Spatial structure of ant–plant mutualistic networks

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The structure of mutualistic networks provides insights into ecological and coevolutionary dynamics of interacting species. However, the spatial effect has only recently been incorporated as a factor structuring mutualistic networks. In this study, we evaluated how the topological structure and species turnover of ant–plant mutualistic networks vary over a spatial gradient. We showed that although the ant and plant composition of networks changed over space, the central core of generalist species and the structure of networks remained unaltered on a geographic distance of up to 5099 m in the southern Brazilian Amazon. This finding indicates that independently of variation in local and landscape environmental factors, the nonrandom pattern organization of these interacting assemblages do not change. Finally, we suggest that a stable core can increase the potential for coevolutionary convergence of traits among species from both sides of the interaction within the community. These findings contribute to our understanding of the maintenance of biodiversity and coevolutionary processes.

The study of mutualistic networks has provided important insights into the mechanisms that contribute to the structural organization of plant–animal interactions (Rezende et al. 2007, Morales and Vázquez 2008, Vázquez et al. 2009). Using measures of graph theory to characterize the network topology, several studies have found non-random patterns of interaction in a wide range of ecological interactions (Bascompte et al. 2003, Lewinsohn et al. 2006, Guimarães et al. 2007, Vázquez et al. 2009). Among their main features, some of these networks are highly nested and exhibit an asymmetrical pattern of interactions (Lewinsohn et al. 2006, Guimarães et al. 2007). This indicates that species with few interactions are a subset of highly connected species (Bascompte et al. 2003, Thompson 2005). Moreover, generalist species are more important for the stability and functioning of the system as a whole than are the peripheral species, mainly because the central core of species interacts with virtually all species of the network (Bascompte et al. 2003, Guimarães et al. 2011).

Recently, some theoretical and empirical studies have shown that when new species are introduced into a network, they can influence the ecological dynamics of the entire network (Olesen et al. 2002, Memmott et al. 2007, Aizen et al. 2008, Díaz-Castelazo et al. 2010). These studies have focused on evaluating how the entry of invasive alien species affects the structural organization of species interactions. However, because the geographical distributions and abundances of all interacting species of a community rarely coincide, the associations among them can also change over space (Thompson

2005). Therefore, in order to understand the consequences of spatial variation in mutualistic networks, it is essential to determine how space modulates the dynamics of interacting species (Olesen and Jordano 2002, Burkle and Alarcón 2011). A next step in the analysis of species networks is to understand how species turnover affect the organization of interacting assemblages.

We used the mutualistic interaction between ants and plants with extrafloral nectaries (EFNs) to evaluate how the structure of mutualistic networks varies through space. In ant–plant mutualistic networks plants produce nutritious liquid for ants, which respond by defending the plants against herbivores (Rico-Gray and Oliveira 2007). However, different factors can change the nature of ant–plant interactions, such as competition (Blüthgen and Fiedler 2004), abundance and quality of resources (Rico-Gray and Oliveira 2007), seasonality of nectar production (Díaz-Castelazo et al. 2004), and other biotic and abiotic factors (Rico-Gray et al. 2012, Dáttilo et al. 2013), and the spatial distributions of ants on plants can be affected by all these factors (Barton 1986, Heil et al. 2000, Apple and Feener 2001). In tropical forests, many plant species are spatially aggregated (Newbery et al. 1986, Condit et al. 2000, Köhler et al. 2000), and ant workers forage and disperse only on small spatial scales (Fourcassié et al. 2003). Therefore, is expected that the compositional similarity among plant communities should decrease as the distance between points increases, due to the limited dispersal of organisms and environmental gradients (Chave and Leigh 2002, Gilbert and Lechowicz 2004).

Here we hypothesisized that the degree of high spatial aggregation of plants in tropical regions and the low mobility of ants would produce a mosaic of interactions with different partners over a relatively small geographic space, and this mosaic could generate differences in the structure of these networks (Thompson 2005, Morales and Vázquez 2008, Burkle and Alarcón 2011). In order to test this hypothesis, we examined 12 ant–plant mutualistic networks in the southern Brazilian Amazon, and analyzed their network topology. Subsequently, we calculated the dissimilarity of network topology over the geographic distance among sampling plots, in order to examine whether: 1) species turnover affects the topological structure of ant–plant mutualistic networks, and 2) the core of generalist species remains stable at the geographic scale studied.

