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Soil and vegetation features determine the nested pattern of ant–plant networks in a tropical rainforest

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Abstract. 1. Recently, several studies have focused on structural properties of ant–plant networks. However, little is known about the role of abiotic factors on these networks.

2. As a result of different abiotic factors that can affect the patterns of ant–plant interactions, it was tested whether soil pH and canopy cover contribute to variation in the nestedness of mutualistic (plants with extrafloral nectar–EFN) and neutral (plants without EFN) ant–plant networks.

3. It was shown that only mutualistic networks were affected by soil pH. It was suggested that this may occur because the variation in soil pH directly influences the secreted nectar, and as there is a preference for nectar composition by ants, this could change the patterns of interaction in mutualistic networks. As prey availability is possibly the main factor influencing ants' presence on plants without EFN, soil pH should have little or no influence on the patterns of interaction in neutral networks.

4. On the other hand, nestedness was not affected by canopy cover in mutualistic and neutral networks. In spite of that canopy cover (light availability) is directly related to the amount of nectar secreted, the volume of nectar may not be important for the structure of the networks. However, canopy cover varied little in this study site. This small variation could not be enough to change the nested pattern in mutualistic and neutral networks.

5. In short, the present results show that the abiotic factors that affect the availability and quality of food resources may have important effects on the structure of trophic interactions in non-symbiotic ant–plant networks.

Key words. Abiotic factors, ant–plant interactions, Brazilian Amazon, ecological networks, nestedness

Introduction

Many species of plants in the tropics have extrafloral nectaries (EFN) (Elias, 1983; Koptur *et al*., 1998; Rico–Gray & Oliveira, 2007) which secrete a liquid rich in carbohydrates and amino acids (Baker *et al*., 1978; Koptur *et al*., 1998; Rico-Gray & Oliveira, 2007). This liquid attracts ants that, in exchange for food, protect the host plant against herbivores (Horvitz & Schemske, 1984; Del-Claro *et al*., 1996; Oliveira *et al*., 1999; Rico-Gray & Oliveira, 2007). However, there is a large variation in EFN quality, particularly among sites, and different abiotic factors can change the quantity and quality of the nectar secreted by plants in a community of EFN-bearing plants (Heil *et al*., 2000; Díaz-Castelazo *et al*., 2004; Herrera *et al*., 2006; Rico-Gray & Oliveira, 2007). Thus, ants do show preference for nectar with higher concentrations of carbohydrates and amino acids (Lanza & Krauss, 1984; Blüthgen & Fiedler, 2004a,2004b; Rico-Gray & Oliveira, 2007).

Soil features have been suggested as one of the main factors affecting nectar composition (Campbell & Halama, 1993;

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Gardener & Gillman, 2001; Heil *et al*., 2001; Burkle & Irwin, 2008; Farkas *et al*., 2012). Some previous studies have shown that the soil nutrients directly influence carbohydrate and amino acid nectar concentrations (Gardener & Gillman, 2001; Mevi-Schütz *et al*., 2003; Burkle & Irwin, 2008; Baude *et al*., 2011). Nectar production by plants located in environments with soil close to a neutral pH tends to have nectar with higher concentrations of sugars and amino acids (Gardener & Gillman, 2001; Burkle & Irwin, 2008; Yao *et al*., 2009). This mainly occurs because soil characteristics affect the energy allocated for growth and reproduction, resulting in an increase in plant fitness and productivity (Sperens, 1997; Monaco *et al*., 2003). Moreover, environments with higher nutrient availability and microbial activity tend to have higher values of soil pH (Ekenler & Tabatabai, 2003; Yao *et al*., 2009). Therefore, it is expected that soil pH will also influence nectar quality.

Additionally, the amount of nectar secreted by plants of tropical rainforest understory is influenced by the light availability (Szabo, 1980; Kersch & Fonseca, 2005). In dense tropical forests, less than 2% of solar radiation incidence on the forest canopy reaches the understory (Chazdon & Fetcher, 1984; Oberbauer *et al*., 1988; Canham *et al*., 1990). Thus, as a result of the importance of light in the photosynthetic and other metabolic processes of plants, light availability can also affect the amount of the nectar secreted (Szabo, 1980; Kersch & Fonseca, 2005; Radhika *et al*., 2010). EFN plants inserted in environments with high luminosity tend to increase the amount of nectar secreted, mainly because nectar is a carbon-based defence derived from photosynthesis (Radhika *et al*., 2010; Yamawo & Hada, 2010). So, as the amount and quality of EFN secreted by plants in a community can vary according to local ecosystem features, as soil pH or canopy cover, the trophic interactions between EFN and their visitors can also change (Frazee & Marquis, 1994; Kersch & Fonseca, 2005; Muñoz *et al*., 2005; Burkle & Irwin, 2010; Cardoza *et al*., 2012).

