

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

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16 **Abstract**

17 **Background.** Ecological communities of interacting species analyzed as complex networks have  
18 shown<sup>ed</sup> that species dependence on their counterpart<sup>s</sup> is more complex than expected at random.  
19 As for other potentially mutualistic interactions, ant-plant networks mediated by extrafloral  
20 nectar show a nested (asymmetric) structure with a core of generalist species dominating the  
21 interaction pattern. Proposed factors structuring ecological networks include encounter  
22 probability (e.g. species abundances and habitat heterogeneity), behavior, phylogeny, and body  
23 size. While the importance of underlying factors that influence the structure of ant-plant networks  
24 have been separately explored, the simultaneous contribution of several biological and ecological  
25 attributes inherent to the species, guild or habitat level has not been addressed.

26 **Methods.** Within ~~For~~ a tropical seasonal site we recorded (in 48 censuses) the frequency of  
27 pairwise ant-plant interactions mediated by extrafloral nectaries (EFN) at different habitats and  
28 studied the resultant network structure. We addressed for the first time the role of mechanistic  
29 versus neutral determinants at the ‘fine-grain’ structure (pairwise interactions) of ant-plant  
30 networks, studying the simultaneous contribution of several attributes of plant and ant species (i.e.  
31 EFN abundance and distribution, ant head length, behavioral dominance and invasive status), and  
32 habitat attributes (i.e. vegetation structure) in prevailing interactions as well as in overall network  
33 topology (community).

34 **Results.** Our studied network was highly-nested <sup>and</sup>~~and~~ non-modular, with core species having high  
35 species strengths (higher strength values for ants than plants) and low specialization; plants had  
36 higher dependences on ants <sup>than vice versa</sup>. We found that habitat heterogeneity in vegetation  
37 structure (open vs. shaded habitats) was the main factor explaining network and fine-grain  
38 structure, with no evidence of neutral (abundance) effects.

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39 **Discussion.** Core ant species are relevant to most plants species at the network, showing  
40 adaptations to nectar consumption and deterrent behavior. Thus, larger ants interact with more  
41 plants species, ~~altogether~~ with higher dependence of plants on ants, suggest~~ings~~ potential biotic  
42 defense at a community scale. At our study site, ~~spatiotemporal~~ heterogeneity in the ant-plant  
43 interactions among habitats is so prevailing, that emerges at community-level structural properties,  
44 ~~depicting the effect of abiotic factors in facultative mutualism.~~ High frequency of morphologically  
45 diverse and temporarily-active EFNs across all habitats suggests phenotypic plasticity in plant  
46 strategies for biotic defense. ~~Frequent occurrence of morphologically diverse EFNs at all habitats~~  
47 ~~suggests plasticity in plant strategies for biotic defense provided by ants.~~ ~~The robust survey of~~  
48 ~~ecological interactions and their biological/ecological correlates that we addressed.~~ We provides  
49 insights ~~of~~ into the interplay between adaptive-value traits and neutral effects in ecological  
50 networks.

**Commented [MS2]:** In the network? OR at the network level?

**Commented [MS3]:** Dominant?

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## Introduction

The interactions among species occurring ~~in a~~ a community have been ~~recently~~ studied ~~recently~~ with a complex network perspective, where interacting species (i.e. plants and animals) are graphically represented as nodes and their feeding interactions as links (Bascompte et al., 2003). Such studies have paid important attention to network structure and its underlying factors, both for mutualistic or antagonistic interactions. Unraveling how interactions among species are structured in communities or ecosystems is crucial for understanding the ecological and evolutionary processes that support ecosystem function and diversity (Herrera & Pellmyr, 2002); furthermore, understanding the architecture of species relationships may help predict how ecosystems respond either to abiotic or human-derived changes (Bascompte, 2010).

Ecological network studies have ~~showed~~ ~~shown~~ that interactions among species are frequently asymmetric and species dependence on their counterparts is more complex than expected at random (Bascompte, Jordano & Olesen, 2006; Guimarães et al., 2007). For networks of mutualistic interactions a nonrandom “~~“““~~“~~”””~~” nested” structure is frequently observed, where more specialist species tend to interact with specific subsets of those species interacting with the more generalist species (Almeida-Neto et al., 2008; Bascompte, 2010); thus nested structure implies that interactions occur asymmetrically in a group of generalist species that comprise most interactions in the network (network core) (Dáttilo et al., 2013b) and a group of specialist species that maintain few interactions mostly or exclusively with generalist species. Such a nested architecture has been found to increase network robustness against loss of species (Mommott et al., 2004; Bascompte et al., 2006) and to maximize the number of coexisting species supported by these networks (Bastolla et al., 2009; Thébault & Fontaine, 2010). 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

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interacting species (Thompson, 2005; Stang et al., 2006; Stang, 2007; Rezende, Bascompte & Jordano, 2007).

Another nonrandom structural pattern in ecological interaction networks is ‘modularity or compartmentalization’ which is characterized by a group of species interacting more strongly among themselves than with other species or subsets in the network (Bascompte, 2010); the modular pattern is more frequently observed for networks of antagonistic interactions. Like nestedness in mutualistic networks, modularity is thought to increase the persistence of species in antagonistic networks ~~The contrasting structures of antagonistic and mutualistic networks are the very ones that also increase the persistence of species in each network type, which is the driving force of network architecture~~ (Thébault & Fontaine, 2010).

Proposed mechanisms affecting overall network structure are diverse, including habitat heterogeneity constraints (Pimm & Lawton, 1980; López-Carretero et al., 2014), phylogeny (Rezende et al., 2007; Cagnolo, Salvo & Valladares, 2011), body size (Cohen et al., 2005; Rezende, Bascompte & Jordano, 2007; Chamberlain & Holland, 2009), and encounter probability based on natural abundance of species (Vázquez, Chacoff & Cagnolo, 2009; Blüthgen, 2010; 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; Junker et al., 2013; López-Carretero et al., 2014). Environmental changes may alter network structure and thus, favor evolutionary responses in opposing directions for different species; the reorganization of network structure because of the indirect effects of coevolution may explain why and how mutualisms persist amid the turnover of species and interactions across space and time (Guimarães et al., 2017).

Several aggregate network properties such as nestedness, connectance (the proportion of realized interactions from all the ones possible given the number of species), and interaction

100 asymmetry (i.e. asymmetry of dependence of plants on animals and vice versa) may also emerge  
101 due to properties inherent to communities. These causes include the different abundances of  
102 species, community sampling biases (that affect the detectability of some interactions), and the  
103 spatio-temporal overlap of species (i.e. co-occurrence) (Vázquez et al., 2007, [2009](#); Blüthgen et  
104 al., 2008; [Vázquez et al., 2009](#)).

105 Although relative species abundance (Vázquez et al., 2009; Dáttilo et al., 2014a) and  
106 spatio-temporal overlap -considered as ‘neutral’ causes of network structure- could explain  
107 overall network structure, they fall short of predicting the frequency of pairwise interactions.  
108 Indeed, the frequency of interactions occurring for any given pair of species within the network  
109 can vary ~~significantly~~[importantly](#) even if the overall network topology remains the same  
110 (Vázquez et al., 2005, 2007, 2009; Díaz-Castelazo et al., 2010; Dáttilo et al., 2014d; Sánchez-  
111 Galván et al., 2012).