Material and methods

Study area

We conducted this study on São Nicolau Farm (9°48′S, 58°15′W), located in the municipality of Cotriguaçu, northern Mato Grosso State, Brazil. According to the Köppen classification, the climate is tropical humid (Am). Mean annual temperature is 24°C, mean annual relative humidity is 85%, and mean annual rainfall ranges from 2000–2300 mm (Dáttilo et al. 2012). Moreover, in this region there are two well-defined seasons, a rainy season from November to April, and a dry season from May to October. The study area is a dense rainforest in the southern Brazilian Amazon and recovers ca 7000 ha of continuous forest, surrounded by a much larger area of intact forest. The topography is undulating, varying in elevation from 200–250 m. The canopy reaches up to 45 m in height and the understory is relatively open and dominated by the palm *Orbignya phalerata* (Arecaceae). In the Brazilian Amazon, it is usual to find between 18 and 53% of plant species in different physiognomies having EFNs (extrafloral nectaries), and these plants may reach up to 50% of spatial coverage in a given physiognomy (Rico-Gray and Oliveira 2007).

Data collection

All fieldwork was conducted in a site (module) managed by the Brazilian Research Program in Biodiversity (PPBio) (<http://ppbio.inpa.gov.br>) on São Nicolau Farm. This PPBio module consists of six parallel north–south trails and two parallel east–west trails. A permanent plot 250 × 25 m (6250 m^2) is located every 1 km along the trail, with a total of 12 sampling plots in the entire module. We considered each of the 12 sampling plots independent samples of ants and plants, generating 12 different ant–plant interaction networks. This is due to the fact that, ants and plants are sessile organisms, the distance among each sampling plot is enough to guarantee that one species *i* found in a plot would never interact with one species *j* on another sampling plot.

We collected the data in December 2010 and January 2011. At each of the 12 sampling plots we looked for EFN plants from 0.5 m to 3 m tall. This size was used because it is easily accessed by researchers without disturbance. On each plant, we recorded all occurrences of ants collecting liquids in EFN. We selected plants at least 10 m distant from each other, in order to minimize the possibility of collecting ants from the same colony that were foraging on different plants. Plants and ants were identified to the lowest possible taxonomic level by morphologic comparisons with species deposited in collections from the Entomological Section of the Zoological Collection of the Universidade Federal de Mato Grosso, Brazil (CEMT), and the Herbário Centro-Norte Mato-Grossense (CNMT). Moreover, different specialists of these institutions also helped us.

Data analysis

To evaluate how topological properties of ant–plant mutualistic networks vary over space, we calculated the dissimilarity among the 12 sampling plots of the following metrics: connectance, network specialization and nestedness. We chose these metrics because we consider it a way to compare community organization within our study and with others published previously. The connectance (*C*) is the proportion of possible links that are actually realized (Jordano 1987). We calculated the level of specialization networks using the specialization index (H_2'), which ranges from 0 (minimum specialization) to 1 (maximum specialization) using the bipartite package (Dormann et al. 2009) in the R software ver. 2.13.1. This index is robust to the number of interacting species and to changes in sampling intensity (more details in Blüthgen et al. 2006). We estimated the nestedness value of each network using the NODF metric (nestedness metric based on overlap and decreasing fill) (Almeida-Neto et al. 2008) in the ANINHADO software (Guimarães and Guimarães 2006). We tested the nestedness observed for each network with 1000 networks generated by null model II, in order to assess if the nestedness value observed was higher than that expected by random patterns of interaction. In this null model, we assume that the probability of an interaction occurring is proportional to observed number of interactions of both plant and ant species (Bascompte et al. 2003). We also calculated the nestedness value, standardizing the difference in richness, connectance and heterogeneity of interactions among the sampling plots, using the z-cores to allow cross-network comparisons. z-score is defined as: $Z_{nodf} = (x - \mu)/\sigma$, where x = NODF value observed, μ = mean NODF value of randomized matrices, and σ = standard deviation of the randomized matrices (Ulrich et al. 2009).

