UNIVERSIDADE FEDERAL DE MATO GROSSO
INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE

STRUCTURE OF COMPLEX NETWORKS AND THE ROLE OF SPATIAL VARIATIONS AND ABUNDANCE IN PLANT-ANT INTERACTIONS

WESLEY FRANCISCO DÁTTILO DA CRUZ

CUIABÁ – MATO GROSSO
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Dissertação apresentada ao Programa de Pós- Graduação, do Instituto de Biociências, para obtenção do título de Mestre em Ecologia e Conservação da Biodiversidade.

CUIABÁ – MATO GROSSO
March 2012

Cruz, Wesley Francisco Dáttilo da.

S586s

Structure of complex networks and the role of spatial variations and abundance in plant-ant interactions. / Wesley Francisco Dáttilo da Cruz. Cuiabá, Mato Grosso, Brazil, 2012.

99f.: Il.

Dissertação (Mestrado em Ecologia e Conservação da Biodiversidade) – Programa de Pós-Graduação em Ciências Biológicas, Instituto de Biociências, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, 2011.

Orientador: Prof. Dr. Thiago Junqueira Izzo.

Co-orientador: Prof. Dr. Paulo Roberto Guimarães Júnior.

1. Aninhamento. 2. Neutralidade. 3. Coevolução. 4. Interações planta-animal. 5. Substituição espacial. I. Título. 574

CDU: 574 (817.2)

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I dedicate this dissertation to all those who supported me
throughout this journey. In particular my parents
and my wife, who were often deprived of
attention, but always stayed by my side.

“Interactions between species are as evolutionarily malleable
as the species themselves and have played a central role in the
diversification and organization of life.”
(John N. Thompson 1999)

ACKNOWLEDGEMENTS

The work presented in this dissertation benefited from many people’s comments, discussion, collaboration and encouragement.

First and foremost, I thank my advisor, Dr. Thiago J. Izzo, for their guidance, support and inspiration throughout. Besides an excellent researcher is a great friend I made in 2007 at the Instituto Nacional de Pesquisas da Amazônia (INPA) where I was his intern working with ant-plant symbiosis. Despite his busy schedule, Thiago Izzo always finds the time to discuss anything from intriguing experimental results to soccer. His dedication and commitment to science is truly inspiring and remarkable. I would also like to thank my co-advisor, Dr. Paulo R. Guimarães-Jr, I am very appreciative of his generosity with his time, advice, data analysis and all help with this dissertation. Thanks for also welcoming me into in his lab at the Universidade de São Paulo (USP). Without his support, this project would not have been possible. Thiago Izzo and Paulo Guimarães both brought unique perspectives to my research, enriching it greatly. Theirs encouragement and enthusiasm were important for the completion of this project.

To Dra. Soraia Diniz and Dr. Roberto Silveira, I express my gratefulness for the discussion and interpretation of some results presented in this thesis. Many additional colleagues provided valuable information that helped my dissertation, and I am grateful to all of them for their assistance.

I cannot forget to thank my dissertation committee members for their valuable comments and constructive criticism; thank you Dr. Mário Almeida-Neto (Universidade Federal de Goiás), Dr. Jerry Penha (UFMT) and Dr. Fernando Vaz-de-Mello (UFMT).

I am grateful also to my true friends at the Universidade Federal de Mato Grosso who over the years have patiently endured my highs and lows and have kept me sane and entertained. In particular, I thank Fernando Tortato (Galdério), Mateus Souza (Ventania), Marcela Gigliotti (Marcelita), Miquéias Ferrão (Kiki), Rafael Nunes (Bino), Vitor Azarias (Zé Colméia). Sorry for something. I extend my heartfelt salute to all my colleagues at the Community Ecology Lab. of UFMT (Ricardo Vicente, Jéssica Falcão and Daniela Monteiro). It was an honour and a pleasure to work among folks of such commitment and fun.

My studies were funded by a scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), with additional funding from the

Brazilian Program for Biodiversity Research (PPBio) and the logistical support from the Office National des Forêts Brazil. I gratefully acknowledge this support.

Finally, I would like to express my deepest gratitude to Jéssica Falcão (my wife) for everything from technical and scientific support to emotional support. I could not have done it without you. Thank you for being there for me from the very beginning.

Thank you for believing in me.

SUMMARY

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ABSTRACT: The structural organization of mutualism networks provides insights into processes shaping biodiversity. Understanding the mechanisms that shape this organization is essential for us to understand the ecological and evolutionary dynamics of the interacting species. Recent studies have suggested that species abundance is one of the most fundamental criteria shaping mutualistic networks. However, the role of species abundance on mutualistic networks is still unclear. Moreover, only recently has the spatial effect been incorporated as a mechanism structuring mutualistic networks. In this work I studied plants with extrafloral nectaries and associated ants to show that the natural abundance of ants on vegetation explained just a part of the frequency of mutualistic interactions and that it is independent of ant species compositions. In addition, the generalist core of these networks interacts more among themselves than expected by their abundances. This generalist core was formed by competitively superior ants that have behavioral and ecophysiological traits to use liquid food and are that exclude other species from the same resource. I also showed that even the fact that ant and plant composition of networks changes over space, the generalist core species and the topological structure of networks remain unaltered. This finding indicates that independently of local and landscape environmental factors the nonrandom pattern of community organization is not changed. Such generalist core conformation being stable over space and time could have serious implications on coevolutionary process of the system. In short, contributing thus to our understanding of the maintenance of biodiversity.

Keywords: nestedness, neutrality, coevolution, plant-animal interactions, spatial turnover.

RESUMO: A organização estrutural das redes mutualísticas provê idéias sobre processos que modulam a biodiversidade. Conhecer os mecanismos que modulam essa organização é essencial para entendermos a dinâmica ecológica e evolutiva das espécies que interagem. Recentes estudos têm sugerido que a abundância das espécies é um dos principais critérios que modulam essas redes. Entretanto, o papel da abundância relativa das espécies nas redes mutualísticas ainda é incerto. Além disso, apenas recentemente o efeito espacial tem sido incorporado como mecanismo que estrutura redes mutualísticas. Neste trabalho, eu estudei plantas com nectários extra-florais para mostrar que a abundância natural das formigas sobre a vegetação explica apenas uma parte da freqüência das interações mutualísticas independente da composição de espécies de formigas. Adicionalmente, o núcleo generalista dessas redes interage mais entre si do que esperado pelas suas abundâncias. Este núcleo generalista foi formado por formigas competitivamente superiores que tem características comportamentais e ecofisiológicas para utilizar alimentos líquidos e que excluem as demais espécies do mesmo recurso. Eu também mostrei que mesmo que a composição de formigas e plantas das redes muda ao longo do espaço, o núcleo de espécies generalistas e a estrutura topológica das redes permanecem inalterados. Esse resultado indica que independente de fatores locais ou ambientais o padrão não-aleatório da organização da comunidade não é mudado. Tal conformação do núcleo generalista sendo estável ao longo do espaço e do tempo poderia ter sérias implicações sobre os processos coevolutivos do sistema. Por fim, contribuindo dessa forma para nosso entendimento da manutenção da biodiversidade.

Palavras-chave: aninhamento, neutralidade, coevolução, interações planta-animal, substituição espacial.

CHAPTER 1

GENERAL INTRODUCTION

CHAPTER 1 - GENERAL INTRODUCTION

Most interspecific interactions involving multiple species, resulting in the interactions networks that may be beneficial, neutral or harmful among the individuals involved (Lewinsohn et al. 2006). Among the various forms of interactions, the study of mutualism in community level was overlooked for a long time (Stanton 2003). However, recently the study of cooperative interactions among species has become one of the central issues in the community ecology (Bronstein 2001; Thompson 2005; Bronstein 2006, Ferrière et al. 2007). Nevertheless, it is likely that all organisms on Earth are involved in at least one event of mutualistic interactions throughout their life history (Bronstein 2001; Toby-Kiers et al. 2010). In this type of interaction, a species provides a service or product that the partner can not achieve alone, and in exchange receive some type of reward (Janzen 1985; Hoeksema & Bruna 2000). This makes mutualistic interactions influences directly the ecological and evolutionary dynamics of interacting species in different ecosystems around the world (Bronstein 2001; Thompson 2005; Bascompte et al. 2006; Montoya et al. 2006; Guimarães et al. 2007). Thus, understand how these factors act on the interaction patterns is helpfull on the management and conservation of the interacting species (Janzen 1974; Burslem et al. 2005; Del-Claro & Torezan-Silingardi 2009; Dyer et al. 2010)

Recent studies have focused on the structure of mutualistic networks among free-living species. This studies found non-random patterns of interaction on different systems and habitats throughout the Earth (Bascompte et al. 2003, Thompson 2005; Lewinsohn et al. 2006; Guimarães et al. 2007; Vázquez 2009). The metrics used in the study of interaction networks are derived from graph theory, first proposed in 1735 by Swiss mathematician Leonhard Euler (Mello 2010). Among the main features found in such networks is that they are highly nested and exhibit asymmetrical pattern of interactions. This means that species associated with few other species (specialists) preferentially interact with species that interact with many others (generalists), causing asymmetric specialization between interacting partners (Bascompte et al. 2003; Thompson 2005; Burgos et al. 2009). However, generalist species tend to interact with one another, forming a dense core of symmetric interactions (Bascompte et al. 2006; Vázquez et al. 2007; Guimarães et al. 2011). The nested pattern has already been observed in different mutualistic networks, such as: plant-pollinator, plant-ant, plant-disperser, clownfish-anemone and marine fish cleaning symbioses (Bascompte et al. 2003; Guimarães et al.

2006; Lewinsohn et al. 2006; Guimarães et al. 2007; Ollerton et al. 2007). Several factors have been proposed to explain the origin of these patterns in mutualistic networks (for more information, please see: Medan et al. 2007; Morales & Vázquez 2008; Nielsen & Bascompte 2007; Rezende et al. 2007; Stang et al. 2009; Vázquez et al. 2009). However, symbiotic networks are not nested, because they present great compartmentalization of interactions among the species involved (Guimarães et al. 2007).

Mutualistic interactions networks can be viewed in different ways, however, there are two main ways to visualize these interactions through: bipartite graphs (Figure 1A) or/and ordered matrices (Figure 1B). Using as example a network of interactions between plant-animals, in bipartite graphs, the left nodes represent different animal species, and the right nodes correspond plant species that interact positively with the animals (Figure 1A). Lines, also called "links", connect positively interacting species; On the other hand, the visualization of interactions in ordered matrices indicates that each column represents one plant species and each row represents a animal species, and filled cells represent positive interactions among species. (Figure 1B).

