



UNIVERSIDADE  
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HELON SIMÕES OLIVEIRA

**DIVERSIDADE FUNCIONAL DE COMUNIDADES DE AVES  
FLORESTAIS EM RESPOSTA A GRADIENTES TEMPORAIS  
E ESPACIAIS NA MATA ATLÂNTICA**

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2023

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Tese apresentada ao Programa de Pós-graduação em Ciências Biológicas da Universidade Estadual de Londrina - UEL, como requisito parcial para a obtenção do título de Doutor em Ciências Biológicas (Biodiversidade e Conservação de Habitats Fragmentados).

Orientador: Prof. Dr. Luiz dos Anjos

Londrina  
2023

Ficha de identificação da obra elaborada pelo autor, através do Programa de Geração Automática do Sistema de Bibliotecas da UEL

O48d Oliveira, Helon Simões.  
Diversidade funcional de comunidades de aves florestais em resposta a gradientes temporais e espaciais na Mata Atlântica / Helon Simões Oliveira. - Londrina, 2023.  
112 f.

Orientador: Luiz dos Anjos.  
Tese (Doutorado em Ciências Biológicas) - Universidade Estadual de Londrina, Centro de Ciências Biológicas, Programa de Pós-Graduação em Ciências Biológicas, 2023.  
Inclui bibliografia.

1. Diversidade funcional - Tese. 2. Dinâmica comunitária - Tese. 3. Ocupação de nicho - Tese. 4. Regras de assembleia - Tese. I. dos Anjos, Luiz. II. Universidade Estadual de Londrina. Centro de Ciências Biológicas. Programa de Pós-Graduação em Ciências Biológicas. III. Título.

CDU 574

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Londrina, 03 de março de 2023.

## **AGRADECIMENTOS**

Agradeço, em primeiro lugar, a Deus, pelas oportunidades que me proporcionou ao longo de minha carreira acadêmica e pelas pessoas e instituições listadas a seguir.

Aos meus pais, Helena S. Alves e Araclides Oliveira, por me prover as bases necessárias para minha carreira.

À minha amada esposa, Agnes Giovanna T. A. e Oliveira, por me apoiar incondicionalmente em meus projetos; por me aturar em todos os momentos em que eu queria lhe dar aulas sobre diversidade funcional; nunca hesitar em fazer o possível para me ajudar, enfrentando todas as dificuldades ao meu lado. Sem ela essa trajetória teria sido totalmente diferente ou mesmo não teria existido. Muito obrigado!

Aos meus sogros, Angela M. Araujo e Gil Araujo, pelo incentivo e por acreditarem em minha capacidade de crescer.

Ao meu orientador, Prof. Dr. Luiz dos Anjos, por não me tratar como um aluno, mas sim como um pesquisador; por acreditar em mim e me proporcionar oportunidades ímpares; por ter ido até Aracaju-SE ser meu avaliador na defesa de mestrado; por me confiar dados de extrema importância ecológica e arduamente obtidos ao longo da última década; por todas as noites que saímos para comer ou tomar nossa cerveja Weiss; pelas nossas conversas descontraídas, assim como, por ouvir minhas angústias pessoais e se importar com comigo; por se fazer meu amigo. Muito obrigado, Luiz!

Aos amigos, Marcelo Jardim, Matheus Tavares e Carlos Araújo, por terem aberto suas casas para me hospedar em minhas muitas viagens para Londrina e Foz do Iguaçu. Muito obrigado pelos ótimos momentos juntos.

À Universidade Estadual de Londrina e seus professores pelas diversas oportunidades ao longo do meu doutorado e por contribuírem para o enriquecimento do meu conhecimento durante as disciplinas que cursei na UEL.

À Pró-Reitoria de Pesquisa e Pós-graduação e ao Prof. Dr. Fernando Jerep, por todo apoio e tratamento humanizado durante as dificuldades financeiras encontradas durante o primeiro ano de meu doutorado.

Ao Instituto Chico Mendes de Conservação da Biodiversidade e seus Analistas Ambientais: Carlos Alberto de O. M. Junior (*in memoriam*) e Antonio Guilherme C. da Silva, responsáveis pela Reserva Biológica das Perobas; Rosane Nauderer, Thais Oliveira e Apolinio N. S. Rodrigues, responsáveis pelo Parque Nacional do Iguaçu, pelas autorizações de pesquisa (21879-2 e 24483, respectivamente) e por todo apoio e facilitações durante as realizações das amostragens em campo realizadas pelo Dr. Luz dos Anjos, que perduram por mais de uma década.

Ao Museu de Zoologia da Universidade de São Paulo (MZUSP) e ao curador das Coleções Ornitológicas, Luís Fábio Silveira, pelo acesso e permissão para medir espécimes de aves.

Às Dra. Gabriela Menezes Bochio, Dra. Barbara Rocha Arakaki Lindsey, Dra. Larissa Corsini Calsavara e Edson Mendes Francisco pela medição dos exemplares de aves no MZUSP e pela obtenção das variáveis vegetais em campo.

"O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001

"This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001"

“O sofrimento é uma pedra de afiar para uma mente forte.”

J.R.R. Tolkien

OLIVEIRA, Helon Simões. **Diversidade funcional de comunidades de aves florestais em resposta a gradientes temporais e espaciais na Mata Atlântica.** 2023. 112 f. Tese (Doutorado em Ciências Biológicas) – Universidade Estadual de Londrina, Londrina, 2023.

## RESUMO

A manutenção da biodiversidade tem sido comprometida ao longo da história humana devido as alterações e destruição dos habitats. Ao longo do tempo, as comunidades apresentam alterações taxonômicas, com mudanças na riqueza e composição de espécies. Embora os avanços nos estudos sobre diversidade funcional sejam evidentes na última década, ainda é vago o entendimento de como as alterações taxonômicas podem afetar a diversidade de funções nas comunidades em ambientes florestais. Assim, o foco desse estudo foi investigar o comportamento das facetas da diversidade funcional de assembleias de aves florestais frente às dinâmicas taxonômicas decorridas ao longo de uma década em uma floresta tropical com alto nível de conservação. Também avaliamos as respostas da diversidade funcional nas assembleias de aves em relação ao gradiente de estado de conservação vegetal oriundo do corte seletivo de árvores. Para tanto, avaliamos a diversidade de traços funcionais e a estrutura do espaço de nicho ocupado pelas assembleias no Parque Nacional do Iguazu e na Reserva Biológica das Perobas. Foram obtidas as métricas: riqueza de espécies; riqueza, uniformidade, divergência e dispersão funcional; e a média ponderada da comunidade de cada traço funcional avaliado. Além disso, comparamos os valores de diversidade funcional observados com os aqueles esperados ao acaso para identificar os mecanismos latentes às montagens das assembleias. Essas métricas foram avaliadas com o uso de modelos aditivos generalizados mistos e modelos lineares Bayesianos. Os resultados apontam que as comunidades passam por uma dinâmica taxonômica temporal, mesmo em ambientes altamente preservados. As alterações taxonômicas são possíveis devido à substituição aleatória gerada por processos de dispersão, porém, a redundância entre as espécies permite a estabilidade funcional geral da comunidade. Entretanto, as espécies Passeriformes insetívoras especialistas apresentaram uma redução taxonômica com prevalência do aninhamento funcional, quando comparado a composição funcional entre os anos, o que indica uma erosão funcional silenciosa nas assembleias. Identificamos, ainda, que as assembleias tendem a aumentar a riqueza de espécies em florestas com reduzido estado de conservação vegetal. Contudo, esse aumento na riqueza de espécies leva ao adensamento do espaço nicho devido à intensificação da influência dos filtros ambientais sobre a estruturação das assembleias. Dessa forma, as comunidades em vegetações menos íntegras apresentam maior risco de extinções locais devido às exclusões competitivas entre espécies redundantes. Isso demonstra que avaliações isoladas da riqueza de espécies são potencialmente ilusórias e podem levar a medidas de conservação malsucedidas, como propor a extração seletiva de madeira em florestas primárias com base no suposto benefício do aumento da riqueza de espécies de aves. Além disso, a composição funcional tende a mudar com as mudanças no estado de conservação da vegetação, alterando assim o papel funcional prestado pelas comunidades.

**Palavras-chave:** Dinâmica comunitária; Diversidade funcional ao longo do tempo; Erosão da biodiversidade funcional; Ocupação de nicho; Regras de assembleia.

OLIVEIRA, Helon Simões. **Functional diversity of forest bird communities in response to temporal and spatial gradients in the Atlantic Forest.** 2023. 112 p. Thesis (Doctorate degree in Biological Sciences) – Universidade Estadual de Londrina, Londrina, 2023.

## ABSTRACT

The maintenance of biodiversity has been compromised throughout human history due to the alteration and destruction of natural habitats. Over time, natural communities show taxonomic alterations, with changes in species richness and composition. Although advances in functional diversity studies are evident in the last decade, the understanding of how taxonomic alterations may affect the diversity of functions in communities in forest environments is still vague. Thus, the focus of this study was to investigate the behavior of functional diversity facets of forest bird assemblages in the face of taxonomic dynamics over a decade in a tropical forest with a high level of conservation. We also evaluated the responses of functional diversity in bird assemblages in relation to the gradient of vegetation conservation status arising from selective logging. To this end, we evaluated the diversity of functional traits and the structure of niche space occupied by assemblages in the Iguaçu National Park and the Perobas Biological Reserve. We obtained the metrics: species richness; functional richness, functional evenness, functional divergence, and functional dispersion; and the weighted average of the community for each functional trait evaluated. In addition, we compared the observed functional diversity values with those expected by chance to identify latent mechanisms in assemblage assemblies. These metrics were evaluated using generalized additive mixed models and Bayesian linear models. The results indicate that communities undergo temporal taxonomic dynamics, even in highly preserved environments. Taxonomic changes are possible due to random turnover generated by dispersal processes, but redundancy among species allows for overall functional stability of the community. However, the specialist insectivorous Passerine species showed a taxonomic reduction with prevalence of functional nesting when comparing the functional composition between years, indicating a silent functional erosion in the assemblages. We also identified that assemblages tend to increase species richness in forests with reduced vegetation conservation status. However, this increase in species richness leads to a densification of the niche space due to the intensified influence of environmental filters on the structure of assemblages. Thus, communities in less intact vegetation are at greater risk of local extinctions due to competitive exclusions among redundant species. This demonstrates that isolated assessments of species richness are potentially illusory and can lead to unsuccessful conservation measures, such as proposing selective logging in primary forests based on the supposed benefit of increased bird species richness. Furthermore, functional composition tends to change with changes in vegetation conservation status, thus altering the functional role provided by communities.

**Key-words:** Assembly rules; Community dynamics; Erosion of functional biodiversity; Functional diversity over time; Niche occupation.

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## LISTA DE ABREVIATURAS E SIGLAS

BSR	Bird species richness
CI	Credible interval
CWM	Community weighted mean
Edf	Estimated degrees of freedom
FDis	Functional dispersion
FDiv	Functional divergence
FEve	Functional evenness
FRic	Functional richness
GAMM	Generalized additive mixed model
GAM	Generalized additive model
INP	Iguaçu National Park
IPA	Index of Point Abundance
MCMC	Monte Carlo Markov Chains
MNND	Mean nearest neighbor distance
MZUSP	Zoology Museum of São Paulo
NP	Non-passerines
OP	Other passerines
PBR	Perobas Biological Reserve
PCoA	Principal Coordinate Analysis
REA	Rapid ecological assessment
S	Species richness
SACC	South American Classification Committee
SAF	Semideciduous Atlantic Forest
sd	Standard deviation
SES	Standardized effect size

SIP	Specialists insectivores passerines
$\beta_{Sin}$	Simpson dissimilarity index
$\beta_{Sne}$	Nestedness
$\beta_{SOR}$	Sørensen dissimilarity index

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## 1. INTRODUÇÃO GERAL

Os serviços ecossistêmicos são essenciais para a sobrevivência e o bem-estar humano. Entretanto, nossa espécie tem alterado o mundo ao seu redor de diversas maneiras ao longo da História, por meio de atividades como mudanças no uso do solo, extração de minérios, exploração de organismos, desmatamento e manufatura de bens de consumo. Tais ações acarretam impactos aos ecossistemas, comprometendo a sobrevivência de organismos e inviabilizando a capacidade do fornecimento dos serviços ecossistêmicos (Beaumont et al., 2019; Cardinale et al., 2012; Hautier et al., 2015; IPBES, 2019; Penuelas et al., 2020). Independente da fonte de alteração, a destruição dos habitats naturais é uma consequência evidente ao redor do Globo, que por sua vez é apontada como a principal responsável pela extirpação das espécies, juntamente com seus traços funcionais (Almeida et al., 2016; Pimm and Raven, 2000). Até o final do século XXI, é esperado que um milhão de espécies estejam extintas (IPBES, 2019). Isso tem acendido uma preocupação sobre a viabilidade funcional dos ecossistemas (Gagic et al., 2015), tornando necessária a obtenção de dados quantitativos capazes de rastrear mudanças na diversidade biológica sobre o espaço e tempo e de métricas que reflitam adequadamente a diversidade de funções ecossistêmicas mediante as variações da biodiversidade (Gagic et al., 2015; Magurran, 2004, 2021).

A diversidade funcional é o componente da biodiversidade capaz de predeterminar a forma como os ecossistemas funcionam (Tilman, 2001). Inicialmente, a riqueza de espécies foi tratada como forma mais simples de mensurar a diversidade de funções em sistemas ecológicos (Cardinale et al., 2012). O pensamento mais intuitivo é: quanto maior o número de espécies presentes em uma taxocenose maior será o rol de funções ecológicas fornecidas por esse grupo de espécies. Contudo, a relação riqueza de espécies e diversidade funcional nem sempre é verdadeira (Díaz and Cabido, 2001; Wardle et al., 1997) e pode ser contexto dependente, influenciada pelo pool de espécies regional, variabilidade fenotípica, filogenia e a condição ambiental (Biswas and Mallik, 2011; Cardinale et al., 2012; Naeem and Wright, 2003). A riqueza de espécies por si só não é uma boa métrica para avaliações funcionais, pois assume equivalência entre as espécies (Gagic et al., 2015; McGill et al., 2006). Destarte, ao longo das últimas três décadas, tem se consolidado o consenso de que para avaliar mecanismos de montagem de comunidades e seus efeitos sobre o funcionamento ecossistêmico, é preciso observar a diversidade de traços funcionais presentes nas taxocenoses e seu comportamento em relação ao acúmulo de espécies (Díaz and Cabido, 2001; Mouchet et al., 2010; Pigot et al., 2016; Swenson and Weiser, 2014; Tilman, 2001). Tais traços funcionais

são características fenotípicas (e.g. morfológicas, fisiológicas e comportamentais), obtidas a nível de indivíduos, capazes de afetar a ocorrência das espécies e dos processos ecossistêmicos (Violle et al., 2007).

Em sistemas naturais, a riqueza de espécies só será um substituto satisfatório para a diversidade funcional se a expansão do espaço de nicho ocupado for proporcional ao aumento no número de espécies (Díaz and Cabido, 2001). Entretanto, esse cenário não é comum na natureza e mesmo que a riqueza funcional aumente com a riqueza de espécies, ela é muito mais influenciada pelos mecanismos de montagem de assembleias (Díaz and Cabido, 2001; Mouchet et al., 2010). Muitas vezes a intensidade com que a riqueza funcional cresce é menor ou maior que a intensidade do acúmulo de espécies (Karadimou et al., 2016; Oliveira et al., 2020). Isso ocorre em função dos mecanismos latentes à (des)montagem das comunidades, denominados de regras de assembleia (Weiher and Keddy, 1999). Esses mecanismos atuam pela ação de filtros ecológicos (dispersão, filtros ambientais e interações interespecíficas) sobre a presença de traços e determinam a estrutura funcional das comunidades ao limitar o número e identidade das espécies que observamos em uma assembleia (Bello et al., 2021; Mouchet et al., 2010).

Dois mecanismos principais são foco dos estudos sobre a montagem de assembleias baseadas em nicho: a seleção por filtros ambientais e interação interespecífica, em especial a similaridade limitante com exclusões competitivas. As comunidades moldadas sob maior influência dos filtros ambientais tendem a apresentar composição de espécies agrupadas funcionalmente, pois as condições ambientais agem como filtros, restringindo à permanência de uma pequena faixa de características que possibilitam a sobrevivência naquele ambiente em questão. Por outro lado, a similaridade limitante postula a coexistência de espécies funcionalmente distintas pela exclusão competitiva entre espécies funcionalmente redundantes. Ainda, deve-se citar a teoria neutra que assume a coexistência de espécies independentemente de suas características, sendo as espécies equivalentes entre si, de tal modo que a composição da comunidade é uma obra de eventos ao acaso como a dispersão (Hubbell, 2001; Hutchinson, 1957; MacArthur and Levins, 1967; Mouchet et al., 2010).

Através do estudo dos mecanismos de formação de assembleias, é possível identificar as vias pelas quais as espécies deixam de ocorrer em determinados locais. Por exemplo, várias foram as tentativas de explicar a redução do número de espécies em relação ao tamanho de fragmentos florestais, inclusive com a aplicação da teoria da biogeografia de ilhas (MacArthur and Wilson, 1967) para o contexto de fragmentos florestais (Diamond, 1975) e, mais recente, passando pela hipótese do montante de habitat (Fahrig, 2017). Entretanto, nenhuma dessas

visões considerou as variações nas características espécie específicas. Entre os anos de 2016 e 2018, desenvolvemos um estudo com objetivo de identificar os mecanismos latentes à desmontagem de comunidades de aves em relação à redução no tamanho de fragmentos florestais na Mata Atlântica (Oliveira et al., 2020). Os resultados desse estudo implicaram que o surgimento da relação espécie-área, no mosaico florestal estudado, se deve à intensificação da similaridade limitante com a redução da área dos fragmentos florestais. À medida que a área diminuiu, junto com a disponibilidade de recursos, se intensificou a similaridade limitante nas assembleias, gerando exclusões competitivas entre as espécies mais próximas funcionalmente. Por outro lado, fragmentos maiores apresentaram assembleias sob uma similaridade limitante enfraquecida, de modo a se enquadrarem como assembleias agrupadas aleatoriamente. O estudo de Oliveira et al. (2020) acicatou os questionamentos que motivam essa tese: Qual o comportamento funcional temporal de assembleias de aves em habitats intocados ou sob baixo impacto antrópico? Qual a influência que a vegetação e seus níveis de conservação exercem sobre a estrutura e diversidade funcional de assembleias de aves florestais?

Embora seja prático e comumente investigado quais são os efeitos causados a curto prazo por impactos ambientais sobre as comunidades, estas não são unidades estáveis no espaço e tempo e sim dinâmicas, variando tanto em composição e abundância, quanto na riqueza de espécies (Buckley et al., 2019; Ryo et al., 2019), mesmo em ambientes não perturbados (Blake and Loiselle, 2016). Devido à mutabilidade da natureza, somado à complexidade de efeitos causados por impactos ambientais, torna-se primordial identificar suas dinâmicas, o que nos possibilitará prever seu comportamento futuro e contribuir para o manejo da biodiversidade (Alvarez-Cobelas et al., 2019; Magurran et al., 2010). Estudos de longo prazo tem contribuído desproporcionalmente para os avanços na ecologia, promovendo bases empíricas para o entendimento sobre as dinâmicas naturais e os efeitos das alterações do ambiente sobre a produtividade, estabilidade, estrutura e composição funcional de ecossistemas, assim como nos processos mecanísticos fundamentais para a manutenção da biodiversidade (ver revisão detalhada em Hughes et al. (2017)).

Alguns estudos recentes apontaram mudanças em comunidades de aves em florestas tropicais preservadas ao longo do tempo (escalas temporais maiores que 10 anos). As comunidades estudadas apresentaram variações da dominância em número de indivíduos entre guildas tróficas na Amazônia, Manaus, Brasil (Stouffer et al., 2020) e na riqueza de espécies envolvendo o desaparecimento de espécies comuns e a colonização por novas espécies na Tiputini Biodiversity Station, Orellana, Equador (Blake and Loiselle, 2016).

Embora a perda de espécies seja vista, quase sempre, como algo danoso, até o momento não se sabe qual o impacto das substituições de espécies sobre a funcionalidade em comunidades de aves em florestas preservadas.

As assembleias podem manter seus papéis ecológicos, mesmo com a perda ou substituições de espécies, caso possuam espécies similares em traços funcionais, o que minimizaria impactos nos processos ecossistêmicos (Díaz and Cabido, 2001). Traços funcionais semelhantes entre espécies distintas sugerem que as funções ecológicas sejam igualmente semelhantes, é o que se chama redundância funcional (Walker, 1992). Essa característica é associada à resiliência do ecossistema frente à distúrbios, de modo que assembleias com maior redundância funcional tendem a ter uma maior estabilidade, mesmo que algumas espécies sejam perdidas ao longo do tempo (Kang et al., 2015; Walker, 1992). Assim, mesmo em ambientes preservados, se as alterações na riqueza e composição de espécies ocorrem entre espécies redundantes, o volume funcional ocupado pela comunidade se manterá estável, o que sugere que o impacto para a funcionalidade do ecossistema deve ser baixo (veja um contexto contrário em Oliveira et al. (2020)).

As escalas de monitoramentos temporais variam desde meses (Lees and Moura, 2017; Rushing et al., 2016; Zhang et al., 2018) a séculos de monitoramento (Silvertown et al., 2006). Todavia, séries de monitoramentos de longo prazo são difíceis de realizar devido à mão de obra especializada escassa e custo elevado (Targetti et al., 2012), principalmente, em florestas tropicais (Gardner et al., 2008). Consequentemente, vários estudos não possuem séries temporais e se limitam a comparações entre amostras pontuais. Por exemplo, Brown and Gurevitch (2004) avaliam comunidades vegetais sobre os efeitos do corte seletivo de madeira 150 anos após sua execução, no entanto o fazem através de comparações com outras áreas que passaram por esse tipo de exploração madeireira mais recentemente (50 anos). No estudo desenvolvido por Thiollay (1992), foi comparado a diversidade de aves em áreas com históricos entre 1-2 anos e 8-12 anos de recuperação após a exploração de madeira por corte seletivo, com outras áreas não exploradas. Embora estes trabalhos apresentem dados e resultados importantes para conservação de espécies, em áreas seletivamente exploradas, eles não retornam a dinâmica das comunidades ao longo dos anos e possuem baixo potencial de previsão de respostas futuras da comunidade (Buckley et al., 2019; Ryo et al., 2019).

