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Estimating the impacts of habitat loss induced by urbanization on bird local extinctions

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ABSTRACT

Habitat loss and fragmentation can be long-term processes driving extinction debts, especially in cities. Because of a lack of temporal data, long-term impacts are generally investigated less frequently than short-term impacts. However, these effects are equally important for understanding biodiversity loss. We developed a Bayesian Island Biogeography model combining historical imagery and current species distribution to investigate the long-term impacts of urbanization-induced habitat loss and isolation on birds. We surveyed 101 bird species in 43 urban forest patches in a South American city with different combinations of size, isolation, and time since the last abrupt change in area. Based on the current and historical landscape configuration, we estimated the temporal dynamics between species extinction rate and area, and between immigration rate and isolation. Additionally, we used model parameters to forecast bird extinction debts. Large patches had lower extinction rates than small patches, and immigration rates were lower in more isolated patches. Furthermore, current bird species richness was better explained by current landscape configuration than by past configuration, suggesting that birds rapidly respond to changes in urban landscapes and there are no apparent extinction debts. Indeed, we found that habitat loss reduces species diversity to a new equilibrium in relatively short period (less than 10 years), and model projections indicate that bird richness will remain similar to the present if patch area is maintained. Habitat loss is the most important cause of species local extinctions in urban areas, and tropical cities could rapidly promote biodiversity by restoring forest cover.

1. Introduction

Understanding the process of biodiversity loss is fundamental to perform conservation actions in a changing world. Among the several causes of species loss, urbanization has one of the most severe impacts due to the intensification of habitat conversion into cities, leading to species local extinctions (Hahs et al., 2009; Sol et al., 2014). Extinctions in urban environments result mostly from the size reduction (Beninde et al., 2015) and isolation of natural patches (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 understood. Theoretical studies suggest that long periods after fragmentation, a new dynamic equilibrium can be reached with a subset of the original species due to the new balance between extinction and immigration rates (Halley and Iwasa, 2011; Hugueny, 2017).

Projections for the long-term dynamic equilibrium in species richness can be made by using the Island Biogeography Theory (IBT; MacArthur and Wilson, 1967). The IBT emphasizes that the variation in area and isolation affect species richness through the change in the dynamic balance between extinction and immigration rates. Extinction rate is mostly related to area, as the probability of extinction increases in smaller areas due to small population sizes (Lande, 1993). In contrast, immigration rate is usually affected by isolation, given that species immigrate into fragments that are highly connected to others and within reach via dispersal (MacArthur and Wilson, 1967; Lasky et al., 2017). The effect of area and isolation on species richness is applicable to landscapes with complex surrounding matrices and relatively homogeneous habitat fragments (Simberloff and Wilson, 1969; Burns, 2015), such as urban environments (Fattorini et al., 2018; Maseko et al., 2020). However, rapid changes in the urban landscape make it necessary to incorporate temporal dynamics in species responses (Watson, 2002;

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Ramalho and Hobbs, 2012).

Species loss might be a result of a gradual delay between the original and new balance of extinction-immigration rates because in the long-term the community would enter into a lower equilibrium level (Diamond, 1972). This temporal gap between the two equilibrium points is known as extinction debt, in which some species are committed to extinction due to habitat loss (Tilman et al., 1994). The time required to reach this new dynamic equilibrium is dependent on area, the time since fragmentation (Halley and Iwasa, 2011; Hugueny, 2017), and how species respond to these factors (Jacquet et al., 2017). This delay in species extinction can be observed in urban environments, as this landscape is constantly being modified (Hahs et al., 2009). Although cities are rapidly expanding, there are only few statistical models available that explicitly integrate the temporal change in patch configuration to estimate extinction delays (Ramalho and Hobbs, 2012). Correlative methods that associate the time since habitat modification and species diversity (e.g. Almeida-Rocha et al., 2017) are not able to precisely quantify the amount of extinction debt or to incorporate the temporal changes in patch configuration to estimate when predicted extinctions will occur. In contrast, dynamic ecological models require long temporal sequences of species records in forest fragments; data that are rarely available (Figueiredo et al., 2019).