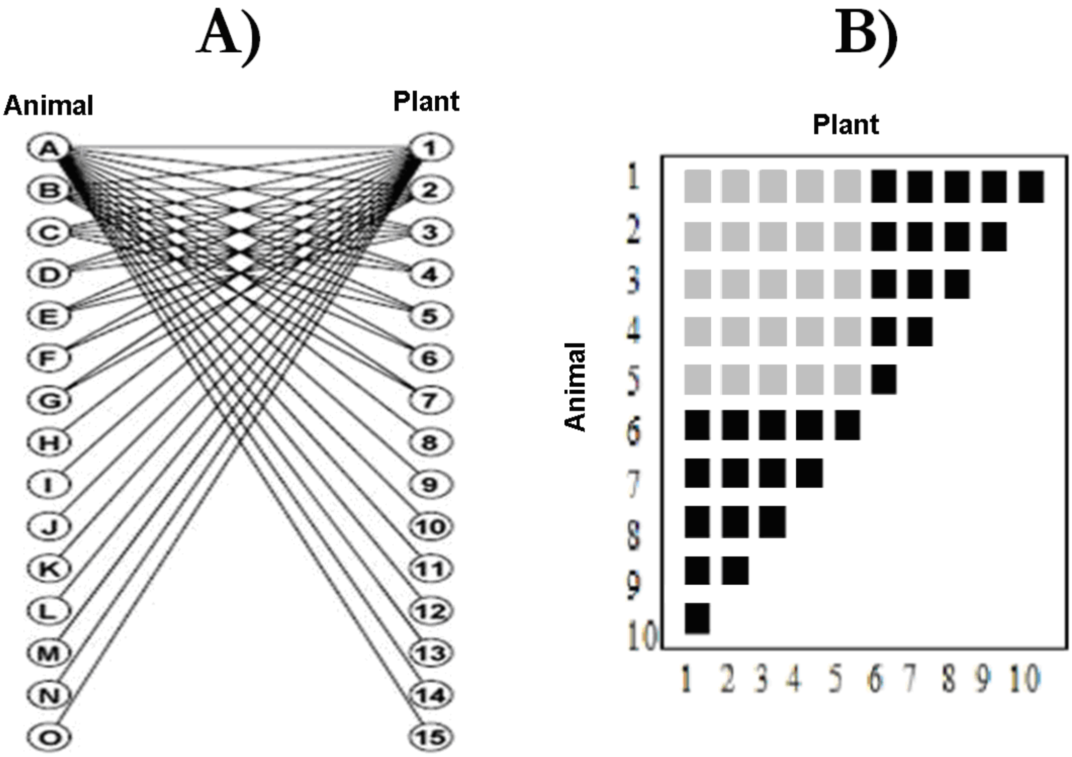

Figure 1. Main ways to view the structure of an interaction networks nested and asymmetric: A) bipartite graphs and B) ordered matrices. Both forms of representation are ordered according to interactions number of the species, where species that have fewer interactions are subsets of species with more interactions. Cells painted of gray in Figure

1B represent the core of generalists species (Figures modified from Lewinsohn et al. 2006).

According to Thompson (2005) and Stanton (2003), studies of interactions only among pairs of species are insufficient to understand the evolutionary and coevolutionary processes in mutualistic interactions. Several authors have studied the implications of coevolution in mutualistic networks of interacting species (Jordano et al. 2003; Thompson 2005, Bascompte et al. 2006; Guimarães et al. 2007; Jordano et al. 2010; Guimarães et al. 2011). The focus of these studies is mainly in the core of generalist species, due the symmetric strength of the interacting species (Jordano et al. 2003; Bascompte et al. 2006; Guimarães et al. 2011). The generalist core can drive the evolution of the whole community because the species of the core interact with virtually all species of the matrix (Jordano et al. 2003; Bascompte et al. 2006; Guimarães et al. 2007; Jordano et al. 2010; Guimarães et al. 2011). Moreover, the generalist core can act as a coevolutionary vortex of more specialized interactions, where the convergence of traits on both sides (e.g. animals and plants) of the interaction increases over evolutionary time (Thompson 2005; Guimarães et al. 2007). Finally, understand the feature and factors that influence the interactions of the species generalist core is essential to understand the current view of coevolutionary process in mutualistic interactions (Bascompte et al. 2003; Thompson, 2005; Bascompte et al. 2006; Jordano et al. 2010).

My aim of this dissertation was, to 1) evaluate the topology of mutualistic (ants and plants with extrafloral nectaries) and neutral (ants and plants without extrafloral nectaries) networks in ant-plant interactions; 2) evaluate the turnover of species composition among these networks; 3) determine through a simples mathematical model the role of relative abundance of species in the probability of pairwise interactions in ant-plant mutualistic networks; 4) evaluate how the topological properties and the spatial turnover of species composition of ant-plant mutualistic vary along an spatial scale. My dissertation was divided into two interrelated chapters. In Chapter 1, I show that the topology of mutualistic and neutral networks are different, and which the core of generalist species interact more among themselves than expected by their abundance in mutualistic networks. Moreover, is little the turnover of ants composition among the mutualistic and neutral networks. In Chapter 2, I show that in mutualisms between ants and plants with EFNs the networks topology remains unaltered at the spatial scale studied (5.099 m). In addition, even that ants and plants composition of networks changes over space, the species of core generalist remains the same along a regional scale on a *terra-firme* forest in Brazilian Meridional Amazon. Finally, the list of ants and plants species collected in this study addition of the instructions for authors of the journals that I will submit the manuscripts are included in four appendices at the end of this dissertation.

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Chapter 2

The structure of ant-plant mutualistic networks: is abundance enough?*

**** This manuscript will be submitted to Ecology***

Submitted to Ecology

Running head: *The effect of abundance in ant-plant networks*

The structure of ant-plant ecological networks: is abundance enough?

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ABSTRACT.

The structural organization of mutualism networks provides insights into processes shaping biodiversity. To know the mechanisms that shape this organization is essential for us to understand the ecological and evolutionary dynamics of the interacting species. Recent studies have suggested that species abundance is one of the most fundamental criteria shaping mutualistic networks. However, the role of species abundance on mutualistic networks is still unclear. In this work we studied plants with extrafloral nectaries and associated ants to show that the natural abundance of ants on vegetation explained just a part of the frequency of mutualistic interactions and that it is independent of ant species compositions. In ant-plant mutualistic networks, the nestedness was higher than predicted by the abundance. In addition, the generalist core of these networks interacts more among themselves than expected by their abundances. This generalist core was formed by competitively superior ants that have behavioral and ecophysiological traits to use liquid food and are that exclude other species from the same resource. Such generalist core conformation being stable over space and time could have serious implications on coevolutionary patterns of the system.

KEYWORDS: coevolution, nestedness, neutrality, plant-animal interactions.

1. INTRODUCTION

A central goal of ecology is to understand the mechanisms that determine the structure of ecological communities at different spatial and temporal scales (Turner 1990, Levin 1992, Williams and Martinez 2008, Zhou and Zhang 2008). Recent studies have focused on the network structure of mutualisms and found non-random patterns of interaction on a wide range of ecosystems (Bascompte et al. 2003, Lewinsohn et al. 2006, Guimarães et al. 2007, Vázquez 2009a). These non-random patterns influence the whole ecological and evolutionary dynamics of the interacting species (Jordano et al. 2003, Thompson 2005, Bascompte et al. 2006, Montoya et al. 2006, Guimarães et al. 2011).

Relative species abundance is one of the most fundamental criteria shaping the ecological networks, and it seems to be an important factor in the probability of interactions (Vázquez et al. 2007, 2009b, Verdú and Valiente-Banuet 2011). In this case, abundant species should interact most frequently with each other and with other less abundant species, but less abundant species will rarely interact with them (Krishna et al. 2008, Vázquez et al. 2007, 2009b). However, the role of species abundance on mutualistic networks is still unclear.

A strictly system to study questions on abundance and dominance on interaction networks is the ant-plant system. Ant-plant interactions are commonly found in tropical rainforests, in which more than 94% of arthropods and 86% of the biomass collected in canopies are ants (Majer 1990, Tobin 1995). The observed high frequency of ant foraging on the surface of plants is due to the high availability of different food and nesting sites within their structures (Andersen 1990, Blüthgen et al. 2000, Davidson et al. 2003). The interactions between ants and plants with extrafloral nectaries (EFNs) are key-ecological interactions in tropical rainforests and well documented in literature. In these associations, plants produce nutritious liquid to attract ants (Baker et al. 1978, Koptur et al. 1998, Rico-Gray and Oliveira 2007). In exchange for food, the ants defend plants against potential herbivores (Del-Claro et al. 1996, Oliveira et al. 1999, Rico-Gray and Oliveira 2007). However, despite nectar being a key resource for ants foraging on plants, there is an adaptive filter in which only a few ant species have adaptations for the acquisition, storage and digestion of liquid resources (Fowler et al. 1991, Oliveira and Brandão 1991, Davidson et al. 2003, 2004).

With the use of the network theory in ecological interaction studies in recent years, some authors have found the existence of a dense core of symmetric interactions in ant-plant mutualistic networks, where generalist species tend to interact with one another (Guimarães et. al. 2006, Chamberlain et al. 2010, Sugiura 2010). Moreover, these studies show that species associated with few other species (specialists) preferentially interact with species that interact with many others (generalists), forming an asymmetrical and nested pattern of interaction (Guimarães et. al. 2006, Chamberlain et al. 2010, Sugiura 2010). Several factors have been proposed to explain the origin of these non-random patterns in mutualistic networks, such as spatial distribution of individuals and species (Morales and Vázquez 2008, Burkle and Alarcón 2011), species richness (Medan et al. 2007), foraging behavior (Vázquez et al. 2009a), sampling effects (Nielsen and Bascompte 2007), phylogeny (Rezende et al. 2007), and phenotypic traits of interacting individuals (Stang et al. 2007). However, species abundance seems to be the best predictor in ant-plant mutualistic networks (Vázquez et al. 2007, Chamberlain et al. 2010). Thus, abundant species tend to find individuals of other abundant species more often than individuals of rare species (Vázquez et al. 2009b). As EFNs are a food resource, their discovery and dominance by ants being dependent only of abundance, imply no actual competition. However, this is not supported by literature once the nectar secreted is a predictable resource and rich in energy, and different ant species compete for the same resource (Hölldobler and Wilson 1990, Dreisig 2000, Blüthgen and Fiedler 2004ab).

On the other hand, among the arboreal ant communities, some species do not have adaptations for feeding liquid resources, but forage on vegetation for prey, for example (Andersen 1990). In plants without the presence of EFNs and honeydew secreted by homopterous insects, resources cannot be predicted, and ants randomly forage using the plant only as substrate (Blüthgen et al. 2000). The presence of such ants in a plant may be driven by neutral, not-deterministic factors, such as the available foraging area. Thus, we expect the existence of two subsets with different composition of ant species foraging on plants with and without EFNs. These subsets should be maintained possibly by the adaptive physiological characteristics of ants, as well as competition where some ants monopolize EFNs plants.

In this study, we hypothesized that there is a particular ant species assembly foraging on plants with EFNs determined by behavior and ecophysiological factors (adaptations for liquid diets and monopolizing the resource) that differ from those ants randomly foraging in the foliage, generating two different subsets. This assembly of nectar-feeding ants monopolizes the resource and interacts with plants more among themselves than expected by their abundance. Moreover, we expected that, due to the liquid-energy food source of EFNs, ants would not interact randomly with plants. Therefore, the topological structure of networks generated through deterministic (plants with EFNs) and non-deterministic (plants without EFNs) processes in ant-plant interactions could be different. In order to test our hypothesis, we evaluated the topology of the ecological networks between ants and plants with and without EFNs, and the turnover of ant species composition among these networks through the additive partitioning of diversity. We also determined through a simple mathematical model the role of the relative species abundance in the pairwise probability interactions in networks of ants and plants with EFNs in a tropical rainforest inserted in the Brazilian Meridional Amazon.

2. METHODS

2.1) Study area

We conducted this study at the São Nicolau Farm (9º48’S and 58º15’W, elev. 254m), located in the municipality of Cotriguaçu, north of Mato Grosso, Brazil. According to the Köppen classification, the climate is tropical wet (Am) with annual average of: 24 °C temperature, 85% humidity, and 2.300 mm precipitation (Camargo et al. 2010, Dáttilo et al. 2012). The study region has two distinct seasons, a rainy season between November and April and a dry season between May and October. The area is characterized as a *terra-firme* dense rainforest inserted in the Brazilian Meridional Amazon (Veloso et al. 1991, Camargo et al. 2010). The reserve area covers 7.000 ha of continuous forest, surrounded by a much larger area of continuous forest. The terrain is undulating with altitudinal variation of 50 m between the plateaus and the river side terrains. Canopy trees range from 30-40 m high with some emergent trees reaching 50 m. The understory is relatively open, with high frequency of *Orbignya phalerata* Mart. (Arecaceae).