112 [The](#) pattern and frequency of pairwise interactions is what we refer [to](#) here as, the ‘fine-  
113 grain’ structure of the network, and is relevant since it could potentially ~~evidence~~[indicate](#)  
114 convergence or complementarity between species (Thomson, 2005; Guimarães, Jordano &  
115 Thompson, 2011). Thus, a current challenge in ecological network studies is to infer which  
116 processes are involved in the structuring [the fine-scale](#) patterns of interaction networks and how  
117 these may change over time (Ramos-Robles et al., 2016). Temporal changes in network structure  
118 and species composition may occur because of seasonal variability in weather (Rico-Gray et al.,  
119 2012), food abundance (Carnicer, Jordano & Melián, 2009; López-Carretero et al., 2014; Ramos-  
120 Robles, Andresen & Díaz-Castelazo et al., 2016), or plant traits (López-Carretero et al., 2016).  
121 Progress in understanding the determinants of network patterns requires datasets with detailed  
122 information of natural history such as spatial or temporal variation, morphological, behavioral, or  
123 life-history traits, which explain interspecific differences observed between species in the number

and strength of interactions (Stang et al., 2006; Carnicer, Jordano & Melian, 2009; Junker et al., 2013; López-Carretero et al., 2016).

The study of ant-plant interactions at a community level, has also been approached with the theoretical/analytical framework of ecological networks (Chamberlain & Holland, 2009; Díaz-Castelazo et al., 2010; Dáttilo et al., 2013a; Fagundes et al., 2017). These ant-plant interactions are mediated by several plant rewards for ants, such as extrafloral nectar, food bodies, fleshy diaspores, or plant domatia. At a community-level, plants providing good-quality extrafloral nectar are highly attractive to ants and accumulate more interactions with aggressive and territorial ant species (Blüthgen et al., 2004; Dáttilo et al., 2014c), but more importantly, ant visits may render reduced herbivory damage (Oliveira et al., 1999; Cautle & Rico-Gray, 2003; Fagundes et al., 2017). ~~Plenty~~ Variation in EFN attributes exist, including nectar volume, the amount of secreted sugar, variable gland size and morphology, position of EFNs within plant organs and differential attractiveness to ant foragers. Many of these attributes show phenotypic plasticity or context-dependency (Koptur, 1992; Rudgers, 2004; Wäckers & Bonifay, 2004). In this context, plant investment in nectar production and nectar quality ~~is~~ are very important factors modifying the benefit received by plants through biotic defense, and fitness-related outcomes of the interaction (Rudgers & Gardner, 2004; Holland, Chamberlain & Horn, 2009).

Ant-plant networks, including potentially mutualistic interactions ('potentially', because benefits ~~were~~ have been assessed only for a few interactions, see: Horvitz & Schemske, 1984; Rico-Gray et al., 1989; ~~Oliveira et al., 1999; Cautle & Rico-Gray, 2003;~~ Cautle, Rico-Gray & Díaz-Castelazo, 2005; Rico-Gray & Oliveira, 2007), have been recently addressed focusing on ~~their~~ its spatio-temporal variation (Díaz-Castelazo et al., 2010; Sánchez-Galván et al., 2012; Díaz-Castelazo et al., 2013; Dáttilo et al., 2013b, 2014b) and/or determining biotic/abiotic factors. Among the latter, temperature and precipitation (Rico-Gray et al., 2012), soil pH (Dáttilo et al.,

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Network approach has been used to...

2013a), and the temporal variation in the percentage of plants with active extrafloral nectaries that mediate the interaction (Lange, Dáttilo & Del-Claro, 2013), have important effects on the structure (i.e. nestedness, specialization) 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., 2013a), however, other community-level studies (not using a network approach) have proved that attributes of EFNs have important effects on frequency of ant-plant interactions or ant forager abundance (Rudgers & Gardner, 2004).~~

Some studies have shown that ~~the~~ variation in the abundance of ants among different types of vegetation, partially explains the network structure of mutualistic interactions, where by abundant ant species usually interact with more plant species (Dáttilo et al., 2014b). Similarly, the abundance of plants bearing extrafloral nectaries (Lange, Dáttilo & Del-Claro, 2013) and plant size are important predictors of asymmetric (i.e. nested) interactions between plants and ants in ant-plant networks. Ant species attributes that may influence structure in ant-plant networks, ~~is include~~ the social recruitment behavior of ants, as well as its invasive potential. Once a worker ant forager finds a profitable food source (i.e. EFnectar) it will (or not if it is a solitary forager) recruit nestmates using variable strategies (Dornhaus & Powell, 2010), such as group recruitment, tandem running, mass recruitment by pheromone trail, trunk trails, and team transport, ~~etc.~~ which are highly variable depending on ant species/genus or ecological context; often, aggressive behavior of ants and numerical dominance are attributes that influence the recruitment and competition abilities (Parr & Gibb, 2010). Ant dominance hierarchy determined by ant behavior, also influences network structure ~~since given that~~ ant species found in the central core of the network are frequently competitively superior (i.e. showing massive recruitment and resource domination) compared with peripheral species with fewer interactions (Dáttilo et al.,

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2014c). Furthermore, invasive ant species, given their opportunism, recruitment behavior, and numeric dominance (Ness & Bronstein, 2004; Lach & Hooper-Bui, 2010), could rapidly become important components of the core of ant-plant networks even if they do not displace other ant species (Díaz-Castelazo et al., 2010; Falcão et al., 2017).

While the importance of abiotic/biotic factors have been separately explored for ant-plant networks, ~~either addressing a couple of biological or abiotic factors~~, the simultaneous relative contribution of biological attributes of species and ecological and habitat level attributes (i.e. ecological correlates) in a facultative mutualistic ant-plant network, is addressed here for the first time. Attributes of the species sets considered here are in accordance with the foraging theory perspective required for a mechanistic understanding of ecological networks (Ings et al., 2009). Our study system provides the opportunity to test simultaneously the effect of several ecological and biological attributes of interacting species including morphology, behavior, and abundance as well as their inter-habitat (spatial) variation on the overall and ‘fine-grain’ structure of a quantitative mutualistic network. In particular we addressed the following questions: 1) What is the network structure of this intensively-sampled ant-plant community mediated by extrafloral nectaries?; 2) Which is the “fine-grain” structure emerging from the frequency (strength) of pairwise interactions?; 3) Which is the position of species in the core/periphery structure of the network?; and 4) Which is the relative contribution of biological or ecological correlates (ant, plant or habitat attributes) in rendering the “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 sub-humid with rainy season between June and September, a 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 sub-deciduous forest, tropical deciduous forest, coastal dune scrub, mangrove forest, freshwater marsh, and deciduous flood forest (Castillo-Campos & Travieso-Bello, 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., 2004; Rico-Gray & Oliveira, 2007). Marked seasonality at the study site (rainy, dry, and cold-front seasons) influences primary productivity and have a strong effect in animal-plant interactions (Rico-Gray 1993; Díaz-Castelazo et al. 2004; Sánchez-Galván et al. 2012; López-Carretero et al. 2014; Ramos-Robles, Andresen & Díaz-Castelazo, 2016; Martínez-Adriano, 2017).

