UNIVERSIDADE ESTADUAL DE SANTA CRUZ – UESC
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE – PPGECB

FERNANDO CÉSAR GONÇALVES BONFIM

EFEITOS DE MUDANÇAS NA ESTRUTURA DA PAISAGEM SOBRE A DIVERSIDADE DE AVES FRUGÍVORAS E AS CONSEQUÊNCIAS PARA AS INTERAÇÕES PLANTA-FRUGÍVORO

ILHÉUS - BAHIA
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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.
Área de concentração: Ecologia e Conservação da Biodiversidade
Discente: Fernando César Gonçalves Bonfim
Orientadora: Drª Eliana Cazetta

ILHÉUS – BAHIA
2022

B713 Bonfim, Fernando César Gonçalves.

Efeitos de mudanças na estrutura da paisagem sobre a diversidades de aves frugívoras e as consequências para as interações planta-frugívoro / Fernando César Gonçalves Bonfim. – Ilhéus, BA: UESC, 2022.

121f. : il.

Orientadora: Eliana Cazetta

Tese (Doutorado) – Universidade Estadual de Santa Cruz. Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade – PPGECB.

Inclui referências.

1. Desmatamento. 2. Taxonomia numérica. 3. Diversidade funcional. 4. Mutualismo. 5. Mata Atlântica. I. Título.

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CDD 631.61

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Ilhéus, 26 de agosto de 2022.

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Dedico esta tese aos meus pais,
Nilva Ferreira Gonçalves e Nivaldo Santiago Bonfim,
por tudo que fizeram por mim ao longo da vida
e por sempre me incentivar a estudar.

AGRADECIMENTOS

A construção desta tese teve a participação direta ou indireta de diversas pessoas, órgãos e entidades públicas, às quais agradeço imensamente.

Sou imensamente grato à Universidade Estadual de Santa Cruz, por toda infraestrutura disponível e ao Laboratório de Ecologia Aplicada à Conservação, o qual tive a oportunidade de conhecer pesquisadores incríveis e discutir as mais diversas questões. Agradeço também ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade pelo suporte, em especial às secretárias Amábille e Iky e também aos coordenadores.

À CAPES pelas bolsas de demanda social e sanduíche, e à Prefeitura Municipal de Apuarema pela licença concedida durante os quatro anos do doutorado.

Ao professor Dr. Pavel Dodonov por toda paciência disponibilidade e vontade de ensinar. Aprendi muita coisa de estatística e R graças a ele.

Ao professor Dr. Paulo R. Guimarães por toda disponibilidade para ensinar, conversar e discutir ciência. Foi um enorme prazer poder trabalhar com você.

Aos meus amigos Lidiane Gomes, Elaine Rios, Albérico Queiroz, Clemensou Reis, Diego Flores, Joanison Vicente e Maria Salles por todos os momentos incríveis que tive a oportunidade ter com vocês. Por me ouvir sobre os mais diversos assuntos e pelos incentivos em momentos difíceis.

À minha amiga Lidiane Gomes, agradeço demais pela ajuda com scripts e diversas dúvidas que me ajudou a solucionar. Além de ler meus artigos e discutir sobre ciência e sobre a vida. Admiro muito você Lidi!

À minha amiga Elaine Rios, por todos os scripts e dúvidas no R que me ajudou, mas sobretudo pelas conversas e conselhos dos mais gerais possíveis. Tenho grande admiração pela pesquisadora que você é!

Aos meus amigos Edson, Simeão, Uilian e Lânio por me suportar falando sobre assuntos acadêmicos-científicos mesmo eles não estando na academia. Em especial agradeço a Edson pela amizade que vem desde 2005, pelos conselhos e por ser uma pessoa com a mente aberta, que me ajuda mesmo estando longe.

Agradeço aos meus colegas de laboratório na Universidade de Miami Fabio, Sofany, Seokmin e Jacque pela acolhida. Em especial agradeço a Jacque e Alex pela confiança, por compartilhar sua casa comigo durante o período que estive em Miami. E também ao meu amigo Joro (o cachorro) por tornar os meus dias menos tensos. Sinto sua falta!

Às minhas colegas de orientação Ketlen Bona, Milena Gama, Geanne Pereira e Cynthia Oliveira pelas resenhas e discussões em nosso grupo de estudo e também pela parceria que estamos formando.

Ao Dr. Mauro Galetti por me receber em seu laboratório em Miami, por todo suporte na minha pesquisa, pelas conversas sobre projetos e todos os ensinamentos. Aprendi muito durante o período que estive em seu laboratório e tenho uma grande admiração pela forma como você pensa na formação de seus alunos e pelo cientista que você é.

À minha orientadora Drª. Eliana Cazetta, pelas oportunidades ao longo do meu doutorado, por confiar na minha capacidade e por me incentivar a me tornar um pesquisador cada vez melhor. Sob sua supervisão eu tive a oportunidade de trabalhar com alguns dos pesquisadores mais renomados na área e ampliar minha visão sobre ciência, ecologia e análise de dados. Tenho enorme admiração pela pesquisadora que você é e pela forma que você orienta. Certamente, muito do que tenho me tornado devo a você.

À minha namorada Bruna Stefani, por entender os diversos momentos que estive ausente, pela paciência e companheirismo de sempre.

À minha família, que forma o pilar que me sustenta. Meus irmãos, Fred e Rael e meu sobrinho-irmão Sávio obrigado por torcerem por mim. Aos meus pais, Nilva e Nivaldo, meu eterno agradecimento à criação que vocês me deram e todo o incentivo a sempre estudar.

SUMÁRIO

RESUMO

A crescente conversão da vegetação nativa em habitats antropizados é considerado um dos principais fatores que afetam a biodiversidade. Desvendar como mudanças na estrutura da paisagem afetam a biodiversidade é crucial para entender como essas ações irão afetar os processos ecológicos. Esse entendimento é ainda mais importante em áreas com alta relevância ecológica, como a Mata Atlântica, e para grupos que exercem importantes serviços ecossistêmicos, como as aves frugívoras. Dessa forma, o objetivo desta tese foi avaliar como mudanças na estrutura da paisagem afetam a diversidade taxonômica e funcional de aves frugívoras, os traços funcionais relacionados à dispersão de sementes, a ocorrência individual das espécies e a estrutura das redes de interações entre aves e plantas na Mata Atlântica. No primeiro capítulo, utilizamos um banco de dados para todo o bioma e demonstramos que a composição da paisagem (cobertura florestal) foi o preditor mais importante da diversidade taxonômica e funcional das aves frugívoras, com efeito positivo na riqueza e negativo na diversidade funcional. Por outro lado, tanto a composição quanto a configuração são importantes e afetam os traços das espécies quando há interação entre elas. No segundo capítulo, utilizamos um banco de dados com 25 redes de interações entre aves e plantas para entender como a perda de floresta afeta a estrutura das redes de interações frugívoro-planta, a robustez das redes, traços funcionais e o papel das aves frugívoras. Demonstramos que a perda de floresta tem efeitos negativos sobre a estrutura das redes de interações. Além disso, mostremos que a perda de floresta altera as espécies que exercem importantes papéis nas redes de interações. No terceiro capítulo, demonstramos que a ocorrência individual dos frugívoros é afetada de diferentes formas em relação ao uso da terra. Especificamente, mostramos que algumas espécies prosperam em paisagens modificadas pelo homem, enquanto outras perecem, onde há substituição de espécies sensíveis à perda de floresta por espécies generalistas. Do mesmo modo, alguns traços, principalmente os relacionados à sensibilidade à perda de habitat, foram afetados negativamente pela perda de floresta. De forma geral, nossos resultados reforçam o efeito perverso das paisagens modificadas pelo homem sobre as aves frugívoras que perpassam desde a diversidade taxonômica, funcional, traços, relações mutualísticas e ocorrência individual das espécies. Ainda assim, mostramos uma relação ganhador-perdedor, onde espécies generalistas de floresta, em geral, sobrevivem em paisagens antropizadas e as especialistas perecem.

Palavras-chave: Desmatamento, Mata Atlântica, diversidade taxonômica, diversidade funcional, mutualismo

ABSTRACT

The increasing conversion of native vegetation into anthropogenic habitats is considered one of the main factors that affect biodiversity. Uncovering how changes in landscape structure affect biodiversity is crucial to understanding how these actions will affect ecological processes. This understanding is even more important in areas with high ecological relevance, such as the Atlantic Forest, and for groups that perform important ecosystem services, such as frugivorous birds. Thus, this thesis aimed to evaluate how changes in landscape structure affect the taxonomic and functional diversity of frugivorous birds, the functional traits related to seed dispersal, the individual occurrence of species and the structure of networks of interactions between birds and plants. In the first chapter, we used a database for the entire biome and demonstrated that landscape composition (forest cover) was the most important predictor of taxonomic and functional diversity of frugivorous birds, with a positive effect on richness and a negative effect on functional diversity. On the other hand, both composition and configuration are important and affect species traits when there is interaction between them. In the second chapter, we used a database with 25 networks of interactions between birds and plants to understand how forest loss affects the structure of frugivore-plant interaction networks, the robustness of networks, functional traits and the role of frugivorous birds. We demonstrate that forest loss has negative effects on the structure of interaction networks. Furthermore, we show that forest loss alters the species that play important roles in interaction networks. In the third chapter, we showed that the individual occurrence of frugivores is affected in different ways in relation to land use. Specifically, we show that some species thrive in human-modified landscapes, while others perish, where species sensitive to forest loss are replaced by generalist species. Likewise, some traits, mainly those related to sensitivity to habitat loss, are negatively affected by forest loss. In general, our results reinforce the perverse effect of human-modified landscapes on frugivorous birds that range from taxonomic and functional diversity, traits, mutualistic relationships and individual species occurrence. Even so, we show a win-lose relationship, where generalist forest species, in general, survive in anthropized landscapes and the specialists perish.

Keywords: Deforestation, Atlantic Forest, taxonomic diversity, functional diversity, mutualism.

INTRODUÇÃO GERAL

Desde os primórdios de sua existência o ser humano tem modificado o ambiente no qual vive. O crescente aumento da população humana evidenciado nos últimos séculos impacta de forma massiva os ecossistemas devido à busca cada vez maior por recursos para satisfazer o bem-estar da humanidade (BUTCHART et al., 2010; LAURENCE; SAYER; CASSMAN, 2014). A exploração dos recursos ecossistêmicos acarreta supressão da vegetação nativa e representa uma das principais ameaças à biodiversidade podendo causar mudanças nas comunidades, redução de populações, comprometimento dos serviços ecossistêmicos e extinção de espécies (OWENS; BENNETT, 2000; VALIENTE-BANUET et al., 2015; MCCONKEY; O'FARRIL, 2016).

Modificações na vegetação nativa ocorrem através da conversão em diversos tipos de usos da terra, principalmente para agricultura, pecuária e exploração madeireira (CURTIS et al., 2018). Esta conversão da vegetação nativa em diferentes tipos de habitats acarreta em modificações na estrutura da paisagem. Essas modificações podem ocorrer através de mudanças na composição (i.e., a quantidade relativa de diferentes tipos de usos e cobertura da terra) e na configuração (i.e., o arranjo espacial das manchas de habitat e não-habitat) do habitat (DUNNING et al.1992). Ambas as formas de modificação na estrutura da paisagem são esperadas que afetem a diversidade de espécies (FAHRIG 2013; HADDAD et al 2015). Entretanto, a hipótese da quantidade de habitat postulou que a riqueza de espécies pode ser predita com base na quantidade de habitat ao redor da paisagem, independente do tamanho do fragmento ou isolamento (FAHRIG, 2013). Além disso, um longo debate tem ocorrido sobre se a configuração da paisagem tem efeitos positivos, negativos ou neutros sobre a biodiversidade (FAHRIG, 2017, 2019; FLETHCER et al., 2018).

Nesse contexto, um bom modelo de estudo sobre os efeitos de modificações na estrutura da paisagem é a Mata Atlântica, uma das florestas tropicais mais impactadas por ações humanas no mundo (MYERS et al., 2000; JOLY et al., 2014). Considerada um *hotspot* de biodiversidade por apresentar alto grau de ameaça, riqueza de espécies e endemismos (MYERS et al., 2000; JOLY et al., 2014), a Mata Atlântica originalmente cobria uma área de 1.5 milhões de quilômetros quadrados abrangendo desde a Argentina e Paraguai até o Nordeste do Brasil (JOLY et al., 2014). No entanto, um intenso processo de conversão da floresta para agricultura, pecuária, centros urbanos e industriais (DEAN, 1996) e a presença de cerca de 70% da população brasileira causaram drástica perda da vegetação nativa e atualmente resta menos de 30% da cobertura de floresta original (RIBEIRO et al., 2009; Rezende et al 2018). Atualmente, os fragmentos de floresta remanescentes são pequenos (80% possuem menos de 50 hectares) e isolados, imersos diferentes tipos de matriz (JOLY et al., 2014; RIBEIRO et al., 2009). A Mata Atlântica abriga cerca de 20 mil espécies de plantas, 936 de aves, 306 de répteis, 306 de peixes de água doce, 516 de anfíbios e 312 de mamíferos (MITTERMEIER et al., 2011).

Figura 1: Fotografia de uma paisagem da Mata Atlântica mostrando um fragmento de floresta circundado por matrizes de eucalipto e pastagem.

Entender como as modificações na estrutura da paisagem afetam as múltiplas facetas da biodiversidade (i.e., taxonômica, funcional, filogenética) é de extrema importância para guiar estratégias de conservação não somente focadas na diversidade taxonômica. Além disso, os efeitos de modificações na estrutura da paisagem sobre as espécies também afetam a diversidade de interações (MCCONKEY; O'FARRIL, 2016; VALIENTE-BANUET et al., 2015). Alguns estudos avaliaram os efeitos de modificações na biodiversidade e mostraram que a composição é o principal preditor da diversidade de morcegos (ARROYO-RODRÍGUEZ et al., 2016), aves (CARRARA et al., 2015), mariposas (MERCKX et al., 2019) e primatas (GÁLAN-ACEDO et al., 2019) com efeitos positivos na riqueza desses grupos. Por outro lado, alguns autores argumentaram que a configuração da paisagem também é um importante preditor da diversidade de espécies (EWERS; DIDHAM, 2006; HADDAD et al., 2015). Estudos que avaliaram os efeitos da configuração sobre a diversidade mostraram efeitos positivos para a riqueza de morcegos (ARROYO-RODRÍGUEZ et al., 2016) e pequenas aves onívoras não-dependentes de floresta (COELHO et al., 2016) e negativos sobre pequenas aves insetívoras (COELHO et al., 2016).

As aves constituem uma das radiações de vertebrados mais estudados no mundo (JETZ et al., 2012). Elas contribuem com importantes serviços ecossistêmicos como controle de pragas, ciclagem de nutrientes, polinização, herbivoria, predação e dispersão de sementes (SEKERCIOGLU et al., 2004; WENNY et al., 2011). Diversos estudos tentaram desvendar os efeitos de modificações na estrutura da paisagem sobre as aves e mostraram resultados divergentes. Por exemplo, a riqueza e abundância de toda a comunidade não foi afetada pela perda de floresta (MORANTE-FILHO et al., 2015). Entretanto, a riqueza e abundância de aves especialistas de floresta foram afetadas positivamente pelo aumento na quantidade de floresta (CARRARA et al., 2015; MORANTE-FILHO et al., 2015), enquanto as espécies generalistas mostraram o padrão oposto (CARRARA et al., 2015; MORANTE-FILHO et al., 2015). Em relação a configuração da paisagem, tanto espécies generalistas quanto especialistas de floresta foram afetadas positivamente pela quantidade de borda e número de fragmentos na paisagem (CARRARA et al., 2015). Outros estudos demonstraram que espécies e grupos sensíveis à perda de habitat são positivamente afetados pelo aumento na porcentagem de cobertura florestal na paisagem, enquanto a riqueza das espécies e grupos não-dependentes de floresta são afetados negativamente (MARTENSEN et al., 2012; COELHO et al., 2016; MORANTE-FILHO et al., 2018a). Por exemplo, frugívoros dependentes de floresta foram afetados positivamente pelo aumento na cobertura florestal (MORANTE-FILHO et al 2018a). Por outro lado, espécies de frugívoros não dependentes de floresta foram afetados positivamente pelo aumento na quantidade de borda (Morante-Filho et al 2018). As aves frugívoras constituem um dos grupos mais importantes nos ecossistemas terrestres pois por meio da dispersão e predação de sementes contribuem para a reprodução das plantas, regeneração das florestas e funcionamento dos ecossistemas (KISSLING et al., 2009). Especificamente, em alguns habitats tropicais, entre 50 e 90% das árvores e arbustos dependem dos frugívoros para dispersar suas sementes (FLEMING, 1987).

Dessa forma, percebemos que os efeitos das modificações na paisagem podem não ser iguais para todas as espécies. De fato, algumas espécies prosperam em paisagens modificadas pelo homem, enquanto outras perecem (MCKINNEY; LOCKWOOD, 1999; FILGUEIRAS, et al., 2021). As espécies que prosperam em paisagens modificadas são principalmente as generalistas de habitat e dieta, enquanto as que perecem são as mais sensíveis a distúrbios e especialistas de habitat e dieta (MCKINNEY; LOCKWOOD, 1999; FILGUEIRAS, et al., 2021). Por exemplo, Newbold et al. (2014) estimaram que a perda de habitat levou a diminuição de 11% na abundância de aves frugívoras e aumento de 4% na abundância de herbívoros. Do mesmo modo, Morante-Filho et al. (2021) mostraram que a ocupação de espécies de aves dependentes de floresta (e.g., *Myrmotherula urostica*, *Lipaugus vociferans*, *Crypturellus soui*) tem relação positiva com a cobertura florestal na paisagem, enquanto a ocupação de espécies generalistas (e.g., *Elaenia flavogaster*, *Camptostoma obsoletum*) diminui com o aumento na cobertura florestal.

Portanto, modificações na estrutura da paisagem afetam as espécies de forma não aleatória (NEWBOLD et al., 2014). Logo, é esperado que em paisagens modificadas pelo homem as espécies exibam traços funcionais adaptados a tais distúrbios. De fato, estudos mostraram que o tamanho corporal, área de vida e especialização na dieta são bons preditores do risco de extinção (OWENS; BENNET, 2000; PURVYS et al., 2000; LEE; JETZ, 2011). Assim, espécies com maior massa corporal, menor área de vida e com dieta restrita a um item alimentar (i.e., frutos ou insetos) são mais sensíveis e mais propensas a serem extintas (OWENS; BENNET, 2000; PURVYS et al., 2000; LEE; JETZ, 2011). Por exemplo, espécies de aves de corpo grande e maior abertura do bico como das famílias Cracidae, Cotingidae e Ramphastidae, em geral, ocorrem somente em áreas não desmatadas, enquanto espécies com pequeno tamanho corporal como das famílias Thraupidae e Turdidae ocorrem tanto em áreas com pouca floresta quanto em áreas com muita floresta (GALETTI et al., 2013; VIDAL et al., 2019). A perda de espécies com maior abertura do bico em áreas desmatadas pode ocasionar mudanças evolutivas, como mudanças no tamanho das sementes por eles dispersadas (GALETTI et al., 2013). Por outro lado, estudos recentes mostraram que pode haver uma dinâmica compensatória (MORANTE-FILHO et al., 2018b), onde espécies adaptadas a distúrbios substituem aquelas não adaptadas. Assim como a substituição de espécies (MORANTE-FILHO et al., 2018b), outro estudo mostrou que a perda de habitat não acarreta perda de funções, mas sim em mudanças nas funções desempenhadas pelas espécies presentes (de COSTER; BANKS-LEITE; METZGER, 2016). Dessa forma, ainda precisamos compreender melhor como os diferentes traços das espécies são afetados pelas modificações na paisagem e as consequências para os processos ecológicos.

Além de afetar a diversidade de espécies e os traços funcionais, modificações na estrutura da paisagem podem afetar a diversidade funcional (i.e., as funções desempenhadas pelas espécies (PETCHEY; GASTON, 2006)). Por exemplo, a riqueza funcional de aves foi afetada positivamente pelo tamanho do fragmento (BOVO et al., 2018), enquanto paisagens desmatadas mostraram aumento na riqueza funcional de aves florestais e aumento na dispersão funcional de aves não florestais (MATUOKA; BENCHIMOL; MORANTE-FILHO, et al., 2020). Além disso, a perda de floresta em escala de paisagem também teve efeito negativo na diversidade funcional de frutos zoocóricos (PESSOA et al., 2017) e na diversidade funcional de atributos reprodutivos das plantas (ROCHA-SANTOS et al., 2019). Por outro lado, poucos estudos investigaram os efeitos de mudanças na configuração na diversidade funcional (Hatfield; HARRISON; BANKS-LEITE, 2018), tais estudos mostraram efeitos positivos ou neutros, mas nenhum foi feito em escala de paisagem. Dessa forma, ainda existe uma lacuna de conhecimento sobre como modificações na configuração da paisagem afetam a diversidade funcional.

Enquanto diversos estudos investigaram os efeitos de mudanças na estrutura da paisagem sobre a riqueza de espécies (MORANTE-FILHO et al., 2015, 2018; COELHO et al., 2016; CARRARA et al., 2015; MARTENSEN et al., 2012), poucos avaliaram como as interações entre as espécies são afetadas (mas veja Vidal et al. (2019)). A perda de interações pode preceder a perda de espécies (MCCONKEY; O'FARRIL, 2016; VALIENTE-BANUET et al., 2015). Dessa forma, modificações na estrutura da paisagem podem ter impactos negativos na estrutura das redes de interações mutualísticas antes da perda de espécies ser notada. Alguns estudos usaram o tamanho do fragmento como proxi para perda de habitat e mostraram impacto negativo sobre o número de espécies de aves, plantas, número de interações e número de links por espécies (de ASSIS BOMFIM et al., 2018; EMER et al., 2019). Por outro lado, o aninhamento (i.e., interações de espécies especialistas são um subconjunto das interações dos generalistas (BASCOMPTE et al., 2003)) mostrou um padrão divergente, aumentando (de ASSIS BOMFIM et al., 2018) ou diminuindo com o tamanho do fragmento (EMER et al., 2019). Do mesmo modo, poucos estudos em escala da paisagem investigaram os efeitos de modificações na paisagem sobre a estrutura das redes de interações. Esses estudos mostraram que o número de interações, aninhamento, grau médio das espécies de plantas e aves e conectância aumentam com o aumento da cobertura florestal na paisagem (VIDAL et al., 2019; MENEZES et al., 2021). Dessa forma, ainda precisamos aumentar nossa compreensão dos efeitos de modificações na estrutura da paisagem sobre as interações mutualísticas. Ainda, mudanças na estrutura da paisagem acarretam alterações na composição de espécies, portanto, é esperado que essas modificações na paisagem determinem quais espécies desempenham papéis centrais nas redes de interações, entretanto esse tópico permanece pouco explorado.

Figura 2: Interação mutualística entre uma ave (*Xipholena atropurpurea*) e uma planta (*Euterpe edulis*) na Mata Atlântica.

A fim de desvendar os efeitos de mudanças na estrutura da paisagem sobre a diversidade de aves frugívoras e as consequências para as interações mutualísticas na Mata Atlântica, esta tese está estruturada em três capítulos. No primeiro, nós usamos um banco de dados para toda a Mata Atlântica Brasileira e avaliamos a importância relativa e tamanho de efeito da composição e configuração da paisagem sobre a diversidade taxonômica e funcional das aves frugívoras e os traços relacionados à dispersão de sementes. No segundo, usamos um banco de dados com interações entre aves frugívoras e plantas e avaliamos como a perda de floresta afeta a estrutura, robustez, traços relacionados à dispersão de sementes e o papel das aves nas redes de interações mutualísticas. No terceiro capítulo, nós ampliamos o banco de dados do primeiro capítulo e avaliamos como diferentes usos da terra (porcentagem de floresta, agricultura e pasto) afetam a riqueza, ocorrência individual e traços funcionais dos frugívoros e como a filogenia molda essas relações.

CAPÍTULO I

LANDSCAPE COMPOSITION IS THE MAJOR DRIVER OF THE TAXONOMIC AND FUNCTIONAL DIVERSITY OF TROPICAL FRUGIVOROUS BIRDS

(https://doi.org/10.1007/s10980-021-01266-y)
Artigo publicado na Landscape Ecology

Landscape composition is the major driver of the taxonomic and functional diversity of tropical frugivorous birds

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Abstract

Context Anthropogenic land use and cover changes impact biodiversity worldwide. However, ecological groups are differently affected by landscape composition and configuration. Understanding which groups are negatively affected and which thrive in human modified landscapes is of paramount importance for conservation management, especially for species such as the frugivorous birds, which play an essential role in seed dispersal.

Objectives We evaluated the relative importance of landscape composition and configuration, explaining taxonomic and functional diversity and their effects on frugivorous birds in the Brazilian Atlantic Forest. Methods We used a robust dataset encompassing 153 forest fragments in the Atlantic Forest hotspot. We classified species as frugivores based on the percentage of fruits in the diet, and used functional traits related to seed dispersal to measure functional diversity.

Results Our results showed that landscape composition was more important than landscape configuration explaining taxonomic and functional diversity of frugivorous birds. In addition, the interaction between landscape composition and configuration explained the loss of functional traits.

Conclusions We demonstrate a disproportional importance of landscape composition explaining taxonomic and functional diversity of frugivorous birds, whereas the traits related to seed dispersal were explained by both compositional and configurational variables. Thus, we highlighted the need to maintain high habitat amount to increase taxonomic and functional diversity of frugivorous birds. However, the interaction of landscape composition and configuration is of paramount importance to sustain functional traits of frugivores in tropical forest landscapes.

Keywords Habitat loss. Land-use. Atlantic forest. Seed dispersal. Fragmentation

Introduction

The increase in habitat conversion to anthropogenic land uses leads to severe changes in the structure and composition of once pristine landscapes (Dunning et al 1992; Newbold et al 2016). These changes have accelerated in recent decades, mainly due to increased growing human requirements for food, energy, agricultural commodities, timber, and other naturals resources (Laurance et al. 2014; Barlow et al. 2018). Alterations in human-modified landscapes include changes in landscape composition (the relative amount of different land use and cover types) and configuration (the spatial arrangement of habitat and non-habitat remnants, e.g. whether the habitat is more continuous or more fragmented) (Dunning et al. 1992). Both are predicted to affect species and population persistence.

Although landscape composition and configuration can affect population persistence (Galán-Acedo et al. 2019), there is an ongoing debate on which of the two is the most important and whether species richness increases or decreases with increasing fragmentation (Fahrig 2017; Fletcher et al. 2018). Landscape composition has been proposed as the main driver of species persistence (Fahrig 2013): the habitat amount hypothesis posits that species richness can be predicted based on the amount of habitat in the surrounding landscape - independent of either patch size or isolation (Fahrig 2013). Several studies found that forest cover, a proxy of habitat amount and the most used landscape composition variable, has positive effects on species richness of different taxonomic groups such as birds (Carrara et al. 2015; Kormann et al. 2018), bats (Arroyo-Rodríguez et al. 2016), macro-moth (Merckx et al. 2019), and primates (Galán-Acedo et al. 2019).

On the other hand, some authors reinforce that the spatial arrangement of habitat remnants is also important, suggesting that habitat fragmentation also affects biodiversity

(Ewers and Didham 2006; Haddad et al. 2015). In fact, some studies showed that landscape configuration can positively (Arroyo-Rodríguez et al. 2016; Coelho et al. 2016) or negatively (Coelho et al. 2016) affect species richness. Additionally, some studies suggested that fragmentation effects only occur at low (Andrén 1994) or intermediate (Pardini et al. 2010) levels of forest cover. Thus, additional studies are necessary to understand which landscape attributes affect species richness and the ecosystem services provided by different species, as well as the direction of these effects.

Disentangling the effects of landscape composition and configuration on species richness is of paramount importance to guide conservation strategies. However, the relative importance of landscape composition and configuration might also depend on the taxonomic group evaluated (Klingbeil and Willig 2009). For instance, forest-dependent species are generally more impacted by forest loss than generalist species (Morante-Filho et al. 2015). Forest-dependent frugivorous birds are especially sensitive to anthopogenic disturbances (Coelho et al. 2016; Kupsch et al. 2019), declining in deforested landscapes, whereas habitat generalist frugivorous species increase (Morante-Filho et al. 2018b). Frugivorous birds play a key role in seed dispersal (Wenny et al. 2011), mainly in tropical forests where up to 90% of woody species depend on animal services for seed dispersal (Jordano 2014). Overall, these forest-dependent species are replaced by non-forest species in less forested landscapes in a sort of compensatory dynamics (Morante-Filho et al. 2018b, a).

