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Taxonomic and functional diversity in bird assemblages in an urban area in the Cerrado hotspot

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Diversidade taxonômica e funcional em assembleias de aves em um área urbana no hotspot do Cerrado

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Tese apresentada como requisito para a obtenção do título de **Doutora em Ecologia**, pelo Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Mato Grosso do Sul.

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“You cannot get through a single day without having an impact on the world around you. What you do makes a difference, and you have to decide what kind of difference you want to make.”

Jane Goodall

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Table of Contents

General abstract

High rates of urbanization and rapid habitat loss in urban centers pose major challenges for biodiversity conservation, making cities complex ecosystems for sustaining diverse biological communities. Increased population density is often associated with reduced biodiversity, as it intensifies the negative effects of urbanization on ecosystems. Together, these processes create significant challenges for the persistence of certain bird species in urban environments. The new conditions imposed by urban areas reduce the availability of green spaces, which can negatively affect the occurrence of less tolerant species, the so-called urban avoiders, while favoring those more adapted to disturbance. Thus, cities that preserve fragments of native vegetation and structures capable of harboring local bird species can sustain greater urban diversity, playing a key role in the conservation and maintenance of these communities. To understand how the urbanization process impacts biodiversity in a tropical city located in the Cerrado biome, one of the world's main biodiversity hotspots, this thesis used birds as a model group. I investigated different levels of urbanization in the city of Campo Grande (MS), and the potential effect of tree cover on the structure of bird assemblages. In Chapter 1, I examined how tree cover, building density, and population density influence bird abundance and species richness in urban areas. In addition, I evaluated whether these patterns vary among different ecological guilds (habitat, trophic niche, and primary lifestyle) and which component of beta diversity (turnover or nestedness) explains variation in community composition. The results showed that tree cover was the most important variable, having a positive effect on the richness and abundance of forest species while negatively affecting species associated with human-modified environments, granivores, and terrestrial species. Beta diversity between sites was mostly explained by the turnover component (97%), indicating species replacement along the urban gradient. Variation in community composition was significantly associated with tree cover, with areas of greater

vegetation cover hosting more similar communities, in contrast to highly urbanized areas, which exhibited greater heterogeneity and a predominance of generalist species. In Chapter 2, I evaluated how environmental variables (tree cover, building density, and population density) at three spatial scales (75 m, 200 m, and 500 m) influence the functional diversity of bird communities across 30 urban locations. Four complementary functional diversity metrics (richness, evenness, divergence, and functional dispersion) were calculated from morphological traits (beak, tail, wing length, and body mass). The results showed that functional evenness (FEve) was negatively related to tree cover at all scales and positively related to the proportion of urban area at the 75 m and 200 m scales, indicating a more homogeneous distribution of functions in more urbanized environments. The other functional diversity metrics (FRic, FDis, and FDiv) showed no significant relationships with environmental variables. Moreover, the community-weighted means (CWMs) of morphological traits indicated a positive effect of urbanization on wing length, suggesting that species with greater flight capacity tend to be favored in more urbanized areas. In Chapter 3, I assessed the potential of urban road verges (median strips between avenues) to maintain and conserve bird communities across different levels of urbanization (low <50%, intermediate 50–90%, and high >90%). The alpha, beta, and gamma diversity of bird assemblages sampled in 30 urban road verges distributed among these classes were compared. The results showed that sites with low urbanization had higher average species richness (alpha diversity) and higher total species numbers (gamma diversity) than those with intermediate and high urbanization. Total beta diversity was also higher in the low and intermediate urbanization classes, reflecting greater heterogeneity among communities. In contrast, highly urbanized areas exhibited more homogeneous communities, with lower species turnover and greater nestedness. Turnover was the main component of the driving variation in beta diversity, especially in less urbanized areas. These results indicate that urban road verges with greater vegetation cover and lower urbanization intensity play an important role in maintaining local and regional diversity, functioning as complementary habitats and potential ecological corridors for birds in highly modified urban landscapes. Our findings highlight the importance of managers and decision-makers prioritizing the maintenance and expansion of native vegetation along the urban gradient. Heterogeneous environments within anthropogenic areas favor more diverse bird communities, with greater resource availability and, consequently, enhanced ecosystem service provision. Strengthening programs for the restoration and proper management of native vegetation, therefore, represents an essential strategy for conserving urban biodiversity and promoting more sustainable and resilient cities.

Resumo geral

As altas taxas de urbanização e a rápida perda de habitat nos centros urbanos representam grandes desafios para a conservação da biodiversidade, tornando as cidades ecossistemas complexos para sustentar comunidades biológicas diversas. O aumento da densidade populacional está frequentemente associado à redução da biodiversidade, uma vez que intensifica os efeitos negativos da urbanização sobre os ecossistemas. Em conjunto, esses processos representam grandes desafios para a persistência de algumas espécies em ambientes urbanos, inclusive espécies de aves. As novas condições impostas pelos ambientes urbanos reduzem a disponibilidade de áreas verdes. Essa redução pode afetar negativamente a ocorrência de espécies menos tolerantes, ou chamadas de evitadoras urbanas, e favorecer aquelas mais adaptadas às perturbações. Dessa forma, cidades que mantêm fragmentos de vegetação nativa e estruturas capazes de abrigar espécies de aves locais podem sustentar uma maior diversidade urbana, desempenhando um papel fundamental na conservação e manutenção dessas comunidades. Para compreender como o processo de urbanização impacta a biodiversidade em uma cidade tropical localizada no bioma Cerrado, um dos principais *hotspots* de biodiversidade do mundo, esta tese utilizou as aves como grupo modelo.
Assim, investiguei diferentes níveis de urbanização na cidade de Campo Grande (MS) e o potencial efeito da cobertura arbórea na estrutura das assembleias de aves. No Capítulo 1, investiguei como a cobertura arbórea, a densidade de construções e a densidade populacional influenciam a abundância e a riqueza de espécies de aves em áreas urbanas. Além disso, avaliei se esses padrões variam entre diferentes guildas ecológicas (habitat, nicho trófico e estilo de vida primário) e qual componente da diversidade beta (*turnover* e *nestedness*) explica a variação na composição das comunidades. Os resultados mostraram que a cobertura arbórea foi a variável mais importante, apresentando efeito positivo sobre a riqueza e a abundância de espécies florestais, enquanto teve efeito negativo sobre espécies associadas a

