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Author for correspondence:
Wesley Dáttilo
e-mail: wdattilo@hotmail.com

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Unravelling Darwin's entangled bank: architecture and robustness of mutualistic networks with multiple interaction types

Wesley Dáttilo[1], Nubia Lara-Rodríguez[2], Pedro Jordano[3],
Paulo R. Guimarães Jr[4], John N. Thompson[5], Robert J. Marquis[6],
Lucas P. Medeiros[4], Raul Ortiz-Pulido[7], Maria A. Marcos-García[2]
and Victor Rico-Gray[8]

[1]Red de Ecoetología, Instituto de Ecología A.C., Carretera Antigua a Coatepec 351, El Haya, 91070 Xalapa,
Veracruz, Mexico
[2]Centro Iberoamericano de la Biodiversidad (CIBIO), Universidad de Alicante, 03690 Alicante, Spain
[3]Integrative Ecology Group, Estación Biológica de Doñana, 41092 Sevilla, Spain
[4]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05508-900
São Paulo, Brazil
[5]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA
[6]Department of Biology and the Whitney R. Harris World Ecology Center, University of Missouri—St Louis,
St Louis, MO 63121-4499, USA
[7]Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo 42001,
Mexico
[8]Instituto de Neuroetología, Universidad Veracruzana, 91190 Xalapa, Veracruz, Mexico

WD, 0000-0002-4758-4379

Trying to unravel Darwin's entangled bank further, we describe the architecture of a network involving multiple forms of mutualism (pollination by animals, seed dispersal by birds and plant protection by ants) and evaluate whether this multi-network shows evidence of a structure that promotes robustness. We found that species differed strongly in their contributions to the organization of the multi-interaction network, and that only a few species contributed to the structuring of these patterns. Moreover, we observed that the multi-interaction networks did not enhance community robustness compared with each of the three independent mutualistic networks when analysed across a range of simulated scenarios of species extinction. By simulating the removal of highly interacting species, we observed that, overall, these species enhance network nestedness and robustness, but decrease modularity. We discuss how the organization of interlinked mutualistic networks may be essential for the maintenance of ecological communities, and therefore the long-term ecological and evolutionary dynamics of interactive, species-rich communities. We suggest that conserving these keystone mutualists and their interactions is crucial to the persistence of species-rich mutualistic assemblages, mainly because they support other species and shape the network organization.

1. Introduction

Within the natural environment, there is a high diversity of interaction types between plant and animal species, including herbivory, pollination, ant protection and seed dispersal [1]. These ecological interactions regulate populations and biological communities, and play a key role in structuring biodiversity [2]. Fascinated by the variety of life forms and interactions between them, Darwin [3] called this complexity the 'entangled bank' in his seminal book *On the origin of species*.

In recent decades, studies have attempted to unravel the interaction structure of Darwin's entangled bank [4–6]. Tools derived from network science

have been used to investigate how the complex organization of these species interactions varies over space and time, and the degree to which they are susceptible to perturbations [7–10]. In ecological networks, species are depicted as nodes and their interactions as links [11]. Such studies have focused on the structural properties of these networks in different ecosystems, and have advanced our understanding of the ecological and evolutionary dynamics of plant–animal interactions [4,12].

Traditionally, studies of ecological networks have considered only one type of ecological interaction (e.g. plant–pollinator or plant–disperser) within bipartite subnetworks (i.e. networks consisting of two interacting guilds or trophic levels; reviewed in [6]). There is no doubt that these studies have contributed to our current and comprehensive view of species interactions. However, in ecological communities, species are involved in multiple kinds of interactions [2,13,14]. For example, a plant species can be visited by pollinators, herbivores and seed dispersers, and generate complex networks of merged interactions [14]. The challenge is to understand how these coupled ecological networks are linked and the dynamical consequences for the resulting multi-interaction networks [14]. Despite the need to merge different types of interactions, only a few studies have evaluated these merged ecological multi-interaction networks [13].

Theoretical approaches to the study of coupled antagonism–mutualism networks have suggested that ecological networks involving different types of interactions would promote community robustness to perturbations [2]. We extended this view by evaluating whether an empirical, species-rich network involving multiple interaction types, but all mutualisms, would also show evidence of a structure that promotes robustness. We hypothesize that the multiple interaction types in the same ecological network beget robustness in the system, more so than the effects of a single interaction type, owing to the increase in connectance or species richness [2,15]. Owing to the high diversity of species and interactions in the tropics, tropical ecosystems could give us a system to study structure–robustness relationships by merging different types of mutualistic subnetworks. In tropical environments, approximately 90% of the woody plant species depend on the interaction with pollinators and seed dispersers to complete their life cycles [16]. Moreover, in such environments, many plant species bear extrafloral nectaries (EFNs) to attract ants that protect their host plants against herbivory [17].

Specifically, we tackled the following issues. What is the structure of an ecological network combining different types of mutualistic interactions? Which mutualism types contribute most to the patterns of organization of a mutualistic network with multiple, coupled types of interactions? Are multi-interaction mutualistic networks more robust to loss of species than bipartite plant–animal mutualistic subnetworks? What are the effects of each of the three types of mutualism on the robustness of this multi-interaction network? We tested the hypothesis that merging different types of mutualistic subnetworks would increase robustness in the system by studying a species-rich multi-interaction network involving different types of mutualism (animal pollination, seed dispersal by frugivorous birds and antiherbivore defence by protective ants) sampled by us in a coastal tropical environment in Mexico [18–20].
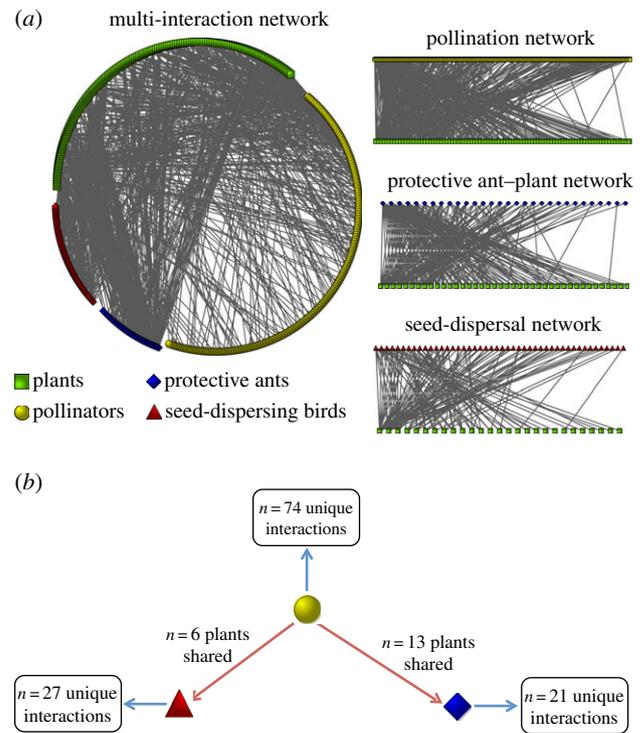

Figure 1. (a) A multi-interaction network of coupled plant–animal mutualisms recorded at Centro de Investigaciones Costeras La Mancha (CICOLMA), located on the central coast of Gulf of Mexico, state of Veracruz, Mexico. Each node represents one plant or animal species, and lines represent the presence of pairwise plant–animal interactions. (b) Number of unique and shared plant species between each network. (Online version in colour.)

2. Material and methods

(a) Datasets

Our study compiled a series of surveys carried out at Centro de Investigaciones Costeras La Mancha (CICOLMA), located on the central coast of the Gulf of Mexico, Veracruz, Mexico (19°36′ N, 96°22′ W; elevation less than 100 m) [18]. The dataset compiled by our research group involved three general types of plant–animal mutualistic interaction: pollination (by both insects and hummingbirds) [20], seed dispersal by frugivorous birds [19], and the protective mutualisms between ants and plants with EFNs [18]. Observations of all these plant–animal interactions were conducted by walking along six representative pre-established trails that covered the different vegetation associations present in the field station and surrounding area. Each of these broad categories includes a variety of ways in which species interact, but our goal here was to evaluate how the three main, fundamentally different ways in which plants interact mutualistically with animals fit together within a community. The resulting database is one of the largest compiled so far with respect to species richness, number of interactions and sampling effort. It comprises 141 plant species, 173 pollinator species, 46 frugivorous bird species and 30 ant species (figure 1). The dataset comprises 753 interactions in our plant–animal mutualistic multi-interaction network, 417 representing plant–pollinator interactions (55% of all recorded interactions), 128 plant–disperser interactions (17% of all recorded interactions) and 208 ant–plant interactions (28% of all recorded interactions). No plant species was involved in all three types of mutualistic interaction, and 122 plant species had only one type of mutualism (86.5% of the total plant species). Among the plant species with only one type of mutualistic interaction, plant–pollinator was the most common interaction ($n = 74$ species), followed by disperser–plant (27 species) and ant–plant (21 species). Nineteen plant

species had two types of mutualistic interactions (13.5% of the total plant species): 13 interacted with ants and pollinators and six interacted with seed-dispersing birds and pollinators (figure 1b). No plant species interacted with both ants and seed-dispersing birds. No animal was involved in more than one type of mutualism. This study is therefore a step in evaluating the structure and dynamics of multiple forms of interaction networks in species-rich communities, combining a unique set of studies and years to assess the patterns that emerge at a single locality. In that sense, the results and conclusions can serve as a working hypothesis for future studies that may be in a better position to undertake multi-year, multi-interaction data collection and analyses that hold more variables constant. Detailed information on sampling of mutualistic interactions and study area is presented in electronic supplementary material, appendix S1.

(b) Data analysis

We used only qualitative networks (binary data), because this approach allowed us to compare the effect of each type of mutualism without bias based on different types of sampling. Moreover, this is a conservative approach, because characterization of interaction strengths is always difficult, especially when addressing distinct types of interaction modes over multiple years of sampling. Considering all plant–animal interactions compiled, we built an interaction matrix A, in which elements $a_{ij} = 1$ represent the presence of an interaction between plant species i and animal species j, and zero for no observed interaction [11]. Initially, we built a matrix for each type of mutualism (pollination, seed-dispersing birds and protective ants) and one matrix including all types of mutualisms together (mutualistic multi-interaction network). We then characterized the structure of each of the four mutualistic networks using the following network descriptors (calculated using the bipartite package in R): nestedness, modularity and robustness.

Nestedness (NODF-metric) describes a pattern of interaction in which species with fewer interactions often interact with a proper subset of the partners of more connected species [21]. Moreover, we tested whether within each network there were groups of species interacting more strongly with each other than with the species in the other groups in the network (i.e. modular pattern). For this, we calculated the modularity index (M) proposed by Barber [22] (range from 0, no subgroups, to 1, totally separated subgroups). Then, we generated random matrices ($n = 1000$ randomizations for each network) to test the significance of nestedness and modularity according to a null model in which the probability of an interaction occurring is proportional to the number of species with which a focal species is observed to interact [11]. We calculated the nestedness and modularity values, standardizing the difference in richness, connectance and heterogeneity of interactions among the networks, using z-scores to allow cross-network comparisons [21].

