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Relative contribution of ecological and biological attributes in the fine-grain structure of ant-plant networks

Cecilia Díaz-Castelazo, Victor Rico-Gray

Background. Ecological communities of interacting species analyzed as complex networks, revealed that species dependence on their counterpart is more complex than expected at random. For ant-plant networks (mediated by extrafloral nectar), links among species are asymmetric (nested), forming a core of generalist species. Proposed factors affecting network organization include encounter probability (species abundances, habitat heterogeneity), behavior, phylogeny and body size. While the importance of underlying factors that influence structure of ant-plant networks have been separately explored, simultaneous contribution of several biological and ecological attributes inherent to the species, guild or habitat level have not been addressed. Methods. For a tropical seasonal site we recorded frequency of pairwise ant-plant interactions mediated by extrafloral nectaries, attributes of interacting species, habitat attributes, cover of plants with EFNs, and studied the resultant network structure. We addressed for the first time the role of mechanistic versus neutral determinants at the “fine-grain” structure (pairwise interactions) of ant-plant networks, studying the simultaneous contribution of several plant, ant, and habitat attributes in prevailing interactions as well as in overall network topology (community). Results. Our studied network was highly-nested, non-modular, with core species in general having high species strengths (higher strength values for ants than plants) and low specialization; plants had higher dependences on their counterparts. The significant factor explaining network and fine-grain structure was habitat heterogeneity in vegetation structure (open vs. shaded habitats), with no evidence of neutral (abundance) effects. Discussion. Core ant species are relevant to most plants species at the network, the latter depending more on the former, core ants showing adaptations to nectar consumption and deterrent behavior, suggestive of potential biotic defense at a community scale. At our study site spatiotemporal heterogeneity is so strong, that emerges at community-level structural properties, depicting influence of abiotic factors in facultative mutualism. Frequent occurrence of morphologically-diverse EFNs at all habitats suggests plasticity in plant strategies for biotic defense provided by ants.

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Title: **Relative contribution of ecological and biological attributes in the fine-grain structure of ant-plant networks**

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Abstract

Background. Ecological communities of interacting species analyzed as complex networks, revealed that species dependence on their counterpart is more complex than expected at random. For ant-plant networks (mediated by extrafloral nectar), links among species are asymmetric (nested), forming a core of generalist species. Proposed factors affecting network organization include encounter probability (species abundances, habitat heterogeneity), behavior, phylogeny and body size. While the importance of underlying factors that influence structure of ant-plant networks have been separately explored, simultaneous contribution of several biological and ecological attributes inherent to the species, guild or habitat level have not been addressed.

Methods. For a tropical seasonal site we recorded frequency of pairwise ant-plant interactions mediated by extrafloral nectaries, attributes of interacting species, habitat attributes, cover of plants with EFNs, and studied the resultant network structure. We addressed for the first time the role of mechanistic versus neutral determinants at the "fine-grain" structure (pairwise interactions) of ant-plant networks, studying the simultaneous contribution of several plant, ant, and habitat attributes in prevailing interactions as well as in overall network topology (community).

Results. Our studied network was highly-nested, non-modular, with core species in general having high species strengths (higher strength values for ants than plants) and low specialization; plants had higher dependences on their counterparts. The significant factor explaining network and fine-grain structure was habitat heterogeneity in vegetation structure (open vs. shaded habitats), with no evidence of neutral (abundance) effects.

Discussion. Core ant species are relevant to most plants species at the network, the latter depending more on the former, core ants showing adaptations to nectar consumption and deterrent behavior, suggestive of potential biotic defense at a community scale. At our study site spatiotemporal heterogeneity is so strong, that emerges at community-level structural properties, depicting influence of abiotic factors in facultative mutualism. Frequent occurrence of morphologically-diverse EFNs at all habitats suggests plasticity in plant strategies for biotic defense provided by ants.

Introduction

Interspecific interactions have been recently analyzed at the ecological community level with a complex network perspective, where important attention have been paid at network organization and its underlying factors both for mutualisms or antagonisms. Ecological network studies show that links among species are frequently asymmetric and species dependence on their counterpart is more complex than expected at random (Bascompte et al. 2006, Guimarães et al. 2007). Proposed mechanisms affecting network organization include habitat heterogeneity constraints (Pimm and Lawton 1980; López-Carretero et al. 2014), phylogeny (Rezende et al. 2009; Cagnolo et al. 2011), body size (Cohen et al. 2005; Chamberlain and Holland 2008; Rezende et al. 2009), and encounter probability based on natural abundance of species (Váquez, Chacoff and Cagnolo 2009; Dáttilo et al. 2014a), or variation in spatiotemporal co-occurrence (Rico-Gray et al 2012; Sánchez-Galván et al. 2012; Díaz-Castelazo et al. 2013; López-Carretero et al. 2014). For quantitative networks, species with a higher interaction frequency have a higher number of links, indicating that these species are possibly more abundant and/or competitive Dáttilo et al 2014a).

A nested pattern of links in mutualistic interaction networks could result from several ecological and evolutionary processes. For instance, the complementarity and convergence of phenotypic traits between both sets of interacting species (Thompson 2005; Stang et al. 2006; Stang 2007; Rezende et al. 2007), or by ‘forbidden interactions or links’, those that are impossible due to physical or biological constraints, such as phenological asynchrony or morphological mismatching (Jordano et al. 2003). However, several aggregate network properties such as nestedness, connectance and interaction asymmetry may also occur due to properties inherent to communities, such as species abundance, community sampling biases and the spatio-temporal overlap of species (Vázquez et al. 2007; 2009; Blütghen et al. 2008). Although relative species abundance (Dáttilo et al. 2014b) and spatio-temporal overlap could explain overall network structure, they fall short of predicting the frequency of pairwise interactions, which is the "fine-grain" structure potentially evidencing convergence or complementarity (Thomson 2005; Guimarães et al. 2011), thus leaving much unexplained variation (Vázquez et al. 2009). Progress in understanding the determinants of network patterns requires datasets with detailed natural history information such as spatial or temporal variation, morphological, behavioral, or life-history traits, which explain interspecific differences observed between species in the number and strength of interactions (Stang et al. 2006; Carnicer et al. 2009; Junker et al. 2013).