The vast majority of studies have focused on species richness, but habitat loss and fragmentation could also affect other facets of biodiversity in contrasting ways (Bregman et al. 2016; Chapman et al. 2018; Hatfield et al. 2018). For instance, functional diversity, which is related to the functions performed by species in relation to ecosystem services (Petchey and Gaston 2006), was observed to increase with increasing forest cover, whereas the effects of landscape configuration were inconsistent (Hatfield et al. 2018). Here, we used a robust dataset on frugivorous birds (Hasui et al. 2018) encompassing 153 forest fragments in the Brazilian Atlantic Forest to: (1) evaluate the relative importance of landscape composition and configuration and (2) their effect size on taxonomic and functional diversity of frugivorous birds. We hypothesized that landscape composition (measured as the amount of forest cover at the landscape scale) is more important than landscape configuration (measured as edge density and mean nearest neighborhood distance) explaining both taxonomic and functional diversity of frugivorous birds. We expected positive effects of forest cover on frugivorous birds richness due to factors such as decreased isolation among patches, changes in plant community composition, increased supplementary resources (Dunning et al. 2017) and increased vegetation complexity (Morante-Filho et al. 2018a) which in turn results in more resource availability in highly forested areas (Dunning et al. 2007; Pessoa et al. 2017b). We also expected positive effects of forest cover on functional diversity of frugivorous birds (Hatfield et al. 2018) because anthropogenic disturbances affect species with extreme traits such as large body size (Vollstädt et al. 2017), thus decreasing the functional space filled by the species (Laliberté and Legendre 2010) present in these areas.

Methods

Study area

We used a published dataset on bird species (Hasui et al. 2018) encompassing the Brazilian Atlantic Forest (Fig. 1). Originally, this tropical forest covered an area of around 1.5 million square kilometers along the Brazilian coast (Joly et al. 2014). However, as a result of anthropogenic land use changes, less than 30% of its original forest cover still remain (Rezende et al. 2018). The Atlantic forest is one of the top five global biodiversity hotspots, presenting high species diversity, levels of endemism and number of threatened species

(Myers et al. 2000; Joly et al. 2014). It harbors nearly 900 species of birds, 213 of which are endemic and 112 are threatened with extinction (Moreira-Lima 2014).

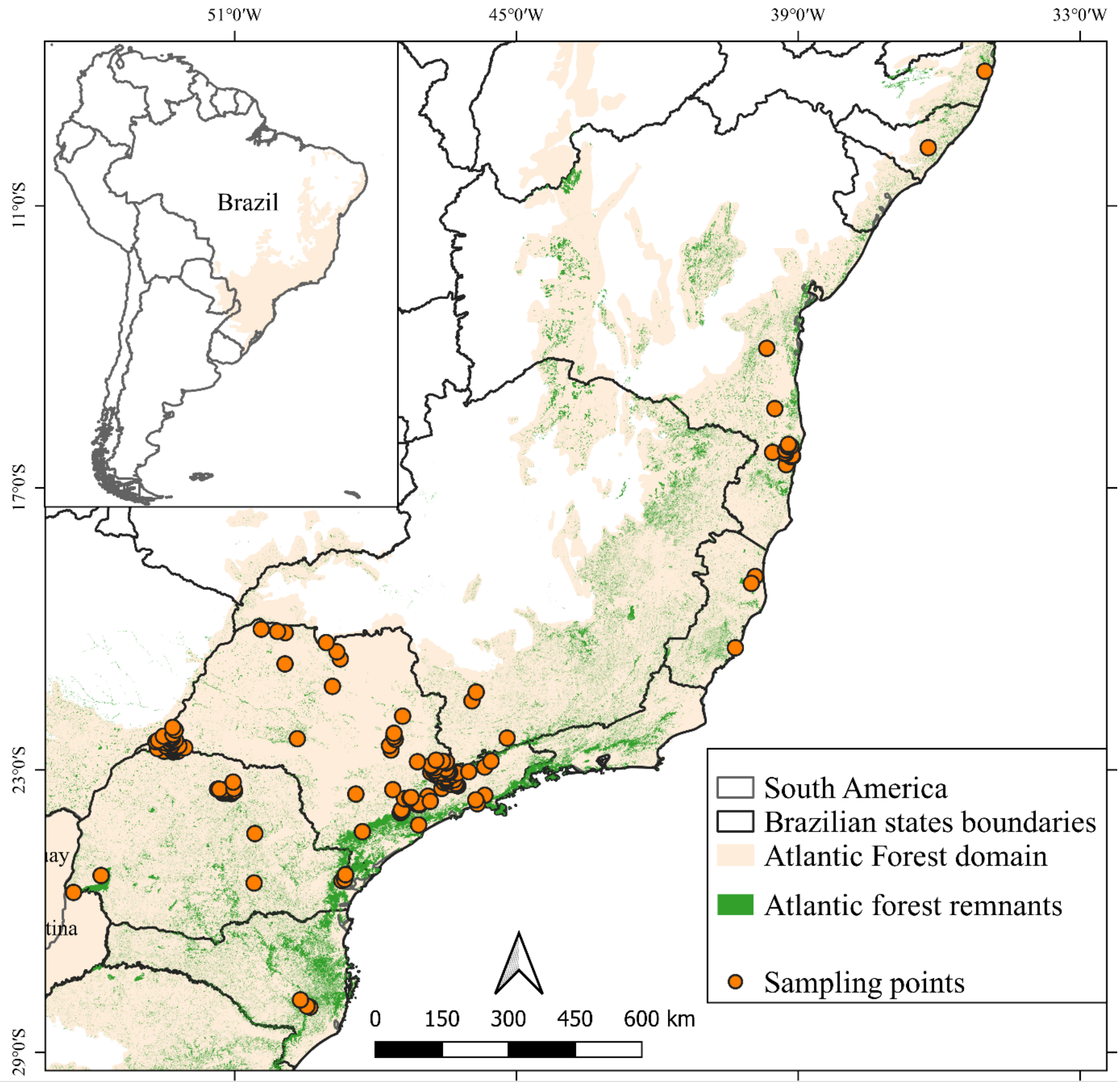

Fig. 1 Map of the 153 study forest fragments in the Brazilian Atlantic Forest obtained from Hasui et al. (2018).

Bird assemblage selection

The database used here compiled bird studies for the whole Brazilian Atlantic Forest. This database cataloged 832 bird species in more than 4,000 sampling points using data from museum, on-line database, literature sources and unpublished records. Considering the three main quantitative sampling methods to inventory birds (mist net, point count and line transect) the dataset encompasses 576 communities (Hassui et al. 2018). We used only studies performed by Point counts (46% of studies out of 329) to standardize the methods and decrease the bias of different methodologies. In addition, point count is the most effective methodology for surveying birds in the Neotropics (Bibby et al 1992). We first used as inclusion criteria the precision of the geographic coordinate to select each assemblage. Thus, we only selected studies that had the coordinate of the central patch, coordinates of the four vertices of the patch, or the central coordinate of the mosaic of sampled habitat (see Hasui et al. 2018). We excluded studies carried out in anthropogenic habitats, restinga (coastal vegetation, including sand dunes and some types of coastal forest), or semideciduos urban forest. We included only fragments that had a minimum distance of two kilometers from one another to minimize spatial autocorrelation. When fragments were located within this distance, we chose the ones that had higher sampling effort. Our final dataset was composed of 153 forest fragments and 562 bird species. The year of sampling ranged from 1991 to 2014, and total effort ranged from 9 to 570 hours (68.6± 88.2 mean ±SD).

Frugivore classification

From the 562 bird species recorded, we classified the frugivores following Kissling et al. (2009), which classify bird species based on nine categories of food items consumed (fruits, fish, nectar, vertebrates, terrestrial invertebrates, aquatic invertebrates, plant material, carrion, and seeds) and consider a species as frugivore if its diet is composed of more than 50% fruits. Thus, in our final dataset, only species that eat more than 50% fruits were included.

Functional traits

For all frugivorous species, we obtained four morphological traits that describe functions related to frugivory and seed dispersal by birds from the published literature (Table 1). Body mass reflects the amount of fruits that can be consumed by each species (Jordano and Schupp 2000), and was obtained from Wilman et al. (2014). Hand-wing index indicates the flight capability for long-distance dispersal (Weiss and Ray 2019) and was obtained from Bovo et al. (2018). Gape width represents the maximum fruit size that can be ingested (Wheelwright 1985). This trait was obtained from Bello et al. (2017) and Rodrigues et al. (2019). Foraging strata correspond to where the species forage and is an indicator of habitat use. For this trait we used Wilman et al. (2014) to determine the main forage strata used by each species. When a species used more than one stratum in equal proportion we classified it as “mixed” (Table 1).

Table 1: Bird functional traits used and the percentage of species for which we were able to obtain information for each functional trait. For continuous traits we also show the range, mean, and standard deviation.

Traits	Category	Range (mean±SD)	% species with information
Body mass	Continuous	9.34-2,600g (186.00±364.75)	98.95
Hand-wing index	Continuous	0-50.96 (20.31±7.85)	66.66
Gape width	Continuous	5.0-33.91 (11.59±6.25)	89.58
Foraging strata	Categorical	ground; understory; midhigh; canopy; mixed	100

Functional diversity

We calculated two functional diversity indexes that can be used for presence data (Laliberté and Legendre 2010) and are widely used to detect shifts in assembly processes related to disturbance (Mason et al. 2013). Functional richness (FRic) describes the niche space occupied by the community (Mason et al. 2005) and functional dispersion (FDis) depicts the mean distance of one species to the centroid of all species in the community (e.g. the spread of functional traits in the community) (Laliberté and Legendre 2010). To calculate the functional diversity indexes, we constructed a matrix of functional distance based on our matrix of species *versus* traits using Gower dissimilarity to account for categorical and continuous traits in our data (Podani and Schmera 2006). We used the package FD that tolerates missing data (Na's) (Laliberté et al. 2014) to generate functional diversity index in R version 3.5.3 (R Core Team 2019). We excluded twelve sites that had less than four species because the "dbFD" function only calculates functional indexes if the number of species is equal to or higher than the number of traits (Laliberté et al. 2014).

We used null models to estimate the extent to which the functional diversity of bird communities is above or below that expected by chance (Gotelli and McCabe 2002). We standardized the effect size (SES) only for FRic because FDis is not affected by species richness (Laliberté and Legendre 2010). Standardized effect size for FRic (SESFRic) was calculated as (observed FRic – mean of expected FRic) / SD of expected FRic. Here, the expected FRic is the one expected under a null model based on the permutation of the presence/absence matrix (samples (rows) x species (columns)), with the trait matrix maintained as originally. We calculated these null models using the "independent swap" algorithm that randomizes the data matrix maintaining occurrence and sample richness (Gotelli 2000). The matrix was permuted 999 times according to the example from Plass-Johnson et al. (2016). Positive SES values indicate low functional redundancy, which can result from competitive exclusion, whereas negative values indicate high redundancy, which can be caused by environmental filtering (Mouchet et al. 2010).

Landscape descriptors

We calculated four metrics to describe landscape composition and configuration. We measured the percentage of forest cover as a descriptor of landscape composition and the number of fragments, mean nearest neighborhood distance, and edge density as metrics of landscape configuration. We used maps derived from 30m resolution Landsat satellite images from MapBiomas (MapBiomas Project - Collection 3.1 of the Annual Series of Coverage and Land Use Maps in Brazil, accessed in [14/06/19]: [http://www.mapbiomas.org]). MapBiomas provides annual maps of land use and cover from 1985 to 2017. We downloaded maps considering the year each study started its sampling. We calculated all landscape metrics in QGIS (QGIS Development Team 2016) in the plugin LecoS (Jung 2016). All landscape metrics were calculated in a buffer radius of 1 km around the central point of each forest fragment. We choose this scale because each species respond differently to the landscape (Boscolo and Metzger 2009) and this scale represents the daily movement range of medium and small birds (Sekercioglu et al. 2007), which are the majority of species in our data. Our final dataset are representative of forest amount at the landscape scale in which 40 fragments (26%) have less than 30% of forest cover, 50 fragments (33%) have between 30 and 70% of forest cover and 63 fragments (41%) have more than 70% of forest cover (Supplementary material fig 1). See supplementary material for information on the mean, variance and range of each landscape predictor (Table S1).

Data analysis

We adjusted generalized linear mixed models using frugivorous bird richness as response variable for taxonomic diversity and linear mixed models for FDis and SESFRic for functional diversity. We used the study ID as random effect to account for studies that sampled multiples forest sites. We also used the coordinates of each forest fragment as covariate to account for spatial auto correlation in the form of spatial gradients (Beale et al. 2010). Because studies differ in sampling effort, we log transformed the sampling effort and included as offset in species richness models. We checked for collinearity among the explanatory variables with the variance inflation factor (VIF) (Dormann et al 2013), which resulted in less than four for all variables. However, we excluded the number of patches because its exclusion reduced VIF to 2.5 and because of its high correlation ($r^2 = 0.79$) with mean nearest neighborhood distance. Thus, the explanatory variables for the final analysis were forest cover, mean nearest neighborhood distance and edge density. Because our variables have different scales, and to enable comparisons, we scaled and standardized all variables. For frugivore richness we used poisson distribution and for SESFRic and FDis we used normal distribution. We constructed models to test the effect of individual variables and of variable combinations as well as their interaction. Overall, we constructed 15 models (See script as supplementary resource). To account for the effect of landscape composition and configuration on functional traits (body mass, bill width and hand-wing index) we also constructed the same models using the mean value of each trait as response variable. We checked the spatial distribution of residuals (supplementary figure 2) and semivariograms for all full models before the analysis.

To calculate variable importance, we used the function *"AICctab"* from package bbmle (Bolker 2020). We constructed a table with model weights and summed the Akaike weights (w_i) of the models contained the variable in question (Burnham and Anderson 2002). We used the MuMIn package (Barton 2019) to perform model averaging (Burnham and Anderson 2002) to find the relative effect size of the explanatory variables using conditional coefficients. Model averaging calculates the average effect of each variable weighted by the

Akaike weights of the models in which this variable occurs (Burnham and Anderson 2002). We performed all analysis in R version 3.5.3 (R Core Team 2019). The data and R codes used are available at https://github.com/CesarEco/Publications.

Results

From 562 bird species in our dataset, 96 were classified as frugivores (Appendix). Mean frugivore richness was 12.75±7.03 SD (range 1 - 36). The most frequent species were *Chiroxiphia caudata*, *Euphonia chlorotica*, *Patagioenas cayennensis, Psittacara leucophthalmus* and *Tangara sayaca*, all present in more than 70 fragments. Eleven species occurred in a single fragment: *Amazona farinosa, Aratinga solstitialis, Chlorophanes spiza, Chlorophonia cyanea, Crax fasciolata, Crypturellus strigulosus, Ortalis guttata, Pipraeidea bonariensis, Pteroglossus inscriptus, Tangara peruviana* and *Xipholena atropurpurea.*

Landscape composition was the most important variable explaining taxonomic diversity of frugivorous birds (Fig. 2). Forest cover showed positive and significant effects on frugivore richness (Fig. 3, Table SII), whereas edge density and mean nearest neighborhood distance did not explain frugivore taxonomic diversity. In addition, the interactions between forest cover and edge density and forest cover and mean nearest neighborhood distance did not explain frugivorous richness (Fig. 3, Table SII).

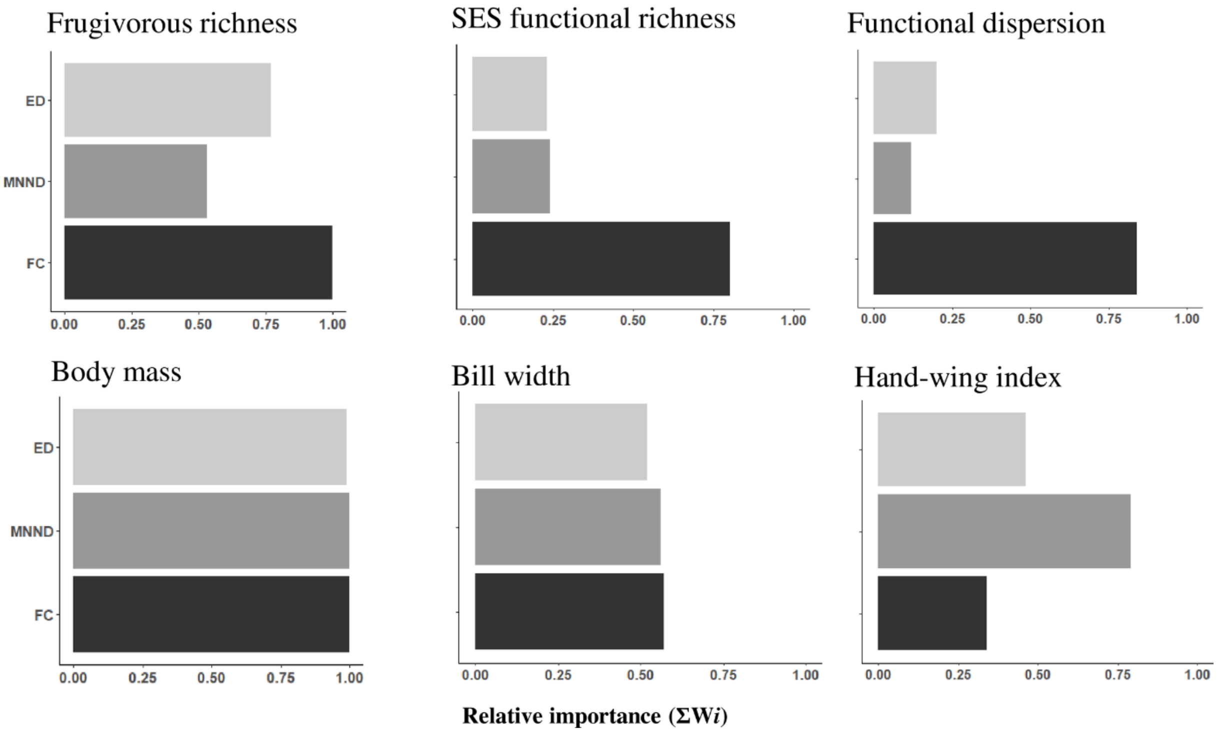

Fig. 2 Predictor variables and their importance for taxonomic and functional diversity and the traits of frugivorous birds in the Brazilian Atlantic Forest. The sum of Akaike weights (Σwi) shows the relative importance of each predictor variable for each response variable. FC = forest cover; ED = edge density; MNND = mean nearest neighborhood distance.

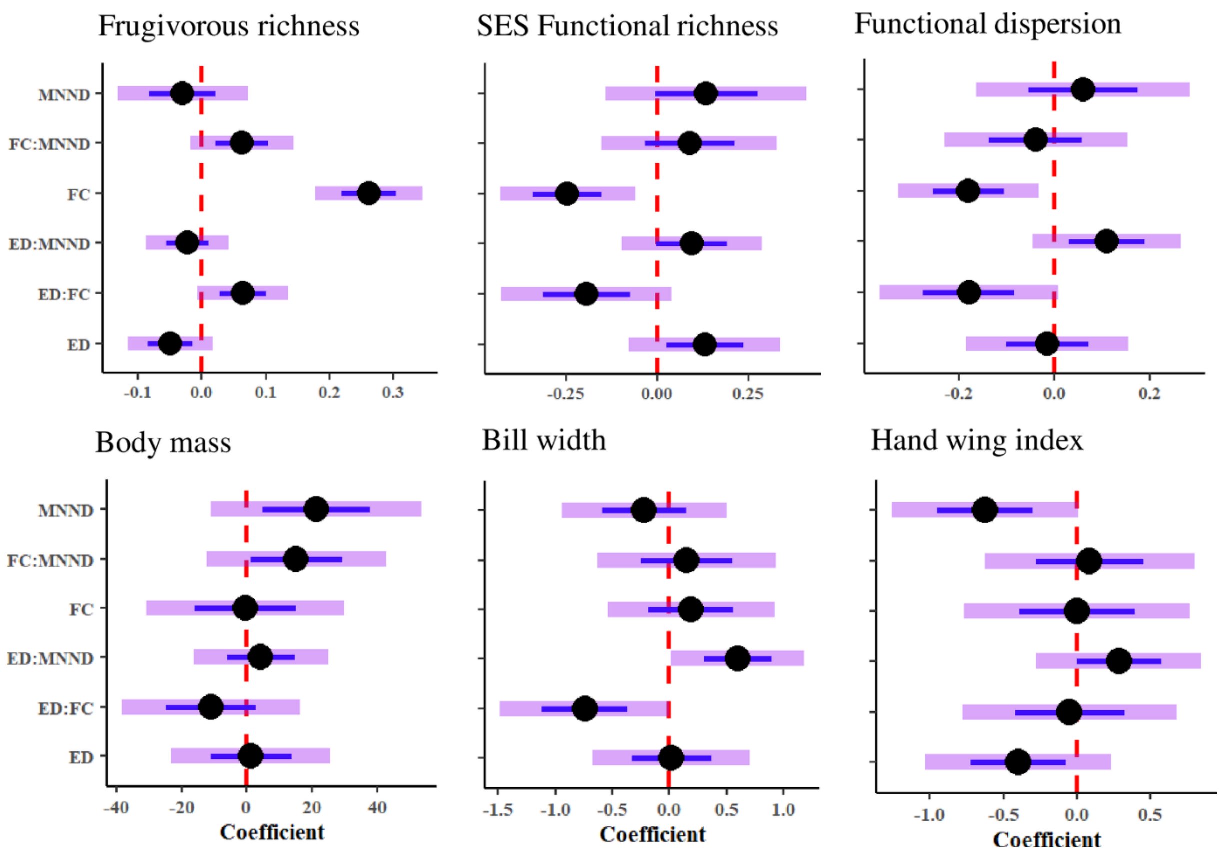

Fig. 3 Landscape effects on taxonomic and functional diversity and traits of frugivorous birds in the Brazilian Atlantic Forest. Significant results are those where the 95% confidence set do not overlap zero. Black dots are the estimate, blue lines are the adjusted standard error and the purple lines are the minimum and maximum confidence set. FC = forest cover; ED = edge density; MNND = mean nearest neighborhood distance; FC : ED =interaction between forest cover and edge density; FC : MNND = interaction between forest cover and mean nearest neighborhood distance; ED : MNND = interaction between edge density and mean nearest neighborhood distance.

Considering functional diversity, forest cover was the most important variable (Fig. 2), negatively and significantly affecting both SESFRic and FDis (Fig 3). Neither landscape configurational predictors nor interactions were significant for SESFRic or FDis.

Regarding the functional traits, the configurational predictor mean nearest neighborhood distance was important explaining hand-wing index, whereas for body mass and gape width forest cover, edge density and mean nearest neighborhood distance were equally important predictors (Fig. 2). However, no compositional or configurational metric alone were significant explaining functional traits (Fig. 3). Even so, for bill width, the interaction between forest cover and edge density was negative, meaning that increases in forest cover reduce the negative effects of edge density on bill width and vice-versa. In contrast, the interaction between edge density and mean nearest neighborhood distance were positive, showing that the bill sizes decreased with MNND, but this decrease is smaller when edge density is high (Fig. 4, Table SII).

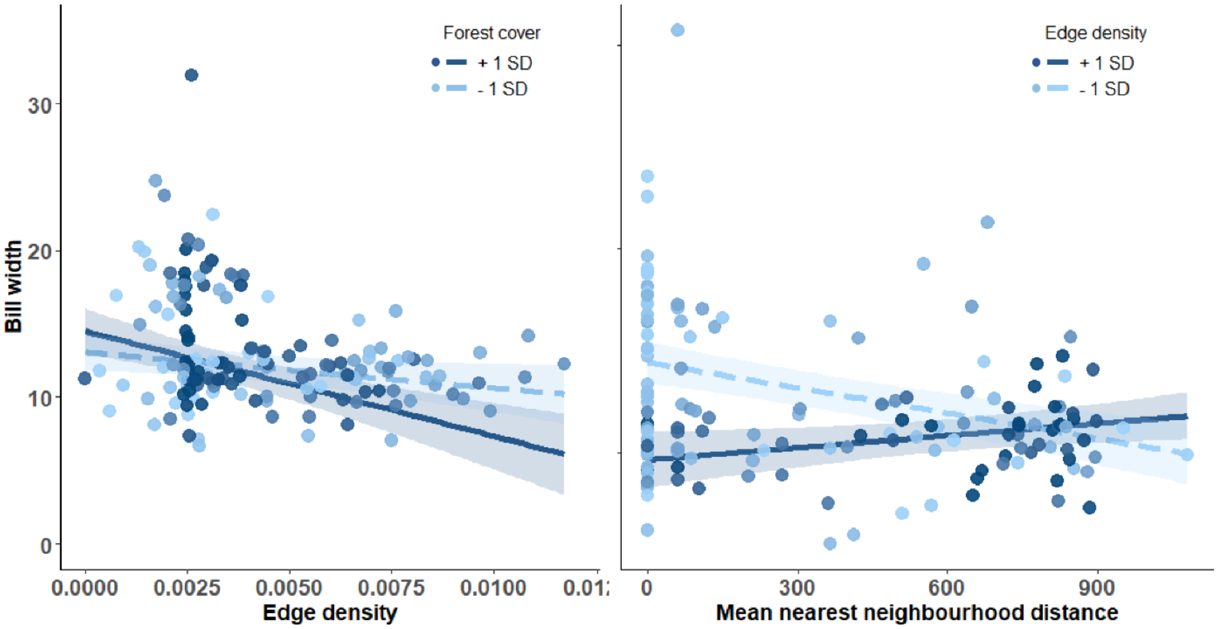

Fig. 4 Interactions that showed significant response for taxonomic, functional diversity and traits of frugivorous birds in the Atlantic Forest. The dark blue line and dots represents higher values for the variable and the dashed light blue line and dots represents lower values for the variable.

Discussion

Our results encompassing the whole Brazilian Atlantic Forest show a disproportional importance of landscape composition than configuration for frugivorous birds. As predicted, forest loss has detrimental effects on frugivore diversity. However, we add important information showing that these effects are also pervasive on functional diversity with possible consequences for seed dispersal process. Interestingly, the combined effect of forest loss and fragmentation are affecting frugivore traits related to seed dispersal with a faster decline when fragmentation increase combined with high levels of habitat amount. These results emphasize that to sustain ecological processes performed by birds it is paramount to maintain high levels of forest amount as well as low levels of fragmentation.

We found that landscape composition affects the taxonomic diversity of frugivorous birds in the Atlantic Forest. As predicted, and consistent with several previous studies (Carrara et al. 2015; Arroyo-Rodríguez et al. 2016; Coelho et al. 2016; Godet et al. 2016; Galán-Acedo et al. 2019; Merckx et al. 2019), we demonstrated the importance of forest cover for species richness. On the other hand, edge density and mean nearest neighborhood distance were less important predictors of frugivore richness. But interestingly, forest cover did not interact with edge and isolation, explaining frugivore richness. It is worth noting that some studies pointed to an indirect effect of habitat configuration via habitat loss (Püttker et al. 2020) or even an intensified effect of landscape configuration at high levels of habitat loss (Metzger and Villard 2014). Our findings do not support these ideas, as we do not find interacting effects of habitat loss and fragmentation for species richness.

The positive effects of forest cover on frugivorous birds richness were expected. Our findings are consistent with previous studies that found increases in frugivorous birds diversity in forested landscapes (Morante-Filho et al. 2015; Coelho et al. 2016; Kupsch et al.

2019). Two main mechanisms might explain this pattern. First, local vegetation complexity increases in forested landscapes (Rocha-Santos et al. 2017), which results in an increase in niche width and resource exploitation (e.g. food, refuge, nesting sites) (MacArthur and MacArthur 1961). It has been shown that vegetation complexity directly affects forest-dependent frugivorous birds in the Brazilian Atlantic Forest (Morante-filho et al. 2018a). Second, landscape scale forest loss may reflect in the availability (Pessoa et al. 2017b) and quality (Pessoa et al. 2017 a) of fruit resources, which in turn results in increased fruit consumption in forested landscapes (Menezes et al. 2016).

On the other hand, landscape configuration did not show significant effects on frugivorous richness. This result corroborates with those observed by Fahrig (2017), in which fragmentation *per se* (fragmentation independent of habitat amount) had in general positive or neutral effects on biodiversity. However, neutral effects were far more prevalent presented in more than 70% of the studies (Fahrig et al. 2019). However, other studies found negative effects of fragmentation and they argument that some species can be sensitive to habitat configuration, mainly when habitat amount is low (Martensen et al. 2012; Püttker et al. 2020), which for example, decreases functional connectivity and thus increases Allee effects (the fitness of individuals related to population density) (Villard and Metzger 2014) and decreases immigration rates of forest dependent species (Pardini et al. 2010; Martensen et al. 2012). Thus, our findings add important evidence that the fragmentation effects on richness of frugivorous birds may be absent.

Forest cover had negative effects on functional richness (either SESFRic or FDis), indicating lower functional redundancy in deforested landscapes. This result is in line with previous works (Prescott et al. 2016; Matuoka et al. 2020), which showed that bird communities in oil plantation and deforested landscapes had higher values of standardized functional diversity, respectively. In fact, forest loss can act as an environmental filter where forest-dependent species are negatively affected (Morante-Filho et al. 2018b). Yet, niche filtering excludes species with traits poorly adapted to ecosystem changes (Mouchet et al. 2010). On the other hand, positive SESFRic values can be found in deforested landscapes probably due to competitive exclusion, where the coexistence of dissimilar species is favored (Mouchet et al. 2010). In deforested landscapes a shift in bird species composition occurs (Morante Filho et al. 2015), where forest-dependent species are replaced by non-forest dependent ones, probably functionally distinct from one another, explaining the lower functional redundancy in deforested landscapes. Also, the negative effects of forest cover on functional dispersion means that in forested landscapes the traits of species are near to the centroid of all species in the community (Laliberté and Legendre 2010)), revealing that forested landscapes can buffer functional traits against the extinction.

