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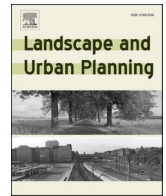
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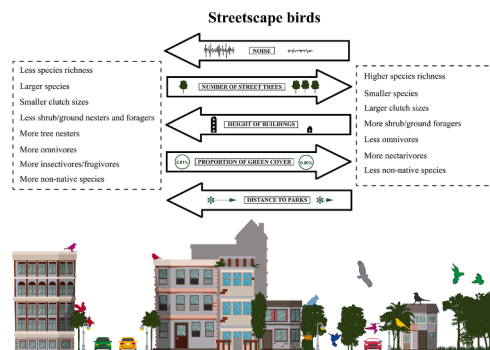
## The relationships between urbanization and bird functional traits across the streetscape

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## HIGHLIGHTS

- We assessed bird traits-environment relationships across a tropical streetscape.
- Environmental attributes presented diverse relationships with species and traits.
- Mostly noise and green cover modulated birds' functional and taxonomic compositions.
- We observed streets with similar community profiles shaped by environmental conditions.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

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## ABSTRACT

The urbanization process leads to changes in bird communities' taxonomic and functional compositions. Highly urbanized areas generally exhibit a reduced number of bird species sharing few functional traits. However, most urban bird studies focused on vegetation patches in temperate cities. In this study, we investigate how urban environmental attributes – noise, height of buildings, and urban vegetation characteristics – modulate species occurrences and the distribution of functional traits across the streetscape of a tropical metropolis. We predicted diverse trait-environment relationships, but that highly urbanized contexts (e.g., noisy streets with tall buildings) would be mostly occupied by a lower number of species sharing generalist traits. We also predicted to observe

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streets with similar community composition (profiles) shaped by environmental conditions and interspecific interactions. We applied hierarchical modelling of species communities as a flexible framework for analysis of community data. We observed that, increased noise exposure and reduced green cover were negatively related with species richness due to their negative relationships with most species' occurrences. On the other hand, larger number of trees and higher proportion of green cover presented mostly positive relationships with occurrences, and thus with species richness. Throughout our streetscape, community composition was highly heterogeneous and similar conditions led to similar profiles. For example, noisy streets may favor the presence of omnivorous and large-bodied species, while wooded streets may allow for the presence of smaller-bodied forest specialist species that exploit lower vegetation strata. Our results indicate that streetscapes may have the potential to harbor functionally and taxonomically diverse bird communities.

## 1. Introduction

Birds comprise a highly conspicuous group in which species present different sensitivities to urbanization. Consequently, represent one of the most frequently studied organisms inhabiting urban landscapes. One of the main factors that determine if a bird species will thrive or perish within cities is its specific combination of morphological and life-history characteristics (hereafter functional traits), such as diet, body size, foraging strategies, and nesting behavior (Crocì, Butet, & Clergeau, 2008; Jokimäki, Suhonen, Jokimäki-Kaisanlahti, & Carbó-Ramírez, 2016; Lepczyk et al., 2008; Patankar, Jambhekar, Suryawanshi, & Nagendra, 2021). As urbanization intensity increases, we tend to observe a reduction in overall bird species richness and abundance, while few species sharing generalist traits tend to dominate highly urbanized areas (e.g. rock dove and house sparrow) (Sol, González-Lagos, Moreira, Maspons, & Lapedra, 2014; Sol et al., 2020). However, urban landscapes are composed by a mosaic of habitats (e.g. wooded streets, urban parks, buildings, vacant lots) that differ in occupation histories, socioeconomic characteristics, and environmental conditions that vary not only between cities but also throughout the same urban landscape (Lepczyk et al., 2017; Melo et al., 2022; Ramalho & Hobbs, 2012; Sol, Bartomeus, González-Lagos, & Pavoine, 2017; Sol et al., 2020). Therefore, species that will thrive or perish throughout the different urban habitats will not only vary in their taxonomic and functional compositions but can also be diverse both within and among cities. As an example, urbanization may inflict strong negative effects on reproduction, since the loss of vegetation strata and the abundance of predators in highly urbanized areas may exclude birds with unique and restrictive reproductive traits, such as shrub and ground nesters (Brown & Graham, 2015; Coetzee & Chown, 2016; Crocì et al., 2008; Jokimäki et al., 2016; Pinho et al., 2016). On the other hand, high vegetation complexity (e.g. presence of standing dead trees and high canopy cover) in more preserved forest patches can facilitate the presence of specialized migratory species (Buron, Hostetler, & Andreu, 2022) or species that need natural hollows to reproduce (Campos-Silva & Piratelli, 2020). These differences indicate that birds select urban habitats based on the variation of local conditions that offer adequate resources according with species' functional traits (Buron et al., 2022). Therefore, it is not possible to determine an ideal combination of traits for birds to thrive across urban landscapes worldwide (Crocì et al., 2008; Sol et al., 2014).

Despite the increasing number on urban biodiversity studies in tropical cities in the last decade, especially in Latin American countries (McDonald et al., 2020), most studies assessing urban bird trait-environment relationships were conducted in temperate cities and focused on communities inhabiting vegetation patches or other urban green spaces (e.g., cemeteries, wastelands) (Patanekar et al., 2021; Pena & Martello, n.d.). Nevertheless, disturbances such as exposure to noise and higher temperatures may be buffered within these areas, and birds may respond differently from those inhabiting unusual urban habitats (Curzel, Bellocq, & Leveau, 2021; McDonald et al., 2020; Melo et al., 2022; Pena et al., 2017; Schütz & Schulze, 2015). For instance, the streetscape (i.e., all components related to streets in cities, including streets and roads, sidewalks, surrounding vegetation, buildings, and other structures) is a highly harmful urban context for birds. The

elevated noise levels have negative effects on bird taxonomic and functional diversities, and communities are dominated by a reduced number of species sharing few generalist traits (Curzel et al., 2021; Pena et al., 2017). On the other hand, some aspects of the streetscape design, mostly related to characteristics of the roadside vegetation, can mitigate the negative influences of disturbances on bird communities by providing resources, refuges and substrate for nesting, perching and foraging (Falfán & MacGregor-Fors, 2016; Leveau & Leveau, 2020; Morelli, Beim, Jerzak, Jones, & Tryjanowski, 2014). Higher tree species richness, larger trees, and higher proportion of green cover across the streetscape are positively related to functional and taxonomic richness of birds in the streets (Curzel et al., 2021; Leveau & Leveau, 2020; Pena et al., 2017). Thus, birds inhabiting the streetscape are an interesting model for assessing how highly stressful urban conditions modulate bird functional traits. Despite the potential of the streetscape vegetation to offer habitat and resources for urban bird communities (Leveau & Leveau, 2020; Pena et al., 2017; Wood & Esaian, 2020; Young, Daniels, & Johnston, 2007), there is a knowledge gap regarding studies addressing trait-environment relationships of birds inhabiting tropical streetscapes (Pena & Martello, n.d.).