Because our mutualistic multi-interaction network was significantly nested and modular (see Results), we explored whether the three types of mutualisms contribute equally to these non-random patterns. For this analysis, we estimated the degree to which the interactions of plant or animal species increase or decrease the network's overall nestedness (cn_i) and compared it with our random expectations [23]. Additionally, we recorded the network roles of species in the modular structure by computing (i) the standardized within-module degree (z_i), which is a measure of the extent to which each species is connected to the other species in its module, and (ii) the among-module connectivity (c_i), which describes how evenly distributed are the interactions of a given species across modules [24]. We then used a one-way ANOVA with Bonferroni's correction for multiple comparisons to assess differences in the mean values of cn_i, c_i and z_i among the three types of mutualism. See electronic supplementary material, appendix S2 for details on methods of calculation for all metrics,

descriptors and null model. Additionally, we used a principal component analysis (PCA) on the correlation matrix among k_i (number of interactions), c_i (among-module connectivity), z_i (standardized within-module degree) and cn_i (contribution to nestedness) values to synthesize the species' contributions to connectivity, nestedness and modularity according to Vidal et al. [25]. The first principal component (PC1) was used as a new descriptor summarizing species' contribution to network structure, and the higher scores assigned to each species indicate greater contributions to all analysed structural aspects described above. Biologically, species with a higher contribution to the network structure are those with many interactions in an environment and tend to have the highest niche overlap.

Robustness (R) of each of the two trophic levels (plants and animals) to the loss of species of the other trophic level was calculated based on the area below the extinction curve after simulations of cumulative removals of species from the network. Robustness values range from 0 (less robust network) to 1 (more robust network) [26]. We removed either plants or animals from networks based on three different extinction scenarios: (i) systematic removal from least to most connected species (e.g. expected by differences in abundance among species, where less abundant species have a higher extinction risk); (ii) systematic removal from most to least connected species (e.g. expected in a catastrophic scenario, where most connected species have a higher extinction risk); and (iii) random species deletion, which represents a benchmark (null model) to compare with the two types of systematic removals. Afterwards, we compared the values of robustness between the multi-interaction network and the three independent mutualistic subnetworks: pollination, seed-dispersing birds and protective ants. Therefore, if the multi-interaction network has higher values of robustness than each mutualistic subnetwork, then these mutualistic subnetworks together could contribute to the robustness of the multi-interaction network over and above their individual contribution. The measure of robustness as performed here assumes that if all the mutualistic partners of one species for a given type of interaction were removed, but not the mutualist partners for another type of interaction, then this species would still persist. In reality, it is possible that a species might require different types of mutualisms simultaneously in order to persist. However, many of these mutualistic interactions are 'facultative' (i.e. characterized by low specificity), so that the loss of an interaction involves a fitness reduction but not necessarily extinction in ecological time. This approach does not necessarily represent real extinctions in nature, but is a first approximation for understanding the robustness of networks to loss of species in different extinction scenarios.

We further analysed how each of the three types of mutualism contributes to the architecture and robustness of our mutualistic multi-interaction network by removing the central core of highly interacting plant and animal species from the multi-interaction network and from each subnetwork independently. We removed only the central core of highly interacting species because these are species that are relatively more important than others for maintaining community structure (high number of interactions), and have the potential to drive the ecological and coevolutionary dynamics within species-rich networks [12]. For this analysis, we first defined the core species of a certain network as the species with a standardized degree higher than 1, following Dáttilo et al. [27] (electronic supplementary material, appendix S3 and S4). In other words, a core species has more interactions compared with the mean (weighted by the standard deviation) number of the interactions of species in the network. We then performed four independent analyses in which we removed the core species of the multi-interaction network or of each of the three subnetworks, and quantified the change in the multi-interaction network descriptors. We expected
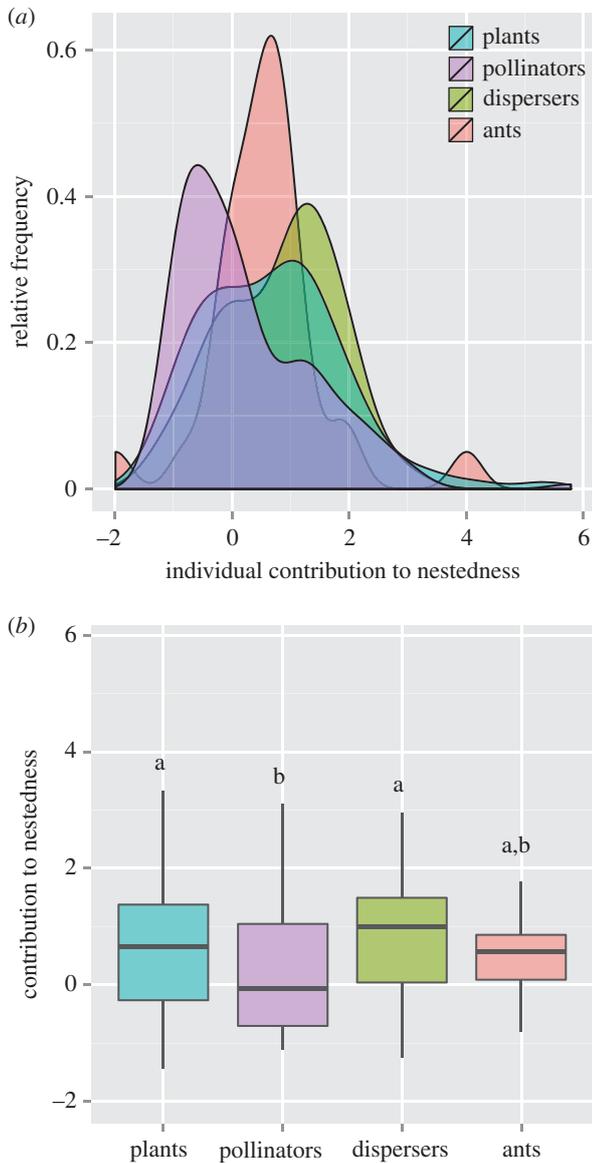
Figure 2. (*a*) Relative frequency and (*b*) the absolute values of individual nestedness contribution for all species within each of the four groups of partners (plants, pollinators, seed-dispersal birds and protective ants) in the mutualistic multi-interaction network. Boxplots sharing the same case letters are not significantly different according to *post hoc* tests. (Online version in colour.)

Figure 3. Network roles of different species of plants, pollinators, seed-dispersal birds and protective ants in the multi-interaction network. Within-module degree (z) describes the standardized number of interactions of a species compared with other species in its module. Among-module connectivity (c) describes the distribution of interactions of a given species across partner species in different modules. (Online version in colour.)

that removing the core species would cause a decrease in nestedness and robustness, and an increase in modularity, mainly because the exclusion of this central core of highly interacting species will disconnect modules within the network. For each core species removal analysis, we performed 100 simulations in which we randomly removed the same number of species and calculated the network descriptors for the 100 randomly species-rarefied networks. With those simulations, we tried to answer the following question: do the core species of a given network contribute more to the multi-interaction network structure and robustness than randomly chosen species from that network? We quantified the contribution of the core species to each network descriptor by calculating standardized (i.e. z-score) network descriptors and p-values, using the randomly rarefied networks (details in electronic supplementary material, appendix S3). We accounted for the changes in network connectance by performing four additional analyses in which we removed only the links between the core species and quantified the change in the multi-interaction network descriptors (electronic supplementary material, appendix S3).

3. Results

Our multi-interaction network exhibited a significantly nested ($NODF_{s.d.} = 14.77$) and modular ($M_{s.d.} = 12.01$) pattern of interactions ($p < 0.05$). All three mutualistic subnetworks were also significantly nested (pollination: $NODF_{s.d.} = 10.57$, seed-dispersing birds: $NODF_{s.d.} = 6.07$ and protective ants: $NODF_{s.d.} = 9.60$). However, only the pollination subnetwork was significantly modular (pollination: $M_{s.d.} = 3.01$, seed-dispersing birds: $M_{s.d.} = -0.33$ and protective ants: $M_{s.d.} = -2.00$). Only a few animal species contributed strongly to the nested pattern within each individual network (figure 2a; electronic supplementary material, appendix S3). Animal species also differed greatly in the degree to which they contributed to nestedness in the mutualistic multi-interaction network (ANOVA: $F_{3,387} = 5.556$; $p < 0.001$). In general, seed-dispersing birds (mean $\pm$ s.e.: 0.83 ± 0.14) and plants (0.71 ± 0.08) contributed more to nestedness than pollinators (0.23 ± 0.08) (figure 2b). Protective ants (0.58 ± 0.18), seed-dispersing birds, plants and pollinators contributed equally to nestedness.

For the multi-interaction network, contributions to modularity also differed greatly among plant and animal species. Most plant and animal species were peripherals ($n = 129$ plant species, 159 pollinator species, 45 seed-dispersing birds and 21 ant species), followed by connectors ($n = 10$ pollinator species, four plant species and three ant species) and module hubs ($n = 8$ plant species, four pollinator species, two ant species and one seed-dispersing bird). Only four species, all ants, were network hubs (figure 3). We found no significant differences in the among-module connectivity (c) values between the four groups (plants, pollinators, seed-dispersers and ants, $p = 0.14$). However, within-module degree (z) values differed among the four groups ($p < 0.001$). When compared separately, z-values did not differ between plants and pollinators ($p > 0.05$), plants and seed-dispersing birds ($p > 0.05$), and pollinators and seed-dispersing birds ($p > 0.05$). Ants had higher z-values (mean $\pm$ s.e.: $0.881 \pm$

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Table 1. Robustness (R) of plants and animals to the loss of species based on three different extinction scenarios: (i) systematic removal from least to most connected species; (ii) systematic removal from most to least connected species and (iii) random species deletion, calculated for the original mutualistic networks with the central core (CC) of highly interacting species and for the resultant interaction networks after removal of the central core of highly interacting species (without CC).

mutualistic network	trophic level	least to most connected species		most to least connected species		random species deletion	
		with CC	without CC	with CC	without CC	with CC	without CC
multi-interaction network	plants	0.886	0.775	0.319	0.357	0.655	0.575
	animals	0.934	0.822	0.411	0.494	0.731	0.678
seed-dispersal network	plants	0.904	0.871	0.323	0.326	0.678	0.643
	animals	0.909	0.930	0.427	0.419	0.710	0.724
protective ant–plant network	plants	0.927	0.881	0.481	0.304	0.791	0.651
	animals	0.957	0.929	0.459	0.438	0.790	0.707
pollination network	plants	0.869	0.781	0.292	0.378	0.619	0.617
	animals	0.923	0.830	0.418	0.473	0.709	0.719

0.293) than plants (-0.012 ± -0.084, $p < 0.05$), pollinators (-0.152 ± 0.054, $p < 0.05$) and seed-dispersing birds (0.063 ± 0.072, $p < 0.05$).

In addition, we found that species differed strongly in their contribution to the organization of the multi-interaction network, and that only a few species contributed to the structuring of these patterns in the multi-interaction network (electronic supplementary material, appendix S5). The first principal component (PC1) resulting from the PCA was positively associated with k_i, cn_i, z_i and c_i, retaining much of the information provided by network measurements (96.1%). We found that k_i, z_i and cn_i were almost always positively correlated with each other (Pearson's $r > 0.42$, $p < 0.0001$). In other words, plant and animal species with many links tend to establish interactions within modules and to exhibit a greater contribution to nestedness. Moreover, these species tended to be classified as module hubs (electronic supplementary material, appendix S6). A list of all species recorded in this study with their values of contribution to network structure is presented in electronic supplementary material, appendix S6.

We found that the robustness to loss of species varied disproportionately among the three different mutualistic networks (pollination, seed-dispersal or protective ant–plant networks) and over different extinction scenarios (table 1). In general, the multi-interaction network was not greater in robustness compared with each independent mutualistic network. In fact, the protective ant–plant network was the most robust to loss of species across all models of extinction.

