Pollination networks of oil-flowers: a tiny world within the smallest of all worlds

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Summary

1. In the Neotropics, most plants depend on animals for pollination. Solitary bees are the most important vectors, and among them members of the tribe Centridini depend on oil from flowers (mainly Malpighiaceae) to feed their larvae. This specialized relationship within 'the smallest of all worlds' (a whole pollination network) could result in a 'tiny world' different from the whole system. This 'tiny world' would have higher nestedness, shorter path lengths, lower modularity and higher resilience if compared with the whole pollination network.

2. In the present study, we contrasted a network of oil-flowers and their visitors from a Brazilian steppe ('caatinga') to whole pollination networks from all over the world.

3. A network approach was used to measure network structure and, finally, to test fragility. The oil-flower network studied was more nested ($NODF = 0.84$, $N = 0.96$) than all of the whole pollination networks studied. Average path lengths in the two-mode network were shorter (one node, both for bee and plant one-mode network projections) and modularity was lower ($M = 0.22$ and four modules) than in all of the whole pollination networks. Extinctions had no or small effects on the network structure, with an average change in nestedness smaller than 2% in most of the cases studied; and only two species caused coextinctions. The higher the degree of the removed species, the stronger the effect and the higher the probability of a decrease in nestedness.

4. We conclude that the oil-flower subweb is more cohesive and resilient than whole pollination networks. Therefore, the Malpighiaceae have a robust pollination service in the Neotropics. Our findings reinforce the hypothesis that each ecological service is in fact a mosaic of different subservices with a hierarchical structure ('webs within webs').

Key-words: community structure, melittophyly, modules, mutualism, subwebs.

Introduction

In some localities, up to 98% of all angiosperms depend on animals for pollination (Bawa 1990). Solitary bees are the major pollinators (Roubik 1989), and most of them look for nectar and pollen in flowers. But species of the tribe Centridini (Hymenoptera: Apidae) also look for oil in specialized flower structures (elaiophores) mainly among the Malpighiaceae in the Neotropics (Vogel 1990; Machado 2004). Used to feed the larvae, oil is a crucial resource (Alves-dos-Santos, Machado & Gaglianone 2007). The population ecology of oil-flower systems is well known (Machado 2004), but this interaction has not been studied at the community level from a complex network perspective. This approach could allow us to assess properties of species and interactions together in

the framework of universal patterns, such as the 'small-world phenomenon' (Bascompte & Jordano 2007).

Pollination networks share some invariant properties with other mutualisms (Bascompte *et al.* 2003), and have been suggested as being 'the smallest of all worlds', because of their high cohesiveness and short path lengths (Olesen *et al.* 2006). The subsystem formed by oil-flowers and bees may be a 'tiny world', i.e. even more cohesive, because of the high phylogenetic relatedness within both sides of the interaction, Centridini oil-collecting bees and Malpighiaceae oil-flowers. This is likely, because within a lower clade such as a tribe, species tend to be more similar to each other. Furthermore, small differences between otherwise very similar systems (e.g. interaction intimacy, Guimarães Jr. *et al.* 2007) can result in differences in the structure and fragility of networks. These differences can generate 'webs within webs' (Newman, Barabasi & Watts 2006) or 'mutualistic modules' (Jordano 1987),

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indicating a hierarchical structure. If this oil-flower subsystem is indeed a tiny world, then we should expect it to also be more resilient, as extinctions could be more easily compensated (Costa 2004). Furthermore, modules formed by oil-bees and oil-flowers have already been detected in whole pollination networks, supporting the hypothesis of a hierarchical structure (Olesen *et al.* 2007).

The goal in the present study was to test whether the tiny world formed by the ensemble (sensu Fauth *et al.* 1996) of oil-flowers and their visitors is more cohesive and resilient than whole pollination networks. More specifically, we expected the oil-flower network to be: (i) more nested than whole pollination systems, because this specialized interactions could result in higher connectivity, and ultimately in higher nestedness; (ii) a small world with short distances between most partners, because of the high phylogenetic relatedness of both bees and plants. We also expected the modularity of the oil-flower network to be lower than the average of the whole pollination networks, because it comprised fewer clades; and (iii) more resilient to extinctions, because of the high cohesiveness and its compensatory effects (Albert, Jeong & Barabasi 2000).