Within a natural environment different species can interact with each other and generate complex ecological networks of interactions (Lewinsohn *et al*., 2006). Focused on the structure of these ecological networks, some studies have recently shown that mutualistic networks between ants and EFN-plants are highly nested (Guimarães *et al*., 2006; Chamberlain *et al*., 2010; Díaz-Castelazo *et al*., 2010; Sugiura, 2010; Dáttilo, 2012; Rico-Gray *et al*., 2012). This shows that species with few links interact with a subset of interactive species with several interactions (Bascompte *et al*., 2003; Thompson, 2005). Biologically, nestedness describes the organisation of niche breadth of a biological community, in which more nested networks tend to have the highest niche overlap (Bastolla *et al*., 2009; Blüthgen, 2010). In spite of the importance of nectar for ant colony fitness (Byk & Del-Claro, 2011), little is known about how nectar composition can affect ant–plant networks. Only one previous study has been conducted showing that the number of nectaries is not an important factor contributing to the nested pattern in ant–plant networks (Chamberlain *et al*., 2010). However, it is not known how the factors that affect the amount and quality of nectar can structure ant–plant networks.

Furthermore, ants can also randomly forage for prey on plants without EFNs or without honeydew secreted by homopterous insects, using the plant only as foraging substrate (Andersen, 1990; Blüthgen *et al*., 2000). These interactions are different from agonistic interactions involving leaf-cutting ants and plants, and therefore, the presence of ants on these plants reflects the spatial abundance of these species in the vegetation without the aggregation caused by the resource (Blüthgen *et al*., 2000; Yamamoto, & Del-Claro, 2008). Some previous studies have suggested that, within a biological community, the difference in species abundance can generate nested patterns (Fischer & Lindenmayer, 2002; Lewinsohn *et al*., 2006; Blüthgen, 2010). It is expected that owing to non-determinist and neutral foraging on plants without EFN, most abundant ant species will tend to find individuals of other abundant plant species more often than individuals of rare species, generating the nested pattern.

Here we hypothesised that soil pH and canopy cover may directly influence the amount and quality of nectar, both factors can therefore affect nestedness in ant–plant mutualistic networks. We also postulate that owing to non-deterministic foraging ants in search of prey on plants without EFNs, the soil pH and canopy cover does not affect nestedness in these neutral networks. Therefore, we expected that the factors that affect the availability of prey on plants are possibly the main factors determining the neutral networks. We studied only nestedness as a dependent variable, once small changes in the patterns of ant–plant interaction is reflected in this network descriptor (Rico-Gray *et al*., 2012).

Materials and methods

Study area

We conducted this study in a non-disturbed dense *terra-firme* rainforest within the southern Brazilian Amazon (9°48′S and 58°15′W, elev. 254 m), municipality of Cotriguaçu, north of Mato Grosso State, Brazil. *Terra-firme* forests are tropical rain forests inserted in environments that do not suffer the influence of periodic and annual cycles of flooding of the great rivers of Amazon. The reserve area covers 7000 ha of continuous forest, surrounded by a much larger area also of continuous forest. The climate is wet tropical (Am) with annual means of 24 °C temperature, 85% humidity, and 2300 mm precipitation (Köppen classification). The region has two distinct seasons, a November–April rainy season and a May–October dry season. Canopy trees range 30–40 m high, with some emergent trees reaching 50 m. The understory is relatively open, with a high frequency of *Orbignya phalerata* Mart. (Arecaceae) (Camargo *et al*., 2010; Dáttilo *et al*., 2012).

Experimental design and abiotic factors

Ant–plant interactions were sampled, and soil and vegetation features in a module managed by the Brazilian Research Program in Biodiversity (PPBio) (http://ppbio.inpa.gov.br). The module consists of two parallel east–west 5-km trails, 1 km apart. Along each trail, we marked one sampling plot of 250 m × 25 m (6250 m^2) every km, totaling 12 sampling points.

The central trail in each plot was located to minimise variations of altitude and soil features, increasing the precision of estimates for predictor variables (soil pH and canopy cover) (Magnusson *et al*., 2005).

