UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO
EM
ECOLOGIA E BIODIVERSIDADE

INTER-RELAÇÕES ENTRE DIVERSIDADE FILOGENÉTICA, ESTRUTURA DA PAISAGEM E REDES DE INTERAÇÕES ENTRE PLANTAS E AVES FRUGÍVORAS

ERISON CARLOS DOS SANTOS MONTEIRO

Rio Claro - SP
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Orientador: MARCO AURELIO PIZO

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia e Biodiversidade.

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TÍTULO DA TESE: Inter-relações entre diversidade filogenética, estrutura da paisagem e redes de interações entre plantas e aves frugívoras

AUTOR: ERISON CARLOS DOS SANTOS MONTEIRO
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Rio Claro, 28 de fevereiro de 2020

Opus Monteiro

Para Lúcia, a professora da vida.

7-4-8-3 5-6-8-11-3 8-10-4-9-6 8-2-2 4-1-9-7-9 3-9-8-6-7

O apanhador de desperdícios- Manoel de Barros

Uso a palavra para compor meus silêncios.
Não gosto das palavras
fatigadas de informar.
Dou mais respeito
às que vivem de barriga no chão
tipo água pedra sapo.
Entendo bem o sotaque das águas
Dou respeito às coisas desimportantes
e aos seres desimportantes.
Prezo insetos mais que aviões.
Prezo a velocidade
das tartarugas mais que a dos mísseis.
Tenho em mim um atraso de nascença.
Eu fui aparelhado
para gostar de passarinhos.
Tenho abundância de ser feliz por isso.
Meu quintal é maior do que o mundo.
Sou um apanhador de desperdícios:
Amo os restos
como as boas moscas.
Queria que a minha voz tivesse um formato
de canto.
Porque eu não sou da informática:
eu sou da invencionática.
Só uso a palavra para compor meus silêncios.

Um Coração Que Mora Dentro Do Olho Do Jaguar-
Matilde Campilho, Jóquei.

O Verão, rapazes – como disse C. Adams -
implica uma insistência nos mergulhos
e uma desistência breve das respostas.
Importante é passar as mãos pelas escarpas,
afagar o pescoço das andorinhas do mar,
verificar o oxigênio nos tubinhos de plástico
que ajuda a respirar na cala azul turquesa
e permitir que o Senhor ressuscite o sangue
dos espadartes a todas as manhãs de 29ºC.
Estas são as tarefas que devem ser realizadas

e – como disse Adams – bom mesmo é chegar
ao fim da estação sem nenhuma resposta.

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Esse trabalho foi feito graças ao tempo e energia de diversos pesquisadores que foram a campo e coletaram dados de plantas com frutos, aves se alimentando, uma série de

bases filogenéticas, mapas de vegetação, milhares de códigos, equações, métricas, gráficos, métodos e lindas teorias sobre como compreender melhor[6] a natureza e suas inter-relações, a todos esses cientistas, muito obrigado.

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Inter-relações entre diversidade filogenética, estrutura da paisagem e redes de interações entre plantas e aves frugívoras

Resumo

A dispersão de sementes é um dos principais processos responsaveis pela manutenção e regeneração das florestas tropicais. É através dela que um numero tão grande de espécies de plantas ocorrem nas florestas tropicais. Esta interação com vantagens mútuas ocorre a milhões de anos e gerando atributos cada vez mais eficientes em trazer nutrientes para os animais e qualidade de dispersão para as plantas. Por isso, buscamos entender se existe seleção por um dos lados da interação e como é possivel através de caracteristicas filogenéticas, entender a estrutura das redes mutualistas (cap.1). E como variações na quantidade de floresta e conectividade influenciam a diversidade filogenética e interações entre especies evolutivamente distintas, e o efeito disso na robustez das redes (cap.2). No primeiro capítulo, descobrimos que a diversidade filogenética das plantas, mais que a das aves está ligada a especialização nas redes de interações, o que sugere um efeito “button up” das plantas selecionando as interações com aves mais generalistas ao longo do tempo evolutivo. No segundo capítulo descobrimos que areas mais florestadas e mais conectadas mantém até 18 vezes mais diversidade filogenética e interações entre espécies evolutivamente distintas, o que tem grande efeito na robustez das redes de interações. Esses achados mostram a importancia das grandes florestas em manter informação evolutiva e consequentemente a saúde e a resistencia dos processos ecológicos contra as mudanças ambientais.

Palavras-chave: Ecologia, Ecologia da paisagem, Mutualismo, Evolução

Abstract

Seed dispersal is one of most important ecological process in tropical forests: most of the plant species depends on animals to disperse their seeds and a lot of vertebrates depend on essential nutritional resources obtained from fruits. These interactions have been occurring during millions of years and several different forces influenced the

evolution to increase the diversity of interactions in the tropics. Here, using a great data set of feeding bouts of frugivorous birds on plants we tested how phylogenetic diversity drive the diversity of interactions and how phylogenetic relationships are associated to network specialization between plants and frugivorous birds (cap.1). And what is the effect of forest cover and landscape connectivity to the phylogenetic diversity (PD) of interacting birds and plants and the evolutionary distinctiveness of the interactions (EDi) between them, and (2) how EDi and plant/bird PD affect the robustness of the interaction networks (cap.2). In the first chapter we found that the phylogenetic diversity of plants is the driver of specialization in frugivory interactions, indicating an important bottom-up effect on the network specialization between plants and frugivorous birds. And in the second We found that more forested areas keep plant and bird PD and EDi that is 18 times greater than areas with lower forest cover. Landscape connectivity is an important factor to predict bird PD, but not plant PD, suggesting that seeds may not move among forest fragments as easily as birds. Furthermore, interactions networks of areas with higher PD and EDi had great robustness both to plant and bird simulated extinction, which is in favor of the importance of larger forested areas to keep evolutionary information and consequently the health and natural resistance of seed dispersal networks against environmental change.

Key-words: Ecology, Landscape ecology, Mutualism, Evolution

Sumário

Introdução Geral

> "*Observing plant-animal interactions in nature has remained one of the most fascinating aspects of our scientific activity. We recall the unforgettable experience of witnessing frugivorous birds feeding on fruit or hummingbirds pollinating flowers. These are mutually beneficial interactions: animals move the genes of the plants across the landscape, and obtain a food reward for this service. Mutualisms in nature are widespread and have played a major role in the diversification of life on Earth. A persistent challenge is to understand how these mutualistic interactions evolve and coevolve in species rich communities." (Bascompte e Jordano, 2014 pg xi*).

As interações mutualistas exercem um grande fascínio naqueles que as observam na natureza. Aqui, fascinados por elas, particularmente pela dispersão de sementes por aves, procuramos avançar na sua compreensão ao investigar como elas evoluem e como resistem a mudanças da cobertura vegetal, fragmentação e degradação de habitats no Antropoceno. Para isso, e motivados por esse fascínio e desafio, apresentamos uma perspectiva que vai além das espécies, envolvendo suas interações ecológicas, a quantidade de informação evolutiva que essas interações carregam e o efeito que as mudanças na paisagem exercem sobre elas.

A dispersão de sementes é um importante processo ecológico que mantem e participa da restauração das florestas tropicais. É, em grande parte, graças a ela que temos tão grande diversidade de espécies e atributos funcionais que possibilitam enorme variação de nichos tanto para plantas quanto para animais frugívoros (Janzen 1971). Algumas vezes, a dispersão de sementes envolve invertebrados, mas é principalmente com os vertebrados, como mamíferos e aves, que a maioria dessas interações ocorrem (Kaufmann et al. 1991, Bascompte 2019). É uma interação ecológica de milhões de anos, durante os quais diversos atributos morfológicos e comportamentais foram selecionados para possibilitar a interação entre plantas e vertebrados cada vez mais eficiente (Howe e Miriti 2004) e com vantagens mútuas. Entre essas vantagens estão a grande variação na qualidade nutricional dos frutos, com uma grande variedade de sais, açúcares, proteínas e lipídios, que atraem uma enorme variedade de animais e são recursos importantes na dieta de vertebrados (Bairlein 1996). Em contrapartida, os animais podem promover a quebra da dormência e[9] a ativação da germinação das sementes, mas principalmente as carregam

para longe da planta mãe, aumentando suas chances de sobrevivência (Jordano et al. 2010).

O Antropoceno, nossa atual época geológica, é marcada por intensas modificações no ambiente, tanto em aspectos físicos como biológicos, o que – ao mesmo tempo que compromete a manutenção da biodiversidade e de funções ecossistêmicas – propicia novos cenários potenciais de inter-relações entre espécies (Johnson et al. 2017). As causas dessas modificações são principalmente a queima de combustíveis fósseis, o desmatamento, mudanças na paisagem e a defaunação (Crutzen 2006), o que pode levar a um efeito cascata e ao colapso de processos ecológicos, entre eles a dispersão de sementes (Perez-Mendez et al. 2016). Diante disso, muitos ecólogos tentam entender como as espécies se adaptam a essas mudanças e como podemos mitigar, prever e evitar a extinção não só das espécies, mas também das interações das quais elas participam no ecossistema (Bascompte e Jordano 2007, Galetti et al. 2013).

Buscando responder sobre questões relacionadas à filogenia, efeito da estrutura da paisagem e redes de interações planta-aves, estruturamos essa tese em dois capítulos. O primeiro foi elaborado em uma parceria com o Dr. Mathias Schleuning durante seis meses de intercâmbio em Frankfurt-Alemanha no Senckenberg Biodiversity and Climate Research Centre. Nesse capítulo, usamos 26 redes de interações entre plantas e aves frugívoras, distribuídas entre os biomas do Cerrado brasileiro e a Floresta Atlântica, para entender como a diversidade filogenética das plantas e aves frugívoras refletem a diversidade nas redes de interação e como essa diversidade filogenética está associada à especialização nessas redes. Os resultados obtidos nos dão indícios sobre quais dos grupos (plantas ou aves) exerceu maior força de seleção no passado evolutivo das interações.

No segundo capítulo, ampliamos a base de dados anterior para 29 redes de interações e restritringimos as análises para a Floresta Atlântica. Aqui procuramos entender como a quantidade de floresta, área do fragmento e conectividade funcional, interferem nas relações filogenéticas e na robustez das redes de interações entre plantas e aves frugívoras. Nossos resultados permitiram, quantificar o efeito da fragmentação na extinção de interações bem como a importância evolutiva dessas interações na robustez das redes de interações frente às mudanças antrópicas.

Referências bibliográficas

Bairlein, F. (1996). Fruit-eating in birds and its nutritional consequences. Comparative Biochemistry and Physiology Part A: Physiology, 113(3), 215–224.

Bascompte, J., Jordano, P., Pascual, M., & Dunne, J., 2007. The Structure of Plant-Animal Mutualistic Networks. Ecological Networks , 143–159.

Bascompte, J. and Jordano, P. 2014. Mutualistic networks. Monographs in Population Biology Series, no. 53. Princeton University Press, Princeton, USA.

Bascompte, J. (2019). Mutualism and biodiversity. Current Biology, 29(11), R467–R470.

Crutzen, P. J. (2006). The anthropocene. In Earth System Science in the Anthropocene (pp. 13–18).

Galetti, M., Guevara, R., Côrtes, M. C., Fadini, R., Von Matter, S., Leite, A. B., Labecca, F[10]., Ribeiro, T., Carvalho, C. S., Collevatti, R. G., Pires, M. M., Guimarães, P. R., Brancalion, P. H., Ribeiro, M. C., & Jordano, P. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. Science, 340(6136), 1086–1090.

Howe, H. F., & Miriti, M. N. (2004). When Seed Dispersal Matters. BioScience, 54(7), 651–660.

Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L., & Wilmshurst, J. M., 2017. Biodiversity losses and conservation responses in the Anthropocene. *Science*, *356*(6335), 270–275.

Jordano, P., Forget, P., Lambert, J. E., Böhning-gaese, K., Traveset, A., Wright, S. J., & Bo, K., 2010. Frugivores and seed dispersal : mechanisms and consequences for biodiversity of a key ecological interaction Subject collections Frugivores and seed dispersal : mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters*, *7*(3), 321–323.

Jordano, P., Forget, P., Lambert, J. E., Böhning-gaese, K., Traveset, A., Wright, S. J., & Bo, K. (2010). Frugivores and seed dispersal : mechanisms and consequences for biodiversity of a key ecological interaction Subject collections Frugivores and seed dispersal : mechanisms and consequences for biodiversity of a key ecological interaction. Biology Letters.

Kaufmann, S., Mckey, D. B., Hossaert-Mckey, M., & Horvitz, C. C. (1991). Adaptations for a Two-Phase Seed Dispersal System Involving Vertebrates and Ants in a Hemiepiphytic Fig (Ficus microcarpa : Moraceae). American Journal of Botany, 78(7), 971–977.

Pérez[11]-Méndez, N., Jordano, P., García, C., & Valido, A. (2016). The signatures of Anthropocene defaunation: Cascading effects of the seed dispersal collapse. Scientific Reports, 6(December 2015), 1–9.

Ramphocèle Scarlatte.

J. Thiod. Descourtils del. *Lith. de Callier.*

Capítulo 1

The structure of mutualistic networks between plants and frugivorous birds is associated with their phylogenetic diversity

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Abstract

Seed dispersal is one of most important ecological process in tropical forests: most of the plant species depends on animals to disperse their seeds and a lot of vertebrates depend on essential nutritional resources obtained from fruits. These interactions have been occurring during millions of years and several different forces influenced the evolution to increase the diversity of interactions in the tropics. Here, using a great data set of feeding bouts of frugivorous birds on plants we tested how phylogenetic diversity drive the diversity of interactions and how phylogenetic relationships are associated to network specialization between plants and frugivorous birds. We found that the phylogenetic diversity of plants and frugivorous birds influence the diversity of interactions occurring among them. Furthermore, communities with phylogenetically clustered bird species had greater network diversity, suggesting that in general phylogenetically homogeneous bird communities tend to explore a greater number of different plant species. Finally, the phylogenetic diversity of plants is the

driver of specialization in frugivory interactions, indicating an important bottom-up effect on the network specialization between plants and frugivorous birds. It shows that evolutive features are important traits to understand the ecological interactions and also that effort on forest recover concentrated on plants more than bird phylogenetic diversity potentially have greater effect on network diversity.

Introduction

One of the most exciting, largely unsolved issues in the ecology of biological interactions is to understand how complex networks of interacting species have formed and are maintained. This calls for a deeper understanding of the ecological and evolutionary mechanisms that regulate the occurrence of biological interactions (Bascompte and Jordano 2014).

On the ecological side, abiotic and biotic factors interact with species traits to influence community assembly and thus the pool of potentially interacting species (Bascompte et al. 2007). Environmental filtering caused by abiotic factors may lead to phylogenetic clustering of interacting species when they are more closely related than expected by chance (Webb et al. 2002, Sargent & Ackerly 2008). On the other hand, if competition is an important biotic force to shape the phylogenetic structure of biological interactions, similarity in resource use due to shared ancestry may lead to competitive exclusion, and the community of interacting species will be characterized by phylogenetic overdispersion, with species more distantly related than expected by chance (Webb et al. 2002, Sargent & Ackerly 2008).

Mutualisms can influence the phylogenetic community structure either in direction of clustering or overdispersion depending on the nature of the interaction (Sargent & Ackerly 2008). Mutualistic interactions are expected to promote phylogenetic clustering when they are specialized enough to enhance the coexistence of phylogenetically similar species (Cavender-Bares et al. 2009). The increase of phylogenetic clustering may be a pattern, at the community level, resulting from benefits accrued to plant congeners through shared pollinators (Moeller 2005, Sargent & Ackerly 2008). Since seed dispersal mutualisms tend to be less specialized than pollination (Blüthgen et al. 2007), we may expect greater phylogenetic overdispersion

unless the environment has previously filtered a particular phylogenetic subset of the potential species pool.

Shared evolutionary histories are known to structure communities of interacting plants and frugivorous birds (Rezende et al. 2007). How these evolutionary processes drive mutualistic networks at the macroscale is, however, poorly known (Fleming et al. 1987, Kissling & Schleuning 2015). Particularly challenging is to know which side of the bird-plant interaction exerts greater selective pressure on the other and how phylogenetic approaches can reflect this selection. Bottom-up effects are at play when the phylogeny of plants explains a significant fraction of the variation observed in interaction networks, as has been observed in Mediterranean communities of fleshy-fruited plants and frugivorous birds (Bascompte & Jordano 2014). In this case, the functional diversity of plants may drive the richness and functional diversity of birds (Vollstädt et al. 2017). On the contrary, top-down effects occur when the richness of frugivorous birds shape the interaction niches of plants, potentially influencing the recruitment probability of the plants they disperse (García & Martinez 2012, Albrecht et al. 2018).