We calculated the additive partitioning of diversity in ant–plant networks (Veech et al. 2002), to assess the spatial turnover among the sampling plots, in plant and ant species composition (β-diversity). From the total richness of the same trophic level found at two sampling plots (γ-diversity), we calculated the α-diversity, defined as: $\alpha = (\alpha_1 + \alpha_2)/2$, where α_1 = species richness at sampling plot 1, and α_2 = species richness at sampling plot 2. Then, we calculated the β-diversity, defined as: $\beta = (\gamma - \alpha)$. We also calculated the turnover of β-diversity only for plants and ants on generalist core species. We defined core or peripheral species components of the networks through: $Gc = (k_i - k_{mean})/\sigma_k$, where k_i = mean number of links for a given plant/ant

species, k_{mean} = mean number of links for all plant/ant species in the network, and σ_k = standard deviation of the number of links for plant/ant species. $Gc > 1$ are species with the larger number of interactions in relation to other species of the same trophic level, and are therefore considered as species constituting the generalist core. $Gc < 1$ are species with lower number of interactions in relation to other species of the same trophic level, and are therefore considered as species constituting the periphery of networks.

We used Mantel tests to determine the existence of a relationship between the turnover in different network metrics described above, and the matrices of geographic distances among all the sampling plots. Mantel tests were done using the vegan package (Oksanen et al. 2007) in the R-project software ver. 2.13.1, using Euclidean distance to calculate the dissimilarity in the metrics and geographic distances among sampling plots. In these analyses, we also tested the correlation coefficient (r) using this analysis. We composed all graphs using the software GraphPad Prism ver. 5.0 (Motulsky 1999).

Results

In this study, we recorded 70 plant species (or morphospecies) with EFNs, belonging to 24 genera and 16 families. The family Bignoniaceae comprised 26.3% of plant species, followed by 22.8% Mimosaceae and 10.5% Caesalpiniaceae. The plant species richness per sampling plot was 21.41 ± 3.77 (mean ± SD). For ants, we recorded 121 species in 19 genera and eight subfamilies. The subfamily Myrmicinae comprised 42.28% of ant species, followed by 26.1% for Formicinae

and 14.9% for Dolichoderinae. The ant species richness per sampling plot was 23.16 ± 5.85. A list of all ant–plant interactions recorded can be viewed in the Supplementary material Appendix A1. In general, the mean connectance value of 12 different ant–plant networks was 0.140 ± 0.035 (mean ± SD) and the network specialization was 0.088 ± 0.049. All networks were significantly nested in comparison to randomized matrices (NODF metric: 21.01 ± 4.40, p < 0.05, and z-score 3.63 ± 1.50; null model: 13.76 ± 2.81).

On the spatial scale studied, we found no trend in variation in connectance (Mantel statistic r = 0.044, p = 0.374) and network specialization (H_2) (Mantel statistic r = 0.004, p = 0.457) across communities (Fig. 1A–B). For nestedness, we obtained different results before and after accounting for the species richness, connectance and heterogeneity of interactions. We found no trend in variation in NODF values across space (Mantel statistic r = 0.078, p = 0.283). However, we observed significant correlations in nestedness calculated by the z-score (Mantel statistic r = 0.315, p < 0.01) (Fig. 1C–D), indicating after controlling for other network patterns the degree of nestedness vary across space.

