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Cheaters in mutualism networks

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Mutualism-network studies assume that all interacting species are mutualistic partners and consider that all links are of one kind. However, the influence of different types of links, such as cheating links, on network organization remains unexplored. We studied two flower-visitation networks (Malpighiaceae and Bignoniaceae and their flower visitors), and divide the types of link into cheaters (i.e. robbers and thieves of flower rewards) and effective pollinators. We investigated if there were topological differences among networks with and without cheaters, especially with respect to nestedness and modularity. The Malpighiaceae network was nested, but not modular, and it was dominated by pollinators and had much fewer cheater species than Bignoniaceae network (28% versus 75%). The Bignoniaceae network was mainly a plant–cheater network, being modular because of the presence of pollen robbers and showing no nestedness. In the Malpighiaceae network, removal of cheaters had no major consequences for topology. In contrast, removal of cheaters broke down the modularity of the Bignoniaceae network. As cheaters are ubiquitous in all mutualisms, the results presented here show that they have a strong impact upon network topology.

Keywords: cheaters; modularity; nestedness; network topology; pollination

1. INTRODUCTION

Species are organized into complex networks through their interactions or links (e.g. Bascompte 2009). In almost all studies, links are only of one kind, e.g. predatory or parasitic (but see Melián *et al.* 2009). In mutualism networks, we assume that all interactions are beneficial, e.g. the exchange of pollination service for floral rewards (e.g. Elberling & Olesen 1999). In plant–animal mutualisms, rewards and services are also exploited by non-mutualistic species. In pollination networks, 'pollinator' is used as a generic term for all kinds of flower visitor (Elberling & Olesen 1999). This is a common simplification. However, animals visit flowers for many reasons, e.g. florivory, ovule/seed predation and nectar and pollen harvesting

with or without pollen transfer (e.g. Inouye 1983; Strauss & Whittall 2006).

The implications of this link diversity to the structure, stability and dynamics of networks are unknown. Melián *et al.* (2009), for example, found that strong links and a high ratio of mutualistic : consumer/resource links were important for the diversity of networks. In food webs, parasites are major determinants of stability (Lafferty *et al.* 2006), strongly affecting network features. Among network features recorded in mutualistic networks are nestedness, in which the links of specialists are subsets of the links of more generalized species (Bascompte *et al.* 2003), and modularity, in which species are organized into small, strongly linked groups or modules, which are loosely interlinked (Olesen *et al.* 2007).

We investigated two flower-visitation networks: a set of Malpighiaceae and Bignoniaceaee species and their flower visitors. For both, visitors were categorized as pollinators, cheaters or both. A flower visitor was a pollinator, if it contacted anthers and stigma, or a cheater, if it obtained its reward without any contact (Inouye 1983). In the Bignoniaceae network, cheaters were further categorized as either nectar or pollen robbers. First, the topology of networks was described and then cheaters were removed to analyse their influence. If cheaters interact with generalist plants, their removal may reduce nestedness and increase modularity by reducing the number of across-module interactions (Olesen *et al.* 2007). If cheaters interact with different sets of related species, their elimination may decrease modularity. We addressed the questions: what are the differences and similarities in topology of the visitation, pollination and plant–cheater networks, especially with respect to modularity and nestedness? And how are cheater species distributed within networks?

2. MATERIAL AND METHODS

(a) *Study site and dataset*
We used data from literature to identify the types of interaction between flower visitors and (i) Malpighiaceae (Sigrist 2001; Sigrist & Sazima 2004) and (ii) Bignoniaceae (Amaral 1992) in a 250 ha fragment of semi-deciduous, seasonal forest (Santa Genebra Municipal Reserve, SGR), Campinas, SE Brazil (22°49′ S, 47°7′ W).

The networks are presented as adjacency matrices depicting plant–animal interactions, in which matrix element $r_{ij} = 1$, if plant species i interacts with animal species j and zero otherwise (e.g. Bascompte *et al.* 2003). Each visitation network was split into two submatrices, *viz.* a pollination matrix of plants and pollinators and a plant–cheater matrix (electronic supplementary material). Additionally, we operated with two kinds of cheater for Bignoniaceae, *viz.* nectar and pollen robbers, and split the plant–cheater matrix into a pollen robbery matrix of plants and pollen robbers, and a nectar robbery matrix of plants and nectar robbers.

(b) *Network statistics*
The linkage level L of a species denotes its number of links (Olesen *et al.* 2007). The level of nestedness n was estimated using the NODF metric (Almeida-Neto *et al.* 2008) and the software ANINHADO (Guimarães & Guimarães 2006). Significance of NODF was tested using a null model described in Bascompte *et al.* (2003).

