Biotropica

WILEY

SPECIAL ISSUE Urban Ecology

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

ORIGINAL ARTICLE OPEN ACCESS

How Management Practices Shape the "Local Habitat Signature" That Modulates Bird Communities in Urban Green Spaces

Tulaci Bhakti[1,2] | Diego Pujoni[3] | Marcos Rodrigues[2] | João Carlos Pena[4]

[1]Programa de Pós-graduação em Ecologia Conservação e Manejo da Vida Silvestre, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil | [2]Laboratório de Ornitologia, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil | [3]Laboratório de Limnologia, Ecotoxicologia e Ecologia Aquática, Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil | [4]Araucária Innovation and Sustainability Lab, Environmental Studies Center, São Paulo State University, Rio Claro, SP, Brazil

Correspondence: Tulaci Bhakti (tulaci.faria.duarte@gmail.com)

Received: 13 January 2025 | **Revised:** 14 November 2025 | **Accepted:** 22 November 2025

Associate Editor: Eleanor Slade | **Handling Editor:** John G Blake

Keywords: bird functional traits | green space management | partial redundancy analysis (pRDA) | tropical metropolis | urban biodiversity | urban ecology

Palavras-chave: Análise de redundância parcial (pRDA) | Biodiversidade urbana | Ecologia urbana | Manejo de áreas verdes | Metrópole tropical | Traços funcionais de aves

ABSTRACT

Urban biodiversity is often studied along urbanization intensity gradients, which can overlook the critical influence of site-specific habitat characteristics. We argue that local-scale management, which creates a unique "local habitat signature," is a primary driver of community composition. We surveyed birds at 60 points across a diverse range of green spaces in a tropical metropolis, recording 148 species. Focusing on the 34 most frequent species, we used Redundancy Analysis (RDA) and variance partitioning to disentangle the effects of local, landscape, and spatial factors on bird communities. Our results showed that local-scale predictors consistently explained the largest proportion of unique variance for both taxonomic (9%) and functional (16%) compositions. The taxonomic analysis identified three ecological groups based on their habitat requirements: (1) Open-Area Specialists, (2) Arboreal Understory Specialists, and (3) Urban Tree-Dwellers and Generalists. Similarly, the functional analysis separated traits associated with forest interiors from those adapted to disturbed environments. The distribution of these groups was strongly tied to specific management practices, especially of soil cover, such as the presence of unmanaged tall grass or litter. Our findings demonstrate that urban biodiversity is mostly shaped by a mosaic of local habitat conditions. However, the surrounding landscape and the spatial arrangement of habitats also influenced community composition, underscoring the importance of a multi-scale approach to assess urban biodiversity composition for effective urban planning.

RESUMO

A biodiversidade urbana é frequentemente estudada ao longo de gradientes de intensidade de urbanização, o que pode negligenciar a influência crítica das características do habitat específicas do local. Argumentamos que o manejo em escala local, que cria uma "assinatura de habitat local" única, é um dos principais impulsionadores da composição da comunidade. Amostramos aves em 60 pontos distribuídos em uma gama diversificada de espaços verdes em uma metrópole tropical, registrando 148 espécies.

Focando nas 34 espécies mais frequentes, utilizamos a Análise de Redundância (RDA) e a partição da variância para separar os efeitos de fatores locais, da paisagem e espaciais sobre as comunidades de aves. Nossos resultados mostraram que os preditores em escala local explicaram consistentemente a maior proporção da variância única tanto para a composição taxonômica (9%) quanto para a funcional (16%). A análise taxonômica identificou três grupos ecológicos com base em suas exigências de habitat: (1) Especialistas de Áreas Abertas, (2) Especialistas de Sub-bosque Arbóreo e (3) Generalistas e Habitantes de Árvores Urbanas. Da mesma forma, a análise funcional separou traços associados ao interior de florestas daqueles adaptados a ambientes perturbados. A distribuição desses grupos esteve fortemente ligada a práticas de manejo específicas, especialmente de cobertura do solo, como a presença de grama alta não manejada ou serapilheira. Nossos achados demonstram que a biodiversidade urbana é moldada principalmente por um mosaico de condições locais de habitat. No entanto, a paisagem circundante e o arranjo espacial dos habitats também influenciaram a composição da comunidade, ressaltando a importância de uma abordagem em múltiplas escalas para avaliar a composição da biodiversidade urbana visando um planejamento urbano eficaz.

1 | Introduction

The complexity of urban landscapes is closely linked to how cities grow and develop, often resembling ecosystems that are constantly changing (Ramalho and Hobbs 2012). Those changes also influence the form, composition and function of urban green spaces across space and time, including wooded streets, gardens, small parks, recreational areas, cemeteries, schools, and railway corridors (Aronson et al. 2017). Among these spaces are included more traditional protected areas which often comprise patches of vegetation that resemble the natural phytophysiognomy at the local or regional scale (Rupprecht et al. 2015; Soanes et al. 2019). Furthermore, informal green spaces, which are not officially recognized by local governments, commonly appear in periurban areas as remnants of native vegetation that were left—often within private properties—during the process of urban expansion (Snep et al. 2006; Vizzari and Sigura 2015).

The urban landscape typically shows a gradient of urbanization, ranging from periurban fringes to dense urban cores. This gradient strongly influences biodiversity, and birds are often used as key indicators due to their varied responses to the urban environment. For example, the response to urbanization levels can differ between forest and non-forest bird species (Santos et al. 2024). Generally, this urban gradient leads to less vegetation in city centers compared to their peripheries. This results in lower taxonomic diversity in urban cores, as species presence is often higher in areas with more vegetation (Escobar-Ibáñez et al. 2020), which can buffer the negative impacts of urbanization (Filloy et al. 2019). This pattern can be explained by the "soft edges" of cities, where the urban border presents higher vegetation amount and lower population density. In these areas, the built environment forms a mosaic with natural features like native vegetation patches, providing more available habitat for different species. In contrast, urban centers have higher human densities and are dominated by impermeable surfaces (Bhakti et al. 2021).

However, urban expansion is multifaceted and influenced by historical, political, and socioeconomic factors, which challenge the simple periurban–urban gradient model (Ramalho and Hobbs 2012). Biodiversity patterns within cities are not defined by this gradient alone; instead, intra-urban regions can support high taxonomic, phylogenetic, and functional diversities that are influenced by local environmental factors. This idea is supported by research on functional traits, which are morphological (e.g., body mass) and behavioral characteristics (e.g., diet, foraging strategy) that describe how species interact with their environment (Jacoboski and Hartz 2020; Nock et al. 2016; Wilman et al. 2014). For instance, studies show that birds with generalist traits, such as omnivores, are positively associated with reduced vegetation cover and taller buildings in the surroundings, as well as, higher noise exposure (Pena et al. 2023). Likewise, vegetation patches with a more complex understory and more mid-level vegetation can provide habitat for birds, such as insectivorous species, that avoid more intensely urbanized areas (Matsuba et al. 2016). Other key elements include the presence of standing dead trees for cavity-nesting birds (Campos-Silva and Piratelli 2021), a denser tree canopy for understory insectivores (Bhakti et al. 2018), and the proximity to watercourses, which is known to boost local bird diversity (Barbosa et al. 2020; Suri et al. 2017; Wong et al. 2023).

To highlight the need for frameworks that consider a more detailed description of local conditions when assessing patterns of urban biodiversity, we frame our study in terms of what we call the "Local Habitat Signature." This approach focuses on the unique "signature" of local habitat conditions, which is directly related to planning and management practices. If the diversity of highly mobile organisms such as birds and bees can be more determined by local rather than landscape conditions (Gomes et al. 2023; Pena et al. 2023), urban biodiversity can be higher across urban landscapes even in the city core, depending on how we plan and manage urban green spaces. Thus, this perspective shows how site-specific factors can significantly influence species distribution, offering new insights for urban ecology and management (Aronson et al. 2017; Rupprecht et al. 2015). In contrast, broader frameworks like the periurban–urban gradient often oversimplify urban complexity by failing to account for landscape heterogeneity and local variations and mask important biodiversity patterns within urban green spaces (Almazán-Núñez et al. 2025; Ramalho and Hobbs 2012).

In this study, we surveyed bird communities across diverse green spaces in a tropical metropolis to test the effects of both landscape-scale and local-scale factors. Our primary goal is to demonstrate the pivotal role of the "local habitat signature"—the specific, site-level characteristics of green spaces driven by management practices, such as the presence of dead trees, leaf litter depth, and canopy openness. We first hypothesized that green spaces in less urbanized surroundings would have higher species richness and support more specialized functional

