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O IMPACTO DA FRAGMENTAÇÃO E PERDA DE HABITAT NA DIVERSIDADE DE AVES EM AMBIENTES URBANOS

Santa Maria, RS

2020

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade Animal da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do título de **Mestre em Biodiversidade Animal**.

Orientador: Prof. Dr. Cristian de Sales Dambros
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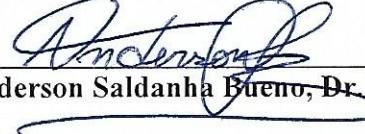
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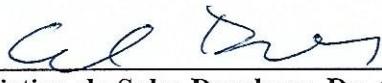
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RESUMO

O IMPACTO DA FRAGMENTAÇÃO E PERDA DE HABITAT NA DIVERSIDADE DE AVES EM AMBIENTES URBANOS

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A perda da biodiversidade em ambientes urbanos é causada principalmente por perda e fragmentação de habitat. Enquanto a perda de habitat pode levar a redução imediata na diversidade, a fragmentação pode isolar as comunidades biológicas, reduzindo a riqueza de espécies ao longo do tempo. Apesar da diversidade de espécies em cidades ser bastante estudada, não existem projeções sobre sua redução a longo prazo. Ademais, não há um estudo integrativo que investigue diferenças na diversidade de espécies e atributos ecológicos associados às funções ecossistêmicas ao longo do gradiente de urbanização. Portanto, eu analisei o impacto de curto e longo prazo da perda e fragmentação de habitat causadas pela urbanização nas taxas de imigração e extinção de espécies de aves, e a associação entre essas taxas com o tamanho da área e isolamento. Além disso, investiguei a influência de variáveis ambientais, como tamanho da área, isolamento, ruído sonoro e tipo de habitat (urbano, subúrbio, natural) na estruturação das comunidades de aves, considerando a diversidade funcional e filogenética. Dados acerca da presença de espécies e das variáveis ambientais foram obtidos em 43 fragmentos florestais urbanos da Ilha da Santa Catarina, município de Florianópolis, Santa Catarina, Brasil, durante a primavera de 2018, nos meses de setembro a novembro. Para mensurar os efeitos de curto e longo prazo da urbanização na riqueza de espécies foi implementado um modelo Bayesiano com base na Teoria de Biogeografia de Ilhas. Encontrei que o tamanho da área é o principal preditor para a riqueza de espécies de aves, em que fragmentos maiores apresentam maior riqueza por apresentarem menor taxa de extinção. O isolamento também apresentou um efeito na riqueza de espécies, em que fragmentos mais isolados apresentam menores taxas de imigração, resultando em menor número de espécies. A riqueza de espécies foi constante ao longo do tempo, evidenciando pequeno débito de extinção, ou seja, a perda de área tem um efeito de curto-prazo nas espécies de aves. Além disso, encontrei que a maior riqueza de espécies está concentrada em fragmentos naturais, enquanto que a riqueza funcional é maior em fragmentos localizados no subúrbio, sugerindo grupos ecologicamente distintos na transição entre áreas naturais e áreas intensamente urbanas. Por fim, foi evidenciado um padrão de substituição na composição taxonômica e filogenética ao longo do gradiente de urbanização, indicando que alguns grupos de espécies são muito sensíveis às atividades antrópicas, principalmente à poluição sonora. Portanto, a preservação de grandes áreas de vegetação e a diminuição da poluição sonora são fundamentais para a manutenção da diversidade de aves em áreas urbanas, e devem ser levados em consideração para a implementação de um planejamento urbano sustentável.

Palavras-chave: Urbanização; Teoria de Biogeografia de Ilhas; extinções em débito; riqueza de espécies, riqueza funcional, diversidade filogenética.

ABSTRACT

IMPACTS OF HABITAT LOSS AND FRAGMENTATION ON BIRD DIVERSITY IN URBAN AREAS

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Biodiversity loss in urban environments is mainly caused by habitat loss and fragmentation. While habitat loss can lead to immediate diversity reduction, fragmentation can isolate biological communities, decreasing species richness over time. Although species diversity in cities is well studied, there are no predictions on long-term species reduction. Besides, there are no integrative study addressing the impact of urbanization on species diversity and on ecological traits associated to species ecosystem function. Therefore, I quantified the short and long- term impact of habitat loss and fragmentation caused by urbanization on bird species extinction and immigration rates, based on fragments area and isolation. Besides, I investigated the roles of environmental variables (e.g. area, isolation, noise and habitat type – urban, suburban, natural) in structuring of bird communities, in terms of functional and phylogenetic diversity. Birds survey and environmental data collection were performed at 43 urban forest fragments in the Santa Catarina Island, municipality of Florianópolis, Santa Catarina, Brazil, during the spring season of 2018, from September to November. To measure the short and long-term effects of urbanization on species richness, accounting for species detectability and the effect of anthropic noise on species occupancy, I implemented a Bayesian model based on the Island Biogeography Theory. I found that area was the main predictor for bird species richness, in which larger fragments had lower extinction rates. Immigration rate also influenced species richness: less isolated fragments had higher immigration rates. Species richness was constant over time, evidencing small extinctions debts, i.e. habitat loss has short-term effect on bird species. I also found that species richness was higher in natural fragments, while higher functional richness occurred at suburban fragments, suggesting different functional groups in the transition between natural and highly urbanized areas. In addition, I found a replacement pattern of taxonomic and phylogenetic composition along the urbanization gradient, indicating that some species are sensitive to anthropic activities, mainly noise pollution. Therefore, these imply that increase of area and decrease of noise are important predictors for maintaining bird diversity in urban areas, useful for sustainable urban planning.

Key-words: urbanization; Island Biogeography Theory; extinction debt; species richness; functional richness; phylogenetic diversity.

SUMÁRIO

INTRODUÇÃO

A urbanização é responsável por grande parte da perda da biodiversidade, causando impactos significativos no ecossistema, sobretudo devido à extinção local de espécies (MCKINNEY, 2006; GRIMM et al., 2008). A extinção de espécies em áreas urbanas é provocada pela redução do tamanho de áreas naturais e pelo aumento do isolamento entre essas áreas (FATTORINI et al., 2018). Entretanto, o impacto destes fatores (redução da área e aumento do isolamento) sobre a diversidade pode não ser imediato, e as consequências em longo prazo podem ser subestimadas (HAHS et al., 2009). Dessa forma, projeções sobre a perda de diversidade a longo prazo em cidades são necessárias para melhorar o entendimento acerca da real situação das espécies em áreas urbanas.

A urbanização impulsiona a fragmentação da paisagem natural, e essa paisagem pode ser estudada através de uma analogia a ilhas oceânicas, denominada Teoria de Biogeografia de Ilhas (MACARTHUR & WILSON, 1967; FATTORINI et al., 2018). Essa teoria prediz que o tamanho da área e grau de isolamento entre áreas moldam a quantidade de espécies em um local (MACARTHUR & WILSON, 1967), com áreas maiores possuindo mais espécies em comparação a áreas menores, e áreas mais próximas de uma área fonte (e.g. continente) apresentando mais espécies que as áreas mais distantes (e.g. mais isoladas). Dessa forma, a riqueza de espécies em um determinado local é modulada pelo equilíbrio dinâmico entre as taxas de imigração (colonização) e extinção (perda) de espécies. No entanto, em ambientes urbanos, as taxas de imigração e extinção podem não estar em equilíbrio devido ao atraso temporal entre a perda de habitat e a perda de espécies (HAHS et al., 2009). Com isso, algumas espécies podem não responder imediatamente a fragmentação e perda de habitat, gerando débito de extinção (DIAMOND, 1972), ou seja, extinções previstas para o futuro devido a eventos de perda de habitat no passado.

Além da riqueza de espécies, outros aspectos da diversidade devem ser levados em consideração em estudos ecológicos, como as diversidades funcional e filogenética das comunidades biológicas (TILMAN et al., 2006; CADOTTE et al., 2012). Em áreas urbanas, o tamanho da área, grau de isolamento e poluição sonora podem agir como um filtro ambiental, excluindo algumas espécies, grupos funcionais (grupos ecológicos, como espécies insetívoras) e/ou evolutivos (espécies mais aparentadas entre si) (ARONSON et al., 2016). Geralmente, áreas

pequenas possuem menor quantidade de recurso, restringindo o número de espécies e de grupos funcionais nesses locais (BENINDE et al., 2015). Áreas mais isoladas podem apresentar apenas grupos com alta capacidade de dispersão, limitando a diversidade filogenética (LEIBOLD et al., 2010). Por fim, a poluição sonora pode excluir espécies e grupos funcionais muito sensíveis à ruídos antrópicos, como tráfego e construção (BARBER et al., 2010). Desta forma, é importante considerar os aspectos funcionais e evolutivos de cada espécie para investigar quais processos ecológicos moldam os padrões de diversidade de espécies em áreas urbanas, a fim de minimizar os efeitos antrópicos e maximizar a conservação da biodiversidade nessas áreas.

Estudos sobre ecologia urbana utilizam as aves como objeto de estudo, por serem organismos comuns, fáceis de observar e sensíveis a alterações ambientais (NIELSEN et al., 2014). As aves formam um grupo muito diverso, apresentando diferentes estratégias alimentares, grupos evolutivos e ocupando uma vasta gama de nichos ecológicos, inclusive em ambientes urbanos. Algumas espécies de aves são bem adaptadas em ambientes urbanos por apresentarem dieta generalista e por serem menos sensíveis às perturbações antrópicas, enquanto que outras espécies são restritas a ambientes florestais (SOL et al., 2014) (Figura 1).

A maioria dos estudos que abordam os impactos dos centros urbanos sobre as comunidades as aves são realizadas na Europa, Ásia e América do Norte (NIELSEN et al., 2014). Nesse contexto, é importante que sejam realizadas pesquisas avaliando o impacto da urbanização sobre esse grupo tão diverso nas regiões tropicais do globo. Para preencher essa lacuna geográfica, essa dissertação foi realizado na parte insular do município de Florianópolis, capital do estado de Santa Catarina, região sul do Brasil. O município faz parte da porção litorânea sul do bioma Mata Atlântica, cuja vegetação predominante é floresta ombrófila mista, juntamente com vegetação litorânea (KLEIN, 1969). Devido a isso, Florianópolis apresenta grande heterogeneidade de paisagens, possuindo desde florestas densas até manguezais, restingas e enseadas (KLEIN, 1969). Essa vasta heterogeneidade ambiental proporciona grande riqueza de espécies de aves – foram contabilizadas 310 espécies da avifauna para Florianópolis (GHIZONI-Jr et al., 2013). Apesar da grande riqueza natural, o município vem sofrendo intensa urbanização a partir da década de 1970. Como consequência, a fragmentação da paisagem natural de Florianópolis apresenta remanescentes florestais de diferentes tamanhos e tempos de isolamento ao longo de um gradiente de urbanização – de áreas mais intensamente urbanizadas até áreas preservadas por lei. Assim, é possível avaliar a influência que o tamanho, o grau de isolamento e

o tempo de isolamento dos fragmentos exercem sobre as comunidades de aves. Aliado a isso, a presença de grandes áreas de vegetação nativa também permite estimar como as comunidades alteradas diferem das comunidades naturais, a fim de prever os impactos da expansão dos centros urbanos a longo prazo.

O objetivo desta dissertação foi quantificar o impacto de curto e longo prazo da fragmentação e perda de habitat causadas pela urbanização nas taxas de imigração e extinção de espécies de aves, baseado no modelo teórico da Teoria de Biogeografia de Ilhas. Além disso, este estudo também visou elucidar como a diversidade de aves está distribuída ao longo do gradiente de urbanização, em termos de diversidade taxonômica, funcional e filogenética.
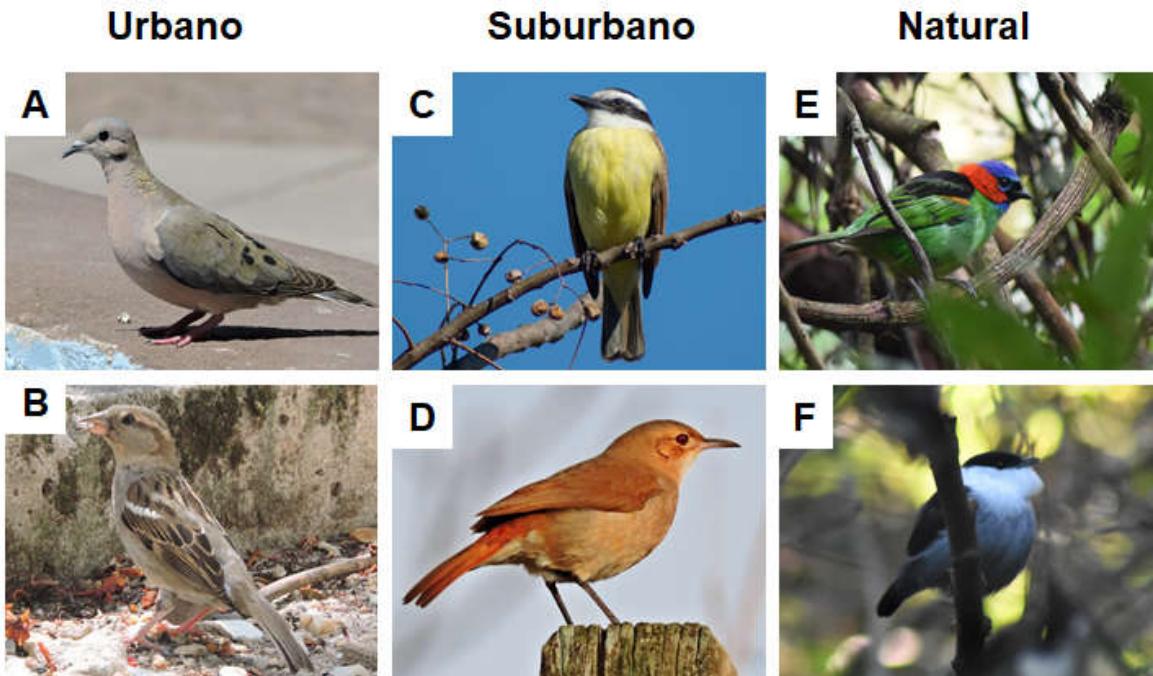
Figura 1 – Espécies de aves encontradas em diferentes ambientes ao longo do gradiente urbano-natural na Ilha de Santa Catarina, município de Florianópolis, Santa Catarina. **(A)** Pombo-doméstico (*Columba livia*); **(B)** Pardal (*Passer domesticus*); **(C)** Bem-te-vi (*Pitangus sulphuratus*); **(D)** João-de-barro (*Furnarius rufus*); **(E)** Saíra-militar (*Tangara cyanocephala*); **(F)** Rendeira (*Manacus manacus*).

Estrutura da Dissertação

Esta dissertação está estruturada de acordo com as normas de "Artigos científicos integrados" do "Manual de Dissertações e Teses da UFSM", contendo dois capítulos redigidos no formato de artigos científicos.

Capítulo I: **Estimating the short and long-term impacts of habitat loss induced by urbanization on bird local extinctions.**

Estimando os impactos de curto e longo prazo da perda de habitat induzida pela urbanização na extinção local de aves. Este capítulo está estruturado em formato *Letters*, conforme as normas da revista *Ecology Letters*.

Nesse capítulo, eu apresento a dinâmica entre as taxas de imigração e extinção de espécies de aves, com o objetivo de investigar se existe débito de extinção em áreas urbanas. A partir do histórico do tamanho dos fragmentos florestais urbanos e do isolamento entre esses fragmentos, implementei um modelo teórico baseado na Teoria de Biogeografia de Ilhas. Com esse modelo, foi possível prever a riqueza de espécies do passado e do futuro e, com isso, estimar um possível débito de extinção.

Capítulo II: **Suburban forest patches can preserve functional diversity and evolutionary history of birds.**

Fragmentos florestais de subúrbio podem preservar diversidade funcional e história evolutiva de aves. Este capítulo está estruturado em formato *Research Article*, conforme as normas da revista *Urban Ecosystems*.

Nesse capítulo, eu analiso a diversidade taxonômica, funcional e filogenética de espécies de aves em um gradiente de urbanização, com o objetivo de verificar em qual região desse gradiente encontra-se a maior diversidade. Além disso, eu apresento quais as influências de variáveis ambientais, como tamanho da área, isolamento e ruído sonoro nesses índices de diversidade.