Biweekly observations were conducted between October 1998 and September 2000 (Rico-Gray, 1993; Díaz-Castelazo et al., 2004), ~~rendering resulting in an~~ intensive sampling of 48 censuses along six 1km trails that sampled vegetation types representative of the plant communities in the study region: 1) pioneer dune vegetation (PDV), 2) coastal dune scrub (CDS), 3) tropical sub-deciduous forest in young soil (TSF-Y), 4) tropical sub-deciduous forest in old soil (TSF-O), 5) tropical deciduous flood forest with wetland (TDF-W), and 6) mangrove forest ecotone (MFE) (nomenclature as in Martínez-Adriano et al., 2016; derived from Castillo-Campos and Travieso-Bello, 2006, following methods from Rico-Gray, 1993 and Díaz-Castelazo et al., 2004). Vegetation associations differ in their structural complexity provided partly by arboreal plant cover and contrasting physiognomies occur between “open” and “shaded” habitats, ~~with the first three habitats being included in the former physiognomy the first three habitats~~ (PDV, CDS, and (TSF-Y) ~~being included in the former physiognomy~~, and ~~in the later~~ the other three habitats (TSF-O, TDF-W, and MFE) ~~included in the latter~~ (Díaz-Castelazo et al. 2004; López-Carretero et

al. 2014). Habitats 1, 2 and 3 are also different from 4, 5, and 6 in their floristic similarity of flowering plants (Chao-Jaccard Similarity Index, see Martínez-Adriano et al., 2016) and in the mean density of ants observed in honey baits placed in (Díaz-Castelazo et al., 2004). At these six vegetation types we recorded all occurrences of ants collecting liquids directly from all the plants at the transects (ant-plant interactions); we considered all plant life forms but only from those below 4 m in height, since no canopy censuses were performed. We also estimated the abundance of EFN-bearing plants through their line cover within each transect (Díaz-Castelazo et al., 2004 or Sánchez-Galván et al., 2012 for details). On each visit at each transect we recorded: ant species, plant species, the plant organ where the extrafloral nectaries were located, and its distribution. Once an individual plant was marked as visited by ants, it was subsequently re-checked throughout the study; when doubt existed on the nectar source, EFN-secretion was confirmed with glucose reagent stripses (Clinistix, Bayer). 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 (Rico-Gray, 1993). For estimating the abundance of EFN-bearing plants we measured the linear cover of each species along the trails or transects at each vegetation association (Díaz-Castelazo, et al. 2004). Further information on the ant-plant interaction censuses showed at the present study (including seasonal variations of species and attributes) is detailed in Díaz-Castelazo, et al. 2004 (i.e. Appendix 1, Figure 1).

## Plant and ant attributes

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243 Regarding the distribution of EFNs among plant organs, we used a general characterization  
244 (Díaz-Castelazo et al., 2005) differentiating the EFNs which are glands circumscribed to  
245 particular plant organs or whorls (at specific or modular locations) from the ones dispersed  
246 among plant organs (i.e. secretory trichomes on leaves or surfaces of vegetative tissues). Díaz-  
247 Castelazo et al. (2005) results ~~raised the idea that~~ indicated that gland distribution on plant organs  
248 could follow an aggregated (i.e. circumscribed) location ~~against compared to~~ a widely dispersed  
249 location ~~and, that this~~ could result in distinct ant visitor arrays (Díaz-Castelazo et al., 2004), in a  
250 similar way that EF-nectar sources may differ from honeydew sources in their associated ant  
251 assemblages (Blüthgen & Fiedler, 2004; Blüthgen et al., 2000). Circumscribed EFNs include:  
252 elevated glands, hollow glands (vascularized), transformed glands (vascularized), capitated  
253 trichomes (non-vascularized), and unicellular trichomes (non-vascularized). Dispersed EFNs  
254 include: flattened glands, peltate trichomes, and scale-like trichomes (Díaz-Castelazo et al.,  
255 2005).

256 Attributes for plants included: (1) the abundance of plants with extrafloral nectaries,  
257 ~~conforming the interaction network (cover of these plant species along transects representative of~~  
258 ~~vegetation associations);~~ (2) species distribution in vegetation associations with distinct habitat  
259 structure (open or shaded habitats) ~~it is an important factor influencing the richness and~~  
260 ~~abundance of ant-plant interactions (Díaz-Castelazo et al., 2004), interactions with other insects~~  
261 ~~(López-Carretero et al., 2014), and the spatio-temporal variation of interactions given the~~  
262 ~~seasonality of those communities (Rico-Gray, 1993; Rico-Gray & Oliveira, 2007; Díaz-Castelazo~~  
263 ~~et al., 2010);~~ and (3) the distribution of the EFNs among plant organs (Table 1) ~~given that~~  
264 ~~different distribution of liquid food sources of plants could favor different ant assemblages or~~  
265 ~~mosaics (Majer, 1993; Blüthgen & Fiedler, 2004); this attribute is essential for the optimal~~

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defense of valuable plant organs compared to vegetative ones (Rico-Gray, 1993; Wäckers & Bonifay, 2004; Holland, Chamberlain & Horn, 2009).

Attributes for ants included the following: (1) behavioral dominance, found to be one of the most important features in mutualistic ant-plant interactions given that competitive species may exclude submissive ones (Andersen, 2000; Ness & Bronstein, 2004; Lach & Hooper-Bui, 2010; Dáttilo et al., 2014e); the behavioral dominance scores we used were based on the classification of ant functional groups proposed by Andersen (1995; 2000) in relation to plant life-forms, stress, and disturbance; (2) head length, a robust estimator of body mass in ant species (Kaspari & 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 ant-plant networks (Chamberlain & Holland, 2009); and (3) species status as invasive, since some of these species may outnumber their native counterparts in the study site (Díaz-Castelazo et al., 2010) or disrupt mutualistic interactions (Schultz & McGlynn, 2000; Holway et al., 2002); the invasive status that we used was based in Holway et al. (2002), with adjustments to include ‘tramp’ species status as well (McGlynn, 1999; Lach & Hooper-Bui, 2010; Falcão et al., 2017) (Table X2).

We provide further detail on species attribute selection at the present study. We selected these attributes because as follows. Cover and distribution of EFN-bearing plant species (among habitats with different vegetation structures) they give us relevant information about (1) the cover of plant species along transects representative of the vegetation associations, (2) habitat structure is an important factor influencing the richness and abundance of ant-plant interactions (Díaz-Castelazo et al., 2004), interactions with other insects (López-Carretero et al., 2014), and the spatio-temporal variations due to seasonality (Rico-Gray, 1993; Rico-Gray & Oliveira, 2007; Díaz-Castelazo et al., 2010). Similarly, and (3) the differential distribution of EFNs among plant

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organs could favor different ant assemblages (Majer, 1993; Blüthgen & Fiedler, 2004); this attribute is essential for the optimal defense of valuable reproductive plant organs compared to vegetative ones (Rico-Gray, 1993; Wäckers & Bonifay, 2004; Holland, Chamberlain & Horn, 2009). With regard to ant attributes, the (1)-behavioral dominance is a relevant feature in mutualistic ant-plant interactions given that the competitive species may exclude submissive ones (Andersen, 2000; Ness & Bronstein, 2004; Lach & Hooper-Bui, 2010; Dáttilo et al., 2014c); (2) head length has been shown to be positively correlated with important network level properties such as the “degree” of ant species, which is the number of plant species. AQUÍ FALTA ALGO EN EL DOCUMENTO ORIGINAL Y POR ESO LA ORACION NO SE ENTIENDE EL ORIGINAL DICE “to be positively correlated with important network level properties such as the number of plant species ants interact with (degree) each ant species interacts with in ant-plant networks (Chamberlain & Holland, 2009); regarding AND (3) the invasive status of ant species, this is a relevant attribute since many invasive species given their behavior or foraging strategies, may outnumber their native counterparts (Díaz-Castelazo et al., 2010) or even disrupt mutualistic interactions (Schultz & McGlynn 2000; Holway et al., 2002).

### 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).

The pairwise interaction matrix here considered is a highly informative sub-web taken from Díaz-Castelazo et al. (2010), where we excluded those interactions that occurred at considerably very low frequencies (interactions recorded on less than three occasions from the whole 48

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314 censuses), in order to perform better multivariate analysis (NMDS), interpretation of biplot  
315 ordinations, and adjustment of explanatory variables. This also reduced the probability of  
316 considering a species with a single or very few interactions as a “specialist”, when it was ~~just~~  
317 simply a very rare species. Further, removing rare interactions ~~and~~ helped to avoid ~~the~~  
318 overestimation of specialization, nestedness, and strength asymmetry (Blüthgen et al., 2008).