ambientes humanos modificados, granívoras e terrestres. A diversidade beta entre os locais foi majoritariamente explicada pelo componente de *turnover* (97%), indicando substituição de espécies ao longo do gradiente urbano. A variação na composição das comunidades foi significativamente associada à cobertura arbórea, com áreas de maior cobertura arbórea apresentando comunidades mais semelhantes entre si, em contraste com áreas mais urbanizadas, que mostraram maior heterogeneidade e predominância de espécies generalistas. No Capítulo 2, avaliei como variáveis ambientais (cobertura arbórea, densidade de construções e densidade populacional) em três escalas espaciais (75 m, 200 m e 500 m) influenciam a diversidade funcional das comunidades de aves em 30 locais urbanos. Foram consideradas quatro métricas complementares de diversidade funcional (riqueza - FRic, uniformidade - FEve, divergência - FDiv e dispersão funcional - FDis), calculadas a partir de características morfológicas (comprimento do bico, cauda e asa, e massa corporal). Os resultados mostraram que a uniformidade funcional (FEve) apresentou relação negativa com a cobertura arbórea em todas as escalas e positiva com a proporção de área urbana nas escalas de 75m e 200m, indicando uma distribuição mais homogênea das funções nas áreas mais urbanizadas. As demais métricas de diversidade funcional (FRic, FDis e FDiv) não apresentaram relações significativas com as variáveis ambientais. Além disso, as médias ponderadas das características morfológicas (CWMs) indicaram um efeito positivo da urbanização sobre o comprimento da asa, sugerindo que espécies com maior capacidade de voo tendem a ser favorecidas em ambientes mais urbanizados. Por fim, no Capítulo 3, avaliei o potencial das *urban road verges* (canteiros centrais entre avenidas) em manter e conservar comunidades de aves em diferentes níveis de urbanização (baixa <50%, intermediária 50–90% e alta >90%). Foram comparadas a diversidade alfa, beta e gama das assembleias de aves amostradas em 30 *urban road verges*, distribuídas entre essas classes de urbanização. Os resultados mostraram que os locais com baixa urbanização apresentaram maior riqueza média de espécies (diversidade alfa) e maior número total de espécies (diversidade gama) em comparação às áreas com urbanização intermediária e alta. A diversidade beta total também foi mais elevada nas classes de baixa e intermediária urbanização, refletindo uma maior heterogeneidade entre as comunidades. Em contraste, áreas com alta urbanização apresentaram comunidades mais homogêneas, com menor substituição (*turnover*) de espécies e maior aninhamento (*nestedness*). A substituição (*turnover*) foi o principal componente responsável pela variação na diversidade beta, especialmente nas áreas menos urbanizadas. Esses resultados indicam que as *urban road verges* com maior cobertura vegetal e menor intensidade de urbanização têm um papel relevante na manutenção da diversidade local e regional, funcionando como habitats complementares e potenciais corredores ecológicos para aves em ambientes urbanos altamente modificados. Nossos resultados destacam a importância de que gestores e tomadores de decisão priorizem a manutenção e o aumento da vegetação nativa ao longo do gradiente urbano. Ambientes heterogêneos dentro de áreas antrópicas favorecem comunidades de aves mais diversas, com maior disponibilidade de recursos e, consequentemente, maior oferta de serviços ecossistêmicos. Assim, o fortalecimento de programas de restauração e manejo de vegetação nativa adequado representa uma estratégia essencial para a conservação da biodiversidade urbana e para a promoção de cidades mais sustentáveis e resilientes.

General Introduction

The urbanization process represents one of the main threats to biodiversity conservation worldwide. Several studies have highlighted the negative consequences of urbanization. For example, the growth of urban areas can cause habitat loss and fragmentation, causing the extinction of more sensitive species (Sol et al. 2014; Dri et al. 2021). Furthermore, the presence of exotic species may pose an additional threat to native species in urban areas, either through competition or predation (Shochat et al. 2010). Finally, other factors such as changes in microclimatic conditions and environmental pollution can also affect the occurrence of species in urban environments (Pereira et al. 2012; Yang et al. 2015). Therefore, since there is a tendency for the human population living in cities to increase in the coming decades (United Nations 2022), new studies are urgently needed to assess how species and communities may react to the growth of urban areas.

Most studies assess the impact of urbanization on animal and plant community structures from a taxonomic perspective, focusing on changes in abundance, richness, and species composition. For instance, McKinney (2008), reviewed patterns of species richness across multiple taxa, such as birds, plants, mammals, reptiles, amphibians, and terrestrial arthropods. Malloch et al. (2020) investigated changes in the structure of microarthropod communities in urban parks in Canada, while Lososová et al. (2016) examined beta diversity patterns of exotic plants across different urban habitats in seven European cities. On the other hand, some studies also evaluate the impact of urbanization on functional and phylogenetic diversity, providing a more integrative understanding of biodiversity loss. For example, Sol et al. (2020) analyzed how urbanization filters bird species according to their functional traits and evolutionary history across multiple cities worldwide, while Devictor et al. (2007) tested the functional homogenization process using bird communities in disturbed landscapes.

However, although urban areas are recognized as inhospitable environments for many species, some factors can mitigate these negative effects, contributing to biodiversity conservation in these environments. For example, the presence of isolated trees can provide shelter, food, and nesting sites for some species in urban areas (Pena et al. 2017; Von Thaden et al. 2021). Furthermore, remnants of native vegetation and protected areas can serve as refuge for populations of more endangered species of several animals, such as birds, bats, frogs, and butterflies (Kruger et al. 2015; Threlfall et al. 2017; Tzortzakaki et al. 2019; Von Thaden et al. 2021). Finally, other green elements in cities, such as gardens and road verges, can positively impact biodiversity in urban environments (Bell et al. 2025; Doğan et al. 2025). Therefore, the great challenge for cities is how to reconcile the expansion of urban areas with the maintenance of landscape elements that can guarantee the conservation of biodiversity in these environments. This is especially worrying in biodiversity hotspots, where urban growth is expected to be greatest in the coming decades (Güneralp and Seto 2013).