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CAPÍTULO I

ESTIMATING THE SHORT AND LONG-TERM IMPACTS OF HABITAT LOSS INDUCED BY URBANIZATION ON BIRD LOCAL EXTINCTIONS

ESTIMANDO OS IMPACTOS DE CURTO E LONGO PRAZO DE PERDA DE HABITAT INDUZIDOS PELA URBANIZAÇÃO NA EXTINÇÃO LOCAL DE AVES

Cuspidor-de-máscara-preta

Conopophaga melanops (Vieillot, 1818)

Estimating the short and long-term impacts of habitat loss induced by urbanization on bird local extinctions

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Abstract

The impact caused by urbanization on biodiversity might be immediate or delayed, resulting in extinction debts. However, these long-terms impacts are rarely investigated due to the lack of temporal biodiversity data. To overcome this limitation and investigate the short and long-term impacts of habitat loss and fragmentation on biodiversity, we developed a Bayesian Island Biogeography model combining historical imagery and current species distribution. We estimated the association between extinction rates and fragment area and between immigration rates and isolation across time. We used model parameters to forecast bird extinction debts in urban forest fragments. As expected, large fragments have lower extinctions rate than small fragments, and immigration rate slightly decreases in more isolated fragments. Our results suggest that species richness is better explained by current landscape configuration than by past configuration, indicating that species rapidly respond to changes in urban landscape and a lack of extinction debts in urban areas.

Key-words: Extinction debts; Fragmentation; Island Biogeography Theory; Mechanistic model; Species richness

Introduction

Urbanization has intensified in recent decades leading to species local extinctions (Hahs *et al*.

2009). Extinctions in urban environments result mostly from the reduction in size (Beninde *et al*.

2015) and in isolation of forest fragments (Fattorini *et al*. 2018). However, the impact of these

factors on species diversity might not be immediate (Tilman *et al*. 1994), and the long-term

consequences of urbanization are poorly known. Theoretical studies suggest that after the initial

diversity lost, the dynamic equilibrium can again be reached after long periods of time posterior

to fragmentation, when the new balance between extinction and immigration rates is reached

(Halley & Iwasa 2011; Hugueny 2017).

Projections for the long-term dynamic equilibrium in species richness and be made using

the Island Biogeography Theory (IBT; MacArthur & Wilson 1967). The IBT emphasizes that the

variation on area and isolation affect species richness through the dynamic balance between

extinction and immigration rates. Extinction rates is related to area, as in larger areas species are

less likely to go extinction, whereas immigration rate is associated with isolation, in which less

isolated areas have higher immigration rates due to easy dispersal (MacArthur & Wilson 1967).

Nonetheless, a temporal, gradual delay might exist between the original and new balance,

because in long-term the community would enter into a low equilibrium level, represented by the

new extinction-immigration balance (Diamond 1972). This temporal gap between the two

equilibrium points is known as extinction debt, in which some species are committed to extinct

due to habitat loss (Tilman 1994). The time required to reach this new dynamic equilibrium is

dependent on area and the age of fragments (Halley & Iwasa 2011; Hugueny 2017), and how

species respond to these factors (Jacquet *et al*. 2017). Therefore, delay in species extinction can

be intense in urban environments, as this landscape is constantly being modified (Hahs *et al*.

2009).

Studies about extinction debts usually consider either the effect of current or past area and isolation (Halley & Iwasa 2011; Bommarco *et al*. 2014). However, integrate into a single mechanistic model the effects of area, isolation, and age of the fragments can be attractive to investigate the simultaneous effect of area and isolation on species richness through time (Hugueny 2017). Furthermore, few studies use mechanistic approaches to directly estimate changes in extinction and immigration rates and their effects on species occupancy, despite the urgent need for more mechanistic and dynamic frameworks in fragmentation studies (Figueiredo *et al*. 2019). This is likely due to the lack of temporal community data required in classical statistical models.

To overcome this limitation and to estimate changes in extinction and immigration rates through time, we developed a Bayesian Island Biogeography Model that integrates historical landscape data obtained from aerial imagery and current species distribution data (i.e. species occurrence). We then used this model to quantify the short and long-term impacts of habitat loss and isolation caused by urbanization on the local extinction and immigration of bird species. As predicted by the Island Biogeography Theory, we expect higher extinction rates in small fragments and lower immigration rates in more isolated fragments. In addition, we also expect that small and old fragments are in equilibrium, whereas large and recent fragments have not reached equilibrium in species richness, evidencing extinction debts in urban environments.

Material and methods

Study area and sampling design

The study was carried out in Florianópolis (27º35'S, 48º32'W; Figure 1), southern Brazil. Florianópolis is a continental island, located in the Atlantic Ocean, separated by approximately

500 m from the continent. The city has undergone intense urbanization at the end of the 20th century (IBGE, 2017), creating many forest fragments.

The spatial landscape configuration of Florianópolis was obtained from aerial imagery available in Google Earth, from 1984 to 2018 (one image per year, 35 images). From these images, we selected urban forest fragments with different combinations of area, isolation and age. This process resulted in a total of 43 fragments considered as sampling units. To quantify these geographical measures, we draw polygons for each fragment for each year (43 fragments in 35 years, 1505 shapefiles) using the Quantum GIS software (QGIS Development Team 2019; version 2.18.20). We then calculated fragments area (ha), isolation and age since the fragment was created/isolated. Isolation was measured based on network degree of centrality (Estrada & Bodin 2008), in which the higher values represent the more isolated fragments. Age represents the time since the most abrupt change in area over the 35 years of sampling. Hereafter the terms "past" and "current" corresponds to area and isolation before and after (respectively) to the most abrupt change in area.

Fragments current area ranged from 0.066 ha to 836.502 ha (mean = 73.342 ± 182.166). Some forest fragments were non-existent in 1984, and for these fragments we considered that past area was equal to zero. In contrast, some forest fragments have not changed in area since 1984, and thus past and current area remained the same. Therefore, the smallest area in the past was zero and the largest area remained with the same size currently observed (mean = 88.509 ± 208.693). The isolation measured for each of the 35 years has not changed over time, and ranged from 0.125 to 0.228 (mean = 0.157 ± 0.030), indicating that more isolated fragments in the past are still the more isolated today (see Table S1 in Supporting Information).

Bird survey

In the 43 fragments (sampling units), we surveyed bird species using 10 minutes point counts (Bibby *et al*. 2014) in the spring season from September to November of 2018. In order to have accurate estimates of species occupancy in larger fragments where sampling is more difficult, the number of surveyed points (n = 62) in each fragment ranged from one to four. The replicate points were used to estimate occupancy at the fragment level, and the differences in sampling effort were corrected in the Bayesian model (see below). In all fragments, points were separated by at least 300 m from each other. Each point count was surveyed twice, thus some fragments have both spatial and temporal replicates that were used to improve species detection and occupancy models. Surveys were conducted between 5:30 and 9:30 am, only in favorable climatic conditions (i.e. avoiding windy and rainy days). To ensure that the survey time would not influence species detection, all fragments were surveyed at dawn in at least one survey. All birds seen or heard within a 50 m radius from the observer were counted and recorded using a sound recorder and a photographic camera for posterior identification. We only counted bird individuals that were using the fragment (i.e. not flying above the survey point), thus the number of species included in the analyzes was 101 (Table S2). Surveys lasted 38 days, totaling 20.7 hours of field observation.

We also collected noise data, measured as the number of decibels in the environment, with Akso AK820 digital decibelmeter during the bird survey. Because noise could reduce species detection rates and the occurrence of sensitive species, we included this variable as co-variate of both detection and occupancy in our models (Herrera-Montes & Aide 2011). The average noise level obtained from all points and replicates of each fragment was used as a predictor. We registered noise from one minute randomly chosen during the 10 minutes of sampling for the analyses (Table S1).

Statistical models

Regression model

To verify the association of species richness with current and past fragment area and isolation, we performed a Bayesian linear regression for each individual predictor variable. We log-transformed area and isolation to linearize the relationship between species richness and these predictor variables. To determine the existence or not of these associations and to make coefficients comparable, all predictor and response variables were standardized prior to the analyses. A threshold of 0.1 was used to determine the existence of a practical effect of area and isolation on species richness. An association was assumed to be of practical importance if the regression coefficients were lower than -0.1 or higher than 0.1 with 95% of posterior probability (Highest Density Interval of 95% excluding the interval between -0.1 and 0.1).

Occupancy model

To investigate extinction debts and the mechanisms associated with the possible extinction delays in urban forest fragments, we developed a multi-species mixed-effects model within a hierarchical Bayesian approach based on the Island Biogeography Theory. The model is divided into two parts that account for 1) observation errors and 2) the dynamic ecological processes (Fig. 2). Therefore, the model defines the absence of a species as a result of non-detection (imperfect detection) or from the species unsuitability to occur due to its response to noise, and to the balance between extinction and immigration (ecological processes).

Species detection probability is imperfect and it varies according to the characteristics of the survey point (e.g. amount of noise decibels in the area; Herrera-Montes & Aide 2011). A low detectability can affect species richness estimates (Chao *et al*. 2009) and bias the results. Therefore, the model estimates detectability θ_{sfp} of each individual species *s* at each survey point

p and fragment f (regional pool; Mackenzie *et al*. 2003), considering the noise as a detection co-variate in a logit scale (Eq. 1):

$$\theta_{sfp} = \frac{e^{(b_{0s}+b_{1s} \times Noise_{fp})}}{1+e^{(b_{0s}+b_{1s} \times Noise_{fp})}} \qquad \text{Eq. 1}$$

When the true species presence and absence are estimated, species occupancy may still depends on noise (Herrera-Montes & Aide 2011) and on species extinction and immigration rates (MacArthur & Wilson 1967). Because noise data for the past was not available (differently from area and isolation), we could not integrate the effect of past noise into the Island Biogeography Model to estimate its effect on past extinction and immigration rates. Thus, the noise was only included as a co-variate of species occupancy, without any association with mechanistic process (Fig. 2).

To predict extinction debts in a scenario where extinction and immigration are the main processes determining species occupancy, it is necessary to use a dynamic (non-equilibrium) model of the Island Biogeography Theory. Therefore, we added a historical perspective to the model (fragments age) to predict species occupancy through time (Hugueny 2017). The effect of time on species occupancy was determined by comparing the past and current time periods, which represent the time since the most abrupt change in area, and estimating the relative contribution of past and current extinction and immigration rates on current species occupancy. Finally, based on current extinction and immigration rates, the model was used to forecast species occupancy in the future (adding 100 years), based on the maintenance of current landscape configuration. Estimation uncertainty was calculated in the Bayesian framework, and we present the range of probable diversity in each fragment based on the posterior probabilities obtained from the model projection.

The estimation of current and past extinction and immigration rates is theoretically

possible because if these rates change over time and species responses are largely delayed, then species current occupancy will be more strongly associated with past landscape configuration. In contrast, fragments with distinct past configuration but similar current configuration, will have similar occupancy and diversity if species responses are immediate. The estimation of these parameters is only possible because fragments in our study site differ in area, isolation, and time since the area reduction, and the sampling design was defined to avoid correlation between these factors (e.g. older fragments do not tend to be larger fragments).

In the classical theory, extinction and immigration rates were only dependent on area and isolation (MacArthur & Wilson 1967). However, it is known that species differ in their dispersal capacity and extinction rates (Jacquet *et al*. 2017). Therefore, in addition to allowing extinction and immigration rates to vary through time, the model also allows these rates to vary across species. We have not included species traits as predictors of extinction and immigration (as in the Trophic Theory of Island Biogeography; Jacquet *et al*. 2017) to avoid overparameterizing the model. However, we included interspecific variability as random effects.

Equation 2 was modified from Simberloff (1969) and represents the occupancy of each individual species (*s*) at individual fragments (*f*; ψ_{sf}) as a function of the dynamic balance between current and past extinction and immigration rates (E, I, E_0, I_0), accounting for fragment age (*ngen)*. The relaxation time depends on the magnitude of extinction and immigration rates. If these rates are low, then there will be a long period between two equilibrium points. However, if these rates are high, then the process must be almost immediate, as would be expected by the immediate species loss due to local environmental changes and to the immigration of a high dispersal group. In this way, we evaluated the temporal changes as a result of the magnitude of the rates, as shown in equation 2.

$$\psi_{sf} = \frac{I_{0sf}}{I_{0sf}+E_{0sf}} + \left(\frac{I_{sf}}{I_{sf}+E_{sf}} - \frac{I_{0sf}}{I_{0sf}+E_{0sf}}\right) \times \left[1 - e^{\left(-I_{sf}+E_{sf}\right)^{ngen_f}}\right] \qquad \text{Eq. 2}$$

Both extinction and immigration rates were modeled as exponential responses to area and isolation, respectively. Current and past fragment area are associated with the coefficient c_0 and c_1 (Eq. 3 and 4), and current and past isolation are associated with the coefficients d_0 and d_1 (Eq. 5 and 6). Because the equilibrium in species richness in the Island Biogeography Model depends on the relative contribution of extinction and immigration (and not the absolute values), these rates were standardized to range from 0 to 1.

$$E_{fs} = c_{0s} \times e^{-c_1 \times X_{1f}} \qquad \text{Eq. 3}$$

$$E_{0fs} = c_{0s} \times e^{-c_1 \times X_{1sf}} \qquad \text{Eq. 4}$$

$$I_{fs} = d_{0s} \times e^{-d_1 \times X_{2f}} \qquad \text{Eq. 5}$$

$$I_{0fs} = d_{0s} \times e^{-d_1 \times X_{2sf}} \qquad \text{Eq. 6}$$

The multi-species model allows estimating the occupancy probability of individual species in each fragment. Therefore, we can estimate current species richness (after corrected imperfect detection) and predict species richness for the past and for the future. Species richness in each fragment was calculated as the sum of the occupancy of all species in each fragment.

We used Monte Carlo Markov Chains (MCMC) to estimate the posterior probability distribution for each model parameter (Fig. 2). We ran 3 chains using 200 000 MCMC iterations, with a burn-in phase of 20 000. MCMC samples were thinned at a rate of 500 to reduce the use of computational disk space and non-informative priors were used for all model parameters. Initial values for parameters associated with extinction (c_0, c_1) and immigration (d_0, d_1) (Fig. 2), were obtained by Maximum Likelihood (ML) using the Broyden, Fletcher, Goldfarb and Shanno (BFGS) method. In the ML model, we estimated parameter values that best explained the species

occupancy data, following the response of extinction rates to fragment areas and immigration rates to isolation, as in the main model. The initial values for species occupancy were based on the naïve (observed) species counts. All model parameters converged to the same distribution in each of the MCMC chains. More details about the model, parameters, and equations are available in Supporting Information (see Appendix S1-S4) and on GitHub (https://github.com/gfdri).

All analyses were performed in R version 3.5.2 (R Development Core Team 2019) and JAGS version 4.3.0 (2017), using the R-JAGs interface. We used the coda (Plummer *et al*. 2006), runjags (Denwood 2016), rjags (Plummer 2018), rgdal (Bivand *et al*. 2019), sp (Pebesma & Bivand 2005), vegan (Oksanen *et al*. 2019), rgeos (Bivand & Rundel 2018) and igrah (Csardi & Nepusz 2006) packages to run the analyses.

Results

We recorded 1009 individual counts from 101 bird species. The number of observed species per fragment varied from eight to 42 (mean = 22 ± 8; Table S3). Observed species richness was positively associated with current area, but not to past area (Fig. 3 A-B). In addition, the observed species richness was not associated with both current and past isolation (Fig. 3 C-D).

Birds were imperfectly detected ($\theta = 0.17 \pm 0.02$; Figure S1A), and observed species richness was lower than estimated in all fragments (Figure S2). The number of species estimated per fragment ranged from 34 to 57 (mean = 46 ± 6; Table S3). Species detectability was not associated with noise ($mb_1 = 0.05 \pm 0.06$; Figure S3).

Species occupancy was mostly explained by the relative contribution of extinction and immigration rates, as defined by the Island Biogeography part of the model and not by noise ($a = 0.9$; Figure S1B). For most species, extinction rates declined in larger fragments (Fig. 4A) and immigration rates slightly decreased in more isolated fragments (Fig. 4B; Figure S1C-D).

Fragment area was the best predictor of species richness, with higher species richness recorded in larger fragments than smaller fragments regardless of isolation (Fig. 4C). Based on model projections (i.e. different values for *ngen* in equation 2), predicted species richness were similar for the past, current, and future time periods, except for those fragments that were recently created, in which current species richness was higher than past species richness (Fig. 5).