319 For this informative network we analyzed nestedness (NODF) (Nestedness based on  
320 Overlap and Decreasing Fill) (Almeida-Neto et al., 2008) using ANINHADO (Guimarães &  
321 Guimarães, 2006). This metric is very robust ~~to at~~ correctly detecting ~~a nestedness pattern~~ since it  
322 is less sensitive to matrix size and shape (Almeida-Neto et al., 2008). Significance of the NODF  
323 value for our network was obtained with ANINHADO after comparing it with 1000 simulations  
324 using null model Ce (Guimarães & Guimarães, 2006), which corresponds to Null Model II of  
325 Bascompte et al. (2003) and assumes that the probability of an interaction occurring is  
326 proportional to the observed number of interactions of both plant and ant species (Bascompte et  
327 al., 2003; Dáttilo et al., 2013b). We then estimated network topology or structural metrics  
328 (connectance, dependence asymmetry, weighted nestedness, and niche overlap) using different  
329 ~~indices~~ ~~exes~~ included in the function “network-level” of the “bipartite” package (Dormann &  
330 Gruber, 2009) in ‘R’ (R Core Team, 2014).

331 In addition, we tested the existence of a modular structure at the network, estimating  
332 modularity index (M) (range: 0-1) with simulated annealing optimization approach (SA)  
333 (Guimerà & Amaral, 2005), based on Barber’s modularity metric for bipartite networks ( $Q_B$ )  
334 (Barber, 2007) with the software MODULAR (Marquitti et al., 2013). The statistical significance  
335 of modularity (M) was calculated using Monte Carlo tests with 1000 randomizations (Guimerà,  
336 Sales-Pardo & Amaral, 2004). High values of M indicate the occurrence of ants and plants in

337 cohesive subgroups that generate compartments or modules in which these species interact more  
338 closely than with the other species in the network (Olesen et al., 2007).

339 We calculated the core-periphery structure of the network and its component species (i.e.  
340 which species constitute the cohesive core of generalists, and which low-degree species constitute  
341 the periphery) with a function developed by Martínez-Adriano (2017) in R software based on the  
342 formula proposed by Dáttilo, Guimarães & Izzo (2013), where the species with values equal or  
343 larger than up-close-to 1 are considered as core components and species < 1 are considered  
344 peripheral.

345 For calculation of the “fine-grain” structure of the network we used the “species-level”  
346 function (Dorman, 2011) in the “bipartite” package. The metrics calculated for this objective  
347 were “species strength” and “ $d^2$ ”. the first Species strength is defined as the sum of dependences  
348 of the plants visited by this animal (or vice versa). It is a measure of the importance of this animal  
349 from the interaction service provided to the plants at the studied community (network); Thus,  
350 species strength is a quantitative extension of the metric “species degree” and provides  
351 information about the relevance of a species for their interacting counterpart, being thus a more  
352 meaningful measure of network complexity (Bascompte, Jordano & Olesen, 2006). While, The  
353 second metric,  $d'$  is the specialization of each species based on its discrimination from random  
354 selection of partners (Blüthgen et al., 2008).

355 In order to explore the among-species dissimilarities resulting in the interaction pattern of  
356 the network, we generated the ordination of interaction frequencies with the multivariate  
357 technique “Non-metric Multidimensional Scaling (NMDS)” (Quinn & Keough, 2002). This  
358 method is specifically designed to graphically represent relationship between objects (i.e.  
359 species/sites) in a multidimensional space provided by non-metric dissimilarities among objects.  
360 NMDS is one of the most effective methods for the ordination of ecological data and the

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identification of underlying gradients, because it does not assume a linear relationship among the variables (Quinn & Keough, 2002). NMDS reduces the dimensionality of a matrix of among sample similarity coefficients, based on particular number of dimensions (Borg & Groenen, 1997). We chose the Bray-Curtis [dissimilarity](#) 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, where values range from zero to one (values of 0.2 and below are 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 Vegan package (Dixon, 2009) on R [Studio software \(Ver. 3.5.1., 0.99.902\), R Core Team, 2014\).](#)

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 ([Dixon, 2009](#)) on [R software \(Ver. 3.5.1., R Core Team, 2014\).](#) ~~[RStudio software \(Ver. 0.99.902\), R software](#)~~. This function fit 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).

384 To test if the frequency of ants was different when foraging in the different EFN  
 385 morphological types we performed a  $\chi^2$  test. To test if between-group floristic similarity  
 386 ([Sorensen's floristic similarity index, Češka, 1966](#))-was higher than within group floristic  
 387 similarity we performed one-way ANOVA contrasting open and shaded habitats. [With this](#)  
 388 [analysis we further confirm that open and shaded habitats differ in their vegetation structure and](#)  
 389 [in turn, provide differential biotic and abiotic conditions for inhabitant species, presumably](#)  
 390 [affecting the resultant network structure of ant-plant interactions](#). To explore if a relation with ant  
 391 head length and species degree in the network (the number of plant species interacting with ants)  
 392 existed, we performed a Spearman rank correlation (Quinn & Keough, 2002).

393

## 394 Results

### 395 Network-level and fine-grain structure

396 Our ant-plant network consisted ~~of~~ 31 EFN-bearing plant species and 19 ant forager species  
 397 linked by 1302 quantitative interactions ([overall frequency of interactions](#)) derived from 157  
 398 species associations ([links among species](#)). The general topology shows a highly and  
 399 significantly nested network ( $NODF = 49.13$ ,  $NODF(Ce) = 34.93$ ,  $P(Ce) < 0.001$ ); although five  
 400 modules were detected ~~in~~ the modularity analysis (Barber's  $Q_B$ ) the network was not  
 401 significantly modular ( $M = 0.288$ ,  $P = 0.55$ ), thus no true compartments exist ~~at~~ [in](#) the network  
 402 (Fig. 1). Network-level indexes were: connectance = 0.267, dependence asymmetry = 0.669  
 403 (implying that plants depend more on ants than the opposite), niche overlap among ant species =  
 404 0.223, niche overlap among plant species = 0.425, and weighted nestedness = 0.554 (implying  
 405 [that is network still nested when considering the frequency of pair-wise interactions](#)). Four plant  
 406 species ([Fig. 1, Table 1](#)) and three ant species ([Fig. 1, Table 2](#)) constituted the central core of this  
 407 network, the remaining species were peripheral; plant core species were: *Cordia spinescens*,

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 Maybe:  
 implying that the network is still nested even when the frequency of  
 pair-wise interactions is taken into account

408 *Cedrela odorata*, *Callicarpa acuminata*, and *Crotalaria incana*, while ant core species were:  
409 *Camponotus planatus*, *Camponotus mucronatus*, and *Camponotus atriceps*.

410 Regarding to 'species strength' mMost plant species exhibited low strength values (below  
411 1), thus and therefore had littlehaving a modest\_relevance for\_to the ant community. However,  
412 some plant species, namely -*Cordia spinescens*, *Cedrela odorata*, *Callicarpa acuminata*, and  
413 *Turnera ulmifolia*, did havestand out with higher strength values (around 2), indicating their  
414 which are *Cordia spinescens*, *Cedrela odorata*, *Callicarpa acuminata*, and *Turnera ulmifolia*.  
415 These plant species are the most importance as EF\_nectar sources for ant foragers at a  
416 community level.

417 Species-level specialization values ( $d'$ , considered as a measure of selectiveness) for plant  
418 species were also generally low (around 0.1), and only those plant species with few (or-peculiar  
419 atypical)-associated ant species (ant species with interaction patterns atypical or different from  
420 the rest) showed values above 0.3. These findings are in accordance to the generalized, highly  
421 nested structure of this network.