We observed a positive relationship between plant and ant composition and distance (β-diversity) (plants: Mantel statistic r = 0.401, p < 0.01, ants: Mantel statistic r = 0.307, p = 0.013) (Fig. 2A–B). However, we observed no trend in the turnover in core species composition, for both plants and ants, over the geographic distance (plants: Mantel statistic r = 0.007, p = 0.437, ants: Mantel statistic r = −0.088, p = 0.734 (Fig. 2C–D). Indeed, the core species composition was very stable for both ants and plants. Of 121 ant species, just one to three species of ants were present in the generalist
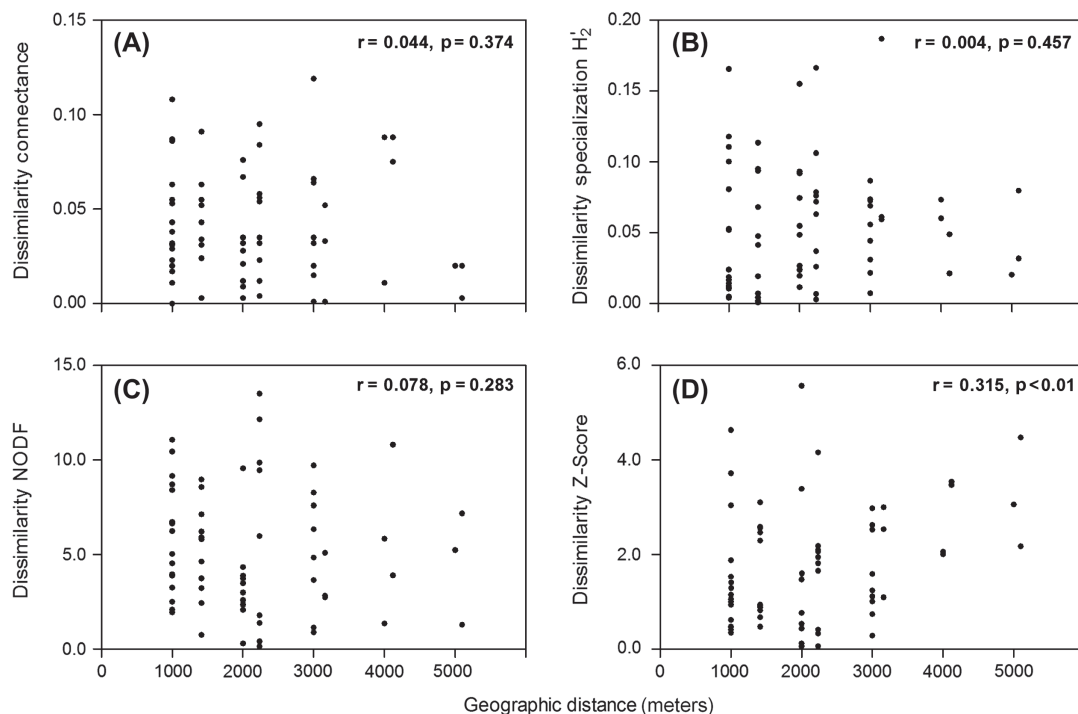