In spite of the low effect of noise on species occupancy and species richness (a = 0.1), species occupancy decreased with noise (h_1 = -108.09 ± 63.46). The complete model including noise, and current and past extinction and immigration rates explained 60% of the variation in species richness among fragments.

Discussion

We assessed how landscape configuration (i.e. area and isolation) in an urban environment was associated to species short- and long-term extinction and immigration rates to shape bird diversity. Variation in bird species richness among fragments was mostly associated with differences in the balance between area-driven extinction and isolation-driven immigration rates, although are had much higher influence than isolation (Fig. 4). Surprisingly, species richness was strongly determined by current landscape configuration and even recent fragments with zero species in the past were close to the expected equilibrium based on their size and isolation (Fig. 3). These results indicate the absence of bird extinction debts in urban environments, as habitat loss reduces species diversity to a new equilibrium in very short periods of time (less than 10 years).

Fragment area and the habitat amount in the landscape have been suggested to determine species richness in fragmented landscapes (Fahrig 2003; Beninde *et al*. 2015; Fattorini *et al*. 2018; Bueno & Peres 2019). Larger fragments usually have higher environmental heterogeneity,

which might allow the co-existence of species with differences in resource use (a niche process; Tilman *et al*. 1994; Tilman 2004). The reduction in fragment area could remove micro-habitats, rapidly increasing the extinction rates, as observed here. Additionally, the low number of individuals in smaller fragments could increase extinction rates because stochastic fluctuations in population size locally eliminate species in a relatively short time (a neutral process; Halley & Iwasa 2011). In line with these expectations of IBT, and niche and neutral processes, our results indicate that extinction rates are higher in smaller fragments, and consequently these fragments have lower species richness (Halley & Iwasa 2011; Beninde *et al*. 2015; Lasky *et al*. 2017). The number of species at the dynamic equilibrium between extinction and immigration was 57 species for a fragment of 836.502 ha, whereas 34 species are estimated to occur in a fragment of 0.066 ha (Fig. 4). Therefore, differences in bird diversity can be explained almost entirely by differences in extinction rates between areas.

In spite of the clear effect of area on extinction rates, previous theoretical metapopulation (e.g. Levins 1969; Hanski & Ovaskainen 2003) and metacommunity models (Leibold *et al*. 2004) have also demonstrated that fragment isolation affect the long-term equilibrium in species persistence by altering immigration rates. However, several empirical studies fail to find an association between species richness and isolation (Cirtwill & Stouffer 2016; Henneron et al. 2019). In our model, which combines both the mechanisms of theoretical models and empirical data on bird species distribution, we found evidence for a negative relationship between immigration rate and fragment isolation. However, the effect of isolation was much lower than the area effect, which might explain why some previous correlative studies have not detected the effect of isolation on species immigration rates.

In addition to the much stronger effect of area then isolation, a potential cause for the disagreement between theoretical and empirical studies might be the fact that in most empirical

studies, fragment size, isolation, and total amount of habitat are correlated to each other (Hanski 2015). Thus, it is important a sampling design that allows tease apart their effects. Moreover, statistical models used in empirical studies are rarely mechanistic (but see Lasky *et al*. 2017), with few direct quantification of how area and isolation directly affect species extinction and immigration rates. Finally, previous empirical studies do not take into account potential delays between fragmentation and biodiversity loss (Fattorini *et al*. 2018). In spite of all these potential problems in empirical studies, we demonstrated that habitat amount is more determinant than isolation using uncorrelated data, in a mechanistic model, and considering short and long-term dynamics.

By integrating the history of urban fragmentation into mechanistic models, we demonstrated that bird communities in urban landscape are likely to be at equilibrium or near equilibrium (i.e. few years predicted to reach the equilibrium), with no extinction debts. Fragment age (time since most abrupt change in area) does not influence species richness because fragments with different ages converged to the dynamic equilibrium (or near it) based on its current area (Fig. 4). In other words, larger fragments had higher species richness than smaller ones regardless of the age (Fig. 5). Although there are historical and socio-economical differences among cities, the majority of the urban areas are affected by similar ecological processes (Grimm *et al*. 2008). Hence, our results on extinction and immigration of bird species are likely to hold to other cities around the world. At the scale of a city or local disturbed areas, species can disperse from one fragment to another and extinctions are likely to occur rapidly after habitat change (Krauss *et al*. 2010). It is important to note that at broader geographic scales, extinction rates within regions and immigration rates between distant regions might be much lower than observed here. The relative importance of habitat loss and isolation might be different than reported here and their processes could still create long extinction delays (Hahs *et al*. 2009;

Cousins & Vanhoenacker 2011; Bommarco *et al*. 2014). Therefore, future research should integrate mechanistic models at broader spatial scales to understand the long-term impact of urbanization globally.

Acknowledgements

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Figures caption

Fig. 1 – Study area (Florianópolis, Southern Brazil) showing the differences in area and isolation of surveyed fragments in 1984 and 2018. In the area some fragments remained with similar size, whereas others appeared or decrease in size, especially at the north and center of the island. Fragments isolation (measured as the degree of centrality in a network) remained very similar over time.

Fig. 2 – Conceptual framework of the Island Biogeography Model describing the associations among data, observer and ecological processes, and parameters. This model accounts for species imperfect detection, influence of noise and influence of the balance between extinction and immigration rates on species occupancy. We used both current and past area and isolation to estimate changes on extinction and immigration rates through time. The parameters obtained for each individual species were combined to generate community level estimates of diversity. Species were jointly analyzed and their parameters combined in higher-level parameters (hyperparameters) which are not shown for simplicity.

Fig. 3 – Association between observed species richness with area and isolation at both current and past landscape configuration. Species richness is only associated with current area composition (a). The bold black line indicates the strength of the association from the most probable line representing each association, and gray lines indicate other 3000 possible associations. Posterior probability distribution of the slope parameters is represented at the small graphs in the right.

Fig. 4 – Influence of area and isolation on bird species extinction and immigration rates. (a) Area has a negative effect on extinction rates and (b) isolation has a slightly negative influence on

immigration rates. (c) Island Biogeography Theory dynamic equilibrium of species richness, varying from 34 to 57 species, depends mostly on fragments size. Less isolated fragments (degree of centrality from 0.12 to 0.15; light red) have higher immigration rates compared to more isolated fragments (degree of centrality from 0.16 to 0.22; dark red); however it has only a slightly influence on species richness and the main predictor for species richness in each fragment is area. Larger fragments (from 1.9 to 836 ha; darker blue) have lower extinction rates and reach the equilibrium between extinction and immigration rates with more species than smaller fragments (from 0.066 to 1.8 ha; light blue).

Fig. 5 – Association among species richness predictions through time. Strong association between (a) current and past, and (b) current and future species richness is an evidence of the lack of extinction debts in urban environments. The term "past" represents the spatial composition of area and isolation before the most abrupt change in area, while "current" corresponds to the composition after the most abrupt change in area, and "future" represents the predictions for spatial composition of 100 years from now. Gray arrows represent the standard deviation.
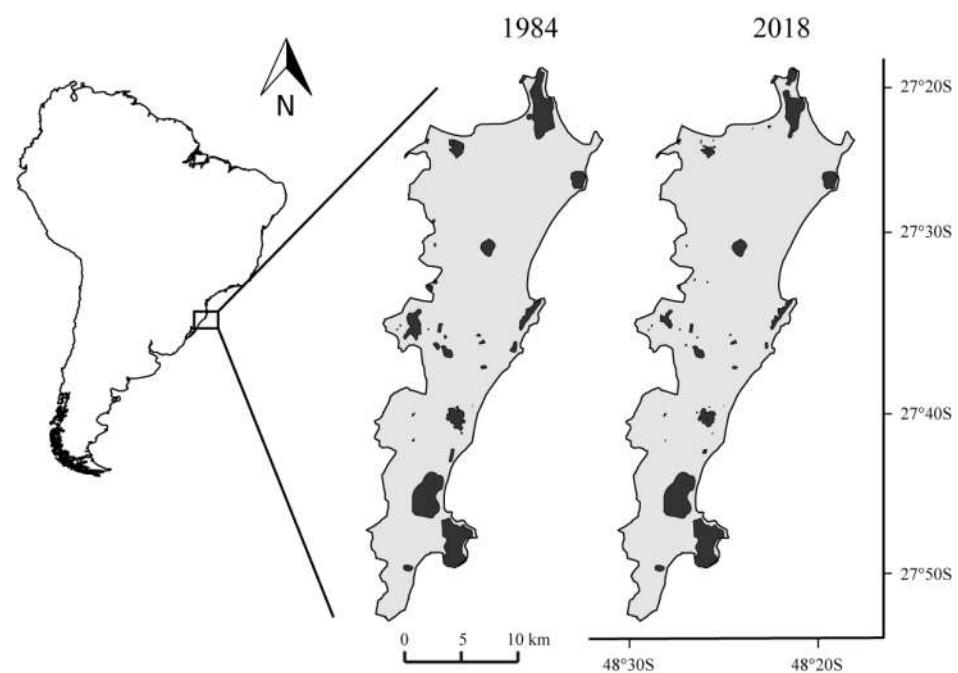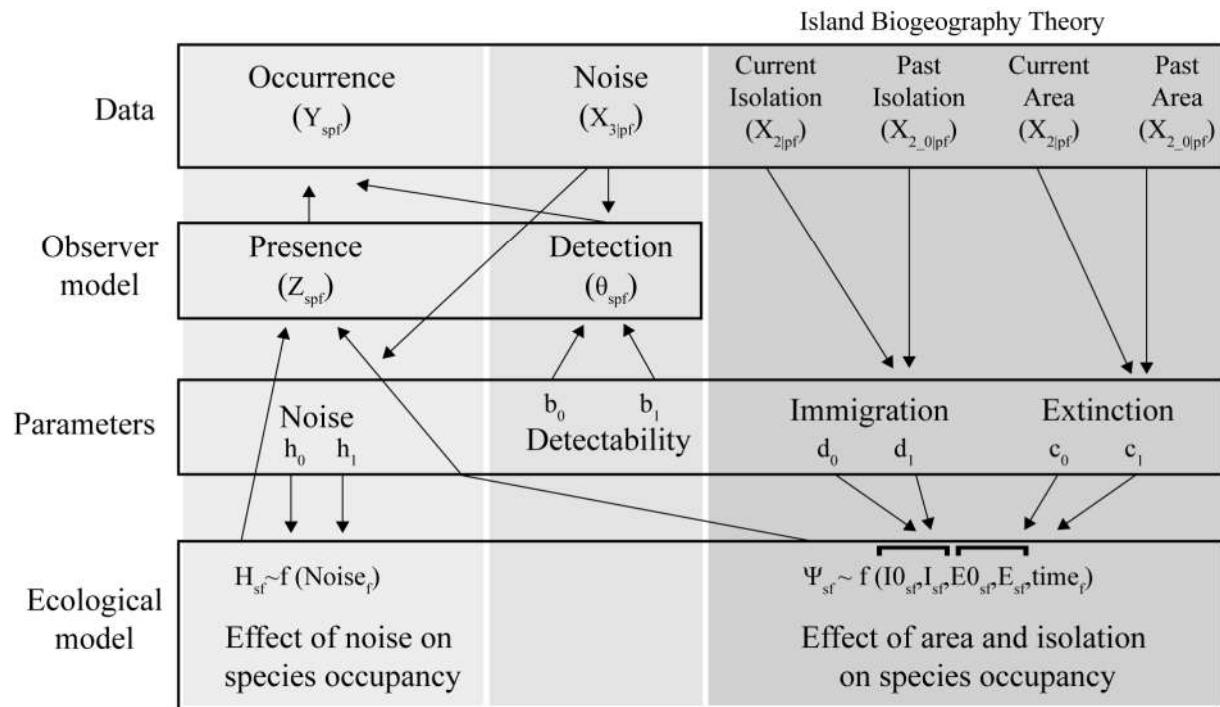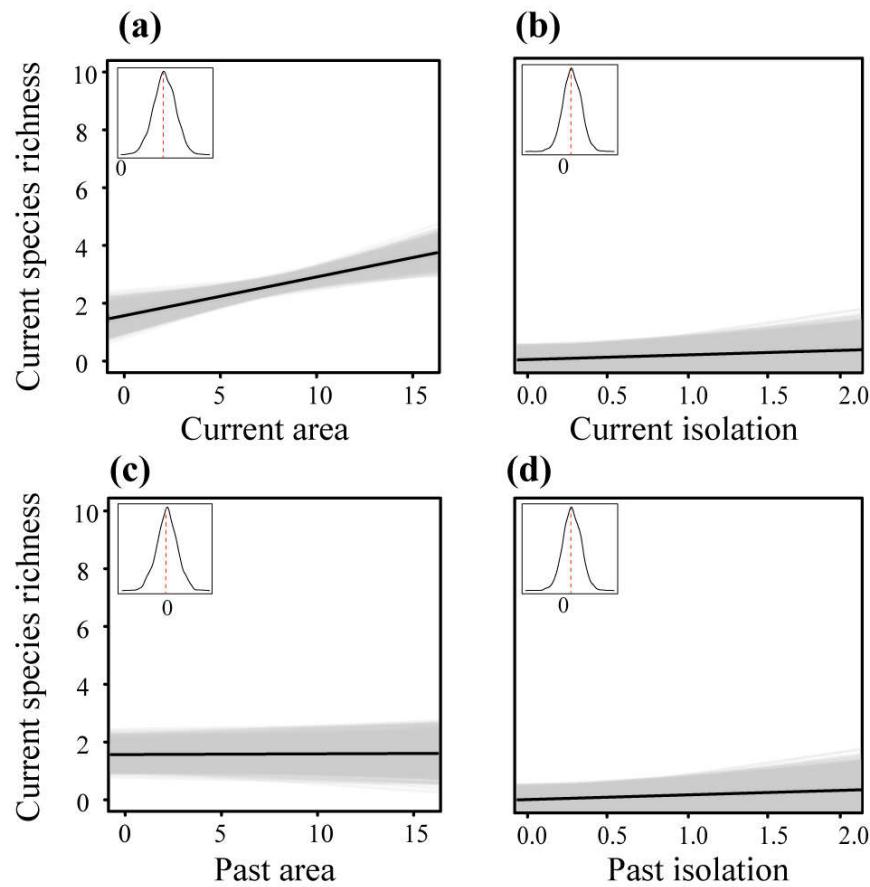
Fig. 1

