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Andrei Langeloh Roos

INFLUÊNCIA DE FATORES AMBIENTAIS, GEOGRÁFICOS E BIÓTICOS SOBRE A DIVERSIDADE E COMPOSIÇÃO DE METACOMUNIDADES DE AVES NA PORÇÃO SUL DA MATA ATLÂNTICA

Florianópolis
2021

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Tese submetida ao Programa de Pós-graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do título de Doutor em Ecologia.
Orientadora: Profª. Drª. Malva Isabel Medina Hernández
Coorientador:Prof. Dr. Eduardo Luís Hettwer Giehl

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Influência de fatores ambientais, geográficos e bióticos sobre a diversidade e composição de metacomunidades de aves na porção sul da Mata Atlântica

Por

Andrei LangelohRoos

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutor em Ecologia.

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Ata de sessão de defesa de Tese de Doutorado de Andrei Langeloh Roos

Aos vinte e seis dias do mês de Julho de 2021, às 8h00min, por videoconferência, realizou-se a sessão de apresentação e defesa da Tese de Andrei Langeloh Roos, como parte dos requisitos para a obtenção do título de Doutor em Ecologia, da Universidade Federal de Santa Catarina. A Comissão Examinadora, consoante à Portaria nº 015/2021/PPGECO, esteve constituída pelos membros Doutores Milton Cezar Ribeiro - participação por videoconferência (Universidade Estadual Paulista), Michele de Sá Dechoum - participação por videoconferência (Universidade Federal de Santa Catarina) e Andros Tarouco Gianuca - participação por videoconferência (Universidade Federal do Rio Grande do Norte) como Membros Titulares, e Marcos Robalinho Lima - participação por videoconferência (Universidade Estadual de Londrina) e Nivado Peroni - participação por videoconferência (Universidade Federal de Santa Catarina) como Membros Suplentes. A Tese apresentada teve o seguinte título: “INFLUÊNCIA DE FATORES AMBIENTAIS, GEOGRÁFICOS E BIÓTICOS SOBRE A DIVERSIDADE E COMPOSIÇÃO DE METACOMUNIDADES DE AVES NA PORÇÃO SUL DA MATA ATLÂNTICA”. Após a exposição do trabalho pelo candidato, o mesmo foi arguido pelos membros da Comissão Examinadora e coube ao candidato responder aos questionamentos da Comissão. Andrei Langeloh Roos foi considerado APROVADO. A Comissão Examinadora solicitou as seguintes alterações na Tese:
CONSIDERAR AS SUGESTÕES E RECOMENDAÇÕES FEITAS PELOS MEMBROS DA BANCA, INCORPORANDO AQUELAS QUE JULGAR PERTINENTES

O aluno terá até 60 (sessenta) dias, a partir da presente data, para fazer as alterações solicitadas pela Comissão Examinadora e submeter a cópia corrigida da Tese à Biblioteca Universitária (UFSC). Caso não haja alteração, o prazo é de 30 (trinta) dias. **O não cumprimento deste prazo acarretará em consequências legais de acordo com a legislação vigente nesta Universidade**.

Após o encerramento da sessão, eu, Dr. Eduardo Luís Hettwer Giehl, lavrei a presente ata que, se aprovada, vai assinada pelos demais membros da Comissão Examinadora e pelo Doutorando.

Florianópolis, 26 de julho de 2021.

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Andrei Langeloh Roos
Doutorando

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Quando meus olhos estão sujos de civilização, cresce por dentro deles um desejo de árvores e aves.

Manuel de Barros, 2010

Todos esses que aí estão
Atravancando meu caminho,
Eles passarão...
Eu passarinho!

Mario Quintana, 1984

RESUMO

Os padrões de diversidade, abundância e composição das espécies são consequências de processos relacionados aos filtros ambientais, interações bióticas, dispersão e deriva demográfica. Esses fatores variam no tempo e no espaço, não são mutuamente excludentes e atuam de forma distinta nos diferentes grupos de uma comunidade. A interação entre as diferentes comunidades, influenciada por esses processos, passa a formar metacomunidades. Assim, a compreensão dos padrões de distribuição da diversidade biológica, das interações entre as espécies e de sua manutenção em uma paisagem fragmentada possui uma grande importância para a elaboração de políticas públicas voltadas à conservação de espécies e áreas protegidas. Sob essa perspectiva, buscamos compreender a formação e dinâmica de manutenção das metacomunidades de aves da Mata Atlântica de Santa Catarina em dois ecossistemas diferentes. Em um primeiro capítulo analisamos as metacomunidades de aves de seis manguezais do litoral catarinense medidas em 40 pontos-de-escuta, bem como as características do hábitat e da conectividade entre as áreas de manguezal. Embora a riqueza de espécies de aves seja semelhante entre os diferentes manguezais, encontramos mais espécies nos manguezais maiores e uma alta substituição de espécies entre estes locais, indicando que cada mangue contribui com espécies diferentes ao conjunto regional de espécies, com a dinâmica interna das áreas sendo o principal mecanismo que define a composição da metacomunidadede aves dos manguezais, com pouca influência das características de cada hábitat e da conectividade. No segundo capítulo analisamos as metacomunidades de aves em 21 áreas florestais remanescentes de Floresta Ombrófila Densa, incluindo três unidades de conservação e fragmentos de diferentes tamanhos. Por meio de gravações com unidades autônomas (ARU), realizamos inventários das metacomunidades de aves com posterior identificação automatizada e medição das características das áreas a nível de hábitat e paisagem. Encontramos uma forte dependência da riqueza das aves com grandes manchas florestais e com aquelas próximas às áreas de referência (áreas protegidas) e uma influência secundária da estrutura de cada hábitat na composição final da metacomunidade de aves. Nossos resultados mostram que as metacomunidades de aves em uma floresta subtropical atlântica são determinadas em grande parte por filtros ambientais caracterizados pelo tamanho dos fragmentos, com a dispersão e características do hábitat local com efeitos secundários. Visando não só a manutenção da maior diversidade taxonômica possível, mas também da diversidade funcional, as estratégias para conservação e manutenção da biodiversidade na Mata Atlântica devem ser localmente adaptadas, levando-se em consideração a quantidade de hábitat presente na paisagem, para que as ações sejam bem-sucedidas e os objetivos de conservação alcançados adequadamente.

Palavras-chave: Conservação, ecologia, hábitat, tamanho de área, manguezal, floresta subtropical

ABSTRACT

Patterns of diversity, abundance and species composition are consequences of processes related to environmental filters, biotic interactions, dispersal, and demographic drift. These factors vary in time and space, are not mutually exclusive, and act differently on different groups within a community. The interaction between the different communities – influenced by these processes – form metacommunities. Thus, understanding the distribution patterns of biological diversity, interactions between species, and their maintenance in a fragmented landscape is of great importance for the development of public policies aimed at the conservation of species and protected areas. From this perspective, we sought to understand the formation and maintenance dynamics of bird metacommunities in the Atlantic Forest of Santa Catarina state in two different ecosystems. In the first chapter, we analyzed the bird metacommunities of six mangroves inthe coastline of the State of Santa Catarina measured at 40 point-counts, as well as the habitat characteristics and connectivity between mangrove areas. Although bird species richness is similar among different mangroves, we found more species in the largest mangroves and a high species turnover, indicating that each mangrove contributes different species to the regional assemblage of species, with the internal dynamics of the areas being the main mechanism that defines the composition of the mangrove bird metacommunity, with little influence from local habitat characteristics and connectivity. In the second chapter we analyzed bird metacommunities in 21 remaining subtropical rainforest patches, including protected areas and fragments of different sizes. Using recordings with autonomous units (ARU), we conducted inventories of bird metacommunities with subsequent automated identification and related it with measurement of patches characteristics at the habitat and landscape level. We found a strong dependence of bird richness with large forest patches and with those near referencesites (protected areas) and a secondary influence of the habitat structure of the forest patches on the final composition of the bird metacommunities. Our results show that bird metacommunities in an Atlantic subtropical forest are largely determined by environmental filters characterized by patch size, with dispersal and local habitat characteristics having secondary effects. In order to maintain not only the greatest possible taxonomic diversity, but also functional diversity, strategies for conservation and maintenance of biodiversity in the Atlantic Forest must be locally adapted, taking into account the amount of habitat present in the landscape, if actions are to be successful and conservation objectives are to be adequately achieved.

Keywords: Conservation, ecology, habitat, area size, mangrove, subtropical forest

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AM AudioMoth – equipamento de gravação automática ou autônoma
APP Área de Proteção Permanente
ARU Automatedor Autonomous Recording Units (Unidade de Gravação Autônoma ou Automática)
CBRO Comitê Brasileiro de Registros Ornitológicos
GIS GeographicInformation System (Sistema de Informações Geográfico - SIG)
ICMBioInstituto Chico Mendes de Conservação da Biodiversidade
IMA Instituto de Meio Ambiente de Santa Catarina
PA Protected Area (Áreas Protegidas – sinônimo de Unidades de Conservação)
PESF Parque Estadual da Serra Furada
PEST Parque Estadual da Serra do Tabuleiro
PNSI Parque Nacional da Serra do Itajaí
PNSJ Parque Nacional de São Joaquim
REBIO Reserva Biológica
ESEC Estação Ecológica
RESEX Reserva Extrativista
UC Unidade de Conservação

SUMÁRIO

1 INTRODUÇÃO

1.1 APRESENTAÇÃO

A presente tese propõe um estudo sobre os processos que estruturam as metacomunidades de aves na Mata Atlântica da região sul do Brasil, analisando como tais aspectos contribuem para a composição e manutenção da biodiversidade em uma paisagem fragmentada. A compreensão dos padrões de distribuição de espécies e dos mecanismos que influenciam a composição e determinam a permanência das espécies a longo prazo nas paisagens, sejam elas naturais ou alteradas pelas atividades humanas, pode auxiliar de forma significativa para a conservação da biodiversidade. As diferentes estratégias de conservação serão mais ou menos exitosas, de acordo com os organismos para as quais são focadas, suas relações intra e interespecíficas, bem como suas interações com o ambiente na paisagem na qual estão inseridos.

A Mata Atlântica se estende por praticamente todo o litoral atlântico brasileiro, cobrindo 13% do território nacional. Devido à essa localização, coincidente com as regiões mais urbanizadas e com maior ocupação humana, esse bioma foi bastante impactado pela perda de hábitat e fragmentação, que transformaram enormemente sua paisagem. A substituição dos ecossistemas naturais por áreas agrícolas, de pastagem e urbanas criou uma série de manchas dos ecossistemas naturais, alterando as dinâmicas dos ecossistemas e afetando as interações entre espécies. O estado de Santa Catarina destaca-se nesse cenário, pois embora também tenha sofrido todo esse processo, apresenta uma quantidade expressiva de cobertura florestal remanescente em muitos fragmentos pequenos, mas também abriga grandes áreas florestais naturais. Tais áreas estão resguardadas principalmente em unidades de conservação, mas também em propriedades privadas, que compõem uma paisagem bastante heterogênea, mas com alta cobertura florestal e conectividade, principalmente na região do litoral.

Dois ecossistemas se destacam na Mata Atlântica litorânea de Santa Catarina: a Floresta Ombrófila Densa, ocupando todo a planície litorânea do estado, desde a região costeira até os contrafortes da serra; e os Manguezais, distribuídos ao longo de todo o litoral em baías e estuários. Esses dois ecossistemas abrigam uma diversa avifauna e devido às suas características de distribuição fragmentada, com variados tamanhos e níveis de conectividade, um de origem antrópica e outro natural, se apresentam como interessantes cenários para o estudo de metacomunidades.

No primeiro capítulo da tese, avaliamos como a riqueza e a composição das metacomunidades de aves são influenciadas pela distância entre manchas de Manguezais, pelas características da paisagem e pelas características locais dos manguezais. Para isso, realizamos inventários da avifauna por meio de pontos de escuta e tomamos medidas da vegetação em seis manguezais do litoral do estado, sendo dois localizados na região do município de Joinville e quatro nas baías norte e sul da Ilha de Santa Catarina (pontos 1 e 2 da figura1-1).

No segundo capítulo avaliamos as metacomunidades de aves da Floresta Ombrófila Densa em três regiões com diferentes coberturas florestais e referenciadas por unidades de conservação. Buscamos compreender como mecanismos na escala local (filtros ambientais) e na escala regional (fatores geográficos) influenciam a diversidade e a composição das espécies (diversidade taxonômica alfa e beta) nos fragmentos florestais remanescentes. Por meio de gravações com unidades autônomas (ARU), realizamos inventários das metacomunidades de aves em 48 pontos de 21 áreas de remanescentes florestais e das unidades de conservação, com posterior identificação automatizada. Para avaliação dos fatores locais e regionais, realizamos a medição das características do fragmento a nível local (hábitat) e regional (área e distância) (pontos 3, 4 e 5 da figura 1-1).

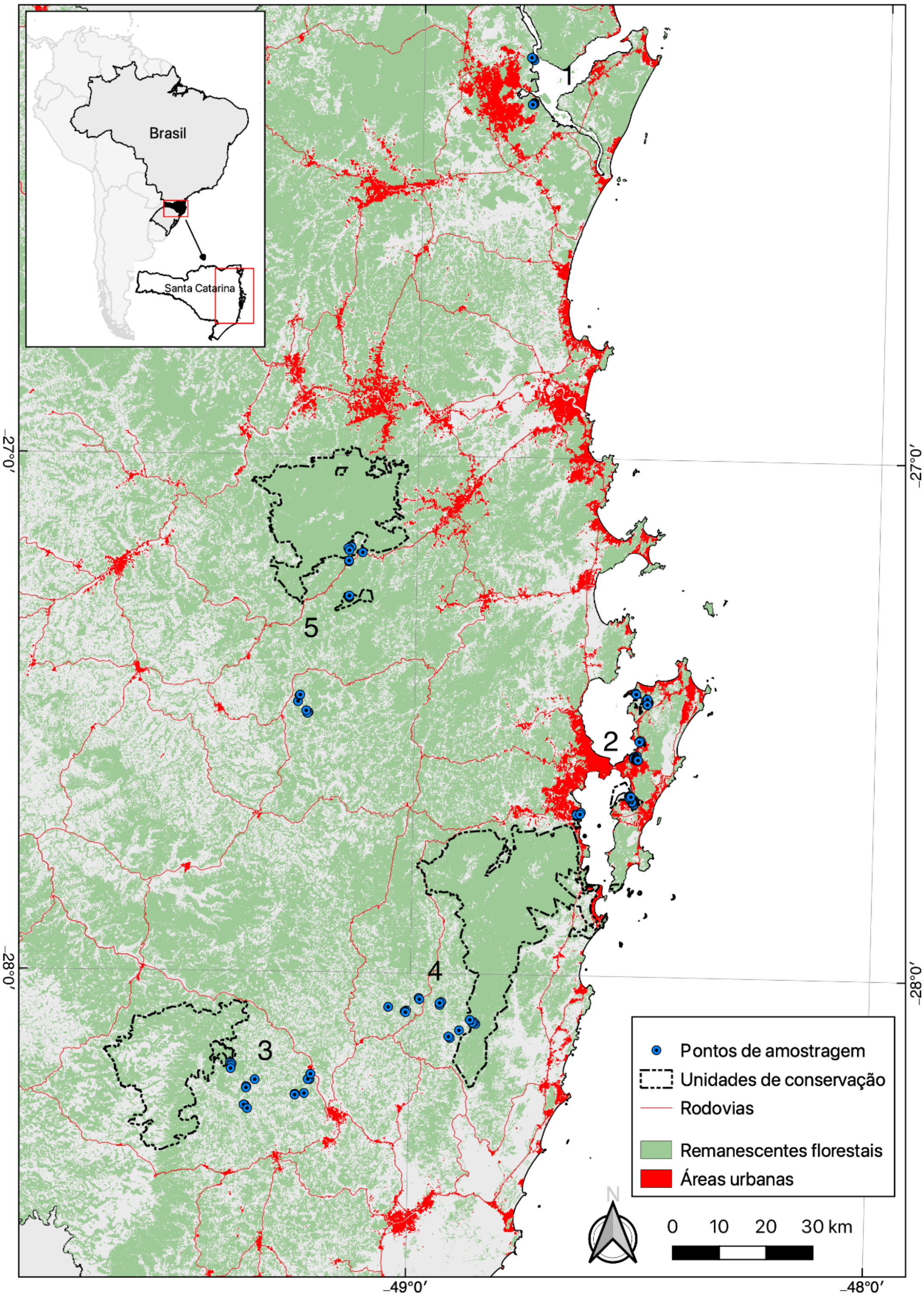

Figura1-1: Localização das áreas de estudo no litoral do estado de Santa Catarina, sul do Brasil. A figura apresenta os remanescentes florestais e a localização das principais unidades de conservação (federais e estaduais) na composição da paisagem estudada (dados de uso do solo: Mapbiomas – compilação 2020). 1- Manguezais do município de Joinville; 2 – Manguezais das baías da Ilha de Santa Catarina (Palhoça e Florianópolis); 3 – Mosaico: Parque Nacional São Joaquim e Parque Estadual da Serra Furada; 4 – Parque Estadual da Serra do Tabuleiro; 5 – Mosaico Parque Nacional da Serra do Itajaí e Reserva Biológica Estadual Canela Preta. Capítulo 1 compreende as regiões 1 e 2 ; Capítulo 2 compreende as regiões 3, 4 e 5.

1.2 FUNDAMENTAÇÃO TEÓRICA

A Ecologia de Comunidades busca compreender os padrões de distribuição da diversidade biológica e as interações entre as espécies que compõem as comunidades. Nas décadas de 50 e 60, o estudo da ecologia de comunidades foi fortemente influenciado por trabalhos que mostravam fortes relações entre as espécies e seus ambientes. A expansão do conhecimento teórico ocorrida posteriormente, bastante auxiliada pelos avanços da matemática aplicada à ecologia, proporcionaram um florescimento da ecologia de comunidades nas décadas seguintes (CHASE; BENGTSSON, 2010; RICKLEFS; SCHLUTER, 1993; SCHLUTER; RICKLEFS, 1993; VELLEND, 2010). O reconhecimento das conexões locais, biogeográficas e históricas na formação e manutenção da diversidade, ocorreu posteriormente com o acúmulo de pesquisas empíricas e teóricas. Esse novo olhar trouxe o reconhecimento de que a composição e diversidade de espécies a nível local depende da composição regional de espécies, que é resultado dos processos de especiação ocorridos ao longo do tempo (CHASE; BENGTSSON, 2010; SCHLUTER; RICKLEFS, 1993; VELLEND, 2010).

Outro processo que influencia fortemente a diversidade é a dispersão dos organismos, ou seja, a movimentação de indivíduos entre áreas e hábitats. Sua importância é bastante destacada na ‘Teoria de Biogeografia de Ilhas’ (MACARTHUR; WILSON, 1967) e continua assumindo um papel de destaque no conceito atual de metacomunidades, já que interage em diferentes escalas com os outros processos influenciando a dinâmica das metacomunidades (RICKLEFS; SCHLUTER, 1993; VELLEND, 2010). Além disso, os conceitos da Teoria Neutra da Genética, trazidos para a ecologia por Hubbell, inseriram a deriva demográfica como mais um importante processo na estruturação das comunidades (ROSINDELL; HUBBELL; ETIENNE, 2011; VELLEND, 2010).

Todo o arcabouço teórico da conceituação de metacomunidades já estava presente, ainda que de forma esparsa, nas discussões teóricas da ecologia de comunidades há muitos anos (BROWN et al., 2017; VELLEND, 2010). Contudo, o conceito atual surge da síntese proposta por HOLYOAK e colaboradores (2005) que definem a metacomunidade como “um conjunto de comunidades locais de espécies potencialmente interatuantes que são interligadas pela dispersão” (CHASE; BENGTSSON, 2010; LEIBOLD et al., 2004; VELLEND, 2010; WILSON, 1992). Tal conceito teórico de metacomunidades é bastante influenciado pelo estudo das metapopulações e da biogeografia de ilhas, com terminologia em comum, embora a amplitude de escalas no contexto de metacomunidades é bem mais amplo, podendo variar de gradientes ambientais em pequena escala a estudos biogeográficos em escala continental (CHASE; BENGTSSON, 2010). Assim, a teoria de metacomunidades nos permite integrar, em diferentes escalas espaciais, os processos locais e regionais que regulam a estruturação das comunidades (CHASE et al., 2020; CHASE; BENGTSSON, 2010; HOLYOAK; MOUQUET; HOLT, 2005; LEIBOLD et al., 2004, 2020) (Figura 1-2). Diferentes combinações desses processos, que hoje são traduzidos como filtros ambientais, interações bióticas, dispersão e deriva ecológica (CHASE et al., 2020; LEIBOLD et al., 2020) formam as comunidades e definem, de forma clássica, os quatro modelos da teoria da metacomunidades.

Esses quatro modelos ou paradigmas teóricos deram a base para a conceituação teórica de metacomunidades, os quais têm sido observados também de modo empírico (BROWN et al., 2017; CHASE; BENGTSSON, 2010; DRISCOLL, 2008; LEIBOLD et al., 2004). Um dos modelos é a ‘dinâmica de manchas’ (“patch-dynamics”), no qual se assume que há vários fragmentos idênticos ou homogêneos em termos de hábitat e a composição das espécies dentro deles é mais influenciada pelas habilidades inerentes de cada espécie em colonizar e competir em cada área (CHASE; BENGTSSON, 2010; LEIBOLD et al., 2004). Essa abordagem assume a estocasticidade nos processos de colonização e extinção nos fragmentos, mas também assume que as espécies podem coexistir ao variarem as suas taxas intrínsecas de colonização e competição (CHASE; BENGTSSON, 2010; LEIBOLD et al., 2004).

O segundo modelo conhecido como ‘alocação de espécies’ (“species-sorting”) não admite a estocasticidade exposta no modelo anterior e foca nos processos determinísticos resultantes das diferentes respostas que as espécies possuem aos ambientes heterogêneos. Desta forma, assume que as espécies só irão ocorrer e permanecer em um determinado hábitat se este apresentar as condições favoráveis à permanência das mesmas (CHASE; BENGTSSON, 2010; LEIBOLD et al., 2004).

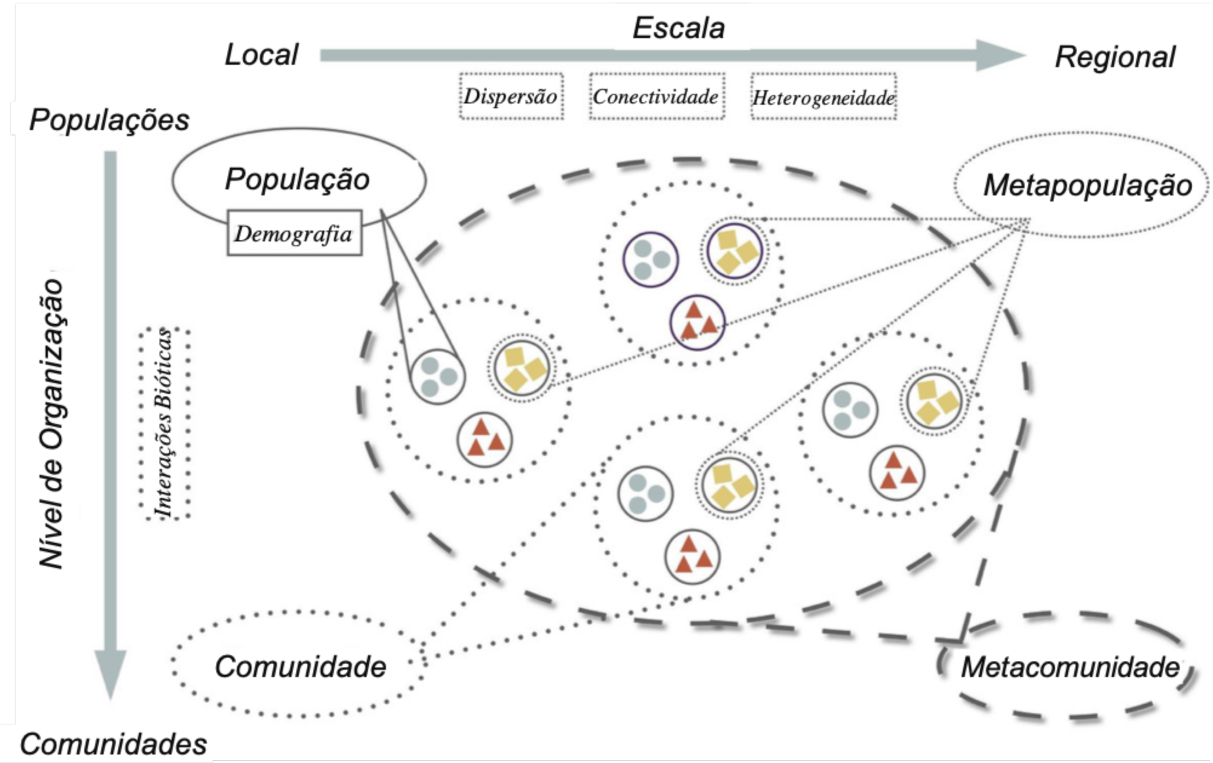

Figura1-2: Representação conceitual que demonstra os diferentes níveis integrados pela Ecologia de Metacomunidades. As populações estão inseridas nas comunidades locais, enquanto as metapopulações estão inseridas nas metacomunidades regionais. Eixo superior mostra as escalas espaciais, do local ao regional, com influência da dispersão, conectividade e heterogeneidade de hábitats. O eixo lateral indica os níveis de organização da população à comunidade, onde atuam as interações bióticas (adaptado de Chase et al. 2020).

Quando são considerados que os fragmentos possuem diferentes condições ambientais, mas são excessivamente conectados, e as espécies possuem diferentes taxas de colonização e extinção, isso resulta em um efeito de fonte-sumidouro entre manchas de hábitat. A coexistência de espécies com diferentes habilidades competitivas é favorecida pelas compensações regionais proporcionadas pela dispersão. Esse balanço entre dispersão, colonização e extinção, que são os aspectos dos dois modelos anteriores combinados, configuram o terceiro modelo conhecido como ‘efeito de massa’ (“mass-effect”) (CHASE; BENGTSSON, 2010; LEIBOLD et al., 2004). Nesse modelo, a dispersão tem um papel bem importante na dinâmica local e regional das comunidades e assume um papel duplo, tanto ao aumentar a densidade de espécies suplementando as taxas de nascimento, quanto ao diminuir a densidade devido a perdas, de forma diferente que o esperado para comunidades fechadas (LEIBOLD et al., 2004).

Quando não existem pressupostos relacionados aos atributos das espécies ou às suas respostas ambientais, ou seja, assume-se que as espécies sejam neutras com relação às interações interespecíficas e aos ambientes, temos o modelo ‘neutro’ (“neutral”) conforme proposto por Hubbell (2001) (CHASE; BENGTSSON, 2010; DRISCOLL; LINDENMAYER, 2009; LEIBOLD et al., 2004; TILMAN et al., 1994). Esse modelo pode ser considerado como uma hipótese nula de todos os outros modelos, uma vez que considera que os padrões de distribuição, abundância e interações dos organismos, tanto a nível local quanto regional são o resultado de eventos estocásticos (CHASE; BENGTSSON, 2010; LEIBOLD et al., 2004).

Esses modelos apresentados dentro da teoria de metacomunidades não são mutuamente excludentes, pois contemplam diferentes mecanismos envolvidos na estruturação das comunidades (BROWN et al., 2017). Além disso, também não são estáticos no tempo e não compreendem todo o espaço de inferência da teoria de metacomunidades (BROWN et al., 2017; LEIBOLD et al., 2020; LOGUE et al., 2011). Assim, apesar de sua utilidade em enfatizar os diferentes conjuntos de dinâmicas nas comunidades, eles devem ser interpretados com cautela e com a possibilidade de que diferentes parcelas das metacomunidades possam ser determinadas por diferentes processos (BROWN et al., 2017; CHEN et al., 2019; LEIBOLD et al., 2020). Isso porque, por exemplo, diferentes processos que formam comunidades (filtragem ambiental, interações bióticas, dispersão e estocasticidade) agem de forma diferente sobre diferentes grupos de espécies dentro de uma comunidade (CHASE et al., 2020).

Alterações de uso do solo e gestão da água (incluindo perda e fragmentação de hábitat), mudanças climáticas, invasões biológicas, poluição e sobre-exploração são atualmente as principais modificações de origem antrópica e consideradas as principais causas de extinção de espécies no mundo (DÍAZ et al., 2019; MCGILL et al., 2015; SOULE, 1985). Essas forças, oriundas das modificações humanas nos ambientes naturais, influenciam os processos das metacomunidades que determinam os padrões de distribuição da biodiversidade, podendo ocorrer de forma direta modificando, ou indireta, amplificando os efeitos antrópicos sob os demais processos da metacomunidade (CHASE et al., 2020). Compreender os padrões de distribuição dos organismos e suas relações com o ambiente, e como essas influências antrópicas interferem nos mesmos, possui uma grande importância para a conservação da biodiversidade, fornecendo importantes subsídios no sentido de prever e mitigar os impactos negativos das modificações antrópicas. Deste modo, a teoria de metacomunidades têm papel fundamental no campo da conservação aplicada (CHASE et al., 2020; DRISCOLL, 2008; SOCOLAR et al., 2016).