We showed that functional traits were affected by both landscape composition and configuration. In fact, some studies point to an increased resource availability for frugivorous species, for example, comparing edge with the fragment interior (Saavedra et al. 2014) or increasing habitat amount (Pessoa et al. 2017b). In addition, among the traits related to frugivory, gape width was affected by the interactions between forest cover and edge density and mean nearest neighborhood distance and edge density. Our results showed that increasing edge amount led to a decrease in bill width, but at higher amounts of forest cover this decrease is faster. This result can also be explained by niche filtering, where more forested landscapes retain small species which ultimately has small gape. Yet the increase in edge amount favors plant species that in general are pioneer and have small fruits (Santos et al. 2012), attracting frugivorous with small bill width. For example, small-gaped species such as *Chiroxiphia pareola* and *Manacus manacus* can be attracted to the edge searching for small fruits, reducing the mean bill width in more forested landscapes. Conversely, reducing edge amount favors large-gaped frugivores. The increase in mean nearest neighborhood distance interacting with high edge density amount increases bill width (greater bill widths at landscapes with high isolation and edge density), whereas decreasing edge amount decreases this attribute. This finding could reflect that landscapes with high isolation and high edge amount can lead to species spillover into the matrix, favoring species that are able to cross the matrix and that use the fruits located at edges (Boesing et al. 2018). On the other hand, landscapes with high levels of isolation and with low edge amount would favor more generalist species, with smaller gape widths, due to the small fruit quality in deforested landscapes (Pessoa et al. 2017a). However, for hand-wing index and body mass, the lack of significant effects may indicate a compensation between large- and small-bodied species, as previously shown for forest and non-forest dependent frugivorous (Morante-Filho et al. 2018b).

Conclusions

This work unveiled the patterns related to the importance and magnitude of the effects of landscape composition (namely forest cover) and configuration for frugivorous birds in the Brazilian Atlantic Forest. Our approach showed that landscape composition is the strongest determinant of taxonomic and functional diversity of frugivorous birds in the Brazilian Atlantic forest. However, landscape composition and configuration interact affecting frugivorous traits related to seed dispersal. We reinforce that conservation initiatives in this biodiversity hotspot should emphasize the maintenance of large habitat amounts at the landscape scale and low edge amount and isolation to hold species and functions performed by frugivorous birds. This group performs the important function of seed dispersal that is essential for regeneration and diversity of tropical plants (Jordano 2014). Here, we showed that habitat loss affects frugivorous birds and can have pervasive consequences for seed dispersal by them, such as a decrease in the number of fruits consumed and dispersal distance (McConkey et al. 2012). Additionally, we showed that forest cover is a strong environmental filter selecting species with redundant functions, which can prevent functional extinction. In addition, the combined effects of landscape composition and configuration affect functional traits of frugivorous birds. This is especially worrying because the Atlantic Forest suffered from intense deforestation creating isolated fragments. Also, more than 40% of remaining forest patches in the Brazilian Atlantic Forest are at a distance of 100 meters or less from edges (Haddad et al. 2015), which could synergistically with habitat loss drive a functional debt related to seed dispersal. Thus, the maintenance of high habitat amount, in combination with low levels of fragmentation in the landscape, can favor a higher number of frugivorous birds and maintain the functions performed by them.

Acknowledgements

We are thankful for Anderson Saldanha

Bueno, Érica Hassui and Luis dos Anjos for helpful comments on an earlier version of this manuscript. We also thank Elaine Rios, Amanda Cerqueira and Maria Sales for helpful comments and ideas on the earliest version of the manuscript. We also are grateful to the editor and two anonymous reviewers for invaluable comments to improve the manuscript. This study was financed in part by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

References

Andrén, H 1994 Effects of habitat fragmentation on birds and mammals
in landscapes with different proportions of suitable habitat: a review.
Oikos 71: 355–366.

Arroyo-Rodríguez V, Rojas C, Saldaña-Vázquez RA, Stoner KE (2016) Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot. Biol Conserv 198:84–92. https://doi.org/10.1016/j.biocon.2016.03.026

Barlow J, França F, Gardner TA et al (2018) The future of hyperdiverse tropical ecosystems. Nature 559:517–526. https://doi.org/10.1038/s41586-018-0301-1

Barton K (2019) MuMIn: Multi-Model Inference. R package version 1.43.6. https://CRAN.R-project.org/package=MuMIn.

Beale CM, Lennon JJ, Yearsley JM, et al (2010) Regression analysis of spatial data. Ecol Lett 13:246–264. https://doi.org/10.1111/j.1461-0248.2009.01422.x

Bello C, Galetti M, Montan D et al (2017) Atlantic frugivory: a plant–frugivore interaction data set for the Atlantic Forest. Ecology 98:1729. https://doi.org/10.1002/ecy.1818

Bibby, CJ, Burgess, ND, Hill, DA. 1992. Bird Census Techniques. Academic Press, New York.

Boesing AL, Nichols E, Metzger JP (2018) Biodiversity extinction thresholds are modulated by matrix type. Ecography (Cop) 41:1520–1533. https://doi.org/10.1111/ecog.03365

Bolker B, R Development Core Team (2020). bbmle: Tools for General Maximum Likelihood

Estimation. R package version 1.0.23.1. https://CRAN.R-project.org/package=bbmle

Boscolo D, Metzger JP (2009) Is bird incidence in Atlantic Forest fragments influenced by landscape patterns at multiple scales? Landsc Ecol 24:907–918. https://doi.org/10.1007/s10980-009-9370-8

Bovo AAA, Ferraz KMPMB, Magioli M et al (2018) Habitat fragmentation narrows the distribution of avian functional traits associated with seed dispersal in tropical forest. Perspect Ecol Conserv 16:90–96. https://doi.org/10.1016/j.pecon.2018.03.004

Bregman TP, Lees AC, MacGregor HEA et al (2016) Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proc R Soc B Biol Sci 283:20161289. https://doi.org/10.1098/rspb.2016.1289

Burnham KP, Anderson, DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, et al (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biol Conserv 184:117–126. https://doi.org/10.1016/j.biocon.2015.01.014

Chapman PM, Tobias JA, Edwards DP, Davies RG (2018) Contrasting impacts of land-use change on phylogenetic and functional diversity of tropical forest birds. J Appl Ecol 55:1604–1614. https://doi.org/10.1111/1365-2664.13073

Coelho MTP, Raniero M, Silva MI, Hasui É (2016) The effects of landscape structure on functional groups of Atlantic Forest birds. Wilson J Ornithol 128:520–534. https://doi.org/10.1676/1559-4491-128.3.520

Dormann CF, Elith J, Bacher S, et al (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop) 36:27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142. https://doi.org/10.1017/S1464793105006949

Fahrig L (2017) Ecological Responses to Habitat Fragmentation Per Se. Annu Rev Ecol Evol Syst 48:1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig L (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. J Biogeogr 40:1649–1663. https://doi.org/10.1111/jbi.12130

Fahrig L, Arroyo-Rodríguez V, Bennett JR, et al (2019) Is habitat fragmentation bad for biodiversity? Biol Conserv 230:179–186. https://doi.org/10.1016/j.biocon.2018.12.026

Fletcher RJ, Didham RK, Banks-Leite C et al (2018) Is habitat fragmentation good for biodiversity? Biol Conserv 226:9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Galán-Acedo C, Arroyo-Rodríguez V, Cudney-Valenzuela SJ, Fahrig L (2019) A global assessment of primate responses to landscape structure. Biol Rev 94:1605–1618. https://doi.org/10.1111/brv.12517

Godet L, Devictor V, Burel F et al (2016) Extreme landscapes decrease taxonomic and functional bird diversity but promote the presence of rare species. Acta Ornithol 51:23–38. https://doi.org/10.3161/00016454ao2016.51.1.003

Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621. https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2

Gotelli NJ, McCabe DJ (2002) Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. Ecology 83:2091–2096. https://doi.org/10.1890/0012-9658(2002)083[2091:SCOAMA]2.0.CO;2

Haddad NM, Brudvig LA, Clobert J et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:1–10. https://doi.org/10.1126/sciadv.1500052

Hasui É, Metzger JP, Pimentel R et al (2018) ATLANTIC BIRDS: a data set of bird species from the Brazilian Atlantic Forest. Ecology 99:497. https://doi.org/10.1002/ecy.2119

Hatfield JH, Harrison MLK, Banks-Leite C (2018) Functional Diversity Metrics: How They Are Affected by Landscape Change and How They Represent Ecosystem Functioning in the Tropics. Curr Landsc Ecol Reports 3:35–42. https://doi.org/10.1007/s40823-018-0032-x

Joly CA, Metzger JP, Tabarelli M (2014) Experiences from the Brazilian Atlantic Forest: Ecological findings and conservation initiatives. New Phytol 204:459–473. https://doi.org/10.1111/nph.12989

Jordano P (2014) Fruits and frugivory. In: Gallagher RS (ed) Seeds: the ecology of regeneration in plant communities, 3rd edn. CAB International, London, pp 18–61

Jordano P, Schupp EW (2000) Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. Ecol Monogr 70:591–615

Jung M (2016) LecoS - A python plugin for automated landscape ecology analysis. Ecol Inform 31:18–21. https://doi.org/10.1016/j.ecoinf.2015.11.006

Kissling WD, Böhning-Gaese K, Jetz W (2009) The global distribution of frugivory in birds. Glob Ecol Biogeogr 18:150–162. https://doi.org/10.1111/j.1466-8238.2008.00431.x

Klingbeil BT, Willig MR (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. J Appl Ecol 46:203–213. https://doi.org/10.1111/j.1365-2664.2008.01594.x

Kormann UG, Hadley AS, Tscharntke T, et al (2018) Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization. J Appl Ecol 55:1288–1298. https://doi.org/10.1111/1365-2664.13084

Kupsch D, Vendras E, Ocampo-Ariza C et al (2019) High critical forest habitat thresholds of native bird communities in Afrotropical agroforestry landscapes. Biol Conserv 230:20–28. https://doi.org/10.1016/j.biocon.2018.12.001

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Laliberté E, Legendre P, Shipley B (2014) Package FD – Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Version1.0–12.

Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. Trends Ecol Evol 29:107–116. https://doi.org/10.1016/j.tree.2013.12.001

MacArthur R, MacArthur J (1961) On bird species diversity. Ecology 42: 594–598.

MapBiomas – Coleção [3.1] da Série Anual de Mapas de Cobertura e Uso de Solo do Brasil. http://www.mapbiomas.org. Accessed 14 June 2019

Martensen AC, Ribeiro MC, Banks-Leite C et al (2012) Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance. Conserv Biol 26:1100–1111. https://doi.org/10.1111/j.1523-1739.2012.01940.x

Mason NWH, De Bello F, Mouillot D et al (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. J Veg Sci 24:794–806. https://doi.org/10.1111/jvs.12013

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional Richness, Functional Evenness and Functional Divergence : The drimary components of functional diversity. Oikos 111:112–118

Matuoka MA, Benchimol M, Morante-Filho JC (2020) Tropical forest loss drives divergent patterns in functional diversity of forest and non-forest birds. Biotropica 52:738–748. https://doi.org/10.1111/btp.12795

McConkey KR, Prasad S, Corlett RT et al (2012) Seed dispersal in changing landscapes. Biol Conserv 146:1–13. https://doi.org/10.1016/j.biocon.2011.09.018

Menezes I, Cazetta E, Morante-Filho JC, Faria D (2016) Forest Cover and Bird Diversity: Drivers of Fruit Consumption in Forest Interiors in the Atlantic Forest of Southern Bahia, Brazil. Trop Conserv Sci 9:549–562. https://doi.org/10.1177/194008291600900128

Merckx T, Dantas de Miranda M, Pereira HM (2019) Habitat amount, not patch size and isolation, drives species richness of macro-moth communities in countryside landscapes. J Biogeogr 46:956–967. https://doi.org/10.1111/jbi.13544

Morante-Filho JC, Arroyo-Rodríguez V, de Andrade ER et al (2018a) Compensatory dynamics maintain bird phylogenetic diversity in fragmented tropical landscapes. J Appl Ecol 55:256–266. https://doi.org/10.1111/1365-2664.12962

Morante-Filho JC, Arroyo-Rodríguez V, Pessoa MS et al (2018b) Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. Ecol Appl 28:2024–2032. https://doi.org/10.1002/eap.1791

Morante-Filho JC, Faria D, Mariano-Neto E, Rhodes J (2015) Birds in anthropogenic landscapes: The responses of ecological groups to forest loss in the Brazilian Atlantic forest. PLoS One 10:1–18. https://doi.org/10.1371/journal.pone.0128923

Moreira-Lima L (2014) Aves da Mata Atlântica: riqueza, composicão, status, endemismos e conservacão. Dissertation, Universidade de São Paulo.

Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. Funct Ecol 24:867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity Hotspots for Conservation Priorities. Nature 403:853–858

Newbold T, Hudson LN, Arnell AP, et al (2016) Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353: 288-291

Pardini R, de Bueno AA, Gardner TA, et al (2010) Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. PLoS One 5:. https://doi.org/10.1371/journal.pone.0013666

Pessoa MS, Hambuckers A, Benchimol M et al (2017a) Deforestation drives functional diversity and fruit quality changes in a tropical tree assemblage. Perspect Plant Ecol Evol Syst 28:78–86. https://doi.org/10.1016/j.ppees.2017.09.001

Pessoa MS, Rocha-Santos L, Talora DC et al (2017b) Fruit biomass availability along a forest cover gradient. Biotropica 49:45–55. https://doi.org/10.1111/btp.12359

Petchey OL, Gaston KJ (2006) Functional diversity: Back to basics and looking forward. Ecol Lett 9:741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Plass-Johnson JG, Taylor MH, Husain AAA et al (2016) Non-random variability in functional composition of coral reef fish communities along an environmental gradient. PLoS One 11:1–18. https://doi.org/10.1371/journal.pone.0154014

Podani J, Schmera D (2006) On dendrogram-based measures of functional diversity. Oikos 115:179–185. https://doi.org/10.1111/j.2006.0030-1299.15048.x

Prescott GW, Gilroy JJ, Haugaasen T, et al (2016) Reducing the impacts of Neotropical oil palm development on functional diversity. Biol Conserv 197:139–145. https://doi.org/10.1016/j.biocon.2016.02.013

Püttker T, Crouzeilles R, Almeida-Gomes M, et al (2020) Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. Biol Conserv 241:108368. https://doi.org/10.1016/j.biocon.2019.108368

QGIS Development Team. 2016. QGIS Geographic Information System. Version 3.4.13. Open Source Geospatial Foundation Project. Retrieved from https://www.qgis.org

R Development Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Rezende CL, Scarano FR, Assad ED et al (2018) From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspect Ecol Conserv 16:208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Rodrigues RC, Hasui É, Assis JC et al (2019) ATLANTIC BIRD TRAITS: a data set of bird morphological traits from the Atlantic forests of South America. Ecology 100:1–2. https://doi.org/10.1002/ecy.2647

Saavedra F, Hensen I, Beck SG et al (2014) Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. Oecologia 176:837–848. https://doi.org/10.1007/s00442-014-3056-x

Santos GGA, Santos BA, Nascimento HEM, Tabarelli M (2012) Contrasting Demographic Structure of Short- and Long-lived Pioneer Tree Species on Amazonian Forest Edges. Biotropica 44:771–778. https://doi.org/10.1111/j.1744-7429.2012.00882.x

Sekercioglu CH, Loarie SR, Brenes FO (2007) Persistence of forest birds in the Costa Rican agricultural countryside. Conserv Bio. 21:482–494. https://doi.org/10.1111/j.1523-1739.2007.00655.

Villard MA, Metzger JP (2014) Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. J Appl Ecol 51:309–318. https://doi.org/10.1111/1365-2664.12190

Vollstädt MGR, Ferger SW, Hemp A et al (2017) Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. Glob Ecol Biogeogr 26:963–972. https://doi.org/10.1111/geb.12606

Weiss KCB, Ray CA (2019) Unifying functional trait approaches to understand the assemblage of ecological communities: Synthesizing taxonomic divides. Ecography 42:1–9. https://doi.org/10.1111/ecog.04387

Wenny DG, DeVault TL, Johnson MD, et al (2011) The Need to Quantify Ecosystem Services Provided by Birds. Auk 128:1–14. https://doi.org/10.1525/auk.2011.10248

Wheelwright NT (1985) Fruit-Size, Gape Width, and the Diets of Fruit-Eating Birds. Ecology 66:808–818

Wilman H, J. B, J. S et al (2014) EltonTraits 1 . 0 : Species-level foraging attributes of the world ' s birds and mammals. Ecology 95:2027

Supplementary Material

Table S1 Exploratory analyses showing mean, standard deviation and range of the landscape composition and configuration predictors included in the models.

Variable	Mean	SD	Range
Forest cover	58.15	31.04	0.4-100
Edge density	0.004	0.002	0.0000008-0.0117
Mean nearest neighborhood distance	342.02	347.52	0-1000

Table S2 Results of the model averaging. Models for frugivorous richness were adjusted using negative binomial, models for SES functional richness, functional dispersion, body mass, bill widht and hand-wind index were adjusted using normal distribution. For frugivorous richness the log sampling effort was included as an offset and for all models the coordinates of each point were included as covariate.

Response variable	Predictor variable	Estimate	Adjusted SE	p-Value
Frugivore richness	FC	0.262	0.042	**0.000**
	ED	-0.049	0.034	0.145
	MNND	-0.030	0.052	0.565
	FC:ED	0.064	0.036	0.077
	FC:MNND	0.062	0.041	0.131
	ED:MNND	-0.023	0.032	0.479
SES Functional richness	FC	-0.246	0.094	**0.009**
	ED	0.129	0.105	0.339
	MNND	0.133	0.140	0.218
	FC:ED	-0.193	0.118	0.102
	FC:MNND	0.088	0.122	0.471
	ED:MNND	0.094	0.098	0.334
	FC	-0.179	0.074	**0.016**

Functional dispersion	ED	-0.015	0.086	0.855
	MNND	0.059	0.113	0.603
	FC:ED	-0.179	0.095	0.060
	FC:MNND	-0.039	0.097	0.686
	ED:MNND	0.109	0.078	0.166
Body mass	FC	-0.425	15.51	0.331
	ED	1.349	12.41	0.978
	MNND	21.33	16.46	0.913
	FC:ED	-10.94	13.88	0.431
	FC:MNND	15.17	13.96	0.277
	ED:MNND	4.313	10.46	0.680
Bill width	FC	0.191	0.371	0.606
	ED	0.019	0.351	0.955
	MNND	-0.219	0.368	0.552
	FC:ED	-0.740	0.377	**0.049**
	FC:MNND	0.149	0.397	0.709
	ED:MNND	0.599	0.298	**0.044**
Hand wing index	FC	0.000	0.393	0.999
	ED	-0.398	0.323	0.217
	MNND	-0.623	0.324	0.054
	FC:ED	-0.049	0.372	0.895
	FC:MNND	0.088	0.363	0.808
	ED:MNND	0.286	0.287	0.319

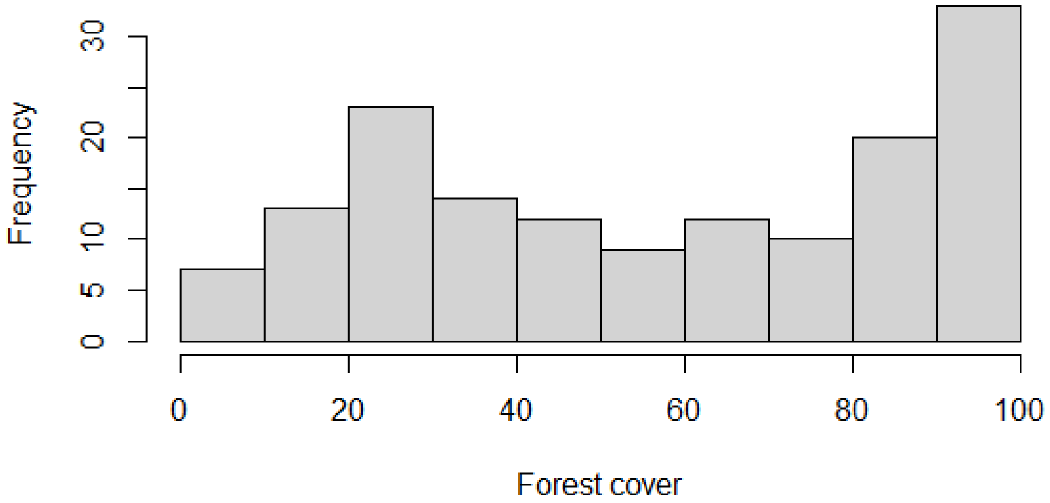

Fig 1 Frequency distribution of forest cover in 153 forest fragments in the Altantic forest.

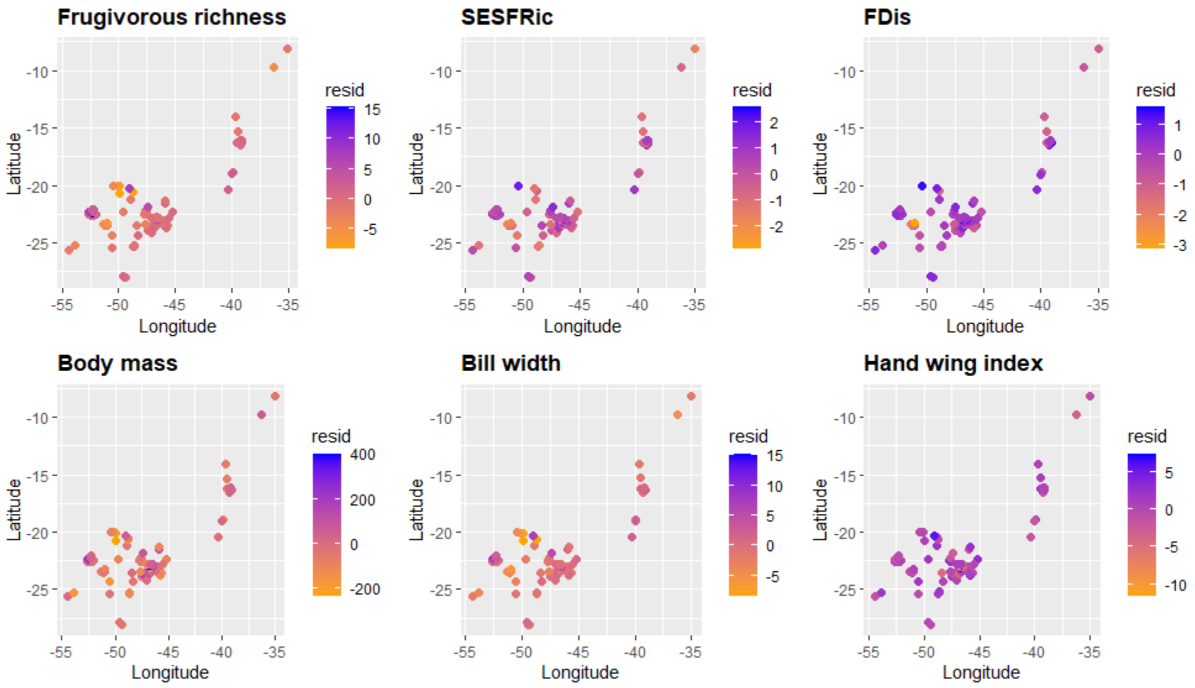

Fig 2 Spatial distribution of residuals from models.

CAPÍTULO II

HABITAT LOSS SHAPES THE STRUCTURE AND SPECIES ROLES IN TROPICAL PLANT-FRUGIVORE NETWORKS

Artigo em revisão na revista Oikos

Habitat loss shapes the structure and species roles in tropical plant-frugivore networks

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ABSTRACT

Habitat loss is a global threat to biodiversity with pervasive effects on species and populations. These impacts may generate cascading effects on ecological processes propagating across ecological networks. Thus, understanding how habitat loss affects ecological networks is fundamental for conservation. We used a database of 25 plant-frugivore networks distributed across the whole Brazilian Atlantic Forest to understand how landscape-scale habitat loss shapes network structure, robustness, species role and traits related to seed dispersal. We compared whether these network properties have linear or non-linear relationships and used centrality metrics and indirect effects to evaluate if habitat loss change the role of species in plant-frugivore networks. We found linear and non-linear relationships with negative effects of habitat loss on the network structure. As a consequence of shifts in species richness and number of links, the number of interactions and the proportion of possible interactions observed (connectance) were negatively associated with habitat loss. In contrast, nestedness increased with habitat loss. Network robustness, mean bill width and mean seed size were not significantly related to habitat loss. In addition to changes in interaction patterns at network level, habitat loss also favors changes in interaction among species, shifting the species playing central roles in network organization or contributing to indirect effects in the networks. In forested landscapes, obligate frugivores are the main central species in the network, and the ones potentially contributing to indirect effects, while in deforested landscapes these roles are fulfilled by occasional frugivores. Thus, our results emphasize the widespread effect of habitat loss on plant-frugivore systems, adding evidence that its pervasive effects on biodiversity also proliferate on mutualistic interactions with negative consequences for seed dispersal that potentially go beyond the direct pairs of interacting species.

Keywords: Atlantic Forest; plant-animal interactions; mutualistic networks; forest cover; birds; deforestation

INTRODUCTION

Habitat loss is one of the main threats to biodiversity, with pervasive effects on species, populations, and ecosystem services (Barnes et al. 2017, Newbold et al. 2015). In the tropical region, species have been impacted by human actions in unprecedented ways in the last decades (Barlow et al. 2018). These consequences are not limited to the direct loss caused by human activities. Rather, biodiversity loss might trigger cascading effects disrupting key ecological processes such as seed dispersal (Memmott et al. 2004, Valiente-Banuet and Verdú 2013).

Evidence of the negative effects of habitat loss on biodiversity has been shown for several clades, such as mammals (Pardini et al. 2010, Arroyo-Rodríguez et al. 2016, Muylaert et al. 2016), birds (Martensen et al. 2012, Morante-Filho et al. 2015), and plants (Rocha-Santos et al. 2017). However, species can exhibit divergent responses to disturbance, as certain generalist or disturbance-tolerant species can thrive in human-modified landscapes (Filgueiras et al 2021). For instance, among birds, generalist species such as, *Camptostoma obsoletum* and *Elaenia flavogaster* increase their occupancy in deforested landscapes, whereas forest-dependent species, such as, *C. rubrocapilla* and *Dixiphia pipra* thrive in forested landscapes (Morante-Filho et al. 2021). Also, sensitivity to deforestation in bird species is known to be shaped by ecological traits (Owens and Bennet 2000; Purvys et al. 2000), such as body size (Gaston and Blackburn 1995).

Habitat loss can lead to non-linear declines in biodiversity (Pardini et al. 2010, Martensen et al. 2012, Morante-Filho et al. 2015, Muylaert et al. 2016). In a seminal review, Andrén (1994) showed that in deforested landscapes, patch size decrease and isolation increase. Consequently, studies showed non-linear relationship between forest loss and biodiversity metrics due to the combined effects of habitat loss and fragmentation (Swift and Hannon 2010), with a threshold below which species richness and abundance of particular groups might decline or increase (Pardini et al. 2010, Morante-Filho et al. 2015, Muylaert et al. 2016).

Biodiversity loss also manifests as the loss of ecological interactions, which can precede species loss (Valiente-Banuet and Verdú 2013, McConkey and O'farril 2016). For instance, the disruption of ecological interactions can reshape the organization and function of ecosystems (Paine 1966, Estes et al. 2011). Ecological interactions form networks upon which the ecosystem depends on (Valiente-Banuet et al. 2015). Thus, the anthropogenic disruption of ecological interactions (Valiente-Banuet and Verdú 2013) may lead to cascading effects that propagate across the ecosystems. Understanding how habitat loss affects the structure and robustness of ecological networks is crucial to identifying thresholds below which the loss of interactions cannot be reversed and the ecosystem collapses (Valiente-Banuet and Verdú 2013, McConkey and O'farril 2015, Heleno et al. 2020). Previous work using patch-scale approaches provided insights on the relationship between habitat loss and the structure of frugivory networks (de Assis Bomfim et al. 2018, Emer et al. 2020), and a next step is to explore how human activities may shift patterns at broader spatial scales (Guimarães 2020). Indeed, ecological patterns are always associated with particular scales (Levin 1992) and, therefore, we need to access the spatial scale in which patterns are more clearly predicted by explanatory variables (Jackson and Fahrig 2015). There is an urgent need to assess landscape-scale effects of habitat loss on ecological networks because biodiversity responses to anthropogenic drivers might vary across spatial scales (Fahrig et al. 2019).

Theory predicts that response of ecological systems to perturbation will depend on network structure (Silva et al 2007). In frugivory networks, nestedness is a common pattern, in which the interactions of specialists are a subset of the interactions performed by generalist species (Bascompte et al. 2003). Nested networks confer functional redundancy and the possibility of alternative routes against disturbance (Bascompte and Jordano 2007). Studies have shown both positive and negative responses of nestedness patterns to disturbances (Laurindo et al. 2019; Morrison et al. 2020; Vidal et al. 2019). The uncertainty of how network patterns respond to habitat loss extends to estimates of the robustness of ecological networks to extinctions (Fortuna and Bascompte 2006, Evans et al. 2013, Vidal et al. 2019). Network robustness measures the system's tolerance to secondary extinctions (Dunne et al. 2002, Memmott et al. 2004). Interestingly, more intensely degraded landscapes may have more connected networks (Morrison et al. 2020), leading to higher robustness. Also, network structure responds non-linearly to habitat loss, with a sudden decay at a certain level of habitat destruction (Fortuna and Bascompte 2006, Fortuna et al. 2013, Vidal et al. 2019). Habitat loss can also shape the role species play in the network, e.g., central species, connecting different parts of the networks. In this sense, we still do not know if, by changing the central species in ecological networks, habitat loss may generate far-reaching effects to ecological assemblages, as those generated by indirect effects, i.e., effects that propagates across species that do not directly interact with each other. Specifically, we still need empirical datasets to analyze how landscape-scale forest loss affects such networks and if its effects translate into changes in the traits related to seed dispersal (Galetti et al.