To overcome the limitation of temporal biological data 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 occurrences). Our model uses an explicit dynamic approach to quantify species loss while accounting for 1) species variability in extinction and immigration rates (Gilpin and Armstrong, 1981; Jacquet et al., 2017) and 2) imperfect species detection, which is likely to bias the estimation of these rates. We use this model to quantify the impacts of habitat loss and isolation caused by urbanization on local extinction and immigration rates of bird species and to simultaneously estimate species occupancy for the past and the future. We expect higher extinction rates in small patches and lower immigration rates in more isolated patches. Equilibrium in species richness should be more evident in small patches than large ones (Halley and Iwasa, 2011). Additionally, we expect old patches to be in or closer to equilibrium because long periods might be required to balance immigration and extinction rates. In contrast, we expect recently created patches to have more species than expected in equilibrium, evidencing extinction debts (Watson, 2002; Hugueny, 2017). Many studies discuss the effects of area on species extinction. However, few studies try to estimate the precise effect of area on extinction rates and integrate the interplay between area and time since the patch change into the models. The dynamic model used here allows making predictions about the number of species at equilibrium and the time required to reach this equilibrium in the urban landscape.

2. Material and methods

2.1. Study area and sampling design

The study was carried out in Florianópolis (27°35′S, 48°32′W; Fig. 1), Southern Brazil, representing one of the few studies on Neotropical urban ornithology. Florianópolis is a continental island, located in the Atlantic Ocean, separated by approximately 500 m from the continent. The city is part of the Atlantic Forest bioregion with a mosaic encompassing different types of habitats. We restricted this study to forest areas (moist broad-leaf tropical forest) because it is the predominant original habitat in the region. The intense urbanization process in Florianópolis at the end of the 20th century resulted in a fragmented landscape, but some areas were naturally regenerated later, creating new patches (Mattei, 2015).

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 patches with different combinations of area, isolation, and time since the patch change. Patches were selected opportunistically to have a gradient of size and isolation, and for these two variables to be independent of each other. The process of patch selection resulted in a total of 43 patches considered as sampling units. Because patch selection was also based on accessibility, and thus not all patches available were surveyed, we extract the central coordinates of 25 non-sampled patches to account for isolation measures in the models.

To quantify the geographical measures for each patch, we drew polygons for each patch for each year (43 patches in 35 years, 1505 shapefiles) using the Quantum GIS software (QGIS Development Team,