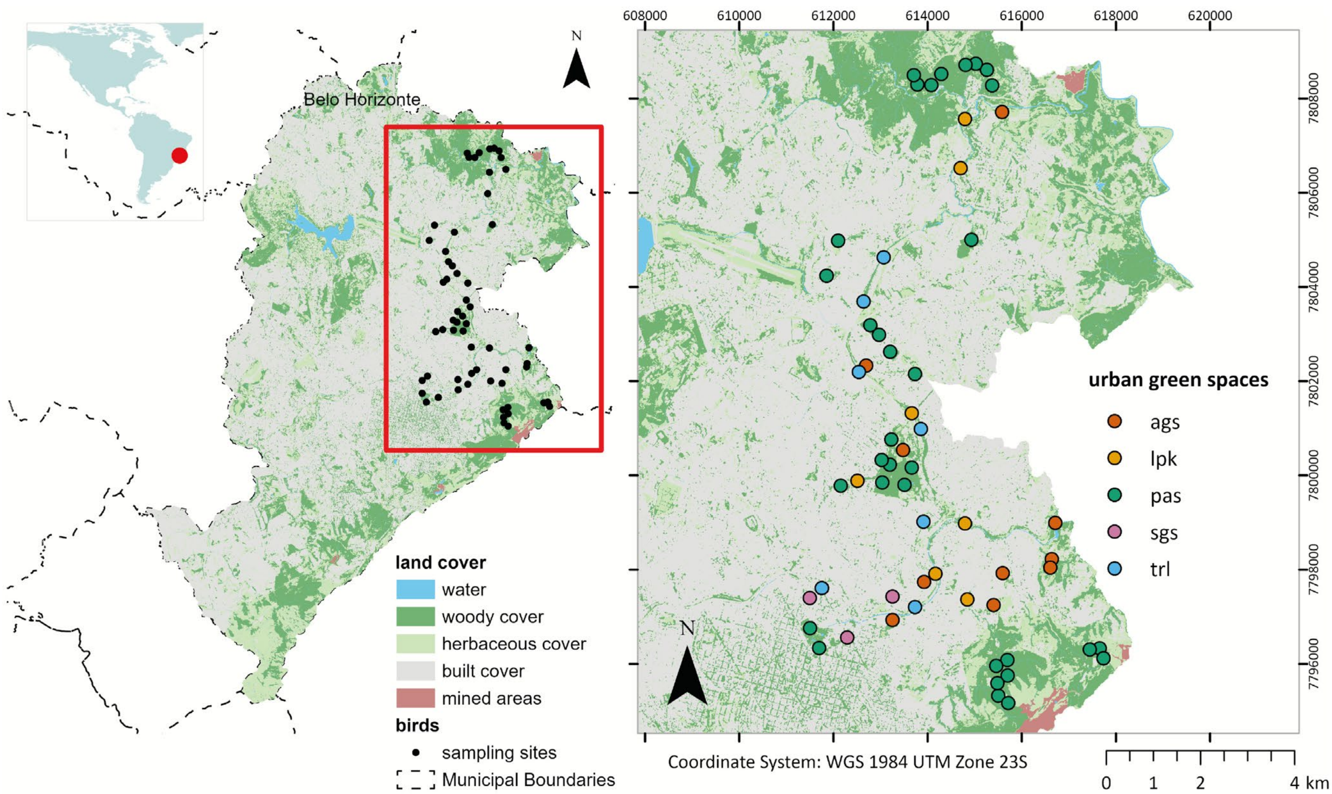

FIGURE 1 | Map of the study area showing the land cover classification and the distribution of the 60 sampling points. The main polygon represents the municipal boundary of Belo Horizonte (Minas Gerais, Brazil). Sampling points are classified according to the type of urban green space: protected areas (PAS), linear parks (LPK), small green spaces (SGS), alternative green spaces (AGS), and railway lines (TRL). The inset map shows the location of Belo Horizonte and its surrounding municipalities.

traits, such as those for understory foraging. Furthermore, we expected that landscape configuration would also be influential, leading to more similar taxonomic and functional compositions in nearby green spaces. However, we predicted that the local habitat signature would ultimately have the strongest effect on bird communities, meaning that local management can create high-quality habitats for a high diversity of species and functional traits regardless of the surrounding vegetation amount or the green space location across the landscape. By emphasizing these local factors, our study provides a more detailed framework for urban ecology, showing how site-specific variations impact biodiversity and offering a more nuanced understanding of the relationship between birds and their urban habitats.

2 | Methods

2.1 | Study Area and Bird Surveys

We conducted our study in the municipality of Belo Horizonte, State of Minas Gerais, Brazil (approx. 19.90° S, 43.96° W), a city characterized by a highly urbanized landscape with lower population density in its periurban regions (Belo Horizonte 2019; Bhakti et al. 2024). The city is situated within the ecotone between the Atlantic Forest and Cerrado biodiversity hotspots (Brandão and Araújo 1992; Myers et al. 2000) and contains over 90 protected areas, including public and private reserves (Xavier 2018). Beyond these formally protected areas, a variety of other urban green spaces are found throughout the municipality, such as linear parks, public squares, wooded streets, cemeteries, and other vegetated areas.

To sample bird communities across this landscape, we established 60 sampling points distributed across 33 distinct urban green spaces. These sites spanned a gradient from the city core to its periurban fringes (Figure 1; Table S1). We classified the 33 urban green spaces into five categories based on their primary form and function, as follows:

- Protected Areas (PAS): Formally designated areas with some degree of legal protection, such as municipal parks or ecological reserves, as defined by the Municipal Master Plan (Belo Horizonte 2019).
- Linear Parks (LPK): Linear green corridors along roads or watercourses, often used for recreation and ecological restoration (Chin and Kupfer 2020).
- Small Green Spaces (SGS): Compact, isolated vegetated areas like public squares or pocket parks, often containing large lawns or impermeable surfaces (da Silva et al. 2021).
- Alternative Green Spaces (AGS): Other types of green areas not included in the above categories, such as cemeteries and the vegetated grounds of private clubs.
- Railway Lines (TRL): Vegetation strips along active or inactive railway lines that can function as ecological corridors (Vandevelde and Penone 2017).

TABLE 1 | List and description of the functional traits used to characterize the bird communities.

Trait category	Variable name	Description
Morphology	body_mass (g)	Average body mass of the species.
	size (cm)	Average total length of the species.
Nesting & Reproduction	clutch_size	Average number of eggs per clutch.
	tree_nesters	Species primarily builds nests in trees.
	shrub_nesters	Species primarily builds nests in shrubs or bushes.
	primary_excavators	Species excavates its own nesting cavity in trees.
	secondary_cavity_nesters	Species uses pre-existing cavities for nesting.
	ground_nesters	Species primarily builds nests on the ground.
	brood_parasites	Species lays its eggs in the nests of other species.
Diet	invertebrates	Diet includes invertebrates (e.g., insects, spiders).
	mammals_birds	Diet includes small mammals, other birds, or eggs.
	amphibians_reptiles	Diet includes amphibians or reptiles.
	fish	Diet includes fish.
	carrion	Diet includes carrion.
	fruits	Diet includes fruits.
	flowers_nectar	Diet includes flowers or nectar.
	seeds	Diet includes seeds or grains.
	plant	Diet includes other plant parts (e.g., leaves, buds).
Foraging Strata	water	Forages on or near water.
	ground	Forages on the ground.
	understory	Forages in the understory (low vegetation).
	midhigh	Forages in mid to high levels of vegetation.
	canopy	Forages in the tree canopy.
	air	Forages in flight (aerial).

Note: The "Variable Name" corresponds to the variable in the dataset. Trait information was compiled from the specialized literature (e.g., Sick 1997; Wilman et al. 2014). A comprehensive list of all sources used to compile trait data is provided in the Supporting Information I (see Table S3).

We allocated one to four sampling points per green space, based on its size. To minimize spatial autocorrelation and ensure independent samples, all points were separated by a minimum distance of 200 m (Table S1: Supporting Information I).

Bird surveys were conducted from October 2020 to April 2021, coinciding with the breeding season for most bird species in the region, which increases their detectability (Sick 1997). Each of the 60 sampling points was surveyed three times, with a minimum interval of 30 days between surveys. These repeated visits were designed to compile a comprehensive species list at each point across the season. All surveys were conducted for 20 min within the first 4 h after sunrise and were avoided on rainy or windy days. During each survey, we identified and counted all birds seen or heard within a 50-m radius, excluding individuals that were only flying over the area without using the habitat (Bhakti et al. 2018; Pena et al. 2017, 2023). A species' abundance at a given point was defined as the maximum number of individuals recorded in any of the three surveys. To characterize the bird community's functional structure, we gathered data on several traits from specialized literature (Sick 1997; Wilman et al. 2014), which were complemented by other sources. A complete list of all bibliographic sources is provided in the legend of Table S2: Supporting Information I. A list of the traits used and their descriptions is provided in Table 1.

2.2 | Multi-Scale Characteristics of Green Spaces and Statistical Analysis

The complete dataset of all predictor variables (local and landscape) measured for each of the 60 sampling points is provided in Table S2: Supporting Information I. To analyze this data, we performed two sets of Redundancy Analyses (RDA): one focusing on the taxonomic composition of the community and another on its functional composition.

For the taxonomic analysis, we started with the full abundance matrix of 148 recorded species and progressively removed the least frequent species until the reduced community matrix remained highly correlated (Mantel test: $r = 0.95$, $p < 0.001$) with the full matrix. This procedure resulted in a subset of 34 species, which happened to occur in at least 11 of the 60 sampling points (i.e., > 18% frequency) and adequately represented the overall community patterns. This 34-species abundance matrix was then Hellinger-transformed prior to the analysis (Legendre and Gallagher 2001).

For the functional analysis, we first compiled a comprehensive trait matrix for all recorded species. Trait information obtained from the literature, often descriptive or in percentages, was standardized using a fuzzy coding approach. This involved converting the data into a 0–4 ordinal scale representing the species' degree of reliance on each trait category (e.g., diet, nesting substrate). A detailed description of this coding protocol, including how quantitative, qualitative, and multi-source data were standardized, is provided in the legend of Table S3. The final response variable was the Community-Weighted Mean (CWM) of these functional traits for each sampling point, derived from a matrix multiplication of the trait-by-species matrix with the species-by-site relative-abundance matrix. All statistical computations were conducted using the R programming language v. 4.4.1 (R Core Team 2024).

2.2.1 | Local Scale Characteristics

To characterize the local habitat at each of the 60 bird sampling points, we established a 100-m transect centered on each point. The orientation of each transect was adjusted to fit the shape of the green space. Along this transect, we assessed habitat variables at three locations: at the center (the sampling point itself), and at 50 m to each side along the line. At each of these three locations, we used a 3 × 3 m quadrat to measure variables related to vegetation structure, microclimate, and soil cover (Figure 2a). It is important to clarify that bird surveys were conducted only at the central point of the transect; the two additional points along the transect were used exclusively for habitat characterization to ensure a more representative assessment of the local environment.

We measured several local habitat variables within each of the 3 × 3 m quadrats. To assess vegetation structure, we first measured canopy openness using a camera with a fisheye lens (Bower 8 mm F3.5) positioned 0.5 m from the ground. Within the same quadrats, we recorded the height and circumference at breast height (CBH) for any tree with a CBH of 10 cm or greater. The presence of standing dead trees, shrub cover (vegetation below 1.0 m), and lianas was also recorded as binary (presence/absence) variables (Figure 2). To characterize microclimatic conditions at the start of each count, we recorded relative humidity (%) and wind speed (m/s) during the first minute of the 20-min observation period using a Brunton Atmospheric Data Center PRO portable meteorological station.

We also characterized the ground layer within each quadrat by measuring leaf litter depth and recording the presence of various surface cover types. Leaf litter depth was measured to the nearest centimeter at the four corners of each quadrant using a ruler, and the average value was recorded. The surface cover types were classified according to the following categories:

- Managed Lawn (ML): Mowed and regularly maintained turfgrass.
- Unmanaged Tall Grass (UTG): Spontaneous and unkempt tall grasses, often found in areas with little to no regular mowing.
- Native Grassland (NG): Areas dominated by native grass species.
- Exposed Soil (ES): Bare ground without significant vegetation or other cover.
- Rocky Soil (RS): Surface predominantly covered by rocks or gravel.
- Sandy Soil (SS): Surface predominantly covered by sand.
- Concrete (CON): Paved surfaces made of concrete.
- Asphalt (ASP): Paved surfaces made of asphalt.
- Urban Waste (UW): Presence of significant amounts of garbage or construction debris.

