

The network structure of myrmecophilic interactions

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Abstract. 1. Ants establish mutualistic interactions involving a wide range of protective relationships (myrmecophily), in which they provide defence against enemies and partners provide food rewards and/or refuge. Although similar in the general outcome, myrmecophilic interactions differ in some characteristics such as quantity and quality of rewards offered by partners which may lead to different specialisation levels and, consequently, to different network properties.

2. The aim of this study was to identify structural patterns in myrmecophilic interaction networks, focusing on aspects related to specialisation: network modularity, nestedness and taxonomic relatedness of interaction ranges. To achieve this, a database of networks was compiled, including the following interactions: ants and domatia-bearing plants (myrmecophytes); ants and extrafloral nectary-bearing plants (EFNs); ants and floral nectary-bearing plants (FNs); ants and Lepidoptera caterpillars; and ants and Hemiptera.

3. Myrmecophilic networks differed in their topology, with ant–myrmecophyte and ant–Lepidoptera networks being similar in their structural properties. A continuum was found, ranging from highly modular networks and phylogenetically structured interaction ranges in ant–myrmecophyte followed by ant–Lepidoptera networks to low modularity and taxonomically unrelated interaction ranges in ant–Hemiptera, EFN and FN networks.

4. These results suggest that different network topologies may be found across communities of species with similar interaction types, but also, that similar network topologies can be achieved through different mechanisms such as those between ants and myrmecophytes or Lepidoptera larvae. This study contributes to a generalisation of myrmecophilic network patterns and a better understanding of the relationship between specialisation and network topology.

Key words. Ants, ecological networks, interaction range, modularity, mutualism, nestedness, specialisation, taxonomic relatedness.

Introduction

Ants (Hymenoptera: Formicidae) are one of the most successful groups of animals, being dominant in most terrestrial ecosystems (Hölldobler & Wilson, 1990). Their ubiquity, abundance and active behavior have made ants keystone organisms in the functioning of communities (Blüthgen *et al.*, 2000). Some of the most important roles of ants in ecosystems are performed by establishing mutualistic interactions with organisms such as plants, fungi and other insects (Rico-Gray & Oliveira, 2007).

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Myrmecophily involves a wide range of protective interactions in which ants provide defence against enemies in return for food rewards and/or refuge (Heil & McKey, 2003). The most relevant groups involved in myrmecophilic interactions are trophobiont insects (e.g. Hemiptera: Aphididae, Coccoideae, Delphacidae; and Lepidoptera: Lycaenidae and Riodiniidae) and plants bearing extrafloral nectaries (EFNs) and/or domatia (hereafter called ‘myrmecophytes’) (Rico-Gray & Oliveira, 2007; Stadler & Dixon, 2008). Although myrmecophilic interactions have similar general outcomes, they differ in some characteristics, such as the spatiotemporal distribution and nutritional composition of rewards, and the existence of morphological and ethological traits that facilitate interactions (Heil & McKey, 2003; Stadler & Dixon, 2008) (Table S1, Document S1).

It is known that mutualistic interactions entail costs and benefits for both partners; accordingly, by investing more in ants, partners can increase protective benefits (Fonseca & Ganade, 1996). Based on this fact, we propose that constant, abundant and high-quality rewards could lead to higher partner performance (Chamberlain & Holland, 2009a), which in turn could promote higher investment in the interaction, leading to high specialisation (Table S1, Document S1). For example, hemipterans produce honeydew at a higher rate and more constantly than EFNs, favouring resource monopolisation that may result in specialisation processes (Blüthgen *et al.*, 2000, 2004; Katayama *et al.*, 2013). In turn, myrmecophytes offering nesting sites and high-quality food rewards receive more protection than EFN plants (Heil & McKey, 2003; Blüthgen & Fiedler, 2004). Also, these plants possess traits that promote the evolution of ant–plant symbiosis (Davidson *et al.*, 1989). For example, some plants emit chemical volatiles that help specific ants to find them (Edwards *et al.*, 2006; Dáttilo *et al.*, 2009). In other cases, domatia structure and stem texture (e.g. waxy cuticle or epidermal trichomes) represent exclusion filters for non-obligated ant partners (Davidson *et al.*, 1989; Quek *et al.*, 2004). In the case of lepidopteran caterpillars, it is known that they produce higher food quality than any other ant partner (Kaminski *et al.*, 2013), have specialised organs and produce signals to attract particular ant species, resulting in highly intimate interactions between them (Pierce *et al.*, 2002). Accordingly, we expect higher specialisation of ant–myrmecophyte and ant–Lepidoptera interactions than of ant–Hemiptera and ant–EFN interactions.