2013) as a consequence of the extinction and replacement of frugivorous birds in relation to forest loss (Morante-Filho et al. 2018).

Here, we use an empirical database of 25 avian frugivory networks encompassing the Brazilian Atlantic Forest, to evaluate how forest loss affects these networks. Specifically, we assessed how habitat loss shapes network structure, robustness, traits related to seed dispersal (bill width and seed diameter), and the role of different bird species in mutualistic networks. We hypothesized that non-linear relationships, based on Andrén's threshold (Andrén 1994), best describe the relationship between interactions and habitat loss due to the sensitivity of birds (Martensen et al. 2012, Morante-Filho et al. 2015) and plants (Rigueira et al. 2013, Lima and Mariano-Neto 2014) to the extinction threshold (Swift and Hannon 2010). We expected that this non-linear trend could be extended to the network structure and robustness, as suggested by empirical and simulated studies (Fortuna and Bascompte 2006, Evans et al. 2013, Fortuna et al. 2013, Vidal et al. 2019). Additionally, we predicted that forest loss would have negative effects on the network structure and robustness, shaping the role of bird species in mutualistic networks. These changes are expected because obligate and occasional frugivore species composition change with habitat loss (Morante-Filho et al. 2018) and functional roles of frugivores, e.g., the patterns of interaction of species within networks, vary across species in seed dispersal networks (Mello et al. 2015, Dehling et al. 2021). Finally, we also expected that this replacement of species due to habitat loss will negatively affect the traits related to seed dispersal, such as bill width (Galetti et al. 2013).

METHODS

We gathered information from published studies on frugivory networks in the Brazilian Atlantic Forest. This biodiversity hotspot has suffered from intense deforestation, and currently less than 30% of its forest still remains (Rezende et al. 2018, Galetti et al. 2021). The Atlantic Forest is considered a hotspot of biodiversity in the world due to the high diversity, levels of endemism and the presence of threatened species (Myers et al. 2000). In the Atlantic Rainforest, seed dispersal by animals is mainly performed by a diverse coterie of bird species, especially in areas in which large mammals died out due to multiple forms of human impact. In this paper, we have focused in the seed dispersal by birds.

Data on plant-bird networks were obtained in the largest published database on interactions available for the Brazilian Atlantic Forest (Fig. 1), the ATLANTIC FRUGIVORY (Bello et al. 2017). This database compiled more than 8000 frugivory interactions from 331 vertebrates and 788 plant species recorded in 166 studies. From the database we selected only network studies focusing on birds. Our dataset includes only community-level studies (i.e., those that recorded the interactions between bird and plant assemblages in a forest fragment, using different methodologies such as focal observations, feeding bouts, etc). Thus, we excluded from the database studies focusing on plant or animal populations. We completed the data searching for additional studies on plant-bird interactions in the Web of Science and Scopus using the following search terms: ("ecological network*" OR "mutualistic network*" OR "frugivor*") AND ("bird*") AND (“Atlantic Forest”) in TOPIC. From this search, we included only network studies that have the coordinates of the sampling fragment and provided the matrix of interactions. Our final database is composed of 25 qualitative plant-bird frugivory networks from different forest fragments, 12 from the ATLANTIC FRUGIVORY and 13 from the literature search (Fig. 1, Table S1).

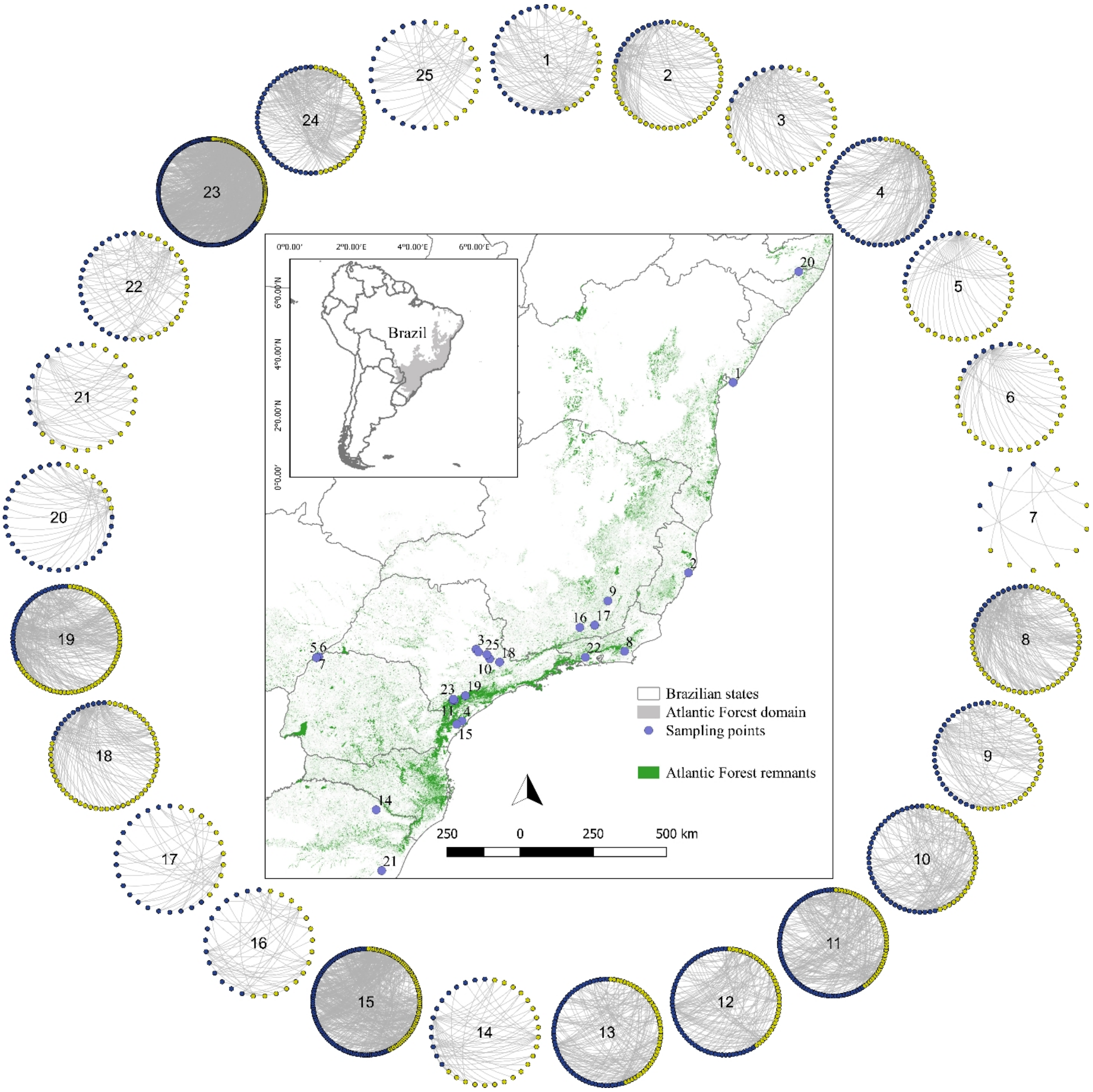

Figure 1. Location of the 25 forest fragments highlighting the structure of the plant-bird frugivore interaction networks in the Brazilian Atlantic Forest. In each network blue dots represent plant species, yellow dots bird species and the gray lines the interaction among them. Figure based on Emer et al. 2019.

Descriptors of network structure

To describe each network, we calculated the number of bird and plant species and the total number of interactions. We also calculated the following descriptors of network structure:

connectance (proportion of realized interactions in relation to all possible interactions, Gardner and Ashby 1970, Jordano 1987); the ***average number of links per species*** (sum of links divided by the number of species); the level of ***nestedness*** (a pattern where the interactions performed by specialist species are a subset of those of generalist species, Almeida-Neto et al. 2008). We selected those metrics because they are commonly used in network studies and describe the diversity of species and interactions in the entire network, providing insights into the structure and dynamics of ecological networks (Dehling 2018, Guimarães 2020). Nestedness was calculated using the Nestedness metric based on Overlap and Decreasing Fill" (NODF) index (Almeida-Neto et al. 2008) using the function "*networklevel*" in the package *bipartite* (Dorman et al 2009). We used null models to test if nestedness shows patterns that are higher than expected by both species richness and the variation in the number of links across species. We used the Patefield algorithm that randomizes the distribution of links between species while maintaining the number of links per species (Dormann et al. 2009). We created 1000 null models for each site and used Z-scores to test if the observed value of the network differs significantly from the theoretical benchmark provided by the null model. Z-scores were calculated as:

$Z = \frac{O - E}{\sigma}$, where O = observed value; E = average value for the ensemble of null model networks and σ = standard deviation of the ensemble of null model networks.

We assumed that robustness can be described by simple coextinction dynamics in which if all partners of a given species die out the species also dies out. We then calculated ***network robustness***, which measures the area under the secondary extinction curve – the curve describing the number of remaining plant species after the sequential removal of animal species - after simulating bird extinction assuming a random extinction process (Memmott et al. 2004). Simulations were performed through 100 randomizations using the functions "*second.extinct*" and "*robustness*" in package bipartite (Dorman et al 2009).

We then turned our attention to descriptors of roles of bird species in network structure. For each bird species, we calculated ***betweenness centrality***, which assesses the importance of each species in connecting different parts of the network (Dáttilo and Rico-Gray 2018). Species may also be important by creating pathways that indirectly connect species, allowing the propagation of indirect effects (Guimarães et al. 2017).

To compute the potential for indirect effects associated with a given bird species, we assumed a model in which indirect effects are stochastic perturbations that propagates across interacting species in the network (see Pires et al. 2020 for a similar approach for coextinction cascades). Potential indirect effects were calculated considering that stochastic perturbations propagate through links connecting interacting species (see Pires et al. 2020 for a similar approach). Specifically, we assumed that an effect propagates from a given species i to its partner j with probability λ. Similarly, with the same probability λ, an effect propagates from species j to its partner k. Thus, with probability λ^2, the effect propagates from i to k through j. We compute the potential of a species to propagate indirect effects in a network with S species, T_{out}, as $T = V(I - \lambda W)^{-1}$ (Pires et al. 2020), in which **T** is a Sx1 row vector in which each element describes the T_{out} of each system in the network, **V** is an all-ones, Sx1 row vector, **I** is an SxS identity matrix, W is a SxS row stochastic matrix in which each element is $w_{ij} = 1/k_i$ if there is an interaction between i and j and zero otherwise and k_i is the number of species interacting with species i. The values of λ are bounded between 0 and 1 and the higher the value, the stronger is the impact of indirect pathways on the T_{out}. We set $\lambda = 0.95$, since our aim is characterizing the potential for indirect pathways and, consequently, the potential of indirect effects. Note that T_{out} is an application of Katz centrality (Katz 1953) for row stochastic matrices.

To assess the functional basis of the changes promoted by habitat loss on the role of species in plant-frugivore networks, we gathered information on two important traits related to the seed dispersal process, bill width and seed diameter. The bill width (from Bello et al. 2017 and Rodrigues et al. 2019) is an important trait that can trigger phenotypic evolutionary changes in the dispersed plants, such as evolution of decreased seed size (Galetti et al. 2013). Seed diameter limits which frugivores will be able to consume the fruit, and is related to seed fitness (Stanton 1984, Silvertown 1989). We collected information on seed diameter from Bello et al. (2017) and from the Neotropical Tree Communities database (TreeCo version 4.0): http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start.

Landscape descriptors

To estimate forest cover, a proxy of habitat amount, we used land use and cover maps derived from classified Landsat satellite images with 30m spatial resolution from the project MapBiomas version 5.0 (Souza et al. 2020). We calculated the percentage of forest cover (corresponding to natural forest formations) (Souza et al. 2020), within circular buffers with radius varying from 500 to 2000 m at 100 m intervals, to assess the scale of effect. We used these buffers to include the scale of effect previously found for birds in the Atlantic Forest (600 m Morante-Filho et al 2015) and the median between-patch dispersal found for frugivorous (Mueller et al. 2014). All maps were downloaded based on the year that each study started sampling the interactions. To calculate the percentage of forest cover in each radius we used the package *landscapemetrics* (Hesselbarth et al. 2019) in R version 3.5.3 (R Core Team 2019).

Data analysis

To take into account the possible effects of sampling effort on network metrics, we constructed a generalized additive model, with Gaussian distribution for continuous and Poisson distribution for count variables, using sampling effort, provided by each study, as predictor and network metrics as response variables (Table S2). Because some network metrics were related to sampling effort, we extracted the residuals of all models and used them as response variables (i.e., response corrected for sampling effort). We also tested the scale of effect, i.e., the spatial scale at which each response variable best responded to the predictor (Jackson and Fahrig 2015). To do this, we constructed models for each response variable in each radius segment and for different types of models (i.e., linear and non-linear). Afterwards, we compared the Akaike weights of these models to choose the appropriate scale of effect, corresponding to the model with the largest Akaike weight (Fig. S1).

We compared five models to evaluate the effects of forest cover on network structure: a null model, which represents the absence of relationship. A linear model, expected when the response variables increase linearly with increasing forest cover, and three non-linear models: quadratic, power law, and piecewise (see Appendix S1 for explanation about each model). Linear relationships imply constant increase or decrease of the response variable with the explanatory variable, whereas non-linear models imply a variable and often suddenly decay or increase.

We used the best scale of effect (Fig. S1) and compared the different models based on their delta Akaike Information Criteria corrected for small sample size (ΔAICc; Buhran and Anderson 2002) using the *MuMIn* package (Barton 2020). We selected as the most plausible the simplest model between those with $\Delta AICc \leq 2$; when two models with $\Delta AICc \leq 2$ were equally simple (i.e., had the same number of parameters), we selected the one with the lowest $\Delta AICc$. When the null model was included in those with $\Delta AICc \leq 2$ we consider it as the best model. All models were checked for normality of the model residuals. We also checked for spatial auto correlation using Moran I ($p>0.05$ for all models) in the best models prior to the comparisons using the function *Moran.I* from package *ape* (Paradis and Schliep 2019). All analyses were implemented in R version 3.5.3 (R Core Team 2019) and the script and data are available at https://github.com/CesarEco/Publications/tree/main/Paper_mutualism.

To assess whether species roles in plant-frugivore networks change in relation to habitat loss, we first classified landscapes according to three levels of forest loss: I. deforested (less than or equal to 30% of remaining forest cover); II. Intermediate (more than 30% and less than or equal to 60% forest cover); and III forested (more than 60% forest cover). We defined these levels of forest loss based on studies that suggest low levels as less than 30% of remaining habitat (Fahrig 1998) and intermediate levels between 30-60% of remaining habitat (Oliveira-Filho and Metzger 2006). We then classified each species as occasional frugivorous (i.e., those that consume less than 80% fruits in their diet) or obligate frugivorous (i.e., those that feed heavily on fruits and whose diet is constituted of more than 80% of fruits), following Wilman et al. (2014). For each fragment we verified the percentage of occasional and obligate frugivorous species in the entire network and also for central species (i.e., species with the highest value of betweenness centrality).

RESULTS

In the 25 plant-bird interaction networks, 469 plant and 215 bird species were recorded. The mean number of plant species was 32.0 ±32.5 (mean ± SD per network, ranging from 5 to 150), mean number of bird species was 31.7 ± 18.4 (ranging from 8 to 76), and the mean number of interactions per network was 147.2 ± 184.1 (ranging from 13 to 883). The most frequent plant species were *Casearia sylvestris* (recorded in 10 networks), *Guapira opposita* (9 networks) and *Trema micrantha* (8 networks). The most frequent bird species were *Turdus rufiventris* (18 networks) and *Pitangus sulphuratus* (17 networks).

The scale of effect varied among the response variables, but the 500m radius was found to be the best scale for 12 out of 36 models (Fig. S1). We observed a positive quadratic relationship ($y=\beta x^2+\alpha$) between forest cover and both the number of plants (α = -0.14 ± 0.06, β = 0.002 ± 0.001) and number of interactions (α = -0.14 ± 0.13, β = 0.002 ± 0.001), indicating that species-rich systems with multiple interactions are observed in areas with higher amounts of forest cover, whereas at intermediate levels of forest cover, low number of plants and interactions are observed (Fig. 2). The number of bird species (β = 0.04 ± 0.01) and links per species (β = 0.03 ± 0.01) increased with forest cover in a linear way (Fig. 2). In contrast, nestedness (NODF) decreased linearly with forest cover ($y=\beta x+\alpha$,β = -0.01 ± 0.04, Fig 2). Also, we observed a piecewise relationship between forest cover and connectance (β = -0.02 ± 0.006) indicating an increase in connectance until ~90% of forest cover and a sudden decay in highly forested areas (Fig. 2). Finally, network robustness, mean bill width and seed diameter showed no significant relationship with habitat amount (Fig. 2, Table S2).

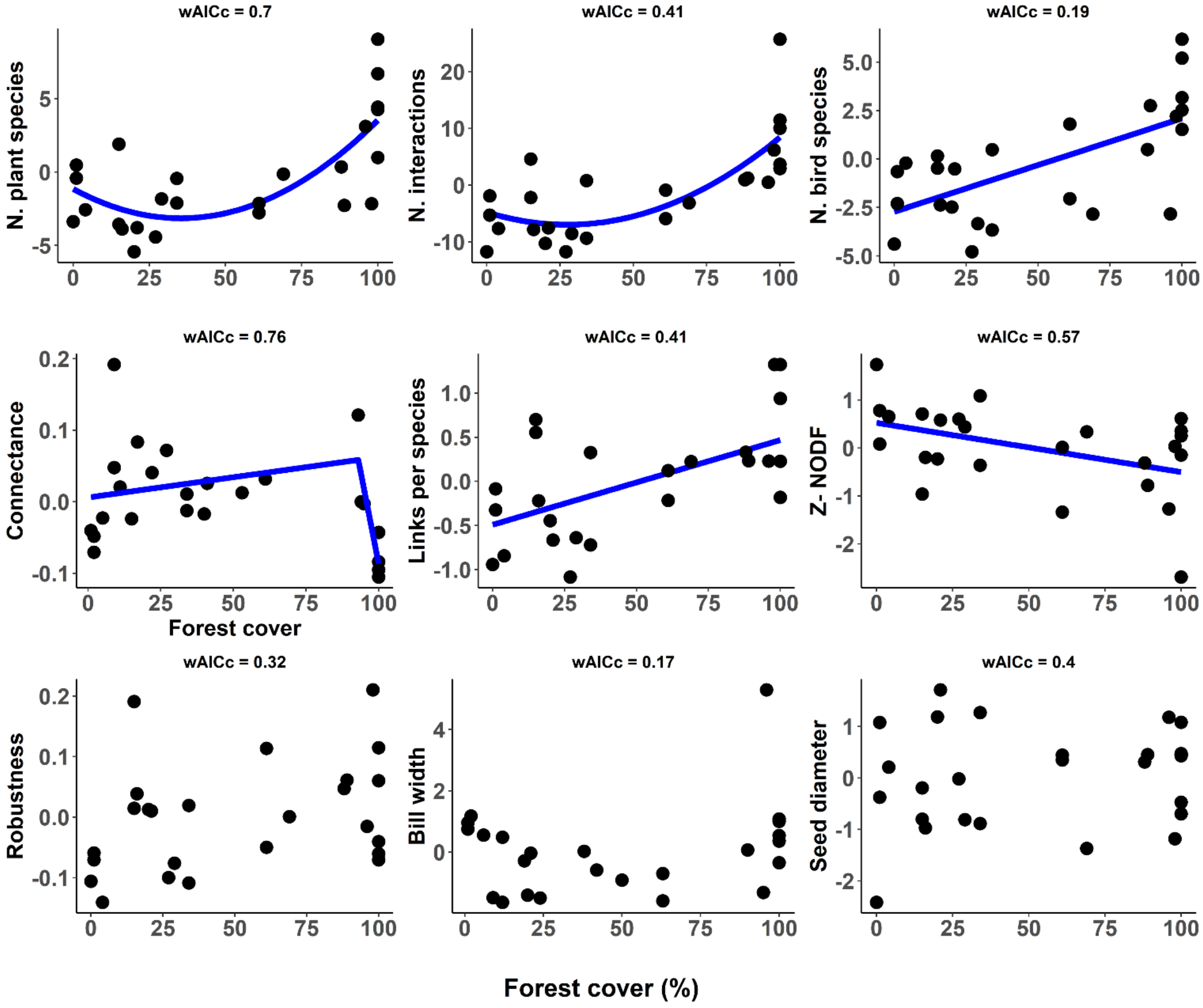

Figure 2. Effects of forest cover on plant-frugivore interaction network descriptors in the Brazilian Atlantic Forest. All metrics were first related to sampling effort and the residuals were used in the analyses. Blue lines represent the fitted values and are shown only when the null model was not included in ΔAICc≤2. Negative values appear because we used residuals to correct for sampling effort (see analysis).

Regarding the role of each species within networks, our results showed that obligate frugivores have greater indirect effects (one way ANOVA $p<0.05$, $\beta = -13.79$), whereas occasional frugivores have higher betweenness centrality (one way ANOVA $p>0.05$, $\beta = 0.03$, Fig. 3, Table S4 and S5). Our analysis showed that increasing forest cover reorganizes the contribution of different species to network structure. In fact, increasing forest cover was associated with the percentage of occasional and obligate frugivorous species in the entire network and those species that occupy central positions and contributing to indirect effects (Fig. 4). Specifically, in deforested landscapes, there is a high proportion of occasional frugivorous birds (90%), that assume a central role in these networks (i.e., high values of betweenness centrality, 90% of species) or contribute largely to indirect effects (i.e., high values of indirect effects, 88% of species). On the other hand, as forest cover increases, so does the proportion of species that are strictly dependent of fruits (28%), resulting in these species assuming central roles (43%) or contributing more to indirect effects in the networks (38%, Fig. 4).

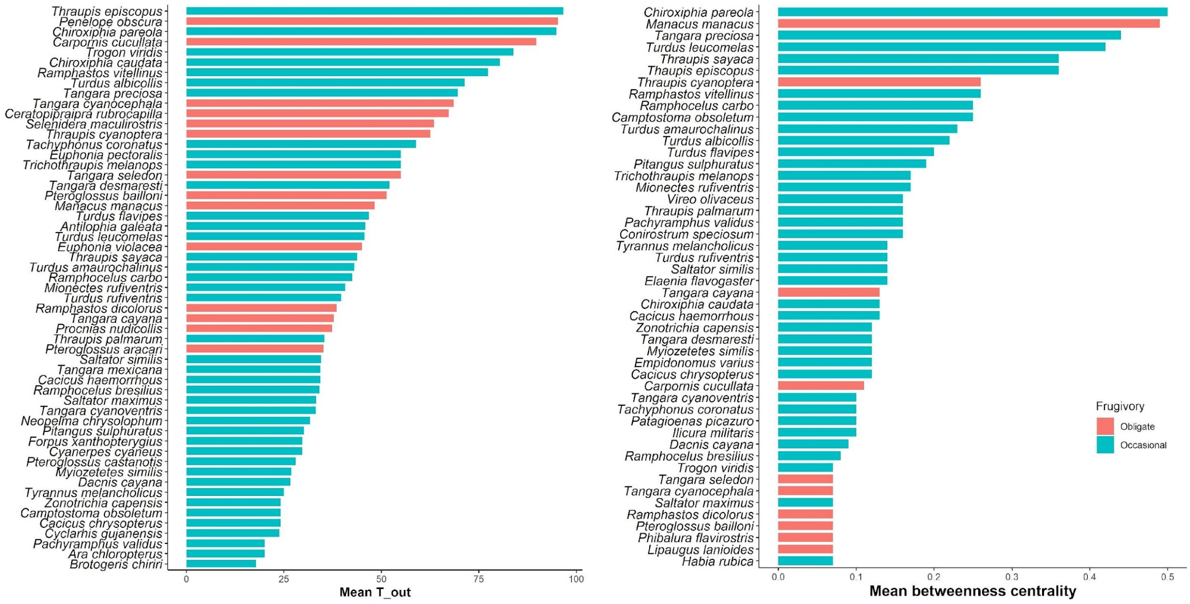

Figure 3. Mean values of contribution to indirect effects (T_out) and betweenness centrality of the species with the highest values of these metrics. Mean values were computed for the five species with highest values across all 25 mutualistic seed dispersal networks in the Brazilian Atlantic Forest.

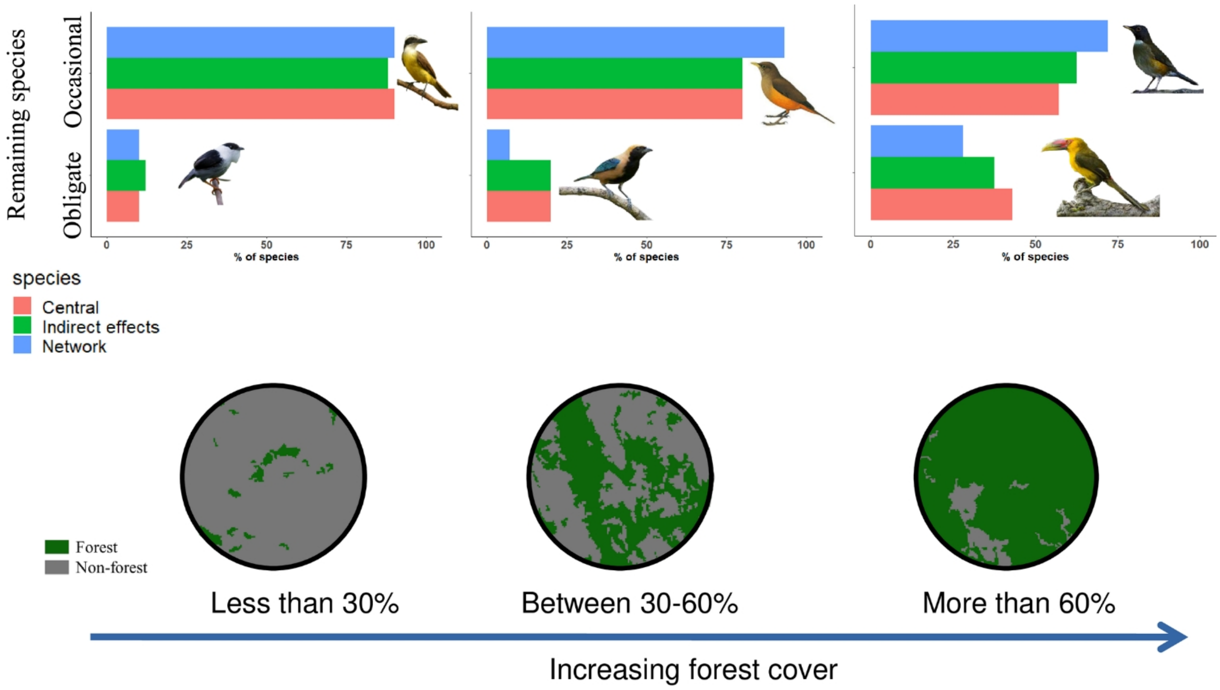

Figure 4. Percentage of obligate and occasional frugivorous species across networks and their role in network organization. Blue bars indicate the mean percentage of obligate and occasional frugivorous species in the entire network. The percentage of obligate frugivorous birds increases with forest cover. Similarly, when considered only the five species with the highest values of betweenness centrality (red bars) and indirect effects (green bars), the percentage of obligate frugivorous increases with forest cover. Bird pictures were downloaded from https://wikiaves.com.br after permission from authors. Examples of occasional species from left to right: *Pitangus sulphuratus, Turdus rufiventris* and *Turdus albicollis*. Examples of obligate frugivorous species: *Manacus manacus, Tangara cayana* and *Pteroglossus bailloni.*

DISCUSSION

Here, we explored the relationship between habitat loss at the landscape scale and the structure and robustness of frugivory networks. The changes in frugivory networks associated with forest loss may be the direct outcome of habitat loss or an indirect consequence of forest loss such as increased hunting pressure associated with deforestation (Constantino 2016) or the demographic instability of small forest patches. By now and using an empirical data set, we showed for the first time that some responses to forest loss, when significant, were linearly distributed (number of bird species, number of links per species and nestedness), and non-linear relationships were observed for number of plants, interactions and connectance. Forest loss was negatively associated with all network descriptors except for nestedness. Our results also showed that forest loss did not significantly affect the two functional traits evaluated (bill width and seed diameter) nor robustness. Moreover, our results highlight the potential role of habitat loss in reshaping the importance of different species in these mutualistic systems by changing the role of the species to the network organization along the deforestation gradient.