To create a final dataset for analysis, the data from the three quadrants at each sampling point were consolidated to generate a single value per variable. For continuous variables (e.g., canopy openness, litter depth, tree height), the mean value from the three quadrants was used. All other variables were treated in a presence/absence format. For structural features like standing dead trees, lianas, and shrub cover, the sampling point was assigned a "1" (presence) if the feature was detected in at least one of the three quadrants, and a "0" otherwise. This same logic was applied to the ground cover types: each category (e.g., Managed Lawn, Exposed Soil, Concrete) was converted into its own binary variable, receiving a "1" if present in at least one quadrant and a "0" if absent from all three.

2.2.2 | Landscape-Scale Characteristics

Landscape-scale characteristics were derived from a land cover map created for the study area. This map was based on Planet Scope satellite imagery (3-m resolution, four spectral bands) acquired in September 2020 (Bhakti et al. 2024; Planet Labs PBC 2017). We performed a supervised classification on this imagery using the Maximum Likelihood algorithm in ArcGIS 10.X, which generated four land cover classes: woody vegetation, herbaceous vegetation, impermeable surfaces (comprising built structures and exposed soil), and mining areas. A fifth class, water (including rivers, lakes, and reservoirs), was added to the map using official hydrographic vector data from the Belo Horizonte City Hall data portal (http://bhmap.pbh.gov.br/). The final five-class map showed high overall accuracy, confirmed by a Kappa coefficient of 0.86.

From the land cover map, we calculated landscape metrics around each of the 60 sampling points. First, we created four concentric buffers with radii of 50, 100, 150, and 500 m (Figure 2b). For each buffer, we calculated the total area of green cover (in m^2) by summing the areas of the "woody vegetation" and "herbaceous vegetation" classes. Second, we calculated the distance to water by measuring the distance from each sampling point to the nearest pixel of the "water" class.

2.2.3 | Spatial Autocorrelation

To account for spatial autocorrelation in our data, we generated spatial predictor variables using Distance-Based Moran's Eigenvector Maps (dbMEM), following the methodology of Dray et al. (2006). These variables, hereafter referred to as MEMs, were calculated from the geographic coordinates of our 60 sampling points. Generally, the first MEMs (e.g., MEM1–MEM4) describe broad-scale structures, such as the North–South spatial gradient illustrated by MEM1. Subsequent MEMs (e.g., MEM5, MEM9) describe finer-scale patterns, such as the local clusters of neighboring points seen in MEM5 and MEM9 (Figure 2c) (the complete set of eigenvector maps is provided in Supporting Information II).

2.3 | Statistical Analysis

For each of the three predictor sets (local, landscape, and spatial), we first conducted an independent forward

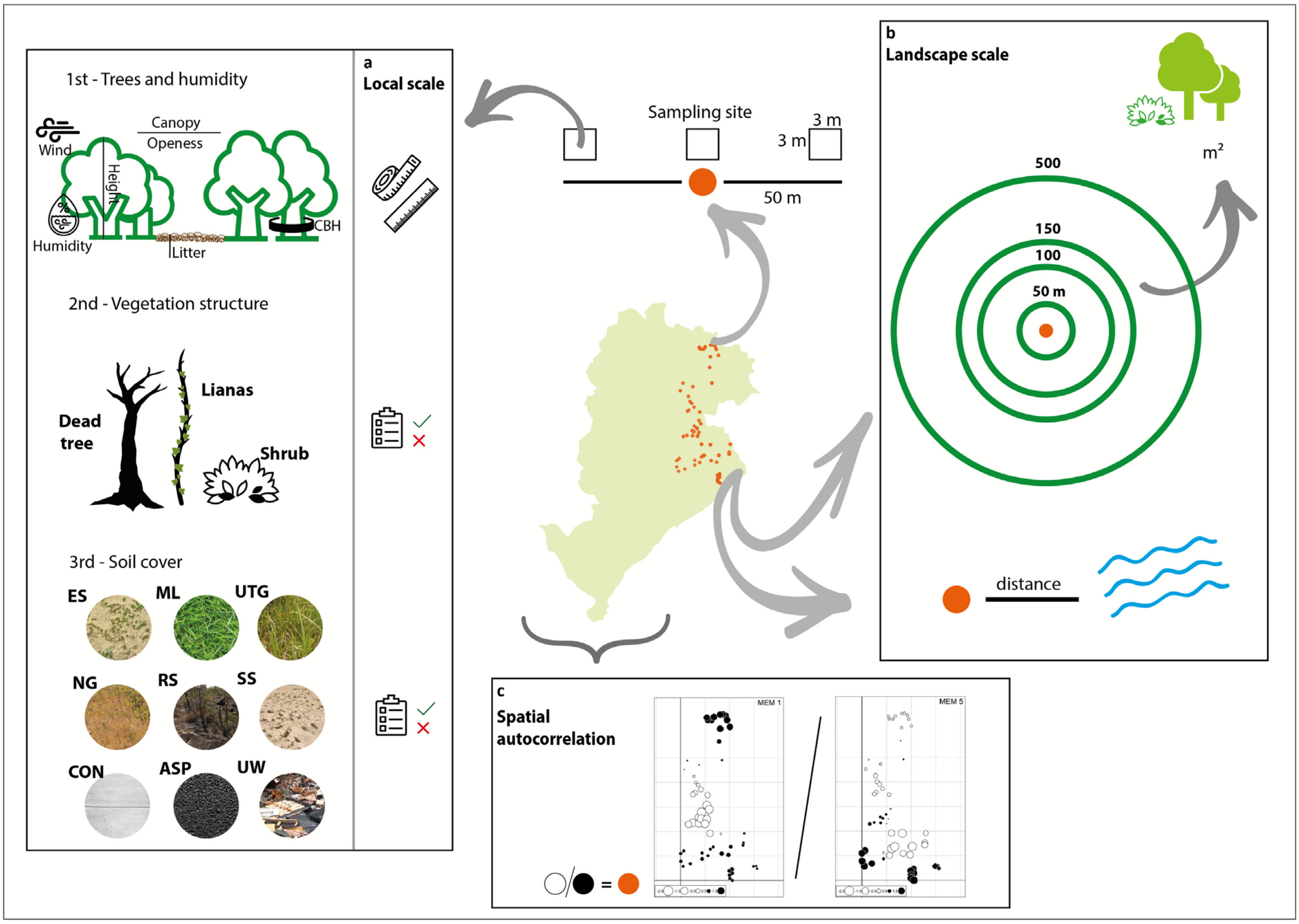

FIGURE 2 | Illustration of variables analyzed at different spatial scales in Belo Horizonte (Minas Gerais, Brazil). (a) At the local scale, quantitative variables included canopy openness, litter depth, relative humidity, wind (m/s) and circumference at breast height (CBH). Other variables were recorded as the presence or absence of a feature within the quadrats, including standing dead trees, lianas, shrubs, and each of the following ground cover types: Exposed Soil (ES), Managed Lawn (ML), Unmanaged Tall Grass (UTG), Native Grassland (NG), Rocky Soil (RS), Sandy Soil (SS), Concrete (CON), Asphalt (ASP), and Urban Waste (UW). (b) At the landscape scale, concentric buffers with 50, 100, 150, and 500 m radii around each sampling point were used to assess the total area of green cover and distance to water bodies. (c) Spatial variables were represented by Moran's Eigenvector Maps (MEMs). This panel illustrates how MEMs model spatial patterns at different scales, where circle diameter is proportional to the eigenvector's value, and black and white circles represent positive and negative values, respectively. The panels shown illustrate an example of a broad-scale North–South gradient (MEM 1) and a fine-scale local cluster (MEM 5), respectively. Icon credits: The Noun Project.

selection procedure to identify the most significant variables, following the methodology of Blanchet et al. (2008). The final Redundancy Analysis (RDA) was then performed using only the subset of significant variables selected from each set.

Subsequently, to partition variance among the three predictor sets, we conducted a Partial Redundancy Analysis (pRDA), extracting eight distinct fractions of variation: the pure effects of local [L], landscape [P], and spatial [S] variables; the shared effects between each pair of predictor sets [LP, SL, SP]; the variation shared by all three sets [LPS]; and the unexplained residuals [U] (Borcard et al. 2011). Specifically, we employed the rda and varpart functions from the "vegan" package (Oksanen et al. 2013) and the forward.sel and dbmem functions from the "adespatial" package (Dray et al. 2018).

3 | Results

3.1 | Bird Community Overview and Survey Results

We recorded a total of 148 bird species across the 60 sampling points during 60 h of observation (see Table S3: Supporting Information I for the complete species list and functional traits). From this total, the 34 most frequent species were selected for further analysis (see Table S4: Supporting Information I for this list). A comparison between total abundance and frequency of occurrence for these species revealed a wide range of ecological strategies. At one extreme of abundance, the Blue-and-white Swallow (*Pygochelidon cyanoleuca*) was the most numerous species (238 individuals) but occurred in only 33% of sampling points. This pattern of high abundance in relatively few sites was

TABLE 2 | List of the 21 bird species most strongly associated with environmental variables in the RDA.