O corte seletivo é um método de extração madeireira em que se extrai da floresta apenas espécies e caules específicos, de alto interesse econômico (Edwards et al., 2014b). Apesar de não provocar o corte raso por grandes áreas e preservar muitos serviços ecossistêmicos (Edwards et al., 2014b), esse método ainda provoca alterações na vegetação

como a diminuição de cobertura de dossel, tanto pela derrubada de grandes árvores, criando clareiras, quanto pela abertura de estradas para o trânsito do material extraído (Thiollay, 1992; Uhl et al., 1991). Distúrbios como a queda de grandes árvores ou quedas de grandes galhos criam alterações na estrutura no nicho ecológico que possibilitam o estabelecimento de espécies distintas daquelas presentes em florestas intocadas (Verburg and van Eijk-Bos, 2003), incluindo espécies invasoras (Arellano-Cataldo and Smith-Ramírez, 2016; Brown and Gurevitch, 2004; Driscoll et al., 2016). Tais alterações geram níveis distintos de conservação dentro de um mesmo bloco florestal, durante o período pós corte seletivos, que pode exercer uma força de seleção sobre as espécies, afetando tanto taxocenoses vegetais (Gálhidy et al., 2006; He et al., 2019), quanto invertebrados (França et al., 2016; Perry et al., 2018; Smolders et al., 2018) e vertebrados (Johns et al., 1992). As respostas de comunidades ao corte seletivo são variáveis, tanto para vegetais quanto para animais (Burivalova et al., 2015; Verburg and van Eijk-Bos, 2003). A vegetação pode apresentar biomassa e riqueza de espécies reduzidas (Gatti et al., 2014), e mesmo após 150 anos de restauração, pode não retornar aos seus parâmetros originais em termos de estrutura e composição de espécies (Brown and Gurevitch, 2004).

Em comunidades de aves tropicais, têm sido frequentemente detectado o aumento da riqueza de espécies pós corte seletivo (Aleixo, 1999; Burivalova et al., 2014; Edwards et al., 2014a). Contudo, há uma considerável alteração na composição de espécies (Aleixo, 1999), com um efeito seletivo que favorece espécies generalistas de habitat, enquanto as especialistas são extirpadas (Burivalova et al., 2014; Thiollay, 1992). Além disso, em curto prazo, espécies de aves frugívoras e insetívoras tendem a responder negativamente, enquanto as onívoras, granívoras e nectarívoras respondem positivamente em termos de abundância (Burivalova et al., 2015). Uma vez que o corte seletivo tende a impulsionar variações nas abundâncias e composição de espécies de aves (Aleixo, 1999), é esperado variações na diversidade funcional das taxocenoses resultantes (Burivalova et al., 2015; Cadotte et al., 2011; dos Anjos et al., 2019; Flynn et al., 2009). Assim, embora a riqueza de espécies *per se* aumente, não se sabe qual o impacto disso nos processos ecossistêmicos e na estrutura funcional, já que a alteração na composição específica acarreta mudanças nos pacotes de traços funcionais (Cardinale et al., 2012; Mouillot et al., 2013). Neste sentido, a depender de como as espécies estão distribuídas no espaço do nicho ecológico, podem ser observados dois padrões distintos em sua ocupação (Perre et al., 2020; Pigot et al., 2016): a expansão do espaço do nicho ocupado ou o seu adensamento, o que tem sido chamado de empacotamento do nicho. No primeiro caso, de acordo com a teoria da similaridade limitante, o acúmulo de espécies na assembleia

pode levar à expansão do espaço de nicho ocupado, uma vez que espécies similares tendem à exclusão competitiva, assim uma nova espécie precisaria ocupar novas regiões do espaço de nicho para persistir em dado local (MacArthur and Levins, 1967). No segundo caso, o aumento da riqueza de espécies pode levar ao empacotamento do espaço de nicho devido a uma especialização mais fina ou a sobreposição de espécies funcionalmente similares no espaço de nicho ocupado (Karr and James, 1975; Klopfer and MacArthur, 1961).

Diante dos fatos expostos, foi delineado o monitoramento de taxocenoses de aves ao longo de uma escala temporal de dez anos em uma floresta tropical madura preservada (Parque Nacional do Iguaçu-PNI) e o levantamento de taxocenoses de aves ao longo de um gradiente de conservação vegetal em fina escala em uma floresta tropical com histórico de corte seletivo não regulamentado (Reserva Biológica das Perobas-REBIOP). Essa tese possui dois objetivos gerais: (1) Investigar a variação funcional e as dinâmicas temporais de suas facetas em taxocenoses de aves em uma floresta sob baixa influencia antrópica; (2) investigar se as mudanças na diversidade taxonômica das aves através do gradiente de status de conservação da vegetação, resultantes do corte seletivo, também influenciam a diversidade e estrutura funcional das comunidades. Com esses objetivos, almejamos promover bases empíricas para o desenvolvimento de práticas de conservação que melhor protejam as funções e serviços cruciais das florestas tropicais impactadas ou não.

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## 2. CAPÍTULO 1

### **Silent changes in functionally stable bird communities of a large protected tropical forest monitored over 10 years.**

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<https://doi.org/10.1016/j.biocon.2021.109407> Received 1 July 2021; Received in revised form 12 November 2021; Accepted 20 November 2021 0006-3207/© 2021 Elsevier Ltd. All rights reserved.

**Artigo publicado no periódico Biological Conservation.**

**Normas do periódico disponíveis em:**

<https://www.elsevier.com/journals/biological-conservation/0006-3207/guide-for-authors>

#### **Citação recomendada**

Oliveira, H. S., & dos Anjos, L. (2022). Silent changes in functionally stable bird communities of a large protected tropical forest monitored over 10 years. *Biological Conservation*, 265, 109407. <https://doi.org/10.1016/j.biocon.2021.109407>

**Abstract**

Temporal taxonomic changes have been noted in bird communities in protected tropical forests. However, it is not known whether these changes compromise the conservation of functional diversity. Here we monitored bird communities in an Atlantic Forest Protected Area in southern Brazil annually during 10 years. We assess temporal trends in taxonomic and functional diversity metrics and compare the observed functional diversity values with expected values to identify the mechanisms that drive community assembly. We also verified temporal beta diversity and the prevalence of its components. We found variations in species richness over time when assessing the entire community, passerines, non-passerines, and specialized insectivorous passerines. Taxonomic turnover was predominant in the temporal beta diversity of these groups. Nonetheless, no significant variations in functional richness were recognized, indicating functional redundancy between the changing species. However, functional nestedness was predominant in the group of specialist insectivorous passerines, which indicates functional erosion in this group. There were also increases in the dispersion of the entire community and functional divergence in non-passerines. These alterations seem to reflect the occurrence of rare species with unique functional traits and the optimization of the use of available resources. Our data suggest that the communities had random functional structures. Consequently, taxonomic alterations are possible due to random substitution generated by dispersal processes however, the redundancy between species allows overall functional stability of community. We also highlight that different groups of species can present different temporal trajectories and their evaluations are necessary to unveil silent alterations in their functional roles.

**Key-words:** Conservation of functional diversity, temporal beta diversity, erosion of functional biodiversity, specialist insectivores, Atlantic Forest, community change.

## 1. Introduction

Tropical forests are home to more than half of all known species around the world (Wright, 2005) but it is also the biome that suffers most from habitat destruction and consequent loss of biodiversity (Pimm and Raven, 2000). Currently, tropical forest fragments have an average size of 17 ha, with a predicted decrease to 0.25 ha over the next 50 years (Taubert et al., 2018). In the midst of this destruction scenario, protected areas are irreplaceable places to achieve long-term nature conservation, preventing extinctions, and providing essential ecosystem services for human well-being (Le Saout et al., 2013; SCBD and COP 10, 2010). As a result, protected areas are expected to be highly effective in maintaining biodiversity and populations of target species. For example, Donald et al. (2007) developed statistical models that predict that for every given additional 1% increase in the area of protected areas in Europe, the chances of bird species increasing in population increase by 4% and with a 7% increase for the target species. However, the effectiveness of conservation in these protected areas needs to be evaluated beyond taxonomic diversity, because a counterpoint view that considers the other dimensions of biodiversity (e.g. genetic, phylogenetic, and functional) can be taken to create more effective measures to achieve conservation of ecosystem services.

Recently, considerable literature has emerged on the topic of taxonomic dynamics of bird community in preserved tropical forests. Stouffer et al. (2020) identified changes in abundance between guilds, with a decline in insectivorous species and an increase in frugivores over an interval of >35 years of monitoring in an area of preserved Amazon forest, Manaus, Brazil. Over 14 years at the Tiputini Biodiversity Station, Orellana, Ecuador, Blake and Loiselle (2016) detected a decrease in the richness of bird species once common in the protected area, which was particularly pronounced in the guild of insectivores. The authors also mention that there were colonization of species that did not previously occur at the site (Blake and Loiselle, 2016). Although the impact of bird losses could be evaluated individually for each species, to date it is not known what the impact of these replacements will be on ecosystem functionality. Important issues to be investigated are the scope of this phenomenon in other preserved areas and whether colonizers are replacing the ecological roles of species that are lost. In other words, are the ecological roles of bird communities being conserved in a protected area where temporal taxonomic changes are occurring?

The maintenance of ecological roles in a community is possible even with the loss or replacement of species, if they have similar functional traits (Díaz and Cabido, 2001). Similar functional traits between different species suggest that ecological functions would be less

affected; this is called functional redundancy (Walker, 1992). Functional redundancy is associated with ecosystem resilience to disturbances, so that assemblages with greater functional redundancy tend to have greater stability even if some species with redundant functions are lost over time (Kang et al., 2015; Walker, 1992). Thus, if alterations in species richness and composition occur among species with similar traits, the functional volume occupied by the community will remain stable, suggesting that the impact on ecosystem functionality should be low. See an opposing context in Oliveira et al. (2020).

Among all biomes worldwide, tropical forests have the highest values of bird species richness (Jetz et al., 2012). Likewise, these habitats present the highest levels of specialization and packing of ecological niche associated with species richness (Belmaker et al., 2012; Morelli et al., 2021; Pellissier et al., 2018; Pigot et al., 2016). Thus, three hypothetical scenarios can be proposed regarding the consequences of species substitutions over large temporal scales on the functional diversity of bird communities in preserved tropical forest environments. If the temporal replacements of species occur between functionally redundant species, the functional volume will tend to remain stable over the years (scenario 1, Fig 1a). On the other hand, there may be a reduction in functional volume if the species that appear are not redundant to those that have disappeared, but rather to others that already exist in the area (scenario 2, Fig 1b). In the scenario of surrogate species having new traits, functional replacement will occur, which may influence the volume of functional space occupied by the community (scenario 3, Fig 1c). However, changes in the volume of functional space are commonly presented as a result of natural transformations in environmental conditions and availability of local resources or as a result of anthropic activities (Pagani-Núñez et al., 2019; Pellissier et al., 2018; Pigot et al., 2016), which is not the case of the Protected Area studied herein.

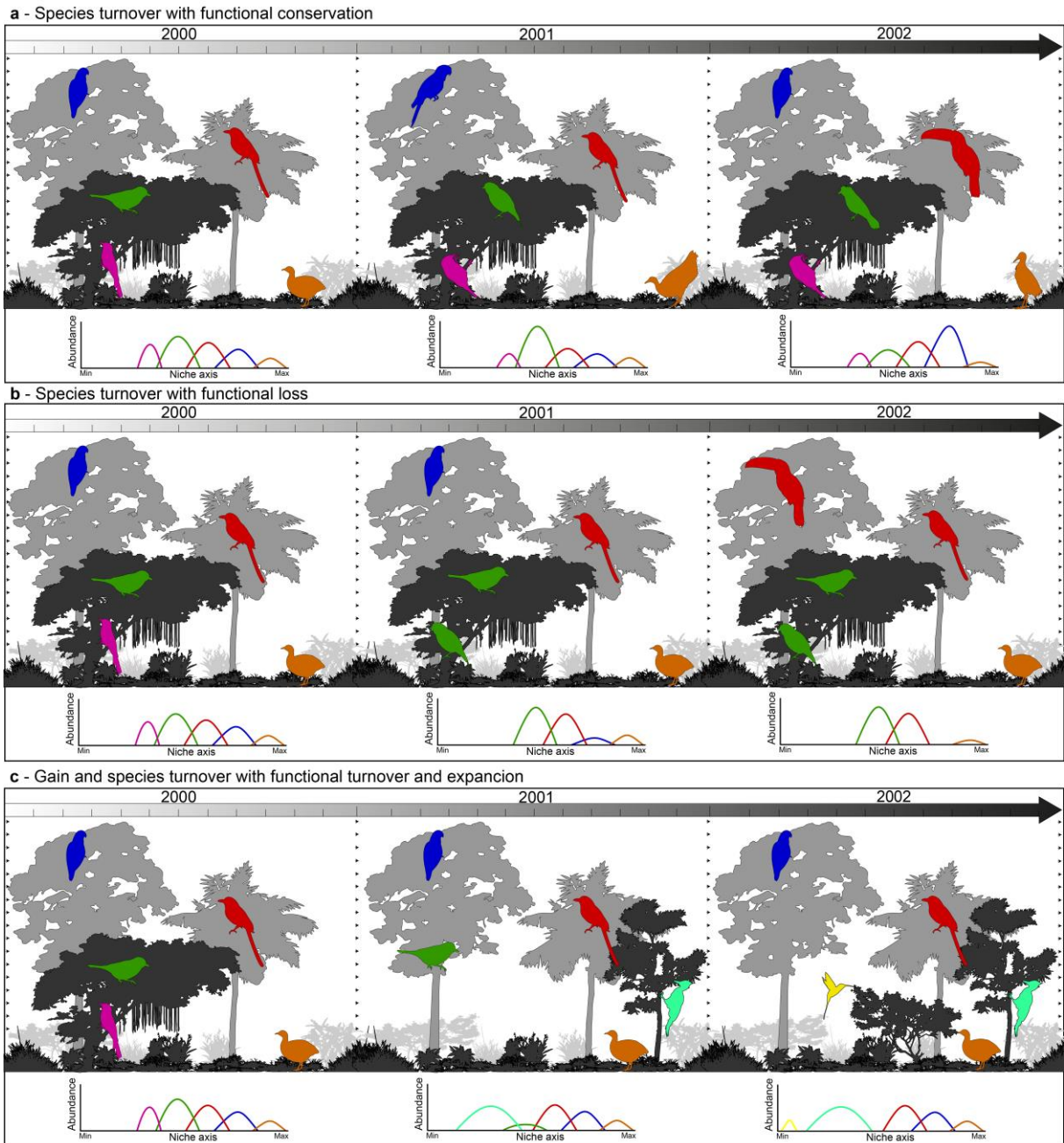


Fig. 1. Schematic representation of possible functional scenarios in the presence of temporal replacement of species in preserved tropical forests. In scenario I, the species that appear along the temporal trajectory are functionally similar to those that disappeared. In this way, all ecological roles are maintained in the community even with alterations in species abundances. The species that appear in scenario II are not equivalent to those that disappear, but rather to others that already exist in the location. In this scenario, the replacement of species causes the disappearance of ecological roles along with the lost species. Finally, in scenario III there are alterations in the habitat that cause taxonomic changes along with functional replacements and the expansion of the functional space occupied by the community. Equally colored species represent functional redundancy.

Variations in the number of coexisting species are commonly related to spatial gradients, such as altitudinal variation (Ding et al., 2019; Dreiss et al., 2015; Goerck, 1999) and area extent (Matthews et al., 2016; Triantis et al., 2012), or environmental such as the heterogeneity of natural habitat (Lee and Martin, 2017) and anthropogenic origin (Burivalova et al., 2015; Burivalova et al., 2014; Perillo et al., 2017; Perry et al., 2018). However, ecological communities are dynamic units in time and space (Damgaard, 2019), even in the absence of anthropogenic disturbances, ranging from hourly intervals to millions of years (McDowell et al., 1995). Species are constantly under the effect of natural stochasticity and deterministic factors such as environmental filters and interspecific interactions such as competition (Mutshinda et al., 2009; Oliveira et al., 2020; Shurin, 2007), whose effects are reflected in alterations in species richness and community composition (e.g. Blake and Loiselle, 2015, 2016; Faaborg et al., 2007; Stouffer et al., 2020; Stouffer et al., 2011). Environmental filters and interspecific interactions, especially competition, comprise the niche-based assembly rules. Communities assembled by these mechanics tend to be functionally clustered or overdispersed, respectively (Hutchinson 1957; MacArthur and Levins, 1967; Kraft et al. 2015). However, the neutral theory of biodiversity suggests that stochastic processes (e.g. dispersal and ecological drift) prevail over niche-based processes, generating a random assembly of the community (Hubbell, 2001).

The Atlantic Forest is one of the largest and richest areas of tropical forests, with more than 745 species of birds being found (Hasui et al., 2018). Despite its large geographic extension, covering approximately 29° latitudinal areas, the Atlantic Forest is currently represented by only 28% of its original coverage, of which only 30% is in protected areas (IUCN Categories I-IV) (Rezende et al., 2018). As in the entire tropical belt (Taubert et al., 2018), the Atlantic Forest is represented by an enormous mosaic of forest remnants in which few exceed 100 000 ha of continuous forest (Ranta et al., 1998; Rezende et al., 2018). Although the need to preserve these remnants is obvious for biodiversity conservation (SCBD and COP 10, 2010), long-term ecological studies are needed to identify alterations in different aspects of biodiversity and assess their effects on maintaining the ecological roles provided by the communities (Hughes et al., 2017).

Here we analyzed forest bird communities monitored for ten years within a large continuous forest area, the Iguçu National Park (INP) in the Atlantic Forest domain in southern Brazil. Based on the species richness and abundance data obtained annually, we investigate temporal variations in taxonomic and functional diversities of the bird community in the forest core. Considering that the INP is an “untouched” protected area, our first

hypothesis was that there is no variation in both diversities. However, based on studies in Ecuador (Blake and Loiselle, 2016) and in the Manaus region (Stouffer et al., 2020) there is a second hypothesis in which there is a taxonomic alteration. In this case, we seek to understand the impact of the change in species composition on the conservation of functional diversity and to investigate the mechanisms behind such changes. Protected areas like INP are the most efficient places for biodiversity conservation because they are supposedly minimally influenced by human actions (Le Saout et al., 2013; SCBD and COP 10, 2010). Anthropogenic actions can generate variations in habitat conditions that relate to adjusting the coexistence of species in several ways: by changing the requirement of specific functional traits for establishment in the habitat (Ding et al., 2019; Kraft et al., 2015); by changing reproductive fitness, with consequent changes in the dynamics of dominance and competitive exclusion (MacArthur and Levins, 1967; Oliveira et al., 2020), or by causing the emergence of new environmental conditions which enable the colonization of new species, native or invasive (Brown and Gurevitch, 2004). These considerations imply that, from a perspective of assemblage structuring by niche-based assembly rules, variations in species richness and composition are not expected unless there are alterations in the habitat. Therefore, if taxonomic temporal dynamics are found to be independent of functional diversity, stochasticity should be the mechanism responsible for the changes in the community.

The analyses were performed on five distinct groups of birds (all birds, non-passerines, passerines, specialist insectivorous passerines, and other passerines), as studies have shown that distinct groups of birds show distinct temporal variations, especially insectivorous species (Blake and Loiselle, 2016; Stouffer et al., 2020). Sherry et al. (2020) argue that Neotropical habitats which are rich in insectivorous species tend to present a continuous diffuse competition for resources, which favors evolutionary specialization generating species with smaller niche breadth but with high overlap. This suggests that specialist insectivorous passerines are more likely to fall into hypothetical scenario 1 described above (Fig. 1a).

## **2. Material and Methods**

### *2.1. Study area*

The study was carried out in the Iguaçu National Park (INP) located in the west of the state of Paraná, Brazil (25°27'38.89" S; 53°55'19.54" W). Officially established as a

Protected Area in 1939 by Decree-Law No. 1035, the INP is the second national park created in Brazil and is the largest remnant of continuous forest in the south of the country, covering an area of 185 262 ha. The predominant vegetation is of the Seasonal Semideciduous Forest of the Atlantic Forest domain, its climatic zone, defined by the Köppen-Geiger table, is of the Cfa type with mean annual precipitation of 1712 mm and mean temperature of 20.7°C (Peel et al., 2007). The predominant soil is deep, fertile, and well-drained Eutroferric Red Nitosol and the terrain is smooth with a lack of steep slopes (Maack, 1981). The INP is home to the Iguazu Falls, one of the most spectacular natural landscapes in South America and considered a Natural Heritage of Humanity by UNESCO. Adjacent to the INP is the Iguazú National Park in Argentina with a protected area of 67 620 ha. These parks have a high level of biodiversity and are of great importance for conservation in the Atlantic Forest (Silva et al., 2018). This region preserves populations of large and medium-sized mammals and birds threatened with extinction such as *Tapirus terrestris*, *Mazama nana*, *Myrmecophaga tridactyla*, and the conservation symbol of the INP the *Panthera onca* (Silva et al., 2018), as well as the *Harpia harpyja* (Anfuso et al., 2008). Surrounding the INP are urban areas, fragments of secondary forest, pastures, and crops for the production of grain, mainly soybean, corn, and wheat.