Our study system is valuable in this sense, since it provides the opportunity to test simultaneously the effect of several ecological and biological attributes of interacting species focusing on morphological aspects, habitat and spatial variation, as well as species abundance data, in order to test its contribution to the "fine-grain" structure of a mutualistic network, given by the frequency and strength of pairwise interactions.

Ant-plant networks, including potentially mutualistic interactions, have been recently addressed focusing on its spatio-temporal variation (Díaz-Castelazo et al. 2010; Sánchez-Galván et al. 2012; Díaz-Castelazo et al. 2013; Dáttilo et al. 2014b) and/or determining biotic/ abiotic factors. Among the latter, temperature and precipitation (Rico-Gray et al. 2012), soil pH (Dáttilo et al. 2013a), and the percentage of plants with active extrafloral nectaries (Lange et al. 2013) have important effects on the structure of ant–plant networks mediated by extrafloral nectaries

(EFNs). At a network-level it has been suggested that the amount of extrafloral nectar secreted is not a factor determining network attributes (Dáttilo et al. 2013), however, other community-level studies have proved that attributes of EFNs have important effects on frequency of ant-plant interactions or ant forager abundance (Rudgers and Gardner 2004).

Some studies have shown that the variation in abundance among ants on vegetation partially explains the network structure of mutualistic interactions, where abundant ant species usually interact with more plant species (Dáttilo et al. 2014b). Similarly, abundance of plants bearing extrafloral nectaries (Lange et al. 2013), plant size and ant body size (Chamberlain et al 2010) are important predictors of symmetric interactions between plants and ants, as well as nestedness in ant-plant networks Among other correlates of ant-plant network structure is the social recruitment behavior of ants, which determines the dominance hierarchy: ant species found in the central core of the network are frequently competitively superior, showing massive recruitment and resource domination, compared with peripheral species with fewer interactions (Dáttilo et al. 2014c).

While the importance of abiotic/biotic factors have been separately explored for ant-plant networks -either addressing a couple of biological factors or a group of abiotic ones-, the simultaneous relative contribution of several species biological attributes and ecological and habitat level attributes (i.e. ecological correlates) providing a facultative mutualistic ant-plant network, is addressed here for the first time. Furthermore, besides overall network topology, the present study focus in the “fine-grain” scale within an ant-plant interaction network that resides in the frequency and strength of pairwise interactions. Attributes of the species sets are in accordance with the foraging theory perspective required for a mechanistic understanding of ecological networks within a community (Ings et al. 2009); thus our study deepens in the underlying factors that influence network and community structure in ant-plant interactions

Attributes for plants include (1) the abundance of plants with extrafloral nectaries conforming the interaction network (cover of these plant species along vegetation association transects), (2) species distribution in vegetation associations with distinct habitat structure (open or shaded habitats), since it is an important factor influencing the richness and abundance of associated ant species (Díaz-Castelazo et al. 2004) and other interactions with insects (López-Carretero et al. 2014), and a highly seasonal component of the community (Rico-Gray 1993; Rico-Gray and Oliveira 2007); and (3) the distribution of the EFNs among plant organs, which are the secretory structures that mediate the interaction, since different distribution of liquid food sources could favor different ant assemblages or mosaics (Majer 1993; Blüthgen and Fiedler 2004). This attribute is essential for the optimal defense of valuable plant organs compared to vegetative ones (Rico-Gray 1993; Wäckers and Bonify 2004; Holland et al. 2009). A previous study on the morphology and distribution of EFNs (Díaz-Castelazo et al. 2005) raised the idea that gland distribution on plant organs could follow an aggregate or circumscribed location against a widely disperse location, that could result in distinct visitor arrays (Díaz-Castelazo et al. 2004), such as EF-nectar vs. honeydew ant assemblages may differ (Blüthgen and Fiedler 2004).

Attributes for ants include (1) behavioral dominance, found to be one of the most important features in mutualistic ant-plant interactions (Andersen 2000; Ness and Bronstein 2004; Dáttilo et al. 2014c); (2) head length, a robust estimator of body mass in ant species (Kaspari and Weiser 1999), which in turn have been shown to be positively correlated with important network-level properties such as the number of plant species ants interact with (degree) in EFN-mediated ant-plant networks (Chamberlain and Holland 2009); and (3) species status as invasive, since they may outnumber their native counterparts in the study site (Díaz-Castelazo et al. 2010) or disrupt mutualistic interactions (Schultz and McGlynn 2000; Holway et al. 2002).

In particular we addressed the following questions: 1) Which is the network structure of this ant-plant community mediated by extrafloral nectaries?; 2) Which is the detailed "fine-grain" structure resulting from the frequency (strength) of pairwise interactions?; and 3) Which is the relative contribution of biological or ecological correlates (ant, plant or habitat attributes) in rendering the pair-wise "fine-grain" and overall network structure?

Materials & Methods

Study site and data collection

Field work was carried out at Centro de Investigaciones Costeras La Mancha (CICOLMA), located on the coast of the state of Veracruz, Mexico (19° 36' N, 96 ° 22' W; elevation <100 m). The climate is warm and subhumid; a rainy season occurs between June and September, total annual precipitation is ca. 1500 mm, and mean annual temperature is 22°-26° C. The major vegetation types in the study area are tropical deciduous forest, tropical dry forest, sand dune scrub, mangrove forest, freshwater marsh, and flooded deciduous forest (Moreno-Casasola 2006). Changes in the abundance of associations between ants and plants bearing extrafloral nectaries (EFNs) suggest that ant–plant interactions are strongly influenced by climatic conditions as a result of marked seasonality (Díaz-Castelazo et al. 200; Rico-Gray and Oliveira 2007).