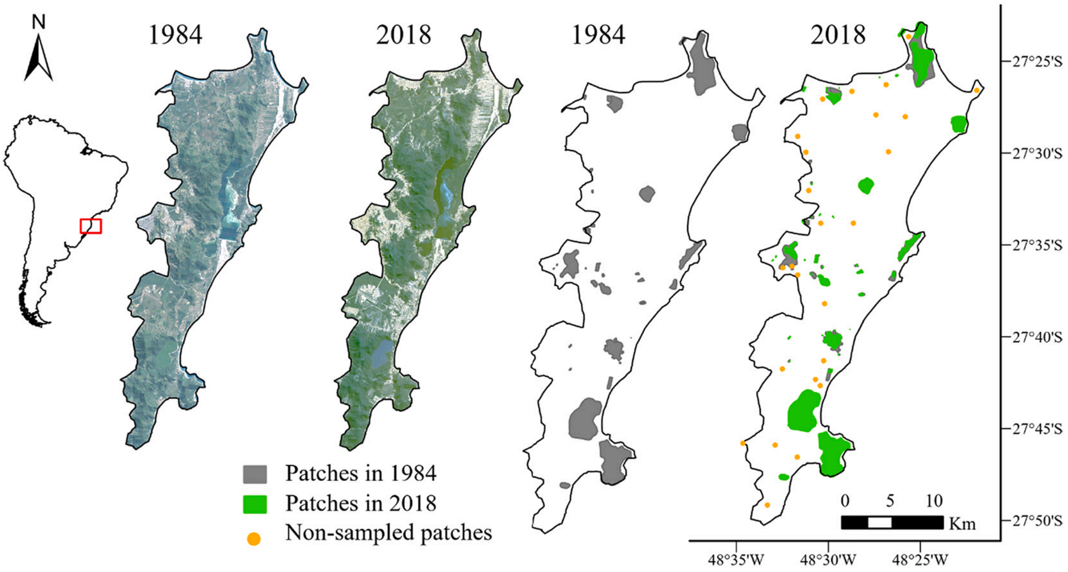

Fig. 1. Study area (Florianópolis, Southern Brazil) showing the differences in area and isolation of surveyed patches in 1984 (gray polygons) and 2018 (green polygons). Some patches remained similar in size, whereas others increased or decreased in size. Patch isolation (measured as the degree of centrality) remained constant over time. Orange dots represent 25 non-surveyed patches included in the isolation calculations. Two regional maps on the left show the urbanization level in 1984 and 2018. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2019; version 2.18.20). We then calculated patch area (ha), isolation, and time since the patch change (Table A1). Isolation was measured based on network analysis to determine the degree of centrality of each patch regarding their locations – patches that are surrounded by other patches are more connected and thus less isolated – with high values representing more isolated patches (Estrada and Bodin, 2008). The time since the patch change is the point in time where each patch suffered the most dramatic area loss/gain due to urbanization. The urbanization process has a very complex temporal dynamic (Ramalho and Hobbs, 2012) and accounting for these changes in a simple model requires some simplifications. Although some patches suffered more than one event of area change over the years, the time since the patch change (i.e. the time since the most abrupt change in area) marks the peak of city expansion regarding that patch. Moreover, despite the absence of aerial imagery before 1984, 40 years is a reasonable baseline for patch size and isolation, given that Florianópolis was at the beginning of the urbanization expansion at this period. Hereafter the terms "past" and "current" corresponds to the average area and isolation before and after the most abrupt change in area considering the baseline of 1984.

We also calculated isolation as the minimal distance between patches. Area and isolation were not highly correlated to each other and could be used as independent predictor variables (centrality degree cor = 0.38; minimal distance cor = 0.00).

2.2. Bird survey

We surveyed bird species in 43 patches using 10 minute point counts (Bibby et al., 1992) in the peak of the breeding season from September to November of 2018. To have accurate estimates of species occupancy in larger patches, the number of surveyed points ($n = 62$) in each patch ranged from one to four. Points were separated by at least 300 m from each other to be sure of their independence. Each point count was surveyed twice with one month difference, thus some patches 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). Patches surveyed on the same day had the order shifted in the second survey to ensure the time of the day (5:30 or near 9) would not influence species detection. All birds seen or heard with an estimation of 50 m radius from the observer were counted by the same researcher. Additionally, we used a sound recorder (Sony ICD-PX470) to allow later identification of individuals in some cases. We only counted bird individuals that were using the patch (i.e. not flying above the survey point) thus the number of bird species included in the analyses was 101. Surveys lasted 38 days, totaling 20.7 h 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. We used the noise at each point as a predictor for species detection probability. We registered noise from 1 min randomly chosen during the 10 min of sampling for the analyses. Because we surveyed each point twice (temporal replicate), any potential bias of a noise peak in the 1-minute sampling would be smoothed by the second survey.

2.3. Statistical models

2.3.1. Regression model

To verify the association of species richness with current and past patch area and isolation, we performed a Bayesian linear regression for each predictor variable in separate models. We log-transformed species richness, area, and isolation to linearize the relationship, which is well described by the power-law function of species-area relationship at local and regional scales ($S = cA^z$) (Martín and Goldenfeld, 2006). To determine the existence or not of these associations and to make coefficients comparable, all predictor and response variables were z-standardized prior to the analyses. Because an absolute zero effect is impossible to occur or detect using classical or Bayesian methods (Kruschke, 2018), a threshold of $r = |0.1|$ ($r^2 = 1\%$) 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 credibility (Highest Density Interval of 95% excluding the interval between −0.1 and 0.1).

We performed another regression model to test the interaction effect between area and isolation on species richness and we found no evidence for the interaction ($-0.1 < r < 0.1$ with 95% of credibility) and therefore we have not included this interaction in subsequent models.

2.3.2. Occupancy model

To investigate extinction debts and the mechanisms associated with the possible extinction delays in urban forest patches, we developed a multi-species mixed-effects model within a hierarchical Bayesian framework based on the Island Biogeography Theory. The model is divided into two parts that account for 1) observation errors (i.e. bias in detectability; Eq. (1)) and 2) the dynamic ecological processes (Fig. A1). The model defines the absence of a species as a result of non-detection (imperfect detection) or from species responses to noise, isolation, and/or local extinction (ecological processes). If detectability was not taken into account in the observer part of the model, a low detectability could bias species occupancy and species richness estimates at the patch level (Chao et al., 2009).

Similarly to mixed-effect models and other occupancy models (Mackenzie et al., 2003) where two sources of uncertainty are incorporated, patch identity was incorporated as a binomial random variable in the observer model (Appendix B). The observer model is described by the equation:

$$Y_{sfp} \sim Bernoulli\left(\theta_{sfp} \times Z_{sf}\right) \tag{1}$$

where Y is the presence/absence of species *s* at each patch *f* and survey point *p*, θ represents the detectability of species *s* at each patch *f* and survey point *p*, and Z is the true occurrence of species *s* at each patch *f* that could be affected by noise and the extinction and immigration rates. Note that Z is defined at the patch scale and only the true occurrences at this scale result from the ecological processes in our model.