Materials and methods

DATA COLLECTION

Data on bee–Malpighiaceae interactions were collected in the Parque Nacional do Catimbau (hereafter Catimbau), in the municipality of Buíque (PE), northeastern Brazil (8°24′00″–8°36′35″ S and 37°09′30″–37°14′40″ W). Catimbau covers 60·7 km², and has a semi-arid regional climate (BSh – Köppen classification). The park's vegetation is a mixture of Caatinga (Brazilian steppe), Cerrado (Brazilian savanna) and Campos Rupestres (montane savanna) (Rodal *et al.* 1998; SNE, 2002). The annual average rainfall is 600 mm and the annual average temperature is 26 °C, with a rainy season occurring between April and June (SUDENE, 1990).

Field work was carried out during three different periods: from January to December 2003, from January to December 2005 and from August to December 2006. We focused on plants of the family Malpighiaceae, because this is the most important family of oil-flowers in the Neotropics (Vogel 1990). One hundred and thirty-eight individual plants in natural clumps of 13 Malpighiaceae species were monitored in the study area. Plant vouchers were deposited in the Herbarium UFP (Departamento de Botânica, Universidade Federal de Pernambuco, Brazil). During the flowering peak of each species, we recorded the number of bee visits to flowers over four consecutive days, from 5.00 to 17.00. We conducted a total of 1392 h of observation. Bee vouchers were collected, preserved dry and deposited in the collection of the Floral and Reproductive Biology Laboratory of the Departamento de Botânica, Universidade Federal de Pernambuco.

Additionally, we used 22 data sets downloaded from the Interaction Web Database (hereafter IWD; Vazquez & Melian 2008) in order to compare data from whole pollination networks with our data focused on the ensemble of oil-collecting bees and oil-flowers. Those data sets refer to pollination networks from all over the world including different biomes (see Table S3 in Supporting Information). We also used results published by Olesen *et al.* (2007) that describe the modularity and the number of modules for 29 whole pollination networks from all over the world (see Supporting Information, Table

S1, of the mentioned paper), and by Olesen *et al.* (2006) from 37 other pollination networks, in order to compare them with our own data on oil-flowers.

DATA ANALYSIS

We organized data on bee visits to plants as an adjacency matrix $P \times A$, with plant species listed as rows (P) and bee species listed as columns (A). Each cell was filled with the number of recorded visits of a bee species j to flowers of a plant species i, and thus the matrix was weighted with frequencies of visitation. Then, we analysed the matrix as one- or two-mode networks, depending on the prediction to be tested (see explanations that follow). We also counted the number of animal and plant species in the matrix, and its richness ratio, a good indicator of network structure (plants/animals, see Guimarães *et al.* 2007a), and compared those values with the ones observed in the whole networks. We presented the studied network as graphs using Pajek 1·24 (Batagelj & Mrvar 1998).

First, high nestedness was hypothesized for our network because the network was thought to have a higher connectivity, as explained in the Introduction. Connectivity seems to be positively related to nestedness (Almeida-Neto *et al.* 2008). Nestedness is one kind of asymmetry of interactions characterized by a core of highly connected species (generalists) that interact mainly with each other, and a subset of species with fewer connections (specialists) that interact mainly with the generalists (Bascompte *et al.* 2003). So, to test the first prediction of high nestedness, we transformed the weighted data into binary data (presence/absence of interaction) and calculated the degree of nestedness in the network using the new metric *NODF* (Almeida-Neto *et al.* 2008), which fits better the concept of nestedness than the classic T metric (Atmar & Patterson 1993). However, we also calculated the N metric, which is derived from T, and expressed as $N = (100-T)/100$, in order to allow comparisons with previous studies. Values of *NODF* were compared with values observed in the 22 worldwide networks from IWD. The significance of both metrics was estimated with Monte Carlo procedures (1000 iterations) in Aninhado 3·0 (Guimarães & Guimarães 2006), using a null model (*Ce*), where the probability of interaction between two species is proportional to the number of interactions of those species (Bascompte *et al.* 2003).