In this context, this thesis investigates the effect of environmental and demographic variables on the taxonomic and functional diversity of birds in an urban area of the Cerrado biome. Birds represent an excellent model group for evaluating the impacts of urbanization on species and communities because their functional traits are well known, and they include a wide range of species with different responses to environmental change, such as urban avoiders and tolerant species (Vandewalle et al. 2010; Xu et al. 2018). Moreover, there are still relatively few studies assessing how bird communities respond to urbanization in areas of the Cerrado biome, one of the most threatened in Brazil. For instance, Almeida-Gomes et al. (2025) investigated whether the taxonomic and functional diversity of bird communities can be explained by historical changes in the landscape. Carvalho et al. (2025) analyzed the effects of vegetation on bird communities and bird–plant interactions in urban riparian areas, while Souza et al. (2019) examined how urbanization influences bird communities by focusing on the richness of bird feeding guilds.

The thesis is structured into three chapters. In Chapter 1, I evaluated the effect of tree cover, urbanization (building density), and human population density on bird species abundance and richness (considering all species and different ecological guilds - habitat, trophic niche, and primary lifestyle). We also evaluated which beta-diversity process (nesting or turnover) explains most of the variation in community composition. In Chapter 2, I investigated how tree cover, urban area, and human population density at three spatial scales (75 m, 200 m, and 500 m) influence the functional diversity of bird communities in thirty urban locations. We evaluated four complementary metrics of functional diversity (functional richness, evenness, divergence, and dispersion) to understand different aspects of the functional structure of assemblages. To describe functional space, we used four quantitative morphological characteristics: beak length, tail length, wing length, and body mass, which reflect ecological strategies related to foraging, dispersal, and habitat use. This approach allows us to assess how bird species respond to urbanization gradients and which morphological traits are associated with their persistence in tropical urban environments.

In Chapter 3, I evaluated the potential of urban road verges to maintain and conserve bird communities across different levels of urbanization (low <50%, intermediate 50–90%, and high >90%). Specifically, we compared the alpha, beta, and gamma diversity of bird assemblages sampled in 30 urban road verges distributed across these three urbanization levels. This approach allowed us to assess how increasing urban intensity influences both local and regional patterns of bird diversity, and to identify whether urban road verges can function as important habitat elements contributing to biodiversity conservation within highly modified landscapes. I understand that the findings of this study provide valuable insights for the development of robust environmental policies aimed at conserving urban avifauna. These results can also inform the design of restoration projects and support the preservation and proper management of existing green areas within urban environments, ensuring their continued contribution to urban biodiversity.

Chapter 1: Tree cover influences bird assemblage composition in a city within the Cerrado biodiversity hotspot*

*This chapter is in the process of publication in Urban Ecosystem.

Abstract

Declines in biodiversity in urban environments have frequently been reported, with factors such as tree cover and degree of urbanization affecting community responses in urban landscapes. Some ecological guilds may be more affected by urbanization than others, especially urban avoiders, due to their ecological and morphological traits. We evaluated the effect of tree cover, urbanization (building density), and human population density on bird abundance and species richness (considering all species and different ecological guilds) in the city of Campo Grande, Mato Grosso do Sul, Brazil. We also evaluated which beta-diversity process (nestedness or turnover) explains most of the variation in community composition. We recorded 2,140 individuals of 89 bird species. For forest species richness and abundance, we found a positive effect of tree cover. On the other hand, we found a negative effect of tree cover on abundance for human-modified habitat species, granivore species, and terrestrial species. Beta diversity was mainly caused by species turnover rather than by nestedness, with turnover being explained primarily by tree cover and human population density. Overall, our results showed that tree cover is important in determining bird assemblage composition in urban environments.

Introduction

The urbanization process represents one of the main threats to biodiversity (Simkin et al. 2022a). Among the consequences of the expansion of urban areas are the reduction of green areas (Nor et al. 2017; Li et al. 2019), increased air and water pollution (Luo et al. 2019; Wei et al. 2021), greater light and noise pollution (Morelli et al. 2023), changes in ecological processes (Moll et al. 2019; Theodorou 2022), and loss of biodiversity and ecosystem services (Aronson et al. 2017; Cox et al. 2018). Several studies have reported the loss of species in urban areas for different taxa, including birds (Ordóñez-Delgado et al. 2022; Almeida-Gomes et al. 2025), amphibians (Ganci et al. 2022), insects (Knop 2016), and bats (Mena et al. 2022). As 28% of the world's population will be concentrated in cities with at least one million inhabitants by 2030 (United Nations 2018), it is urgent to find ways to reconcile urban development and biodiversity conservation (Soga et al. 2014).

The maintenance of biodiversity in urban areas may depend on the presence of different landscape elements, such as fragments of native vegetation, isolated trees, and urban parks (White et al. 2005; Bryant 2006; Litteral and Wu 2012; Sushinsky et al. 2013; Pena et al. 2017). Among these elements, native vegetation can be particularly important for supporting more sensitive species (Sushinsky et al. 2013; Aronson et al. 2017). Several studies have reported positive effects of native vegetation remnants on different taxonomic groups, including bees (Prendergast et al. 2022), birds (White et al. 2005; Palmer et al. 2008), butterflies (Soga et al. 2014), and amphibians (Hamer and Parris 2011). For example, frugivorous birds (*Turdus leucomenas*), mammals (*Sapajus nigritus*), and reptiles (*Salvator merianae*) have high occupancy rates when resources are available in urban environments (Rigacci et al. 2021). For ground beetle species, there is a decline in populations as forest areas decrease (Fujita et al. 2008). Although urban areas may attract species when suitable habitat is present, they can function as ecological traps or habitat sinks for some bird species, leading to poor population viability. For example, fledglings of Spotted Towhee (*Pipilo maculatus*) near edges had a higher probability of dying in a forested urban park (Shipley et al. 2013). Moreover, insufficient food supply can cause low reproduction rates in the Eurasian kestrel (*Falco tinnunculus*) in the city of Vienna (Sumasgutner et al. 2014).