Biweekly observations were conducted between October 1998 and September 2000 (Díaz-Castelazo et al. 2004; also see Rico-Gray 1993) along six arbitrarily selected but representative

1-km trails that sampled different vegetation associations: Trail 1, sand dune pioneer species; Trail 2, deciduous forest; Trail 3, deciduous forest–dry forest ecotone; Trail 4, dry forest and sand dune scrub; Trail 5, sand dune scrub; and Trail 6, sand dune–fresh water lagoon ecotone and mangrove forest. We recorded all occurrences of ants collecting liquids from plants. On each visit we noted ant species, plant species, and the plant organ where the extrafloral nectaries mediating the ant–plant interaction were located. Once an individual plant was marked as visited by ants, it was subsequently re-checked throughout the study. We considered extrafloral nectar either produced by the surface of reproductive structures such as the spike, pedicel, bud, calyx, or fruit, or secreted by special structures on vegetative parts such as leaves, shoots, petioles, bracts, or stems. Ants were considered to be feeding on nectar when they were immobile, with mouthparts in contact with nectar secreting tissues, for periods of up to several minutes. Nectar-feeding ants often showed obviously distended gasters (Rico-Gray 1993).

The two distinctive distributions of EFNs on plant organs were circumscribed and disperse nectaries. The first category included: elevated glands, hollow glands (vascularized), transformed glands (vascularized), capitated trichomes (non-vascularized) and unicellular trichomes (non-vascularized). Disperse EFNs include: flattened glands, peltate trichomes, and scale-like trichomes (Díaz-Castelazo et al. 2005).

Data analysis

The ant-plant network analyzed here consists of a quantitative species-species matrix given by the frequency of occurrence of each pairwise ant-plant interaction. Ecological and biological attributes of the species were of different kinds and considered as highly important in modulating the mutualistic interaction (Díaz-Castelazo et al. 2004; 2005).

In order to perform an informative analysis, we excluded from the original ant-plant interaction matrix, those interactions that occurred at considerably low frequencies (interactions recorded on less than three occasions).This reduced the probability of representing a species with a single or very few interactions within the network, as a ‘‘specialist’’, when it may be a rare species, thus partially avoiding an overestimation of specialization, nestedness, and strength asymmetry, and thus deflating connectance and interaction diversity (Blütghen et al. 2008).

For this informative network we analyzed nestedness (NODF) (Nestedness based on Overlap and Decreasing Fill) (Almeida-Neto et al., 2008) using ANINHADO (Guimarães and Guimarães, 2006). This metric is very robust to correctly detect a nested pattern since it is less sensitive to matrix size and shape (Almeida-Neto et al., 2008). Significance of the NODF value for our network was obtained with ANINHADO after comparing it with 1000 simulations using null model Ce (Guimarães and Guimarães 2006), which corresponds to Null Model II of Bascompte et al. (2003) and assumes that the probability of an interaction occurring is proportional to the observed number of interactions of both plant and ant species (Bascompte et al. 2003; Dáttilo et al. 2013b). We then estimated network topology or structural metrics (connectance, dependence asymmetry, weighted nestedness and niche overlap) using different indexes included in the “network-level” section of the“Bipartite” package in “R” (Dormann and Gruber 2009). After graphic exploratory and “network-level” analysis were performed in “Bipartite”, the fact that no compartments existed within the network and its high nested structure render the formal modularity analysis unnecessary.

The detailed or “fine-grain” structure of the network, was estimated with the “species-level” function in the Bipartite” package in “R” (Dormann and Gruber 2009), the strength of each species, which is a more meaningful measure of network complexity (Bascompe et al.

2006). The strength of an animal species (ants in this case), is defined as the sum of dependences of the plants visited by this animal. It is a measure of the importance of this animal from the perspective of the plant set; thus, “species strength” is a quantitative extension of the species degree. We also estimated d’, which is the specialization of each species based on its discrimination from random selection of partners (Blüthgen et al. 2006), using the same species-level function in the Bipartite package of software “R”.

In order to explore the among-species dissimilarities resulting in the interaction pattern of the network, we generated the ordination of interaction frequencies with the multivariate technique known as Non-metric Multidimensional Scaling (NMDS) (Quinn and Keough 2002). This method is specifically designed to graphically represent relationship between objects (i.e. species / sites) in a multidimensional space provided by non-metric dissimilarities among objects. NMDS is one of the most effective methods for the ordination of ecological data and the identification of underlying gradients, because it does not assume a linear relationship among the variables (Quinn and Keough 2002). NMDS reduces the dimensionality of a matrix of among-sample similarity coefficients, based on particular number of dimensions (Borg and Groenen 1997). We chose the Bray-Curtis coefficient to construct the similarity matrices because joint absences do not influence among-sample similarity, and then we chose a two dimension configuration. The fit of an NMDS ordination, known as “stress”, is determined by how well the ordination preserved the actual sample dissimilarities. Stress values can range from zero to one, being values of 0.2 and below valid configurations to be interpreted. Because NMDS analysis offers more than one solution, we carried out an iterative process to find the model with smallest stress value using the metaMDS function in the MASS routine and Vegan package of software R (Dixon 2009). Then, in order to explore the simultaneous relative contribution of several biological attributes of species, ecological and habitat level attributes on the interaction pattern (NMDS ordination), we fitted those ecological/biological factors and vectors using the envfit function from the "Vegan" package of software "R". This function fits the vectors (continuous variables) and factors (categorical variables) of the environmental variable to the NMDS ordination, providing statistical significance by comparing our real model of pairwise interactions with 1000 permutations of a given null model; the envfit function provides a measure of correlation (r) and a significance value based on the probability that 1000 random permutations of simulated (environmental) variables would have a better fit than the real variables (Oksanen 2009). Thus the analysis allows testing ecological/biological/environmental variables as mechanistic proxies of network structure. (López-Carretero et al. 2014).