As expected, the removal of the central core of the multi-interaction network decreased nestedness (electronic supplementary material, appendix S7). This change in nestedness was significant relative to random species removal (electronic supplementary material, appendix S7). Removing either the core of the pollination subnetwork or the protective ants subnetwork significantly decreased nestedness (electronic supplementary material, appendix S7). Removal of the seed-dispersal core decreased modularity (electronic supplementary material, appendix S7). Overall, removal of the multi-interaction network, pollination or seed-dispersal core species

significantly decreased network robustness, except for the most to least connected species extinction scenario (table 2). Surprisingly, for the most to least connected species extinction scenario, robustness greatly increased after removal of the core species (table 2). Finally, removal of the protective ants core had an overall weak effect on network robustness except for two extinction scenarios (table 2: random animal extinction and most to least connected animal extinction). Results for the core links removal simulations are presented in electronic supplementary material, appendix S8 and S9.

4. Discussion

Our study shows that the overall organization of mutualistic interactions involving plants and animals depends, in part, on the types of mutualism in which the plants participate (pollination by animals, seed dispersal by birds and plant protection by ants), and how these species integrate in the multi-interaction network. In general, we found that our mutualistic network with multiple interaction types exhibited a nested and modular pattern of species interactions. Seed-dispersing birds and plants contributed more to nestedness than did pollinators, whereas ants tended to decrease modularity. Additionally, we found that the multi-interaction network did not promote community robustness over different simulated scenarios of species extinction compared with each of the three independent mutualistic networks, possibly owing to low overlap of mutualism types among plant species. However, when the central core of the multi-interaction network is removed the network robustness collapses (except for the most to least extinction scenario). Moreover, few species contribute to the multi-interaction network central core, and loss of these species results in network structures that are likely more vulnerable than networks with these generalists. These results indicate that merging different types of mutualism can change our estimates of the relative importance of the species to the organization of mutualistic networks when compared with isolated networks. Our results suggest that the organization of coupled mutualistic networks within larger

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Table 2. Robustness values, standardized robustness values (z-score) with the associated p-values (see electronic supplementary material, appendix S3 for explanation) and the number of species removed for each simulation analysis of core species removal. The network robustness values were quantified for the intact multi-interaction network (no core removal) or for the multi-interaction network after the removal of its own core (general core removal) or the core of one of the subnetworks (pollination core removal, ants core removal and dispersal core removal).

extinction scenario	trophic level for extinction	core removal scenario	robustness value	robustness z-score	p-value	number of species removed
random	plants	no core removal	0.651	—	—	0
		general core removal	0.574	−9.096	0	39
		pollination core removal	0.624	−3.746	0	27
		ants core removal	0.640	−0.982	0.18	10
		dispersal core removal	0.638	−2.510	0	10
random	animals	no core removal	0.728	—	—	0
		general core removal	0.679	−5.211	0	39
		pollination core removal	0.718	−1.330	0.1	27
		ants core removal	0.707	−2.408	0.03	10
		dispersal core removal	0.733	1.712	0.97	10
least to most connected	plants	no core removal	0.884	—	—	0
		general core removal	0.774	−11.237	0	39
		pollination core removal	0.769	−13.602	0	27
		ants core removal	0.884	−0.068	0.38	10
		dispersal core removal	0.858	−8.051	0	10
least to most connected	animals	no core removal	0.934	—	—	0
		general core removal	0.835	−8.591	0	39
		pollination core removal	0.818	−11.023	0	27
		ants core removal	0.932	0.238	0.57	10
		dispersal core removal	0.907	−5.434	0	10
most to least connected	plants	no core removal	0.320	—	—	0
		general core removal	0.354	3.813	1	39
		pollination core removal	0.382	7.212	1	27
		ants core removal	0.303	−1.783	0.04	10
		dispersal core removal	0.328	2.401	0.99	10
most to least connected	animals	no core removal	0.409	—	—	0
		general core removal	0.499	5.567	1	39
		pollination core removal	0.485	5.770	1	27
		ants core removal	0.432	2.593	1	10
		dispersal core removal	0.420	2.134	0.99	10

and more diversified multi-interaction networks could be essential to the maintenance of ecological communities as shown in previous studies on multi-interaction networks [13,28,29], once the multi-interaction network exhibited non-random patterns that promote persistence of biological communities.

When we evaluated each type of mutualism as independent networks, we observed that all networks were significantly nested. By contrast, only the pollination network exhibited a modular pattern of interaction. The structure of these independent networks was consistent with previously described patterns in the literature (see [11,29–31]). In addition, despite our large sampling effort, no species of plant was involved in all three types of mutualism, and most plants are involved in only one type of mutualism. This is probably because plants with EFNs are only a minor

subset of the plant community in a given environment, and the presence of ants foraging on these plants could repel pollinators and frugivorous birds by aggressive attacks, affecting pollination efficiency [17]. Moreover, there is evidence that some plants with biotic pollination tend to have abiotic seed dispersal and vice versa in the study area (W.D. and V.R-G. 2014, personal data), which also decreases the shared record of mutualistic interactions, suggesting a trade-off between animal pollination and animal dispersal.

Probably owing to high specialization of species interactions within each mutualism and the low overlap between types of mutualisms, the multi-interaction network did not promote community robustness over different extinction scenarios. Thus, our original hypothesis was not supported. However, our mutualistic multi-interaction network was both nested and modular. This combined structure plays an important role in the persistence of biological communities, beyond the ability to support high levels of biodiversity [7,32,33] for two main reasons. First, because there is a core of highly connected species in nested networks, when one of the central core species goes extinct other species can 'dampen' the system [34,35]. Second, in modular networks, any perturbation that occurs within a module decreases the likelihood of cascading effects propagating to other modules [13,36,37]. Therefore, both non-random patterns may enhance the stability of plant–animal mutualisms in complementary ways [38].

Nestedness describes the organization of niche breadth, in which more nested networks tend to have the highest niche overlap [39]. Here, we observed that frugivorous birds and protective ants were the mutualistic agents that contribute most to nestedness. This is possibly related to interactions between plants and seed-dispersing birds, and plant and ants tending to be more functionally redundant and generalized compared with interactions with pollinators [40]. Moreover, ants also had an important role in network connectivity and in the robustness of the modular pattern, and were classified as network hubs. In this case, EFN is a seasonal resource and ants can use other resources available on foliage, which makes ant–plant interactions less specialized and more facultative [41], and therefore, more robust to loss of species over different extinction scenarios as shown in this study. Therefore, ant–plant interactions could have a remarkable impact on the architecture and robustness of mutualistic multi-interaction networks. However, the high plant specificity among pollinators could explain the high frequency of functional peripheral roles of pollinating species within the modular structure. Despite the importance of nestedness and modularity to the robustness and species coexistence in mutualisms, only a few species contributed to the structuring of these patterns in the multi-interaction network. Therefore, if the goal is to conserve mutualistic interactions within an environment, then a key task is to identify the 'keystone mutualists'. These species and their interactions play disproportionately important roles in the community either through many direct or indirect links to other species that help guarantee the persistence of a mutualistic community rich in species [42,43]. The loss of keystone mutualists has important consequences for the ecological and evolutionary dynamics of the system, because the extinction of these highly connected species can lead to co-extinctions of other species and reduce the long-term overall species persistence [23,25].

Using different approaches, some recent studies have highlighted the importance of identifying key positions within ecological networks (i.e. highly connected species) in order to conserve the ecological and evolutionary processes in an environment [44,45]. This is mainly because different types of ecological networks vary disproportionately in their robustness over different extinction scenarios and types of interactions [42]. We further explored the role of these highly connected species in structuring and promoting robustness in the multi-interaction network by removing the central core of highly interacting species. We observed that the core species of our mutualistic multi-interaction network, as well as the core species of our pollination and protective ants subnetworks contribute to a nested pattern of interactions. These patterns, in turn, promoted robustness to most extinction scenarios studied here. However, the removal of the core species of our multi-interaction network or of each of the three types of mutualisms led to an increase in network robustness in a scenario where the most connected species have a higher extinction risk. Therefore, environmental impacts that selectively affect these highly connected core species [25] may disrupt network organization and make the network very susceptible to future impacts of the same kind that target the remaining species in the community. We did not observe important changes in network robustness when removing only the interactions between the core species from any of our networks. Thus, we suggest that interactions between core and periphery species, rather than just the interactions among the core species, are important to maintain the multi-interaction network robust to extinctions.

Finally, our results suggest that studying only one type of mutualistic network does not necessarily lead us to erroneous conclusions about system stability. Many of the network statistics have similar values in the multi- versus single-mutualism type networks. Moreover, the multi-mutualism network is no more robust than the mutualistic subnetworks considered individually. However, multi-interaction networks can more clearly show the relative importance of the species to maintenance of ecological communities, mainly because species can differ in their contributions to network structure. In summary, our study provides one of the few empirical examples available in the literature highlighting the importance of combining different interaction types within ecological multi-interaction networks to better characterize their architectural patterns of plant–animal mutualisms of free-living species. The next step is to assess the determinants of these mutualistic multi-interaction network structures, such as phylogenetic constraints and trait matching, and how they vary over space and time, and whether these multi-interaction networks respond collectively to perturbations.

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Supplementary Materials for

4

Unraveling Darwin's entangled bank: architecture and robustness of

mutualistic networks with multiple interaction types

Wesley Dáttilo*; Nubia Lara-Rodríguez; Pedro Jordano, Paulo R. Guimarães; John N.

Thompson; Robert J. Marquis; Lucas P. Medeiros, Raul Ortiz-Pulido; Maria A.

Marcos-García and Victor Rico-Gray

11

*Corresponding author: wdattilo@hotmail.com

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Appendix S1. Study area and sampling mutualistic interactions.

        The climate in the study area is warm and sub-humid and experiences three

well defined seasons: the dry season from February to May, rainy season from June to

September, and 'Nortes' or cold front season from October to January. Total annual

precipitation is ca. 1500 mm, and mean annual temperature is between 22°-26°C. The

major vegetation types in our study area are tropical dry and deciduous forests,

mangrove forest, sand dune scrub, freshwater marsh, and flooded deciduous forest

(Rico-Gray 1993).

        Sampling for pollination was conducted during five days per month between

March 2007 and March 2008 in periods of 15-20 min, between 08:00 and 16:00. We

considered a pollinator-plant interaction to occur when a floral visitor (insect or bird)

was seen feeding in a flower in a way such that its body touched the floral

26 reproductive structures. Sampling of seed dispersal by frugivorous birds was done

27 during three days per month between April 1992 and March 1993, starting 30 min

28 before sunrise until 11:00, and from 16:00 until sunset. A bird disperser-plant

29 interaction was described by observing birds eating fruits from ornithocoric plant

30 species. All observations were made with the aid of binoculars and field guides. We

31 considered all birds feeding on fruits as a potential seed disperser given that species

32 classified as "seed predators" can also occasionally disperse seeds (Heleno et al.

33 2011). For ant-plant interactions biweekly field observations (three days per visit)

34 were made between May 1989 and April 1991, and all occurrences of ant species

35 feeding on EFNs present on the spike, pedicel, bud, calyx, leaves, shoots, petioles,

36 bracts or stems were recorded (from 08:00 to 13:00 h). Ants were considered to be

37 feeding on nectar when they were immobile for periods of up to several minutes and

38 obviously exhibiting distended gasters (Rico-Gray 1993). Observations of all these

39 animal–plant interactions were conducted by walking along six representative pre-

40 established trails that covered the different vegetation associations present in the field

41 station and surrounding area: Trail 1, sand dune pioneer species; Trail 2, deciduous

42 forest; Trail 3, deciduous forest–dry forest ecotone; Trail 4, dry forest and sand dune

43 scrub; Trail 5, sand dune scrub; and Trail 6, sand dune–freshwater lagoon ecotone.