A Mata Atlântica ocupa cerca de 13% do território brasileiro, e atualmente abriga 57% das áreas urbanas do Brasil, que mantêm cerca de 72% da população brasileira, com mais de 61% do bioma ocupado por áreas agrícolas e de pastagem (MAPBIOMAS, 2020). A Mata

Atlântica é classificada como um dos ecossistemas mais ameaçados do mundo e uma das principais áreas mundiais prioritárias (‘Hotspot’) para a conservação (MYERS et al., 2000; MITTERMEIER et al., 2004). Essa classificação advém da sua alta diversidade e grande número de endemismos, desde plantas vasculares, aves, mamíferos, répteis e anfíbios (BROOKS; TOBIAS; BALMFORD, 1999; CARDOSO DA SILVA; CARDOSO DE SOUSA; CASTELLETTI, 2004; GOERCK, 1997; MARINI; GARCIA, 2005; MITTERMEIER et al., 2004; MOREIRA LIMA, 2014; RIBEIRO et al., 2009; TABARELLI et al., 2010). A nível nacional, a Mata Atlântica, está reduzida a cerca de 12% da sua cobertura original, distribuídos em inúmeros fragmentos e dispersos em uma paisagem altamente fragmentada (RANTA et al., 1998; RIBEIRO et al., 2009) e com somente 30% localizado em unidades de conservação (REZENDE et al., 2018). Embora a região da Mata Atlântica do Sul/Sudeste do Brasil, mais especificamente a Serra do Mar, apresente a maior porcentagem de remanescentes florestais (32%) em relação à cobertura florestal original, o padrão de paisagem fragmentada ainda persiste (RIBEIRO et al., 2009; VIBRANS et al., 2013), com os fragmentos remanescentes sofrendo com processos de erosão da biodiversidade e da biomassa (DE LIMA et al., 2020).

No estado de Santa Catarina, na região sul do Brasil, encontramos uma elevada proporção de remanescentes florestais (27%), alcançando de 40 a 47% se considerada apenas a Floresta Ombrófila Densa (VIBRANS et al., 2013). Boa parte dessa cobertura florestal é resultado de um processo de regeneração que ocorreu no estado entre 1975-1995 (BAPTISTA; RUDEL, 2006) e que substituiu florestas originais por áreas em regeneração que, entretanto, não possuem a mesma qualidade de hábitat que as florestas originais (BAPTISTA; RUDEL, 2006; DE LIMA et al., 2020; RIBEIRO et al., 2009). Várias foram as causas desse processo de recuperação vegetal, que incluem abandono de algumas práticas agrícolas, processos de urbanização e industrialização, o reforço de medidas legais limitando exploração e corte, bem como a criação de áreas protegidas na forma de unidades de conservação (BAPTISTA; RUDEL, 2006). A manutenção de inúmeros fragmentos, de variados tamanhos, de remanescentes de vegetação nativa, que sofreram pouca modificação ou de regeneração, juntamente com as unidades de conservação, têm garantido uma boa conectividade na paisagem na Mata Atlântica de Santa Catarina (MAPBIOMAS, 2020). Nesse cenário, bastante heterogêneo, as Unidades de Conservação possuem um alto valor, pois representam grandes e importantes áreas mantenedoras dos processos ecológicos e fontes de espécies na paisagem fragmentada e se confirmam como uma importante ferramenta na conservação *in-situ* da biodiversidade

(BRUNER et al., 2001; CHAPE et al., 2005; DEFRIES et al., 2005; FERREIRA; VENTICINQUE; ALMEIDA, 2005; GASTON et al., 2008; HANNAH et al., 2007; MEDEIROS et al., 2011; NEPSTAD et al., 2006).

Além dos fragmentos de floresta, na região litorânea, os manguezais são um importante ecossistema dentro da Mata Atlântica. Os manguezais são ambientes de alta produtividade, importantes berçários da vida marinha e desempenham importantes funções ecológicas, como ciclagem de nutrientes, sequestro de carbono ("blue carbon") e manutenção das linhas de costa (ALVES, 2001; HATJE et al 2021; HUTCHINGS; SAENGER, 1987; KATHIRESAN; BINGHAM, 2001; LUGO; ROVAI et al 2021; SNEDAKER, 1974; MCLEOD et al., 2011; SOBRINHO; BRESOLIN; KLEIN, 1969). Também são hábitat primário para diversas espécies de aves, que os utilizam para reprodução e alimentação (KUTT, 2007; LUGO; SNEDAKER, 1974; NAGELKERKEN et al., 2008). Os manguezais são ambientes naturalmente fragmentados e distribuídos em manchas isoladas com tamanhos variados (ALVES, 2001; LEFEBVRE; POULIN, 1997; LUGO; SNEDAKER, 1974; RIBEIRO et al., 2009), características essas que os transformam em importantes corredores ecológicos aumentando a conectividade dos ambientes costeiros (HUTCHINGS; SAENGER, 1987; KUTT, 2007; MOHD-AZLAN; NOSKE; LAWES, 2012).

Esta paisagem composta de manchas de hábitat, impactada pela perda de habitat e fragmentada a partir de duas distintas origens (antrópica no caso das florestas e natural no caso dos manguezais), mas que ainda preserva uma alta proporção de cobertura florestal, é um cenário importante para se compreender os padrões e mecanismos que geram a diversidade e mantém a composição das comunidades animais da Mata Atlântica. Paralelamente, a compreensão do papel das Unidades de Conservação e das áreas legalmente protegidas (APP e Reservas Legais) compondo essa paisagem, permite ampliar as discussões sobre o melhor aproveitamento de recursos disponíveis, o papel de corredores ecológicos e demais políticas públicas ambientais.

1.3 AVES COMO MODELOS DE ESTUDO

As aves foram utilizadas como grupo focal para análise dos padrões de diversidade, por serem um dos grupos de vertebrados mais bem conhecidos, além de serem globalmente distribuídas e consideradas boas bioindicadoras (GARDNER et al., 2008; PIRATELLI et al., 2008; PIZO; TONETTI, 2020). As aves apresentam grande diversidade e desempenham diversos papéis ecológicos, de modo que sua extinção massiva levaria a uma redução dos processos e serviços ecossistêmicos de grande importância para a humanidade (SEKERCIOGLU; DAILY; EHRLICH, 2004; SODHI et al., 2011; WHELAN; ŞEKERCIOĞLU; WENNY, 2015).

Localizado na região Neotropical, que é considerada a região mais rica em diversidade de aves e em endemismos, o Brasil ainda figura como um dos três países com a maior diversidade de espécies de aves (DEVELEY, 2021). Com mais de 1900 espécies de aves (PIACENTINI et al., 2015), também lidera no número de espécies endêmicas e em táxons ameaçados de extinção (DEVELEY, 2021). Cobrindo toda a costa leste do Brasil, a Mata Atlântica abriga a segunda maior riqueza avifaunística dos biomas brasileiros e uma grande quantidade de endemismos (CARDOSO DA SILVA; CARDOSO DE SOUSA; CASTELLETTI, 2004; MARINI; GARCIA, 2005; MOREIRA LIMA, 2014; TABARELLI et al., 2010).

Mesmo com todo o histórico de perda de hábitat e fragmentação, se esperaria um grande número de espécies de aves extintas na Mata Atlântica, mas os registros de extinções recentes são poucos ou subestimados (DEVELEY et al., 2021), embora exista um número expressivo de espécies ameaçadas (BROOKS; TOBIAS; BALMFORD, 1999; DEVELEY et al., 2021; MOREIRA LIMA, 2014). Têm se postulado algumas possíveis explicações para essa baixa taxa de extinções na Mata Atlântica, incluindo também uma possível defasagem no tempo das extinções (BROOKS; TOBIAS; BALMFORD, 1999; TILMAN et al., 1994; UEZU; METZGER, 2016) e a possibilidade de que muitas espécies sobrevivam em ambientes não florestados (BROOKS; TOBIAS; BALMFORD, 1999), em manchas florestais secundárias (CASAS et al., 2016), ou mesmo uma persistência de sobrevivência em paisagens fragmentadas (AWADE; METZGER, 2008; BOSCOLO et al., 2008; UEZU; METZGER; VIELLIARD, 2005), desde que resguardada alguma quantidade de hábitat (ANDRÉN, 1994; BANKS-LEITE et al., 2014; BOESING; NICHOLS; METZGER, 2018; MARTENSEN et al., 2012). Até mesmo em algumas espécies de aves, reconhecidas como negativamente afetadas pela fragmentação (AWADE; METZGER, 2008; GIUBBINA; MARTENSEN; RIBEIRO, 2018; HANSBAUER et al., 2008; LEES; PERES, 2009; UEZU; METZGER; VIELLIARD, 2005), têm se confirmado sua capacidade de deslocamento entre fragmentos (AWADE; METZGER, 2008; BOSCOLO et al., 2008; HANSBAUER et al., 2008; MARTENSEN; PIMENTEL; METZGER, 2008; UEZU; METZGER; VIELLIARD, 2005).

Embora boa parte dos estudos com aves se concentrem em regiões florestais, a riqueza de espécies de aves dos manguezais é bastante significativa e relevante no bioma. Apesar dos manguezais apresentarem uma baixa diversidade arbórea, sua riqueza de aves é bastante influenciada pelos ecossistemas que o cercam (MESTRE; KRUL; MORAES, 2007; MOHD-AZLAN; LAWES, 2011; OLMOS; SILVA, 2001). Elas desempenham importantes papéis ecológicos e contribuem com os processos e funcionamento dos manguezais através do controle de invertebrados herbívoros, polinização de plantas e ciclagem de nitrogênio inorgânico (CANNICCI et al., 2008; MOHD-AZLAN; NOSKE; LAWES, 2012; NOSKE, 1995).

As aves têm uma grande capacidade de deslocamento, mas muitas espécies de aves são restritas a hábitats contínuos ou de boa qualidade, de forma que o tamanho dos fragmentos é considerado um bom preditor de riqueza de espécies (HANSBAUER et al., 2008; MARTENSEN; PIMENTEL; METZGER, 2008). Enquanto mensurar a capacidade de dispersão das espécies de aves não é uma tarefa fácil e pode ser realizada com diferentes abordagens (AWADE; METZGER, 2008; HANSBAUER et al., 2008; LEES; PERES, 2009; MARINI, 2010), estudos recentes propõem o uso do índice alar (‘hand-winged index’ - HWI) como um indicador, na forma de um único valor, da eficiência de voo e capacidade de dispersão das aves (SHEARD et al., 2020).

A manutenção da diversidade de aves na Mata Atlântica é um grande desafio, e passa por buscar compreender como as comunidades de aves se mantêm nas paisagens alteradas e fragmentadas, de forma a subsidiar estratégias para a conservação desse grupo na Mata Atlântica. Nesse sentido, a compreensão dos padrões de distribuição das espécies de aves em dois sistemas complementares, com diferentes estruturas espaciais é de grande importância para a conservação da diversidade no Bioma Mata Atlântica.

1.4 OBJETIVOS

1.4.1Objetivo Geral

O objetivo geral da tese foi o de avaliar como fatores que estruturam as comunidades (filtros ambientais, interações bióticas e dispersão), em diferentes escalas espaciais (local e regional), influenciam a diversidade e a composição das espécies de aves (diversidade taxonômica alfa e beta) em dois ecossistemas da Mata Atlântica do sul do Brasil.

1.4.2 Objetivos Específicos

Artigo 1 - Local species turnover increases regional bird diversity in mangroves
Objetivo: Avaliar a influência da distância entre manchas, características da paisagem, características de hábitat e interações entre espécies na diversidade e composição das comunidades de aves encontradas nos manguezais do sul do Brasil.

Artigo 2 - Bird diversity losses and changes in small fragments: a call for conservation in the southern ranges of the Atlantic Forest
Objetivo: Avaliar os processos que estruturam as metacomunidades de aves na Mata Atlântica do sul do Brasil, analisando como os mecanismos em escala local (filtragem de hábitat - fatores ambientais locais - e interações ambiente - características das aves) e em escala regional (fatores geográficos - tamanho dos fragmentos e distância das áreas protegidas) influenciam a diversidade de espécies e mudanças na composição das espécies (diversidade taxonômica alfa e beta).

2 CAPÍTULO 1 – LOCAL SPECIES TURNOVER INCREASES REGIONAL BIRD DIVERSITY IN MANGROVES

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2.1 ABSTRACT, RESUMO E RESUMEN

Abstract

Understanding patterns of species diversity and distribution is crucial for the development of adequate public conservation policies. Despite the conservation value of mangroves, we still have a limited understanding of the influence of the habitat characteristics and patch connectivity of mangroves on bird species composition and diversity at local and regional scales. Here we used 40 point-counts in six mangroves in southern Brazil to test the effects of landscape connectivity and habitat characteristics on the composition and diversity of mangrove bird communities. We measured environmental variables locally and calculated land cover to describe the landscapes in which the patches of mangrove habitat were inserted. We also generated spatial variables as proxies for connectivity. We found that local bird species richness was similar in the different mangroves, ranging from 22 to 33 species, but with more species being found in larger patches. The partitioning of the beta diversity revealed a high species turnover, indicating that each patch of mangrove contributes different species to the regional pool of 57 species. Variance partitioning analysis also indicated that the composition of the mangrove bird metacommunity is driven mainly by local patch dynamics, whereas habitat characteristics and connectivity had a minor influence. These findings indicate that the maintenance of multiple large patches of mangrove at a regional scale will ensure a high species turnover and is the key to the maintenance of a diverse regional biota.

Keywords: Bird, conservation, mangrove, metacommunity, species turnover.

Resumo

Compreender os padrões de diversidade e distribuição das espécies é essencial para o desenvolvimento de políticas públicas adequadas à conservação. Apesar da importância dos manguezais, ainda compreendemos pouco a influência das características do hábitat e da conectividade entre manchas de mangue na composição e diversidade das comunidades de aves, seja na escala local ou regional. Neste trabalho, amostramos 40 pontos-de-escuta em seis manguezais no sul do Brasil para testar os efeitos da conectividade entre manchas e das características de hábitat na composição e diversidade das comunidades de aves dos manguezais. Medimos variáveis ambientais em cada mancha e calculamos a cobertura por distintos usos do solo na matriz em que as manchas de mangue estão inseridas. Para avaliar a conectividade entre os manguezais, usamos variáveis espaciais. Verificamos que a riqueza de espécies de aves é semelhante entre os diferentes manguezais, variando de 22 a 33 espécies, sendo que mais espécies são encontradas nos manguezais maiores. A partição da diversidade beta revelou uma alta substituição de espécies, indicando que cada mangue contribui com espécies diferentes ao conjunto regional de 57 espécies. Com uma análise de partição de variância identificamos que a dinâmica interna das manchas é o principal mecanismo definindo a composição da metacomunidadede aves dos manguezais, com pouca influência das características do hábitat e da conectividade. Assim, apontamos que a melhor estratégia para a conservação dos manguezais é a manutenção de muitas manchas de mangue e com os maiores tamanhos possíveis em uma escala regional, o que garantirá alta substituição de espécies entre manchas e a manutenção de uma biota regional diversificada.

Palavras-chave: Ave, conservação, manguezal, metacomunidade, substituição de espécies.

Resumen

Comprender los patrones de diversidad y la distribución de especies es crucial para el desarrollo de políticas públicas de conservación adecuadas. A pesar del valor de conservación de los manglares, todavía tenemos un conocimiento limitado de la influencia de las características del hábitat y la conectividad de los manglares sobre la composición y diversidad de especies de aves a escala local y regional. Aquí usamos 40 puntos de conteo en seis manglares en el sur de Brasil para probar los efectos de la conectividad del paisaje y de las características del hábitat sobre la composición y diversidad de las comunidades de aves de los manglares. Medimos las variables ambientales localmente y calculamos la cobertura del suelo para describir el paisaje en el cual se insieren los parches de hábitat de manglares. También generamos variables espaciales como una aproximación de la conectividad. Encontramos que la riqueza local de especies de aves fue similar en los diferentes manglares, con un rango de 22 a 33 especies, pero con más especies en los parches más grandes. La partición de la diversidad beta reveló un altorecambio de especies, lo que indica que cada parche de manglar aporta diferentes especies a la riqueza regional de 57 especies. Mediante el análisis de partición de la varianza identificamos que la composición de la metacomunidad de aves de manglar es impulsada principalmente por la dinámica de parches, mientras que las características del hábitat y la conectividad tienen una influencia menor. Estos hallazgos indican que el mantenimiento de múltiples fragmentos de grandes manglares a escala regional, lo que asegurará un alto recambio de especies, siendo clave para el mantenimiento de una biota regional diversa.

Palabras clave: Aves, conservación, manglar, metacomunidad, recambio de especies.

2.2 INTRODUCTION

The understanding of patterns of diversity at the metacommunity level can provide essential insights for management and conservation actions (Driscoll 2008; Chase and Bengtsson 2010; Socolar *et al.* 2016). A metacommunity is a series of local communities connected by the dispersal of potentially interacting species (Leibold and Mikkelson 2002; Leibold *et al.* 2004; Driscoll 2006; Brown *et al.* 2017; Chase and Bengtsson 2010). At the metacommunity level, multiple processes such as environmental filtering, biotic interactions, dispersal, and stochastic events combine to drive the distribution and abundance of species,, and patterns of community composition (Presley *et al.* 2010; Vellend 2010; Leibold and Mikkelson 2002). These processes can drive local (alpha) diversity, create, or maintain the dissimilarity in species composition among communities (beta diversity), and thus account for regional (gamma) diversity (Socolar *et al.* 2016). Beta diversity can be further partitioned into components of nestedness or turnover, with varying implications for conservation (Baselga

2010, 2012). Nestedness arises when species-poor communities are subsets of species-rich ones, which implies that conservation initiatives would be more efficient by focusing on species-rich sites because they are more important for the maintenance of the regional species pool. By contrast, turnover refers to the mutual replacement of species among sites along environmental or spatial gradients, which reinforces the need for the conservation of multiple sites across the landscape to ensure the maintenance of the regional species pool. The identification of the drivers of diversity at different scales and the quantification of the components of beta diversity are thus important steps for the development of management actions to optimise the effectiveness of conservation efforts.

Mangrove bird communities occur in ecosystems of high conservation value, which may benefit from metacommunity-level studies (Lugo and Snedaker 1974; Kathiresan and Bingham 2001; Nagelkerken *et al.* 2008).Mangroves are typically inserted within other types of habitat and consist of patches of varying size and shape (Lefebvre and Poulin 1997; SEMADS 2001; Ribeiro *et al.* 2009; Lugo and Snedaker 1974; Kathiresan and Bingham 2001). These characteristics of mangrove patches are the primary determinants of its species composition, and for many animals, including birds, mangrove patches are important steppingstones (Hutchings and Saenger 1987; Kutt 2007). This is especially true for the mangrove birds that are good dispersers, e.g., water birds (Morris 2012; Almeida *et al.* 2016). By contrast, mangrove-dependent species or species with low dispersal ability are unlikely to move between mangroves separated by other habitat types or by relatively large distances (Grose 2016; Chupil and Monteiro-Filho 2018; Kathiresan and Bingham 2001). In recent years, changes in land use has led to increasing habitat loss, which reduces alpha diversity because less habitat is available (Thompson *et al.* 2017; Fahrig 2017), and fragmentation, which affects beta diversity through the reduction of connectivity.

Despite their reduced tree diversity, South American mangroves have a considerable diversity of bird species (Olmos and Silva 2001; Mestre *et al.* 2007; Mohd-Azlan and Lawes 2011). In contrast with the rich endemic mangrove-dependent fauna of the mangroves of the Indo-Pacific region, South American bird species are less mangrove-dependent (Luther and Greenberg 2009). While some of these bird species are strongly associated with mangroves (Mohd-Azlan *et al.* 2012), many generalist bird species that inhabit adjacent habitats may also forage in mangroves (Mohd-Azlan*et al.* 2012), but tend to be associated only weakly with this ecosystem. Biotic interactions may limit the number of species found in a given mangrove, and can be assessed indirectly through the assessment of the composition of different foraging guilds or groups of different body size (Bregman et al 2016, Casas et al 2016). The identification of the potential drivers of diversity at the metacommunity level can provide important insights for the understanding the dynamics of bird communities in mangrove environments.

In the present study, we assessed the influence of the distance between patches, landscape features, habitat characteristics, and species interactions on the diversity and composition of the bird communities found in the mangroves of southern Brazil. We tested two hypotheses, that (i) thediversity of the bird communities is driven by specific features of the mangrove (habitat characteristics) and landscape (patch shape and area), and (ii) the influence of the distance between patchesis negligible because most mangrove bird species are good dispersers. Overall, we expected the composition of the mangrove bird communities to be similar, even between distant patches, but with specific differences determined by features of the mangrove patches and the landscape. We also verified whether guild structure and the distribution of body mass reflected a rule determining biotic interactions in mangrove bird communities.

2.3 METHODS

Study area

The present study focused on six mangroves located on the coast of the state of Santa Catarina, in southern Brazil. Two of the mangroves (Ma1, Ma2) were located innorth-eastern Santa Catarina, in the municipality of Joinville, while three (Ma3, Ma4, Ma5) were on Santa Catarina Island in the municipality of Florianópolis, on the central coast, and the other (Ma6) is in a nearby estuary in the municipality of Palhoça. These sites extend along the coastline of Santa Catarina between 26.2° S and 27.6° S. Sites Ma1 and Ma2 are partly connected, although they are separated by tidal channels, bays, and urban areas. The other mangroves are located in different estuaries and are unconnected to other mangroves, even though associated habitats, such as swamps or other types of wetland. The distances between neighboring pairs of mangroves varied from 9 to 12 km.

Each mangrove was surrounded by habitats such as forest and wetlands, including marshes, and varying levels of anthropogenic impact (Figure 1). The area of the patches of mangrove ranged from 156 ha to 683 ha and four are protected areas (Table 1). The mangroves of Santa Catarina are composed of three tree species: *Rhizophora mangle* L., *Laguncularia racemosa* (L.) C.F.Gaertn, and the tallest and largest (basal area), *Avicennia schaueriana* Stapf & Leechm. ex Moldenke. These species form mixed or monospecific stands in different parts of the mangrove, but with no clear relationship with soil conditions. The mangrove at Palhoça represents the Brazilian southern limit of the distribution of *Rhizophora mangle* (ICMBIO 2018; Soares *et al.* 2012). The present study was conducted between November 2017 and January 2018, a period that coincides with the breeding season of most Brazilian birds, when they are more vocally active (Sick 1997; Marini and Durães 2006).

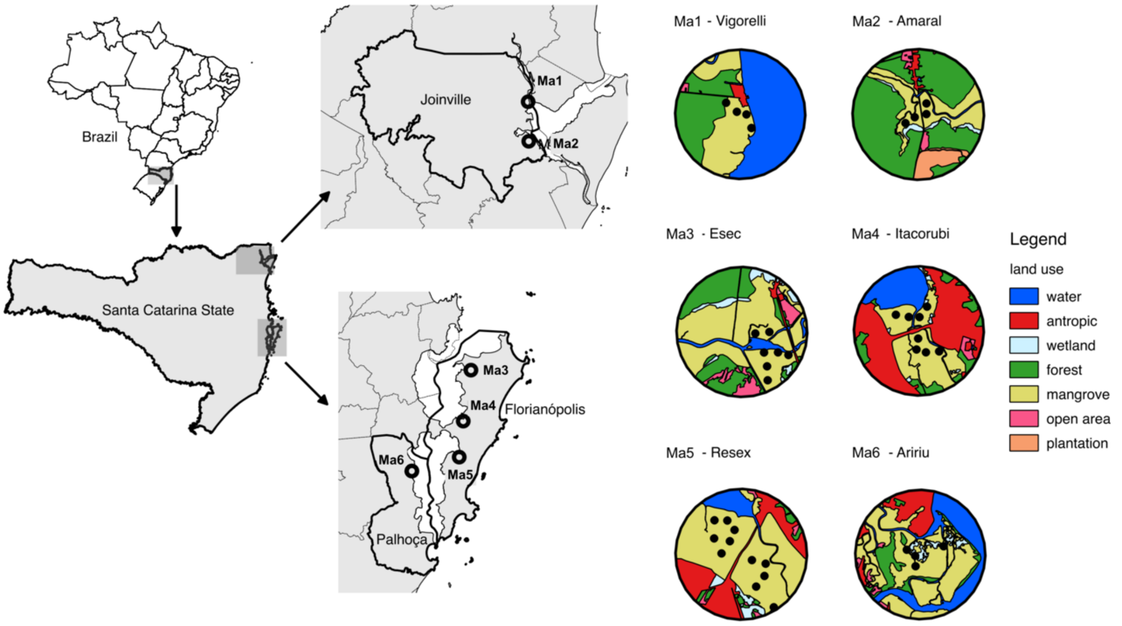

Figure 2-1.Location of the six mangroves studied in Santa Catarina state, in the municipalities of Joinville, Florianópolis, and Palhoça, in southern Brazil. Sample points (black dots) and land-cover classes within the 500-ha buffers are also shown. The site identification codes follow Table 2.

Table 2-1. Mangrove bird diversity sampled in six mangrove patches of Santa Catarina state, southern Brazil, during summer of 2017-2018.

Mangrove	Locality	Protected Area IUCN category	N of sample points	Area (ha)	Bird richness	Estimate richness	Exclusive species	Sample coverage (%)
Ma1	Vigorelli	No category	4	229	15	24	2	63
Ma2	Amaral	No category	4	156	10	22	2	23
Ma3	Carijós	Ecological Station - Ia	9	554	30	33	9	76
Ma4	Itacorubi	Municipal Park - II	8	173	22	25	6	84
Ma5	Pirajubaé	Extractive Reserve - VI	11	683	30	30	7	84
Ma6	Aririú	State Park - II	4	237	18	23	4	79
	Overall	-	40	-	57	95	-	90

Bird sampling

Birds were sampled by 10-minute point counts conducted within a fixed 100-m radius at intervals of 200 m, between 6 am and 11 am (following Volpato *et al.* 2009; dos Anjos *et al.* 2010). We obtained four to 11 point-counts per mangrove, depending on the size of the patch and its accessibility (Table 1). This included four point-counts (each) in Ma1, Ma2, and Ma6, eight counts in Ma4, nine in Ma3, and 11 in Ma5 (Figure 1, Table 1), with a total of 40 sampling points. The field observations were complemented with sound recordings, obtained using a Zoom H4N digital sound recorder with a Sennheiser ME66 microphone, which were analysed in the laboratory for the confirmation of the species. All bird species observed and recorded within the mangrove environment were registered, but birds flying over the mangrove and migratory species were excluded. The taxonomy and systematic orders followed CBRO (Piacentini *et al.* 2015). The principal habitat of each species was obtained from Stotz *et al.* (1996), and body mass data for the size classification were obtained from Dunning (2008).

The bird species were assigned to one of five dietary categories, based on the predominant resource used, *sensu* Eltontraits 1.0 (Wilman *et al.* 2014): (i) plant-seed (seeds, nuts, leaves, and other plant material), (ii) fruit-nectar (fruit, nectar, and pollen), (iii) invertebrates, (iv) vertebrates (including fish and carrion), and (v) omnivore (≤ 50% of any of the preceding categories).

Environmental variables

We recorded environmental characteristics at both local habitat and landscape scales in all six study mangroves. At the habitat scale, we collected data at every other bird sampling point, that is, at a total of 18 points. We decided not to sample each point because of the considerable environmental homogeneity found within each mangrove, and the assumption that the sampling of every other site would provide a more reliable characterisation of each study area. The environmental data were summarised for each mangrove.

We used the point-centred quarter method of Cottam and Curtis (1956) to evaluate vegetation structure. The distance, height and circumference at breast height (CBH) to the nearest tree in each quadrant was measured. We measured trees with a diameter of at least 5 cm and used the data to calculate tree density (per hectare) and mean basal area (Cintron and Novelli 1984; Cottam and Curtis 1956). The distance and CBH of each tree were measured with a surveyor’s tape and the CBH was used to calculate the diameter at breast height (DBH) and basal area, in m^2 (Cintron and Novelli 1984). We quantified the number of crab holes and the coverage of aerial roots within a 1 × 1 m square placed at 2.5 m from the central point in each quarter. We took a canopy photograph from each central point to calculate the Canopy Cover Index using the GLAMA application (Tichý, 2015, 2016). We used (1) tree density, (2) mean basal area, (3) the canopy cover index, (4) the number of crab holes, and (5) aerial root cover as the explanatory variables of the local environment at each sampling point. We separated the data into vegetation (1 to 3) and substrate variables (4 and 5) for analysis. All the variables were measured after the bird point counts.

At the landscape scale, we defined a buffer of 500 ha around the centroid of the sample points in each mangrove. This buffer is two orders of magnitude larger and encompasses the known territory size of the most Brazilian terrestrial birds (Lefebvre *et al.* 1992; Duca *et al.* 2006; Ribon and Marini 2016). Within each buffer, we calculated land use and vegetation cover manually using high-resolution satellite images from Google Earth in the QuickMapServices plug-in in the QGIS 2.18.13 software (QGIS Development Team 2018). Finally, we checked our data against the Santa Catarina Island land cover (Neves *et al.* 2017).