In this study, we assessed how environmental attributes describing streetscape conditions may modulate taxonomic and functional compositions of an urban bird community inhabiting the streetscape of a tropical metropolis. Since the incrementation of aspects related with the roadside vegetation (e.g. amount of green cover, tree species diversity) would lead to a higher bird species richness and a more diverse composition of functional traits (e.g. da Silva, Pena, Viana-Junior, Vergne, & Pizo, 2020; Leveau & Leveau, 2006; Leveau & Leveau, 2020; Pena et al., 2017), while increasing noise exposure and the height of buildings would lead to an impoverished community dominated by generalist functional traits (e.g. omnivorous birds) (Curzel et al., 2021; Leveau & Leveau, 2006; Leveau & Leveau, 2020; Loss, Will, Loss, & Marra, 2014; Machtans, Wedeles, & Bayne, 2013; Pena et al., 2017), we predicted that streets in greener areas (higher number of most native street trees, higher proportion green cover, near urban parks, with lower traffic noise, and surrounded by houses), would harbor a higher species richness of mainly native bird species with diverse functional traits' compositions. Since characteristics at the local scale (e.g. number and diversity of street trees) would influence the ability of birds to exploit streets as habitats based on their functional traits composition, (Buron et al., 2022; Leveau & Leveau, 2020; Pena et al., 2017), we predicted to find a variety of traits and species compositions between sites across the streetscape. At the same time, since the bird community may be partially shaped by the influences of similar environmental attributes between sites (e.g., high noise exposure) and by species-to-species interactions not related to the environment (e.g., negative relationships between native and non-native bird species) (Ovaskainen et al., 2017), we also predicted that sites with similar environmental conditions would harbor similar species and traits compositions (community profiles) and to observe positive and negative associations between species across the streetscape. Testing these hypotheses may add to our knowledge on how urban environmental conditions modulate bird communities inhabiting urban contexts outside the boundaries of green spaces.

## 2. Material and methods

### 2.1. Study area and bird community data

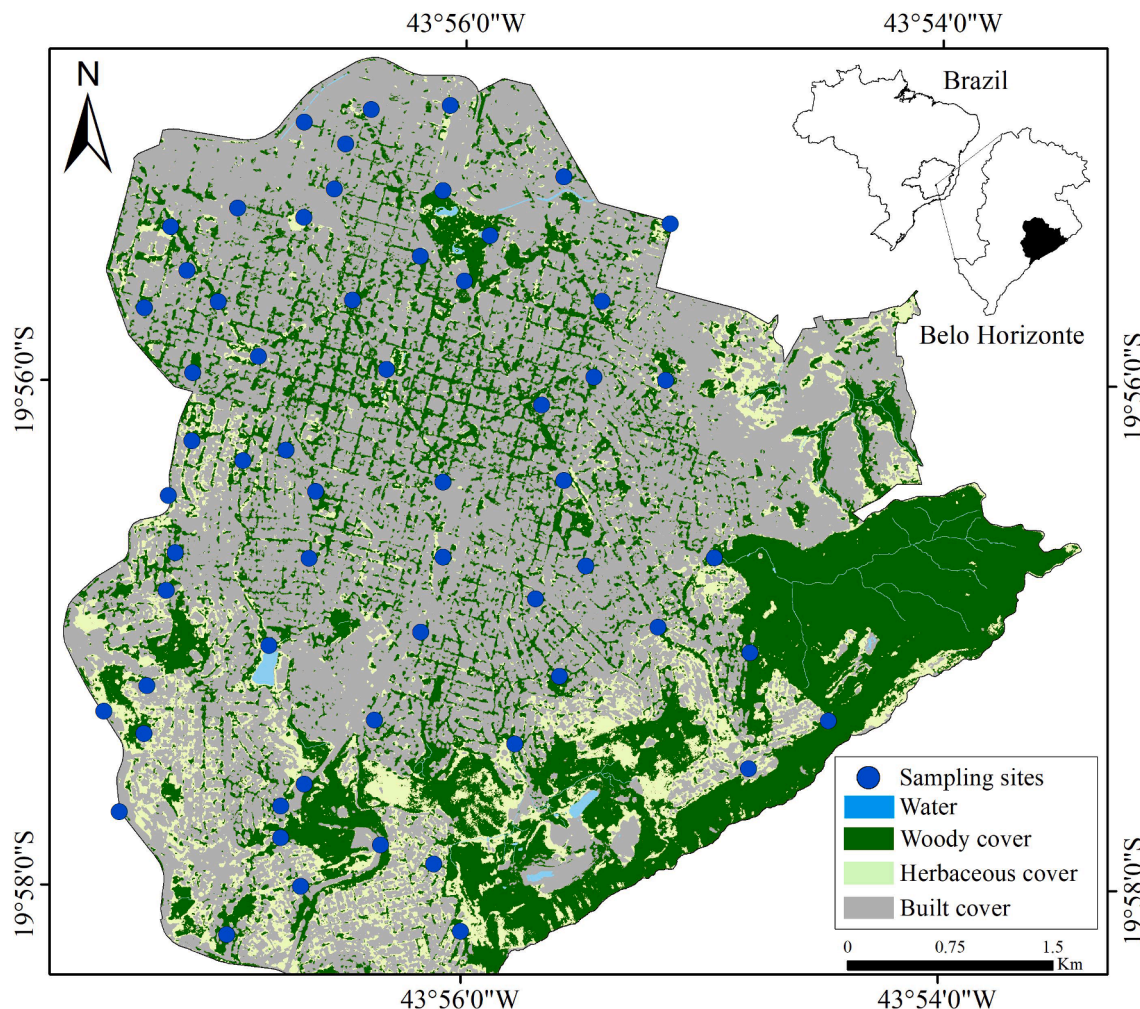
We conducted this study in Belo Horizonte (19°55'08"S 43°56'18"W; ~850 m a.s.l.), one of the largest Brazilian metropolises, with a population of over 2.5 million people and an area of 331 km<sup>2</sup> (IBGE, 2022). The city is located in the transition zone between the Atlantic Forest and Cerrado biomes and is divided into nine administrative regions, each one with its own socioeconomic (e.g., wage level, human development index) and environmental (e.g., amount of vegetation, number of protected areas) characteristics (Goulart, Teixeira, & Young, 2010). The study area is the southern region of Belo Horizonte, which includes the oldest part of the city established in 1897 and a highly heterogeneous streetscape, from residential streets to high traffic avenues and highways (Fig. 1). The southern region of Belo Horizonte covers 31.7 km<sup>2</sup> and almost half of its landscape is occupied by woody and herbaceous vegetation (14.44 km<sup>2</sup>) concentrated within urban parks, gardens and streets (Pena et al., 2016) (Fig. 1). The urban afforestation process is composed of a large tree species pool (475 species), but dominated by a few species, mainly non-natives to Brazil (Pena et al., 2016).

