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**ILHAS FLORESTAIS, REDES DE INTERAÇÃO
FORMIGA-PLANTA E A CONSERVAÇÃO DE
PROCESSOS ECOLÓGICOS**

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Manaus, Amazonas

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Sinopse:

Estudo sobre o efeito da fragmentação e da perda de habitat provocados pela construção da hidrelétrica de Balbina nas redes de mutualismo formiga-planta na Amazônia Central. Foram testados os efeitos da posição na paisagem (floresta, borda do lago, ilha) e de área, isolamento, forma e vizinhança das ilhas sobre a riqueza e densidade de plantas, riqueza e densidade de formigas, número de plantas desocupadas, riqueza de interações, aninhamento, conectância e modularidade das interações.

Palavras-chave: mirmecófitas, redes de mutualismo, co-extinção, hidrelétrica, Balbina, Amazônia

Dedicatória

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RESUMO

Ilhas florestais, interação formiga-planta e a conservação de processos ecológicos

O mutualismo formiga-planta é uma característica importante da biodiversidade na Amazônia. Tal trajetória co-evolutiva gerou redes de interação fortemente compartimentadas, atualmente ameaçadas por alterações ambientais. A recente demanda brasileira por energia tem levado a construção de uma série de hidrelétricas que causam perda de habitat e fragmentação devido à inundação provocada pelo represamento dos rios. O objetivo deste trabalho é testar como a fragmentação e a perda de habitat afetam a estrutura de redes de mutualismo formiga-planta, especificamente riqueza e densidade de espécies, conectância, modularidade e aninhamento. Nós comparamos as redes da floresta contínua com aquelas das ilhas e da borda do lago, bem como a mudança das redes das ilhas em relação à área, isolamento, forma e vizinhança. O estudo foi desenvolvido na Reserva Biológica do Uatumã na Amazônia Central, que inclui a floresta contínua em torno dos 3127 km² do reservatório da hidrelétrica de Balbina e mais de 3500 ilhas. A comunidade formiga-mirmecófita foi investigada em plotes de 600 x 5 m em 20 ilhas, 5 áreas na borda do lago e 6 áreas na floresta contínua. A riqueza e a densidade de plantas e formigas foram menores nas ilhas e na borda do lago em relação à floresta, aumentou com a área e diminuiu com o isolamento das ilhas. A densidade de todas as espécies de plantas diminuiu da floresta para borda do lago e para as ilhas. A porcentagem de plantas desocupadas sem proteção de formigas foi três vezes maior nas ilhas em relação à floresta. As comunidades de plantas e de formigas, bem como as interações nas ilhas e na borda do lago são aninhadas com a comunidade da floresta. A rede de interação formiga-mirmecófita na floresta foi altamente compartimentada, enquanto que as redes das ilhas e da borda do lago perderam espécies, interações e compartimentos e ganharam novas espécies oportunistas de formigas. A conectância se manteve constante com a fragmentação da paisagem e não esteve relacionada a nenhuma característica das ilhas. História natural, características da paisagem, quebra de processos ecológicos, coextinção e novas interações foram discutidos como os principais fatores envolvidos no aninhamento das comunidades, mudanças nas redes, perda de espécies e manutenção da conectância. Coextinção e perda de interações por fragmentação por hidrelétricas podem influenciar processos evolutivos com importantes implicações para a conservação.

ABSTRACT

Forest islands, ant-plant interactions, and the conservation of ecological processes

Ant-plant mutualism is an important feature of the Amazon biodiversity. Its coevolutionary trajectories which generated tight compartmented networks are nowadays threatened by habitat alteration. The recent Brazilian demand for energy is leading to the construction of a series of hydroelectric which causes habitat loss and fragmentation. Our goal is to test how dam fragmentation affects the structure of ant-plant mutualistic networks, in particular species density and richness, connectance, modularity, and nestedness. We compared the networks of continuous forest with those from islands and lake edges as well as how networks change among islands varying in area, isolation, shape, and neighborhood. We developed the study in the Biological Reserve of Uatumã in Central Amazon, which includes the continuous forest around the 3147 km² of the Balbina dam reservoir and more than 3500 islands. Ant-plant communities were surveyed along 600 x 5 m plots in 20 islands, 5 lake edges, and 6 forests sites. Plant and ant richness and density was lower in islands and lake edge in comparison with forest, increased with island area and decreased with isolation. Density of all myrmecophyte species decreased from forest to lake edge and island. Unoccupied plants percentage was three times higher on islands than on forest. Plant and ant community, as well as interactions on islands and lake edge were nested with forest. Forest network was highly compartmented, while island and lake edge networks lost species, interactions and compartments and won new opportunistic ant species. Connectance didn't change among habitats and was not related to islands traits. Natural history, landscape traits, ecological processes decay, coextinction, and new interactions were discussed as the main factors involved on nested communities, networks changes, species loss and connectance constancy of our community. Coextinction and interaction loss by dam fragmentation can influence evolutionary processes with important implications for conservation.

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1. INTRODUÇÃO

As interações animal-planta conectam as espécies em redes mutualísticas e antagônicas que constituem a arena ecológica e evolutiva onde a biodiversidade é criada e perpetuada (Thébault & Fontaine 2010). A estrutura de redes mutualísticas reflete a história de trajetórias evolutivas muito próximas e de benefícios mútuos entre as espécies (Thompson 2005; Bascompte & Jordano 2007; Leigh Jr. 2010). Mudanças em tais relações mutualísticas podem ser detectadas pela análise dos padrões das redes de interações e servem como um importante preditor do status de conservação do ecossistema (Dunn et al. 2009; Morris 2010).

O mutualismo formiga-planta varia no grau de associação entre as espécies, desde espécies de vida livre, que apenas utilizam o parceiro como parte do recurso, até associações obrigatórias, onde as espécies dependem do parceiro para sobreviver e reproduzir (Benson 1985; Davidson & McKey 1993). Nos sistemas formiga-mirmecófita, as formigas nidificam exclusivamente dentro das domáceas, estruturas modificadas de plantas mirmecófitas que servem como sítios de nidificação para as formigas (Beattie 1985; Benson 1985; Fonseca 1999). Na Amazônia Central, a comunidade formiga-mirmecófita envolve mutualismos assimétricos: enquanto as plantas podem hospedar um grande número de parceiros que variam na eficiência em defesa anti-herbivoria, as formigas são mais específicas e dependem dos seus hospedeiros para estabelecimento da colônia e crescimento (Fonseca & Ganade 1996; Fonseca 1999; Guimarães Jr et al. 2006). A rede de interações resultante deste mutualismo revela uma estrutura compartimentada, com subgrupos de espécies interagindo exclusivamente entre si e formando compartimentos bem definidos com fortes interações interespecíficas (Fonseca & Ganade 1996). Esta relação de forte dependência interespecífica pode indicar um processo co-evolutivo onde o benefício ao parceiro tornou-se uma vantagem para adquirir maior sucesso reprodutivo (Thompson 2005; Leigh 2010).

Compartimentos são raros em comparação com os padrões aninhados encontrados na maioria dos mutualismos animal-planta, como nas redes planta-polinizador, onde espécies especialistas interagem com um subgrupo de espécies generalistas. De acordo com a teoria ecológica clássica, redes compartimentadas apresentam maior resiliência e aumentam a estabilidade do ecossistema, considerando que a perturbação permanece no compartimento e não se difunde para o restante da comunidade, como esperado em redes aninhadas onde as espécies estão mais conectadas entre si e não divididas em compartimentos (May 1972; Pimm & Lawton 1980). No entanto, mesmo redes compartimentadas podem ser rompidas se uma espécie-chave desaparece da comunidade. A perda de uma espécie-chave em interações mutualísticas pode

induzir a um processo de co-extinção, onde espécies são extintas em função do desaparecimento do seu parceiro (Dunn et al. 2009). Tal processo tem sido considerado uma das principais causas de perda de biodiversidade no planeta (Dunn et al. 2009).

Distúrbios antropogênicos podem levar a ruptura de redes de interações e a processos de coextinção (Tylianakis et al. 2010). Diversos estudos baseados na Teoria de Biogeografia de Ilhas, que definiu área e isolamento como os principais determinantes da extinção e colonização de espécies em ilhas, contribuíram para entendermos as conseqüências da fragmentação florestal para a biodiversidade (MacArthur & Wilson 1967; Laurance 2008; Laurance et al. 2010). A fragmentação da paisagem afeta negativamente a riqueza, densidade e composição de espécies, desequilibra comunidades e processos ecológicos e pode levar à extinção local de espécies (Terborgh et al. 2001; Laurance et al. 2010). Por outro lado, algumas espécies podem se beneficiar da falta de competidores e/ou do aumento de recursos no novo ambiente, aumentando sua população local (Feeley & Terborgh 2008). No entanto, as conseqüências da fragmentação são influenciadas pela combinação de diversos fatores, tais como a área e o isolamento dos fragmentos, a qualidade da matriz e as características das espécies, que variam conforme a configuração da paisagem (Swift & Hannon 2010).