While some species cannot tolerate the environmental changes associated with urbanization or have lower population viability, generalist species or urban explorers often increase their populations in urbanized areas (Sol et al. 2020b), dominating these environments. For example, some ants are tolerant to dry conditions and warmer temperatures, which can be abundant in urban areas in Raleigh, North Carolina (Menke et al. 2011). For birds, granivorous species are often abundant in urban environments, thriving and expanding their distribution within human-dominated landscapes (Kark et al. 2007; Conole and Kirkpatrick 2011). Finally, the invasive and generalist bee species *Apis mellifera* is highly tolerant to urban environments and dominates urban plant-bee interactions in neotropical cities (Giannini et al., 2015, Tavares-Brancher et al., 2024). This adaptation to the urban environment occurs for species with functional and morphological characteristics that are likely to be favored in these locations, such as body size, diet, nesting behavior and foraging strategies (Jokimäki et al. 2016; Patankar et al. 2021; Pena et al. 2023).

Birds can be good models for understanding the effects of environmental changes on biodiversity in urban environments (de Toledo et al. 2012). For example, birds inhabiting wetlands and open spaces in a city in China were the most affected by habitat loss and fragmentation (Xu et al. 2018). Moreover, Baker et al., (2010) found a reduction in bird species diversity with increasing urbanization in Bristol, England, which was characterized by the loss of carnivores and piscivores, and an increase in the prevalence of granivorous and insectivorous species. Furthermore, insectivorous birds tend to be more sensitive to urban green space changes (Wu et al. 2024; Schillé et al. 2025). On the other hand, urban environments can favor generalist species, such as *Passer domesticus* and *Columba livia,* which can thrive in simplified and human-modified habitats due to their ecological flexibility (Jokimäki et al. 2016; Callaghan et al. 2019). The composition of the bird community is strongly influenced by the availability and quality of habitat in urban landscapes (Kang et al. 2015). Loss of native vegetation can reduce habitat complexity and resource availability, affecting species with narrow ecological niches and leading to communities dominated by urban-tolerant species (Croci et al. 2008; Conole and Kirkpatrick 2011; Dale 2018; Mbiba et al. 2021). These changes can be driven by key urban factors such as vegetation cover, which provides food and nesting resources (James Reynolds et al. 2019), building density which contributes to habitat loss and fragmentation (Dri et al. 2021) and population density, which is often associated with disturbance levels and reduced habitat quality (Kang et al. 2015).

Considering that different bird species and guilds can present distinct responses to urban environments, according to their life-history traits, and that landscape structure can affect the spatial distribution of urban bird attractiveness (Suarez-Castro et al. 2024), it is crucial to understand which species can or not thrive in urbanized areas and the role of landscape composition in shaping these communities. For example, Campos-Silva and Piratelli (2021) demonstrated that the structure of vegetation positively influenced the presence of native bird species that depend on forest resources, highlighting the vulnerability of more specialized groups. In contrast, Neate-Clegg et al. (2023) in a global analysis showed that species associated with urban areas tended to have broader diets and habitat preferences, confirming the urban tolerance of some species. These findings are especially important in tropical cities with high bird diversity and rapid urban growth. In this study, we evaluated whether tree cover, building density, and human population density can affect bird communities (species richness, abundance and community composition) along an urbanization gradient in a medium-sized tropical city, Campo Grande, Mato Grosso do Sul, Brazil, embedded within the Cerrado biome. We hypothesized that bird species richness and abundance (particularly forest-dependent species) would be positively related to tree cover, because of the higher resource availability provided by trees, such as nesting sites and food (Thaweepworadej and Evans 2022; Humphrey et al. 2023), which can positively improve bird attractiveness in urban areas (Suarez-Castro et al. 2024). We also hypothesized that bird species richness and abundance would be negatively related to urbanization (building density) and human population density, because of the higher level of disturbance in densely urbanized and populated areas. Finally, since urban areas can act as an ecological filter for bird species (Croci et al. 2008; Aronson et al. 2016; Silva et al. 2016; MacGregor-Fors et al. 2022), limiting which species can occur in these habitats, we hypothesized that the difference in community composition between areas will be explained mostly by the turnover rather than nestedness component of beta diversity, with the level of urbanization as the main variable responsible for this pattern. This result was found for amphibians in ponds in the same city (Ganci et al., 2022).

Material and methods

Study area

We conducted this study in the urban perimeter of the municipality of Campo Grande (20° 28′ 13″S, 54° 37′ 25″W), state of Mato Grosso do Sul, Brazil (Fig. S1). The study area was formerly entirely covered by Cerrado, including dry forests, grasslands, wetlands, shrublands, and savannahs (Ribeiro & Walter, 1998, MapBiomas platform collection 7.0, 2021). However, most of the native vegetation (~80%) has been replaced by pastures, crops, and urban areas (Ganci et al., 2022). There is a dry season (from April to September) and a rainy season (October to March), with an average annual precipitation of 1,530 mm and an average annual temperature ranging from 18 °C to 29 °C (Ferreira et al., 2017). The city has nearly

900,000 inhabitants and an average population density of 104 inhabitants/km2 (Ferreira et al., 2017).