We assigned the vegetation and land use to five classes: (i) mangrove, (ii) native vegetation cover (wetland, vegetation with marine influence or dense lower montane ombrophilous forest), (iii) urban or human infrastructure, (iv) open areas (fields, pasture or exposed soil), and (v) water (Figure 1). The total area of each mangrove was also calculated from satellite images when this datum was not available from other sources (Carvalho *et al.* 2007; ICMBIO 2018). We considered four parameters as landscape explanatory variables (1) the total area of each mangrove patch, (2) extent of mangrove within the buffer, (3) native vegetation cover within buffer, and (4) extent of urban area within the buffer.

Spatial variables

We used the linear distance between mangroves as a proxy for dispersal. Geographic distances between patches is the usual proxy for dispersal limitation or connectivity, given that patches separated by smaller distances will likely be more connected by dispersing individuals (Maurer *et al.* 2013; Driscoll and Lindenmayer 2009; Leibold *et al.* 2004). To generate variables representing the spatial structure of the patches, we calculated the Euclidian distances from the coordinates of each mangrove, and truncated the greatest distances to generate a neighbourhood matrix, which was used to run a Principal Coordinates Analysis to obtain the eigenvectors (PCNMs; Borcard and Legendre 2002).

Data analyses

The alpha diversity of the birds was compared by interpolation and extrapolation curves compiled using the iNEXT package (Chao *et al.* 2014; Hsieh *et al.* 2016). We used the base sample size as proposed by Chao *et al*. (Chao *et al.* 2014) for the comparisons. This method permits the comparison of the species richness of all sample areas at an equivalent sample size. We then correlated patch size and estimated species richness for each mangrove. We then partitioned the beta diversity into its two components, i.e., replacement (turnover) and nestedness, from the total dissimilarity. We computed the dissimilarities for multiple sites and pairwise using the *betapart* package (Baselga *et al.* 2018). All analyses were computed in the R program version 3.6.0 (R Core Team 2019).

For each set of explanatory variables, i.e., the vegetation and ground characteristics, and landscape features, we used a Principal Components Analysis (PCA) to select the axes with the highest eigenvalues. We then created a new matrix with the first PCA axes for each group of environmental variables. This new set of explanatory variables was used to summarise both habitat and landscape factors, while reducing multicollinearity and maintaining the degrees of freedom for further analysis. We ran a redundancy analysis (RDA) for each set of variables and selected the best model in each case based on the adjusted-R^2 criterion. The species matrix was transformed with the Hellinger method prior to analysis to satisfy the assumption of linear relationships for the RDA. We then used variance partitioning to analyse the contributions of the environmental (E) and spatial (S) variables on the composition of the mangrove bird communities. For this, we ran a partial redundancy analysis (pRDA) to measure the amount of variation attributed to each set of explanatory variables (Cottenie 2005; Peres-Neto *et al.* 2006). All the ordinations were computed in the *vegan* package (Oksanen *et al.* 2018) of the R program version 3.6.0 (R Core Team 2019).

Finally, to assess whether biotic constraints regulate mangrove bird communities, we plotted graphs of the relative abundance of the different feeding guilds and mean body mass for each mangrove. This allowed us to verify whether community structure was influenced by the partitioning of resources, which represented a proxy for biotic interactions.

2.4 RESULTS

Composition and diversity of mangrove bird communities

We recorded a total of 57 bird species representing 25 families and 14 orders in the six study mangroves (Table 1). Total species richness was estimated to be 95 species (CI: 70–162 spp.; Table 2). The most diverse orders were the Passeriformes, with 29 species (51% of the total), the Columbiformes, Gruiformes and Pelicaniformes with four species (7%), and the Piciformes with three species (5%). Only four bird species (7%) were found in all six mangroves: Grey-necked Wood-Rail *Aramides cajaneus*, Glittering-throated Emerald *Amazilia fimbriata*, Great Kiskadee *Pitangus sulphuratus* and Tropical Parula *Setophaga pitiayumi*, while five other species occurred in at least four mangroves. Only five taxa (9%) are mangrove dependent: Yellow-crowned Night-Heron *Nyctanassa violacea*, Little Blue Heron *Egretta caerulea*, Mangrove Rail *Rallus longirostris*, Gray-necked Wood-Rail *Aramides cajaneus avicenniae* and Bicolored Conebill *Conirostrum bicolor*. Most (75%) of the species recorded in the surveys prefer arboreal-shrubby habitats, while the others were marsh habitat species (11% of the total), open area species (5%), or waterbirds (5%).

Estimated bird species richness per mangrove ranged from 22 to 33. Estimated species richness was correlated significantly ($r = 0.89$; $p = 0.018$) with patch area (Table 2). Although sampling effort varied among the mangroves, with values ranging from 23% to 84% of coverage (Appendix S1), estimated richness was similar among the mangroves, considering that patch Ma2 was under-sampled (Figure 2).

The analysis of beta diversity considerable differences among the communities, with dissimilarity ranging from 57% to 81% (Table 3). The partitioning of the beta diversity indicated that this dissimilarity was derived primarily from turnover, even in nearby mangroves (0.74; Table 3). Species replacement was high among patches, given that 30 of the 57 species were recorded at only one site and ten species were recorded in only two mangroves (Figure 3). The largest mangroves, which had the most species (Ma3 and Ma5) shared 18 species, but all the dissimilarity between them was due to species turnover, with 12 different species in each area. These sites had also the largest numbers of exclusive species, with nine species in Ma3 and seven in Ma5. The greatest dissimilarity was found between Ma2 and Ma4, with a high turnover (17 unshared species).

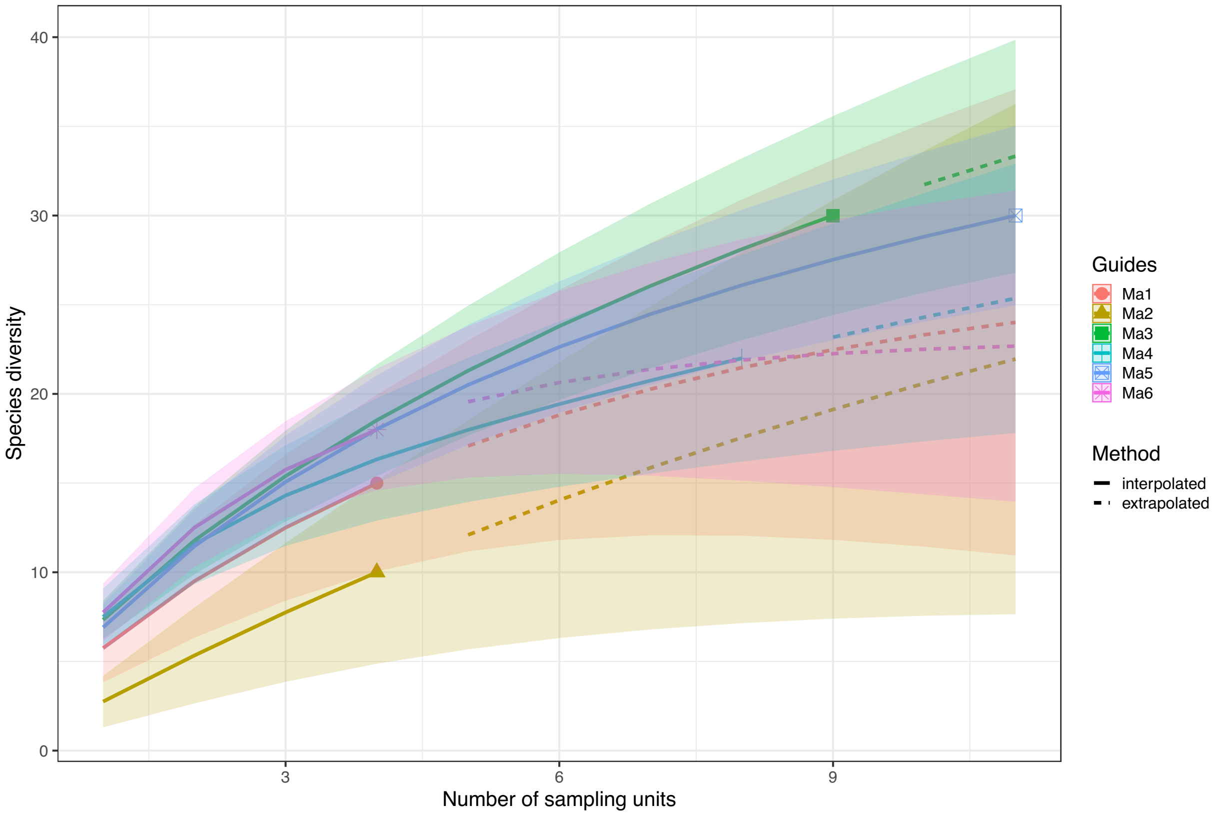

Figure 2-2. Rarefaction (solid lines) and extrapolation (dashed lines) sample size-based curves for species richness (q=0) and the associated 95% confidence intervals (shaded areas) of bird species in six mangroves in Santa Catarina state, southern Brazil (see Table 2 for identification codes).

Table 2-2. Bird richness registered in six mangroves of Santa Catarina state, southern Brazil, during summer 2017-2018. Values representing point-counts occurrence frequency.

Taxon	English Name	Habitat†	Guild‡	Size§	Ma1	Ma2	Ma3	Ma4	Ma5	Ma6
Galliformes Linnaeus, 1758										
Cracidae Rafinesque, 1815										
Ortalis squamata (Lesson, 1829)	Scaled Chachalaca	lFe	FN	l	0	0	2	0	0	0
Suliformes Sharpe, 1891										
Phalacrocoracidae Reichenbach, 1849										
Nannopterum brasilianus (Gmelin, 1789)	Neotropic Cormorant	C	VFS	l	0	0	0	2	1	0
Pelecaniformes Sharpe, 1891										
Ardeidae Leach, 1820										
Nyctanassa violacea (Linnaeus, 1758)	Yellow-crowned Night-Heron	M	VFS	l	0	0	1	2	1	0
Ardea alba Linnaeus, 1758	Great Egret	fM	VFS	l	0	0	1	0	0	0
Egretta caerulea (Linnaeus, 1758)	Little Blue Heron	M	In	m	0	0	0	1	2	0
Threskiornithidae Poche, 1904										
Plegadis chihi (Vieillot, 1817)	White-faced Ibis	fM	In	l	0	0	0	4	0	0
Accipitriformes Bonaparte, 1831										
Accipitridae Vigors, 1824										
Rupornis magnirostris (Gmelin, 1788)	Roadside Hawk	lFe	VFS	m	0	1	0	0	0	0
Gruiformes Bonaparte, 1854										
Rallidae Rafinesque, 1815										
Rallus longirostris Boddaert, 1783	Mangrove Rail	sM	O	m	0	0	0	1	0	0
Aramides cajaneus (Statius Muller, 1776)	Gray-necked Wood-Rail	M	O	m	1	1	3	3	5	2
Pardirallus nigricans (Vieillot, 1819)	Blackish Rail	fM	In	m	0	0	0	1	0	0
Gallinula galeata (Lichtenstein, 1818)	Common Gallinule	fM	O	m	0	0	0	1	0	0
Charadriiformes Huxley, 1867										
Charadriidae Leach, 1820										

Taxon	English Name	Habitat†	Guild‡	Size§	Ma1	Ma2	Ma3	Ma4	Ma5	Ma6
Vanellus chilensis (Molina, 1782)	Southern Lapwing	P	In	m	1	0	6	4	3	0
Columbiformes Latham, 1790										
Columbidae Leach, 1820										
Columbina talpacoti (Temminck, 1810)	Ruddy Ground-Dove	sS	PS	s	0	1	0	0	0	0
Patagioenas picazuro (Temminck, 1813)	Picazuro Pigeon	lFe	PS	m	0	0	0	0	1	2
Patagioenas plumbea (Vieillot, 1818)	Plumbeous Pigeon	lF	O	m	1	0	0	0	0	0
Leptotila rufaxilla (Richard & Bernard,1792)	Gray-fronted Dove	rF	PS	m	0	0	1	0	0	0
Cuculiformes Wagler, 1830										
Cuculidae Leach, 1820										
Piaya cayana (Linnaeus, 1766)	Squirrel Cuckoo	lF	In	m	0	0	0	0	3	0
Guira guira (Gmelin, 1788)	Guira Cuckoo	sS	VFS	m	0	0	0	1	0	0
Apodiformes Peters, 1940										
Trochilidae Vigors, 1825										
Eupetomena macroura (Gmelin, 1788)	Swallow-tailed Hummingbird	lFe	FN	s	0	0	0	0	1	0
Amazilia fimbriata (Gmelin, 1788)	Glittering-throated Emerald	rF	FN	s	2	1	1	1	3	3
Coraciiformes Forbes, 1844										
Alcedinidae Rafinesque, 1815										
Megaceryle torquata (Linnaeus, 1766)	Ringed Kingfisher	R	VFS	m	0	0	0	1	2	0
Chloroceryle amazona (Latham, 1790)	Amazon Kingfisher	R	O	m	0	0	1	0	0	1
Piciformes Meyer & Wolf, 1810										
Picidae Leach, 1820										
Veniliornis spilogaster (Wagler, 1827)	White-spotted Woodpecker	mF	In	s	0	1	3	0	5	0
Colaptes melanochloros (Gmelin, 1788)	Green-barred Woodpecker	lFe	In	m	0	0	0	0	1	0
Celeus flavescens (Gmelin, 1788)	Blond-crested Woodpecker	lF	In	m	3	0	8	5	7	1
Falconiformes Bonaparte, 1831										

Taxon	English Name	Habitat†	Guild‡	Size§	Ma1	Ma2	Ma3	Ma4	Ma5	Ma6
Falconidae Leach, 1820										
Milvago chimachima (Vieillot, 1816)	Yellow-headed Caracara	P	VFS	m	0	1	2	5	3	2
Psittaciformes Wagler, 1830										
Psittacidae Rafinesque, 1815										
Forpus xanthopterygius (Spix, 1824)	Blue-winged Parrotlet	rF	O	s	1	0	0	0	0	0
Amazona aestiva (Linnaeus, 1758)*	Turquoise-fronted Parrot	lFe	O	m	0	0	1	0	1	0
Passeriformes Linnaeus, 1758										
ThamnophilidaeSwainson, 1824										
Dysithamnus mentalis (Temminck, 1823)	Plain Antvireo	mF	In	s	0	0	1	0	0	0
Thamnophilu scaerulescens Vieillot, 1816	Variable Antshrike	mF	In	s	0	0	0	0	0	2
Furnariidae Gray, 1840										
Furnarius rufus (Gmelin, 1788)	Rufous Hornero	sS	In	s	1	0	0	3	0	1
Synallaxis spixi Sclater, 1856	Spix'sSpinetail	sS	In	s	0	0	0	0	0	1
Tyrannidae Vigors, 1825										
Camptostoma obsoletum (Temminck, 1824)	Southern Beardless-Tyrannulet	sF	In	s	1	0	1	0	1	0
Elaenia flavogaster (Thunberg, 1822)	Yellow-bellied Elaenia	sS	O	s	0	0	1	0	0	0
Elaenia obscura (d'Orbigny & Lafresnaye, 1837)	Highland Elaenia	mF	O	s	0	0	0	0	1	0
Serpophaga subcristata (Vieillot, 1817)	White-crested Tyrannulet	lFe	In	s	0	0	0	0	1	0
Myiarchus ferox (Gmelin, 1789)	Short-crested Flycatcher	rF	O	s	0	0	1	3	3	0
Pitangus sulphuratus (Linnaeus, 1766)	Great Kiskadee	sF	O	s	4	1	9	8	11	4
Myiodynastes maculatus (Statius Muller, 1776)	Streaked Flycatcher	lFe	O	s	0	0	1	0	0	0
Tyrannus melancholicus Vieillot, 1819	Tropical Kingbird	sF	In	s	1	0	1	0	0	0
Satrapa icterophrys (Vieillot, 1818)	Yellow-browed Tyrant	P	In	s	0	0	1	0	0	0
VireonidaeSwainson, 1837										
Cyclarhis gujanensis (Gmelin, 1789)	Rufous-browed Peppershrike	lFe	In	s	0	0	0	0	0	1

Taxon	English Name	Habitat†	Guild‡	Size§	Ma1	Ma2	Ma3	Ma4	Ma5	Ma6
Corvidae Leach, 1820										
Cyanocorax caeruleus (Vieillot, 1818)	Azure Jay	lF	O	m	0	0	1	0	0	0
Troglodytidae Swainson, 1831										
Troglodytes musculus Naumann, 1823	Southern House Wren	sS	In	s	1	0	2	1	5	1
Turdidae Rafinesque, 1815										
Turdus leucomelas Vieillot, 1818	Pale-breasted Thrush	lFe	In	s	1	0	0	0	1	0
*Turdus amaurochalinus*Cabanis, 1850	Creamy-bellied Thrush	lFe	FN	s	1	1	2	0	1	1
Turdus albicollis Vieillot, 1818	White-necked Thrush	lF	In	s	0	1	1	0	0	1
Parulidae Wetmore, Friedmann, Lincoln, Miller, Peters, van Rossem, Van Tyne & Zimmer 1947										
Setophaga pitiayumi (Vieillot, 1817)	Tropical Parula	mF	In	s	2	2	2	1	2	2
Geothlypis aequinoctialis (Gmelin, 1789)	Masked Yellowthroat	rT	In	s	0	0	1	0	1	0
Icteridae Vigors, 1825										
Icterus pyrrhopterus (Vieillot, 1819)	Variable Oriole	lF	In	s	0	0	0	0	2	0
Thraupidae Cabanis, 1847										
Tangara cyanocephala (Statius Muller, 1776)	Red-necked Tanager	lF	FN	s	0	0	0	0	0	1
Tangara sayaca (Linnaeus, 1766)	Sayaca Tanager	lFe	O	s	0	0	3	5	3	3
Conirostrum bicolor (Vieillot, 1809)	Bicolored Conebill	M	O	s	2	0	5	6	2	2
Dacnis cayana (Linnaeus, 1766)	Blue Dacnis	lF	O	s	0	0	1	0	0	0
Coereba flaveola (Linnaeus, 1758)	Bananaquit	lF	FN	s	0	0	0	0	1	0
Fringillidae Leach, 1820										
Euphonia violacea (Linnaeus, 1758)	Violaceous Euphonia	lFe	FN	s	0	0	0	1	0	0
Passeridae Rafinesque, 1815										
Passer domesticus (Linnaeus, 1758)*	House Sparrow	sS	PS	s	0	0	2	0	2	0

Values representing point counts occurrence frequency. † Principal birds habitats: C – Coastal waters, fM – freshwater Marshes, sM – saltwater/brackish Marshes, M – Mangroves, rT – riparian Thickets, rF – river-edge Forest, R – Rivers, P – Pastures/agricultural lands, sS – second-growth Scrub, sF – secondary Forest, lFe- tropical lowland evergreen Forest + forest edge, lF – tropical lowland evergreen Forest and mF – mon- tane evergreen Forest (adapted from Stotz et al. 1996); ‡ Guild; § Size: small – birds <100 g; medium – birds >100 g and <500 g; large – birds >500 g. * Invasive exotic species.

Table 2-3. Dissimilarities values for species composition in six mangroves in Santa Catarina state, south of Brazil. Total dissimilarity between pair-wise mangrove patches is showed is first table. Partition of dissimilarities in turnover and nestedness is showed in subsequent tables. Total dissimilarity is composed by sum of turnover and nestedness values. Mangroves patches names follow Table 2.

Jaccard dissimilarities 0.84

	Ma1	Ma2	Ma3	Ma4	Ma5
Ma2	0.75				
Ma3	0.68	0.75			
Ma4	0.68	0.81	0.70		
Ma5	0.68	0.79	0.57	0.59	
Ma6	0.63	0.67	0.67	0.67	0.70

Total turnover 0.74

	Ma1	Ma2	Ma3	Ma4	Ma5
Ma2	0.67				
Ma3	0.42	0.33			
Ma4	0.57	0.67	0.63		
Ma5	0.42	0.46	0.57	0.48	
Ma6	0.57	0.46	0.50	0.62	0.56

Total nestedness 0.10

	Ma1	Ma2	Ma3	Ma4	Ma5
Ma2	0.08				
Ma3	0.26	0.42			
Ma4	0.11	0.15	0.08		
Ma5	0.26	0.33	0.00	0.11	
Ma6	0.05	0.21	0.17	0.05	0.14

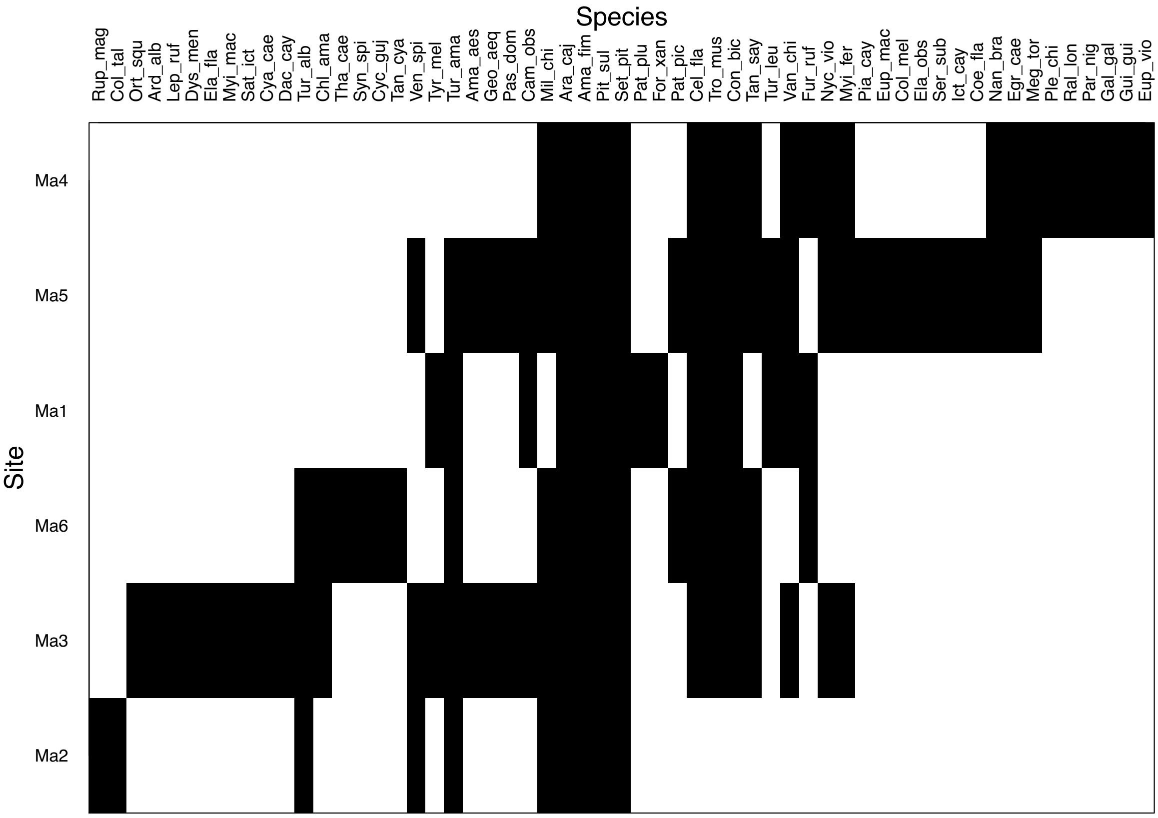

Figure 2-3. Occurrence of species in each study mangrove showing the highest turnover between sites. Each small rectangle represents one species. The order of the sites and species is based on reciprocal averaging scores. See Table 2 for site names. Species codes are based on the first three letters of the species epithet (see Table 1).

Habitat, landscape, and spatial distance as drivers of composition differences

Before verifying the association between the bird communities and potential drivers, we summarised the variation in habitat (vegetation and ground) and landscape factors in three PCAs. The first PCA, which analysed the vegetation variables, indicated a relationship with canopy cover and tree density, which together explained 63% and 29% of the variation on the first two axes. In the second PCA (ground characteristics), crab holes and aerial root coverage had equal contributions to the first (67% of the observed variation) and second (32%) axes. In the case of the landscape variables, the total area of mangrove contributed 60% of the variation on the first axis, while the area of urban development within the buffer contributed 32% of the variation, on the second axis. All other variables made only minor contributions to the overall variation (Appendix S2).

The partitioning of the variables (pRDA) indicated that the environmental (E) and spatial (S) variables explained 17% of the variation in species composition among the mangroves. Approximately 13% of the variation in species composition was explained by the environmental variables with the spatial variables contributing 8%. The environmental variables without the contribution of the spatial variables (E|S) explained 9% of the variation, whereas in the absence of the environmental contribution (S|E), the spatial variables contributed only 4% of the variation (Appendix S3). Overall, a large proportion of the variance in species composition could not be explained by any of the variables analysed.

Community guild structure and body mass distribution

Four of the species recorded in the present study have a plant-seed diet, while seven were frugivore-nectarivores, 16 were omnivores, 23 species feed predominantly on invertebrates, and seven has a vertebrate diet (Table 1). All five guilds were recorded in four of the mangroves (Ma2, Ma3, Ma5, and Ma6), while the plant-seed guild erewere not recorded in Ma1 or Ma4, and vertebrates consumers were not registered in Ma1. Major variation in body size was restricted to the largest mangroves, where the largest bird species were found (Appendix S4).

2.5 DISCUSSION

Our results contradicted our initial hypothesis that the composition of mangrove bird communities would be similar between patches; we found community change being driven by mangrove differences at the habitat and landscape levels. Even so, we did find a high rate of species turnover among the mangrove patches, which indicates a high level of beta diversity and, consequently, that the whole set of patches is important for the maintenance of the diversity of mangrove birds at the regional scale. From a conservation viewpoint, a high species turnover among areas reinforces the need for the protection of multiple sites. Conservation strategies should also maximise mangrove patch size, irrespective of whether the patches are continuous or disjunct (Socolar *et al.* 2016), given that the largest patches had the highest alpha diversity.

We found little support for our initial hypothesis, that species composition would be determined by characteristics of the environment. This is because, at a landscape level, species richness was influenced only by patch size. Up to a point, this reflects the overall lack of pertinent variation in the structure of local mangrove habitats, although it is also important to note their composition was also relatively homogeneous, with a predominance of *Avicennia schaueriana* (Sobrinho *et al.* 1969; Pagliosa *et al.* 2016). Thus bird species composition is not responding to vegetation zonation, which also has only marginal responses related to the frequency of flooding or soil salinity (Souza *et al.* 1994; Lugo and Snedaker 1974; Sobrinho *et al.* 1969). This pattern contrasts with bird metacommunity studies in other ecosystems (Meynard and Quinn 2008, Uezu and Metzger 2011, Gianuca *et al.* 2013, Bonthoux and Balent 2015, Casas *et al.* 2016, Gonçalves *et al.* 2017, Bhakti *et al.* 2018) in which either environmental gradients, habitat structure, or both, were important drivers of the composition of the local bird metacommunity and supported a process of species sorting (Leibold *et al.* 2004). We thus believe that internal dynamics, based on competition-colonisation trade-offs play a key role in the structuring of mangrove bird communities, suggesting a process of patch dynamics (Chase *et al.* 2005; Leibold *et al.* 2004). Nevertheless, landscape factors, especially patch size, do appear to have a small, but relevant influence on the composition of the mangrove bird community, with larger mangroves having more species than smaller patches, which is a pattern often reported (Fahrig 2013; Uezu and Metzger 2011; Bhakti *et al.* 2018).

Locally, this variation may be related to factors that were unevaluated or unrelated to habitat structure *per se*, such as nest predation, food limitations, intraspecific attraction, and competition (Jones 2001). Moreover, many bird species inhabiting mangroves are generalists insectivores and omnivores that tend to be less affected by patch size and isolation (Uezu and Metzger 2011), typically finding resources in any habitat.

In general, even small mangrove birds are competent fliers and are well able to disperse between neighbouring habitat patches, although the distance between patches does have a substantial influence on the composition of the avian community. A number of aquatic, coastal, and forest birds exploit mangroves during their daily movements, to rest and feed. Important dormitory and reproductive colonies of aquatic birds are also found in the mangroves of Santa Catarina (Bisinela *et al.* 2014; Grose *et al.* 2014; Vieira *et al.* 2014; Vieira 2016; Mestre *et al.* 2007; Grose 2016). In this context, mangroves are crucial to the connectivity of coastal environments, facilitating bird dispersal (Lugo and Snedaker 1974; Hutchings and Saenger 1987; Kutt 2007).

In this study, the regional species richness of the mangrove bird communities was lower (i.e. 57 species) than the numbers reported in other studies of Brazilian mangroves which range from 68 to 247 species (De Araujo *et al.* 2006; Silva and Olmos 2007; Almeida and Barbieri 2008; Periquito *et al.* 2008; Olmos and Silva 2001; Mestre *et al.* 2007) although these studies included migratory species and either sampling in associated ecosystems or long-term sampling effort. Other possible determinants of these disparities may be the variation in the size of the mangroves or latitudinal gradients, which is reinforced by patch size being a good predictor of species richness (Hansbauer *et al.* 2008; Martensen *et al.* 2008). The mangroves of Santa Catarina are at the southern limit of the distribution of this ecosystem in the Atlantic (Soares *et al.* 2012; ICMBIO 2018). The relatively low temperatures in this region may limit mangrove growth, and thus the size of mangrove patches (Soares *et al.* 2012; ICMBIO 2018). We anticipate that bird species richness of mangroves increases with increasing habitat complexity, a pattern observed in the bird assemblages of the subtropical Brazilian Atlantic rain forest (Casas *et al.* 2016). Moving forward it would be interesting to investigate the existence of a possible gradient in species richness in the southernmost Santa Catarina mangroves.