To estimate the level of modularity, module number and species network role, we used an algorithm by Guimerà & Amaral (2005; see the electronic supplementary material, Olesen *et al.* 2007). Among-module distribution of cheater species was assessed by a co-occurrence analysis (electronic supplementary material).

3. RESULTS
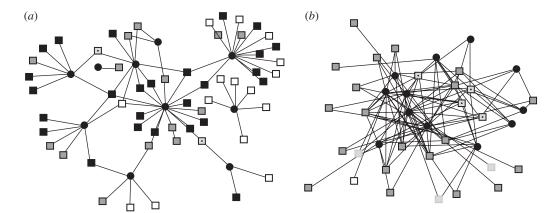The topology of the visitation networks clearly looks different in the two families (figure 1). The

Figure 1. Network indicating different roles of animal species and links to plant species in (*a*) Bignoniaceae and (*b*) Malpighiaceae. Dark grey filled square, pollinator; unfilled square, pollen robber; black filled square, nectar robber; light grey filled square, oil robber; black square with centre dot, mix role (pollinator/robber); black filled circle, plants.

Table 1. Descriptive statistics for the matrices of Malpighiaceae and Bignoniaceae and their visitors. Number of visitors $\leq$ (number of pollinators + number of cheaters) because some visitors were both pollinator and cheater. The cheating matrix is the combined nectar and pollen robbery matrices. A and P, number of animal and plant species, resp.; I, number of interactions; C, connectance (I/AP); $\langle L_m \rangle$ and $\langle L_n \rangle$, average animal and plant linkage level, resp.; s.d., standard deviation; M and N, observed modularity and nestedness, resp.

matrix	Malpighiaceae			Bignoniaceae				
	visitation	pollination	cheating	visitation	pollination	cheating	nectar robbery	pollen robbery
A	29	25	8	57	16	43	29	14
P	12	12	10	10	9	8	7	5
I	116	91	25	75	20	55	41	14
C	0.33	0.30	0.31	0.13	0.14	0.16	0.20	0.20
range of A	1–11	1–11	1–7	1–4	1–2	1–4	1–4	1
range of P	3–18	1–15	1–6	1–19	1–5	2–14	1–13	1–5
$\langle L_m \rangle \pm$ s.d.	4.0 ± 3.01	3.6 ± 2.8	3.1 ± 2.2	1.3 ± 0.69	1.3 ± 0.45	1.3 ± 0.73	1.4 ± 0.87	1.0 ± 0
$\langle L_n \rangle \pm$ s.d.	9.7 ± 5.3	7.6 ± 4.1	2.5 ± 1.8	7.5 ± 5.7	2.2 ± 1.4	6.9 ± 4.4	5.9 ± 4.3	2.8 ± 2.0
M	n.s.	n.s.	n.s.	0.65**	n.s.	0.63*	n.s.	0.70*
N	0.59**	0.57**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

$p > 0.05$ n.s.
*$p < 0.05$.
**$p < 0.01$.

Malpighiaceae network had fewer species but more links and thus a higher connectance than the Bignoniaceae network (table 1). The Malpighiaceae network was nested, but not modular, whereas the Bignoniaceae network was modular, but not nested (table 1). Removing cheaters from the visitation networks had completely different outcomes in the two networks: it did not affect nestedness in the Malpighiaceae network, but destroyed modularity in the Bignoniaceae network (table 1). Thus, pollinators caused nestedness in the Malpighiaceae network, and cheaters caused modularity in the Bignoniaceae network. These differences may be due to a smaller proportion of cheaters in the Malpighiaceae network (28% versus 75%, table 1) and/or a higher food–plant specificity among Bignoniaceae cheaters (1.3 versus 3.1, table 1).

The visitation matrix of Bignoniaceae had nine modules, each with 2–14 species. Most species were peripherals (N = 62%, figure 2), i.e. with only one to two links to other species, but three species were connectors between modules, *viz.* the nectar-robbing bees *Xylocopa suspecta*, *Oxaea flavescens* and *Euglossa*

annectans. The plants *Adenocalyma bracteatum* and *Anemopaegma chamberlaynii* were module hubs, whereas *Arrabidea triplinervia* was a network hub (figure 2). Cheaters show much less co-occurrence among modules in the Bignoniaceae visitation matrix than expected by chance (C score = 0.86, P = 0.0002), indicating that cheaters were overdispersed among modules. However, one module was composed exclusively of cheaters and *Lundia obliqua*. The plant–cheater matrix of Bignoniaceae had seven non-connected modules with 3–12 peripheral species. Here, the same bee species as in the visitation matrix were classified as connectors, whereas *A. bracteatum* and *A. triplinervia* were module hubs. The pollen robbery matrix had five modules with two to six species, and all animals were peripherals (L_m = 1.0, table 1).