2.2) Data Collection

We collected data in a module managed by the Brazilian Research Program in Biodiversity (PPBio) inserted at São Nicolau Farm. The module consists of two 5 km parallel trails East-West one kilometer apart. In both trails, one sampling point with 250 m x 25 m (6.250 m^2) was made every km., totaling 12 sampling points in the entire module. The central trail of each plot was established minimizing variations of soil and altitude, and increasing the precision of estimates for predictor variables (Magnusson et al. 2005) (additional details about module and trails please see http://ppbio.inpa.gov.br). Here, we considered each of the 12 sampling points as independent samples of ants and plants, generating 12 different ant-plant interaction networks. We assume that ants and plants are sessile organisms (Fourcassié et al. 2003) and the distance between sampling points is enough so as to guarantee that organisms of a given plot can never interact with the organisms of another plot.

We collected ants and plants in December 2010 and January 2011 always between 9:00 h and 15:00 h. In each of the 12 sampling points, we collected ants foraging in all plants with EFNs that were accessible to the collector (from 0.5 m to 3 m). For ant collection, we used a method similar to the entomological umbrella in which the branches were shaken and all the ants that fell were collected in a white squared cloth board of 1.2 m² previously placed under the branch (Bestelmeyer et al. 2000). This method is very effective as some species, particularly of the genera *Camponotus* and *Ectatomma* drop from the plant at the slightest sign of disturbance made by the collector (W. Dáttilo, pers. obs.). We observed and collected additional ants, especially more secretive species before and after performing this procedure in order to register ants feeding on EFNs. For each plant with EFNs where ants were collected, we selected a plant without EFNs with similar structure (height, width and number of branches) nearby. No plants with homopterous and other visible liquid-resource sources were considered when sampling plants without EFNs. All selected plants should be at least 10 m apart to minimize the possibility of collecting the same ant colony foraging on different plants. We used the entomological umbrella methodology instead of feeding baits to minimize biases towards ant species with efficient recruitment behavior and ants with particular feeding habits.

Plants and ants were identified to the lowest possible taxonomic level using taxonomic keys and with the help of specialists. Ant specimens were deposited in the Entomological Section of the Zoological Collection of Universidade Federal de Mato Grosso, Brazil (CEMT), and the plants were deposited in the Herbário Centro-Norte Mato-Grossense (CNMT).

2.3) Network topology

Mutualistic interactions networks can be viewed in two main ways: bipartite graphs or/and ordered matrices. In bipartite graphs, nodes represent different animal species and links are positive interactions among species. On the other hand, the visualization of interactions in ordered matrices indicates that each column represents one animal species and each row represents a plant species, and filled cells represent positive interactions among species. Thus, in order to describe the network topology of the ecological networks of the ants and plants with and without EFNs, we calculated the difference in the number of species (ants and plants) and the interaction frequency of the ecological networks between ants and plants with and without EFNs. In addition, we also calculated the following metrics: connectance, mean and variance of number of links per plant and ant species, modularity and nestedness in each of the 12 interaction networks between ants and plants with and without EFNs. The connectance (C) is the proportion of possible links that are actually made (Jordano 1987). Mean and variance of number of links per plant and ant species were obtained from the arithmetic mean of the number of interactions in which each species was involved.

We calculated modularity using the modularity index *M* (range 0 - 1), which estimates the degree in which groups of species (ants and plants) interact more among each other than with species in other groups in the network (Guimerà and Amaral 2005). The *M* index decreases when the fraction of between-module links increases in the total network. High values of *M* indicate that the ants and plants form modules that are semi-independent of other interactions within the network (Olesen et al. 2007). We tested the significance of index *M* for each network through 1.000 simulated networks generated by a null model, in order to assess whether the value of *M* observed in the empirical network is higher than expected for networks of equal size and with similar heterogeneity in interactions among species (Null Model II, Bascompte et al. 2003). We made the null model network through a routine in MATLAB, and the *M* indices of all networks were calculated by the software Netcarto (Guimerà and Amaral 2005).

We used the NODF index (Nestedness metric based on Overlap and Decreasing Fill) to estimate the nestedness value of networks, using ANINHADO software (Guimarães and Guimarães 2006). This metric is a much better nestedness metric than others and less prone to type-I statistical error, since it is based on the nestedness of all pairs of columns and rows in the matrix (Almeida-Neto et al. 2008). To assess if the nestedness value observed was higher than expected by random patterns of interaction, we tested the nestedness degree of each network with 1.000 networks generated by Null Model CE (Null Model II). In addition, we also calculated the nestedness value standardizing the difference of richness, connectance and heterogeneity of interactions among the networks using the Z-Score metric, which is defined as: $Z_{nodf} = (x - \mu) / \sigma$, where x= NODF value observed, μ = NODF mean value of randomized matrices, and σ= is the standard deviation of the randomized matrices (Almeida-Neto et al. 2008, Ulrich et al. 2009). To test the difference of all the metrics described above for the ecological networks of ants and plants with and without EFNs, we used the paired T-Test (paired per plot) using R-Project software (R Development Core Team 2010).

2.4) Overrepresentation of species interactions

To determine if the matrices of interaction networks of ants and plants with EFNs have their structure determined by abundance, we developed a simple mathematical model that allowed us to differentiate in which regions of the observed matrices the ant-plant interactions occurred more than expected by the abundance. In this model we used the ant records of neutral interactions as a measure of ant abundance in the foliage. As plants without EFNs offer no predictable resource to the ants, the frequency of ants in these plants reflects the spatial abundance of these species in the vegetation without the aggregation caused by the resource (Blüthgen et al. 2000).

Initially, we built an interaction matrix between ants and plants, where a_{ij}= number of interactions between plant species *i* and ant species *j*. The theoretical matrix of abundance was determined by $b_{ij} = \left(\frac{F_i}{F_p} . \frac{F_j}{F_a} \right)$, where F_i is the absolute frequency of a given plant with EFNs in the plot, F_p is the total frequency of plants with EFNs found in the plot, F_j is the absolute frequency of a given ant collected in plants without EFNs in the plot, F_a is the total frequency of ants collected in plants without EFNs found in the plot. The probability of any particular interaction between ants and plants occurs was determined as $P_{(aij)} = \frac{a_{ij}}{\sum_{n}^{p} \sum_{m}^{a} a_{nm}}$, where a_{ij} is the number of interaction events of the matrix and $\sum_{n}^{p} \sum_{m}^{a} a_{nm}$ is the total number of interaction events between ants and plants with EFNs. The probability of an interaction occurring is determined by the abundance of interacting partners as $P_{(bij)} = \frac{b_{ij}}{\sum_{o}^{p} \sum_{g}^{a} a_{og}}$, where b_{ij} is the number of interaction events of the matrix and $\sum_{o}^{p} \sum_{g}^{a} a_{og}$ is the total number of interaction events in plants without EFNs. Finally, we computed the differences between the actual probability of a given interaction occurring and the probability derived from the species abundances, $C_{ij} = (A' - B')$. We standardized C_{ij} to $C_{ij}' = \frac{C_{ij}}{|\max(C_{ij})|}$, where $|\max(C_{ij})|$ was the maximum value of C_{ij} of matrix to allow across-plot comparisons. $C_{ij}<0$ are cases in which plant *i* and ant *j* interact less than expected by their abundances; $C_{ij}>0$ are cases in which plant *i* and ant *j* interact more than expected from their abundances; and values equal to 0 representing the cases where ant species collected in plants without EFNs was not collected in plants with EFNs.

2.5) Additive partitioning of diversity

To evaluate the turnover of ant species composition (β-diversity) between the networks of ants and plants with and without EFNs, we calculated the additive partitioning of diversity as proposed by Veech et al. (2002). From the total ant richness found in each plot (γ-diversity), we calculated the α-diversity, defined as: $\alpha_{mean} = (\alpha_1 + \alpha_2) / 2$); where α_1 = ant richness of plant networks with EFNs found in plot; α_2 = ant richness of plant networks without EFNs found in plot. Then, we calculated the β-diversity, defined as: $\beta = \gamma - \alpha_{mean}$. In addition, to summarize the composition of the ant community in plants with and without EFN, we ordered the similarity between points using Non-Metric Multidimensional Scaling (NMDS) and tested the difference in the ant species composition through a permutation test (10.000 permutations) based on an analysis of similarities (ANOSIM) (Supplementary information). Additionally, to exclude the effect of the presence of EFNs and evaluate if the presence of EFNs was a factor which caused an increase in ant species richness, we randomized the plants classification (presence or absence of EFNs) while keeping fixed the plant richness from sampling points (γ-diversity). We performed this randomization 1.000 times. In the end of each set of randomization, we counted the ant network richness of plants with EFNs (α_1) and plants without EFNs (α_2), in order to assess whether the ant network richness of plants with EFNs is higher than expected by ant network richness of plants without EFNs. The average of these values (α_{mean}) was subtracted from the γ-diversity to obtain the β-diversity. We did this randomization using MATLAB.

3. RESULTS

In this study, we recorded 238 plant species (72 with EFNs) and 149 ant species. The number of plant species with EFNs was lower (Mean ± SD: 21.4 ± 3.77) than plants without EFNs (27.2 ± 3.97, t= -3.093, df= 11, *P*= 0.011). However, the number of ant species on plants with EFNs (23.2 ± 5.85) was not different from plants without EFNs in the sampling points studied (23.3 ± 4.11) (t= -0.0647, df= 11, P= 0.949). Likewise, the interaction frequency was also equal between networks of ants and plants with EFNs (77.91 ± 12.58) and plants without EFNs (75.58 ± 10.46) (t= 1.239, df= 11, P= 0.241). The mean and variance as to the number of links per plant with EFNs (Mean ± Variance: 3.46 ± 0.28) were higher than plants without EFNs (Mean ± Variance: 2.69 ± 0.48) (t= -3.876, df= 11, P= 0.003, Figure 1A). For ants, the mean and variance of the number of links per ant did not differ between networks of plants with EFNs (Mean ± Variance: 2.67 ± 0.14) and without EFNs (Mean ± Variance: 2.64 ± 0.10) (t= 0.258, df= 11, P= 0.801) (Figure 1B).

The network connectance of ants and plants with EFNs were higher (Mean ± SD: 0.140 ± 0.03) than the network connectance of ants and plants without EFNs (0.109 ± 0.02) (t= -3.528, df=11, P= 0.005) (Figure 1C). In none of our sampling points did we observe significantly higher modularity than expected by the heterogeneity of interactions (P> 0.05). However, there is a tendency that the modularity index was lower in networks of ants and plants with EFNs (0.459 ± 0.059) than in the networks of ants and plants without EFNs (0.519 ± 0.061) (t= 3.552; df= 11; P= 0.005) (Figure 1D).

The nestedness was higher in networks of ants and plants with EFNs (Mean ± SD: 21.01 ± 4.46) than the nestedness in networks of ants and plants without EFNs (15.75 ± 3.33) (t= -3.427; df= 11; P= 0.006) (Figure 1E), as well as their standard normal deviate (Z-Score metric): networks of ants and plants with EFNs (3.63 ± 1.51) and networks of ants and plants without EFNs (2.34 ± 1.35) (t= -2.270; df= 11; P= 0.04) (Figure 1F).

The model developed in this study showed that the species of ants and plants that form the generalist core region interact more among themselves than expected by their abundances (Figure 2). Moreover, the species on the periphery of the network interact less than expected by their abundances. This same pattern was repeated in the 12 networks evaluated in this study.