To test the second hypothesis of a small-world structure, two more predictions were derived. First, the original two-mode network was transformed in Pajek 1·24 into two one-mode networks, plants and bees separated, defined by interactions with the same partners. Then, we tested our second prediction in this study: a short average path length between pairs of species, i.e. the number of nodes between two nodes in the network. Values of path lengths were compared with values from 37 networks published by Olesen *et al.* (2006). Then, we tested our third prediction: a low value of modularity. For this test we used the software Netcarto, so we could calculate the M index and detect modules with a simulated annealing algorithm (Guimerà & Amaral 2005). We compared the value of modularity observed in the oil-flower network with values of 29 pollination networks from all over the world published by Olesen *et al.* (2007).

To test for network resilience, simulated removals of species in the binary matrix were used in order to determine the degree to which the network structure changed and the number of extinctions that were caused. The fourth prediction was a small change in the network's degree of nestedness and few coextinctions, as observed in most scale-free and broad-scale networks (Albert *et al.* 2000). The fifth prediction was that generalists were expected to cause larger changes than specialists because they usually play the role of hubs or

connectors (Olesen *et al.* 2007). One species and all of its interactions were removed from the network at a time in a jack-knife procedure. If there were species that were connected only to the removed species, they and their interactions were removed as well (a coextinction). This procedure was the same as that used in previous sensitivity analyses (Memmott, Waser & Price 2004; Rezende *et al.* 2007). After each removal, the relative change in nestedness ($NODF_r$) of the whole network was measured as: $NODF_r = (NODF_{obs}–NODF_{ori})/NODF_{ori}$, where $NODF_{obs}$ is the observed value of $NODF$ after the species was removed, and $NODF_{ori}$ is the original value of $NODF$ of the full matrix. Finally, the number of coextinctions (C) was counted. We ran a logistic regression to test whether species with more interactions were more likely to cause decreases in nestedness. The software Ataque (F.M.D. Marquitti & M.A.M. Aguiar, unpublished data), was used to remove species and interactions according to the explained criteria. Average values of C and $NODF_r$ were calculated for 23 networks from IWD, and were compared with the oil-flower network.

Finally, because species richness may influence the structure of a network (Guimarães *et al.* 2007a), we controlled for this factor by correlating $NODF$, $NODF_r$, C and M to species richness in all networks. Even if species richness is indeed a correlate of those four metrics, we expected the oil-flower network to deviate from the average trends because of its higher phylogenetic relatedness (as explained before). Thus, the residuals of this network in each correlation were expected to be higher than average in the case of $NODF$, but lower than average in the three other correlations.

Results

The pollination network of oil-flowers and oil-collecting bees was composed of 26 species in our study area, and therefore the species richness was lower than the average of all of the whole networks (mean ± SD: total richness = 126 ± 159 species, N = 22). The studied network had a perfectly balanced proportion of plants and animals of 1 : 1 (13 × 13 species), and as such was more balanced than 90% of the whole networks from Olesen *et al.* (2006) that were used for comparison (plant : animal ratio of 0·43 ± 0·40). In our study, there were a total of 28 224 visits to the flowers and 71 connections between bees and flowers, and all Malpighiaceae species interacted only with the Apidae bees. Out of the 13 visiting bee species, 10 were oil-collecting bees that are members of the tribe Centridini. The other three species (*Apis mellifera* Linnaeus, 1758, *Xylocopa grisescens* Lepeletier, 1841 and *Xylocopa* sp.) only took pollen from Malpighiaceae flowers, and do not collect oil. The genus *Centris* was the major bee group represented, with nine species that conducted 94% of all pollination events (see Supporting Information, Table S1).