We obtained bird community data from Pena et al. (2017). Between September 2014 and January 2015 (Spring-Summer in the Southern Hemisphere), the authors conducted three 20 min visits in 60 sampling sites distributed throughout the streetscape of the study area (Fig. 1). Time frame was defined by the authors after a pilot study, because they

continued to find new species after 10 min point counts (Pena et al., 2017). The database was comprised of 73 bird species (distributed in 26 families and 12 orders) from which 68 were considered in our analyses (Table S1) as we removed two species that were not fully identified to species level and three species with singular habits (e.g., *Ardea alba*, the only aquatic species). As bird functional traits, we selected mean clutch size (number of eggs per clutch), body mass (g), diet (carnivorous, seed/fruits, invertebrates/fruits, nectarivorous or omnivorous), foraging substrate (ground, lower vegetation strata or upper vegetation strata), and nesting location (tree, shrub/ground or cavity), which are phenotypic characteristics related to bird responses and survivability to environmental changes (Brown & Graham, 2015; Luck, Lavorel, McIntyre, & Lumb, 2012). Data about the functional traits were obtained from published literature (Del Hoyo, Elliot, Sargatal, & Christie, 2004; Wilman et al., 2014). We also classified each species according to its origin (native or non-native to Brazil).

### 2.2. Multiscale urban environmental attributes

As predictor variables, we selected urban environmental attributes that have previously been shown to be related to distributions of bird traits within urban landscapes (Alberti et al., 2016; Leveau & Leveau, 2020; Pena et al., 2017). To describe noise exposure (dB), we used ambient noise data measured by Pena et al. (2017) simultaneously with the bird observations and calculated the average Equivalent Continuous Sound Level ( $L_{eq}$ ) index for each survey site (S1 Text). We also



**Fig. 1.** Land cover map of the southern region of Belo Horizonte (Minas Gerais, Brazil), highlighting the 60 survey sites where bird data was gathered by Pena et al. (2017).

calculated, the average Euclidian distance (m) between each survey site and all urban parks in the study area. To obtain information about the height of buildings, the proportion of green cover, the number of street trees (hereafter number of trees), and the proportion of native street tree species (hereafter proportion of native trees) surrounding the survey sites across the streetscape, we adopted a multiscale approach (S1 Text). We extracted data from buffers of various sizes and compared Pearson's correlation between the values extracted for each environmental attribute and bird species richness across the streetscape (S1 Text, Figs S1-S4). For each environmental attribute, the predictor variable was defined as the buffer size of which the values presented the highest correlation with species richness (S1 text, Figs S1-S4). Thus, for average height of buildings we extracted data from 750 m radius buffer; for proportion of green cover, 75 m radius buffer; number of trees, 200 m radius buffer; proportion of native trees, 50 m radius buffer. All the final predictor variables presented Pearson's  $r < 0.53$ , which we assessed by a pairwise comparison considering all predictors (Fig. S5). The approaches adopted for obtaining information on each streetscape environmental attribute are described in the Supporting Information (S1 Text).

### 2.3. Data analysis and scenarios' simulations

We analyzed the data with Hierarchical Modelling of Species Communities (HMSC) as a general, flexible Bayesian framework for modern analysis of community data. While non-manipulative data allow for only correlative and not causal inference, this framework facilitates the formulation of data-driven hypotheses regarding the processes that structure communities (Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017), an approach that belongs to the class of Joint Species Distribution Models (JSDM; Warton et al., 2015). In these analyses, we considered each point count as one sampling unit. In the HMSC analyses, we included data on species abundances (matrix  $Y$  of sampling units times species), environmental variables (matrix  $X$  of sampled locations times the included predictor variables), species traits (matrix  $T$  of species times the included traits), taxonomic relationships among the species (a taxonomic tree with levels of species, genus, family, and order; assuming equal branch length for each taxonomic level), and the spatial coordinates.

As the response variable (i.e., components of the matrix  $Y$ ), we considered the vector of species counts for each survey site. To account for the zero-inflated nature of the data, we applied a hurdle approach in which we first modelled species occurrences (i.e., presence-absence) with a probit regression and then modelled their abundance conditional on presence with a log-normal regression. As potential predictor variables (i.e., fixed effects included in the matrix  $X$ ), we included (predictor P1) average  $L_{eq}$  (i.e. noise – dB), (P2) average building height (m), (P3) number of trees, (P4) proportion of native trees, (P5) average distance to urban parks (m), and (P6) proportion of green cover. We utilized the geographic coordinates of the sampling locations to include a spatially explicit community-level random effect. As species traits (i.e., components of the matrix  $T$ ), we included (trait T1) the  $\log_{10}$ -transformed mean body mass, (T2) mean clutch size, (T3) an indicator variable describing if the species was non-native from the Brazilian territory, (T4) a classification of nesting site location as tree, shrub/ground or cavity, (T5) a classification of foraging substrate as ground, upper vegetation strata or lower vegetation strata, (T6) a classification of diet as carnivorous, seed/fruits, invertebrates/fruits, nectivorous, and omnivorous, and (T7) an indicator variable describing if the species was an inter-Neotropical migrant (hereafter migratory species).

To avoid the risk of overfitting, we reduced the number of models to be compared by first ranking the potential predictor variables *a priori* in terms of their expected importance considering previous findings (Pena et al., 2017) and our interest in assessing their relationships with bird traits. The predictor variables are ordered above in that order, i.e., we hypothesized that P1 is the most and P6 the least important. We then

constructed seven models out of which Model 0 is the null model containing no predictors, Model 1 contains predictor P1 (i.e. noise) only, Model 2 predictors P1 (i.e. noise) and P2 (i.e. average height of buildings), and so on, with Model 6 finally containing all predictor variables P1-P6. We compared these models by tenfold cross-validation and assessed their predictive power for presence-absence data by Tjur's  $R^2$  (defined as the difference between the mean predicted occurrence probability for the occupied units and the mean predicted occurrence probability for the empty units), and by the standard  $R^2$  for abundance conditional on presence.

We fitted all models with the R-package Hmsc (Tikhonov et al., 2020). For the preliminary analyses related to variable selection, we applied a single MCMC chain of length 15,000 iterations, out of which we ignored a transient of 5000 iterations and thinned the chain by 10 to yield 1000 posterior samples. For the final analyses with the selected model, we applied four MCMC chains each of length 1,500,000 iterations, out of which we ignored a transient of 500,000 iterations and thinned the chain by 1000 to yield 1000 posterior samples per chain and hence 4000 posterior samples in total.

We followed Ovaskainen et al. (2017) to perform a variance partitioning between the included environmental predictors and random effect. We examined the posterior distributions of the parameters  $\beta$  (species-specific responses to environmental predictors),  $\rho$  (phylogenetic signal in species responses to environmental covariates) and  $\Omega$  (residual species associations) of the HMSC model (Ovaskainen et al. 2017). To examine how the functional compositions of local communities depend on environmental predictors in more detail, we conducted a set of scenario simulations. In these simulations, we considered one of the environmental predictors (such as average building height) as the focal environmental predictor, the value of which we varied from the smallest to the largest observed in the data. We generated 4000 simulated communities (sampling the model parameters from the joint posterior distribution independently for each replicate) for each value that we assumed for the focal environmental predictor. When generating the predictions, we set the values of the non-focal environmental predictors to their mean value conditional on the value of focal environmental predictors. For each of the simulated communities, we computed its species richness, as well the community-weighted mean value of each trait. Finally, we identified streets with common bird community profiles by clustering sites with similar predicted bird communities. To do so, we applied k-means clustering to posterior means of the predicted occurrence probabilities.