To measure soil pH, we collected six soil samples (50-m equidistant points) in the centre of each 12 sampling points to a depth of 5 cm. We obtained the pH value for each sample from a solution of dry ground soil with distilled water with a pH meter, according to the protocol of the Brazilian Agricultural Research Corporation (Embrapa-Solos, 1999). In addition, along the centre of each plot, we also measured the canopy cover at six equidistant points (50 m) using a concave densiometer. At each point we made four measures according to geographical references (north, south, east, and west). The value representing the canopy cover of each plot is the average of the measurements of the geographical references and subsequently the average of six points.

Data collection of ant–plant interactions

We recorded ant–plant interactions in December 2010 and January 2011, always between 09.00 and 15.00 hours. At each of the 12 sampling points, we collected ants foraging on all EFN–plants that were accessible to the collector (from 0.5 to 3 m high). We recorded all occurrences of ants collecting liquids on EFN of each plant. For each EFN-bearing plant where ants were collected, we selected a plant without EFNs with a similar structure (height, width, and number of branches) nearby (neutral networks). No plants with Hemiptera or other visible liquid sources were included when sampling plants without EFNs. We did not use the agonistic interactions involving leaf-cutting ants and plants. In plants without EFNs, resources cannot be predicted, and ants forage randomly, using the plant only as substrate (Blüthgen *et al*., 2000; Yamamoto, & Del-Claro, 2008). Therefore, our neutral networks are possibly generated by differences in species abundance. All selected plants were at least 10 m apart to minimise the possibility of collecting the same ant colony foraging on different plants.

Nestedness and statistical analyses

To estimate nestedness of the networks, we used the *NODF* index (Nestedness Overlap and Decreasing Fill) using ANINHADO software (Guimarães & Guimarães, 2006). To assess if the nestedness value observed was higher than expected by random interaction patterns, we tested the nestedness of each network with 1000 networks generated by Null Model II (CE). In this null model, the probability of an interaction occurring is proportional to the level of degree (mean number of links or interactions) of plant and ant species (Bascompte *et al*., 2003). To test the difference of nestedness between ecological networks of ants and plants with and without EFNs, we used a paired *t*-test (paired per plot).

In order to evaluate the statistical variation of our explanatory variables (pH and canopy cover) around their own mean, we used a Student's *t*-test for one sample. To test how different factors affect the nested pattern in ant–plant networks, we used general linear models (GLM). We used nestedness as dependent variable, network type (mutualistic or neutral), soil pH and canopy cover and interactions between network type and soil pH and canopy cover as a fixed factors, and network size as a cofactor. In the cases that the interaction was significant, we used *a posteriori* simple regressions to best describe the differences on tendencies between neutral and mutualistic networks. Note that we only used GLM because both soil pH and canopy cover were not correlated factors (Pearson's correlation: $r = 0.11$, $P = 0.28$). We performed all statistical analyses using R-software version 2.13.1 (R Development Core Team, 2012).

Results

We recorded 238 plant species (72 with EFNs) and 149 ant species. The mean number of plant species per sampling plot on mutualistic networks was lower (mean ± SD: 21.4 ± 3.77) than plant species on neutral networks (27.2 ± 3.97, $t = -3.093$, d.f. = 11, $P = 0.011$). However, the mean number of ant species on mutualistic networks per sampling point (23.2 ± 5.85) did not differ from the number on neutral networks (23.3 ± 4.11) ($t = -0.0647$, d.f. = 11, $P = 0.949$). In addition, soil pH and canopy cover did not influence ant or plant richness in both mutualistic and neutral ant–plant networks (All P-value > 0.05) (Table 1).

Both mutualistic and neutral ant–plant networks show nested patterns of interactions (all $P < 0.05$). However, average values of nestedness are different between mutualistic and neutral networks (GLM: $F = 3.625$, $P = 0.04$). NODF values were higher in mutualistic networks (mean ± SD: 34.71 ± 10.21) than in neutral networks (15.76 ± 3.34). First, we observed that both explanatory variables varied significantly (*t*-test; soil pH: $P = 0.03$; and canopy cover: $P = 0.04$), indicating that these variables had a sufficient magnitude to affect the nestedness of networks. Posteriorly, we observed that small changes on soil pH values can exert related changes on the NODF values of ant–plant networks (GLM: $F = 4.371$, $P = 0.04$). However, there is an interaction between network type (mutualistic and neutral) and soil pH (GLM: $F = 8.879$, $P = 0.01$). In mutualistic networks, an increase in soil pH is positively related to NODF values ($r^2 = 0.37$; $F = 5.912$; $P = 0.03$). But, this tendency was not observed on neutral networks ($r^2 = 0.131$; $F = 1.506$; $P = 0.248$) (Fig. 1a). Moreover, nestedness was not affected by canopy cover in mutualistic or neutral networks (GLM: mutualistic: $F = 0.119$; $P = 0.738$, neutral: $F = 0.196$; $P = 0.668$) (Table 1) (Fig. 1b). The network size did not affect the nestedness of networks (GLM: $F = 0.041$, $P = 0.84$). Additionally, the 24 networks studied (both mutualistic and neutral) tended to not have groups or modules of species of one trophic level that interact more frequently with a group of species of another trophic level (Fig. 2a,b).