Here we take advantage of analytical developments in the field to study how phylogenetic diversity of plants and birds is associated with the structure of seed-dispersal networks at the community level (Crisp et al. 2009, Purvis et al. 2000). We related phylogenetic metrics like phylogenetic diversity which gives the amount of different phylogenetic branch lenght, Next Relatedness Index (NRI), which reflects the clustering/overdispersion of the species in clades, and phylogenetic evenness that shows the evenness of species along the phylogenetic tree (Tucker et al. 2017, Martin-González et al. 2015). To network metrics we use Shannon Network diversity and H2 complementary specialization to understand the role of different aspects of phylogenetic diversity in shaping mutualistic networks between plants and frugivorous birds. By integrating these two sets of metrics, we aim at exploring how different phylogenetic relationships reflect on frugivory interactions between plants and birds. (Cattin et al. 2004, Lewinsohn et al. 2005, Rezende et al. 2007a). For this we built a dataset with 26 plant-frugivore mutualistic networks in different sites of the Atlantic Forest and Brazilian Cerrado. Specifically, we addressed two questions: 1) What is the relationship between phylogenetic diversity and phylogenetic

clustering/overdispersion of plant and bird communities on network diversity?, and 2) How does the phylogenetic diversity of both groups is associated with network specialization? Some studies show evidences that bottom-up effects of plant diversity (Matson and Hunter 1992, Blüthgen et al. 2004, Scherber et al. 2010) and, more specifically, the phylogenetic diversity of plants drives communities and interactions at the multitrophic level (Bascompte and Jordano 2014). Therefore, we hypothesized that the phylogenetic diversity of plants and their phylogenetic overdispersion have a higher effect on network diversity (bottom-up effect) than the corresponding bird metrics (top-down effect). We further expect that phylogenetic overdispersion of plant communities will promote generalization of seed-dispersal networks.

Methods

Study area

This study was carried out with literature data collected in Brazilian Cerrado and the Atlantic forest. Cerrado that covers some 2 million km² of central Brazil and adjacent countries (the same size as Western Europe; Oliveira and Marquis 2002). The climate is typical of the rather moister savanna regions of the world, with an average precipitation of 800–2000 mm for over 90% of the area, and a well-marked dry season during the southern winter (aprox. April– September), while average annual temperatures are 18–28 C (Dias, 1992). The typical Cerrado vegetation landscape varied from dense grassland, usually with a sparse covering of shrubs and small trees of 12–15 m, to forested areas following the water courses (gallery forests). The most important plant families are Leguminosae, Compositae, Myrtaceae and Rubiaceae (Ratter, 1997).

The Atlantic Forest is the second largest rainforest of the Americas that in the past covered more than 1.5 million km² (Morellato and Haddad 2000). The large geographic coverage, combined with extreme heterogeneity in composition and large altitudinal gradient ranging from sea level to 2900 m have favoured high diversity and endemism among more than 20,000 species of plants and 688 species of birds (Goerck, 1997; Mittermeier et al., 1999; da Silva and Casteleti, 2003). Both the

Cerrado and Atlantic Forest are among the world's 25 biodiversity hotspots (Myers et al. 2000).

The data set

In Brazil is very common a kind of frugivory research with plant focus, a lot of undergraduate studies, MSc dissertations, and PhD theses and local journals are available about this subject. We searched this literature in thesis repositories and scientific journals for records of frugivorous birds feeding on plants. We retrieved all studies with information on the interacting bird and plant species, the number of feeding visits by birds to fruiting plants, and the sampling effort in hours. This resulted in 109 published papers and unpublished theses carried out from 1988 to 2013 in natural reserves, rural areas, and urban parks in the Atlantic Forest and Cerrado. We pooled the results of different studies conducted in the same area, and selected only the studies that focused on a minimum of three plant species at the same locality. We used plant and bird species names to build the phylogenetic trees and feeding visits to build bipartite quantitative interaction network matrices. To make studies comparable, we weighted the number of interactions of each study by its sampling effort. .

Overall, we retained data from 26 studies totaling 28,849 interactions, 199 plant species, 235 bird species, conducted in 26 different localities running from northeast to south Brazil (15 studies in the Atlantic Forest and 11 in Cerrado). The biggest network had 1,400 interactions involving 38 plants, and 48 bird species while the smallest had 68 interactions, six plants, and six bird species (See data set details on Fig. 1, Table S1).

Plant and bird phylogeny

For the construction of the bird phylogenetic tree, we standardized the nomenclature using the species list provided by the South American Classification Committee (Remsen 2017). We submitted the corrected bird species list to birdtree.org (Jetz et al. 2012) using the Hackett subset with 10,000 trees sorting by 5,000 trees. This website gives a multiphylo archive (".tre") output with 5,000 phylogenetic trees. To condense

all the trees we used the TreeAnnotator v1.8.4 (Bouckaert et al. 2014). This program uses bayesian evolutionary analises to compare all trees and condenses the multiphylo archive in the phylogenetic tree by the most frequent resolution of each clade division by parsimony. The generated phylogenetic tree was visualized on “Interactive Tree of Life” (iTOL v3) (Ciccarelli et al. 2006).

To obtain the plant phylogenetic tree, we used The Plant List (2013) as standard for plant nomenclature. We submitted the species list to plantminer.com, an online tool that uses a species list as input and gives an output with the most probable correct names in a “phylomatic taxa” format (Carvalho 2017). For this, it compares the species names between the input list and the repository taxa. We then submitted the output to Phylomatic (Webb, 2005), a tool that prunes the phylogenetic megatree based on the input list. The output is a phylogenetic tree in a nexus archive, which can be visualized on iTOL. We estimated the branch lengths with the bladj function from Phylocom (Webb *et al*., 2008), using the calibration from Gastauer and Meira Neto 2017. We solved the politomies using the function “multi2di” from “ape” package. It transforms all multichotomies into a series of dichotomies with one (or several) branch(es) of length zero. We solved all politomies 1000 times and selected the most frequent resolution.

Phylogenetic signal

To assess the phylogenetic signal on the interactions among birds and plants, we built four distance matrices, one with the phylogenetic distances among plants and another among birds, a network distance matrix among plants and another among birds. Branch length phylogenetic distances in millions of years were depicted in cophenetic distance matrices for birds and plants, which give the phylogenetic distance between each pair of species in each phylogenetic tree (Sneath and Sokal, 1973). Using the Horn-Morisita index for quantitative data (Faith et al. 1987, Krebs 1989), we got network dissimilarity matrixes, one for plants and one for birds, based on the shared interactions between each pair of species, i.e. bird species that exploited the same plants with similar frequencies have greater indexes in the matrix than birds

that shared a smaller number of plants and/or do it in a lower frequency. The same rationale was applied to plants in relation to interacting bird species. We used Mantel tests with 9999 permutations to calculate the correlation between phylogenetic and network distances for each study as an indirect form to find phylogenetic signal on interactions (Legendre and Legendre, 2012).

Phylogenetic metrics

To both plant and bird phylogenetic tree we calculated the Faith's Phylogenetic Diversity (PD), which is a measure of the sum of the total phylogenetic branch length by the minimum spanning tree that links all species in a community. PD describes how are the cladistic/phylogenetic relationships among taxa (Faith 1992, Cadotte et al. 2009). The second metric was the Net Relatedness Index (NRI), which uses the community sample and the phylogenetic pairwe distance to give the NRI (Webb et al. 2008). Essentially, NRI shows how clustered (positive values) or overdispersed (negative values) are the interactions between the species in our phylogenetic trees, i.e what is the kinship degree of the community. An important concept about NRI is the idea that a community with more closely species was likely selected by environmental filters, while a community with overdispersed species probably experienced competitive exclusion (Cavender-Bares et al. 2009).

Finally, we used the Phylogenetic Species Evenness (PE), a metric complementary and contrary to Phylogenetic Diversity that indicates the evenness of species along the phylogenetic tree. The maximum attainable value of Phylogenetic Evenness (i.e., 1) occurs if species abundances are equal and all species have the same phylogenetic distances (Dehling et al. 2014, Helmus et al. 2007).

Network metrics

For each study we built a network matrix with plants in columns, bird species in rows and the number of interactions in each matching cells. We used the R function “networklevel” from the package bipartite (Dormann 2020) to calculate three metrics to investigate diversity and specialization/generalization in the networks. We used the Shannon Network Diversity as an estimate of the diversity of interactions in the

network. This metric is similar to the Shannon Diversity used for species communities, but is based on the frequency of interactions (Eagle et al. 2010). In addition, we used H2' complementary specialization to access the specialization level of the interactions in our communities. This is a scale-independent index to characterize specialization at the level of the entire network. H2’ can be standardized between 0 and 1 for extreme generalization versus extreme specialization, respectively, meaning that high values correspond to a high degree of niche partitioning, while low values are associated to a high degree of niche overlap (Blüthgen *et al.* 2006). For an additional method to assess specialization/generalization, we used the Interaction Evenness. Based on the Shannon diversity evenness, this metric range from 0 to 1 and describes to what extent a quantitative network is dominated by a few strong interactions, thus estimating the homogeneity of the distribution of interactions among species (Tylianakis et al. 2007).

Statistical analyses

To describe how bird and plant phylogenies drive network attributes, we fitted threelinear regression models testing separately the relationship between the Shannon network diversity, complementary specialization (H2'), and interaction evenness with all phylogenetic metrics (PD, NRI and PE). For all models we used log-transformed Phylogenetic Diversity of plants since this metric did not have a normal distribution. We then used the Akaike Information Criterion (AIC) to evaluate the relative goodness of fit of each model. We selected models with delta AIC < 2 and used their average as the best explication of our data.

We tested for spatial autocorrelation in our networks using the geographic coordinates of each study and estimating the spatial dependence among them measured by the “Moran's I similarity” index at discrete distance classes. We expected a clustered pattern of points denoting the different studied localities in case of positive, and an overdispersed pattern on the negative spatial autocorrelation scenario (*Material Suplementar*., Figure 1, 2 and 3).

Results

Overall, Tyrannidae formed the most representative bird family in the networks with 75 species. *Elaenia* (Tyrannidae) was the most frequent bird genus (5 species), while *Turdus leucomelas* (Turdidae) was the bird species with the greatest number of interactions (984). For plants, Melastomataceae was the most representative plant family with 60 species, *Miconia* the most frequent genus (58 species), and *Miconia chamissois* (Melastomataceae) was the plant species with the greatest number of interactions (628).

Pooling all networks together we found 28,849 interactions, with a mean ± standard deviation of 1,109.6 ± 1,305.9 interactions (range 63-4,904 interactions). The average number of plant species per network was 10.6 ± 8.1 (range 3 - 38 species), while the average number of bird species was 36.1±17.9 (6-74 species) (see supl. Material Table S2 to more details).

Eleven out of 26 networks had significant ($p<0.05$)correlations between phylogenetic and network distances for birds. For plants, phylogenetic and interaction distances in the networks were not correlated (supl. material tab 2S).

In relation to our first question, we found that the phylogenetic diversity of birds, phylogenetic diversity of plants, and bird NRI had positive effects on network diversity (Fig.2, Table1). In relation to the second question, the phylogenetic diversity of plants had positive effect on Interaction Evenness, and negative effect on H2 complementary specialization (Fig.3; Tab.2).

Discussion

Our findings show that the phylogenetic diversity of plants and frugivorous birds influences the diversity of interactions occurring among them. This is denoted by the strong correlation between network and phylogenetic diversity in both groups at the community level, the positive correlation between plant and bird phylogenetic diversity with Shannon network diversity, and the positive correlations between bird phylogenies and network distances. We found that, communities with phylogeneticaly clustered bird species had greater network diversity, suggesting that in general phylogeneticaly homogeneous bird communities tend to explore a greater number of different plant species. Finally, the phylogenetic diversity of plants is the driver of

specialization in frugivory interactions, indicating an important bottom-up effect on the network specialization between plants and frugivorous birds.

We had thus evidence that both plant and bird phylogenetic diversities have strong contribution to shape network architecture. This underscores the limitation of explanations based exclusively on ultimate ecological factors (Ives and Godfray 2006, Rezende et al. 2007a, Rezende et al., 2007b), and asks for an integrative approach with different ecological mechanisms simultaneously considered in association with phylogenetic information (Bascompte and Jordano 2014). In addition, in species-rich networks formed by multiple-partner mutualists, such as pollination and seed dispersal, indirect effects of phylogeny are more likely to shape interactions over the evolutionary history (Guimarães Jr. et. al 2017). This corroborates our hypotheses and the theory saying that phylogenetic relatedness among participating species can influence interaction patterns because phylogenetically related groups of species tend to show similar interaction patterns by sharing traits that mediate the interactions (Reich et al 2003, Bascompte and Jordano 2014).

Here, the phylogenetic clustering of bird species increased network diversity, i.e. the greater the phylogenetic clustering of birds the more diverse are their interactions with fruiting plants. This finding may be influenced by the dominance of specific phylogenetic groups of birds in several of the networks we analyzed, in particular passerines, which form the most speciouse bird order, with a diversity of morphological and physiological attributes permitting them to exploit a variety of plant species (Kissling et al. 2009). Passerines are the dominant avian frugivores in a variety of communities, especially in Neotropical degraded areas (Pizo 2007). Moreover, mutualisms and other positive interactions should promote phylogenetic clustering whenever mutualists are spatially aggregated and specialized enough to enhance the survival of phylogenetically similar species (Cavender-Bares et al. 2009). While positive interactions may promote phylogenetic clustering when they enhance fitness of phylogenetically similar species, they may also promote high phylogenetic diversity (overdispersion) if they increase the co-occurrence of distantly related species (Cavender-Bares et al., 2009 Ives and Godfray 2006). This suggests that phylogenetically closer bird species tend to explore a great number of plant species, which increases network diversity.

Our results show a strong bottom-up effect of plant phylogeny on the network structure of plant-frugivorous bird interactions. This is attested by the negative linear relationship between plant phylogenetic diversity and H2' complementary specialization and the positive relationship with Interaction Evenness, suggesting that phylogenetic diversity of plants are driving networks in favor of more generalist interactions. Jordano and Bascompte (2014) also reported bottom-up effects when they tested for phylogenetic signal in plant-bird interactions and found that the signal of plant phylogeny was stronger than the phylogenetic signal of frugivores. Other analyses also found a greater effect of plant phylogeny on other animal-plant interaction systems, including host-parasitoid interactions (Ives and Godfray 2006), and pollination (Vázquez et al. 2009). It is known that plant diversity tend to decrease specialization in both pollination and seed dispersion networks (Schleuning et al. 2012). The mechanism behind such relationship has to do with variability of fruit traits that tends to increase with plant phylogenetic diversity, consequently increasing the variability of different interactions and decreasing the specialization of interactions.

Together, our findings point to the importance of phylogenetic diversity both of plants and birds in driving frugivory interactions, and the importance of phylogenetic diversity of interacting species to understand the structure of mutualistic networks. In this phylogeny-driven scenario, we have on one side the bottom-up effect of plant phylogenies leading to more generalist interactions, and on the other side the clustering of bird phylogeny increasing interaction diversity.

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References

Albrecht, J., Hagge, J., Schabo, D. G., Schaefer, H. M., & Farwig, N., 2018. Reward regulation in plant–frugivore networks requires only weak cues. Nature communications, 9(1), 1-11.

Albrecht, J., Berens, D. G., Jaroszewicz, B., Selva, N., Brandl, R., & Farwig, N., 2014. Correlated loss of ecosystem services in coupled mutualistic networks. Nature Communications 5, 3810.

Bartomeus, I., Gravel, D., Tylianakis, J.M., Aizen, M.A., Dickie, I.A. & Bernard-Verdier, M., 2016. A common framework for identifying linkage rules across different types of interactions. Functional Ecology, 30, 1894–1903.

Bascompte, J. and Jordano, P., 2014. Mutualistic networks. Monographs in Population Biology Series, no. 53. Princeton University Press, Princeton, USA.

Bascompte, J., 2007. Networks in ecology. Basic and Applied Ecology, 8, 485–490.

Bascompte, J., Jordano, P., Pascual, M., & Dunne, J., 2006. The structure of plant-animal mutualistic networks. In M. Pascual & J. Dunne (Eds.), Ecological networks: linking structure to dynamics in food webs. (pp. 143–159). Oxford, UK: Oxford University Press.

Bascompte, J.; Jordano, P.; Melián, C.J. & Olesen, J.M., 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences of the USA 100: 9383-9387.

Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B., & Blüthgen, N., 2007. Specialization, constraints, and conflicting interests in mutualistic networks. Current biology 17(4): 341-346.

Blüthgen, N., Menzel, F., & Blüthgen, N., 2006. Measuring specialization in species interaction networks. BMC Ecology, 6(9).

Blüthgen, N., Stork, N. E., & Fiedler, K., 2004. Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. Oikos, 106(2), 344–358.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C-H., Xie, D., Suchard, MA., Rambaut, A., & Drummond, A. J., 2014. BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. PLoS Computational Biology, 10(4).

Cadotte, M. W., Cavender-bares, J., Tilman, D., & Oakley, T. H., 2009. Using Phylogenetic, Functional and Trait Diversity to Understand Patterns of Plant Community Productivity. 4(5), 1–9.

Cadotte, M.W., Cardinale, B.J. & Oakley, T.H., 2008. Evolutionary history and the effect of biodiversity on plant productivity. Proc. Natl. Acad. Sci. U.S.A., 105, 17012–17017.

Carvalho G. (n.d). The Plantminer. Retrieved June 15, 2017, from http://www.plantminer.com/

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W., 2009. The merging of community ecology and phylogenetic biology. Ecology Letters, 12, 693–715.