Na Amazônia brasileira, estima-se que mais de dez milhões de hectares de floresta já tenham sido perdidos devido ao represamento de rios para construção de hidrelétricas (Fearnside 2006). Neste processo, a fragmentação e a perda de habitat ocorrem simultaneamente: enquanto as partes mais baixas do relevo são inundadas, as partes mais altas são transformadas em ilhas florestais e habitat naturais são substituídos por uma matriz aquática (Fahrig 2003, Swift & Hannon 2010). A perda de biodiversidade é prontamente percebida pela submersão da vegetação, morte ou deslocamento de animais e extinção de habitat, além do usual impacto social em comunidades tradicionais e indígenas (Fearnside 1989). Além disso, a emissão de gases de efeito estufa pela matéria orgânica em decomposição, como CO₂ e CH₄, podem atingir níveis superiores aos emitidos por termoelétricas (Fearnside 2006). A matriz aquática resultante atua como uma importante barreira física para o deslocamento da maioria dos organismos terrestres e cria um ambiente hostil nos fragmentos remanescentes, especialmente para espécies adaptadas ao interior de floresta. Além disso, é esperado que as condições ambientais nas ilhas florestais com matriz aquática se tornem muito diferentes do ambiente no interior da floresta, tornando a sobrevivência da maioria das espécies ainda mais difícil do que previamente reportado em fragmentos com matriz terrestre (Laurance et al. 2010; Swift & Hannon 2010). No

entanto, como as interações animal-planta respondem a tais impactos permanece fracamente documentado.

2. OBJETIVOS

O objetivo deste estudo foi testar como redes de mutualismo formiga-mirmecófita respondem a distúrbios antropogênicos. Especificamente, testamos como a modularidade, o aninhamento e a conectância das redes de interação, bem como a riqueza e densidade da comunidade formiga-planta responde à fragmentação e perda de habitat. Para tal, utilizamos duas abordagens: (i) análise comparativa da estrutura das redes formiga-planta em floresta perturbada (ilhas e borda do lago) e não perturbada (controle); (ii) análise do efeito das métricas das ilhas (área, isolamento, forma, vizinhança) na estrutura das redes e na comunidade formiga-planta.

Capítulo 1

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3. ARTIGO CIENTÍFICO

COMPARTMENTALIZATION COLLAPSE ON ANT-PLANT MUTUALISTIC NETWORKS UNDER FRAGMENTATION AND HABITAT LOSS

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Abstract

Ant-myrmecophyte mutualism shows a highly compartmentalized network with low connectance. We tested how ant-myrmecophyte mutualistic network responds to human-made disturbance, regarding to species density and richness, connectance, nestedness, and modularity. We compare networks of undisturbed and disturbed forests, and how networks respond to island area, isolation, shape, and neighborhood. Data were surveyed along 600 x 5 m plots in 20 islands, 5 lake edges, and 6 forests sites in Central Amazon. Forest network was highly compartmented while islands and lake edges networks show random structures, lost species, interactions and compartments. Opportunistic ants colonized unoccupied plants on disturbed forests, which reduced compartmentalization and kept connectance constant. Ant-myrmecophyte community on islands was nested with forest. Species richness and density decreased on disturbed forests, smaller areas and higher isolation. Compartmentalization did not guarantee stability to mutualistic networks jeopardizing classical theories and favoring recent models that attribute stability to nestedness on mutualistic networks.

Keywords: network theory, coevolution, fragmentation, hydroelectric power plants, water matrix, habitat loss, conservation

Introduction

Mutualism networks are major component of biodiversity, being highly developed in the tropics where a single plant can be associated to a number of pollinators, seed-dispersers, mycorrhizae, N-fix bacteria, and ant-defenders. These networks reflect both the coevolutionary history of the partners and the resource-use opportunities provided in the ecological arena (Hutchinson 1979; Thompson 2005). Mutualistic networks, similarly to antagonistic ones, can vary from highly nested to highly compartmentalized, or both, with consequences to community stability (Lewinsohn & Prado 2006; Montoya *et al.* 2006; Bascompte & Jordano 2007; Olesen *et al.* 2007). Simulation models analyzing how community structure affects stability can be traced back to Robert May seminal paper (May 1972) which suggested that lower connectance and higher compartmentalization could enhance stability. Since May, the theory relating compartmentalization to stability was mainly developed over trophic systems (Pimm & Lawton 1980; Krause *et al.* 2003; Montoya *et al.* 2006; Rezende *et al.* 2009). Tough there is some evidence of compartments as coevolutionary units that would enhance stability in mutualistic networks too (Thompson 2005; Dupont & Olesen 2009). On mutualistic systems, model simulations have shown that nestedness benefit community tolerance to species extinction, increases robustness, biodiversity and minimize competition (Bascompte *et al.* 2003; Memmott *et al.* 2004; Bastolla *et al.* 2009). A recent theoretical model incorporating the architecture of networks of both mutualistic and antagonistic interactions showed that stability of mutualistic networks increases when interactions are highly nested and connected, while compartmentalization and low connectance benefit antagonistic networks, as predicted on May's model (Thébault & Fontaine 2010). However, we still don't know empirically how a mutualistic network respond to disturbance in a fragmented world, particularly in a special case of a mutualism that evolved with a network structure considered stable according to May, but would

enhance stability only in foodwebs, following Thébault & Fontaine (high compartmentalization and very low connectance).

Ant-plant mutualistic networks are architecturally diverse (Fonseca & Ganade 1996; Blüthgen *et al.* 2007; Guimarães *et al.* 2007). The networks of myrmecophytes, which are plants that provide nesting space (myrmecodomatia) to their specialized ant-defender partners, exhibit very low connectance and highly compartmentalized structure, with independent and unconnected modules (Benson 1985; Davidson & McKey 1993; Fonseca & Ganade 1996). Ant-myrmecophyte compartments are constituted of phylogenetically-related plants associated to specialized ants from a more diverse phylogenetic background (Fonseca & Ganade 1996), although some phylogenetic signal can be also detected (Ward & Downie 2005). In contrast, networks of extrafloral nectary plants, which provide only nectar to their generalist ant partners, exhibit *higher connectance*, weak and asymmetric interactions, and nested structure (Guimarães Jr *et al.* 2006; Guimarães *et al.* 2007; Díaz-Castelazo *et al.* 2010).

Human-induced disturbance leads to network disruption by species extinction, alien species invasion, and by altering the number, type, and strength of ecological links. Habitat replacement has been demonstrated to modify networks of host-parasitoids (Tylianakis *et al.* 2007), plant-herbivore-parasitoids (Macfadyen *et al.* 2011), and plant-pollinators (Aizen *et al.* 2008; Sabatino *et al.* 2010). Habitat fragmentation causes alteration of natural communities, for instance, by causing species replacement, breakdown of ecological process and the establishment of new ecological links (Terborgh *et al.* 2001; Laurance *et al.* 2010; Gonzalez *et al.* 2011). Alien species can successfully integrate both compartmented and nested community network, usually through the interaction with high generalist species, altering species links but not network structure (Memmott & Waser 2002; Aizen *et al.* 2008; Sugiura 2010).

In the Brazilian Amazon, more than ten million hectares are estimated to be lost due to river impoundment by hydroelectric power plants, causing habitat loss and fragmentation (Fearnside 2006). While lower topographic areas are flooded, top hills remain as islands. The water matrix acts as a hard physical barrier to the movement and dispersion of most terrestrial organisms (Prevedello & Vieira 2010). Besides, the environmental conditions on the remaining forest islands become harsher to the survival of many species. The present study was developed in the 3147 km² artificial lake of the Balbina dam (Central Amazon) which contains more than 3500 islands as well as in its continuous forest surroundings. We tested how fragmentation and habitat loss affects ant-myrmecophyte networks, in particular, modularity, connectance, nestedness, species density and richness. We adopted two approaches. First, we compare the networks of undisturbed forests with those from disturbed forests (lake edges and islands). Second, we tested how island networks respond to the effect of area, isolation, shape, and neighborhood. We hypothesized that (i) if May's model is right, the low connectance and high compartmentalization of the ant-myrmecophyte network will be robust to disturbance, enhancing community stability; otherwise, (ii) if Thébault & Fontaine model is correct, then the compartmentalized structure won't be robust and will disrupt under disturbance. We considered that ant-myrmecophyte network is robust to disturbance if network structure preserves its main properties, i.e., the same number of compartments, and compartments remain unconnected among them, which benefit community stability. Here, we refused May's model to mutualistic network and partially support Thébault & Fontaine's model due to the collapse of the compartmentalized structure of the ant-myrmecophyte networks on disturbed forests.

Methods

Study area

The study was carried out on the forest islands and on the Amazonian forests surrounding the reservoir of the Balbina hydroelectric dam in Central Amazon (1°24' – 1°53'S, 59°13' – 59°51'W, Appendix 1). The hydroelectric power plant was inaugurated in 1989, 16 months after the impoundment of Uatumã River, a major tributary of Amazon River. As a consequence of the relatively flat topography and poor drainage of the area, 3147 km² of pristine forest were flooded, inducing the formation of a lake with more than 210 km of extension, 4582 km of dendritic margins, and mean water depth of only 7.4 m that caused the isolation of more than 3500 forest islands (Fearnside 1989). The mean annual temperature is 27°C and the mean annual rainfall is 2360 mm, with a slightly drier season between August and October causing a 4 m fluctuation on the Balbina lake water level. Vegetation is Submontane Dense Rainforest, located in a transitional zone between Guiana Shield and Central Amazon basin. Myrmecophyte community composition is very similar to that described to another Central Amazonian study site by Fonseca & Ganade (1996).

Sampling design

Site selection was initially based on satellite images of Landsat TM5 1997 (orbit/point 231/61 and 230/61; [available on http://www.dgi.inpe.br/CDSR/](http://www.dgi.inpe.br/CDSR/)). Site selection was designed to allow comparisons between three main habitats: (i) undisturbed forests (control), (ii) forest sites located on the adjacency of the lake edge, and (iii) water-isolated forest islands. The selection of islands was designed to represent the whole spectrum from small (c.a. 10 ha) to large islands (> 1000 ha) which are available on Balbina Lake, allowing to test the effect of area and other landscape traits on ant-myrmecophyte network.