Our results indicate that the mangroves of Santa Catarina harbour only five habitat-specialist bird species (Yellow-crowned Night-Heron *Nyctanassa violacea*, Little Blue Heron *Egretta caerulea*, Mangrove Rail *Rallus longirostris*, Gray-necked Wood-Rail *Aramides cajaneus avicenniae* and Bicolored Conebill *Conirostrum bicolor*). The distribution of these species is associated primarily with that of mangroves and other wetlands. In Santa Catarina, Yellow-crowned Night-Heron and Little Blue Heron occur only in mangroves and associated coastal ecosystems (WikiAves 2019a, b). All records of Gray-necked Wood-Rail *Aramides cajaneus avicenniae* in Santa Catarina are associated with mangroves and the saltmarsh or coastal wetlands that replace the mangrove in the south of the state (Soares *et al.* 2012; Just *et al.* 2018, WikiAves 2019c). The geographic ranges of Mangrove Rail and Bicolored Conebill are strictly related with the distribution mangroves along the entire Brazilian coast. The southernmost limit of the distribution of mangroves in Brazil is Laguna, in southern Santa Catarina, which is also the southern limit of Mangrove Rail (WikiAves 2019d). The Aririú mangrove (Ma6) represents the southern limit of the distribution of Bicolored Conebill (WikiAves 2019e). As few studies have focused on South American mangrove birds, little is known of the degree of dependence on mangrove habitats. Mangrove-dependent species use mangroves as primary habitats for feeding, breeding, and resting. Previous studies only indicate Bicolored Conebill as a mangrove-dependent species, despite the occurrence of the other four species (*Nyctanassa violacea*, *Egretta caerulea*, *Rallus longirostris*, and *Aramides* *cajaneus avicenniae*) being always associated with the mangrove and associated habitats, indicating their dependence on mangroves. Despite the absence of endemic mangrove bird species, the dependence of these birds on mangroves is a crucial question for their conservation.

The avian specific richness of Pacific mangroves is influenced strongly by the contribution of the surrounding matrix (Kutt 2007; Mohd-Azlan and Lawes 2011). A similar role of the landscape matrix is found in Brazilian mangroves (Olmos and Silva 2001; De Araujo et al. 2006; Silva and Olmos 2007; Mestre et al. 2007). This matrix effect may account for the larger numbers of non-mangrove dependent species and the enhanced flight capacity of the species recorded in the present study. All the mangroves surveyed here were in a matrix where other vegetation types or anthropogenic habitats were common, thus being a source of species and supporting a high species turnover between patches. Non-mangrove dependent birds also use mangroves to feed and are typically recorded in either the mangrove or surrounding areas (Vieira et al. 2014; Vieira 2016).

Despite being under legal protection with highly restricted use (Magris and Barreto 2010), mangrove conservation is a major challenge in Brazil given the law is scarcely put into practice. Conservation status is even worse for the associated wetland habitats that are uncovered by state or federal legislation. Although its importance as transitional and buffer zones, these associated habitats are normally the first to be impacted by human activities and disfigured (Trindade 2009; Magris and Barreto 2010; Espinoza and Rosa 2009; Kilca *et al.* 2019; Pagliosa *et al.* 2006). This reduces the availability of suitable habitats for mangrove bird species and contributes to a decline in regional diversity. In addition to direct human impacts, mangroves experience environmental imbalances. Pest outbreaks such as the caterpillar of the mouth *Hyblaea* sp. (Lepidoptera: Hyblaeidae) have caused extensive damage to trees in several mangroves in the state (Silva 2001; Menezes and Mehlig 2005; Kilca*et al.* 2019), aggravating habitat loss and affecting species richness of the mangroves.

Because each mangrove patch has a distinct bird community, thus adding to the reginal pool of species, protecting as many of such patches as possible and of the largest possible size is essential to guarantee the conservation of mangrove birds. Actions to maximise conservation should also put limits to uses that degrade mangroves, while promoting restoration and sustainable uses, and expand the legal protection to associated habitats. Although the adoption of such strategies is now a huge challenge, especially because environmental and scientific policies are instead losing governance and resources in Brazil (Rovai *et al.* 2012; Loyola 2014; Vieira *et al.* 2019; Ferrante and Fernside 2019; Tollefson 2019), we believe these could promote the conservation of mangroves, in general, and the maintenance of the regional mangrove bird diversity, in particular.

2.6 CONFLICTS OF INTEREST

No conflict of interest has been declared by the author(s).

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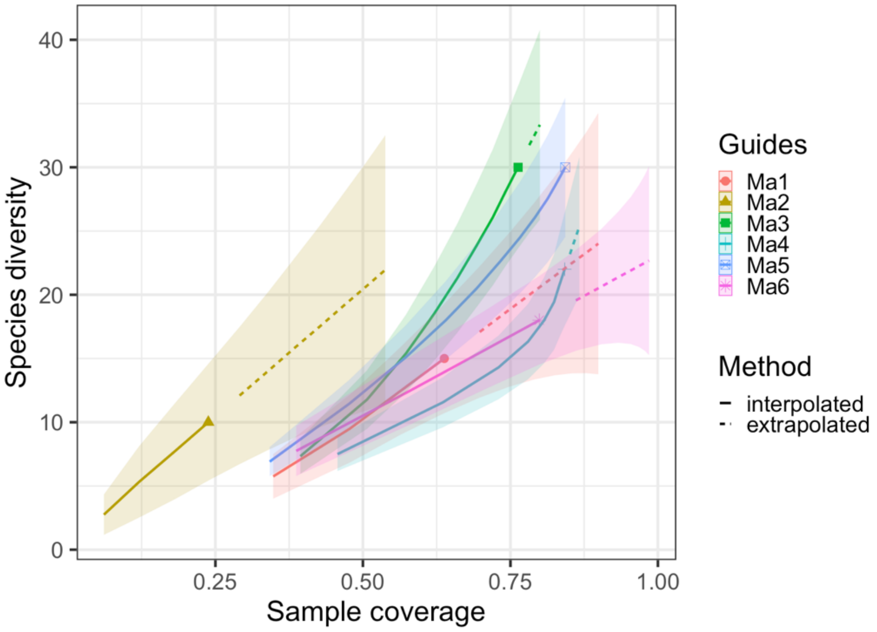
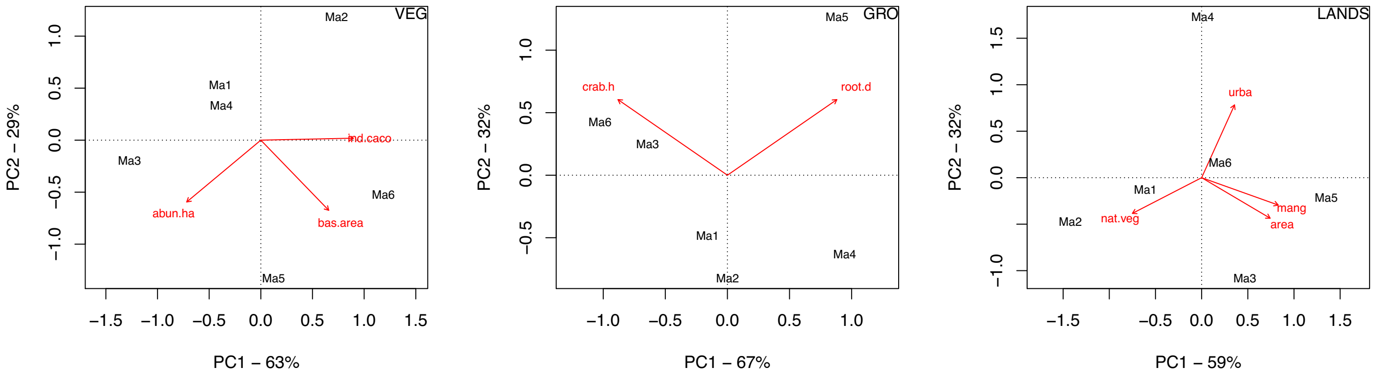
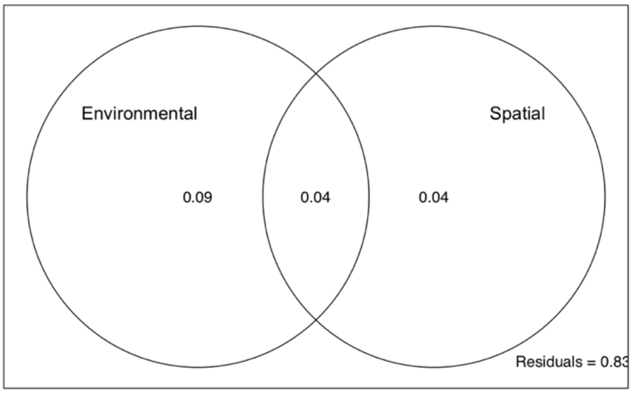
2.9 SUPPORTING INFORMATION



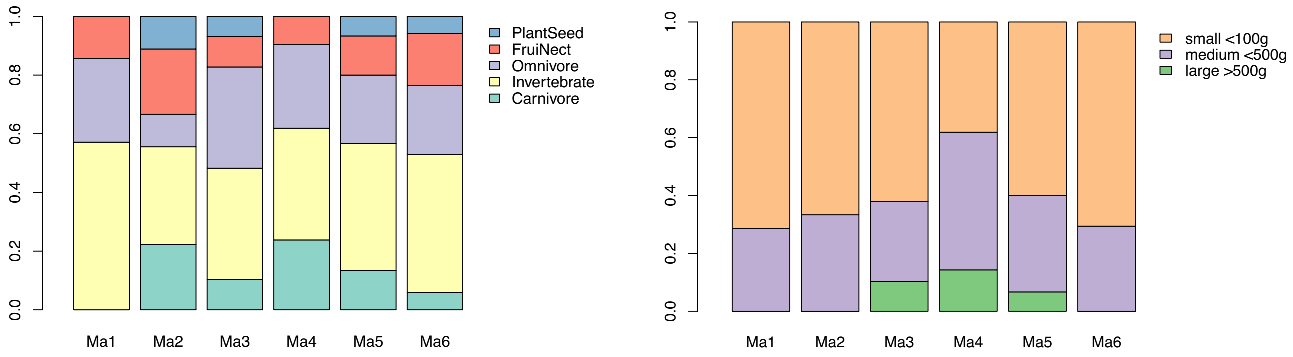
Appendix S1: Sampling coverage sample-size-based curves and the associated 95% confidence intervals of bird species in six mangroves of Santa Catarina state, southern Brazil (see Table 2 for guide codes).



Appendix S2: PCA analysis for environmental variables: VEG – vegetational variables (abund.ha - tree abundance; area.basal - average basal area; ind.caco canopy index), GRO – ground variables (crab.h - crab holes; root.d - aerial roots percentage) and LANDS – landscape variables (area - total area of mangroves patches; mang - 500 ha-mangrove area; nat.veg - 500 ha-native tree vegetation area; urba - 500 ha-urban area for each mangrove patch).



Appendix S3: Venn diagram showing the percentages of variance explained by environmental and space variables in six mangroves of Santa Catarina state, southern Brazil, during summer 2017-2018.



Appendix S4: Relative proportions of bird functional characteristics distribution in six mangroves of Santa Catarina state, southern Brazil (see Table 2 for mangrove codes). Guild classes: *sensu* Eltontraits 1.0 (Wilman et al. 2014): Plant-seed – seeds, nuts, leaves, other plant material; Fruit-nectarivore – fruits, nectar, pollen; Invertebrate – invertebrates in general; Carnivores – vertebrates, fish and carrion and, Omnivore - score of <= 50 in all four categories. Size: small – birds< 100g; medium – birds >100g and <500g; large – birds >500g.

3 CAPÍTULO 2 – BIRD DIVERSITY LOSSES AND CHANGES IN SMALL FRAGMENTS: A CALL FOR CONSERVATION IN THE SOUTHERN RANGES OF THE ATLANTIC FOREST

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3.1 ABSTRACT E RESUMO

Abstract

The metacommunity framework allows an assessment of processes driving diversity and composition of communities at different spatial scales. Factors such as patch size and isolation act together with species and local habitat characteristics on the dynamics of metacommunities, changing the relative importance of processes such as environmental filtering, dispersal, and biotic interactions on biodiversity. Understanding how different combinations of such factors operate to structure bird metacommunities in fragmented landscapes may then aid decisions aimed at biodiversity conservation. In 2018-19 (spring-summer southern hemisphere seasons), we sampled bird species in 21 sites in a relatively well-connected Atlantic forest landscape in southern Brazil and measured geographical and environmental variables at regional and local scales. We found a total of 160 species in the region. Species richness was strongly influenced by patch size, with the turnover component of beta bird-diversity increasing towards smaller forest patches. Distance from protected areas (reference sites) and vegetation structure also helped to explain bird richness and differences in species composition but played a secondary role to that of patch size. This study reinforces the importance of considering patch size of remnants for conservation, since patch size was key to maintain a richer diversity at regional scale, specialist species and ecosystem processes.

Fragments should be considered in conservation strategies, by focusing in their restoration or aiming at increasing total area and connectivity across the landscape, thus promoting higher levels of regional diversity.

Key-words: Conservation, fragmented landscape, dispersal, Atlantic rain forest

Resumo:

A estrutura de metacomunidades nos permite compreender os processos que moldam a diversidade e composição das comunidades em diferentes escalas espaciais. Fatores como tamanho e isolamento de fragmentos florestais, atributos das espécies e variáveis locais do hábitat atuam na dinâmica das metacomunidades e influenciam os processos de filtragem ambiental, dispersão e interações bióticas que regem as metacomunidades. Entender como as diferentes combinações destes fatores operam na estruturação das metacomunidades de aves nas paisagens fragmentadas, nos ajuda a tomar decisões que visam à conservação da biodiversidade. Durante a primavera-verão de 2018-19, amostramos a diversidade de espécies de aves em 21 locais dentro de uma região de Mata Atlântica relativamente bem conectada no sul do Brasil e, as variáveis geográficas e ambientais foram medidas nas escalas regional e local. Encontramos uma riqueza regional de 160 espécies que é fortemente influenciada pelo tamanho dos fragmentos, com um padrão de substituição de espécies na diversidade-beta conforme o tamanho dos fragmentos diminui. O grau de isolamento dos fragmentos e a estrutura da vegetação são fatores secundários na explicação da riqueza de aves e diferenciação na composição das espécies, reforçando os padrões determinados pelo tamanho dos fragmentos. Este estudo reforça a importância de considerar o tamanho dos fragmentos em estratégias de conservação, uma vez que eles são capazes de manter uma maior diversidade na escala regional, bem como mais espécies especialistas e processos ecossistêmicos. Fragmentos devem ser considerados nas estratégias de conservação, concentrando-se em sua restauração e visando aumentar a área total e a conectividade em toda a paisagem, promovendo assim níveis mais altos de diversidade regional.

Palavras-Chave: Conservação, paisagem fragmentada, dispersão, Mata Atlântica

3.2 INTRODUCTION

Biodiversity conservation is a particular challenge in developing countries because it needs to balance economic development, food security, and social welfare with the maintenance of diversity. Because the vast majority of ecosystems has already been altered by human activities and are now found as fragmented landscapes, the focus of conservation biology shifts from just stopping or reducing habitat loss, and consequent species loss, to also finding ways of keeping ecological processes (Sekercioglu et al. 2004; Sekercioglu 2012). In a modern view, biodiversity conservation aims to maintain sustainable and resilient relationships between human societies and the natural environment (Mace 2014). Habitat loss and fragmentation impact biodiversity (Fahrig 2003; Haddad et al. 2015; Fletcher et al. 2018), so understanding the distribution of species in remnant areas, as well as species interactions, habitat suitability, and dispersal ability, might aid in the understanding of processes that maintain species diversity and, thus, could guide effective conservation strategies integrated with human activities (Driscoll 2008; Mace 2014; Socolar et al. 2016; Chase et al. 2020). The metacommunity framework allows us to integrate and inspect, at different spatial scales, such local and regional processes underlying community assembly and thus can help us to understand community diversity and composition in anthropogenic fragmented areas (Leibold et al. 2004, 2020; Holyoak et al. 2005; Chase & Bengtsson 2010; Chase et al. 2020).

The Theory of Island Biogeography (MacArthur & Wilson 1967) laid out key roles for habitat size and isolation (distance from source areas) as drivers of species richness and composition, a knowledge now extensively applied in fragmented landscapes (Laurance 2008). Habitat size and isolation act at regional scales in the metacommunity dynamics, changing the environmental heterogeneity and affecting species dispersal (Leibold et al. 2004; Chase & Bengtsson 2010; Chase et al. 2020). At the landscape scale, the amount of habitat also contributes to further change connectivity and environmental heterogeneity, further affecting dispersal, metacommunity richness, and composition (Andrén 1994). At the local scale, metacommunities are driven by biotic and trophic interactions, where interactions between species and the abiotic factors determine the habitat suitability for a given species (Chase & Bengtsson 2010; Chase et al. 2020). Different combinations of these processes (environmental filtering, changing biotic interactions, and dispersal) will then determine the composition and richness of metacommunities from local to regional scales (Chase et al. 2020; Leibold et al. 2020).

Bird species richness and abundance in Atlantic Forest metacommunities have been shown to persist after extensive forest loss at the landscape level (Morante-Filho et al. 2015). However, the species composition of these communities changed depending on the amount and structure of habitats and landscape connectivity since fragmented landscapes favor generalist species (Casas et al. 2016; Morante-Filho et al. 2016). This often results in variation in species composition when comparing bird communities from small forest patches with those from large patches (Banks-Leite et al. 2012). Distinct ecological groups generally differ in their responses to disturbances and habitat modifications (Banks-Leite et al. 2013; Morante-Filho et al. 2015; Casas et al. 2016; Ribon & Marini 2016; Keinath et al. 2017; Bhakti et al. 2018). For instance, forest specialist birds – frugivorous, granivorous, and understory insectivores – decline when forest cover goes under 50% in a landscape (Morante-Filho et al. 2015). Such specialized groups are more sensitive to habitat change and are adversely impacted by habitat loss (Keinath et al. 2017). Thus, differing dispersal ability and habitat suitability for each species result in greater beta diversity between forest patches (Hansbauer et al. 2008, 2010; Lees & Peres 2009). Furthermore, species traits play an important role in the functioning and stability of ecosystems and are influenced by changes in biodiversity and the composition of metacommunities across scales (Chase et al. 2020).

The Atlantic Forest is a global diversity hotspot extending over 13% of the Brazilian territory. However, 57% of Brazilian urban lands fall in the range of Atlantic Forest and more than 61% of its original extent has been converted to agriculture or pasture, resulting in a landscape dominated by mosaics with less than 27% of its original forest cover (Ribeiro et al. 2009; Vibrans et al. 2013). In this scenario, the effects are strong and negative for both habitat loss (Andrén 1994; Banks-Leite et al. 2012) and edge-effect on forest fragments (Banks-Leite et al. 2010, 2012; Püttker et al. 2020). With such small remaining forest cover and due to the history of habitat loss and fragmentation, a large number of bird species losses could be expected (Banks-Leite et al. 2010). Nevertheless, just a few extinctions have been documented, even though several species are now threatened (Brooks et al. 1999; Moreira-Lima 2014). Such few recorded extinctions of Atlantic Forest birds have been suggested, in an alarming scenario, as resulting from “time lags” or “extinction debts” (Brooks et al. 1999; Uezu & Metzger 2016) or, in a less alarming one, as resulting from the ability of bird species to survive on either fragmented landscapes (Uezu et al. 2005; Boscolo et al. 2008; Awade & Metzger 2008), secondary and small forest patches (Casas et al. 2016; Barbosa et al. 2017) or non-forested environments (Brooks et al. 1999). Out of the entire range of the Atlantic Forest, its southern limit, located in the southern states of Brazil, shows some of its largest remaining forest covers and is home to some of its largest remnants (Ribeiro et al. 2009, 2011; Vibrans et al. 2013). Since few studies addressed the effects of fragmentation and habitat loss effects on bird diversity in this southern region, here we assessed factors that could drive and maintain bird diversity and composition in such fragmented but still with high forest cover region.

This study aimed to unveil the structuring processes of bird metacommunities in a fragmented landscape analyzing how mechanisms at the local scale (habitat filtering) and at regional scale (geographic factors) influence species diversity and species composition differences (taxonomic alfa e beta diversity). To analyze habitat filtering at the local scale we assessed environmental factors on each patch. We used specialization indexes based on bird trait to study how species interact with environment to changes community composition across sites. Patch size and patch distance to potential "sources" (protected areas) were assessed as geographic factors at the regional scale. Our hypothesis is that more specialized species with lower dispersal capacity will disappear from smaller fragments of those more distant from the source areas. Three predictions should support this hypothesis. First, species richness should decrease towards small forest patches, with species compositional changes mainly driven by nestedness (accordingly Baselga, 2012). Second, bird composition similarity should decrease depending on the distance from patches to protected areas, irrespective of patch size. Third, birds with specialized traits should be associated with large fragments, and birds with high dispersal capabilities will be widespread, no matter the distance from patches to protected areas.

3.3 MATERIAL AND METHODS

Study region

The study area covered the southern range of the Atlantic Forest, in the central-east part of the State of Santa Catarina. Total forest cover in the State of Santa Catarina is ~ 30% and has been reduced in some regions (about 16% since 1985, MapBiomas 2020; Baptista and Rudel 2006). Notwithstanding this overall pattern, the coastal Atlantic Rainforest found in Santa Catarina (or Ombrophilous Dense Forest following other classifications) has still 40% of its original cover–but spread over thousands of small fragments–and hosts the largest remnants found in southern Brazil (Ribeiro et al. 2009; Vibrans et al. 2013; MapBiomas 2020). Our samplings were in the coastal extent of the Atlantic Rainforest across plains and submontane areas (27.15°S; 49.40°W to 28.30°S; 48.80°W) with altitudes ranging from 108 up to 918 m. The climate of the region is humid subtropical with hot summers and without dry season, with average temperatures ranging from 13ºC to 25ºC (Alvares et al. 2013).

To evaluate whether the bird diversity patterns can be generalized, we repeated sampling in three regions referenced by protected areas (hereafter "reference PAs"): São Joaquim National Park/Pedra Furada State Park mosaic (region 1), Serra do Tabuleiro State Park (region 2), and Serra do Itajaí National Park (region 3; see sampling design – figure 3-1). Forest cover was obtained for regions 1-3 by drawing a 20 km radius circle centered on centroid points of each region with data from MapBiomas (2020). The forest cover of 53%, 61% and, 75% was found for regions 1-3, with varied connectivity and distinct anthropic matrices (varying amounts of area used for agriculture, pastures, or non-native tree monocultures).

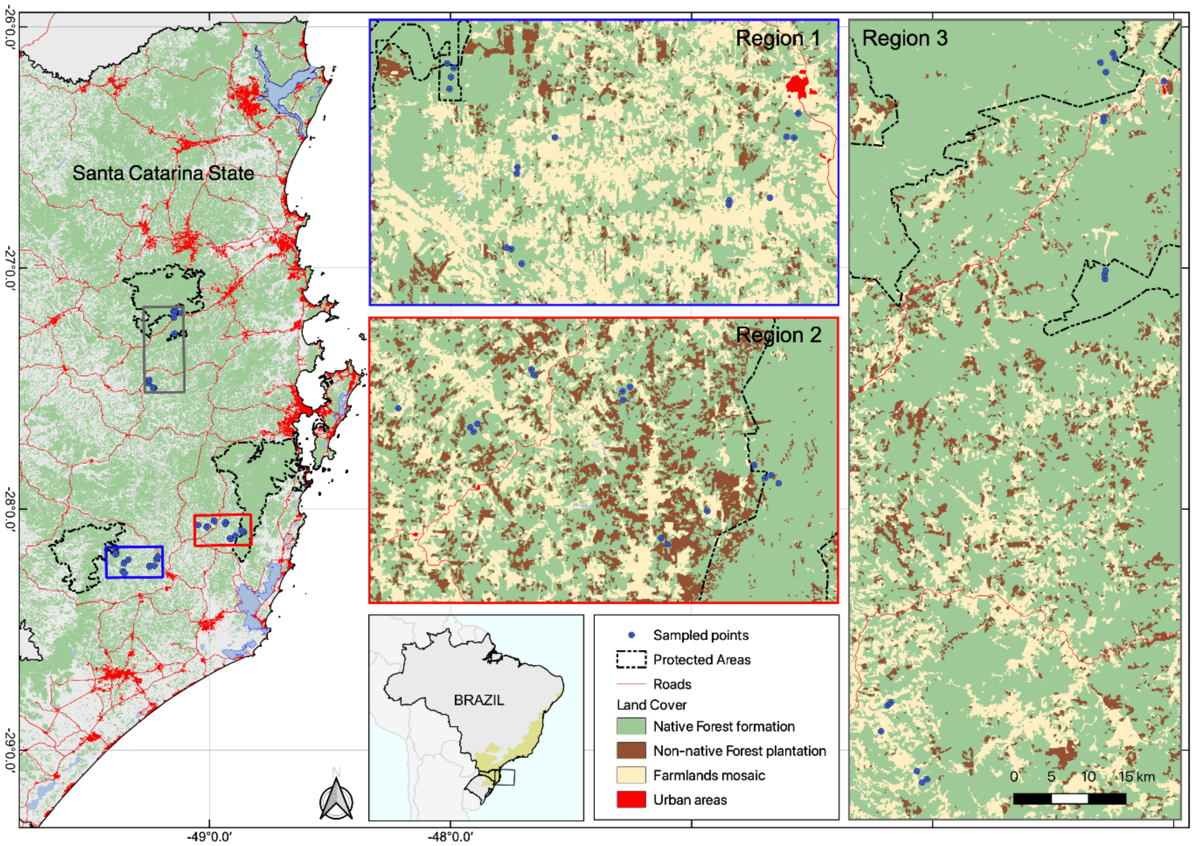

Figure 3-1: Location map of studied areas on the State of Santa Catarina. The figure shows forest remnants, with emphasis on the studied patches and sampling points. Protected areas (reference PAs) in each region are: region 1 – Mosaic Sao Joaquim National Park and Serra Furada State Park; region 2 – Serra do Tabuleiro State Park; region 3 – Mosaic Serra do Itajai National Park and CanelaPreta State Biological Reserve (land use data from Mapbiomas 2020)

Sampling design

To test the geographical factors in each region, we selected forest patches in two classes of distance to the region's reference Protected Area (PA) ('Near' when the distance from PA ≤ 12 km; and 'Far' when the distance from PA > 12 km) and of different sizes ('Small' patches: ≤ 5 ha; 'Medium' patches: > 5 and ≤ 100 ha; 'Large' patches: > 100 ha). We took one additional sample on the Protected Area of each region, totaling seven samples per region and 21 samples across regions (figure3-1). Patch selection was based on the analysis of up-to-date satellite images (Google Earth images), land use maps (MapBiomas, 2020), and field checking. The number of sample points was defined according to patch area: one sample point in small, two in medium, three in large patches, and four in reference PAs, totaling 48 sample points. There was one exception in region 3, where the near and large patch had ~ 2,500 ha and was located inside the State Biological Reserve Canela Preta considered a medium patch.

Far forest patches of region 3 were located up to 30 km from reference PA due to the absence of small forest patches in a 12 km radius.

Environmental variables

Environmental variables were measured at regional and local scales (Table S1 Supplementary material). To analyze the geographical factors at the regional scale, we calculated the patch area and distance from protected areas at each region (reference PA) using GIS tools (QGIS Development Team 2018). To analyze habitat filtering at the local scale, in each sample point, we assessed vegetation structure by using the point-centered quarter method (Cottam & Curtis 1956). On each point and each quarter, we measured tree and shrub density and height. On each sample point, we took four measurements, one for each quarter, and values were averaged for each point. For trees, on each quarter, we measured height, diameter at breast height (DBH), the distance of the closest tree, and the biggest tree and canopy cover calculated from digital photos obtained with the GLAMA app (Tichý 2016). For shrubs, we measured height, diameter at root collar (DRC), and the distance to the first shrub taller than 1 m (Bibby et al. 1998a, 1998b). We took a photo in each quarter, at 1 m above the soil and 3m away from a white fabric (1 × 1 m) opened at 50 cm from the ground. Afterward, we converted photos in black and white and calculated the percentage of black pixels with ImageJ software (Abràmoff et al. 2004) and averaged all four photos as a proxy for understory density per sample point (adapted from Marsden et al. 2002).

To reduce the multicollinearity of such a large set of habitat variables, we ran a Principal Component Analysis (PCA). The first two axes of the PCA explained ~51% of the variation in vegetation structure (PC1: 33.7%; PC2: 16.9%; figure 3-2). The first axis was positively related to tree and shrub height, and negatively related to understory density. The second axis was positively related to the density of trees, sub-forest bushes, and more strongly with the density of the biggest tree. However, patches and Protected Areas were grouped by neither region, size, nor distance, suggesting habitat structure to be heterogeneous and to represent a stabilized environment. This is reinforced by all sampled regions being under low deforestation rates and, even though all likely suffered selective logging in the past, all forest patches already existed and are stable in extent since 1985 (MapBiomas 2020).