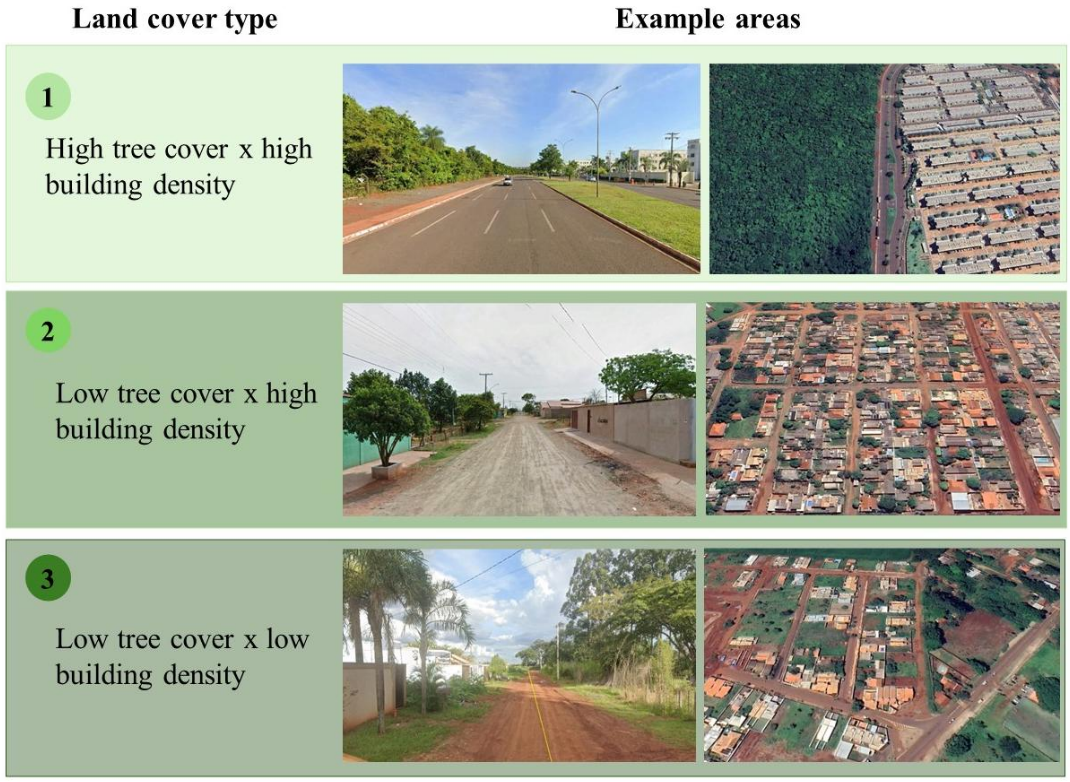

Figure 1. Representation of the sampled areas. These three areas represent the different levels of urbanization (building density) and tree cover in our study area.

Landscape and demographic metrics

To carry out landscape and demographic metric analyses, we created buffers with a radius of 500 meters for each of the thirty sampled locations, to calculate the percentage of tree cover, population density and building density. We calculated the percentage of tree cover in each buffer using imagery dated July 19, 2022, from the Sino-Brazilian Earth Resources Satellite (CEBRS 04A) with medium-resolution remote sensing (8m). To accomplish this, we employed bands 2 (Green), 3 (Red), and 4 (Near Infrared) to generate a false-color composite highlighting vegetation pixels. Additionally, we conducted a pan-sharpening process with the Panchromatic band to facilitate sample selection based on spectral signatures during the land-use and land-cover classification process. We utilized the Semi-Automatic Classification Plugin developed by Congedo (2021) in QGIS to generate a raster with the tree cover class. Tree cover (using a buffer of 500 m around transects) ranged from 2.47 to 50.65%.

Population density (number of human inhabitants per hectare) data were obtained from the SiSGRAN, a system managed by the Municipality of Campo Grande. These density data are available per neighborhood and represent the number of inhabitants per hectare. To extract population density information for each buffer, we utilized an intersection algorithm. However, when our samples overlapped with multiple neighborhoods, we employed the arithmetic mean to represent the population density of the sample. Population density (using a buffer of 500 m around transects) ranged from 8.03 to 55.94%.

We use the OpenStreetMap (OSM) indicator on the Google Engine platform for building density data (buildings per km²). OSM building density denotes the total building area in a region. It is a proxy for the quantitative estimation of construction data in urban areas (Zhou 2018). Building density (using a buffer of 500 m around transects) ranged from 609.27 to 3349.48 buildings per km².

Bird sampling

Bird sampling took place between July and November 2022, and was performed between 06:00 and 10:00, because most species in the region are active at that time (Souza et al. 2019).We did not sample birds on days with adverse weather conditions (e.g. rainy days), to avoid any bias in the detectability of some species. Each transect (N = 30) was sampled three times on distinct days. On each sampling event, two observers (simultaneously) walked a 200 m transect in a direction (unidirectional sampling) at a speed of approximately 1 km/h, which resulted in a duration of 12 minutes per transect. We recorded bird species through visual and acoustic identification (total sampling effort of 36 h for all transects). These methods allow a larger sample area to be covered in the same time when compared to other methods such as point sampling (Bibby 2000; Gregory et al. 2004; Pejchar et al. 2008; Karp et al. 2011). Moreover, the sampling effort we used was similar to those found in other studies in urban areas (Xie et al. 2016; Guo et al. 2019; Leveau and Leveau 2020).

To evaluate whether our sampling effort was appropriate, we calculated the sample coverage for each transect using the iNEXT package (Hsieh et al. 2016) and the exponent $q = 0$ for the Hill numbers (species richness) (Chao et al. 2023). Sample coverage represents the proportion of the total number of individuals that belong to the species detected in the sample (Hsieh et al. 2016). This analysis showed that our transects were properly sampled, as the mean sample coverage for all transects was 0.87 (range: 0.80 to 0.94) (Fig. S3).

Ecological guilds

We classified species according to their ecological guilds, using the AVONET dataset (Tobias et al. 2022) and the taxonomic classification from eBird (Clements et al. 2019). Species were classified according to their habitat (forest, grassland, human-modified, and shrubland), trophic niche (granivore, invertivore and omnivore), and primary lifestyle (insessorial and terrestrial), which allows us to predict the different responses of birds to environmental changes (Tobias et al. 2022). A complete description of the AVONET dataset can be found in (Tobias et al. 2022).

To ensure statistical robustness and avoid biases from small sample sizes, we selected only trait categories represented by at least 10 species. This selection allowed for more reliable inferences about the environmental variables, which are central to understanding how bird communities respond to urbanization.