The β-diversity turnover of ant and plant networks with and without EFNs involves approximately one third of the total diversity, indicating limited turnover of ant composition among the networks. In addition, when we randomized the plant classification (presence or absence of EFNs), there was no difference between the observed and expected values for β-diversity. In other words, the presence of EFNs did not propitiate an increase in the number of ant species (t= 1.448, df= 11, P= 0.176) and the species turnover does not change in intensity in the networks. Thus, the ant species present in plants with EFNs were similar to those in plants without EFNs (Figure 3). Additional NMDS ordination of the ant community followed by ANOSIM showed similar results (see supplementary information).

4. DISCUSSION

Recently, some studies have shown that the relative species abundance is an important factor structuring mutualistic networks (Krishna et al. 2008, Vázquez et al. 2007, 2009b, Verdú and Valiente-Banuet 2011). Such studies show that the asymmetric interaction among species results from their abundances and that species abundance explains almost a third of the nested pattern in mutualistic networks. Here we showed that the topological structure of networks generated through deterministic process (plants with EFNs) is different than that of the networks generated by the natural abundance of ants on vegetation. Moreover, the core of generalist species in the ant and plant networks with EFNs interact more among themselves than expected by their abundance.

Some studies have suggested that, within a biological community, the difference in species abundances and sampling techniques can generate nested patterns (Fischer and Lindenmayer 2002, Lewinsohn et al. 2006, Blüthgen 2010), including simulated neutral networks (Blüthgen et al. 2008). This possibly explains the nested pattern on our ant and plant networks without EFN, as less abundant species tend to be subsets of the more abundant species (Vázquez et al. 2009b). When comparing the ecological networks in ant-plant interactions, however, we showed that the ant and plant networks with EFNs are more connected and nested than the ant and plant networks without EFNs, possibly due to difference in networks size. However, in this study nestedness cannot be explained by different patterns of richness, connectance and heterogeneity of interactions, since we controlled these variables through the Z-Score metric. Also the nestedness found is not explained by richness and mean number and nor is its variance of links per ant species, since they are similar in both ecological networks and controlled by the Z-Score metric. Thus, this points out that the structure of mutualistic ant-plant interactions found in this study is fundamentally different from what we should expect from connectances, species richness and abundances alone.

According to Bastolla et al. (2009) the nested pattern in mutualistic networks between plants and their animal pollinators or seed dispersers reduces interspecific competition enhancing the number of coexisting species. This is due to the small number of shared partners when compared with fully connected and compartmentalized networks (Bastolla et al. 2009). In the interaction ant and plant networks with EFNs studied here, we showed that within the matrices there is a region, or a "hard-core", where generalist plant and ant species interact more among themselves than expected by their abundances. In this study, similar to other mutualism networks, we assumed that all resources offered are nutritionally equal; however, we know that the quantity and quality of nectar may vary among species and plant individuals (Schupp and Feener 1991, Heil 2000). Maybe the core of generalist plant species has better resources and only ant species competitively superior (i.e. more recruitment or aggressive) monopolize the resources (Blüthgen and Fiedler 2004ab, Heil and McKey 2003) independent of its spatial abundance. Thus, we hypothesize that the hard-core region might be formed by competitively superior ant species that can exclude others. This hard-core region can be generated by ants that have ecophysiological and behavioral traits that enable them to find, dominate, and use the resource efficiently and over a longer time period.

In interactions between ants and plants with EFNs, only a few ant species of the subfamilies Myrmicinae, Formicinae and Dolichoderinae are known to have physiological adaptations for the acquisition, storage and digestion of liquid resources secreted by EFNs (Fowler et al. 1991, Oliveira and Brandão 1991, Davidson et al. 2003, 2004). Although there is an adaptive filter for the ants that feed on the liquid resources secreted by EFNs, we found a low turnover of ant species foraging on plants with and without EFNs. The absence of a particular ant species composition foraging on plants with EFNs was also observed by Schoereder et al. (2010). Therefore, the nested pattern observed in both ecological networks also studied here can not be explained by the ant species composition, as the presence of EFNs does not influence a particular ant species composition associated with this resource. Some ant genera that do not have adaptations for feeding on liquids resource can carry liquids externally, and these genera strongly associate with EFN bearing plants (e.g. *Acanthoponera*, *Ectatomma*, *Heteroponera*, *Pachycondyla*, *Paraponera*, *Pseudomyrmex*) (Oliveira and Brandao 1991, Almeida and Figueredo 2003, Davidson et al. 2003, 2004). But, in this study, the ant species composing the "hard-core" compartment show adaptations for liquid diet, such as: *Azteca*, *Brachymyrmex*, *Camponotus*, *Crematogaster*, *Dolichoderus.*

Here we showed that abundance is important in the nested pattern (Vázquez and Aizen 2006, Blüthgen et al. 2008, Vázquez et al. 2009b, Verdú and Valiente-Banuet 2011), but the core of generalist species interact more than expected by their abundance. Such core conformation implies that the generalist core can act as a coevolutionary vortex of more specialized interactions, where the convergence of traits occurs on both sides of the interaction, increasing over evolutionary time (Bascompte et al. 2003, Thompson 2005, Guimarães et al. 2007). Furthermore, it is possible that the hard-core is less variable over space and time, and can affect the ecological and evolutionary dynamics of these interactions. For instance, a stable core will have unknown implications to the geographic mosaic of coevolution (Thompson 2005). Finally, we suggest studies evaluating the consequences of spatial and temporal variations in ant-plant and other types of mutualistic networks as being the next step in the analysis of stability in core interactions.

ACKNOWLEDGEMENTS

We would like to thank Jéssica Falcão for your help during the fieldwork and for comments on earlier versions of this manuscript. We also thank Office National des Forêts Brazil for logistical support and Brazilian PPBio project for financial support. WD was granted with a master fellowship from the Coordination for the Improvement Higher Education Personnel (CAPES-Brazil). PRG and FMDM acknowledge the financial support of FAPESP. This is publication XXX in the NEBAM technical series.

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Figure 1

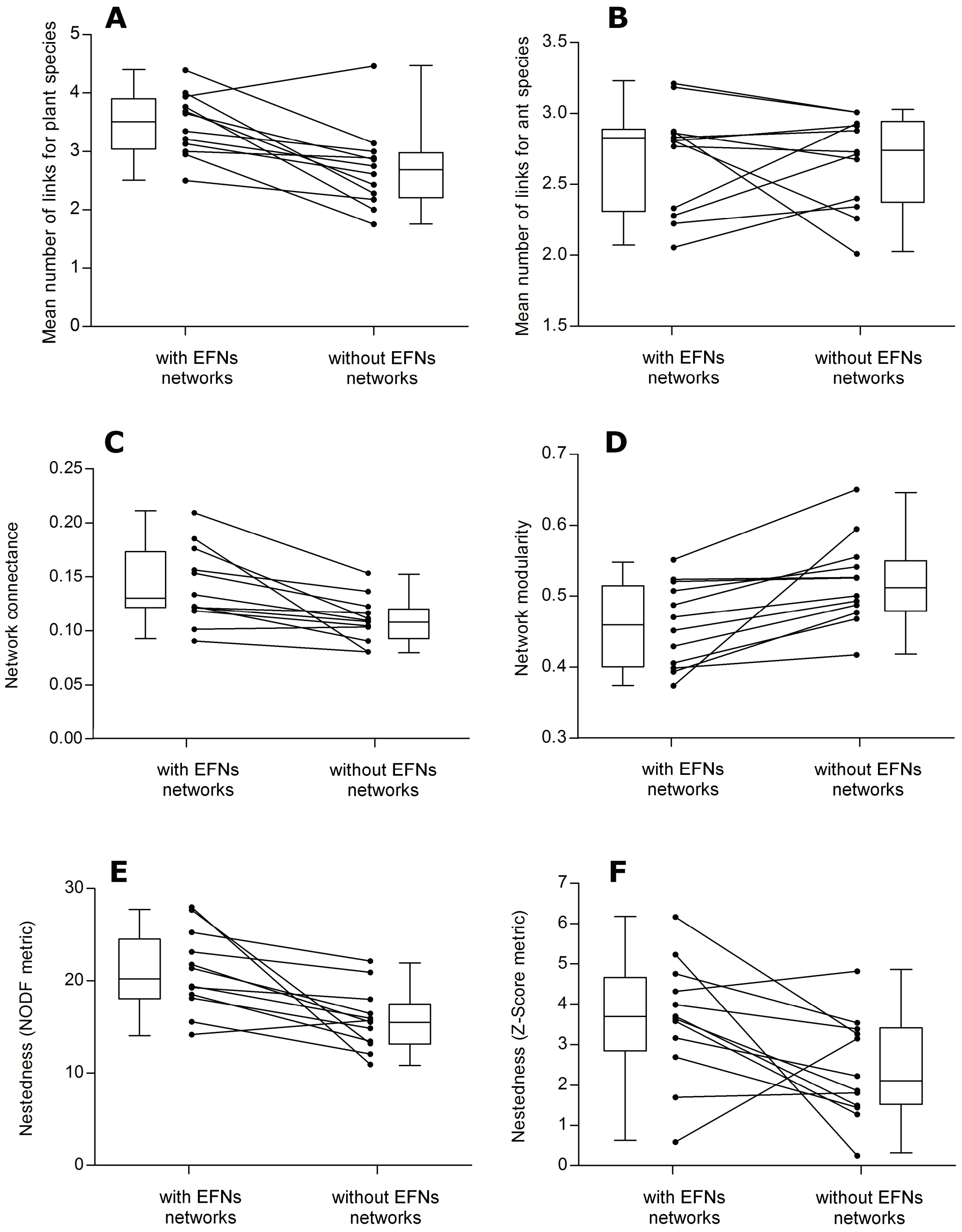

Figure 1. Relationship for the different metrics used in both ecological networks of ants and plants with and without extrafloral nectaries (EFNs): A) mean number of links for plant specie; B) mean number of links for ant specie; C) connectance; D) modularity*; E) nestedness (NODF metric); F) nestedness (Z-Score metric). Each line represents one of the

12 paired plots. It is also shown the boxplots with the distribution of the data set based on their descriptive parameters. Only the mean number of links for ant specie (B) was not significant (paired t-test: t= 0.258, df=11, P= 0.801).

* In any of the plots studied were observed modularity significantly higher than expected by the heterogeneity of interactions.

Figure 2

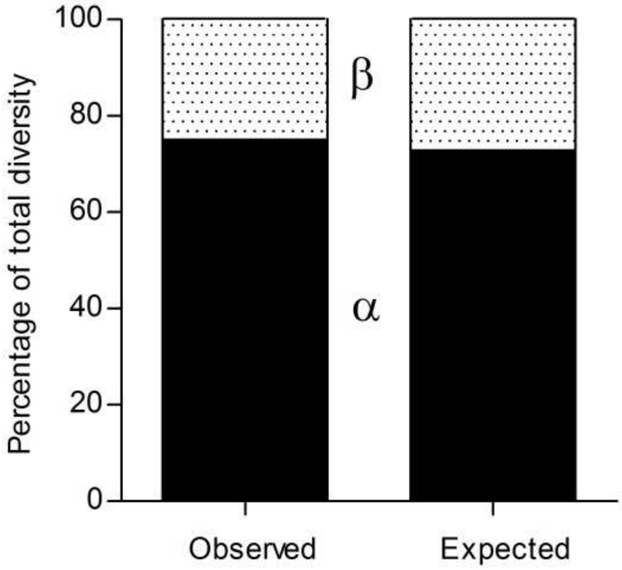

Figure 2. Average percentage of additive partitioning of total diversity of ants collected on plants with and without extrafloral nectaries in 12 plots of an *terra-firme* dense rainforest in the Brazilian Meridional Amazon. α-diversity represents the mean of ants richness collected on plants with and without extra-floral nectaries (EFNs). β-diversity represent the turnover of ant species composition collected on plants with and without EFNs in the plots. The total ant richness in both networks was determined by γ-diversity. The values of the additive partitioning of diversity expected were calculated excluding the effect of the presence of EFNs through 1,000 randomizations of plants classification (presence or absence of EFNs).