422 In contrast with plants, some ant species had higher strength values. Seven ant species had  
423 values above 1, and two core ant species, *Camponotus planatus* and *C. mucronatus*, have strength  
424 values over 6, being thus very important visitors of\_to EFN-bearing plants.

425

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

427 Attributes of species are summarized as follows: plant species with circumscribed\_nectaries  
428 produced larger mean nectar volumes (2.06  $\mu$ l), than those plants with dispersed\_nectaries (0.53  
429  $\mu$ l). However, the numberamount of active glands in a plant individual may be higher for  
430 dispersed\_nectaries, since these glands are structurally simpler than those of circumscribed  
431 nectaries. The frequency of ants foraging on the different EFN morphological types (Díaz-

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Castelazo et al. 2005; Díaz-Castelazo et al. 2017) were different ( $\chi^2_8 = 1091.7$ ,  $P < 0.01$ ).

Moreover, the range of total associated ant species visiting plants considered within each type of nectary is different among EFN distribution types. Moreover, the range of visits to circumscribed nectaries (9-17 ant species) was between nine and 17 ant species, while it was between 20 and 23 ant species lower than the number of ant species visiting for dispersed nectaries (20-23 ant species). Thus, similar to gland morphology, EFN distribution in plant organs may influence visitation rates but mostly by attracting 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 considerably 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, either of “open or shaded habitats”.

The stress value of the multivariate Non-Metric Multidimensional Scaling (NMDS) obtained at the fourth run of the iterative process was the lowest (0.17), and being an acceptable value suggesting that the NMDS two-dimensional solution of the ordination suitably represented 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.

In Fig. 2, 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 zero, are those plant species with the highest relevance for the associated ant community. For ants, no generic or grouping trends are apparent in the NMDS

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**Commented [MS17]:** This isn't a result as such – and it's in the figure legend. No need to repeat here

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community analysis (Fig. 2). Axis NMDS2 divides plant species are primarily separated according to the main habitats where they occur (Fig. 2). The vegetation associations with differential structure (open vs. shaded habitats) were the variables that determined the variation in the frequency of ant-plant pairwise interactions mediated by EFNs ( $r^2 = 0.24$ ,  $P = 0.005$ ). On the upper part of the ordination, the plant species of within shaded habitats (low light) with modest light incidence follow a 'humidity' gradient from the most humid forests to the drier habitats: the higher values for NMDS2 show (in decreasing order) plants (and associated ants) from the MFE, followed TSF-W, and TSF-O (Fig. 2). At the bottom of the bi-plot NMDS2 the plants and ants occurring mostly in open vegetation types with high light incidence: from zero to the lowest values of NMDS2, the interacting species are arranged through TSF-Y, CDS, and PDV.

The results of fitting the biological/ecological variables in the NMDS ordination showed that vegetation associations with differential structure (open vs. shaded habitats) were the variables 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.

None of the variables of ant species (behavioral dominance, invasive status or head length) were significant to explain the network's fine-grained structure. 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,  $r_s = 0.565$ ,  $P < 0.05$ ). A trend at the NMDS ordination is that Further, the invasive (tramp) ant species at our study (*Solenopsis geminata*,

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*Wasmannia auropunctata*, *Tetramorium spinosum* and *Paratrechina longicornis*) separate from the rest of ant species ~~at the interaction display in the ordination~~, suggesting differential associations from the rest of the community (Fig. 2). However, when all ant attributes are simultaneously considered, they do not provide significant contribution to the variation in the observed ant-plant association pattern.

## Discussion

### Network-level and fine-grain network structure

Our studied network, ~~comprising 31 plant and 19 ant species with attached by 157 interaction links, has a general nested structure, thus is highly nested or is~~ asymmetric in its specialization patterns (see also Díaz-Castelazo et al., 2010; Díaz-Castelazo et al., 2013). ~~The network and~~ shows no modular structure, as occurs commonly in theoretical mutualistic networks, especially for facultative non-symbiotic interactions (Guimarães et al., 2007). ~~A relatively small core of A few~~ species with very high interaction frequencies exists within our network (eight plant and four ant species), referred to as ‘super-generalists’. Super-generalist species are fundamental ~~components for~~ the maintenance of convergence at the community-level within highly diversified mutualistic assemblages (Guimarães, Jordano & Thompson, 2011). In our study, super-generalist species may favor trait convergence: core ant species belong to the same functional group (Subordinate Camponotini) and share adaptations ~~for~~ foraging on plant-derived liquids sources such as EFnectar (Davidson, Cook & Snelling, 2004). Similarly, core plants species show mostly “dispersed” EFNs, a gland distribution that may favor a more diverse array of associated ant visitors.

In our study system, ~~the fact that~~ the plant ‘guild’ shows higher dependence asymmetry values than ants, implying that ~~at in~~ the studied community plants ‘depend’ more on ants as a

guild than the opposite. This 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. Three of the four plant species constituting the core of this network had high strength values (*Cordia spinescens*, *Cedrela odorata*, and *Callicarpa acuminata*), suggesting that 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; Díaz-Castelazo et al., 2017), nor gland distribution or ~~mere~~ plant abundance explained core composition and species strength of plant species. Instead, this pattern seems to emerge from degree and interaction frequencies, possibly ye driven by other higher-scale factors (i.e. habitat structure, species co-occurrence, abiotic variables, etc.).

The rest of the plant species showed very low strength values having ~~thus a modest~~ low importance 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 (with an atypical interaction pattern) 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 and for~~ facultative ant-plant interactions ~~such as the ones~~ mediated by extrafloral nectar, low specialization or selectiveness for each species (and the whole network) is the general trend (Bascompte et al., 2003; Vázquez & Aizen, 2004; Díaz-Castelazo et al., 2010).

In contrast with plants (which have very low species strength values), the ant species that constituting the core of this network (*Camponotus planatus*, *Camponotus mucronatus*, and

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528 *Camponotus atriceps*) had species strength values above 1; *C. planatus* and *C. mucronatus* have  
 529 strength values above 6, being thus remarkably important visitors of EFN-bearing plants. Species  
 530 belonging to this genus are frequent visitors of EFNs (Díaz-Castelazo et al., 2004; Díaz-  
 531 Castelazo et al., 2013) and solitary leaf foragers that cover high foliar areas. *Camponotus* species  
 532 have high ability ~~to~~ rapidly ~~up~~ take ~~up~~ nectar given their proventricular adaptations that  
 533 allow passive damming of sugary liquids, large crop capacities, and seeping canals to nourish the  
 534 midgut (Davidson, Cook & Snelling, 2004). Thus, this group of ants is highly adapted to forage  
 535 in nectar and sugary liquids. Therefore, it is unsurprising that ~~It is understandable that at in the~~  
 536 ~~our present~~ study *Camponotus* species have high degree (links with plant species), high strength  
 537 values, and low levels of specialization or selectiveness (d'), ~~given that these ants are~~  
 538 ~~physiologically adapted to forage in all available extrafloral nectar sources, not having any~~  
 539 ~~trophic restriction, they~~ These species tend to be generalist visitors of EFN-bearing plants,  
 540 although some other ecological aspects, ~~such as competitive~~ ~~on~~ ability of other ant species and  
 541 resource attractiveness (Dáttilo et al., 2014c) ~~may differentiate visitation patterns~~ of these core  
 542 ant species. ~~At~~ Within our studied community the core ant species are relevant to most plants  
 543 species at the network, ~~thus the plant species depending more of ant species~~, and evident nectar  
 544 consumption adaptations and deterrent behavior of core ants, suggest potential biotic defense at a  
 545 community scale.