These results showed that the number of plant species, interactions, and connectance decreased non-linearly as forest is lost at the landscape scale. These relationships point to a decrease in the number of plants and interactions at intermediate levels of habitat loss, as reported for fruit removal in the Atlantic Forest (Cazetta et al. 2019). When habitat is lost, a decrease in the total amount of habitat itself occurs, however, at intermediate levels of habitat loss, there is an increase in the number of fragments which result in more edges (Fahrig 2017), favoring pioneer plant species (Santos et al. 2012), decreasing fruit removal (Cazetta et al. 2019), and consequently the number of interactions. The loss of interactions can also be attributed to the loss of specialized frugivores such as toucans, trogons and cotingas that are absent or present in low densities at low habitat amount (i.e., below 60%) (Vidal et al. 2019). These specialized frugivores are known to consume more fruits and disperse seeds farther than less specialized species (Godínez-Alvarez et al. 2020). In deforested landscapes, generalist frugivorous birds, such as tanagers and thrushes, with limited dispersal effectiveness prevail (Schupp et al. 2010). We also found that the connectance increased until ~90% of forest cover and then decayed suddenly. This might be due to the increase in plant and bird species in more forested landscapes increasing the number of possible interactions while realized interactions are limited by selection and phenotypic constraints acting on the number of partners of any given species. However, given the small number of samples in highly forested regions, this result must be interpreted with caution; regardless, in areas with less than 100% of forest cover, connectance decreased linearly.

In contrast, number of bird species, number of links per species and nestedness respond linearly to forest loss. In forested landscapes the number of frugivorous birds is high (Morante-Filho et al. 2018, Bonfim et al. 2021) possibly reflecting the increase in fruit availability and forest structure complexity (Morante-Filho et al. 2018). Our results showed that connectance increases as forest cover increases at the landscape scale. This is the result of the increase in the number of links per species in less disturbed landscapes, as previously shown for pollinators (Vanbergen et al. 2017) and frugivorous birds (Vidal et al. 2019). On the other hand, our results using empirical mutualistic networks show that increasing forest cover decreases nestedness. Indeed, some studies showed that disturbed areas are less nested (Traveset et al. 2018, de Assis Bomfim et al. 2018, Vidal et al. 2019), while the opposite pattern was observed by others, in which disturbed areas present higher nestedness (Menke et al. 2012, Vanbergen et al. 2017, Morrison et al. 2020). Our result is in line with those that point to a decrease in nestedness in forested landscapes. Nestedness may decrease due to reduction of niche overlap between species or because niche overlap expands, reducing the heterogeneity in the number of interactions across species and, consequently, the structure of nested subsets (Almeida-Neto et al. 2007, 2008). We suggest that high overlap in fruit consumption could be observed in areas with low forest cover, where the number of frugivorous bird and plant species are low (Rocha-Santos et al. 2017, Morante-Filho et al. 2018), and species might share the same resource. This would be especially likely if species having other resources, as observed in the case of occasional frugivorous. Low overlap in fruit consumption is more likely to emerge in areas with high forest cover, in which the increase of plant species provides different resources and organisms can rely upon fruits as a major component of diet. The co-occurrence of multiple obligate frugivores may promote competition, which, in turn favor specialization in different resources, decreasing niche overlap and, consequently, nestedness.

Our results did not find significant effects of forest loss on network robustness, bill width, or seed diameter. Robustness measures the system tolerance to secondary extinction (Memmott et al. 2004). Thus, our results imply that robustness to extinction is maintained even in deforested landscapes. Previous studies found that robustness can even increase in disturbed areas, for instance, forest edges (more disturbed) showed higher robustness than forest interior (Mencke et al. 2012). In fact, increasing forest loss reduce the number of plant and bird species (Rocha-Santos et al. 2017, Morante-Filho et. al 2018), however the remaining species in deforested landscapes are less specialized and possibly share resources, thus buffering the extinction of the plants foraged by them. Yet, for mean bill width and mean seed diameter our results could reflect the impoverishment of large-bodied species even in more forested landscapes which result in less consumption of seeds with large diameter by species with large bill width. Another possible explanation could be the replacement of large forest-dependent species by large frugivorous species that do not depend on forest and have large bill width (the correlation between body mass and bill width in our dataset was 0.88). For example, the large-bodied forest dependent species *Pipile jacutinga* (a ~ 1 kg cracid bird) is present only in areas with high forest cover, but this game bird species can be replaced by *Penelope superciliaris*, a large bodied species from the same family, that is present in less forested landscapes. Indeed, one mechanism that may explain the persistence of central frugivore clades is mutualistic networks against extinction dynamics, even at long temporal scales, is the replacement of extinct species by closed-related species (Burin et al. 2021).

Although functional traits of species did not change with forest cover, the role of different species did change. We showed that, as forest cover increases, there is a shift in species that play central roles in these mutualistic networks. Whereas in less forested landscapes the species in the overall network and those playing central roles are mainly those that use fruits occasionally (90% for both the overall network and those playing central roles), in more forested landscapes these groups are replaced by obligate frugivores (28% for the whole network and 43% for species playing central roles). In fact, studies showed that, as habitat amount increases, there is a sort of compensatory dynamics at the landscape scale, with forest-dependent and obligate frugivores increasing in more forested landscapes, whereas the richness of species that do not depend on forest increases in less forested areas (Morante-Filho et al. 2018). This fact probably results from more plentiful resources for those that depend on them in more forested landscapes, whereas less forested ones offer different types of resources favoring species that do not depend exclusively on fruits. Indeed, as pointed by Vidal et al. (2019), in less forested landscapes (e.g., 30%) mainly thrushes and tanagers remain, whereas species that heavily depend on fruits such as cotingas and toucans occur mainly in areas with more than 60% of habitat at the landscape scale.

Previous studies have shown that obligate and occasional frugivorous species play complementary roles in seed dispersal (Dehling et al. 2021). However, our study contributes to the understanding of how the role of obligate and occasional frugivorous in plant-frugivore networks is reshaped by forest loss. Obligate frugivores have higher dispersal effectiveness than occasional frugivores (Schupp et al. 2010). Also, several obligate species are also large-bodied frugivores, responsible for consuming large number of fruits and dispersing seeds over larger distances (Godínez-Alvarez et al. 2020). Obligate frugivores also contribute more to indirect effects, thus the loss of these species can propagate extinction cascades for the whole network (Pires et al. 2020). Therefore, the loss of obligate frugivores has pervasive effects on mutualistic seed dispersal process, contributing not only with direct interactions, but supporting ecosystem integrity (through centrality) and potentially affecting indirectly multiple species in the network.

CONCLUSIONS

There is a solid body of research showing the negative effects of habitat loss on species richness (Foley et al. 2005, Newbold et al. 2015, Arroyo-Rodríguez et al. 2016, Muylaert et al. 2016, Rocha-Santos et al. 2017, Barnes et al. 2017, Morante-Filho et al. 2018). We extended these findings by unveiling an overlooked component of biodiversity, the loss of species interactions (Valient-Banuet et al. 2015), as well as the non-linear nature of these relationships. As far as we know, this is the first empirical study to evaluate how landscape-scale habitat loss affects the structure and robustness of mutualistic networks and also to show the non-linear effects of habitat loss. These losses have consequences for network structure, such as reduction in mean number of interactions per species and connectance, which means that in less forested areas birds interact with fewer plant species, potentially reducing their long-term persistence. We also showed a replacement of species when habitat is lost. The loss of obligate frugivores species can compromise seed dispersal reducing the number of seeds consumed and seed dispersal distance with potential cascading effects. We did not find effects of habitat loss on bill width and seed diameter, which can indicate that the defaunation of large seed dispersers is occurring even in forested landscapes or that bird species that do not strictly depend on forest compensate the loss of those forest-dependent species maintaining the mean value of bill width in deforested landscapes. Our findings add important information on how habitat loss shapes mutualistic network structure in tropical forest and how seed dispersal process can be impacted.

ACKNOWLEDGMENTS

We are thankful to Renato Augusto Ferreira de Lima for sharing the data from TreeCo, an initiative financed by São Paulo Research Foundation (FAPESP) grant 2013/08722-5. We thanks to Leandro G. Cosmo for helping with Fig. 1. We also thank to Leonardo Casadei, Maria Jucá, Renério Almeida, Gabriel Mello and Dario Sanches, birdwatchers from WikiAves that shared photos for Fig. 3. We are grateful to Debora Rother, Pâmela Friedemann and Leandro G. Cosmo for helpful comments on the manuscript. This study was financed in part by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. PRG thanks CNPq (307134/2017-2), FAPESP (2018/14809-0), and the Royal Society, London (CHL/R1/180156) for financial support. EC thanks CNPq (306373/2018-1).

DATA AVAILABILITY STATEMENT

Data available from the Zenodo Digital Repository <https://doi.org/10.5281/zenodo.6208475> (Bonfim et al 2022).

REFERENCES

Almeida-Neto, M. et al. 2007. On nestedness analyses: rethinking matrix temperature and anti-nestedness. - Oikos 116: 716–722.

Almeida-Neto, M. et al. 2008. A Consistent Metric for Nestedness Analysis in Ecological Systems: Reconciling Concept and Measurement. - Oikos 117: 1227–1239.

Andrén, H. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. - Oikos 71: 355–366.

Arroyo-Rodríguez, V. et al. 2016. Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot. - Biol.

Conserv. 198: 84–92.

Barlow, J. et al. 2018. The future of hyperdiverse tropical ecosystems. - Nature 559: 517–526.

Barnes, A. D. et al. 2017. Direct and cascading impacts of tropical land-use change on multi-trophic biodiversity. - Nat. Ecol. Evol. 1: 1511–1519.

Barton, K. 2015. Package "MuMIn".Model selection and model averaging based on information criteria. R package version 1.15.11.

Bascompte, J. and Jordano, P. 2007. Plant-animal mutualistic networks: The architecture of biodiversity. - Annu. Rev. Ecol. Evol. Syst. 38: 567–593.

Bascompte, J. et al. 2003. The nested assembly of plant-animal mutualistic networks. - Proc. Natl. Acad. Sci. 100: 9383–9387.

Bello, C. et al. 2017. ATLANTIC-FRUGIVORY: a plant–frugivore interaction data set for the Atlantic Forest. - Ecology 98: 1729.

Bonfim, F. C. G. et al. 2021. Landscape composition is the major driver of the taxonomic and functional diversity of tropical frugivorous birds. - Landsc. Ecol. 36: 2535–2547.

Bonfim et al. 2022. Data from: Habitat loss shapes the structure and species roles in mutualistic seed dispersal networks. Zenodo Digital Repository, <https://doi.org/10.5281/zenodo.6208475>.

Burnham KP and Anderson D. R.2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Burin, G. et al. 2021. Macroevolutionary stability predicts interaction patterns of species in seed dispersal networks. - Science 372: 733–737.

Cazetta, E. et al. 2019. Forest amount, not structure, influences fruit removal of two pioneer species in Atlantic forest remnants. - Biotropica 51: 674-681.

Constantino, P. A. L. 2016. Deforestation and hunting effects on wildlife across Amazonian indigenous lands. – Ecology and Society 21:3.

de Assis Bomfim, J. et al. 2018. Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. - Ecography (Cop.). 41: 1899–1909.

Dáttilo, W. and Rico-gray, V. 2018. Ecological Networks in the Tropics: An Integrative Overview of Species Species-Rich Habitats on Earth (W Dáttilo and V Rico-Gray, Eds.). - Springer International Publishing.

Dehling, D. M. 2018. The structure of ecological networks. Pages 29-42 in W. Dáttilo and V. Rico-Gray. Ecological networks in the tropics. Springer International Publishing.

Dehling, D. M. et al. 2021. Specialists and generalists fulfil important and complementary functional roles in ecological processes. - Funct. Ecol. 35: 1810–1821.

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

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

Emer, C. et al. 2020. Seed dispersal networks in tropical forest fragments: Area effects, remnant species, and interaction diversity. - Biotropica 52: 81–89.

Estes, J. A. et al. 2011. Trophic downgrading of planet earth. - Science 333: 301–306.

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

Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. - J. Biogeogr. 40: 1649–1663.

Filgueiras, B. K. C. 2021. Winner–Loser species replacements in human-modified landscapes. - Trends Ecol. Evol. 36: 545–555.

Foley, J. A. et al. 2005. Global consequences of land use. - Science 309: 570–574.

Fortuna, M. A. and Bascompte, J. 2006. Habitat loss and the structure of plant-animal mutualistic networks. - Ecol. Lett. 9: 281–286.

Fortuna, M. A. et al. 2013. Habitat loss and the disassembly of mutalistic networks. - Oikos 122: 938–942.

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

Galetti, M. et al. 2021. Causes and consequences of large-scale defaunation in the Atlantic Forest. Pages 297-324 in M. C. M. Marques and C. E. V. Grelle. The Atlantic Forest. Springer.

Gardner, M. R. and Ashby, W. R. 1970. Connectance of large dynamic (Cybernetic) systems: Critical values for stability. - Nature 228: 784.

Gaston, K. J. and Blackburn, T . M. 1995. Birds, body size, and the threat of extinction. - Phil. Trans. R. Soc. Lond. B 205:212.

Godínez-Alvarez, H. et al. 2020. Are large frugivorous birds better seed dispersers than medium- and small-sized ones? Effect of body mass on seed dispersal effectiveness. - Ecol. Evol. 10: 6136–6143.

Guimarães, P. R. 2020. The structure of ecological networks across levels of organization. - Annu. Rev. Ecol. Evol. Syst. 51: 433–460.

Guimarães, P. R. et al. 2017. Indirect effects drive coevolution in mutualistic networks. - Nature 550: 511–514.

Heleno, R. H. et al. 2020. Scientists’ warning on endangered food webs. - Web Ecol. 20: 1–10.

Hesselbarth, M. H. K. et al. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. - Ecography (Cop.). 42: 1648–1657.

Jackson, H. B. and Fahrig, L. 2015. Are ecologists conducting research at the optimal scale? - Glob. Ecol. Biogeogr. 24: 52–63.

Jordano, P. 1987. Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance, Dependence Asymmetries, and Coevolution. - Am. Nat. 129: 657–677.

Katz, L. 1953. A new status index derived from sociometric analysis. - Psychometrika 18: 39–43.

Laurindo, R. S., R. L. M. Novaes, J. Vizentin-Bugoni, and R. Gregorin. 2019. The effects of habitat loss on bat-fruit networks. - Biodiver. Conserv. 28:589–601.

Levin, S. A. 1992. The problem of pattern and scale in ecology. - Ecology 73: 1943–1967.

Lima, M. M. and Mariano-Neto, E. 2014. Extinction thresholds for Sapotaceae due to forest cover in Atlantic Forest landscapes. - For. Ecol. Manage. 312: 260–270.

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

McConkey, K.R. and G. O'Farrill. 2015. Cryptic function loss in animal populations. - Trends Ecol. Evol. 30, 182-189.

McConkey, K.R. and G. O'Farrill. 2016. Loss of seed dispersal before the loss of seed dispersers. - Biol. Conser. 201: 38–49.

Mello, M. A. R. et al. 2015. Keystone species in seed dispersal networks are mainly determined by dietary specialization. - Oikos 124: 1031–1039.

Memmott, J. et al. 2004. Tolerance of pollination networks to species extinctions. - Proc. R. Soc. B Biol. Sci. 271: 2605–2611.

Menke, S. et al. 2012. Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. - Oikos 121: 1553–1566.

Morante-Filho, J. C. et al. 2015. Birds in anthropogenic landscapes: The responses of ecological groups to forest loss in the Brazilian Atlantic forest. - PLoS One 10: 1–18.

Morante-Filho, J. C. et al. 2018. Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. - Ecol. Appl. 28: 2024–2032.

Morante-Filho, J. C. et al. 2021. Landscape composition is the strongest determinant of bird occupancy patterns in tropical forest patches. Landscape Ecology 36: 105–117.

Morrison, B. M. L. et al. 2020. Agricultural intensification drives changes in hybrid network robustness by modifying network structure. - Ecol. Lett. 23: 359–369.

Mueller, T. et al. 2014. Large frugivorous birds facilitate functional connectivity of fragmented landscapes. - J. Appl. Ecol. 51: 684–692.

Muylaert, R. L. et al. 2016. Threshold effect of habitat loss on bat richness in cerrado-forest landscapes. - Ecol. Appl. 26: 1854–1867.

Myers, N. et al. 2000. Biodiversity Hotspots for Conservation Priorities. - Nature 403: 853–858.

Newbold, T. et al. 2015. Global effects of land use on local terrestrial biodiversity. - Nature 520: 45–50.

Oliveira Filho F. J. B., and J. P. Metzger. 2006. Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. - Landscape Ecol 21:1061–1073.

Owens, I. A. F. and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. - PNAS 97: 12144 –12148.

Paine, R. T. 1966. Food Web Complexity and Species Diversity. - Am. Nat. 100: 65–75.

Paradis, E., and K. Schliep. 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. - Bioinformatics 35: 526–528.

Pardini, R. et al. 2010. Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. - PLoS One 5: e13666.

Pires, M. M. et al. 2020. The indirect paths to cascading effects of extinctions in mutualistic networks. - Ecology 101: 1–8.

Purvis, A. et al. 2000. Predicting extinction risk in declining species. - Proc. R. Soc. Lond. B 267:

1947-1952.

Rezende, C. L. et al. 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. - Perspect. Ecol. Conserv. 16: 208–214.

Rigueira, D. M. G. et al. 2013. Forest cover, extinction thresholds and time lags in woody plants (Myrtaceae) in the Brazilian Atlantic Forest: Resources for conservation. - Biodivers. Conserv. 22: 3141–3163.

Rocha-Santos, L. et al. 2017. Functional decay in tree community within tropical fragmented landscapes: Effects of landscape-scale forest cover. - PLoS One 12: 1–18.

Rodrigues, R. C. et al. 2019. ATLANTIC BIRD TRAITS: a data set of bird morphological traits from the Atlantic forests of South America. - Ecology 100: e02647.

Santos, G. G. A. et al. 2012. Contrasting Demographic Structure of Short- and Long-lived Pioneer Tree Species on Amazonian Forest Edges. - Biotropica 44: 771–778.

Schupp, E. W. et al. 2010. Seed dispersal effectiveness revisited: A conceptual review. - New Phytol. 188: 333–353.

Silva, W.P.R., Guimaraes, P., dos Reis, S. F. 2007. Investigating fragility in plant-frugivore networks: a case study for Atlantic Forest. Pages 561-578 in A.J. Dennis, E.W. Schupp, R.J. Green, D.W. Wescott. Seed dispersal: theory and its application in a changing world. Wallingford. Wallingford: CAB International.

Silvertown, J. 1989. The paradox of seed size and adaptation. - Trends Ecol. Evol. 4: 24–26.

Souza, C. M. et al. 2020. Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. - Remote Sens. 12: 2735.

Stanton, M. L. 1984. Seed Variation in Wild Radish : Effect of Seed Size on Components of Seedling and Adult Fitness. - Ecology 65: 1105–1112.

Swift, T. L. and Hannon, S. J. 2010. Critical thresholds associated with habitat loss: A review of the concepts, evidence, and applications. - Biol. Rev. 85: 35–53.

Traveset, A. et al. 2018. Effects of habitat loss on the plant–flower visitor network structure of a dune community. - Oikos 127: 45–55.

Valiente-Banuet, A. and Verdú, M. 2013. Human impacts on multiple ecological networks act synergistically to drive ecosystem collapse. - Front. Ecol. Environ. 11: 408–413.

Valiente-Banuet, A. et al. 2015. Beyond species loss: The extinction of ecological interactions in a changing world. - Funct. Ecol. 29: 299–307.

Vanbergen, A. J. et al. 2017. Network size, structure and mutualism dependence affect the propensity for plant–pollinator extinction cascades. - Funct. Ecol. 31: 1285–1293.

Vidal, M. M. et al. 2019. Predicting the non-linear collapse of plant–frugivore networks due to habitat loss. - Ecography (Cop.). 42: 1765–1776.

Wilman, H. et al. 2014. EltonTraits 1 . 0 : Species-level foraging attributes of the world ’ s birds and mammals. - Ecology 95: 2027.

SUPPLEMENTARY MATERIALS

Appendix S1. Supporting Methods

Non-linear models

We constructed four non-linear models to describe the relationship between forest cover and network descriptors. A quadratic relationship could be observed because fragmentation can increase at intermediate levels of forest cover (i.e., more edge density or number of patches) (Fahrig 2017). Thus, a quadratic relationship between network structure and habitat amount would result from a combined effect of fragmentation and habitat amount. A power law model describes a relationship where at low or high levels of forest cover, network metrics increase or decrease rapidly with small changes in forest cover. This type of relationship is consistent with Andren's proposed threshold (Andrén 1994), with a fast but not abrupt decay of species richness below a certain threshold. We predicted that this pattern could happen with frugivore-plant interactions. This model was constructed by assuming that the network structure (F(x)) changes with fragmentation (x) following a power law, $F(x) = ax^b$, in which *a* is a scaling constant and *b* describes how fast network structure changes with fragmentation (Bolker 2008). We used the function *gnls* from package *nls2* (Grothendieck 2013) to fit the model and used the brute-force algorithm to find the best initial values based on a list with combined values for *a* and *b*. Finally, we constructed a piecewise model that models an abrupt decay in values of the response variable in relation to the predictor variable. To fit this model, we constructed a linear model and used the function *segmented* from package *segmented* (Muggeo 2017) to find the breakpoints. This model is also consistent with Andrén's proposed threshold, but assumes a qualitative and abrupt change in network patterns. Finally, we included a null model that depicts no effect of forest cover on the response variable.

CITED LITERATURE

Andrén, H. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. Oikos 71:355–366.

Bolker, B. 2008. Ecological models and data in R. Princeton University Press, Princeton, New Jersey, US.

Fahrig, L. 2017. Ecological Responses to Habitat Fragmentation Per Se. Annual Review of Ecology, Evolution, and Systematics 48:1–23.

Grothendieck, G. 2013. nls2: Non-linear Regression with Brute Force. R package version 0.2, http://CRAN.R-project.org/package=nls2

Muggeo, M. V. M. R. 2017. Package "segmented". Biometrika 58:525–34.

TABLES

Table S1: Description of the 25 seed-dispersal networks used in this study. The year represents when the study started. Sampling effort are reported in hours.

Network*	Latitude	Longitude	Year	Sampling effort	Number of Plants	Number of Birds	Number of Iinteractions
1	-12.9333	-38.4	2009	245	22	17	79
2	-19.7415	-39.9961	1993	543	12	41	103
3	-22.4833	-47.5923	2008	242	8	29	88
4	-25.0513	-48.095	2001	648	42	16	118
5	-22.7653	-53.2583	2009	84	11	31	40
6	-22.7488	-53.2233	2009	168	7	29	41
7	-22.7811	-53.3031	2009	168	5	9	13
8	-22.5532	-42.2805	1997	195	13	45	181
9	-20.75	-42.88	2000	250	25	28	91
10	-22.8237	-47.104	1988	2520	36	29	145
11	-24.3166	-48.4166	1999	1200	71	47	241
12	-24.3047	-48.3647	1999	1200	55	37	150

13	-24.2783	-48.4077	1999	1200	54	43	159
14	-28.2258	-51.1688	1996	168	13	21	54
15	-25.1667	-48.2833	2011	1288	90	67	493
16	-21.7	-43.8833	2004	3178	14	15	45
17	-21.6167	-43.35	2001	1400	19	11	33
18	-22.9433	-46.7499	2002	308	13	48	124
19	-24.1414	-47.974	2013	646	30	63	255
20	-8.9666	-36.05	2007	3600	28	8	41
21	-30.3998	-50.9682	2003	1106	10	17	43
22	-22.7667	-43.6833	2010	103	20	20	59
23	-24.2653	-48.4069	1999	8160	150	76	883
24	-22.5762	-47.5088	2011	646	35	31	165
25	-22.6719	-47.206	2011	565	16	14	35

*References

1. Andrade, P. C. 2011. Interações mutualísticas entre aves frugívoras e plantas em um fragmento urbano de Mata Atlântica, Salvador, BA. Revista Brasileira de Ornitologia 19: 63-73.

2. Argel-de-Oliveira, M. M. 1999. Frugivoria por aves em um fragmento de floresta de restinga no Estado do Espírito Santo, Brasil. PhD Thesis. UNICAMP Campinas.

3. Athiê, S. 2009. Composição da Avifauna e Frugivoria por Aves em Um Mosaico de Vegetação Secundária em Rio Claro, Região Centro-leste de São Paulo. MSc Dissertation. UFSCar São Carlos.

4. Castro, E. R. 2007. Fenologia reprodutiva da palmito Euterpe edulis (Arecaceae) e sua influência na abundância de aves frugívoras na floresta Atlântica. PhD Thesis. UNESP Rio Claro.

5. Castro, S. L. R. 2011. Rede de interações aves-plantas arbóreas em fragmentos de floresta ripária na região noroeste do Paraná Rede de interações aves-plantas arbóreas em fragmentos de floresta ripária na região noroeste do Paraná. PhD Thesis. UEM Maringá.

6. Castro, S. L. R. 2011. Rede de interações aves-plantas arbóreas em fragmentos de floresta ripária na região noroeste do Paraná Rede de interações aves-plantas arbóreas em fragmentos de floresta ripária na região noroeste do Paraná. PhD Thesis. UEM Maringá.

7. Castro, S. L. R. 2011. Rede de interações aves-plantas arbóreas em fragmentos de floresta ripária na região noroeste do Paraná Rede de interações aves-plantas arbóreas em fragmentos de floresta ripária na região noroeste do Paraná. PhD Thesis. UEM Maringá.

8. Correia, J. M. S. (1997). Utilização de espécies frutíferas da Mata Atlântica na alimentação da

avifauna da Reserva Biológica de Poços das Antas, RJ. MSc Dissertation. UNB Brasília.

9. Fadini, R. F. and P. D. de Marco. 2004. Interações entre aves frugívoras e plantas em um fragmento de mata atlântica de Minas Gerais. Ararajuba 12:97–103.

10. Galetti, M. and M. A. Pizo. 1996. Fruit eating by birds in a forest fragment in southeastern Brazil. Ararajuba 4: 71-79.

11. Hasui, É. 2003. Influência da vairação fisionômica da vegetação sobre a composição de aves frugívoras na Mata Atlântica. PhD Thesis. UNICAMP Campinas.

12. Hasui, É. 2003. Influência da vairação fisionômica da vegetação sobre a composição de aves frugívoras na Mata Atlântica. PhD Thesis. UNICAMP Campinas.

13. Hasui, É. 2003. Influência da vairação fisionômica da vegetação sobre a composição de aves frugívoras na Mata Atlântica. PhD Thesis. UNICAMP Campinas.

14. Kindel, A. (1996). Interações entre plantas ornitocóricas e aves frugívoras na Estação Ecológica de Aracuri, Muitos Capões, RS. MSc Dissertation. UFRGS Porto Alegre. MSc

Dissertation. UFRGS Porto Alegre.

15. Machado-de-Souza, T., R. P. Campos, M. Devoto, and I. G. Varassin. 2019. Local drivers of the structure of a tropical bird-seed dispersal network. Oecologia 189:421–433.

16. Manhães, M. A. et al. 2010. Diet of understorey birds in two Atlantic Forest areas of southeast Brazil. Journal of Natural History 44:469–489.

17. Manhães, M. A. et al. 2010. Diet of understorey birds in two Atlantic Forest areas of southeast Brazil. Journal of Natural History 44:469–489.

18. Pizo, M. A. 2004. Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeast Brazil. Ornitologia Neotropical 15:117–126.

19. Rodrigues, S. B. M. 2015. Rede de interações entre aves frugívoras e plantas em uma área de Mata Atlântica do sudesde do Brasil. MSc Dissertation. UFSCar São Carlos.

20. Sarmento, R. et al. 2014. Partitioning of seed dispersal services between birds and bats in a fragment of the Brazilian Atlantic Forest. Zoologia 31:245–255.

21. Scherer, A. et al. 2007. Padrões de interações mutualísticas entre espécies arbóreas e aves frugívoras em uma comunidade de Restinga no. Acta Botanica Brasilica 21:203–212.

22. Silva, R. F. M. 2011. Interações entre plantas e aves frugívoras no Campus da Universidade Federal Rural do Rio de Janeiro. Undergrad

Dissertation. UFRJ Rio de Janeiro.

23. Silva, W. R. et al. 2002. Patterns of fruit – frugivore bird communities of South-Eastern Brazil: implications for conservation. Seed Dispersal and Frugivoty: Ecology, Evolution and Conservation:423–435.

24. Silva, F. R. et al. 2015. The restoration of tropical seed dispersal networks. Restoration Ecology 23:852–860.

25. Silva, F. R., D. Montoya, R. Furtado, J. Memmott, M. A. Pizo, and R. R. Rodrigues. 2015. The restoration of tropical seed dispersal networks. Restoration Ecology 23:852–860.

Table S2: Parameter estimates from generalized additive models from all response variables evaluated in relation to sample size of 25 mutualistic networks in the Brazilian Atlantic Forest.

Response variable	**Estimate**	**Deviance explained (%)**	**p-value**
Robustness	0.703	2.54	0.838
N. bird species	3.434	17.6	<0.01
N. plant species	3.344	46.1	<0.01
N. interactions	4.841	50.2	<0.01
Connectance	0.165	10.2	0.119
N. link per species	1.894	25.8	0.05
Nestedness	-2.341	37.1	<0.01
Bill width	10.106	0.27	0.804
Seed diameter	4.968	32	<0.05

Table S3: Model selection for each response variable in the best scale of effects (Fig. S1). Best models are highlighted in bold. We selected the best model based on Akaike Information Criteria (AIC, see analysis). wAICc = weights of the model; ΔAICc = delta AIC corrected for small sample size.