Figure 3

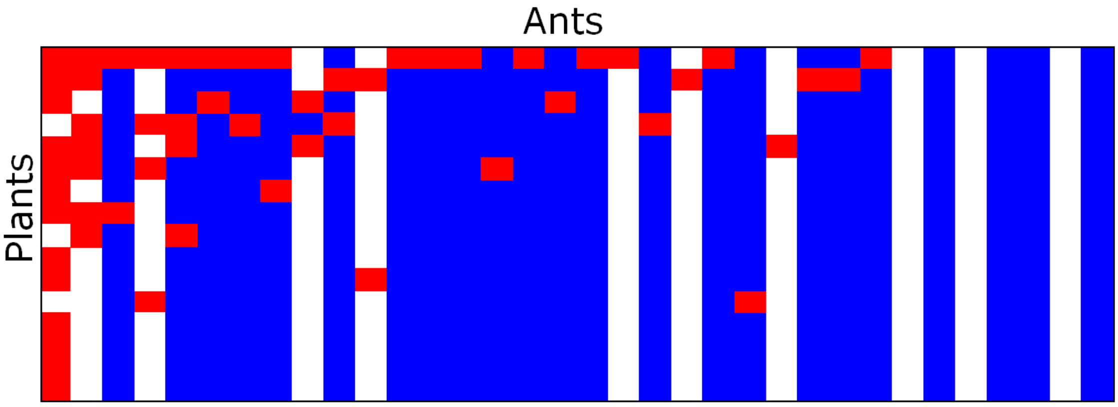

Figure 3. Graphical representation of one of the 12 interaction matrices among ants with extrafloral nectaries (EFNs) plants studied. This matrix shows the cases of an interaction between ants and plants mediated by the relative species abundance of both plants and ants. The red cells represents that the interaction occurs less than expected by the abundance, blue cells represents the interaction occurs more than expected by the abundance, white cells represents ant species collected in plants without EFNs was not collected in plants with EFNs.

Supplementary Information

To summarize the composition of the ant community in plants with and without EFNs, we ordered the similarity between points using Non-Metric Multidimensional Scaling. The ordinations analyses were performed from a distance matrix calculated from the Sorensen's dissimilarity index (qualitative data) and Bray-Curtis's dissimilarity index (quantitative data: frequency occurrence of ants on plants). Additionally, we tested the difference in the ant species composition through a permutation test (10,000 permutations) based on analysis of similarities (ANOSIM) (Clarke 1993). Both the ordination and analysis of similarities were made through the software R Development Core Team (version 2.13.1).

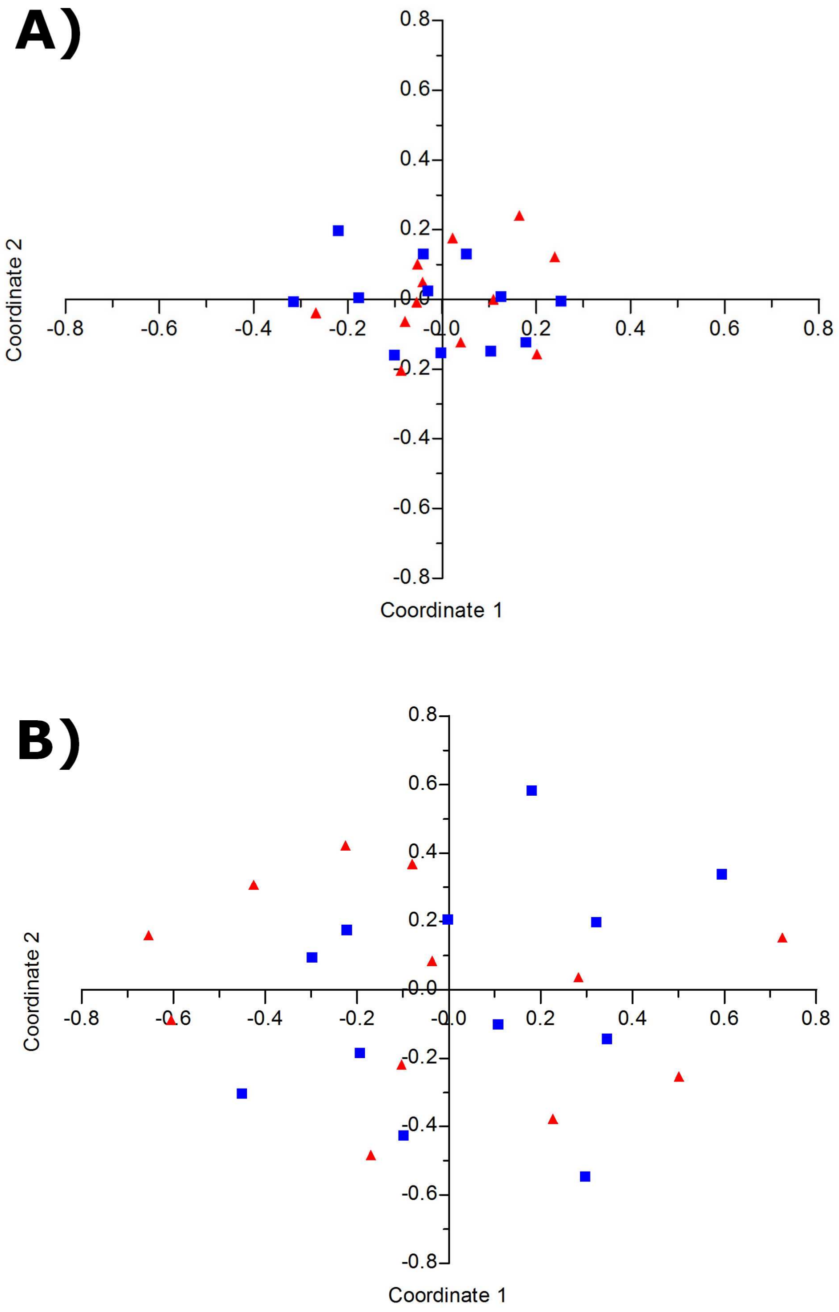

Figure 4. Non-metric multidimensional scaling of ants collected in plants with (triangles) and without extrafloral nectaries (squares) in 12 plots of an *terra-firme* dense rainforest in the Brazilian Meridional Amazon. This ordination analysis was calculated from the (A) Sorensen's dissimilarity index (Stress= 0.351 ; Axis 1 + Axis 2= 34.9% of explanation) and (B) Bray-Curtis's dissimilarity index (Stress= 0.318 ; Axis 1 + Axis 2= 43.7% of explanation).

CHAPTER 3

Spatial structure of ant-plant mutualistic networks*

**** This manuscript will be submitted to Oikos***

Submitted to Oikos

Running head: *Effect of space in ant-plant networks*

Spatial structure of ant-plant mutualistic networks

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ABSTRACT:

The topological structure of mutualism networks provides insights into ecological and evolutionary dynamics of interacting species. However, only recently has the spatial effect been incorporated as a mechanism structuring mutualistic networks. Here we used the ant-plant mutualistic networks to evaluate for the first time how the topological structure and species turnover of mutualistic networks varies over spatial gradient. Even the fact that ant and plant composition of networks changes over space, the generalist core species and the topological structure of networks remain unaltered. This finding indicates that independently of local and landscape environmental factors the nonrandom pattern of community organization is not changed. In short, contributing thus to our understanding of the maintenance of biodiversity and coevolutionary processes.

Keywords: beta diversity, coevolution, generalist core, nestedness, spatial turnover.

1. Introduction

The study of mutualistic networks has provided important insights into the mechanisms that contribute to the structural organization of plant-animal interactions. (Medan et al. 2007, Morales and Vázquez 2008, Nielsen and Bascompte 2007, Rezende et al. 2007, Stang et al. 2007, Vázquez et al. 2007, 2009). Using measures of graph theory to characterize the network topology, several studies have found non-random patterns of interaction on a wide range of ecosystems (Bascompte et al. 2003, Lewinsohn et al. 2006, Guimarães et al. 2007, Vázquez 2009a). However, little is known as such metrics vary over space (Morales and Vázquez 2008, Vázquez et al. 2009, Burkle and Alarcón 2011). In addition, to understand the consequences of spatial variation in mutualistic networks it is essential to determine how the space modulates the dynamics of interacting species (Burkle and Alarcón, 2011).

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, mainly because of the dominance hierarchy and species abundance of interactions can be modified (Solé and Montoya 2001, Olesen et al. 2002, Memmott et al. 2007, Aizen et al. 2008, Olesen et al. 2008, Díaz-Castelazo et al. 2004). Such studies have focused on evaluating how the entry of invasive alien species affects the structural organization of the network. However, very little is still known on how the species turnover along space affects the structure of networks.

When we compared this with other systems, eg. plant-polinator, ant-plant mutualistic networks have been studied on a small scale (Guimarães et. al. 2006, 2007, Chamberlain et al. 2010, Sugiura 2010) and the knowledge of space effect on these networks is null. Thus, we used the interactions between ants and plants with extrafloral nectaries (EFNs), to evaluate for the first time how the topological structure of mutualistic networks varies over the spatial gradient. In ant-plant mutualistic networks, plants produce nutritious liquid for ants (Baker et al. 1978, Rico-Gray and Oliveira 2007), which in exchange for the food provided, the ants defend the plants against potential herbivores (Del-Claro et al. 1996, Oliveira et al. 1999, Rico-Gray and Oliveira 2007).

On the other hand, different parameters can change the nature of ant-plant interactions, such as: competition, abundance and quality of resources, seasonality of nectar production, and other biotic and several abiotic factors (Blüthgen and Fiedler 2004, Díaz-Castelazo et al. 2004, Rico-Gray and Oliveira 2007, Rico-Gray et al. 2011). All these factors can be affected by the spatial distributions of ants on plants (Bentley 1976, Barton 1986, Heil 2000, Apple and Feener 2001, Cogni et al. 2003). In fact, in tropical forests, it is known that several plant species are spatially aggregated (Newbery et al. 1986, Condit et al. 2000, Köhler 2000), and that the foraging and dispersal of ants is limited to small spatial scales (Soares and Schoereder 2001, Fourcassié et al. 2003). So, according to neutral theory the compositional similarity among plant communities will decrease as the distance between two points increases, due to the limited dispersal of organisms and environmental gradients (Hubbel 2001, Chave and Leigh 2002, Gilbert and Lechowicz 2004).

Here we predicted that due to high spatial aggregation of plants in tropical regions and low ant mobility there is a mosaic of interactions with different partners over a relatively small geographic space, and this could generate differences in the topological structure of these networks (Thompson 2005, Morales and Vázquez 2008, Burkle and Alarcón, 2011). In order to test this hypothesis, we collected twelve ant-plant mutualistic networks in a *terra-firme* forest in Brazilian Meridional Amazon and analyzed their network topology. Subsequently, we calculated the dissimilarity of network topology over geographic distance among sampling points in order to examine whether: (1) species turnover over spatial gradient influences the topological structure of ant-plant mutualistic networks, and (2) the core of generalist species remains stable on a geographic scale of up to 5.099 meters.