Species	Code	Frequency of occurrence (%)	Total abundance
Coereba_flaveola	Coefla	53	90
Troglodytes_musculus	Tromus	50	98
Patagioenas_picazuro	Patpic	45	170
Thraupis_sayaca	Thrsay	44	99
Turdus_leucomelas	Turleu	44	89
Pitangus_sulphuratus	Pitsul	43	152
Columbina_talpacoti	Coltal	42	171
Chionomesa_lactea	Chilac	39	49
Tyrannus_melancholicus	Tyrmel	38	88
Megarynchus_pitangua	Megpit	38	68
Piaya_cayana	Piacay	37	44
Euphonia_chlorotica	Eupchl	35	53
Pygochelidon_cyanoleuca	Pygcya	33	238
Thraupis_palmarum	Thrpal	32	63
Furnarius_rufus	Furruf	31	65
Camptostoma_obsoletum	Camobs	29	36
Brotogeris_chiriri	Brochi	27	153
Volatinia_jacarina	Voljac	27	68
Myiarchus_ferox	Myifer	27	40
Galbula_ruficauda	Galruf	25	40
Thamnophilus_caerulescens	Thacae	25	39
Basileuterus_culicivorus	Bascul	24	45
Eupetomena_macroura	Eupmac	23	34
Hemithraupis_ruficapilla	Hemruf	22	50
Turdus_amaurochalinus	Turama	22	47
Elaenia_flavogaster	Elafla	21	29
Estrilda_astrild	Estast	20	147
Myiozetetes_similis	Myisim	20	40
Rupornis_magnirostris	Rupmag	20	21
Synallaxis_frontalis	Synfro	19	30
Columba_livia	Colliv	18	133
Sicalis_flaveola	Sicfla	18	47
Herpsilochmus_atricapillus	Heratr	18	42
Empidonomus_varius	Empvar	18	29

(Continues)

TABLE 2 | (Continued)

Note: The table shows the frequency of occurrence (the percentage of the 60 sampling points where each species was recorded) and the total abundance (the total number of individuals recorded across all points) for each species.

also observed in other gregarious species, such as the Yellow-chevroned Parakeet (*Brotogeris chiriri*; 153 individuals at 27% of sites) and the Common Waxbill (*Estrilda astrild*; 147 individuals at 20% of sites). In contrast, the Bananaquit (*Coereba flaveola*) exemplified a different strategy, being the most frequent species (present in 53% of points) despite a more moderate total abundance (90 individuals). At the other extreme, the Roadside Hawk (*Rupornis magnirostris*) was also relatively widespread (present in 20% of sites) but was one of the least abundant species in this group, with only 21 individuals recorded in total.

The redundancy analysis (RDA) revealed that a significant portion of the variation in bird community composition was explained by the environmental and spatial variables. To aid interpretation, we visually inspected the ordination biplot and identified 21 of the 34 selected species positioned further from the origin, indicating stronger alignment with the main environmental gradients (Table 2; Figure 3). These species formed three groups that emerged from their clustering in the ordination space, corresponding to different habitat characteristics: (1) Open-Area Specialists, (2) Arboreal Understory Specialists, and (3) Urban Tree-Dwellers and Generalists. The 13 remaining species, which were clustered near the origin indicating weaker associations with the predictors, are shown in Figure S1: Supporting Information I.

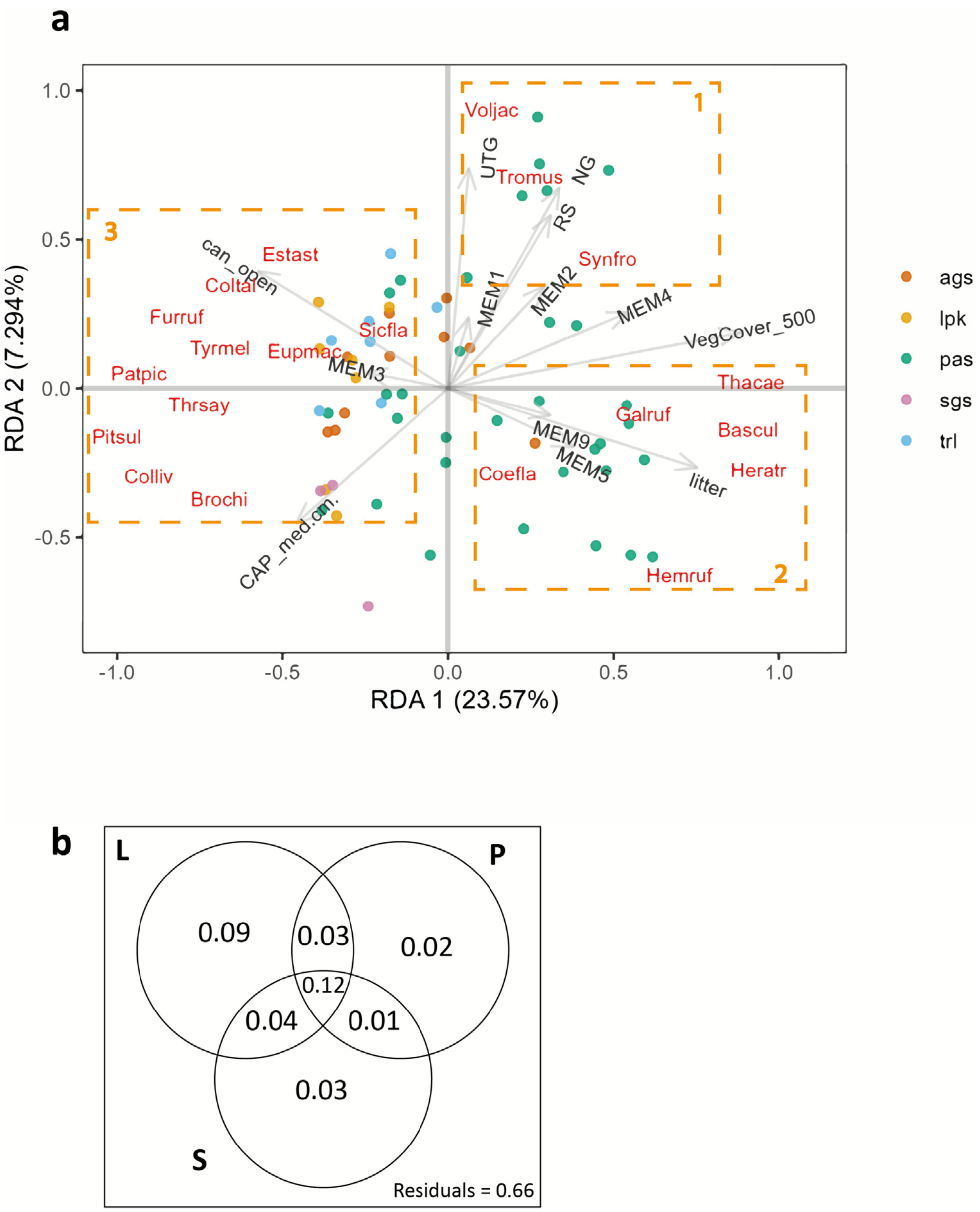

FIGURE 3 | Results of the Redundancy Analysis (RDA) and variance partitioning for the taxonomic composition of bird communities in Belo Horizonte, Brazil. (a) RDA ordination diagram showing the 21 bird species most strongly associated with the significant predictor variables. Species are represented by their codes (see Table 2 for full names). The three main ecological groups are visually highlighted: (1) the Open-Area Specialists, (2) the Arboreal Understory Specialists, and (3) the Urban Tree-Dwellers and Generalists. Significant environmental variables are shown as vectors. Centroids for the five green space types are shown as colored squares: Protected areas (PAS), linear parks (LPK), small green spaces (SGS), alternative green spaces (AGS), and railway lines (TRL). (b) Venn diagram illustrating the partitioning of the explained variance (R^2_{adj} = 34%) among the pure effects of local [L], landscape [P], and spatial [S] variables, and their shared effects. All MEMs can be viewed in Supporting Information II.

3.2 | Variance Partitioning and Redundancy Analysis

The main environmental and spatial gradients structuring the bird community were revealed by the RDA. The detailed relationships between predictor variables and species composition are illustrated in the ordination plot in Figure 3a, while the relationships with functional traits are shown in Figure 4a. To quantify the relative importance of the different spatial scales, we performed a variance partitioning analysis for both community components (Figures 3b and 4b).

For taxonomic composition, the predictor variables explained a total of 34% of the variation. The pure local-scale fraction [L] was the largest unique contributor (9%), while the fraction shared by all three predictor sets [LPS] was also substantial at 12% (Figure 3b). The model for functional composition was stronger, explaining 51% of the variation. Here, the pure local fraction [L] was again the most important unique factor (16%), and the three-way shared fraction [LPS] was also very large (14%) (Figure 4b). Together, these results highlight the primary importance of local-scale predictors, while also demonstrating a complex interplay among local, landscape, and spatial factors.