### 3. Results

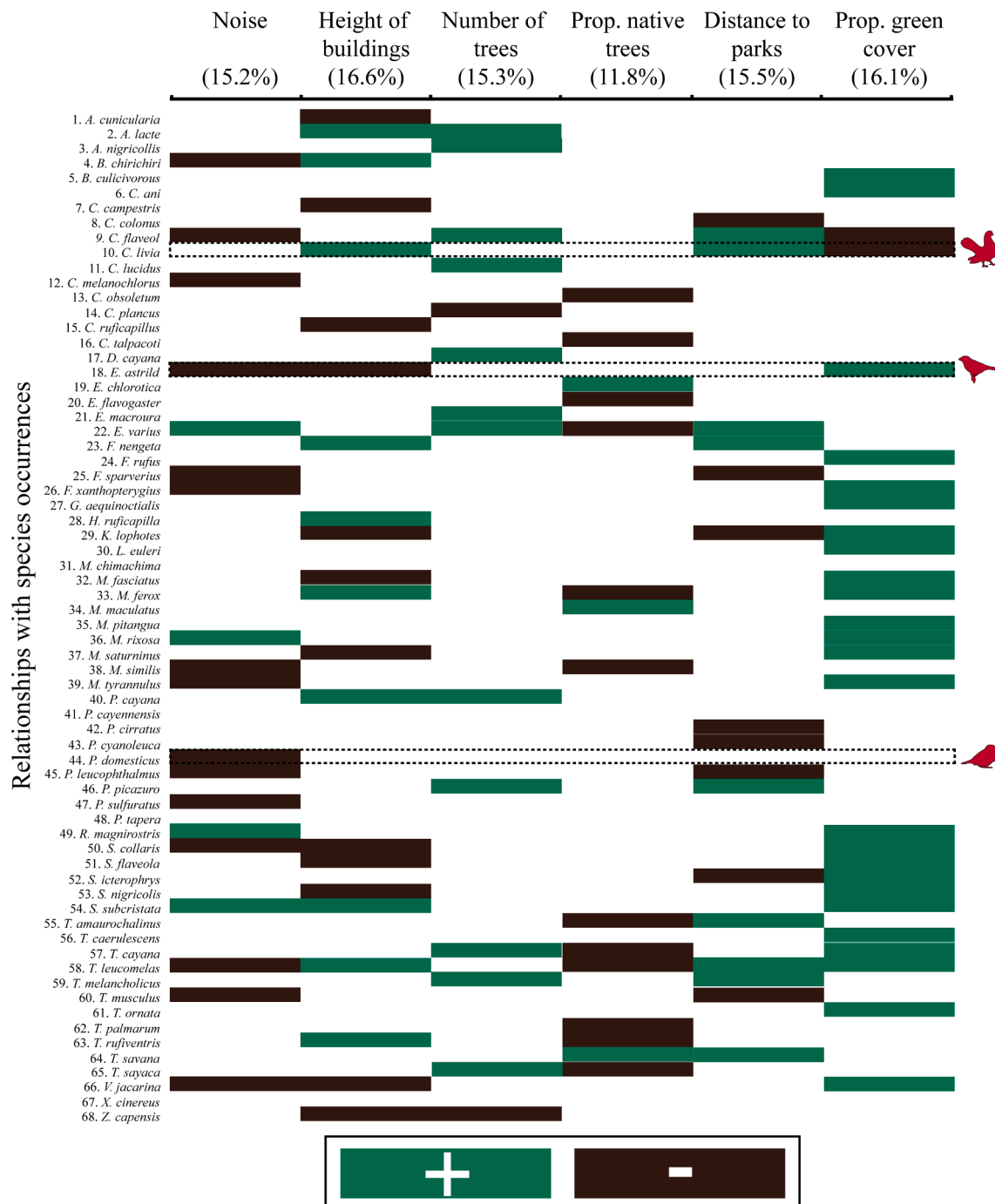
For the presence-absence data, Model 6 (which include all the predictors; P1-P6) was best supported in terms of predictive power, as it had the highest Tjur's  $R^2$  on average in the cross validation (0.042, Table 1, Text S2). For abundance conditional on presence, most models captured noise rather than signal, as most models except the null model (Model 0) had negative predictive power in the cross-validation. Thus, we did not pursue abundance analyses any further.

An evaluation of the MCMC convergence of the selected Model 6 showed satisfactory results, as the effective sample size was generally close to the actual sample size of 4000, and as the potential scale reduction factor was generally close to one (Text S2). The variance partitioning attributed (on average over the species) 15.2 % of the explanatory power to exposure to noise, 16.6 % to average height of buildings, 15.3 % to the number of trees, 11.8 % to proportion of native trees, 15.5 % to the distance to urban parks, 16.1 % to the proportion of green cover (Fig. 2), and 9.5 % to the random effect of the site. Among the species whose occurrences were associated to these six environmental predictors with a high level of statistical support, most species' presence was negatively related to exposure to noise, proportion of native trees, and distance to urban parks, and positively related to the number of trees and proportion of green cover, whereas some species

**Table 1**

Results from the model selection of the presence-absence model of birds inhabiting the streetscape of Belo Horizonte (Minas Gerais, Brazil). The measure of model fit (Tjur R<sup>2</sup>) is based either on explanatory power (model fitted to all data) or predictive power (tenfold cross-validation, indicated in the table by CV). (P1) average L<sub>eq</sub> (i.e. noise – dB); (P2) average building height (m); (P3) number of trees; (P4) proportion of native trees; (P5) average distance to urban parks (m); and (P6) proportion of green cover.

Model and the included predictors	6 (P1 to P6)	5 (P1 to P5)	4 (P1 to P4)	3 (P1 to P3)	2 (P1 and P2)	1 (P1)	0 (no predictors)
mean Tjur R <sup>2</sup>	0.147	0.128	0.116	0.096	0.071	0.045	0
mean Tjur R <sup>2</sup> (CV)	0.042	0.035	0.033	0.027	0.021	0.01	-0.015