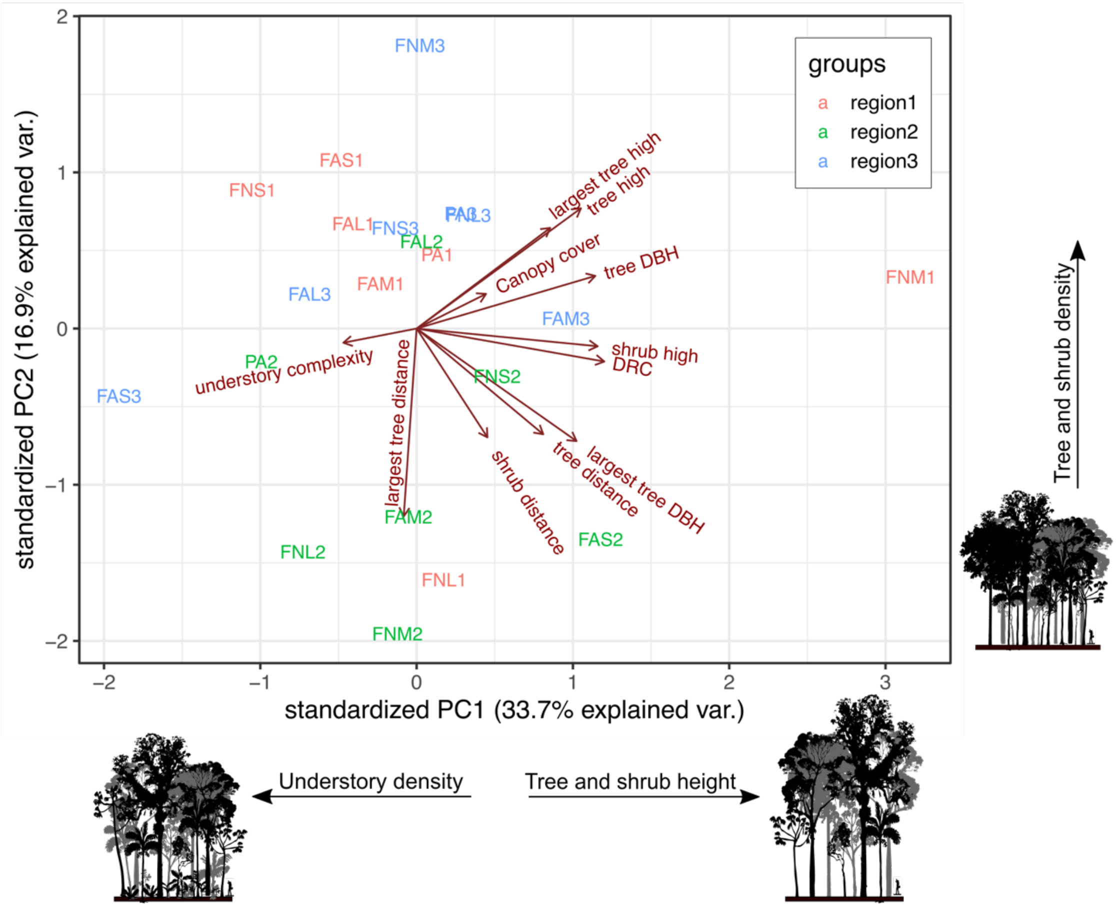

Figure 3-2: Principal component analysis (PCA) for the environmental variables showing the two first axis. Forest patches codes in Table 1. Color codes represent patches by region. Figures represent the vegetation in the interpretation of axes. Patch code: sequence of 3 letters and one number, first letters PA protected areas or F forest patches, ongoing letters refer to size and distance: N near, A far away, S small, M medium, L large, and the last number refers to a region.

Bird sampling

To measure bird species diversity at the local scale, we used Automatic Recording Units (AudioMoth, AM version 1.0, Hill et al., 2019, 2018) to record acoustic samples in 48 points of all 21 sample areas. We arranged AMs inside forest patches at least 100 m away from forest edges and 200 m apart and fixed them on tree branches at ~1.5 m from the ground. Recordings were carried out from November 2018 to March 2019 – Spring and Summer in the southern hemisphere. AM units were programmed to record 1min and then rest 9 min (6 min/h), resulting in 144 recordings per day at a sampling rate of 48Khz (Campos-Cerqueira et al. 2021). Each point was sampled for 5 consecutive days with a total of 720 1-min recordings per point. Due to technical problems, we ended up with a slightly smaller sample in two points (710 1-min recordings in point of PA1 and 561 in point of FAM2). All recordings were stored in the RFCx-Arbimon platform (Aide et al. 2013) and are available in the project 'Arquivo Bioacústico Catarinense' (https://arbimon.rfcx.org/project/arqbiocatarinense).

Out of the 34,391 samples, an experienced bird expert (ALR) listened to ~10% (3,578 min) of the 1-min recordings, with an average of 74 samples per point and distributed along the day. Bird songs and calls were manually annotated during this stage. For each bird species, one sample of a common song and one for a simple call, where applicable, were chosen as a template (accordingly LeBien et al., 2020). With such templates, we created a database of Atlantic Forest birds in the project on the RFCx-Arbimon platform, where they were permanently stored and are available online (on the project's link above). In addition, we created templates for species undetected in the samples listened to, but present in regional bird lists, using sounds available in the WikiAves database (http://www.wikiaves.com). Next, we used the procedure of multi-species/multi-label classification to automatically detect bird species in the remaining ~90% samples using RFCxArbimon (LeBien et al. 2020). In this process, the 'pattern matching' function with a threshold of 0.1 and one detections by 1-min record (n=1) was used. The results of all automatic detections were checked by ALR and post-validation generated a presence-absence / species-by-point matrix.

Bird trait environment interactions

We used bird functional traits in association with geographic and environmental factors (bird trait-environment interactions) to study how species presence-absence depends on traits to allow their distribution across sites. We gathered bird traits from different datasets (Table S2 Supplementary material). We compiled and chose the traits related to the selected explanatory variables and that could explain the presence of birds on forest patches. As proxies for dispersal ability, we chose the avian hand-wing index (HWI) and body mass (Wilman *et al.* 2014; Sheard *et al.* 2020). To relate traits with vegetation structure and ecosystem functioning, we chose the specialization index per species calculated from diet and foraging strata data (Stotz et al. 1996; Wilman et al. 2014). From data of habitat preferences (Stotz et al. 1996), we calculated a habitat specialization index with all habitat data and, in addition, the forest specialization index, based only on forest habitats. We chose to calculate these two indexes because we kept non-forest birds in the analyses. Specialization indexes were calculated by applying the Gini coefficient of inequality (see Morelli et al., 2019) using the R package *DescTool* (Signorell & et al. 2020) (see details in Table S2 Supplementary material). All index values ranged from 0 (least specialized) to 1 (most specialized). We also calculated a forest dependency index from data of habitat preferences (Stotz et al. 1996) as follows: *Fdi* =*F* - *nF*, where *F* is the proportion of forest habitats and *nF* is the proportion of nonforest habitats a species has been found to use. This index ranges from '-1' (forest-independent) to '+1' (forest-dependent). Hand-wing index (HWI), body mass, and range size were log-transformed before the analysis.

The Atlantic forest bird endemism follows Vale et al (2018) and species nomenclature follows Piacentini et al (2015).

Data analysis

Initially, we estimated bird diversity for each patch in each region, and then we used these values to compare the bird community's richness. Because observed species richness increased with sampling effort (i.e. number of 1-min recordings; $r = 0.78$)(Figure S1 in Supplementary material), we standardized species richness estimates at the sampling effort of 1440 1-min samples per point, with seven sites with effort below, five equal to, and nine above this limit (Chao et al. 2014). Extrapolated or interpolated species richness was computed using the iNEXT package (Hsieh et al. 2016). In addition, we calculated sample coverage with the same package and for each forest patch to check for sampling sufficiency.

To estimate beta diversity inside regions, we used Jaccard dissimilarities between the species composition of protected areas and patches. Dissimilarities were further decomposed into components: species turnover and nestedness (Baselga 2010, 2012) using the R package *betapart* (Baselga et al. 2018).

To investigate the relationships between patch (size and source distance) and habitat variables (PC1 and PC2 axes) on estimated species richness, we used Generalized Linear Mixed Models (GLMM). Afterward, we investigated the relationships of the set of predictors on beta diversity and its components (dissimilarity, turnover, and nestedness). We used regions as a random variable to control for variation across regions that were left unassessed. We fitted GLMMs and checked for outliers and the assumptions of normality and homogeneity of dispersion of model residuals using the R packages *glmmTMB* (Brooks et al. 2017) and *DHARMa* (Hartig 2020).

To evaluate the biotic interactions and influence of dispersal-related traits in a metacommunity composition, we used a Community Assembly by Trait Selection regression method (CATS regression; Warton, Shipley, and Hastie 2015). This analysis fits predictive models for the species matrix as a function of environmental variables and their interaction with species traits, which allowed us to analyze how species composition within patches is driven by species traits, habitat, and patches characteristics (see complete method description in Warton, Shipley, and Hastie 2015). The region was included as an "explanatory variable" to control for regional differences in species pools or other region-level unassessed factors (as mixed-effects models are still unavailable for CATS regression). CATS regression was calculated in R-package *mvabund* (Wang et al. 2020). We kept all other recorded species, even singletons because rare species with similar traits could show a similar relationship with environmental variables and build up stronger trait-environment interactions.

All analyses were run in R version 3.6.0 (R Core Team 2019).

3.4 RESULTS

Bird metacommunities

We registered 160 bird species at the regional scale after validating 7,609 automatic detections (Table S3 in Supplementary material). These bird species belong to 49 families. Thraupidae (19 species), Tyrannidae (15), Thamnophilidae (14), and Furnariidae (10) had the highest species richness. The most widespread species were *Basileuterus culicivorus* and *Dacnis cayana*, being found in 21 and 20 patches, respectively. Nine species were nocturnal. Thirty species were registered in only one patch, 26 being found in a single point, and out of these, 13 in a single sound record. Almost 50% (70 species) are endemic to the Atlantic Forest and two are vulnerable to extinction: *Ramphastos vitellinus* and *Procnias nudicollis* (IUCN, 2021).

We found similar estimated species richness across regions (Table 3-1; Figure S2 and S3 in Supplementary material), even though the three regions differ in remaining forest cover. Protected areas had the highest species richness, as expected, with values of 84, 71, and 65 observed species. In all regions, the largest patches had higher observed species richness, followed by the medium and small ones and, in each size category, those closest to the reference area had also the highest richness (Table 3-1). Despite small differences, the same pattern was found for estimated richness (Figure 3-3). Sample coverage was > 88% in all patches (with sample effort of 1440 1-min recordings), suggesting sample sufficiency in all patches (Table 3-1, Figure S4 Supplementary material).

Table 3-1: Description of Protected Areas and patches (size, geographical distance) and estimates of bird species richness in southern Atlantic Forest. Patch code: sequence of letters and one number: first letters PA protected area or F forest patch, ongoing letters refer to size and distance: N near, A far-away; S small, M medium, L large, and the number refers to the region. Rec: number of recorders used to sample each site. Effort: Sampling effort corresponding to the total number of 1-min recordings took in each patch. S obs: total observed species richness. S est and Coverage: estimated richness and sample coverage standardized at a 1440 1-min sample. LCI and UCI: lower and upper confidence interval for estimated species richness.

Region	Patch code	PA distance (km)	Size (ha)	Rec	Effort	Coverage	Sobs	S est	S est (LCI–UCI)
1	PA1		26,014.01	4	2,870	0.964	84	75	71.6–78.4
	FNS1	5.95	6.74	1	720	0.997	51	56.3	48.2–64.4
	FNM1	5.13	20.43	2	1,440	0.970	58	58	52.3–63.7
	FNL1	8.69	199.49	3	2,160	0.954	79	71.1	66.2–76.1
	FAS1	16.90	4.32	1	720	0.936	42	54.5	43.1–66
	FAM1	14.70	40.94	2	1,440	0.978	59	59	53.8–64.2
	FAL1	16.86	273.31	3	2,160	0.959	61	55.3	51.4–59.2
2	PA2		84,543.8	4	2,880	0.909	71	60	56.1–64
	FNS2	5.38	5.96	1	720	0.990	27	30.3	24.3–36.4
	FNM2	8.12	43.93	2	1,440	0.974	66	66	60.8–71.2
	FNL2	8.08	517.79	3	2,160	0.929	59	51.4	45.2–57.5
	FAS2	19.32	3.39	1	720	0.997	28	29.9	23.9–35.9
	FAM2	13.07	20.97	2	1,281	0.910	43	45.1	38.7–51.5
	FAL2	15.59	473.16	3	2,160	0.919	49	44.8	41–48.6
3	PA3		56,928.17	4	2,880	0.947	65	53.1	48.6–57.6
	FNS3	3.26	2.02	1	720	0.931	19	24.6	16.9–32.4
	FNM3	3.26	24.11	2	1,440	0.952	37	37	32.7–41.4
	FNL3	11.47	2,521.39	3	2,160	0.962	60	54.7	50.9–58.5
	FAS3	34.99	3.45	1	720	0.932	29	37.1	27–47.3
	FAM3	33.60	50.48	2	1,440	0.935	36	36	31.9–40.1
	FAL3	36.71	228.42	3	2,160	0.883	45	38.9	34.5–43.4
Region 1			-	16	11,510	1.000	126	129.7	126.8–142.6
Region 2			-	16	11,361	1.000	115	118.5	115.7–132.9
Region 3			-	16	11,520	0.997	115	131.2	120.3–164.5

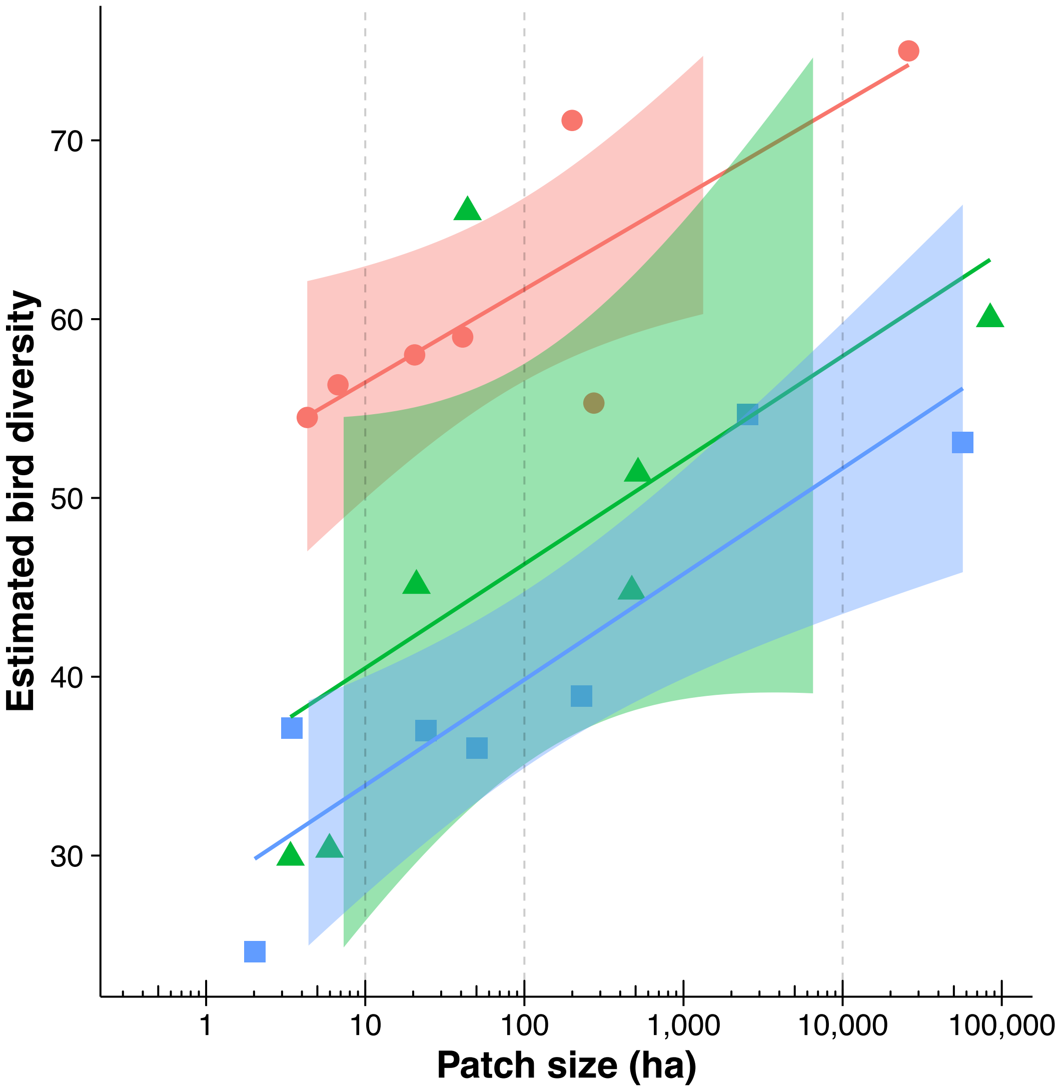

Figure 3-3: Estimated bird diversity (at 1440 1-min effort) by patch size and protected area. Symbols and color by region: red circles = region 1; green triangles = region 2 and blue squares = region3. Regression lines and confidence intervals are also represented followed region's colors.

Compositional dissimilarity from patches to reference PAs ranged from 40% up to 89%, depending on patch size and geographical distance. The highest of such dissimilarities was found for small patches, decreasing with increasing patch size (Figure 3-4 A). This pattern shows an important effect of patch size on the composition of bird metacommunities. Patch distance from protected area stands to increase dissimilarities, with smaller differences than found for patch size.

By partitioning beta diversity, we found that species turnover accounts for major changes in species composition, adding up from 62% to 94% of total dissimilarity (Figure 3-4B and C. Table S4 Supplementary material). Turnover peaked in small patches, suggesting changes in composition to be more than a consequence of species loss – although the same fragments had the lowest species richness. Such high turnover was found to be in part because small patches had species typical of open and non-forest areas, pointing at an increasing influence of the nearby landscape matrix on bird composition. The highest values of the nestedness component were also found for small patches (FAS1, FNS2, and FNS3), indicating an effect of size on species loss. Notably, dissimilarities between small patches and their reference PAs increased with forest cover in each region (dissimilarity: region 1 > region 2 > region 3; forest cover: 53%, 61% and, 75%). This suggests as the proportion of forest cover in the landscape decreases, the contribution of small patches increases in their value in maintaining diversity.

In all regions, dissimilarities within large patches were smaller than between them and nearby patches of distinct sizes (dissimilarities values for each patch pair in Table S4 Supplementary material). One medium-size patch (FNM2) in region 2 had dissimilarities that were lower than expected, indicating size and distance from reference PAs have to be eventually complemented by additional factors for better explanations of all patterns. Region 3 had the highest overall forest cover and patches were close to the reference PA, with the large patch (FLN3) immersed in a large continuous area. Not surprisingly, FLN3 had a bird composition that was very similar to that of its reference PA (i.e., relatively low dissimilarity: ~50%). For this reason, the patches far from the reference PA had higher values of dissimilarities and were more similar to each other than to the reference PA (Table S4 Supplementary material).

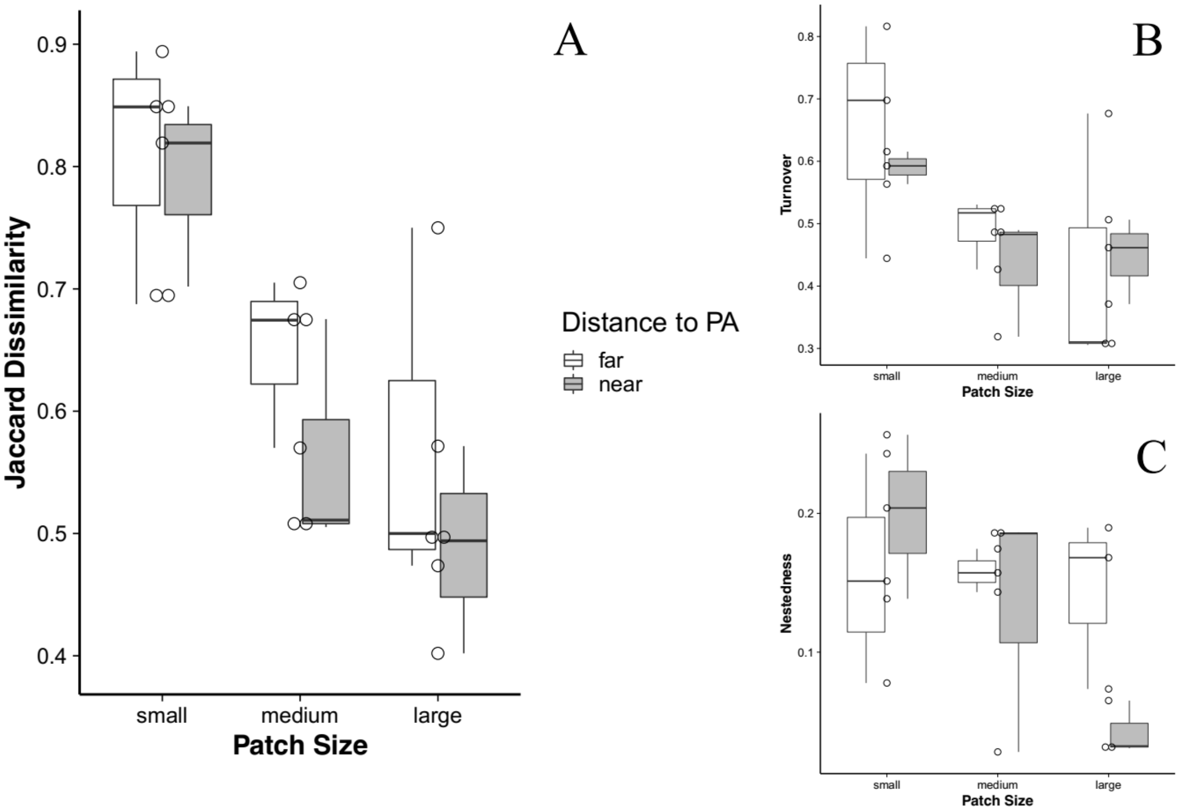

Figure 3-4: Beta diversity relationships between patch size and distance to reference Protected Areas: A - Jaccard dissimilarity; B- Turnover component, C – Nestedness component.

Effects of environmental and geographic factors on diversity

Patch size was a key predictor of bird diversity (Table 3-2, Figure 3-5, Table S5 Supplementary material). Alpha diversity (estimated bird richness) increased with increasing patch size, while beta diversity (overall dissimilarity, turnover, and nestedness components) increased with decreasing patch size. In combination, such results highlight key differences between large patches and small patches to maintain diversity alongside PAs. Spatial distance between patches and reference PAs was of little importance to explain diversity patterns, except for overall dissimilarity, which slightly increased with spatial distance (Table 3-2). In addition, local habitat characteristics correlated with alpha and beta diversity to varying degrees (Table 3-2). Bird richness slightly increased under opener vegetation (inverse relation with PC2's values, Figure 3-5). While overall dissimilarity was uncorrelated with habitat characteristics, turnover decreased and nestedness increased towards tall vegetation with open understory (weak correlations with PC1values, Table 3-2). In addition, nestedness increased towards more open vegetation (strong correlation with high PC2-values, Figure3-5).

Table 3-2: Relationships between patch and habitat characteristics on diversity (alpha: estimated species richness; beta: Jaccard dissimilarity, and turnover and nestedness components) of bird metacommunities in Santa Catarina Atlantic rain forest. PC1 axis has a positive relation with trees and shrubs height and negative relation with understory density; PC2 axis has negative relation with trees, shrub, and dominant tree density. Numbers indicate z values and * significance of relationships (‘*’/ P < 0.05; ‘**’ / P< 0.01; ‘***’/P <0.001).

	Patch characteristic		Habitat characteristic	
Response variable	Patch size (log)	Distance to reference PA (log)	PC1	PC2
Estimated bird richness	4.502 ***			-2.566 *
Jaccard dissimilarity	-8.999 ***	2.32 *		
Turnover component	-5.009 ***		-2.198 *	
Nestedness component	-4.182 ***		1.981 *	3.351 ***

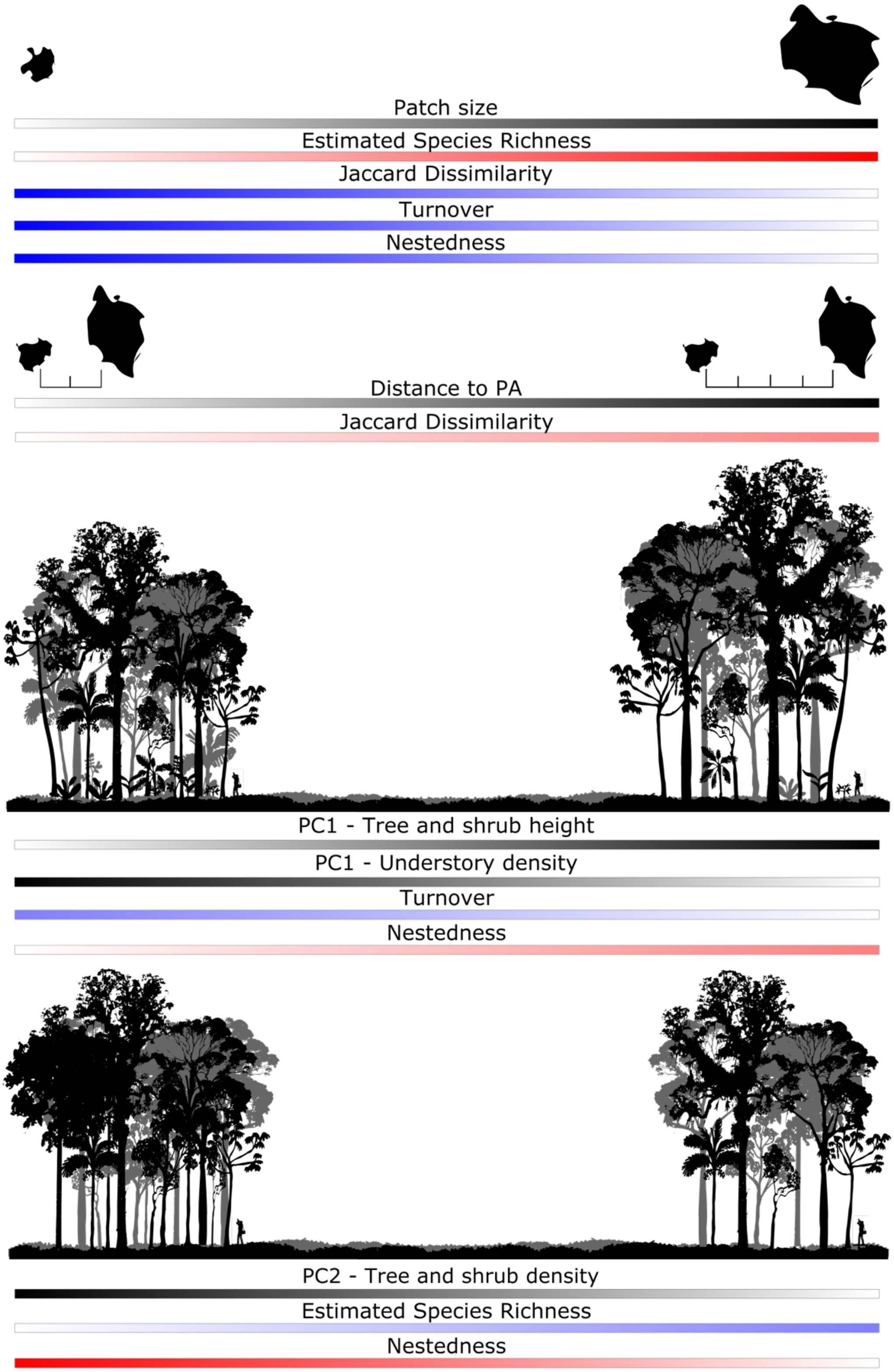

Figure 3-5: Relationships between environmental and geographic factors on alpha and beta bird diversity. Black bar represents positive relationships with patch and habitat characteristics. Red color represents positive, and blue, negative relationships with beta diversity components. Color intensity shows the strength of relationships.

Trait-environment interactions and local bird species compositions

Overall, 151 species were classified as diet specialists (Gini specialization index > 0.8), foraging strata specialists comprise 122 bird species, 143 bird species were classified as habitat specialists of which 71 are forest-specialists. Forest dependence (values >0) was detected on 149 birds with 16 are fully forest-dependent. Bird traits and specialization indexes for all 160 species are shown in Table S6 (Supplementary material). Patch size interacted strongly with bird traits in explaining the distribution of bird species and, thus, community composition. Patch size had a strong positive correlation (>0.3) with habitat specialism and forest dependence, a moderate positive correlation with forest specialism and foraging substrate, and more lightly with dispersal ability (HWI) (Figure 3-6, Table S7 Supplementary material). Most such relationships suggest only large patches support birds that are specialized in forests – especially preserved ones, with many vegetation layers – and, to some extent, with good dispersal ability. Patch size and body mass have weak inverse relationships and, thus, indicate large fragments are home to small, forest-specialized bird species, such as understory insectivores. Patch distance to reference PAs had a weak positive correlation with diet specialism, which likely results from frugivorous birds flying large distances to find their food.