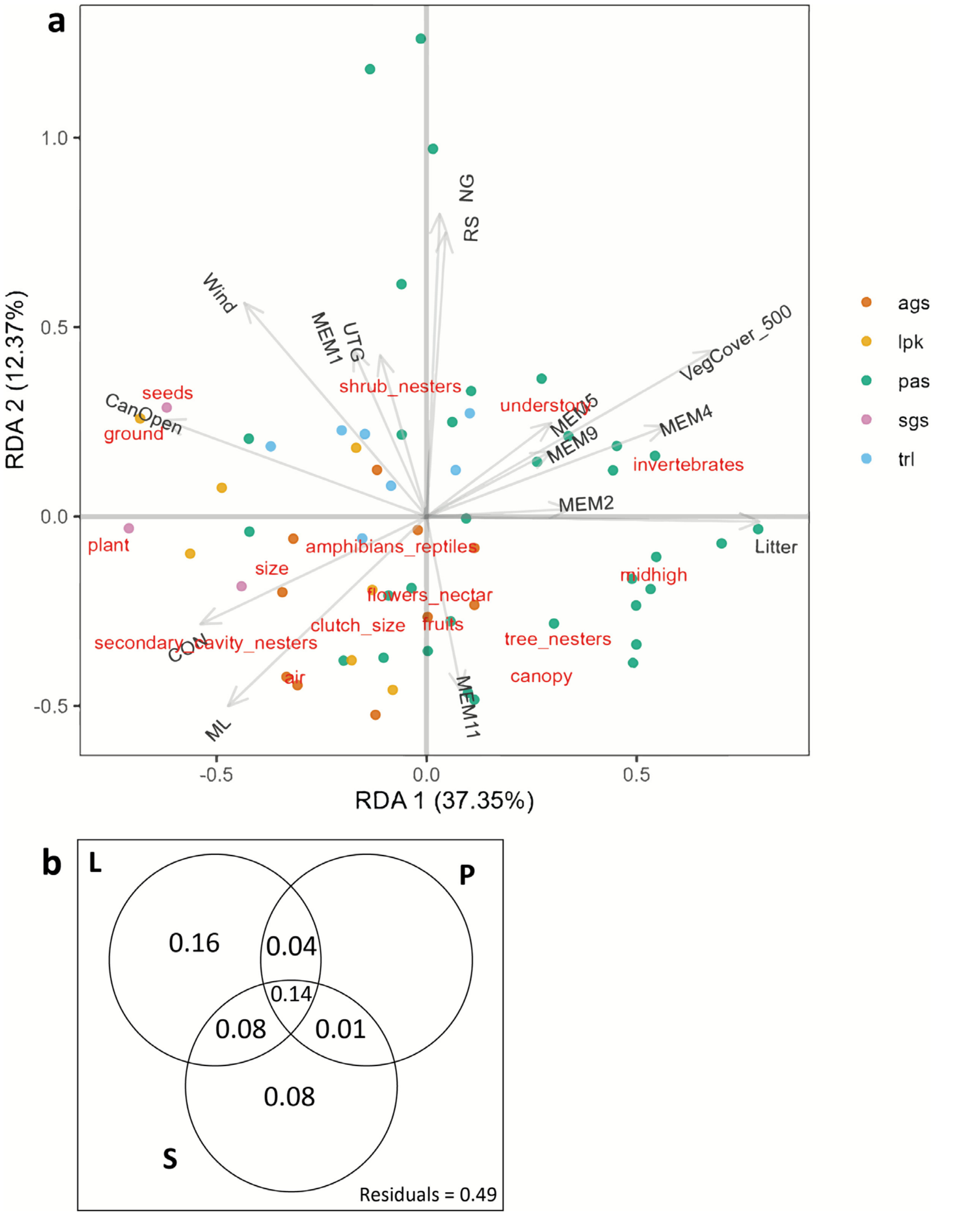

FIGURE 4 | Results of the Redundancy Analysis (RDA) and variance partitioning for the functional composition of bird communities in Belo Horizonte, Brazil. (a) RDA ordination diagram showing the relationships between bird functional traits and the significant predictor variables. The plot illustrates the main gradients of ecological strategies, showing how different functional traits (e.g., morphology, diet, foraging, and nesting strategy) are associated with specific environmental conditions. (b) Venn diagram illustrating the partitioning of the explained variance in functional composition ($R^2_{adj} = 51\%$) among the pure effects of local [L], landscape [P], and spatial [S] variables, and their shared effects. All MEMs can be viewed in Supporting Information II.

3.2.1 | Predictors of Bird Community Composition

The forward selection procedure identified six local, one landscape, and six spatial variables (Figure 3a) that significantly explained the variation in the composition of the 21 key bird species (see Table S5: Supporting Information I—for full model statistics). Among the local-scale predictors, leaf litter depth was the most influential variable ($R^2 = 0.15$, $p < 0.001$), followed by the presence of Native Grassland (NG; $R^2 = 0.09$, $p < 0.001$) and Unmanaged Tall Grass (UTG; $R^2 = 0.04$, $p < 0.001$). Canopy openness ($R^2 = 0.03$, $p < 0.001$), Rocky Soil (RS; $R^2 = 0.03$, $p = 0.006$), and mean tree CBH ($R^2 = 0.02$, $p = 0.037$) also contributed significantly to the model. At the landscape scale, the total area of green cover within a 500-m radius (VegCover_500) was a significant predictor of community composition ($R^2 = 0.19$, $p < 0.001$).

Spatial structure, as modeled by the MEM variables, was also significant. The final model retained four broad-scale predictors (MEM1, MEM2, MEM3, and MEM4), which correspond to the major geographic gradients across the study area (such as the North–South pattern defined in the Methods), and two fine-scale predictors (MEM5 and MEM9), which represent the local clustering of sites. This indicates that the bird community is organized by geographic patterns occurring both across the entire city and at more local, neighborhood scales. The first two ordination axes of the RDA explained a total of 30.86% of the constrained variance in species composition. The primary axis explained 23.57% of the variance and primarily separated species based on habitat structure. The second axis explained an additional 7.294% and separated species based on their degree of habitat specialization (Figure 3a). To aid interpretation, we visually inspected the ordination biplot and identified 21 of the 34 selected species positioned further from the origin, indicating stronger alignment with the main environmental gradients (Table 2; Figure 3a). These species formed three groups that emerged from their clustering in the ordination space, corresponding to different habitat characteristics: (1) Open-Area Specialists, (2) Arboreal Understory Specialists, and (3) Urban Tree-Dwellers and Generalists. The 13 remaining species, which were clustered near the origin indicating weaker associations with the predictors, are shown in Figure S1: Supporting Information I. Functionally, this group was highly heterogeneous, comprising species with varied nesting strategies (e.g., trees, cavities, shrubs), diets (primarily insectivores and frugivores), and foraging behaviors across all vertical strata. This ecological versatility explains their position near the origin of the RDA, as they are not strongly associated with any single, specific set of habitat predictors.

The first group, positioned on the upper-right side of the RDA plot, consists of three species: *Volatinia jacarina*, *Troglodytes musculus*, and *Synallaxis frontalis*. These species were positively associated with the presence of Unmanaged Tall Grass (UTG), Native Grassland (NG), and Rocky Soil (RS). This environmental association aligns with their functional traits, which show a predominance of nesting in shrubs and foraging near the ground for a diet of invertebrates and seeds. Spatially, this group was associated with broad-scale predictors (MEM1, MEM2, and MEM4), suggesting that their preferred open, low-vegetation habitats are widely distributed throughout the urban matrix rather than being clustered in specific areas.

The second group, located on the lower-right side of the plot, includes six species typical of forest interiors: *Basileuterus culicivorus*, *C. flaveola*, *Galbula ruficauda*, *Hemithraupis ruficapilla*, *Herpsilochmus atricapillus*, and *Thamnophilus caerulescens*. This group showed a strong positive association with deep leaf litter and a negative association with canopy openness, indicating a preference for shaded, forest-like conditions. Their functional traits support this result, with a prevalence of insectivores that forage in the understory (e.g., *B. culicivorus* and *T. caerulescens*) and species that forage predominantly in the midstory and canopy (e.g., *H. ruficapilla* and *H. atricapillus*), highlighting a reliance on the full vertical structure of these forest patches. This group was exclusively associated with fine-scale spatial predictors (MEM5 and MEM9), indicating that the high-quality forest habitats they depend on are not widespread, but occur in spatially aggregated patches within the city.

The third group, occupying the left side of the RDA plot, is composed of 12 species, including many of the most abundant recorded, such as *Columbina talpacoti*, *Pitangus sulphuratus*, *P. cyanoleuca*, and *Thraupis sayaca*. This group was positively associated with greater canopy openness and larger trees (high mean CBH, which are mainly old trees in the oldest streets and green spaces of the city), and negatively with deep leaf litter. Functionally, this guild is highly diverse. Nesting sites are varied, including trees and anthropogenic structures (e.g., buildings used by *P. cyanoleuca* and *C. livia*), while foraging strategies span all vertical strata with a varied diet of invertebrates, fruits, nectar, and seeds. The association with a broad-scale spatial predictor (MEM3) suggests that this group of highly urban-adapted species is widely and homogeneously distributed. The urban character of this group is highlighted by the strong presence of species from families known for their success in tropical cities, such as Columbidae (e.g., *Columba livia*, *C. talpacoti*) and Psittacidae (e.g., *B. chiriri*).

Finally, the ecological groups showed a clear association with specific green space types. Both specialist guilds, the Open-Area Specialists (Group 1) and the Arboreal Forest Species (Group 2), were predominantly found in Protected Areas, (PAs), and both groups were also positively associated with the landscape variable of vegetation cover (VegCover_500), indicating a greater dependence on vegetation cover (woody or herbaceous vegetation) in their surroundings. In contrast, the Urban Tree-Dwellers and Generalists (Group 3) were widespread across all green space categories.

3.2.2 | Functional Composition

The forward selection procedure for the functional traits identified eight local, one landscape, and six spatial variables that significantly explained the variation in functional composition (Figure 4a). Among the local predictors, leaf litter depth was again the most influential variable ($R^2=0.24$, $p<0.001$), followed by Native Grassland (NG; $R^2=0.09$, $p<0.001$) and canopy openness ($R^2=0.04$, $p=0.002$). The presence of Concrete (CON; $R^2=0.03$, $p=0.006$), Unmanaged Tall Grass (UTG; $R^2=0.03$, $p=0.015$), Managed Lawn (ML; $R^2=0.02$, $p=0.027$), and wind speed ($R^2=0.02$, $p=0.036$) also explained a significant portion of the variation. At the landscape scale, the total area of green cover within a 500-m radius (VegCover_500) was the only variable retained ($R^2=0.20$, $p<0.001$). The final model also included six spatial predictors representing both broad-scale (MEM1, MEM2, MEM4) and fine-scale patterns (MEM5, MEM9, MEM11).

The primary axis separated traits along a gradient of urbanization and habitat complexity. On one side, traits associated with complex, forest-like habitats were positively correlated with deep leaf litter and were most frequent in Protected Areas (PAS). This functional group of traits included insectivorous diets, foraging in the understory, mid-story, and canopy, and nesting in trees. These traits were negatively associated with high wind speeds, concrete surfaces, and managed lawns. Spatially, this group was associated with a mix of both broad- and fine-scale predictors, indicating a complex spatial distribution rather than a simple aggregated or dispersed pattern.

Conversely, the other side of the gradient grouped traits characteristic of highly urbanized or disturbed conditions. The traits in this group were composed of species with larger body sizes and clutch sizes, that nested in secondary cavities and had generalist diets (plants, fruits, nectar, and vertebrates). These traits were positively correlated with the presence of Concrete (CON) and Managed Lawns (ML), and negatively with the amount of green cover in the surrounding landscape (VegCover_500). Spatially, this functional group showed no significant association with any spatial predictor.

The analysis also revealed other distinct functional groups. Shrub-nesting, for example, was strongly associated with a matrix of Unmanaged Tall Grass (UTG), Native Grassland (NG), and Rocky Soil (RS), and with higher wind speeds characteristic of open environments. In another pattern, seed-eating and ground-foraging traits were positively associated with greater canopy openness and negatively with deep leaf litter, indicating a preference for open areas. Spatially, these open-habitat traits were associated with a broad-scale predictor (MEM1), suggesting that their required resources are widely and homogeneously distributed across the landscape.

4 | Discussion

By evaluating the relationships between bird communities and the characteristics of urban green spaces across multiple scales, we found that local environmental conditions exert the greatest influence on both species occurrence and functional trait composition. This observation aligns with the "local habitat signature," which highlights that the specific use and management of a green space is a key driver of species composition. Cities contain a diversity of green spaces and their ecological character is shaped by how they are managed; for example, whether standing dead trees are retained, and whether a complex understory is allowed to develop or is instead replaced by mowed lawns. This is particularly important for local stakeholders, as it provides valuable insights into how individual green spaces can be managed more effectively. Furthermore, our findings suggest that the spatial distribution of these habitat characteristics does not necessarily follow a traditional periurban–urban gradient. In other words, local factors such as vegetation structure and specific ground cover types (e.g., litter or asphalt) may have a more significant role in shaping bird communities than the broader intensity of urbanization, which in this study was represented by the proportion of surrounding green cover.