As expected, nestedness was very high in the studied network as measured by both indices ($NODF$ = 0·84, P < 0·001; N = 96, P < 0·001). We observed a core of generalist plants interacting mainly with generalist *Centris* bees, and a subset of other plants and bees with few interactions that were connected only to the main core (Fig. 1). There were no interactions among specialists, indicating a highly nested structure. The degree of nestedness was substantially higher than the values observed in 22 whole pollination networks from IWD ($NODF$ = 0·32 ± 0·18).
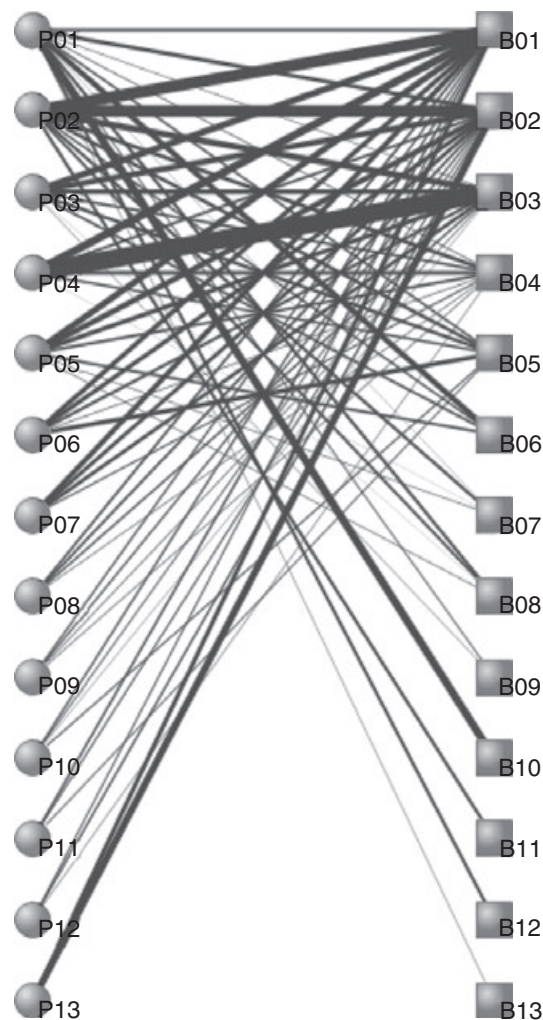

Fig. 1. A two-mode ordered graph representing the pollination ensemble formed by pollinating bees (boxes) and plants of the family Malpighiaceae (ellipses). Edges represent pollination interactions, and the thickness of the line indicates the number of visits by the bee species to the plant species (the thicker the line, the higher the number of visits). See the legend for species labels in Table S2.

The average path length between bees was very short (one node), and the same pattern was observed among plants (one node). Thus, all nodes were indirectly connected to each other in the network through interactions with partners, a shorter distance than observed in all 37 of the whole pollination networks studied by Olesen *et al.* (2006) (path length: animals = 1·73 ± 0·28, plants = 1·47 ± 0·29). Only four compartments were detected in the simulated annealing analysis (Fig. 2), and modularity was significant but lower (M = 0·20, P = 0·04) than in all 29 of the whole pollination networks studied by Olesen *et al.* (2007) (number of compartments = 8·76 ± 3·72; M = 0·47 ± 0·09). Six bee species and one plant species had a central position in the network (Fig. 2).