Cattin, M-.F. et al., 2004. Phylogenetic constraints and adaptation explain food web structure. Nature 427: 835–839.

Ciccarelli, F. D., Doerks, T., von Mering, C., Creevey, C. J., Snel, B., & Bork, P., 2006. Toward Automatic Reconstruction of a Highly Resolved Tree of Life. Science, 311(5765), 1283 LP-1287.

Crisp, M. D., Arroyo, M. T. K., Cook, L. G., Gandolfo, M. A., Jordan, G. J., McGlone, M. S., … Linder, H. P., 2009. Phylogenetic biome conservatism on a global scale. Nature, 458(7239), 754-756.

Dehling, D. M., Fritz, S. A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K., & Schleuning, M., 2014. Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography, 37(11), 1047-1055.

Dias, B.F. de S., 1992. Cerrados: Uma Caracterização. In: Dias B.F. de S., ed. Alternativas de Desenvolvimento dos Cerrados : Manejo e Conservação dos Recursos Naturais Renovaveis. Brasília, DF, Brazil: FANATURA.

Eagle, N., Macy, M., & Claxton, R., 2010. Network diversity and economic development. Science, 328(5981), 1029-1031.

Ebeling, A., Klein, A. M., & Tscharntke, T., 2011. Plant-flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. Basic and Applied Ecology, 12(4), 300–309.

Faith, D. P., 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation, 61(1), 1–10.

Faith, D. P, Minchin, P. R. and Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68.

Fleming, T. H., 1987. Patterns of tropical vertebrate frugivore diversity. Annual Review of Ecology and Systematics, v. 18, n. 1, p. 91-109.

Fleming T.H., Kress W.J., 2011. A brief history of fruits and frugivores. Acta Oecologica 37, 521–530.

García, D., & Martínez, D., 2012. Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. Proceedings of the Royal Society B: Biological Sciences, 279(1740), 3106-3113.

Gastauer, Markus, & Meira Neto, João Augusto Alves., 2017. Updated angiosperm family tree for analyzing phylogenetic diversity and community structure. Acta Botanica Brasilica, 31(2), 191-198.

Githiru, M., Lens, L., Bennur, L.A., Ogol, C[5]., 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. Oikos 96, 320–330.

Goerck, J. M., 1997. Patterns of Rarity in the Birds of the Atlantic Forest of Brazil: Patrones de Rareza en las Aves del Bosque Atlántico de Brasil. Conservation Biology, 11(1), 112-118.

Guimarães Jr, P. R., Pires, M. M., Jordano, P., Bascompte, J., Thompson, J. N., 2017. Indirect effects drive coevolution in mutualistic networks. Nature, 550: 511-514.

Helmus M.R., Bland T.J., Williams C.K. & Ives A.R., 2007. Phylogenetic measures of biodiversity. American Naturalist, 169, E68-E83.

Ives, A.R. and Godfray, H.C.J., 2006. Phylogenetic analysis of trophic associations. American Naturallist, 168, 1–14.

Janson, C. H., 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. Science 219: 187-189.

Jordano, P., 2016. Sampling networks of ecological interactions. Functional Ecology, 30, 1883–1893.

Jetz W., G. H. Thomas, J. B. Joy, K. Hartmann, A. O. Mooers, 2012. The global diversity of birds in space and time. Nature, 491: 444-448.

Kissling, D. W., Carsten, R., 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. Proceedings of the royal society B, 274: 799-808.

Kissling, W. D. and Schleuning, M., 2015. Multispecies interactions across trophic levels at macroscales: retrospective and future directions. – Ecography 38: 346 – 357.

Kissling, D. W., Field, R., Böhning-Gaese., 2008. Spatial patterns of woody plant and bird diversity: functional relationships or enviromental effects? Global Ecology and Biogeography. 17:327-339.

Kissling, D., Böhning–Gaese, K., Jetz, W., 2009. The global distribution of frugivory in birds. Global Ecology and Biogeography 18: 150-162

Krebs, C. J., 1989. Ecological Methodology. Harper Collins, New York.

Legendre, P. and Legendre, L., 2012. Numerical Ecology. 3rd English Edition. Elsevier.

Lewinsohn, T. M., Novotny, V., & Basset, Y., 2005. Insects on plants: diversity of herbivore assemblages revisited. Annu. Rev. Ecol. Evol. Syst., 36, 597-620.

Martin-González, A. M. ., Dalsgaard, B., Nogués-bravo, D., Graham, C. H., Schleuning, M., Maruyama, P. K., … Mcguire, J. A., 2015. The macroecology of phylogenetically structured hummingbird – plant networks. Global Ecology and Biogeography, 1–13.

Matson, P. A., and Hunter, M. D., 1992. The Relative Contributions to Top-Down and Bottom-Up Forces in Population and Community Ecology. Ecology, 73(3), 723.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B. et al., 2007. Evolution and the latitu- dinal diversity gradient: speciation, extinction and biogeography. Ecology Letters, 10, 315–331.

Mittermeier, R. A, G. A. B. Fonseca, A. Rylands and C. G. Mittermeier., 1999. Atlantic Forest. In: R. A. Mittermeier, N. Myres, P. R. Gil & C. G. Mittermeier (eds.). Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. pp. 136-147. Cemex. Washington, DC.

Moeller, D.A., 2005. Pollinator community structure and sources of spatial variation in plant–pollinator interactions in Claria xantiana ssp xantiana. Oecologia, 142, 28–37.

Morellato, L. P. C., & Haddad, C. F., 2000. Introduction: the Brazilian Atlantic forest. Biotropica, 32(4), 786-792.

Muller-Landau H. C. & Hardesty B. D., 2005. Seed dispersal of woody plants in tropical forests: Concepts, examples and future directions. In B. F. R. P. Burslem, M. A.

Muñoz M.C., Schaefer H.M., Böhning-Gaese K., Neuschulz E.L. and Schleuning M., 2017. Phylogenetic and Functional Diversity of Fleshy-Fruited Plants Are Positively Associated with Seedling Diversity in a Tropical Montane Forest. Front. Ecol. Evol. 5:93

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., & Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature, 403(February), 853–858.

Oliveira, P. S. & Marquis, R. J., 2002. The cerrados of Brazil: ecology and natural history of a neotropical savanna. Columbia University Press.

Pizo, M. A. 2007. Frugivory by birds in degraded areas of Brazil. In: Dennis, A. J., E. W. Schupp, R. J. Green e D. W. Westcott (eds.), Seed dispersal: theory and its application in a changing world. CABI Publishing, Wallingford, UK. pp. 615-627

Pizo, M. A. & M. Galetti., 2010. Métodos e perspectivas do estudo da frugivoria e dispersão de sementes por aves." Ornitologia e Conservação: Ciência Aplicada, Técnicas de Pesquisa e Levantamento. Technical Books, Rio de Janeiro, Rio de Janeiro : 492-504.

Poisot, T., Stouffer, D. B., & Kéfi, S., 2016. Describe, understand and predict: why do we need networks in ecology? Functional Ecology, 30, 1878–1882.

Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M., 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B: Biological Sciences, 267(1456), 1947–1952.

Ratter, J. A., Ribeiro, J. F., & Bridgewater, S., 1997. The Brazilian cerrado vegetation and threats to its biodiversity. Annals of botany, 80(3), 223-230.

Reich, P. B., Wright, I. J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B., 2003. The evolution of plant functional variation : Traits , spectra , and strategies. International. Journal Of Plant Sciences, 164, 143–164.

Remsen, J. V., Jr., J. I. Areta, C. D. Cadena, S. Claramunt, A. Jaramillo, J. F. Pacheco, J. Pérez-Emán, M. B. Robbins, F. G. Stiles, D. F. Stotz, and K. J. Zimmer. Version [28 April 2017]. A classification of the bird species of South America. American Ornithologists' Union.

Rezende, E.L., Lavabre, J.E., Guimaraes, P.R., Jordano, P. & Bascompte, J. 2007a Non-random coextinctions in phylogenetically structured mutualistic networks. Nature, 448, 925–928.

Rezende, E.L., Jordano, P., Bascompte, J., 2007b. Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. Oikos, 116: 1919-1929.

Sargent R.D. and Ackerly D.D., 2008. Plant–pollinator interactions and the assembly of plant communities. Trends in Ecology & Evolution, 23, 123–130.

Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., ... Tscharntke, T., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature, 468, 553–556.

Schleuning, M., Frund, J., Klein, A., Abrahamczyk, S., Alarcón, R., Albrecht, M., … Blüthgen, N., 2012. Specialization of Mutualistic Interaction Networks Decreases Toward Tropical Latitudes. Current Biology, 22(20), 1925–1931.

Schleuning et al. 2014. Ecological, historical and evolutionary determinants of

modularity in weighted seed-dispersal networks. Ecol Lett. doi: 10.1111/ele.12245

Srivastava et al. 2012. Phylogenetic diversity and the functioning of ecosystems. Ecol Lett. doi: 10.1111/j.1461-0248.2012.01795.x

da Silva, J. M. C., & Casteleti, C. H. M., 2003. Status of the biodiversity of the Atlantic Forest of Brazil. The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook. CABS and Island Press, Washington, 43-59.

Sneath, P.H.A. and Sokal, R.R., 1973. Numerical Taxonomy: The Principles and Practice of Numerical Classification, p. 278 ff; Freeman, San Francisco.

The Plant List, 2013. Version 1.1. Published on the Internet; http://www.theplantlist.org/ (accessed 22 April 2017).

Thompson, J. N., 2005. The geographic mosaic of coevolution. Chicago University Press: Chicago.

Tiffney, B. H., 1986. Evolution of seed dispersal syndromes according to the fossil record. Pp. 273-305 in D.R. Murray (Ed) Seed dispersal. Academic Press. Sydney.

Traveset A., 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. Perspect. Plant Ecol. Evol. Syst. 1, 151–190.

Traveset A., Robertson A.W., Rodríguez-Pérez J., 2007. A review on the role of endozoochory in seed germination. In: Dennis AJ, Schupp EW, Green RJ, Westcott DA (eds) Seed dispersal. Theory and its application in a changing world. CABI Publishing, Wallingford, U.K, 78-103.

Trøjelsgaard, K. & Olesen, J.M., 2016. Ecological networks in motion: micro- and macroscopic variability across scales. Functional Ecology, 30, 1926–1935.

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S. , Fritz, S. A., Grenyer, R. , Helmus, M. R., Jin, L. S., Mooers, A. O., Pavoine, S. , Purschke, O. , Redding, D. W., Rosauer, D. F., Winter, M. and Mazel, F., 2017, A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biol Rev, 92, 698-715.

Tylianakis, Jason M. Tscharntke, Teja and Lewis , Owen T., 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. Nature volume 445, pages 202–205.

Van Der Pijl, L., 1982. Principles of dispersal in higher plants, third edition. Springer-Verlag, Berlin.

Vázquez, D. P., Chacoff, N. P., & Cagnolo, L., 2009. Evaluating multiple determinants of the structure of plant–animal mutualistic networks. Ecology, 90(8), 2039-2046.

Vollstädt, M. G. R., Ferger, S. W. , Hemp, A., Howell, K.M., Topfer, T., Böhning-Gaese, K., Schleuning, M., 2017. Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. Global Ecol Biogeogr, 26, 963– 972.

Webb, C. O., Ackerly, D. D., & Kembel, S. W., 2008. Phylocom : software for the analysis of phylogenetic community structure and trait evolution, 24(18), 2098–2100.

Webb C.O., Donoghue M. J., 2005. Phylomatic: tree assembly for applied phylogenetics Molecular Ecology Notes, 5 (1) 181-183.

Webb, C. O., Ackerly, D. D., McPeek, M. a., & Donoghue, M. J., 2002. Phylogenies and Community Ecology. Annual Review of Ecology and Systematics, 33(1), 475–505.

Wheelwrigth, N. T. and G. H. Orians., 1982. Seed dispersal by animals: Contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist 119: 402-413.

Tables and Figures

Table 1. Model-averaged coefficients of the best linear model (delta AIC < 2) between Shannon Network Diversity and the five phylogenetic metrics with significant p-values to Net Relatedness Index of birds, Phylogenetic Diversity of birds and plants.

Shannon Network Diversity

	Estimate	Std. Error	z value	Pr(>|z|)
NRI_bird	0.180	0.075	2.251	0.024*
Phylo Diversity_bird	0.454	0.073	5.878	<0.001***
Log Phylo Diversity_plant	0.410	0.076	5.096	<0.001***
NRI_plant	0.068	0.088	0.748	0.454
Phylo Evenness_bird	0.037	0.065	0.553	0.580

*p-value<0.05; **p-value<0.01; ***p-value<0.001

Table 2. a) Model-averaged coefficients of the best linear model (delta AIC<2) between H2' complementary specialization and the phylogenetic metrics with significant p-value to Phylogenetic Diversity of plant. b) Model-averaged coefficients of the best linear model (delta AIC < 2) between Interaction Evenness and Phylogenetic Diversity of Plants.

H2 specialization

	Estimate	Std. Error	z value	Pr(>|z|)
Log Phylogenetic Diversity of Plants	-0.097	0.029	3.116	0.001**
Phylogenetic Evenness of birds	-0.029	0.033	0.877	0.380
Phylogenetic Evenness of plants	0.009	0.022	0.424	0.671

Interaction Evenness

Phylogenetic Diversity of birds	-0.015	0.013	1.116	0.264
Log Phylogenetic Diversity of plants	0.034	0.011	2.802	0.005**
Phylogenetic Evenness of birds	0.002	0.007	0.353	0.724
NRI of plant	0.002	0.006	0.283	0.777
NRI of bird	0.001	0.006	0.272	0.785

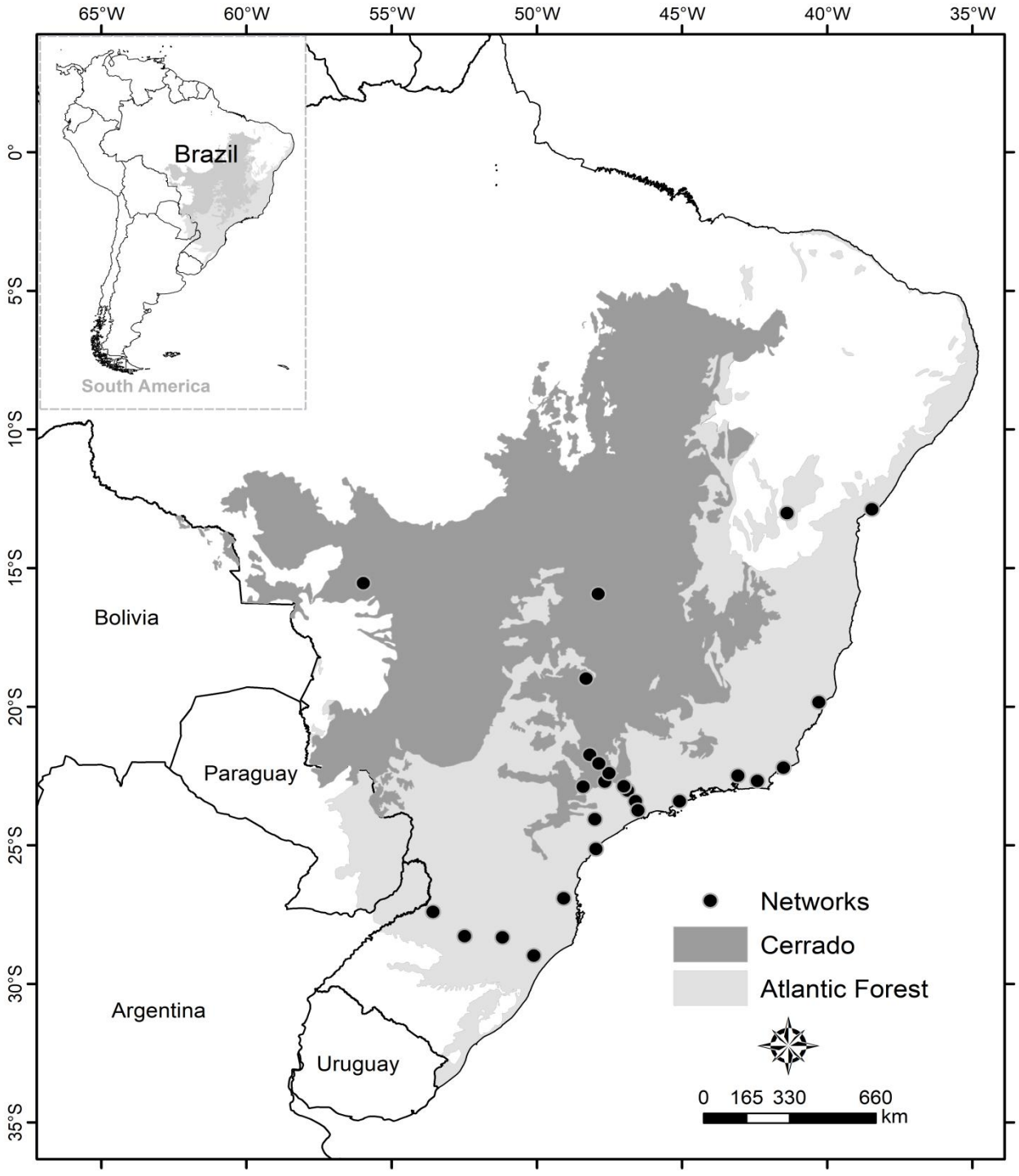


Figure 1. Distribution of the 26 interactions networks, 11 in Cerrado (Brazilian Savanna) and 15 in Atlantic Forest.