The bird species in our study clustered into three distinct ecological groups based on their differing habitat requirements and life-history traits. The first group, the Urban Tree-Dwellers and Generalists, is composed of 12 species common to urban landscapes in Brazil, many of which are gregarious, such as columbids, parrots, and swallows (similar result as Kark et al. 2007; Silva et al. 2023). Those species present a strong association with high canopy openness and larger trees (i.e., larger CBH), indicating their preference for highly urbanized sites, such as streets and linear parks. Among our studied green spaces, the oldest trees are concentrated in sites such as streets and small public urban green spaces. The intimate relationship with high urbanized sites is evident in the non-native *C. livia*, which is hyperabundant but is only present in 30% of the studied sites. Other columbids, such as the native *Patagioenas picazuro* and *C. talpacoti*, were more frequent across the landscape, indicating a larger niche breadth, possibly related to a diet that favors their occurrence in both more and less urbanized areas (Fontoura and Orsi 2013; Wilman et al. 2014). Among these 12 species, we also observed birds with diverse dietary habits (omnivorous, insectivorous, and granivorous), suggesting that these species are able to forage and nest in more stressful urban contexts, such as the streetscape (e.g., *Sicalis flaveola*, *Furnarius rufus*, and *T. sayaca*) (Pena et al. 2023; Richardson et al. 2023). Similarly, hummingbird species like *Eupetomena macroura* are favored by the diversity of urban plants, both exotic and native; their territorial and aggressive behavior may further contribute to their success in urban environments (Anselmo et al. 2023; Cardoso Araujo et al. 2024; Rodrigues and Araujo 2011). The presence of species with such diverse strategies in highly urbanized areas highlights the potential of urban vegetation to support biodiversity, which is closely related to landscaping decisions that provide key resources for different species (Smith et al. 2018; Threlfall et al. 2017).

In contrast to the highly adaptable urban species, our study also identified two distinct guilds of specialist birds. These groups were predominantly found in more preserved green spaces, such as Protected Areas. Their association with a higher proportion of surrounding vegetation also highlights their dependence on a more continuous vegetated landscape. The first of these specialist groups, the Open-Area Specialists, consists of three species associated with grassy, low-management spaces, such as parks that protect rocky outcrops and other areas with minimal mowing. These birds exploit lower vegetation strata for nesting and foraging; for instance, the granivorous *V. jacarina* depends on unmanaged grasses for seeds, while the insectivorous *S. frontalis* forages in tall grasses and bushes. Both species use this low vegetation for nest construction (Sick 1997). The third species in this group, *T. musculus*, is a synanthropic species known for its adaptability. It is primarily an insectivore, but is also known to consume seeds. This adaptability in both diet and nesting (using a wide range of sites from ornamental vegetation and rocky crevices to various secondary cavities) (Pena et al. 2023; Sick 1997) likely explains why it was the second most frequent species in this study. Spatially, this group's association with broad-scale predictors and its negative correlation with large trees indicate that these preferred open habitats are widely distributed across the urban matrix rather than being clustered.

The second specialist guild, the Arboreal Understory Specialists, comprises six species characteristics of forest-like sites that show a strong positive association with deep leaf litter and a negative association with canopy openness. This guild includes a range of insectivores that utilize different vertical strata. Species like *B. culicivorus* and *T. caerulescens* depend on a well-structured understory for foraging, while others prefer the upper strata, such as *G. ruficauda*, which is often associated with vegetation near watercourses, and the Atlantic Forest endemic *H. ruficapilla*, which depends on forested canopies (Bhakti and Rodrigues 2020; Vale et al. 2018). Interestingly, the highly frequent Bananaquit (*C. flaveola*) was also strongly associated with this group. As a nectarivore known to exploit a wide array of floral resources in urban areas (D'angelo 2021), this association may highlight its dependence on the greater resource diversity found in woody, well-structured sites, a pattern previously observed in Belo Horizonte where nectar-feeding species responded positively to the number of street trees (Pena et al. 2023). Spatially, this group's association with fine-scale spatial predictors (MEM5 and MEM9) shows that these high-quality forested habitats are spatially aggregated, different from the more widespread open–grassland habitats.

The distinct habitat requirements of the three ecological groups highlight how management decisions modulate the ability of bird species with a variety of functional traits to occupy urban green spaces. Mowing frequency, for example, can determine whether a granivorous bird finds food resources, or an insectivorous species finds adequate substrate for foraging and nesting.

The analysis of functional traits also revealed the primary influence of local-scale characteristics. This influence was structured along a main ecological gradient that separated two groups of traits. One end of this gradient, largely corresponding to Protected Areas, grouped traits associated with more preserved, forest-like conditions, such as deep leaf litter, low canopy openness, and low wind speed. This cluster of green spaces also presents a higher amount of vegetation within a 500 m radius buffer, which is related to the increase in the abundance of species that forage in the understory. This is consistent with the positive association between the number of trees and bird species richness across streets in Belo Horizonte (Pena et al. 2017, 2023). Other functional traits associated with these protected areas are the dependence of understory, mid-high, and canopy vegetation strata to forage and the use of trees for nesting. Furthermore, insectivorous species are also associated with these preserved forested spaces, which may be related to the occurrence of species such as antbirds and warblers. This result reinforces that understory insectivorous birds are sensitive to urbanization and may be restricted to more preserved vegetated areas within urban landscapes (Avilla et al. 2021; Matsuba et al. 2016; Stagoll et al. 2010). It was also observed that some protected areas are characterized by rocky soil and native grass, which explains the association of shrub-nesting birds with such places. This result aligns with the findings of Marini et al. (2012), who detailed the nesting biology of birds in the Cerrado and noted the importance of vegetation types in their nesting behavior. The association between the abundance of these functional traits and both broad and fine-scale predictors highlights the diversity of vegetation structure among protected areas. This is consistent with the spatial patterns found for the species themselves, where forested protected areas present a more clustered distribution across the landscape, while grassy green spaces are widely distributed.

Contrastingly, a second ecological strategy was evident, defined by a suite of functional traits related to a lower dependence on preserved vegetation patches. The green spaces associated with this strategy are characterized by higher wind speed, greater canopy openness, and the presence of concrete, managed lawns, and unmanaged tall grass. Consequently, we observe a higher abundance of traits related to open habitat and generalist bird species such as those that forage on the ground, feed on seeds, have larger body sizes and clutch sizes, and can exploit human-made structures for nesting (secondary cavity nesters) (as in Pena et al. 2023). The association between those functional traits and a broad-scale spatial predictor (MEM1) indicates that they are widely distributed across the landscape, which would be expected since they are also related to a high diversity of green space types. These finds based on functional trait abundances, indicate that the urban ecosystem can provide habitat and resources for species with different habitat requirements and sensitivities to human disturbances according to local management practices (Richardson et al. 2023).

The landscape scale, although it did not have a pure influence as a predictor but rather was associated with a combination of the local and spatial predictors, had influences on the occurrence of species and the abundance of functional traits when considering green cover within a 500 m radius buffer. A greater proportion of green cover correlates with an increased frequency of birds associated with woody vegetation, such as understory insectivores. This association suggests that multiple green spaces within this distance can be interconnected based on the functional traits of the birds found in similar locations. The presence of vegetation around these green spaces may facilitate bird movement across the urban matrix, further supporting the connection between green areas and bird distribution (Villaseñor et al. 2020), and specifically in Belo Horizonte (Horta et al. 2018).

Our study emphasizes the effects of local predictors on the taxonomic and functional compositions of urban bird communities, highlighting how birds interact with and exploit habitats based on local-scale characteristics. Our approach, which grouped birds into distinct ecological guilds, also exposed the functional heterogeneity among the different types of green spaces. These results challenge the oversimplification that can arise from using broad urban gradients in biodiversity research, which often ignore crucial local characteristics in favor of a single proxy for urbanization. This aligns with a growing trend in urban ecology to include local-scale variables to better understand biodiversity patterns and their complex relationship with the urban environment (Callaghan et al. 2021; Morelli et al. 2018; Rega-Brodsky et al. 2022). However, this focus on local factors does not exclude the importance of other scales. The influence of spatial predictors cannot be overlooked, nor can the role of landscape characteristics, such as surrounding vegetation, in potentially mitigating the negative effects of urbanization on biodiversity.

Another important aspect was our decision to evaluate only the 34 most frequent species. While this approach may have excluded rarer species that could be more sensitive to urbanization, it allowed us to focus on the factors influencing the most prevalent birds in the community. This focus is critical for understanding the key ecological processes these common species drive, such as seed dispersal and pollination, which are essential for urban ecosystem dynamics. Our findings show that local-scale management practices, often dictated by patterns of human use, significantly shape the environmental characteristics of green spaces. For example, areas along railway lines, with their limited human access, were associated with unmanaged grass. In contrast, green spaces with more frequent human use, such as small parks and recreational areas, typically had well-maintained grass, reflecting regular management activities (de Toledo et al. 2012; Hwang et al. 2019; Matsuba et al. 2016). This spatial patterning of management was also evident in soil cover, with more peripheral protected areas maintaining higher litter depth, likely due to reduced human access (Bhakti et al. 2024). While this multi-site approach provides robust insights, we recognize its limitations. The specific variability of urban environments means that sampling a wide diversity of green spaces may not always be feasible in other cities, and the relationships we found may be context-dependent as baseline biodiversity can vary. These factors should be considered when generalizing our findings to different urban contexts.

To enhance bird biodiversity across urban landscapes, particularly for sensitive species, we recommend increasing habitat heterogeneity through targeted management practices, such as incorporating diverse vegetation structures and allowing for some natural growth (Hwang et al. 2019; Kowarik 2018). This approach can support a wider range of bird species, including those sensitive to urbanization. Managing green spaces to include various tree types, maintaining standing dead trees, when possible (Campos-Silva and Piratelli 2021), developing understory vegetation, and creating corridors to connect green spaces (Matsuba et al. 2016) can improve habitat quality and enhance bird communities across urban landscapes. By adopting these strategies, urban planners and managers can contribute to preserving and enhancing bird diversity in cities.