Six undisturbed forest sites were randomly established on a 25 km² grid of the Biodiversity Research Program (PPBIO/CNPq) in the Uatumã Biological Reserve, at least 3 km from Balbina Lake. Five lake edge sites were established on the surroundings of Balbina lake (200 – 400 m from the border), and potentially could be affected by edge effects. Finally, we selected 20 islands, widespread through the Balbina lake, based on an area-based stratified sampling procedure. Four islands were selected in each one of the five area classes (ha): 6.6 – 12.7, 17.3 – 41.6, 60.6 – 126, 205.8 – 475.4, and 689.6 – 1815.

Sampling procedure

From December 2009 to July 2010, a sample plot of 600 x 5 m (3000 m²) was established in each of the 31 study sites (on islands, plots were positioned at least 100 m from the edge, when possible, to minimize edge effects). Each plot was intensively surveyed, without time constraints, for domatia-bearing plants, the so called myrmecophytes and their associated ant partners. Unoccupied myrmecophytes were also recorded. Plant and ant vouchers were collected to allow identification. Ant species were classified either as plant-ants (those occurring on the undisturbed forest sites and those classified as such in the specialized taxonomic and ecological literature) or opportunistic ants (those recorded exclusively on disturbed sites and cited by the literature or by ant taxonomists as free-living species). Ant vouchers were deposited in the entomological collection of the Instituto Nacional de Pesquisas da Amazônia (INPA).

Island metrics

Islands were quantitatively described by four landscape metrics: area, isolation, shape, and neighborhood (measured on ArcGIS v9.3). Island area (ha) was simply defined as the log₁₀-transformed area of the island. Isolation (m) was the shortest Euclidean distance between the island and the lake edge. Shape was defined as the residual of the linear regression between

perimeter (\log_{10}) and area (\log_{10}) for the 20 studied islands. Positive residuals indicate islands whose shapes are less linear and more dendritic than the sample mean. The metric PROX, from the program Fragstats v3.3 (McGarical *et al.* 2002), estimates how much an island is isolated from nearby forest patches which occur on a given *a priori* defined buffer. It is calculated as the sum, over all forest patches whose edges are within the buffer radius of the focal island, of each forest patch area divided by the square of its distance from the focal island. Since Prox was well correlated to island area ($r = 0.941$, $p < 0.001$), for the analyses we used the variable neighborhood, defined as the residual of the linear regression between Prox and island area, with a 1km buffer. As required by the multiple regression models, these four island metrics were not well correlated ($-0.278 \leq r \leq 0.562$).

Network metrics

Modularity maximization analyses were performed to test if ant-plant networks have a compartmentalized structure (Guimera & Amaral 2005a; Guimera & Amaral 2005b). In bipartite ($m \times n$) ant-plant networks, plant and ant species are represented by nodes and their interactions are represented by links. A module is characterized by a sub-group of species that are more strongly connected among them than with species outside the module. The program Netcarto (gently available by R. Guimerá) detects modules by a simulated annealing procedure and calculates the modularity (M) of the system as:

$$M \equiv \sum_{s=1}^{N_M} \left[\frac{l_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right],$$

where N_M is the number of modules, L is the number of links in the network, l_s is the number of links between nodes in module s , and d_s is the sum of the number of links of the nodes in module s . In our community, each node is a plant species or an ant species, links are interaction among them, and modules are called compartments. Since Netcarto was designed for unipartite ($S \times S$)

networks, the significance of M could not be trusted. Therefore, in order to test the significance of M we built a bipartite null model where the interactions of the ant-plant network ($m \times n$) were randomly re-allocated, respecting the marginal totals, to produce a set of simulated M_{rand} values ($N = 100$ runs).

Nestedness analyses were performed to test if ant-myrmecophyte networks (m plants, n ants) exhibit a nested structure. The element a_{ij} takes the value of one when plant species i interact with ant species j , and zero when they do not interact. Separated analyses were performed for undisturbed forests, lake edges and islands. The nested structure was tested with the index NODF, the significance being tested by a Monte Carlo simulation with 1000 runs in the program ANINHADO (Guimarães & Guimarães 2006; Almeida-Neto *et al.* 2008). Also, nestedness analyses were applied to test if plant species, ant species, and ant-plant interactions found on islands and lake edges represent a sub-set of the species and interactions found on undisturbed forests. In order to verify if islands were sub-sets of undisturbed and lake edge forests, we compared the site ranks by the non-parametric Kruskal-Wallis test.

The connectance (C) of a community matrix is defined as the ratio between the number of realized interactions (I_r) and the number of possible interactions (I_p). However, in the literature, connectance has been calculated in a variety of ways (e.g. $C = I_r / S.S$ which can include all interaction types, including amensalism (-,0), and commensalism (+,0); $C = I_r / S.S-1$, to avoid intraspecific interactions; $C = L / m.n$, to avoid intra-guild interactions) making connectance not comparable among studies. Furthermore, for all these definitions, connectance has been demonstrated to be strongly affected by species richness (S). Here, we follow the community allometry approach of Fonseca & John (1996) which solves these problems (Fonseca & John 1996). As any allometry study, we start by fitting a power function between the number of realized interactions and the number of possible interactions ($I_r = aI_p^b$), a and b being empirical

parameters. In principle, the number of possible interactions is calculated as $S \times S$, which allows all the interactions between a given species i and the other species of the community to be represented. In bipartite studies (ant-plants, plant-pollinators, plant-dispersers), however, the total number of possible interactions is $2mn$, since intra-guild interactions ($m.m$ and $n.n$) are not being considered. In order to evaluate how connectance varies with community size, we test if the slope β is significantly different from one. If $\beta = 1$, connectance does not increase with community size (isometric model); if $\beta > 1$, connectance increases with community size (positive allometry); if $\beta < 1$, connectance decreases with community size (negative allometry). Furthermore, the residuals of the power function can be used as measure of connectance which is fully independent of community size, being called standardized connectance (C_{std}). Here, we tested how standardized connectance varied among habitats by a one-way Anova.

Statistical analyses

Moran's I test failed to detect significant spatial autocorrelation on the island metrics, density and richness of the mutualistic partners, and ant-plant network descriptors, as tested by the software Spatial Analysis in Macroecology (Rangel *et al.* 2010). Therefore, all analyses were not corrected by spatial autocorrelation.

A MANOVA was used to test how the density of all myrmecophyte species changes among habitats (undisturbed forests, lake edges, and islands). Differences among the three habitats on the dependent variables plant richness, plant density, ant richness, ant density, number of unoccupied plants, connectance, and modularity were tested by one-way ANOVA, followed by Tukey test. When necessary, plant density, ant density, number of records, and total species richness were included in the model as covariants. A linear regression was used to test if species richness influenced modularity and connectance among habitats. The effects of the interaction between habitat and species richness on modularity was tested with General Linear

Models. The effect of island metrics (area, isolation, shape, and neighborhood) on these dependent variables was tested by multiple regressions, with recursive backward elimination procedure when necessary. We performed statistical analyses on Systat 11, except when otherwise specified.

Results

Habitat networks

The structure of the ant-myrmecophyte network exhibited by undisturbed Amazonian forests differed from that exhibited by forests located on edges of the artificial lake and on water-isolated islands (Fig. 1). The undisturbed forests network was highly compartmented ($M = 0.776$; $M_{\text{rand}} = 0.71$; $\text{sd} = 0.022$, $p < 0.01$; Fig. 1a). Twelve myrmecophytes were associated to 15 ant partners by 21 links, in a structure containing six completely unconnected compartments (notice that *Tococa bullifera* was recorded but it was not colonized).

Forests on lake edges, in contrast, lost the compartmentalized structure, exhibiting only four recognized compartments ($M = 0.639$, $M_{\text{rand}} = 0.617$, $\text{sd} = 0.022$, $p = 0.14$; Fig. 1b). In relation to undisturbed forests, forests on lake edges lost three plant species (*Cecropia concolor*, *Cecropia purpurascens*, and *Tococa bullifera*) and eight ant species. Additionally, the pioneer *Pourouma heterophylla* and its main ant partner, *Allomerus vogeli*, together with three additional opportunistic ants were recorded in the lake edge network. As a whole, forests on lake edges had only 19 links, four being made by opportunistic ants.

On islands, the ant-myrmecophyte network also exhibited only four compartments, but the compartmentalized structure remained marginally significant ($M = 0.550$; $M_{\text{rand}} = 0.520$; $\text{sd} =$

0.019, $p = 0.04$; Fig. 1c). In relation to the undisturbed forests network, the island network was invaded by eight opportunistic ants that established 40% of the network links (10 out of 25) of the system. Additionally, islands lost 5 myrmecophyte species (*Hirtella duckei*, *Maieta poeppigii*, *Cecropia concolor*, *Cecropia purpurascens*, and *Tococa bullifera*) and eight ant species that have been recorded on undisturbed forest sites. We did not detect a nested structure on the ant-myrmecophyte networks of undisturbed forests (NODF = 7.19, $p = 0.95$), lake edges (NODF = 11.00, $p = 0.93$), and islands (NODF = 19.92, $p = 0.78$).

Site networks

The effect of disturbance on ant-myrmecophyte networks was verified at the site level. Site modularity (M) was lower on islands (0.371 ± 0.062 [SE]) when compared to lake edges (0.568 ± 0.053) and undisturbed forests (0.636 ± 0.038 , $F_{2,27} = 3.84$, $p = 0.034$). Furthermore, species richness affects more strongly modularity on forest islands ($\beta = 0.070 \pm 0.013$, $p < 0.001$, $r^2 = 0.64$) than on lake edge ($\beta = 0.021 \pm 0.010$, $p = 0.116$, $r^2 = 0.62$), and undisturbed forests ($\beta = 0.018 \pm 0.002$, $p = 0.002$, $r^2 = 0.94$) (habitat-species richness interaction; $F_{2,24} = 5.739$, $p = 0.009$).