## 2.2. Bird surveys

The monitoring of avifauna in the INP was carried out annually from 2011 to 2020 using the method of point counts (Vielliard et al., 2010). Sampling was carried out over five transects (Fig. 2). At each transect, sampling points were established every 200 m to reduce overestimates in species abundance (Vielliard et al., 2010). Six points were plotted on each transect, totaling 30 points. In addition, all five transects were positioned within the forest at a minimum distance higher than 300 m from the edge in order to concentrate records on bird species that live within the forest. Each transect was sampled once a year during the breeding season (September-January). The points of each transect were sampled sequentially on the same morning from dawn. The observer remained at each point for 15 min and took a 15 min interval between points. The detection radius at each point was 50 m (Vielliard et al., 2010). Only one observer (L.A.) performed all sampling events, in order to standardize the accuracy of species detection.

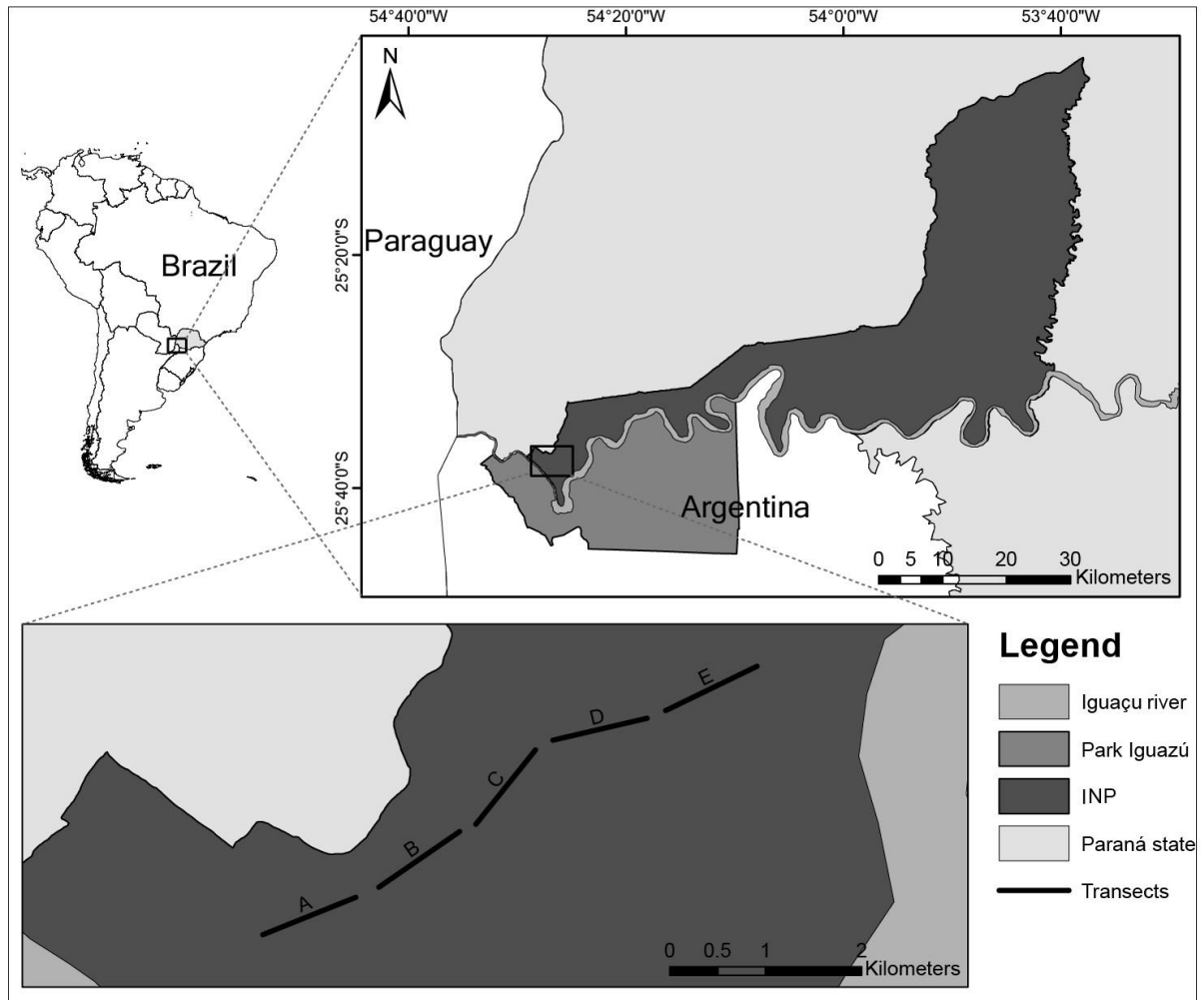


Fig. 2. Location of sample areas in the Iguazu National Park, western Paraná State, southern Brazil.

The bird species were separated into five groups: all birds (all species recorded), non-passerines (all species that do not belong to the order Passeriformes), passerines (only species of the order Passeriformes), specialist insectivorous passerines (only specialist insectivorous species of the order Passeriformes), and other passerines (only species of the order Passeriformes with the exception of specialist insectivores). The separation of insectivorous passerines into specialists was based on dietary data from Wilman et al. (2014). Passerine birds with invertebrate consumption making up  $\geq 70\%$  of the prevalence of food items in the diet were considered to be specialist insectivores (see Anjos et al., 2019). The analyses of this study were carried out separately for each group. The taxonomic identification of the species followed the South American Classification Committee (SACC; Remsen et al., 2020). The Index of Point Abundance (IPA) was calculated for each species per transect annually to

allow for the representation of the temporal fluctuation of the relative abundance of each species (Vielliard et al., 2010). The IPA was calculated by dividing the number of contacts of each species by the total number of points sampled in each transect, that is, by six (Appendix 1).

### 2.3. *Functional traits*

Since many ecological roles provided by birds come from their resource exploitation (Mahendiran and Azeez, 2018), in the current study, functional traits of birds were used that reflect the variation in the ability and exploitation strategies of the resource available in the habitat, in particular the food.

Two functional traits data sets of functional traits were used (Appendix 2). The first was used when the functional space was modeled for the entire community or for non-passerines only. In total, 20 functional traits were evaluated for each species, divided into three categories: Food Item (referring to the percentage of food items in the diet - invertebrates; mammals and birds; reptiles and amphibians; scavenge; fruits, nectar; seeds; other plant materials), Forest Stratum for Foraging (referring to the percentage of use of the forest stratum for foraging – surface water; soil; understory; middle levels; canopy; aerial), and Morphometry (body mass, beak length, beak height, width length of beak, wing length, and tail length). Morphometry was previously obtained, using a caliper, of five individuals of each species at the Zoology Museum of São Paulo (MZUSP). Values for percentages of food items in the diet, use of forest stratum for foraging, and body mass were obtained from Wilman et al. (2014).

The second functional traits data set was used only when the functional space was modeled for passerines. This database maintains the same traits present in the first one and adds three new categories of traits, which reflect a spectrum of variations associated with the foraging behavior. By using these additional traits, we can raise the refinement of the functional space by bringing into focus the high specialization of Neotropical passerines, especially insectivores (Sherry et al., 2020). In total there are 19 functional traits associated with these categories of eating behavior: Foraging Substrate (litter, live leaves, dead leaves, vines, bamboo, branches, trunks, dead trunks, moss/lichens, bromeliads, aerial); Direction of Foraging (substrate, target), and Locomotion Strategy (perch, walk/hop, climb, sally/strike, sally/hover, hawk). To obtain these traits, the literature was consulted (Chesser, 2004; Fitzpatrick et al., 2004; Krabbe and Schulenberg, 2003a; Krabbe and Schulenberg, 2003b;

Remsen, 2003; Snow, 2004a, b; Whitney, 2003; Zimmer and Isler, 2003), and importance values were assigned to each category. We assigned a value of three if the literature suggests that the species is based on or prefers the character, a value of two if the importance of the character is not mentioned but it is stated or implied that the species exhibits the character, a value of one if the literature indicates that the species only occasionally displays the character, and zero if the character is absent.

#### 2.4. Alpha diversity

Species richness was used to represent taxonomic diversity, while, to provide a more complete perspective on the distribution of species and their abundances along the functional space, four functional diversity metrics were calculated: functional richness (FRic), evenness (FEve), divergence (FDiv), and dispersion (FDis) (Laliberté and Legendre, 2010; Villéger et al., 2008). To obtain the functional diversity indices, a matrix of functional distances between bird species was created using the Gower distance (Gower, 1971). As categorical traits with different numbers of categories were used, with continuous traits, different weights were assigned to each trait so that all traits had equal influence in the construction of the n-dimensional space. Thus, all traits were assigned proportional values for the calculation of functional diversity indices by calculating the weight:

$$Wi = \frac{1}{Ni},$$

where  $Ni$  is the number of characters by which a categorical trait is divided (Laliberté and Legendre, 2010). Functional distance matrices were used in the Principal Coordinate Analysis (PCoA). Later, the first axes, whose sum totaled  $\geq 80\%$  of the data variation of the functional distance matrix, were used as new independent traits to generate the n-dimensional functional space. The values of the functional diversity metrics were computed by the dbFD function from the FD package (Laliberté and Legendre, 2010) in the R software, version 4.0.2 (R Core Team, 2020).

In order to investigate the processes that drive temporal patterns of functional diversity, we compared observed values of alpha functional diversity indices and values expected by chance generated by null models. The observed values were compared with randomly generated values by the matrix-swap null model (Manly and Sanderson, 2002; Mason et al., 2013), through the use of the standardized effect size (SES) of Gotelli and McCabe (2002). Simulated assemblages were created through randomization (999 permutations) of all species recorded in all years, maintaining the abundance and richness of

species observed in each transect in each year. The SES measures the number of standard deviations ( $SD$ ) that the observed value is above or below the mean of the values obtained for each simulated assembly, and was calculated according to the following equation:

$$SES = \frac{Observed - mean(Expected)}{SD(Expected)}$$

Assuming a normal distribution, 95% of the SES values will be within the confidence interval of 1.96 and -1.96. Values outside this confidence interval are considered significantly different from what is expected by chance, with  $\alpha = 0.05$  (Wittman et al., 2010), suggesting that local assembly was driven by deterministic processes (Mouchet et al., 2010). Higher than expected SES values by chance indicate an overdispersion of traits (i.e., coexisting species are functionally *overdispersed*, complementary, and form local assembly driven by limiting similarity), while lower than expected SES values indicate trait convergence (i.e., coexisting species are functionally clustered and form local assembly driven by environmental filters) (Mouchet et al., 2010). Increases or decreases in SES beyond the confidence interval over time may indicate the intensifying influence of deterministic factors on community assembly (see Oliveira et al., 2020 for a spatial-scale example).

## 2.5. Beta diversity

As a means of investigating community dynamics on the temporal scale, variations in taxonomic and functional compositions in bird groups were measured. For this, the taxonomic and functional temporal beta diversities were calculated, as proposed by Baselga (2010) and Villéger et al. (2011), respectively. Both beta diversities were partitioned into nestedness and turnover (Baselga, 2010) and were measured by comparing each current configuration to the previous year, following the sequence on the temporal scale. The Sørensen dissimilarity index ( $\beta_{SOR}$ ) was calculated as a representation of the total difference in a community between pairs of consecutive years over the ten-year period of this study. The increase in  $\beta_{SOR}$  value indicates an increase in dissimilarity (beta diversity) between communities. The turnover ( $\beta_{SIM}$ ), represented by the Simpson dissimilarity index, measures how much of the difference between two communities is represented purely by species replacement. Finally, the nestedness ( $\beta_{SNE}$ ), which results from the difference between  $\beta_{SOR}$  and  $\beta_{SIM}$ , represents how much of a community is composed of a subset of a richer community (Baselga, 2010; Villéger et al., 2013). For the calculations of taxonomic beta diversity ( $\beta_{SOR-Tax}$ ) a matrix of species occurrence per year in the INP was used. For the functional beta diversity ( $\beta_{SOR-Fun}$ ), the

same occurrence matrix was used along with the matrix of functional traits by species. As the functional beta diversity calculations are based on the intersections of the functional spaces (convex hulls) occupied by the communities (Villéger et al., 2013), the same functional space generated for the functional alpha diversity was used in the functional beta diversity calculations by bird group (Villéger et al., 2011). Beta diversity calculations were performed using the *betapart* package (Baselga and Orme, 2012), in the R software.

## 2.6. Analysis

To explore the possibly non-linear behavior of facets of bird diversity over the last ten years in the INP, Generalized Additive Mixed Models (GAMMs) were fitted to the alpha diversity metrics (S, FRic, SESFRic, FEve, SESFEve, FDis, SESFDis, FDiv, and SESFDiv) and Generalized Additive Models (GAMs) for beta diversity metrics ( $\beta_{\text{SOR-Tax}}$  and  $\beta_{\text{SOR-Fun}}$ ). The GAMM models were adjusted to obtain smoothing terms by cubic regression, where the identity of the transects was entered into the models as a random factor. A first-order autocorrelation structure was added to all models to explain the temporal dependence between samples. Species richness (S) was modeled with the negative binomial distribution with a log link function (Zuur et al., 2009) as a way to deal with overdispersion in the model. The other metrics were modeled using the Gaussian distribution after checking the normality of the data by the Shapiro-Wilk test (Legendre and Legendre, 2012). However, metrics that did not approach a normal distribution were transformed by  $\log(x+1)$ . The homoscedasticity of the residuals of all models was inspected using plots of standardized residuals against adjusted values (Zuur et al., 2009). To verify the prevalence of a process underlying the measures of temporal beta diversity over the last decade, Wilcoxon rank sum tests were performed between  $\beta_{\text{SNE}}$  and  $\beta_{\text{SIM}}$  (Hollander et al., 2014). All analyses were carried out in R software, the GAMM and GAM were created using the *mgcv* package (Wood, 2011).

## 3. Results

Over the ten years of monitoring, 138 bird species were registered in the sampled area of INP (Appendix 1). The group of passerines presented the highest average of species and also greater variation than non-passerines throughout the time (Table 1).

**Table 1** Mean, median, and standard deviation of species richness per bird group recorded in the Iguazu National Park between 2011 and 2020.

<b>Group</b>	<b>Mean</b>	<b>Median</b>	<b>SD</b>
<b>All birds</b>	71.8	74.0	10.05
<b>Non-Passerines</b>	26.1	28.0	4.72
<b>Passerines</b>	45.7	47.0	6.04
<b>Specialist Insectivorous Passerines</b>	32.9	33.5	3.25
<b>Other passerines</b>	12.8	13.5	3.68

### 3.1. Trends in alpha diversity

We found significant changes in species richness over the past ten years in the entire community, in non-passerines, in passerines, and in specialist insectivorous passerines (Fig. 3). The smoothing term of the GAMM indicated that the species richness, when considering the entire community and the non-passerines, oscillated in such a way that, approximately, every three years the species richness alternated between moments of descent and ascent (estimated degrees of freedom [edf] = 3.652,  $F = 3.465$ ,  $p = 0.01$ ; edf = 3.909,  $F = 3.572$ ,  $p < 0.01$ ). With respect to passerines and specialist insectivorous passerines, there was an approximately linear and linear reduction, respectively, in the number of species recorded per year (edf = 1.293,  $F = 5.473$ ,  $p < 0.05$ ; edf = 1,  $F = 4.653$ ,  $p < 0.05$ ). Regarding functional diversity, we found significant trends only for FDis and FDiv in specific groups. The FDis of the entire community increased significantly over the final four years (edf = 2.041,  $F = 3.615$ ,  $p < 0.05$ ), while the non-passerines group presented a significant linear increase in the FDiv (edf = 1,  $F = 4.524$ ,  $p < 0.05$ ), (Fig. 4).

All groups of birds evaluated in this study presented trends in standardized effect sizes (SES) of functional diversity metrics centered between the 1.96 and -1.96 confidence intervals. Among them, only SESFDis and SESFDiv from the entire community showed a significant temporal change (edf = 1,  $F = 5.305$ ,  $p < 0.05$ ; edf = 1,  $F = 4.755$ ,  $p < 0.05$ ), increasing and decreasing linearly. Other indices did not show significant trends (Appendix 3).

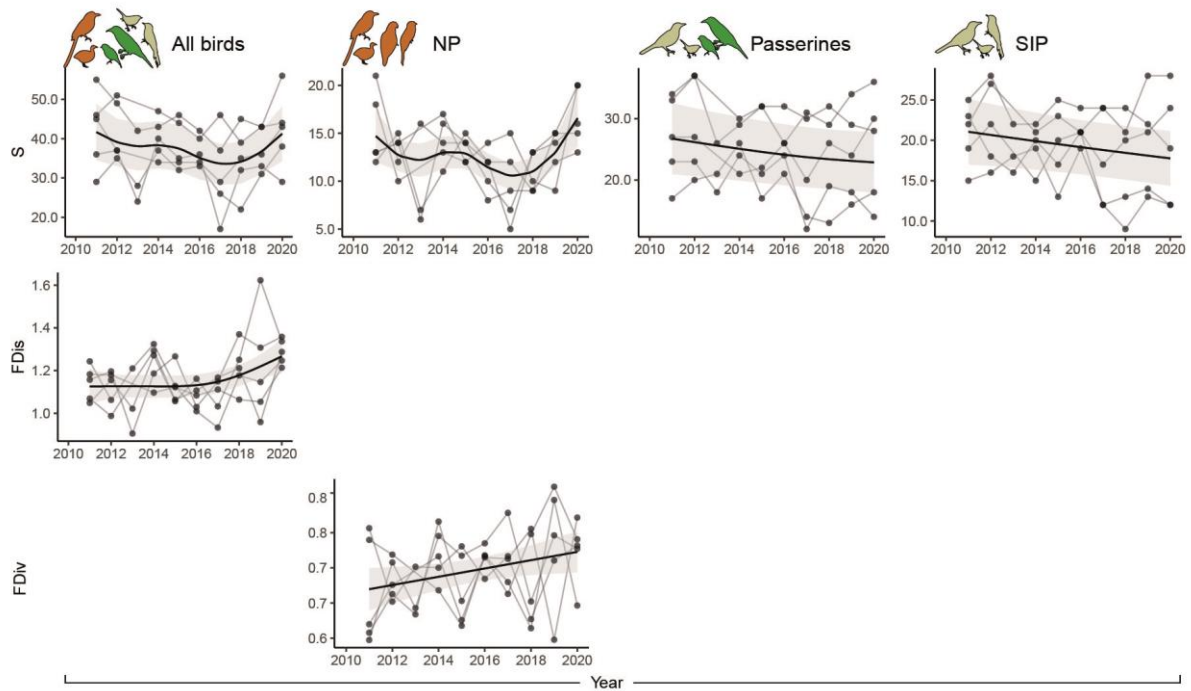


Fig. 3. Significant temporal trends in taxonomic and functional alpha diversity. Black lines represent significant generalized additive mixed-model (GAMM) general smoothing terms over time. Shaded areas represent confidence intervals. NP: Non-passerines; SIP: Specialist Insectivorous Passerines.

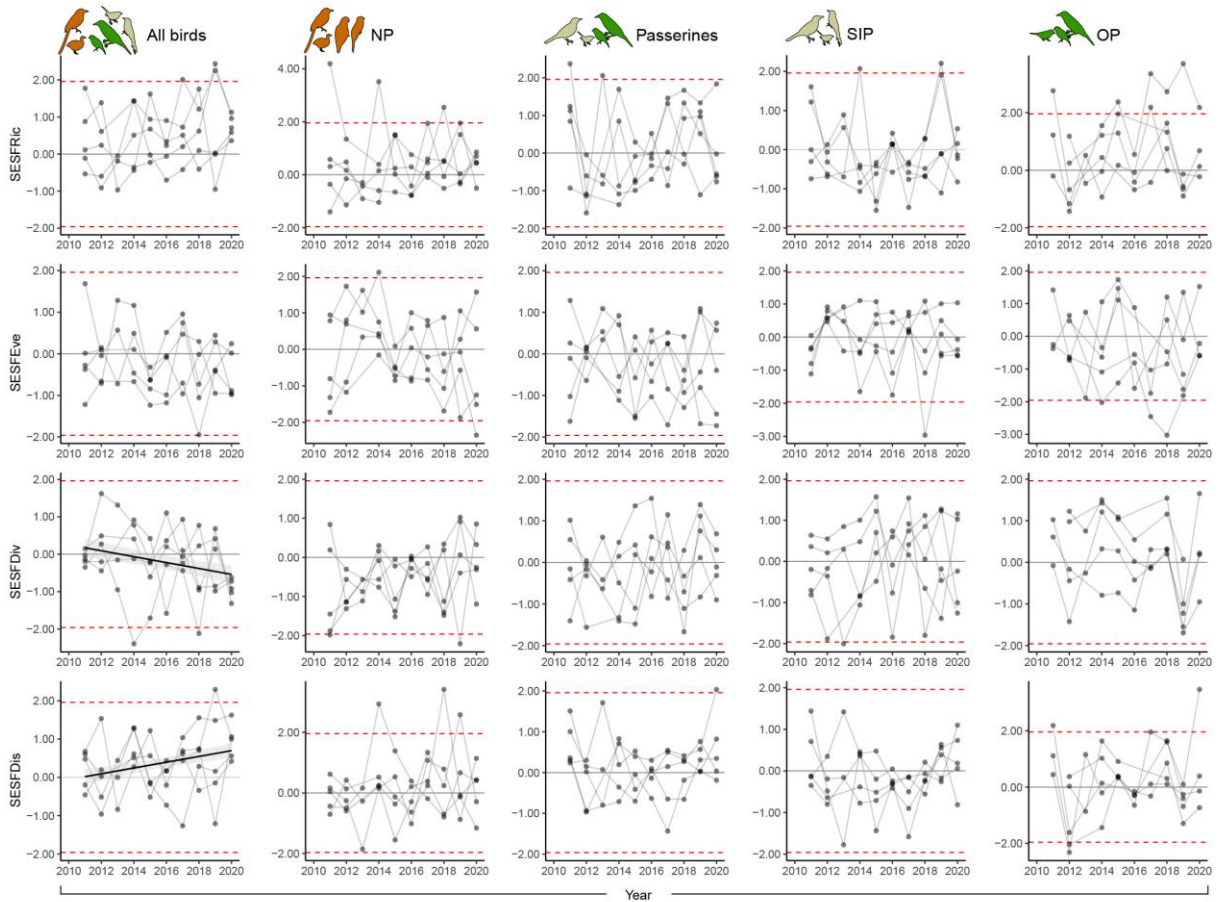


Fig. 4. Standardized effect sizes for differences between observed and expected values for the functional beta diversity of each species group. The dashed red lines represent the lower and upper limits (1.96; -1.96). Black lines represent significant generalized additive mixed-model (GAMM) general smoothing terms over time. Shaded areas represent confidence intervals. NP: Non Passerines; SIP: Specialist Insectivorous Passerines; OP: Other Passerines.