Discussion

Our results suggest that, in the Brazilian Amazonian rainforest, different abiotic factors can affect the nested pattern of

Table 1. Values of soil pH, canopy cover (%), ant and plant richness, and nestedness (NODF metric) from mutualistic and neutral ant–plant networks in 12 sampling points in the Brazilian Amazon (see text for more information).

			Mutualistic networks			Neutral networks		
Plot	pH	Canopy (%)	Ants	Plants	NODF	Ants	Plants	NODF
1	4.40	39.90	25	28	18.33	21	31	15.70
2	4.10	41.60	16	22	38.92	13	29	22.15
3	4.13	41.18	31	19	28.26	26	32	13.43
4	4.33	43.47	27	16	39.00	27	30	15.52
5	4.06	41.18	28	21	27.23	23	28	12.06
6	4.36	40.35	30	23	33.92	27	22	15.91
7	4.23	41.18	25	22	29.89	25	26	14.83
8	4.36	40.35	18	28	37.41	21	23	20.91
9	4.40	40.14	20	17	44.50	23	33	13.20
10	4.20	41.18	14	21	21.64	20	22	17.99
11	4.86	40.35	17	18	53.98	26	27	10.94
12	4.33	42.01	27	22	43.43	27	23	16.44

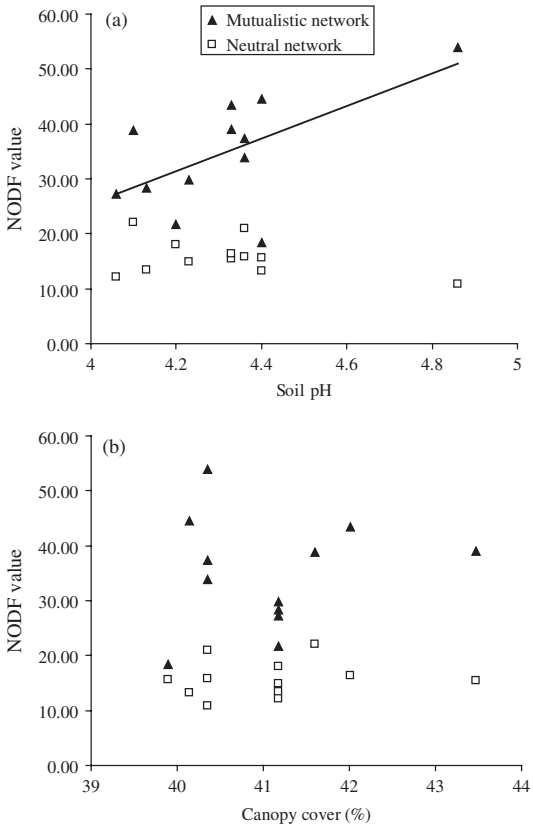

Fig. 1. Regressions between (a) soil pH and nestedness (NODF) of mutualistic ($r = 0.37$; $P = 0.03$) and neutral ant–plant networks ($r^2 = 0.01$; $P = 0.248$), and (b) canopy cover and nestedness of mutualistic ($r^2 = 0.01$; $P = 0.738$) and neutral ($r^2 = 0.01$; $P = 0.668$) ant–plant networks.