Species detection probability θ is allowed to be imperfect (lower than 1) and to vary according to the characteristics of the survey point (e.g. noise decibels; Herrera-Montes and Aide, 2011). We modeled the association of $\theta_{s\,f\,p}$ with noise using a logit function (Eq. (2)):

$$\theta_{sfp} = \frac{e^{\left(b_{0s}+b_{1s}\times Noise_{fp}\right)}}{1+e^{\left(b_{0s}+b_{1s}\times Noise_{fp}\right)}} \tag{2}$$

To predict extinction debts in a scenario where extinction and immigration are the main processes determining species occupancy between two equilibrium states, it is necessary to use a dynamic model, adding a historical perspective to predict species occupancy through time (Hugueny, 2017). The effect of time on species occupancy was determined by comparing the past and current periods, and by estimating the relative contribution of past and current extinction and immigration on current species occupancy. Based on the rates, we forecast species occupancy in the future (adding 100 years), considering the maintenance of the current landscape configuration.

In the classical Island Biogeography Theory, extinction and immigration rates were only dependent on area and isolation (MacArthur and Wilson, 1967). However, species differ in their dispersal capacity and extinction rates (Jacquet et al., 2017). Therefore, besides 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) and we have not accounted for the difference in surrounding landscapes because the matrix separating distant patches was very complex and almost unique for each pair of patches. However, we included interspecific variability by allowing species to vary in their response to area and isolation around average parameter values.

To estimate the effect of area, isolation, and time since the patch change on species occupancy and richness, we used an equation (Eq. (3)) modified from Simberloff (1969). The equation represents the occupancy of each species *s* at individual patch *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 time since the patch change (*t*) (see Supplementary material Appendix B for more details on model construction and simulations). The relaxation time (the time required for the community to return to the equilibrium level; Diamond, 1972) depends on the magnitude of extinction and immigration rates. If these rates are low, there will be a long period between two equilibrium points. However, if these rates are high, the process must be almost immediate, as would be expected by the immediate species loss due to local environmental changes or the immediate immigration of a high-dispersal group when a patch is highly connected.

$$\psi_{sf} = \frac{I_{0sf}}{I_{0sf} + E_{0sf}} + \left(\frac{I_{sf}}{I_{sf} + E_{sf}} - \frac{I_{0sf}}{I_{0sf} + E_{0sf}}\right) \times \left(1 - e^{-\left(I_{sf}+E_{sf}\right)t_f}\right) \tag{3}$$

where I_{0sf} and E_{0sf} represent the estimated original immigration and extinction rates for each species *s* in each patch *f*, I_{sf} and E_{sf} represent the estimated future immigration and extinction rates, and *t* represents the elapsed time since these rates changed.

By using Eq. (3), we have made two main assumptions regarding the urban landscape dynamic. First, we assume that the history of each patch can be divided into two periods, before and after the most abrupt change in area. Extinction and immigration rates associated with area and isolation can differ between each time period and between patches but remain constant within each time period for a given patch. Second, we assume a patch was at its equilibrium in species richness in the past period (baseline). In our study system, human population density remained relatively low until the mid-late 1980s and the increase occurred during the 1990s and 2000s, periods within the time span of our study (Mattei, 2015). Therefore, these two assumptions are likely to have a low impact in model estimates considering the context of our study region and we believe similar contexts are likely to hold in other urban regions. The baseline condition is only assumed to be at near equilibrium, but not necessarily to represent the natural condition in the area.

Both extinction and immigration rates were modeled as exponential responses to area (inverse log) and isolation (kernel dispersal). Past and current patch area ($X_1|_{t=0}$ and X_1) are associated with the coefficients c_0 (intercept) and c_1 (slope) (Eqs. (4)–(5)), and past and current isolation ($X_2|t=_0$ and X_2) are associated with the coefficients d_0 (intercept) and d_1 (slope) (Eqs. (6)–(7)), in which each species has its own intercept to account interspecific variability. 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 by dividing the extinction and immigration values by the maximum value.

$$E_{fs} = c_{0s} \times e^{-c_1 \times X_{1f}} \tag{4}$$

$$E_{0fs} = c_{0s} \times e^{-c_1 \times X_{1|t=0f}} \tag{5}$$

$$I_{fs} = d_{0s} \times e^{-d_1 \times X_{2f}} \tag{6}$$

$$I_{0fs} = d_{0s} \times e^{-d_1 \times X_{2|t=0f}} \tag{7}$$

The multi-species model allows estimating the occupancy probability for individual species in each patch. Therefore, we were able to estimate current species richness (after correcting for imperfect detection) and predict species richness for the past and the future. Species richness in each patch was calculated as the sum of the occupancy of all species in the patch combining the two surveys.