44 For specific information about our design and sampling effort, please see the original

45 studies from which the data were compiled (pollinators: Hernández-Yáñez et al. 2013;

46 seed dispersers: Ortiz-Pulido et al. 2000; protective ants: Rico-Gray 1993).

47   Sampling a single sub-network is a challenging task and the characterization

48 of a network of networks is an almost unfeasible, leading to some undesired sampling

49 solutions. In our work, sampling the different forms of mutualistic interactions was

50 conducted in different years. Having said that, all sampling was done on the same

51 trails, and sampling effort was very similar among them: monthly sampling ranging

52 from 12 to 13 months. Changes in the phenology of plants with larger temporal

53 periods and in the population cycles of animals (mainly insects) could influence the

54 sampling of interactions. However, we note that the variation in sampling between

55 years may be less than if the sampling had been performed in different seasons due to

56 the clear seasonality of the area.

57

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72

73 <u>**Appendix S2.**</u> Methods of calculation for all metrics and null model used in this

74 study.

75

76 <u>**Robustness:**</u>

77    $R = \int_0^1 f(x)$, in which R is the robustness (Burgos *et al.* 2007), *f(x)* is the function

78   describing how the cumulative number of species of set B decay with the extinction of

79   species of set A. *f(x)* is numerically estimated using the BIPARTITE package

80   (Dormann *et al.* 2009) in R. Initially, we removed one species from one trophic level,

81   and when species from the other trophic level were connected only to the initial

82   removed species, they were also removed from the network, indicating secondary

83   losses. We removed all remaining species until all species from the trophic level

84   chosen died out. In this way an extinction curve, *f(x)*, was generated by plotting the

85   number of remaining species on the one trophic level against the cumulative number

86   of species removed from the trophic level. The area below the extinction curve (R)

87   was calculated as a measure of the robustness of the whole system.

88

89   **Nestedness:**

90    $N = 2 \frac{\Sigma_i^P \Sigma_j^P N_{ij} + \Sigma_k^A \Sigma_l^A N_{kl}}{P(P-1) + A(A-1)}$, where N is the observed nestedness (*NODF*) , N_{ij} is a

91   measure of nestedness among pairwise animals and N_{kl} plant species (see Almeida-

92   Neto *et al.* 2008 for further details); P is the number of plant species; and A is the

93   number of animal species in the interaction network.

94

95   **Modularity**:

96    $$M_B = \sum_{m=1}^{N_m} \left[\frac{l_m}{I} - \left(\frac{d_m^A d_m^B}{I^2} \right) \right]$$, where N_m is the number of modules in the network,

97   l is the total number of links, l_m is the number of links between species in module m,

98   and d_m^A and d_m^B are the sum of the links of all species in module s which belong to

99   *A-set* and *B-set* respectively (Barber 2007).

100

Null Model:

102 $\left(\dfrac{ki}{P} + \dfrac{kj}{A}\right)$,, where k_i is the number of interactions of plant species i, k_j is the number

103 of interactions of animal j, and T and A are the number of plant and animal species. P-

104 value was defined as the probability of a null model replicate being equally or more

105 nested/modular than the observed networks (Bascompte *et al.* 2003). The null model

106 used probabilistically controls the heterogeneity of interactions, e.g., the variation in

107 the number of interactions per species. Thus, we generated a benchmark for expected

108 nestedness and modularity if interactions were random but preserving the

109 heterogeneity in the number of interactions.

110

Contribution to nestedness:

112 This metric is a z-score relative to null models and is defined as follows:

113 $cn_i = \left(\dfrac{N - N_i}{\sigma_{Ni}}\right)$, where N is the observed nestedness (*NODF*) of the network, N_i is

114 the average of nestedness when randomizing just the interactions of the species i, and

115 σ_{Ni} is the standard deviation of nestedness when randomizing just the interactions of

116 the species i (n = 100 randomizations). Positive values of cn_i indicate a higher

117 contribution of species (i) to the nested structure (Saavedra et al. 2011).

118

Functional roles:

120 $$1.)\quad z_i = \frac{k_{is} - k_s}{SD_{ks}}$$

121 and,

122 $$2.)\quad c_i = 1 - \sum_{t=1}^{N_m} \left(\frac{k_{it}}{k_i} \right)^2$$

123 where k_{is} is the number of interactions of the species i with other species within its

124 module s, k_s is the average of interactions within module k of all species in s, SD_{ks} is

125 the standard deviation of interactions within module k of all species in s, N_m is the

126 number of modules in the network, k_i is the total number of interactions of species i in

127 the network, and k_{it} is the number of interactions of species i with the other species of

128 module t (Olesen et al. 2007). We used the frequency distribution of z and c values to

129 define the threshold to separate the role of species within and among the modules. In

130 other words, we created cutoffs of the frequency distribution of z and c values at the

131 95% (based on the mean, from lowest to highest values) and classified species as

132 peripherals ($z \leq 1.51$ and $c \leq 0.13$, *i.e.*, with a few interactions with other species),

133 connectors ($z \leq 1.51$ and $c > 0.13$, *i.e.*, connects several modules to each other), module

134 hubs ($z > 1.51$ and $c \leq 0.13$, *i.e.*, has several interactions within its module), or network

135 hubs ($z > 1.51$ and $c > 0.13$, *i.e.*, the species is a connector and has several interactions

136 in the module) (Olesen et al. 2007).

137

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156

157   **Appendix S3.** Core species, and core links removal simulations

158   **Definition of core species:**

159   We defined the core species of a given network (multi-interaction network,

160   pollination sub-network, seed-dispersal sub-network or protective ants sub-network)

161   as species within that network with a standardized degree higher than 1 (Dáttilo et al.

162   2013). The standardized degree is calculated as $G_c = (K_i - K_{mean})/\sigma_k$ where $K_i =$

163   number of links for a given plant or animal species i, K_{mean} = mean number of links

164   for all plant or animal species in the network, and σ_k = standard deviation of the

165   number of links for plant or animal species (Dáttilo et al. 2013). A list of core species

166   is presented in the Appendix S4.

167

168   **Standardized network descriptors and p-value:**

169   We quantified a given network descriptor (mean number of links,

170   specialization, nestedness, modularity or robustness) after the removal of all core

171 species as D_{core}. We then performed 100 simulations in which the same number of

172 species were removed but removed species were randomly selected. Then, we

173 calculated the standardized network descriptor as $D_{std} = (D_{core} - D_{mean})/\sigma_D$, where

174 D_{mean} = mean of the network descriptor for the corresponding 100 randomly rarefied

175 networks and σ_D = standard deviation of the network descriptor of the corresponding

176 100 randomly rarefied networks. We expected that removing the core species would

177 cause a decrease in the mean number of links, nestedness and robustness and an

178 increase in specificity and modularity. Based on those expectations we calculated a p-

179 value as the proportion of randomly rarefied networks (n=100) that had the network

180 descriptor value greater/lesser than D_{core}.

181

182 **Simulating the removal of core links:**

183   We were able to control for the changes in species richness while removing

184 the core species by performing simulations of random species removal. However,

185 removing the core species may also change network connectance. To control for the

186 changes in network connectance, we performed four additional analyses (one for each

187 network) in which we only removed the links between the core species and quantified

188 the change in the multi-interaction network descriptors. We first removed the links

189 between the core species from the multi-interaction network and from each of the

190 three sub-networks independently and quantified all network descriptors. We then

191 performed 100 simulations for each of the four link removal analyses, in which we

192 randomly removed the same number of links and calculated the network descriptors

193 for the 100 randomly link-rarefied networks. All 100 randomly link-rarefied networks

194 had the same species richness and connectance as the corresponding network without

195 the core links. Finally, we calculated the standardized network descriptors and p-

196   values for link removal simulations in the same way as described above for the

197   species removal simulations.

198

199

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203 **Appendix S4.** List of plant and animal species that were components of the highly

204 generalized core of each of the mutualistic networks (pollination, seed disperser, and

205 protective ants). The number of links (*i.e.*, interactions) observed for each species is

206 also shown. All other plant and animal species were considered as species constituting

207 the periphery of networks.

208

Pollination networks			
plant species	no. of links	pollinator species	no. of links
Bauhinia divaricata	24	*Apis melifera*	30
Bidens pilosa	24	*Lasioglossum* sp1	18
Randia laetevirens	22	*Trigona nigra*	12
Turnera diffusa	16	*Ascia monuste*	10
Lantana camara	14	*Euglossa viridissima*	9
Waltheria indica	14	*Scaptotrigona pectoralis*	8
Palafoxia lindenii	13	*Ceratina* sp1	8
Tecoma stans	13	*Danaus gilipus*	7
Hyptis suaveolens	12	*Sphecidae* sp2	7
Piscidia piscipula	11	*Centris inermis*	7
Turnera ulmifolia	11	*Amazilia yucatanensis*	7
Crusea longiflora	10	*Dryas julia*	6
Cynanchum sp1	10	*Phoebis agarithe*	6
		Chlorostilbon canivetti	6

Seed dispersal networks			
plant species	no. of links	seed-dispersal birds	no. of links
Ficus cotinifolia	27	*Psilorhinus morio*	10
Bursera simaruba	20	*Tyrannus forficatus*	7
		Ortalis vetula	6
		Myiozetetes similis	6
		Psarocolius montezuma	5
		Pitangus sulphuratus	5
		Dumetella carolinensis	5
		Empidonax alnorum	5

Protective ants networks			
plant species	no. of links	ant species	no. of links
Cedrela odorata	17	*Camponotus planatus*	33
Cordia spinescens	15	*Camponotus mucronatus*	22
Turnera ulmifolia	15	*Paratrechina longicornis*	18
Callicarpa acuminata	11		
Crotalaria incana	11		
Calopogonium caerulium	10		
Mansoa hymanoea	10		

209 **Appendix S5.** Animal (A) and plant (B) species' contribution to network structure

210 (details in Methods). Species are arranged in order of decreasing contribution to

211 network structure. An ordered list of the position of each species according their