Figure 1. Relationship among the dissimilarity of network topology: (A) connectance, (B) network specialization, (C) nestedness (NODF metric) and (D) nestedness by z-score metric, with dissimilarity of geographic distance of 12 sampling plots examined on São Nicolau Farm, Mato Grosso State, southern Brazilian Amazon. Correlation coefficient (r) and significance (p computed using Mantel tests) are also shown (n = 66 points in each of the metrics calculated).
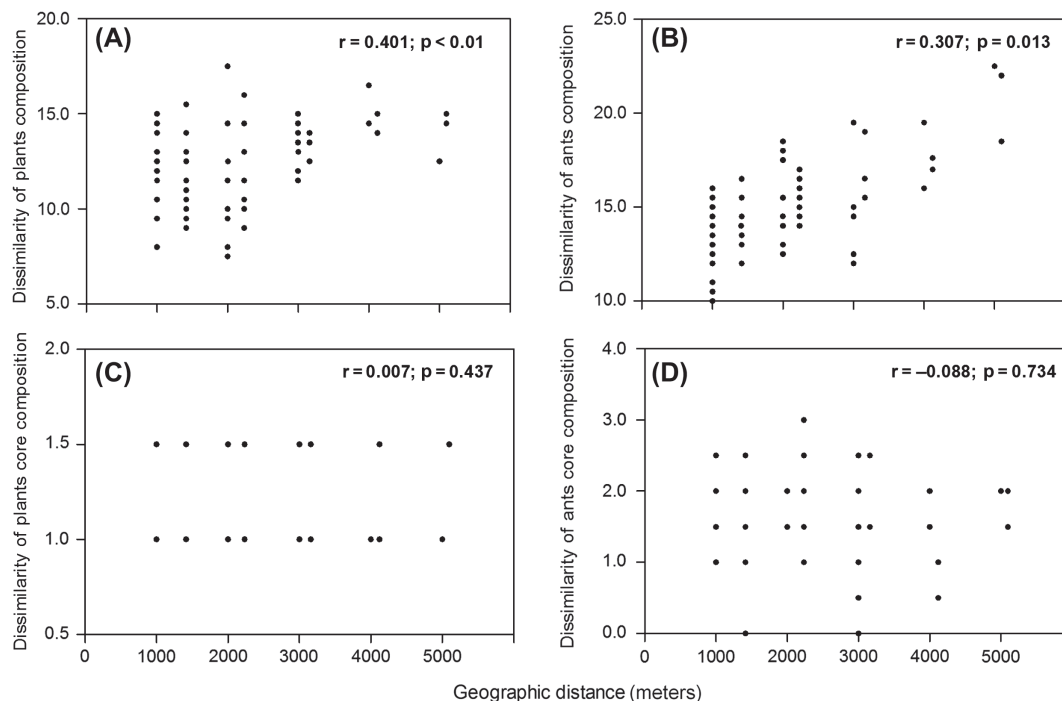
Figure 2. Relationship among the dissimilarity of: (A) plant species composition, (B) ant species composition, (C) plant core composition and (D) ant core composition, with dissimilarity of geographic distance of 12 sampling plots examined on São Nicolau Farm, Mato Grosso State, southern Brazilian Amazon. Correlation coefficient (r) and significance (p computed using Mantel tests) are also shown (n = 66 points in each of the metrics calculated).

core of networks, and the species *Azteca* sp. 2, *Brachymyrmex* sp. 1 and *Crematogaster* sp. 8 were present in the core at more than 58% of the sampling plots. For plants, one or two species were present in the generalist core of networks, and *Inga* sp. 12, *Mabea* sp. 2, *Protium* sp. 1 and *Stryphnodendron* sp. 1 were present in the core in more than 66% of the sampling plots.

Discussion

Previous studies have shown that disparate mutualistic networks of free-living species have a nested and asymmetrical pattern, such as plant–pollinator, fruit–frugivore, ant–plant, clownfish–anemone and marine fish cleaning symbioses (reviewed by Hagen et al. 2012). However, few studies have evaluated how the structure of these networks varies over spatial gradients. The few studies that evaluated the role of spatial variations in mutualistic networks showed that local and landscape environmental factors, as well as spatial aggregation and animal mobility, are important factors that structure the plant–animal interactions (Morales and Vázquez 2008, Burkle and Alarcón 2011). In this study, standardizing the network metrics, collection effort and habitat, we showed that for ant–plant mutualistic networks, the structure remains unaltered over the spatial scale studied. In addition, although the ant and plant composition of networks changes over space, the core of generalist species remains stable along the 5099 m measured in a dense rainforest in the southern Brazilian Amazon.

Studying ant–plant networks on different islands, Sugiura (2010) showed that the size of islands strongly influenced

the connectance, the nestedness and the number network interactions. However, the islands studied by Sugiura (2010) are quite different from the sites we studied, once each island is separated from the other by a impermeable matrix. It makes the landscape much more heterogeneous than a continuous forest or other more connected landscapes. On the other hand, a study made by Chamberlain and Holland (2009) in eight locations of the Sonoran Desert, show that despite the species richness of ant–plant networks vary among sites, the number of interactions per species remains similar. These same authors also found that the correlation between the degree and the ant body size also remains stable over all eight communities studied. In our study, within a relatively homogeneous forest inserted in southern Brazilian Amazon, there are almost no changes in the networks descriptors among the sample points. Therefore, we hypothesize that the topology of ant–plant networks tend to be more stable over homogeneous environments where there is no direct spatial limitation (i.e. deserts and tropical rainforests) than in isolated environments such as islands.