We used Monte Carlo Markov Chains (MCMC) to estimate the posterior probability distribution for each model parameter (Fig. A1). We ran 3 chains using 200,000 MCMC iterations, with a burn-in phase of 20,000 to achieve parameter convergence. MCMC samples were thinned at a rate of 500 to reduce the use of computational disk space. Initial values for parameters associated with extinction and immigration rates 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 rate to area and immigration rate to isolation as in the main model. The initial values for species occupancy were based on the observed species counts. All model parameters converged to the same distribution in each of the MCMC chains. More details about the model and codes and data to replicate our results are available in Supplementary material (see Appendix B) and in Figshare repository (https://doi.org/10.6084/m9.figshare.12217694).

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. (Pedesma and Bivand, 2005), vegan (Oksanen et al., 2019), rgeos (Bivand and Rundel, 2018) and igrah (Csardi & Nepusz, 2006) packages to run the analyses.

We ran the analyses in three different ways: (i) isolation calculated as centrality degree, isolation calculated as the minimal distance between patches, and (iii) incorporating non-sampled patches in the isolation metrics, obtaining qualitatively similar results (Figs. A2–4). Therefore, we only show results of isolation based on the degree of centrality and with surveyed patches in the main text. We also ran a separate model accounting for the effect of area on species detectability and we found a slightly negative influence on patch area on detection (Fig. A5). We were not able to include this effect on the main model because we could not reach chain convergence to estimate the parameters. However, the effect of the area was incorporated in the model when we conducted more survey points on larger patches.

3. Results

We recorded 3009 individual counts from 101 bird species. The number of observed species per patch varied from eight to 42 (mean = 22; sd =8; Table A1). Observed species richness was positively associated with current area, but not to past area (Fig. 2A–C). In addition, the observed species richness was not associated with either current or past isolation (Fig. 3B–D).

Birds were imperfectly detected at each survey point ($\theta = 0.17$; sd = 0.02; Fig. A5A; Table A2). Detection probability ranged from 31% in patches with only temporal replicates (i.e. one survey point with one temporal replicate) to 77% in patches with eight replicates (i.e. four survey points with one temporal replicate each). Due to imperfect detection, observed species richness was lower than estimated in all patches (Fig. A7). The number of species estimated per patch ranged from 31 to 59 (mean = 45; sd = 7; Table A1). Species detectability was not associated with noise ($mb_1 = 0.03$; sd = 0.06; Fig. A8).

Species occupancy measured in the biological part of the model was mostly explained by the relative contribution of extinction and immigration rates and not by noise (a = 0.9; Fig. A5B). For most species, extinction rates declined in larger patches (Fig. 3A) and immigration rates slightly decreased in more isolated patches (Figs. 3B; A5C–D). Patch area was the best predictor of species richness, with more species recorded in larger patches regardless of isolation (Fig. 3C). Based on model projections (i.e. different values for *t* in Eq. (3)), predicted species richness was similar for the past, current, and future periods, except for those patches that were recently created, in which current species richness was higher than past species richness (Fig. 4).

For all models, either correlative or mechanistic, current patch area was more strongly associated with current species richness than past area (Figs. 2–4). Although past area was associated with species richness