### 3.2. Trends in temporal beta diversity

The GAM indicated a significant decrease in the temporal  $\beta_{\text{SOR-Tax}}$  for passerines (edf = 1,  $F = 10.36$ ,  $p = 0.014$ ) and for the other passerines (edf = 1,  $F = 8.77$ ,  $p = 0.02$ ) (Fig. 5 e,i).  $\beta_{\text{SIM-Tax}}$  was the predominant mechanism (Wilcoxon rank sum tests,  $p < 0.001$ ) in the differentiations of the bird community over the years, except for the group of other passerines (Fig. 5 b,d,f,h,j). The functional beta diversity showed a significant negative trend in passerines (edf = 1,  $F = 6.847$ ,  $p < 0.05$ ) and other passerines (edf = 1.149,  $F = 7.467$ ,  $p = 0.02$ ; Fig. 5 o,s). Unlike the taxonomic approach, functional nesting was the predominant mechanism in specialist insectivorous passerines ( $W = 15$ ,  $p < 0.05$ ; Fig. 5 r).

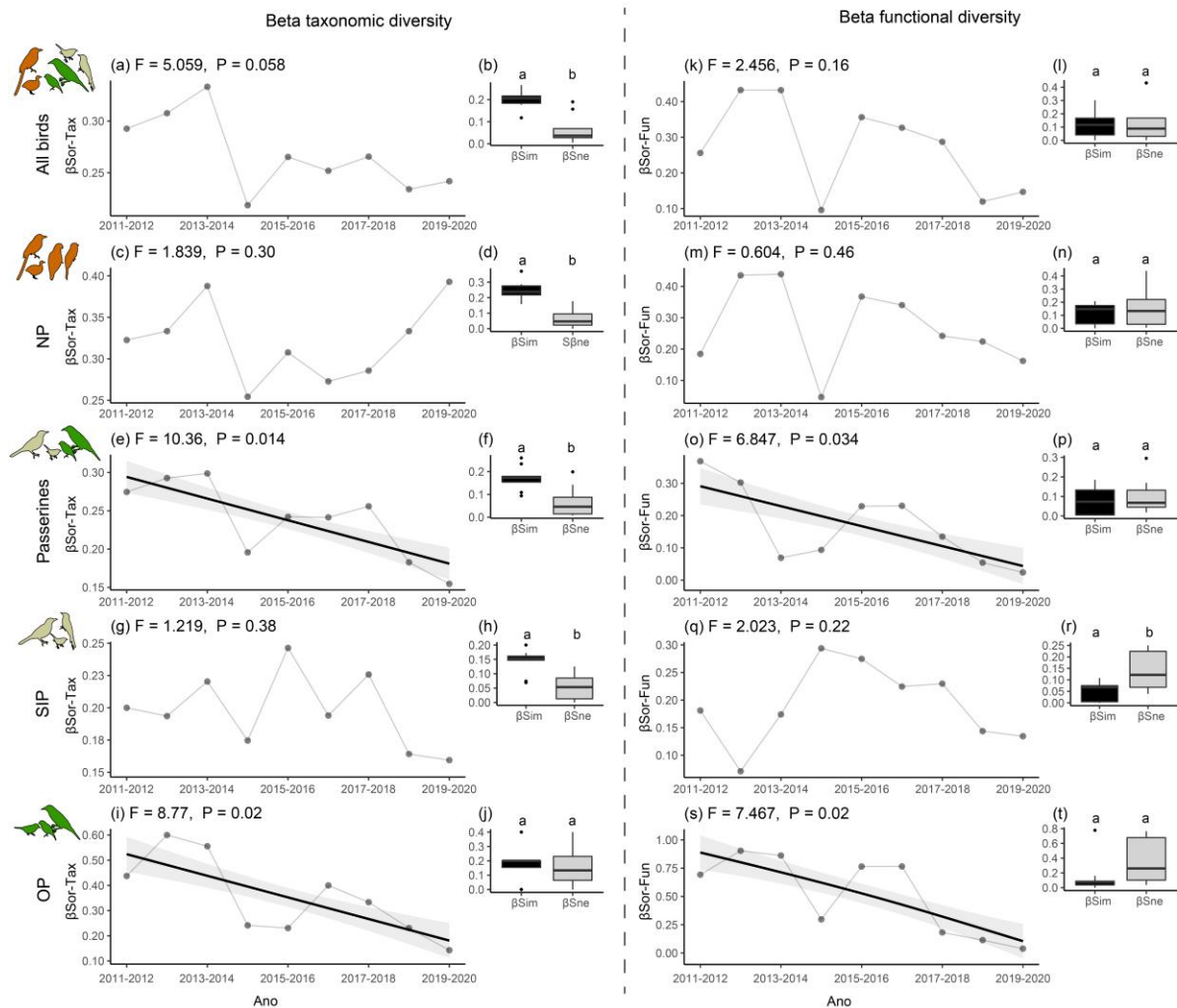


Fig. 5. Scatterplots of the taxonomic and functional temporal beta diversity values of the bird groups between two consecutive years, together with their respective box-plots for the nestedness components ( $\beta_{SNE}$ ) and temporal turnover ( $\beta_{SIM}$ ). Black lines represent significant generalized additive model (GAM) smoothing terms over time. Different letters above the box-plots represent a significant difference. Shaded areas represent confidence intervals. NP: Non-passerines; SIP: Specialist Insectivorous Passerines; OP: Other Passerines.

#### 4. Discussion

As reported for other study areas in the Neotropical region, we found that the forest bird communities in the sampled area of INP showed taxonomic changes over the temporal scale. In this study, taxonomic turnover was the main mechanism transforming species composition from one year to the next, except for the group of other passerines. However, although there was a taxonomic dynamic, the volume occupied by the communities within the functional space remained stable over the 10 years at the evaluated forest core area of INP.

Thus, we can answer that the sampled area of INP has maintained stable the functional richness of the bird community over time, even with variations in species richness and composition.

One of the many hypotheses to explain the great diversity of tropical forests is based on the temporally constant environmental conditions that, supposedly, could support the maintenance of highly diverse and stable biological resources and communities in tropical regions (e.g. Connell and Orias, 1964; Pianka, 1966). Contrary to this expected taxonomic stability, untouched areas in the Ecuadorian Amazon showed a significant reduction in the number of bird species (Blake and Loiselle, 2015), as well as a gradual variation in community composition over 14 years (Blake and Loiselle, 2016). Concomitantly, there was a reversal in guild abundance in an intact area in the Brazilian Amazon, with a decrease in insectivorous birds and an increase in frugivores captured in an interval of >35 years (Stouffer et al., 2020). This recurrent pattern suggests that bird communities present a dynamic system in the coexistence of species, resulting in variations in their species richness and composition over time, even in “untouched” tropical environments. Nevertheless, despite the significant variation in the number of species and prevalence of taxonomic turnover in bird communities over the 10 years in the sampled area of INP, all groups of birds showed stability in the functional volume occupied (FRic). Furthermore, no significant variation in the distribution of the abundance of individuals in the functional space (FEve) was recognized. These results suggest that the general taxonomic dynamics of forest bird communities in the area sampled in the INP apparently correspond to hypothetical scenario 1, where the greatest volume of alterations occurs among functionally redundant species (Díaz and Cabido, 2001) or at least a partial redundancy in fact.

#### *4.1. Mechanisms of community assembly over time*

According to the neutral theory of biodiversity, ecological communities are open and unbalanced in co-occurrence. Communities are assembled randomly by neutral dispersal, local stochastic extinction, and ecological drift; so communities are randomly structured and independent of species characteristics (Hubbell, 2001). In fact, the species richness metric can be sensitive to the size of the temporal scale of observations due to the temporal turnover generated by dispersal processes. (Adler and Lauenroth, 2003; Song et al., 2018). According to neutral theory, the results of this study demonstrate that all functional metrics standardized effect size (SESRic, SESFEve, SESFDiv, SESDis) presented trends within the confidence

interval (1.96 and -1.96). Although the SESFDis and SESFDiv from the entire community showed significant trends over time, these metrics remained within the confidence interval over the entire time scale, meaning that the observed values of the functional diversity metrics did not diverge from that expected by chance. These results indicate the random assembly of these communities (Mouchet et al., 2010) over the ten-year period of this study. Since the general species richness fluctuated along the time scale, it is possible that this is a naturally random phenomenon and that it presents a stationary trajectory on a larger time scale (Ryo et al., 2019), like the pattern of the number of species captured by Blake and Loiselle (2016) and Faaborg et al. (2007).

Variation on a fine temporal scale may be related to the effect of sampling clusters from the regional species pool (the entire area of the protected area). Since the samples in this study did not cover the entire vast area of the INP, it is true that only a fraction of an intra-forest metacommunity was sampled (Leibold et al., 2004). In fact, a total of 230 bird species have been historically recorded in the INP (Torezan et al. 2020). It seems clear that even within large forest areas, there are places with a greater or lesser probability of occurrence of certain species (Cintra and Cancelli, 2008, Tonetti and Pizo, 2016). Therefore, it is very possible that individuals of certain species search for more suitable sites within the forest. This dispersal process may have caused the disappearance of species or generated new occurrences in the sampled area of the INP over the ten years of monitoring. Species such as *Cacicus chrysopterus*, *Colonia colonus*, and *Dromococcyx pavoninus* were registered only in 2011, while some others, such as *Manacus manacus*, *Celeus galeatus*, and *Leucochloris albicollis*, were registered only from 2019 onwards. In addition, there were species that occurred in 2011 but were only registered again in 2019, as occurred with *Claravis pretiosa* and *Colaptes melanochloros* (Appendix 1). In other words, in the sampled area of INP, the annual samples were composed of a random grouping of species that occur in the protected area, which local bird dispersion events within the forest result in unregularly occurrences over time. We also believe that these dynamic dispersal events could explain species absences as reported by Faaborg et al. (2007), and Blake and Loiselle (2015, 2016).

#### 4.2. Configuration and dispersion of species in trait space

Temporal changes in the composition and distribution of the abundance of individuals in a community lead to changes in the configuration and dispersion of species in the space of functional traits (Mouillot et al., 2013). From 2016, some new species with extreme traits

were recorded in the sampling zone (e.g. *Celeus galeatus*, *Coccyzus melacoryphus*, *Accipiter striatus*, *Caracara plancus*, and *Leucochloris albicollis*) and maintained low IPA values. The occurrence of these species provided an increase in the mean deviation (functional dispersion-FDis) of the values of traits of the species of the entire community in relation to the centroid of the functional space filled by the community, that is, a greater dissimilarity between the niches occupied by the species in the community (Laliberté and Legendre, 2010; Mouillot et al., 2013). The functional dispersion of vertebrate assemblages may be high due to the high primary productivity in tropical environments (Gorczynski et al., 2021). This mechanism is based on the increase in the abundance of rare resources with the increase in biomass in the environment, which makes rare species with specialized niches viable (Evans et al., 2005). Future projections highlight the decrease in FDis in bird assemblages due to global climate change, with the expectation of a decrease in functionally specialist species, especially frugivorous bird species (Bender et al., 2019), which suggests the importance of continuity of monitoring in the INP.

Regarding the functional divergence, the portion of the community composed of non-passerines showed a significant increase over the 10 years. This is due to the increase in the abundance of dominant species and with more extreme functional traits. (e.g. *Trogon surrucura*, *Baryphthengus ruficapillus* and *Selenidera maculirostris*). This result indicates an increase in the differentiation of the niche occupied by the dominant non-passerine species, in relation to the rest of the community, resulting in less competition for resources (Villéger et al., 2008). The absence of strong competitive relationships could explain these increases in abundance, as the absence of competition can favor the maximum use of specific fitness adjusted to the environment, with a consequent population increase (MacArthur and Levins, 1967). Thus, the increase in functional divergence in communities may indicate better use of available ecosystem resources in the INP sample area (Mason et al., 2005).

#### 4.3. *The case of passerines*

Differently from all community, we found that the passerines showed a reduction in species richness, with the specialist insectivorous passerines accounted for much of this variation. The data presented here differ from other studies which suggest that passerine species tend to be faithful to their territories of occupation, maintaining stable population densities and composition, possibly due to environmental stability in tropical forests (Greenberg and Gradwohl, 1986), even in 20 years (Martínez and Gomez, 2013).

Nevertheless, insectivorous birds tend to be sensitive to vegetation disturbance (Stouffer and Bierregaard, 1995). This sensitivity may be related to its food specificity, and to small variations in vegetation and micro-habitat (Henle et al., 2004; Sodhi et al., 2004), since forest degradation causes structural (Cazzolla Gatti et al., 2014) and microclimatic alterations within the forest (Gascon et al., 2000; Laurance, 2008) with a consequent change in the proportion of food resources (arthropods) (Hamer et al., 2015; Perry et al., 2018). Although the INP has not undergone any apparent transformation, one possibility is that the global climate change can generate local microclimatic alterations compromising food resources for those specialized birds (Riddell et al., 2019).

Indeed, some studies have indicated that climate change is responsible for avian decline (e.g. Blake and Loiselle, 2015, Riddell et al., 2019). However, these global changes can employ negative or positive effects depending on the physiological requirements of each species (Gregory et al., 2009). For example, in the Mojave Desert, the main factor associated with nearly half of the variation in decline of insectivore species over the past century has been the cost of body cooling which has been increasing due to climate change and especially threatens larger species (Riddell et al., 2019). Nores (2009) stated that the bird activity and diversity have decline in the tropical and subtropical forests of South America, which could be a result from climate change. However, changes in the forest bird community in the INP caused by climate change would mean changes due to deterministic factors (e.g. environmental filters). In contrast, the results of this study indicate that all metrics standardized by size (SES) also indicate that the passerine group and specialist insectivorous passerines, in the sampled area of INP, were also driven by random processes of community assembly. Therefore, the possibility of a stationary trend in species richness over a longer time scale than that assessed in this study cannot be ruled out (Ryo et al., 2019).

None of the passerine groups showed clear trends of change over time in occupied functional volume (FRic). Indeed, it is assumed that those neotropical insectivorous bird species tend to exhibit a high overlap in resource use (Sherry et al., 2020), this highlights the high level of redundancy among these species and a greater chance of conserving the functional volume occupied by this portion of the community if taxonomic changes occur (Kang et al., 2015; Walker, 1992). On the other hand, the group of specialist insectivorous passerines was the only one to present functional nestedness as the predominant mechanism in the conformation of temporal functional beta diversity. This means that the portion of the community composed of these species has lost diversity of functional traits with the reduction in the number of species (Villéger et al., 2011). Despite the ambiguity discussed above about

the trajectory of alpha diversity in this group, it can be suggested that the reduction in species to date far has occurred with greater intensity among species with unique functional trait values (Villéger et al., 2011). Functional nestedness measures the portion of the diversity of functional traits in which a community is represented by a subset of another more functionally rich community (Villéger et al., 2013). Relating the results obtained for temporal functional beta diversity and the tendency to a reduction in species richness, the group of specialist insectivorous passerines may be undergoing a gradual and silent functional erosion (Carmona et al., 2021).

## **5. Conclusion**

Although the studied bird community experiences variations in species richness and composition, the overall functional space occupied remains stable due to redundancies, which brings stability to the system. However, we found a different result when we analyzed passerines, with a prevalence of functional nestedness in specialist insectivorous passerines over time. For this particular group, we found a concerning result that may compromise functional stability in the system in the future.

## **Acknowledgements**

The Museum of Zoology of the University of São Paulo allowed us to measure bird specimens, where we were assisted by L.F.S. The Chico Mendes Institute for Conservation of Biodiversity (ICMBio, Brasília) gave us permission (24483) to study birds in the Iguassu National Park, where we had the assistance of A.N.S.R., R. N., and T. O. We thank Ph.D. Gabriela Menezes Bochio, Ph.D. Barbara Rocha Arakaki Lindsey, and Ph.D. Larissa Corsini Calsavara for measuring the bird specimens at the Zoology Museum of São Paulo (MZUSP). We also thank Ph.D. Bia de Arruda Almeida for her help in brainstorming at the beginning of this study, and to the editor and two anonymous reviewers for comments that improved earlier versions of the manuscript.

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**Appendix 2.** Information on traits related to food item, forest stratum for foraging, body mass, morphometry, foraging substrate, direction of foraging and locomotion strategy.

Order	Species	Used for all bird																																									
		Used only for passerines																																									
		Diet								Foraging forest strata							Body mass	Morphological measurements					Foraging substrate							Foraging orientation			Locomotion strategy										
Diet-Inv	Diet-ManBif	RepAmP	Diet-Scav	Diet-Fruit	Diet-Nect	Diet-Seed	Diet-OPlant	ForStrat-waterround	ForStrat-ground	ForStrat-understory	ForStrat-midhigh	ForStrat-canopy	ForStrat-aerial	Mass	Bill length	Bill width	Bill height	Wing length	Tail length	Lite r	Live leaves	Dead leaves	Vines	Bambo o	Branches	Trunks	Dead trunks	Moss/Lichen	Bromeliads	Aerial	Substrate	Target	Perc h	Walk, Hop	Climb	Sally, Strike	Sally, Hover	Hawk					
Accipitriformes	<i>Accipiter striatus</i>	0	100	0	0	0	0	0	0	0	0	25	25	25	25	130.6	16.2	8.4	10.1	183.3	153.9																						
Psittaciformes	<i>Amazona aestiva</i>	0	0	0	0	50	0	50	0	0	0	30	40	30	0	451.0	31.0	18.3	29.8	213.2	154.4																						
Passeriformes	<i>Anabacerthia lichtensteini</i>	100	0	0	0	0	0	0	0	0	0	0	50	50	0	21.0	20.7	4.7	5.4	79.2	76.7	0	1	2	1	0	2	0	0	1	1	0	2	0	2	0	1	0	0	0	0		
Passeriformes	<i>Automolus leucophthalmus</i>	100	0	0	0	0	0	0	0	0	0	80	20	0	0	34.5	28.1	5.7	6.5	84.1	86.6	1	1	2	0	2	0	0	0	0	0	0	2	0	1	2	0	0	0	0	0		
Coraciiformes	<i>Baryphengus ruficapillus</i>	60	10	10	0	20	0	0	0	0	0	50	20	30	0	141.7	43.5	12.1	12.9	147.4	231.2																						
Passeriformes	<i>Basileuterus culicivorus</i>	80	0	0	0	20	0	0	0	0	0	70	30	0	0	10.5	14.7	4.5	3.9	55.5	58.4	0	2	0	1	0	2	0	0	0	0	0	0	2	1	2	0	0	0	1	0		
Passeriformes	<i>Cacicus chrysopterus</i>	50	0	0	0	50	0	0	0	0	0	80	20	0	0	36.2	23.9	7.7	8.9	99.7	95.6	0	1	0	0	0	1	0	0	2	2	0	2	0	2	0	0	0	0	0	0		
Passeriformes	<i>Cacicus haemorrhous</i>	60	0	0	0	20	20	0	0	0	0	20	60	20	0	83.7	31.5	8.0	10.2	154.1	108.3	0	1	0	0	0	1	0	0	2	2	0	2	0	2	0	0	0	0	0	0		
Passeriformes	<i>Cacicus solitarius</i>	100	0	0	0	0	0	0	0	0	0	40	60	0	0	79.8	25.0	10.8	13.0	NA	104.7	0	1	0	0	0	0	2	2	0	2	0	2	0	0	0	0	0	0	0	0		
Piciformes	<i>Campophylus robustus</i>	100	0	0	0	0	0	0	0	0	0	30	40	30	0	200.0	49.5	13.0	13.9	191.8	138.2																						
Passeriformes	<i>Campostoma obsoletum</i>	70	0	0	0	30	0	0	0	0	0	80	20	0	0	8.1	12.5	3.4	3.0	50.6	44.6	0	2	0	0	0	0	0	0	0	0	2	0	2	1	0	0	1	1	1	1		
Passeriformes	<i>Capsiempis flaveola</i>	90	0	0	0	10	0	0	0	0	0	100	0	0	0	7.7	13.2	4.3	3.7	48.0	49.9	0	1	0	2	2	0	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	
Falconiformes	<i>Caracara plancus</i>	20	0	20	60	0	0	0	0	0	0	100	0	0	0	1078.6	41.2	27.4	27.6	369.0	260.4																						
Piciformes	<i>Celeus flavescens</i>	70	0	0	0	30	0	0	0	0	0	20	30	50	0	139.0	34.5	10.8	10.4	152.9	109.2																						
Piciformes	<i>Celeus galeatus</i>	100	0	0	0	0	0	0	0	0	0	50	50	0	0	124.0	35.1	9.4	9.5	172.0	135.3																						
Passeriformes	<i>Chamaeza campanisona</i>	70	0	0	0	30	0	0	0	0	0	80	20	0	0	90.6	28.5	6.6	6.6	95.0	67.6	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	
Passeriformes	<i>Chiroxiphia caudata</i>	50	0	0	0	50	0	0	0	0	0	50	50	0	0	25.6	13.5	5.7	5.3	77.4	65.0	0	2	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	0	
Passeriformes	<i>Chlorophonia cyanea</i>	10	0	0	0	90	0	0	0	0	0	0	20	80	0	14.0	10.3	5.7	5.2	62.0	34.9	0	2	0	0	0	1	0	0	2	0	0	2	1	2	0	0	0	1	2	0	0	
Apodiformes	<i>Chlorostilbon lucidus</i>	10	0	0	0	0	90	0	0	0	0	90	10	0	0	3.5	19.5	3.1	2.1	49.9	30.6																						
Passeriformes	<i>Cissopis leverianus</i>	30	0	0	0	70	0	0	0	0	0	20	30	20	0	76.0	18.5	8.8	10.1	113.5	168.8	0	1	0	0	0	0	2	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0
Columbiformes	<i>Claravis pretiosa</i>	20	0	0	0	0	0	80	0	0	0	0	0	0	0	68.2	17.2	2.4	3.6	111.8	85.4																						
Cuculiformes	<i>Coccyzus melacoryphus</i>	100	0	0	0	0	0	0	0	0	0	50	30	20	0	49.7	25.3	6.7	7.8	113.6	145.8																						
Piciformes	<i>Colaptes melanochlorus</i>	80	0	0	0	10	10	0	0	0	0	50	50	0	0	127.3	31.2	8.5	8.0	144.1	123.8																						
Passeriformes	<i>Colonia colonus</i>	100	0	0	0	0	0	0	0	0	0	30	70	0	0	18.3	12.5	5.4	4.1	80.5	162.0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	2
Passeriformes	<i>Canirostrum speciosum</i>	70	0	0	0	10	0	10	10	0	0	60	20	20	0	8.8	10.5	3.5	3.2	57.9	46.3	0	2	0	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	1	0	0	
Passeriformes	<i>Canopias trivirgatus</i>	100	0	0	0	0	0	0	0	0	0	30	70	0	0	24.4	13.8	5.5	5.3	64.9	54.5	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	2	
Passeriformes	<i>Conopophaga lineata</i>	100	0	0	0	0	0	0	0	0	0	40	0	0	0	25.2	21.1	5.4	4.8	67.3	52.5	2	2	0	0	2	0	0	0	0	0	0	2	0	2	2	0	0	0	0	0	0	