The pollination network was very resilient to extinctions, as expected, because the average absolute change in nestedness caused by single-species extinctions was very low (N_r = 0·4 ± 1·5%; see Supporting Information, Table S2).
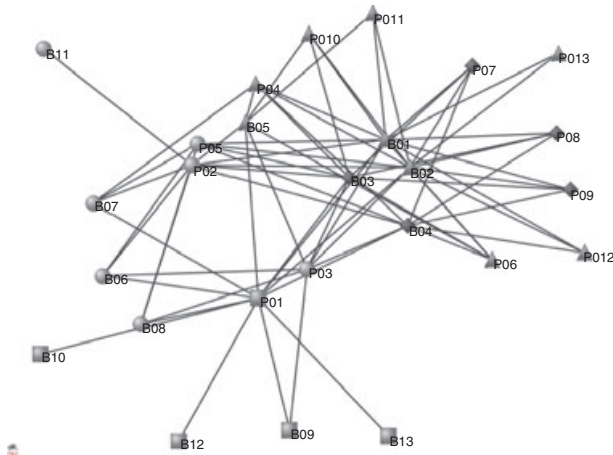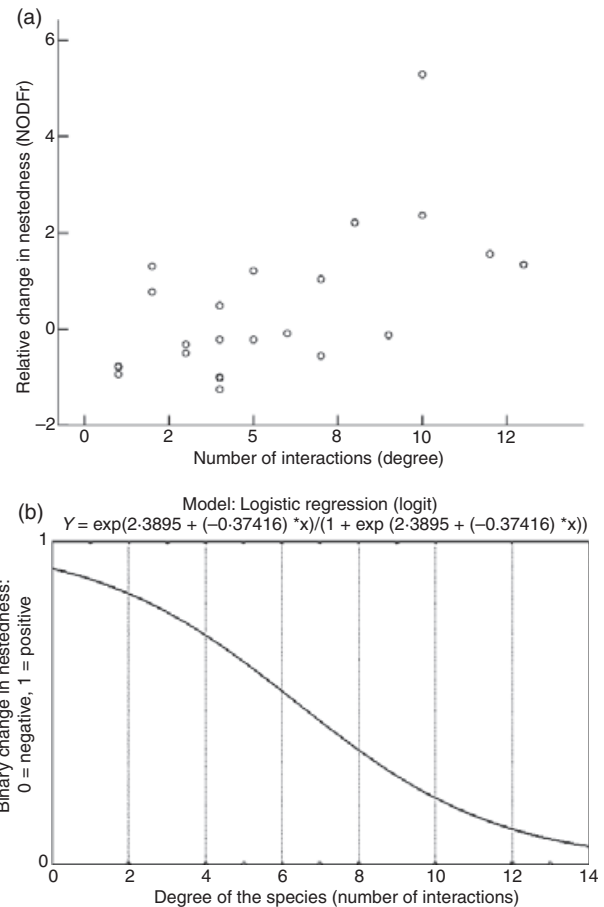
Fig. 2. The whole network is represented as an energy two-mode graph (Kamada–Kawai free method) with the four modules identified in Netcarto represented with different symbols (ellipses, triangles, diamonds and boxes).


Fig. 3. Results are shown from cases in which the network was submitted to simulated single-species extinctions: (a) relationship between the degree of the removed species and the absolute change in nestedness caused by its removal; and (b) relationship between the probability of a decrease (0) or increase (1) in nestedness and the degree (number of interactions) of the removed species.

Most species caused no change in nestedness when removed from the network. There were some outliers, like the most important bee (*Centris caxiensis* Ducke, 1907), which alone caused a decrease of 5·3% in nestedness, and the most important plant [*Banisteriopsis muricata* (Cav) Cuatrec.] that was responsible for an increase of 1·6% in nestedness. Almost all plant and bee species caused no coextinctions, but one plant species (*B. muricata*) caused four coextinctions in the network when removed. In the 22 IWD whole networks, an average of 95% of the extinctions resulted in at least one coextinction ($C = 2·2 \pm 4·5$, varying from 0 to 6) and an average change of 2·0 $\pm$ 7·3% in nestedness (varying from −21·9 to 25·9%) was observed.

On average, bees caused stronger changes than plants ($U = 39·5$, $P = 0·006$) and generalists caused stronger changes in nestedness than specialists ($r^2 = 0·38$, $P = 0·001$) (Fig. 3). Additionally, the higher the degree of the removed species, the higher the probability of a decrease in nestedness, and an increase of one interaction in the species degree represented an increase in 0·68% in the probability of a decrease in nestedness ($\chi^2 = 8·36$, $P = 0·004$, odds ratio = 0·68).