In tropical rainforests, the main factors that explain the distribution and diversity of ants are competitive interactions, habitat complexity (abundance of food and nesting sites), climate stability and natural barriers that prevent the dispersal of ant queens (Benson and Harada 1988, Hölldobler and Wilson 1990). Thus, along a spatial scale, different biotic and abiotic factors can influence the richness and diversity of interactions between ants and plants in several ways (Díaz-Castelazo et al. 2004, Rico-Gray and Oliveira 2007, Rico-Gray et al. 2012, Lange et al. 2013). Here, the values of connectance varied widely among the sampling plots, which influenced the values of

nestedness using the NODF metric. In fact, when we calculated the dissimilarity among the values of this metric, there was no relationship to geographic distance. On the other hand, when we controlled for the connectance and species richness effects, we found the dissimilarity of nestedness increased with geographic distance. Why were networks closer to each other more similar? This can be explained because closer networks have a lower turnover of plant and ant composition, as we observed. Therefore, it was expected that the number of ant and plant species, as well as the number of interactions would be more similar for closer networks. Additionally, the metric used to calculate the network specialization is also robust with respect to networks with different connectance values (Blüthgen et al. 2006, Blüthgen 2010), which indicates that the low specialization found here is a non-random pattern of ant–plant mutualistic networks. Thus, we showed that the topological structure of ant–plant mutualistic networks is stable and predictable over a spatial scale of up to 5099 meters in rainforest in the southern Brazilian Amazon, independent of variations in biotic and abiotic factors at the sampling plots.

The core of generalist species remained stable over the spatial scale studied. One factor that could explain the stability of this core of species over space is abundance, because abundant species could interact most frequently with each other and with less-abundant species (Vázquez et al. 2007, 2009). However, Dáttilo et al. (unpubl.), found that in ant–plant mutualistic networks, the members of the generalist core interacted with each other more than expected by their abundances. This finding indicates that ants of the generalist core possibly have mechanisms that maintain these species in the core over space. Because competition for resources is an important factor structuring ant communities in tropical regions (Delabie et al. 2000), we believe that the core generalist species are competitively superior (i.e. more recruitment-oriented or aggressive) and monopolize resources. In addition, our results support the notion that the generalist core is less variable in time and space than the network periphery (Bascompte et al. 2003).

In general, the dispersal capacity of most tree species and the foraging of ant workers in tropical forests are limited to small spatial scales (a few meters to a few hundred meters) (Hölldobler and Wilson 1990). The stability of the generalist core over up to 5099 m in our study site indicates that different populations of plants and ants can interact in the same way. Moreover, it was hypothesized that the generalist core species has the potential to drive the coevolution of the entire network (Guimarães et al. 2011). Thus, the spatially and temporally stable generalist core can act as a coevolutionary vortex for more specialized interactions, where the convergence of traits on both sides of the interaction increases over evolutionary time, and in turn allows the evolution of a subset of specialists that exploit the resource (Bascompte et al. 2003, Thompson 2005, Guimarães et al. 2007).

In conclusion, we showed that, in general, the topological structure of ant–plant mutualistic networks remained stable across space in a dense rainforest in the southern Brazilian Amazon. Moreover, even though the composition of interacting ants and plants changed along this spatial scale, the generalist core remained stable. This finding indicates that independently of local and landscape environmental factors, the nonrandom pattern of community organization did not change. These observations contribute to the understanding of the maintenance of biodiversity and coevolutionary processes. However, the consequences of temporal variations and the resilience of the generalist core over larger spatial scales remain unknown (but see Olesen et al. 2011, Lange et al. 2013). There is still much to do to acquire a better understanding of patterns and processes related to spatiotemporal variation in ant–plant interaction systems.

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Supplementary material (available as Appendix oik-00562 at <www.oikosoffice.lu.se/appendix>). Appendix A1.