5 | Conclusions

Urban landscapes are complex ecosystems, constantly evolving, which increases the challenge of studying biodiversity patterns in cities. In this study, we focused on the "local habitat signature," emphasizing the significance of local-scale characteristics, which reflect how green spaces are managed and used by urban populations, ultimately shaping urban biodiversity. By shedding light on the importance of local environmental conditions, we argue for the need to move beyond the simplistic "urban gradient" model, recognizing cities as highly heterogeneous ecosystems (Malkinsona et al. 2018). A mere proxy for urbanization intensity at the landscape scale may fail to fully capture the dynamics of biodiversity patterns (Aoki-Gonçalves et al. 2023). By identifying distinct ecological groups based on species and functional traits, our approach provides a clear framework for pinpointing the key local factors that structure bird communities. This framework not only deepens our understanding of urban biodiversity but also enables the design of more targeted and effective management strategies. Ultimately, recognizing that different management actions create distinct habitat signatures allows urban planners and managers to implement specific, on-the-ground changes to enhance habitat quality and support diverse bird communities in increasingly urbanized regions.

Author Contributions

Tulaci Bhakti: conceptualization; data curation, methodology; project administration, data analysis; lead the investigation; writing – original draft; visualization. **Diego Pujoni:** methodology; data curation; writing – review and editing; visualization. **Marcos Rodrigues:** methodology; writing – review and editing; supervision. **João Carlos Pena:** conceptualization; methodology; data curation; lead the investigation; writing – review and editing; visualization; supervision.

Acknowledgments

We thank all the Institutions and Companies that allowed the fieldwork across Belo Horizonte: Belo Horizonte City Hall/Fundação de Parques, Fundação João Pinheiro, Fundação Benjamin Guimarães/Hospital da Baleia, Minas Tênis Clube, COMUPRA, CBTU-BH, Casa de Francisco, MHNJB/UFMG, COPASA, ASPRA, IRS, and IEF (license: 025/2020). T.B. received scholarships from the Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES process: 88887.364396/2019-00) and thanks to Fundo Brasileiro para a Biodiversidade (FUNBIO/Humanize), Idea Wild. M.R. has received a research scholarship from CNPq. J.C.P. received funding from FAPESP (#2018/00107-3; 2021/10195-0; 2023/17971-0). We are grateful to the Subject Editor and two anonymous reviewers for their constructive comments that significantly improved the manuscript. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in the Zenodo digital repository at https://doi.org/10.5281/zenodo.177151466.

References

Almazán-Núñez, R. C., E. A. Alvarez-Alvarez, D. K. Poblete-López, R. Rodríguez-Godínez, and P. Sierra-Morales. 2025. "Impulsores Locales y paisajísticos de los cambios en la comunidad de aves en parques urbanos de una ciudad neotropical." *Acta Biológica Colombiana* 30, no. 1: 105–120. https://doi.org/10.15446/abc.v30n1.113739.

Anselmo, P. A., J. C. F. Cardoso, P. R. Siqueira, and P. K. Maruyama. 2023. "Non-Native Plants and Illegitimate Interactions Are Highly Relevant for Supporting Hummingbird Pollinators in the Urban Environment." *Urban Forestry & Urban Greening* 86, no. June: 128025. https://doi.org/10.1016/j.ufug.2023.128025.

Aoki-Gonçalves, F., J. C. Pena, T. Toledo-Aceves, and I. MacGregor-Fors. 2023. "Urban Epiphytes: Bromeliad Diversity in a Green Cover Gradient Across a Neotropical Streetscape." *Urban Forestry & Urban Greening* 83: 127901. https://doi.org/10.1016/j.ufug.2023.127901.

Aronson, M. F. J., C. A. Lepczyk, K. L. Evans, et al. 2017. "Biodiversity in the City: Key Challenges for Urban Green Space Management." *Frontiers in Ecology and the Environment* 15, no. 4: 189–196. https://doi.org/10.1002/fee.1480.

Avilla, S. S., K. E. Sieving, M. Anciães, and C. Cornelius. 2021. "Phenotypic Variation in a Neotropical Understory Bird Driven by Environmental Change in an Urbanizing Amazonian Landscape." *Oecologia* 196, no. 3: 763–779. https://doi.org/10.1007/s00442-021-04976-x.

Barbosa, K. V. C., A. D. Rodewald, M. C. Ribeiro, and A. E. Jahn. 2020. "Noise Level and Water Distance Drive Resident and Migratory Bird Species Richness Within a Neotropical Megacity." *Landscape and Urban Planning* 197: 103769. https://doi.org/10.1016/j.landurbplan.2020.103769.

Belo Horizonte. 2019. "Plano Diretor do Município de Belo Horizonte—Lei no 11.181 (p. Lei no 11.181)." http://portal6.pbh.gov.br/dom/iniciaEdicao.do?method=DetalheArtigo&pk=1215565.

Bhakti, T., F. Goulart, C. S. de Azevedo, and Y. Antonini. 2018. "Does Scale Matter? The Influence of Three-Level Spatial Scales on Forest Bird Occurrence in a Tropical Landscape." *PLoS One* 13, no. 6: e0198732. https://doi.org/10.1371/journal.pone.0198732.

Bhakti, T., J. C. Pena, A. C. M. Moura, D. Pujoni, L. Saliba, and M. Rodrigues. 2024. "Urban Biodiversity Suitability Index: Decoding the Relationships Between Cities and Birds." *Urban Ecosystems* 27, no. 1: 305–319. https://doi.org/10.1007/s11252-023-01446-5.

Bhakti, T., J. C. Pena, B. B. Niebuhr, et al. 2021. "Combining Land Cover, Animal Behavior, and Master Plan Regulations to Assess Landscape Permeability for Birds." *Landscape and Urban Planning* 214: 104171. https://doi.org/10.1016/j.landurbplan.2021.104171.

Bhakti, T., and M. Rodrigues. 2020. "Nidificação da ariramba-da-cauda-ruiva *Galbula ruficauda* em área altamente urbanizada." *Atualidades Ornitológicas* 218: 22–23.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008. "Forward Selection of Explanatory Variables." *Ecology* 89, no. 9: 2623–2632. https://doi.org/10.1890/07-0986.1.

Borcard, D., F. Gillet, and P. Legendre. 2011. *Numerical Ecology With R*. Vol. 2. Springer.

Brandão, M., and M. G. Araújo. 1992. "Cobertura vegetal do município de Belo Horizonte, MG." *Daphne: Revista Do Herbário PAMG* 2, no. 2: 5–12.

Callaghan, C. T., A. G. B. Poore, R. E. Major, W. K. Cornwell, J. H. Wilshire, and M. B. Lyons. 2021. "How to Build a Biodiverse City: Environmental Determinants of Bird Diversity Within and Among 1581 Cities." *Biodiversity and Conservation* 30: 217–234. https://doi.org/10.1007/s10531-020-02088-1.

Campos-Silva, L. A., and A. J. Piratelli. 2021. "Vegetation Structure Drives Taxonomic Diversity and Functional Traits of Birds in Urban Private Native Forest Fragments." *Urban Ecosystems* 14: 375–390. https://doi.org/10.1007/s11252-020-01045-8.

Cardoso Araujo, A., C. Silveira Souza, V. Akemi Nakamura, L. da Cruz Rodrigues, and A. Traveset. 2024. "Floral Abundance and Corolla Length Predict the Importance of Species in Connecting Urban Green Areas." *Landscape and Urban Planning* 248, no. May: 105108. https://doi.org/10.1016/j.landurbplan.2024.105108.

Chin, E. Y., and J. A. Kupfer. 2020. "Identification of Environmental Drivers in Urban Greenway Communities." *Urban Forestry & Urban Greening* 47: 126549. https://doi.org/10.1016/j.ufug.2019.126549.

da Silva, B. F., J. C. Pena, A. B. Viana-Junior, M. Vergne, and M. A. Pizo. 2021. "Noise and Tree Species Richness Modulate the Bird Community Inhabiting Small Public Urban Green Spaces of a Neotropical City." *Urban Ecosystems* 24, no. 1: 71–81. https://doi.org/10.1007/s11252-020-01021-2.

D'angelo, G. B. 2021. *História Natural das relações alimentares de aves com plantas em um parque urbano no Sudeste do Brasil*. Universidade Estadual de Campinas.

de Toledo, M. C. B., R. J. Donatelli, and G. T. Batista. 2012. "Relation Between Green Spaces and Bird Community Structure in an Urban Area in Southeast Brazil." *Urban Ecosystems* 15, no. 1: 111–131. https://doi.org/10.1007/s11252-011-0195-2.

Dray, S., D. Bauman, G. Blanchet, et al. 2018. "adespatial: Multivariate Multiscale Spatial Analysis." R Package Version 0.3-2. https://cran.r-project.org/package=adespatial.

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. "Spatial Modelling: A Comprehensive Framework for Principal Coordinate Analysis of Neighbour Matrices (PCNM)." *Ecological Modelling* 196, no. 3–4: 483–493. https://doi.org/10.1016/j.ecolmodel.2006.02.015.

Escobar-Ibáñez, J. F., R. Rueda-Hernández, and I. MacGregor-Fors. 2020. "The Greener the Better! Avian Communities Across a Neotropical Gradient of Urbanization Density." *Frontiers in Ecology and Evolution* 8: 500791. https://doi.org/10.3389/fevo.2020.500791.

Filloy, J., G. A. Zurita, and M. I. Bellocq. 2019. "Bird Diversity in Urban Ecosystems: The Role of the Biome and Land Use Along Urbanization Gradients." *Ecosystems* 22: 213–227. https://doi.org/10.1007/s10021-018-0264-y.

Fontoura, P. M., and M. L. Orsi. 2013. "Ecological Partitioning of Three Columbidae Species in Northern Paraná, Southern Brazil." *Biota Neotropica* 13, no. 3: 44–49. https://doi.org/10.1590/S1676-06032013000300005.

Gomes, I. N., C. Bosenbecker, V. H. D. Silva, J. C. F. Cardoso, J. C. Pena, and P. K. Maruyama. 2023. "Spatiotemporal Availability of Pollinator Attractive Trees in a Tropical Streetscape: Unequal Distribution for Pollinators and People." *Urban Forestry & Urban Greening* 83: 127900. https://doi.org/10.1016/j.ufug.2023.127900.