We also included in our analyses ant–flower visitation (hereafter ant–FN) networks as a similar interaction type in terms of outcome, but not classified as myrmecophily *sensu stricto*. Although floral nectar is an essential component in their diet (Blüthgen *et al.*, 2004; Davidson *et al.*, 2004; Rico-Gray & Oliveira, 2007), most ants visiting floral nectaries have a negative influence on plant reproduction by damaging its sexual organs or competing with legitimate pollinators (Gómez & Zamora, 1992; Galen & Butchart, 2003; Rico-Gray & Oliveira, 2007; Dáttilo *et al.*, 2012).

There is a growing interest in the study of ecological networks in general, and of myrmecophilic networks in particular (Fonseca & Ganade, 1996; Guimarães *et al.*, 2007a; Chamberlain & Holland, 2009b; Dáttilo *et al.*, 2013a). Although the way in which specialisation processes shape interaction network structure remains to be tested, network modularity appears as one of the possible patterns emerging from specialised interactions at the community level (Lewinsohn *et al.*, 2006). Modules are revealed when species interact more often within a group than with the rest of the network (Pimm & Lawton, 1980). Such structures may arise through different mechanisms, including tight coevolution, as expected for symbiotic interactions (Thompson, 1999). This hypothesis predicts that clades of partners will mirror each other in their patterning of speciation events.

At the network level, a modular topology of ant–myrmecophyte interactions in the Amazonian rainforest has been reported (Fonseca & Ganade, 1996; Dáttilo *et al.*, 2013b). Likewise, a comparison of ant–myrmecophyte and ant–EFN networks revealed that symbiotic interactions resulted

in modular networks, whereas non-symbiotic interactions displayed nested topologies (Guimarães *et al.*, 2007a) and were less prone to species co-extinctions (Dáttilo, 2012). Furthermore, it was demonstrated that ant–EFN interaction networks depict a nested topology, a particular organisation of networks in which interaction partners of less connected species are proper subsets of those of more connected ones (Bascompte *et al.*, 2003), similar to that observed in ant–FN (Santos *et al.*, 2014) and pollination networks (Guimarães *et al.*, 2006).

Network patterns could be a consequence of phylogenetic constraints on interactions, as related species may share characteristics to which partners have to be adapted. It was shown that species interactions are phylogenetically conserved (Gómez *et al.*, 2010) and that phenotypic complementarity and phylogenetic history were associated with mutualistic network structure (Rezende *et al.*, 2007). Few studies have evaluated the phylogenetic signal of myrmecophilic interactions and most of them have focused on ant–myrmecophyte interactions (but see Díaz-Castelazo *et al.*, 2013). For example, it was revealed that plant trichomes can ‘filter’ ant species based on their size but the presence of trichomes had independent origins in the different taxa (Davidson *et al.*, 1989), suggesting the possibility of ‘diffuse co-evolution’ between ants and plants (Ward, 1991). Interaction restrictions are necessarily related to network modularity (Lewinsohn *et al.*, 2006), and could be related to specialisation degree, particularly when there is a phylogenetic basis for partner selection (e.g. Prado & Lewinsohn, 2004; Cagnolo *et al.*, 2011). Despite fundamental advances in the search of patterns in ant-involved networks, to date no study has compared patterns in network topology across a broad spectrum of myrmecophilic interactions. Here, we aim to identify and describe structural patterns in myrmecophilic interaction networks (ant–myrmecophyte, ant–EFN, ant–FN, ant–Hemiptera and ant–Lepidoptera), focusing on aspects related to ecological specialisation: network modularity, nestedness and taxonomic relatedness of interaction ranges (Lewinsohn *et al.*, 2006). Specifically, we intend to answer the following questions: (i) do myrmecophilic interactions compose networks of similar structure regardless of the organisms involved; and (ii) do different myrmecophilic partners differ in the taxonomic relatedness of their interaction ranges?