Furthermore, we observed that the degree of nestedness (*NODF*) decreased with species richness in all pollination networks analysed, including the oil-flower network ($r^2 = -0·49$, $P = 0·02$) (Fig. 4). However, the residual of the oil-flower network (0·47) was positive and higher than in all other residuals (0·00 $\pm$ 0·16), indicating that this particular network had a higher than expected nestedness. Species richness also explained the number of coextinctions (*C*) that occurred after single-species extinctions, which were higher in richer networks ($r^2 = 0·52$, $P = 0·01$). Again, the oil-flower network differed from the others because its residual (−0·87) was much lower than the residual of 86% of the whole networks (0·00 $\pm$ 1·33). There was no correlation between species richness and the relative change in nestedness (*NODF*$_r$) after single-species extinctions ($r^2 = 0·004$, $P = 0·97$), and the degree of modularity ($r^2 = 0·18$, $P = 0·33$).

Discussion

The network formed by oil-flowers and their pollinating bees was a 'tiny world' within 'the smallest of all worlds' (whole pollination networks, Olesen *et al.* 2006). In summary, the network was more cohesive and resilient than whole pollination networks. Together, these findings suggest that ensembles within larger networks may have different properties, and it reinforces the hypothesis that a given ecological service may be a mosaic of hierarchical subservices (Jordano 1987).

One very important finding in the present study was that the studied network of oil-flowers was different from other studied cases despite the positive correlation observed between species richness and degree of nestedness and the negative correlation between species richness and the number of coextinctions. This was due to the nestedness and resilience values for oil-flowers, which were higher than expected considering its richness. This finding reinforces our hypothesis that a phylogenetically restricted ensemble may represent a hierarchical subweb within a whole network.
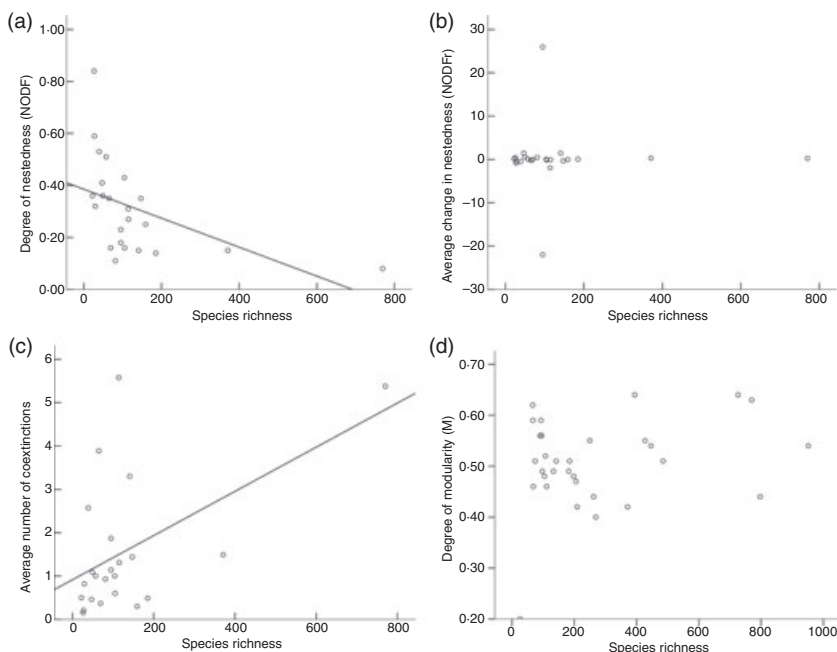
Fig. 4. Relationship between species richness and different network metrics: (a) degree of nestedness (*NODF* index); (b) relative change in nestedness caused by single-species extinctions; (c) number of coextinctions caused by single-species extinctions; and (d) modularity (*M* index).