2. Material and Methods

2.1) Study area

We conducted this study at São Nicolau Farm (9º48'S e 58º15'W, elev. 254m), located in the municipality of Cotriguaçu, north of Mato Grosso State, Brazil. According to the Köppen classification, the climate is tropical humid (Am) with average annual temperature: 24 °C, humidity 85 %, and 2.300 mm of precipitation (Camargo et al. 2010, Dáttilo et al. 2012). It has two well defined seasons, a rainy season between November and April and dry season between May and October. The area is characterized as a *terra-firme* dense rainforest inserted in the Brazilian Meridional Amazon (Veloso et al. 1991, Camargo et al. 2010). The reserve area covers 7.000 ha of continuous forest, surrounded by a much larger area of intact forest. The terrain is undulating with altitudinal variation of 50 m between the plateaus and the riverside terrains. Canopy trees range from 30-40 m high with some emergent trees which reach 50 m in height. The understory is relatively open, with high frequency of *Orbignya phalerata* Mart. (Arecaceae). In the Brazilian Amazon, it is usual to find between 18 and 53% of plant species in different physiognomies having EFNs, reaching up to 50% coverage of these plants in a given physiognomy (Morellato and Oliveira, 1991, Rico-Gray and Oliveira 2007).

2.2) Data Collection

We collect data in a site (module) managed by the Brazilian Research Program in Biodiversity (PPBio) (PPBio: http://ppbio.inpa.gov.br) inserted at São Nicolau Farm. The module consists of six parallel trails in the North-South and two parallel trails East-West.

Every 1 Km trail is one permanent plot with 250 m x 25 m (6.250 m²), total of 12 sampling points in the entire module.

We collected ants and plants between December 2010 and January 2011. In each of the 12 sampling points, we looked for EFN plants reaching from 0.5 m to 3 m height. This size was used because of its easily accessible size to researchers without disturbance. In each plant, we recorded all occurrences of ants collecting liquids in EFN. The plants should be at least 10 meters away from each other, in order to minimize the possibility of collecting ants from the same colony foraging on different plants. Plants and ants were identified to the lowest possible taxonomic level using taxonomic keys and with the help of specialists. Ant specimens were deposited in the Setor de Entomologia of Coleção Zoológica of Universidade Federal de Mato Grosso, Brazil (CEMT).

2.3) Network topology

To evaluate how topological properties of ant-plant mutualistic networks vary over space, we calculated the dissimilarity among the 12 sampling points of the following metrics: connectance, network specialization, and nestedness. 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') (ranges from zero (extreme generalization) to one (extreme specialization) through R-Project software version 2.13.1 (bipartite packpage, R Development Core Team 2005). This index is mathematically derived from the Shannon entropy, and based on the deviation from the expected probability distribution of the interactions (Blüthgen et al. 2006). In addition, the index is robust to changes in sampling intensity and the number of interacting species (see more details of this index in Blüthgen et al. 2006, 2007).

We calculated the NODF metric (Nestedness metric based on Overlap and Decreasing Fill) (Almeida-Neto et al. 2008) to estimate the nestedness value of networks, using ANINHADO software (Guimarães and Guimarães 2006). We tested the nestedness observed for each network with 1.000 networks generated by Null Model II, in order to assess if the nestedness value observed was higher than expected by random patterns of interaction. In this null model, the probability of an interaction occur is proportional to the level of generalization (degree) of plant and animal species (Bascompte et al. 2003). We also calculated the nestedness value standardizing the difference in richness, connectance and heterogeneity of interactions among the sampling points studied using the Z-Score metric to allow cross network comparisons. Z-Score is defined as: $Z_{nodf} = (x - \mu) / \sigma$, where x= NODF value observed, μ= NODF value of randomized matrices, and σ= is the standard deviation of the randomized matrices (Ulrich et al 2009).

2.4) Spatial turnover of species composition

We calculated the additive partitioning of diversity in ant-plant networks as suggested by Veech et al. (2002) to access the spatial turnover among the sampling points studied on plant and ant species composition (β-diversity). From the total richness of the same trophic level found in two sampling points (γ-*diversity*), we calculated the α-diversity, defined as: $\alpha = (\alpha_1 + \alpha_2)/2$, where α_1 = species richness of same trophic level of plot 1, α_2 = species richness of the same trophic level of plot 2). Then, we calculated the β-diversity, defined as: $\beta = (\gamma - \alpha)$. Moreover, we calculated which species belongs to the generalist core through: $Cg = \left(\frac{x-y}{z}\right) > 1$, where *x* = mean number of links for given plant/ant species, *y* = mean number of links for all plant/ant species in network , e *z* = standard deviation of the number of links for plant/ant species. Thus, we also calculated the turnover of β-diversity (as described above) just for plants and ants inserted on generalist core species.

2.5) Statistical analysis

We used Mantel tests to determine the existence of a relationship between the turnover on different network metrics described above and the matrices of geographic distances among all the sampling points studied. We conducted these tests using the vegan package (Oksanen et al. 2007) in the R-Project software version 2.13.1 (R Development Core Team 2005) using Euclidean distance to calculate the dissimilarity in the metrics and geographic distances among sampling points. In these analyses, we also tested the correlation coefficient (r) using this analysis. We made all graphics using the software GraphPad Prism version 5.0 (Motulsky, 1999).

3. Results

In this study, we recorded 72 plant species (or morphospecies) with EFNs, belonging to 24 genera and 16 families. The Bignoniaceae family corresponded to 26.3% of plant species, followed by 22.8% of Mimosaceae and 10.5% of Caesalpiniaceae. The plant species richness per sampling points was 21.41 ± 3.77 (Mean ± SD). For ants, we recorded 149 species, inserted into 23 genera and eight subfamilies. The subfamily Myrmicinae corresponded to 42.28% of ant species, followed by 26.1% for Formicinae and 14.9% for Dolichoderinae. The ant species richness per sampling points was 23.16 ± 5.85. The mean and standard deviation of metrics used in this study were: Connectance: (0.140 ± 0.035), Network specialization: (0.088 ± 0.049), NODF: (21.01 ± 4.406), nestedness Z-Scores (3.63 ± 1.50).

In the spatial scale studied, we did not find significant correlation of dissimilarity of geographic distance with the dissimilarity of connectance (Mantel statistic r= 0.044, P= 0.374) and network specialization (H_2’) (Mantel statistic r= 0.004, P= 0.457) (Figure 1A-B). When analyzed we had different results in the two metrics that describe the nested pattern in ant-plant interactions. We did not observe significant correlation of dissimilarity of nestedness calculated by NODF metric with geographic distance (Mantel statistic r= 0.078, P= 0.283). However, we observed significant correlation of dissimilarity of geographic distance with the dissimilarity of nestedness calculated by Z-Score metric (Mantel statistic r= 0.315, P< 0.01) (Figure 1C-D).

We observed a turnover of species composition (β-diversity), for both plants and ants, along the geographic distance (Plants: Mantel statistic r= 0.401, P< 0.01, Ants: Mantel statistic r= 0.307, P= 0.013) (Figure 2A-B). However, we did not observe a turnover on core species composition, for both plants and ants, along the geographic distance (Plants: Mantel statistic r= 0.007, P= 0.437, Ants: Mantel statistic r= -0.088, P= 0.734 (Figure 2C-D). In addition, the number of ant species present in the generalist core of networks ranged between one and three species, and the species *Azteca* sp2, *Brachymyrmex* sp1 and *Crematogaster* sp8 were present in the core in more than 58 % of sampling points. For plants, the number of species present in the generalist core of networks ranged between one and two species, and the species *Inga* sp12, *Mabea* sp2, *Protium* sp1, *Stryphnodendron* sp1 were present in the core in more than 66 % of sampling points.

4. Discussion

We know from previous studies that mutualistic networks of free-living species show a nested and asymmetrical pattern in different habitats and ecosystems such as plant-pollinator, fruit-frugivore, ant-plant, clownfish-anemone and marine fish cleaning symbioses (Bascompte et al. 2003, Guimarães et al. 2006, Guimarães et al. 2007, Ollerton et al. 2007, Mello et al. 2011). However, how the topological structure of these networks varies over spatial gradients has often been ignored. The few studies that evaluated the role of spatial variations in mutualistic networks, show us that local and landscape environmental factors, beyond 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 in ant-plant mutualistic networks, the topological structure remains unaltered in the spatial scale studied. In addition, even the fact that ant and plant composition of networks changes over space, the generalist core species remain stable along the 5.099 m on a *terra-firme* forest in Brazilian Meridional Amazon.

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 ant queen dispersal (Benson and Harada 1988, Hölldobler and Wilson 1990, Reyes-Lopes et al. 2003). Thus, along a spatial scale, different biotic and abiotic factors can influence the richness and diversity of interactions between ants and plants differently (Brühl et al. 1999, Díaz-Castelazo et al. 2004, Rico-Gray and Oliveira 2007, Rico-Gray et al. 2011). In this study, there was a wide variation in the values of connectance among sampling points, influencing the values of nestedness using NODF metric. In fact, when we calculated the dissimilarity among these metrics, there was no relation with geographic distance. On the other hand, when we controlled the connectance effects, we found different patterns and nestedness values using Z-Score metric, since the dissimilarity of nestedness increased with geographic distance. So why are closer sampling points more similar? This can be explained because closer sampling points have lower turnover of plant and ant composition, as we observed. Therefore, it was expected that the number of ant and plant species, beyond number of interactions would be more similar in closer sampling points. Additionally, the metric used to calculate the network specialization is also robust with respect to networks with different connectance values (Blüthgen et al. 2006, 2007, 2010), which indicated us 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 5.099 meters, independent of variations in biotic and abiotic factors of sampling points studied.

Interestingly, we showed that the core of generalist species remained stable over the spatial scale studied. One factor that could explain the stability of the core over space is the species abundance, where abundant species could interact most frequently with each other and with other less abundant species (Vázquez et al. 2007, 2009b). However, in a previous paper by Dáttilo et al. *in preparation*, showed that in ant-plant mutualistic networks, the generalist core interact with each other more than expected by their abundances. This finding indicates that ants of the core possibly have mechanisms which maintain such species in the core over space. Due to the fact that competition for resource is an important factor in the structuring of ant communities in tropical regions (Djieto-Lordon & Dejean. 1999, Delabie et al 2000), we believe that the core of generalist ant species are competitively superior (i.e. more recruitment orientated or aggressive) and monopolize resources. In addition, we propose that this generalist core is less variable in time and space than the network periphery as originally proposed by Bascompte et al. (2003). Moreover, the interaction strength among interacting partners of generalist core species is symmetrical (Bascompte et al. 2006, Vázquez et al. 2007, Guimarães et al. 2011). This implies that the 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 (Bascompte et al. 2003; Thompson 2005; Guimarães et al. 2007). The existence of a geographic stable hard-core enhances the coevolutionary importance of such a vortex, once several individuals of ants and plants that belong to the core, in a given region, will have an increased chance of interacting with each-other. Additionally, Díaz-Castelazo et al. (2010), showed that the proportion of generalist core species in ant-plant interaction did not change in 10 years on a local scale. Thus, the generalist core being stable over space and time at different spatial scales, can generate the geographic mosaic of coevolution, where the number of interacting species increases over evolutionary time (Thompson 2005).

In conclusion, our study shows that in general, the topological structure of ant-plant mutualistic networks is stable over a relatively small geographic space inserted in a *terra-firme* forest in Brazilian Meridional Amazon. Moreover, even that a turnover on interacting ant and plant composition changes along this spatial scale, the generalist core remains stable. This finding indicates that independently of local and landscape environmental factors the nonrandom pattern of community organization is not changed. In short, contributing thus to our understanding as to the maintenance of the biodiversity and coevolutionary processes. However, it is not known what the consequences of temporal variations and resilience of the generalist core in larger spatial scales is. There is still much to do to better understand patterns and processes related to spatiotemporal variation in ant-plant systems. Finally, other empirical studies that assess the spatial effect in different mutualistic networks are essential to understanding the current view of coevolutionary processes in mutualistic interactions.