Material and methods

Database construction

We compiled a database of 34 interaction networks from different sources (Table S2, Document S1). Four networks were extracted from the ‘Interaction Web Database’ (<http://www.nceas.ucsb.edu/interactionweb>), two were provided by the authors and the remaining 28 were compiled directly from papers. Thirty-one interaction networks involve myrmecophilic interactions *sensu stricto* [ant–myrmecophyte (hereafter referred to as domatia, $N=6$), ant–EFN ($N=7$), ant–Hemiptera ($N=10$), and ant–Lepidoptera ($N=8$) interactions] and three are ant–FN interactions (floral nectary-bearing plants).

Network description

We described each network by calculating its connectance (proportion of realised links from the total possible, noted as C), link density (average number of links per species, Ld), clustering coefficient (measure of the degree to which species in a network tend to cluster together, Cc), co-occurrence index (measure of the segregation in species interaction ranges, Cs), mean normalised degree (average number of links per species normalised by the number of partners available, dn), mean number of shared partners (average of shared partners by every species pair in a network, Sp), nestedness [NODF index (Almeida-Neto *et al.*, 2008), N] and modularity [Newman and Girvan's Q (Newman & Girvan, 2004), M]. Network statistics were calculated using the BIPARTITE (Dormann *et al.*, 2009) and TNET packages (Opsahl, 2013) in the R program (R Development Core Team; <http://www.R-project.org>); for modularity analyses we used the MODULAR program by applying simulated annealing as the module searching technique (Marquitti *et al.*, 2014). These metrics provide a comprehensive description of network structural patterns, and also allows a direct comparison among networks in the present study and in previously reported studies (Dormann *et al.*, 2009). A detailed explanation of network statistics calculations and references can be found in Table S3 of Document S1.

To facilitate comparisons, we corrected modularity and nestedness values for among-network variation in number of species and interactions by using relative modularity [$M_{rel} = (M - \overline{M}_{random}) / \overline{M}_{random}$] and nestedness [$N_{rel} = (NODF - \overline{NODF}_{random}) / \overline{NODF}_{random}$], where \overline{M}_{random} and \overline{NODF}_{random} were average modularity and nestedness, respectively, of 1000 null matrices with the same size, connectance and proportional marginal sums (Bascompte *et al.*, 2003). Negative values of M_{rel} and N_{rel} correspond to lower than expected values, whereas positive values represent the opposite (Olesen *et al.*, 2007).

To consider additional sources of variability on network structure, we estimated each study sampling effort by recording the sampling area (geographic range) and its temporal duration. Geographic range was recorded directly from the publication when available or estimated by calculating the area inside a polygon determined by the extreme geographic points reported in the study. Study duration was extracted from papers as the number of months from the first to the last interaction recorded. We also considered taxonomic resolution of networks by calculating the proportion of nodes not identified to species or morphospecies level.

Data analysis

Evaluation of systematic variation of additional factors. Our dataset was compiled from several sources; hence, it is possible that different interaction types may be subject to consistent variation in sampling effort, taxonomic resolution or network size. To evaluate whether networks varied consistently across the mentioned factors, we included them as response variables with ant's partner type as the categorical predictor in generalised linear models (GLMs) with type III sums of squares. Significant

differences may indicate the existence of consistent variation in the response variable across network types.

Finally, as ant sub-families differ in their foraging strategies, adaptations and dependence on liquid food resources (Davidson *et al.*, 2004), we evaluated whether the 'sub-families range' (with the number of species within sub-families as an 'abundance' measure) of our dataset is biased towards particular network types through cluster analysis with Euclidean distances and Ward's clustering method (Legendre & Legendre, 1998).