Data analysis

Since predictor variables were measured at different scales, we standardized all of them to have a zero mean and unit variation, using the function decostand in the package vegan (Dixon, 2003; R Core Team, 2021). We used the variance inflation factor (VIF) in the usdm package (Naimi et al. 2014) to check for multicollinearity among our variables, but all of them had VIF < 2 and remained for analyses. We pooled the data from the three sampling events per transect to quantify differences in species richness in bird assemblages. For abundance and species composition, given that many tropical birds are highly site-faithful, we considered the maximum count per species per transect across visits, to reduce the risk of over-counting individuals observed multiple times.

To identify the effect of building density, human population density, and tree cover on abundance and species richness (considering all species and each ecological guild separately), we selected guilds represented by at least ten species in ecological guilds related to “habitat”, “trophic niche”, and “primary lifestyle” and with expected responses to urbanization or tree cover loss. We opted for “trophic niche” instead of “trophic level” because the former is more refined in terms of food preference. For example, the guild herbivore in “trophic niche” is decomposed into seven categories in the ecological variable “trophic level” (frugivore, granivore, herbivore aquatic, herbivore terrestrial, nectarivore, and omnivore). Therefore, the selected guilds were forest, human-modified (“habitat”), granivore, invertivore, and omnivore (“trophic niche”), and insessorial and terrestrial (“primary lifestyle”). We did not use the guild frugivore because of the low variation in species richness (0 to 3 species) and because of the low abundance for most sites (only six out of 30 sites with at least five individuals).

We employed a model selection approach to assess the effect of different scenarios on bird richness and abundance, considering two social variables (building density and population density) and one environmental variable (tree cover). The candidate models considered for each response variable were: (1) a null model, assuming no effect of social and environmental variables; (2) three models containing only social variables (building density and human population density); (3) a model containing only the environmental variable (tree cover); and (4) three additive models combining social and environmental variables.

We used generalized linear models (GLMs) with Poisson-distributed residuals. We used the “check_overdispersion” function from the ‘performance’ package to assess for overdispersion in Poisson models. As we detected overdispersion for models with abundance data, we used the negative binomial distribution using the “glm.nb” function in the package ‘MASS’ (Venables et al. 2013). The models were compared using the Akaike Information Criterion corrected for small samples (AICc) and Akaike weights (*wi*) using the MuMIn package (Burnham and Anderson 2004). Models with ΔAICc ≤ 2 were considered plausible. The relative importance of each explanatory variable was obtained from the sum of the weights of the models in which the variable was present (*Σwi*). Plausible models were subsequently subjected to model averaging (MuMIn package) (Burnham and Anderson 2004) to obtain mean coefficient estimates and standard errors. Finally, we obtained (for each model) Nagelkerke’s R^2 using the tab_model function from the sjPlot package (Lüdecke 2013).

To evaluate variation in species composition (the species present in a community) among bird assemblages, we used the approach proposed by Baselga (2010) to separate total beta-diversity into turnover and nestedness components. These two components of β-diversity reflect the underlying mechanisms responsible for changes in species identities across the landscape, the replacement of species (turnover) or their loss (nestedness) (Bevilacqua and Terlizzi 2020). We used abundance data and the Bray-Curtis index and conducted our analyses in the betapart R package (Baselga et al. 2018). Moreover, we conducted a distance-based Redundancy Analysis (db-RDA) using the Principal Coordinates extracted from the three dissimilarity matrices to test which explanatory variables (building density, human population density, and tree cover) best explained each beta diversity component. We conducted the analysis in the vegan package (Oksanen et al. 2020). We performed all analyses in R software v.4.3.2 (R Core Team, 2023).

Results

We recorded 2140 individuals of 89 bird species at 30 sampling transects during the breeding season. The list of all bird species recorded in this study is provided in the supplementary material (Table S1).

For total species richness and the species richness considering the guilds human-modified, granivore, invertivore, omnivore, insessorial and terrestrial, the null model was a plausible model (Supplementary Material; Table S2, S4-S9). We found two plausible models for forest species richness, one with only tree cover (wi= 0.40; $R^2 = 0.352$) and an additive model with tree cover and human population density (wi= 0.19; $R^2 = 0.408$) (Supplementary Material; Table S3). The most important variable was tree cover (Σwi =0.78). Model averaging showed that tree cover (β ±SE: 0.011 ± 0.004; Fig. 2A) and human population density (0.005 ± 0.005) had a positive effect on forest species richness.

For total abundance and the abundance considering the guilds invertivore, omnivore and insessorial, the null model was a plausible model (Table S10, S14-S16). For the abundance of forest species, we found two plausible models, considering only tree cover (wi= 0.41; $R^2 = 0.296$) and an additive model with tree cover and human population density (wi= 0.25; $R^2 = 0.361$) (Table S11). The most important variable was tree cover (Σwi =0.84). Model averaging showed that tree cover (0.012 ± 0.004; Fig. 2B) and human population density (0.006 ± 0.005) had a positive effect on the abundance of forest species. We found two plausible models for the abundance of human-modified species, with only tree cover (wi=

0.53; $R^2 = 0.550$) and an additive model with tree cover and building density (wi= 0.22; $R^2 = 0.576$) (Table S12). The most important variable was tree cover (Σwi =0.99). Model averaging showed that tree cover had a negative effect (-0.017 ± 0.004; Fig. 2C), while building density (0.00007 ± 0.00007) had a positive effect on the abundance of human-modified species. We found a single best-fit model to explain the abundance for granivore species, containing only the variable tree cover (wi= 0.55; $R^2 = 0.608$) (Table S13). Tree cover (-0.012 ± 0.005) showed a negative effect on the abundance of granivore species (Fig. 2D). We found two plausible models for the abundance of terrestrial species, considering only tree cover (wi = 0.54; $R^2 = 0.623$) and an additive model with tree cover and human population density (wi= 0.23; $R^2 = 0.649$) (Table S17). The most important variable was tree cover (Σwi =1.00). Model averaging showed that both variables, tree cover (-0.018 ± 0.004; Fig. 2E), and human population density (-0.004 ± 0.004) had a negative effect on terrestrial species abundance.