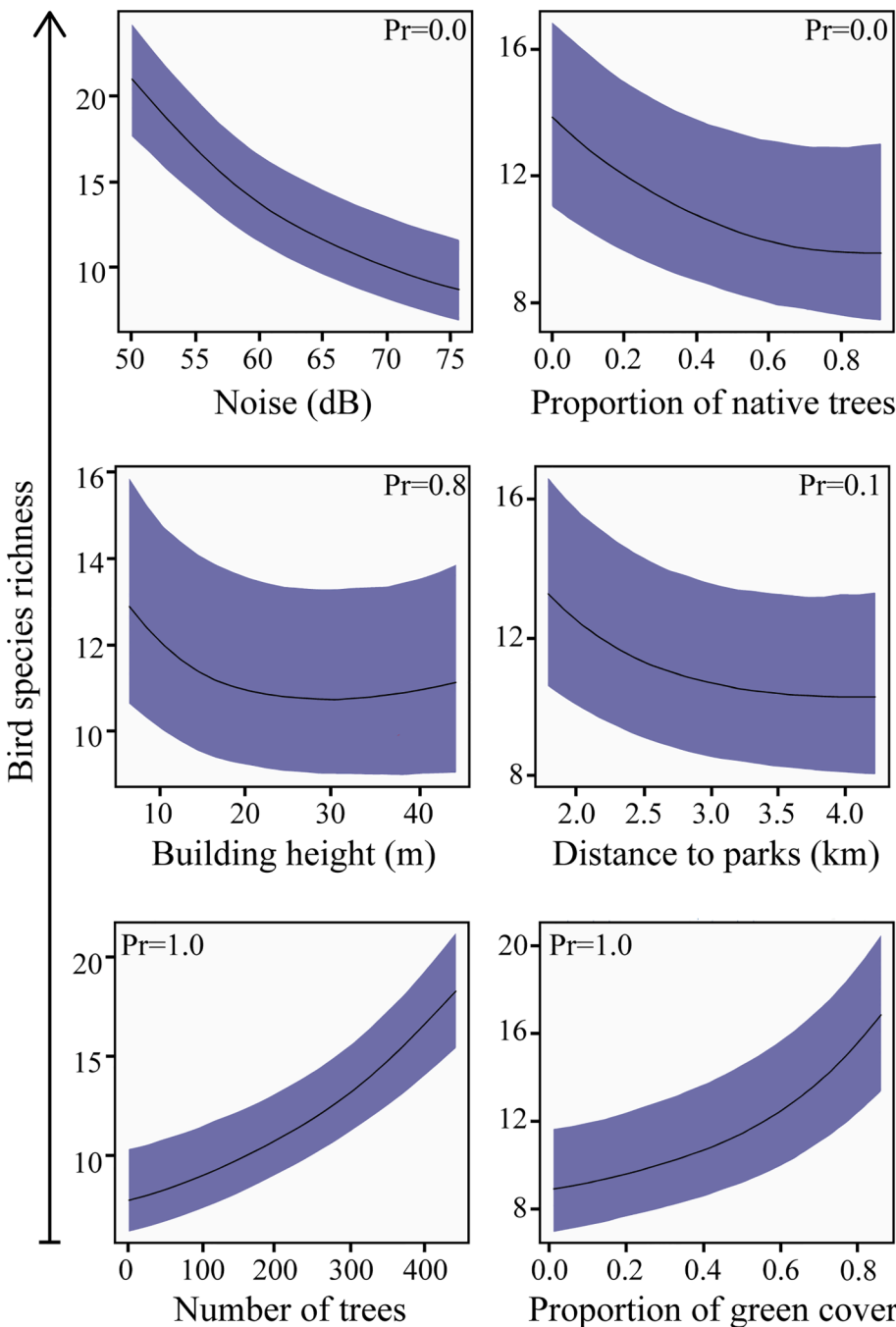


**Fig. 2.** Relationships between environmental predictors and species occurrences across the streetscape of the southern region of Belo Horizonte (Minas Gerais, Brazil). Colored lines indicate negative (brown) and positive (green) relationships between each environmental predictor and each species that are supported by at least 95% posterior probability. Values in parentheses indicate the proportion of variance explained by each environmental predictor. The numbers indicate each observed bird species according with [Table S1](#). Dotted lines highlight the results for non-native species.

presented positive and others negative relationships with the average height of buildings (Fig. 2, Table S1). As a result, species richness decreased with exposure to noise, proportion of native trees, and the distance to urban parks, increased with the number of trees and proportion of green cover, and was invariant in relation to the average height of buildings (Fig. 3). Interestingly, some of the streets with the highest proportions of native tree species are in some of the most urbanized regions of our streetscape (Fig. S4).

In terms of the influence of traits on the species responses to the environmental predictors, we found several statistically supported relationships (Table 2, Fig. 4). For example, the community-weighted mean body mass increased with noise (Table 2, Fig. 4A) and decreased with the number of trees (Table 2), and the proportion of species that nest and forage on the ground or lower vegetation strata decreased with noise (Table 2, Fig. 4A). We observed few statistically supported

residuals indicating positive associations between six native species: the Palmn (*Tangara palmarum*) and the Sayaca (*Tangara sayaca*) tanagers, the Boat-billed (*Megarynchus pitangua*) and the Social (*Myiozetetes similis*) flycatchers, the Bananaquit (*Coereba flaveola*), and the Yellow-chevroned Parakeet (*Brotogeris chiriri*) (Fig. S3). We did not obtain statistical support for or against the presence of taxonomic signal in the responses of the species to these environmental predictors, as the posterior median (95 % credibility interval) of the parameter  $\rho$  was 0.35 (0.00–0.94). We identified 10 common profiles across the streetscape presenting similar community compositions ( $R^2 = 0.62$ ), for example, in downtown and in greener residential areas near urban parks (Fig. 5). Some of these profiles are related to the noisiest and greyest streets, where low bird species richness (between 1 and 11 species) was also observed (Pena et al., 2017) (Figs. 5 and S4).