Do myrmecophilic interactions compose networks of similar structure regardless of the organisms involved? We ordered networks according to the statistics described earlier (Table S2, Document S1), using principal components analysis (PCA). The PCA arranges networks in an ordination space according to their descriptor statistics, where networks close to each other have similar structural properties, and networks spaced far apart have dissimilar structure (Legendre & Legendre, 1998).

We used relative modularity and nestedness values as response variables to evaluate the effects of ant's partner type on myrmecophilic interaction network topology using GLMs with type III sums of squares. We included network size, taxonomic resolution, geographic range and temporal duration of studies as covariables to control for their effects on network topology. Finally, we performed *post hoc* comparisons using Tukey's honestly significant difference (HSD) test for unequal sample sizes (Spjotvoll & Stoline, 1973).

Do different myrmecophilic partners differ in the taxonomic relatedness of their interaction ranges? To answer this question, we assigned all species to hierarchically organised taxonomic nodes using classifications from web resources: The Encyclopedia of Life (Wilson, 2003), The Tree of Life Web Project (Maddison & Schulz, 2007) and Illustrated Lists of American Butterflies (Warren *et al.*, 2013). We measured the taxonomic distance between a pair of species by counting the number of steps necessary to reach a common node, using the ADE4 package (Dray & Dufour, 2007) in R (R Development Core Team, 2010). The use of taxonomic trees instead of phylogenetic distances has the disadvantage of underestimating evolutionary distances, because all steps are considered equal (i.e. a jump from species to species has the same value as jumping between families) (Weiblen *et al.*, 2006). Nonetheless, considering the differences in availability and quality among insect and plant phylogenies, we decided to use rough but comparable taxonomic distances instead of phylogenetic distances of different reliability among groups.

After constructing the taxonomic distance matrix for all species on each side of a bipartite network, we calculated the average taxonomic distance of interaction partners of every species and calculated the difference from the average taxonomic distance of 1000 randomly chosen, same number, species groups. Finally, we estimated the average difference between expected and observed taxonomic distance values (d) for ants and partners of every interaction network.

We used the d -values to evaluate differences in taxonomic distances of interaction ranges between network types using

a linear mixed effects model applied with the NLME package (Pinheiro & Bates, 2000) in R. As phylogenetic signal on interactions could vary for different sides of a bipartite network (Gómez *et al.*, 2010; Cagnolo *et al.*, 2011), we included network side (ants or partners) as a factor and ‘study’ as a random factor to control for the dependency of different sides of a bipartite network belonging to a unique study. We also included network size, geographic range and taxonomic resolution as covariables.

In all cases, covariables were removed from final analyses when no significant effects on response variables were observed. Model residuals were tested for normality and homoscedasticity and network size and geographic range were \log_{10} -transformed, and taxonomic resolution was arcsine-square-root-transformed to meet the assumptions of analyses.

Results

Evaluation of systematic variation of additional factors

We found no consistent differences in network size ($F_{4,29} = 1.371$, $P = 0.268$), taxonomic resolution ($F_{4,29} = 1.687$, $P = 0.181$) or study duration ($F_{4,29} = 2.638$, $P = 0.060$) across different kinds of networks; however, geographic range varied consistently ($F_{4,29} = 2.943$, $P = 0.039$), with ant–Lepidoptera studies being more extensive than ant–Hemiptera networks (Tukey HSD, $P = 0.049$). Finally, cluster analysis of sub-family composition of different ant–myrmecophilic networks revealed no bias towards different ant partners (Figure S1, Document S1).

Do myrmecophilic interactions compose networks of similar structure regardless of the organisms involved?

Axis 1 of the PCA explained more than half of the network structural properties, being negatively associated with modularity and C -score and positively associated with nestedness, links per species, clustering coefficient, mean number of shared partners, connectance and normalised degree. Along axis 1, ants associated with myrmecophytes and lepidopteran trophobionts composed networks of similar structural properties, being tightly grouped on the left-centre side of the graph. Ant–EFN networks appeared sparse on the right-hand side and ant–FN networks on the centre of the ordination. Networks including hemipteran partners were sparsely distributed across the entire graph. While ant–myrmecophyte and ant–Lepidoptera networks were associated with high modularity, ant–EFN networks were associated with high nestedness and low modularity (Fig. 1).