Acknowledgements

We would like to thank Jéssica Falcão for your help during the fieldwork and for their comments on earlier versions this manuscript. We also thank Office National des Forêts Brazil by logistical support and Brazilian Program for Biodiversity Research by financial support. WD is granted by a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior master's fellowship. PRG acknowledge the financial support of Fundação de Amparo à Pesquisa do Estado de São Paulo. This is publication XXX in the Núcleo de Estudos da Biodiversidade da Amazônia Mato-Grossense technical series.

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Figures

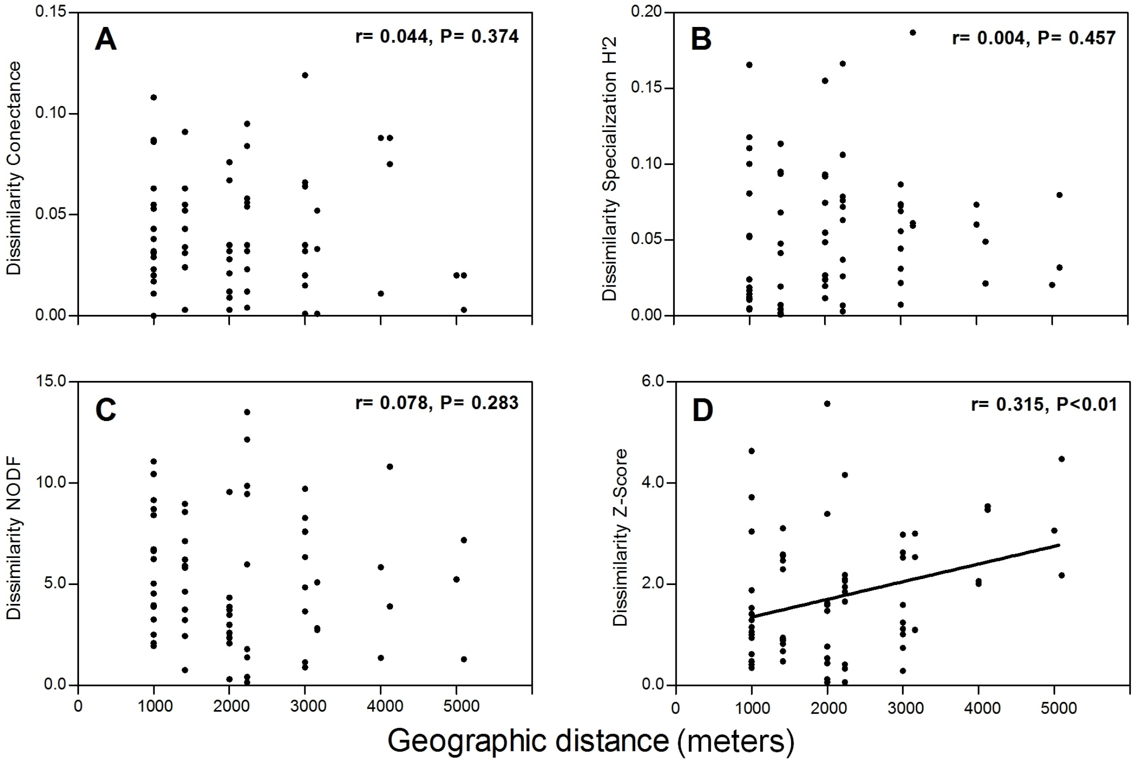

Figure 1. Relationship among the dissimilarity of: a) connectance, b) network specialization, c) nestedness by NODF metric and d) nestedness by Z-Score metric, with dissimilarity of geographic distance of 12 plots collected in the São Nicolau Farm, Mato Grosso State, Brazilian Meridional Amazon. Correlation coefficient (*r*) and significance (*P* computed using Mantel tests) also are shown. (n= 66 points in each of the metrics calculated).

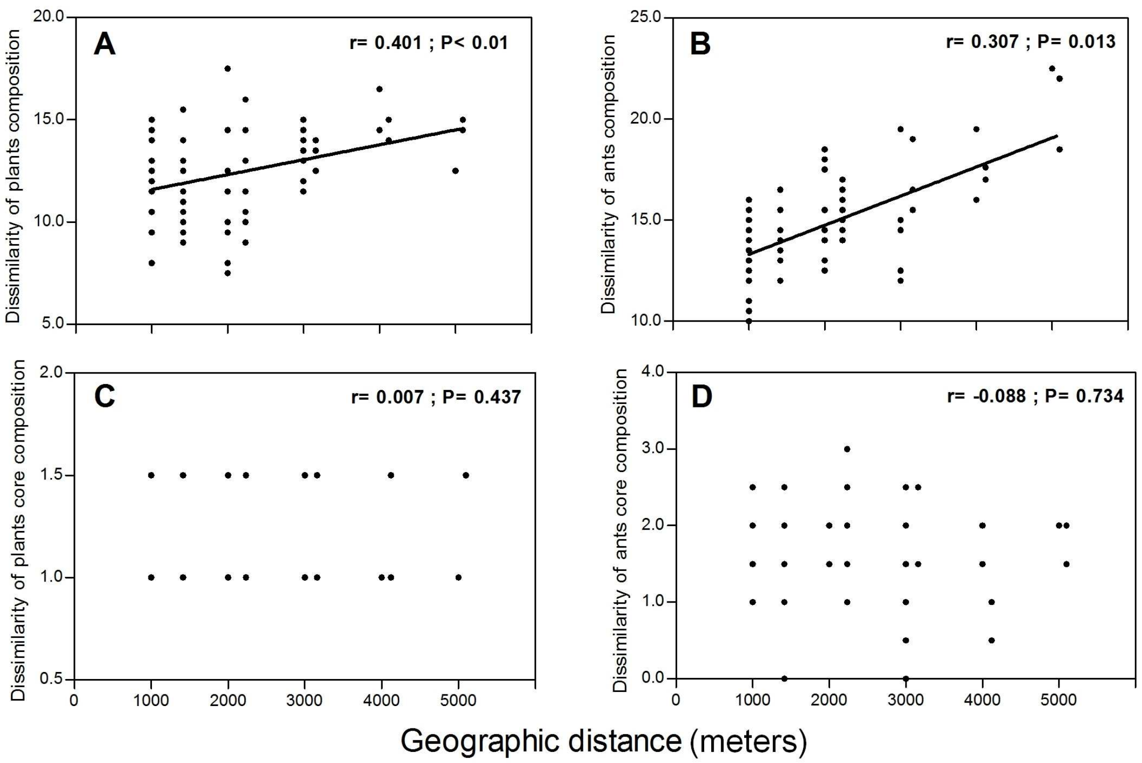

Figure 2. Relationship among the dissimilarity of: a) plants species composition, b) ants species composition, c) plants core composition and b) ants core composition, with dissimilarity of geographic distance of 12 plots collected in the São Nicolau Farm, Mato Grosso State, Brazilian Meridional Amazon. Correlation coefficient (*r*) and significance (*P* computed using Mantel tests) also are shown. (n= 66 points in each of the metrics calculated).

FINAL CONCLUSION

Here I showed that the topological structure of networks generated through deterministic process (plants with EFNs) is different than that of the networks generated by the natural abundance of ants on vegetation. Moreover, the core of generalist species in the ant and plant networks with EFNs interact more among themselves than expected by their abundance. Moreover, standardizing the network metrics, collection effort and habitat, I showed that in ant-plant mutualistic networks, the topological structure remains unaltered in the spatial scale studied. In addition, even the fact that ant and plant composition of networks changes over space, the generalist core species remain stable along the 5.099 m on a *terra-firme* forest in Brazilian Meridional Amazon.

APPENDIX 1

List of 238 plant species with and without extrafloral nectaries (EFNs) collected in 12 plots (250 x 25 m) in an terra-firme forest in the Brazilian Meridional Amazon located in the municipality of Cotriguaçu, north of Mato Grosso State, Brazil. The plants were collected between between December 2010 and January 2011.

	with EFNs	without EFNss
Anacardiaceae		
Astronium sp1		X
Tapirira sp1		X
Thyrsodium sp1		X
Anonaceae		
Annona sp1		X
Annona sp2		X
Duguetia sp1		X
Xylopia sp1		X
Xylopia sp2		X
Xylopia sp3		X
Apocynaceae		
Aspidosperma sp1		X
Aspidosperma sp2		X
Aspidosperma sp3		X
Bignoniaceae		
Jacaranda sp1	X	
Jacaranda sp2		X
Unidentified sp1	X	
Unidentified sp2	X	
Unidentified sp3	X	
Unidentified sp4		X
Unidentified sp5	X	
Unidentified sp6	X	
Unidentified sp7	X	
Unidentified sp8	X	

Unidentified sp9		X
Unidentified sp10		X
Unidentified sp11	X	
Unidentified sp12	X	
Unidentified sp13	X	
Unidentified sp14		X
Unidentified sp15	X	
Unidentified sp16	X	
Unidentified sp17	X	
Unidentified sp18		X
Unidentified sp19	X	
Unidentified sp20		X
Bixaceae		
Bixa sp1		X
Bombacaceae		
Eriotheca sp1		X
Burseraceae		
Protium pilosum	X	
Protium sp1	X	
Trattinnickia sp1		X
Trattinnickia sp2		X
Caesalpiniaceae		
Bauhinia sp1	X	
Bauhinia sp2	X	
Bauhinia sp3	X	
Bauhinia sp4	X	
Bauhinia sp5	X	
Bauhinia sp6		X
Hymenaea sp1		X
Unidentified sp1	X	
Unidentified sp2		X
Tachigali sp1		X
Tachigali sp2		X
Tachigali venusta		X

Celastraceae		
Cheiloclinium sp1	X	
Hypocrateae sp1		X
Chrysobalanaceae		
Hirtella sp1		X
Hirtella sp2		X
Licania sp1		X
Combretaceae		
Combretum sp1	X	
Costaceae		
Costus sp1	X	
Costus sp2	X	
Costus sp3	X	
Cucurbitaceae		
Unidentified sp1	X	
Elaeocarpaceae		
Sloanea sp1		X
Sloanea sp2		X
Sloanea sp3		X
Euphorbiaceae		
Hevea sp1		X
Mabea sp1	X	
Mabea sp3		X
Unidentified sp1	X	
Unidentified sp1	X	
Fabaceae		
Dipteryx sp1		X
Erythrina sp2	X	
Machaerium sp1	X	
Machaerium sp2	X	
Machaerium sp3	X	
Machaerium sp4		X
Unidentified sp1		X
Ormosia sp1		X

Platymiscium sp1		X
Platymiscium sp2		X
Platymiscium sp3		X
Vatairea sp1	X	
Flacourtiaceae		
Casearia sp1		X
Casearia sp3		X
Casearia sp3	X	
Laetia sp1		X
Laetia sp2		X
Laetia sp3		X
Heliconiaceae		
Heliconia sp1		X
Humiriaceae		
Vantanea sp1		X
Lacistemataceae		
Lacistema sp1		X
Lauraceae		
Aniba sp1		X
Unidentified sp1		X
Unidentified sp2		X
Ocotea sp1		X
Ocotea sp2		X
Lecytidaceae		
Couratari sp1	X	
Malpighiaceae		
Byrsonima sp1		X
Marantaceae		
Ischnosiphon sp1		X
Melastomataceae		
Bellucia sp1		X
Miconia sp1		X
Meliaceae		
Guarea sp1		X