Fig. 2
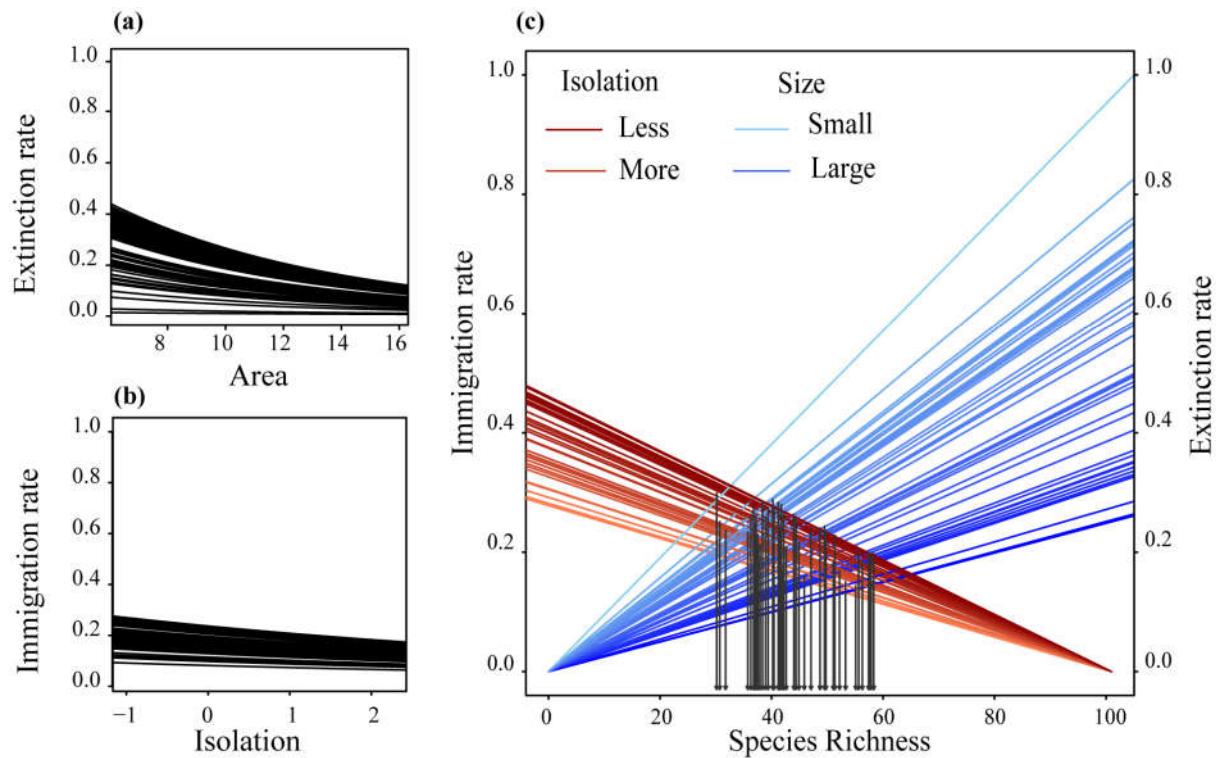
Fig. 3

Fig. 4

Fig. 5
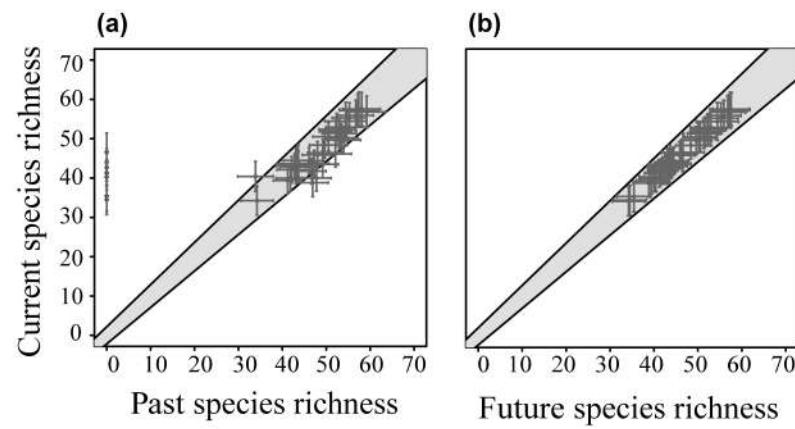
SUPPORTING INFORMATION

Appendix S1 Island Biogeography Model: effect of noise and extinction and immigration rates

on species occupancy

Species occupancy can be a result from both habitat characteristics such as noise or from the

balance between extinction and immigration rates. Equation 5 represents the effect of noise (H)

and the dynamic equilibrium between extinction and immigration rates (ψ) on species s

occupancy Z at each fragment f. These two processes are associated with the parameter "a" that

determines which predictor better explains species occupancy at a fragment. The parameter "a"

range from 0 to 1, and if "a" is lower than 0.5 then noise is the main predictor for species

occupancy. Conversely, "a" higher than 0.5 indicates that Island Biogeography Model play the

key role on species occupancy, and thus we need to consider the balance between extinction and

immigration rates on species occupancy probability.

$$Z_{fs} Bernoulli \left(a \times \psi_{fs} + (1-a) \times H_{fs} \right) \quad \text{Eq. 7}$$

Appendix S2 Dynamic model of Island Biogeography Theory accounting for species imperfect

detection, species interspecific variability, past and current fragments area and isolation and

fragments age.

```
# creating the Bayesian model
OccIBTDetModel <- "
model{
for(s in 1:nsp){ # species
for(f in 1:nfrag){ # fragments
for(p in 1:nrep){ # replicates within fragments
y[f,p,s]~dbern(theta[f,p,s]*Z[f,s]) # species occurrence
logit(theta[f,p,s])<-b0[s]+b1[s]*X3[f,p] # species detectability
}


Z[f,s]~dbern(a*psi[f,s]+(1-a)*H[f,s]) # occurrence depends on noise and IBT
logit(H[f,s])<-(h0+h1*X3[f,2]) # noise
psi[f,s]<-(i0[f,s]/(i0[f,s]+e0[f,s]))+(i[f,s]/(i[f,s]+e[f,s])-(i0[f,s]/(i0[f,s]+e0[f,s])))*(1-exp(-(i[f,s]
+e[f,s])*(ngen[f]))) # IBT


# parameters
# current immigration and extinction rates based on isolation and area (respectively)
e[f,s]<-c0[s]*exp(-c1*X1[f]) # current extinction rate for each species
i[f,s]<-d0[s]*exp(-d1*X2[f]) # current immigration rate for each species


# past immigration and extinction rates
e0[f,s]<-c0[s]*exp(-c1*X1_0[f]) # past extinction rate for each species
i0[f,s]<-d0[s]*exp(-d1*X2_0[f]) # past immigration rate for each species
}


# hyperparameters
b0[s]~dnorm(mb0,1/sdb0^2) # mean intercept for all species
b1[s]~dnorm(mb1,1/sdb1^2) # mean slope for all species


c0[s]~dnorm(mc0,1/sdc0^2) # mean extinction rate for all species
d0[s]~dnorm(md0,1/sdd0^2) # mean immigration rate for all species
}


# estimating values for Noise=NA
for(f in 1:nfrag){
for(p in 1:nrep){


X3[f,p]~dnorm(n1,1/sdn1^2)
}
}


# priors
n1~dnorm(0,1/100^2)
sdn1~dunif(0,100)
mb0~dnorm(0,1/100^2)
mb1~dnorm(0,1/100^2)
sdb0~dunif(0,100)
sdb1~dunif(0,100)
c1~dnorm(0,1/100^2)
d1~dnorm(0,1/100^2)
mc0~dnorm(0,1/100^2)
md0~dnorm(0,1/100^2)
sdc0~dunif(0,100)
sdd0~dunif(0,100)
a~dunif(0,1)
h0~dnorm(0,1/100^2)
```

```
h1~dnorm(0,1/100^2)}"


# Export the model
writeLines(OccIBTDetModel,"OccIBTDetModel.txt")


# Name the variables
y<-NaiveOcc3d
Noise<-Noise_pr
nyears<-yearoldnew[,2]-yearoldnew[,1]
dist_scale2<-scale(distanceoldnew2) # scaling isolation variable
area_scale<-log(areaoldnew) # scaling area variable


# Name the predictor variables as in the model
X1<-area_scale[,2]
X1_0<-area_scale[,1]
X2<-dist_scale2[,2]
X2_0<-dist_scale2[,1]


# Organize the data
data2<-
list(y=NaiveOcc3d,X3=scale(Noise),X1=area_scale[,2],X1_0=area_scale[,1],X2=dist_scale2[,2],X2_0=dist_scale
2[,1],ngen=nyears,nsp=101,nfrag=43,nrep=8)


# Give initial values for the parameters
inits2<-list(mc0=resu3.2$par[3],md0=resu3.2$par[1],d1=resu3.2$par[2],c1=resu3.2$par[4] ,Z=occpre)


# Check if the model works
IBTDetTest2<-jags.model("OccIBTDetModel.txt", data=data2, n.chains=3, n.adapt = 20000,inits = inits2)


# Run the MCMC model
IBTDetMcmc2<-coda.samples(IBTDetTest2, variable.names = c("b0","b1","mb0","mb1","sdb0","sdb1", "c0",
"mc0", "sdc0","d0","md0","sdd0","c1","d1","X3[1,3]","n1","sdn1","h0","h1","a"),n.iter = 200000, thin =
500)


# Transform in data.frame to better deal with the results
IBTDetMatrix2<-as.data.frame(as.matrix(IBTDetMcmc2))


# Parameters median
ParamMed2<-apply(IBTDetMatrix2,2,median)


# Extract the parameters results in a matrix
d0mat2<-as.matrix(IBTDetMatrix2[,paste0("d0[",1:101,"]")]) # species immigration rate
d1mat2<-as.matrix(IBTDetMatrix2[,"d1"]) # isolation on immigration rate
c0mat2<-as.matrix(IBTDetMatrix2[,paste0("c0[",1:101,"]")]) # Species extinction rate
c1mat2<-as.matrix(IBTDetMatrix2[,"c1"]) # area on extinction rate


h0mat2<-as.matrix(IBTDetMatrix2[,"h0"])
h1mat2<-as.matrix(IBTDetMatrix2[,"h1"])
amat2<-as.matrix(IBTDetMatrix2[,"a"])


# Creating an empty array that after will be filled with runs values
ir2<-array(NA,c(43,101,1200))
er2<-array(NA,c(43,101,1200))
i0r2<-array(NA,c(43,101,1200))
e0r2<-array(NA,c(43,101,1200))


# One mcmc result for fragments (rows), species (columns) and a third dimension for each mcmc run
for(i in 1:1200){
  ir2[,,i]<-exp(-d1mat2[i]*X2)%*%t(d0mat2[i,]) # current immigration
  er2[,,i]<-exp(-c1mat2[i]*X1)%*%t(c0mat2[i,]) # current extinction
  i0r2[,,i]<-exp(-d1mat2[i]*X2_0)%*%t(d0mat2[i,]) # past immigration
  e0r2[,,i]<-exp(-c1mat2[i]*X1_0)%*%t(c0mat2[i,])} # past extinction
```

```
# Species occurrence probability in each fragment
# Past
psi_02<-(i0r2/(i0r2+e0r2))+(ir2/(ir2+er2)-(i0r2/(i0r2+e0r2)))*(1-exp(-(ir2+er2)*(ngen*0)))
hist(psi_02) # most not between 0-1
hist(psi_02[areaoldnew[,1]>0,,])


# Future
psi_1002<-(i0r2/(i0r2+e0r2))+(ir2/(ir2+er2)-(i0r2/(i0r2+e0r2)))*(1-exp(-(ir2+er2)*(ngen+100)))


# Current
psi_c2<-(i0r2/(i0r2+e0r2))+(ir2/(ir2+er2)-(i0r2/(i0r2+e0r2)))*(1-exp(-(ir2+er2)*(ngen)))


# Species richness in each fragment
# Past
S_02<-apply(psi_02,3,rowSums)
S_0m2<-rowMeans(S_02)
S_0sd2<-apply(S_02,1,sd)


# Future
S_1002<-apply(psi_1002,3,rowSums)
S_100m2<-rowMeans(S_1002)
S_100sd2<-apply(S_1002,1,sd)


# Current
S_c2<-apply(psi_c2,3,rowSums)
S_cm2<-rowMeans(S_c2)
S_csd2<-apply(S_c2,1,sd)


# Verify if observed species richness in associated with predicted species richness
plot(S_cm2,sprich)


# Relationship between current and past species richness
plot(S_0m2,S_cm2,xlim=c(0,70),ylim=c(0,70),pch=21,bg=1,cex=0.7,xlab="Past Species Richness",ylab="Current
Species Richness")
abline(0,1,lty=2)
polygon(c(-30,80,80,-30),c(-30,0.9*80,1.1*80,-30),col="#e0e0e0")
points(S_0m2,S_cm2,xlim=c(0,70),ylim=c(0,70),xlab="Past Species Richness",ylab="Current Species
Richness",pch=21,bg=1,cex=0.7)
arrows(S_0m2,S_cm2-S_csd2,S_0m2,S_cm2+S_csd2,length = 0.02,code = 3,angle = 90,col="gray40")
arrows(S_0m2-S_0sd2,S_cm2,S_0m2+S_0sd2,S_cm2,length = 0.02,code = 3,angle = 90,col="gray40")


# Relationship between current and future species richness
plot(S_100m2,S_cm2,xlim=c(0,70),ylim=c(0,70),xlab="Future Species Richess",ylab="Current Species
Richness",pch=21,bg=1,cex=0.7)
abline(0,1,lty=2)
polygon(c(-30,80,80,-30),c(-30,0.9*80,1.1*80,-30),col="#e0e0e0")
points(S_100m2,S_cm2,xlim=c(0,70),ylim=c(0,70),xlab="Future Species Richess",ylab="Current Species
Richness",pch=21,bg=1,cex=0.7)
arrows(S_100m2,S_cm2-S_csd2,S_100m2,S_cm2+S_csd2,length = 0.03,code = 3,angle = 90,col="gray40")
arrows(S_100m2-S_100sd2,S_cm2,S_100m2+S_100sd2,S_cm2,length = 0.03,code = 3,angle = 90,col="gray40")


# Relationship between observed and expected species richness
plot(sprich,S_cm2,xlim=c(0,70),ylim=c(0,70),ylab="Predicted species richness",xlab="Observed species
richness",pch=19,las=1,col="grey50")
abline(lm(S_cm2~sprich))
abline(0,1)


## Immigration and Extinction rates ##
# Mean of fragments immigration rate
irmean2<-apply(ir2,c(1,3),mean)


# Median of fragments immigration (one rate per fragment)
```

```
irmed2<-apply(irmean2,1,median)


# Mean of fragments extinction rate
ermean2<-apply(er2,c(1,3),mean)


# Median of fragments extinction (one rate per fragment)
ermed2<-apply(ermean2,1,median)


# Relationship between species extinction rate and area
areagraph<-seq(min(area_scale[,2]),max(area_scale[,2]),length.out = 1000)


plot(areagraph,areagraph,ylim=c(0,1),type="n",ylab="Extinction rate",xlab="Area size",las=1)


for(i in 1:101){
  elinha2<-(ParamMed2[paste0("c0[",i,"]")]*exp(-ParamMed2["c1"]*areagraph)/max(ermean2))
  lines(areagraph,(elinha2))}


# Relationship between species immigration rate and isolation
isolgraph2<-seq(min(dist_scale2[,2]),max(dist_scale2[,2]),length.out = 1000)


plot(isolgraph2,isolgraph2,ylim=c(0,1),type="n",ylab="Immigration rate",xlab="Geographical
isolation",las=1)


for(i in 1:101){
  ilinha2<-(ParamMed2[paste0("d0[",i,"]")]*exp(-ParamMed2["d1"]*isolgraph2)/max(irmean2))
  lines(isolgraph2,(ilinha2))}


## Immigration and Extinction rates and species richness ##
plot(S_cm2,41.55601*S_cm2/max(S_cm2),ylim=c(0,50)) # extincao
points(S_cm2,31.11425-31.11425*S_cm2/max(S_cm2),col="red")


seqx<-c(0,101)
mypallete<-colorRampPalette(c("skyblue","blue")) # extinction
mypallete2<-colorRampPalette(c("darkred","coral")) # immigration


colors<-mypallete(100)[cut(area_scale[,2],100)]
colors2<-mypallete2(100)[cut(dist_scale2[,2],100)]
plot(seqx,41.55601*seqx/max(seqx),ylim=c(0,1),type="n",xlab="Species Richness",ylab="Immigration
Rate",zlab="Extinction Rate",las=1) # plot


mei2<-max(ermed2,irmed2)


for(i in 1:43){   lines(seqx,(ermed2[i]*seqx/max(seqx))/mei2,ylim=c(0,80),xlim=c(0,60),col=colors[i])
lines(seqx,(irmed2[i]-irmed2[i]*seqx/max(seqx))/mei2,col=colors2[i])}


for(i in 1:43){ # linhas verticais mostrando o equilibrio
  v<-max(seqx)*irmed2[i]/(ermed2[i]+irmed2[i])
  h<-ermed2[i]*max(seqx)*irmed2[i]/(ermed2[i]+irmed2[i])/max(seqx)
  arrows(v,h/mei2,v,-0.03,length = 0.1,col = "grey20")}
```

Appendix S3 Maximum Likelihood model to estimate the parameters initial values for the main

model.

```
# creating the model
nlogLik4<-function(parms,S_s,D,A){
  d0<-parms[1]
  d1<-parms[2]

  c0<-parms[3]
  c1<-parms[4]

  I<-exp(d0+d1*D)
  E<-exp(c0+c1*A)

  Spred<-matrix(I/(I+E),nrow(S_s),ncol(S_s))

 -sum(dbinom(S_s,1,prob = Spred, log=TRUE))

}

# using the model
nlogLik4(c(d0,d1,c0,c1),S_s,D,A)

# use this results in the Bayesian model
resu4<-optim(c(d0=7.7,d1=0.009,c0=10.62,c1=-
0.34),nlogLik4,S_s=occpre,D=dist_scale[,2],A=log(areaoldnew[,2]))

I2<-resu4$par[1]+resu4$par[1]*dist_scale[,2]
E2<-resu4$par[3]+resu4$par[4]*areaoldnew[,2]

# species richness
S2<-(I2/(I2+E2))*101

# relationship between observed species richness and richness predicted by the model
plot(S2,rowSums(occpre))
```