The nested structure found in the studied ensemble has been observed in many facultative mutualisms, such as pollination and seed dispersal (Bascompte *et al.* 2003), and even marine-cleaning symbiosis (Guimarães *et al.* 2007b), where the opportunities to establish partnerships are more diversified than in symbiotic interactions. Nestedness is assumed to be an evolutionarily stable strategy in facultative mutualisms because more vulnerable species (specialists) are linked preferentially to a strong core of generalists (Bascompte, Jordano & Olesen 2006). Moreover, deleterious influences are thought to be diluted in nested networks, while their effects could be amplified and could result in a higher number of coextinctions in compartmented systems (Guimarães Jr. *et al.* 2007). It is interesting to notice that the degree of nestedness observed in the oil-flower network was much higher than that observed in whole pollination networks. There are different explanations for the origin of a nested structure (Krishna *et al.* 2008), and in our case we suppose that phylogenetic relatedness may result in higher connectivity due to a higher ecological similarity among partners and, ultimately, in a higher nestedness. The new nestedness metric used here, *NODF*, increases with connectivity, as it is coherent with the original nestedness concept (Almeida-Neto *et al.* 2008).

Considering the high asymmetry of interactions in the network, a high cohesiveness was also expected, and indeed was observed. All species of the same group (i.e. plants or animals) are indirectly connected to each other by just one common partner. This is a strong 'small-world' structure (Newman *et al.* 2006), and thus influences are easily percolated or diluted throughout the network. This pattern may be beneficial for the Malpighiaceae, because the loss of one mutualist bee is probably compensated by other mutualists.

The sum of those cohesiveness-increasing properties resulted in a resilient network. Most simulated extinctions caused no coextinctions, and resulted in changes of nested-

ness smaller than 2%. On average, bees were more important for network structure than plants, probably because of the influence of effective pollinators. Resilience to extinctions was higher than in the whole pollination networks selected for comparison, and were also higher than in another set of pollination networks studied by Memmott *et al.* (2004). As expected, generalists caused higher changes in network structure. Hubs and connectors are known to be more important for the whole network structure in many scale-free (Albert *et al.* 2000) and broad-scale systems (Memmott *et al.* 2004). Besides, the removal of generalists tended to cause decreases in nestedness, while the removal of specialists resulted in increases. On the one hand, one likely explanation is that the removal of a specialist also removes interactions with other specialists, thus enhancing the nested structure. On the other hand, the removal of a generalist may lessen the difference between subsets of the network, thus decreasing nestedness.

Regarding the importance of particular species in the network, the plant *B. muricata* deserves special attention, because its removal caused three coextinctions and an increase in nestedness of 1·6% (much higher than the average). This is also the case of the bee *Centris caxiensis*, which was not responsible for coextinctions, but caused a change in nestedness of 5·3%. Other hub and connector bees, like *C. aenea* Lepeletier, 1841 and *C. fuscata* Lepeletier, 1841, were also important for network structure. Evidence suggests that the most common and generalistic species are the main keepers of an ecological service.

In summary, the pollination network of oil-flowers and bees is one of the smallest worlds studied so far, considering subwebs defined on a biological basis (in this case, oil collection). Results of the present study indicate that small ensembles within whole networks may exhibit different properties. Thus, future studies should investigate the hierarchical structure of ecological services such as pollination and seed

dispersal in others to increase our understanding of how different subservices contribute to the larger ecological service. Conservation plans that aim to protect the Malpighiaceae and their products should pay attention not only to charismatic bee or plant species, but also to hub and connector species that glue the system together and maintain ecological services.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Ordered matrix of interactions observed between oil-flowers of the family Malpighiaceae (rows) and oil-collecting bees (columns) in the studied Caatinga area. Cell values represent the number of visits that a *j* bee species made to an *i* plant species. 'Degree' is the number of interactions (binary) observed for a given species.

Table S2. Results from the extinction simulations based on removal of single species from the network. For each species we present information on its taxonomic group (animal or plant), its ecological category (see Methods), the label used to identify it in graphs, its scientific name, its degree (K – number of interactions), relative degree (Kr – proportion of interactions), relative change in nestedness caused by its removal ($NODF_r$) and the number of coextinctions caused by its removal (C). *Bees that are not oil-collectors.

Table S3. Thirty-two data sets downloaded from the website 'Interaction Web Database' (Vazquez & Melian 2008) that we used in the present study for comparison with the oil-flower subnetwork.

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