Connectance decreases with network size, as indicated by the shallow slope ($\beta = 0.580$ [IC_{95%}: 0.527 – 0.634]) of the power function between number of realized interactions (I_R) to number of possible interactions (I_p) ($I_R = .922I_p^{0.580}$). Standardized connectance, as represented by the residuals of the I_R - I_p relationship, was not different among undisturbed forest sites and lake edge island sites ($F_{2,28} = 0.628$, $p = 0.541$, Fig. 2).

Local richness and density of mutualistic partners

Plant density was higher on undisturbed forests than on forests located on lake edges and islands; this general pattern being followed by most myrmecophyte species (Wilks' Lambda:

$F_{26,32} = 23.054$, $p < 0.001$; Fig. 3). *Maieta guianensis*, *Tachigali polyphylla*, and *Tachigali myrmecophila* showed the higher decreased in density, being 32, 6, and 4 times lower on islands compared to forests, respectively. *Cecropia concolor*, *Cecropia purpurascens*, and *Tococa bullifera* were recorded exclusively on undisturbed forests. *Hirtella duckey* and *Maieta poeppigii* were recorded exclusively on forest and lake edge but not on islands. The rare pioneer *Pourouma heterophylla* was the only plant species recorded on lake edges and islands but not on forest.

Myrmecophyte richness was twice as high on undisturbed forests and lake edges when compared to islands ($F_{2,28} = 9.03$, $p < 0.001$, $r^2 = 0.39$; Fig. 4a). However, when plant density is controlled for, the significance disappears ($F_{2,27} = 1.16$, $p = 0.329$, $r^2 = 0.74$). Plant density on forest was 4 times higher than on islands, and 1.8 times higher than on lake edges ($F_{2,28} = 14.02$, $p < 0.0001$, $r^2 = 0.50$; Fig.4b).

Ant richness was twice as low on islands than on undisturbed forests and lake edges ($F_{2,28} = 5.804$, $p = 0.008$, $r^2 = 0.29$; Fig. 3c). However, when ant density is controlled for, there was no significant difference among habitats ($F_{2,27} = 0.599$, $p = 0.557$, $r^2 = 0.73$). Compared to undisturbed forests, ant density was 4.5 times lower on islands and 1.6 times lower on lake edges ($F_{2,28} = 13.13$, $p < 0.0001$, $r^2 = 0.48$; Fig. 3d).

Unoccupied plants corresponded to 16.7% of all plant records. The proportion of unoccupied plants was higher on islands ($34.4\% \pm 6.3[\text{SE}]$) than on undisturbed forests ($18.0\% \pm 4.0$), and lake edge ($6.6\% \pm 3.7$), this being highly significant (Deviance = -27.883, $df = 2$, $F = 13.941$, $p < 0.001$).

Effect of island metrics on mutualistic networks

The ant-myrmecophyte networks recorded on islands turned out to be sub-sets of the larger networks naturally found in forest communities (Fig. 4). Nested structure was detected for

plants (NODF = 62.66, $p < 0.01$; Kruskal-Wallis = 7.709, $p = 0.021$), ants (NODF = 45.54, $p < 0.01$; KW = 6.567, $p = 0.037$), and for the ant-plant interactions (NODF = 32.37, $p < 0.01$; KW = 6.275, $p = 0.043$).

The modularity of ant-myrmecophyte networks declined from larger to smaller islands (Log Area, $\beta_{std} = 0.647$, $t = 4.163$, $p = 0.001$), and from lesser isolated to more isolated ones (Isolation, $\beta_{std} = -0.429$, $t = -2.757$, $p = 0.014$). Area and isolation explained together 61% of the modularity variance ($F_{2,16} = 12.698$, $p < 0.001$). Connectance, however, was not related to any of the island metrics.

Area and isolation were the most important island metrics affecting the density and richness of the mutualistic partners (Table 1). Plant richness was positively related to area and isolation, but this effect was strongly attributed to plant density. Similarly, ant richness was positively affected by area and negatively by isolation, but the effect was due to the effect of ant density. Plant and ant density were positively related to area and neighborhood, and negatively related to island isolation. Furthermore, smaller islands had a higher proportion of unoccupied plants (Logit Regression, $\beta = -0.145 \pm 0.045$, $t = -3.256$, $p = 0.004$).

Discussion

We detected the collapse of the compartmentalized structure of the ant-myrmecophyte networks under human-induced disturbance in Amazon Forest. The highly compartmented and low connected network was not efficient to guarantee stability to the mutualistic network under fragmentation and habitat loss caused by the damming of Uatumã River. Our results refute May' model regarding to mutualistic systems under real disturbance likely because he used random interactions, without considering evolutionary traits neither spatial heterogeneity that are

important to define our community, for example. On the other hand, we can support Thébault & Fontaine model in the sense that compartmentalization do not provide stability on mutualistic networks; however, our network was not nestedness to be able to test if this structure enhance stability, as they demonstrated. Besides, Thébault & Fontaine measured stability as persistence (the proportion of species remaining on community after disturbance) and resilience (speed rate to return to equilibrium after disturbance), whereas we considered stability as the maintenance of unconnected number of compartments, since we were not able to access if equilibrium was reached or not after disturbance.

Contrary to recent studies that found both nested and compartmented structure in the same mutualistic or trophic network (Olesen *et al.* 2007; Fortuna *et al.* 2010) our undisturbed network were highly and only compartmentalized. While in mutualistic networks compartmentalization do not enhance stability, in foodwebs, it is an advantageous strategy acting as a buffer constraining disturbance, as coextinctions, inside compartments (Thébault & Fontaine 2010; Stouffer & Bascompte 2011). Our network suffered coextinction inside compartments as in foodwebs; however the disturbance was not constrained but propagated on the network through the new interactions made by remaining species with generalist ones from outside the system, as found on simulation models of mutualistic networks when a generalist species is removed (Memmott *et al.* 2004; Bascompte & Jordano 2007).

Why the network collapsed?

1. Loss of compartments and coextinctions

Some compartments on disturbed forests were loss due to directly effects of habitat loss. Species that lives exclusively on lower forest microhabitats, as *Maieta guianensis* and *Maieta*

poepigii had the local population promptly extinguished when Balbina Lake flooded all lower habitats along Uatumã riverbed, concomitantly extinguishing its associated ants that formed a closed compartment on undisturbed forests. Besides, habitat changes on forest dynamics on disturbed sites were likely affecting the occurrence of the pioneers *Cecropia concolor* and *C. purpureascens* and its associated ants, as reported on fragments with a terrestrial matrix (Bruna et al. 2005). Both *Cecropias* are light demanding, usually growing on gaps of undisturbed forests and were expected to occur on islands and on lake edges, where light availability is expected to be higher. Even species adapted to higher habitats, as *Tachigali myrmecophila*, *Duroia saccifera* and *Hirtella myrmecophila*, suffered a population decline on disturbed forests, or were locally extinguished, as *Hirtella duckeyi*.

The decline of plant myrmecophytes community affected directly the community of plant-ants whose occurrence is dependent of host availability (Fonseca 1999). On disturbed forests, when the host plant was absent, so did the reciprocal ants, characterizing coextinction. Coextinction is considered one of the main causes of biodiversity loss due to its consequences on ecological and evolutionary times, potentially leading to a cascade effect where other species dependent of the system, as predators, parasites or seed dispersers, will also be affected (Dunn et al. 2009; Morris 2010). We detected coextinction on the loss of the whole *Cecropia* compartments on disturbed forests, and on the loss of the interaction between *Maieta poepigii* and *Crematogaster flavosensitiva*. Therefore, one can expect that coextinction become stronger along the time on disturbed forests because recover on islands is unlikely and edge effects tend to increase, leading to Allee effects by the already seen very low species density.

2. Unoccupied plants

One third of myrmecophytes on forest islands was unoccupied, without ant protection. Empty plants are part of the ant-myrmecophyte colonization process, but the high proportion of

unoccupied plants found on islands, twice higher than on forest, indicates that plant-ants are failing to colonize host plants on disturbed forests. We supposed that plant-ants are not been able to disperse from the forest to island fragments, neither from island to island. The difficult to cross the water matrix and the long distance among patches may explain the decline of plant-ant colonization on forest islands. dispersion The other possible explanation is that plant-ants are dispersing but not reproducing successfully on islands due to changes on quality or quantity of resource (Hölldobler & Wilson 1991). Such decline on plant-ant density on islands leads to less plant defenses and can increase herbivory, which consequently can harm plant fitness and would explain the decline of plant density on islands as a cascade effect (Terborgh *et al.* 2001; Palmer *et al.* 2008). Once plant-ants are absent, space was opened for opportunistic species that successfully occupied some empty domatia on islands and lake edges.

3. Opportunistic ants

The opportunistic ants on disturbed forest networks substituted the lost of obligatory plant-ants keeping connectance, and strongly affecting compartmentalization. The opportunistic ants directly affecting compartmentalization are those that interacted with more than one compartment, i.e., *Crematogaster brasiliensis*, *Crematogaster tenuicula*, and *Pheidole* 13. These species are known to be generalist when foraging for nesting space, i.e., they can use an array of available cavities on forest ground to establish their colony, which include empty domatia. The genus *Solenopsis* and *Azteca* are unresolved taxonomically and could have failed identification which unlikely would change network results. The only morphotype that is connecting different compartments and could generate some changes on modularity is *Solenopsis* 02; the other ones entered on the system affecting connectance, but are not connecting compartments.