Response Variable\Model	**Linear**		**Quadratic**		**Power-law**		**Piecewise**		**Null**	
	wAICc	ΔAICc	wAICc	ΔAICc	wAICc	ΔAICc	wAICc	ΔAICc	wAICc	ΔAICc
Robustness	0.39	0	0.12	2.4	0.001	90.5	0.17	1.6	**0.32**	**0.4**
Nº bird species	**0.19**	**2**	0.31	1	-	-	0.5	0	0.001	12.9
Nº plant species	0.03	6.1	**0.70**	**0**	-	-	0.26	2	0.001	21.7
Nº interactions	0.25	0.9	**0.41**	**0**	0.001	16.9	0.34	0.4	0.001	16.6

Connectance	0.13	3.5	0.11	4	-	-	**0.76**	**0**	0.001	116.8
Links by species	**0.41**	**0.2**	0.11	2.7	0.003	9.7	0.45	0	0.009	7.8
NODF	**0.57**	**0**	0.18	2.3	-	-	0.11	3.3	0.14	2.8
Bill width	0.22	1.3	0.43	0	0.07	3.5	0.11	2.8	**0.17**	**1.9**
Seed diameter	0.13	2.2	0.03	4.7	0.16	1.8	0.26	0.8	**0.4**	**0**

Table S4: Bird species showing highest betweenness centrality in 25 seed dispersal networks in the Brazilian Atlantic Forest. FC=forest cover. The numbers inside parentheses means the times a species appeared as one of the five central considering all 25 networks.

FC ≤ 30%	**Frugivory**	**30% < FC ≥ 60%**	**Frugivory**	**FC > 60%**	**Frugivory**
Cacicus chrysopterus (1)	Ocasional	*Tangara cayana* (2)	Obligate	*Carpornis cucullata* (3)	Obligate
Cacicus haemorrhous (1)	Ocasional	*Cyclarhis gujanensis* (1)	Ocasional	*Lipaugus lanioides* (1)	Obligate
Camptostoma obsoletum (1)	Ocasional	*Myiozetetes similis* (1)	Ocasional	*Penelope superciliaris* (1)	Obligate
Chiroxiphia caudata (3)	Ocasional	*Thraupis palmarum* (1)	Ocasional	*Phibalura flavirostris* (1)	Obligate
Chiroxiphia pareola (1)	Ocasional	*Thraupis sayaca* (2)	Ocasional	*Procnias nudicollis* (2)	Obligate
Coereba flaveola (1)	Ocasional	*Turdus leucomelas* (1)	Ocasional	*Pteroglossus bailloni* (1)	Obligate
Conirostrum speciosum (1)	Ocasional	*Turdus rufiventris* (1)	Ocasional	*Ramphastos dicolorus* (1)	Obligate
Cyanerpes cyaneus (1)	Ocasional	*Vireo olivaceus* (1)	Ocasional	*Tangara cyanocephala* (3)	Obligate
Dacnis cayana (2)	Ocasional			*Tangara cyanoptera* (1)	Obligate
Elaenia flavogaster (2)	Ocasional			*Tangara seledon* (2)	Obligate
Empidonomus varius (1)	Ocasional			*Tityra cayana* (2)	Obligate
Euphonia chlorotica (1)	Obligate			*Turdus flavipes* (1)	Obligate
Manacus manacus (1)	Obligate			*Chiroxiphia caudata* (2)	Ocasional
Mionectes rufiventris (1)	Ocasional			*Dacnis cayana* (2)	Ocasional
Myiozetetes similis (2)	Ocasional			*Euphonia pectoralis* (1)	Ocasional
Neopelma chrysolophum (1)	Ocasional			*Habia rubica* (1)	Ocasional
Pachyramphus validus (1)	Ocasional			*Ilicura militaris* (1)	Ocasional

Patagioenas picazuro (1)	Ocasional			*Mionectes rufiventris* (1)	Ocasional
Pitangus sulphuratus (3)	Ocasional			*Myiarchus ferox* (1)	Ocasional
Ramphastos toco (1)	Ocasional			*Myiozetetes similis* (1)	Ocasional
Ramphocelus carbo (3)	Ocasional			*Patagioenas plúmbea* (1)	Ocasional
Saltator similis (2)	Ocasional			*Ramphastos vitellinus* (1)	Ocasional
Tachyphonus coronatus (1)	Ocasional			*Ramphocelus bresilius* (1)	Ocasional
Tangara cayana (2)	Obligate			*Saltator maximus* (1)	Ocasional
Tangara cyanoventris (1)	Ocasional			*Tachyphonus coronatus* (1)	Ocasional
Tangara preciosa (1)	Ocasional			*Tangara desmaresti* (1)	Ocasional
Thraupis sayaca (5)	Ocasional			*Thraupis sayaca* (1)	Ocasional
Thraupis episcopus (1)	Ocasional			*Trogon viridis* (1)	Ocasional
Thraupis palmarum (1)	Ocasional			*Turdus albicollis* (4)	Ocasional
Trichothraupis melanops (3)	Ocasional			*Turdus rufiventris* (2)	Ocasional
Turdus albicollis (3)	Ocasional				
Turdus amaurochalinus (2)	Ocasional				
Turdus flavipes (1)	Obligate				
Turdus leucomelas (4)	Ocasional				
Turdus rufiventris (2)	Ocasional				
Tyrannus melancholicus (2)	Ocasional				
Zonotrichia capensis (1)	Ocasional				

Table S5: Bird species with highest amount of potential indirect effects, T_{out}, found in 25 seed dispersal networks in the Brazilian Atlantic Forest. FC=forest cover. The numbers inside parentheses means the times a species appeared as one of the five contributing to indirect effects considering all 25 networks.

FC≤30	**Frugivory**	**30<FC≤60**	**Frugivory**	**FC>60**	**Frugivory**
Antilophia galeata (1)	Ocasional	*Cyclarhis gujanensis*	Ocasional	*Carpornis cucullata* (3)	Obligate

		(1)			
Ara chloropterus (1)	Ocasional	*Myiozetetes similis* (1)	Ocasional	*Chiroxiphia caudata* (4)	Ocasional
Brotogeris chiriri (1)	Ocasional	*Tangara cayana* (2)	Obligate	*Dacnis cayana* (1)	Ocasional
Cacicus chrysopterus (1)	Ocasional	*Thraupis sayaca* (3)	Ocasional	*Euphonia pectoralis* (2)	Ocasional
Cacicus haemorrhous (1)	Ocasional	*Turdus leucomelas* (2)	Ocasional	*Manacus manacus* (1)	Obligate
Camptostoma obsoletum (1)	Ocasional	*Turdus rufiventris* (1)	Ocasional	*Mionectes rufiventris* (1)	Ocasional
Ceratopipraipra rubrocapilla (1)	Obligate			*Myiozetetes similis* (1)	Ocasional
Chiroxiphia caudata (5)	Ocasional			*Penelope obscura* (1)	Obligate
Cyanerpes cyaneus (1)	Ocasional			*Procnias nudicollis* (1)	Obligate
Dacnis cayana (3)	Ocasional			*Pteroglossus bailloni* (1)	Obligate
Euphonia violácea (1)	Obligate			*Ramphastos dicolorus* (1)	Obligate
Forpus xanthopterygius (1)	Ocasional			*Ramphastos vitellinus* (1)	Ocasional
Manacus manacus (4)	Obligate			*Ramphocelus bresilius* (1)	Ocasional
Mionectes rufiventris (2)	Ocasional			*Saltator maximus* (1)	Ocasional
Myiozetetes similis (2)	Ocasional			*Selenidera maculirostris* (1)	Obligate
Neopelma chrysolophum (1)	Ocasional			*Tachyphonus coronatus* (2)	Ocasional
Pachyramphus validus (1)	Ocasional			*Tangara cyanocephala* (2)	Obligate
Pitangus sulphuratus (3)	Ocasional			*Tangara desmaresti* (1)	Ocasional
Pteroglossus aracari (1)	Obligate			*Tangara seledon* (2)	Obligate
Pteroglossus castanotis (2)	Ocasional			*Thraupis cyanoptera* (1)	Obligate
Ramphocelus carbo (4)	Ocasional			*Thraupis sayaca* (1)	Ocasional
Saltator maximus (1)	Ocasional			*Trichothraupis melanops* (2)	Ocasional
Saltator similis (2)	Ocasional			*Trogon viridis* (1)	Ocasional
Tachyphonus coronatus (2)	Ocasional			*Turdus albicollis* (5)	Ocasional
Tangara cayana (2)	Obligate			*Turdus flavipes* (1)	Obligate
Tangara cyanoventris (1)	Ocasional			*Turdus rufiventris* (1)	Ocasional
Tangara mexicana (1)	Ocasional				
Thraupis sayaca (9)	Ocasional				
Tangara preciosa (1)	Ocasional				
Thraupis episcopus (1)	Ocasional				
Trichothraupis melanops (2)	Ocasional				

Turdus albicolis (4)	Ocasional
Turdus amaurochalinus (1)	Ocasional
Turdus leucomelas (5)	Ocasional
Turdus rufiventris (2)	Ocasional
Tyrannus melancholicus (1)	Ocasional
Zonotrichia capensis (1)	Ocasional

FIGURES

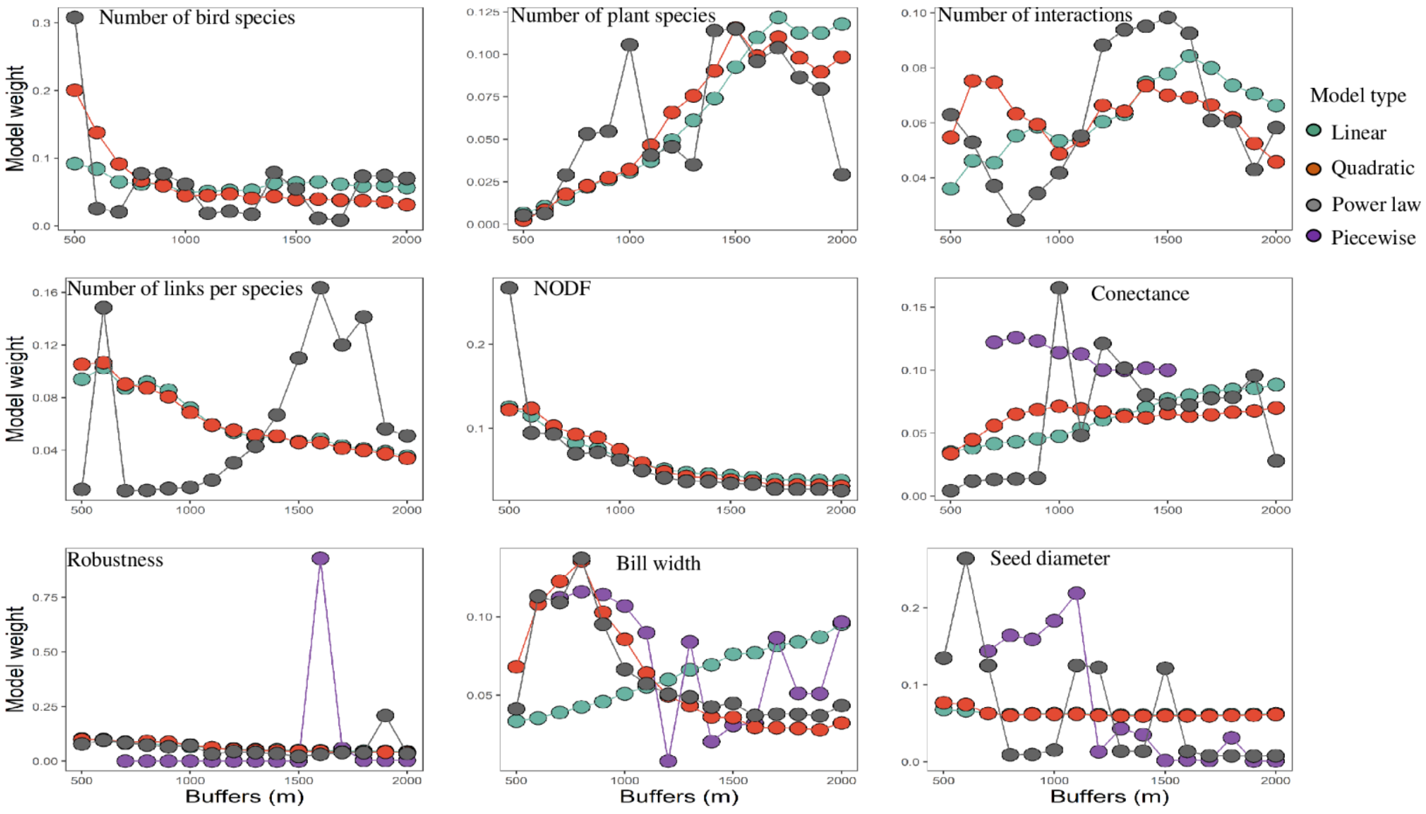

Figure S1. Scale of effects for all response variable included in the analyses. Green circle = linear model; orange circle = quadratic model; purple circle = power law model; gray circle = piecewise model.

CAPÍTULO III

ECOLOGICAL TRAITS AND PHYLOGENY SHAPE THE RESPONSE OF FRUGIVOROUS BIRD ASSEMBLAGES TO LAND-USE CHANGES IN HUMAN-MODIFIED TROPICAL LANDSCAPES

Manuscrito formatado nas normas da revista Perspectives in Ecology and Conservation

Ecological traits and phylogeny shape the response of frugivorous bird assemblages to land-use changes in human-modified tropical landscapes

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ABSTRACT

Understanding how human-modified landscapes can maintain biodiversity is crucial to mitigating the impacts of habitat disturbance in the face of the increasing human pressure on forest ecosystems. Given that responses to disturbances are species-specific, it is pivotal to understand how landscape changes may shape patterns of species persistence (i.e., occurrence), especially for keystone forest species, such as frugivores. Here, we used a comprehensive bird dataset covering the entire Brazilian Atlantic Forest to understand how species richness and individual occurrences of frugivorous birds respond to land-use spatial predictors, and subsequently assess how functional traits and phylogeny modulate these responses. Using Bayesian hierarchical modeling, we found that the richness of frugivorous birds was positively associated with the amount of forest, and negatively with agriculture and pasture amount at the landscape scale. Conversely, species occurrence and functional traits showed positive, negative and neutral responses in relation to the spatial predictors carried by a weak phylogenetic signal. Our study unveils frugivore responses to human-modified landscapes showing that land-use simplification (i.e., the conversion of forest to pasture) has pervasive consequences for species highly dependent on forested areas. In contrast, some generalist species thrive in deforested areas, replacing species sensitive to habitat disturbances. This replacement goes beyond species, also affecting functional traits and translates into a softening of the harmful effects of habitat loss.

Key words: Deforestation, traits, land-use, seed dispersal, Atlantic Forest

INTRODUCTION

Land-use changes, in combination with other anthropogenic pressures such as hunting and overexploitation, comprise the main threats to biodiversity worldwide (Newbold et al., 2019, 2015). The increasing human influence on forests and the conversion of intact forest tracts into agricultural landscapes have altered many of the earth's ecosystems (Lewis et al., 2015; Potapov et al., 2017), with developing countries facing the highest conversion rates. In fact, the conversion of primary forests was one of the main sources of new agricultural lands in the last century (Gibbs et al., 2010). As a result, most of the natural forest ecosystems have turned into human-modified landscapes (Curtis et al., 2018), which ultimately affect species persistence (Morante-Filho et al., 2020; Valente and Betts, 2019).

Species occurrence in modified habitats depends on their tolerance to disturbance (Lindenmayer et al., 2020; Morante-Filho et al., 2020). Indeed, some species thrive in human-modified landscapes as "winners", whereas others perish as "losers" (Filgueiras et al., 2021; McKinney and Lockwood, 1999). In general, the winners in these landscapes are mainly habitat generalist species, whereas losers are mostly composed of species highly sensitive to disturbances and dependent on specific habitat characteristics (Filgueiras et al., 2021; McKinney and Lockwood, 1999). Therefore, land-use effects are not random, negatively affecting species that present specific ecological traits such as large body mass, small home range, and high dependency on natural habitats (Lee and Jetz, 2011; Owens and Bennett, 2000; Andy Purvis et al., 2000).

Functional redundancy (i.e., species that share similar ecological traits performing similar functions (Lawton and Brown, 1993)) and complementarity (i.e., replacement of functionally similar species (Frost et al., 1994; Rosenfeld, 2002)) are mechanisms that structure biological communities and influence ecosystem functioning in human-modified landscapes. While the former has poor evidence (Rosenfeld, 2002), some studies showed that functional complementarity occurs along environmental gradients (Frost et al., 1995). In this sense, the turnover of species sensitive to habitat disturbance with tolerant ones may reduce the loss of ecological functions. In fact, it is also expected that the loss of ecological traits of those sensitive species is compensated by traits of resilient ones. This process, known as compensatory dynamics, has been demonstrated for forest species such as birds (Frishkoff and Karp, 2019; Morante-Filho et al., 2018a) and could also be translated into ecological traits (De Coster et al., 2015; Frost et al., 1995).

Indeed, some studies showed that species' traits modulate their response to land-use intensity, but contrasting responses have so far being found. For example, land-use changes showed negative effects on forest-dependent bird species, especially those primarily frugivores or insectivores (Newbold et al., 2013). In the threatened Brazilian Atlantic Forest, however, habitat loss showed none or positive effects on birds' functional traits, which was explained by the turnover of species exerting the same ecological function or by the replacement of specialists by generalists (De Coster et al., 2015). Yet, traits like small home range size, large body mass, high trophic level, and foraging specialization are the main correlates of extinction risk in human-modified landscapes (Lee and Jetz, 2011; Owens and Bennett, 2000; Andy Purvis et al., 2000). Despite these different findings, some clear trends emerge. For example, large forest frugivorous birds, such as members of Cracidae and Cotingidae families, decline in highly deforested landscapes (Galetti et al., 2013; Vidal et al., 2019). Also, the richness of forest-dependent frugivore species is negatively impacted by the increase of cattle pasture (Bennett et al., 2022; Cabral et al., 2021), whereas these species are positively affected by the increase of native forest cover (Morante-Filho et al., 2018b). Furthermore, the occurrence of forest-dweller birds increased in patches inserted in highly forested landscapes, whereas non-forest birds decreased (Lindenmayer et al., 2020; Morante-Filho et al., 2020).

Yet, it is expected that phylogenetically related species will respond similarly to environmental conditions (i.e., phylogenetic signal) because their niches are conserved over evolutionary timescales (Wiens and Graham, 2005). Previous studies found that altered landscapes lead to a decrease in bird phylogenetic diversity (Frishkoff et al., 2014; Morante-Filho et al., 2018a), with some heterogeneous agricultural areas supporting more evolutionary history than intensive monoculture but less than forest habitats (Frishkoff et al., 2014). Furthermore, the response of species to human disturbance is mediated by a strong phylogenetic signal (Frishkoff et al., 2014). Under this scenario, it is expected that human-modified landscapes act as a strong spatial filter, resulting in a proliferation of disturbance-adapted species and leading to phylogenetic homogenization (Nowakowski et al., 2018).

Frugivorous birds comprise the main group of seed dispersers across the tropics, yet exhibit the greatest extinction rates among birds (Şekercioğlu et al., 2004). Consequently, the loss of frugivores can trigger further extinction cascades (Rogers et al., 2021), disrupting key ecological functions such as seed dispersal (Menezes Pinto et al., 2021; Vidal et al., 2019). Thus, understanding how frugivorous birds respond to land-use change is crucial to foresee ecosystem changes in human-modified landscapes. Here, we evaluate how spatial land use predictors (landscape composition *sensu* Fahrig (2013)) affect the richness and individual occurrence of frugivorous birds in Brazilian Atlantic forest remnants, which is one of the most threatened biodiversity hotspots on Earth (Marques and Grelle, 2021). We also unveil how specific functional traits related to frugivory and phylogenetic signal modulate these responses. We hypothesize negative effects on the richness of frugivorous birds in landscapes presenting low amounts of forest cover and dominated by agricultural areas and pastures (Newbold et al., 2015, 2014). Given that individual responses to spatial predictors are species-specific, we also predict that the individual occurrence of species sensitive to anthropogenic changes will be greatly and positively associated with forest cover, and negatively associated with pasture cover (De Coster et al., 2015; Morante-Filho et al., 2018b). In contrast, we expect that an increase in the proportion of agricultural areas will positively affect habitat-generalist frugivores, but exert a negative effect on forest-specialist frugivorous birds (Bennett et al., 2022; Sekercioglu et al., 2007). We also hypothesize that traits related to frugivory have a detrimental effect on species occurrence patterns (Newbold et al., 2014). Specifically, we presume that bird species more vulnerable to human pressures, such as those presenting greater body mass, low flight capacity, more dependence on fruits, and greater specialization at a foraging stratum, will respond negatively to forest loss and to an increase in anthropogenic land uses, such as pastures and agriculture (Lee and Jetz, 2011; Owens and Bennett, 2000; Andy Purvis et al., 2000). Finally, we expect that phylogenetically related species will respond similarly to the spatial predictors (Wiens and Graham, 2005).

METHODS

Study area and data

We chose the Brazilian Atlantic Forest as our study case (Figure 1), one of the most threatened biodiversity hotspots on Earth. This biome originally covered more than 1.5 million square kilometers ranging from northeast Brazil to Argentina (Marques et al., 2021; Muylaert et al., 2018), but due to the conversion of natural forests into agricultural, urban and industrial land use in addition to the presence of more than 70% of the Brazilian population, less than 30% of its original cover remains (Rezende et al., 2018; Solórzano et al., 2021). The remaining forest remnants are mostly small and isolated from each other, being immersed within degraded matrices, such as pasture and agriculture (Joly et al., 2014; Ribeiro et al., 2009). Despite its intensive history of deforestation and degradation, the Atlantic Forest is home to 830 bird species (Hasui et al., 2018), mostly comprised of frugivorous species.

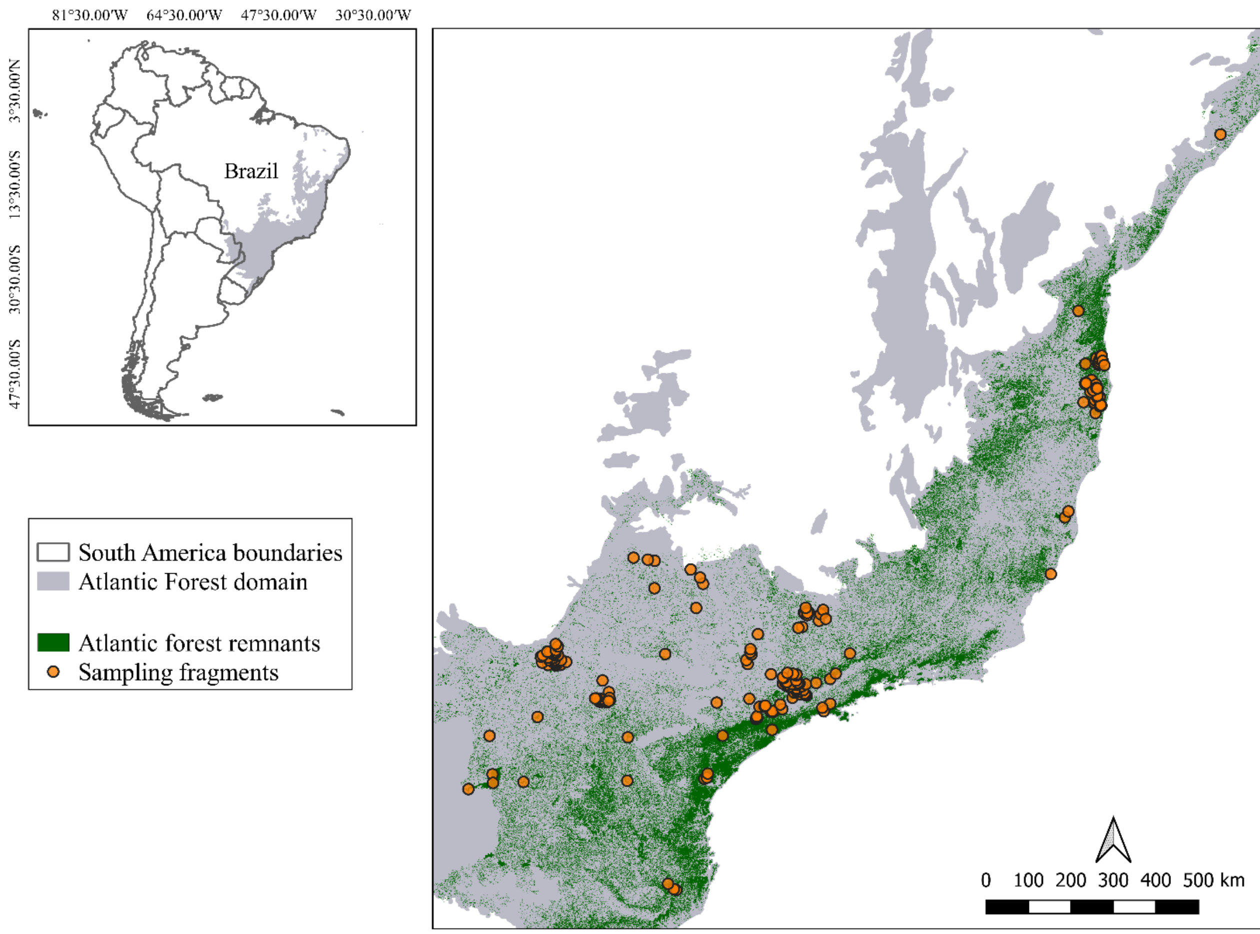


Figure 1: Location of the 194 sampling forest fragments in the Brazilian Atlantic Forest used in this study.

We extracted information on frugivore species occurrence from the largest dataset of birds available for the biome, the ATLANTIC BIRDS (Hasui et al., 2018). From this dataset, we selected only studies that sampled birds using the point count methodology, in order to minimize the bias of using different sampling techniques. In addition, point count is the most effective method for sampling birds in the neotropics, given that it enables both acoustic and visual records and, therefore, detects a wide range of bird species occurring at different vegetation strata (Bibby et al., 1992). As inclusion criteria, all studies should have: (1) explicitly presented the geographic coordinates of the sampled fragments, (2) carried out samplings in natural forest fragments (i.e., we excluded those performed in anthropic habitats such as urban areas), (3) presented a minimum distance of two kilometers among fragments to minimize spatial autocorrelation, (4) collected data from 1985 to date, because our satellite images to calculate landscape predictors do not cover previous years. To see a full description of the study selection criteria, see Bonfim et al. (2021). We also compiled additional information by conducting a comprehensive literature search using both Web of Science and Scopus, using as keywords "bird*" and "Atlantic Forest" in English and Portuguese. We first searched in the title and abstract, and if the study fitted our criteria, we checked the entire paper and supplementary material to verify if the occurrence table and sampling effort were both provided. Our final dataset was composed of 194 forest fragments (153 described in Hassui et al. (2018) and 41 from other studies, Figure S1). Considering that our target group comprises frugivorous species, we classified each species recorded at least in one forest fragment as frugivorous or non-frugivorous, based on its diet composition. According to Wilman et al. (2014), we consider as frugivores those species with a diet composed of at least 50% of fruits (Fleming et al., 1987). Considering all sampling forest fragments, data on a total of 105 frugivorous birds were obtained and used in the subsequent analyses.

Frugivore Occurrence

For each frugivore species, we first determined its natural geographic distribution based on the polygons provided by the International Union for Conservation of Nature (BirdLife International, 2021), coupled with the incidence data from Hassui et al. (2018). We carefully examined the geographic distribution obtained for each species, and whenever geographic range inconsistencies were found, the polygon was revised, and the distribution increased. This step was required given that in some cases, species detection was recorded outside the proposed distribution by IUCN. For each frugivorous species, we subsequently overlapped the revised polygon with the occurrences compiled in our database and assigned [1] (presence) if the species was recorded in a determined forest fragment or [0] (absence) if the species was expected to occur but was not detected.

Ecological traits

For each species, we compiled five traits related to seed dispersal or vulnerability to anthropogenic disturbance: (i) body mass (from Wilman et al. (2014)), which reflects the number of fruits that can be consumed (Schupp et al. 2010) and is one of the main predictors of species extinction (Owens and Bennett 2000); (ii) degree of frugivory (from Wilman et al. (2014)), which is related to the number of visits and fruits consumed by frugivores (Schupp et al., 2010); (iii) hand-wing index (HWI), used as a proxy for flight efficiency and dispersal ability (from (Sheard et al., 2020)). We finally gathered information on foraging strata (from Wilman et al. (2014)), which provides the percentage of foraging time that a species spends in each stratum (ground, understory, mid-high, and canopy).