The different types of myrmecophilic networks studied here showed no differences in nestedness values associated with partner type ($F_{5,28} = 0.139$, $P = 0.966$) (Fig. 2a), geographic range ($F_{1,25} = 1.369$, $P = 0.257$), taxonomic resolution ($F_{1,25} = 0.785$, $P = 0.357$) or study duration ($F_{1,25} = 0.455$, $P = 0.408$), but were positively associated with network size ($F_{1,25} = 10.698$, $P = 0.004$). On the other hand, modularity levels differed between kinds of myrmecophilic partners ($F_{5,28} = 5.520$, $P = 0.001$). Modularity was highest in ant–myrmecophyte

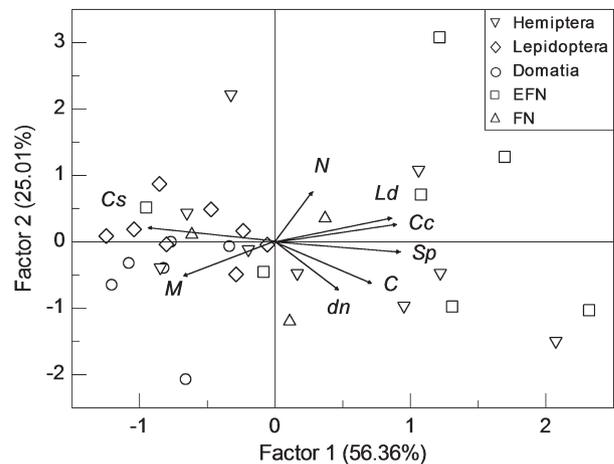


Fig. 1. Principal components analysis ordination of myrmecophilic networks (point symbols) and network statistics (arrows). C , connectance; Ld , link density; Cc , clustering coefficient; Cs , C -score; Sp , mean number of shared partners; dn , normalised degree; N , relative nestedness; M , relative modularity; EFN, extrafloral nectary-bearing plants; FN, floral nectary-bearing plants.

interaction networks, at least doubling the M -values of the rest of the network types. The lowest modularity values were observed in ant–EFN and ant–Hemiptera networks (Fig. 2b). No significant effects of network size ($F_{1,25} = 0.272$, $P = 0.609$), geographic range ($F_{1,25} = 0.709$, $P = 0.411$), resolution ($F_{1,25} = 2.504$, $P = 0.132$) or duration ($F_{1,25} = 0.029$, $P = 0.865$) were detected, and we therefore removed them from the final model.

Do different myrmecophilic partners differ in the taxonomic relatedness of their interaction ranges?

Although we found no significant differences in ant species’ taxonomic relatedness within interaction ranges across different types of myrmecophilic networks ($F_{4,21} = 2.006$, $P = 0.149$), we observed a tendency towards higher taxonomic distances of ants visiting FNs and lower distances in ant–myrmecophyte networks (Fig. 3). On the other hand, taxonomic distances of ant partners differed consistently across different types of myrmecophilic networks ($F_{4,21} = 4.327$, $P = 0.009$). Myrmecophytes showed the lowest taxonomic distances, whereas the remaining networks did not differ (Fig. 3). In both cases, network size (ants, $F_{1,21} = 2.006$, $P = 0.149$; partners, $F_{1,21} = 0.295$, $P = 0.594$), taxonomic resolution (ants, $F_{1,21} = 2.641$, $P = 0.126$; partners, $F_{1,21} = 1.557$, $P = 0.244$), geographic range (ants, $F_{1,21} = 3.265$, $P = 0.087$; partners, $F_{1,21} = 0.588$, $P = 0.454$) and study duration (ants, $F_{1,21} = 0.434$, $P = 0.520$; partners, $F_{1,21} = 0.578$, $P = 0.457$) did not show significant effects and were removed from the final models.