Passeriformes	<i>Manacus manacus</i>	10	0	0	0	90	0	0	0	0	0	80	20	0	0	16.7	13.7	5.0	4.1	47.7	38.8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	2	0	0				
Passeriformes	<i>Megarynchus pitangua</i>	70	0	0	0	10	0	10	0	0	0	10	50	40	0	69.9	31.0	17.0	11.8	110.4	92.7	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	2	2	0			
Strigiformes	<i>Megascops choliba</i>	90	0	0	0	0	0	0	0	0	0	40	50	0	0	132.0	19.1	16.1	14.0	178.4	100.0																									
Piciformes	<i>Melanerpes formicivorus</i>	30	0	0	0	40	0	30	0	0	0	50	50	0	0	57.8	29.9	6.6	6.1	111.2	68.8																									
Falconiformes	<i>Microastur ruficollis</i>	0	20	80	0	0	0	0	0	0	0	40	30	30	0	0	177.6	19.7	8.5	12.2	165.8	198.6																								
Falconiformes	<i>Microastur semitorquatus</i>	0	80	20	0	0	0	0	0	0	0	50	30	20	0	0	621.7	30.7	12.0	18.3	265.0	293.0																								
Passeriformes	<i>Mionectes rufiventris</i>	50	0	0	0	50	0	0	0	0	0	10	90	0	0	13.3	17.4	5.0	3.9	66.1	58.3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	2	1		
Passeriformes	<i>Myiarchus swainsoni</i>	70	0	0	0	20	0	10	0	0	0	100	0	0	0	25.1	21.4	8.2	5.7	87.5	87.3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	2	1	
Passeriformes	<i>Myiodinastes maculatus</i>	40	0	30	0	30	0	0	0	0	0	0	100	0	0	43.2	21.4	12.3	8.8	106.6	87.0	0	2	0	0	0	2	0	0	0	0	0	0	0	2	0	2	0	1	0	0	0	2	2		
Passeriformes	<i>Myiopagis caniceps</i>	80	0	0	0	20	0	0	0	0	0	0	0	100	0	10.5	12.5	5.7	4.4	62.8	65.4	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	2	0	
Passeriformes	<i>Myiopagis viridicata</i>	60	0	0	0	20	0	20	0	0	0	0	50	50	0	11.5	12.4	4.9	3.8	60.3	58.8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	2	2	0	
Passeriformes	<i>Myiornis auricularis</i>	100	0	0	0	0	0	0	0	0	0	50	50	0	0	5.3	13.1	3.4	2.5	36.9	29.6	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	2	2	0		
Passeriformes	<i>Myiathypis leucoblephara</i>	100	0	0	0	0	0	0	0	0	0	50	50	0	0	15.1	16.6	4.8	3.8	63.3	66.2	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	2	2	0	0	0	0		
Passeriformes	<i>Myiathypis rivularis</i>	100	0	0	0	0	0	0	0	0	0	80	20	0	0	13.5	16.3	5.2	4.1	62.9	60.9	2	2	0	0	0	0	0	0	0	0	2	0	0	0	0	2	1	0	2	0	2	0	0		
Piciformes	<i>Nonnula rubecula</i>	100	0	0	0	0	0	0	0	0	0	50	50	0	0	18.4	23.2	6.6	6.6	61.2	64.1																									
Piciformes	<i>Natharchus swainsoni</i>	80	0	0	0	0	0	0	10	0	33	33	33	0	0	60.7	39.5	14.5	13.8	107.7	89.9																									
Galliformes	<i>Odontophorus capueira</i>	0	0	0	0	80	0	20	0	0	0	100	0	0	0	425.4	19.3	9.8	12.2	144.9	85.5																									
Passeriformes	<i>Pachyrhamphus polychaetus</i>	50	0	0	0	50	0	0	0	0	0	0	100	0	0	20.8	17.2	7.5	6.2	73.6	70.8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	2	0	
Columbiformes	<i>Patagioenas cayennensis</i>	0	0	0	0	70	0	30	0	0	0	20	0	40	40	0	229.0	23.9	4.4	5.0	183.0	112.8																								
Columbiformes	<i>Patagioenas picazuro</i>	10	0	0	0	30	0	30	30	0	0	30	30	30	10	0	279.0	26.8	4.6	6.1	213.2	126.2																								
Galliformes	<i>Penelope superciliosa</i>	10	0	0	0	90	0	0	0	0	0	33	0	33	33	0	895.0	36.6	11.3	10.7	250.6	310.2																								
Apodiformes	<i>Phaethornis eurynome</i>	10	0	0	0	0	90	0	0	0	0	100	0	0	0	5.3	34.9	2.9	2.7	55.1	61.5																									
Passeriformes	<i>Philydor atricapillus</i>	100	0	0	0	0	0	0	0	0	0	33	33	33	0	22.2	16.1	7.5	5.9	82.4	75.6	0	1	2	1	0	2	0	0	1	2	0	0	2	0	2	0	2	0	0	1	0	0	0		
Passeriformes	<i>Philydor rufum</i>	100	0	0	0	0	0	0	0	0	0	0	40	60	0	25.0	22.6	5.2	5.6	83.2	90.9	0	2	1	1	0	2	0	0	1	1	0	2	0	2	0	0	1	0	0	0	0				
Passeriformes	<i>Phyllomyias fasciatus</i>	80	0	0	0	20	0	0	0	0	0	0	0	100	0	10.3	9.8	4.9	3.3	60.0	53.1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	2	2	0		
Passeriformes	<i>Phyllomyias virescens</i>	70	0	0	0	30	0	0	0	0	0	10	50	40	0	8.2	10.2	5.3	3.1	60.2	56.6	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	2	2	0		
Passeriformes	<i>Phylloscartes eximius</i>	100	0	0	0	0	0	0	0	0	0	0	100	0	0	7.5	14.3	4.9	3.1	53.3	51.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	2	0		
Passeriformes	<i>Phylloscartes paulista</i>	100	0	0	0	0	0	0	0	0	0	50	50	0	0	7.5	13.9	2.9	3.1	45.0	44.1	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	2	0		
Passeriformes	<i>Phylloscartes ventralis</i>	100	0	0	0	0	0	0	0	0	0	0	100	0	0	8.3	15.5	3.4	3.6	49.4	51.2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	2	0		
Cuculiformes	<i>Piaya cayana</i>	100	0	0	0	0	0	0	0	0	0	0	20	80	0	102.0	32.2	9.3	10.8	168.6	344.8																									
Piciformes	<i>Picumnus temminckii</i>	100	0	0	0	0	0	0	0	0	0	80	20	0	0	11.5	11.4	6.4	4.9	53.3	34.8																									
Psittaciformes	<i>Pionopsitta pileata</i>	0	0	0	0	40	0	30	30	0	0	0	60	40	0	119.0	18.0	12.3	17.7	144.2	88.8																									
Psittaciformes	<i>Pionus maximiliani</i>	0	0	0	0	10	0	70	20	0	0	30	50	20	0	293.0	24.7	18.7	23.9	184.8	106.4																									
Passeriformes	<i>Pipra fasciicauda</i>	10	0	0	0	90	0	0	0	0	0	50	50	0	0	15.9	10.8	5.3	4.1	63.5	31.3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	2	0		



Passeriformes	<i>Turdus albicollis</i>	60	0	0	0	40	0	0	0	0	80	0	20	0	0	54.0	26.5	6.0	6.1	112.5	90.2	2	2	0	0	0	0	0	0	0	0	0	2	0	2	2	0	0	0	0	
Passeriformes	<i>Turdus amaurochalinus</i>	40	0	0	0	60	0	0	0	0	20	20	30	30	0	57.9	24.5	5.5	6.1	112.4	96.5	2	2	0	0	0	0	0	0	0	0	1	2	1	2	2	0	1	0	0	
Passeriformes	<i>Turdus leucometas</i>	70	0	0	0	30	0	0	0	0	60	20	20	0	0	69.1	26.0	6.0	6.2	121.0	102.3	2	1	0	0	0	0	0	0	0	0	0	2	0	1	2	0	0	0	0	
Passeriformes	<i>Turdus rufiventris</i>	50	0	0	0	50	0	0	0	0	100	0	0	0	0	69.4	26.3	6.0	6.6	118.7	102.3	2	1	0	0	0	0	0	0	0	0	2	0	1	2	0	0	0	0		
Passeriformes	<i>Turdus subalaris</i>	40	0	0	0	60	0	0	0	0	20	40	40	0	0	49.5	19.3	11.0	6.8	109.7	87.1	0	2	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0		
Piciformes	<i>Veniliornis spilogaster</i>	80	0	0	0	20	0	0	0	0	0	50	50	0	0	40.3	26.7	6.1	5.7	96.6	63.4																				
Passeriformes	<i>Vireo olivaceus</i>	60	0	0	0	20	0	20	0	0	0	0	20	80	0	16.1	19.9	4.1	4.1	70.8	55.9	0	2	0	0	0	1	0	0	0	0	0	0	0	1	2	2	0	0	0	0
Passeriformes	<i>Xenops rutilans</i>	100	0	0	0	0	0	0	0	0	0	20	80	0	0	11.2	16.6	3.7	4.9	64.3	56.3	0	0	0	1	0	2	2	1	0	0	0	0	2	0	0	0	2	0	0	0
Passeriformes	<i>Xiphocolaptes albicollis</i>	80	10	0	0	0	0	0	0	0	0	0	100	0	0	118.0	44.5	11.7	10.3	127.9	117.0	0	0	0	1	0	1	2	2	1	2	0	2	1	0	0	2	1	0	0	
Passeriformes	<i>Xiphorhynchus fuscus</i>	100	0	0	0	0	0	0	0	0	0	50	50	0	0	21.8	24.0	8.4	5.6	79.6	71.9	0	0	1	1	0	1	2	0	2	2	0	2	0	0	0	2	1	0	0	

**Appendix 3.** Information on the General Additive Mixed Modeling (GAMM) of alpha diversity indices (taxonomic and functional) and the Standardized Effect Size (SES) of alpha functional diversity indices, as well as the General Additive Modeling of temporal taxonomic and functional beta diversity.

Table A1. General additive mixed modeling of alpha diversity indices through time for bird communities in Iguazu National Park, Paraná, Brazil. Significant p-values are shown in bold. S = species richness; FRic = Functional richness; FEve = Functional evenness; FDis = Functional dispersion; FDiv = Functional divergence.

<b>Alfa diversity index</b>	<b>Estimated degrees of freedom</b>	<b>F statistics</b>	<b>p-value</b>	<b>Adj. R-square</b>
S_All birds	3.652	3.465	<b>0.011</b>	0.078
S_Non-passerines	3.909	3.572	<b>0.009</b>	0.301
S_Passerines	1.29	5.473	<b>0.027</b>	-0.001
S_Specialist Insectivorous Passerines	1	4.653	<b>0.036</b>	0.008
S_Other passerines	2.09	2.397	0.103	0.071
FRic_All birds (log+1)	2.028	1.235	0.288	0.022
FRic_Non-passerines (log+1)	2.293	1.456	0.193	0.059
FRic_Passerines (log+1)	1.725	0.587	0.406	-0.005
FRic_Specialist Insectivorous Passerines	1.502	0.454	0.425	0.018
FRic_Other passerines (log+1)	1	0.021	0.885	-0.027
FEve_All birds	1	0.219	0.642	-0.020
FEve_Non-passerines	3.526	2.358	0.162	0.105
FEve_Passerines	1	1.356	0.25	0.013
FEve_Specialist Insectivorous Passerines	1	0.097	0.756	-0.015
FEve_Other passerines	1	1.215	0.277	-0.004
FDis_All birds	2.041	3.6015	<b>0.029</b>	0.131
FDis_Non-passerines (log+1)	1	0.899	0.348	-0.001
FDis_Passerines	1.784	0.991	0.257	0.004
FDis_Specialist Insectivorous Passerines (log+1)	1	1.309	0.258	-0.005
FDis_Other passerines	1	0.024	0.877	-0.025
FDiv_All birds	1	2.843	0.098	0.024
FDiv_Non-passerines	1	4.524	<b>0.038</b>	0.073
FDiv_Passerines	1	0.171	0.681	-0.020
FDiv_Specialist Insectivorous Passerines	1	1.206	0.278	-0.036
FDiv_Other passerines	1	2.456	0.125	0.014

Table A2. General additive mixed modeling of the standardized effect size (SES) of alpha functional diversity indices across time for bird communities in Iguazu National Park, Paraná, Brazil. Significant p-values are shown in bold. S = species richness; FRic = Functional richness; FEve = Functional evenness; FDis = Functional dispersion; FDiv = Functional dispersion.

<b>SES(Index)</b>	<b>Estimated</b>	<b>F statistics</b>	<b>p-value</b>	<b>Adj. R-square</b>
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	degrees freedom	of		
FRic_All birds	1		3.153	0.082
FRic_Non-passerines	1		0.206	0.652
Fric_Passerines	1.413		0.238	0.589
FRic_Specialist	2.005		1.553	0.22
Insectivorous Passerines				
FRic_Other passerines	1		0.603	0.442
FEve_All birds	1		2.169	0.148
FEve_Non-passerines	1		3.159	0.082
FEve_Passerines	1		1.346	0.252
FEve_Specialist	1		0.045	0.823
Insectivorous Passerines				
FEve_Other passerines	1		1.014	0.32
FDis_All birds	1		5.305	<b>0.025</b>
FDis_Non-passerines	1		1.305	0.259
FDis_Passerines	2.407		2.763	0.058
FDis_Specialist	2.156		2.615	0.071
Insectivorous Passerines				
FDis_Other passerines	1		0.49	0.488
FDiv_All birds	1		4.755	<b>0.034</b>
FDiv_Non-passerines	1		3.979	0.052
FDiv_Passerines	1		1.627	0.209
FDiv_Specialist	1.232		0.225	0.774
Insectivorous Passerines				
FDiv_Other passerines	1		2.367	0.132

Table A3. General additive modeling of temporal taxonomic and functional beta diversity (Sorensen dissimilarity index -  $\beta_{\text{SOR}}$ ) through time for bird communities in Iguazu National Park, Paraná, Brazil. Significant p-values are shown in bold. Tax = Taxonomic; Fun = Functional.

Sorensen index	dissimilarity	Estimated degrees freedom	F statistics	p-value	Adj. R-square
$\beta_{\text{SOR-Tax}}$	All birds	1	5.059	0.059	0.337
$\beta_{\text{SOR-Tax}}$	Non-passerines	2.35	1.839	0.307	0.313
$\beta_{\text{SOR-Tax}}$	Passerines	1	10.36	<b>0.014</b>	0.539
$\beta_{\text{SOR-Tax}}$	Specialist	1.691	1.219	0.376	0.158
Insectivorous Passerines					
$\beta_{\text{SOR-Tax}}$	Other passerines	1	8.77	<b>0.020</b>	0.493
$\beta_{\text{SOR-Fun}}$	All birds	1	2.456	0.161	0.154
$\beta_{\text{SOR-Fun}}$	Non-passerines	1	0.604	0.462	-0.052
$\beta_{\text{SOR-Fun}}$	Passerines	1	6.847	<b>0.034</b>	0.42
$\beta_{\text{SOR-Fun}}$	Specialist	2.479	2.023	0.217	0.419
Insectivorous Passerines					
$\beta_{\text{SOR-Fun}}$	Other passerines	2.097	7.467	<b>0.021</b>	0.543

### 3. CAPÍTULO 2

#### **High vegetation conservation brings greater taxonomic and functional stability to bird communities of Atlantic rainforest although lower species richness**

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**Artigo a ser publicado no periódico Journal for Nature Conservation**

<https://www.elsevier.com/journals/journal-for-nature-conservation/1617-1381/guide-for-authors>

**Abstract**

Although selectively logged tropical forests have high bird species richness, it is known that their species composition is substantially changed when compared with intact forests. Thus, we need to improve the understanding on how functional trait diversity of birds is affected in this habitat type in order to support the development of more effective conservation actions to maintain functional roles and community stability. Here, we evaluate traits responses to variations in vegetation conservation status and how the pattern of niche occupancy is affected by this increase in species richness. We then evaluated the effects of vegetation conservation status in the Atlantic Forest on range of trait space occupied, niche packing, and trait composition in local bird communities. We also evaluate the mechanisms driving niche expansion and packing using null models. Our results show that trait composition changes in communities: (1) lower vegetation's conservation increases foraging in understory and consumption of grains and ectothermic vertebrates by birds; (2) higher vegetation's conservation drives higher and wider beaks and increase foraging for invertebrates in canopy. We also found that lower vegetation's conservation not only is associated with the increase of species richness, but also with both expansion and packing of niche space occupied by the community. However, only niche packing had predominantly smaller values than expected by chance, indicating a strong effect of environmental filters on niche occupancy density. Although bird assemblages in more intact forests have lower species richness, they have greater functional distance between bird species suggesting greater stability, with a low probability of local extinctions due to a lower intensity of interspecific competition. This demonstrates that isolated assessments of species richness are potentially illusory and can lead to unsuccessful conservation measures, such as proposing selective logging in primary forests based on the supposed benefit of increased bird species richness. Furthermore, the functional composition tends to change with changes in vegetation conservation status, thus altering the functional role provided by communities. Consequently, forests with high vegetation conservation status should be maintained, despite the lower species richness.

**Keywords:** Environmental filters; forest conservation; niche packing; selective logging; species richness; trait composition

## 1. Introduction

The distribution of bird species is closely related to vegetation structure, which filters food availability, microhabitat, locomotion, and nesting sites for a given community (Hewson, Austin, Gough & Fuller, 2011; James, 1971; Lu, Jia, Lloyd & Sun, 2012; Mason, 1996). Some factors, such as canopy cover, foliage height, and plant species diversity are recognized to positively affect bird species richness in different ecoregions (Joshi, Bhatt & Thapliyal, 2012; Kukreti, 2020). In some situations, human actions that interfere with vegetation density can affect bird species richness and composition (Beskardes, et al., 2018; Hanle, Duguid & Ashton, 2020). In a study case in Venezuela, increased understory density in selectively logged forest was the main environmental factor driving the dissimilarity between bird communities when compared to original integrity forests (Mason, 1996). These dissimilarities are due to the different responses of the species to the variations in the integrity of the vegetation structure, which can vary according to the type of habitat, latitude, and regional species pool (Almazán-Núñez, Arizmendi, Eguiarte & Corcuera, 2015; Burivalova, et al., 2015; Burivalova, Şekercioğlu & Koh, 2014; Yamamoto, 2000). But, some questions are yet unclear when there is a change in the integrity of the forest vegetation, such as: how is the functional diversity of the bird community affected, which functional traits are affected, and how are the species distributed in the niche space (Ibarra, Martin, Cockle & Martin, 2017; Pigot, Trisos & Tobias, 2016; Schaaf, Gomez, Tallei, Vivanco & Ruggera, 2021).

Birds play vital roles in ecosystem functioning, such as seed dispersal, pest control, and pollination (Sekercioglu, 2006). However, classical diversity metrics are limited in understanding the influence of disturbances on the functional roles provided by communities (Díaz & Cabido, 2001). Conversely, in a functional diversity perspective, species are seen as “packages” of functional traits, which may have an “effect” on other trophic levels or on ecological processes (see Bello, et al., 2021). Accordingly, the ecological functions provided by communities depend on how these traits are affected by variations in habitat (Bender, et al., 2019; Burivalova, et al., 2015; Cosset & Edwards, 2017). It should also be noted that the occurrence and fitness of a species depend on the adjustment of its “response” traits to the set of environmental conditions (Balda, 1975; Bello, et al., 2021; McGarigal, Wan, Zeller, Timm & Cushman, 2016). Therefore, the diversity of functional traits allows for better understanding and prospection of the impacts generated by alterations in the specific composition of communities (Díaz & Cabido, 2001).

In this study, our focus is to understand how the decrease in the conservation status of

the vegetation integrity, due to selective logging, affects bird communities in seasonal semideciduous forest in the Atlantic Forest. Selective logging can generate severe alterations in vegetation structure, due to the opening of clearings and roads, which impact the global biogeochemistry of the forest ecosystem (Schliemann & Bockheim, 2011; Thiollay, 1992; Uhl, Veríssimo, Mattos, Brandino & Vieira, 1991). Among the main abiotic alterations are the increase in light and temperature input, decrease in relative humidity, and alterations in the physicochemical characteristics of the soil (He, et al., 2019; Yamamoto, 2000). In the case of vegetation, it may show a reduction in the number of species and biomass (Gatti, et al., 2014), even after 150 years of restoration, may not return to its original integrity (Brown & Gurevitch, 2004), which is often a consequence of the establishment of invasive plants (Arellano-Cataldo & Smith-Ramírez, 2016; Driscoll, et al., 2016).