Guarea sp2		X
Guarea sp3		X
Guarea sp4		X
Trichilia micrantha		X
Trichilia pallida		X
Trichilia sp1		X
Trichilia sp2		X
Memecylaceae		
Mouriri sp1		X
Menispermaceae		
Abuta grandifolia		X
Abuta sp1		X
Mimosaceae		
Abarema sp1	X	
Abarema sp1	X	
Enterolobium sp1	X	
Inga sp1	X	
Inga sp2	X	
Inga sp3	X	
Inga sp4	X	
Inga sp5	X	
Inga sp6	X	
Inga sp7	X	
Inga sp8	X	
Inga sp9	X	
Inga sp10	X	
Inga sp11	X	
Inga sp12	X	
Inga sp13	X	
Inga sp14	X	
Inga sp15	X	
Inga sp16		X
Inga sp17		X
Mimosa sp1	X	

Mimosa sp2	X	
Parkia sp1		X
Parkia sp2		X
Samanea sp1	X	
Senegalia sp1	X	
Stryphnodendron sp1	X	
Moraceae		
Brosimum sp1		X
Brosimum sp2		X
Brosimum sp3		X
Ficus sp1		X
Ficus sp2		X
Ficus sp3		X
Ficus sp4		X
Ficus sp5		X
Pseudolmedia cf laevigata		X
Pseudolmedia sp1		X
Pseudolmedia sp2		X
Sorocea sp1		X
Myristicaceae		
Cybianthus sp1		X
Virola sp1		X
Virola sp2		X
Nyctaginaceae		
Guapira sp1		X
Ochnaceae		
Cespedezia sp1		X
Olacaceae		
Dulacia sp1		X
Piperaceae		
Piper sp1		X
Piper sp2		X
Piper sp3		X

Piper sp4		X
Polygonaceae		
Coccoloba sp1		X
Quiinaceae		
Quiina pteridofila		X
Rubiaceae		
Capirona sp1		X
Duroia sp1		X
Unidentified sp1		X
Palicourea sp1	X	
Palicourea sp2		X
Palicourea sp3		X
Palicourea sp4		X
Psychotria sp1		X
Remijia amazonica		X
Remijia sp1		X
Remijia sp2		X
Uncaria sp1	X	
Rutaceae		
Esenbeckia sp1		X
Metrodorea sp1		X
Metrodorea sp2		X
Zanthoxylum sp1		X
Sapindaceae		
Paullinia sp1		X
Serjania sp1		X
Thalisia sp1		X
Thalisia sp2		X
Thalisia sp3	X	
Sapotaceae		
Ecclinusa sp1		X
Ecclinusa sp2		X
Ecclinusa sp3		X
Ecclinusa sp4		X

Manilkara hulberia		X
Manilkara sp1		X
Manilkara sp2		X
Pouteria sp1		X
Pouteria sp2		X
Pouteria sp3		X
Pouteria sp4		X
Simaroubaceae		
Simarouba amara		X
Siparunaceae		
Siparuna sp1		X
Siparuna sp2		X
Siparuna sp3		X
Solanaceae		
Unidentified sp1		X
Unidentified sp2		X
Sterculiacea		
Theobroma sp1		X
Theobroma sp2		X
Theobroma sp3		X
Theobroma sp4		X
Theophrastaceae		
Clavija sp1		X
Tiliaceae		
Luehea sp1		X
Ulmaceae		
Celtis sp1		X
Trema micrantha	X	
Urticaceae		
Urera sp1	X	
Urera sp1		X
Vouchysiaceae		
Vouchysia sp1		X

Unidentified sp1		X
Unidentified sp2		X
Unidentified sp3		X
Unidentified sp4		X
Unidentified sp5		X
Unidentified sp6		X
Unidentified sp7		X
Unidentified sp8		X
Unidentified sp9	X	
Unidentified sp10		X
Unidentified sp11		X
Unidentified sp12		X
Unidentified sp13	X	
Unidentified sp14		X
Unidentified sp15		X
Unidentified sp16	X	
Unidentified sp17	X	
Unidentified sp18		X
Unidentified sp19		X
Unidentified sp20		X
Unidentified sp21		X
Unidentified sp22	X	
Unidentified sp23		X
Unidentified sp24		X
Unidentified sp25		X
Unidentified sp26		X
Unidentified sp27		X

APPENDIX 2

List of 149 ant species collected on plants with and without extrafloral nectaries (EFNs) collected in 12 plots (250 x 25 m) in an terra-firme forest in the Brazilian Meridional Amazon located in the municipality of Cotriguaçu, north of Mato Grosso State, Brazil. The plants were collected between between December 2010 and January 2011.

	Occurrence on plants	
FAMLIY FORMICIDAE	**With EFNs**	**Without EFNs**
SUBFAMILY DOLICHODERINAE		
Tribe Dolichoderini		
Azteca sp1	X	X
Azteca sp2	X	X
Azteca sp3	X	X
Azteca sp4	X	X
Dolichoderus sp1	X	X
Dolichoderus sp2	X	X
Dolichoderus sp3	X	X
Dolichoderus sp4	X	X
Dolichoderus sp5	X	X
Dolichoderus sp6	X	X
Dolichoderus sp7	X	X
Dolichoderus sp8	X	X
Dolichoderus sp9	X	X
Dolichoderus sp10	X	X
Dolichoderus sp11	X	X
Dolichoderus sp12	X	X
Dolichoderus sp13	X	X
Dolichoderus sp14	X	X
Tapinoma sp1	X	X
Tapinoma sp2	X	X
Tapinoma sp3	X	X
SUBFAMILY ECITOTINAE		

Tribe Ecitonini		
Eciton sp1		X
SUBFAMILY ECTATOMMINAE		
Tribe Ectatommini		
Ectatomma tuberculatum	X	X
SUBFAMILY FORMICINAE		
Tribe Camponotini		
Camponotus latangulus	X	X
Camponotus sp1	X	X
Camponotus sp2	X	X
Camponotus sp3	X	X
Camponotus sp4	X	X
Camponotus sp5	X	X
Camponotus sp6	X	X
Camponotus sp7	X	X
Camponotus sp8	X	X
Camponotus sp9	X	X
Camponotus sp10	X	X
Camponotus sp11	X	X
Camponotus sp12	X	X
Camponotus sp13	X	X
Camponotus sp14	X	X
Camponotus sp15	X	X
Camponotus sp16	X	X
Camponotus sp17	X	X
Camponotus sp18	X	X
Camponotus sp19	X	X
Camponotus sp20	X	X
Camponotus sp21	X	X
Camponotus sp22	X	X
Camponotus sp23	X	X
Camponotus sp24	X	X

Camponotus sp25	X	X
Camponotus sp26	X	X
Tribe Plagiolepidini		
Brachymyrmex sp1	X	X
Brachymyrmex sp2	X	X
Brachymyrmex sp3	X	X
Brachymyrmex sp4	X	X
Brachymyrmex sp5	X	X
Brachymyrmex sp6	X	X
Nylanderia sp1	X	
Nylanderia sp2	X	X
Nylanderia sp3	X	X
Nylanderia sp4	X	X
Nylanderia sp5	X	
Nylanderia sp6	X	
SUBFAMILY MYRMICINAE		
Tribe Attini		
Sericomyrmex sp1		X
Trachymyrmex sp1	X	
Tribe Blepharidattini		
Wasmannia auropunctata	X	X
Tribe Cephalotini		
Cephalotes atratus	X	X
Cephalotes sp1	X	X
Cephalotes sp2	X	X
Cephalotes sp3	X	X
Cephalotes sp4	X	X
Cephalotes sp5	X	X
Cephalotes sp6	X	X
Cephalotes sp7	X	X
Cephalotes sp8	X	X
Tribe Crematogastrini		
Crematogaster sp1	X	X

Crematogaster sp2	X	X
Crematogaster sp3	X	X
Crematogaster sp4	X	X
Crematogaster sp5	X	X
Crematogaster sp6	X	X
Crematogaster sp7	X	X
Crematogaster sp8	X	X
Crematogaster sp9	X	X
Crematogaster sp10	X	X
Crematogaster sp11	X	X
Crematogaster sp12	X	X
Tribe Formicoxenini		
Nesomyrmex sp1	X	
Nesomyrmex sp2	X	X
Nesomyrmex sp3	X	
Tribe Ochetomyrmecini		
Ochetomyrmex neopolitus	X	X
Ochetomyrmex semipolitus	X	X
Tribe Pheidolini		
Pheidole sp1	X	X
Pheidole sp2	X	X
Pheidole sp3	X	X
Pheidole sp4	X	X
Pheidole sp5	X	X
Pheidole sp6	X	X
Pheidole sp7	X	X
Pheidole sp8	X	X
Pheidole sp9	X	X
Pheidole sp10	X	X
Pheidole sp11	X	X
Pheidole sp12	X	X
Pheidole sp13	X	X
Pheidole sp14	X	X
Pheidole sp15	X	X

Pheidole sp16	X	X
Pheidole sp17	X	X
Pheidole sp18	X	X
Pheidole sp19	X	X
Pheidole sp20	X	X
Pheidole sp21	X	X
Pheidole sp22	X	X
Pheidole sp23	X	X
Pheidole sp24	X	X
Tribe Solenopsidini		
Megalomyrmex sp1	X	
Solenopsis sp1	X	X
Solenopsis sp2	X	X
Solenopsis sp3	X	X
Solenopsis sp4	X	X
Solenopsis sp5	X	X
Solenopsis sp6	X	X
Solenopsis sp7	X	X
Solenopsis sp8	X	X
Solenopsis sp9	X	X
SUBFAMILY PARAPONERINAE		
Tribe Paraponerini		
Paraponera clavata	X	X
SUBFAMILY PONERINAE		
Tribe Ponerini		
Odontomachus sp1	X	X
Pachycondila sp1	X	X
Pachycondila sp2	X	X
Pachycondila sp3	X	X
Pachycondila sp4	X	X
Pachycondila sp5	X	X
Pachycondila sp6	X	X

Pachycondila sp7	X	X
Pachycondila sp8	X	X
Pachycondila sp9	X	X
Pachycondila sp10	X	X
Pachycondila sp11	X	X
SUBFAMILY PSEUDOMYRMICINAE		
Tribe Pseudomyrmecini		
Pseudomyrmex sp1	X	X
Pseudomyrmex sp2	X	X
Pseudomyrmex sp3	X	X
Pseudomyrmex sp4	X	X
Pseudomyrmex sp5	X	X
Pseudomyrmex sp6	X	X
Pseudomyrmex sp7	X	X
Pseudomyrmex sp8	X	X
Pseudomyrmex sp9	X	X
Pseudomyrmex sp10	X	X
Pseudomyrmex sp11	X	X

APPENDIX 3

Instructions for Authors – *Ecology*

Articles. While a Report is a concise scientific statement on a single simple topic, an Article tells a more complicated story with distinct components. The greater length of Articles relative to Reports must be justified by their greater complexity. We are asking authors to submit shorter, better-organized pieces that make use of Ecological Archives for digital publication of appendices and supplements. The target length for Articles is 20-30 manuscript pages (double-spaced, 12-point font, including everything from Title Page through the last figure). Longer Articles (those between 30 and 50 manuscript pages) should be accompanied by a detailed justification for the length in the cover letter at the time of submission. The abstract can have a maximum of 350 words. Manuscripts longer than 50 pages may be considered for Ecological Monographs, at the editor's discretion.

Requirements for submission

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APPENDIX 4

Instructions for Authors – *Oikos*

Author Guidelines

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