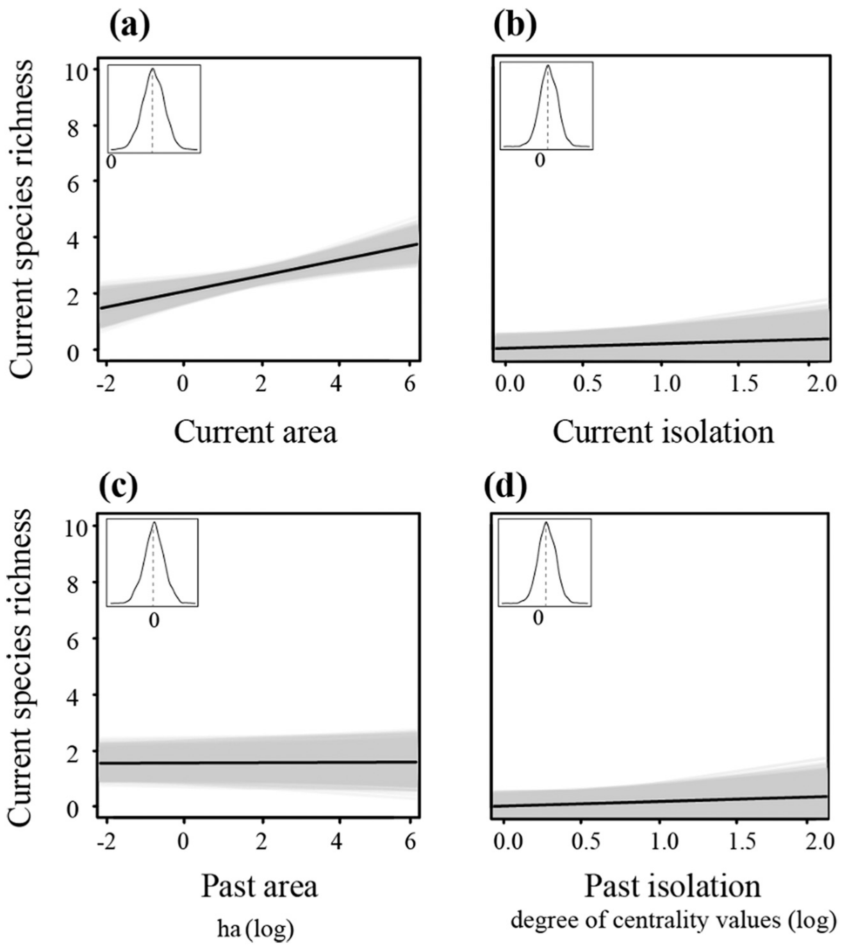

Fig. 2. Associations between observed species richness with area and isolation at both current and past landscape configurations. Species richness is only associated with current area (a). Black lines indicate the strength of the association from the most probable line representing each association, and gray lines indicate 3000 other possible associations. Posterior probability distribution of the slope parameters are at the small graphs in the top left. Species richness, area and isolation were log-transformed.

in simple regression models using observed or predicted species richness ($p < 0.001$; $R^2_{obs} = 0.25$; $R^2_{pred} = 0.55$; log-log scale regression), almost all the variation explained by past area could be attributed to the tendency of larger fragments to remain large over time ($R^2_{\text{exclusive past}} < 0.04$; $R^2_{\text{shared explained; obs}} = [0.25;\ 0.52]$; $R^2_{\text{shared explained; pred}} = 0.52$). In contrast, current area explained more variation in species richness ($p < 0.001$; $R^2_{obs} = [0.47;0.76]$; $R^2_{pred} = 0.76$; log-log scale regression) and a large portion of the variation could not be attributed to past patch area ($R^2_{\text{exclusive present}} > 0.23$ $R^2_{\text{shared explained; obs}} = 0.25$; $R^2_{\text{shared explained; pred}} = 0.52$). In addition, recently created patches rapidly accumulated species – the most recently created patch (8 years old) had 22 species observed.

Despite the low effect of noise on species occupancy and species richness ($a = 0.1$), species occupancy decreased with noise ($h_1 = -108.09$; $sd = 63.46$). The complete model including noise, and current and past extinction and immigration rates (ecological process) explained 58% of the variation in species richness among patches.

4. Discussion

We assessed how area and isolation of urban forest patches in a South American city were associated with temporal changes of birds extinction and immigration rates. Variation in bird richness among patches was mostly associated with differences in the balance between area-driven extinction and isolation-driven immigration rates, although area had greater influence than isolation (Fig. 3). Species richness was strongly determined by current landscape configuration and even recent patches were close to the expected equilibrium based on their size and isolation (Fig. 2). These results indicate an absence of bird local extinction debts in urban environments as habitat loss may reduce species diversity to a new equilibrium in very short periods (less than 10 years; see results).

Patch area has been suggested to determine species richness in fragmented urban landscapes (Beninde et al., 2015; Fattorini et al., 2018). Larger patches 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 patch area can remove micro-habitats and decrease population size, rapidly increasing extinction rates (Halley et al., 2016). Additionally, the low number of species in smaller patches could increase extinction rates because stochastic fluctuations locally eliminate species in a relatively short time (a neutral process; Halley and Iwasa, 2011). In line with these expectations, our results indicate that extinction rates are higher in smaller patches, and consequently these patches have lower species richness (Halley and Iwasa, 2011; Beninde et al., 2015). For example, we found the number of species at the dynamic equilibrium was 58 species for a patch of 836.502 ha, whereas 31 species were estimated to occur in a patch of 0.066 ha (Fig. 3; Table A1). Further, the largest patch is more isolated but it still holds 2 fold more species than the smallest but less isolated patch. Although, in occupancy model, species richness could have been overestimated in small patches due to the presence of transient species and the low detection rates, the high number of species accumulated with the increase in area indicates that most species are affected by the increase of forest cover. Moreover, results using raw species counts (not correcting for detection) still show qualitatively similar results, demonstrating a rapid increase in species richness with area, likely caused by the reduction in local extinction. Therefore, differences in bird diversity can be explained almost entirely by differences in extinction rates between areas.