Several studies indicate that bird species richness tends to increase in selectively logged tropical forests (Aleixo, 1999; Burivalova, et al., 2014; Edwards, et al., 2014). However, there is a considerable alteration in species composition (Aleixo, 1999), with a selective effect that favors habitat generalist species, while forest specialist species are extirpated (Burivalova, et al., 2014; Thiollay, 1992). Thus, although species richness per se increases, the impact of this on ecosystem processes and functional structure is not known, as the change in specific composition leads to changes in the “packages” of functional traits (Díaz & Cabido, 2001). In this sense, depending on how the species are distributed in the ecological niche space, two distinct occupation patterns can be observed (Pigot, et al., 2016; Swenson & Weiser, 2014): the expansion of the occupied niche space or its densification. In the first case, within the limiting similarity theory, the accumulation of species in the assemblage can lead to the expansion of the occupied niche space, since similar species tend toward competitive exclusion, so a new species would need to occupy new regions of the niche space (MacArthur & Levins, 1967). In the second case, the increase in species richness can lead to a more tightly packed niche space due to a finer specialization or the overlap of functionally similar species in the occupied niche space (Karr & James, 1975; Klopfer & MacArthur, 1961).

Changes in vegetation would enable the emergence of novel regions of niche space that could be filled by new trait packages, thus expanding the niche space occupied (Oliveira & dos Anjos, 2022), but niche expansion and packing are not exclusive and may occur simultaneously. Nevertheless, results from recent studies (dos Anjos, et al., 2019; Oliveira, Gouveia, Ruiz-Esparza & Ferrari, 2020), indicate that alterations in habitat can cause changes in the influence of deterministic processes on community assembling, causing one of these

models to become predominant in communities (Pigot, et al., 2016). Thus, it is uncertain if the reduction in conservation status due to selective logging, which leads to lower vegetation integrity and higher bird species richness, will drive a predominance of niche packing or an expansion of the niche by the occupation. Therefore, the present study has the key objective of investigating whether changes in the taxonomic diversity of birds across the vegetation conservation status gradient, resulting from selective logging, also influence the diversity and functional structure of the communities. Here, we used ecomorphological traits on a fine spatial scale to obtain indices that represent different facets of functional diversity (Bello, et al., 2021). Based on these indices, we seek to understand how the functional composition and the occupation of the ecological niche space of communities change with the integrity of the vegetation.

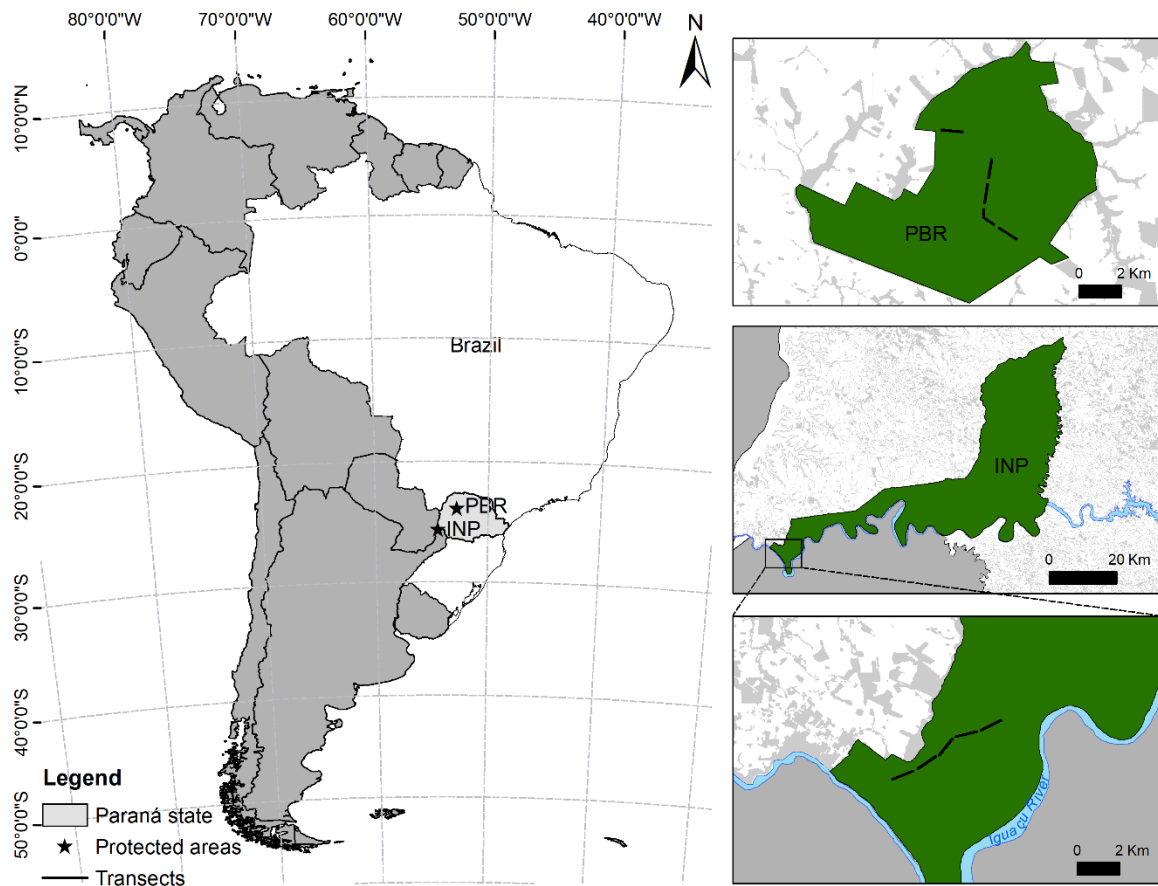
Theoretically, environments with greater resource availability and complexity tend to provide niche packing by providing an increase in specialization, smoothing the limiting similarity rule (MacArthur, 1965; Sherry, Kent, Sánchez & Şekercioğlu, 2020). That said and based on previous studies, we expect that: a) bird species richness increases with the reduction in conservation of vegetation integrity, but without significant expansion of the niche space occupied by the introduction of functionally close species (Ibarra, et al., 2017; Mouchet, Villéger, Mason & Mouillot, 2010; Schaaf, et al., 2021); b) for the same reason, assemblies in areas of lower vegetation conservation status presents greater niche packing than expected due to the increased influence of environmental filters on the assembling of the communities; and c) the composition of functional traits gradually changes along the conservation of vegetation integrity gradient due to changes in the ecological niche generated by vegetation alterations, with the main changes being in the proportions of consumption of food items and in the average body mass of taxocenosis with the decrease in vegetation conservation status (Burivalova, et al., 2015; Burivalova, et al., 2014; Hewson, et al., 2011).

## **2. Materials and methods**

### **Study area**

This study was carried out in two protected areas located in the state of Paraná, in southern Brazil (Fig. 1): Iguaçu National Park (INP, 25°37'44.56"S, 54°27'49.69"W), with an extension of 185.262 ha, and the Perobas Biological Reserve (PBR, 23°51'38.98"S, 52°44'21.70"W), with an extension of 8.716 ha. These protected areas are located in the Cfa climate zone, defined by the Köppen-Geiger classification system, characterized by a humid

subtropical climate with hot and humid summers and mild to cold winters, with annual average precipitation and temperature of 1712mm and 20.7 °C (Peel, Finlayson & McMahon, 2007). The predominant phytophysionomic formation in both units is Semideciduous Atlantic Forest (SAF) (Dettke, Crespão, Siquerolo, Siqueira & Caxambú, 2018; Souza, Machado, Galvão & Figueiredo-Filho, 2017).



**Fig. 1.** Location of sample areas in western Paraná state, southern Brazil.

These protected areas were chosen for this study because they are the two largest remnants of SAF in Paraná and because of their histories of environmental preservation. The INP was established in 1939 and has great relevance for the preservation of plant species in southern Brazil such as *Euterpe edulis* and *Aspidosperma polyneuron* (Souza, et al., 2017). Its well-preserved vegetation allows the maintenance of large mammal assemblages, such as *Tapirus terrestris* and *Panthera onca*, whose populations are reasonably stable and with high occupancy rates along the INP (Silva, Paviolo, Tambosi & Pardini, 2018). On the other hand, the PBR was only established in 2006, after having been selectively exploited for at least 40 years (Magalhães-Júnior & Tomanik, 2012). The most exploited species was the *A. polyneuron*, so that currently the remaining individuals are those with trunk deformities,

which reduces their commercial interest (Dettke, et al., 2018). The highest intensity of selective logging in the PBR occurred between 100 and 200 m from the edges of an old trail that crosses the unit. Thus, even though different stages of ecological succession can still be found in internal areas of the PBR, including the presence of several areas with well-preserved vegetation with large numbers of *A. polyneron* individuals, the general vegetation of the PBR can be considered in an intermediate stage of ecological succession (Castella & Britz, 2004).

### **Bird surveys**

Sampling of bird communities was carried out during the breeding seasons (October – November) of the years 2016, 2017, and 2018 using the point counts method (Vielliard, Almeida, dos Anjos & Silva, 2010). In both protected area, 20 fixed points were established every 200 m and divided into five transects, along preexisting trails: the Poço Preto trail in the INP and the Central Trail in the PBR. The transects were at least 300 m from the forest edge in order to concentrate the samples in the forest core and avoid the edge effect. The points of each transect were sampled once a year, sequentially on the same morning, starting at dawn and with a detection radius of 50 m (Vielliard, et al., 2010). The observer remained at each point for 15 minutes, with a 15-minute interval between points. All sampling events were performed by only one observer in order to standardize the detection accuracy of the species.

The Index of Point Abundance (IPA) was calculated to represent the relative abundance of each species per point during the sampling period (Vielliard, et al., 2010). Thus, the IPA was calculated for each point, dividing the number of contacts of each species by the total number of times each point was sampled, that is, by three (Appendix A). The taxonomic identification of the species followed the South American Classification Committee (SACC; Remsen, et al., 2022).

### **Status of conservation of the forest**

The status of conservation of forest was measured through the Rapid Ecological Assessment (REA), according to Medeiros and Torezan (2013). The REA is an efficient index based on ecological indicator variables related to plant community structure and was developed to assess the ecological conservation status of vegetation in SAF ecosystem. The ecological variables used are: 1 – number of dead trees standing; 2 – presence and coverage of exotic grasses; 3 – presence of other exotics; 4 – abundance of tangles of vines; 5 - types of ecological units present (they are intended to indicate different degrees of vegetation structure

development through clearing phase regeneration); 6 – abundance of vascular epiphytes (except Orchidaceae); 7 – abundance of Orchidaceae; 8 – abundance of figer trees (*Ficus* spp, Moraceae); 9 – abundance of juçara palms (*Euterpe edulis*, Arecaceae); and 10 – abundance of peroba-rosa (*Aspidosperma polyneuron*, Apocynaceae). Each variable is given a value from 1 to 5 so that the overall index can vary between 10 and 50, with the value 10 representing very low conservation while the value 50 indicates excellent conservation status. For details on the REA method, see Medeiros and Torezan (2013).

REA values were obtained at the fixed point level for sampling bird community at three vegetation assessment points 30 m equidistant in two transects, perpendicular to the fixed point, 100 m long by 30 m wide. Vegetation data collection was carried out from September to December 2017 during the spring in order to avoid seasonal variations. The ten variables of REA were independently estimated by two senior biologists. Then, the mean values of the observations of the biologists were used to calculate a single value of REA index per point.

### **Functional traits**

The ecomorphological traits used in this study reflect the variation in the capacity and exploitation strategies of the available resources in the habitat, in particular food, since many ecological roles provided by birds are related to the exploitation of resources (Mahendiran & Azeez, 2018). Information was compiled on 18 functional traits, grouped into three categories (Appendix B): Food item (invertebrates; mammals and birds; reptiles and amphibians; fruits, nectar; seeds; other plant materials), forest stratum for foraging (soil; understory; middle stratum; canopy; aerial stratum), morphometric attributes (beak length, beak height, beak width, wing length, and tail length, and body mass). Values corresponding to food items and forest strata are percentages of use of each item (Wilman, et al., 2014). Morphometry was obtained according to Eck, et al. (2011), from five individuals of each species at the Museu de Zoologia de São Paulo (MZUSP).

### **Bird Diversity Index**

The bird species richness (BSR) was calculated as a representation of taxonomic diversity, which is the number of species recorded at each count point (Magurran, 2004). Functional diversity was evaluated using functional richness (FRic; Laliberté & Legendre, 2010) and the mean Gower nearest neighbor distance (MNND; Ricklefs & Travis, 1980). Functional richness (FRic) represents the size of the functional volume occupied by a

community, where the species with the most extreme values of traits represent the vertices of the volume of a convex hull. In other words, an increase in FRic represents an expansion of the functional volume occupied by the community in a niche space. Meanwhile, the MNND reports on the density of occupation of the space of multivariate traits by the assemblage. The higher the value of the MNND, the smaller the packing of the occupied niche space (Pigot, et al., 2016; Swenson & Weiser, 2014).

We used the Community Weighted Mean (CWM) of the functional traits in order to explore changes in the functional composition of assemblages along the vegetation conservation status gradient, based on the IPA values of the bird species (Lavorel, et al., 2008). The IPA matrix by species together with the matrix of functional traits were used to obtain the metrics of functional diversity. The trait matrix was converted into a matrix of functional distances between species using the Gower distance (Gower, 1966). As categorical traits with different numbers of categories were used, with continuous traits, different weights were assigned to each trait so that they all had the same influence on the construction of the n-dimensional space, through the calculation of the weight:  $Wi = \frac{1}{Ni}$ , where  $Ni$  is the number of characters by which a categorical feature is divided (Laliberté & Legendre, 2010). Subsequently, a principal coordinate analysis (PCoA) was calculated from the functional distance matrix. The first three axes of PCoA were used as "new" independent functional traits to generate n-dimensional space. These metrics were calculated in R software (R Core Team, 2022) for each fixed point: FRic and the CWMs of the 18 traces were obtained through the dbFD function of the FD package (Laliberté & Legendre, 2010).

### **Null model**

We sought to determine the presence of deterministic processes on the pattern of occupation of the niche space. Therefore, we compared the empirical values of FRic and MNND with those obtained by a matrix-swap null model of 1000 values for each assembly (Manly & Sanderson, 2002), using the Standardized Effect Size (SES). We calculated the SES of the FRic (SESEFRic) and MNND (SESMNND) using the formula:  $SES = \frac{Obs - Exp}{SDexp}$ , where Obs is the empirical value of the metric, Exp is the average of the 1000 values obtained in the null model, and SDexp is the standard deviation of the distribution of expected values by chance (Gotelli & McCabe, 2002).

An SES greater than zero indicates overdispersion of species in the functional space, which translates into less niche packing when evaluating SESMNND and greater expansion

of the occupied niche in the case of SESFRic. This would indicate a greater influence of limiting similarity on community assembly (MacArthur & Levins, 1967). In contrast, when SES is less than zero, this indicates that the species are more functionally closer than expected, suggesting that niche packing is higher than expected when evaluating SESMNND and there is less occupied niche expansion than expected in the case of SESFRic. This result would indicate that environmental filters are predominant in the functional structuring of communities (Zobel, 1997). However, the SES values are only considered significantly (with  $\alpha = 0.05$ ) different from the expected by chance if they are greater than  $|1.96|$  (Gotelli & McCabe, 2002). Furthermore, it is important to highlight that these mechanisms can act simultaneously in the community assembling (Helmus, Savage, Diebel, Maxted & Ives, 2007; Mouchet, et al., 2010) and that along gradients, it is possible to notice sequential variations in the strength of influence of each one (Oliveira, et al., 2020; Zobel, 1997).

### Data analysis

To verify the association of bird diversity metrics with SAF vegetation conservation status, Bayesian linear regression models were performed. The linear model for BSR was performed with Poisson distribution with log link function, described as:

$S_i \sim Poisson(\lambda)$ ; where  $S_i$  is the BSR at each fixed point and  $\lambda$  corresponds to lambda, being obtained by the link function to the linear predictor  $log(\lambda_i) = \beta_0 + \beta_1 X_i$ ; where  $\beta_0$  and  $\beta_1$  are the coefficients of the relationship and  $X_i$  is the value of the explanatory variable in each sample.

The FRic, MNND, and CWMs of continuous value traits were modeled via simple linear regression models (assuming normal distribution and identity link function), according to the equation:

$Y_i \sim Normal(\mu, \sigma)$ ; where  $\mu$  is the mean of the distribution of  $Y$  obtained by the linear predictor  $\mu = \beta_0 + \beta_1 X_i$ , and  $\sigma$  is the standard deviation and has its own prior in the model. This same model was used to verify the relationship of SESFRic and SESMNND with BSR, in order to verify possible intensifications of niche expansion or packaging along the accumulation of species.

The other CWMs, corresponding to the traits of proportion variables, were modeled via beta regression models, where continuous values are assumed with limits 0 and 1. We run the beta regression model as:

$Y_i \sim Beta(Alpha_i, Beta_i)$ ; where  $Alpha_i$  is the proportion that corresponds to that trait and  $Beta_i$  is the proportion that does not match.  $Alpha_i = \mu_i * \Phi$  and  $Beta_i = (1 - \mu_i) * \Phi$ , where  $\mu_i$  is obtained by connecting logit to the linear predictor:  $logit(\mu_i) = \beta_0 + \beta_1 X_i$ .  $\Phi$  has its own prior in the

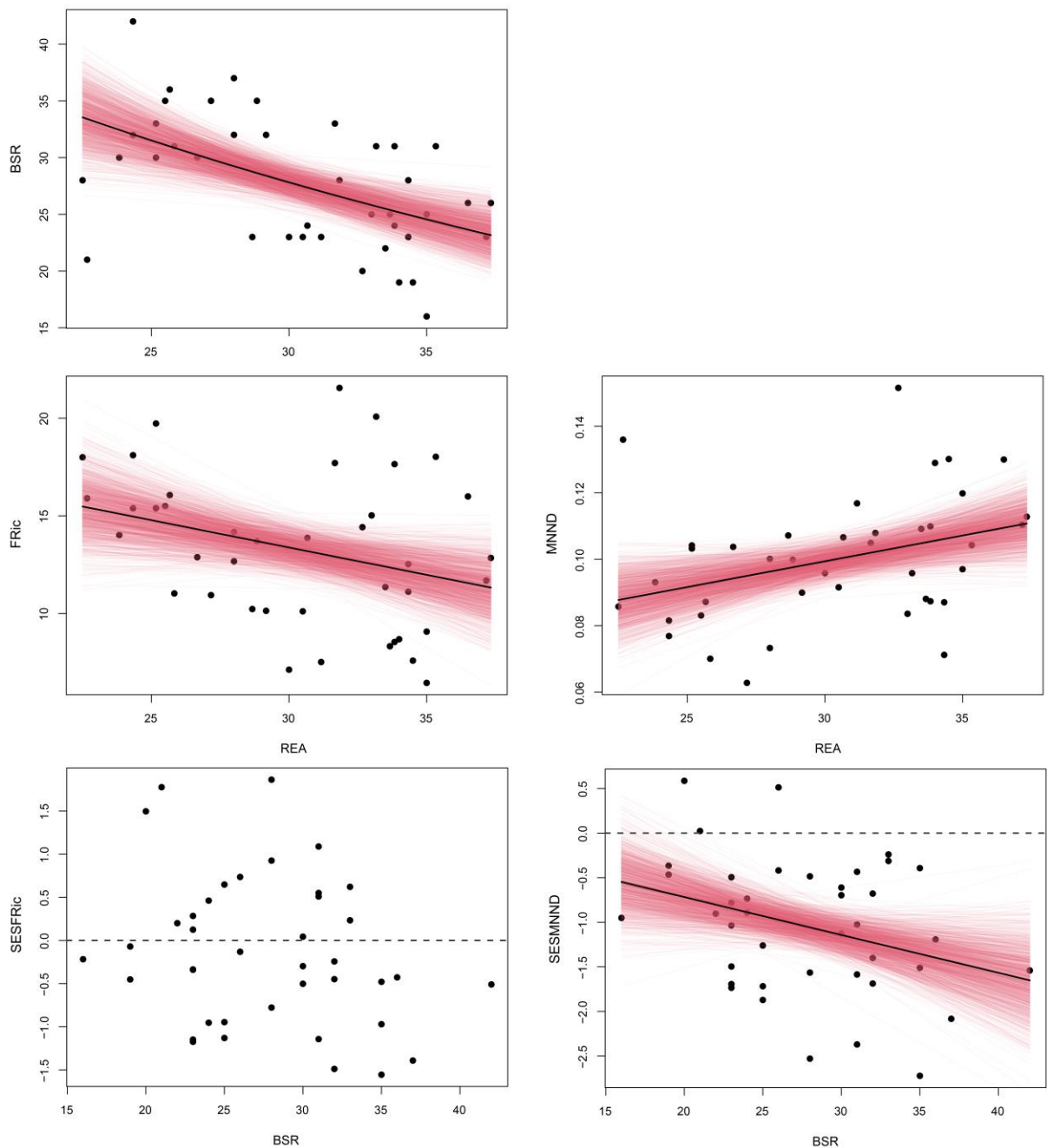
model.

The models were performed in JAGS software (Plummer, 2003) using the rjags package (Plummer, 2022) in R software. The parameters of all models were estimated using the Monte Carlo method via Markov Chains (MCMC) with non-informative (flat) priors for all model parameters. We ran three chains of length of 60,000 iterations each after an initial burn phase of 30,000 for the adaptation period. Convergence of the MCMC was assessed by verifying that the Gelman-Rubin statistic was less than 1.1 and by visually inspecting the chains using traceplots, with both measures indicating a reasonable assumption of convergence. The effect of SAF vegetation conservation status was considered statistically significant on any diversity metric when 95% of the Bayesian credible interval (CI) of the slope coefficient ( $\beta_1$ ) did not overlap the value zero. The model scripts can be found in the Appendix C (online supplementary material).