Horta, M. B., T. Bhakti, P. F. Cordeiro, S. M. Carvalho-Ribeiro, G. W. Fernandes, and F. F. Goulart. 2018. "Functional Connectivity in Urban Landscapes Promoted by *Ramphastos toco* (Toco Toucan) and Its Implications for Policy Making." *Urban Ecosystems* 21, no. 6: 1097–1111. https://doi.org/10.1007/s11252-018-0789-z.

Hwang, Y. H., Z. E. J. Yue, S. K. Ling, and H. H. V. Tan. 2019. "It's Ok to Be Wilder: Preference for Natural Growth in Urban Green Spaces in a Tropical City." *Urban Forestry & Urban Greening* 38: 165–176. https://doi.org/10.1016/j.ufug.2018.12.005.

Jacoboski, L. I., and S. M. Hartz. 2020. "Using Functional Diversity and Taxonomic Diversity to Assess Effects of Afforestation of Grassland on Bird Communities." *Perspectives in Ecology and Conservation* 18, no. 2: 103–108. https://doi.org/10.1016/j.pecon.2020.04.001.

Kark, S., A. Iwaniuk, A. Schalimtzek, and E. Banker. 2007. "Living in the City: Can Anyone Become an 'Urban Exploiter'?" *Journal of Biogeography* 34, no. 4: 638–651. https://doi.org/10.1111/j.1365-2699.2006.01638.x.

Kowarik, I. 2018. "Urban Wilderness: Supply, Demand, and Access." *Urban Forestry & Urban Greening* 29: 336–347. https://doi.org/10.1016/j.ufug.2017.05.017.

Legendre, P., and E. D. Gallagher. 2001. "Ecologically Meaningful Transformations for Ordination of Species Data." *Oecologia* 129: 271–280. https://doi.org/10.1007/s004420100716.

Malkinsona, D., D. Kopela, and L. Wittenberg. 2018. "From Rural–Urban Gradients to Patch—Matrix Frameworks: Plant Diversity Patterns in Urban Landscapes." *Landscape and Urban Planning* 169: 260–268. https://doi.org/10.1016/J.LANDURBPLAN.2017.09.021.

Marini, M. Â., F. J. A. Borges, L. E. Lopes, et al. 2012. "Breeding Biology of Birds in the Cerrado." *Ornitologia Neotropical* 23: 385–405.

Matsuba, M., S. Nishijima, and K. Katoh. 2016. "Effectiveness of Corridor Vegetation Depends on Urbanization Tolerance of Forest Birds in Central Tokyo, Japan." *Urban Forestry & Urban Greening* 18: 173–181. https://doi.org/10.1016/j.ufug.2016.05.011.

Morelli, F., P. Mikula, Y. Benedetti, R. Bussière, and P. Tryjanowski. 2018. "Cemeteries Support Avian Diversity Likewise Urban Parks in European Cities: Assessing Taxonomic, Evolutionary and Functional Diversity." *Urban Forestry & Urban Greening* 36, no. May: 90–99. https://doi.org/10.1016/j.ufug.2018.10.011.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. "Biodiversity Hotspots for Conservation Priorities." *Nature* 403, no. 6772: 853–858. https://doi.org/10.1590/2179-8087.011119.

Nock, C. A., R. J. Vogt, and B. E. Beisner. 2016. "Functional Traits." In *Encyclopedia of Life Sciences*, 1–8. Wiley. https://doi.org/10.1002/9780470015902.a0026282.

Oksanen, J., F. G. Blanchet, R. Kindt, et al. 2013. "vegan: Community Ecology Package." https://cran.r-project.org/package=vegan.

Pena, J., F. Martello, M. C. Ribeiro, R. A. Armitage, R. J. Young, and M. Rodrigues. 2017. "Street Trees Reduce the Negative Effects of Urbanization on Birds." *PLoS One* 12, no. 3: e0174484. https://doi.org/10.1371/journal.pone.0174484.

Pena, J., O. Ovaskainen, I. MacGregor-Fors, C. P. Teixeira, and M. C. Ribeiro. 2023. "The Relationships Between Urbanization and Bird

Functional Traits Across the Streetscape." *Landscape and Urban Planning* 232: 104685. https://doi.org/10.1016/j.landurbplan.2023.104685.

Planet Labs PBC. 2017. "Planet Application Program Interface: In Space for Life on Earth." Image 2017 Planet Labs PBC. https://api.planet.com.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Ramalho, C. E., and R. J. Hobbs. 2012. "Time for a Change: Dynamic Urban Ecology." *Trends in Ecology & Evolution* 27, no. 3: 179–188. https://doi.org/10.1016/j.tree.2011.10.008.

Rega-Brodsky, C. C., M. F. J. Aronson, M. R. Piana, et al. 2022. "Urban Biodiversity: State of the Science and Future Directions." *Urban Ecosystems* 25, no. 4: 1083–1096. https://doi.org/10.1007/s11252-022-01207-w.

Richardson, J., A. C. Lees, E. T. Miller, and S. J. Marsden. 2023. "Avian Diversity and Function Across the World's Most Populous Cities." *Ecology Letters* 26, no. 8: 1301–1313. https://doi.org/10.1111/ele.14238.

Rodrigues, L. C., and A. C. Araujo. 2011. "The Hummingbird Community and Their Floral Resources in an Urban Forest Remnant in Brazil." *Brazilian Journal of Biology* 71, no. 3: 611–622. https://doi.org/10.1590/s1519-69842011000400005.

Rupprecht, C. D. D., J. A. Byrne, J. G. Garden, and J. M. Hero. 2015. "Informal Urban Green Space: A Trilingual Systematic Review of Its Role for Biodiversity and Trends in the Literature." *Urban Forestry & Urban Greening* 14, no. 4: 883–908. https://doi.org/10.1016/j.ufug.2015.08.009.

Santos, E. G., H. C. Wiederhecker, V. T. Pompermaier, et al. 2024. "Urbanization Reduces Diversity, Simplifies Community and Filter Bird Species Based on Their Functional Traits in a Tropical City." *Science of the Total Environment* 935, no. March: 173379. https://doi.org/10.1016/j.scitotenv.2024.173379.

Sick, H. 1997. *Ornitologia Brasileira*, edited by J. F. Pacheco. Nova Fronteira.

Silva, P., A. G. Cherutte, A. C. S. Gomes, et al. 2023. "The Ecological Role and Potential Impact of an Alien Tree Highly Attractive to Native Nectar-Feeding Birds in Urban Areas." *Urban Ecosystems* 26: 1029–1040. https://doi.org/10.1007/s11252-023-01345-9.

Smith, W. S., F. L. da Silva, S. R. de Amorim, and M. S. Stefani. 2018. "Urban Biodiversity: How the City Can Do Its Management?" *Biodiversity International Journal* 2, no. 2: 246–251. https://doi.org/10.15406/bij.2018.02.00068.

Snep, R. P. H., P. F. M. Opdam, J. M. Baveco, et al. 2006. "How Peri-Urban Areas Can Strengthen Animal Populations Within Cities: A Modeling Approach." *Biological Conservation* 127, no. 3: 345–355. https://doi.org/10.1016/j.biocon.2005.06.034.

Soanes, K., M. Sievers, Y. E. Chee, et al. 2019. "Correcting Common Misconceptions to Inspire Conservation Action in Urban Environments." *Conservation Biology* 33, no. 2: 300–306. https://doi.org/10.1111/cobi.13193.

Stagoll, K., A. D. Manning, E. Knight, J. Fischer, and D. B. Lindenmayer. 2010. "Using Bird-Habitat Relationships to Inform Urban Planning." *Landscape and Urban Planning* 98, no. 1: 13–25. https://doi.org/10.1016/j.landurbplan.2010.07.006.

Suri, J., P. M. Anderson, T. Charles-Dominique, E. Hellard, and G. S. Cumming. 2017. "More Than Just a Corridor: A Suburban River Catchment Enhances Bird Functional Diversity." *Landscape and Urban Planning* 157: 331–342. https://doi.org/10.1016/j.landurbplan.2016.07.013.

Threlfall, C. G., L. Mata, J. A. Mackie, et al. 2017. "Increasing Biodiversity in Urban Green Spaces Through Simple Vegetation Interventions." *Journal of Applied Ecology* 54, no. 6: 1874–1883. https://doi.org/10.1111/1365-2664.12876.

Vale, M. M., L. Tourinho, M. L. Lorini, H. Rajão, and M. S. L. Figueiredo. 2018. "Endemic Birds of the Atlantic Forest: Traits, Conservation Status, and Patterns of Biodiversity." *Journal of Field Ornithology* 89, no. 3: 193–206. https://doi.org/10.1111/jofo.12256.

Vandevelde, J., and C. Penone. 2017. "Ecological Roles of Railway Verges in Anthropogenic Landscapes: A Synthesis of Five Case Studies in Northern France." In *Railway Ecology*, edited by L. Borda-de-Água, R. Barrientos, P. Beja, and H. Pereira, 261–276. Springer. https://doi.org/10.1007/978-3-319-57496-7_16.

Villaseñor, N. R., L. A. Chiang, H. J. Hernández, and M. A. H. Escobar. 2020. "Vacant Lands as Refuges for Native Birds: An Opportunity for Biodiversity Conservation in Cities." *Urban Forestry & Urban Greening* 49: 126632. https://doi.org/10.1016/j.ufug.2020.126632.

Vizzari, M., and M. Sigura. 2015. "Landscape Sequences Along the Urban–Rural–Natural Gradient: A Novel Geospatial Approach for Identification and Analysis." *Landscape and Urban Planning* 140: 42–55. https://doi.org/10.1016/j.landurbplan.2015.04.001.

Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. "EltonTraits 1.0: Species-Level Foraging Attributes of the World's Birds and Mammals." *Ecology* 95, no. 7: 2027. https://doi.org/10.1890/13-1917.1.

Wong, J. S. Y., M. C. K. Soh, B. W. Low, and K. B. H. Er. 2023. "Tropical Bird Communities Benefit From Regular-Shaped and Naturalised Urban Green Spaces With Water Bodies." *Landscape and Urban Planning* 231: 104644. https://doi.org/10.1016/j.landurbplan.2022.104644.

Xavier, E. R. S. 2018. "Áreas Protegidas Urbanas e conservação de um ecótone Cerrado-Mata Atlântica [Universidade Federal de Minas Gerais]." In *Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silcvestre*. https://doi.org/10.13140/RG.2.2.11607.32169.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Supporting Information: I. Supporting Information: II.**