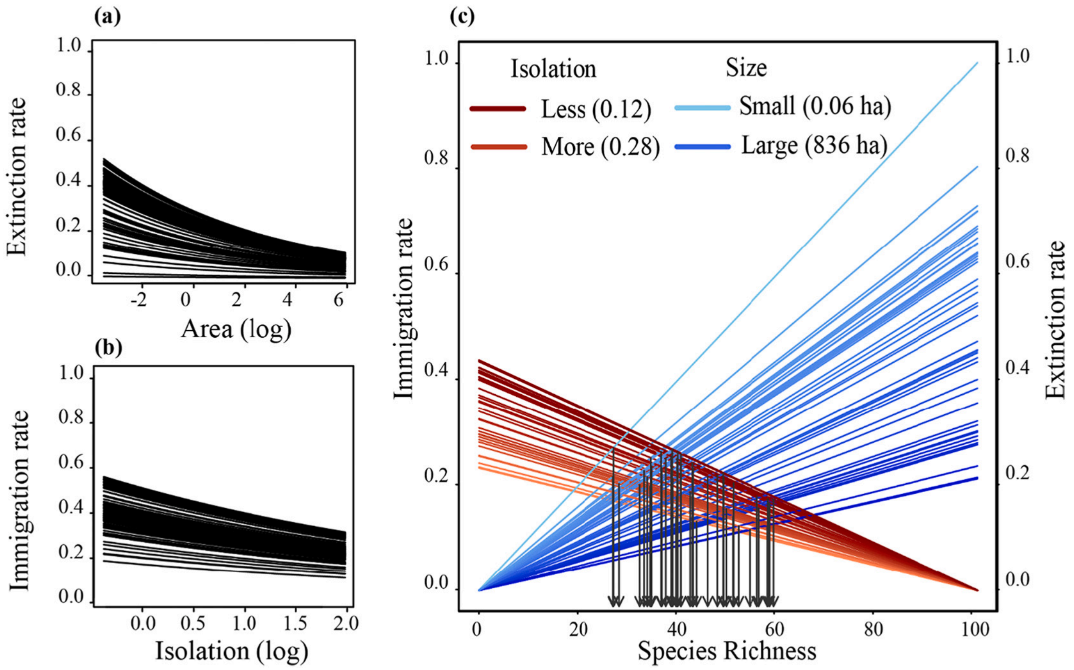

Fig. 3. Influence of area and isolation on bird species extinction and immigration rates. (a) Area has a negative effect on extinction rates and (b) isolation has a slightly negative influence on immigration rates. (c) Island Biogeography Theory dynamic equilibrium of species richness, varying from 31 to 59 species, depends mostly on patch size. Less isolated patches (dark red) have higher immigration rates compared to more isolated patches (light red); however, the influence of isolation is small as area is the main predictor for species richness. Larger patches (darker blue) have lower extinction rates and reach the equilibrium between extinction and immigration rates with more species than smaller patches (light blue). The numbers following the “Less and More”, “Small and Large” in the legend indicate the range of values analyzed. Area and isolation were log-transformed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

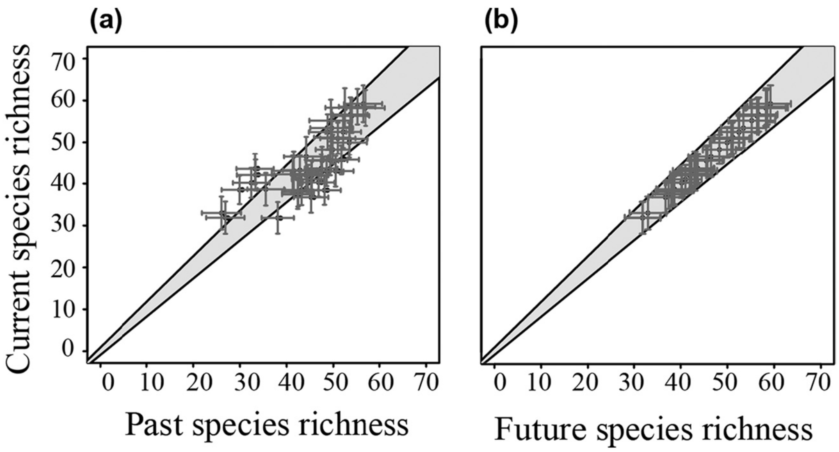

Fig. 4. Associations among species richness predictions through time. Strong association between (a) current and past, and (b) current and future species richness is an evidence of the lack of extinction debts in urban environments. The term “past” represents the spatial configuration of area and isolation before the most abrupt change in area, while “current” is the configuration after the most abrupt change, and “future” represents the predictions 100 years from now. Gray lines represent the expectation of balance of extinction and immigration rates. As all data points are within the gray line, this indicates a balance in species richness among periods. If the system were not in balance (i.e. extinction debt) future projections for bird richness could be much less than is currently projected. Gray arrows represent the standard deviation.