Results

Network-level and fine-grain structure

Our ant-plant network (a highly informative subweb taken from 2000 data (Díaz-Castelazo et al. 2010) consisted in 31 EFN-bearing plant species and 19 ant forager species linked by 1302 quantitative interactions derived from 157 species associations. The general topology shows a highly and significantly nested (NODF 49.13) (NODF (Ce) 34.93, P (Ce) < 0.001) network, with no modules or compartments at all (Fig 1). Network-level indexes were: connectance = 0.267, dependence asymmetry = 0.669 (implying that plants depend more on ants than the opposite), niche overlap among ant species = 0.223, niche overlap among plant species = 0.425, and weighted nestedness = 0.554 (implying that is network still nested when considering the frequency of pair-wise interactions). Eight plant species and four ant species constituted the central core of this network, the remaining species were peripherical (see also Díaz-Castelazo et al. 2010); plant core species were: *Cordia spinescens, Cedrela odorata, Callicarpa acuminata, Turnera ulmifolia, Canavalia rosea Crotalaria incana, Calopogonium caerulium* and *Mansoa hymenaea,* while ant core species were: *Camponotus planatus, Camponotus mucronatus, Crematogaster brevispinosa, Paratrechina longicornis.*

The species strength parameter is a quantitative version of species degree, which provides information on the relevance of a species for their interacting counterpart. Plant species *Cordia spinescens, Cedrela odorata, Callicarpa acuminata, Turnera ulmifolia* and *Canavalia rosea* showed the highest values for species strength (around 2), and are important nectar sources for ant foragers. Most plant species exhibited very low strength values, thus having, a modest relevance for the ant community. Species-level specialization values (d', considered as a measure of selectiveness) for plant species were also generally low (around 0.1), and only those plant species with few (or peculiar) associated ant species showed values above 0.3. These findings are in accordance to the generalized, highly nested structure of this network.

In contrast with plants, some ant species had important strength values. Eight ant species had values above 1, and two core ant species, *Camponotus planatus* and *C. mucronatus,* have strength values over 6, being thus important visitors of EFN-bearing plants.

Relative contribution of attributes to the assemblage of pair-wise interactions

Attributes of species are summarized as follows: plant species with circumscribed nectaries produced larger mean nectar volumes (2.06 µl), than those plants with disperse nectaries (0.53 µl). However, the amount of active glands in a plant individual may be higher for disperse nectaries, since these glands are structurally simpler than those of circumscribed nectaries. The frequency of ants foraging on the different EFnectary types clearly differs (χ^2_8= 1091.7).

Moreover, the range of total associated ant species visiting plants considered within each type of nectary is different among EFN distribution types. The range of visits to circumscribed nectaries was between nine and 17 ant species, while it was between 20 and 23 ant species for disperse nectaries. Thus, similar to gland morphology, EFN distribution in plant organs may influence visitation rates but mostly by a distinct composition of associated ant species.

We considered the two main vegetation structural associations (open vs. shaded habitats) to be natural groups, because floristic similarity between them is considerable lower (15.80) and significantly different ($F_{1,13} = 15.79$, $P < 0.01$) to that occurring within each group (36.06 and 41.28 for open and shaded habitats, respectively). See Methods for information on the vegetation associations.

The NMDS stress values that we obtained at the fourth run of the iterative process was the lowest (0.17), being an acceptable representative value suggested that the two-dimensional solution of the ordination suitably represented ant-plant assemblage dissimilarity; NMDS ordination being thus a valid configuration to be interpreted. This configuration having as well very low residuals (max res 0.0004) indicating a good concordance between the calculated dissimilarities and the distances among objects.

In Fig. 2, NMDS2 divides plant species according to the main habitats where they occur. On the superior part of the ordination, the plant species of shaded habitats with modest light incidence following a “humidity” gradient: the higher values for NMDS2 show (in decreasing order) plants (and associated ants) from the mangrove forest, followed by flooded subdeciduous forest and old-growth subdeciduous forest. At the bottom of the bi-plot the plants (and ants) occurring mostly in open vegetation with high light incidence: from cero to the lowest values of NMDS2, the interacting species are arranged through subdeciduous forest (ecotone with dune scrub), dune scrub vegetation and, pioneer vegetation in sand dunes. Axis NMDS1 is related to the contribution or importance of plant species to the ant forager community. Those plant species that are ordered at either low (negative) or higher (positive) values of the axis NMDS1, have low species strength values; in contrast, those plant species aggregated near the cero scale for this axis, are exactly those plant species with the highest strengths and thus higher relevance for the associated ant community. For ants, no generic or grouping trends are apparent. Sympatric ants are quite separated in the multivariate display. Detailed visitation frequencies of the ant species recorded for the network are shown in Table 2.

The results of fitting the biological/ecological variables into the multivariate Non-metric Multidimensional Scalings ordination shows that vegetation associations with differential structure (open vs. shaded habitats) were the only variable that determined the variation in the frequency of ant-plant pairwise interactions mediated by EFNs ($r^2 = 0.24$, $P < 0.005$). Two contrasting groups were formed along NMDS2, which were plant species (and their associated ant forager species) located either in open or shaded habitats (Fig. 2). Neither the distribution of EFNs on plant organs, nor the abundance of extrafloral-nectary bearing plants at each vegetation type, had a significant contribution to the variation in the observed ant-plant association patterns.