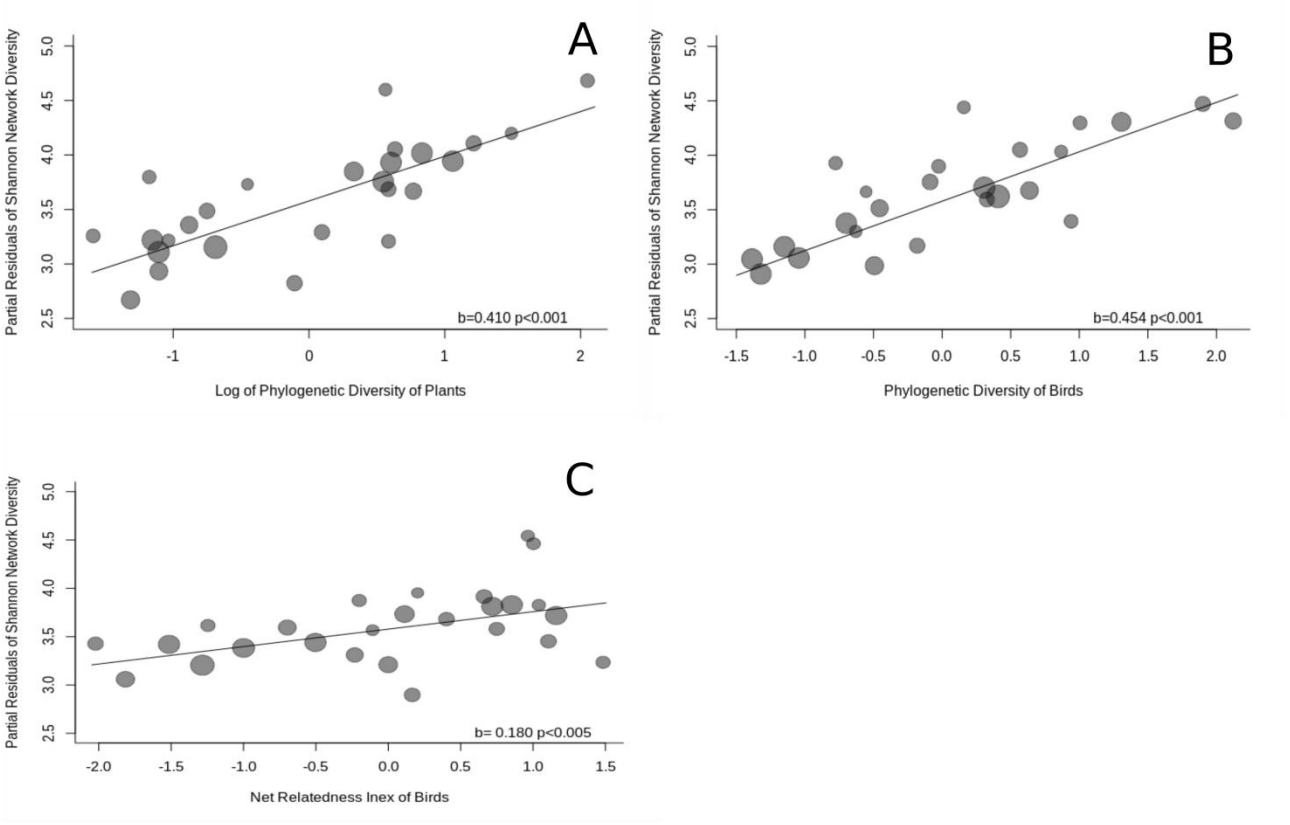


Figure 2. The partial residuals of the best general linear model of Shannon Network Diversity against Log of Phylogenetic Diversity of Plants (A), Phylogenetic Diversity of Birds (B), and Net Relatedness Index (C). The smallest values of NRI represent over dispersion, while high values denote clustering. The size of the circles is proportional to the sampling time used to construct each network.

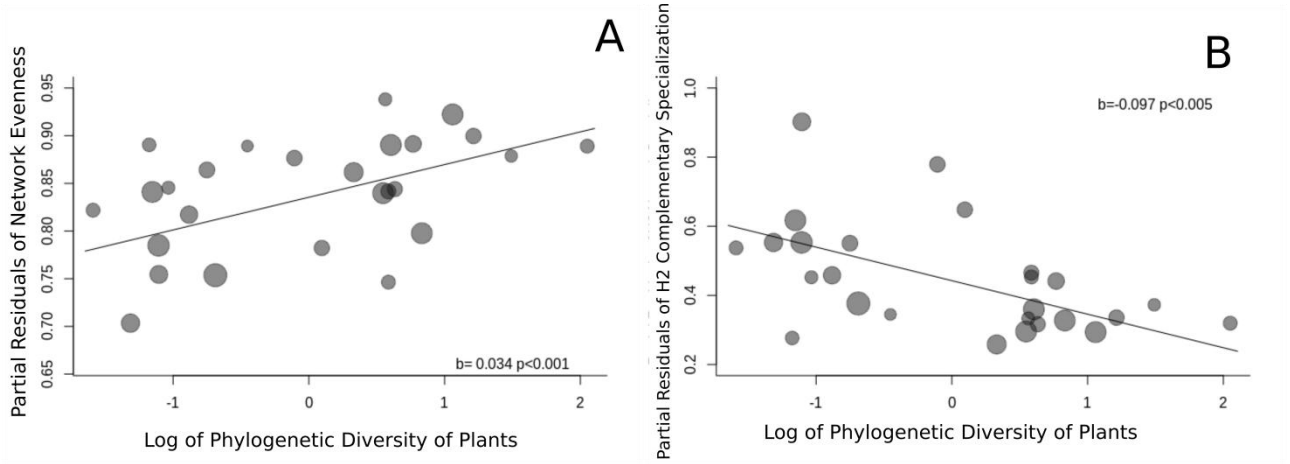


Figure 3. Partial residuals of the best general linear model of Network Evenness against Log of Phylogenetic Diversity of plants (A) and partial residuals of H2' complementary specialization against Log of Phylogenetic Diversity of plants (B). The size of the circles is proportional to the sampling time used to construct each network.

Suplementary Material

Table S1. The work list with the Code, Local city, vegetation type (AF- Atlantic Forest, C- Brazilian Cerrado), the sample time in hours, number of interactions, number of species of plants, birds, Authors name and year of publications. *Non published data.

Code	Local	Vegetation	Sample time	Interactions	Plant species	Bird species	Year
w1	Brasília-DF	C	128	4904	19	68	1991
w100	Piracicaba-SP	AF	27	199	6	28	2015
w104	Jurubatiba, RJ	AF	30	63	16	14	2006
W110	Interior RS	AF	120	181	13	17	2014
w14D	Blumenau-SC	AF	571	228	3	56	1996
w15G	Rio Claro-SP	AF	457	862	16	85	2001
w16	Itatiba-SP	AF	211	1135	15	50	Profix*
w2	Araraquara-SP	C	45	1400	40	50	2002
w20L	Uberlandia-MG	C	3683	2620	26	213	2013
W22E	Campinas-SP	C	532	1033	9	57	2005
W28H	São Carlos-SP	C	2401	4722	13	212	1993
w4	Silva Jardim-RJ	AF	150	500	13	45	1997
w44	Muitos Capões-RS	AF	40	190	16	21	1996
W46J	Sarra dos Orgãos	AF	499	1145	24	101	2008
w5	Mucugê-BA	AF	30	68	10	9	2004
W52K	Ubatuba-SP	AF	97	1948	14	74	2005
w57	Passo Fundo-RS	AF	180	760	3	24	2011
W60F	Cuiabá-MT	C	325	453	3	48	2014
w62	Cantareira-SP	AF	177	199	3	17	2013
w63	Salvador-BA	AF	245	403	18	16	2011
W67A	Carlos Botelho	AF	2947	468	4	47	2014
w6	Cambará do Sul-RS	AF	48	330	4	26	2006
w7	Botucatu-SP	AF	110	1363	4	38	2000
W72B	Ilha do Cardoso-SP	AF	449	724	4	60	2009

w8	Aracruz-ES	AF	63	2659	19	44	1999
w9	São Paulo-SP	AF	3	292	26	23	1994

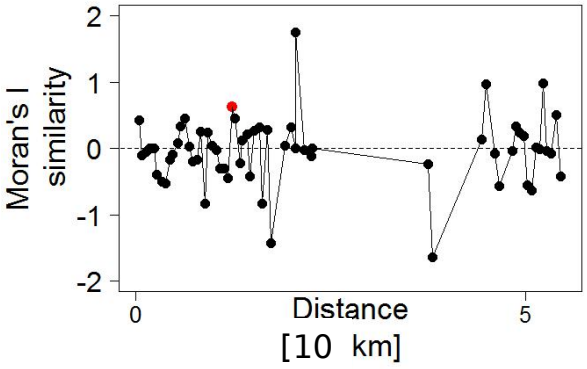
Table S2. The network information with the number of interactions, number of species of birds, plants, Shannon Diversity, H2 Specialization and the Interaction Evenness for each one of the 26 networks.

Code	Interactions (n)	Plant species	Bird species	Shannon_d	H2	interaction evenness
w1	4904	19	68	4.9655	0.3490	0.8675
w100	199	6	27	3.5329	0.3458	0.8986
w104	63	16	15	3.5695	0.2469	0.9490
w110	181	12	14	3.1696	0.3029	0.8535
w14D	228	3	29	3.6527	0.2494	0.9074
w15G	862	5	32	3.3254	0.5794	0.8225
w16	1135	13	44	3.9796	0.2847	0.8342
w2	1400	38	48	4.8163	0.3508	0.8661
w20L	2620	17	74	4.6922	0.4303	0.8608
w22E	1033	9	41	3.3920	0.6606	0.7856
w28H	4722	10	64	4.3486	0.3188	0.8347
w4	500	13	45	4.9038	0.3044	0.9413
w44	190	13	20	3.5907	0.3247	0.9133
w46J	1145	7	53	3.9906	0.4658	0.8380
w5	68	6	6	1.9792	0.7877	0.9008
w52K	1948	13	60	3.8246	0.4915	0.7296
w57	760	3	23	2.4721	0.5364	0.7133
w6	453	4	25	3.0706	0.3982	0.8269
w60F	199	3	42	2.8687	0.9193	0.7410
w62	403	3	17	2.5776	0.6250	0.8466
w63	468	15	16	3.5736	0.3096	0.8227
w67A	330	4	38	3.0572	0.3739	0.7437
w7	1363	4	37	3.5487	0.5532	0.8667
w72B	724	3	38	3.0235	0.5632	0.7769
w8	2659	12	41	3.9471	0.4749	0.8365
w9	292	25	22	3.8670	0.3764	0.8876

Table S3. Phylogenetic information about R^2 and p-values of the correlation between phylogenetic and network distances (*significant correlation), Phylogenetic Diversity (PD), Net Relatedness Index (NRI), and Philogenetic Evenness for each one of the 26 networks. Cells in white for birds and grey for plants.

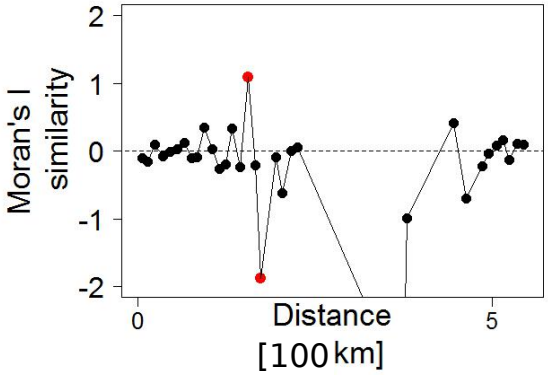
Network code	r^2	p value	PD	NRI	Phylogenetic Evenness	r^2	p value	PD	NRI	Phylogenetic Evenness
w1	0.1939	0.0001	1.9004	0.4020	-0.4474	0.0917	0.1559	1.1993	-0.8817	-0.0088
w100	-0.1125	0.8636	-0.5541	0.2027	-0.1018	-0.2997	0.7722	-0.5872	0.3132	-0.2147
w104	-0.0019	0.4461	-1.3211	1.1598	2.0290	-0.0067	0.4886	0.9403	-0.8662	1.4383
w110	0.0801	*0.2857	-1.0442	-0.5032	-0.6209	0.0391	0.3707	0.2450	0.0385	-1.1669
w14D	-0.0427	0.7280	-0.7764	1.0034	1.3549	0.9731	0.3333	-0.9243	-0.3473	1.3696
w15G	0.1042	*0.0212	-0.0253	-0.2004	-1.6144	0.0507	0.6000	-1.0555	2.5722	-0.6569
w16	0.2842	*0.0001	0.5677	-2.0219	0.9279	-0.0360	0.5451	0.3466	0.0029	-0.4187
w2	0.0850	0.0563	1.0058	-1.2462	-1.2039	0.0441	0.1626	3.1852	-0.7678	-0.4973
w20L	0.1142	*0.0046	2.1218	-0.2315	0.0337	0.0694	0.3143	0.5166	1.4973	-1.0600
w22E	0.0924	*0.0211	-0.1815	1.1065	-0.4842	0.1333	0.1833	-0.1991	0.0211	-0.1950
w28H	0.0325	0.1582	1.3072	0.1122	-1.9520	-0.0199	0.5418	0.0152	-0.6039	0.2323
w4	0.0848	*0.0367	0.1585	0.9643	1.3020	0.0540	0.3615	0.2640	0.1436	1.0267
w44	0.2369	*0.0108	-1.1503	0.7187	1.2492	0.1211	0.1998	0.3116	0.0909	0.2468
w46J	0.1142	*0.0028	0.8677	1.0399	-0.7834	0.8837	0.1429	-0.8704	3.2681	-1.0359
w5	-0.1773	0.7333	-1.7453	0.1656	-0.5532	-0.2888	0.8889	-0.3588	-0.8950	-0.8100
w52K	0.0487	*0.1801	0.9402	1.4836	-1.3103	0.1229	0.1375	0.2905	-0.4220	-0.1236
w57	0.0858	0.1027	-0.4934	-0.0003	0.8076	0.8283	0.3333	-0.9721	-0.0631	0.7841
w6	0.2082	*0.011	-0.4554	-0.6975	1.3793	0.1211	0.3333	-0.8066	-0.0871	-1.9337
w60F	-0.0100	0.5408	0.6370	-1.8154	0.2409	NA	NA	-0.8978	-0.5134	2.5090
w62	-0.2257	0.9425	-0.6982	-1.5145	-0.6651	1.0000	0.3333	-0.9157	-0.4017	-1.2578
w63	0.0879	0.2194	-1.3853	0.8534	0.5180	-0.0687	0.6921	0.6028	0.1784	-0.2286
w67A	0.0158	0.3512	0.4071	-1.2842	0.0578	-0.4358	0.9167	-0.7155	-0.7607	-0.1004
w7	0.1311	*0.011	-0.0877	0.6618	0.3420	-0.5609	0.8333	-0.7460	-0.4366	1.3059
w72B	0.1090	*0.0122	0.3076	-0.9998	-0.0793	-0.6550	0.8333	-0.8986	-0.6127	0.7849
w8	0.0836	0.0586	0.3264	0.7492	-0.3806	0.0991	0.2047	0.2896	-0.1133	-0.2221
w9	0.0315	0.3575	-0.6294	-0.1081	-0.0456	0.0569	0.1986	1.7409	-0.3538	0.2325

Figures

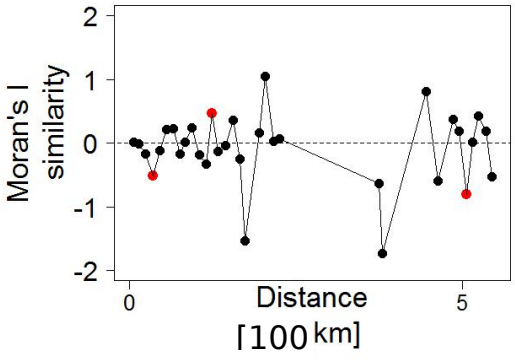


Increment=100

Figure S1. Spatial Auto-correlation between Shanon Network Diversity (SD) and phylogenetic Index (Phylogenetic Diversity, NRI and Phylogenetic Species Evenness)



Increment=100
Figure S2. Spatial Auto-correlation between H2' complementary specialization (SD) and phylogenetic Index (Phylogenetic Diversity, NRI and Phylogenetic Species Evenness)



Increment=100
Figure 3. Spatial Auto-correlation between Interactio Evennes (SD) and phylogenetic Index (Phylogenetic Diversity, NRI and Phylogenetic Species Evenness)

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Capítulo 2

Landscape degradation has pervasive effects on the maintenance of evolutionary distinct interactions in seed dispersal networks

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Abstract

Seed dispersal by animals is one of the most important ecological processes in tropical forests, entailing millions of years of evolutionary adaptations of plants and frugivorous animals that forms networks of interactions that ultimately contribute to the resilience of such forests. In a constantly threatened hotspot of biodiversity, we used 29 seed dispersal networks with data on visiting frequency of frugivorous birds to fruiting plants to ask (1) what is the effect of forest cover and landscape connectivity to the phylogenetic diversity (PD) of interacting birds and plants and the evolutionary distinctiveness of the interactions (EDi) between them, and (2) how EDi and plant/bird PD affect the robustness of the interaction networks. We found that more forested areas keep plant and bird PD and EDi that is 18 times greater than areas with lower forest cover. Landscape connectivity is an important factor to predict bird PD, but not plant PD, suggesting that seeds may not move among forest fragments as easily as birds. Furthermore, interactions networks of areas with higher PD and EDi had great robustness both to plant and bird simulated extinction, which is in favor of the importance of larger forested areas to keep evolutionary information and consequently the health and natural resistance of seed dispersal networks against environmental change.