Despite the clear effect of area on extinction rates, previous theoretical metapopulation (e.g. Levins, 1969; Hanski and Ovaskainen, 2003) and metacommunity models (Leibold et al., 2004) have also demonstrated that patch isolation affects 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 and Stouffer, 2016; Maseko et al., 2020). In our model, which combines both the mechanisms of theoretical models and empirical data on bird species distribution, we found evidence for a slightly negative relationship between immigration rates and patch isolation. Importantly, in our model we considered the matrix as homogeneous and unfavorable for all species persistence, which could soften the effect of isolation (Cook et al., 2002). Additionally, our study area is an island at only 500 m off the coast, with potential immigration events coming from the mainland. However, supporting our conclusion of the small effect of immigration on species richness, we tested two different metrics of isolation and the result remained similar: small effects of isolation on species richness (Figs. A2–4). Hence, a greater importance of area on species richness and, thus, the large effect of extinction rates, might explain why some previous correlative studies have found habitat area to be much more important than isolation/ fragmentation per se on species diversity (Fahrig et al., 2019).

In addition to the stronger effect of area than isolation, a potential cause for the disagreement between theoretical and empirical studies could be that in most empirical studies, patch size and isolation are correlated with each other (Hanski, 2015). Moreover, statistical models used in empirical studies are rarely mechanistic (but see Lasky et al., 2017), with few direct quantifications of how area and isolation directly affect species extinction and immigration rates. Finally, previous empirical studies do not consider potential delays between fragmentation and biodiversity loss (Figueiredo et al., 2019). In spite of all these potential problems in empirical studies, we demonstrated that habitat size is more deterministic than isolation in the urban context by using uncorrelated data in a mechanistic Island Biogeographic model. Though we were unable to capture all landscape alterations (e.g., novel foods sources or unfamiliar enemies; Sol et al., 2013), by capturing the main alterations in the landscape caused by urbanization (habitat loss and isolation) we were able to explain 58% of all variation in species richness.

By integrating the history of urban fragmentation into mechanistic models, we demonstrated that bird communities in urban landscapes are likely to be at equilibrium or near equilibrium, with no apparent extinction debts. Larger patches had higher species richness regardless of the time since the patch change (Figs. 3–4), corroborating the great effect of area on species richness (Halley and Iwasa, 2011). This result could be explained by birds having a short-term response to habitat loss (short relaxation time), in which current habitat configuration and species richness are associated, or it could be that habitat loss has not been dramatic enough to induce the long-term effects (extinction debts). However, the second scenario is less likely because some patches suffered area loss of almost 85% (Table A1). Additionally, the fact that a recently created patch (less than 10 years since the patch change) already has 22 species (see results) corroborates the rapid response of birds to habitat loss.

5. Conclusions

Our results indicate that both small and large patches are close to equilibrium and the similar response of species in all patches, regardless of size or fragmentation history, may suggest that birds have a quick response to habitat loss with no apparent extinction debts. Habitat loss is the most important cause of species local extinctions in urban areas, and cities could rapidly promote biodiversity by maintaining or restoring forest cover. This result likely applies to other cities around the world with similar urban contexts (i.e. recent urban expansion in tropical environments). At the scale of a city or local disturbed areas, species can disperse from one patch to another and extinctions are likely to occur rapidly after habitat change (Krauss et al., 2010). However, 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 at broad scales might be different than for a single city scale, and extinction and immigration processes could still create long extinction delays (Hahs et al., 2009; Bommarco et al., 2014). Therefore, future research should integrate mechanistic models at broader spatial scales to understand the long-term impact of urbanization globally.

Data accessibility

The data supporting the results as well as R codes to run our models and replicate our results are archived in Figshare repository (https://doi.org/10.6084/m9.figshare.12217694) under the CC-BY 4.0 license (free to use and distribute).

CRediT authorship contribution statement

Gabriela Dri: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – Original Draft, Visualization. **Carla Fontana:** Conceptualization, Methodology, Writing – Review & Editing. **Cristian Dambros:** Conceptualization, Methodology, Formal analysis, Writing – Review & Editing, Visualization.

Declaration of competing interest

The authors have no competing interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109064.

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