212 contribution to network structure is presented in the Appendix S6.
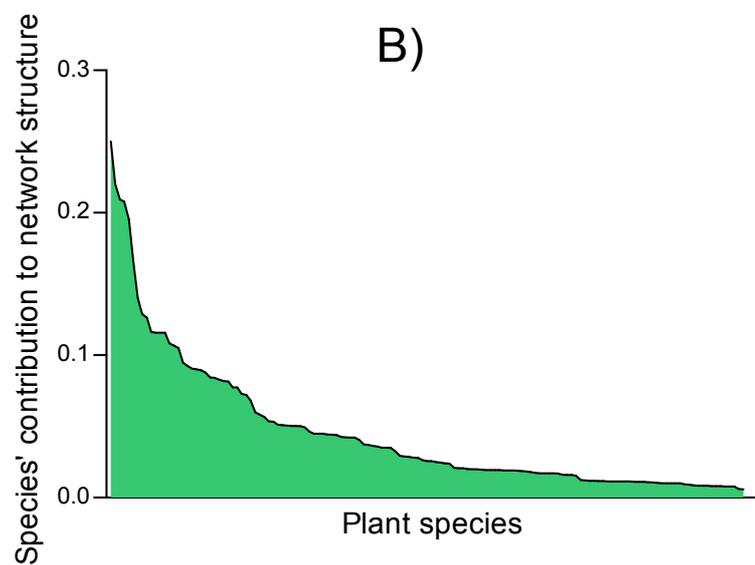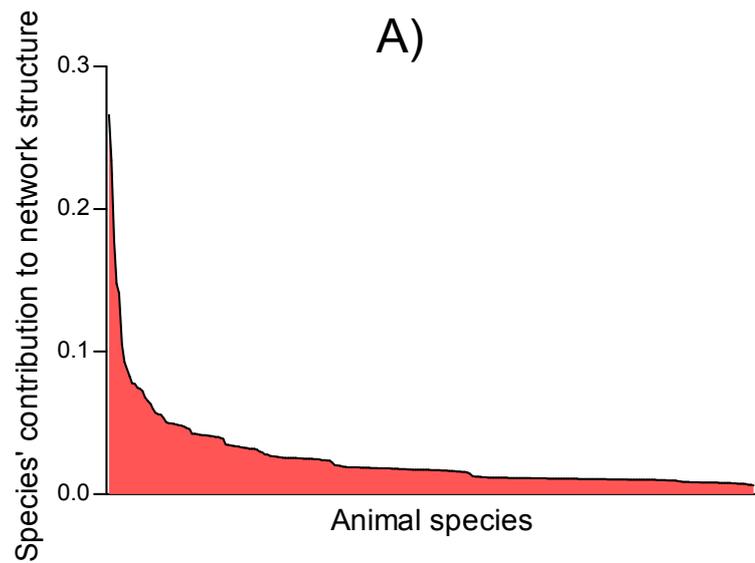
213

214   **Appendix S6.** List of animal and plant species showing their functional roles, number of interactions (K_i), standardized within-module degree

215   (z_i), among-module connectivity (c_i), contribution to nestedness (cn_i), and contribution to network structure (details in Methods). Species are

216   ordered according their contribution to network structure.

Species	Organism	Functional Role	k_i	z_i	c_i	cn_i	Contribution to network structure
Camponotus planatus	Protective ant	Network Hub	33.00	6.37	0.22	4.35	0.27
Bidens pilosa	Plant	Module Hub	31.00	4.12	0.06	7.36	0.25
Apis melifera	Pollinator	Module Hub	30.00	6.10	0.00	8.25	0.23
Ficus cotinifolia	Plant	Module Hub	27.00	3.62	0.00	5.15	0.22
Turnera ulmifolia	Plant	Module Hub	26.00	3.45	0.00	6.61	0.21
Randia laetevirens	Plant	Module Hub	26.00	3.45	0.00	7.42	0.21
Bauhinia divaricata	Plant	Module Hub	24.00	3.11	0.00	5.21	0.20
Camponotus mucronatus	Protective ant	Module Hub	22.00	4.73	0.09	1.88	0.18
Bursera simaruba	Plant	Module Hub	20.00	2.44	0.00	2.63	0.17
Paratrechina longicornis	Protective ant	Network Hub	18.00	3.42	0.20	0.84	0.15
Lasioglossum sp1	Pollinator	Module Hub	18.00	3.68	0.10	4.41	0.14
Cedrela odorata	Plant	Module Hub	17.00	1.77	0.11	3.14	0.14
Turnera diffusa	Plant	Module Hub	16.00	1.77	0.00	4.64	0.13
Cordia spinescens	Plant	Peripheral	15.00	1.60	0.00	1.29	0.13
Waltheria indica	Plant	Peripheral	14.00	1.43	0.00	2.16	0.12
Crotalaria incana	Plant	Peripheral	14.00	1.43	0.00	2.41	0.12
Canavalia rosea	Plant	Peripheral	14.00	1.43	0.00	2.50	0.12
Lantana camara	Plant	Peripheral	14.00	1.43	0.00	2.50	0.12
Palafoxia lindenii	Plant	Peripheral	13.00	1.26	0.00	2.00	0.11
Psychotria erythrocapa	Plant	Peripheral	13.00	1.26	0.00	2.98	0.11
Crematogaster brevispinosa	Protective ant	Network Hub	13.00	2.66	0.16	1.08	0.11
Tecoma stans	Plant	Peripheral	13.00	1.26	0.00	3.83	0.11
Hyptis suaveolens	Plant	Peripheral	12.00	1.09	0.00	4.88	0.09
Trigona nigra	Pollinator	Module Hub	12.00	2.36	0.00	3.90	0.09
Callicarpa acuminata	Plant	Peripheral	11.00	0.93	0.00	1.29	0.09
Opuntia stricta	Plant	Peripheral	11.00	0.93	0.00	2.52	0.09
Chamaecrista chamaecristoides	Plant	Peripheral	11.00	0.93	0.00	2.78	0.09
Piscidia piscipula	Plant	Peripheral	11.00	0.93	0.00	3.21	0.09
Crusea longiflora	Plant	Peripheral	10.00	0.76	0.00	-0.69	0.09

Species	Role	Topology					
Camponotus atriceps	Protective ant	Network Hub	11.00	2.04	0.20	1.90	0.09
Calopogonium caerulium	Plant	Peripheral	10.00	0.76	0.00	1.33	0.08
Mansoa hymanoea	Plant	Peripheral	10.00	0.76	0.00	1.37	0.08
Azteca sp1	Protective ant	Connector	10.00	1.17	0.18	1.05	0.08
Cynanchum sp1	Plant	Connector	10.00	0.76	0.32	1.41	0.08
Macroptilium atropurpureum	Plant	Peripheral	10.00	0.76	0.00	2.70	0.08
Terminalia catappa	Plant	Peripheral	10.00	0.76	0.00	2.87	0.08
Cyanocorax morio	Disperser	Module Hub	10.00	1.84	0.00	3.27	0.08
Ascia monuste	Pollinator	Module Hub	10.00	1.84	0.00	3.47	0.08
Achatocarpus nigricans	Plant	Peripheral	9.00	0.59	0.00	0.45	0.08
Malpighia glabra	Plant	Peripheral	9.00	0.59	0.00	0.48	0.08
Euglossa viridissima	Pollinator	Connector	9.00	1.31	0.20	0.32	0.07
Pseudomyrmex gracilis	Protective ant	Connector	9.00	1.31	0.20	0.85	0.07
Petiveria alliaceae	Plant	Peripheral	9.00	0.59	0.00	3.13	0.07
Cephalotes minutus	Protective ant	Module Hub	9.00	1.57	0.00	1.67	0.07
Cayaponia attenuata	Plant	Peripheral	9.00	0.59	0.00	3.57	0.07
Cordia sp1	Plant	Peripheral	8.00	0.42	0.00	0.92	0.07
Pachycondyla villosa	Protective ant	Peripheral	8.00	1.31	0.00	-0.45	0.07
Scaptotrigona pectoralis	Pollinator	Connector	8.00	0.78	0.41	1.00	0.07
Ceratina sp1	Pollinator	Connector	8.00	1.05	0.22	2.19	0.06
Ipomoea pescaprae	Plant	Peripheral	7.00	0.25	0.00	0.85	0.06
Amazilia yucatanensis	Pollinator	Connector	7.00	0.00	0.49	0.21	0.06
Caesalpinia crista	Plant	Peripheral	7.00	0.25	0.00	1.72	0.06
Sphecidae sp2	Pollinator	Connector	7.00	0.78	0.24	1.02	0.06
Cordia dentata	Plant	Peripheral	7.00	0.25	0.00	2.69	0.06
Centris inermis	Pollinator	Peripheral	7.00	1.05	0.00	1.77	0.06
Tyrannus forficatus	Disperser	Peripheral	7.00	1.05	0.00	1.95	0.06
Unknown sp11	Plant	Peripheral	6.00	0.08	0.00	-0.33	0.05
Danaus gilipus	Pollinator	Peripheral	7.00	1.05	0.00	3.34	0.05
Bursera fagaroides	Plant	Peripheral	6.00	0.08	0.00	-0.14	0.05
Amphilophium paniculatum	Plant	Peripheral	6.00	0.08	0.00	1.12	0.05
Porophyllum punctatum	Plant	Peripheral	6.00	0.08	0.00	1.18	0.05
Conocarpus erectus	Plant	Peripheral	6.00	0.08	0.00	1.39	0.05
Pseudomyrmex brunneus	Protective ant	Peripheral	6.00	0.78	0.00	0.28	0.05
Ipomoea sp1	Plant	Peripheral	6.00	0.08	0.00	1.50	0.05
Cardiospermum alicabrum	Plant	Peripheral	6.00	0.08	0.00	1.55	0.05
Commelina erecta	Plant	Peripheral	6.00	0.08	0.00	1.65	0.05

Wasmannia auropunctata	Protective ant	Peripheral	6.00	0.78	0.00	0.63	0.05
Dorymyrmex bicolor	Protective ant	Peripheral	6.00	0.78	0.00	0.81	0.05
Chlorostilbon canivetti	Pollinator	Connector	6.00	0.52	0.28	0.71	0.05
Psittacanthus calyculatus	Plant	Peripheral	6.00	0.08	0.00	2.16	0.05
Tetramorium spinosum	Protective ant	Peripheral	6.00	0.78	0.00	1.24	0.05
Phoebis agarithe	Pollinator	Peripheral	6.00	0.78	0.00	1.53	0.05
Myiozetetes similis	Disperser	Peripheral	6.00	0.78	0.00	1.68	0.05
Dryas julia	Pollinator	Peripheral	6.00	0.78	0.00	2.08	0.05
Ortalis vetula	Disperser	Peripheral	6.00	0.78	0.00	2.65	0.05
Gomphrena sp1	Plant	Peripheral	5.00	0.00	0.00	-1.10	0.05
Pheidole sp1	Protective ant	Peripheral	5.00	0.00	0.32	-1.46	0.05
Casearia corymbosa	Plant	Connector	5.00	0.00	0.48	-1.48	0.04
Karwinskia humboldtiana	Plant	Peripheral	5.00	-0.08	0.00	-0.13	0.04
Coccoloba barbadensis	Plant	Peripheral	5.00	-0.08	0.00	-0.09	0.04
Delonix regia	Plant	Peripheral	5.00	-0.08	0.00	0.08	0.04
Dendropanax arboreus	Plant	Peripheral	5.00	-0.08	0.00	0.33	0.04
Celtis caudata	Plant	Peripheral	5.00	-0.08	0.00	0.47	0.04
Ipomoea sp2	Plant	Peripheral	5.00	-0.08	0.00	1.08	0.04
Acacia cornigera	Plant	Peripheral	5.00	-0.08	0.00	1.27	0.04
Camponotus hirsutinasus	Protective ant	Peripheral	5.00	0.52	0.00	0.30	0.04
Forelius analis	Protective ant	Peripheral	5.00	0.52	0.00	0.36	0.04
Tabebuia rosea	Plant	Peripheral	5.00	-0.08	0.00	1.44	0.04
Empidonax trailli	Disperser	Peripheral	5.00	0.52	0.00	0.49	0.04
Cissus rhombifolia	Plant	Peripheral	5.00	-0.08	0.00	1.51	0.04
Urbanus proteus	Pollinator	Peripheral	5.00	0.52	0.00	0.65	0.04
Dumetella carolinensis	Disperser	Peripheral	5.00	0.52	0.00	0.80	0.04
Leptothorax echinatinodis	Protective ant	Connector	5.00	0.00	0.32	0.89	0.04
Monomorium cyaneum	Protective ant	Peripheral	5.00	0.52	0.00	1.05	0.04
Pitangus sulphuratus	Disperser	Peripheral	5.00	0.52	0.00	1.23	0.04
Hibiscus tiliaceus	Plant	Connector	5.00	-0.08	0.44	1.16	0.04
Anartia fatima	Pollinator	Peripheral	5.00	0.52	0.00	1.31	0.04
Junona evarete	Pollinator	Peripheral	5.00	0.52	0.00	1.53	0.04
Psarocolius montezuma	Disperser	Peripheral	5.00	0.52	0.00	1.60	0.04
Epargyreus aspina	Pollinator	Peripheral	5.00	0.52	0.00	2.09	0.04
Agraulis vanillae	Pollinator	Peripheral	5.00	0.52	0.00	2.26	0.04
Unknown sp2	Plant	Peripheral	4.00	-0.25	0.00	-0.69	0.04
Sesuvium maritimum	Plant	Peripheral	4.00	-0.25	0.00	-0.47	0.04