547 Relative ~~attributes contributions of the attributes~~ to the assemblage of pair-wise  
 548 interactions  
 549 Major vegetation associations grouped according to habitat structure, were the only factors that  
 550 explained variations in pair-wise interactions or fine-grain structure of the network. Open and  
 551 shaded (i.e. forest) habitats at the study site seems to differ structurally in vegetation and ~~on~~ in

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**Commented [MS23]:** ¿? Plant species are more dependent on the ant?

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552 their abiotic conditions, which may in turn be important determinants of insect-plant interactions  
553 (López-Carretero et al., 2014). Although, some studies have discussed the possible effects of  
554 abiotic variables on ant-plant networks (Díaz-Castelazo et al., 2010; Rico-Gray & Oliveira, 2007  
555 (references therein); Rico-Gray et al., 2012, Sánchez-Galván et al., 2012), ours is the only one  
556 addressing habitat abiotic effects ~~jointly-together~~ with species-level biological attributes and  
557 neutral explanations (i.e. abundance) in a quantitative ant-plant network.

558 A mechanistic explanation for the differential ant-plant association pattern between open  
559 and shaded habitats (suggesting habitat complexity effects, Dáttilo et al., 2013b), may include  
560 light incidence (under light conditions, jasmonic acid-induced EFN secretion is higher than in  
561 dark conditions (Radhika et al., 2010), ‘attractiveness’ or nutritional value of extrafloral nectar  
562 secreted by ‘light demanding’ plant species compared to ‘shade tolerant’ ones, and the  
563 physiological tolerance of ants to high temperatures. Increased photosynthetic activity of plants in  
564 open light-rich habitats (Radhika et al., 2010) could result in higher carbohydrates availability in  
565 extrafloral nectar, and thus increased attractiveness to ants, or a higher density of EFN-bearing  
566 plant life forms (such as vines). EFN-bearing plants growing in sunlight obtain a measurable  
567 benefit from ant visitation, whereas the same plant species growing under shaded conditions has  
568 no such a benefit (e.g., Bentley, 1976; Frank & Fonseca, 2005). For some plant species, the size  
569 of EFNs and quantity of nectar secretion are higher under intense light conditions compared to  
570 low light conditions (Yamawo & Hada, 2010) and a similar trend is found for the ant abundance  
571 foraging on these glands (Rudgers & Gardener 2004, Yamawo & Hada, 2010). This effect of site  
572 conditions on EFN abundance and secretory activity could also exist in our study system, since  
573 vegetation types with canopy cover (shaded) versus open habitats do sustain different species  
574 abundances, floristic similarities (Díaz-Castelazo et al., 2004), and patterns of specific insect-  
575 plant interactions (López-Carretero et al., 2014).

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Among-habitat heterogeneity in vegetation structure (as well as seasonality) at our study

site is so prevalent (having a strong effect in animal-plant interactions as seen in Rico-Gray,

1993; Díaz-Castelazo et al., 2004; Sánchez-Galván et al., 2012; López-Carretero et al., 2014; and

Ramos-Robles, Andresen & Díaz-Castelazo, 2016); that it is clearly detected in the ant-plant

interaction pattern, in contrast to other studies where vegetation structure differences are not so

outstanding to have an effect in other ant-plant networks (Dáttilo et al., 2013b), with more/fewer

interactions occurring along a humidity gradient.... Further evidence of among-habitat

heterogeneity transcending to ant-plant network structure, is provided at in the present study by

the multivariate analysis, where the component explaining more variance in the lack of

independence among ant and plant species (NMDS1), displays habitats following a decreasing

humidity gradient, from MFE, followed by TSF-W and TSF-O, TSF-Y, CDS and PDV. Indeed,

open habitats at the study site, such as coastal dune scrub (CDS) and pioneer dune vegetation

(PDV), have the most extreme temperatures, solar radiation (Moreno-Casasola, 1982; Moreno-

Casasola & Travieso-Bello, 2006), and are subject to continual disturbance (López-Carretero et

al., 2014) because sand movement, strong winds, and abrasion (Pérez-Maqueo, 1995).

~~Our results showed that no n~~Neutral effects derived from variation in species abundances

~~aredid not structuring the studied~~ ant-plant network in our study. Abundance of EFN-bearing

plant species was considered ~~inat~~ our analysis ~~but~~; rendered ~~eding~~ no significant contribution to

explain the frequency of pairwise ant-plant interactions. Similar results were found in plant-

herbivore network study at the for another ecological network at the same study site such as a

plant-herbivore network (López-Carretero et al. 2016), where network parameters were not

influenced by plant cover (abundance) but by biological and seasonality aspects. AtIn our study,

Aalthough we did not directly explore the effect of ant abundance ~~was not included in order to~~

explore its effect in on network structure, we know from robust estimates of ant density (honey

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You've already presented the Results- just discuss

baits) at the same periods of time and vegetation types, that average ant density is higher in open habitats than in shaded ones (Díaz-Castelazo et al., 2004). In other studies of ant-plant interactions, the abundance of interacting species partially explain some features of network structure (Vázquez et al. 2007; Dáttilo et al., 2014a). However, Dáttilo et al. (2014a) show that although more abundant ant species interact with more plant species with EFNs ~~plant species~~, information on the difference in abundance among interacting species was insufficient to explain ant-plant network organization: nestedness was 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.

Other potentially mutualistic networks have shown that species abundance or temporal overlap ~~are far from do not~~ accurately predicting the frequency of pair-wise interactions, ~~leaving much unexplained variation~~ (Vázquez et al., 2009). Poisot et al. (2015) ~~highlight that interaction networks should benefit from a population-level approach given the fact that the same species may happen to interact differently when their local abundances or trait distribution changes, or when the environment affects either of these factors. These authors~~ outline several direct (abundance-based and trait-based) and indirect (biotic modifiers and indirect effects of co-occurrence) effects ~~to that may~~ account for interactions occurrence. Given that perspective, at the sampling intensity and duration of our ant-plant interaction survey (a biweekly two-year census that capture the high seasonality at the study site, reflecting that could reflect detailed temporal and spatial variation; see Díaz-Castelazo et al. 2004), neither the abundance-based nor the trait-based modifiers seems to be relevant enough to account for variation in pairwise ant-plant interactions, even if at other scales ant abundance could partially explain an overall network pattern (Dáttilo et al., 2014a). In contrast, an indirect effect given by habitat structure (biotic

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modifiers through co-occurrence, *sensu* Poissot et al., 2015) ~~explain~~ more thoroughly explains the quantitative interaction pattern ~~at the present in our~~ study.

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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 potential effect on ant foraging patterns at other sites or when within habitat information is considered** (Dáttilo et al. 2013a, 2014b). At our study site, besides the overwhelming evidence of seasonality and habitat heterogeneity ~~(and we did find an effect of habitat structure in ant-plant interactions within the network)~~, the high occurrence frequency of morphologically diverse EFNs at vegetation associations (Díaz-Castelazo et al., 2005) ~~that have a temporal activity (i.e. seasonality) (Díaz-Castelazo et al., 2004),~~ suggests phenotypic plasticity in plant strategies for biotic defense, as that showed for other anti-herbivory plant defenses at the study site (López-Carretero et al., 2016; López-Carretero et al., 2018), ~~information on the contribution to plant fitness of the EFN occurring among plant organs~~ could shed light on the optimal defence-value of EFN resources as an indirect defence (Holland, Chamberlain & Horn, 2009) mediated by ants, an issue not yet explored at a community-level.