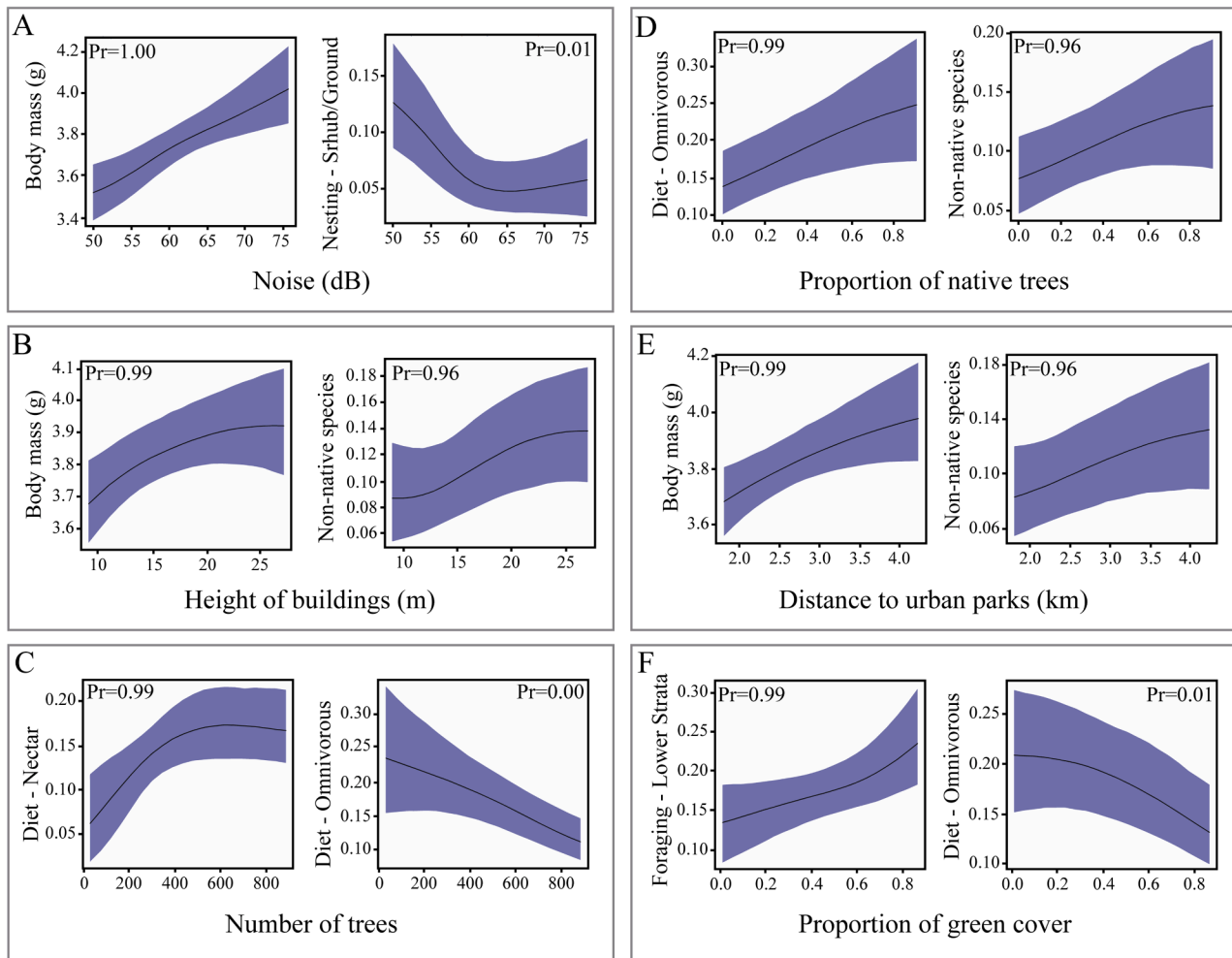


**Fig. 3.** Relationships between urban environmental predictors and bird species richness across the streetscape of the southern region of Belo Horizonte (Minas Gerais, Brazil). The lines and the shaded areas show the posterior means and 95 % credibility intervals of the model predictions. The value of probability (Pr = ...) on the top of each panel shows the posterior probability by which the species richness is higher for the highest value of the predictor than for the lowest value of the predictor. For example, value of Pr = 0.0 means the posterior probability by which the species richness is higher for the lowest value of the predictor, than for the highest value of the predictor is 1.0. Thus, Pr values close to zero and close to one correspond to statistically supported results.

**Table 2**

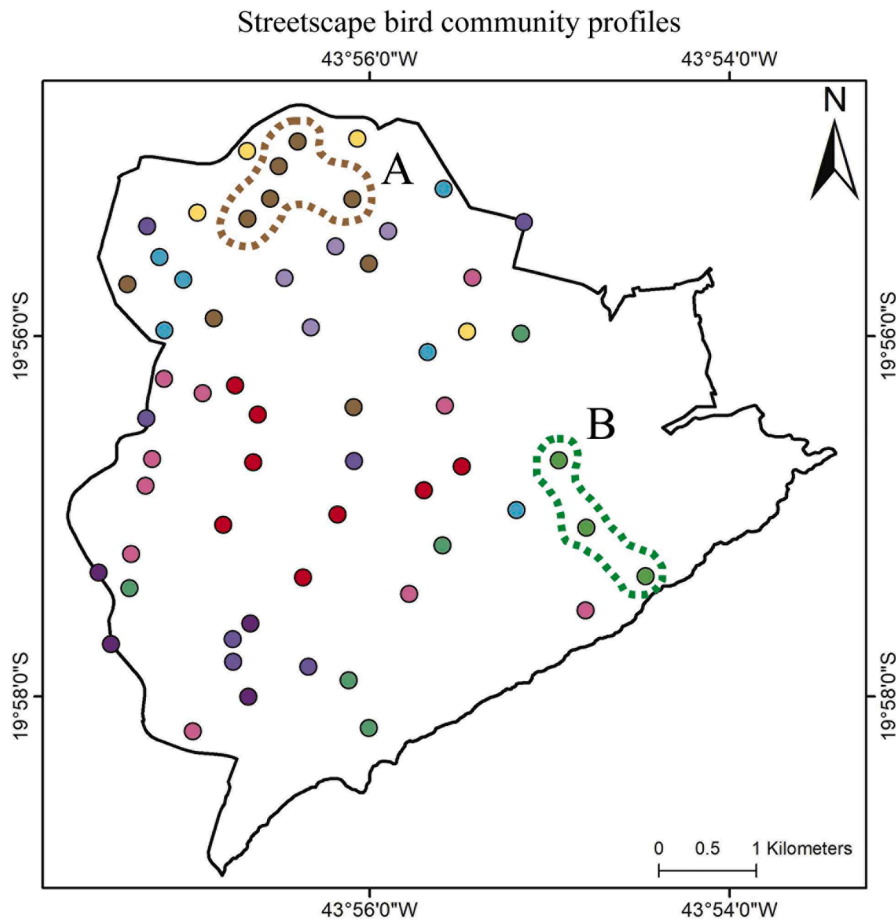
Relationships between environmental attributes and functional traits of birds inhabiting the streetscape of the southern region of Belo Horizonte (Minas Gerais, Brazil). Values show the posterior probabilities by which the community-weighted mean trait is higher when the environmental attribute has its maximal value (as observed in our data) compared to when the environmental attribute has its minimal value. Results highlighted in bold indicate positive (+) and negative (–) relationships with at least 95 % posterior support.  $L_{eq}$ : Average Equivalent Continuous Sound Level; Build. Height: Average height of buildings; #Trees: Number of trees; Prop. Native: Proportion of native tree species; Dist. Parks: Average distance to urban parks; Prop. Green: Proportion of Green Cover (woody + herbaceous cover).

Bird traits	$L_{eq}$	Build. Height	#Trees	Prop. Native	Dist. Parks	Prop. Green
Body mass	<b>1.000 +</b>	<b>0.986 +</b>	<b>0.000 –</b>	0.909	<b>0.998 +</b>	<b>0.003 –</b>
Clutch size	<b>0.000 –</b>	0.134	<b>0.981 +</b>	0.609	<b>0.009 –</b>	<b>0.998 +</b>
Nesting Shrub/Ground	<b>0.010 –</b>	<b>0.051 –</b>	0.232	0.087	0.826	0.890
Nesting Trees	<b>0.999 +</b>	0.661	0.536	0.649	0.713	0.138
Foraging Low Veg. Strata	<b>0.001 –</b>	0.384	0.619	0.309	0.470	<b>0.994 +</b>
Foraging Up. Veg. Strata	0.938	0.719	0.913	0.363	0.218	<b>0.024 –</b>
Diet Nectar	0.127	0.290	<b>0.999 +</b>	0.662	0.171	<b>0.040 –</b>
Diet Inv./Fruits	<b>0.957 +</b>	0.888	0.074	<b>0.023 –</b>	<b>0.978 +</b>	0.295
Diet Omnivorous	<b>0.974 +</b>	0.892	<b>0.003 –</b>	<b>0.994 +</b>	0.933	<b>0.014 –</b>
Migrant	<b>0.999 +</b>	0.705	<b>0.004 –</b>	0.763	<b>0.992 +</b>	0.113
Non-native	0.802	<b>0.959 +</b>	0.058	<b>0.963 +</b>	<b>0.963 +</b>	<b>0.046 –</b>



**Fig. 4.** Predictions over environmental gradients, exemplifying statistically supported relationships between environmental predictors and functional traits of birds inhabiting the streetscape of the southern region of Belo Horizonte (Minas Gerais, Brazil). The lines and the shaded areas show the posterior means and 95% credibility intervals of the model predictions. The value on the top of each panel shows the posterior probability by which the response variable is higher for the highest value of the predictor than for the lowest value of the predictor. A. Noise (db); B. Height of buildings (m); C. Number of trees; D. Proportion of native trees; E. Distance to urban parks (km); F. Proportion of green cover.