Cupania dentata	Plant	Peripheral	4.00	-0.25	0.00	-0.07	0.04
Sida sp1	Plant	Peripheral	4.00	-0.25	0.00	0.20	0.04
Bromelia pinguin	Plant	Peripheral	4.00	-0.25	0.00	0.65	0.04
Caesalpinia bonduc	Plant	Peripheral	4.00	-0.25	0.00	0.67	0.04
Ipomoea sp3	Plant	Peripheral	4.00	-0.25	0.00	0.73	0.03
Solenopsis geminata	Protective ant	Peripheral	4.00	0.26	0.00	-0.08	0.03
Vespidae sp1	Pollinator	Connector	4.00	-0.01	0.38	-0.35	0.03
Turdus grayi	Disperser	Peripheral	4.00	0.26	0.00	0.43	0.03
Augochloropsis sp1	Pollinator	Peripheral	4.00	0.26	0.00	0.51	0.03
Mimus polyglottos	Disperser	Peripheral	4.00	0.26	0.00	0.71	0.03
Myiarchus crinitus	Disperser	Peripheral	4.00	0.26	0.00	0.81	0.03
Megarynchus pitangua	Disperser	Peripheral	4.00	0.26	0.00	1.16	0.03
Acacia macracantha	Plant	Peripheral	4.00	-0.25	0.00	2.03	0.03
Achalarus jalapus	Pollinator	Peripheral	4.00	0.26	0.00	1.28	0.03
Icterus galbula	Disperser	Peripheral	4.00	0.26	0.00	1.35	0.03
Icterus gularis	Disperser	Peripheral	4.00	0.26	0.00	1.60	0.03
Xylocopa fimbriata	Pollinator	Peripheral	4.00	0.26	0.00	1.65	0.03
Astraptes fulgerator	Pollinator	Peripheral	4.00	0.26	0.00	1.73	0.03
Sphecidae sp1	Pollinator	Peripheral	4.00	0.26	0.00	2.13	0.03
Sphecidae sp4	Pollinator	Peripheral	4.00	0.26	0.00	2.89	0.03
Urbanus sp1	Pollinator	Peripheral	4.00	0.26	0.00	3.08	0.03
Ipomoea alba	Plant	Peripheral	3.00	-0.42	0.00	-0.81	0.03
Russelia sp1	Plant	Peripheral	3.00	-0.42	0.00	-0.54	0.03
Stemmedenia galeotiana	Plant	Peripheral	3.00	-0.42	0.00	-0.38	0.03
Tabernamontana alba	Plant	Peripheral	3.00	-0.42	0.00	-0.22	0.03
Augochlora sp2	Pollinator	Peripheral	3.00	-0.01	0.00	-0.76	0.03
Byrsonima crassifolia	Plant	Peripheral	3.00	-0.42	0.00	0.01	0.03
Phoebis sp1	Pollinator	Peripheral	3.00	-0.01	0.00	-0.64	0.03
Pseudomyrmex ejectus	Protective ant	Peripheral	3.00	-0.01	0.00	-0.17	0.03
Auglochlora nigrocyanea	Pollinator	Peripheral	3.00	-0.01	0.00	0.07	0.03
Senna occidentalis	Plant	Peripheral	3.00	-0.42	0.00	0.80	0.03
Syrphidae sp9	Pollinator	Peripheral	3.00	-0.01	0.00	0.19	0.03
Syrphidae sp5	Pollinator	Peripheral	3.00	-0.01	0.00	0.32	0.03
Monomorium floricola	Protective ant	Peripheral	3.00	-0.01	0.00	0.49	0.03
Bunchosia lindeliana	Plant	Peripheral	3.00	-0.42	0.00	1.28	0.03
Battus philenor	Pollinator	Peripheral	3.00	-0.01	0.00	0.62	0.03
Petrea volubilis	Plant	Peripheral	3.00	0.00	0.00	0.61	0.03

Species	Type	Role					
Hemiargus ceraunus	Pollinator	Peripheral	3.00	-0.01	0.00	0.68	0.03
Pyrgus communis	Pollinator	Peripheral	3.00	-0.01	0.00	0.70	0.03
Thraupis episcopus	Disperser	Peripheral	3.00	-0.01	0.00	0.76	0.03
Unknown sp1	Pollinator	Connector	3.00	-0.27	0.44	0.11	0.03
Pachycondyla unidentata	Protective ant	Peripheral	3.00	-0.01	0.00	0.80	0.03
Tyrannus verticalis	Disperser	Peripheral	3.00	-0.01	0.00	0.88	0.03
Quasimellana eulogius	Pollinator	Peripheral	3.00	-0.01	0.00	0.91	0.03
Eristalis sp1	Pollinator	Peripheral	3.00	-0.01	0.00	0.96	0.02
Mesoplia regalis	Pollinator	Peripheral	3.00	-0.01	0.00	0.99	0.02
Cephalotes umbraculatus	Protective ant	Peripheral	3.00	-0.01	0.00	1.01	0.02
Paratetrapedia moesta	Pollinator	Peripheral	3.00	-0.01	0.00	1.03	0.02
Enterolobium cyclocarpum	Plant	Peripheral	3.00	-0.42	0.00	1.76	0.02
Syrphidae sp2	Pollinator	Peripheral	3.00	-0.01	0.00	1.15	0.02
Ficus obtusifolia	Plant	Peripheral	3.00	-0.42	0.00	1.87	0.02
Icteria virens	Disperser	Peripheral	3.00	-0.01	0.00	1.19	0.02
Heliconius charithonia	Pollinator	Peripheral	3.00	-0.01	0.00	1.36	0.02
Roystonea dunlapiana	Plant	Peripheral	3.00	-0.42	0.00	2.16	0.02
Danaus eresimus	Pollinator	Peripheral	3.00	-0.01	0.00	1.58	0.02
Cornutia grandiflora	Plant	Peripheral	3.00	-0.42	0.00	2.33	0.02
Agapostemon nasutus	Pollinator	Connector	3.00	-0.27	0.44	1.02	0.02
Phoebis sennae	Pollinator	Peripheral	3.00	-0.01	0.00	1.68	0.02
Melanerpes aurifrons	Disperser	Peripheral	3.00	-0.01	0.00	1.70	0.02
Unknown sp6	Pollinator	Peripheral	3.00	-0.01	0.00	2.56	0.02
Muntigia calabura	Plant	Peripheral	2.00	-0.59	0.00	-0.85	0.02
Callisia fragrans	Plant	Peripheral	2.00	-0.59	0.00	-0.70	0.02
Unknown sp4	Plant	Peripheral	2.00	-0.59	0.00	-0.67	0.02
Lycastrirhyncha sp1	Pollinator	Peripheral	2.00	-0.27	0.00	-1.08	0.02
Pyrisitia proterpia	Pollinator	Peripheral	2.00	-0.27	0.00	-0.97	0.02
Carica papaya	Plant	Peripheral	2.00	-0.59	0.00	-0.41	0.02
Conyza sp1	Plant	Peripheral	2.00	-0.59	0.00	-0.31	0.02
Cordia foliosa	Plant	Peripheral	2.00	-0.59	0.00	-0.26	0.02
Cardinalis cardinalis	Disperser	Peripheral	2.00	-0.27	0.00	-0.75	0.02
Antogonon sp1	Plant	Peripheral	2.00	-0.59	0.00	-0.13	0.02
Eugenia capuli	Plant	Peripheral	2.00	-0.59	0.00	-0.03	0.02
Syrphidae sp6	Pollinator	Peripheral	2.00	-0.27	0.00	-0.50	0.02
Tabebuia chrysantha	Plant	Peripheral	2.00	-0.59	0.00	0.03	0.02
Unknown sp12	Plant	Peripheral	2.00	-0.59	0.00	0.07	0.02

Stachytarpheta sp1	Plant	Peripheral	2.00	-0.59	0.00	0.12	0.02
Rourea glabra	Plant	Peripheral	2.00	-0.59	0.00	0.12	0.02
Urbanus simplicius	Pollinator	Peripheral	2.00	-0.27	0.00	-0.36	0.02
Unknown sp9	Plant	Peripheral	2.00	-0.59	0.00	0.17	0.02
Chioccoca alba	Plant	Peripheral	2.00	-0.59	0.00	0.18	0.02
Pseudomyrmex pallidus	Protective ant	Peripheral	2.00	-0.27	0.00	-0.27	0.02
Melanis pixe	Pollinator	Peripheral	2.00	-0.27	0.00	-0.25	0.02
Empidonax sp2	Disperser	Peripheral	2.00	-0.27	0.00	-0.21	0.02
Prestonia sp1	Plant	Peripheral	2.00	0.00	0.00	-0.66	0.02
Closyne lacinia	Pollinator	Peripheral	2.00	-0.27	0.00	-0.19	0.02
Eulaema polychroma	Pollinator	Peripheral	2.00	-0.27	0.00	-0.13	0.02
Vitis biformis	Plant	Peripheral	2.00	-0.59	0.00	0.46	0.02
Dendroica sp1	Disperser	Peripheral	2.00	-0.27	0.00	-0.07	0.02
Papilio anchisiades	Pollinator	Peripheral	2.00	-0.27	0.00	-0.02	0.02
Tyrannus couchii	Disperser	Peripheral	2.00	-0.27	0.00	-0.01	0.02
Empidonax sp1	Disperser	Peripheral	2.00	-0.27	0.00	-0.01	0.02
Mimoides phaon	Pollinator	Peripheral	2.00	-0.27	0.00	0.12	0.02
Guazuma ulmifolia	Plant	Peripheral	2.00	-0.59	0.00	0.65	0.02
Augochlorella sp1	Pollinator	Peripheral	2.00	-0.27	0.00	0.14	0.02
Scoliidae sp1	Pollinator	Peripheral	2.00	-0.27	0.00	0.16	0.02
Hemipenthes sp1	Pollinator	Peripheral	2.00	-0.27	0.00	0.19	0.02
Archilochus colubris	Pollinator	Peripheral	2.00	-0.27	0.00	0.22	0.02
Phtiria sp1	Pollinator	Peripheral	2.00	-0.27	0.00	0.22	0.02
Geron sp1	Pollinator	Peripheral	2.00	-0.27	0.00	0.23	0.02
Vireo olivaceus	Disperser	Peripheral	2.00	-0.27	0.00	0.26	0.02
Syrphidae sp3	Pollinator	Peripheral	2.00	-0.27	0.00	0.31	0.02
Melete lycimnia	Pollinator	Peripheral	2.00	-0.27	0.00	0.32	0.02
Passiflora holosericea	Plant	Peripheral	2.00	-0.59	0.00	0.92	0.02
Thraupis episcopus	Disperser	Peripheral	2.00	-0.27	0.00	0.42	0.02
Mydas sp1	Pollinator	Peripheral	2.00	-0.27	0.00	0.46	0.02
Nisoniades sp1	Pollinator	Peripheral	2.00	-0.27	0.00	0.49	0.02
Melissodes tepaneca	Pollinator	Peripheral	2.00	-0.27	0.00	0.60	0.02
Papilo thoas	Pollinator	Peripheral	2.00	-0.27	0.00	0.62	0.02
Epargyreus exadeus	Pollinator	Peripheral	2.00	-0.27	0.00	0.71	0.02
Heterocentron suptriplinervium	Plant	Peripheral	2.00	-0.59	0.00	1.27	0.02
Brachymyrmex sp1	Protective ant	Peripheral	2.00	-0.27	0.00	0.75	0.02
Crataeva tapia	Plant	Peripheral	2.00	-0.59	0.00	1.28	0.02