Interactions between habitat characteristics and bird traits had a secondary role in explaining bird distribution with weak relatonships (Figure 3-6, Table S7 Supplementary material). Inside fragments with taller vegetation and more open understory (higher PC1 values), habitat-specialized birds were more common, as were forest specialists. In turn, under short vegetation and close understory (low PC1 values), diet specialists were more common. Although weakly correlated, the inverse relationship between vegetation density (higher PC2 values) and dispersal ability indicates that where vegetation is denser there are birds with lower dispersal ability (lower HWI values).

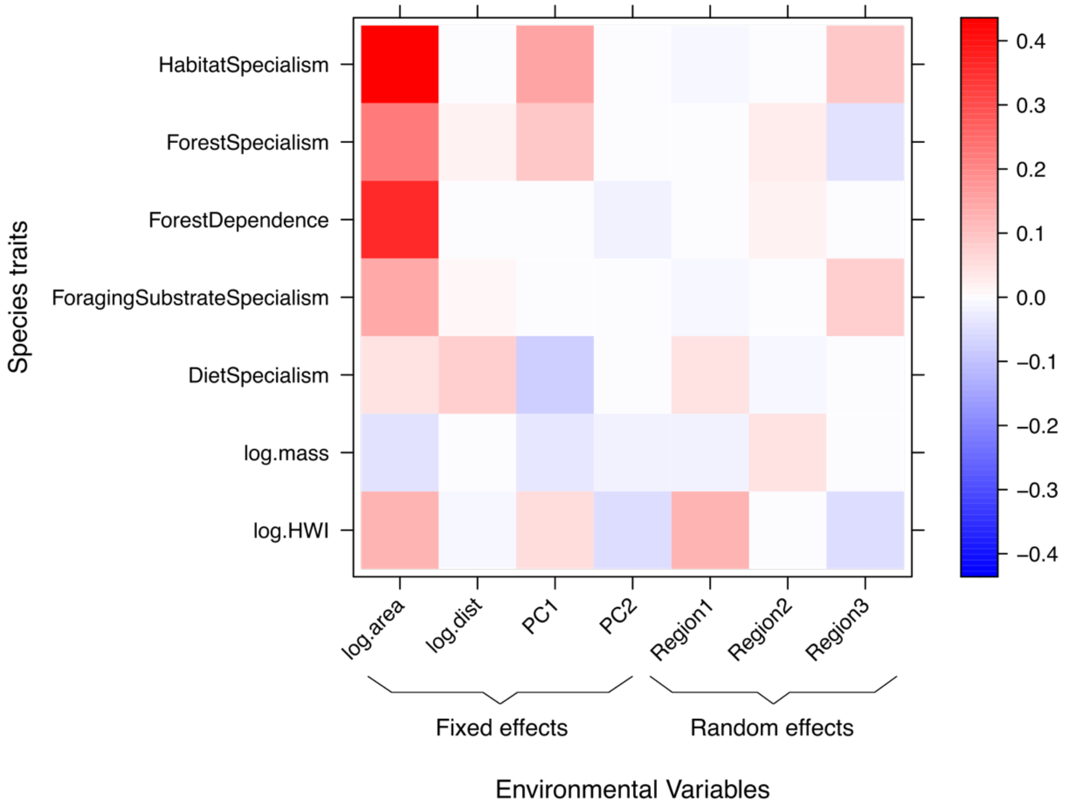

Figure 3-6: Interaction between patch and habitat characteristics and bird traits to explain bird distributions. Variable-trait interactions are colored according to their coefficients, where red indicates a relevant positive trait-variable association, and blue indicates a relevant negative trait-variable association. Color depth indicates the strength of the trait-variable correlation.

3.5 DISCUSSION

Here we found evidence that regional factors – patch size of forest remnants and distance to protected areas – had greater relevance in maintaining bird diversity than those factors measured on the local scale, i.e., local habitat variables. As a matter of concern, we found alpha and beta bird diversity show a typic pattern of degradation in smaller forest patches and at those distant from potential sources of colonizers. Although we assessed bird metacommunities in a part of the Atlantic forest that has still moderate to large amounts of remaining forest cover (Ribeiro et al. 2009; Vibrans et al. 2013), as patch size decreases, bird richness declines. Meanwhile, turnover - which drives most patterns of overall dissimilarity - increases between fragments and reference protected areas, suggesting a threshold between 10 and 20 ha in size for the largest compositional changes. Distance to reference sites and vegetation structure are secondary but still relevant factors in explaining bird richness and differentiation in species composition. In addition, forest specialist birds are more common in larger patches and under tall and more open vegetation, likely contributing to explain patterns in species turnover on different sizes and at distant patches.

We assessed bird metacommunities across moderately to highly connected landscapes, with all three sampled regions showing >50% of forest cover, thus expecting only small to moderate effects of geographic factors – patch size and distance from reference PAs – on bird metacommunities. Despite differing in the amounts of forest loss across regions, we found no differences in bird richness. Similar independence of bird richness on the amounts of remaining forest cover have been found across other regions in the Atlantic Forest (Morante-Filho et al. 2015, 2016). However, lacking relationships between species richness and habitat cover on the landscape level can be misleading when changes in species composition are left unchecked (Banks-Leite et al. 2012).

By indicating key roles for patch size and distance from reference protected areas on bird diversity, our results agree with the key ideas of the theory of island biogeography (MacArthur & Wilson 1967) borrowed to interpret terrestrial fragmented landscapes. In agreement, we found bird richness increases towards larger patches, which seems a recurrent pattern for birds across the fragmented Atlantic Forest (Uezu et al. 2005; Martensen et al. 2012; Hatfield et al. 2020). However, in addition to showing smaller bird richness, small and medium patches had high values of dissimilarity and with turnover as the main component of composition differentiation in relation to PAs. Such a key role for turnover has been suggested as underlying little changes on bird richness and an underestimation of the negative effects of habitat loss on the landscape scale (Banks-Leite et al. 2012). Indeed, species turnover may result from increasing edge-effects in smaller patches, leading to environmental changes that select different sets of bird species than those found in larger patches (Hansbauer et al. 2008; Banks-Leite et al. 2010; Püttker et al. 2020). Futhermore, small patches are more susceptible to high demographic stochasticity, increasing the odds of changes in species richness and species composition that follow a random or nested pattern (Chase et al. 2020). Habitat heterogeneity, which can mediate species-area relationships (Casas et al 2016), was found here to be unrelated to patch size, thus suggesting a direct effect of patch size on species richness.

Dispersal has a significant role in structuring bird metacommunities (Meynard et al. 2011) with geographical distance influencing beta diversity (Morante-Filho et al. 2016). Even with the patch size effect, we found that patches closer to protected areas have more similar species composition, suggesting many forest bird species cross a non-forested matrix (Uezu et al. 2005; Boscolo et al. 2008; Awade & Metzger 2008; Lees & Peres 2009). We used the avian hand-wing index (HWI) as a proxy for dispersal ability (Sheard et al. 2020) and, contrary to our expectations, found lower HWI-values in patches far from reference protected areas. Species turnover in patches far from reference areas can be less related to dispersal than to both, environmental, filters that cause an increase of non-forest species coming from the surrounding matrix (Morante-Filho et al. 2016), and the decrease of forest-dependent species following changes in habitat characteristics (Morante-Filho et al. 2016; Barbosa et al. 2017). Therefore, dispersal ability was a weaker predictor of community composition than, for instance, habitat suitability for different species (Uezu et al. 2005; Hansbauer et al. 2008, 2010; Giubbina et al. 2018).

Patch size is important in landscapes of low connectivity (Uezu & Metzger 2011) and our results suggest the importance of patch size to bird diversity in regions with high degrees of connectivity. In addition, the surrounding matrix affects patch species composition, especially when forest patches are in an unsuitable matrix (Hansbauer et al. 2008; Goulart et al. 2015; Barbosa et al. 2017; Biz et al. 2017; Giubbina et al. 2018; Boesing et al. 2018). Given that most are in a matrix that is still somewhat suitable for forest birds, such as non-native tree monocultures (*Eucalyptus* spp. or *Pinus* spp. plantations), this can help to explain why medium patches showed species-rich communities (Biz et al. 2017; Hatfield et al. 2020). Moreover, in a medium patch surrounded by early-secondary forests or non-native tree monocultures, the dissimilarity and species turnover are smaller than in those surrounded by crops or pasture. In isolated small patches surrounded by crops or pasture, we found high turnover values on beta diversity with bird communities composes of several non-forest species that are known to use edges and could spill over to the interior of small forest patches (Hatfield et al. 2020). Following the rationale that effective strategies can be aided by knowing beta diversity and the spatial structure of diversity (Socolar et al. 2016; Chase et al. 2020), high species turnover in the landscapes suggests a need to protect multiple disjunct patches to ensure the highest diversity.

Bird richness and composition correlated with differences in vegetation structure between forest patches, but such differences were unrelated to region, patch size, or distance from reference sites. Even without a detailed history of each patch, vegetation structure itself, and information from former or current nearby residents suggest some patches are old-growth forests lacking logging for over fifty years and others are late secondary forests. This process of forest recovery taking place in the State of Santa Catarina (Baptista & Rudel 2006) creates an inner heterogeneity in vegetation structure which affected bird richness and composition in different ways, acting as secondary filter on the composition of bird metacommunities. Trees and shrubs were tallest and vegetation closest in old-growth forests, while understory density was highest in secondary forests and near forest edges (DeWalt et al. 2003; Piotto et al. 2009; Magnago et al. 2015). Bird species richness increases towards patches with old-growth forest structures (DeWalt et al. 2003; Piotto et al. 2009). Such kinds of forest patches host more understory insectivores and species of large ground birds (Uezu & Metzger 2011; Casas et al. 2016; Bhakti et al. 2018), a similar pattern as found herein. Bird turnover was, at least in part, also a response of species to a gradient in vegetation structure, with edge species and those from the surrounding matrix being favored in secondary forests or patches with large edge effects (Hatfield et al. 2020).

Species are sorted across patches in a fragmented landscape as a result of the interaction of bird traits with environmental (Neuschulz et al. 2013; Keinath et al. 2017) and geographical factors (Uezu & Metzger 2011; Goulart et al. 2015). Frugivorous and nectarivorous birds are good at flying long distances and moving between distant forest patches (Neuschulz et al. 2013), keeping the connectivity between them (Díaz Vélez et al. 2015). Thus, even though we analyzed functional groups together, there might be some relationship between birds with such a specialized diet and distance between patches or from patches to reference sites. Understory insectivorous birds have, in turn, high dependence on forest habitats, being thus common only in large patches and absent from small or isolated ones. This pattern emerges a typic of tropical forest birds (Uezu & Metzger 2011; Kormann et al. 2018) and contrast with that normally found for temperate species, where habitat specialist birds disperse farther than generalists (Martin & Fahrig 2018).

In this work, we found a positive association between forest patch size and forest dependency, and other bird specialisms, except for diet specialism. Therefore, even if a heterogeneous landscape gains new species regardless of fragmentation, high turnover between fragments of different sizes and patch size and distance associations with bird traits can still lead community functioning or functional diversity to recede (Bregman et al. 2016). Species losses are known to follow habitat loss (Fahrig 2003, 2013; Hanski 2015). The limits of the remaining habitat needed for the maintenance of functional diversity are nevertheless under debate (Andrén 1994; Martensen et al. 2012; Banks-Leite et al. 2014, 2021; Boesing et al. 2018; Arroyo-Rodríguez et al. 2020, 2021). By reducing available habitat in to small patches, forest specialists and large ground species are normally lost (Uezu et al. 2005; Uezu & Metzger 2011; Barbosa et al. 2017; Keinath et al. 2017; Bhakti et al. 2018). Moreover, specialist birds, such as forest frugivorous and granivorous, are greatly reduced when forest cover is below 50% (Morante-Filho et al. 2015, 2016). Therefore, distinct species functional groups suffer different impacts depending on the amount of forest cover in the region contributing to changes in patches composition.

Conservation aims to ensure diversity is maximized, but keeping high species richness does not safeguard community functioning is sustained, especially if species with distinct roles are replaced, which is normally the case for specialists and generalists (Morante-Filho et al. 2016; Kormann et al. 2018). Thus, the maintenance of reference sites such as large areas of well-preserved and old-growth forests, either in protected areas or private lands, has great importance to ensure sensitive species are kept in regional species pools (Kormann et al. 2018; Hatfield et al. 2020). But where such large reference sites are already lost, it is crucial to maintain, recover, connect, and increase small and medium fragments to maintain bird diversity on a regional scale. As a way to expand the available area, the restoration actions of the forest habitats should also contemplate marginal habitats, still contributing to the reduction of the edge effects (Ribeiro et al. 2011). In Brazil, the Native Vegetation Protection Law (NVPL – *Lei de Proteção da VegetaçãoNativa*, in Portuguese) (Law nº.12,727/2012), which replaced the Forest Code, brought advances and setbacks for the protection of vegetation (Brancalion et al. 2016). This law ensures the protection of native vegetation in 20% of the area of the rural property in the Atlantic Forest, as Legal Reserves and, guarantees the protection of riparian forests as Areas of Permanent Protection (APP). This form of protection in the Atlantic Forest combined with the small average size of rural properties in the State of Santa Catarina (about 35 ha (Ferrari et al. 2018)), ensured the high amounts of forest remnants found today in the state.

Conservation strategies for biodiversity in the Brazilian Atlantic Forest must go beyond the simple maintenance of large public areas to encompass small and medium-sized fragments present in private lands, which comprise the majority of forest remnants (Ribeiro et al. 2009) and has played an important role in the conservation of threatened birds (Develey 2021). Agroforestry systems have a high potential to contribute to the increase of landscape areas and connectivity, as well as to the provision of ecosystem services and agricultural products (Santos et al. 2019). Uses that value forest maintenance, such as nature-based tourism and birdwatching, have great potential for social and landowner involvement, should also be encouraged and maximized (Steven et al. 2015; Develey 2021). Public policy actions should act in compliance and law enforcement, as well as reinforce the values and benefits of forest maintenance, encouraging and rewarding landowners who maintain these sustainable activities. However, our study also clearly demonstrates the fundamental importance of preserving large remnants in order to protect specialist forest birds, which could otherwise disapear from the landscape.

3.6 CONCLUSION

We studied bird metacommunities in the southern range of the Atlantic Forest, where a relatively high amount of forest cover remains and where patches of old-growth forest remnants are still common. Even there, our results indicate a loss in bird species from large to small forest patches and a turnover in species composition in relation with PAs, with a threshold around 10 ha of patch size, driven by the selection of species based on their traits relationships with patch geographic and environmental factors. Strategies for conservation and maintenance of biodiversity in the fragmented Atlantic Forest must therefore go beyond maximizing species richness and protect large public areas but aim also at species composition and functional aspects across landscapes and include private forest patches. In the current scenario of budget constraints for conservation and recovery actions, conservation strategies for the Brazilian Atlantic Forest must include sustainable activities and bring benefits to private landowners for the actions to be successful and the conservation objectives to be achieved.

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3.9 SUPPLEMENTARY MATERIAL

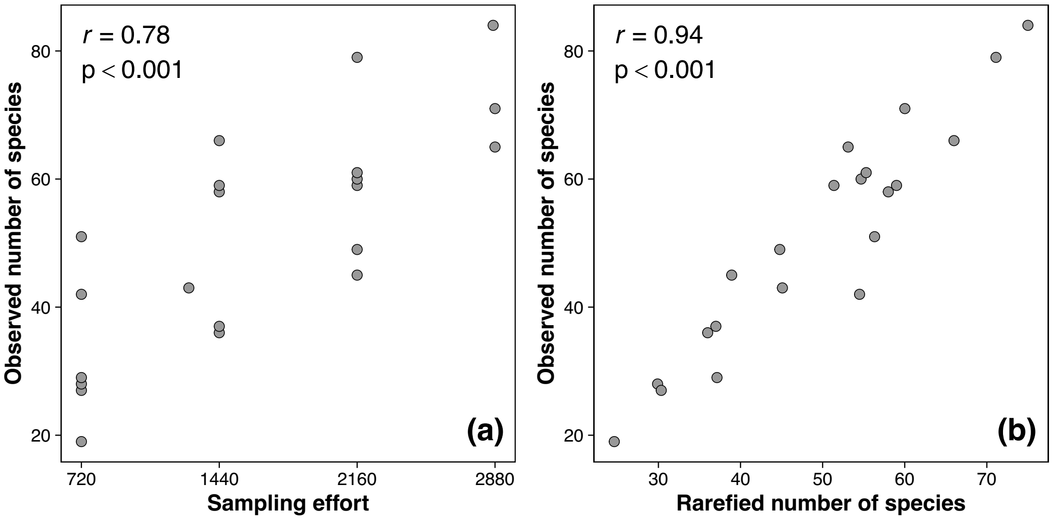

Figure S1: Relations of observed number os species with sampling effort (a) and rarified number os species (b) of bird species recorded on 21 sample areas in the Atlantic rain forest of Santa Catarina state. The Pearson's correlation and p-values are showed above.

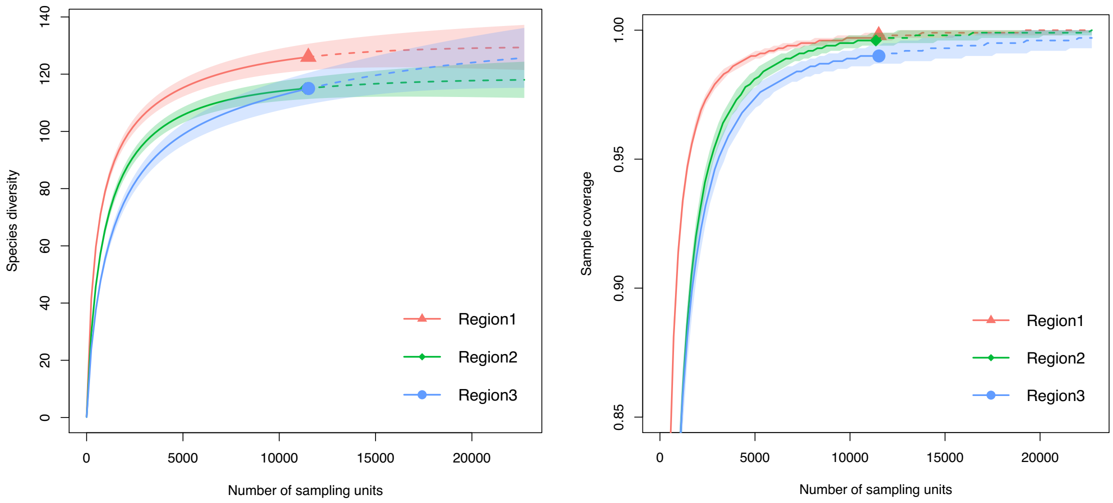

Figure S2: Rarefaction curves and sample coverage for rarefied samples of bird species recorded per region in the Atlantic rain forest of Santa Catarina state. The continuous line is interpolated and the dashed line is extrapolated data.

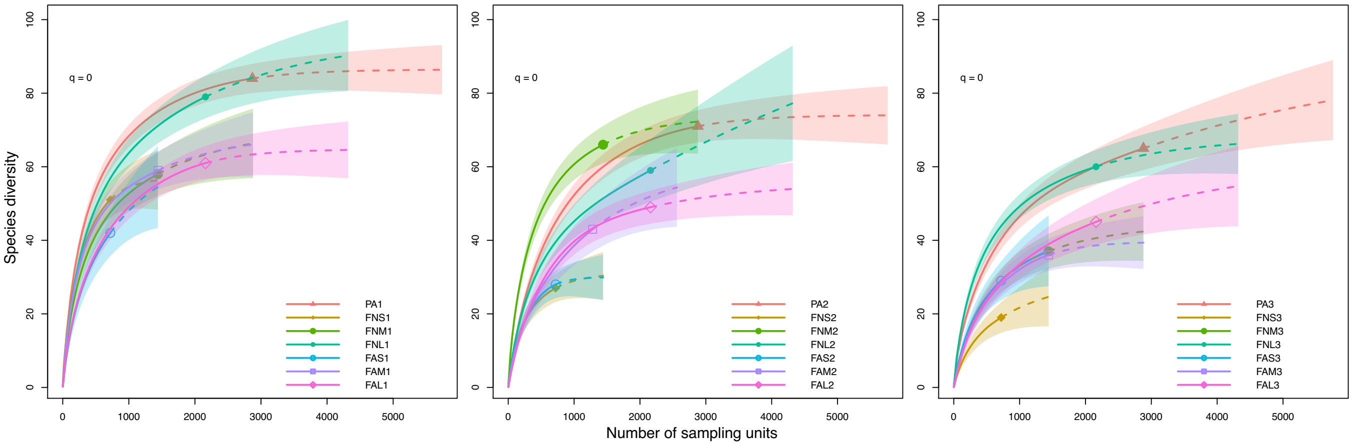

Figure S3: Incidence frequency-based rarefaction curves of bird species richness recorded per patch in the Atlantic rain forest of Santa Catarina state. The continuous line is interpolated and the dashed line extrapolated data. Patches are grouped per region based on the protected area.

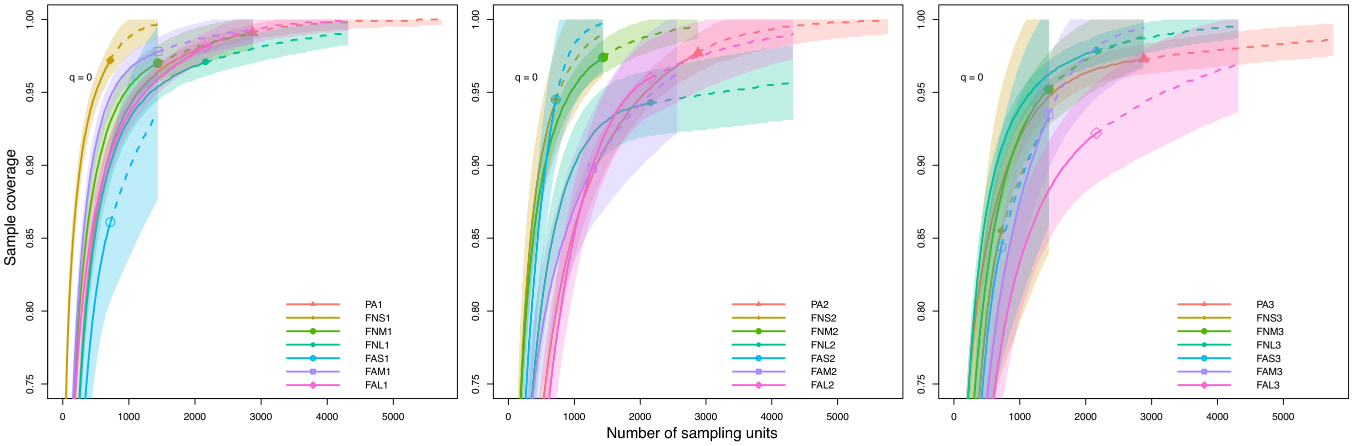

Figure S4: Sample coverage for rarefied samples (solid line) and extrapolated samples (dashed line) as a function of sample size for forest patches in Santa Catarina Atlantic forest.

Table S1: Description of environmental variables

Variable	Description	Scale/fator type
Area	Total area of forest native vegetation calculated by GIS from recent satellite images	Regional/ Geographical factors By pacth
Distance do PA	Distance in Km calculated from central points of protected area sample points to central point of forest patches by GIS tools	Regional/ Geographical factors By patch
Tree height	Tree height measured by laser measure Bosch GLM20	Local/ Habitat factors By point
Tree diameter breast height	Trunk diameter measured at breast height with tape measure	Local/ Habitat factors By point
Tree density	Measured by the average distance from the nearest tree in each quadrant to the center point	Local/ Habitat factors By point
Canopy Cover	Canopy cover index calculated from digital photos obtained with the GLAMA app (Tichý 2016)	Local/ Habitat factors By point
Shrub height	Shrub height measured by laser measure Bosch GLM20	Local/ Habitat factors By point
Shrub density	Measured by the average distance from the nearest shrub in each quadrant to the center point	Local/ Habitat factors By point
Shrub diameter root collar	Diameter of the main stem measured at the base of the aerial part of the plant and the top of the root system (root colar) with tape measure	Local/ Habitat factors By point
Understory density	Average percentage of black pixels of photos took in each quarter, at 1 m above the soil and at 3 m away from a white fabric (1 × 1 m) opened at 50 cm from the ground. Photos converted in black and white binary and calculated the percentage of black pixels with ImageJ software (ABRÀMOFF; et al, 2004).	Local/ Habitat factors By point

Table S2. Description of bird traits and information source

Trait	Description	Data Source
Avian hand-wing index (HWI)	Morphological metric linked to wing aspect ratio. See Sheard et al. 2020 for details.	Sheard et al. 2020
Body mass	(log) Mass of species in grams.	Wilman et al. 2014
Diet specialization index	Wilman et al. 2014 classified bird species by estimated % use in Diet classes: Carnivore, Frugivore/Nectarivore, Invertivore, Omnivore and PlantSeed. Based on this diet data we calculated Gini coefficient of inequality (Morelli et al. 2019) obtained an Index values range between 0 (least specialized) and 1 (most specialized).	Wilman et al. 2014
Foraging strata specialization index	Wilman et al. 2014 classified bird species by estimated % use in Foraging stratum: aerial, canopy, ground, midhigh and understory. Based on this stratum data we calculated Gini coefficient of inequality (Morelli et al. 2019) obtained an Index values range between 0 (least specialized) and 1 (most specialized).	Wilman et al. 2014
Habitat specialization index	Stotz et al. 1996 classified bird species by presence-ausence in forest and non-forest habitats. Based on this habitat presence data we calculated Gini coefficient of inequality (Morelli et al. 2019) obtained an Index values range between 0 (least specialized) and 1 (most specialized).	Stotz et al. 1996
Forest specialization index	Stotz et al. 1996 classified bird species by presence-ausence in forest habitats. Based on this habitat forest presence data we calculated Gini coefficient of inequality (Morelli et al. 2019) obtained an Index values range between 0 (least specialized) and 1 (most specialized).	Stotz et al. 1996
Forest dependence	Index calculated by the formula $Fdi = F - nF$, where F is the proportion of forest habitats and nF is the proportion of nonforest habitats where a species were recorded from data of habitat presence of Stotz et al. 1996.	Stotz et al. 1996

Table S3: List of species registered by sound records in 48 sample points in Santa Catarina Atlantic forest, during summer 2018-2019. Taxonomy and systematic order follow Piacentini et al (2015). End – Atlantic forest endemism; Patch – number of patches with species presence; Point – number of sampled points with species presence; Det – Total number of species detections in all sampled points.