Opportunistic ants can act as parasites of mutualisms, affecting the cost: benefit ratios of interactions and increasing interaction generality (Kiers 2010). The ant *Pseudomyrmex*

nigropilosa is described as a parasite of the ant-acacia mutualism by harvest resources from acacias but do not protect them (Janzen 1975). In an extreme situation, if the effects of disturbance would be strong enough to completely exclude obligatory ants, parasite ants can occupy all or even most of the available host plants, resulting on the extinction of the mutualism, and still do not affect community allometry (Yu 2001; Kiers *et al.* 2010). Therefore, we can do an analogy of opportunistic ants with alien species on networks. Alien invaders are usually highly generalized, able to interact with different species in different compartments, connecting them and reducing or even broken modularity, besides the long-term effects on network functioning and species selection (Memmott & Waser 2002; Aizen *et al.* 2008; Genini *et al.* 2010). While aliens disassemble compartmented networks, on nested communities of ants and extrafloral nectaries bearing-plants, alien species increased the number of links, then increasing nestedness (Sugiura 2010).

4. Effects of island metrics

The spatial nested structure of plants, ants, and interactions on islands in relation to undisturbed forest is a reflection of the impoverishment of the whole ant-myrmecophyte community. Community nestedness on fragmented landscape was also demonstrated for birds, lizards and small mammals on islands of another inundated lake (Wang *et al.* 2010). Therefore, at far we know, it is the first report of interaction nestedness.

Our results match the classical Theory of Island Biogeography which predicts that larger and less isolated islands have higher probability to be colonized, while smaller and more isolated ones have higher probability of local species extinction while (MacArthur & Wilson 1967). However, the relationship of network structure with island area and isolation is relatively new. Sugiura (2010) found that nestedness of ant-bearing plants network increases with area on

oceanic islands and lower number of interactions and species richness on smaller areas were reported to plant-pollinator networks in fragments with agricultural matrix (Sabatino *et al.* 2010).

Edge effects, as increased temperature, dryness and wind exposure, are expected to be higher as island area decreases and become more isolated, which constraint the establishment of species adapted to forest interior, as the case of most myrmecophytes. Concomitantly, as isolation increases, more important is the species ability to disperse long distances and cross different matrix to the maintenance of mutualism. In our community, dispersion syndromes vary among species as well as the distance they can reach. The decline on richness and density in more remote islands is an indicative that some species are not being able to disperse long distances through the water matrix; however this prediction must be tested. On the other side, a “rescue effect” seems to be supplying propagule to islands closer to the forest, reducing the probability of local species extinctions (Brown & Kodric-brown 1997). Therefore, island neighborhood seems to buffer edge effects regarding to plant and ant densities. As most neighborhood included only islands and not forest land, we supposed that closed islands have the role of step-stones, with species dispersing among them instead only from forest (MacArthur & Wilson 1967).

Implications to conservation

The effects fragmentation and habitat loss on mutualistic interactions and species survivorship is certainly much stronger than reported on this study if we consider that many species and its interactions are sensitive to drastic habitat changes as seen on Balbina, besides the crescent number of hydroelectric power plants all around the world. The direct impact of Balbina dam on ant-myrmecophyte community can be estimated by multiplying the mean density of

myrmecophytes per hectare (124,3 plants/ha in the continuous forest) by the flooded area (3147 Km²), which produces an astonishing estimate of 39,1 million ant-plant mutualistic systems vanished due to habitat loss. The lake created a huge edge between water and forest that became a transitional zone from preserved habitats to more depauperate ones. Since our results showed that 724 m \pm 180 from the margin of the lake to the interior forest are affected by edge effects, we can consider that all ant-myrmecophyte interactions on this area are threatened by Balbina lake effects. These results suggest that edge effects produced by a water matrix can be even stronger than those recorded for terrestrial matrix (Laurance *et al.* 2010). Therefore, the maintenance of ant-myrmecophyte mutualism depends primarily to the maintenance of the integrity of its natural habitats, which means that large forest patches are needed because small fragments do not support such specific interactions. We can expect accentuated breakdown on network structure in the future since, in this case, habitat loss and fragmentation are irreversible.

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Literature Cited

Aizen, M. A., C. L. Morales, and J. M. Morales. 2008. Invasive mutualists erode native pollination webs. *PLoS Biology* **6**:396-403.

- Almeida-Neto, M., P. Guimara, P. R. Guimara, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**:1227-1239.
- Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology Evolution and Systematics* **38**:567-593.
- Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America* **100**:9383-9387.
- Bastolla, U., M. A. Fortuna, A. Pascual-Garcia, A. Ferrera, B. Luque, and J. Bascompte. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**:1018-1020.
- Benson, W. W. 1985. Amazon ant-plants. Pages 239-266 in G. T. Prance, and N. Lovejoy, editors. *Amazonia*. Pergamon Press, New York, USA.
- Blüthgen, N., F. Menzel, T. Hovestadt, B. Fiala, and N. Blüthgen. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology* **17**:341-346.
- Brown, J. H., and A. Kodric-brown. 1997. Turnover rates in insular biogeography: effect of immigration on extinction *Ecology* **58**:445-449.
- Bruna, E., H. Vasconcelos, and S. Heredia. 2005. The effect of habitat fragmentation on communities of mutualists: Amazonian ants and their host plants. *Biological Conservation* **124**:209-216.
- Davidson, D. W., and D. B. McKey. 1993. The evolutionary ecology of symbiotic ant-plant relationships. *Journal of Hymenoptera Research* **2**:13-83.
- Díaz-Castelazo, C., P. R. Guimarães, P. Jordano, J. N. Thompson, R. J. Marquis, and V. Rico-Gray. 2010. Changes of a mutualistic network over time: reanalysis over a 10-year period. *Ecology* **91**:793-801.
- Dunn, R. R., N. C. Harris, R. Colwell, L. P. Koh, and N. S. Sodhi. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society Biological Sciences Series B* **276**:3037-3045.
- Dupont, Y. L., and J. M. Olesen. 2009. Ecological modules and roles of species in heathland plant-insect flower visitor networks. *Journal of Animal Ecology* **78**:346-353.
- Fearnside, P. M. 1989. Brazil's Balbina Dam: Environment versus the legacy of the Pharaohs in Amazonia. *Environmental Management* **13**:401-423.
- Fearnside, P. M. 2006. Dams in the Amazon: Belo Monte and Brazil's hydroelectric development of the Xingu River Basin. *Environmental management* **38**:16-27.
- Feeley, K. J., and J. W. Terborgh. 2008. Trophic drivers of species loss from fragments. *Animal Conservation* **11**:366-368.
- Fonseca, C. R. 1999. Amazonian ant-plant interactions and the nesting space limitation hypothesis. *Journal of Tropical Ecology* **15**:807-825.
- Fonseca, C. R., and G. Ganade. 1996. Asymmetries, compartments and null interactions in an Amazonian ant-plant community. *Journal of Animal Ecology* **65**:339-347.
- Fonseca, C. R., and J. L. John. 1996. Connectance: a role for community allometry. *Oikos* **77**:353-358.

- Fortuna, M. A., D. B. Stouffer, J. M. Olesen, P. Jordano, D. Mouillot, B. R. Krasnov, R. Poulin, and J. Bascompte. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology* **79**:811-817.
- Genini, J., L. P. C. Morellato, P. R. Guimarães, and J. M. Olesen. 2010. Cheaters in mutualism networks. *Biology Letters*:494-497.
- Gonzalez, A., B. Rayfield, and Z. Lindo. 2011. The disentangled bank: how loss of habitat fragments and disassembles ecological networks. *American Journal of Botany* **98**:503-516.
- Guimarães Jr, P. R., V. Rico-Gray, S. F. Dos Reis, and J. N. Thompson. 2006. Asymmetries in specialization in ant-plant mutualistic networks. *Proceedings of the Royal Society Biological Sciences Series B* **273**:2041-2047.
- Guimarães, P. R., and P. Guimarães. 2006. Improving the analyses of nestedness for large sets of matrices. *Environmental Modelling & Software* **21**:1512-1513.
- Guimarães, P. R., V. Rico-Gray, P. S. Oliveira, T. J. Izzo, S. F. dos Reis, and J. N. Thompson. 2007. Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Current Biology* **17**:1797-1803.
- Guimera, R., and L. a. N. Amaral. 2005a. Cartography of complex networks: modules and universal roles. *Journal of Statistical Mechanics: Theory and Experiment* **PO2001**.
- Guimera, R., and L. a. N. Amaral. 2005b. Functional cartography of complex metabolic networks. *Nature* **433**:895-900.
- Hölldobler, B., and E. O. Wilson 1991. *The Ants*. Springer, Berlin, Germany.
- Hutchinson, E. 1979. *The ecological theater and evolutionary play*. Editorial Blume, Barcelona.
- Janzen, D. H. 1975. *Pseudomyrmex nigropilosa*: a parasite of a mutualism. *Science* **188**:936-937.
- Kiers, E. T., T. M. Palmer, A. R. Ives, J. F. Bruno, and J. L. Bronstein. 2010. Mutualisms in a changing world: an evolutionary perspective. *Ecology Letters* **13**:1459-1474.
- Krause, A. E., K. A. Frank, D. M. Mason, R. E. Ulanowicz, and W. W. Taylor. 2003. Compartments revealed in food-web structure. *Nature* **426**:282-285.
- Laurance, W. 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation* **141**:1731-1744.
- Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. B. Williamson, J. Benítez-Malvido, H. L. Vasconcelos, K. S. van Houtan, C. E. Zartman, S. A. Bouyle, R. K. Didham, A. Andrade, and T. E. Lovejoy. 2010. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* **144**:56-57.
- Lewinsohn, T. M., and P. I. Prado. 2006. Structure in plant-animal interaction assemblages. *Oikos* **113**:1-184.
- MacArthur, R. H., and E. O. Wilson 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Macfadyen, S., R. H. Gibson, W. O. C. Symondson, and J. Memmott. 2011. Landscape structure influences modularity patterns in farm food webs: consequences for pest control. *Ecological Applications* **21**:516-524.
- May, R. M. 1972. Will a large complex system be stable? *Nature* **238**:413-414.