Ant head length was not significant in determining the variation of pairwise ant-plant interactions, neither ant invasive status. We found, however, a significant positive correlation between ant head length and species degree (the number of plant species interacting with ants) (Spearman rank correlation, rs = 0.5649, $P < 0.05$). Neither ant behavioral dominance categories, nor invasive status of ant species, were significant to explain the network fine-grain structure.

Discussion

Network-level and fine-grain network structure

Our studied network is highly nested or asymmetric in specialization patterns (see also Díaz-Castelazo et al. 2010; Díaz-Castelazo et al. 2013) and shows no modular structure, a common finding in potentially mutualistic networks, specially for facultative non-symbiotic interactions (Guimarães et al. 2007). A relative small core of species with very high interaction frequencies exist within our network (eight plant and four ant species), referred as "super-generalists". Super-generalist species are fundamental components of the maintenance of convergence at the community-level within highly diversified mutualistic assemblages, which, in turn, may be essential for the addition and persistence of more specialized species, influencing them through cascading effects (Guimarães, Jordano and Thompson 2011).

In our study system, the fact that the plant "guild" shows higher dependence asymmetry values than ants, implying that plants "depend" more on ants for maintaining network structure, is also reinforced by the higher species-level strength values of ants than those of plants. This asymmetry could reflect a higher temporal turnover of plants at the network – probably caused by seasonality or disturbance - versus higher ant resilience – probably derived from facultative foraging of ants. Most of the plant species constituting the core of this network had high strength values (*Cordia spinescens, Cedrela odorata, Callicarpa acuminata, Turnera ulmifolia* and *Canavalia rosea)*, suggesting that only the most connected plant species are important resources for the ants at a community level. However, the relative importance of specific plant species for this ant community do not seem related to specific biological attributes or neutral effects, since neither mean nectar volumes secreted by each plant species (Díaz-Castelazo et al. 2005), nor gland distribution or mere plant abundance explain core composition and species strength of plant species. Instead, this pattern seems to emerge from the degree of each species, its interaction frequencies with specific partners, possible driven by other higher-scale factors (i.e. habitat structure, abiotic variables, etc.).

The rest of the plant species showed very low strength values, having thus, a modest relevance for the ant community. Species-level specialization values (d') for plant species were also generally low (around 0.1), and only those plant species with few (or peculiar) associated ant species exhibited values above 0.3. These findings are in accordance to the generalized, highly nested structure of this network. For potentially mutualistic networks such as this (potentially, because benefits were assessed only for few pair-wise interactions) (Horvitz and Schemske 1984; Rico-Gray et al. 1987; Oliveira et al. 1999; Cuautle and Rico-Gray 2003; Cuautle, Rico-Gray and Díaz-Castelazo 2005) and for facultative ant-plant interactions such as the ones mediated by extrafloral nectar, low specialization or selectiveness levels for each species (and the whole network) is the general trend (Vázquez and Aizen 2004; Bascompte et al.,2003; Díaz-Castelazo et al. 2010).

In contrast with plants, some ant species had important strength values. From the ant species constituting the core of this network (*Camponotus planatus, Camponotus mucronatus, Crematogaster brevispinosa, Paratrechina longicornis)* three of them had strength values higher than 1 and the two *Camponotus* species have strength values over 6, being thus remarkably important visitors of EFN-bearing plants. Species belonging to this genus are frequent visitors of EFNs (Díaz-Castelazo et al. 2004; Díaz-Castelazo et al. 2013), considered as solitary leaf foragers that cover high foliar rates, with high ability of rapid uptaking nectar given proventricular adaptations that allow passive damming of sugary liquids, large crop capacities, and seeping canals to nourish the midgut (Davidson et al. 2004), highly adapted thus, to forage in nectar and sugary liquids. It is understandable then that ant species with high-degree and high strength values do not show high levels of specialization or selectiveness (d’), since they are physiologically adapted to forage in all available extrafloral nectar sources, not having any trophic restriction, although some other aspects -such as ant competition ability and resource attractiveness (Dáttilo et al. 2014c)- may differentiate visitation pattern of these core ant species. At our studied community core ant species are relevant to most plants species at the network, the latter depending more on the former, and evident nectar consumption adaptations and deterrent behavior of core ants, suggest potential biotic defense at a community scale.

Relative contribution of attributes to the assemblage of pair-wise interaction

Major vegetation associations according to habitat structure, were the only factors explaining variations in pair-wise interactions or fine-grain structure of the network. Open and shaded (i.e. forest) habitats at the study site seem to differ structurally in vegetation and on their abiotic conditions, which may in turn be important determinants of insect-plant interactions (López-Carretero et al. 2014). Although some studies have discussed the possible effects of abiotic variables on ant-plant networks (Rico-Gray et al. 2012, Sánchez-Galván et al. 2012, Díaz-Castelazo et al. 2010), ours is the only one testing habitat abiotic effects jointly with species-level biological attributes and neutral explanations (i.e. abundance) in a quantitative ant-plant network.

A mechanistic explanation for the differential ant-plant association pattern between open and forested habitats (which in turn do not differ in the abundance of EFN-bearing plant species) may involve light incidence, “attractiveness” or nutritional value of extrafloral nectar secreted by “light demanding” plant species compared to “shade tolerant” ones, and the physiological tolerance of ants to high temperatures. Increased photosynthetic activity of plants in open habitats could result in higher carbohydrate availability in extrafloral nectar, and thus increased attractiveness to ants, or a higher density of EFN-bearing plant life forms (such as vines). EFN-bearing plants growing in sunlight obtain a measurable benefit from ant visitation, whereas the same plant species growing under shaded conditions has no such a benefit (e.g., Bentley 1976; Frank and Fonseca 2005). For some plant species size of EFNs and nectar secretion are higher under intense light conditions compared to low light conditions (Yamawo and Hada 2010), and a similar trend is found for the ant abundance foraging on these glands (Rudgers and Gardener 2004, Yamawo and Hada 2010). This effect of site conditions on EFN abundance and secretory activity could also exist in our study system, since vegetation types with canopy cover (shaded) versus open habitats do sustain different species abundances, floristic similarities (Díaz-Castelazo et al. 2004) and patterns of specific insect-plant interactions (Lopez-Carretero et al. 2014).