Keywords: Atlantic Forest, frugivory, ecosystem functioning, tropical biodiversity

INTRODUCTION

Biotic and abiotic factors, acting for millions of years, structure biological communities, whose phylogenetic profiles are important to the functioning of key ecological processes such as pollination (Fleming et al. 2009, Grab et al. 2019), seed dispersal (Lorts et al. 2008, Pigot et al. 2016), and ecosystem resilience (Pérez-Valera et al. 2018). The pervasive processes of habitat loss and fragmentation are among the main threats to the integrity of such ecological processes and to the conservation of biodiversity worldwide (Butchart et al. 2010, Johnson et al. 2017). Much effort has been done to understand how landscape alteration by human activities influences ecosystem functioning (Srivastava et al. 2012, Cramer et al. 2007). However, little is known about how habitat loss and fragmentation impacts the maintenance of phylogenetic diversity and how these changes can influence the persistence of key ecological processes, such as the seed dispersal by birds.

Fragmentation as a process (sensu Fahrig 2003), which includes habitat loss and fragmentation, results in patch size reduction, increases habitat isolation and magnifies the chance of edge effects, thus affecting species persistence. As a consequence, habitat fragmentation can also reduce landscape connectivity or the ability of the landscape to promote organism movements (sensu Taylor et al. 1993). Altogether, such changes impact a myriad of species, but particularly mutualistic interactions whose effectiveness partially depends on the species movement, such as pollination and seed dispersal (Côrtes and Uriarte 2013). In tropical forest areas, networks of interactions between frugivorous birds and plants are negatively impacted by fragmentation , that impacts particularly large birds that often are the first to be extinct in fragmented landscapes (Emer et al. 2019a). As a consequence, the importance of small generalist tend to increase in such landscapes (Emer et al. 2018, Carreira et al. 2020), which, in the medium-long term, can lead to the homogenization of bird-plant interactions (Tylianakis et al. 2010, Olden et al. 2004). The loss of interactions performed by large animals affects particularly large-seeded plants (Galetti et al. 2013). Therefore, most evolutionarily distinct species (ED, i.e. species that have appeared longer in evolutionary time and share less evolutionary history with the rest of the community) can be lost, resulting in the loss of millions of years of evolutionary history (Emer et al. 2019b). For this reason, considering evolutionary processes in studies of species loss and interactions adds an important dimension to conservation (Crandall et al. 2000, Moritz 2002).

One way to understand how environmental changes lead to the loss of evolutionary information is to take into account the phylogenetic diversity (Faith 1992) and the amount of evolutionary divergence (Emer 2019b) accumulated in a community. Here, we use the amount of accumulated evolutionary divergence between species interacting in a given location to assess how much of that divergence is lost with habitat loss and how such loss influences the robustness of networks of interacting fleshy-fruited plants and frugivorous birds to the extinction of species.

In interaction network theory, robustness allow us to quantify how extinctions in one side of a bipartite network (for example birds) results in secondary extinctions on the other side (for example plants), thus allowing us to assess the level of disturbances caused by species extinctions (Memmott et al. 2004). This metric has the drawback of considering interactions statically as it does not take into account the possibility that interactions might reorganize in response to the extinction of a given species (rewiring). In addition, the robustness analysis does not take into account the abundance of species or interactions. However, the robustness of an interaction networks is a proxy for their resilience to cope with changes in environmental factors such as the reduction of functional landscape connectivity (Vieira and Almeida-Neto 2014, Dunne et al. 2002), habitat loss (Evans et al. 2013) and changes in the behavior of interacting animals (Kaiser-Bunbury et al. 2010). Ultimately, robustness permits to evaluate how networks of ecological interactions are maintained under scenarios of ecological changes (Memmott et al. 2004).

Networks of interactions in well-preserved large blocks of habitats that maintain the complete coterie of interacting species are expected to have more connections among species, which is associated with greater robustness due to the lower likelihood of losing species due to coextinction (Dunne et al. 2002, Burgos et al. 2007, Kaiser-Bunbury and Blüthgen, 2015). On the other hand, networks with fewer connections are more prone to the coextinction of species partners (Vieira and Almeida-Neto 2014). As a consequence, this can compromise the maintenance of the evolutionary history embedded in interactions that Emer et al. (2019b) called Evolutionary Distinctness of Interactions (EDi), which can be defined as “the combined ED that both interacting partner species convey to a given interaction, irrespective of how long they have been interacting with one another”. Losing interactions with high EDi should make the recovery of disturbed forests even more difficult, for instance,

through the limitation in the dispersal of large-seeded plants that generally have a great EDi, thus hindering the regeneration of the forest (Tabarelli and Peres 2002, Costa et al. 2012). Although many efforts has been done to understand how human-induced modifications impact the occurrence, abundance, and species persistence in the Anthropocene (Johnson et al. 2017), it is of utmost importance that we quantify how landscape degradation shape the maintenance of phylogenetic diversity of interacting species and how these changes can influence the robustness of interaction networks that are essential to guarantee key ecological processes, such as seed-dispersal. In addition, this can allow us to estimate how much of evolutionary history can be lost due to landscape degradation affecting only one or both sides of interaction networks.

Here we addressed two questions: (1) How the decrease in forest cover and functional connectivity affects the maintenance of the phylogenetic diversity (PD) and evolutionary distinct Interactions (EDi) between plants and frugivorous birds in a hotspot of biodiversity, the Brazilian Atlantic Forest, and (2) how does plant and bird PD and EDi affect the robustness of interaction networks? We expect that: (1) the loss of forest cover and reduction of functional connectivity causes a decline in phylogenetic diversity of birds and plants, and (2) the loss of PD and the loss of interactions between evolutionarily distinct species would lead to the reduction of robustness in mutualistic networks between plants and frugivorous birds (Fig.1).

METHODS

Study area

The Atlantic Forest is among the top five global biodiversity hotspots in the world (Myers et al. 2000). It is the second largest rainforest in the Americas, which originally covered more than 1.5 million km² that encompassed latitudinal, longitudinal and environmental gradients distributed along the Atlantic coast of Brazil and to the continent interior to reach parts of Argentina and Paraguay (Morellato & Haddad 2000, Young 2003, Muylaert et al. 2018). The extensive geographic coverage, combined with extreme heterogeneity in composition and altitudinal gradient (from sea level to 2900 m) favored great species diversification and endemism, with more than 20,000 species of plants and 688 species of birds (Goerck, 1997, Mittermeier et al., 1998). As a consequence of intense forest loss and fragmentation, the Atlantic

Forest was reduced to less than 16% of its original forest cover (Ribeiro et al. 2009) (fig.2).

Dataset

We searched for studies carried out in the Atlantic Forest with records of interactions between frugivorous birds and plants in scientific journals, data repositories and the gray literature, which included thesis and dissertations. We searched the databases Google Scholar, Scopus, and Web of Science using the terms “bird”, “avian”, “frugivory”, “seed dispersal”, and their Portuguese and Spanish equivalents. To be considered, the study should have (1) a list of plants, birds and information on visit frequency of frugivorous birds to plants, and (2) at least five plant species with interactions with birds recorded (Table S1).

Phylogenetic trees of plants and birds

Plants. Considering the regional pool of species, we first obtained the updated species name from the plantminner.com platform (Carvalho et al. 2019) using The Plant List (2013) as a standard for nomenclature. Then, we obtained the initial mega-phylogeny of plants using the “S.Phylomaker” function (Qian and Jin 2016) based on “scenario 1”, which places unidentified genera and species within their highest taxonomic level as basal polytomies. We proceed to solve the polytomies applying a birth-death model using the “PolytomyResolver” function (Kuhn et al. 2011) to adjust the length of the branches and the BEAST software v. 1.5.4 (Suchard et al. 2018). A Markov Chain Monte Carlo simulation was performed for 10^6 iterations, sampling trees at 10^3 iterations. Finally, we randomly selected 100 solved trees, after burning out the first 25% options. We calculated the phylogenetic metrics for all the 100 trees and used the means of these metrics to subsequent analyses.

Birds. We considered all bird species recorded in the 29 studied networks as our regional pool for the bird phylogenetic tree. We standardize species nomenclature using the South American Classification Committee (Remsen 2017) and submit the corrected names to birdtree.org online database (Jetz et al. 2012). We used the 'Hacket' source tree as our bird’s master phylogeny containing up to 10,000 phylogenetic hypotheses, which resulted in a multiphylo file (“.tre”) containing 100

phylogenetic trees without polytomies and with resolution at the species level. Likewise, the plant phylogeny, we calculated the phylogenetic metrics to all of 100 trees and used the mean to subsequent analyses.

Phylogenetic metrics

Based on the bird and plant phylogenetic trees of our regional pool of species, we estimated the evolutionary history involved in the interactions for each studied network using two complementary metrics calculated at the community level: (i) Phylogenetic Diversity (PD) which accounts for the summed branch lengths of all species within a network (Faith 1992), and (ii) how unique the frugivory interactions are within each network by calculating the Evolutionary Distinctness (ED) of birds and plants followed by the Evolutionary Distinctness of interactions (EDi, sensu Emer et al. 2019b), which represents how many millions of years of evolutionary history is carried by a given interaction, independent of how long they have co-evolved. We estimated ED using the equal splits metric in the "evol.distinct" function in the spicy package for R (Kembel et al. 2010). Equal splits equally divide the phylogenetic distance between a branch and its roots by the number of nodes between them, given higher values of ED for species placed in clades with lower speciation events. We used the averaged ED of bird and plant species calculated over 100 correspondent phylogenetic trees and used this to estimate the EDi. Therefore, EDi is the sum of the average EDs of plants and birds that interact in each network.

Robustness

This metric is calculated from the area under the extinction curve generated by the simulated removal of species from one group of a bipartite network that reflects in secondary extinctions in the interacting group. The size of this area (from 0 to 1) represents the system tolerance to species loss. Thus, R = 1 corresponds to a curve that decays slightly until the total extinction of the species in both sides of the network, indicating a robust system, while R = 0 corresponds to a curve that declines abruptly as soon as the first species is removed from the network, representing a fragile system in which one or a few extinctions lead to the rapid collapse of the network (Dormann et al. 2009). To calculate the robustness by the simulated extinction of birds and plants by ED order, we ranked the species in decreasing order

of ED and used both lists with external methods into the “second.extinct” function from “bipartite” package in R.

Landscape metrics

Vegetation maps were compiled from the FBDS (Brazilian Foundation for Sustainable Development, https://www.fbds.org.br/), SOS-Mata Atlântica 2014 (https://www.sosma.org.br/), and Hansen et al. 2000 (using a 95% NDVI limit to determine what is forest) to obtain a binary map (vegetation, non-vegetation), with 30 m of resolution, and based on Albers Equal Area, Datum SAD69 coordinate system. The extent of the Atlantic Forest used here is the consensual limits defined by several previous extent definitions (Muylaert et al. 2018). Then, for each study area we extracted the (1) forest cover (%), considering the percentage of forest cells within a radius of 4,000 meters from the centroid coordinate provided in each study, and (2) functional connectivity, which represents how much of the vegetation (in ha) is functionally connected to focal forest fragments, given a gap crossing capability. In our case we used a gap crossing of 180 meters, which corresponds to the maximum recorded distance for movement between forest fragments by forest-dependent birds of the Atlantic Forest (Martensen et al. 2008, Awade and Metzger 2008). Forest cover refers to the percentage of vegetation present in a given landscape, and functional connectivity reflects the sum of available forests (in ha) if the organism has the ability to cross up non-forest anthropogenic matrices (such as pasture, agriculture and *Eucalyptus* plantation). Functional connectivity was log-transformed using base 10, similarly to Jorge et al. (2013).

Data analyses

We assessed the explanatory power of forest cover and functional connectivity on explaining the phylogenetic metrics (PD and EDi) of the plants and birds that interacted with each other. For this we built generalized linear models (GLM) with landscape metrics as predictor variables, and PD and Edi as response variables. To evaluate the effect of phylogenetic metrics on the robustness of networks, we built another model with PD and EDi as predictor variables and robustness as the response variable. The explanatory power of each model was measured using the Coefficient of

Determination (r^2); for beta 1 (b1) parameters estimates we present both t-value and p-value.

We controlled for the variation in sampling intensity among studies by using sampling intensity as a covariable in all fitted GLM models:

$$Intensity_{web} = \frac{\sqrt{N_i}}{\sqrt{size_i}}$$

where N_i is the total number of interactions, and $size_i$ is the multiplication of the number of plants by the number of bird species in each network (Schleuning et al., 2012). We used the R language in version 3.6.3 for all analyses.

RESULTS

We found 29 interaction networks in different areas of the Atlantic Forest spanning a great latitudinal gradient of 2.2 thousand kilometers (Fig.1). Most studies were done in non-protected areas (55%) (Table S1). The networks involved 378 species of plants, 203 species of birds, and 8,029 interactions between them (Figure 2). The plant species most commonly consumed by birds was *Matayba elaeagnoides* (Sapindaceae) with 788 interactions (i.e. 9.8%), while the bird species most frequently recorded was *Thraupis sayaca* (Thraupidae) with 661 interactions (8.2%).

The three most forested areas (1, 3 and 5 in Fig. 1) had on average 20,151 millions years (Ma) of cumulative EDi and the three more deforested areas (17, 19 and 26) had an average of 1,106 ma (see supl. material Fig. S1). When we controlled for sampling intensity, areas with high forest cover had greater PD of birds (b1=5.345, SE=1.461, t=3.659, p<<0.001, r^2=0.494) and plants (b1=11.206, SE=6.106, t=1.835, p<<0.001, r^2=0.578), maintaining in addition interactions with higher EDi (b1=0.013, SE=0.004, t=3.030, p<<0.001, r^2=0.389) (Figure 3), this corresponds on average to 270 million years (Ma) of evolutionary distinction in interactions lost by each 1% of forest cover loss(see supl. material methods). Likewise, areas with higher functional connectivity had greater PD of birds (b1=45.220, SE=21.590, t=2.095, p=0.002, r^2=0.345), but connectivity was not able to explain the PD of plants nor EDi (Figure 4).

Moreover, when we controlled for sampling intensity interaction, areas with higher EDi (b1=0.0461, SE=0.0104, t=4.452, p<<0.001, r^2=0.389) and areas with greater PD of plants (b1=3.733e-05, SE=7.749e-06, t=4.818, p<<0.001, r^2=0.431) had

greater robustness calculated by the removal of plants with decreasing order o ED. Likewise, areas with higher EDi (b1=0.088, SE=0.013, t=7.040, p<<0.001, r^2=0.75) and with greater PD of birds (b1=0.17132, SE=0.014, t=12.637, p<<0.001, r^2=0.899) have greater robustness calculated by the removal of birds with decreasing order o ED (Figure 5).

DISCUSSION

We demonstrated that areas with a high forest cover are able to maintain greater phylogenetic diversity of birds and plants, and also maintain interactions between more evolutionarily distinct species (i.e., high PD and EDi). When we lose 1% of forest cover, we also lose on average 270 million years (Ma) of evolutionary distinction in the interactions between plants and frugivorous birds. A mean difference of 19,045 Ma of evolutionary distinction from the three more forested areas (1, 3 and 5 in Fig. 1) to the three more deforested areas (17, 19 and 26) reinforce the importance of maintaining large and well-connected forest blocks as key sources of phylogenetic/evolutionary information (Cadotte et al. 2012, Ribeiro et al. 2009). These findings also emphasizes how important are restoration projects, particularly those that aim to increase functional connectivity between areas with high levels of integrity of ecological processes (Tambosi et al. 2014)

Areas with high functional connectivity between forest fragments are able to maintain higher phylogenetic diversity of frugivorous birds when compared to less connected or isolated forest patches (Fig.3), suggesting that the connection between remnant areas of forests is important for maintaining key ecological processes such as seed dispersal. We know that birds, especially insectivorous and frugivorous ones, are among the most mobile vertebrates and consequently most threatened by the fragmentation of tropical forests (Sekercioglu 2002). Landscapes with higher functional connectivity allow such mobile organisms to seek resources in structurally disperse forest fragments (Boscolo et al. 2008, Martensen et al. 2012). However, this will depend on the ability of species to cross the surrounding anthropogenic matrix, as pastures, agriculture and *Eucalyptus* plantation (Andrade and Marini 2001, Silveira et al. 2016, Giubbina et al. 2018, Ramos et al. 2020). The combination between fragment size, forest cover and functional connectivity can be pivotal for mitigating the negative effects of habitat loss and fragmentation, thus allowing birds to use

multiple functionally connected fragments (Martensen et al. 2008). Therefore, maintaining high levels of functional landscape connectivity for frugivorous birds and high forest cover at landscape level are of utmost importance for guaranteeing high phylogenetic diversity of birds. However, plant phylogenetic diversity is mostly affected by forest cover, while functional connectivity was apparently not a good predictor of the phylogenetic diversity of interacting plant species, suggesting that seeds may not move among forest fragments as easily as birds.