Discussion

Finding patterns in ecological network structure is crucial because they could reveal general principles of organisation

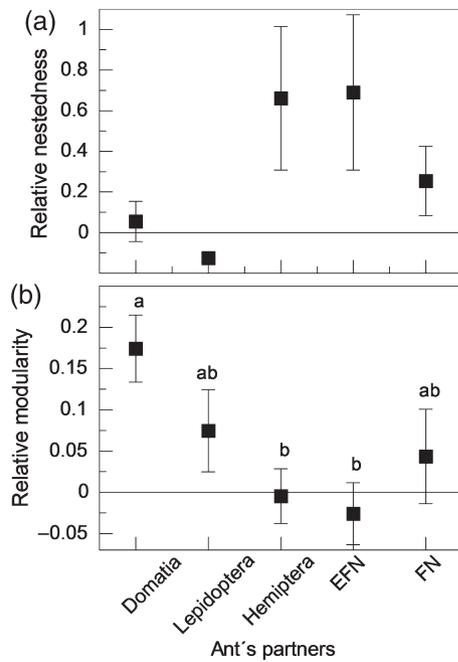


Fig. 2. Relative nestedness (a) and modularity (b) (\pm SE) of different myrmecophilic interaction networks. The horizontal line indicates equality with random expectations, positive values indicate higher than null model expectation, and negative values indicate the opposite. Domatia, domatia-bearing plants; EFN, extrafloral nectary-bearing plants; FN, floral nectary-bearing plants. Different letters refer to significant differences at $\alpha = 0.05$.

that have implications for coevolutionary dynamics, persistence and even community functioning (Dunne, 2005). Important advances in the description of ant interaction network patterns and their causes have been made, but until now, no study has summarised or compared structural properties across the wide spectrum of myrmecophilic interactions. Here we compared the most conspicuous myrmecophilic interactions from a network perspective, focusing on the following key aspects: nestedness, modularity and phylogenetic distance of interaction ranges.

Before starting the detailed discussion of results, there are a number of caveats that may have a bearing on the conclusions of this study. As we compiled data from different sources, it is possible that high heterogeneity has been included in sampling design and effort. To deal with data heterogeneity, we first evaluated whether the extension in space and time varied consistently among studies involving different ant partners. We found no differences in the temporal length of studies among networks, but we did find that ant–Lepidoptera studies covered a more extensive area than the remaining networks analysed. Ant–Lepidoptera interactions are relatively rare compared with the rest of the interactions studied (Lamborn, 1913); because of this, lists of interactions between ants and Lepidoptera larvae consist of data accumulated over greater areas than the remaining myrmecophilic interactions. Nevertheless, similarly to study duration, geographic range did not affect network nestedness, modularity or taxonomic distances of interaction ranges. Accordingly, we assume that differences

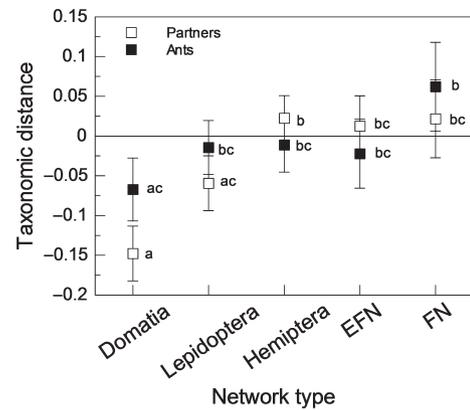


Fig. 3. Relative taxonomic distance of interaction ranges (\pm SE) of ants and partners from different myrmecophilic interaction networks. The horizontal line indicates equality with random expectations, positive values indicate higher than random expectation, and negative values indicate the opposite. Domatia, domatia-bearing plants; EFN, extrafloral nectary-bearing plants; FN, floral nectary-bearing plants. Different letters refer to significant differences at $\alpha = 0.05$.

in sampling effort could not be responsible for the results of our study.

Network size has been reported to be positively associated with nestedness (Bascompte *et al.*, 2003) and modularity levels (Olesen *et al.*, 2007), and also node aggregation in poorly taxonomically resolved studies may underestimate modularity and affect other network parameters (Martinez, 1993). We found no systematic variation in network size or taxonomic resolution among different studies. Although we were not able to control for every aspect of data heterogeneity, we are confident (and these results support our confidence) that the main conclusions of our study are a consequence of biological characteristics of species in the network rather than artifacts resulting from different protocols and sampling efforts.