Among-habitat heterogeneity in vegetation structure (as well as seasonality) at our study site is so strong that is clearly detected in the ant-plant interaction pattern, in contrast to other studies where vegetation structure differences are not that strong to being noticed at other ant-plant networks (Dáttilo et al. 2013a). Further evidence of among-habitat heterogeneity transcending to ant-plant network structure is provided at the present study by the multivariate analysis, where the component explaining more variance in the lack of independence among ant an plant species (NMDS1), display habitats following a decreasing humidity gradient, from mangrove forest, followed by flooded subdeciduous forest and old-growth subdeciduous forest, subdeciduous forest (ecotone with dune scrub), dune scrub vegetation and, pioneer dune vegetation. Indeed, open habitats at the study site, such as dune scrub and pioneer dune vegetation, have the most extreme temperatures and solar radiation (Moreno-Casasola, 1982, 2006), and subject to continual disturbance (López-Carretero et al. 2014) because of sand movement, strong winds and abrasion (Pérez-Maqueo 1995).

Our results show that no neutral effects derived from variation in species abundances are structuring the studied ant-plant network. Abundance of interacting species has been empirically proved to be a key factor affecting network structure (Dáttilo et al. 2013). These authors show that more abundant ant species often interact with more EFN plant species, but also pointed out that information on the difference in abundance among interacting species was insufficient to explain ant-plant network organization: nestedness being higher in networks of ants and plants with EFNs than that observed in networks of ants and plants without EFNs. Thus, the differences in nestedness, connectance and heterogeneity of interactions remained after controlling for the effects of species richness structure (Dáttilo et al. 2013). Other potentially mutualistic networks have shown that species abundance or temporal overlap are far from accurately predicting the frequency of pair-wise interactions, leaving much unexplained variation (Vázquez et al. 2009).

The fact that neither the distribution of EFNs on plant organs nor the abundance of extrafloral-nectary bearing plants at each vegetation type, had a significant simultaneous contribution to the variation in the observed ant-plant association patterns, does not rule out its possible effect on ant foraging patterns at other sites or when within habitat information is considered (Dáttilo et al. 2014). At our study site, besides the overwhelming evidence of seasonality and habitat heterogeneity the high occurrence frequency of morphologically diverse EFN at vegetation associations suggests plasticity in plant strategies for biotic defense.

For ant variables, although ant size (head length) was not a significant factor explaining frequency of pairwise interactions, it was, however, important in explaining other species-level attributes within a mutualistic network, such as species degree (also see Chamberlain and

Holland 2008), suggesting that larger ant species can forage over a greater area than small species, and thus interacting with more plant species. It has been shown that recruitment of ant foragers to a resource in negatively correlated with ant body size (LeBrun 2005). This suggests that body size-driven competition could result in larger ant species visiting more plant species to fulfill their requirements and avoid competition (Chamberlain and Holland 2008).

Overall behavioral dominance as a factor was not significant in explaining variations in the frequency of pair-wise interactions, possibly due to the spectra of factors considered simultaneously within the analysis, since the EFNs considered here include both, disperse EFNs and circumscribed EFNs that could provide resources for both, dominant and non competitive ant species.

Conclusions

While the importance of abiotic / biotic factors have been separately explored for ant-plant networks -either addressing a couple of biological factors or a group of abiotic ones-, the simultaneous relative contribution of several species biological attributes and ecological and habitat level attributes (i.e. ecological correlates) providing a facultative mutualistic ant-plant network, is addressed here by the first time. Besides overall network topology, the focus here is in the “fine-grain” scale within an ant-plant interaction network that resides in the frequency and strength of pairwise interactions.

Our extrafloral-nectary mediated ant-plant network result highly nested, non-modular, show high strengths for core species and low specialization or selectiveness and higher dependence of plants on ants; in accordance to a facultative mutualism scenario. At our studied community core ant species are relevant to most plants species at the network, the latter depending more on the former, and evident nectar consumption adaptations and deterrent behavior of core ants, suggest potential biotic defense at a community scale.

When simultaneously exploring plant, ant, and habitat attributes on network-level and fine-grain structure, the only factor significantly influencing the pair-wise interactions is habitat heterogeneity in vegetation structure (and distribution of EFN-bearing plant species). At our study site this heterogeneity is so strong that is clearly detected in the ant-plant interaction network pattern, both at network topology and at the fine-grain network structure provided by the frequency of pair-wise interactions; being thus, further evidence of abiotic factor influence in facultative mutualism and biotic plant defense.

Habitat heterogeneity in vegetation structure and distribution of EFN-bearing plant species depicts plasticity in plant strategies for biotic anti-herbivory defense: in our study plant species at shaded habitats more frequently have disperse EFnectaries, while plants at open habitats more frequently have circumscribed EFnectaries. The latter EFNs are more structurally complex glands (i.e. elevated or pit nectaries) more effectively protected from nectar evaporation, which is required at these open, insolated, high-temperature sites.

Non-neutral effects were detected at ant-plant interacting community, since EFN-bearing plant abundance per se had no influence in the ant-plant interaction pattern. As we showed before, more ecological/biological factors could influence network structure; thus, possible convergence effects of interacting species at open vs. shaded habitats may be occurring presided by supergeneralist species and thus, the possibility of cascading coevolutionary events taking place. This may deserve further study in other facultative mutualistic networks.