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For ant ~~variables~~ attributes, 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 such as species degree, within a mutualistic network, ~~†This may occur because competition among ant species foraging at EFNs may vary with ant body size, contributing to the degree of species~~ Competition among ant species for EFN resources of plants may vary with ant body size, such as species degree (also see Chamberlain & Holland 2009). ~~These results suggest that larger ant species can forage over a greater area than~~

648 ~~small species, and thus interacting with more plant species.~~ In addition, it ~~For example, it has been~~  
649 shown that recruitment of ant foragers to a resource ~~is~~ negatively correlated with ant body size  
650 (LeBrun, 2005); ~~thereby contributing to the degree of ant species. For example, LeBrun (2005)~~  
651 ~~showed that recruitment of foraging ants to a resource is strongly and negatively correlated with~~  
652 ~~ant body size. As~~ ant body size increases, the number of recruiting foragers decreases, which  
653 can lead to a body size-driven competition hierarchy in which larger ant species visit more plant  
654 species.

655 Overall, ant behavioral dominance as a factor was not significant in explaining variations  
656 in the frequency of pair-wise interactions, possibly due to ~~the spectra of factors considered~~  
657 ~~simultaneously within the analysis, since the EFNs considered here include both~~ dispersed EFNs  
658 and circumscribed EFNs ~~being included; that they~~ could provide resources for both dominant and  
659 non-competitive ant species. However, ant invasive/tramp species at the study site (*Solenopsis*  
660 *geminata*, *Wasmannia auropunctata*, *Tetramorium spinosum* and *Paratrechina longicornis*)  
661 seems to have a slightly different pattern of interaction from the other species (separate from the  
662 rest of ant species at the interaction display), probably due to their ability to access new habitats  
663 or food resources (Ness & Bronstein, 2004; Lach & Hooper-Bui, 2010).

664 ~~This seems in accordance~~ makes sense in to such a human altered ecosystem as La  
665 Mancha, that seems to rapidly reflect ant invasions. At smaller time scales, at the same At our  
666 study site, ant invasiveness does not seem to alter the core structure of the network (Falcão et al.,  
667 2017), despite ~~of~~ other possible functional effects in the community. Effects of invasive ants in  
668 biotic communities and their resultant interaction networks are ~~just about~~ still to be explored.

## 670 Conclusions

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671 Our extrafloral-nectary mediated ant-plant network ~~result was~~ highly nested, non-  
 672 modular, showed high species strength for core species, low specialization or selectiveness, and  
 673 higher dependence of plants on ants. ~~This is not surprising for ; all (in accordance to a~~  
 674 ~~facultative mutualism scenario, mainly considering~~ given that the core ant species at this network  
 675 ~~are well known as good plant-defenders in general~~ (Oliveira et al., 1999; Cuautele & Rico-Gray,  
 676 2003; Dáttilo et al., 2014c)). ~~At our studied community, core ant species are relevant to most~~  
 677 ~~plants species at the network, thus the plant species depending more of ant species, and the~~  
 678 ~~adaptations of nectar consumption and deterrent behavior of core ants, suggest potential biotic~~  
 679 ~~defense at a community scale.~~

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680 When simultaneously exploring plants, ants, and habitat attributes on a network-level and  
 681 fine-grain structure, the only factor that significantly affected the pair-wise interactions ~~was~~  
 682 habitat heterogeneity in vegetation structure (and distribution of EFN-bearing plant species). At  
 683 our study site, this heterogeneity is so strong that is clearly detected in the ant-plant interaction  
 684 network pattern, both ~~in~~ network topology and ~~in~~ the fine-grain network structure provided by  
 685 the frequency of pair-wise interactions. ~~This provides further evidence of abiotic factors influence~~  
 686 ~~in facultative mutualism and biotic plant defense,; being thus, further evidence of abiotic factor~~  
 687 ~~influence in facultative mutualism and biotic plant defense.~~

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688 Habitat heterogeneity in vegetation structure and distribution of EFN-bearing plant  
 689 species depicts ~~plasticity variability~~ in plant strategies for biotic anti-herbivory defense: in our  
 690 study the plant species at shaded habitats more frequently have dispersed EFN ~~snectaries~~, while  
 691 plants at open habitats more frequently have circumscribed EFN ~~snectaries~~. The latter EFNs are  
 692 more structurally complex glands (i.e. elevated or pit nectaries) ~~and are~~ more effectively  
 693 protected from nectar evaporation (Koptur, 1992; Nepi, 2007), which is ~~required valuable~~ at these  
 694 open, ~~insolated~~, high-temperature sites.

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695 Non-neutral effects were detected at ant-plant interacting community, since EFN-bearing  
696 plant abundance per se had no effects in the ant-plant interaction pattern. As we showed before,  
697 more ecological/biological factors, such as habitat/vegetation structure, could affect network  
698 structure (CITA). Thus, possible convergence effects of interacting species at open vs. shaded  
699 habitats may be occurring presided by supergeneralist species and consequently the possibility of  
700 cascading coevolutionary events taking place. This may deserve further study considering  
701 ecological/abiotic and coevolutionary contexts (Guimarães et al. 2017) for mutualistic interaction  
702 networks.

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#### 704 Acknowledgements

705 We wish to acknowledge Mariana Cuautle, Rosa Linda Robles and Gloria Castelazo for their  
706 assistance during specific fieldwork. Fernando Ortega helped with the characterization of  
707 extrafloral nectaries. Paulo R. Guimarães and Pedro Jordano made suggestions that improved this  
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957 **Table 1.** EFN-bearing plant species within the network and its attributes. Plant species code as follows:  
 958 CorSpi= *Cordia spinescens*, TurUlm= *Turnera ulmifolia*, CrotIn= *Crotalaria indica*, CedOdo= *Cedrela*  
 959 *odorata*, CallAc= *Callicarpa acuminata*, CaeCri= *Caesalpinia crista*, BidPil= *Bidens pilosa*, CanRos=  
 960 *Canavalia rosea*, CalCae= *Calopogonium caeruleum*, TerCat= *Terminalia catappa*, SenOcc= *Senna*  
 961 *occidentalis*, OpuStri= *Opuntia stricta*, HibTil= *Hibiscus tiliaceus*, AmphPa= *Amphilophium*  
 962 *paniculatum*, IpoPes= *Ipomoea pescaprae*, ConEre= *Conocarpus erectus*, FicObt= *Ficus obtusifolia*,  
 963 CorGra= *Cornutia grandiflora*, MacAtr= *Macroptilium atropurpureum*, CisRho= *Cissus rhombifolia*,  
 964 IpoSp= *Ipomoea sp.*, ManHym= *Mansoa hymenaea*, TabRos= *Tabebuia rosea*, AcaMac= *Acacia*  
 965 *macracantha*, TriHav= *Trichilia havanensis*, AruDon= *Arundo donax*, PetVol= *Petrea volubilis*,  
 966 ChaCha= *Chamaecrista chamaecristoides*, IreCel= *Iresine celosia*, CorDen= *Cordia dentata*, BunLin=  
 967 *Bunchosia lindeliana*. Plant attributes considered also in Figure 2 are: EFN= Distribution of extrafloral  
 968 nectaries within a plant species ('C' are circumscribed glands and 'D' are disperse glands), Habitat=  
 969 Distribution of plant species between habitats with contrasting vegetation structure ('S' is shaded  
 970 vegetation and 'O' is open vegetation). Abundance (% cover) = Percent cover of EFN-bearing plant  
 971 species.  
 972

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

<b>CalCae</b>	C	O	16.85
<b>TerCat</b>	C	S	0.35
<b>SenOcc</b>	C	S	3.717
<b>OpuStri</b>	D	O	64.35
<b>HibTill</b>	C	O	2.4
<b>AmphPa</b>	D	O	17.55
<b>IpoPes</b>	C	O	49.1
<b>ConEre</b>	C	S	16.383
<b>FicObt</b>	C	S	8.15
<b>CorGra</b>	D	O	2.5
<b>MacAtr</b>	C	O	16.3
<b>CisRho</b>	C	O	3.55
<b>IpoSp.</b>	C	S	12.167
<b>ManHym</b>	C	S	16.3
<b>TabRos</b>	D	S	6.66
<b>AcaMac</b>	C	B	2.75
<b>TriHav</b>	C	S	28.33
<b>AruDon</b>	C	O	151.66
<b>PetVol</b>	D	O	74.1
<b>ChaCha</b>	C	O	32.4
<b>IreCel</b>	C	O	16.55
<b>CorDen</b>	D	S	3.615
<b>BunLin</b>	C	S	1.7

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**Table 2.** 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 spinozum*, 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 (from the most dominant to the least) are: A= Dominant Dolichoderine, B= Specialized Predators, C= Generalized Myrmicine, D= Subordinate Camponotini, E= Hot Climate Specialist, F= Opportunistic; Head length= length (mm) from head apex to anterior clypeal margin of species (minor worker).