Urbanus dorantes	Pollinator	Peripheral	2.00	-0.27	0.00	0.78	0.02
Urbanus esmeraldus	Pollinator	Peripheral	2.00	-0.27	0.00	0.80	0.02
Prestonia mexicana	Plant	Peripheral	2.00	-0.59	0.00	1.33	0.02
Bombycilla cedrorum	Disperser	Peripheral	2.00	-0.27	0.00	0.82	0.02
Dives dives	Disperser	Peripheral	2.00	-0.27	0.00	0.82	0.02
Unknown sp5	Plant	Peripheral	2.00	-0.59	0.00	1.37	0.02
Codactractus sp1	Pollinator	Peripheral	2.00	-0.27	0.00	0.85	0.02
Piranga ludoviciana	Disperser	Peripheral	2.00	-0.27	0.00	0.85	0.02
Pontederia sagitatta	Plant	Peripheral	2.00	-0.59	0.00	1.38	0.02
Euptoieta hegesia	Pollinator	Peripheral	2.00	-0.27	0.00	0.89	0.02
Anartia jatrophae	Pollinator	Peripheral	2.00	-0.27	0.00	0.92	0.02
Neptunia oleracea	Plant	Peripheral	2.00	-0.59	0.00	1.52	0.02
Phyciodes tulcis	Pollinator	Peripheral	2.00	-0.27	0.00	1.00	0.02
Piranga olivacea	Disperser	Peripheral	2.00	-0.27	0.00	1.02	0.02
Trogon melanocephalus	Disperser	Peripheral	2.00	-0.27	0.00	1.09	0.02
Piranga rubra	Disperser	Peripheral	2.00	-0.27	0.00	1.12	0.02
Polythrix mexicanus	Pollinator	Peripheral	2.00	-0.27	0.00	1.15	0.02
Tityra semifasciata	Disperser	Peripheral	2.00	-0.27	0.00	1.25	0.02
Syrphidae sp7	Pollinator	Peripheral	2.00	-0.27	0.00	1.26	0.02
Icterus cucullatus	Disperser	Peripheral	2.00	-0.27	0.00	1.34	0.02
Arundo donax	Plant	Peripheral	2.00	-0.59	0.00	1.92	0.02
Combretum sp1	Plant	Connector	2.00	0.00	0.50	-0.20	0.02
Calliopsis sp1	Pollinator	Peripheral	2.00	-0.27	0.00	1.50	0.02
Scycidium tamnifolium	Plant	Peripheral	2.00	-0.59	0.00	2.13	0.02
Dolichoderus diversus	Protective ant	Peripheral	2.00	-0.27	0.00	1.60	0.02
Astraptes anaphus	Pollinator	Peripheral	2.00	-0.27	0.00	1.69	0.02
Polistes sp1	Pollinator	Connector	2.00	0.00	0.50	0.03	0.02
Trichilia havanensis	Plant	Peripheral	2.00	-0.59	0.00	2.36	0.02
Phocides polybius	Pollinator	Peripheral	2.00	-0.27	0.00	2.04	0.02
Syrphidae sp1	Pollinator	Connector	2.00	0.00	0.50	0.74	0.01
Muscidae sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-1.20	0.01
Anthus spragueii	Disperser	Peripheral	1.00	-0.53	0.00	-1.16	0.01
Pseudaugochlora graminea	Pollinator	Peripheral	1.00	-0.53	0.00	-1.16	0.01
Ipomoea sp4	Plant	Peripheral	1.00	-0.76	0.00	-0.74	0.01
Unknown sp3	Plant	Peripheral	1.00	-0.76	0.00	-0.65	0.01
Paratetrapedia sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-1.01	0.01
Phoradendron tamaulipensis	Plant	Peripheral	1.00	-0.76	0.00	-0.50	0.01

Megachile sp4	Pollinator	Peripheral	1.00	-0.53	0.00	-0.86	0.01
Inga vera	Plant	Peripheral	1.00	-0.76	0.00	-0.44	0.01
Polistes sp2	Pollinator	Peripheral	1.00	-0.53	0.00	-0.80	0.01
Guettarda elliptica	Plant	Peripheral	1.00	-0.76	0.00	-0.39	0.01
Sphecidae sp3	Pollinator	Peripheral	1.00	-0.53	0.00	-0.74	0.01
Tachinidae sp4	Pollinator	Peripheral	1.00	-0.53	0.00	-0.73	0.01
Tyrannus vociferans	Disperser	Peripheral	1.00	-0.53	0.00	-0.73	0.01
Helianthus sp1	Plant	Peripheral	1.00	-0.76	0.00	-0.33	0.01
Pyrgus oileus	Pollinator	Peripheral	1.00	-0.53	0.00	-0.69	0.01
Calliopsis sp2	Pollinator	Peripheral	1.00	-0.53	0.00	-0.68	0.01
Vermivora celata	Disperser	Peripheral	1.00	0.00	0.00	-1.57	0.01
Megachile sp5	Pollinator	Peripheral	1.00	-0.53	0.00	-0.68	0.01
Vespidae sp8	Pollinator	Peripheral	1.00	-0.53	0.00	-0.63	0.01
Vespidae sp3	Pollinator	Peripheral	1.00	-0.53	0.00	-0.61	0.01
Pseudomyrmex ferrugineus	Protective ant	Peripheral	1.00	-0.53	0.00	-0.60	0.01
Passerina versicolor	Disperser	Peripheral	1.00	-0.53	0.00	-0.59	0.01
Rethus arcius	Pollinator	Peripheral	1.00	-0.53	0.00	-0.58	0.01
Heliotropium sp1	Plant	Peripheral	1.00	-0.76	0.00	-0.18	0.01
Aguna claxon	Pollinator	Peripheral	1.00	-0.53	0.00	-0.54	0.01
Tillandsia limbata	Plant	Peripheral	1.00	-0.76	0.00	-0.16	0.01
Myiarchus cinerascens	Disperser	Peripheral	1.00	-0.53	0.00	-0.52	0.01
Unknown sp8	Plant	Peripheral	1.00	-0.76	0.00	-0.15	0.01
Bouchea sp1	Plant	Peripheral	1.00	-0.76	0.00	-0.15	0.01
Psittacanthus schiedeanus	Plant	Peripheral	1.00	-0.76	0.00	-0.14	0.01
Turnefortia hirsutissima	Plant	Peripheral	1.00	-0.76	0.00	-0.13	0.01
Tachinidae sp3	Pollinator	Peripheral	1.00	-0.53	0.00	-0.49	0.01
Palpada sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.49	0.01
Phtiria sp2	Pollinator	Peripheral	1.00	-0.53	0.00	-0.48	0.01
Tachinidae sp5	Pollinator	Peripheral	1.00	-0.53	0.00	-0.47	0.01
Everes comyntas	Pollinator	Peripheral	1.00	-0.53	0.00	-0.45	0.01
Eugenia acapulcensis	Plant	Peripheral	1.00	-0.76	0.00	-0.08	0.01
Pithecellobium calistachys	Plant	Peripheral	1.00	-0.76	0.00	-0.06	0.01
Centris sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.41	0.01
Vespidae sp7	Pollinator	Peripheral	1.00	-0.53	0.00	-0.41	0.01
Adelpha fessonia	Pollinator	Peripheral	1.00	-0.53	0.00	-0.41	0.01
Diptera sp3	Pollinator	Peripheral	1.00	-0.53	0.00	-0.40	0.01
Cnidoscolus sp1	Plant	Peripheral	1.00	-0.76	0.00	0.00	0.01

Diptera sp2	Pollinator	Peripheral	1.00	-0.53	0.00	-0.32	0.01
Colletes sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.32	0.01
Unknown sp4	Pollinator	Peripheral	1.00	-0.53	0.00	-0.30	0.01
Ptiloglossa sp1	Pollinator	Peripheral	1.00		0.00	-1.12	0.01
Coelioxys sp2	Pollinator	Peripheral	1.00	-0.53	0.00	-0.30	0.01
Sostrata bifasciata	Pollinator	Peripheral	1.00	-0.53	0.00	-0.28	0.01
Syrphidae sp4	Pollinator	Peripheral	1.00	-0.53	0.00	-0.27	0.01
Augochlora sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.24	0.01
Bracon sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.24	0.01
Diptera sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.23	0.01
Urbanus procne	Pollinator	Peripheral	1.00	-0.53	0.00	-0.22	0.01
Psidium guajava	Plant	Peripheral	1.00	-0.76	0.00	0.16	0.01
Bombyliidae sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.19	0.01
Lasioglossum sp2	Pollinator	Peripheral	1.00	-0.53	0.00	-0.18	0.01
Hypantidium sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.18	0.01
Staphylus mazans	Pollinator	Peripheral	1.00	-0.53	0.00	-0.16	0.01
Megachile sp6	Pollinator	Peripheral	1.00	-0.53	0.00	-0.15	0.01
Vespidae sp2	Pollinator	Peripheral	1.00	-0.53	0.00	-0.13	0.01
Theope eupolis	Pollinator	Peripheral	1.00	0.00	0.00	-1.01	0.01
Agave angustifolia	Plant	Peripheral	1.00	-0.76	0.00	0.26	0.01
Peponapis crassidentata	Pollinator	Peripheral	1.00	-0.53	0.00	-0.11	0.01
Sarcophagidae sp1	Pollinator	Peripheral	1.00	0.00	0.00	-0.96	0.01
Muscidae sp2	Pollinator	Peripheral	1.00	0.00	0.00	-0.96	0.01
Exomalopsis zexmeniae	Pollinator	Peripheral	1.00	-0.53	0.00	-0.05	0.01
Heliconius erato	Pollinator	Peripheral	1.00	0.00	0.00	-0.94	0.01
Megachile sp1	Pollinator	Peripheral	1.00	-0.53	0.00	-0.03	0.01
Eufriesea mexicana	Pollinator	Peripheral	1.00	-0.53	0.00	-0.02	0.01
Camponotus sericeiventris	Protective ant	Peripheral	1.00	-0.53	0.00	0.00	0.01
Myiarchus tuberculifer	Disperser	Peripheral	1.00	-0.53	0.00	0.01	0.01
Coelioxys sp1	Pollinator	Peripheral	1.00	-0.53	0.00	0.09	0.01
Gliricidia sepium	Plant	Peripheral	1.00	-0.76	0.00	0.46	0.01
Colletes punctipennis	Pollinator	Peripheral	1.00	0.00	0.00	-0.81	0.01
Centris nitida	Pollinator	Peripheral	1.00	-0.53	0.00	0.10	0.01
Vespidae sp5	Pollinator	Peripheral	1.00	0.00	0.00	-0.80	0.01
Rivina humilis	Plant	Peripheral	1.00	-0.76	0.00	0.48	0.01
Sabal mexicana	Plant	Peripheral	1.00	-0.76	0.00	0.49	0.01
Vespidae sp6	Pollinator	Peripheral	1.00	-0.53	0.00	0.12	0.01