### 3. Results

A total of 134 bird species were sampled in the two studied areas with a mean per fixed point of  $27.8 \pm 5.78$  SD and a median of 28 (minimum = 16, maximum = 42). The REA values in the two protected areas were complementary, with the average vegetation conservation status in the INP points being considered as regular (REA = 30 to 37.4, mean =  $34 \pm 1.8$  SD) and in the PBR as low (REA = 22.5 to 31.2, mean =  $26.7 \pm 2.6$  SD).

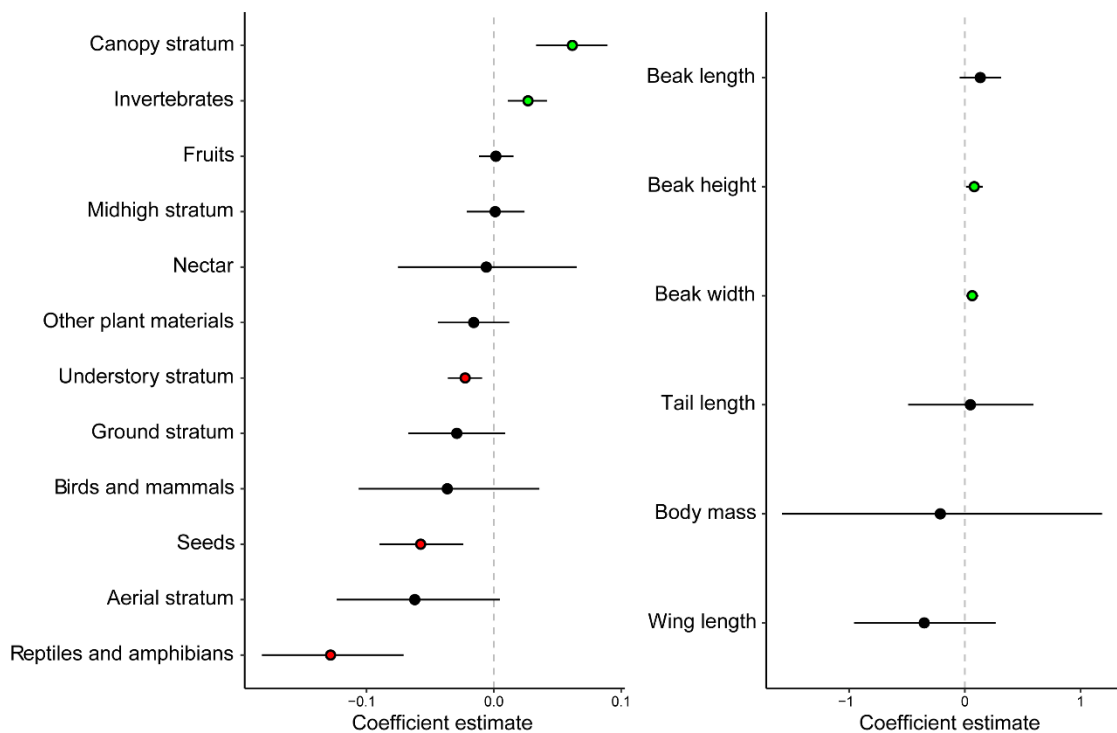
The linear models showed a reduction in BSR (mean of  $\beta_1 = -0.98$ , [95% CI: -0.96 to -0.99]), as well as in FRic (-0.28, [95% CI: -0.55 to -0.01]) with increasing SAF conservation status (Fig. 2). These results indicate an increase in BSR and in the multivariate functional volume occupied by the assemblages in places with lower conservation status of vegetation integrity. However, MNND was positively related to vegetation conservation (0.002, [95% CI: 0.0002 to 0.003]), demonstrating the increase in niche packing in sites with low vegetation conservation. Despite the increase in FRic with the reduction in REA, SESFRic values were randomly distributed around zero (-0.04, [95% CI: -0.09 to 0.01]), indicating that species richness did not enhance niche expansion more than was expected by chance. On the other hand, SESMNND values were mostly below zero and related to BSR (-0.04, [95% CI: -0.08 to -0.001]), that is, while BSR increased, the influence of environmental filters also increased, leading to more densification of niche space occupation than expected by chance.



**Fig. 2.** Patterns of diversity indices in relationship to the vegetation conservation status gradient (REA) and the bird species richness (BSR). Plots with a solid black line (average slope) and light red lines (3000 posterior predictive regression lines, representing uncertainty in the models) indicate CIs that do not overlap zero. FRic = functional richness; MNND = Mean Nearest Neighbor Distance; SESFRic = Standardized Effect Size of FRic; SESMNND = Standardized Effect Size of MNND.

Seven CWMs of the functional traits showed significant associations with the vegetation conservation status (Fig. 3). Among these, the proportion of foraging in the forest

canopy was the most positively affected foraging trait (95% CI: 0.03 to 0.09). In contrast, the proportion of foraging in the understory reduced as the vegetation conservation status increased (95% CI: -0.04 to -0.009). Of the CWMs referring to food items, the proportion of consumption of seeds (95% CI: -0.09 to -0.02), and especially of reptiles and amphibians (95% CI: -0.18 to -0.07), were negatively related to the vegetation conservation. Among the morphometric traits, only beak height (95% CI: 0.01 to 0.15) and beak width (95% CI: 0.01 to 0.12) had a significant positive relationship with SAF conservation. The other functional traits had CIs overlapping zero, therefore had non-significant effects.



**Fig. 3.** Mean and 95% credible intervals (CI) of change of the Community Weighted Means of the birds' functional traits along the vegetation conservation status gradient. Colored circles (red for decreasing, green for increasing) indicate CIs that do not overlap zero.

#### 4. Discussion

We found that BSR increased with reduced vegetation conservation status, which is accordance with several studies (Aleixo, 1999; Burivalova, et al., 2014; Edwards, et al., 2014). In this gradient of species richness increase, it was possible to detect not only the packing of niches, but also their expansion with the reduction in vegetation conservation status (Figure 2). However, only the SESMNND presented values generally below zero and negatively related to BSR, while the SESFRic remained randomly distributed around zero

across the BSR accumulation gradient. That is, this means that increased BSR in vegetation of lower quality involves a high influence of environmental filters, which intensify niche packing. The same does not occur with the expansion of the niche, which remained within that expected by chance.

We also demonstrate that the composition of functional traits presented different responses to the gradient of vegetation conservation, since there is a change in the composition of species and, consequently, in the “packages” of functional traits. The CWMs of proportions of vertebrates (reptile and amphibian) and grain consumption increased in less integral vegetation, while invertebrate consumption showed an opposite pattern, being higher in areas of better vegetation conservation. Following the same inversion trend, while the proportion of foraging in the understory was negatively related to vegetation conservation, foraging in the canopy was positively affected. In addition to these effects, changes in the CWMs of traits related to the beak of the birds were verified, so sites with better vegetation conservation status favored assemblages with greater beak width and height.

### **On taxonomic and functional diversity in niche space**

Species richness is the simplest and most intuitive metric of diversity among many; however, the interpretation of this number can become somewhat illusory (Magurran, 2004). An isolated interpretation of the relationship we obtained for this index with the vegetation conservation status could open a “Pandora’s Box” full of erroneous conclusions that could induce inappropriate conservation measures. The most inappropriate measure would be to subject forests with climax vegetation to selective logging indiscriminately based on the supposed benefit of increased BSR. This is because, the increase in species richness with the reduction in vegetation conservation is associated with a greater overlap of species in the occupied niche driven by environmental filters (Karr & James, 1975; Klopfer & MacArthur, 1961; MacArthur, 1965). This suggests that areas with lower vegetation conservation status have more unstable systems, with a greater probability of local species extinction due to the current strong interspecific competition (MacArthur & Levins, 1967; Swenson & Weiser, 2014). Instead, in places with more integrated vegetation, there is less niche packing, smaller than expected by chance, which can be interpreted as a result of the limiting similarity (Díaz & Cabido, 2001; Hardin, 1960; MacArthur & Levins, 1967; Mouchet, et al., 2010). Due to the competitive exclusions or the displacement of functional traits that have occurred throughout the ecological history of the community, a more stable coexistence is possible through the partition of the occupied niche (Connell, 1980; Sherry, et al., 2020). Thus, places with greater

vegetation conservation will have a lower probability of extinction due to biotic interactions being less unstable.

As new species are inserted into the assemblage, the possibility of including new values of functional traits is also increased, inflating the FRic (Karadimou, Kallimanis, Tsiripidis & Dimopoulos, 2016; Mouchet, et al., 2010). So, the FRic demonstrates a natural correlation with species richness (Mouchet, et al., 2010). Nevertheless, FRic is more influenced by the assembly rules than by the number of species itself (Mouchet, et al., 2010). However, in our study system there were no significant changes in SESFRic. This means that the functional volume of these bird species assemblages is the result of stochastic processes according to the neutral theory (Hubbell, 2001).

### **On the bird functional composition**

In a pantropical meta-analysis, Burivalova, et al. (2014) identified that whenever forest exploitation leads to an increase in bird species richness, there is a marked reduction in the number of specialist species in forest habitats, and that this is offset by a strong increase in generalist species richness. These changes in taxonomic composition can lead to major changes in the composition of the assemblage's functional trait packages (Díaz & Cabido, 2001; Mouchet, et al., 2010). In the current study, we demonstrate that, more informative than the number of species (Díaz & Cabido, 2001), vegetation conservation in SAF influences the functional composition of bird assemblages, which is consistent with the results of Burivalova, et al. (2015).

The CWMs of bird functional traits is directly related to the maintenance of ecosystem functions, such as hummingbird pollination (Tinoco, Santillán & Graham, 2018), and invertebrate control by forest birds (Philpott, et al., 2009). Variations in body mass, for example, depend on environmental conditions such as food availability, which drives individual consumption (Leisler & Winkler, 1985). Although no trend was found for body mass, the more intact vegetation provided the formation of bird assemblages formed by species with greater specialty in foraging in the canopy and in the consumption of invertebrates (especially insects). Inversely, assemblages in points with lower vegetation conservation increased foraging in the understory and consumption of seeds, reptiles, and amphibians. Probably, the reason for this is due to the presence of dense clearings in vineyards and the establishment of grasses in vegetation with lower conservation status values (Medeiros & Torezan, 2013; Yamamoto, 2000). This favored the proportions of granivores and carnivores in bird assemblages with the presence of species such as *Claravis pretiosa* and

*Mackenziaena severa*, as well as those that prefer dense understory for foraging, such as *Basileuterus culicivorus* (Wilman, et al., 2014). Furthermore, gaps in the forest canopy can positively affect reptile abundance, possibly due to thermal requirements, and apparently do not affect amphibians (Agha, et al., 2018; Greenberg, 2001), in this way, these environments can become zones with availability of prey for species of birds that adopt them as a food item.

The adaptive radiations are observed in the functional differences of the sets of morphometric traits linked to the forms of locomotion and strategies for obtaining resources (Leisler & Winkler, 1985; Reif, Hořák, Krištín, Kopsová & Devictor, 2016). Since species do not have energy to use without restrictions, so they are limited to the development of morphological adaptations essential for their lifestyle (Leisler & Winkler, 1985). For example, the size of the tail differs between groups and functions, in woodpeckers and woodcreepers the tail serves to anchor the bird to tree trunks, but in other species the function is more related to flight maneuverability (Leisler & Winkler, 1985; Matyjasiak, Marzal, Navarro, De Lope & Møller, 2009; Sachs, 2007; Thomas, 1993, 1997). In addition, species that forage in the canopy tend to have more developed wings and a high proportion between width and length, which gives them greater speed in vertical movements, important in the aerial hawk strategy (Balmford, Thomas & Jones, 1993; Leisler & Winkler, 1985).

Supposedly, species in environments with denser vegetation should present trait combinations that provide them with better locomotion at low speed, that is, short and wide tails (Leisler & Winkler, 1985). Thus, it was expected that areas with lower vegetation conservation status would present assemblages with higher CWM values for wing and tail length, since these may be associated with aerial Hawk or perch to ground foraging strategies in clearings (Fitzpatrick, 1980; Matyjasiak, et al., 2009; Robinson & Holmes, 1982). However, the vegetation in points with intermediate conservation also presents high densities of understory and tangles of vines, which favors species with smaller, rounded tails and wings, better adapted for movement in this type of habitat (Leisler & Winkler, 1985; Medeiros & Torezan, 2013; Robinson & Holmes, 1982), as occurs in *Platyrrinchus mystaceus* (Wilman, et al., 2014). Thus, apparently our results indicate that vegetation conservation status does not affect the average wing and tail length in forest bird assemblages, at least within the vegetation status values that we contemplated in this study. Despite this, we cannot rule out the influence of vegetation status on other traits linked to the shape of these structures that better inform maneuverability in flight (Thomas, 1993) or even in environments with even lower conservation status.

In addition to the wings and tail, the morphology of the bird's beak is linked to several

aspects of the way of life of each species, from the care of the feathers to the food items that are part of its diet (Barbosa, 1996; Herrel, Podos, Huber & Hendry, 2005). Insectivorous species require combinations of beak morphological traits that are sufficiently adjusted to capture and trap their prey (Lederer, 1975). Both height and width of the beak are related to handling mobile prey in insectivorous birds (Borrás, Cabrera & Senar, 2008). Thus, our results provide some light to better understand the positive relationships of these characteristics of the feeding apparatus in bird assemblages in more intact/integral vegetation may be directly associated with increased specialty in the consumption of invertebrates in the diet of the species that make up these assemblages.

### **Conservation implications**

The functional structure in bird communities has been widely used as a way of investigating how communities are grouped over time and space (Almeida, Sebastián-González, dos Anjos, Green & Botella, 2019; Mouchet, et al., 2010; Oliveira & dos Anjos, 2022; Oliveira, et al., 2020), and has clarified patterns that species richness alone cannot demonstrate (Pigot, et al., 2016). Several studies have shown that the richness and species composition of forest birds are directly affected by anthropic disturbances (Aleixo, 1999; Burivalova, et al., 2014; Thiollay, 1992). However, the assessment of functional structure along environmental gradients can provide insights into how latent mechanisms of community assembly can drive the dismantling of assemblages in altered habitats (Oliveira, et al., 2020). The greater functional distance of bird species in forest environments suggests greater stability, with low probability of local extinctions due to lower intensity of interspecific competition (MacArthur & Levins, 1967; Sherry, et al., 2020). In our study system, changes in vegetation conservation status led to an increase in species richness, but also in niche packing. Since species that are similar in functional attributes tend to be excluded by competition (Hardin, 1960), it suggests that reducing the conservation status of vegetation integrity can increase the risk of local extinctions, especially for species specialized in invertebrates. Therefore, the high richness and functional diversity seem to be momentary, as the recovery of vegetation should act as an environmental filter favoring specialist species and causing the local extinction of generalists (Fox, 2013). Hence, as suggested by Barlow, et al. (2007), an area with high vegetation integrity should be primarily conserved, despite the lower species richness.

### **Acknowledgements**

The Museum of Zoology of the University of São Paulo allowed us to measure bird specimens, where we were assisted by L.F.S. The Chico Mendes Institute for Conservation of Biodiversity (ICMbio, Brasília) gave us permissions to study birds in the Iguassu National Park (24483) and in the Perobas Biological Reserve (21879-2), where we had the assistance of A.N.S.R. and A.G.C.S. We thank Ph.D. Gabriela Menezes Bochio, Ph.D. Barbara Rocha Arakaki Lindsey, Ph.D. Larissa Corsini Calsavara, and Edson Mendes Francisco for measuring the bird specimens at the Zoology Museum of São Paulo (MZUSP) and by obtaining plant variables in the field. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 (88887.484989/2020-00). L. A. receives grant from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brasília, (308523/2021-0). We are grateful for the valuable comments provided by the two anonymous reviewers.

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**Appendix B** – Supporting information of bird traits data set. Diet-Inv = Percent use of invertebrates; Diet-Vend = Percent use of mammals, birds; Diet-Vect = Percent use of reptiles, amphibians; Diet-Fruit = Percent use of fruit; Diet-Nect = Percent use of nectar; Diet-Seed = Percent use of seed; Diet-OPlant = Percent use of other plant material; ForStrat-ground = Percent of foraging on ground; ForStrat-understory = Percent of foraging below 2m in understory in forest, forest edges, bushes or shrubs; ForStrat-midhigh = Percent of foraging in mid to high levels in trees or high bushes (2m upward), but below canopy; ForStrat-canopy = Percent of foraging in or just above (from) tree canopy; ForStrat-aerial = Percent of foraging well above vegetation or any structures; Mass = Body mass in grams; Bill length = From insertion to the tip of the bill (mm); Bill width = Horizontal width at the nostril (mm); Bill height = Vertical width at the nostrils (mm); Wing length = From the insertion of the primary feathers to the wingtip (mm); Tail length = Insertion of rectrices to the tail tip (mm).

Species	Diet_Inv	Diet-Vend	Diet-Vect	Diet_Fruit	Diet_Nect	Diet_Seed	Diet_OPlant	ForStrat_ground	ForStrat_understory	ForStrat_midhigh	ForStrat_canopy	ForStrat_aerial	BodyMass_Value	Bill length	Bill width	Bill height	Wing length	Tail length
<i>Amazona aestiva</i>	0	0	0	50	0	50	0	0	30	40	30	0	451.00	31.00	18.30	29.80	213.20	154.40
<i>Anabacerthia lichtensteini</i>	100	0	0	0	0	0	0	0	0	50	50	0	21.00	20.70	4.70	5.40	79.20	76.70
<i>Automolus leucophthalmus</i>	100	0	0	0	0	0	0	0	80	20	0	0	34.50	28.10	5.70	6.50	84.10	86.60
<i>Baryphthengus ruficapillus</i>	60	10	10	20	0	0	0	50	20	30	0	0	141.65	43.50	12.10	12.90	147.40	231.20
<i>Basileuterus culicivorus</i>	80	0	0	20	0	0	0	0	70	30	0	0	10.50	14.70	4.50	3.90	55.50	58.40
<i>Cacicus haemorrhous</i>	60	0	0	20	20	0	0	0	20	60	20	0	83.71	31.50	8.00	10.20	154.10	108.30
<i>Cacicus solitarius</i>	100	0	0	0	0	0	0	0	40	60	0	0	79.76	24.96	10.80	13.01	138.00	104.68
<i>Campephilus robustus</i>	100	0	0	0	0	0	0	0	30	40	30	0	200.00	49.50	13.00	13.90	191.80	138.20
<i>Camptostoma obsoletum</i>	70	0	0	30	0	0	0	0	0	80	20	0	8.10	12.50	3.40	3.00	50.60	44.60
<i>Campylorhamphus falcularius</i>	100	0	0	0	0	0	0	0	50	50	0	0	42.60	77.40	4.30	6.00	94.90	105.80
<i>Capsiempis flaveola</i>	90	0	0	10	0	0	0	0	0	100	0	0	7.70	13.20	4.30	3.70	48.00	49.90
<i>Celeus flavescens</i>	70	0	0	30	0	0	0	20	30	50	0	0	139.00	34.50	10.80	10.40	152.90	109.20
<i>Chamaeza campanisona</i>	70	0	0	30	0	0	0	80	20	0	0	0	90.58	28.50	6.60	6.60	95.00	67.60
<i>Chiroxiphia caudata</i>	50	0	0	50	0	0	0	0	50	50	0	0	25.60	13.50	5.70	5.30	77.40	65.00
<i>Chlorophonia cyanea</i>	10	0	0	90	0	0	0	0	0	20	80	0	14.00	10.27	5.67	5.23	62.03	34.93
<i>Chlorostilbon lucidus</i>	10	0	0	0	90	0	0	0	0	90	10	0	3.50	19.47	3.10	2.12	49.86	30.60
<i>Cissopis leverianus</i>	30	0	0	70	0	0	0	20	30	30	20	0	76.00	18.50	8.80	10.10	113.50	168.80
<i>Claravis pretiosa</i>	20	0	0	0	0	80	0	100	0	0	0	0	68.20	17.20	2.40	3.60	111.80	85.40
<i>Coccyzus euleri</i>	100	0	0	0	0	0	0	50	30	20	0	0	52.30	27.70	5.83	8.53	93.95	146.00
<i>Coccyzus melacoryphus</i>	100	0	0	0	0	0	0	50	30	20	0	0	49.71	25.30	6.70	7.80	113.60	145.80
<i>Colonia colonus</i>	100	0	0	0	0	0	0	0	30	70	0	0	18.30	12.50	5.40	4.10	80.50	162.00