Appendix S4 Bayesian linear regression with current species richness and current and past area.

```
# Species-area model
lm.bayes<-"
model{
for(i in 1:n){
y[i]~dnorm(ylin[i],1/sd^2)
ylin[i]<-b0+b1*x1[i]+b2*x2[i]
}

#Priors
b0~dnorm(0,1/100)
b1~dnorm(0,1/100)
b2~dnorm(0,1/100)
sd~dgamma(0.001,0.001)
}
"
# Write the model
writeLines(lm.bayes,"lm.bayes.txt")
# Add the data
data<-list(y=scale(log(sprich))[,1],x1=scale(log(areaoldnew[,1]+1))[,1],
x2=scale(log(areaoldnew[,2]+1))[,1],n=nrow(areaoldnew))

# Test the model
lm.test<-jags.model("lm.bayes.txt", data=data, n.chains=3, n.adapt = 1000)

# Run the model
lm.test.mcmc<-coda.samples(lm.test, variable.names = c("b0","b1","b2","sd"),n.iter =
50000,thin=50)

# Parameters chains convergence
plot(lm.test.mcmc[,3])
plot(lm.test.mcmc[,2])
plot(lm.test.mcmc[,1])

# Transform into matrix
lm.test.mcmc.m<-as.matrix(lm.test.mcmc)

# Parameter medianas
b0med<-median(lm.test.mcmc.m[,1])
b1med<-median(lm.test.mcmc.m[,2])
b2med<-median(lm.test.mcmc.m[,3])

# current
plot(log(areaoldnew[,2]),log(sprich),xlab="Fragments area (log)",ylab="Species
richness (log)",main="Current SAR",xlim =c(0,16),ylim=c(0,6))
abline(b0med,b2med,lwd=3) # more likely association
select<-sample(nrow(lm.test.mcmc.m),3000) # 3000 more possible associations
for(i in 1:3000){
abline(lm.test.mcmc.m[select[i],1],lm.test.mcmc.m[select[i],3],col=adjustcolor("grey8
0",0.15),lwd=1)}
```

Supporting figures captions

Figure S1 – Posterior probability distribution for parameters (solid gray) and hyperparameters (red line). (a) species detectability; (b) a value representing that the balance between extinction and immigration rates highly explain species occurrences; (c) extinction rates; (d) immigration rates. For extinction and immigration rates, we used the average of fragments area and connectivity for graph simplification.

Figure S2 – Association between naive species richness (observed) and species richness estimated by the Island Biogeography Theory model accounting for imperfect detection. Although the strong association between observed and estimated species richness, the observed values are lower than values estimated by the model, suggesting detectability issues.

Figure S3 – Influence of noise on species detection probability. The mean detection is less than 20%, even though some species have higher detection. However, detection probability does not change with the increase of noise. Gray lines represent each species and the black line represents the median for all species.
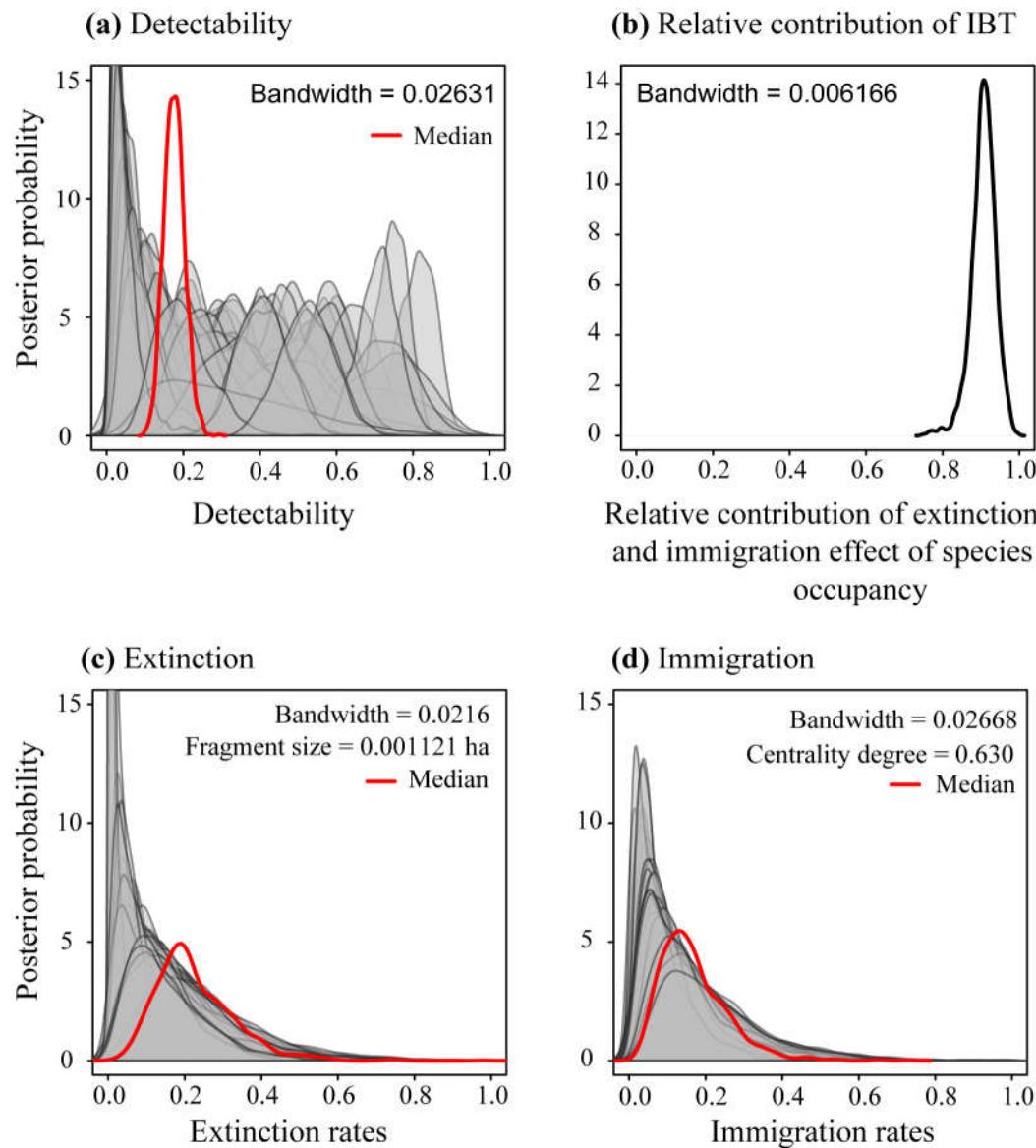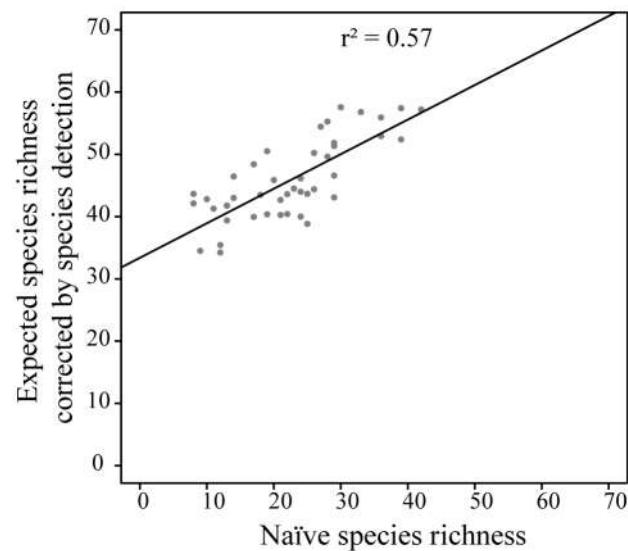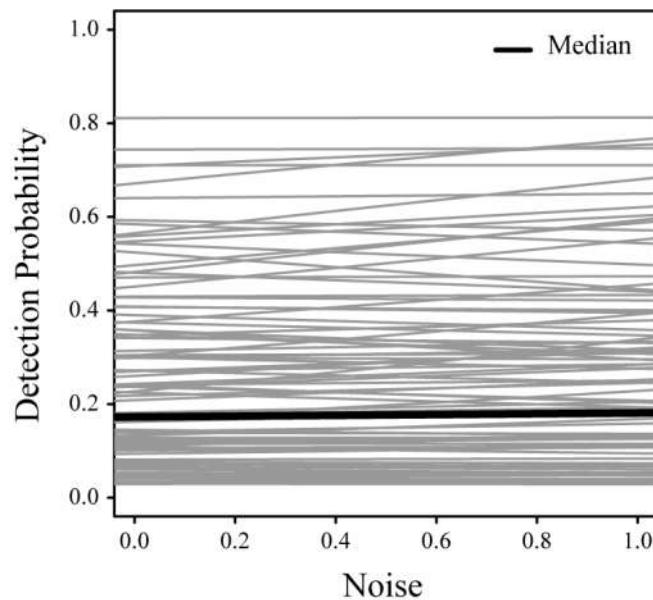
Figure S1

(a) Detectability

(b) Relative contribution of IBT

Relative contribution of extinction and immigration effect of species occupancy

(c) Extinction

(d) Immigration

Figure S2

Figure S3

Supporting table captions

Table S1: Predictor variables for each fragment (n = 43). Area old and area new represent the area (ha) before and after the most abrupt change in fragments size, respectively. Fragments with area = zero means that they were not yet fragmented in 1984. Isolation, measured degree of centrality, as did not change across years. For fragments with more than one survey point, we used an average of noise (decibels) of all points.

Table S2: Taxonomy classification of the 101 bird species surveyed. Classification follows South American Classification Committee (SACC).

Table S3: Species richness in each fragment. Observed species richness (naive) represents the amount of species registered in the bird survey, while the predicted species richness refers to the estimation by the mechanistic model based on the Island Biogeography Theory.

Table S1

Fragment	Points	Past area	Current area	Isolation	Age	Noise
1	1	20.092	17.975	0.131	23	45.02
2	2	235.603	101.962	0.132	25	41.91
3	1	0.795	0.795	0.136	1	62.15
4	1	4.678	2.256	0.129	30	55.11
5	1	22.339	2.976	0.134	34	53.7
6	1	3.966	1.155	0.132	20	56.76
7	1	1.025	1.025	0.135	1	62.45
8	1	25.991	8.743	0.126	27	43.16
9	1	1.303	0.675	0.158	19	43.8
10	1	6.107	0.870	0.126	29	56.04
11	2	0	97.420	0.226	33	49.41
12	1	11.478	11.478	0.131	1	39.7
13	2	22.950	22.950	0.220	1	52.97
14	1	66.486	66.486	0.135	1	52.67
15	1	36.710	36.710	0.228	1	51.73
16	3	206.1983	156.940	0.152	29	39.97
17	3	170.283	170.283	0.187	1	44.97
18	1	26.486	10.308	0.166	23	38.76
19	1	37.213	8.501	0.131	19	51.95
20	1	0	0.499	0.132	22	66.92
21	1	6.800	0.459	0.142	24	47.64
22	1	2.779	2.779	0.156	1	52.69
23	4	836.502	836.502	0.184	1	41.97
24	1	3.094	1.724	0.136	28	43.37
25	3	138.538	138.538	0.136	1	42.78
26	1	10.519	6.924	0.136	21	49.26

27	1	0	0.250	0.181	16	50.56
28	1	0	0.502	0.190	29	44.3
29	2	143.355	119.821	0.129	17	42.39
31	1	20.698	1.231	0.180	33	48.66
32	1	0	1.962	0.178	15	52.6
33	1	134.630	77.670	0.175	26	42.14
34	2	775.051	775.051	0.210	1	44.07
35	1	6.023	1.096	0.149	34	63.5
36	1	0	0.710	0.151	10	54.44
37	1	0.330	3.662	0.195	6	43.3
38	4	818.463	452.022	0.209	33	39.04
39	1	2.050	1.048	0.165	20	44.18
40	1	6.411	9.114	0.181	18	41.72
41	1	0.864	0.864	0.132	1	64.65
42	1	0.066	0.066	0.147	1	52.63
43	1	0	0.649	0.125	17	50.4
44	1	0	1.051	0.126	31	52.17

Table S2

Order	Family	Species
Accipitriformes	Accipitridae	*Rupornis magnirostris*
Apodiformes	Trochilidae	*Amazilia fimbriata*
		Amazilia versicolor
		Aphantochroa cirrochloris
		Chlorostilbon lucidus
		Eupetomena macroura
		Leucochloris albicollis
		Thalurania glaucopis
Cathartiformes	Cathartidae	*Cathartes aura*
		Coragyps atratus
Charadriiformes	Charadriidae	*Vanellus chilensis*
Columbiformes	Columbidae	*Columba livia*
		Columbina talpacoti
		Leptotila rufaxilla
		Leptotila verreauxi
		Patagioenas picazuro
Cuculiformes	Cuculidae	*Crotophaga ani*
		Guira guira
		Piaya cayana
Falconiformes	Falconidae	*Milvago chimachima*
		Milvago chimango
Galliformes	Cracidae	*Ortalis squamata*
Gruiformes	Rallidae	*Aramides saracura*
Passeriformes	Cardinalidae	*Habia rubica*
	Conopophagidae	*Conopophaga melanops*
	Corvidae	*Cyanocorax caeruleus*
	Estrildidae	*Estrilda astrild*
	Formicariidae	*Formicarius colma*
	Fringillidae	*Chlorophonia cyanea*
		Euphonia pectoralis
		Euphonia violacea
		Anabacerthia lichtensteini
		Furnarius rufus
		Philydor atricapillus
		Philydor rufum
		Sittasomus griseicapillus
		Stilpnia preciosa
	Hirundinidae	*Pygochelidon cyanoleuca*
		Syrigma sibilatrix

Icteridae	*Icterus pyrrhopterus*	
	Molothrus bonariensis	
Parulidae	*Basileuterus culicivorus*	
	Geothlypis aequinoctialis	
	Setophaga pitiayumi	
Passerellidae	*Zonotrichia capensis*	
Passeridae	*Passer domesticus*	
Pipridae	*Chiroxiphia caudata*	
	Manacus manacus	
Thamnophilidae	*Dysithamnus mentalis*	
	Herpsilochmus rufimarginatus	
	Myrmoderus squamosus	
Thraupidae	*Coereba flaveola*	
	Dacnis cayana	
	Hemithraupis ruficapilla	
	Pipraeidea bonariensis	
	Saltator similis	
	Sicalis flaveola	
	Tachyphonus coronatus	
	Tangara cyanocephala	
	Thraupis sayaca	
	Thraupis palmarum	
	Trichothraupis melanops	
	Volatinia jacarina	
Tityridae	*Pachyramphus validus*	
	Schiffornis virescens	
Troglodytidae	*Troglodytes aedon*	
Turdidae	*Turdus albicollis*	
	Turdus amaurochalinus	
	Turdus leucomelas	
	Turdus nigriceps	
	Turdus rufiventris	
Tyrannidae	*Attila rufus*	
	Camptostoma obsoletum	
	Elaenia flavogaster	
	Empidonomus varius	
	Lathrotriccus euleri	
	Legatus leucophaius	
	Leptopogon amaurocephalus	
	Mionectes rufiventris	
	Myiarchus ferox	
	Myiodynastes maculatus	
	Myiozetetes similis	

		Pitangus sulphuratus
		Platyrinchus mystaceus
		Serpophaga subcristata
		Tolmomyias sulphurescens
		Tyrannus melancholicus
	Vireonidae	*Vireo olivaceus*
Pelecaniformes	Ardeidae	*Ardea alba*
		Egretta thula
Pelecaniformes	Threskiornithidae	*Phimosus infuscatus*
Pelecaniformes	Ardeidae	*Synallaxis spixi*
Piciformes	Picidae	*Celeus flavescens*
		Colaptes campestris
		Veniliornis spilogaster
		Picumnus temminckii
	Ramphastidae	*Ramphastos dicolorus*
		Ramphastos vitellinus
Psittaciformes	Psittacidae	*Amazona aestiva*
		Pyrrhura frontalis
Tinamiformes	Tinamidae	*Crypturellus obsoletus*