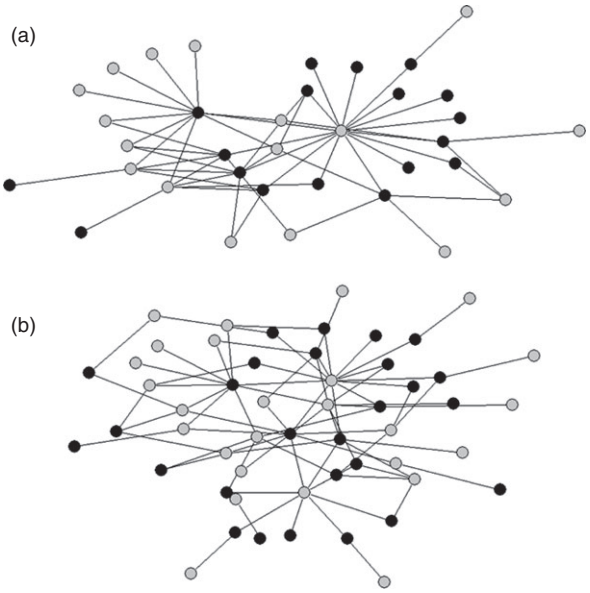

Fig. 2. Graphical representation of one (a) mutualistic network and one (b) neutral network out of the 24 ant–plant networks studied in a tropical rainforest in the southern Brazilian Amazon (December 2010 to January 2011). Each circle represents one ant or plant species, which are represented by grey and black colours, respectively. Lines represent ant–plant interactions. The ant–plant networks are represented as an energy two-mode graph (Kamada–Kawai free method) obtained using the program Pajek.

interactions independently of ant–plant network size. Local features of soil differentially influence the patterns of interactions in mutualistic and neutral ant–plant networks possibly because soil pH differently influences the ants that feed on EFNs compared with ants that used the plants only as substrate. Soil pH was an important factor for the nested pattern only for the mutualistic networks. In addition, we did not find an association between canopy cover and nestedness in both mutualistic and neutral ant–plant networks. According to Rico-Gray *et al*. (2012), abiotic factors probably influence the availability of resources on plants, which in turn affect the number of interactions and thus the nested pattern of ant–plant networks. Vegetation is one of the main factors affecting the

structure of ant communities in an environment (Andersen, 1990; Retana & Cerdá, 2000; Wang & Strazanac, 2001; Lassau & Hochuli, 2004), therefore, factors that influence vegetation features can be an important mechanism determining the structure of ant–plant networks.

Although soil pH did not influence ant and plant richness, this soil feature significantly altered nestedness in mutualistic networks. The present results suggest that soils with a pH closer to neutral generate highly nested mutualistic networks. This possibly occurs because plants growing on soils with a higher neutral pH and nutrient availability tend to have nectar with higher concentrations of sugars and amino acids (Gardener & Gillman, 2001; Burkle & Irwin, 2008; Yao *et al*., 2009). This change in the nectar quality could influence the patterns of ant–plant interactions and reflect on the nestedness of networks. Furthermore, although the ants strongly compete for better quality nectar (Dreisig, 2000; Blüthgen & Fiedler, 2004a), in environments with higher neutral pH, it is possible that all plants tend to have better resources, and therefore we should expect lower competition for resources. Thus, as nestedness reflects the degree of generalisation of a network (Bascompte *et al*., 2003), minimising competition and increasing the number of coexisting species (Bastolla *et al*., 2009), mutualistic networks inserted in highly neutral pH environments would then be highly nested. On the contrary, environments where soil pH is more acidic, it is possible that a few plant species could produce high nectar quality, generating more competition for resources and less nestedness in these sampling points.

Although some plants secrete larger amounts of nectar in environments with higher light availability (Szabo, 1980; Kersch & Fonseca, 2005), we found no effect of canopy cover on the nestedness in mutualistic networks. Two main factors not mutually exclusive could explain this pattern. First, the amount of secreted nectar can not be an important factor affecting the structure of mutualistic networks. Some previous studies have shown that ants may prefer more concentrated nectar instead of large amounts of nectar (Blüthgen & Fiedler, 2004a,2004b; Lach, 2005). It is possible that the presence of ants on plants with EFN is not determined by the amount of nectar available, but by nectar quality. Additionally, as there was little variation in canopy cover in our study area, this could not have influenced the amount of nectar secreted in environments with 'higher light availability'.

In summary, our results show that soil pH and canopy cover can differently structure mutualistic and neutral ant–plant networks. It is possible that nectar quality is the main factor that influences the nested pattern in mutualistic ant–plant networks. We also show that soil pH and canopy cover do not influence nestedness in neutral networks. In fact, ants forage randomly for prey on plants without EFN, using the plant only as a substrate (Andersen, 1990; Blüthgen *et al*., 2000). We suggest that prey availability on plants may be the main factor structuring neutral ant–plant networks. Thus, it is possible that variations in soil pH and canopy cover could have little effect on prey availability and not reflect on nestedness of neutral networks. Finally, different biotic and abiotic factors may influence the patterns of ant–plant interactions in tropical environments, e.g. foraging periods, competitive interactions, and variation in daily in resource availability (Rico-Gray & Oliveira, 2007). Therefore, a fundamental next step is to understand all the main mechanisms and factors that shape the structure of ecological networks involving ants and plants.

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