Total beta-diversity among transects was strongly caused by turnover (97%) rather than nestedness (2.9%). The db-RDA explained 18% of the variance for the turnover component ($R^2 = 0.18$). The percentage of tree cover ($F_{1,26} = 1.96$, $P = 0.010$), human population density ($F_{1,26} = 1.83$, $P = 0.014$) and building density ($F_{1,26} = 1.62$, $P = 0.031$) significantly explained the turnover component (Table S18, Fig. S4). On the other hand, the db-RDA explained a smaller part of the variance ($R^2 = 0.06$) and no variable had a significant effect on the nestedness component (Table S19, Fig. S5). Finally, the db-RDA explained 18% of the variance for the total beta diversity ($R^2 = 0.18$), with tree cover ($F_{1,26} = 2.04$, $P = 0.006$) and human population density ($F_{1,26} = 1.68605$, $P = 0.041$), having a significant effect on the total beta diversity (Table S20, Fig. S6). Most local landscapes with a high percentage of tree cover appear closer to each other in terms of community composition compared to areas with medium or low tree cover (Fig. 3). The ordinations based on human population density (Fig.

S7) and building density (Fig. S8) did not show such a clear pattern as those based on tree cover.

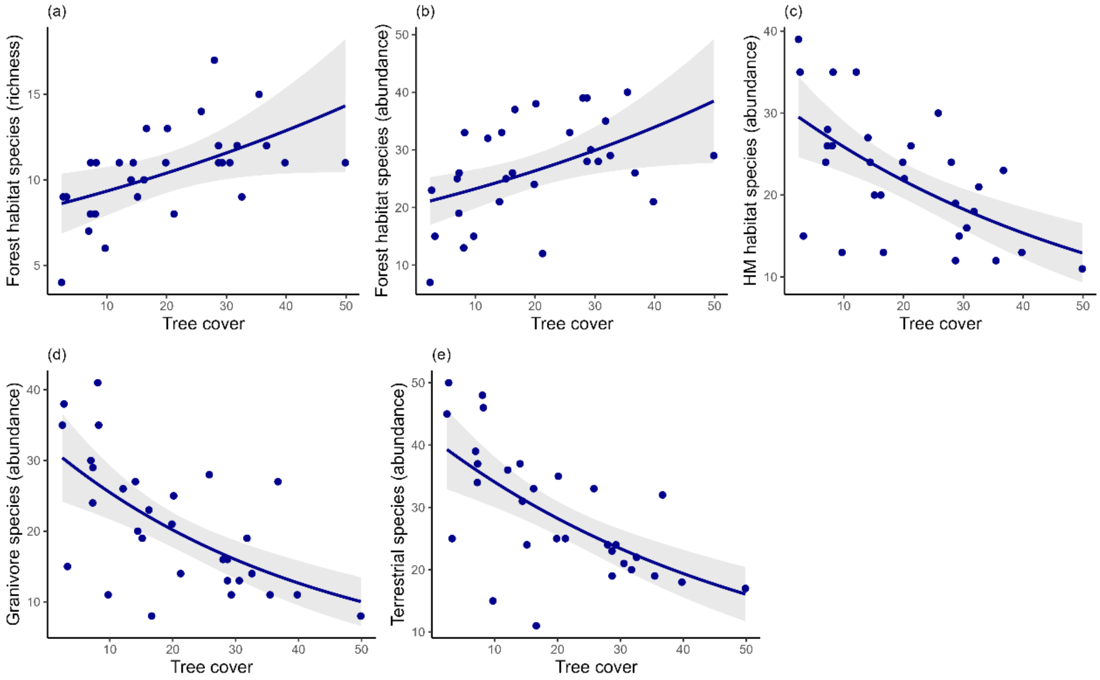

Figure 2. Effects of tree cover (%) on richness and abundance of birds across different ecological guilds. (a) positive relationship between tree cover and species richness of forest habitat species; (b) positive relationship between tree cover and abundance of forest habitat species; (c-e) negative relationship between tree cover and abundance of human-modified (HM) habitat species, granivore and terrestrial species. Only the most important variable for each model was plotted.