<i>Conirostrum speciosum</i>	70	0	0	10	0	10	10	60	20	20	0	0	8.80	10.50	3.50	3.20	57.90	46.30
<i>Conopophaga lineata</i>	100	0	0	0	0	0	0	60	40	0	0	0	25.21	21.10	5.40	4.80	67.30	52.50
<i>Corythopsis delalandi</i>	90	0	10	0	0	0	0	80	20	0	0	0	15.00	14.75	6.30	3.75	63.74	51.23
<i>Crypturellus obsoletus</i>	50	0	0	0	0	50	0	100	0	0	0	0	443.40	34.30	5.70	5.40	165.60	72.60
<i>Crypturellus tataupa</i>	50	0	0	0	0	30	20	50	50	0	0	0	218.80	28.13	5.38	5.88	124.80	49.24
<i>Cyanocorax chrysops</i>	80	0	0	20	0	0	0	10	30	30	30	0	166.00	36.60	11.10	12.60	152.70	175.20
<i>Cyanoloxia glaucocaeerulea</i>	40	0	0	20	0	30	10	50	50	0	0	0	18.20	12.47	9.48	9.86	69.48	65.16
<i>Cyclarhis gujanensis</i>	100	0	0	0	0	0	0	0	40	40	20	0	28.80	19.00	5.40	8.00	69.20	59.10
<i>Dacnis cayana</i>	50	0	0	40	0	0	10	0	0	30	60	10	13.00	14.00	4.20	4.20	65.00	49.50
<i>Dendrocincla turdina</i>	100	0	0	0	0	0	0	0	40	60	0	0	39.00	30.80	8.10	7.10	103.20	91.20
<i>Dendrocolaptes platyrostris</i>	80	0	0	0	0	0	10	50	50	0	0	0	61.70	46.80	9.50	8.50	117.90	120.20
<i>Dramococcyx pavoninus</i>	100	0	0	0	0	0	0	50	50	0	0	0	46.40	24.90	5.40	5.20	124.80	157.40
<i>Dryophila malura</i>	100	0	0	0	0	0	0	40	40	20	0	0	13.00	17.00	3.50	3.30	53.60	73.70
<i>Dryocopus lineatus</i>	80	0	0	10	0	10	0	20	20	60	0	0	183.19	47.20	11.80	10.10	192.80	135.40
<i>Dysithamnus mentalis</i>	90	0	0	10	0	0	0	0	40	40	20	0	14.87	17.00	4.10	4.00	56.00	44.00
<i>Eleoscytalopus indigoticus</i>	100	0	0	0	0	0	0	60	40	0	0	0	16.15	15.80	3.90	3.70	46.70	39.60
<i>Empidonomus varius</i>	60	0	0	40	0	0	0	0	30	70	0	0	27.10	17.90	7.10	5.70	97.00	89.10
<i>Euphonia chlorotica</i>	0	0	0	100	0	0	0	0	0	10	90	0	11.00	8.60	5.40	4.80	56.50	38.90
<i>Euphonia pectoralis</i>	20	0	0	70	10	0	0	0	0	30	70	0	14.40	11.80	5.30	5.00	62.70	41.70
<i>Euphonia violacea</i>	0	0	0	100	0	0	0	0	30	40	30	0	15.00	10.60	5.80	5.60	60.10	39.50
<i>Geothlypis aequinoctialis</i>	100	0	0	0	0	0	0	0	100	0	0	0	13.10	12.88	6.28	4.55	56.47	54.64
<i>Glaucidium brasilianum</i>	60	20	20	0	0	0	0	80	10	10	0	0	75.10	16.44	9.41	10.41	95.55	66.89
<i>Habia rubica</i>	80	0	0	20	0	0	0	0	40	60	0	0	32.46	17.70	8.30	8.90	89.70	89.00
<i>Hemithraupis guira</i>	80	0	0	10	0	10	0	0	0	10	90	0	12.00	12.70	4.70	4.30	64.70	53.50
<i>Hemitriccus diops</i>	100	0	0	0	0	0	0	0	100	0	0	0	10.00	15.70	4.60	3.60	48.80	47.20
<i>Herpetoheres cochinnans</i>	0	0	0	0	0	0	0	33	33	33	0	0	623.58	27.60	13.60	20.40	281.80	239.60
<i>Herpsilochmus rufimarginatus</i>	90	0	0	10	0	0	0	0	0	100	0	0	10.58	18.10	4.20	3.80	46.30	47.20
<i>Hylocharis chrysur</i>	10	0	0	0	90	0	0	0	20	40	30	10	4.50	22.20	2.10	2.40	51.90	34.20
<i>Hylophilus poicilotis</i>	70	0	0	30	0	0	0	0	20	60	20	0	10.40	14.00	3.60	4.00	54.40	56.10
<i>Hypoedaleus guttatus</i>	90	0	10	0	0	0	0	0	0	100	0	0	38.80	24.98	9.62	9.55	79.00	99.56
<i>Icterus pyrrhopterus</i>	70	0	0	0	30	0	0	0	20	40	40	0	35.44	19.35	6.60	6.77	87.94	93.30
<i>Ictinia plumbea</i>	90	0	10	0	0	0	0	0	0	0	20	80	249.90	21.30	9.70	10.10	321.20	171.20
<i>Leptopogon amaurocephalus</i>	80	0	0	20	0	0	0	0	50	50	0	0	11.70	17.10	4.30	4.60	62.60	57.30

<i>Leptotila rufaxilla</i>	10	0	0	10	0	80	0	100	0	0	0	0	157.00	22.70	3.90	4.70	153.80	111.00
<i>Leptotila verreauxi</i>	20	0	0	20	0	60	0	100	0	0	0	0	146.88	21.50	3.40	4.40	149.60	120.60
<i>Mackenziaena severa</i>	60	20	20	0	0	0	0	30	40	30	0	0	51.80	19.82	11.13	8.42	93.92	113.74
<i>Megarynchus pitangua</i>	70	0	0	10	0	10	0	0	10	50	40	0	69.91	30.97	16.96	11.82	110.44	92.75
<i>Megascops choliba</i>	90	0	0	0	0	0	0	40	50	0	0	10	132.00	19.09	16.13	13.95	178.36	100.01
<i>Melanerpes flavifrons</i>	30	0	0	40	0	30	0	0	50	50	0	0	57.78	29.90	6.60	6.10	111.20	68.80
<i>Micrastur ruficollis</i>	0	20	80	0	0	0	0	40	30	30	0	0	177.64	19.70	8.50	12.20	165.80	198.60
<i>Micrastur semitorquatus</i>	0	80	20	0	0	0	0	50	30	20	0	0	621.68	30.70	12.00	18.30	265.00	293.00
<i>Myiodynastes maculatus</i>	40	0	30	30	0	0	0	0	0	100	0	0	43.20	21.39	12.30	8.85	106.57	87.00
<i>Myiopagis caniceps</i>	80	0	0	20	0	0	0	0	0	0	100	0	10.50	12.50	5.70	4.40	62.80	65.40
<i>Myiopagis viridicata</i>	60	0	0	20	0	20	0	0	0	50	50	0	11.51	12.40	4.90	3.80	60.30	58.80
<i>Myiornis auricularis</i>	100	0	0	0	0	0	0	0	50	50	0	0	5.30	13.10	3.40	2.50	36.90	29.60
<i>Myiothlypis flaveola</i>	100	0	0	0	0	0	0	60	40	0	0	0	13.19	16.30	5.30	3.90	64.00	67.00
<i>Nonnula rubecula</i>	100	0	0	0	0	0	0	50	50	0	0	0	18.40	23.20	6.60	6.60	61.20	64.10
<i>Notharchus swainsoni</i>	80	0	0	0	0	0	10	33	33	33	0	0	60.72	39.48	14.50	13.84	107.72	89.94
<i>Odontophorus capueira</i>	0	0	0	80	0	20	0	100	0	0	0	0	425.40	19.30	9.80	12.20	144.90	85.50
<i>Pachyramphus polychopterus</i>	50	0	0	50	0	0	0	0	0	100	0	0	20.80	17.20	7.50	6.20	73.60	70.80
<i>Patagioenas cayennensis</i>	0	0	0	70	0	30	0	20	0	40	40	0	229.00	23.90	4.40	5.00	183.00	112.80
<i>Patagioenas picazuro</i>	10	0	0	30	0	30	30	30	30	30	10	0	279.00	26.80	4.60	6.10	213.20	126.20
<i>Penelope superciliaris</i>	10	0	0	90	0	0	0	33	0	33	33	0	894.99	36.60	11.30	10.70	250.60	310.20
<i>Phaethornis eurynome</i>	10	0	0	0	90	0	0	0	100	0	0	0	5.30	34.90	2.90	2.70	55.10	61.50
<i>Philydor atricapillus</i>	100	0	0	0	0	0	0	0	33	33	33	0	22.20	16.13	7.48	5.91	82.35	75.61
<i>Philydor rufum</i>	100	0	0	0	0	0	0	0	0	40	60	0	25.00	22.60	5.20	5.60	83.20	90.90
<i>Phyllomyias fasciatus</i>	80	0	0	20	0	0	0	0	0	0	100	0	10.30	9.80	4.90	3.30	60.00	53.10
<i>Phyllomyias virescens</i>	70	0	0	30	0	0	0	0	10	50	40	0	8.20	10.22	5.28	3.06	60.21	56.59
<i>Phylloscartes eximius</i>	100	0	0	0	0	0	0	0	0	100	0	0	7.50	14.28	4.86	3.09	53.26	51.46
<i>Phylloscartes paulista</i>	100	0	0	0	0	0	0	0	50	50	0	0	7.48	13.90	2.90	3.10	45.00	44.10
<i>Phylloscartes ventralis</i>	100	0	0	0	0	0	0	0	0	100	0	0	8.30	15.50	3.40	3.60	49.40	51.20
<i>Piaya cayana</i>	100	0	0	0	0	0	0	0	0	20	80	0	101.98	32.20	9.30	10.80	168.60	344.80
<i>Picumnus albosquamatus</i>	100	0	0	0	0	0	0	0	40	30	30	0	11.90	12.04	4.70	4.73	55.69	33.66
<i>Picumnus temminckii</i>	100	0	0	0	0	0	0	0	80	20	0	0	11.50	11.43	6.39	4.89	53.29	34.77
<i>Pionopsitta pileata</i>	0	0	0	40	0	30	30	0	0	60	40	0	119.00	18.00	12.30	17.70	144.20	88.80
<i>Pionus maximiliani</i>	0	0	0	10	0	70	20	0	30	50	20	0	293.00	24.70	18.70	23.90	184.80	106.40

<i>Pipra fasciicauda</i>	10	0	0	90	0	0	0	0	50	50	0	0	15.90	10.80	5.30	4.13	63.54	31.31
<i>Piprites chloris</i>	90	0	0	10	0	0	0	0	0	20	80	0	16.00	16.60	8.40	5.36	63.30	49.48
<i>Platyrrinchus mystaceus</i>	100	0	0	0	0	0	0	0	80	20	0	0	9.70	15.30	8.40	3.50	53.30	33.40
<i>Poecilotriccus plumbeiceps</i>	100	0	0	0	0	0	0	0	100	0	0	0	5.70	13.30	3.90	2.80	42.80	39.20
<i>Psilorhamphus guttatus</i>	100	0	0	0	0	0	0	10	60	30	0	0	11.30	14.30	7.20	4.20	51.00	67.25
<i>Psittacara leucophthalmus</i>	10	0	0	30	0	30	30	20	20	40	20	0	158.00	21.90	16.40	27.70	171.60	160.40
<i>Pteroglossus castanotis</i>	10	10	0	60	0	10	10	0	20	60	20	0	258.09	94.50	26.90	31.40	147.40	168.80
<i>Pyriglena leucoptera</i>	90	0	10	0	0	0	0	40	40	20	0	0	28.80	20.80	4.80	5.00	78.40	82.90
<i>Pyroderus scutatus</i>	40	0	0	60	0	0	0	0	50	50	0	0	357.00	49.80	15.90	16.50	242.40	178.60
<i>Pyrhocomia ruficeps</i>	100	0	0	0	0	0	0	0	80	20	0	0	15.60	13.00	5.80	5.70	62.50	61.50
<i>Pyrrhura frontalis</i>	10	0	0	30	0	30	30	0	30	50	20	0	72.00	16.80	10.80	16.70	130.80	138.20
<i>Ramphastos dicolorus</i>	10	10	0	80	0	0	0	20	0	0	80	0	331.00	91.47	31.10	37.30	195.02	185.94
<i>Ramphastos toco</i>	20	10	0	70	0	0	0	20	10	10	60	0	617.99	152.50	31.50	62.00	243.80	169.00
<i>Saltator fuliginosus</i>	60	0	0	30	10	0	0	0	0	60	40	0	50.50	22.90	11.00	14.60	102.80	109.40
<i>Saltator similis</i>	60	0	0	30	10	0	0	0	70	30	0	0	43.30	21.00	9.60	11.00	96.40	95.10
<i>Schiffornis virescens</i>	50	0	0	50	0	0	0	0	100	0	0	0	25.60	19.20	4.70	4.90	78.20	69.00
<i>Selenidera maculirostris</i>	20	0	0	80	0	0	0	0	20	40	40	0	164.00	58.90	19.80	23.20	121.50	126.90
<i>Setophaga pitiayumi</i>	70	0	0	20	0	0	10	0	0	0	100	0	6.82	13.60	3.90	3.30	51.70	42.90
<i>Sirystes sibilator</i>	80	0	0	20	0	0	0	0	0	0	100	0	32.30	23.80	8.90	6.90	91.90	87.40
<i>Sittasomus griseicapillus</i>	90	0	0	0	0	0	10	0	0	50	50	0	13.12	17.50	4.20	3.50	71.20	79.20
<i>Synallaxis frontalis</i>	100	0	0	0	0	0	0	20	80	0	0	0	14.00	16.70	3.60	3.70	56.00	86.10
<i>Synallaxis ruficapilla</i>	100	0	0	0	0	0	0	20	60	20	0	0	13.80	18.30	4.20	3.90	54.10	81.20
<i>Synallaxis spixi</i>	100	0	0	0	0	0	0	20	80	0	0	0	12.60	11.74	3.28	3.55	51.78	75.02
<i>Tachyphonus coronatus</i>	60	0	0	20	0	20	0	0	20	40	40	0	29.30	15.80	6.80	7.60	84.90	80.90
<i>Tangara sayaca</i>	10	0	0	50	0	40	0	10	0	20	70	0	32.49	15.40	6.80	7.00	89.10	66.90
<i>Tapera naevia</i>	100	0	0	0	0	0	0	50	30	20	0	0	48.42	19.24	7.30	6.76	116.91	150.31
<i>Thalurania glaucopis</i>	10	0	0	0	90	0	0	0	60	40	0	0	4.80	21.80	2.10	1.70	56.90	49.60
<i>Thamnophilus caerulescens</i>	80	0	0	10	0	10	0	0	60	40	0	0	21.10	20.60	4.80	5.40	66.30	64.10
<i>Tinamus solitarius</i>	20	0	0	40	0	20	20	100	0	0	0	0	1386.41	47.00	6.80	6.80	259.40	129.80
<i>Tityra cayana</i>	20	0	0	80	0	0	0	0	50	50	0	0	68.10	36.04	15.11	13.63	200.89	88.91
<i>Tityra inquisitor</i>	20	0	0	80	0	0	0	0	0	100	0	0	43.10	34.31	12.78	9.32	181.00	93.02
<i>Tolmomyias sulphurescens</i>	90	0	0	10	0	0	0	0	30	70	0	0	14.30	19.40	6.70	4.20	67.00	62.80
<i>Trichothraupis melanops</i>	70	0	0	20	0	10	0	30	30	20	10	10	22.58	14.34	7.84	6.20	80.39	74.76

<i>Troglodytes aedon</i>	80	0	0	0	0	0	20	0	100	0	0	0	10.85	14.85	4.71	4.05	51.02	43.42
<i>Trogon rufus</i>	60	0	0	40	0	0	0	10	60	30	0	0	53.80	22.20	10.30	10.10	120.10	163.00
<i>Trogon surrucura</i>	80	0	0	20	0	0	0	0	0	100	0	0	73.29	24.40	10.50	10.40	132.90	160.40
<i>Turdus albicollis</i>	60	0	0	40	0	0	0	80	0	20	0	0	54.00	26.50	6.00	6.10	112.50	90.20
<i>Turdus amaurochalinus</i>	40	0	0	60	0	0	0	20	20	30	30	0	57.90	24.50	5.50	6.10	112.40	96.50
<i>Turdus leucomelas</i>	70	0	0	30	0	0	0	60	20	20	0	0	69.10	26.00	6.00	6.20	121.00	102.30
<i>Turdus rufiventris</i>	50	0	0	50	0	0	0	100	0	0	0	0	69.44	26.30	6.00	6.60	118.70	102.30
<i>Turdus subalaris</i>	40	0	0	60	0	0	0	20	40	40	0	0	49.50	19.27	10.95	6.77	109.69	87.13
<i>Tyrannus melancholicus</i>	100	0	0	0	0	0	0	0	0	50	50	0	37.40	27.40	10.60	7.70	112.30	98.80
<i>Veniliornis spilogaster</i>	80	0	0	20	0	0	0	0	50	50	0	0	40.30	26.70	6.10	5.70	96.60	63.40
<i>Vireo olivaceus</i>	60	0	0	20	0	20	0	0	0	20	80	0	16.06	19.90	4.10	4.10	70.80	55.90
<i>Xenops rutilans</i>	100	0	0	0	0	0	0	0	20	80	0	0	11.20	16.60	3.70	4.90	64.30	56.30
<i>Xiphocolaptes albicollis</i>	80	10	0	0	0	0	0	0	0	100	0	0	118.00	44.52	11.70	10.30	127.86	116.96
<i>Xiphorhynchus fuscus</i>	100	0	0	0	0	0	0	0	50	50	0	0	21.80	24.00	8.36	5.62	79.56	71.90

## Appendix C – Bayesian Linear Models developed for execution in JAGS software.

```
#####
```

```
## Specify model in JAGS language
```

```
#####
```

```
## Bayesian linear regression models
```

```
# Gaussian Regression Model
```

```
Mod_Reg_Gaus <- "model {
  #Likelihood
  for (i in 1:n) {
    Y[i] ~ dnorm(mu[i],1/sd^2)
    mu[i] <- beta0+beta1*X[i]
    Y.err[i] <- Y[i] - mu[i]
  }
  #Priors
  beta0 ~ dnorm(0,1/100^2)
  beta1 ~ dnorm(0,1/100^2)
  sd ~ dgamma(0.001,0.001)
}"
```

```
## Poisson Regression Model
```

```
Mod_Reg_Pois <- "model {
  #Likelihood
  for (i in 1:n) {
    Y[i] ~ dpois(lambda[i])
    log(lambda[i]) <- beta0 + beta1*X[i]
  }
  #Priors
  beta0 ~ dnorm(0,1.0E-06)
  beta1 ~ dnorm(0,1.0E-06)
}"
```

```
## Beta Regression Model
```

```
Mod_Beta_Reg <- " model{
  #Likelihood
  for (i in 1:n) {
    Y[i] ~ dbeta(alpha[i], beta[i])
    alpha[i] <- mu[i] * phi
    beta[i] <- (1-mu[i]) * phi
    logit(mu[i]) <- a + b*X[i]
  }
  #Priors
  phi ~ dgamma(.01,.01)
  a ~ dnorm(0,0.001)
  b ~ dnorm(0,0.001)
}"
```

#### 4. CONCLUSÃO GERAL

As análises desenvolvidas nessa tese nos possibilitaram identificar que de fato as comunidades de aves apresentam uma dinâmica taxonômica temporal, mesmo em ambientes com alto nível de conservação. Apesar dessa dinâmica taxonômica, as comunidades de aves do Parque Nacional do Iguaçu apresentaram estabilidade do volume do espaço funcional ocupado e na uniformidade da distribuição dos indivíduos ao longo desse espaço. Isso significa que as alterações taxonômicas ocorram entre espécies funcionalmente redundantes, o que mantém os papéis funcionais sempre presentes na comunidade. Entretanto, ao analisar os subgrupos de espécies de aves, foram identificadas reduções lineares na riqueza de espécies e a prevalência do aninhamento funcional no grupo dos passeriformes insetívoros especialistas. A respeito desse resultado, alertamos que: se a diversidade taxonômica do grupo dos passeriformes não estiver passando por um momento de declínio de uma dinâmica temporal com tendência estacionária em uma escala temporal maior do que a avaliada neste estudo, então presenciaremos uma erosão silenciosa da diversidade funcional nessas comunidades de aves.

Nossos resultados ainda apontam que o nível de conservação da vegetação florestal pode impulsionar alterações na estrutura funcional de comunidades de aves. As comunidades de aves passaram por um processo de alteração na composição de seus traços funcionais, com modificações nas prevalências de itens alimentares na dieta e no estrato florestal para forrageio, assim como em traços relacionados a morfometria do aparato bucal. Embora a expansão do espaço de nicho ocupado tenha sido reconhecida ao longo do aumento no número de espécies, esse foi um fenômeno resultante da estocasticidade e da relação intrínseca da riqueza de espécies com a riqueza funcional. Por outro lado, as comunidades com maior riqueza de espécies também apresentaram um maior adensamento de nicho. Esse resultado se deve às alterações no nicho ecológico florestal o que intensificou a influência dos filtros ambientais na formação das comunidades. Esse adensamento do espaço de nicho pode provocar extinções locais devido à intensificação das interações competitivas entre as espécies mais próximas em seus traços funcionais. Dessa forma, embora as comunidades em áreas com vegetações florestais mais conservadas apresentem menor riqueza de espécies, estas devem apresentar uma maior estabilidade na coocorrência das espécies com um menor risco de extinções por exclusões competitivas.

Embora os capítulos dessa tese tratem sobre a diversidade de aves em escalas distintas, temporal e espacial, é importante destacar sua importância conjunta para a tomada de decisões

para conservação. Podemos concluir, com esses estudos, que ambientes florestais com maior nível de integridade vegetal podem abrigar comunidades de aves com menor probabilidade de extinções locais por interações bióticas, principalmente a competição interespecífica. Ao longo do tempo isso conferiu às comunidades de aves, encontradas na Trilha do Poço Preto no Parque Nacional do Iguaçu, uma estabilidade funcional ao longo do tempo, mesmo havendo alterações aleatórias na composição de espécies. Essas mudanças taxonômicas aleatórias se devem, principalmente, aos eventos de dispersão dos indivíduos entre diferentes locais dentro do Parque Nacional do Iguaçu. Por outro lado, ambientes florestais com menor integridade da vegetação florestal impuseram uma intensificação na influência dos filtros ambientais sob as comunidades de aves. Esse aumento na influência dos filtros ambientais pode gerar uma série de efeitos em cascata, como o adensamento do espaço de nicho ocupado, o aumento da competição entre espécies funcionalmente redundantes, mudanças na prevalência de traços funcionais nas comunidades e exclusões competitivas que podem inviabilizar a ocorrência de espécies especialistas e favorecer as generalistas.

Dada a importância de dados temporais e de fina escala espacial para tomadas de decisões mais acuradas para a conservação, aconselha-se a manutenção dos monitoramentos aqui desenvolvidos e o incentivo para o estabelecimento de protocolos de monitoramento de longa escala temporal em outras unidades de conservação na região Neotropical.