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Ant species	Invasive status	Dominance hierarchy	Head length
<b>CamPla</b>	NO	D	1.198
<b>CamMu</b>	NO	D	1.418
<b>CamAt</b>	NO	D	1.946
<b>AztSp</b>	NO	E	1.471
<b>ParLo</b>	INV	C	0.638
<b>TetSpi</b>	INV	D	0.968
<b>CepMin</b>	NO	C	1.155
<b>DorBi</b>	NO	C	0.973
<b>PseGra</b>	NO	B	1.738
<b>MonCy</b>	NO	D	0.482

<b>CamHi</b>	NO	D	1.076
<b>PachVi</b>	NO	B	2.88
<b>ForAna</b>	NO	E	0.631
<b>CreBre</b>	NO	D	1.031
<b>PheSp</b>	NO	E	0.553
<b>SolGe</b>	INV	D	0.684
<b>WasAu</b>	INV	D	0.479
<b>PseEje</b>	NO	B	0.8

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1006 **FIGURE LEGENDS**

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1008 **Figure 1.** Quantitative mutualistic networks between EFN-bearing plants (lower trophic level,  
1009 green nodes) and ant visitor species (higher trophic level, red nodes). Blue-colored nodes depict  
1010 species constituting the core of the network. Species codes as in Tables 1 and 2.

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1012 **Figure 2.** Ordination of NMDS representing the assemblage of interactions given the ant-plant  
1013 distances (Bray-Curtis) at the network: ant species in red, plant species in black, codes for species  
1014 names and attributes as in Table 1. *Stress* = 0.17 (fourth iteration) indicates a good two-  
1015 dimensional solution of the ordination suitably representing ant-plant assemblage dissimilarity.

1016 This configuration having as well also has very low residuals (*max res* = 0.0004) indicating a  
1017 good concordance between the calculated dissimilarities and the distances among objects. ~~Distant~~  
1018 Non-overlapping ellipses (i.e. orange and green) circle the attribute (factor) that significantly  
1019 explained ( $r^2=0.24$ ,  $P = 0.005$ ) the pairwise interaction pattern (habitat types).

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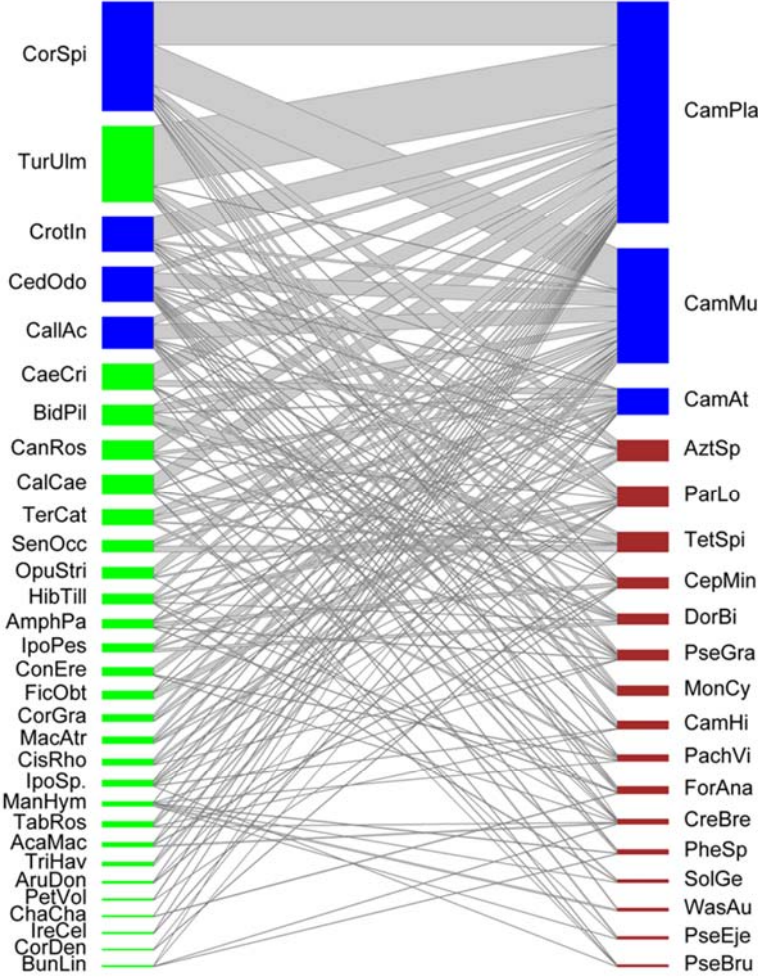
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**Commented [MS40]:** rather than having ant and plant names on nMDS - which are difficult to read – could you better explain the factors and habitat types show on the nMDS. Its not very self-explanatory at the momento.

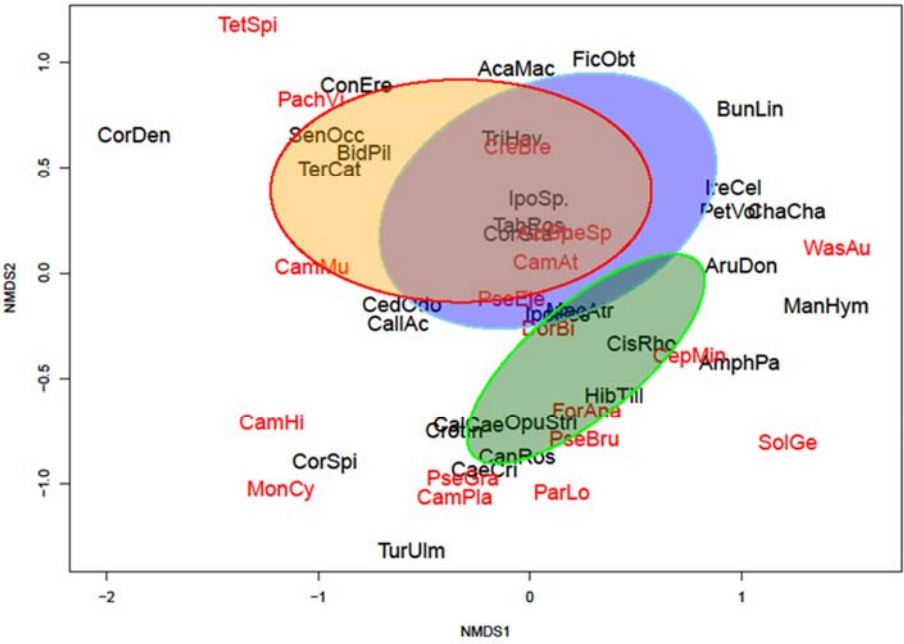
1032    **Figure 1.**



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1035 Figure 2.



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