Taxon	English name	IUCN Status	End	Patch	Point	Det
Tinamidae Gray, 1840						
Tinamus solitarius (Vieillot, 1819)	Solitary Tinamou	NT	Y	3	8	20
Crypturellus obsoletus (Temminck, 1815)	Brown Tinamou	LC		11	19	37
Crypturellus tataupa (Temminck, 1815)	Tataupa Tinamou	LC		9	17	31
Cracidae Rafinesque, 1815						
Penelope obscura Temminck, 1815	Dusky-legged Guan	LC		1	1	1
Ortalis squamata (Lesson, 1829)	Scaled Chachalaca	LC	Y	1	1	16
Odontophoridae Gould, 1844						
Odontophorus capueira (Spix, 1825)	Spot-winged Wood-Quail	LC	Y	10	17	48
Threskiornithidae Poche, 1904						
Theristicus caudatus (Boddaert, 1783)	Buff-necked Ibis	LC		2	2	3
Accipitridae Vigors, 1824						
Rupornis magnirostris (Gmelin, 1788)	Roadside Hawk	LC		4	5	8
Rallidae Rafinesque, 1815						
Aramides saracura (Spix, 1825)	Slaty-breasted Wood-Rail	LC	Y	4	4	6
Charadriidae Leach, 1820						
Vanellus chilensis (Molina, 1782)	Southern Lapwing	LC		6	7	8
Columbidae Leach, 1820						
Columbina talpacoti (Temminck, 1810)	Ruddy Ground-Dove	LC		2	2	7
Patagioenas picazuro (Temminck, 1813)	Picazuro Pigeon	LC		9	12	73
Patagioenas cayennensis (Bonnaterre, 1792)	Pale-vented Pigeon	LC		1	1	3
Patagioenas plumbea (Vieillot, 1818)	Plumbeous Pigeon	LC		2	3	68
Leptotila verreauxi Bonaparte, 1855	White-tipped Dove	LC		15	23	71
Leptotila rufaxilla (Richard & Bernard, 1792)	Gray-fronted Dove	LC		4	6	24
Geotrygon montana (Linnaeus, 1758)	Ruddy Quail-Dove	LC		10	14	37

Taxon	English name	IUCN Status	End	Patch	Point	Det
Cuculidae Leach, 1820						
Piaya cayana (Linnaeus, 1766)	Squirrel Cuckoo	LC		1	1	1
Guira guira (Gmelin, 1788)	Guira Cuckoo	LC		2	2	3
Tapera naevia (Linnaeus, 1766)	Striped Cuckoo	LC		1	1	2
Strigidae Leach, 1820						
Megascops atricapilla (Temminck, 1822)	Black-capped Screech-Owl	LC	Y	3	3	13
Megascops sanctaecatarinae (Salvin, 1897)	Long-tufted Screech-Owl	LC	Y	1	3	51
Pulsatrix koeniswaldiana (Bertoni & Bertoni, 1901)	Tawny-browed Owl	LC	Y	4	4	9
Strix virgata (Cassin, 1849)	Mottled Owl	LC		3	3	18
Glaucidium minutissimum (Wied, 1830)	Least Pygmy-Owl	LC	Y	3	5	25
Nyctibiidae Chenu & Des Murs, 1851						
Nyctibius griseus (Gmelin, 1789)	Common Potoo	LC		7	7	9
Caprimulgidae Vigors, 1825						
Antrostomus sericocaudatus Cassin, 1849	Silky-tailed Nightjar	LC		1	1	63
Lurocalis semitorquatus (Gmelin, 1789)	Short-tailed Nighthawk	LC		10	15	22
Nyctidromus albicollis (Gmelin, 1789)	Common Pauraque	LC		1	1	68
Apodidae Olphe-Galliard, 1887						
Chaetura meridionalis Hellmayr, 1907	Sick's Swift	LC		2	2	2
Trochilidae Vigors, 1825						
Phaethornis eurynome (Lesson, 1832)	Scale-throated Hermit	LC	Y	8	10	61
Stephanoxis loddigesii (Gould, 1831)	Violet-crowned Plovercrest	LC	Y	3	4	5
Amazilia versicolor (Vieillot, 1818)	Versicolored Emerald	LC		5	5	27
Trogonidae Lesson, 1828						
Trogon surrucura Vieillot, 1817	Surucua Trogon	LC		12	21	66
Trogon rufus Gmelin, 1788	Black-throated Trogon	LC		9	17	24
Alcedinidae Rafinesque, 1815						
Megaceryle torquata (Linnaeus, 1766)	Ringed Kingfisher	LC		2	2	3
Baryphthengus ruficapillus (Vieillot, 1818)	Rufous-capped Motmot	LC	Y	3	4	8

Taxon	English name	IUCN Status	End	Patch	Point	Det
Bucconidae Horsfield, 1821						
Malacoptila striata (Spix, 1824)	Crescent-chested Puffbird	NT	Y	2	2	5
Ramphastidae Vigors, 1825						
Ramphastos vitellinus Lichtenstein, 1823	Channel-billed Toucan	VU		9	13	29
Ramphastos dicolorus Linnaeus, 1766	Red-breasted Toucan	LC	Y	12	16	20
Selenidera maculirostris (Lichtenstein, 1823)	Spot-billed Toucanet	LC	Y	2	2	4
Picidae Leach, 1820						
Picumnus temminckii Lafresnaye, 1845	Ochre-collared Piculet	LC	Y	15	28	51
Veniliornis spilogaster (Wagler, 1827)	White-spotted Woodpecker	LC		11	13	20
Piculus aurulentus (Temminck, 1821)	White-browed Woodpecker	NT	Y	5	5	5
Colaptes campestris (Vieillot, 1818)	Campo Flicker	LC		1	1	1
Celeus flavescens (Gmelin, 1788)	Blond-crested Woodpecker	LC		1	1	1
Falconidae Leach, 1820						
Milvago chimachima (Vieillot, 1816)	Yellow-headed Caracara	LC		2	2	2
Micrastur ruficollis (Vieillot, 1817)	Barred Forest-Falcon	LC		6	11	13
Psittacidae Rafinesque, 1815						
Psittacara leucophthalmus (Statius Muller, 1776)	White-eyed Parakeet	LC		5	9	19
Pyrrhura frontalis (Vieillot, 1817)	Maroon-bellied Parakeet	LC	Y	10	20	40
Forpus xanthopterygius (Spix, 1824)	Blue-winged Parrotlet	LC		1	1	1
Brotogeris tirica (Gmelin, 1788)	Plain Parakeet	LC	Y	12	16	39
Pionopsitta pileata (Scopoli, 1769)	Pileated Parrot	LC	Y	5	8	15
Pionus maximiliani (Kuhl, 1820)	Scaly-headed Parrot	LC		2	3	4
Triclaria malachitacea (Spix, 1824)	Blue-bellied Parrot	NT	Y	7	8	11
Thamnophilidae Swainson, 1824						
Myrmotherula unicolor (Ménétriès, 1835)	Unicolored Antwren	NT	Y	7	11	117
Rhopias gularis (Spix, 1825)	Star-throated Antwren	LC	Y	10	13	17
Dysithamnus stictothorax (Temminck, 1823)	Spot-breasted Antvireo	NT	Y	4	5	21
Dysithamnus mentalis (Temminck, 1823)	Plain Antvireo	LC		14	21	40
Herpsilochmus rufimarginatus (Temminck, 1822)	Rufous-winged Antwren	LC		4	6	16

Taxon	English name	IUCN Status	End	Patch	Point	Det
Thamnophilus caerulescens Vieillot, 1816	Variable Antshrike	LC		5	6	15
Hypoedaleus guttatus (Vieillot, 1816)	Spot-backed Antshrike	LC	Y	4	7	18
Batara cinerea (Vieillot, 1819)	Giant Antshrike	LC		4	8	14
Mackenziaena severa (Lichtenstein, 1823)	Tufted Antshrike	LC	Y	1	1	3
Myrmoderus squamosus (Pelzeln, 1868)	Squamate Antbird	LC	Y	15	26	311
Pyriglena leucoptera (Vieillot, 1818)	White-shouldered Fire-eye	LC	Y	11	15	26
Drymophila rubricollis (Bertoni, 1901)	Bertoni's Antbird	LC	Y	1	1	2
Drymophila malura (Temminck, 1825)	Dusky-tailed Antbird	LC	Y	1	1	2
Conopophagidae Sclater & Salvin, 1873						
Conopophaga lineata (Wied, 1831)	Rufous Gnateater	LC		7	10	210
Conopophaga melanops (Vieillot, 1818)	Black-cheeked Gnateater	LC	Y	8	13	26
Grallariidae Sclater & Salvin, 1873						
Grallaria varia (Boddaert, 1783)	Variegated Antpitta	LC		5	9	21
Hylopezus nattereri (Pinto, 1937)	Speckle-breasted Antpitta	LC	Y	1	3	46
Rhinocryptidae Wetmore, 1926 (1837)						
Merulaxis ater Lesson, 1830	Slaty Bristlefront	NT	Y	1	2	7
Scytalopus speluncae (Ménétriès, 1835)	Mouse-colored Tapaculo	LC	Y	1	1	10
Psilorhamphus guttatus (Ménétriès, 1835)	Spotted Bamboowren	NT	Y	1	1	27
Formicariidae Gray, 1840						
Formicarius colma Boddaert, 1783	Rufous-capped Antthrush	LC		1	2	19
Chamaeza campanisona (Lichtenstein, 1823)	Short-tailed Antthrush	LC		11	26	104
Scleruridae Swainson, 1827						
Sclerurus scansor (Ménétriès, 1835)	Rufous-breasted Leaftosser	LC	Y	10	19	50
Dendrocolaptidae Gray, 1840						
Dendrocincla turdina (Lichtenstein, 1820)	Plain-winged Woodcreeper	LC	Y	7	12	36
Sittasomus griseicapillus (Vieillot, 1818)	Olivaceous Woodcreeper	LC		16	31	64
Xiphorhynchus fuscus (Vieillot, 1818)	Lesser Woodcreeper	LC	Y	18	38	101
Dendrocolaptes platyrostris Spix, 1825	Planalto Woodcreeper	LC		15	27	42
Xiphocolaptes albicollis (Vieillot, 1818)	White-throated Woodcreeper	LC		6	12	19

Taxon	**English name**	**IUCN Status**	**End**	**Patch**	**Point**	**Det**
Xenopidae Bonaparte, 1854						
Xenops rutilans Temminck, 1821	Streaked Xenops	LC		12	17	35
Furnariidae Gray, 1840						
Furnarius rufus (Gmelin, 1788)	Rufous Hornero	LC		5	6	20
Lochmias nematura (Lichtenstein, 1823)	Sharp-tailed Streamcreeper	LC		5	5	41
Automolus leucophthalmus (Wied, 1821)	White-eyed Foliage-gleaner	LC	Y	16	29	74
Anabacerthia amaurotis (Temminck, 1823)	White-browed Foliage-gleaner	NT	Y	3	7	130
Philydor atricapillus (Wied, 1821)	Black-capped Foliage-gleaner	LC	Y	9	13	36
Philydor rufum (Vieillot, 1818)	Buff-fronted Foliage-gleaner	LC		13	26	171
Heliobletus contaminatus Pelzeln, 1859	Sharp-billed Treehunter	LC	Y	3	4	103
Cichlocolaptes leucophrus (Jardine & Selby, 1830)	Pale-browed Treehunter	LC	Y	4	7	110
Synallaxis ruficapilla Vieillot, 1819	Rufous-capped Spinetail	LC	Y	10	12	36
Pipridae Rafinesque, 1815						
Ilicura militaris (Shaw & Nodder, 1809)	Pin-tailed Manakin	LC	Y	9	11	18
Chiroxiphia caudata (Shaw & Nodder, 1793)	Swallow-tailed Manakin	LC	Y	15	29	86
Oxyruncidae Ridgway, 1906 (1831)						
Oxyruncus cristatus Swainson, 1821	Sharpbill	LC		1	1	1
Tityridae Gray, 1840						
Schiffornis virescens (Lafresnaye, 1838)	Greenish Schiffornis	LC	Y	17	30	62
Tityra cayana (Linnaeus, 1766)	Black-tailed Tityra	LC		1	1	1
Pachyramphus castaneus (Jardine & Selby, 1827)	Chestnut-crowned Becard	LC		2	3	5
Pachyramphus polychopterus (Vieillot, 1818)	White-winged Becard	LC		14	20	48
Cotingidae Bonaparte, 1849						
Carpornis cucullata (Swainson, 1821)	Hooded Berryeater	NT	Y	7	18	76
Procnias nudicollis (Vieillot, 1817)	Bare-throated Bellbird	VU	Y	3	6	23
Platyrinchidae Bonaparte, 1854						
Platyrinchus mystaceus Vieillot, 1818	White-throated Spadebill	LC		13	20	76
Rhynchocyclidae Berlepsch, 1907						
Mionectes rufiventris Cabanis, 1846	Gray-hooded Flycatcher	LC	Y	3	3	168

Taxon	English name	IUCN Status	End	Patch	Point	Det
Leptopogon amaurocephalus Tschudi, 1846	Sepia-capped Flycatcher	LC		12	18	44
Tolmomyias sulphurescens (Spix, 1825)	Yellow-olive Flycatcher	LC		15	24	52
Hemitriccus obsoletus (Miranda-Ribeiro, 1906)	Brown-breasted Pygmy-Tyrant	LC	Y	1	1	1
Tyrannidae Vigors, 1825						
Camptostoma obsoletum (Temminck, 1824)	Southern Beardless-Tyrannulet	LC		13	20	46
Myiopagis caniceps (Swainson, 1835)	Gray Elaenia	LC		1	1	1
Phyllomyias virescens (Temminck, 1824)	Greenish Tyrannulet	LC	Y	3	4	5
Phyllomyias fasciatus (Thunberg, 1822)	Planalto Tyrannulet	LC		1	1	5
Phyllomyias griseocapilla Sclater, 1862	Gray-capped Tyrannulet	NT	Y	2	5	12
Attila phoenicurus Pelzeln, 1868	Rufous-tailed Attila	LC		13	29	132
Attila rufus (Vieillot, 1819)	Gray-hooded Attila	LC	Y	11	17	61
Legatus leucophaius (Vieillot, 1818)	Piratic Flycatcher	LC		9	13	601
Myiarchus swainsoni Cabanis & Heine, 1859	Swainson's Flycatcher	LC		15	18	221
Pitangus sulphuratus (Linnaeus, 1766)	Great Kiskadee	LC		6	7	10
Myiodynastes maculatus (Statius Muller, 1776)	Streaked Flycatcher	LC		10	18	492
Tyrannus melancholicus Vieillot, 1819	Tropical Kingbird	LC		10	11	14
Empidonomus varius (Vieillot, 1818)	Variegated Flycatcher	LC		1	1	23
Lathrotriccus euleri (Cabanis, 1868)	Euler's Flycatcher	LC		19	32	72
Vireonidae Swainson, 1837						
Cyclarhis gujanensis (Gmelin, 1789)	Rufous-browed Peppershrike	LC		15	21	40
Hylophilus poicilotis Temminck, 1822	Rufous-crowned Greenlet	LC	Y	14	22	43
Vireo chivi (Vieillot, 1817)	Chivi Vireo	LC		15	31	108
Corvidae Leach, 1820						
Cyanocorax caeruleus (Vieillot, 1818)	Azure Jay	LC		7	8	77
Polioptilidae Baird, 1858						
Polioptila lactea Sharpe, 1885	Creamy-bellied Gnatcatcher	NT	Y	2	2	2
Turdidae Rafinesque, 1815						
Turdus flavipes Vieillot, 1818	Yellow-legged Thrush	LC		7	13	26
Turdus leucomelas Vieillot, 1818	Pale-breasted Thrush	LC		3	3	13

Taxon	English name	IUCN Status	End	Patch	Point	Det
Turdus rufiventris Vieillot, 1818	Rufous-bellied Thrush	LC		9	13	108
Turdus subalaris (Seebohm, 1887)	Eastern Slaty Thrush	LC		1	1	2
Turdus albicollis Vieillot, 1818	White-necked Thrush	LC		19	37	194
Passerellidae Cabanis & Heine, 1850						
Zonotrichia capensis (Statius Muller, 1776)	Rufous-collared Sparrow	LC		2	2	11
Parulidae Wetmore, Friedmann, Lincoln, Miller, Peters, van Rossem, Van Tyne & Zimmer 1947						
Setophaga pitiayumi (Vieillot, 1817)	Tropical Parula	LC		17	33	104
Basileuterus culicivorus (Deppe, 1830)	Golden-crowned Warbler	LC		21	44	226
Myiothlypis leucoblephara (Vieillot, 1817)	White-browed Warbler	LC		8	13	54
Icteridae Vigors, 1825						
Cacicus chrysopterus (Vigors, 1825)	Golden-winged Cacique	LC		1	1	2
Mitrospingidae Barker, Burns, Klicka, Lanyon & Lovette, 2013						
Orthogonys chloricterus (Vieillot, 1819)	Olive-green Tanager	LC	Y	1	1	1
Thraupidae Cabanis, 1847						
Pipraeidea melanonota (Vieillot, 1819)	Fawn-breasted Tanager	LC		3	3	4
Tangara seledon (Statius Muller, 1776)	Green-headed Tanager	LC	Y	13	21	70
Tangara cyanocephala (Statius Muller, 1776)	Red-necked Tanager	LC	Y	10	16	37
Tangara desmaresti (Vieillot, 1819)	Brassy-breasted Tanager	LC	Y	3	3	4
Tangara sayaca (Linnaeus, 1766)	Sayaca Tanager	LC		2	3	4
Tangara cyanoptera (Vieillot, 1817)	Azure-shouldered Tanager	NT	Y	6	14	73
Tangara palmarum (Wied, 1821)	Palm Tanager	LC		1	1	1
Tangara ornata (Sparrman, 1789)	Golden-chevroned Tanager	LC	Y	1	1	3
Tangara preciosa (Cabanis, 1850)	Chestnut-backed Tanager	LC		12	23	66
Sicalis flaveola (Linnaeus, 1766)	Saffron Finch	LC		5	7	118
Haplospiza unicolor Cabanis, 1851	Uniform Finch	LC	Y	2	4	69
Hemithraupis ruficapilla (Vieillot, 1818)	Rufous-headed Tanager	LC	Y	5	8	15
Trichothraupis melanops (Vieillot, 1818)	Black-goggled Tanager	LC		7	10	15
Tachyphonus coronatus (Vieillot, 1822)	Ruby-crowned Tanager	LC	Y	14	20	34
Tersina viridis (Illiger, 1811)	Swallow Tanager	LC		2	2	4

Taxon	English name	IUCN Status	End	Patch	Point	Det
Dacnis cayana (Linnaeus, 1766)	Blue Dacnis	LC		20	43	119
Coereba flaveola (Linnaeus, 1758)	Bananaquit	LC		6	8	23
Saltator similis d'Orbigny & Lafresnaye, 1837	Green-winged Saltator	LC		5	7	11
Cardinalidae Ridgway, 1901						
Habia rubica (Vieillot, 1817)	Red-crowned Ant-Tanager	LC		16	24	53
Fringillidae Leach, 1820						
Euphonia chlorotica (Linnaeus, 1766)	Purple-throated Euphonia	LC		2	2	14
Euphonia violacea (Linnaeus, 1758)	Violaceous Euphonia	LC		4	4	9
Euphonia pectoralis (Latham, 1801)	Chestnut-bellied Euphonia	LC	Y	6	11	52
Chlorophonia cyanea (Thunberg, 1822)	Blue-naped Chlorophonia	LC		2	4	83

Table S4: Jaccard dissimilarities and turnover and nestedness components by region. Patch code: sequence of letters and one number: PA protected area or first letters F forest, ongoing letters refer to size and distance: N near, A far-away, S small, M medium, L large, number refers to region.

	Jaccarddissimilaritiesregion 1 - PNSJ						Jaccarddissimilaritiesregion 2 - PEST						Jaccarddissimilaritiesregion 3 - PNSI					
	PA1	FNS1	FNM1	FNL1	FAS1	FAM1	PA2	FNS2	FNM2	FNL2	FAS2	FAM2	PA3	FNS3	FNM3	FNL3	FAS3	FAM3
FNS	70.20%						81.90%						84.90%					
FNM	50.50%	65.40%					51.10%	70.80%					67.50%	63.40%				
FNL	40.20%	66.00%	38.80%				57.10%	69.70%	41.80%				49.40%	83.80%	67.10%			
FAS	68.80%	69.00%	59.20%	60.90%			84.90%	72.10%	79.50%	73.90%			89.40%	93.30%	75.50%	82.90%		
FAM	57.00%	57.10%	50.00%	50.00%	63.50%		67.40%	79.30%	54.70%	58.30%	81.70%		70.50%	90.00%	69.60%	66.70%	70.00%	
FAL	47.40%	63.40%	41.30%	35.30%	52.90%	48.10%	50.00%	75.40%	50.60%	45.70%	81.50%	58.50%	75.00%	85.70%	75.80%	65.40%	76.70%	65.00%

	Turnover component						Turnover component						Turnover component					
	PA1	FNS1	FNM1	FNL1	FAS1	FAM1	PA2	FNS2	FNM2	FNL2	FAS2	FAM2	PA3	FNS3	FNM3	FNL3	FAS3	FAM3
FNS	56.30%						61.50%						59.30%					
FNM	31.90%	62.20%					48.30%	36.40%					49.00%	34.80%				
FNL	37.10%	52.20%	18.80%				50.60%	41.20%	36.10%				46.20%	59.30%	52.00%			
FAS	44.40%	64.50%	47.30%	32.00%			69.80%	71.40%	60.00%	52.60%			81.60%	91.40%	71.10%	71.10%		
FAM	42.70%	52.20%	49.40%	36.10%	52.60%		51.70%	71.40%	34.60%	46.40%	75.60%		53.10%	84.80%	69.10%	50.00%	65.10%	
FAL	30.60%	58.30%	38.90%	17.90%	35.30%	46.80%	31.00%	61.50%	36.70%	36.70%	72.70%	54.20%	67.60%	73.30%	72.40%	57.10%	68.20%	58.80%

	Nestednesscomponent						Nestednesscomponent						Nestednesscomponent					
	PA1	FNS1	FNM1	FNL1	FAS1	FAM1	PA2	FNS2	FNM2	FNL2	FAS2	FAM2	PA3	FNS3	FNM3	FNL3	FAS3	FAM3
FNS	13.90%						20.40%						25.70%					
FNM	18.60%	3.30%					2.80%	34.50%					18.60%	28.60%				
FNL	3.10%	13.80%	20.10%				6.50%	28.50%	5.70%				3.20%	24.60%	15.10%			
FAS	24.30%	4.50%	11.90%	28.90%			15.10%	0.70%	19.50%	21.30%			7.80%	1.90%	4.40%	11.80%		
FAM	14.30%	5.00%	0.60%	13.90%	10.90%		15.70%	7.90%	20.10%	11.90%	6.10%		17.50%	5.20%	0.60%	16.70%	4.90%	
FAL	16.80%	5.10%	2.40%	17.40%	17.60%	1.30%	19.00%	13.90%	14.00%	9.00%	8.80%	4.20%	7.40%	12.40%	3.30%	8.20%	8.50%	6.20%

Table S5: Estimated coefficients from GLMM relating Rarefied Richness and beta diversity (Dissimilarity, Turnover, and Nestedness) to habitat variables and patches characteristics of bird metacommunities of Santa Catarina Atlantic rain forest. Signif. codes: ‘***’ >0.001, ‘**’ >0.01, ‘*’ >0.05.

rareS ~ logdist + logarea + PC1 + PC2 + (1 | region)

AIC 157.9

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	39.9263	7.8413	5.092	3.55e-07 ***
logdist	-0.8088	1.6241	-0.498	0.6185
logarea	2.4134	0.5361	4.502	6.74e-06 ***
PC1	-1.1157	1.6078	-0.694	0.4877
PC2	-5.3025	2.0665	-2.566	0.0103 *

JaccDiss ~ logdist + logarea + PC1 + PC2 + (1 | region)

AIC -33.5

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.733995	0.066785	10.99	<2e-16 ***
logdist	0.048392	0.02086	2.32	0.0204 *
logarea	-0.057213	0.006358	-8.999	<2e-16 ***
PC1	-0.019705	0.014981	-1.315	0.1884
PC2	0.021009	0.018135	1.158	0.2467

Turn ~ logdist + logarea + PC1 + PC2 + (1 | region)

AIC -27.3

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.545631	0.077992	6.996	2.63e-12 ***
logdist	0.040223	0.025427	1.582	0.1137
logarea	-0.038698	0.007725	-5.009	5.46e-07 ***
PC1	-0.040061	0.018224	-2.198	0.0279 *
PC2	-0.039609	0.021938	-1.805	0.0710

Nest ~ logdist + logarea + PC1 + PC2 + (1 | region)

AIC -50.5

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.193945	0.041139	4.714	2.42e-06 ***
logdist	0.005694	0.015056	0.378	0.705281
logarea	-0.018426	0.004406	-4.182	2.89e-05 ***
PC1	0.020555	0.010375	1.981	0.047568 *
PC2	0.053865	0.016074	3.351	0.000805 ***

Table S6: Bird traits and specialization index values. Hand-wing index (HWI)(Sheard *et al.* 2020), body mass, guildand foraging strata (ForagStrata)(Wilman *et al.* 2014), Diet Specialism (DietSpec), Foraging Strata Specialism (StrSpc), Forest Specialism (ForSpec), Forest Dependency (ForDep) and Habitat Specialism (HabSpec) calculated index values. All index values range from 0 (least specialized) to 1 (most specialized). Forest dependency index ranges from ‘-1’ (forest-independent) to ‘+1’ (forest-dependent).

Taxon	**HWI**	**mass(log)**	**Guild**	**DietSpec**	**ForagStrata**	**StrSpec**	**ForSpec**	**ForDep**	**HabSpec**
Tinamus solitarius	13.63739	3.14189	Omnivore	0.733	ground	1	1	1	1
Crypturellus obsoletus	22.46076	2.64680	Omnivore	0.889	ground	1	0.889	0.5	0.947
Crypturellus tataupa	21.08514	2.34005	Omnivore	0.844	understory	0.833	0.778	0.333	0.895
Penelope obscura	4.86363	3.24797	Frugivore/Nectarivore	0.956	under-midhigh	0.6	0.889	0.5	0.947
Ortalis squamata	10.01645	2.73856	Frugivore/Nectarivore	0.978	midhigh-canopy	0.833	0.667	0.25	0.842
Odontophorus capueira	10.45892	2.62880	Frugivore/Nectarivore	0.956	ground	1	0.889	0.5	0.947
Theristicus caudatus	32.15546	3.23704	Invertivore	0.867	ground	0.867	0.778	0.125	0.842
Rupornis magnirostris	25.49195	2.42975	Carnivore	0.8	under-midhigh	0.667	0.444	0.102	0.684
Aramides saracura	11.62119	2.73239	Invertivore	0.867	ground	0.9	0.778	0.333	0.895
Vanellus chilensis	30.98842	2.51455	Invertivore	0.978	ground	0.933	0	-0.5	0.947
Columbina talpacoti	19.91960	1.66314	PlantSeed	0.978	ground	1	0	-0.25	0.842
Patagioenas picazuro	37.64990	2.44560	PlantSeed	0.733	under-midhigh	0.6	1	-0.111	0.895
Patagioenas cayennensis	34.06070	2.35984	Frugivore/Nectarivore	0.933	midhigh-canopy	0.733	0.556	0.2	0.789
Patagioenas plumbea	35.33258	2.25229	Omnivore	0.889	canopy	0.9	0.889	0.5	0.947
Leptotila verreauxi	21.85028	2.16696	PlantSeed	0.867	ground	1	0.556	0.2	0.789
Leptotila rufaxilla	24.39169	2.19590	PlantSeed	0.933	ground	1	0.667	0.25	0.842
Geotrygon montana	26.46937	2.12665	Omnivore	0.844	ground	1	0.778	0.333	0.895
Piaya cayana	11.29984	2.00852	Invertivore	1	canopy	0.933	0.556	0.2	0.789
Guira guira	24.92803	2.14922	Carnivore	0.8	ground	0.867	0	-1	1
Tapera naevia	22.83421	1.68502	Invertivore	0.956	understory	0.8	0.889	0.111	0.895
Megascops atricapilla	24.96298	2.07515	Invertivore	0.978	canopy	0.767	0.778	0.333	0.895
Megascops sanctaecatarinae	18.82169	2.25460	Omnivore	0.889	understory	0.833	0.778	0.333	0.895
Pulsatrix koeniswaldiana	25.65114	2.68215	Carnivore	0.889	under-midhigh	0.567	0.889	0.5	0.947
Strix virgata	20.84569	2.45327	Carnivore	0.8	ground	0.933	0.667	0.25	0.842
Glaucidium minutissimum	21.13955	1.69897	Invertivore	0.867	ground	0.967	0.667	0.25	0.842
Nyctibius griseus	43.83778	2.23563	Invertivore	1	midhigh	0.967	0.556	0.2	0.789
Antrostomus sericocaudatus	49.61674	1.91908	Invertivore	1	midhigh	0.833	0.889	0.5	0.947
Lurocalis semitorquatus	56.77760	1.88024	Invertivore	1	midhigh	0.867	0.889	0.5	0.947
Nyctidromus albicollis	35.75796	1.76223	Invertivore	1	understory	0.667	0.667	0.25	0.842
Chaetura meridionalis	62.63949	1.34635	Invertivore	1	aerial	1	0.889	0.111	0.895
Phaethornis eurynome	60.56840	0.72428	Frugivore/Nectarivore	0.978	understory	1	0.889	0.5	0.947