Areas with greater phylogenetic diversity of both plants and birds, as well as areas with more evolutionary distinct interactions, presented interaction networks with greater robustness . Some authors point out the role of species loss in the robustness of parasite-host interaction networks (Ives and Godfray 2006), herbivorous/predatory insects and plants(Haddad et al. 2009), and pollination (Memmott et al. 2004, Vásquez et al. 2009, Kaiser-Bunbury et al. 2010, Vieira et al. 2013). To our knowledge, however, Rezende et al. (2007) was the only to analyze the robustness of phylogenetically structured mutualistic networks. Indeed, studies have rarely shown how the loss of phylogenetic diversity (PD) and interactions between evolutionarily distinct species (EDi) lead to less robust networks and consequently more likely to collapse in face of anthropic impacts. Our study shows the importance of maintaining large forest blocks and clusters of functionally connected areas with great phylogenetic diversity, which, in turn, can assure high levels of robustness to interaction networks. This agrees with previous studies showing that PD is linked to ecosystem functioning (Flynn et al. 2011, Srivastava et al. 2012) and promotes ecosystem stability (Cadotte et al. 2012), so that when we extinguish species in areas with high phylogenetic diversity, the impact of such extinction is smaller due to the high diversity of interactions.

The possibility of extinction of plants and birds would theoretically lead to co-extinctions and, consequently, to the rapid collapse of networks in these communities. However, the extinction of a species does not necessarily lead to the co-extinction of its interacting partners (Pires 2017). This is because there is the possibility of interaction rewiring within complex networks, though often with unknown consequences for the effectiveness of the interaction (Gilljam et al. 2015). Moreover, we should not expect that from the extinction of a given species the extinction of its interacting partners immediate follows as a time lag is expected to occur in

consequence of the action of secondary seed dispersers (e.g., rodents, ants; Forget et al. 2005) and the long lifespan of species, especially trees (Herrera 1986).

In summary, we found that in addition to the well known extinction of species, deforestation may cause the extinction of the evolutionary information embedded in the interactions between plants and their seed dispersers. As a consequence, it may negatively affect the robustness of the interaction networks formed by these mutualistic partners. Within the Atlantic Forest biodiversity hotspot, every percentage of forest lost at landscape level represents the loss of 270 Ma of evolutionary history in the interactions between plants and frugivorous birds. In critical environmental conditions, when forest cover and functional connectivity is exceedingly low, seed dispersal networks present low phylogenetic diversity and evolutionary distinction (Emer et al. 2019b), which may translate into low ecological resilience and recovery capacity of the ecosystems.

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REFERENCES

Andrade, R.D. and Marini, M.A. et al. 2001. Movement of birds in natural forest patches in southeast Brazil, in: Albuquerque, J.L.B., Candido Jr., J.F., Straube, F.C, Ross, A.L. (ed.), Ornitologia e Conservação: da Ciência às Estratégias. Editora UNISUL, Tubarão- SC pp.125–136.

Awade, M. and Metzger, J. P., 2008. Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. Austral Ecology, 33: 863–871.

Butchart. S. H. M. et al. 2010. Global Biodiversity: Indicators of Recent Declines.- Science 328: 1164-1168

Burgos, E. et al. 2007. Why nestedness in mutualistic networks? – J. Theor. Biol. 249: 307–313.

Cadotte, M. W., Dinnage, R., & Tilman, D., 2012. Phylogenetic diversity promotes ecosystem stability.- Ecology 93:S223–S233.

Carreira, D. C. et al. 2020. Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest.- Scientific Reports 10: 1–11.

Carvalho G. (n.d). The Plantminer. Retrieved October 25, 2019, from http://www.plantminer.com/

Côrtes, M. C., and Uriarte, M. 2013. Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal.- Biological Reviews 88: 255-272.

Costa, J. B. P. et al. 2012. Reduced availability of large seeds constrains Atlantic forest regeneration.- Acta Oecologica 39: 61–66.

Cramer, J. M. et al. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees.- Biological Conservation 37: 425–423.

Crandall, K.A. et al. 2000. Considering evolutionary processes in conservation biology.- Trends in Ecology and Evolution 15: 290–295.

Da Silveira, N.S. et al. 2016. Effects of Land Cover on the Movement of Frugivorous Birds in a Heterogeneous Landscape.- PLoS ONE 11: e0156688.

Dormann, C. F. et al. 2009. Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks.- The Open Ecology Journal 2: 7–24.

Dunne, J. A. et al. 2002. Network structure and biodiversity loss in food webs: Robustness increases with connectance.- Ecology Letters 5: 558–567.

Emer, C. et al. 2019a. Seed dispersal networks in tropical forest fragments : Area effects, remnant species, and interaction diversity.- Biotropica 52: 81– 89.

Emer, C. et al. 2019b. Defaunation precipitates the extinction of evolutionarily distinct interactions in the Anthropocene. Science Advances, June: EAAV6699.

Emer, C. et al. 2018. Seed-dispersal interactions in fragmented landscapes – a metanetwork approach.- Ecology Letters 21: 484–493.

Evans, D. M. et al. 2013. The robustness of a network of ecological networks to habitat loss.- Ecology Letters 16: 844–852.

Faith, D. P., 1992. Conservation evaluation and phylogenetic diversity.- Biological Conservation 61: 1–10.

Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity.- Annual Review of Ecology, Evolution, and Systematics 34: 487–515.

Fleming, T. H. et al. 2009. The evolution of bat pollination: a phylogenetic perspective.- Annals of Botany 104: 1017–1043

Flynn, D. F. B. 2011. Functional and phylogenetic diversity as predictors of biodiversity-Ecosystem-function relationships.- Ecology 92: 1573–1581.

Forget, P.M. et al. (eds.). 2005. Seed fate: predation, dispersal, and seedling establishment. CABI Publishing, Wallingford, Oxfordshire, UK.

Galetti, M. et al. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size.- Science 340: 1086–1090.

Gilljam, D. et al. 2015. Adaptive rewiring aggravates the effects of species loss in ecosystems.- Nature Communications 6: 1–10.

Giubbina, M.F. et al. 2018. Sugarcane and Eucalyptus plantation equally limit the movement of two forest-dependent understory bird species.- Austral Ecology 43: 527-533.

Goerck, J. M., 1997. Patterns of rarity in the birds of the Atlantic forest of Brazil.- Conservation Biology 11:112–118.

Grab, H. et al. 2019. Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services Heather.- Science 363: 282–284.

Haddad, N. M. et al. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure.- Ecology Letters 12: 1029–1039.

Hansen, M. C. et al. 2000. Global land cover classification at 1 km spatial resolution using a classification tree approach.- International Journal of Remote Sensing 21: 1331-1364.

Herrera, C. M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. In Frugivores and seed dispersal (pp. 5-18). Springer, Dordrecht.

Ives A, Godfray H. 2006. Phylogenetic analysis of trophic associations.- American Naturalist 168: E1-14.

Jetz, W. et al. 2012. The global diversity of birds in space and time.- Nature 491: 444–448.

Johnson, C. N. et al. 2017. Biodiversity losses and conservation responses in the Anthropocene.- Science 356: 270-275.

Jorge, M. L. S. P. et al. 2013. Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot.- Biological Conservation 163: 49–57.

Kaiser-Bunbury, C. N., and Blüthgen, N., 2015. Integrating network ecology with applied conservation: A synthesis and guide to implementation.- AoB PLANTS 7: plv076.

Kaiser-Bunbury, C. N. et al. 2010. The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour.- Ecology Letters 13: 442–452.

Kembel, S. W. et al. 2010. Picante: R tools for integrating phylogenies and ecology.- Bioinformatics 26: 1463–1464.

Kuhn, T. S. et al. 2011. A simple polytomy resolver for dated phylogenies.- Methods in Ecology and Evolution 2: 427–436.

Lorts, C. M. et al. 2008. Evolution of fruit types and seed dispersal: A phylogenetic and ecological snapshot.- Journal of Systematics and Evolution 46: 396–404.

Martensen, A. C. et al. 2012. Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance.- Conservation Biology 26: 1100–1111.

Martensen, A. C. et al. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation.- Biological Conservation 141: 2184–2192.

Memmott, J., et al. 2004. Tolerance of pollination networks to species extinctions.- Proceedings of the Royal Society B 271: 2605–2611.

Mittermeier, R. A. et al. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities.- Conservation Biology 12:516–520.

Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it.- Syst. Biol.: 51, 238–254.

Morellato, L. P. C. and Haddad, C. F. 2000. Introduction: the Brazilian Atlantic forest.- Biotropica 32: 786-792.

Muylaert, R. L. et al. 2018. Uma Nota Sobre Os Limites Territoriais Da Mata Atlântica.- Oecologia Australis 22: 302–311.

Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities.- Nature 403: 853–858.

Olden, J. D. et al. 2004. Ecological and evolutionary consequences of biotic homogenization.- Trends in Ecology & Evolution 19: 18–24.

Pérez-Valera, E. et al. 2018. Resilience to fire of phylogenetic diversity across biological domains.- Mol Ecol.27: 2896– 2908.

Pigot, A. L. et al. 2016. Quantifying species contributions to ecosystem processes: A global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. -Proceedings of the Royal Society B: Biological Sciences, 283: 20161597.

Pires, M. M. 2017. Rewilding ecological communities and rewiring ecological networks.- Perspectives in Ecology and Conservation 15: 257–265.

Qian, H. and Jin, Y. 2016. An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure.- Journal of Plant Ecology,9: 233–239.

Ramos, D.L. et al. 2020. Forest and connectivity loss drive changes in movement behavior of bird species.- Ecography 43: 1203-1214.

Remsen, J. V., Jr. et al. Version [28 April 2017]. A classification of the bird species of South America. American Ornithologists' Union.

Rezende, E. L. et al. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks.- Nature 448: 925–928.

Ribeiro, M. C. et al. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation.- Biol. Conserv. 142: 1141–1153.

Schleuning, M. et al. 2012. Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitudes.- Current Biology: 22: 1925–1931.

Sekercioglu, C.H. et al. 2002. Disappearance of insectivorous birds from tropical forest fragments.- Proceedings of the National Academy of Science 99: 263–267.

Srivastava, D.S. et al. 2012. Phylogenetic diversity[3] and the functioning of ecosystems.- Ecol Lett 15: 637-648.

Suchard, M. A. et al. 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10.- Virus evolution 4: vey016.

Tabarelli B. and Peres C.A., 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration.- Biol. Conserv. 106: 165–176.

Taylor, P. D. et al. 1993. Connectivity Is a Vital Element of Landscape Structure.- Oikos 68: 571–573.

The Plant List, 2013. Version 1.1. Published on the Internet; http://www.theplantlist.org/ (accessed 18st January of 2019).

Tylianakis, J. M. et al. 2010. Conservation of species interaction networks.- Biological Conservation 143: 2270–2279.

Vasquez, D. P. et al. 2009. Evaluating multiple determinants of the structure of plant–animal mutualistic networks-. Ecology 90: 2039–2046.

Vieira, M. C., and Almeida-Neto, M., 2014. A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance. Ecology Letters 18: 144–152.

Vieira, M. C. et al. 2013. Plant-pollinator coextinctions and the loss of plant functional and phylogenetic diversity.- PLoS ONE 8: 1–10.

Young, C.E.F., 2003. Socioeconomic causes of deforestation in the Atlantic Forest of Brazil. In: Galindo-Leal, C. and Câmara, I.G. (Eds.), The Atlantic Forest of South America: biodiversity status. Threats, and Outlook. Island Press, Washington, pp. 103–117.

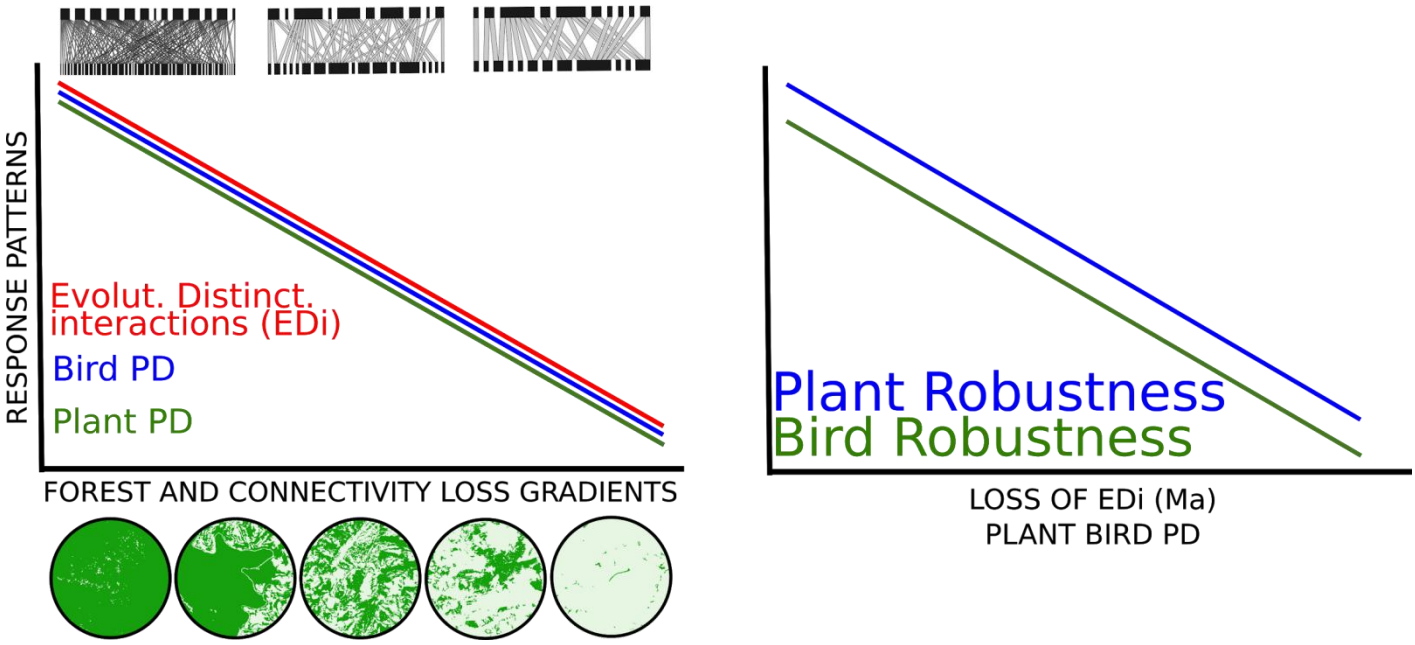

Figure 1. Expected effects of deforestation on the Phylogenetic Diversity (PD) of interacting birds and plants, and the Distinctiveness of Interactions (EDi) between them (left panel). The right panel shows the expected consequences of the decrease in PD and EDi on the robustness of interaction network between plants and frugivorous birds.