4. DISCUSSION
The Bignoniaceae and Malpighiaceae visitation networks have similar number of plants, whereas flower-visiting animal species are twice as frequent in
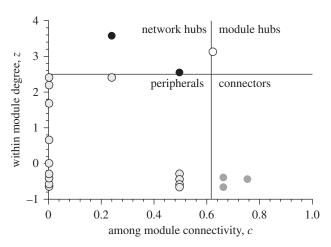
Figure 2. Species roles according to a zc-plot for Bignoniaceae visitation matrix.

the Bignoniaceae network. This is due to the cheaters, which are three times as common in the Bignoniaceae network. Thus, the Malpighiaceae network is essentially a pollination network, whereas the Bignoniaceae network is a plant–cheater network. As in other pollination networks (Bascompte *et al.* 2003), the Malpighiaceae network is nested, but also non-modular, which may reflect its small size (Olesen *et al.* 2007). Another Malpighiaceae–bee network was strongly nested, but, in contrast to ours, showed a low degree of modularity (Bezerra *et al.* 2009).

The Bignoniaceae networks had a completely different topology from our Malpighiaceae networks. In the Bignoniaceae networks, connectance is only half of that in the Malpighiaceae networks, indicating that the Bignoniaceae networks are more specialized. In addition, the Bignoniaceae visitation network was non-nested, but modular. The reason for this was the many specialized links (i.e. one or two animals visiting one plant species only) between pollen robbers and their plants. Pollen robbery is similar to herbivory, and herbivory networks are strongly modular (Lewinsohn *et al.* 2006). An increase in cheating in visitation networks may decrease nestedness, but increase modularity. Large pollination networks are modular (Olesen *et al.* 2007). However, this assumes that all links are pollinatory. We show that, besides phylogenetic clustering and trait convergence (Olesen *et al.* 2007), consumer/resource links, such as cheating links, also contribute to modularity.

Malpighiaceae is pan(sub)tropical with *ca* 1250 species, with oil flower species restricted to the neotropics. Female bees collect pollen and oil, which is used as larval provision and for nest cell walls (Sigrist & Sazima 2004). In this study, 26 of the 29 bee visitor species were known oil collectors (Vogel 1974). The oil-collecting species made 93–96% of all links in the matrices. Thus, the Malpighiaceae visitation and pollination networks are bee pollination–floral-oil systems, and the small cheating networks are a floral-oil harvesting system. However, floral resources in Malpighiaceae species seem difficult to exploit by visiting animals without pollinating. As Bezerra *et al.* (2009) indicated, the phylogenetic and ecological similarity among partners results in a high nested pattern in this flower-oil system.

Bignoniaceae is a predominantly neotropical family with *ca* 800 species pollinated by insects, birds and bats (Gentry 1980). Bignoniaceae flowers are much more diverse than Malpiguiaceae, allowing a much larger array of flower visitors the access to their flower rewards. In the network, 54 per cent, 23 per cent and 23 per cent of the animals were bees, butterflies and others (Diptera, Coleoptera and hummingbirds), respectively. Bees were mainly pollinators or nectar robbers; butterflies and hummingbirds were mainly nectar robbers, and most of the 'others' were pollen robbers. Nectar robbers act as the glue of the Bignoniaceae network, connecting the modules and increasing the cohesiveness of the network, while pollen robbers show more specialized links. The distribution of cheaters among modules might imply that robbers are overdispersed in niche space leading to the observed modular pattern, and/or may be a result of flower features such as calyx thickness and pubescence and corolla shape, which constrains the foraging of bees. Finally, the proportion of cheaters was three times higher in Bignoniaceae networks than in Malpighiaceae networks. The reasons might be that (i) the adaptations of the morphology and behaviour of visitors to flowers of the Malpighiaceae are much tighter, making it more difficult to harvest rewards without pollinating, and (ii) the oil resource is more costly than nectar to produce, resulting in a more specialized, conservative flower-pollination system, and the adapted visitors morphology and behaviour on Malpighiaceae flowers.

Nestedness adds robustness to a network and shortens the distance between species (Bascompte *et al.* 2003). Thus, cheaters, such as Bignonaceae pollen robbers, may have a strong impact upon network stability by destroying nestedness and enforcing modularity. The importance of modularity for networks is less known, although a modular structure may slow down the spread of disturbances (Olesen *et al.* 2007). Cheaters are a ubiquitous part of maybe all mutualisms, and they seem to be important to the overall stability and integration of natural systems.

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