**Fig. 5.** Streets with similar bird community composition identified across the streetscape of the southern region of Belo Horizonte (Minas Gerais, Brazil). Point colors represent the ten distinct community compositions (profiles), highlighting the high heterogeneity observed across the assessed streetscape. It is possible to observe groups of streets with similar community compositions, such as in downtown near the Belo Horizonte Bus Station (brown points surrounded by the brown dashed line, A) and in residential and greener neighborhoods, near urban parks (green points surrounded by the green dashed line, B). This figure has been designed using resources from [Freepik.com](https://www.freepik.com).

A. Noisy streets, surrounded by reduced green cover, tall buildings, low number of trees, and distant from urban parks



- Profile:**
- Non-native species
  - Less native species richness
  - Large-bodied species
  - Omnivorous
  - Exploit upper vegetation strata
  - Smaller clutch sizes

B. Streets with low traffic noise and surrounded by houses, high number of trees and proportion of green cover, and near urban parks



- Profile:**
- Higher native species richness
  - Smaller species
  - Larger clutch sizes
  - Forest specialist species
  - Exploit lower vegetation strata

#### 4. Discussion

We observed that highly urbanized areas in the studied streetscape may be occupied by a reduced number of species that share mostly generalist traits, such as large-bodied birds that exploit upper layers of vegetation for nesting and foraging. Traits and consequently species occurrences presented diverse relationships with each environmental predictor, leading to a high heterogeneity of species and traits composition across the same streetscape, explained by the presence of ten common profiles. We observed positive associations between six native species, all of which exploit upper vegetation strata for nesting and foraging. Thus, the ten common profiles may be mostly determined by similar species responses to the environmental predictors but can also be influenced by species interactions. Therefore, streetscape bird communities can be diverse depending on the variation of local conditions.

Noise exposure modifies bird physiology and communication (frequency, duration and complexity of vocalizations) and reduces reproductive success (Shannon et al., 2015). Thus, as demonstrated in other studies (Curzel et al., 2021; Pena et al., 2017), we recorded less bird species richness in the noisiest streets. The height of buildings can represent a limitation to the presence of birds across the streetscape (low permeability related to window strikes (Loss et al., 2014; Machtans et al., 2013), but may also provide opportunities for species to thrive by providing nesting substrates, for example (Lizée, Mauffrey, Taton, & Deschamps-Cottin, 2011; Partridge & Clark, 2018). Therefore, we did not observe a clear relationship between bird species richness and the average height of buildings surrounding streets.

With regards to the urban vegetation, we observed positive relationships between bird species richness and both the number of trees and the proportion of green cover. Across the streetscape, woody vegetation, especially street trees, provide a variety of biotic and abiotic benefits for birds, such as foraging and nesting substrate, food resources (e.g., fruits, flowers and insects) and attenuation of disturbances such as noise and air pollution (Dias de Oliveira, Biondi, Batista, Nunho dos Reis, & Nesi, 2018; Faeth, Warren, Shochat, & Marussich, 2005; Young et al., 2007). The farther the streets are from urban parks across the assessed streetscape, the lower the bird species richness was in these streets, demonstrating the importance of habitat patches for birds inhabiting the urban matrix (MacGregor-Fors, Morales-Pérez, & Schondube, 2010; Melo et al., 2022). At the same time, the large variance observed in this relationship may be related with the presence of species that preferentially occupy more urbanized areas far from urban parks, such as the Rock Dove (*Columba livia*).

We observed a negative relationship between proportion of native trees and bird species richness. Streets surrounded by the highest proportions of native trees across the studied streetscape are mostly located in highly urbanized regions. Thus, other environmental predictors that explained a higher proportion of the variance on species occurrences may have higher influences on the community, such as exposure to noise and proportion of green cover. At the same time, non-native trees may have an important role providing resources for birds because they usually comprise ornamental plant species with remarkable flowering periods and adaptations to the harsh conditions of cities. Among the most abundant tree species in our study area, most are non-natives (Pena et al., 2016), thus bird species may be more adapted to exploit resources from such trees.

Across the assessed streetscape, noisy streets surrounded by tall buildings may be occupied by large-bodied species, with smaller clutch sizes. Stressful conditions and high abundance of predators may favor species that focus their reproductive effort in smaller breeding attempts and in fact, smaller clutch sizes were already reported for urban dwellers (Sol et al., 2014). Regarding body mass, larger species may deal better with disturbances in urban sites with a high number of vehicles and people in circulation. This result is in accordance to a previous study that showed that large bodied species seem to be less afraid of humans, demonstrated by their smaller flight initiation distances (delBarco-

Trillo, 2018). However, our results do not present substantial support to assess relationships between urban environmental attributes and size of the overall bird diversity. Some large bodied species, such as ground-dwelling large-bodied birds (e.g. Galliformes and Gruiformes), were absent in our study and usually are negatively related to urbanization (Coetzee & Chown, 2016; La Sorte et al., 2018). Global analysis on the relationships between urbanization and birds body size have been observing contrasting results (La Sorte et al., 2018; Sol et al., 2014, 2020), which may be related with the type of analysis or the idiosyncratic influences of urbanization on traits (Sol et al., 2014). Nevertheless, these results are mostly based on temperate urban bird communities (Pena & Martello, n.d.) and our study brings new insights on the species inhabiting a tropical streetscape – mostly comprised by Passeriformes – among which the largest ones may occupy the most urbanized sites.

On the other hand, we observed that birds inhabiting greener streets may be comprised by smaller species. Birds that occupy structurally complex habitats, such as forest specialist species, usually have lower body masses since the process of foraging on small branches and slender vegetation probably favored the selection of smaller body sizes (Polo & Carrascal, 1999). Furthermore, larger and quieter urban green spaces seem to favor the presence of forest-specialist species within urban landscapes (Zorzal et al., 2021). Thus, although larger bodied species seem to deal with streetscape disturbances better, smaller bodied species – comprised mainly by forest specialist species across the assessed streetscape – seem to be favored by the urban afforestation process.

While the presence of species that nest and/or forage on trees and upper vegetation strata increased according to noise and the height of buildings, the occurrence of species that exploit lower layers of vegetation was favored by the increase in the proportion of green cover surrounding streets. Species that preferentially occupy tree canopy are probably less affected by the loss of vegetation strata and disturbances (e.g., traffic noise) and the high abundance of ground dwelling predators (e.g., cats) (Brown & Graham, 2015; Coetzee & Chown, 2016; Croci et al., 2008). Furthermore, natural open habitat patches are almost absent near the noisiest streets across the studied streetscape (Pena et al., 2016), so birds that exploit lower vegetation strata are probably restricted to streets near natural grasslands located in the southern portion of our study area.