Chlosyne theona	Pollinator	Peripheral	1.00	-0.53	0.00	0.12	0.01
Dolichopodidae sp1	Pollinator	Peripheral	1.00	-0.53	0.00	0.13	0.01
Anthidiellum sp1	Pollinator	Peripheral	1.00	-0.53	0.00	0.14	0.01
Jaquinia macrocarpa	Plant	Peripheral	1.00	0.00	0.00	-0.74	0.01
Epicharis lunulata	Pollinator	Peripheral	1.00	0.00	0.00	-0.74	0.01
Passiflora sp1	Plant	Peripheral	1.00	0.00	0.00	-0.72	0.01
Unknown sp3	Pollinator	Peripheral	1.00	-0.53	0.00	0.18	0.01
Strymon alba	Pollinator	Peripheral	1.00	-0.53	0.00	0.19	0.01
Hemipenthes sp2	Pollinator	Peripheral	1.00	-0.53	0.00	0.20	0.01
Unknown sp7	Plant	Peripheral	1.00	0.00	0.00	-0.69	0.01
Eurytides philolaus	Pollinator	Peripheral	1.00	-0.53	0.00	0.21	0.01
Sphecidae sp5	Pollinator	Peripheral	1.00	-0.53	0.00	0.21	0.01
Chioides zilpa	Pollinator	Peripheral	1.00	-0.53	0.00	0.23	0.01
Pompilidae sp2	Pollinator	Peripheral	1.00	-0.53	0.00	0.26	0.01
Anteros carausius	Pollinator	Peripheral	1.00	0.00	0.00	-0.61	0.01
Vespidae sp4	Pollinator	Peripheral	1.00	-0.53	0.00	0.32	0.01
Calcididae sp1	Pollinator	Peripheral	1.00	0.00	0.00	-0.51	0.01
Dryadula phaetusa	Pollinator	Peripheral	1.00	-0.53	0.00	0.39	0.01
Paratrechina sp1	Protective ant	Peripheral	1.00	-0.53	0.00	0.39	0.01
Cycloglypha thrasibulus	Pollinator	Peripheral	1.00	-0.53	0.00	0.41	0.01
Danaus plexippus	Pollinator	Peripheral	1.00	-0.53	0.00	0.46	0.01
Unknown sp10	Plant	Peripheral	1.00	-0.76	0.00	0.97	0.01
Megachile sp3	Pollinator	Peripheral	1.00	0.00	0.00	-0.15	0.01
Kallstroemia maxima	Plant	Peripheral	1.00	-0.76	0.00	1.14	0.01
Leptotes casius	Pollinator	Peripheral	1.00	-0.53	0.00	0.87	0.01
Ancylocelis apiformis	Pollinator	Peripheral	1.00	0.00	0.00	0.09	0.01
Unknown sp13	Plant	Peripheral	1.00	-0.76	0.00	1.37	0.01
Vireo solitarius	Disperser	Peripheral	1.00	-0.53	0.00	1.02	0.01
Pseudomyrmex sp1	Protective ant	Peripheral	1.00	-0.53	0.00	1.08	0.01
Manihot sp1	Plant	Peripheral	1.00	-0.76	0.00	1.50	0.01
Epargyreus spina	Pollinator	Peripheral	1.00	-0.53	0.00	1.17	0.01
Tournefortia sp1	Plant	Peripheral	1.00	-0.76	0.00	1.55	0.01
Rynchosia americana	Plant	Peripheral	1.00	-0.76	0.00	1.58	0.01
Proteides mercurius	Pollinator	Peripheral	1.00	-0.53	0.00	1.21	0.01
Myiarchus tyrannulus	Disperser	Peripheral	1.00	-0.53	0.00	1.22	0.01
Chlosyne janais	Pollinator	Peripheral	1.00	-0.53	0.00	1.25	0.01
Bombyliidae sp2	Pollinator	Peripheral	1.00	-0.53	0.00	1.27	0.01

Marpesia sp1	Pollinator	Peripheral	1.00	-0.53	0.00	1.27		0.01
Unknown sp1	Plant	Peripheral	1.00	-0.76	0.00	1.65		0.01
Spathilepia clonius	Pollinator	Peripheral	1.00	-0.53	0.00	1.31		0.01
Urbanus doryssus	Pollinator	Peripheral	1.00	-0.53	0.00	1.31		0.01
Unknown sp2	Pollinator	Peripheral	1.00	-0.53	0.00	1.32		0.01
Solanum diversifolium	Plant	Peripheral	1.00	-0.76	0.00	1.71		0.01
Unknown sp6	Plant	Peripheral	1.00	-0.76	0.00	1.73		0.01
Tyrannus melancholicus	Disperser	Peripheral	1.00	-0.53	0.00	1.37		0.01
Phtiria sp3	Pollinator	Peripheral	1.00	-0.53	0.00	1.37		0.01
Tachinidae sp6	Pollinator	Peripheral	1.00	-0.53	0.00	1.40		0.01
Fabaceae sp1	Plant	Peripheral	1.00	-0.76	0.00	1.80		0.01
Nymphaea ampla	Plant	Peripheral	1.00	-0.76	0.00	1.81		0.01
Momotus momota	Disperser	Peripheral	1.00	-0.53	0.00	1.44		0.01
Quiscalus mexicanus	Disperser	Peripheral	1.00	-0.53	0.00	1.47		0.01
Piranga bidentata	Disperser	Peripheral	1.00	-0.53	0.00	1.48		0.01
Polytex vibex	Pollinator	Peripheral	1.00	-0.53	0.00	1.50		0.01
Fabaceae sp2	Plant	Peripheral	1.00	-0.76	0.00	1.87		0.01
Icterus spurius	Disperser	Peripheral	1.00	-0.53	0.00	1.56		0.01
Unknown sp5	Pollinator	Peripheral	1.00	-0.53	0.00	1.61		0.01
Hylephila phyleus	Pollinator	Peripheral	1.00	-0.53	0.00	1.70		0.01
Calycopis isobeon	Pollinator	Peripheral	1.00	-0.53	0.00	1.72		0.01
Lerodea dysaules	Pollinator	Peripheral	1.00	-0.53	0.00	1.77		0.01
Tachinidae sp1	Pollinator	Peripheral	1.00	-0.53	0.00	1.93		0.01
Tachinidae sp2	Pollinator	Peripheral	1.00	-0.53	0.00	2.15		0.01
Vinepeius tinga	Pollinator	Peripheral	1.00	-0.53	0.00	2.19		0.01
Megachile sp2	Pollinator	Peripheral	1.00	-0.53	0.00	2.42		0.01
Caparis frondosa	Plant	Peripheral	1.00	-0.76	0.00	2.92		0.01
Iresine celosia	Plant	Peripheral	1.00	-0.76	0.00	3.06		0.01

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221 **Appendix S7.** Network descriptors, standardized network descriptors (z-score) with the associated p-values (see Appendix S3 for explanation)

222 and the number of species removed for each simulation analysis of core species removal. The network descriptor values were quantified for the

223 intact multi-interaction network (No core removal) or for the multi-interaction network after the removal of its own core (General core removal)

224 or the core of one of the sub-networks (Pollination core removal, Ants core removal and Dispersal core removal).

Network descriptor	Core removal scenario	Descriptor value	Descriptor z-score	p-value	Number of species removed
Nestedness	No core removal	6.892	-	-	0
	General core removal	1.825	-12.610	0	39
	Pollination core removal	5.738	-4.164	0	27
	Ants core removal	6.013	-3.052	0	10
	Dispersal core removal	6.990	0.291	0.54	10
Modularity	No core removal	0.653	-	-	0
	General core removal	0.839	14.642	0.00	39
	Pollination core removal	0.676	1.576	0.06	27
	Ants core removal	0.667	0.033	0.46	10
	Dispersal core removal	0.628	-3.801	0.99	10

225 **Appendix S8.** Network descriptors, standardized network descriptors (z-score) with the associated p-values (see Appendix S3 for explanation)

226 for each simulation analysis of core links removal. The network descriptor values were quantified for the intact multi-interaction network (No

227 core removal) or for the multi-interaction network after the removal of the links between its own core (General core removal) or the core links of

228 one of the sub-networks (Pollination core removal, Ants core removal and Dispersal core removal).

Network metric	Link rarefaction scenario	Metric value	Metric z-score	p-value	Number of links removed
Nestedness	No rarefaction	6.892	-	-	0
	General core removal	5.005	-7.684	0.00	79
	Pollination core removal	5.723	-6.349	0.00	43
	Ants core removal	6.494	-3.824	0.00	19
	Dispersal core removal	6.553	-5.185	0.00	12
Modularity	No rarefaction	0.653	-	-	0
	General core removal	0.690	3.186	0.01	79
	Pollination core removal	0.681	2.815	0.00	43
	Ants core removal	0.656	0.298	0.42	19
	Dispersal core removal	0.644	-1.507	0.94	12

229   **Appendix S9.** Robustness values, standardized robustness values (z-score) with the associated p-values (see Appendix S3 for explanation) and

230   the number of links removed for each simulation analysis of core links removal. The network robustness values were quantified for the intact

231   multi-interaction network (No core removal) or for the multi-interaction network after the removal of the links between its own core (General

232   core removal) or the core links of one of the sub-networks (Pollination core removal, Ants core removal and Dispersal core removal).

Extinction scenario	Trophic level for extinction	Link rarefaction scenario	Robustness value	Robustness z-score	p-value	Number of links removed
Random	Plants	No rarefaction	0.651	-	-	0
		General core removal	0.638	1.454	0.94	79
		Pollination core removal	0.643	1.207	0.85	43
		Ants core removal	0.650	0.526	0.67	19
		Dispersal core removal	0.649	0.781	0.73	12
Random	Animals	No rarefaction	0.728	-	-	0
		General core removal	0.722	2.632	0.99	79
		Pollination core removal	0.733	2.886	1.00	43
		Ants core removal	0.724	-0.036	0.49	19
		Dispersal core removal	0.729	0.970	0.82	12
Least-to-most connected	Plants	No rarefaction	0.884	-	-	0
		General core removal	0.880	0.467	0.64	79
		Pollination core removal	0.870	-1.784	0.06	43
		Ants core removal	0.887	0.200	0.55	19
		Dispersal core removal	0.882	-1.103	0.13	12
Least-to-most connected	Animals	No rarefaction	0.934	-	-	0

		General core removal	0.924	-0.068	0.40	79
		Pollination core removal	0.921	-0.431	0.33	43
		Ants core removal	0.931	-0.955	0.19	19
		Dispersal core removal	0.927	-0.376	0.37	12
Most-to-least connected	Plants	No rarefaction	0.320	-	-	0
		General core removal	0.317	3.301	1.00	79
		Pollination core removal	0.322	2.959	1.00	43
		Ants core removal	0.315	0.016	0.43	19
		Dispersal core removal	0.318	0.076	0.50	12
Most-to-least connected	Animals	No rarefaction	0.409	-	-	0
		General core removal	0.409	0.762	0.79	79
		Pollination core removal	0.416	1.677	0.97	43
		Ants core removal	0.414	0.800	0.73	19
		Dispersal core removal	0.415	1.130	0.87	12

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