- McGarical, K. S., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst.
- Memmott, J., and N. M. Waser. 2002. Integration of alien plants into a native flower-pollinator visitation web. *Proceedings of the Royal Society Biological Sciences Series B* **269**:2395-2399.
- Memmott, J., N. M. Waser, and M. V. Price. 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society Biological Sciences Series B* **271**:2605-2611.
- Montoya, J. M., S. L. Pimm, and R. V. Solé. 2006. Ecological networks and their fragility. *Nature* **442**:259-264.
- Morris, R. J. 2010. Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **365**:3709-3718.
- Olesen, J. M., J. Bascompte, Y. L. Dupont, and P. Jordano. 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America* **104**:19891-19896.
- Palmer, T. M., M. L. Stanton, T. P. Young, J. R. Goheen, R. M. Pringle, and R. Karban. 2008. Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African Savanna. *Science* **319**:192-195.
- Pimm, S., and J. H. Lawton. 1980. Are food webs divided into compartments? *Journal of Animal Ecology* **49**:879-898.
- Prevedello, J. A., and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation* **19**:1205-1223.
- Rangel, T. F., J. A. F. Diniz-Filho, and L. M. Bini. 2010. SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography* **33**:46-50.
- Rezende, E. L., E. M. Albert, M. A. Fortuna, and J. Bascompte. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters* **12**:779-788.
- Sabatino, M., N. Maceira, and M. A. Aizen. 2010. Direct effects of habitat area on interaction diversity in pollination webs. *Ecological Applications* **20**:1491-1497.
- Stouffer, D. B., and J. Bascompte. 2011. Compartmentalization increases food web persistence. *Proceedings of the National Academy of Sciences of the United States of America* **108**:3648-3652.
- Sugiura, S. 2010. Species interactions-area relationships: biological invasions and network structure in relation to island area. *Proceedings of the Royal Society Biological Sciences Series B* **277**:1807-1815.
- Swift, T. L., and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological reviews of the Cambridge Philosophical Society* **85**:35-53.
- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**:1923-1926.

- Thébaud, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**:853-856.
- Thompson, J. N. 2005. *The Geographic Mosaic of Coevolution*. The University of Chicago Press, Chicago, USA.
- Tylianakis, J. M., E. Laliberté, A. Nielsen, and J. Bascompte. 2010. Conservation of species interaction networks. *Biological Conservation* **143**:2270-2279.
- Tylianakis, J. M., T. Tschardtke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* **445**:202-205.
- Wang, Y., Y. Bao, M. Yu, G. Xu, and P. Ding. 2010. Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. *Diversity and Distributions* **16**:862-873.
- Ward, P. S., and D. A. Downie. 2005. The ant subfamily Pseudomyrmecinae (Hymenoptera : Formicidae): phylogeny and evolution of big-eyed arboreal ants. *Systematic Entomology* **30**:310-335.
- Yu, D. W. 2001. Parasites of mutualism. *Biological Journal of the Linnean Society* **72**:529-546.

Table 1. Multiple regressions analysis of the effects of island metrics on ant-myrmecophyte community traits.

	Control	Area	Isolation	Edge	Neighborhood	R ²	F
Plant richness		0.48*	-0.52*	-0.06	0.19	0.45	$F_{4,15} = 3.06^*$
Plant richness	Plant density 0.87	-0.10	0.00	-0.11	-0.09	0.56	$F_{5,14} = 3.60^*$
Plant density		0.66***	-0.60***	0.06	0.32*	0.85	$F_{4,14} = 21.44^{***}$
Ant richness		0.54*	-0.52*	-0.06	0.19	0.45	$F_{4,15} = 3.06^*$
Ant richness	Ant density 0.37	0.27	-0.39	0.08	-0.04	0.65	$F_{5,14} = 5.31^{**}$
Ant density		0.73***	-0.48***	0.12	0.32**	0.9	$F_{4,15} = 33.63^{***}$

* Values are the standard coefficient.

† Asterisks denote p significance: * < 0.05, ** < 0.01, *** ≤ 0.001.

Figure legends

Figure 1. Ant-mymecophyte mutualistic networks on different habitats: (a) compartmentalized network of undisturbed forest; (b) random network of disturbed forest of lake edges; (c) random network of disturbed forests on islands. Dotted line represents interaction with opportunistic ants. Plants are on the left column, ants on the right one. Plants and ants are abbreviated by the first syllable of genus and specific epithet as follow: Himy – *Hirtella myrmecophila*, Hiph – *Hirtella physophora*, Hidu – *Hirtella duckei*, Dusa – *Duroia saccifera*, Cono – *Cordia nodosa*, Tamy – *Tachigali myrmecophila*, Tapo – *Tachigali polyphylla*, Magu – *Maieta guianensis*, Mapo – *Maieta poeppigii*, Ceco – *Cecropia concolor*, Cepu – *Cecropia purpurascens*, Pohe – *Pourouma heterophylla*; Aloc – *Allomerus octoarticulatus*, Alse – *Allomerus septemarticulatus*, Alvo – *Allomerus vogeli*, Azt = Azteca, Caba – *Camponotus balzanii*, Crbr – *Crematogaster brasiliensis*, Crfl – *Crematogaster flavosensitiva*, Crte – *Crematogaster tenuicula*, Myfl – *Myrmelachista flavocotea*, Myjy – *Myrmelachista cf. joycei*, Paun – *Pachycondila unidentata*, Phmi – *Pheidole minutula*, Ph13 – *Pheidole sp13*, Psco – *Pseudomyrmex concolor*, Psni – *Pseudomyrmex nigrescens*, Ps01 – *Pseudomyrmex sp1*, So01 – *Solenopsis sp1*, So02 – *Solenopsis sp2*, So03 – *Solenopsis sp3*, So04 – *Solenopsis sp4*.

Figure 2. Connectance of ant-mymecophyte community of all sites of forest, lake edges and islands showed in a non-linear regression between realized and possible interactions. Note that some points are overlapped due to equal results of connectance.

Figure 3. Density of each plant species on undisturbed (Forest) and disturbed forests (Lake edge, Islands) of Balbina Lake. Thinner bars are standard error. Superscript letters are the Tukey test significance for each species among different habitats. Cono – *Cordia nodosa*, Hidu – *Hirtella duckey*, Himy – *Hirtella myrmecophila*, Dusa – *Duroia saccifera*, Tamy – *Tachigali myrmecophila*, Tapo – *Tachigali polyphylla*, Magu – *Maieta guianensis*, Mapo – *Maieta poeppigii*, Tobu – *Tococa bullifera*, Ceco – *Cecropia concolor*, Cepu – *Cecropia purpurascens*, Pohe – *Pourouma heterophylla*.

Figure 4. ANOVA results of the effects of undisturbed (Forest) and disturbed forests (Edge, Islands) on ant-mymecophyte community traits: (a) plant richness; (b) plant density; (c) ant

richness; (d) ant density. Bars are mean (SE) among sites. Letters over SE bars indicate differences among habitats detected with Tukey test.

Figure 5. Spatial nested structure of plant richness (a), ant richness (b), and ant-plant interaction (c) among disturbed and undisturbed forests. Black squares represents species presence or interaction occurrence in the respective site, while white squares represents the absence of the species or interaction in that site. F = Forest, E = Lake Edge, I = Islands; numbers on F and E are site codes, while numbers on I represents a scale from the smaller island area (I01) to larger island area (I20).