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Table 1.

Plant species	Distribution of EFNs	Habitat structure	Abundance (%cover)
CorSpi	D	S	38.833
TurUlm	C	O	6.66
CrotIn	C	O	12.38
CedOdo	D	S	36.143
CallAc	D	B	68.797
CaeCri	C	O	27.15
BidPil	C	S	27.95
CanRos	C	O	76.057
CalCae	C	O	16.85
TerCat	C	S	0.35
SenOcc	C	S	3.717
OpuStri	D	O	64.35
HibTill	C	O	2.4
AmphPa	D	O	17.55
IpoPes	C	O	49.1
ConEre	C	S	16.383
FicObt	C	S	8.15
CorGra	D	O	2.5
MacAtr	C	O	16.3
CisRho	C	O	3.55
IpoSp.	C	S	12.167
ManHym	C	S	16.3
TabRos	D	S	6.66
AcaMac	C	B	2.75
TriHav	C	S	28.33
AruDon	C	O	151.66
PetVol	D	O	74.1
ChaCha	C	O	32.4
IreCel	C	O	16.55
CorDen	D	S	3.615
BunLin	C	S	1.7

Table 1, legend. EFN-bearing plant species within the network and its attributes. Plant species code as follows: *CorSpi= Cordia spinescens, TurUlm= Turnera ulmifolia, CrotIn= Crotalaria indica, CedOdo= Cedrela odorata, CallAc= Callicarpa acuminata, CaeCri= Caesalpinia crista, BidPil= Bidens pilosa, CanRos= Canavalia rosea, CalCae= Calopogonium caerulium, TerCat= Terminalia catappa, SenOcc= Senna occidentalis, OpuStri= Opuntia stricta, HibTil= Hibiscus tiliaceus, AmphPa= Amphilophium paniculatum, IpoPes= Ipomoea pescaprae, ConEre= Conocarpus erectus, FicObt= Ficus obtusifolia, CorGra= Cornutia grandiflora, MacAtr= Macroptilium atropurpureum, CisRho= Cissus rhombifolia, IpoSp= Ipomoea sp., ManHym= Mansoa hymenaea, TabRos= Tabebuia rosea, AcaMac=Acacia macracantha, TriHav= Trichilia havanensis, AruDon= Arundo donax, PetVol= Petrea volubilis, ChaCha= Chamaecrista chamaecristoides, IreCel= Iresine celosia, CorDen= Cordia dentata, BunLin= Bunchosia lindeliana.* Plant attributes considered also in Figure 2 are: EFN= Distribution of extrafloral nectaries within a plant species ("C" are circumscribed glands and "D" are disperse glands), Habitat= Distribution of plant species between habitats with contrasting vegetation structure ("S" is shaded vegetation and "O" is open vegetation). Abundance (% cover)= Percent cover of EFN-bearing plant species.

Table 2.

Ant species	Invasive status	Dominance hierarchy	Head lenght
CamPla	NO	D	1.198
CamMu	NO	D	1.418
CamAt	NO	D	1.946
AztSp	NO	E	1.471
ParLo	INV	C	0.638
TetSpi	INV	D	0.968
CepMin	NO	C	1.155
DorBi	NO	C	0.973
PseGra	NO	B	1.738
MonCy	NO	D	0.482
CamHi	NO	D	1.076
PachVi	NO	B	2.88
ForAna	NO	E	0.631
CreBre	NO	D	1.031
PheSp	NO	E	0.553
SolGe	INV	D	0.684
WasAu	INV	D	0.479
PseEje	NO	B	0.8
PseBru	NO	B	0.768

Table 2, legend. Ant species within the network and its attributes. Ant species code as follows: *CamPla= Camponotus planatus, CamMu= Camponotus mucronatus, CamAt= Camponotus atriceps, AztSp= Azteca sp. 1, ParLo= Paratrechina longicornis, TetSpi= Tetramorium spinosum, CepMin= Cephalotes minutus, DorBi= Dorymyrmex bicolor, PseGra= Pseudomyrmex gracilis, MonCy= Monomorium cyaneum, CamHi= Camponotus mucronatus hirsutinasus, PachVi= Pachycondyla villosa, ForAna= Forelius analis, CreBre= Crematogaster brevispinosa, PheSp= Pheidole sp., SolGe= Solenopsis geminate, WasAu= Wassmannia auropunctata, PseEje= Pseudomyrmex ejectus, PseBru= Pseudomyrmex brunneus.* Ant attributes considered also in Figure 2 are: Invasive status= status as invasive / tramp ant species (INV or NO), Dominance= hierarchies of behavioral dominance (B to E in order of increasing dominance), Head length= length (in mm) from head apex to anterior clypeal margin of species (minor worker).

Figure 1.