Do myrmecophilic interactions compose networks of similar structure regardless of the organisms involved?

Ants interact with a wide range of organisms that provide them with food and/or refuge in return for protection (Heil & McKey, 2003; Rico-Gray & Oliveira, 2007). Despite networks of ants and their partners being similar in terms of the general outcome of their interactions, they were assembled in different ways. Ordination analysis revealed convergent properties of ant–myrmecophyte and ant–Lepidoptera networks that were grouped together, whereas ant–Hemiptera, ant–EFN and ant–FN networks were sparsely distributed in the ordination space. This result suggests there are no differences in specialisation degree of ant–Hemiptera, ant–EFN and ant–FN interactions because, although honeydew can be a more nutritious food compared with nectar, and more stable over space and time (Auclair, 1963; Becerra and Venable, 1989; Fiala, 1990), it is a waste product and trophobionts usually do not have specialised morphological structures, such as nectar glands (Stadler & Dixon, 2005). Moreover, it is known that ants may

consume floral nectar, a reward for pollinators, without giving (in most cases) pollination service in return (Gómez & Zamora, 1992; de Vega, 2009).

Myrmecophytes establish an obligate (symbiotic) interaction with ants, providing living space through different structures that filter the colonisation of particular ant species and, in some cases, providing complete nutritional food rewards (Davidson & Mckey, 1993; Heil & McKey, 2003). Dependence between interaction partners could be reinforced because many myrmecophytes obtain nutrients from ant activities (Mayer *et al.*, 2014). On the other hand, lepidopterans establish mutualistic interactions with ants to obtain protection, manipulating and appeasing aggressive ant behavior through sound and chemical signals and nectar production in specialised organs (Pierce *et al.*, 2002) (see also Table S1, Document S1). For example, some Lycaenidae larvae mimic ant brood pheromones to avoid aggression (Pierce *et al.*, 2002), which may result in highly specialised interactions with particular ant species. The latter characteristics, exclusive to some Lepidoptera species, may be the cause of the highly intimate relationship leading to a particular structural pattern of their interaction networks with ants. Accordingly, myrmecophytes and lepidopterans achieve similar network characteristics through different mechanisms: while ant–myrmecophyte interactions seem to be symmetrical (both sides receiving similar benefits), ant–Lepidoptera interactions seem to be biased toward Lepidoptera benefits.

As observed in the PCA, myrmecophytes showed the highest modularity of all network types explored here, followed by ant–Lepidoptera and ant–FN networks. The high modularity of ant–myrmecophyte networks was previously reported by Fonseca and Ganade (1996) and Dáttilo *et al.* (2013b) and confirmed in a comparison between ant–myrmecophyte and ant–EFN networks (Guimarães *et al.*, 2007a). Our results support those previous findings and allow us to extend our conclusions to a wider range of myrmecophilic interactions.

Tight coevolutionary dynamics between small groups of species were proposed as a mechanism for modularity assembly in networks of symbiotic interactions, such as those between myrmecophytes and ants (Guimarães *et al.*, 2007a). Although ants and Lepidoptera trophobionts are not necessarily symbiotic and sometimes are parasitic, they also compose highly modular networks, but ones that are not significantly different from the remaining network types studied here. On the other hand, ant–EFN and ant–Hemiptera networks may behave as other kinds of mutualistic networks, without major restrictions to interactions, such as those between plants and pollinators (Guimarães *et al.*, 2007b; Vázquez *et al.*, 2009). In the latter cases, most species converge into a series of traits shared by dominant species, so that their networks are highly connected and (generally) present low modularity (Jordano, 1987). An alternative explanation involves interactions occurring randomly between individuals, with probabilities of occurrence being mostly determined by species abundance (Vázquez *et al.*, 2009). However, recent evidence reveals that for ant–EFN networks, some interactions occur more frequently than expected by species abundance, reinforcing the nested structure of the network (Dáttilo *et al.*, 2014b). According to our results, it seems reasonable not to separate EFN and trophobiont

interactions when studying resource use by ants and interaction networks in order to fully understand the patterns and dynamics of ant–partner communities.