All nectarivorous birds we observed are represented by small forest-specialist species. Thus, the negative relationship between their occurrence with the increase in green cover may be related to other types of vegetation, such as cultivated lawns and open habitat patches (Chong et al., 2014). The observed species that feed on invertebrates and fruits are represented by small forest mixed feeders that exploit small fruits and arthropods, such as tanagers and tyrant flycatchers. They may be well adapted to exploiting the resources provided across tropical urban landscapes (Zorzal et al., 2021) and by the dominant non-native tree species in our landscape (Lessi et al., 2016). Thus, they may occupy noisy streets far from urban parks and their occurrence may be negatively related to the proportion of native tree species. Omnivorous birds are frequently associated with highly urbanized contexts. In our study, their occurrence was positively related to the proportion of native trees. This can be explained by the dominance of native tree species in some of the most urbanized sites across the streetscape. These results are indicative of the idiosyncratic influences of urbanization on bird communities (Croci et al., 2008; Sol et al., 2014). For instance, according to our study, it is possible that species that feed on invertebrates and fruits or omnivorous species are able to thrive in the noisiest streets depending on the proportion of native trees.

The occurrence of migratory species was positively related to noisy streets, far from urban parks, and with reduced number of trees. However, migratory birds represented a small proportion of observed species across the studied streetscape. They are mostly represented by species that feed on invertebrates and fruits in the upper vegetation strata, such as the Tropical Kingbird (*Tyrannus melancholicus*) and the Variegated

Flycatcher (*Empidonomus varius*). These migratory species may be able to exploit highly urbanized contexts across the streetscape. Usually Neotropical migratory bird species are highly affected by urbanization, relying on *peri* urban vegetation patches (MacGregor-Fors et al., 2010). They can also occupy urban parks depending on noise levels and the distance from water sources (Barbosa, Rodewald, Ribeiro, & Jahn, 2020).

The occurrence of non-native bird species was positively related to highly urbanized sites. Additionally, their occurrence was positively related to the proportion of native trees, which may also be explained by the tree species distribution across the streetscape. Interestingly, we did not observe negative relationships between the occurrence of native and non-native bird species across the streetscape. The native species we observed, which also comprise some of the most frequent species throughout the study area (Pena et al., 2017), already inhabit highly stressful conditions and may not be considered competitively inferior to non-native species such as the House Sparrow and the Rock Dove. Furthermore, the number and proportion of non-native bird species in cities are relatively low (Aronson et al., 2014) and probably have a limited role in modulating the diversity of urban birds (La Sorte et al., 2018).

We did not observe relationships between some of the bird functional traits and the environmental attributes. Species classified as carnivorous (which are mostly comprised by insectivorous birds) represented almost a third of observed species across the streetscape. Insectivorous birds are usually diverse in Neotropical urban landscapes, probably due the high diversity of tyrant flycatchers in the region (Pena & Martello, n.d.; Zorzal et al., 2021). Thus, they may be spread across the assessed streetscape, and their overall distribution is probably not influenced by the selected environmental attributes. Most of the observed species that feed on seeds and fruits also exploit the ground for foraging. Their presence across the streetscape is probably restricted due to the high level of disturbances (Brown & Graham, 2015; Coetzee & Chown, 2016; Croci et al., 2008; Jokimäki et al., 2016; Pinho et al., 2016) and in fact, they are mostly restricted to streets near natural grassland patches (Pena et al., 2017). Finally, we did not observe relationships between cavity nesting birds and the environmental attributes. This can be explained by the variety of substrates exploited by these species, such as natural hollows in trees, cavities on the ground, and even buildings can be used as substrates by more generalist species (Jokimäki et al., 2016).

Studies have been observing contrasting results when assessing the influences of urbanization on phylogenetic composition of urban bird communities. Global analyses – which are mostly based on data obtained in temperate cities – have shown that urban birds are generally comprised of closely phylogenetically-related species that tend to have similar responses to urbanization because they share traits that influence their ability to overcome the modified conditions of cities (La Sorte et al., 2018; Sol et al., 2017, Sol et al., 2014, Sol et al., 2020). Additionally, the most evolutionary distinct species are also lost within urban landscapes (La Sorte et al., 2018). On the other hand, assessments on three Neotropical cities have observed that the phylogenetic composition of urban bird communities on highly urbanized areas can also be random (Leveau, 2021) or be comprised by the most evolutionary distinct species in the community (Leveau, Isla, & Bellocq, 2020). Thus, the influences of urbanization on phylogenetic composition of bird communities may be idiosyncratic and related to the original species pool and local environmental conditions. Nevertheless, due its harsh environmental conditions, the streetscape may be inhabited by evolutionary and phylogenetic impoverished communities, what may have led to the absence of a taxonomic correlation in the relationships with environmental attributes in our results.

We are aware that our model presented a low predictive power, which may be related to a relatively small sample size and to the large number of rare species observed across the assessed streetscape. This

type of data makes it difficult to predict where each species will be present or absent. At the same time, it is meaningful to include rare species in our analyses, once they contribute to the community level patterns such as species richness and trait distributions, and the statistical methods that we used are optimized by incorporating data on rare species (Ovaskainen & Abrego, 2020). This is reflected in our results by the strong statistical support of many of the relevant parameter estimates, despite the low predictive power of the model. As our study is more focused on inference than prediction, we consider our conclusions to be well supported by the data and the analyses. Therefore, we can make inferences about how the distribution of bird species and functional traits may be influenced by environmental conditions of this streetscape. However, we believe that the use of more comprehensive data – for example, by replicating our study in different cities to obtain independent sampling sites – may lead to higher predictive ability to describe bird-trait-environment relationships across streetscapes. Furthermore, future studies should include a seasonal and daily variation of bird species that exploit the streetscape, which could provide more information on how migratory and resident species exploit resources available across streets and how environmental conditions modulate the streetscape bird community. For example, if the influences of noise on birds are related to sampling biases or spatiotemporal adjustments of birds to the daily variation of noise (Carral-Murrieta, García-Arroyo, Marín-Gómez, Sosa-López, & MacGregor-Fors, 2020).

## 5. Management and planning implications

The patterns we observed here and in other studies can help in the development of guidelines to reduce the harsh environmental conditions of streetscapes. For instance, increasing green cover, especially street trees' density – together with the selection of an adequate set of tree species – were already demonstrated to be important measures to enhance the streetscape's ability to preserve a diverse urban bird community (Curzel et al., 2021; Leveau & Leveau, 2020; Wood & Esaian, 2020). Improvement of public transport services and adoption of cleaner and sustainable transportation options (e.g., cycling ways) can reduce motorized traffic volume and noise and therefore their negative effects on both people and biodiversity through the streetscape. Considering that birds may be able to return to sites when high noise levels are ceased (Carral-Murrieta et al., 2020), strategies such as temporally closing streets for recreational and leisure activities may lead to positive impacts not only for people but also for streetscape birds. In Brasília (Federal District, Brazil), 86 bird species were recorded in a 14 km highway which is closed to motorized traffic every Sunday (Guimarães, Pena, & Corrêa, 2020). These types of initiatives can increase urban landscape permeability for the bird community by allowing a higher diversity of species with different functional traits to exploit the streetscape. In artificial and human-dominated landscapes, it is fundamental to recognize small spaces and novel habitats, and to test creative solutions for reducing the impacts of urbanization on biodiversity (Soanes et al., 2019). Therefore, since adequate environmental conditions may allow for the presence of a taxonomically and functionally diverse bird community, streetscapes may also have an important role in conserving and maintaining biodiversity and ecological functions in cities.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2023.104685>.

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