Table S3

Fragment	Species richness observed	Species richness predicted
1	29	51
2	33	56
3	8	42
4	20	45
5	24	46
6	25	43
7	14	43
8	26	50
9	13	39
10	18	43
11	29	46
12	19	50
13	29	43
14	28	55
15	22	43
16	36	55
17	39	52
18	14	46
19	28	49
20	11	41
21	24	39
22	8	43
23	39	57
24	26	44
25	42	57
26	17	48
27	9	34
28	12	35
29	20	57
31	15	38

32	19	40
33	19	51
34	27	54
35	13	41
36	21	40
37	22	40
38	36	52
39	17	39
40	23	44
41	10	42
42	12	34
43	21	42
44	24	43

CAPÍTULO II

SUBURBAN FOREST PATCHES CAN PRESERVE FUNCTIONAL DIVERSITY AND EVOLUTIONARY HISTORY OF BIRDS

FRAGMENTOS FLORESTAIS DE SUBÚRBIO PODEM PRESERVAR DIVERSIDADE FUNCIONAL E HISTÓRIA EVOLUTIVA DE AVES

Choquinha-lisa
Dysithamnus mentalis (Temminck, 1823)

Suburban forest patches can preserve functional diversity and evolutionary history of birds

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Abstract

Urbanization is one of the major threats to bird conservation due to the reduction of habitats, the isolation of areas and the increase in noise pollution. Highly urbanized areas have lower species richness and distinct species composition compared to natural areas. In addition, species with particular traits might be absent from fragmented areas, which could impact ecosystem functioning. However, it is unknown how changes in species richness and composition are associated to reduction in species functional traits, and consequently ecosystem functioning in urban ecosystems. We investigated how bird communities are structured in terms of taxonomic, functional and phylogenetic diversity along an urbanization gradient, and which anthropogenic related factors (area, isolation and noise) cause the changes in bird diversity. We surveyed birds and collected environmental data from 43 patches divided into natural, suburban and urban patches in a 45 km lenght island of South Brazil. The impact of urbanization was investigated by associating environmental predictors to 1) measures of patch species taxonomic, functional and phylogenetic and 2) changes in the taxonomic, functional and, phylogenetic composition between patches. Species richness was higher in natural patches where noise was minimal, whereas higher functional richness occurred in suburban patches. Suburban patches also preserved taxonomic and phylogenetic composition (i.e. species and phylogenetic history) that are typically present either in urban or natural areas. Our results suggest that in order to minimize the negative effects of urbanization and protect biodiversity in cities it is important to reduce urban noise and preserve habitat diversity and vegetation, as commonly observed in suburban patches.

Keywords: community composition, local diversity, noise, patch area

Introduction

Urbanization is responsible for one of the greatest environmental changes in the world, negatively affecting ecosystems (Seto et al. 2012). The negative effects of urbanization on biodiversity are caused by the reduction of area and habitat quality (Beninde et al. 2015), the isolation of areas (Fattorini et al. 2018) and the increase in noise pollution (Halfwerk et al. 2011). However, it is less clear how these factors affect the diversity of species traits, which is ultimately responsible for ecosystem functioning (Díaz and Cabido 2001). In addition, most studies on urban biodiversity focus on the effect of urbanization on species richness and abundance (Aronson et al. 2014; Callaghan et al. 2019; Chamberlain et al. 2019), but studies considering species identity, functions and evolutionary history are scarce (but see Morelli et al. 2017). Therefore, it is unknown how changes in species richness and composition are associated to reduction in species functional traits and evolutionary history, and the best strategy to preserve community diversity and functions in urban ecosystems.

Ecological communities in urban areas are constrained by the harsh environmental conditions, limited biotic interactions and direct anthropogenic impacts. In such environments, area, isolation and noise pollution can act as environmental filters, excluding species, with a disproportionate impact on species with particular traits and/or evolutionary history (Aronson et al. 2016). Small areas have less resources available for specialist species (Beninde et al. 2015) and more isolated areas may have only species with high dispersal capacity (Leibold et al. 2010). In addition, noise pollution can exclude sensitive species to traffic and construction (Perillo et al. 2017). These constraints reduce the diversity of species from natural to urban areas and which might cause biotic homogenization among urban patches, both in terms of functional and phylogenetic diversity (McKinney 2006).

However, the evidences of biotic homogenization occuring at functional and phylogenetical level may not occur at the taxonomic level, as different facets of diversity may vary in response to urbanization (Morelli et al. 2017). Because of the replacement of specialist by generalist species, reducing functional and phylogenetic diversity (Sol et al. 2017), species richness may remain constant along an urbanization gradient (Aronson et al. 2015). In fact, a recent study suggests a positive responses of species taxonomic diversity to intermediate levels of urbanization (Callaghan et al. 2019). Therefore, it is urgent a study that deeply investigates how biodiversity interacts with urban-induced environments, accounting for species, species functions and evolutionary relationships.

We investigated how bird communities are structured in terms of taxonomic, functional and phylogenetic diversity along an urbanization gradient, and which anthropogenic related factors cause change in bird diversity. We expect the reduction of area (Beninde et al. 2015), and the increase of isolation (Fattorini et al. 2018) and noise (Perillo et al. 2017) to reduce species richness in urban areas. Due to biotic homogenization of species traits and evolutionary history, areas with lower species richness should also have lower functional and phylogenetic diversity.

Methods

Study area

The study was conducted in Florianópolis, a continental island located in Southern Brazil. The climate is subtropical humid (Cfa), with average annual temperature of 20.4ºC and annual precipitation of 1500mm (INMET, 2017; http://www.inmet.gov.br/portal). The island is part of the Atlantic Forest biome, whose predominant vegetation is mixed ombrophilous forest, along with coastal vegetation (Klein, 1969).

We sampled 43 areas (hereafter, "patches"; Fig. 1) in Florianópolis along an urbanization gradient. The patches were divided in three categories from the urbanization gradient as follows: (i) natural patches, defined as predominantly preserved primary forests (n = 13); (ii) suburban patches, defined as residential neighborhoods characterized by moderate human population, composed mostly by houses and buildings single-or doubled-stored, with several green spaces such as lawns, gardens and parks (n = 22); and (iii) urban patches, defined as areas around the city central areas where most of the surface area is covered by multi-store buildings, have high human density and car traffic, and lawns, gardens and parks surrounded by an intense urban matrix (n = 8. Table S1) (Marzluff et al. 2001).

Data collection

Birds were surveyed in the spring season of 2018, from September to November, using point counts (Bibby et al. 1992). Points varied from 1 to 4 in each patch, according patch area (differences in sampling effort were statistically corrected, see below), and points within a patch were far from each other by at least 300 m. In each point, sampling was conducted between 5:30 and 9:30 am. for a period of 10 minutes, in which all birds seen or heard within a 50 m radius from the observer were registered. Each sampling point was sampled twice. A total of 62 sampling points was surveyed in 38 days of sampling, corresponding to 20.7 field hours of observation. We excluded from the data species observed exclusively flying over the patch. Bird counts were conducted by GFD only in favorable climatic conditions (i.e. avoiding windy and rainy days) with the additional help of sound recorder and a photographic camera to register the data.

We also collected environmental data induced by anthropogenic activities: patch area, isolation and noise (Table S1). Isolation was calculated using network analysis and was measured

the centrality degree – a proxy for isolation (Estrada and Bodin 2008). Patch area and isolation

was measured for the patch, whereas noise was collected in each survey point. Noise was

measured as the amount of decibels in the patch using Akso AK820 digital decibelmeter. We have

randomly chosen one minute within the 10 minutes survey in each point to collect this variable,

and for patches that have more than one survey point, we calculated noise as the average of all

points. The two surveys in every individual patch were conducted at different hours of the day

(e.g. first visit around 5:30 and second visit around 8:00) to capture the average noise of the patch

and to avoid introducing differences among patches in the amount of noise due o the time of the

day.

Species functional traits were chosen based on their potential impact on ecosystem

functioning (Díaz and Cabido 2001). We obtained species foraging ecology (diet and foraging

strata) and body mass from Wilman et al. (2014) for each individual species. These traits are

proxy for many life history strategies and are related to species dispersal capacity (Paradis et al.

1998). We obtained phylogenetic information from Jetz et al. (2012) which was constructed

based on the Hackett backbone tree, which is available in the BirdTree platform

(http://www.birdtree.org). The platform provides 100,000 phylogenetic trees, each of

phylogenetic tree is a hypothesis about the phylogenetic relationship among species. To account

for this factor, we used a consensus of 100 phylogenetic.

Diversity measures

To analyze how communities are structured in terms of taxonomic, functional and phylogenetic

diversity along the urbanization gradient, we performed two distinct groups of analyses. First, we

measured local diversity for each patch individually (alpha diversity) and associated local

diversity metrics with anthropogenic-related variables. Second, we calculated the pairwise

similarities between each individual pair of patches using indices that account species identity only, species identity weighted by species traits (functional similarity), and species identity weighted by phylogenetic relationships (phylogenetic similarity). The similarities in pairs of patches were then associated to anthropogenic induced environmental distances between patches.

Measures of alpha diversity

Differences in sampling effort can strongly influence measures of species richness – heavily sampled areas have highest number of observed species (Gotelli and Colwell 2011). To account for the unequal sampling effort among patches, we estimated the species richness (taxonomic diversity) using the abundance-based estimator Chao1 (Chiu et al. 2014). This unbiased richness estimate was then used as response variable representing local species taxonomic diversity in our models.

Observed values of local functional richness was calculated based on the species traits observed in each patch. Functional richness (FRic) describes the total amount of functional space filled by the community (Villéger at al. 2008). Observed local phylogenetic diversity (PD) was measured as the phylogenetic distance between all species of birds surveyed in each patch, which is analogue to species and functional richness metrics but weighted by species phylogeny (Faith, 1992). Measures of species functional and phylogenetic diversity can be affected by differences in species richness between patches (Villéger et al. 2008). In order to test for the effect of predictor variables on these measures independently from their effect on species richness, we created null models controlling for differences in species between patches ad used the deviation from the expectations as unbiased measures of species functional and phylogenetic diversity.

Null communities were created by maintaining constant species richness and frequencies in each patch, and by randomizing species traits (for functional richness) and species

phylogenetic position (for phylogenetic diversity). Species traits and phylogenetic positioning

were randomized 99 and 999 times and the functional and phylogenetic indices were recalculated

in each randomization. Therefore, we created a distribution of expected values of functional and

phylogenetic diversity that could be compared to the observed diversities. Because species

richness was maintained constant, any differences between the observed and expected values

could only be attributed to functional or phylogenetic constraints, not differences in species

richness. The new indices resulting from the comparison between the observed indices and those

obtained from null models were calculated as the Standardize Effect Sizes for each individual

patch (SES; Eq. 1) (Gotelli and McCabe 2002). In some randomization of species traits, only

species with the same trait values were selected and it was not possible to calculate the volume of

the functional space. Therefore, we used only the randomization in which the functional space

was larger than zero.

$$SES = \frac{X_{obs} - X_{null}}{SD_{null}} \qquad \text{Eq. 1}$$

To identify how local taxonomic (species richness estimated by Chao1), functional

(FRic$_{SES}$) and phylogenetic richness (PD$_{SES}$) are influenced by antropogenic-driven environmental

variables along the urbanization gradient, we performed linear regression analyses. Because area,

noise and habitat type (urban, suburban and natural) are related to each other ($r^2 > 0.26$) we

performed a simple linear regression analyses for each response variables. We also performed a

variance partitioning analysis to quantify the unique effect of area, noise and habitat type on

species richness (i.e. the effect of each variable that could not be attributed to other predictor

variables). Although these predictor variables are correlated to each other, we have not found

spatial autocorrelation in the response variables, as measured by a Moran's I test (results not

shown).

Measures of beta diversity

Beta diversity was measured using the Sorensen similarity index between all pairs of communities. In order to avoid biases associated to differences in sampling effort between patches, we used the average species abundance in each survey point to calculate the similarity indices. Functional similarity was calculated based on species occurrences weighted by species functional attributes (Villéger et al. 2013) and phylogenetic similarity was calculated based on species occurrences weighted by the phylogenetic positioning of species (Leprieur et al. 2012). Pairwise community similarity was measured as the turnover component of beta diversity, which represents the diversity replacement (taxonomic, functional or phylogenetic) between pairs of communities (Baselga 2010).

To calculate the functional similarity between communities, we combined continuous traits (body mass) with fuzzy traits (categories within the same functional trait in the form of percentages: diet and foraging strata) in the same distance matrix. We standardized and created a species traits distance matrix using a generalized Gower's distance that allows the treatment of various types of traits (Pavoine et al. 2009). From this distance matrix, we performed a Principal Coordinates Analysis (PCoA) and used the first four ordination axes, which explains 72.5% of the variance in species traits, as variables representing species traits in functional similarity measures. To calculate the phylogenetic similarity between pairs of communities, we used the average pairwise similarity obtained from 100 phylogenetic trees obtained from BirdTree for each community.

To determine how taxonomic, functional and phylogenetic similarities between pairs of communities are related to differences in patch area, isolation, noise, and habitat type, we performed multiple regressions of distance matrices (Lichstein 2007). In addition, to represent graphically the taxonomic, functional and phylogenetic composition in the distinct habitat types,

we performed a NMDS analysis with two dimensions and plotted the NMDS axes against habitat type categories.

All analyses were performed in R version 3.5.2, using the vegan (Oksanen et al. 2019), ape (Paradis and Schliep, 2018), ecodist (Goslee and Urban, 2007), picante (Kembel et al. 2010), FD (Laliberté and Legendre, 2010), betarpart (Baselga et al. 2018) and igraph (Csardi and Nepusz 2006) packages. We used a modified version of the functional.beta.pair function from the betapart package to improve computational performance. The function is available at

https://raw.githubusercontent.com/csdambros/R-functions/master/FunctionalBetaPart.R.

For functional diversity (alpha and beta), we performed the analyses using traits combined and using traits individually. The results were qualitatively the same and, therefore we only show results using all traits combined.

Results

We found 101 bird species, in 14 orders and 35 families (Table S2). The number of species per patch varied from eight to 53 (mean = 28 $\pm$ 11) and the number of individuals per patch ranged from 11 to 99 (mean = 52 $\pm$ 20). The surveyed species feed on invertebrates (50.6%), fruits (21.7%), seeds (10.3%), nectar (7.6 %), vertebrates (7.2 %), and plants (2.6%), and forage in all strata layers (from ground to canopy). Average species body mass was 131 g (ranging from 3.5 g to 1881 g).

Species richness was positively associated with patch area and negatively associated with noise (Table 1). Natural areas had higher species richness than urban and suburban areas (Table 1; Fig. 2). Patch area, noise and habitat type explained 46% of the variance in species richness (Fig. 3).

Functional richness (FRic$_{SES}$) was higher in suburban patches in comparison with natural

patches (Fig. 2; Table 1). We found no evidence for association between $FRic_{SES}$ and other covariates. We have also not found relationship between phylogenetic diversity (PD_{SES}) and environmental predictors, except for a slightly (p = 0.02) negative association with noise (Table 1).

Changes in taxonomic similarity (turnover) between pairs of communities were associated with differences in patch area, noise and habitat type (Table 2; Fig. 4). Habitat type was also associated with changes in phylogenetic similarity (turnover) between patches (Table 2; Fig. 4). We have not found a relationship between functional similarity and any predictor variable.

Discussion

Urban areas are thought as homogenized environments with a reduced set of species when compared to natural areas (McKinney 2006; Sol et al. 2014; Morelli et al. 2017). We corroborate this pattern by finding that natural patches harbor higher species richness than typical urban or suburban patches. Surprisingly, however, we found that suburban forest patches have a disproportionately high functional richness, and also that suburban patches share taxonomic and phylogenetic composition that are typically present uniquely in urban or natural environments, but not both. The higher functional richness in suburban patches could be partially attributed to the habitat heterogenity of these regions, that contributes for the survival of native-specialist and invasive and generalist species (Blair and Johnson 2008).