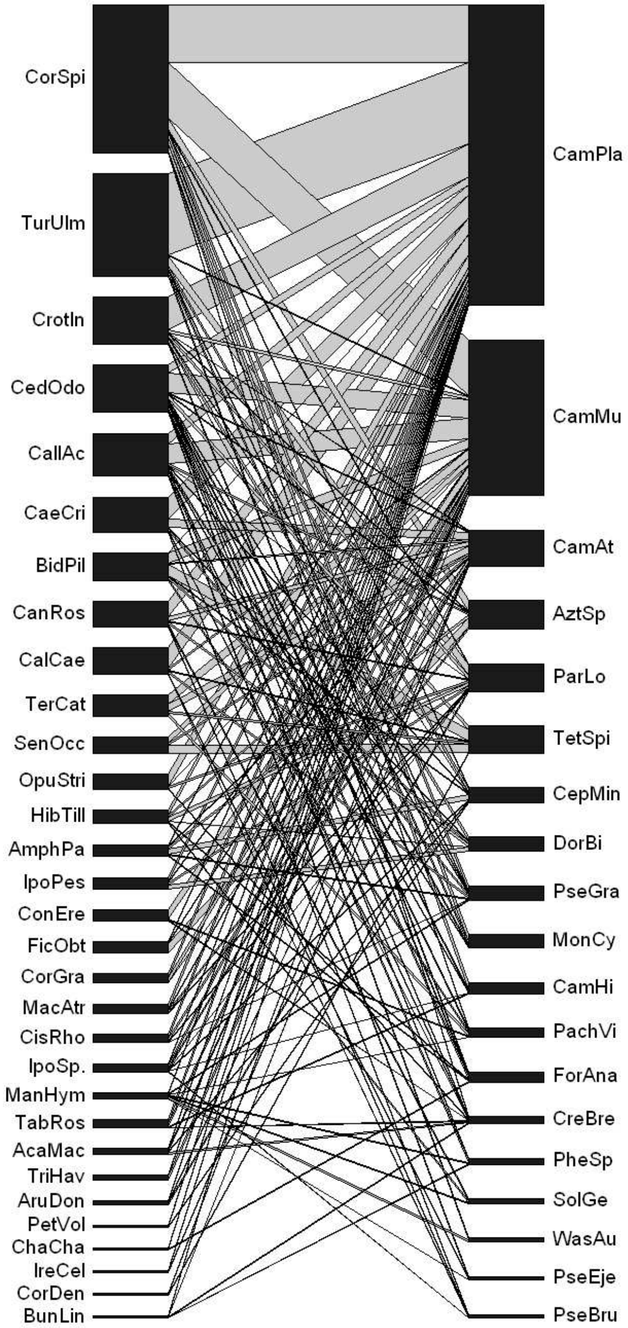

Figure 1, legend. Quantitative mutualistic networks between ants (higher trophic level) and EFN-bearing plants (lower trophic level). Species codes as in Tables 1 and 2.

Figure 2.

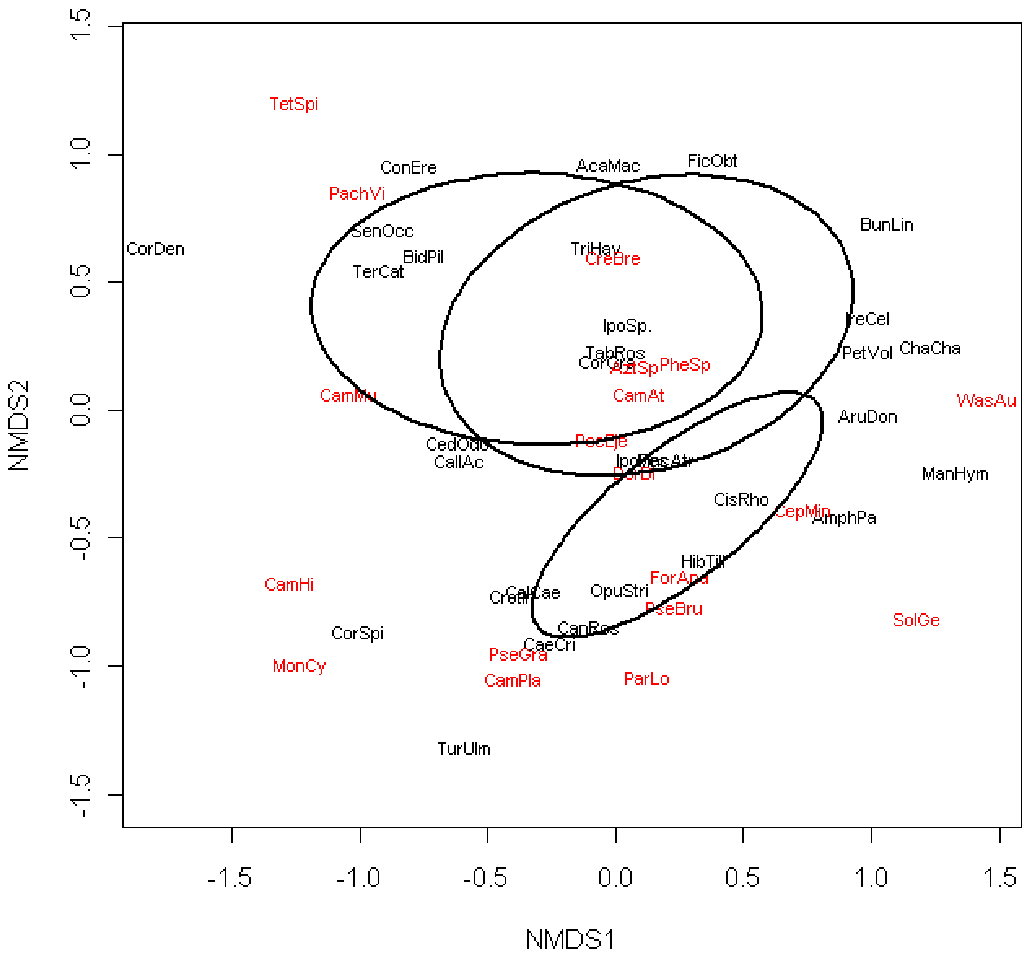

Figure 2, legend. Ordination of NMDS. Stress values:0.17 (fourth iteration) indicating a good two-dimensional solution of the ordination suitably representing ant-plant assemblage dissimilarity. This configuration having as well very low residuals (max res 0.0004) indicating a good concordance between the calculated dissimilarities and the distances among objects. Distant ellipses circle the only attribute (factor) that significantly explained (r^2 =0.24, P <0.005) the pairwise interaction pattern (habitat types). Codes for species and attributes as in Table 1.