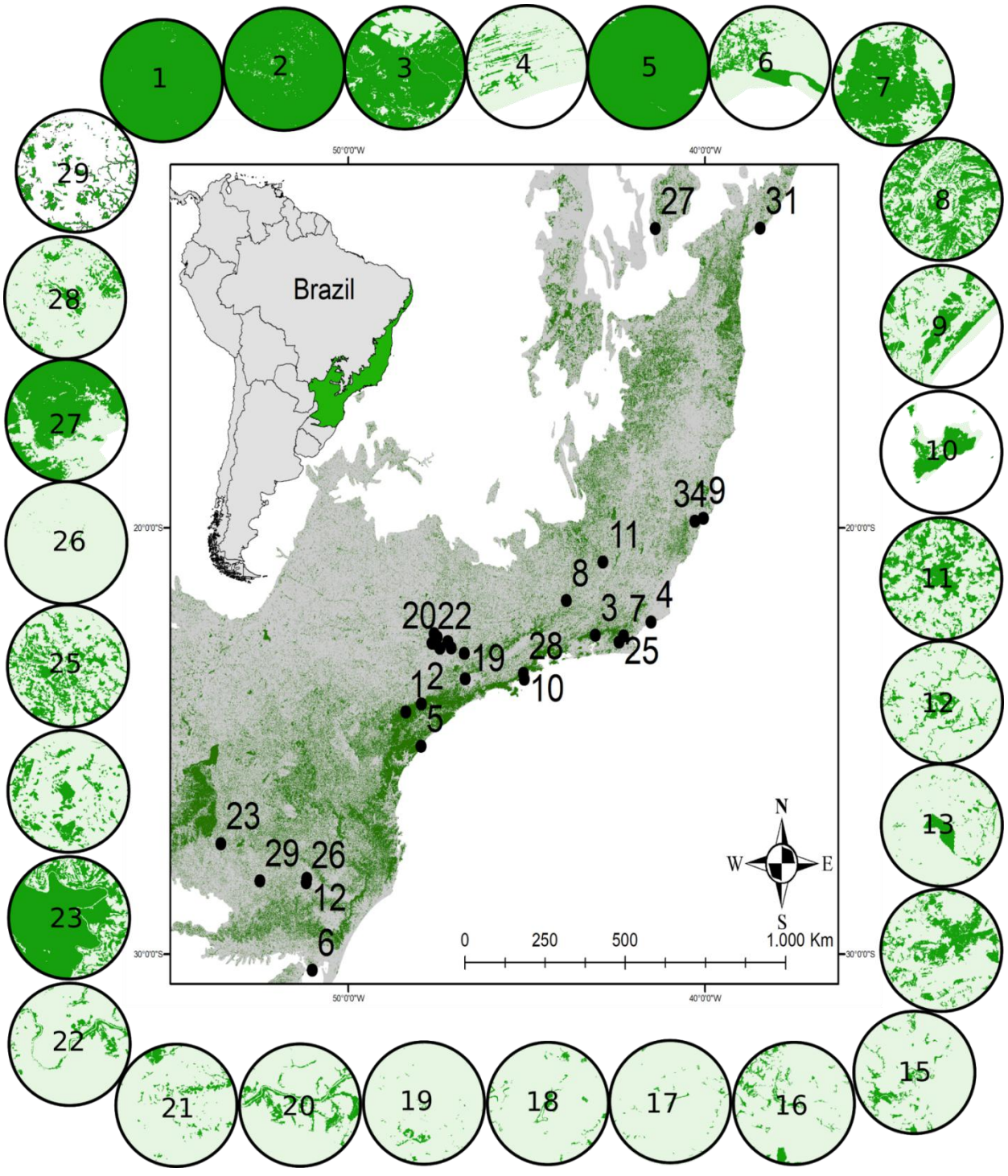

Figure 2. Distribution map of the areas where interaction networks were sampled in the Atlantic Forest with their respective forest cover buffers (4 km radius).

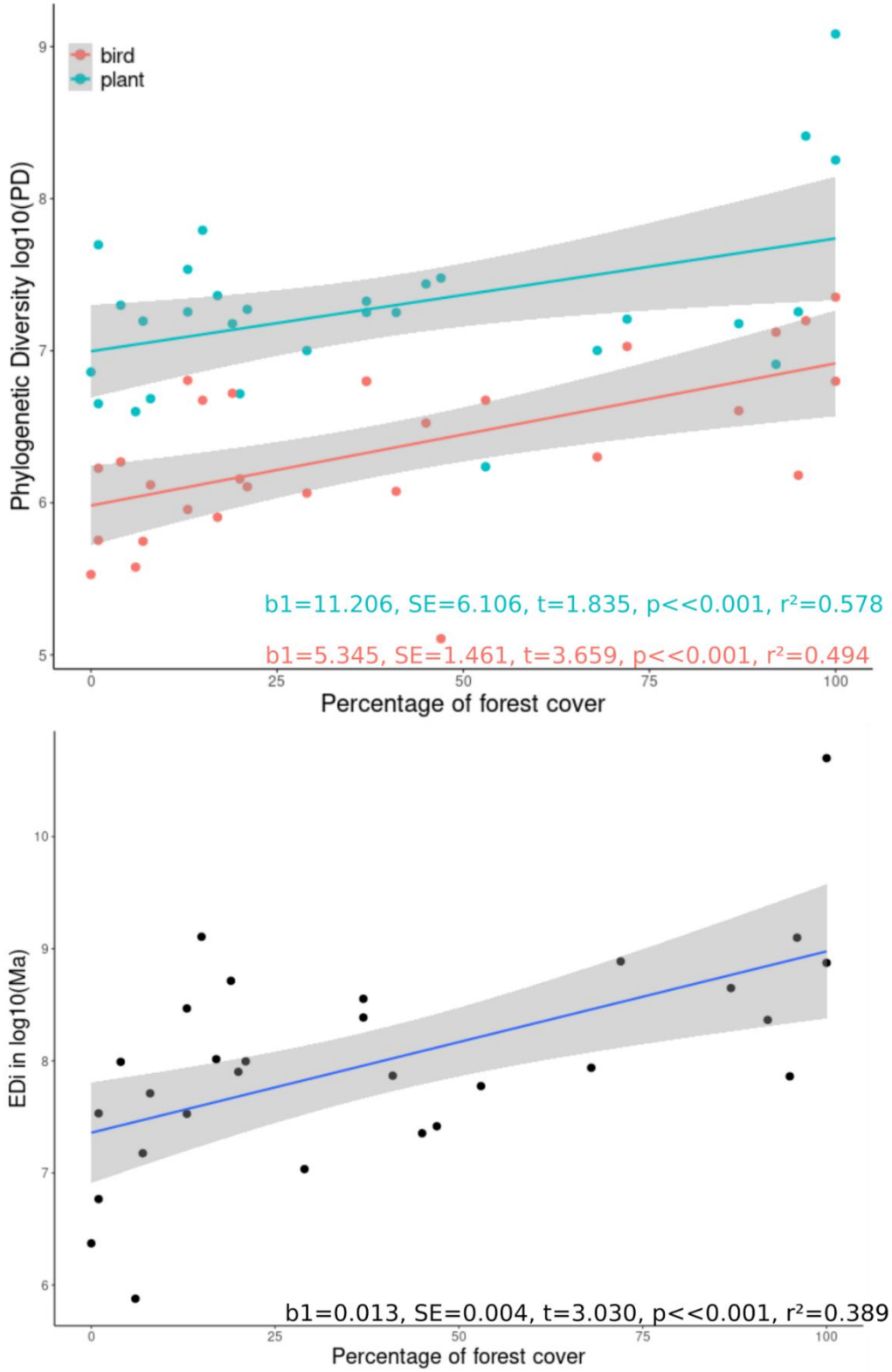

Figure 3. Linear models showing that areas with greater forest coverage in a 4-km radius presented greater Distinctiveness of Interactions (EDi) (a[8]), and greater phylogenetic diversity of both plants and frugivorous birds (b). The gray band represents the 95% confidence interval.

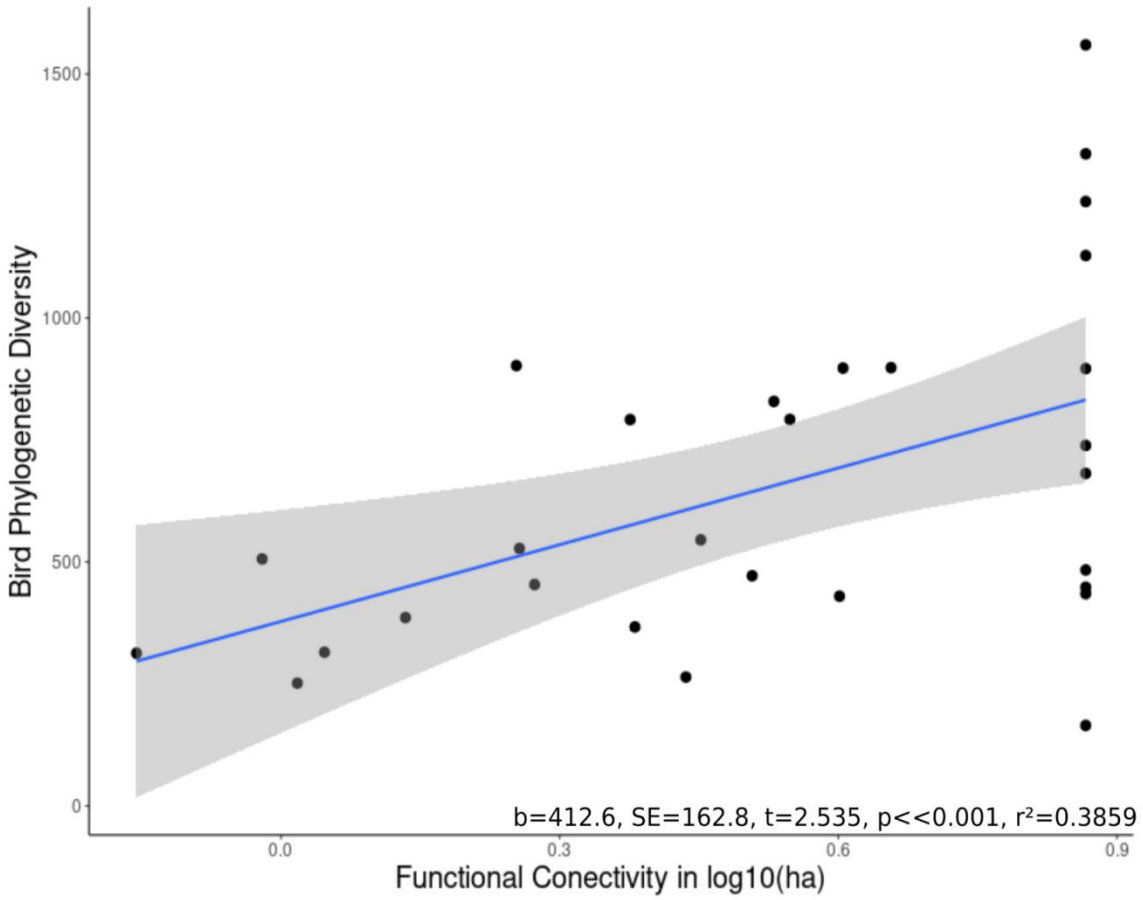

Figure 4. Linear regression between Phylogenetic Diversity (PD) in birds and Functional Connectivity, showing that more connected areas maintain greater phylogenetic diversity of frugivorous birds. The gray band represents the 95% confidence interval.

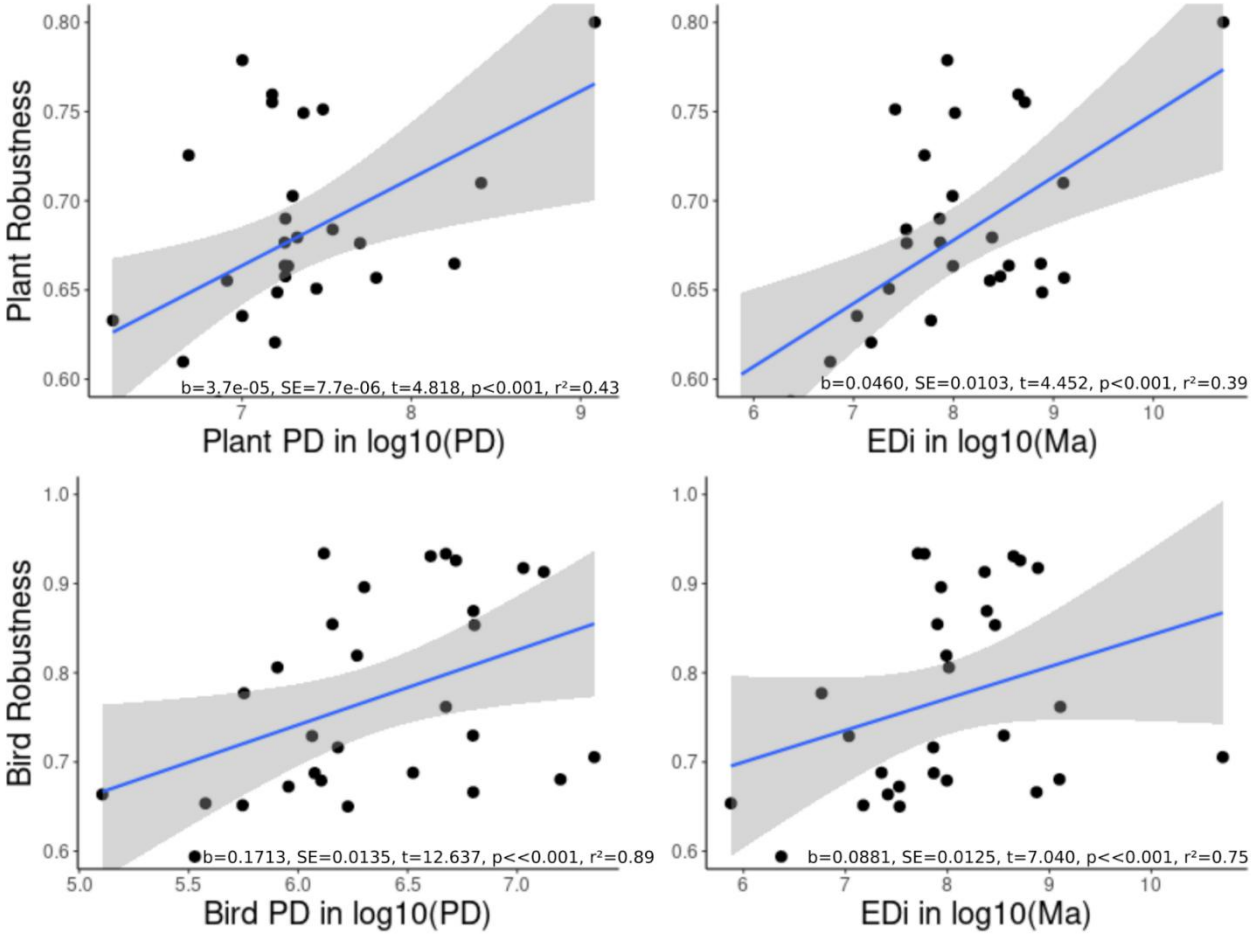

Figure 5. Linear regression showing that areas with greater phylogenetic diversity (PD; a and c) and greater evolutionary distinctiveness (EDi; b and d) have greater robustness in the interaction networks calculated by removing plants (a and b) and birds (c and d) in decrescent order of ED. The gray band represents the 95% confidence interval. EDi and PD were logged-transformed with base 10.

Supplementary Material

Methods

We calculated the amount of EDi (in millions of years - Ma) according to the loss of forest cover using the formula:

$$EDi_p=(EDi1/FC1+EDi2/FC2+EDi3/FC3...)/N_t$$

Where EDi_p is the amount of EDi for each 1% of vegetation, $EDi1$ is the amount of EDi in the first area divided by the percentage of forest cover $FC1$ in this area and N_t is the total number of areas.

Figure S1. The amount of Evolutionary Distinctiveness of Interactions (EDi) in millions of years in each study area, ordered by percentage of forest cover. Red lines mark the average EDi of the three most and three less forested areas, respectively.