Because suburban areas have a diverse set of species with distinct traits, these areas also share several functional traits with both natural and urban areas (Fig. 4B). Therefore, almost the whole trait diversity present in the entire region is encompassed by suburban patches. The diversity replacement between natural and urban patches suggests urbanization can exclude species not adapted to the harsh urban environment resulting in the diversity reduction in city

centers (Sol et al. 2014; Aronson et al. 2016). However, we demonstrate that suburban areas can both preserve a large portion of functional and phylogenetic information present in natural and urban areas. Suburban patches are the transition between natural and urban forests, and are common in recently fragmented urban areas (Blair and Johnson 2008). Our results might suggest that the maintenance of the ecosystem functioning performed by birds and the evolutionary history of species in urban areas can be mediated by preserving suburban areas.

It is important to note that in spite of the results for functional and phylogenetic diversities, species richness can be reduced in suburbs and other cities might have different conditions for birds in these areas. For example, highly noisy suburbans might aggravate the decline in species richness in suburbs. Noise had a negative effect on species richness and species similarity, which could result from the negative effect that noise has on bird vocalizarion (Koper et al. 2016) and breeding (Halfwerk et al. 2011). In addition, we also found a slightly negative response of birds phylogenetic diversity (PD_{SES}) to noise (Table 1; p = 0.02), suggesting that certain bird clades are indeed avoiding loud urban areas (Sol et al. 2017). Despite the well-known negative effects of noise on species richness (Fontana et al., 2011; Perillo et al., 2017), there is a gap in how noise can impact other facets of diversity. It is possible that noise can be a strong barrier for less plastic birds to persist and survive in urban areas (Aronson et al. 2016), and future studies should investigate more deeply if closely related species respond similarly to anthropogenic noise and what are the implications to urban biodiversity conservation.

Urbanization is one of the major threats to biodiversity conservation (Seto et al. 2012). Our findings provide some future avenues for biodiversity conservation and maintenance in urban environments. First, based on the results and on previous findings (Savard, 2000; Callaghan et al. 2019) it is clear the need to maintain and create green areas at the cty center in order to reduce the anthropogenic impact in urban forest patches. Second, it is important to to

establish strict noise limits in cities because noise has a severe impact on taxonomic and potentially on phylogenetic diversity, acting as filter that exclude species from urban patches. Finally, our results show that suburbs can be important for biodiversity conservation in cities. Although suburban forest patches have lower species richness than natural areas, these patches can preserve the functional diversity and evolutionary history of birds, demonstrating that it is possible to have economic and urban development while preserving the functional diversity in ecological communities.

Authors' contributions

GFD, CSD, CSF conceived the ideas and designed methodology; GFD collected the data; GFD and CSD analyzed the data; GFD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data available at Supporting Informarion and at Github (https://github.com/gfdri)

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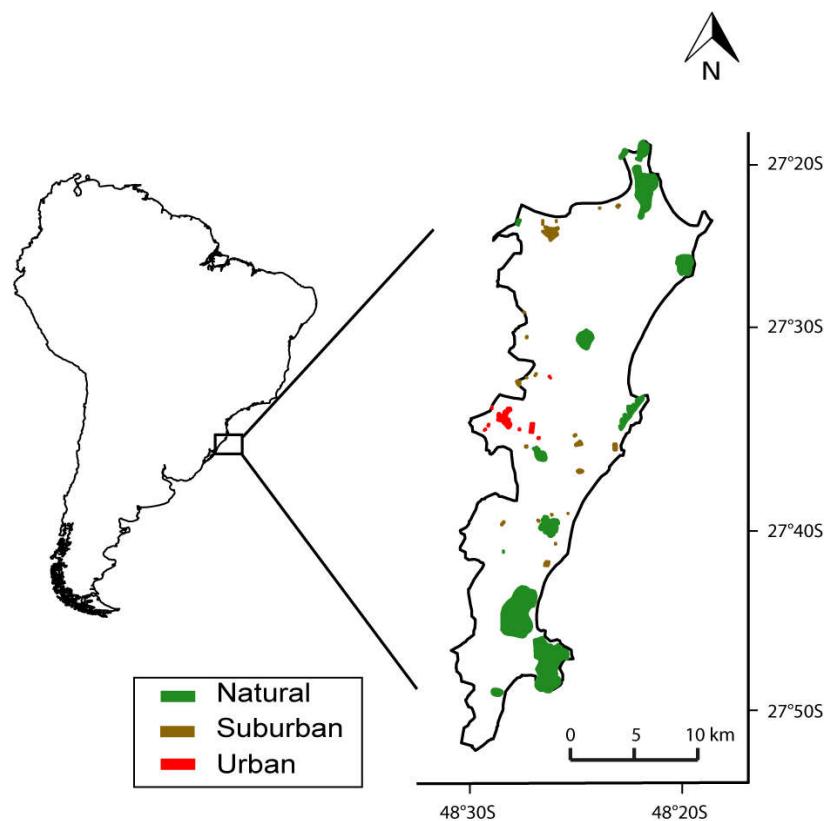
Figures and Tables

Fig. 1 Study area, Florianópolis, Sourthern Brazil. We surveyed at 43 forest patches, with different habitat types represented by colors
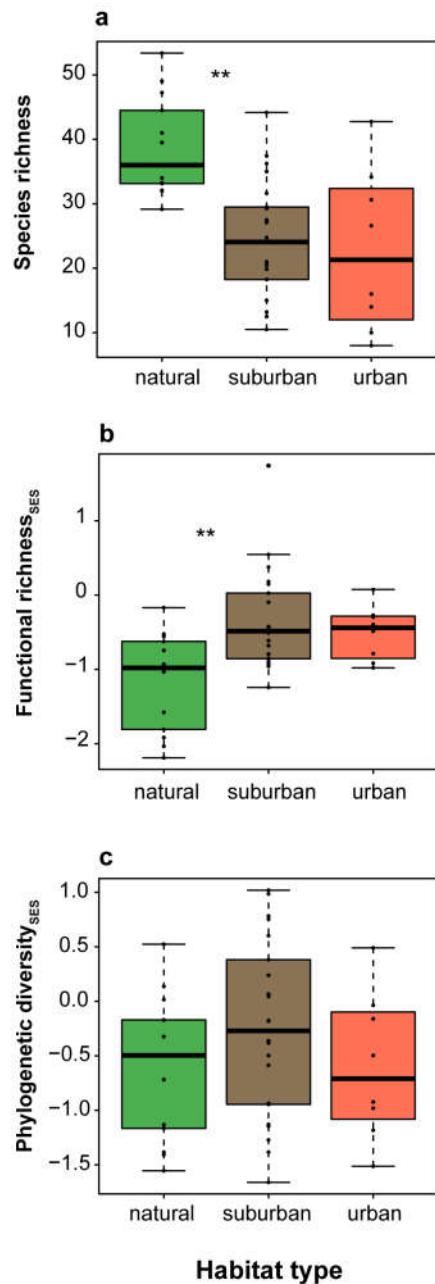
Fig. 2 Local diversity representing the association between species richness (a), functional richness (b), and phylogenetic diversity (c) along the urbanization gradient. Functional richness and phylogenetic diversity indices were corrected by species richness. ** represents significance
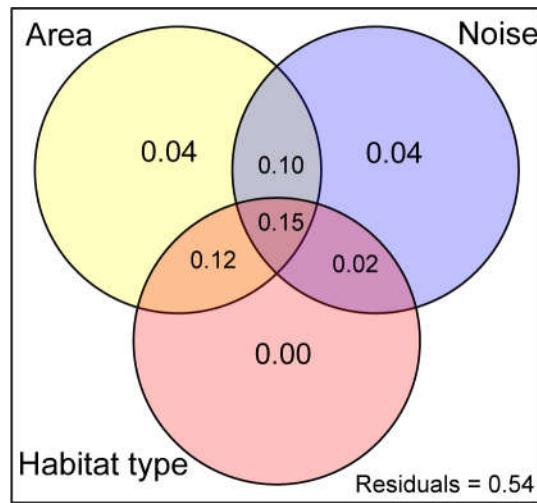
Fig. 3 Venn diagram with the results of variation partitioning analyses for bird species richness at 43 vegetation patches surveyed in Florianópolis, Brazil. Patch area, noise and habitat type explain 46% of the variation on species richness
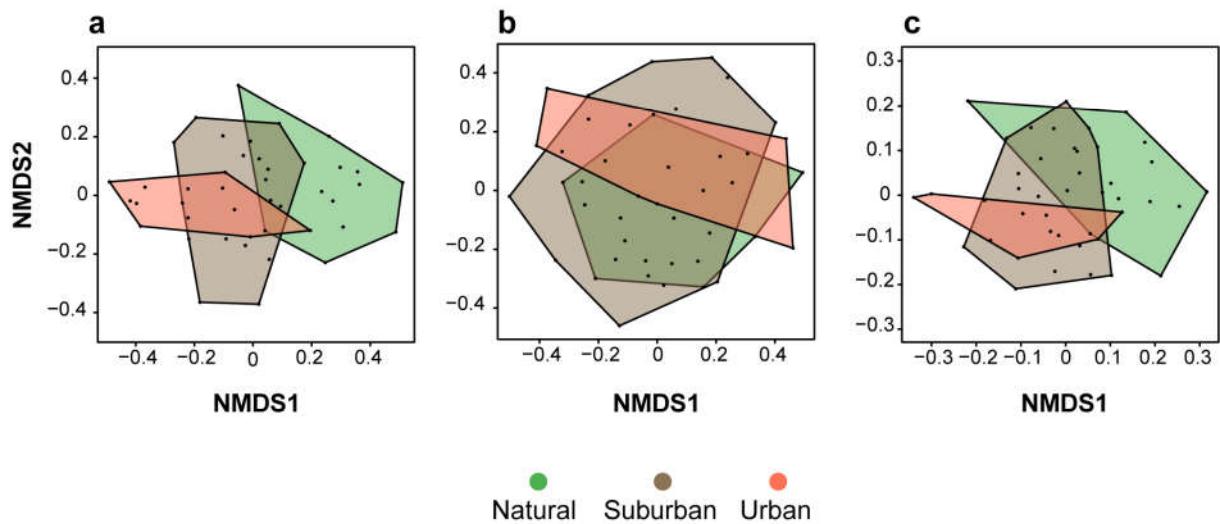
Fig. 4 Birds composition along the urbanization gradient. Natural (green) and urban (red) patches have very distinct taxonomic and phylogenetic composition (a; c). Functional composition (b) is higher in suburban patches (brown)

Table 1 Association among environmental conditions with local diversity, represented by species richness (Chao1), functional richness (FRic$_{SES}$) and phylogenetic diversity (PD$_{SES}$; analogue to species and functional richness). Predictors were associated in separated linear models

	Taxonomic		Functional		Phylogenetic	
	Chao1		FRic$_{SES}$		PD$_{SES}$	
Predictor	Estimate	R²	Estimate	R²	Estimate	R²
Area	**0.65****	0.41	-0.29	0.06	0.16	0.00
Isolation	6.96	0.02	0.05	0.02	0.00	0.02
Noise	**-0.57****	0.30	0.19	0.01	-0.33*	0.08*
Habitat type natural (intercept)	**0.83****	0.28	**-0.74****	0.21	-0.23	0.00
Habitat type suburban	**-1.10****	0.28	**1.12****	0.21	0.45	0.00
Habitat type Urban	**-1.42****	0.28	**0.92****	0.21	0.00	0.00

P-values: ** < 0.01 in bold; * < 0.02

Table 2 Multiple regression matrices indicating the association between environmental distances with taxonomic, functional and phylogenetic similarity between pairs of communities. Habitat type distance represents the distance among urban, suburban and natural habitat type. Predictors were analyzed in the same model

	Taxonomic Similarity	Functional Similarity	Phylogenetic Similarity
Habitat type distance	**-0.23****	0.01	**-0.17****
Area distance	-0.11	0.17	0.00
Isolation distance	-0.06	0.04	-0.12
Noise distance	**-0.24****	-0.10	-0.00
F	**44.20****	11.21	**12.40****
R²	0.16	0.04	0.05

P-values: ** < 0.01 in bold

Table S1 Predictor variables for each fragment (n = 43). Area (hectares), isolation (centrality degree), noise (decibels). For fragments with more than one survey point, we used an average of noise of all points

Patch	Points	Longitude	Latitude	Area	Isolation	Habitat type	Noise
1	1	-48.5109	-27.596	17.975	0.131	urban	45.02
2	2	-48.5335	-27.5888	101.962	0.132	urban	41.91
3	1	-48.5504	-27.5973	0.795	0.136	urban	62.15
4	1	-48.4745	-27.6014	2.256	0.129	suburban	55.11
5	1	-48.5156	-27.6099	2.976	0.134	suburban	53.7
6	1	-48.5052	-27.6036	1.155	0.132	urban	56.76
7	1	-48.5475	-27.5939	1.025	0.135	urban	62.45
8	1	-48.5222	-27.5622	8.743	0.126	suburban	43.16
9	1	-48.4908	-27.6828	0.675	0.158	suburban	43.8
10	1	-48.5153	-27.5584	0.870	0.126	suburban	56.04
11	2	-48.4174	-27.388	97.420	0.226	natural	49.41
12	1	-48.4712	-27.6078	11.478	0.131	suburban	39.7
13	2	-48.4335	-27.3906	22.950	0.220	natural	52.97
14	1	-48.5039	-27.616	66.486	0.135	natural	52.67
15	1	-48.5404	-27.794	36.710	0.228	natural	51.73
16	3	-48.496	-27.6696	156.940	0.152	natural	39.97
17	3	-48.3819	-27.4735	170.283	0.187	natural	44.97
18	1	-48.4983	-27.6978	10.308	0.166	suburban	38.76
19	1	-48.4406	-27.6102	8.501	0.131	suburban	51.95
20	1	-48.5445	-27.5808	0.499	0.132	urban	66.92
21	1	-48.5174	-27.5095	0.459	0.142	suburban	47.64
22	1	-48.5354	-27.6674	2.779	0.156	suburban	52.69
23	4	-48.5222	-27.7346	836.502	0.184	natural	41.97
24	1	-48.5152	-27.5279	1.724	0.136	suburban	43.37
25	3	-48.4659	-27.5294	138.538	0.136	natural	42.78

26	1	-48.4703	-27.6284	6.924	0.136	suburban	49.26
27	1	-48.4902	-27.441	0.250	0.181	suburban	50.56
28	1	-48.4537	-27.4313	0.502	0.190	suburban	44.3
29	2	-48.4275	-27.5839	119.821	0.129	natural	42.39
31	1	-48.5016	-27.442	1.231	0.180	suburban	48.66
32	1	-48.4894	-27.4465	1.962	0.178	suburban	52.6
33	1	-48.4948	-27.4501	77.670	0.175	suburban	42.14
34	2	-48.497	-27.7732	775.051	0.210	natural	44.07
35	1	-48.494	-27.661	1.096	0.149	suburban	63.5
36	1	-48.5054	-27.6655	0.710	0.151	suburban	54.44
37	1	-48.4381	-27.4296	3.662	0.195	suburban	43.3
38	4	-48.4158	-27.4169	452.022	0.209	natural	39.04
39	1	-48.5349	-27.6886	1.048	0.165	natural	44.18
40	1	-48.5222	-27.4419	9.114	0.181	natural	41.72
41	1	-48.5214	-27.597	0.864	0.132	urban	64.65
42	1	-48.4804	-27.66	0.066	0.147	suburban	52.63
43	1	-48.4958	-27.5577	0.649	0.125	urban	50.4
44	1	-48.5077	-27.556	1.051	0.126	suburban	52.17

Table S2 Taxonomy classification of the 101 bird species surveyed. Classification follows South American Classification Committee (SACC) from March 2019