Taxon	**HWI**	**mass(log)**	**Guild**	**DietSpec**	**ForagStrata**	**StrSpec**	**ForSpec**	**ForDep**	**HabSpec**
Stephanoxis loddigesii	60.24557	0.60206	Frugivore/Nectarivore	0.978	understory	0.767	0.889	0.111	0.895
Amazilia versicolor	63.36093	0.61278	Frugivore/Nectarivore	0.978	under-canopy	0.7	0.556	0.2	0.789
Trogon surrucura	39.15323	1.86504	Invertivore	0.956	midhigh	1	0.889	0.5	0.947
Trogon rufus	38.24101	1.73078	Invertivore	0.911	understory	0.833	0.889	0.5	0.947
Megaceryle torquata	23.14126	2.50106	Carnivore	0.867	ground	0.967	0	0	0
Baryphthengus ruficapillus	16.00166	2.15122	Invertivore	0.844	understory	0.767	0.778	0.333	0.895
Malacoptila striata	20.67047	1.64444	Invertivore	1	understory	0.833	0.889	0.5	0.947
Ramphastos vitellinus	11.82236	2.55674	Frugivore/Nectarivore	0.844	midhigh-canopy	0.733	1	1	1
Ramphastos dicolorus	14.00877	2.51983	Frugivore/Nectarivore	0.933	canopy	0.933	0.889	0.5	0.947
Selenidera maculirostris	14.78839	2.21484	Frugivore/Nectarivore	0.956	under-canopy	0.733	0.889	0.5	0.947
Picumnus temminckii	13.25861	1.06070	Invertivore	1	understory	0.933	0.778	0.333	0.895
Veniliornis spilogaster	18.77323	1.60531	Invertivore	0.956	under-midhigh	0.833	0.778	0.333	0.895
Piculus aurulentus	20.36992	1.87500	Invertivore	1	midhigh	1	0.778	0.333	0.895
Colaptes campestris	17.53645	2.19866	Invertivore	0.978	ground	1	0	-0.25	0.842
Celeus flavescens	16.25159	2.14301	Invertivore	0.933	under-midhigh	0.767	0.667	0.25	0.842
Milvago chimachima	29.95759	2.49860	Carnivore	0.533	ground	1	0	-0.25	0.842
Micrastur ruficollis	21.80047	2.24954	Carnivore	0.956	understory	0.7	0.889	0.5	0.947
Psittacara leucophthalmus	42.69600	2.19866	PlantSeed	0.733	under-midhigh	0.6	0.667	0.25	0.842
Pyrrhura frontalis	40.27515	1.85733	PlantSeed	0.733	under-midhigh	0.767	0.778	0.333	0.895
Forpus xanthopterygius	27.83320	1.49136	Omnivore	0.889	ground	1	0.667	0.25	0.842
Brotogeris tirica	35.08376	1.79934	PlantSeed	0.733	canopy	0.8	0.778	0.333	0.895
Pionopsitta pileata	35.71200	2.07555	PlantSeed	0.8	midhigh-canopy	0.867	0.889	0.5	0.947
Pionus maximiliani	35.21821	2.46687	PlantSeed	0.911	under-canopy	0.767	0.667	0.25	0.842
Triclaria malachitacea	30.48128	1.95424	Omnivore	0.733	under-canopy	0.767	0.889	0.5	0.947
Myrmotherula unicolor	12.91489	1.06070	Invertivore	1	midhigh	0.933	0.778	0.333	0.895
Rhopias gularis	11.02971	1.05308	Invertivore	1	understory	0.733	0.889	0.5	0.947
Dysithamnus stictothorax	8.08699	1.20844	Invertivore	0.978	midhigh	0.9	0.889	0.5	0.947
Dysithamnus mentalis	11.69616	1.17231	Invertivore	0.978	under-canopy	0.733	0.889	0.5	0.947
Herpsilochmus rufimarginatus	7.30924	1.02449	Invertivore	0.978	midhigh	1	0.556	0.2	0.789
Thamnophilus caerulescens	10.90784	1.32428	Invertivore	0.844	under-midhigh	0.867	0.444	0.167	0.737
Hypoedaleus guttatus	7.62921	1.58883	Invertivore	0.978	midhigh	1	1	1	1
Batara cinerea	6.63275	2.11727	Invertivore	0.911	under-midhigh	0.7	0.778	0.333	0.895
Mackenziaena severa	9.33047	1.71433	Invertivore	0.867	understory	0.7	0.778	0.333	0.895
Myrmoderus squamosus	9.04097	1.26717	Invertivore	1	ground	0.933	0.889	0.5	0.947
Pyriglena leucoptera	10.30640	1.45939	Invertivore	0.978	understory	0.733	0.889	0.5	0.947
Drymophila rubricollis	9.55325	1.00000	Invertivore	1	midhigh	0.933	0.889	0.5	0.947
Drymophila malura	10.71756	1.11394	Invertivore	1	understory	0.733	1	1	1

Taxon	**HWI**	**mass(log)**	**Guild**	**DietSpec**	**ForagStrata**	**StrSpec**	**ForSpec**	**ForDep**	**HabSpec**
Conopophaga lineata	11.00877	1.40157	Invertivore	1	ground-under	0.867	0.778	0.333	0.895
Conopophaga melanops	13.37713	1.30320	Invertivore	1	ground-under	0.867	1	1	1
Grallaria varia	8.35294	2.07555	Invertivore	1	ground	1	0.889	0.5	0.947
Hylopezus nattereri	10.49964	1.50515	Invertivore	1	ground	1	0.889	0.5	0.947
Merulaxis ater	5.36222	1.54444	Invertivore	1	ground	1	1	1	1
Scytalopus speluncae	12.71422	1.11394	Invertivore	1	ground-under	0.867	0.889	0.5	0.947
Psilorhamphus guttatus	8.96422	1.05308	Invertivore	1	understory	0.833	1	1	1
Formicarius colma	18.98377	1.67210	Invertivore	1	ground	0.933	1	1	1
Chamaeza campanisona	11.66987	1.95703	Invertivore	0.933	ground	0.933	0.889	0.5	0.947
Sclerurus scansor	16.21449	1.56703	Invertivore	1	ground	1	0.889	0.5	0.947
Dendrocincla turdina	20.46650	1.59106	Invertivore	1	under-midhigh	0.867	0.889	0.5	0.947
Sittasomus griseicapillus	21.99259	1.11793	Invertivore	0.978	midhigh-canopy	0.833	0.556	0.2	0.789
Xiphorhynchus fuscus	19.54343	1.33846	Invertivore	1	under-midhigh	0.833	0.889	0.5	0.947
Dendrocolaptes platyrostris	16.75775	1.79029	Invertivore	0.933	understory	0.833	0.778	0.333	0.895
Xiphocolaptes albicollis	14.05666	2.07188	Invertivore	0.933	midhigh	1	0.778	0.333	0.895
Xenops rutilans	23.57903	1.04922	Invertivore	1	midhigh	0.933	0.778	0.333	0.895
Furnarius rufus	16.09109	1.66671	Invertivore	0.956	ground	0.9	0	-0.5	0.947
Lochmias nematura	11.80398	1.34242	Invertivore	1	ground	1	0.778	0.333	0.895
Automolus leucophthalmus	17.35745	1.53782	Invertivore	1	understory	0.933	1	1	1
Anabacerthia amaurotis	15.46413	1.28330	Invertivore	1	understory	0.8	1	1	1
Philydor atricapillus	16.20211	1.34635	Invertivore	1	under-canopy	0.667	1	1	1
Philydor rufum	19.73363	1.39794	Invertivore	1	midhigh-canopy	0.867	0.778	0.333	0.895
Heliobletus contaminatus	19.88404	1.14613	Invertivore	1	midhigh-canopy	0.833	0.889	0.5	0.947
Cichlocolaptes leucophrus	16.75146	1.69897	Invertivore	1	midhigh	0.933	0.889	0.5	0.947
Synallaxis ruficapilla	11.54459	1.13988	Invertivore	1	understory	0.8	0.778	0.333	0.895
Ilicura militaris	22.62957	1.10380	Omnivore	0.889	under-midhigh	0.833	0.889	0.5	0.947
Chiroxiphia caudata	15.81320	1.40824	Omnivore	0.889	under-midhigh	0.833	0.778	0.333	0.895
Oxyruncus cristatus	67.33313	1.62325	Frugivore/Nectarivore	0.956	midhigh-canopy	0.867	0.889	0.5	0.947
Schiffornis virescens	15.66691	1.40824	Omnivore	0.889	understory	1	0.778	0.333	0.895
Tityra cayana	25.41600	1.83315	Frugivore/Nectarivore	0.956	under-midhigh	0.833	0.889	0.5	0.947
Pachyramphus castaneus	18.26537	1.29003	Invertivore	0.978	midhigh	1	0.667	0.25	0.842
Pachyramphus polychopterus	20.81776	1.31806	Omnivore	0.889	midhigh	1	0.667	0.25	0.842
Carpornis cucullata	19.79407	1.87035	Frugivore/Nectarivore	0.956	under-midhigh	0.833	0.889	0.5	0.947
Procnias nudicollis	24.01076	2.23563	Frugivore/Nectarivore	1	under-midhigh	0.833	0.889	0.5	0.947
Platyrinchus mystaceus	16.10833	0.98677	Invertivore	1	understory	0.933	0.889	0.5	0.947
Mionectes rufiventris	13.26675	1.12385	Omnivore	0.889	midhigh	0.967	0.889	0.5	0.947

Taxon	**HWI**	**mass(log)**	**Guild**	**DietSpec**	**ForagStrata**	**StrSpec**	**ForSpec**	**ForDep**	**HabSpec**
Leptopogon amaurocephalus	18.65235	1.06819	Invertivore	0.956	under-midhigh	0.833	0.889	0.5	0.947
Tolmomyias sulphurescens	14.64519	1.15534	Invertivore	0.978	midhigh	0.9	0.444	0.167	0.737
Hemitriccus obsoletus	12.86198	1.06446	Invertivore	1	understory	0.933	1	1	1
Camptostoma obsoletum	14.20584	0.90849	Invertivore	0.933	midhigh	0.933	0.667	0.056	0.737
Myiopagis caniceps	18.47259	1.02119	Invertivore	0.956	canopy	1	1	1	1
Phyllomyias virescens	19.56807	0.91381	Invertivore	0.933	midhigh-canopy	0.8	0.778	0.333	0.895
Phyllomyias fasciatus	17.50534	1.01284	Invertivore	0.956	canopy	1	0.778	0.333	0.895
Phyllomyias griseocapilla	14.20201	0.90309	Invertivore	0.911	understory	0.9	0.889	0.5	0.947
Attila phoenicurus	20.62527	1.50920	Invertivore	0.911	midhigh	0.667	0.889	0.5	0.947
Attila rufus	13.45873	1.62941	Invertivore	0.867	under-midhigh	0.5	0.889	0.5	0.947
Legatus leucophaius	25.44312	1.34635	Frugivore/Nectarivore	0.933	canopy	0.933	0.667	0.25	0.842
Myiarchus swainsoni	16.61983	1.39967	Invertivore	0.911	understory	1	0.667	0.25	0.842
Pitangus sulphuratus	16.70773	1.79831	Omnivore	0.733	understory	0.8	0.889	0	0.842
Myiodynastes maculatus	19.07943	1.63548	Omnivore	0.8	midhigh	1	0.667	0.25	0.842
Tyrannus melancholicus	22.38583	1.57287	Invertivore	1	midhigh-canopy	0.833	0.667	0.12	0.789
Empidonomus varius	20.81863	1.43297	Invertivore	0.911	midhigh	0.9	0.667	0.25	0.842
Lathrotriccus euleri	21.02755	1.05423	Invertivore	1	understory	1	0.778	0.333	0.895
Cyclarhis gujanensis	17.93294	1.45939	Invertivore	1	under-midhigh	0.733	0.667	0.25	0.842
Hylophilus poicilotis	11.76542	1.01703	Invertivore	0.933	midhigh	0.8	0.778	0.333	0.895
Vireo chivi	24.07676	1.20575	Invertivore	0.867	canopy	0.933	0.556	0.2	0.789
Cyanocorax caeruleus	14.46999	2.43457	Omnivore	0.733	midhigh	0.867	0.667	0.25	0.842
Polioptila lactea	11.44192	0.81291	Invertivore	1	under-canopy	0.667	0.889	0.5	0.947
Turdus flavipes	27.64268	1.81385	Frugivore/Nectarivore	0.956	under-canopy	0.6	0.778	0.333	0.895
Turdus leucomelas	22.52270	1.83948	Invertivore	0.933	ground	0.8	0.667	0.25	0.842
Turdus rufiventris	16.85755	1.84161	Omnivore	0.889	ground	1	0.778	0.333	0.895
Turdus subalaris	28.51063	1.69461	Frugivore/Nectarivore	0.911	under-midhigh	0.733	0.778	0.333	0.895
Turdus albicollis	21.41808	1.73239	Invertivore	0.911	ground	0.933	1	1	1
Zonotrichia capensis	17.57931	1.30771	PlantSeed	0.844	ground	1	1	-0.102	0.684
Setophaga pitiayumi	20.87650	0.83378	Invertivore	0.911	canopy	1	0.556	0.2	0.789
Basileuterus culicivorus	18.19343	1.02119	Invertivore	0.956	understory	0.9	0.778	0.333	0.895
Myiothlypis leucoblephara	16.97335	1.17898	Invertivore	1	understory	0.833	0.778	0.125	0.842
Cacicus chrysopterus	17.77785	1.55823	Omnivore	0.889	midhigh	0.933	0.889	0.5	0.947
Orthogonys chloricterus	23.84360	1.60206	Invertivore	0.911	midhigh	1	0.889	0.5	0.947
Pipraeidea melanonota	24.46790	1.32222	Omnivore	0.844	canopy	0.767	0.778	0.333	0.895
Tangara seledon	22.37139	1.27184	Frugivore/Nectarivore	0.911	midhigh-canopy	1	0	-0.5	0.947
Tangara cyanocephala	21.29303	1.25527	Frugivore/Nectarivore	1	canopy	0.8	0.889	0.5	0.947
Tangara desmaresti	20.06473	1.30963	Frugivore/Nectarivore	0.911	canopy	0.7	0.889	0.5	0.947

Taxon	**HWI**	**mass(log)**	**Guild**	**DietSpec**	**ForagStrata**	**StrSpec**	**ForSpec**	**ForDep**	**HabSpec**
Tangara sayaca	22.00809	1.51175	Omnivore	0.933	canopy	0.867	0.667	0.25	0.842
Tangara cyanoptera	24.96394	1.63649	Frugivore/Nectarivore	0.911	canopy	0.8	1	1	1
Tangara palmarum	21.06685	1.59106	Frugivore/Nectarivore	1	canopy	0.767	0	-0.25	0.842
Tangara ornata	26.21138	1.51851	Frugivore/Nectarivore	0.956	canopy	0.867	0.778	0.333	0.895
Tangara preciosa	21.05879	1.35793	Frugivore/Nectarivore	0.933	under-canopy	0.833	0.667	0.25	0.842
Sicalis flaveola	19.79086	1.22763	PlantSeed	1	ground-under	0.867	0	-0.5	0.947
Haplospiza unicolor	18.42121	1.18412	PlantSeed	1	ground	0.933	0.889	0.5	0.947
Hemithraupis ruficapilla	20.31436	1.04139	Invertivore	0.956	canopy	0.967	0.778	0.333	0.895
Trichothraupis melanops	20.20838	1.35372	Invertivore	0.911	under-midhigh	0.533	0.778	0.333	0.895
Tachyphonus coronatus	17.06954	1.46687	Invertivore	0.867	under-canopy	0.733	0.778	0.333	0.895
Tersina viridis	30.97034	1.46240	Frugivore/Nectarivore	0.956	midhigh	0.767	0.778	0.333	0.895
Dacnis cayana	24.41083	1.11394	Omnivore	0.867	canopy	0.833	0.667	0.25	0.842
Coereba flaveola	19.30228	1.00043	Frugivore/Nectarivore	0.933	understory	0.933	0.778	0.04	0.789
Saltator similis	14.76935	1.63649	Invertivore	0.889	understory	0.9	0.778	0.333	0.895
Habia rubica	19.21352	1.51135	Invertivore	0.956	under-midhigh	0.867	1	1	1
Euphonia chlorotica	23.22329	1.04139	Frugivore/Nectarivore	1	canopy	0.967	0.667	0.25	0.842
Euphonia violacea	28.07335	1.17609	Frugivore/Nectarivore	1	under-canopy	0.7	0.778	0.333	0.895
Euphonia pectoralis	21.81239	1.15836	Frugivore/Nectarivore	0.911	canopy	0.9	0.889	0.5	0.947
Chlorophonia cyanea	25.35190	1.14613	Frugivore/Nectarivore	0.978	canopy	0.933	0.889	0.5	0.947

Table S7: Fourth corner coefficients for the interaction of bird traits and environmental variables.

	log.area	log.dist	PC1	PC2	Region1	Region2	Region3
log.HWI	0.1240381	-0.0073502	0.0506008	-0.0512210	0.1275434	0.0000000	-0.0553001
log.mass	-0.0483250	0.0000000	-0.0313806	-0.0202877	-0.0194144	0.0484224	0.0000000
DietSpecialism	0.0422580	0.0757916	-0.0788747	0.0023850	0.0435871	-0.0113830	0.0000000
ForagingSubstrate Specialism	0.1406176	0.0068863	0.0009853	0.0000000	-0.0044315	0.0000000	0.0753630
ForestDependence	**0.3596202**	0.0000000	0.0000000	-0.0150726	0.0000000	0.0140147	0.0000000
ForestSpecialism	0.2232900	0.0166212	0.0917660	0.0000000	0.0000000	0.0262634	-0.0456322
HabitatSpecialism	**0.4359493**	0.0000000	0.1534011	0.0000000	-0.0066147	0.0000000	0.0920367

4 CONCLUSÃO GERAL

A grande maioria dos ecossistemas da Terra já sofreu alguma interferência de atividades humanas, que embora variem em grau e intensidade, vêm causando diversas e profundas modificações ambientais, sugerindo a entrada em uma nova era, o Antropoceno (CARO et al., 2012; MCGILL et al., 2015; STEFFEN et al., 2011). Com a industrialização, as interferências humanas cresceram em extensão e intensidade, se tornando as principais causas de perda de espécies na atualidade. Todas as cinco principais causas atuais de perda de espécies estão associadas com as atividades humanas, sendo elas: a mudança de uso do solo e gestão da água (incluindo perda e fragmentação de hábitat), mudança climática, invasões biológicas, poluição e sobre-exploração (CHASE et al., 2020; MCGILL et al., 2015; SOULE, 1985).

Reconhecida como uma ciência da crise, a 'biologia da conservação' surge como uma forma de aplicar os conhecimentos científicos para resolver os problemas advindos das atividades humanas (SOULE, 1985), reconhecendo que a perda de espécies traz consequências diretas para a humanidade (CARDINALE et al., 2012). A partir de um pensamento inicial de manter a natureza intacta (natureza por ela mesma), o foco da biologia da conservação passa a buscar a redução dos impactos humanos visando parar ou reduzir a perda de hábitat e consequente perda de espécies, e posteriormente com o objetivo de manter os processos ecológicos realizados pelas comunidades nos ecossistemas (MACE, 2014; SEKERCIOGLU et al., 2012; SEKERCIOGLU; DAILY; EHRLICH, 2004). Kareiva e Marvier (2012) expandem o conceito de biologia da conservação e propõem uma 'ciência da conservação', onde as ações também venham a ocorrer em ambientes alterados por humanos e não defender um retorno a ambientes pristinos (KAREIVA; MARVIER; LALASZ, 2012). Essa proposta de conservação propõe que, para ser bem-sucedida, ela deve incluir estratégias simultâneas para garantir a proteção da natureza e manter o bem-estar humano nas áreas utilizadas pelas pessoas, defendendo uma conservação da natureza para as pessoas e não das pessoas (KAREIVA; MARVIER, 2012; KAREIVA; MARVIER; LALASZ, 2012). Com uma abordagem mais recente, a biologia da conservação tem sido integrada com uma visão interdisciplinar das relações dinâmicas entre as pessoas e a natureza, removendo a visão utilitarista da natureza pelos seres humanos, de forma a enfatizar as interações sustentáveis e resilientes entre as sociedades humanas e o ambiente natural (MACE, 2014).

A conservação da biodiversidade é um grande desafio, pois é necessário equilibrar o desenvolvimento econômico, a segurança alimentar e o bem-estar social com a manutenção da diversidade (DOBROVOLSKI et al., 2018; FERRANTE; FEARNSIDE, 2019). Apesar de muitas conquistas nas últimas décadas, a conservação no Brasil atualmente passa por um período de incertezas e restrições orçamentárias (FERNANDES et al., 2017; LEVIS et al., 2020; THOMAZ et al., 2020), de forma que as ações de conservação devem maximizar os ganhos em relação aos seus objetivos. Nessa tendência, as unidades de conservação (UCs) se tornaram uma importante ferramenta na conservação *in-situ* da biodiversidade, pois são importantes áreas mantenedoras da biodiversidade e dos processos ecológicos por ela desempenhados (BRUNER et al., 2001; CHAPE et al., 2005; DEFRIES et al., 2005; FERREIRA; VENTICINQUE; ALMEIDA, 2005; GASTON et al., 2008; HANNAH et al., 2007; MEDEIROS et al., 2011; NEPSTAD et al., 2006).

A manutenção dos processos ecológicos desempenhados pelas comunidades nos ecossistemas deve ser um dos principais alvos da conservação, uma vez que a perda desses irá causar enormes prejuízos à humanidade (SEKERCIOGLU et al., 2012; SEKERCIOGLU; DAILY; EHRLICH, 2004). Deste modo, a conservação deve ser pensada não só em termos de manutenção da diversidade taxonômica, mas também em termos da manutenção de processos das metacomunidades e funcionamento dos ecossistemas em diferentes escalas espaciais, levando-se em conta não somente a qualidade do hábitat dentro das unidades, como também a qualidade do hábitat dos remanescentes na matriz das áreas de entorno e a conectividade entre as comunidades.

No atual cenário da Mata Atlântica, de uma paisagem fragmentada e com diferenças de conectividade entre metacomunidades, conhecer como as espécies estão distribuídas, como interagem com o hábitat, e como ocupam e se dispersam entre as manchas de hábitat, é fundamental para compreender os processos que mantêm a diversidade de espécies, o que contribui diretamente na definição de boas estratégias de conservação (DRISCOLL, 2008; LEIBOLD et al., 2020; SOCOLAR et al., 2016). Compreender ainda o papel das Unidades de Conservação e das áreas legalmente protegidas (APPs e reservas legais) nessa dinâmica, em diferentes escalas espaciais, tem uma grande importância para subsidiar sua manutenção e ampliar as discussões sobre o uso de corredores ecológicos na ampliação da conectividade e demais políticas públicas de meio ambiente.

Assim, no capítulo 1 avaliamos como a distância entre as manchas de hábitat, as características da paisagem e do hábitat, e as interações das espécies influenciam a diversidade e a composição das comunidades de aves encontradas nos manguezais do sul do Brasil. Nossos resultados mostraram uma alta taxa de substituição de espécies (turnover) entre as manchas de manguezais, indicando que cada área de manguezal abriga uma composição particular e, portanto, existe uma alta diversidade beta e regional. Essa diferença na composição teve pouca influência das características do hábitat a nível local, uma vez que as áreas de manguezal, embora bastante diferentes com relação aos impactos antrópicos, não apresentam alterações significativas na estrutura do hábitat. Contudo, a riqueza e a composição da avifauna foram bastante influenciadas pelo tamanho da área dos manguezais, com grandes áreas abrigando mais espécies do que áreas pequenas. Devido à alta capacidade de voo da avifauna dos manguezais, as distâncias entre as manchas não representam uma limitação e, portanto, a distância de dispersão não se configura como barreira à composição das comunidades. A presença de outros ambientes no entorno influencia as comunidades dos manguezais, contribuindo para a composição e riqueza das aves, principalmente de espécies não especialistas de manguezais. Como cada mancha de mangue tem uma comunidade de aves distinta, o conjunto dessas áreas contribui para uma riqueza regional de espécies mais alta, de forma que as estratégias de conservação devem priorizar a quantidade e tamanho das áreas para garantir a conservação das aves.

Com o foco para as áreas florestais da Mata Atlântica do sul do Brasil, no capítulo 2, visamos verificar os processos que estruturam as metacomunidades das aves nos fragmentos remanescentes, analisando como os mecanismos em escala local e regional influenciam a diversidade de espécies de aves (diversidade taxonômica alfa) e as mudanças na composição das espécies (diversidade taxonômica beta). Para tanto, na escala local observamos a filtragem de hábitat, incluindo fatores ambientais locais, e as interações bióticas, medidas indiretamente por meio de características das aves. Na escala regional incluímos fatores geográficos, como o tamanho e a distância dos fragmentos a fontes em potencial (áreas de referência), representadas aqui por grandes áreas protegidas. Conforme esperado, encontramos que a riqueza de espécies é bastante influenciada pelo tamanho dos fragmentos florestais, ocorrendo a perda de espécies de acordo com a diminuição do tamanho desses. A composição das espécies também se modifica, principalmente devido à substituição de espécies (turnover) com maiores valores encontrados para os fragmentos menores. A distância dos fragmentos às áreas de referência, a qual usamos como um indicador da distância de dispersão para as aves, também tem influência na riqueza e composição das espécies que vivem nos fragmentos, mas de forma secundária, reforçando os padrões determinados pelo tamanho das áreas. Ainda relevante, mas com influência mais sutil, a estrutura da vegetação dos fragmentos contribui para a explicar a perda de espécies, bem como a distribuição das espécies especialistas e dependentes florestais. A paisagem estudada é composta por uma grande proporção de cobertura florestal, com muitos fragmentos de floresta madura e, ainda assim, nossos resultados indicam um destaque para as grandes áreas de floresta remanescente na manutenção da biodiversidade das aves da Mata Atlântica.

Desta forma, seja uma paisagem naturalmente fragmentada, ou uma paisagem composta por manchas de hábitat de origem antrópica, o tamanho das áreas remanescentes se configura como uma importante característica para sustentar as dinâmicas das metacomunidades e a funcionalidade delas. Contudo, a valorização dos pequenos remanescentes de vegetação nativa deve ser aumentada, visto que sua importância varia de acordo com a quantidade de hábitat existente na paisagem e complementam a diversidade regional, além de contribuírem de forma fundamental com o aumento da conectividade entre manchas. Assim, os fragmentos remanescentes de todos os tamanhos devem ser protegidos e incluídos em processos de restauração ou de uso sustentável, de forma a aumentar a área disponível e expandir a conectividade da paisagem.

Assim, propomos que as estratégias para conservação e manutenção da biodiversidade na Mata Atlântica fragmentada devem ir além de manter ou aumentar a riqueza taxonômica, envolvendo ações que mantenham a diversidade funcional na paisagem, e impor limites aos usos que diminuem as áreas remanescentes e degradam os hábitats, promovendo ao mesmo tempo a restauração e usos sustentáveis. Embora o estado de Santa Catarina surpreenda com um elevado número de remanescentes florestais, recentes aumentos do desmatamento nos alertam que ações de fiscalização ainda são necessárias, bem como ações focadas na educação e transformação da cultura exploratória para uma substituição por atividades sustentáveis, como a observação de aves (“birdwatching”). Atualmente, a adoção de tais estratégias é um enorme desafio, especialmente porque as políticas ambientais e científicas estão enfrentando muitos retrocessos e perdendo recursos, acarretando um grande enfraquecimento da governança no Brasil (FERRANTE; FEARNSIDE, 2019; LOYOLA, 2014; ROVAI et al., 2012; THOMAZ et al., 2020; TOLLEFSON, 2019; VIEIRA; PRESSEY; LOYOLA, 2019). Contudo, acreditamos que temos plena capacidade de reverter a crise ambiental brasileira e garantir um meio ambiente ecologicamente equilibrado e socialmente justo para as futuras gerações.

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ANEXO A – Autorizações

Autorizações ambientais concedidas para a elaboração da Tese.

Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 60841-1	**Data da Emissão: 12/12/2017 20:24**	**Data para Revalidação*: 11/01/2019**

* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: ANDREI LANGELOH ROOS	CPF: 666.181.341-53
Título do Projeto: Qualidade do habitat e conectividade na conservação da biodiversidade na Mata Atlântica do sul do Brasil: aves como modelo de análise	
Nome da Instituição : UFSC - UNIVERSIDADE FEDERAL DE SANTA CATARINA	CNPJ: 83.899.526/0001-82

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Atividades de campo nos manguezais	11/2017	04/2018

Observações e ressalvas

1	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
2	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
3	Este documento somente poderá ser utilizado para os fins previstos na Instrução Normativa ICMBio n° 03/2014 ou na Instrução Normativa ICMBio n° 10/2010, no que especifica esta Autorização, não podendo ser utilizado para fins comerciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades científicas ou didáticas no âmbito do ensino superior.
4	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
5	O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio, nos termos da legislação brasileira em vigor.
6	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen.
7	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade.

Outras ressalvas

1	1. Comunicar a equipe da unidade de conservação previamente às atividades de campo na mesma. 2. Apresentar os resultados da pesquisa após sua conclusão ao conselho deliberativo da unidade de conservação. 3. Possíveis ressalvas posteriores poderão ser definidas com base em oitiva ao conselho deliberativo.
2	Indicar o apoio logístico necessário com antecedência mínima de uma semana (embarcação, viatura, outros equipamentos de campo). Solicita-se ao pesquisador indicar, no decorrer da pesquisa, aqueles "point counts" que apresentem potencial de acesso e observação para serem utilizados nas atividades educativo-científicas de Observação de Aves na ESEC Carijós.

Equipe

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	JOAO PEDRO KRAUSPENHAR BARROS	Pesquisador aluno	049.953.891-99	2183139 SEJUSP-MS	Brasileira

Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo
1		SC	ESTAÇÃO ECOLÓGICA DE CARIJÓS	UC Federal

Este documento (Autorização para atividades com finalidade científica) foi expedido com base na Instrução Normativa nº 03/2014. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).

Código de autenticação: 27896337

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Ministério do Meio Ambiente - MMA

Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio

Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 64140-1	**Data da Emissão: 02/10/2018 16:14:45**	**Data da Revalidação*: 02/10/2019**

De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: Andrei Langeloh Roos	CPF: 666.181.341-53
Nome da Instituição: UNIVERSIDADE FEDERAL DE SANTA CATARINA	CNPJ: 83.899.526/0001-82

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Analise dos dados	03/2019	06/2019
2	Amostragens auditivas	09/2018	03/2019

Equipe

#	Nome	Função	CPF	Nacionalidade
1	JOAO PEDRO KRAUSPENHAR BARROS	Auxiliar de campo	049.953.891-99	Brasileira

Observações e ressalvas

1	O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio, nos termos da legislação brasileira em vigor.
2	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
3	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
4	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
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