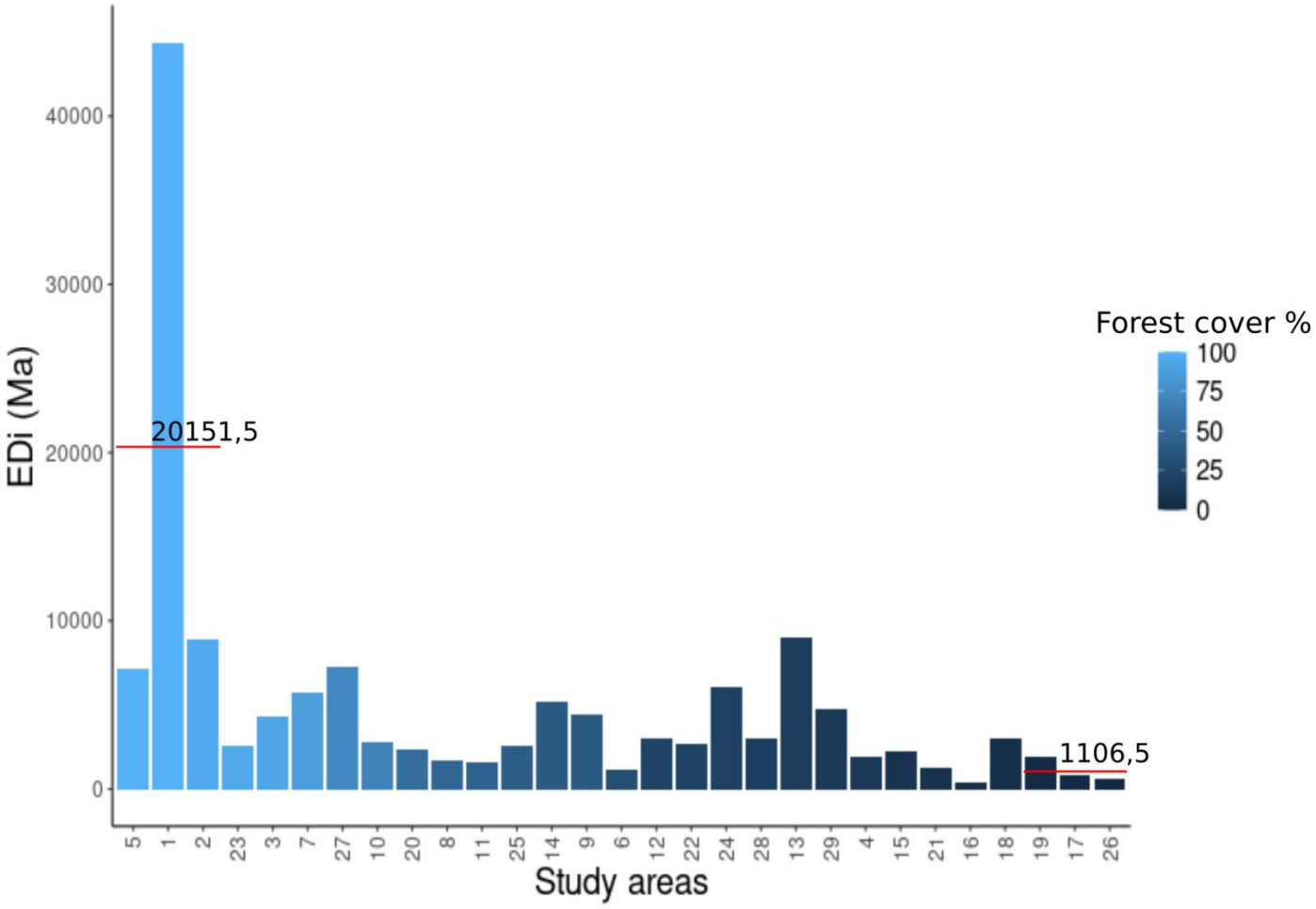

Table S1- Study areas with local coordnates and landscape metrics

Study_site	id	Latitude	Longitude	protected	habitat_pct_4000m	func_connect_0180m_AreaHA
PE Intervales	1	-24.316965	-48.387175	yes	100	7.35219651181922
PARNA S. Órgãos	3	-22.52	-43.07	yes	92	7.35219651181922
PE Ilha do Cardoso	5	-25.127786	-47.957463	yes	100	4.02836788369706
Interior RS	23	-27.410062	-53.57638	not	95	7.35219651181922
Ubatuba-SP	27	-23.418272	-45.084853	yes	72	7.35219651181922
PE Carlos Botelho	2	-24.131389	-47.949167	yes	96	7.35219651181922
fragment MG	11	-20.802611	-42.858746	not	45	7.35219651181922
Rebio Poço Antas	7	-22.536652	-42.276533	yes	87	7.35219651181922
Reserva Comboios	9	-19.774	-40.0432	yes	37	4.53744128340795
PE Ilha Anchieta	10	-23.548369	-45.062541	yes	68	2.83122969386706
Rio Claro-SP	20	-22.706	-47.61	not	53	3.53109554687003
Silva Jardim-RJ	24	-22.681725	-42.402228	not	19	3.39392600658584
Mata Sta Genebra	13	-22.818101	-47.113757	yes	15	2.37657695705651
Itatiba	14	-22.943263	-46.749949	yes	37	7.35219651181922
PE Ibitipoca	8	-21.709	-43.884	yes	47	7.35219651181922
Salvador-BA	28	-12.966824	-38.452749	not	17	2.40483371661994
Araucaria Forest	12	-28.223141	-51.166857	not	21	7.35219651181922
Muitos Capões-RS	25	-28.326808	-51.182164	not	41	7.35219651181922
fragment RC	15	-22.48	-47.5929	not	8	1.8750612633917
Reserva Itapua	6	-30.38087	-51.008115	yes	29	3.99325983143674
restored 25	18	-22.565851	-47.503397	not	4	1.80617997398389
restored 8	22	-22.709772	-47.6526	not	20	3.21563756343506
Aracruz-ES	29	-19.846619	-40.281914	not	13	1.79239168949825
restored 57	16	-22.671644	-47.204638	not	6	2.72835378202123
PARNA Jurubatiba	4	-22.206	-41.5073	yes	13	1.36172783601759
fragment SP	19	-23.545601	-46.720929	not	1	0.954242509439325
fragment RJ	21	-22.764556	-43.692994	not	7	0.698970004336019
restored 15	17	-22.825234	-47.4265	not	1	1.11394335230684
Mucugê-BA	26	-12.977194	-41.389953	not	0	1.04139268515822

Table S2- Study area with network metrics

Study_site	id	robustness_ED_plant	robustness_ED_bird	int_number	samp_int
PE Intervales	1	0.800129939174396	0.705419112668349	1224	0.243839873685241
PARNA S. Órgãos	3	0.65522608226281	0.913107356292879	195	0.462402194494884
PE Ilha do Cardoso	5	0.664750147798512	0.666124384955284	185	0.281175797428991
Interior RS	23	0.689986305801488	0.716379243117151	41	0.494011760029677
Ubatuba-SP	27	0.648661342023722	0.917478585990043	182	0.483045891539648
PE Carlos Botelho	2	0.709999725387043	0.680482514321297	286	0.245171959280596
fragment MG	11	0.650745416608173	0.687993166407321	64	0.405095746833467
Rebio Poço Antas	7	0.759582897442327	0.930787397873281	181	0.569027667678105
Reserva Comboios	9	0.679440350372748	0.869270571976487	122	0.467168994486642
PE Ilha Anchieta	10	0.778837444177545	0.896071289628138	104	0.644980619863884
Rio Claro-SP	20	0.632909203478339	0.933423176846713	57	0.596866819315666
Silva Jardim-RJ	24	0.755267610125306	0.925950530345159	183	0.559303596287842
Mata Sta Genebra	13	0.656775304218616	0.761834673530384	155	0.368088998055512
Itatiba	14	0.66364472603144	0.729618380530015	108	0.45014069095232
PE Ibitipoca	8	0.751248419090825	0.663603832434205	42	0.525657483037847
Salvador-BA	28	0.749251119607222	0.806013040517327	86	0.579601155968481
Araucaria Forest	12	0.663410931773894	0.679192117525162	54	0.444749589996661
Muitos Capões-RS	25	0.676587307842941	0.687492338608757	51	0.44289258986107
fragment RC	15	0.725522735245195	0.933871761451243	62	0.718795288428261
Reserva Itapua	6	0.63539330544723	0.729034814186005	43	0.50293257646586
restored 25	18	0.702723421693209	0.819282456623084	88	0.500711744132541
restored 8	22	0.584889196732875	0.854499104296163	48	0.554700196225229
Aracruz-ES	29	0.65764503541319	0.853543866991121	112	0.477118723613698
restored 57	16	0.585248003209908	0.65358590601538	15	0.52704627669473
PARNA Jurubatiba	4	0.683930690762422	0.672391426441253	41	0.42687494916219
fragment SP	19	0.676278264802109	0.650043119781792	59	0.375697119178271
fragment RJ	21	0.62057521053132	0.651442927378457	25	0.456435464587638
restored 15	17	0.609735521079416	0.77701288008854	20	0.577350269189626
Mucugê-BA	26	0.587647146077104	0.593878110755099	9	0.5

Table S3- Study area with phylogenetic metrics

Study_site	id	EDi	plant.PD	bird.PD	plant_sp	bird_sp
PE Intervales	1	44368.7561593466	8808.89802486193	1559.90482379007	219	94
PARNA S. Órgãos	3	4292.97633139042	1003.12778473155	1238.86722077023	12	76
PE Ilha do Cardoso	5	7143.90020941904	3844.95387109117	897.378373001343	52	45
Interior RS[7]	23	2594.32639359905	1417.1961223075	483.542159812973	12	14
Ubatuba-SP	27	7239.63701917542	1350.45258618139	1128.1215829031	13	60
PE Carlos Botelho	2	8941.96603955322	4501.51342262774	1336.5804429548	61	78
fragment MG	11	1561.82870850449	1701.49507437361	681.677521523643	15	26
Rebio Poço Antas	7	5704.57194709605	1310.19247738063	738.923119136003	13	43
Reserva Comboios	9	4386.9110551814	1518.53830820289	898.324443538933	13	43
PE Ilha Anchieta	10	2800.88346008436	1098.70219802239	545.395937210643	10	25
Rio Claro-SP	20	2379.16347402249	511.3550756305	792.210269077773	5	32
Silva Jardim-RJ	24	6085.03273589012	1310.19247738063	829.167842168003	13	45
Mata Sta Genebra	13	9015.85211015116	2422.11843611352	791.894107674833	26	44
Itatiba	14	5182.17470202112	1410.42449676356	896.345172650333	13	41
PE Ibitipoca	8	1662.32804663833	1768.6925572739	164.990598746773	19	8
Salvador-BA	28	3024.65226088297	1576.05599793809	366.896611725573	16	16
Araucaria Forest	12	2965.10429801345	1439.78284890969	448.251132644733	13	21
Muitos Capões-RS	25	2609.33807618172	1410.76126320919	434.983872024233	13	20
fragment RC	15	2229.74771363694	800.14190198026	453.756141356473	5	24
Reserva Itapua	6	1134.33328990241	1097.94815390281	429.860721268473	10	17
restored 25	18	2951.52741115183	1478.95350503066	527.830984060043	13	27
restored 8	22	2702.09210814445	826.3378649932	471.775328622873	6	26
Aracruz-ES	29	4757.80579964449	1415.93130739089	902.489185471903	12	41
restored 57	16	356.683761464276	734.683154864	264.161114667833	6	9
PARNA Jurubatiba	4	1857.99814129931	1872.94107489648	386.098186667173	15	15
fragment SP	19	1865.55371030081	2201.68313229664	506.221115102273	22	19
fragment RJ	21	1306.51071419632	1332.3860652272	313.060721450873	10	12
restored 15	17	867.910956446366	774.1072749868	315.077915529773	5	12
Mucugê-BA	26	584.728803913925	953.7951004097	251.68004757936	6	6

Conclusão Geral

Dado esses dois passos na expansão do conhecimento sobre como interações mutualistas evoluem e como mudanças no ambiente influenciam sua estrutura, venho então concluir este trabalho, primeiro agradecendo a tantas pesquisadoras e pesquisadores, a maioria brasilenses, que dedicaram tamanha energia observando plantas com frutos para registrar as interações com as aves. Esse tipo de pesquisa básica, tão desvalorizada nos tempos atuais, foi a base da construção dessa tese, que juntou trabalhos realizados em diferentes regiões para entender padrões macro-ecológicos.

Com essa visão macro-ecológica conseguimos entender que a diversidade filogenética de plantas e aves frugívoras é um dos grandes componentes ligados à diversidade de interações. Também encontramos que comunidades com aves mais agrupadas filogeneticamente tendem a ter maior diversidade de interações. Além disso, encontramos um importante efeito *bottom-up* segundo o qual a diversidade filogenética das plantas, mais que a das aves, está relacionada às redes de interações mais generalistas. Pudemos ainda demonstrar que áreas com maior quantidade de florestas, maior diversidade filogenética e interações evolutivamente distintas tendem a manter maior robustez nas redes de interações entre plantas e aves frugívoras.

Chamamos a atenção aqui para a emergência de uma visão cada vez mais multidisciplinar da conservação e do entendimento sobre a extinção das interações no antropoceno. Sob essa ótica, devemos valorizar ainda mais aspectos filogenéticos/evolutivos da diversidade biológica e dos processos ecológicos, assim como o uso conjunto das seguintes métricas: diversidade filogenética (PD), distinção evolutiva das espécies (EDi) e o índice de parentesco líquido (*net relatedness index*-NRI), num contexto de interações mutualistas. Essa visão possibilita interpretações importantes sobre como as relações filogenéticas das espécies fornecem informações sobre as interações ecológicas em ambientes megadiversos.

Também é importante lembrar que, apesar dos enormes esforços dos pesquisadores para registrar interações, elas são efêmeras. Existe uma incerteza sobre suas frequências, se algumas das interações registradas resultam de um rearranjo (*rewiring*) de interações extintas no passado, ou se são interações raras devido a mudanças no ambiente e no comportamento dos frugívoros. Essa incerteza é mais

visível no primeiro capítulo, no qual, apesar de não termos métricas de paisagem, sabemos que parte das áreas amostradas são degradadas ou em fase de regeneração. Neste sentido, este capítulo diferiu do segundo capítulo, que foi desenvolvido após a publicação do *data paper* de Bello el al. (2017), que incluiu na nossa base de dados mais 10 áreas, a maioria delas preservadas, como o Parque Estadual de Carlos Botelho e o Parque Estadual Intervales, que englobam uma grande região protegida de Floresta Atlântica na Serra do Mar.

Uma grande limitação do segundo capítulo é o lapso temporal entre a época de tomada dos dados em campo e a atual situação da paisagem revelada em imagens recentes de satélite. A mediana do o ano de publicação dos trabalhos foi 2005, sendo o trabalho de Zimmerman (1996) o mais antigo, enquanto o de Robinson (2015), o mais recente. Nesse capítulo, devido à dificuldade operacional de mapeamento de cada ano de publicação, decidimos extrair todas as métricas de paisagem para cada local a partir de um mapa temático basal construído em 2014. Apesar dessas limitações, os resultados encontrados sugerem que a perda de florestas leva à perda de diversidade filogenética, interações evolutivamente distintas e à perda de robustez nas redes de interações, demonstrando que a diferença temporal entre as métricas de paisagem e os registros de interações são menos importantes que os padrões ecológicos encontrados.

Encerramos sugerindo novas pesquisas, ou mesmo a continuação desta, de modo a adicionar mudanças temporais na paisagem como uma variável das inter-relações aqui investigadas. Modelos que possam entender o rearranjo das interações e como elas mantêm a robustez das redes e a eficiência da dispersão de sementes mesmo em ambientes impactados ou em restauração (Pires 2017, Raimundo et al.2018, Vizentin Bugoni et al. 2020) também representam um grande passo para a expansão do conhecimento nessa área.

Referências bibliográficas

Bugoni, J. V., Maruyama, P. K., & Sperry, J. H. (2020). Including rewiring in the estimation of the robustness of mutualistic networks. 2020(September 2019), 106–116.

Pires, M. M. (2017). Rewilding ecological communities and rewiring ecological networks. Perspectives in Ecology and Conservation, 15(4), 257–265.

Raimundo, R. L. G., Guimarães, P. R., & Evans, D. M. (2018). Adaptive Networks for Restoration Ecology. Trends in Ecology and Evolution, 33(9), 664–675.

Manifesto

É tudo pra ontem, não no sentido de pressa de corre-corre, sufoco, *dead line*, entrega, não. É no sentido de corrigir o antes. Cada vitória sem precedentes, é o precedente do que vem depois, o solo adubado, a rua asfaltada, s chances de ter uma infância e ter um ambiente preservado.

Somos funcionários do amanhã presos no hoje, consertando tudo que passou. E passou? Se aquela porta continua aberta, se o eco violento das invasões ainda impedem que nossos sonhos germinem livres. Se ainda é necessário que a flor vença o concreto, o hoje, o agora, com tudo que eles oferecem são duas ilusões.

É tudo pra ontem. Não no sentido de pressa, no sentido de pressa, o que é pra ontem, já era, perdeu no sentido da vida, dentro do fluxo do tempo e do espaço. Se o estômago ronca, é um lembrete do vazio que permanece e que foi parido no antes.

A tônica desse lugar é produção, padrões e padrões e padrões e reprodução, se somos mais do que meras engrenagens algo precisa ser corrigido, a linha do tempo precisa ser redigida, se alguma coisa está fora da ordem, é tudo pra ontem.

“Exu atingiu um pássaro ontem com uma pedra que atirou hoje.” Entendeu? Ontem estávamos numa calçada sonhando acreditando estar traçando o destino do universo em guardanapos de papel, ontem. Quando nos sentimos feios, fracos, inúteis, vazios, quando desejamos nos tornar invisíveis ou indiferentes. Fizemos da nossa diferença nossa força, da nossa origem o nosso castelo, do nosso descuido o nosso pior inimigo. E nossa missão? Gritar pela rua que é tudo pra ontem, por quem sangrou e morreu calado. Pra dizer que nos orgulhamos das nossas cicatrizes mas que elas são coadjuvantes, os personagens principais dessa história ainda somos nós e não as nossas dores. Então cá estamos nós... Triunfo se não for coletivo é do sistema. Eternos e efêmeros, cá estamos nós, por trilhas caminhos e ruas um bando de maloqueiro sonhador compreendendo que é no agora que se muda o ontem e que sem isso não se constrói o amanhã. Não se iluda com a pressa, a evolução demanda tempo.

Quantos de nós estão por aí, quantos narizes largos são doutores, quantos cabelos crespos são faxineiros? Quantos pele escura são donos da loja no shopping, quantos são camelôs? A minha presença aqui, um doutor Negro no PPG-Ecologia e Biodiversidade da UNESP de Rio Claro, pelos que não chegaram, não porque não sonharam com isso, não porque acham a ciência chata e desinteressante, mas porque as oportunidades que abriram pra mim, apesar do meu esforço, não abrem pra todos, até que a proporção de negros na universidade seja maior que na cadeia.

Onde estaria a humanidade agora se nosso potencial não fosse cortado a metade da metade? Quantos Darwins mulheres, negras, pobres, não puderam observar os seres vivos porque estavam lutando pra sobreviver? Quantos ainda vivem assim?

Porque quem veio forçado no navio e jamais sonhou com uma diáspora sua chegar tão longe. Pelos que sofreram tanto, por todo o mal que suportaram, por quem um dia sonhou em ver a diáspora do fruto do seu fruto florecer num ambiente fértil, em paz, feliz e justo. Pra que os que germinem por aqui encontre solo adubado. Triunfo de não for coletivo, é do sistema.

(Inspirado e adaptado de Emicida- C&A apresenta LAB, A Rua é Noiz, disponível em: https://yout[4]u.be/fouCSV40sJs)