Order	Family	Species	Patch
Accipitriformes	Accipitridae	*Rupornis magnirostris*	33, 37
Apodiformes	Trochilidae	*Amazilia fimbriata*	9, 10, 13, 20, 21, 24, 31
		Amazilia versicolor	35
		Aphantochroa cirrochloris	6, 10, 11, 13, 25, 33
		Chlorostilbon lucidus	7
		Eupetomena macroura	2, 5, 12, 28
		Leucochloris albicollis	23
		Thalurania glaucopis	1, 5, 16, 17, 19, 23, 25, 34, 36
Cathartiformes	Cathartidae	*Cathartes aura*	38
		Coragyps atratus	11, 34, 37
Charadriiformes	Charadriidae	*Vanellus chilensis*	4, 12, 36, 39, 41, 43
Columbiformes	Columbidae	*Columba livia*	1, 3, 7, 20, 41, 43
		Columbina talpacoti	1, 4, 5, 6, 7, 8, 9, 10, 12, 13, 18, 20, 21, 24, 27, 31, 32, 33, 36, 38, 41, 43, 44
		Leptotila rufaxilla	35, 38
		Leptotila verreauxi	1, 2, 5, 6, 8, 10, 12, 13, 14, 15, 16, 17, 18, 19, 21, 23, 25, 29, 34, 37, 38, 40
		Patagioenas picazuro	1, 2, 5, 12, 13, 14, 16, 17, 23, 24, 25, 26, 28, 29, 33, 36, 37, 38, 40
Cuculiformes	Cuculidae	*Crotophaga ani*	8, 19, 26, 38
		Guira guira	5, 16, 18, 19, 20, 24, 25, 26, 27, 28, 32, 33, 36, 37, 39, 41, 44
		Piaya cayana	1, 2, 4, 8, 13, 16, 17, 25, 29, 33, 36, 38
Falconiformes	Falconidae	*Milvago chimachima*	9, 21, 29, 31, 39, 40
		Milvago chimango	8, 18, 26
Galliformes	Cracidae	*Ortalis squamata*	1, 2, 4, 8, 14, 16, 17, 19, 22, 23, 24, 25, 26, 32, 33, 34, 38, 40, 42, 44
Gruiformes	Rallidae	*Aramides saracura*	1, 2, 4, 5, 6, 8, 9, 11, 12, 13, 15, 16, 17, 19, 23, 24, 25, 34, 37, 38, 40
Passeriformes	Cardinalidae	*Habia rubica*	14, 15, 17, 25, 29, 34
	Conopophagidae	*Conopophaga melanops*	11, 15, 23, 25, 34, 38
	Corvidae	*Cyanocorax caeruleus*	, 2, 6, 8, 9, 11, 13, 15, 16, 17, 18, 19, 21, 23, 24, 25, 28, 29, 31, 32, 33, 34, 35, 37, 38, 40

Estrildidae	*Estrilda astrild*	12, 36, 44
Formicariidae	*Formicarius colma*	2, 5, 11, 14, 15, 16, 17, 19, 23, 25, 29, 34, 38, 44
Fringillidae	*Chlorophonia cyanea*	11
	Euphonia pectoralis	1, 6, 11, 17, 25, 29, 32, 36, 40
	Euphonia violacea	1, 13, 15, 16, 17, 19, 21, 23, 32, 34, 40
	Anabacerthia lichtensteini	25
	Furnarius rufus	1, 3, 4, 5, 7, 8, 9, 10, 11, 12, 13, 16, 18, 19, 20, 2, 24, 26, 27, 28, 29, 31, 32, 34, 36, 37, 38, 39, 41, 42, 43, 44
	Philydor atricapillus	23
	Philydor rufum	14, 17
	Sittasomus griseicapillus	16, 17, 23, 25, 34
	Stilpnia preciosa	34
Hirundinidae	*Pygochelidon cyanoleuca*	21, 24, 41, 43
	Syrigma sibilatrix	4, 28, 39
Icteridae	*Icterus pyrrhopterus*	21, 24
	Molothrus bonariensis	2, 4, 5, 6, 8, 9, 11, 12, 13, 21, 29, 28
Parulidae	*Basileuterus culicivorus*	1, 2, 6, 8, 11, 13, 14, 15, 16, 17, 19, 21, 23, 24, 25, 29, 32, 33, 24, 37, 38, 40, 42
	Geothlypis aequinoctialis	8, 12, 15, 16, 17, 19, 21, 23, 29, 34, 36, 37, 38, 42
	Setophaga pitiayumi	1, 2, 5 6, 7, 8, , 11, 13, 14, 15, 16, 19, 21, 23, 24, 25, 26, 31, 33, 34, 35, 37, 38, 40, 44
Passerellidae	*Zonotrichia capensis*	2, 4, 5, 6, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 29, 31, 33, 37, 38, 42, 43, 44
Passeridae	*Passer domesticus*	1, 3, 7, 20, 31, 41, 43
Pipridae	*Chiroxiphia caudata*	2, 14, 15, 16, 17, 25, 34
	Manacus manacus	2, 14, 16, 17, 29
Thamnophilidae	*Dysithamnus mentalis*	12, 14, 16, 23, 29, 31, 33, 37, 38, 40
	Herpsilochmus rufimarginatus	8, 15, 16, 23, 25, 31, 40
	Myrmoderus squamosus	14, 23, 25, 38
Thraupidae	*Coereba flaveola*	1, 2, 4, 5, 6, 8, 9, 11, 13, 14, 15, 16, 17, 19, 21, 23, 24, 25, 26, 31, 33, 36, 37,

		3, 39, 40, 44
	Dacnis cayana	2, 5, , 8, 11, 12, 13, 14, 16, 17, 3, 24, 25, 29, 38
	Hemithraupis ruficapilla	2, 11, 17, 25, 29
	Pipraeidea bonariensis	5
	Saltator similis	6, 10, 15, 26, 29, 32, 36, 43
	Sicalis flaveola	3, 7, 9, 10, 12, 18, 20, 21, 27, 31, 35, 36, 39, 41, 43, 44
	Tachyphonus coronatus	14, 17, 23, 25, 34, 44
	Tangara cyanocephala	11, 16, 25, 29, 34
	Thraupis palmarum	1, 2, 6, 13, 19, 24, 28, 31, 33, 35, 44
	Thraupis sayaca	1, 2, 3, 4, 5, 6, 7, 8, 10, 13, 18, 19, 20, 21, 24, 26, 27, 28, 31, 32, 33, 35, 36, 38, 41, 42, 43
	Trichothraupis melanops	25
	Volatinia jacarina	2, 13, 14, 15, 16, 17, 24, 31, 33, 36, 44
Tityridae	*Pachyramphus validus*	25, 35
	Schiffornis virescens	16, 23, 25, 34
Troglodytidae	*Troglodytes aedon*	1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 21, 22, 23, 24, 25, 26, 27, 28, 29, 31, 33, 35, 36, 37, 38, 39, 40, 42, 43, 44
Turdidae	*Turdus albicollis*	6, 14, 25
	Turdus amaurochalinus	1, 3, 4, 5, 6, 7, 8, 9, 10, 14, 15, 18, 19, 20, 22, 24, 26, 27, 3, 32, 33, 34, 36, 37, 38, 40, 42, 43, 44
	Turdus leucomelas	1, 4, 5, 8, 10, 11, 12, 17, 22, 27, 29, 31, 33, 35, 39, 42, 43
	Turdus nigriceps	1, 7, 31, 38, 44
	Turdus rufiventris	2, 3, 4, 5, 6, 7, 10, 13, 14, 15, 20, 21, 24, 28, 31, 33, 43
Tyrannidae	*Attila rufus*	2, 11, 14, 16, 17, 23, 25, 33, 38
	Camptostoma obsoletum	1, 8, 10, 17, 19, 22, 23, 25, 26, 28, 31, 32, 33, 36, 37, 38, 40, 43, 44
	Elaenia flavogaster	5, 6, 7, 17, 18, 19, 35, 36, 43
	Empidonomus varius	24, 40

		Lathrotriccus euleri	23
		Legatus leucophaius	2
		Leptopogon amaurocephalus	2, 8, 11, 13, 15, 16, 17, 23, 25, 29, 33, 34, 44
		Mionectes rufiventris	23, 25, 29, 44
		Myiarchus ferox	32, 40
		Myiodynastes maculatus	1, 13, 16, 19, 39, 44
		Myiozetetes similis	11, 17
		Pitangus sulphuratus	1, 2, 3, 4, 5, 6, 7, 8, 9, 0, 11, 12, 3, 14, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 2, 27, 28, 29, 31, 32, 33, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44
		Platyrinchus mystaceus	23, 25, 31, 33, 34
		Serpophaga subcristata	17, 33
		Tolmomyias sulphurescens	23, 25
		Tyrannus melancholicus	1, 2, 4, 10, 11, 13, 14, 17, 19, 21, 23, 24, 26, 28, 29, 32, 33, 35, 36, 38, 39, 42, 43, 44
	Vireonidae	*Vireo olivaceus*	2, 3, 5, 6, 11, 13, 14, 15, 16, 17, 21, 23, 25, 29, 31, 32, 34, 38, 40
Pelecaniformes	Ardeidae	*Ardea alba*	37
		Egretta thula	14, 39, 43
Pelecaniformes	Threskiornithidae	*Phimosus infuscatus*	1, 43
Pelecaniformes	Ardeidae	*Synallaxis spixi*	1, 13, 16, 17, 19, 29, 38
Piciformes	Picidae	*Celeus flavescens*	1, 2, 4, 5, 6, 10, 11, 13, 14, 16, 17, 19, 21, 23, 24, 25, 26, 29, 32, 33, 34, 37, 38, 39, 42, 43, 44
		Colaptes campestris	10, 16, 18, 38
		Veniliornis spilogaster	2, 39
		Picumnus temminckii	1, 2, 4, 6, 8, 1, 12, 13, 14, 16, 17, 19, 21, 23, 24, 25, 29, 31, 32, 34, 37, 38, 39, 44
	Ramphastidae	*Ramphastos dicolorus*	2, 8, 15, 17, 23, 25
		Ramphastos vitellinus	2, 8, 15, 16, 17, 21, 23, 25, 29, 32, 33, 34, 37, 38, 40
Psittaciformes	Psittacidae	*Amazona aestiva*	23
		Pyrrhura frontalis	12
Tinamiformes	Tinamidae	*Crypturellus obsoletus*	11, 23

DISCUSSÃO

Neste trabalho, eu investiguei como os elementos de uma paisagem fragmentada impactam a diversidade de aves em um gradiente temporal (capítulo I) e espacial (capítulo II). Os resultados encontrados corroboram com a Teoria de Biogeografia de Ilhas (MACARTHUR & WILSON, 1967), em que a riqueza de espécies nos fragmentos foi influenciada pelas taxas e imigração e extinção. Embora o isolamento (atuando sobre a taxa de imigração) tenha influenciado a riqueza de espécies, a área (atuando sobre a taxa de extinção) foi o principal preditor para a riqueza de espécies. Além disso, a poluição sonora tem um impacto negativo na diversidade de espécies e suas relações evolutivas. Esses resultados implicam que apesar dos efeitos negativos da urbanização, o aumento de áreas verdes e a diminuição de ruídos sonoros podem ajudar na conservação da biodiversidade em áreas urbanas.

O tamanho da área e a quantidade de habitat na paisagem são preditores importantes para a riqueza de espécies em ambientes fragmentados (FAHRIG, 2003; FATORRINI et al., 2018). Os resultados aqui encontrados evidenciaram que fragmentos maiores apresentaram maior riqueza de espécies de aves em relação a fragmentos menores (de acordo com o gráfico A da Figura 3 e gráfico A e C da Figura 4, capítulo I). No entanto, a riqueza foi associada com o tamanho da área atual, e não com o tamanho no passado ou com o isolamento geográfico (conforme os gráficos da Figura 3, capítulo I). Esse fenômeno sugere a ausência de débito de extinção em áreas urbanas, uma vez que a redução da área tem um efeito quase imediato na riqueza de espécies (KUUSSAARI et al., 2009). Além do tamanho da área, o grau de isolamento entre fragmentos também influenciou a riqueza de espécies, embora essa relação tenha sido mais suave (conforme gráfico B da Figura 4, capítulo I), sugerindo que a riqueza de espécies é principalmente influenciada pelo tamanho da área (HALLEY & IWASA 2011) (ilustrado no gráfico C da Figura 4, capítulo I). Os resultados encontrados sugerem que o efeito da perda de habitat é de curto prazo (conforme os gráficos da Figura 5, capítulo I), dessa forma, um novo episódio de perturbação ambiental poderá desequilibrar as comunidades de aves e, consequentemente, diminuir rapidamente o número de espécies presentes no local.

Além da redução a curto prazo da riqueza de espécies, a perda de habitat e fragmentação induzidas pela urbanização também afetaram as diversidades funcional e filogenética, promovendo um filtro ambiental (ARONSON et al., 2016; MORELLI et al., 2017). Os resultados mostraram que o filtro ambiental imposto pela urbanização é devido ao aumento da poluição

sonora e da cobertura urbana, pois essas variáveis influenciaram a modificações da diversidade de espécies e de relações evolutivas entre ambientes naturais e urbanos (gráficos da Figura 4, capítulo II). A poluição sonora também afetou negativamente a riqueza de espécies e diversidade filogenética (Tabela 1, capítulo II), indicando a perda de espécies e de histórias evolutivos no gradiente de urbanização (PERILLO et al., 2017). No entanto, foi encontrado que áreas de subúrbio possuem maior riqueza funcional (Figura 3, caítulo II). Esse padrão pode devido à heterogeneidade ambiental promovida pela mistura da paisagem urbana com a paisagem natural (CALLAGHAN et al., 2019) que facilita o encontro de espécies generalistas com espécies florestais-especialistas (BLAIR & JOHNSON, 2008). Com isso, os resultados sugerem que a diminuição da poluição sonora e a conservação de áreas naturais no entorno da cidade podem aumentar a diversidade de aves e atenuar os impactos gerados pela urbanização.

Embora existam diferenças históricas e socioeconômicas entre as cidades, a maioria sofre os mesmos processos ecológicos relacionados ao filtro ambiental e a adaptação de espécies (GRIMM et al., 2008; ARONSON et al., 2016). Devido a isso, os resultados apresentados sobre o efeito da área nas taxas de extinção e na riqueza de espécies, e da influência negativa da poluição sonora da diverisdade taxonômica e filogenética, podem ser extrapolados para outras cidades. Apesar deste ser um trabalho em pequena escala espacial e realizado em apenas uma cidade, os resultados encontrados seguem o mesmo padrão de estudos em larga-escala sobre os efeitos negativos da urbanização, principalmente sobre a redução de espécies (ARONSON et al., 2014; BENINDE et al., 2015) e de relações evolutivas (MORELLI et al., 2017; SOL et al., 2017). Porém, a relação de curto prazo da perda de habitat na diversidade de espécies tende a ocorrer mais gradualmente em larga-escala, podendo levar centenas de anos para as comunidades entrarem em um novo equilíbrio de riqueza em escalas continentais (HAHS et al., 2009; COUSINS & VANHOENACKER, 2011). Nesse sentido, é importante entender como a dinâmica entre as taxas de imigração e extinção acontecem em ambas escalas espaciais, a fim de implementar medidas adequadas de conservação de áreas naturais tanto em escala local (cidades) como em escalas mais amplas.

CONCLUSÃO

Ao investigar os impactos da fragmentação e perda de habitat na diversidade de aves em ambientes urbanos, tornam-se evidentes alguns padrões. O tamanho da área apresentou um papel fundamental na permanência das espécies em cidades, devido a sua relação negativa com a taxa de extinção. Além disso, a extinção de espécies ocorreu quase imediatamente após a destruição do habitat natural, ou seja, não há evidência para débito de extinção em Florianópolis. Tal ausência de débito de extinção expõe a importância da preservação de áreas verdes dentro das cidades (e.g. parques e praças), uma vez que sua conversão em construções antrópicas pode provocar extinções em curto prazo.

Além da importância do tamanho da área e da ausência de débito de extinção em ambientes urbanos, também foi encontrado possíveis preditores do filtro ambiental no gradiente de urbanização. A poluição sonora e o tipo de habitat (urbano, suburbano ou natural) influenciaram negativamente a diversidade de espécies e de relações evolutivas. Embora o mesmo padrão não tenha sido observado para a diversidade funcional, em que o ápice ocorre em áreas de subúrbio, esse fenômeno só acontece devido a existência de fragmentos bem preservados adjacentes. Como consequência, um planejamento urbano que reduza a poluição sonora e que intercale áreas construídas com espaços para vegetação aumentaria a biodiversidade urbana.

Portanto, os resultados dessa dissertação mostraram que a redução do tamanho da área possui um efeito quase imediato na riqueza de espécies de aves, sugerindo a ausência de débito de extinção em áreas urbanas (capítulo I). Além do efeito da área, foi encontrado que o ruído sonoro e o tipo de habitat, sendo urbano, suburbano ou natural, afetam as diversidades taxonômica, funcional e filogenética de comunidades de aves (capítulo II). Esses resultados implicam que o aumento do tamanho das áreas verdes urbanas e a redução da poluição sonora são medidas importantes para a manutenção da biodiversidade em cidades. Dessa forma, é crucial que os tomadores de decisão se baseiem nesses resultados para implementaram um planejamento urbano sustentável.

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