Landscape predictors

For each forest fragment, we derived three landscape composition predictors - the amount of native forest, pasture, and agriculture, at different spatial scales. We only calculated landscape composition metrics because they are good predictors of bird species richness and occurrence (Fahrig, 2013; Morante-Filho et al., 2020). In particular, landscape composition was more important than configuration in explaining taxonomic and functional diversity of frugivorous birds (Bonfim et al., 2021). To do this, we used a classified satellite image with 30 m resolution freely available for the entire Atlantic Forest by the MapBiomas Project version 5.0 (Souza Jr. et al., 2020). Based on the year each study started, we estimated the percentage of native forest considering different successional stages (class 3), cattle pasture (class 9), and agriculture cover (merging the classes 18, 19, 39, 20, 21, 36, and 41) considering different buffer radii (i.e., 250 m, 500 m, 750 m and 1000 m, and from 1000 m to 5000 m at 500 m intervals) to further assess the best scale of effect. We used these radii to encompass both the best scale found in previous studies with birds in the Atlantic Forest (600 m in Morante-Filho et al. (2018b)) and because frugivorous are mobile species that can travel long distances.

To account for possible confounding effects of climate and topography, we also calculated the mean altitude, mean annual temperature and precipitation for the same radii, except 250 and 500 m because some coordinates resulted in “no data”. We gathered these variables from rasters from the WorldClim database (Fick and Hijmans, 2017) with 1km^2 resolution. Due to the high correlation (r = -0.92) between altitude and mean annual temperature, the later was excluded from the analyses. All metrics were calculated from the fragment central point using the *landscapemetrics* package (Hesselbarth et al. 2019) in R version 4.1 (R Core Team 2021).

Data analysis

We analyzed occurrence data by using Hierarchical Modelling of Species Communities (HMSC; (Ovaskainen et al., 2017; Ovaskainen and Abrego, 2020; Tikhonov et al., 2020)). HMSC is a Bayesian joint species distribution modeling (Warton et al., 2015) that uses hierarchical layers to understand how species responses to environmental covariates depend on species traits and phylogenetic relationships. For the final analysis, we excluded species with less than five occurrences considering all forest fragments because preliminary analyses showed no convergence for these species. Therefore, our global model included 73 frugivorous bird species.

To detect the best scale of effect for each predictor, we first calculated individual models with the presence-absence matrix in relation to the percentage of forest, agriculture, pasture cover, altitude and mean annual precipitation, separately, for each of 12 buffer radii ranging from 250 to 1000 m with 250 m intervals and from 1000 m to 5000 m with 500 m intervals (60 models, 12 for each spatial predictor: see “*spatial predictors*” section). For these models, we also included the sampling effort (log transformed) as co-variable. The Widely Applicable Information Criteria (WAIC, (Watanabe, 2010)) was used to detect the best scale of effect for each landscape variable. WAIC is equivalent to AIC and has the same asymptotic behaviour as Bayes cross-validation and generalization loss (Watanabe, 2010). Choosing the model with the lowest WAIC maximizes the predictive power of the model (Watanabe, 2010). The final model was therefore fitted using the best scale for each variable (Supplementary Table 1).

We used the 'study ID' as the study design in the HMSC because some fragments are nested in the study ID (i.e., studies that sampled more than one sampling site). Additionally, to account for the spatial nature of the study design, we included the coordinates of the sampling fragment at a random level (Ovaskainen and Abrego, 2020; Tikhonov et al., 2020). We used the landscape predictors (percentage of forest, agriculture, pasture, mean altitude and mean annual precipitation calculated in the best scale of effect) as fixed effects (the matrix X of HMSC; see Ovaskainen et al. (2017)). Also, because studies differ in sampling effort, we used this variable (log-transformed) as a fixed term in the model.

We used the hierarchical structure of HMSC to investigate how species traits (body mass, degree of frugivory, HWI, and foraging strata) and phylogenetic relationships modulate species responses to landscape predictors. The phylogenetic data was obtained from a tree derived from birdtree.org online database (Jetz et al., 2012). We used the Hacket source and gathered 1000 possible combinations of trees. We used the function "*MaxCladeCred"* from the package "phangorn" to get a consensus tree and used it in the HMSC as the phylogenetic tree.

We fitted the HMSC model using the R-package Hmsc (Tikhonov et al., 2020) assuming the default prior (Ovaskainen and Abrego, 2020). We sampled the posterior distribution with four Markov Chain Monte Carlo (MCMC), each of which was run with 375,000 iterations, where the first 125,000 were removed as burn-in. The MCMC convergence was examined by whether the potential scale reduction factor was lower than 1.1 (Gelman and Rubin, 1992). We examined the explanatory power of the probit model through the AUC and TJur'R^2 for each species. We quantified the drivers of the structure of frugivore bird assemblages by partitioning the explained variation among fixed and random effects included in the model (i.e., variance partitioning).

RESULTS

The mean frugivore richness was 31 ± 24 (mean ± SD) per forest fragment, ranging from one to 44 species (Figure S1). Three species occurred only in five forest patches (*Pipile jacutinga*, *Antilophia galeata* and *Tangara cyanoventris*), whereas *Turdus rufiventris* and *Euphonia chlorotica* occurred in 118 and 97 fragments (60 and 50% of the fragments), respectively.

Our model evaluating the response of frugivorous bird richness to forest, agriculture, and pasture cover (incuding altitude and annual precipitation as covariates) showed good convergence. The potential scale reduction factor for the β-parameters, which measures the response of species to environmental covariates (Ovaskainen et al 2017), was on average 1.02 ± 0.21 (min = 0.99, max = 5.60), indicating that the MCMC convergence was satisfactory. The model showed a good fit with mean AUC 0.86 ± 0.06 (min = 0.7, max = 1) and the mean explained deviance (Tjur's R^2) 0.28 ± 0.13 (min = 0.06, max = 0.92).

We found that frugivorous birds richness was positively associated with the percentage of forest (100% of posterior support), and negatively related to agriculture and pasture cover (92% and 100% of posterior support, respectively) (Figure 2).

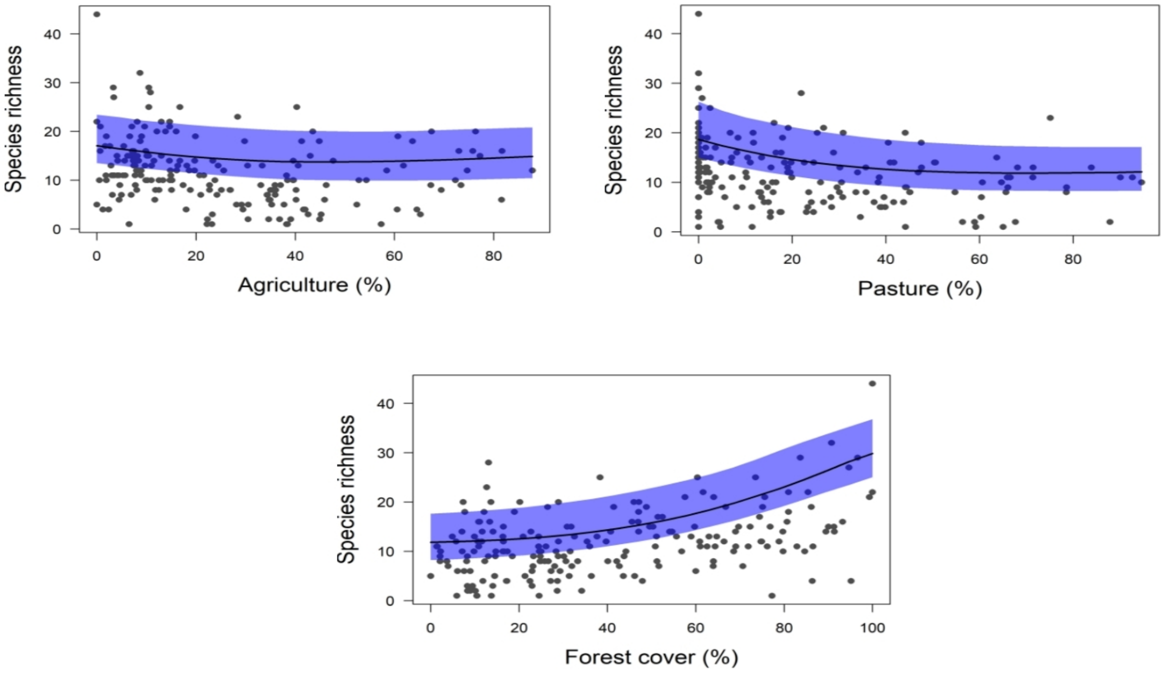


Figure 2. Predicted responses of frugivorous bird richness in relation to the percentage of forest, agriculture, and pasture cover in landscapes located in the Brazilian Atlantic Forest.

Our results on frugivore’s individual responses showed that half of the variance in the models (45.5%) was explained by landscape predictors. In addition, 20.6% was explained by random effects (the nested study design and the coordinates of the forest fragments), 10.2% by sampling effort, 14.8 by altitude and 8.9% by precipitation (Figure 3).

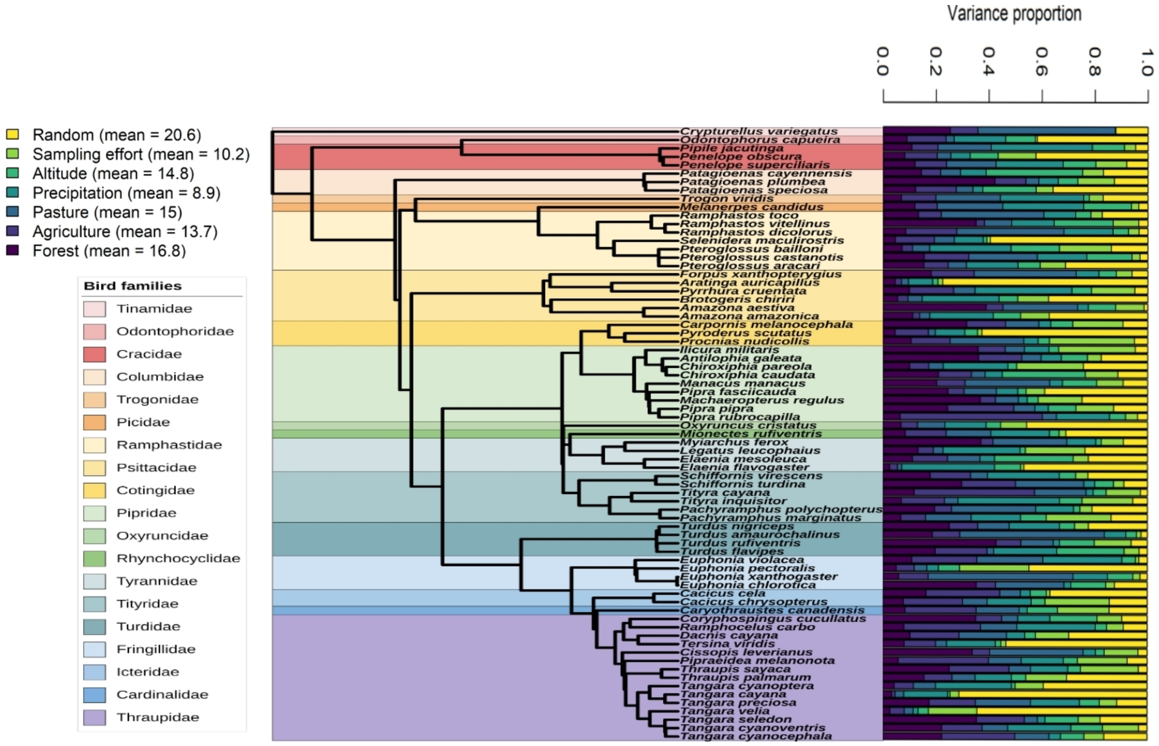


Figure 3. Variance partitioning of each predictor included in the model for each frugivorous bird species. The bars correspond to the explained variance achieved for forest, agriculture, pasture cover, altitude, precipitation, random effects (the nested study design and the coordinates of the forest fragments) and sampling effort on each species. The different colors in the phylogeny represent different bird Families.

Furthermore, a weak phylogenetic signal was identified in the individual responses of frugivorous birds' occurrence to our spatial predictors (ρ = 0.13, 95% CI = 0.09-0.42). Yet, the posterior probability of no phylogenetic signal is Pr(ρ= 0) = 0.44. Most of the species (21 out of 73) responded positively to increasing forest cover, whereas some species from the Ramphastidae, Tyrannidae and Psittacidae families responded negatively. For agriculture cover, the bird response was more scattered, as species from the same clade responded differently. For example, *Ramphastus toco* (Rampahastidae) was negatively affected by increasing agriculture cover, whereas *Pteroglossus bailloni* (Rampahastidae) was positively affected. The same pattern occurs with members from families Turdidae and Thraupidae. On the other hand, most individual responses (20 out of 73) to pasture cover were negative, but also few species were positively affected, such as *Euphonia violacea* and *Patagioenas cayennensis* (Figure 4).

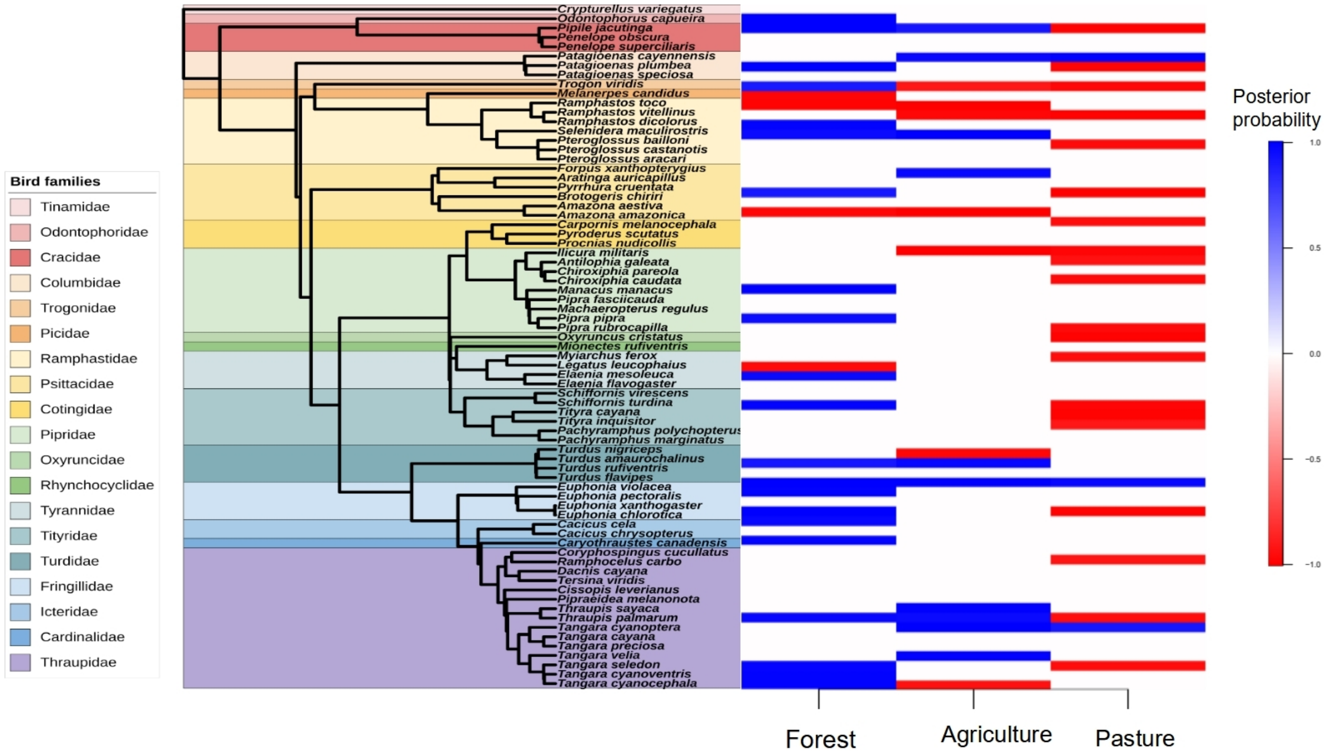


Figure 4: Response of frugivorous birds' occurrence to the amount of forest, agriculture and pasture cover in landscapes located in the Brazilian Atlantic Forest. Red and blue bars mean negative and positive response with ≥ 0.95 posterior probabilities, respectively. The different colors in the phylogeny represent bird Families.

Our findings also evidenced a low influence of ecological traits explaining species responses to landscape predictors (Figure 5). In fact, only 4, 4 and 5% of the proportion of the variance in the species' responses to forest, agriculture, and pasture cover, respectively, were explained by life-history traits. The traits also respond differently to the spatial predictors. Specifically, considering ≥ 95 posterior probability, forest cover had positive effects on species that forage on midhigh stratum but showed negative effects on species with great frugivory degree . The increase in agriculture cover also showed negative effects on species with high frugivory degree. On the other hand, increasing pasture cover had negative effects on species with great body mass.

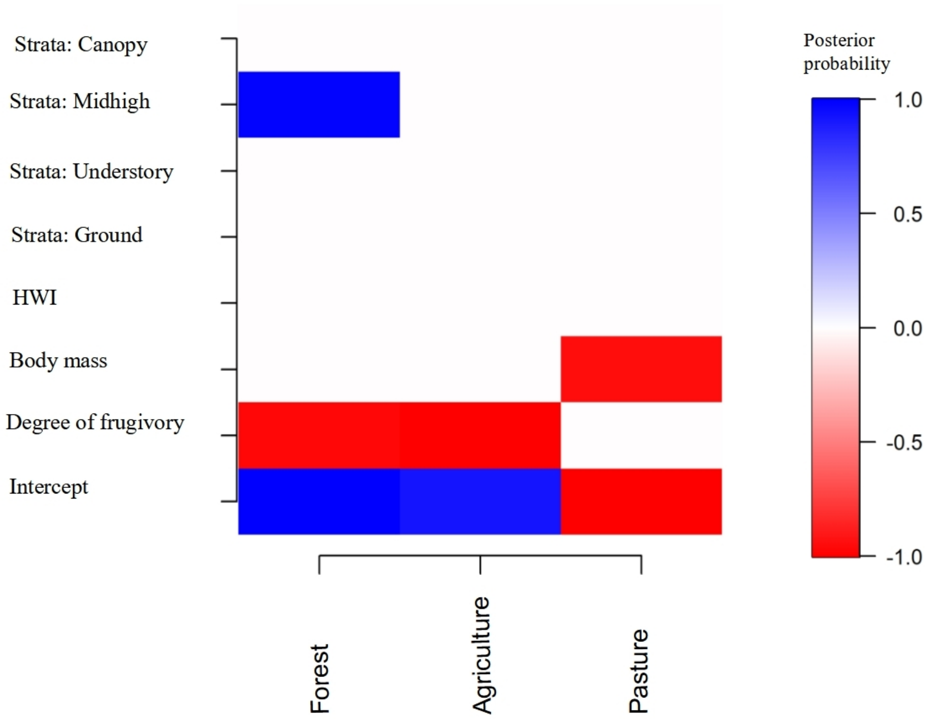


Figure 5: Influence of functional traits of frugivorous birds on the response to the spatial predictors (forest, agriculture, and pasture cover). Red and blue bars mean negative and positive responses, with ≥ 95 posterior probabilities, indicating that species with high trait values respond positively or negatively, respectively.

DISCUSSION

Our study unveils the influence of landscape spatial predictors explaining the richness and occurrence patterns of frugivorous birds in forest remnants of the threatened Brazilian Atlantic Forest, in addition to revealing how functional traits and phylogenetic relationships modulate these responses. Our findings show a trend of increasing richness of frugivorous birds in more forested landscapes and a decrease in landscapes dominated by agriculture and cattle pastures. However, individual species' responses to spatial predictors were highly variable. While species' occurrence in general increase with increasing forest and decreasing pasture cover, the response to agriculture cover widely varies. We also observed that closely related species respond differently to landscape predictors, indicating a weak phylogenetic signal in species response to land use changes. Lastly, the influence of frugivorous traits on species' response to the amount of each land use type also varies. Thus, our results covering the entire Atlantic Forest shed light on understanding how the most important seed disperser group across the tropical region - the frugivorous birds - respond to land-use changes in human-modified landscapes.

As predicted, we found a positive association between frugivorous richness and the amount of forest cover, while agriculture and pasture exerted a negative effect. This pattern is consistent with previous findings showing that forest loss has negative impacts on frugivorous birds (Bregman et al., 2016; Coelho et al., 2016; Kupsch et al., 2019; Morante-Filho et al., 2018b, 2015). In fact, the conversion of undisturbed primary forest to pasture or mechanized agriculture was recently showed to have pervasive effects on birds (Nunes et al., 2022). For example, the richness of forest-dependent frugivorous birds increased in forest fragments surrounded by forested landscapes in the Atlantic Forest (Morante-Filho et al., 2018b). Also, frugivores in the Amazon decreased in highly intensified landscapes, mostly composed of arable agriculture and pasture (Bregman et al., 2016).

We also showed a winner-loser response of frugivorous species to the spatial predictors. For example, 28% of frugivorous birds increase their occurrence as forest cover increase in the landscape, whereas 5% of frugivorous species decreased their occurrence in the same scenario, considering the 95% posterior probability. On the other hand, individual responses to increasing pasture cover were mostly negative (27% of species responded negatively, whereas 4% responded positively, considering 95% posterior probability), which means that frugivore species are sensitive to more intensified land use (Bregman et al., 2016). This negative response possibly reflects the fact that most frugivores cannot cross open matrices given that reduced resource availability and higher predation risk (Da Silva et al., 1996). Still, few species responded positively to pasture cover, such as *Turdus flavipes* and *Patagioenas cayennensis*. These species are associated with open areas, and can be favored by deforestation thriving in these landscapes. This variation in frugivore responses to forest and pasture cover corroborates previous studies showing that some species thrive in forested landscapes, whereas others perish (Lindenmayer et al., 2020; Macchi et al., 2019; Morante-Filho et al., 2020). Furthermore, the winners in deforested areas are mainly habitat and diet generalist species. Our study evidenced that forest loss or the increase in pasture cover is a pervasive threat to frugivorous birds, since the occurrence of species decrease in these scenarios. Furthermore, individual response to agriculture cover varied widely, 13% of species responding positively and 9% responding negatively. For example, *Ramphastus vitellinus* and *Trogon* viridis responded negatively, while *Thraupis sayaca* and *Patagioenas* cayenennsis responded positively to increasing agriculture cover. This means that some species are benefited by the increase in agriculture cover, which reflect dietary, microclimatic and nesting resources use is this land-cover type (Sekercioglu et al., 2007).

We observed a weak phylogenetic signal in frugivore responses to landscape predictors. This suggests that the co-occurrence of bird species in human-modified landscapes is not determined by phylogenetic relationship (Nowakowski et al., 2018; Wiens and Graham, 2005). Yet, human-altered habitats filter species' occurrence, where some generalist clades thrive leading to phylogenetic homogenization (Nowakowski et al., 2018). In our study, species from the same family tended to respond differently to the amount of forest, agriculture, and pasture cover. For example, *Ramphastus toco* and *R. dicolorus*, both Ramphastidae, responded negatively and positively, respectively, to forest cover. Whereas, *Turdus nigriceps* and *T. Amaurochalinus,* both Turdidae, responded negatively and positively, respectively, to agriculture cover. These patterns indicate that life history can be preserved even in human-altered habitats.

Our study evidenced that ecological traits can shape the response of frugivorous birds to spatial predictors. Specifically, increasing forest and agriculture cover showed negative effects on species with greater degree of frugivory. On one hand, this is contrary to our expectation since increasing forest cover also increases fruit biomass (Pessoa et al., 2017). This could be explained because frugivorous complement their diet with other resources (Wilman et al., 2014) perhaps not provided in more forested areas. On the other hand, increasing agriculture cover is expected to decrease fruit availability, therefore decreasing the main resource (i.e., fruits) for frugivores. Also, species that spend more time on the midhigh stratum are positively affected by forest cover. In this foraging strata predominate large-bodied species such as Cracidae, Ramphastidae and Cotingidae, which are among the most sensitive to deforestation (Galetti et al., 2013; Vidal et al., 2019), which possibly reflect resource availability. Yet, species with large bodies also decreased their occurrence in less forested landscapes. This is in accordance to our hypotheses and means that the conversion of native habitat in more intensified land use is a pervasive threat for large bodied frugivorous.

CONCLUSION

By evaluating the responses of frugivorous birds, the most important seed disperser group in the entire Atlantic Forest, we took advantage of a Bayesian hierarchical modeling approach to go beyond previous finds and unveil how human-modified landscapes affect the richness and individual occurrence of frugivorous birds and how the traits related to seed dispersal and phylogeny modulate these responses. Our findings reveal that increasing proportion of cattle pasture or decreasing forest cover at the landscape scale is a pervasive threat to frugivorous birds, as the overall and individual species occurrence decreased in forest fragments embedded within this land use type. Also, these responses are carried by a weak phylogenetic signal, which indicates that phylogenetically related species respond differently to land-use change. Moreover, we found a winner-loser (Filgueiras et al., 2021) response in relation to forest, agriculture and pasture cover, where species that thrive in deforested landscapes are mainly generalist and opportunistic ones. This replacement of species also spreads to traits softening the effects of habitat loss.

We call attention to this scenario because the quality of the function is species-specific, even if a species replaces another in less forested landscapes, the service provided by loser species could not be replaced. Further studies could investigate the consequences of this species replacement for ecosystem services, such as the quality of seed dispersal service provided by the winners. Therefore, the remaining frugivores in these landscapes would not guarantee the quality of seed dispersal services, with consequences for the regeneration of this threatened tropical forest.

REFERENCES

Bennett, R.E., Sillett, T.S., Rice, R.A., Marra, P.P., 2022. Impact of cocoa agricultural intensification on bird diversity and community composition. Conserv. Biol. 36, 1–10. https://doi.org/10.1111/cobi.13779

Bonfim, F.C.G., Dodonov, P., Cazetta, E., 2021. Landscape composition is the major driver of the taxonomic and functional diversity of tropical frugivorous birds. Landsc. Ecol. 36, 2535–2547. https://doi.org/10.1007/s10980-021-01266-y

Bregman, T.P., Lees, A.C., MacGregor, H.E.A., Darski, B., de Moura, N.G., Aleixo, A., Barlow, J., Tobias, J.A., 2016. Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proc. R. Soc. B Biol. Sci. 283, 20161289. https://doi.org/10.1098/rspb.2016.1289

Cabral, J.P., Faria, D., Morante-Filho, J.C., 2021. Landscape composition is more important than local vegetation structure for understory birds in cocoa agroforestry systems. For. Ecol. Manage. 481, 118704. https://doi.org/10.1016/j.foreco.2020.118704

Coelho, M.T.P., Raniero, M., Silva, M.I., Hasui, É., 2016. The effects of landscape structure on functional groups of Atlantic forest birds. Wilson J. Ornithol. 128, 520–534. https://doi.org/10.1676/1559-4491-128.3.520

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science (80-.). 361, 1108–1111. https://doi.org/10.1126/science.aau3445

Da Silva, J.M.C., Uhl, C., Murray, G., 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. Conserv. Biol. 10, 491–503.

https://doi.org/10.1046/j.1523-1739.1996.10020491.x

De Coster, G., Banks-Leite, C., Metzger, J.P., 2015. Atlantic forest bird communities provide different but not fewer functions after habitat loss. Proc. R. Soc. B Biol. Sci. 282, 1–8. https://doi.org/10.1098/rspb.2014.2844

Fahrig, L., 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. J. Biogeogr. 40, 1649–1663. https://doi.org/10.1111/jbi.12130

Fick, S.E. and R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology. 37, 4302-4315.

Filgueiras, B.K.C., Peres, C.A., Melo, F.P.L., Leal, I.R., Tabarelli, M., 2021. Winner–Loser Species Replacements in Human-Modified Landscapes. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2021.02.006

Fleming, T.H., Breitwisch, R., Whitesides, G.H., 1987. Patterns of Tropical Vertebrate Frugivore Diversity. Annu. Rev. Ecol. Syst. 18, 91–109. https://doi.org/10.1146/annurev.es.18.110187.000515

Frishkoff, L.O., Karp, D.S., 2019. Species-specific responses to habitat conversion across scales synergistically restructure Neotropical bird communities. Ecol. Appl. 29, 1–14. https://doi.org/10.1002/eap.1910

Frishkoff, L.O., Karp, D.S., M'Gonigle, L.K., Mendenhall, C.D., Zook, J., Kremen, C., Hadly, E.A., Daily, G.C., 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. Science (80-.). 345, 1343–1346. https://doi.org/10.1126/science.1254610

Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., 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 (80-.). 340, 1086–1090. https://doi.org/10.1126/science.1233774

Gelman, A., Rubin, D.B., 1992. Inference from Iterative Simulation Using Multiple Sequences. Stat.