Do different myrmecophilic partners differ in the taxonomic relatedness of their interaction ranges?

The interaction with closely related species is a widely demonstrated pattern in antagonistic and mutualistic systems (Gómez *et al.*, 2010). Phylogenetically related species are more likely to share similar traits, such as body size, feeding mode and habitat preference than unrelated ones (Futuyma, 2009). We found that different networks studied here presented interaction ranges with consistently different taxonomic distances. Domatia-bearing plants within ant interaction ranges presented the lowest taxonomic distances of all partner types, implying that ants strongly select phylogenetically related species with which to interact. A similar result was reported based on the analysis of one of the datasets used here (Fonseca & Ganade, 1996); therefore, our study confirms and generalises this result as a pattern of myrmecophilic networks involving ants and domatia-bearing plants. In turn, partners in ant–Hemiptera and ant–FN networks showed the highest taxonomic distances of all the studied networks. The selection of phylogenetically related species within ant interaction ranges may have two non-mutually exclusive explanations. One involves the tracking of chemical, morphological or ecological partner traits usually shared by related species (Agrawal, 2007); and the other involves the phylogenetic conservatism of partners because new colonies interact with the same partner lineages as their parents, as proposed for plant–herbivore interactions (Barron, 2001).

Although a previous study reported that EFN-bearing plants were visited by a broader spectrum of ant species and genera than hemipteran aggregations (Blüthgen *et al.*, 2006), our results showed that taxonomic distances within interaction ranges in ant–EFN and ant–Hemiptera networks were not different from each other, and they were not different from what was expected by chance. These results suggest that species phylogeny may not be the most important factor in partner selection, either for ants or for partners. Partner selection by ants could be driven by other factors not necessarily shared by related species, such as phenology (Rico-Gray *et al.*, 2012), abundance (Chamberlain *et al.*, 2010; Dáttilo *et al.*, 2014b), body size (Chamberlain & Holland, 2009b), ant dominance hierarchies (Dáttilo *et al.*, 2014a) and abiotic factors (Rico-Gray *et al.*, 2012), which have been demonstrated to be good predictors of the structure of ant–EFN interaction networks. Moreover, ant visitation to FN was shown to depend on seasonality (Santos *et al.*, 2014), and the presence of floral barriers and repellents, which were in turn independent of plant phylogeny (Junker *et al.*, 2011).

Previous studies revealed structural differences in myrmecophilic interaction networks that could be related to their coevolutionary dynamics (Guimarães *et al.*, 2006, 2007a). In this study we revisited this topic, analysing a more extensive database, which included a broader range of interactions

between ants and partners. In summary, our results showed a continuum, ranging from higher specialisation with highly modular networks and taxonomically structured interaction ranges in ant–myrmecophyte and ant–Lepidoptera networks to more generalised associations with nested networks and no taxonomically related interaction ranges in ant–Hemiptera, ant–EFN and ant–FN plant networks. Our results contribute to a generalisation of myrmecophilic network patterns and a better understanding of the relationship between specialisation and network topology.

Acknowledgements

We thank N. Blüthgen for kindly providing two of the datasets used here, L. Bernaschini for helping with data compilation and W. Dáttilo and one anonymous reviewer who provided helpful comments. L.C. is a career researcher and J.T. a doctoral fellow with Consejo Nacional de Investigaciones Científicas y Técnicas. This work was supported by a grant from FONCYT–ANPCYT (PICT 0973).

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12229

Document S1. Document containing: **Table S1:** Characteristics of different myrmecophilic interactions with a possible influence on specialization analyzed from the ant and partner perspectives; **Table S2:** Interaction type, country, location, size, and references of the analyzed networks; **Table S3:** Statistics used to describe myrmecophytic interaction networks involving different organisms; **Figure S1:** Cluster analysis of sub-family composition of ants in myrmecophytic networks with different interaction partners; **Table S4:** Observed and expected modularity and nestedness and corresponding p values obtained from different myrmecophytic interaction networks and null models that preserved connectance and marginal sums and established the probability of each cell being occupied as the average of the probabilities of occupancy of its row and column.

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Accepted 3 May 2015