Figure 1

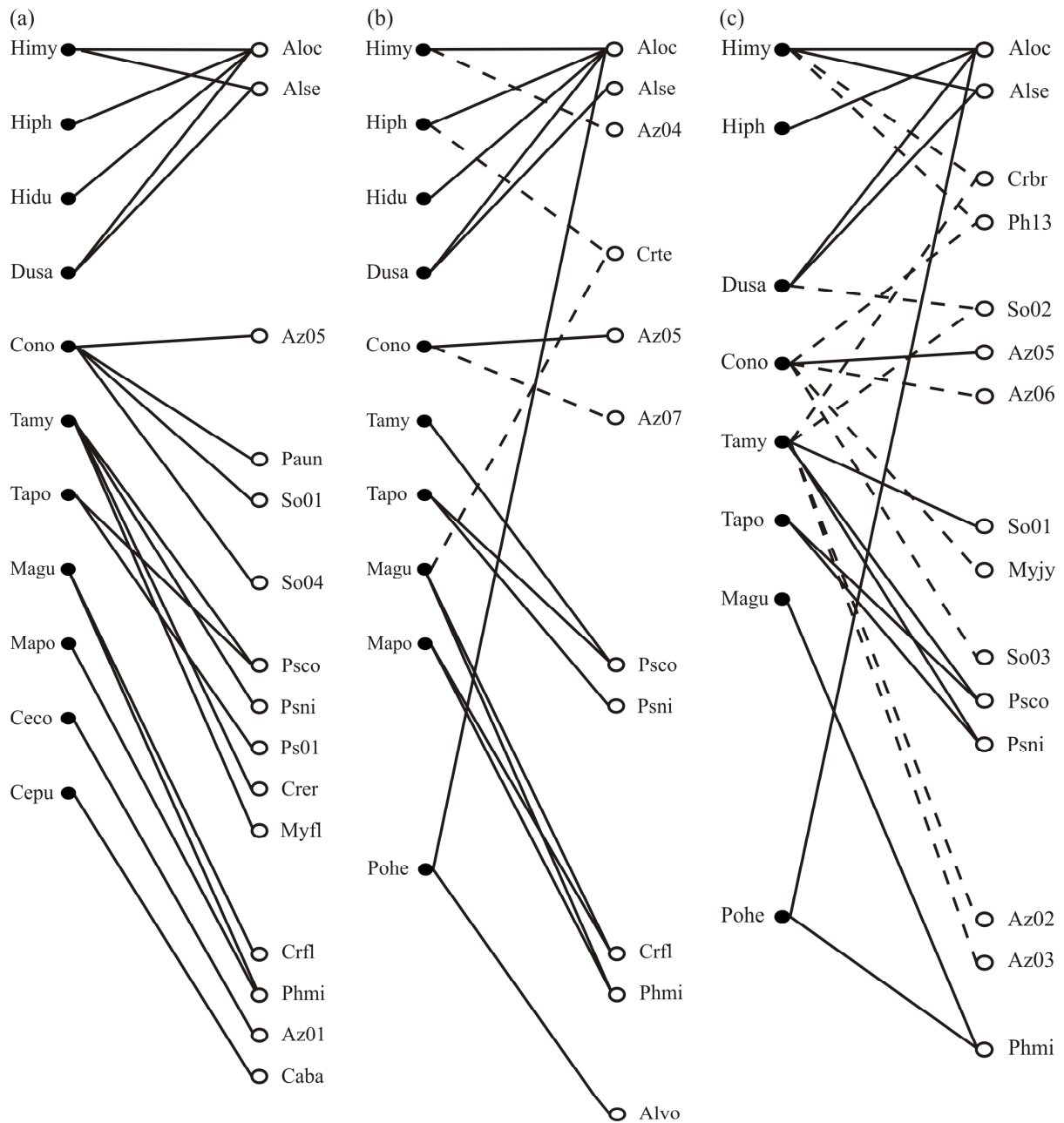


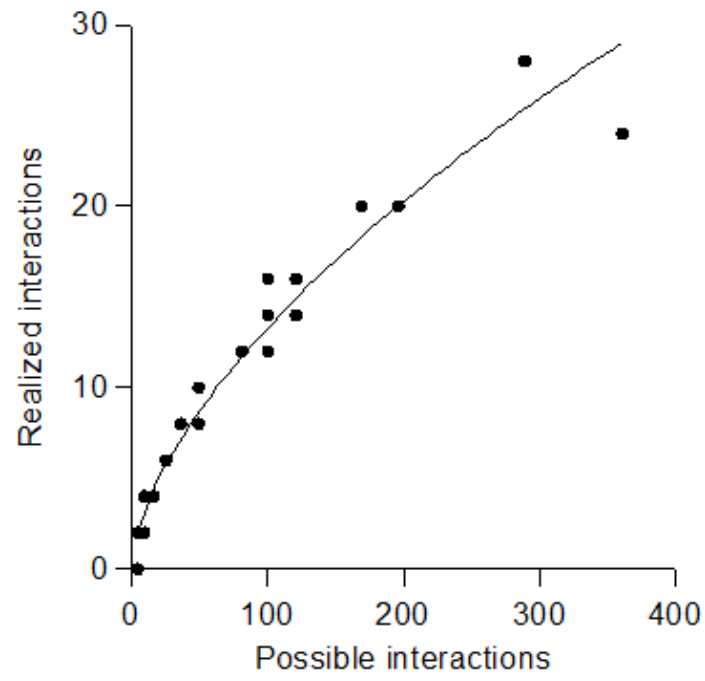
Figure 2

Figure 3

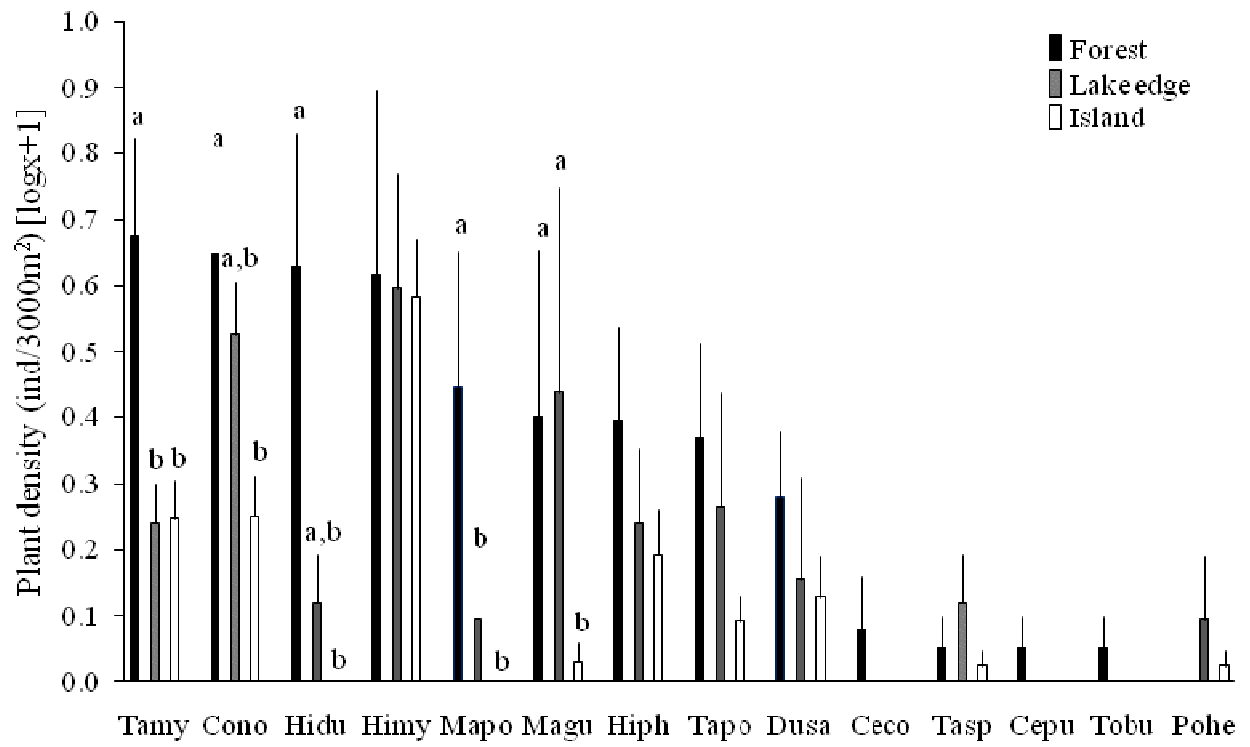


Figura 4

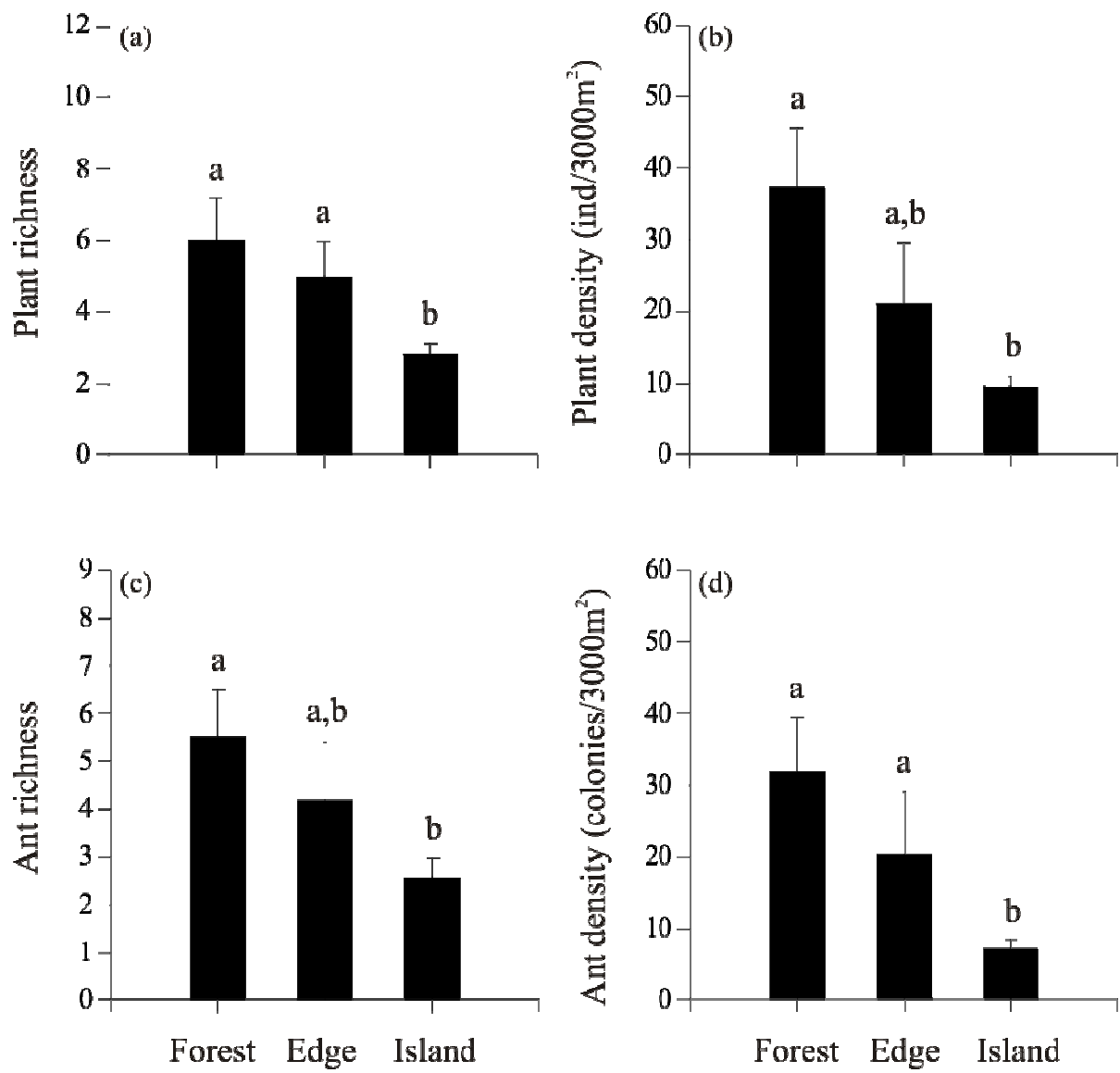
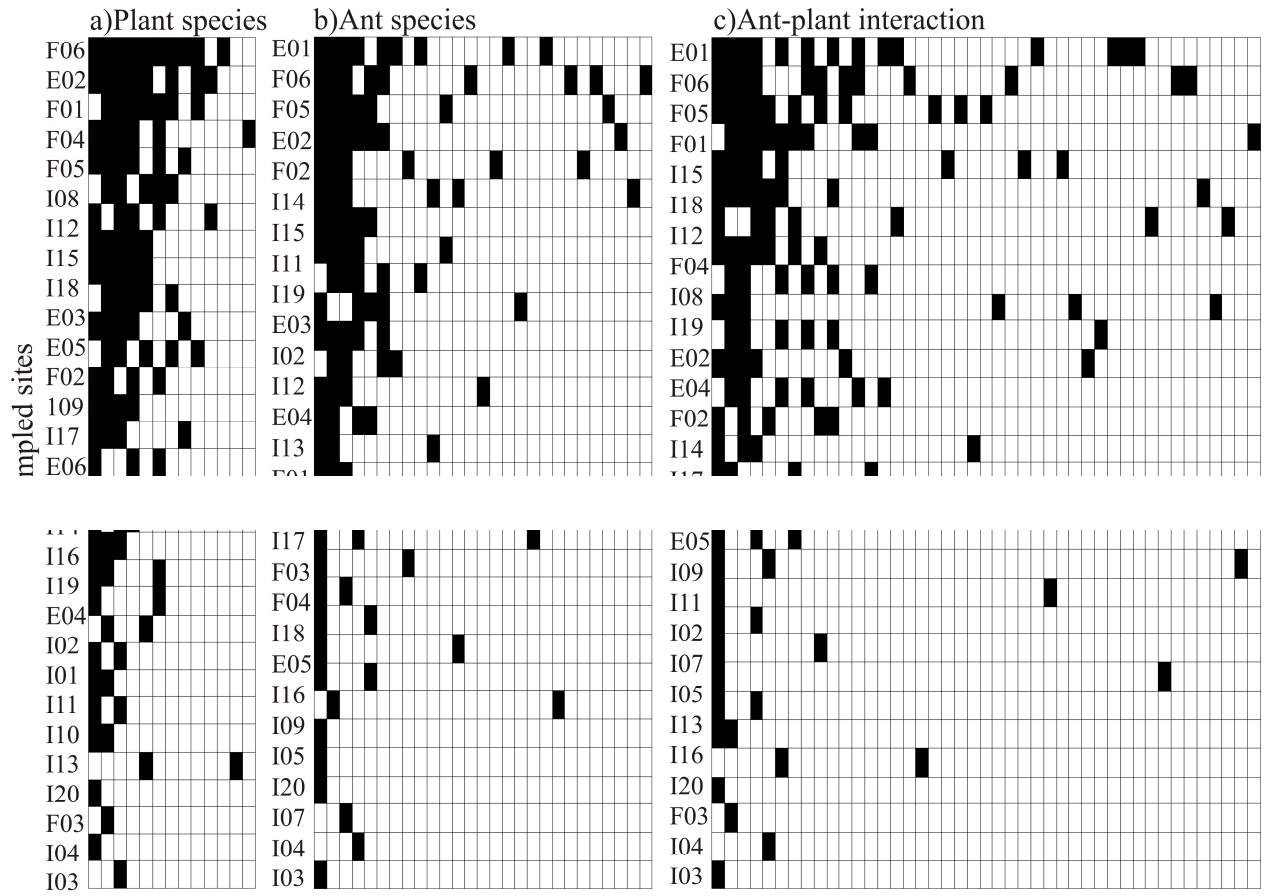
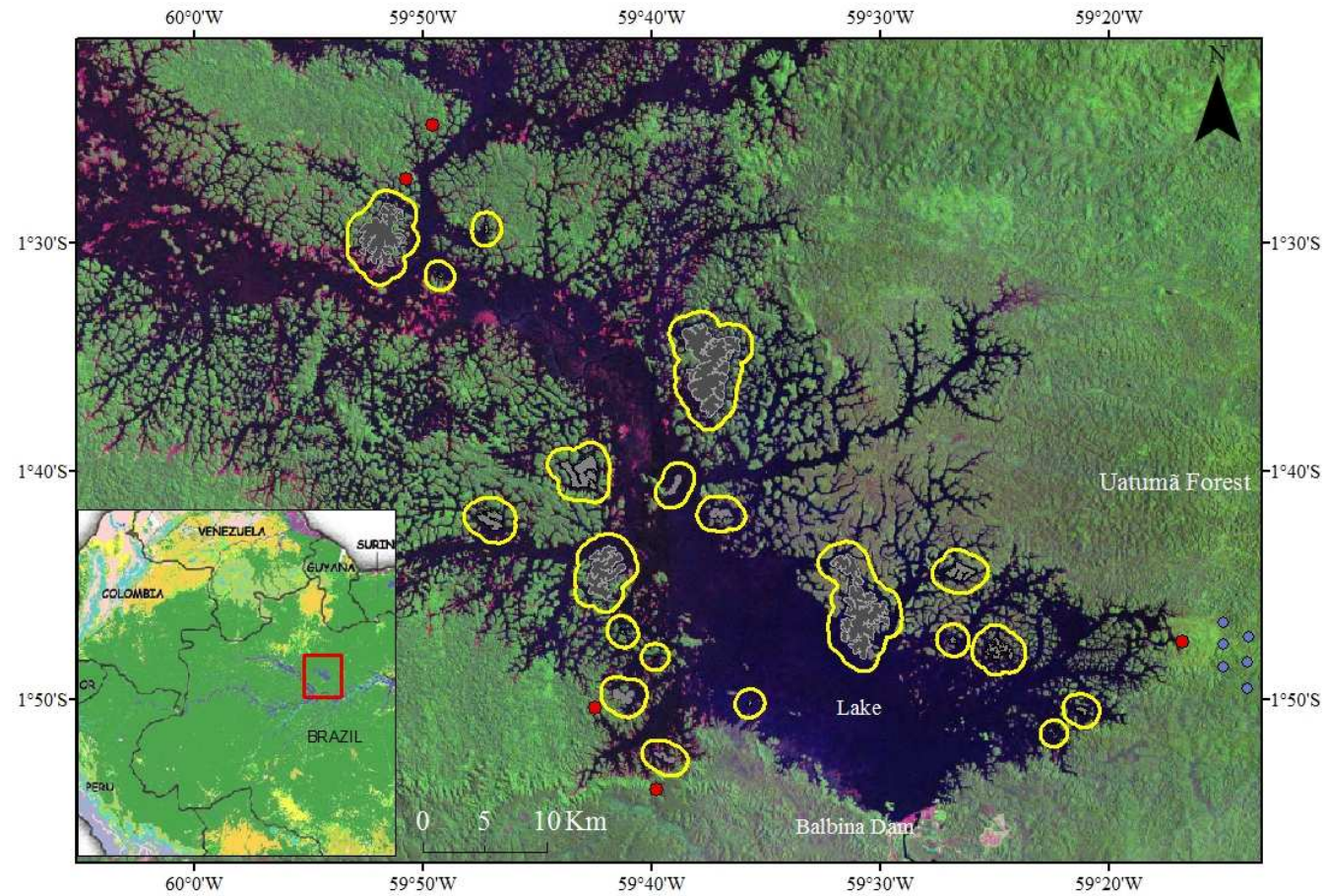


Figure 5



Appendix 1



Map of Balbina Lake and continuous surrounding forest. Yellow circles mark the studied islands. Red points indicate studied sites on lake edges while blue points indicate studied sites on undisturbed forest.

4. CONCLUSÕES

1) A estrutura das redes de mutualismo formiga-planta foram afetadas pela fragmentação e perda de habitat, com perda de espécies, interações e compartimentos.

2) A comunidade formiga-planta está empobrecida nas ilhas e na borda, sendo que área e isolamento foram os principais fatores que explicaram a diminuição da riqueza e densidade de plantas e formigas.

3) O padrão compartimentado das redes de mutualismo formiga-planta permaneceu nas ilhas e na borda do lago, no entanto, a modularidade das redes foi menor e diminuiu com a área e isolamento. As redes das ilhas e da borda do lago perderam interações e compartimentos e ganharam novas espécies de formigas oportunistas.

4) A conectância da comunidade não foi alterada com a fragmentação, se manteve constante nas ilhas e na borda do lago em relação à floresta e não esteve relacionada com nenhuma característica das ilhas. A manutenção da conectância ocorreu devido à entrada de novas espécies de formigas oportunistas nas ilhas e borda do lago.

5) A comunidade de plantas, formigas e as interações formiga-planta são aninhadas com a floresta, ou seja, são sub-grupos depauperados da comunidade original, com algumas interações novas ocorrendo nos ambientes fragmentados (ilhas e borda do lago).

6) Co-extinção de espécies e perda de interações sintetizam os efeitos negativos da construção de hidrelétricas para conservação da biodiversidade, e chamam atenção para os impactos nos processos ecológicos e evolutivos das alterações em redes mutualísticas.