Sci. 7, 457–472. https://doi.org/https://www.jstor.org/stable/pdf/2246093

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc. Natl. Acad. Sci. U. S. A. 107, 16732–16737. https://doi.org/10.1073/pnas.0910275107

Hasui, É., Metzger, J.P., Pimentel, R.G., Silveira, L.F., Bovo, A.A. d. A., Martensen, A.C., Uezu, A., Regolin, A.L., Bispo de Oliveira, A., Gatto, C.A.F.R., Duca, C., Andretti, C.B., Banks-Leite, C., Luz, D., Mariz, D., Alexandrino, E.R., de Barros, F.M., Martello, F., Pereira, I.M. d. S., da Silva, J.N., Ferraz, K.M.P.M. d. B., Naka, L.N., dos Anjos, L., Efe, M.A., Pizo, M.A., Pichorim, M., Gonçalves, M.S.S., Cordeiro, P.H.C., Dias, R.A., Muylaert, R. d. L., Rodrigues, R.C., da Costa, T.V.V., Cavarzere, V., Tonetti, V.R., Silva, W.R., Jenkins, C.N., Galetti, M., Ribeiro, M.C., 2018. ATLANTIC BIRDS: a data set of bird species from the Brazilian Atlantic Forest. Ecology 99, 497. https://doi.org/10.1002/ecy.2119

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. Nature 491, 444–448. https://doi.org/10.1038/nature11631

Joly, C.A., Metzger, J.P., Tabarelli, M., 2014. Experiences from the Brazilian Atlantic Forest: Ecological findings and conservation initiatives. New Phytol. 204, 459–473. https://doi.org/10.1111/nph.12989

Kupsch, D., Vendras, E., Ocampo-Ariza, C., Batáry, P., Motombi, F.N., Bobo, K.S., Waltert, M., 2019. High critical forest habitat thresholds of native bird communities in Afrotropical agroforestry landscapes. Biol. Conserv. 230, 20–28. https://doi.org/10.1016/j.biocon.2018.12.001

Lee, T.M., Jetz, W., 2011. Unravelling the structure of species extinction risk for predictive conservation science. Proc. R. Soc. B Biol. Sci. 278, 1329–1338. https://doi.org/10.1098/rspb.2010.1877

Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. Science (80-.). https://doi.org/10.1126/science.aaa9932

Macchi, L., Baumann, M., Bluhm, H., Baker, M., Levers, C., Grau, H.R., Kuemmerle, T., 2019. Thresholds in forest bird communities along woody vegetation gradients in the South American Dry Chaco. J. Appl. Ecol. 56, 629–639. https://doi.org/10.1111/1365-2664.13342

Marques, M.C.M., Grelle, C.E. V, 2021. The Atlantic Forest, The Atlantic Forest. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-55322-7

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: A few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14, 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Menezes Pinto, Í., Emer, C., Cazetta, E., Morante-Filho, J.C., 2021. Deforestation Simplifies Understory Bird Seed-Dispersal Networks in Human-Modified Landscapes. Front. Ecol. Evol. 9. https://doi.org/10.3389/fevo.2021.640210

Morante-Filho, J.C., Arroyo-Rodríguez, V., de Andrade, E.R., Santos, B.A., Cazetta, E., Faria, D., 2018a. Compensatory dynamics maintain bird phylogenetic diversity in fragmented tropical landscapes. J. Appl. Ecol. 55, 256–266. https://doi.org/10.1111/1365-2664.12962

Morante-Filho, J.C., Arroyo-Rodríguez, V., Pessoa, M. de S., Cazetta, E., Faria, D., 2018b. Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. Ecol. Appl. 28, 2024–2032. https://doi.org/10.1002/eap.1791

Morante-Filho, J.C., Benchimol, M., Faria, D., 2020. Landscape composition is the strongest determinant of bird occupancy patterns in tropical forest patches. Landsc. Ecol. 6. https://doi.org/10.1007/s10980-020-01121-6

Morante-Filho, J.C., Faria, D., Mariano-Neto, E., Rhodes, J., 2015. Birds in anthropogenic landscapes: The responses of ecological groups to forest loss in the Brazilian Atlantic forest. PLoS One 10, 1–18. https://doi.org/10.1371/journal.pone.0128923

Muylaert, R.L., Vancine, M.H., Bernardo, R., Oshima, J.E.F., Sobral-Souza, T., Tonetti, V.R., Niebuhr, B.B., Ribeiro, M.C., 2018. A note on the territorial limits of the Atlantic forest.

Oecologia Aust. 22, 302–311. https://doi.org/10.4257/oeco.2018.2203.09

Newbold, T., Adams, G.L., Robles, G.A., Boakes, E.H., Ferreira, G.B., Chapman, A.S.A., Etard, A., Gibb, R., Millard, J., Outhwaite, C.L., Williams, J.J., 2019. Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being. Emerg. Top. Life Sci. 3, 207–219. https://doi.org/10.1042/ETLS20180135

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324

Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Şekercioğlu, Ç.H., Alkemade, R., Booth, H., Purves, D.W., 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proc. R. Soc. B Biol. Sci. 280. https://doi.org/10.1098/rspb.2012.2131

Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Şekercioğlu, Ç.H., Joppa, L., Alkemade, R., Purves, D.W., 2014. Functional traits, land-use change and the structure of present and future bird communities in tropical forests. Glob. Ecol. Biogeogr. 23, 1073–1084. https://doi.org/10.1111/geb.12186

Nowakowski, A.J., Frishkoff, L.O., Thompson, M.E., Smith, T.M., Todd, B.D., 2018. Phylogenetic homogenization of amphibian assemblages in human-altered habitats across the globe. Proc. Natl. Acad. Sci. U. S. A. 115, E3454–E3462. https://doi.org/10.1073/pnas.1714891115

Nunes, C.A., Berenguer, E., França, F., Ferreira, J., Lees, A.C., Louzada, J., Sayer, E.J., Solar, R., Smith, C.C., Aragão, L.E.O.C., Braga, D. de L., de Camargo, P.B., Cerri, C.E.P., de Oliveira, R.C., Durigan, M., Moura, N., Oliveira, V.H.F., Ribas, C., Vaz-de-Mello, F., Vieira, I., Zanetti, R., Barlow, J., 2022. Linking land-use and land-cover transitions to their ecological impact in the Amazon. Proc. Natl. Acad. Sci. 119, 1–9. https://doi.org/10.1073/pnas.2202310119

Ovaskainen, O., Abrego, N., 2020. Joint Species Distribution Modelling with Applications in R. Cambridge University Press. https://doi.org/10.1017/9781108591720

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., Abrego, N., 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. Ecol. Lett. 20, 561–576. https://doi.org/10.1111/ele.12757

Owens, I.P.F., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. Proc. Natl. Acad. Sci. U. S. A. 97, 12144–12148. https://doi.org/10.1073/pnas.200223397

Pessoa MS, Rocha-Santos L, Talora DC, Faria D, Mariano-Neto E, Hambuckers A, Cazetta E (2017b) Fruit biomass availability along a forest cover gradient. Biotropica. 49,45–55.

Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S., Esipova, E., 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Sci. Adv. 3, 1–14. https://doi.org/10.1126/sciadv.1600821

Purvis, Andy, Agapow, P.M., Gittleman, J.L., Mace, G.M., 2000. Nonrandom extinction and the loss of evolutionary history. Science (80-.). 288, 328–330. https://doi.org/10.1126/science.288.5464.328

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. R. Soc. B Biol. Sci. 267, 1947–1952. https://doi.org/10.1098/rspb.2000.1234

Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., Metzger, J.P., Strassburg, B.B.N., Tabarelli, M., Fonseca, G.A., Mittermeier, R.A., 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspect. Ecol. Conserv. 16, 208–214.

https://doi.org/10.1016/j.pecon.2018.10.002

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Rogers, H.S., Donoso, I., Traveset, A., Fricke, E.C., 2021. Cascading Impacts of Seed Disperser Loss on Plant Communities and Ecosystems. Annu. Rev. Ecol. Evol. Syst. 52, 641–666. https://doi.org/10.1146/annurev-ecolsys-012221-111742

Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98, 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x

Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Seed dispersal effectiveness revisited: A conceptual review. New Phytol. 188, 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x

Şekercioğlu, Ç.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystem consequences of bird declines. Proc. Natl. Acad. Sci. 101, 18042–18047. https://doi.org/10.1073/pnas.0408049101

Sekercioglu, C.H., Loarie, S.R., Oviedo Brenes, F., Ehrlich, P.R., Daily, G.C., 2007. Persistence of forest birds in the Costa Rican agricultural countryside. Conserv. Biol. 21, 482–494. https://doi.org/10.1111/j.1523-1739.2007.00655.x

Sheard, C., Neate-Clegg, M.H.C., Alioravainen, N., Jones, S.E.I., Vincent, C., MacGregor, H.E.A., Bregman, T.P., Claramunt, S., Tobias, J.A., 2020. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. Nat. Commun. 11. https://doi.org/10.1038/s41467-020-16313-6

Souza Jr., C.M., Z. Shimbo, J., Rosa, M.R., Parente, L.L., A. Alencar, A., Rudorff, B.F.T., Hasenack, H., Matsumoto, M., G. Ferreira, L., Souza-Filho, P.W.M., de Oliveira, S.W., Rocha, W.F., Fonseca, A. V., Marques, C.B., Diniz, C.G., Costa, D., Monteiro, D., Rosa, E.R., Vélez-Martin, E., Weber, E.J., Lenti, F.E.B., Paternost, F.F., Pareyn, F.G.C., Siqueira, J. V., Viera, J.L., Neto, L.C.F., Saraiva, M.M., Sales, M.H., Salgado, M.P.G., Vasconcelos, R., Galano, S., Mesquita, V.

V., Azevedo, T., 2020. Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. Remote Sens. 12, 2735. https://doi.org/10.3390/rs12172735

Tikhonov, G., Opedal, Ø.H., Abrego, N., Lehikoinen, A., de Jonge, M.M.J., Oksanen, J., Ovaskainen, O., 2020. Joint species distribution modelling with the r-package Hmsc. Methods Ecol. Evol. 11, 442–447. https://doi.org/10.1111/2041-210X.13345

Valente, J.J., Betts, M.G., 2019. Response to fragmentation by avian communities is mediated by species traits. Divers. Distrib. 25, 48–60. https://doi.org/10.1111/ddi.12837

Vidal, M.M., Banks-Leite, C., Tambosi, L.R., Hasui, É., Develey, P.F., Silva, W.R., Guimarães, P.R., Metzger, J.P., 2019. Predicting the non-linear collapse of plant–frugivore networks due to habitat loss. Ecography (Cop.). 42, 1765–1776. https://doi.org/10.1111/ecog.04403

Warton, D.I., Blanchet, F.G., O'Hara, R.B., Ovaskainen, O., Taskinen, S., Walker, S.C., Hui, F.K.C., 2015. So Many Variables: Joint Modeling in Community Ecology. Trends Ecol. Evol. 30, 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Watanabe, S., 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. J. Mach. Learn. Res. 11, 3571–3594.

Wiens, J.J., Graham, C.H., 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36, 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

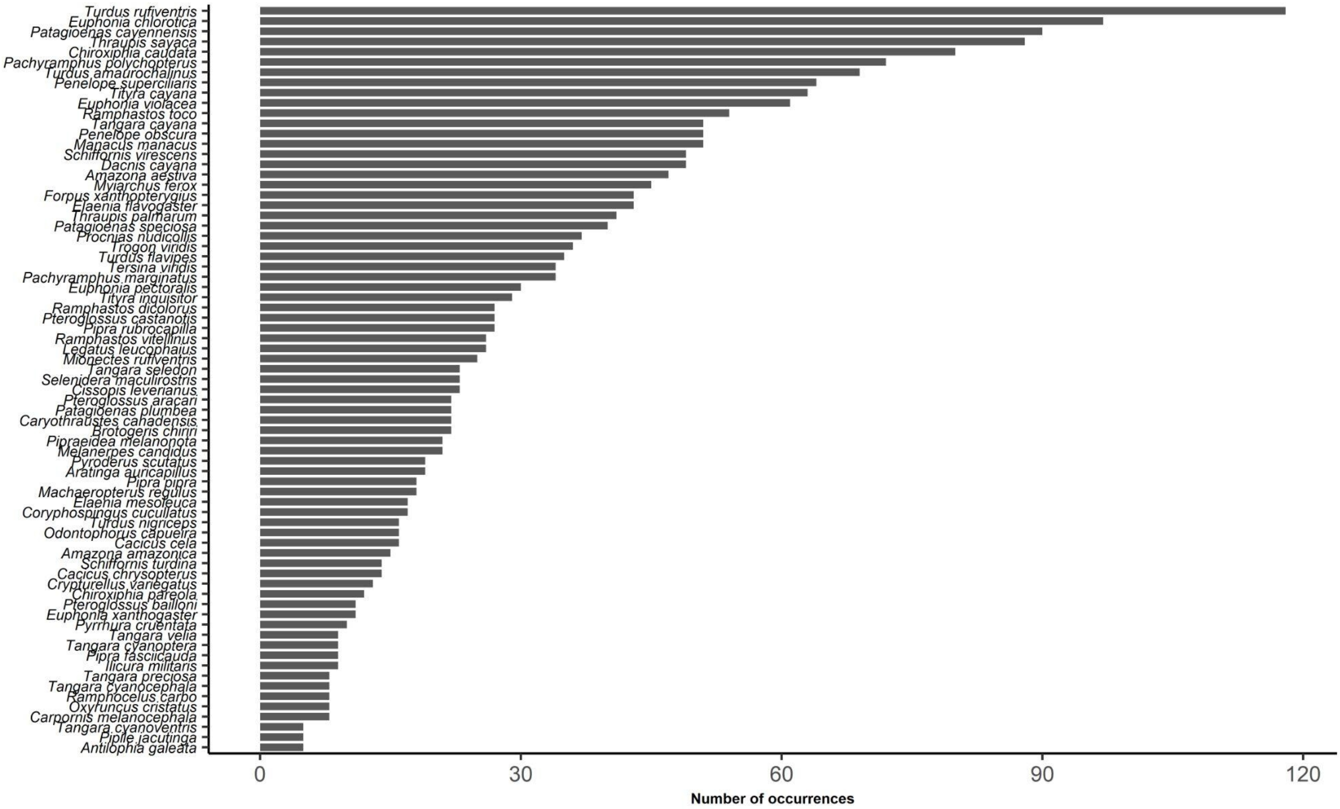
Wilman, H., J., B., J., S., C., de L.R., M., R., W, J., 2014. EltonTraits 1 . 0 : Species-level foraging attributes of the world ' s birds and mammals. Ecology 95, 2027.

Supplementary material

Table S1: Results of the Widely Applicable Information Criteria (WAIC) for the Hierarchical Modeling of Species Communities (HMSC) over the response of frugivorous birds in relation to forest, agriculture, and pasture cover in different radius from the central point. The best scales are highlighted in bold.

Radius (m)/ Variable	Forest cover	Agriculture cover	Pasture cover	Altitude	Bio1	Bio12
250	22.27	22.41	22.66			
500	22.06	22.46	22.59			
750	23.03	22.41	22.83	**22.14**	22.53	22.28
1000	21.97	22.53	**22.45**	22.31	22.24	22.30
1500	21.77	22.54	22.81	22.56	22.55	22.29
2000	21.74	22.56	22.82	22.51	22.65	22.26
2500	21.73	22.54	23.11	22.48	22.38	22.29
3000	21.67	22.48	22.85	22.32	22.69	22.33
3500	21.69	22.35	22.82	22.17	**22.00**	22.21
4000	21.67	22.45	22.71	22.53	22.47	22.23
4500	21.71	22.34	22.92	22.48	22.42	**22.20**
5000	**21.62**	**22.33**	23.16	22.29	22.33	22.54

Figure S1: Number of occurrences recorded for each frugivore species in 195 forest fragments in the Brazilia Atlantic Forest.


Turdus rufiventris
Euphonia chlorotica
Patagioenas cayennensis
Thraupis sayaca
Chiroxiphia caudata
Pachyramphus polychopterus
Turdus amaurochalinus
Penelope superciliaris
Tityra cayana
Euphonia violacea
Ramphastos toco
Tangara cayana
Penelope obscura
Manacus manacus
Schiffornis virescens
Dacnis cayana
Amazona aestiva
Myiarchus ferox
Forpus xanthopterygius
Elaenia flavogaster
Thraupis palmarum
Patagioenas speciosa
Procnias nudicollis
Trogon viridis
Turdus flavipes
Tersina viridis
Pachyramphus marginatus
Euphonia pectoralis
Tityra inquisitor
Ramphastos dicolorus
Pteroglossus castanotis
Pipra rubrocapilla
Ramphastos vitellinus
Legatus leucophaius
Mionectes rufiventris
Tangara seledon
Selenidera maculirostris
Cissopis leverianus
Pteroglossus aracari
Patagioenas plumbea
Caryothraustes canadensis
Brotogeris chiriri
Pipraeidea melanonota
Melanerpes candidus
Pyroderus scutatus
Aratinga auricapillus
Pipra pipra
Machaeropterus regulus
Elaenia mesoleuca
Coryphospingus cucullatus
Turdus nigriceps
Odontophorus capueira
Cacicus cela
Amazona amazonica
Schiffornis turdina
Cacicus chrysopterus
Crypturellus variegatus
Chiroxiphia pareola
Pteroglossus bailloni
Euphonia xanthogaster
Pyrrhura cruentata
Tangara velia
Tangara cyanoptera
Pipra fasciicauda
Ilicura militaris
Tangara preciosa
Tangara cyanocephala
Ramphocelus carbo
Oxyruncus cristatus
Carpornis melanocephala
Tangara cyanoventris
Pipile jacutinga
Antilophia galeata
0
30
60
90
120
Number of occurrences

CONCLUSÃO GERAL

Neste trabalho, nós mostramos os efeitos de modificações na estrutura da paisagem sobre a diversidade taxonômica, funcional, traços relacionados à dispersão de sementes, ocorrência individual das aves frugívoras e estrutura das redes de interações mutualísticas entre aves e plantas na Mata Atlântica. No primeiro capítulo, nós mostramos que a composição da paisagem é a principal preditora da diversidade taxonômica e funcional das aves frugívoras. No entanto, o aumento da cobertura florestal afeta positivamente a diversidade taxonômica, enquanto a diversidade funcional é afetada negativamente. Por outro lado, a interação entre composição e configuração da paisagem afetaram os traços funcionais de diferentes formas. Dessa forma, nossos resultados evidenciam que a quantidade de habitat na paisagem é um importante filtro ambiental para os frugívoros e pode atuar sinergisticamente com a fragmentação do habitat selecionando os traços que sobressaem em paisagens antropizadas.

No segundo capítulo, nós mostramos que a perda de floresta em escala da paisagem tem efeito negativo na estrutura das redes de interações frugívoro-planta na Mata Atlântica, exceto para o aninhamento. Além disso, mostramos que mudanças na cobertura florestal selecionam as espécies centrais ou contribuindo para efeitos indiretos na Mata Atlântica. Especificamente, nossos resultados demonstraram que a perda de floresta tem efeitos negativos e não lineares sobre o número de plantas, interações e conectância e lineares sobre o número de aves e links por espécie. Além disso, mostramos que em áreas com baixa cobertura florestal as espécies que desempenham papéis centrais ou que contribuem mais para efeitos indiretos são os frugívoros ocasionais, enquanto em áreas com alta cobertura florestal essas espécies são substituídas pelos frugívoros obrigatórios. Esses resultados evidenciam que a perda de habitat tem um profundo impacto nas relações mutualística e atua como um filtro sobre as espécies importantes para as redes de interações.

No terceiro capítulo, nós mostramos que a resposta individual das espécies e dos traços funcionais variam em função da quantidade de floresta, agricultura e pasto na paisagem. Nossos resultados mostraram que algumas espécies, principalmente as generalistas de habitat, são afetadas negativamente pela quantidade de floresta e agricultura, enquanto espécies dependentes de floresta, em geral, são afetadas positivamente. Por outro lado, em geral, o aumento na quantidade de pasto tem efeitos negativos para a ocorrência dos frugívoros. Além disso, mostramos que a resposta das espécies exibe um fraco sinal filogenético, o que mostra que a ocorrência dos frugívoros em paisagens modificadas pelo homem não é determinada pela filogenia. Ainda, mostramos que os traços exibem diferentes respostas à modificação na paisagem. Além disso, nós mostramos uma substituição de espécies em relação aos preditores espaciais, onde algumas espécies prosperam com a perda de habitat enquanto outras perecem.

Os resultados desta tese evidenciam que estratégias de conservação bem planejadas devem levar em consideração a quantidade e configuração do habitat na paisagem para manter a diversidade de espécies, funções ecossistêmicas e interações entre as espécies. Tendo em vista que uma paisagem ideal deve conter pelo menos 40% de habitat imerso em matrizes amigáveis e com corredores de habitat (ARROYO-RODRÍGUEZ et al., 2020), nossos achados clamam para a urgente restauração da Mata Atlântica como estratégia para manter sua riqueza de espécies, e consequentemente os serviços ecossistêmicos, haja vista o atual cenário de desmatamento desse bioma. Além disso, espécies generalistas de habitat são beneficiadas com o desmatamento, dessa forma, é preciso avaliar se o papel desempenhado por essas espécies supre o das espécies especialistas.

REFERÊNCIAS BIBLIOGRÁFICAS

ARROYO-RODRIÍGUEZ, V. et al. Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot. **Biological Conservation**, v. 198, p. 84–92, 2016.

ARROYO-RODRIÍGUEZ, V. et al. Designing optimal human-modified landscapes for forest biodiversity conservation. **Ecology Letters**, v. 23, 1404-1420, 2020.

BASCOMPTE, J. et al. The nested assembly of plant-animal mutualistic networks. **Proc. Natl. Acad. Sci.**, v. 100, p. 9383–9387, 2003.

BOVO, A.A.A. et al. Habitat fragmentation narrows the distribution of avian functional traits associated with seed dispersal in tropical forest. **Perspectives in Ecology and Conservation**, v. 16, p. 90–96, 2018.

BUTCHART, S.H.M. et al. Global Biodiversity: Indicators of Recent Declines. **Science**, v.328, p.1164-1168, 2010.

CARRARA, M. et al. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. **Biological Conservation**, v. 184, p. 117–126, 2015.

COELHO, M.T.P. et al. The effects of landscape structure on functional groups of Atlantic forest birds. **Wilson Journal of Ornithology**, v. 128, p. 520–534, 2016.

CURTIS, P.G. et al. Classifying drivers of global forest loss. **Science**, v. 361, p. 1108–1111, 2018.

DE ASSIS BOMFIM, J. et al. Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. **Ecography**, v. 41, p. 1899–1909, 2018.

DEAN, W. With Broadax and Firebrand: The destruction of the Brazilian Atlantic Forest. University of California Press, California, 1996.

De Coster, G.; Banks-Leite, C.; Metzger, J.P. Atlantic forest bird communities provide different but not fewer functions after habitat loss. **Proc. R. Soc.** B, v. 282, 20142844, 2016.

DUNNING, J.B.; DANIELSON, B.J.; PULLIAM, H.R. Ecological processes that affect populations in complex landscapes. **Oikos**, v. 65, p. 169–175, 1992.

EMER, C. et al. Seed dispersal networks in tropical forest fragments: Area effects, remnant species, and interaction diversity. **Biotropica**, v. 52, p. 81–89, 2020.

EWERS, R.M.; DIDHAM, R.K. Confounding factors in the detection of species responses to habitat fragmentation. **Biological Reviews**, v. 81, p. 117–142, 2006.

FAHRIG, L. Ecological responses to habitat fragmentation per se. **Annu Rev Ecol Evol Syst**, v. 48, p. 1–23, 2017.

FAHRIG, L. Rethinking patch size and isolation effects: the habitat amount hypothesis. **Journal of Biogeography**, v. 40, p. 1649–1663, 2013.

FAHRIG, L. et al. Effects of habitat fragmentation on biodiversity. **Biological Conservation**, v. 230, p. 179-186, 2019.

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

FILGUEIRAS, B.K.C. et al. Winner–Loser Species Replacements in Human-Modified Landscapes. **TREE**, v. 36, p. 545-555, 2021.

GALÁN-ACEDO, C. et al. A global assessment of primate responses to landscape structure. **Biological Reviews**, v. 94, p. 1605–1618, 2019.

GALETTI, M. et al. Functional extinction of birds drives rapid evolutionary changes in seed size. **Science**, v. 340, p. 1086-1090, 2013.

JOLY, C.A.; METZGER, J.P.; TABARELLI, M. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. **New Phytologist**, v. 204, p. 459-473, 2014.

HADDAD, N.M. et al. Habitat fragmentation and its lasting impact on Earth's ecosystems. **Science Advances,** v.1, p.1–10, 2015.

HATFIELD, J.H.; HARRISON, M.L.K.; BANKS-LEITE, C. Functional diversity metrics: how they are affected by landscape change and how they represent ecosystem functioning in the tropics. **Current Landscape Ecology Reports**, v. 3, p. 35-42, 2018.

JETZ, W. et al. The global diversity of birds in space and time. **Nature**, v. 491, p. 444-448, 2012.

KISSLING, W. D. et al. The global distribution of frugivory in birds. **Global Ecol. Biogeogr.** v. 18, p. 150–162, 2009.

LAURANCE, W.F.; SAYER, J.; CASSMAN, K.G. Agricultural expansion and its impacts on tropical nature. **Trends in Ecology & Evolution**, v. 29, n. 2, p. 107-116, 2014.

LEE, T.M.; JETZ, W. Unravelling the structure of species extinction risk for predictive conservation science. **Proc. R. Soc. B**, v. 278, p. 1329–1338, 2011.

MARTENSEN, A.C. et al. Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. **Conservation Biology**, v. 26, p. 1100–111, 2012.

MATUOKA, M.A.; BENCHIMOL, M.; MORANTE-FILHO, J.C. Tropical Forest loss drives divergent patterns in functional diversity of forest and non-forest birds. **Biotropica**, v. 52, p. 738-748, 2020.

MCKINNEY, M.L.; LOCKWOOD, J.L. Biotic homogenization: a few winners replacing many losers in the next mass extinction. **TREE**, v. 14, p. 450-453, 1999.

MCCONKEY, K.R.; O'FARRILL, G. Loss of seed dispersal before the loss of seed dispersers. **Biological Conservation**, v. 201, p. 38–49, 2016.

MERCKX, T. et al. Habitat amount, not patch size and isolation, drives species richness of macro-moth communities in countryside landscapes. **Journal of Biogeography**, v. 46, p. 956–967, 2019.

MITTERMEIER, R.A. et al. **Global biodiversity conservation: the critical role of hotspots**, in: ZACHOS, F.E.; HABEL, J.C. (Eds.), Biodiversity hotspots: distribution and protection of conservation priority areas. Springer, 3–22. 2011.

MORANTE-FILHO, et al. Birds in anthropogenic landscapes: the responses of ecological groups to forest loss in the brazilian atlantic forest. **PLoS ONE**, v. 10, n. 6, p. 1-18, 2015.

MORANTE-FILHO, et al. Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. **Ecological Applications**, v. 0, p. 1–9, 2018.

MORANTE-FILHO, et al. Compensatory dynamics maintain bird phylogenetic diversity in fragmented tropical landscapes. **J Appl Ecol.**, v. 55, p. 256–266, 2018.

MORANTE-FILHO, J.C.; BENCHIMOL, M.; FARIA, D. Landscape composition is the strongest determinant of bird occupancy patterns in tropical forest patches. **Landscape ecology**, v. 36, p. 105–117, 2021.

MYERS, N. et al. Biodiversity hotspots for conservation priorities. **Science**, v. 403, p. 853-858, 2000.

NEWBOLD, T. et al. Functional traits, land-use change and the structure of present and future bird communities in tropical forests. **Global Ecology and Biogeography**, v. 23, p. 1073–1084, 2014.

NEWBOLD, T. et al. Global effects of land use on local terrestrial biodiversity. **Nature**, v. 520, p. 45-50, 2015.

OWENS, I.P.F.; BENNETT, P.M. Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. **PNAS**, v. 97, n. 22, 12144–12148, 2000.

Pessoa, M. S. et al. Deforestation drives functional diversity and fruit quality changes in a tropical tree assemblage. **Perspect Plant Ecol Evol Syst**, v. 28, p. 78–86, 2017.

PETCHEY, O.L.; GASTON, K.J. Functional diversity: back to basics and looking forward. **Ecology Letters**, v. 9, p. 741–758, 2006.

PINTO, I. M. et al. Deforestation simplifies understory bird seed-dispersal networks in human-modified landscapes. **Front. Ecol. Evol.**, v. 9, p. 640210, 2021.

PURVYS, A. et al. Nonrandom extinction and the loss of evolutionary history. **Science**, v.288, p. 328-330, 2000.

REZENDE, C.L. et al. From hotspot to hopespot: an opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation, v. 16, p. 208-214, 2018.

RIBEIRO, M.C. et al. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, v. 142, p. 1141–1153, 2009.

ROCHA-SANTOS, L. et al. The loss of functional diversity: A detrimental influence of landscape-scale deforestation on tree reproductive traits. **Journal of Ecology**, v. 108, p. 212-223, 2020.

ŞEKERCIOĞLU, Ç.H.; DAILY, G.C. EHRLICH, P.R. Ecosystem consequences of bird declines. **PNAS**, v. 101, n. 52, p. 18042–18047, 2004.

VALENTE, J.J.; BETTS, M.G. Response to fragmentation by avian communities is mediated by species traits. **Diversity and Distributions**, v. 25, p. 48–60, 2019.

VALIENTE-BANUET, A. et al. Beyond species loss: the extinction of ecological interactions in a changing world. **Functional Ecology**, v. 29, p. 299–307, 2015.

VIDAL, M.M. et al. Predicting the non-linear collapse of plant–frugivore networks due to habitat loss. **Ecography**, v. 42, p. 1765-1776, 2019.

WENNY, D.G. et al. The need to quantify ecosystem services provided by birds. **The Auk**, v. 128, n. 1, p. 1-14, 2011.