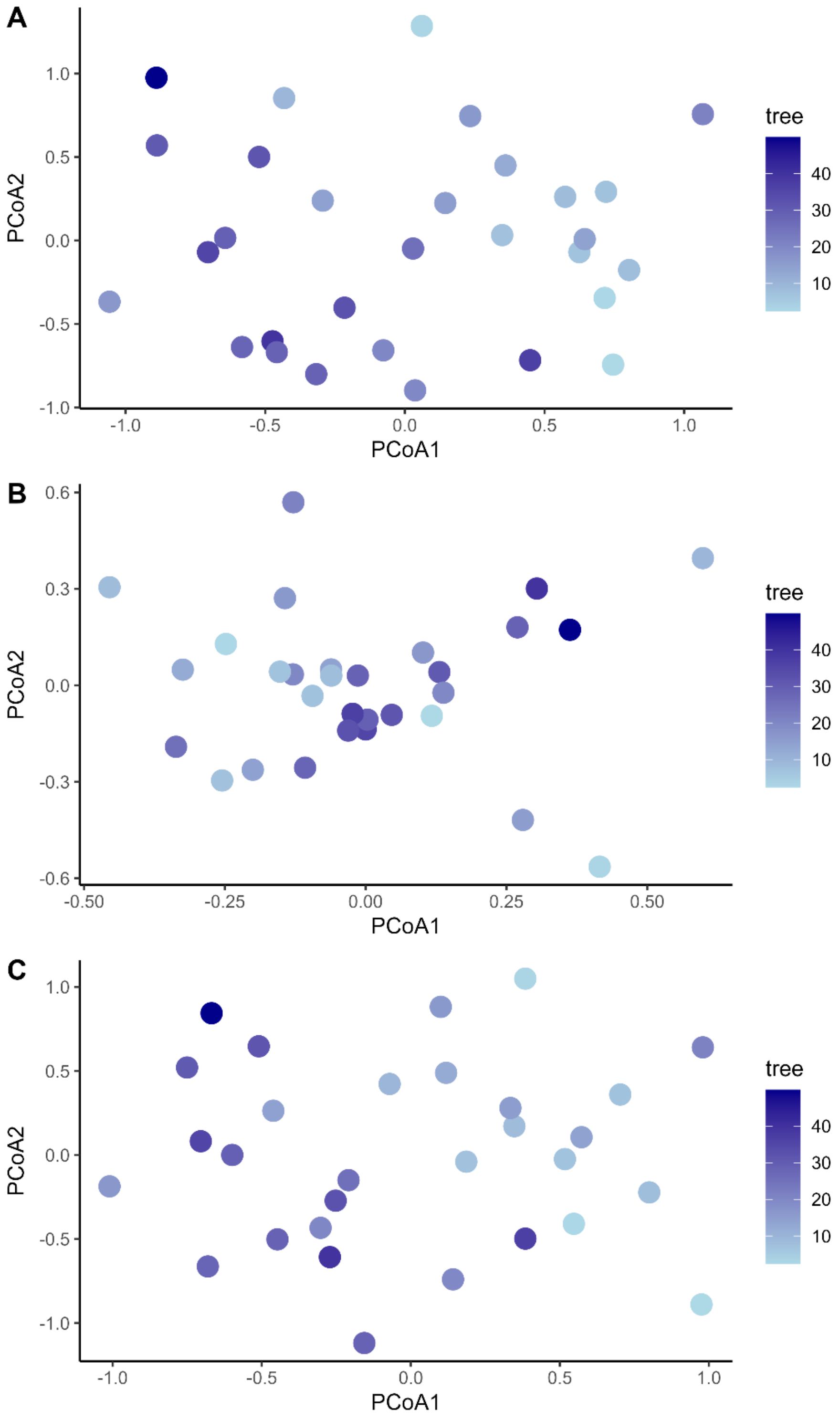

Figure 3. Ordination diagram showing the Principal Coordinates Analysis for the total beta-diversity (A), nestedness (B), and turnover (C) based on the Bray-Curtis dissimilarity. The symbols are shaded according to the percentage of tree cover in a 500 m buffer surrounding each sampled area.

Discussion

We assessed the influence of tree cover, human population density, and building density on the abundance of individuals, species richness and composition of birds in a tropical city. Our results indicate that tree cover was the most important variable in explaining the variation in species richness for forest species, abundance of some guilds and species composition. We also found that the change in community composition was mainly explained by turnover. Overall, our results reinforce the importance of maintaining urban forests or trees to help preserve forest-dependent bird species. This result has been reported in other studies, which show the importance of tree cover for the presence of some bird species and biodiversity conservation (Lepczyk et al. 2017; Amaya-Espinel and Hostetler 2019; Noe et al. 2022).

Species richness and abundance

As we expected, forest species (species richness and abundance) were positively influenced by tree cover. Other studies have found similar results, with forest-dependent bird species having higher species richness and relative abundance in areas with greater forest cover (Villegas and Garitano-Zavala 2010; Beninde et al. 2015; Shoffner et al. 2018; Filloy et al. 2019; Campos-Silva and Piratelli 2021; Thaweepworadej and Evans 2022; Kaushik et al. 2022; Humphrey et al. 2023). Several studies have emphasized the importance of the diversity and complexity of vegetation in urban spaces for the maintenance of (de Toledo et al. 2012; Tiwary and Urfi 2016; Champness et al. 2019). Green spaces are important habitats and provide nesting sites, shelter and food for bird species, especially forest-dependent ones (Ferenc et al. 2014; Jokimäki et al. 2016). For instance, in our study, *Alipiopsitta xanthops*, which is endemic to the Cerrado and near-threatened, and *Crax fasciolata*, a forest-dependent species considered highly vulnerable (BirdLife International 2024, IUCN 2021a, b), were observed at study points with high levels of vegetation cover. Considering that the increased diversity of vegetation structure and reduced fragmentation can improve bird attractiveness in built areas (Suarez-Castro et al. 2024; Oropeza-Sánchez et al. 2024), our study highlights the importance of maintaining green spaces, forest patches and isolated trees in urban environments. Forest specialists are particularly sensitive to anthropogenic disturbance and serve as bioindicators of habitat quality, making the spatial distribution of green areas a key factor for sustaining bird diversity in cities.

On the other hand, we found a negative effect of tree cover on the abundance of human-modified habitat species, granivorous species, and terrestrial species. Some species, such as terrestrial, granivorous, and human-modified species (Allen and O'Connor 2000; MacGregor-Fors et al. 2021; Villaseñor et al. 2021), show a level of urban adaptability and are favored in these environments with low tree coverage, playing a prominent role in structuring urban assemblages. Disturbance of urban environments can increase landscape heterogeneity, i.e., fragmentation, and offer new niche opportunities for exotic species (Andrikou-Charitidou et al. 2020; Marcolin et al. 2024). For example, *Columbia livia* and *Passer domesticus* (the most abundant species in our study) are well-adapted and abundant in urban areas globally (van Heezik et al. 2008; MacGregor-Fors et al. 2010; Alexandre et al. 2022; Ibañez et al. 2023; Leveau 2024). These species illustrate the success that human-modified and ground-foraging granivore species experience in anthropized environments. However, the dominance of these species contributes to biotic homogenization in the urban environment, reducing taxonomic, functional and phylogenetic diversity, which consequently leads to a decrease in diversity (Liang et al. 2019; Marcolin et al. 2024). Consequently, the reduced diversity of native species in such environments may increase susceptibility to invasion and facilitate the establishment of exotic species.

Beta-diversity

Similar to studies on birds (Sidemo-Holm et al. 2022; Petersen et al. 2022), bees (Martins et al. 2017) and frogs (Ganci et al. 2022) in urban environments, we found that differences in beta-diversity were caused primarily by turnover, with species being replaced from one site to another as a result of environmental filtering or dispersal processes (Baselga 2010; Sidemo-Holm et al. 2022; Liu et al. 2024). This result reflects the replacement of specialist species, such as habitat forest species, by generalist species, dominated by the Thraupidae and Tyrannidae families, which are terrestrial foragers and generalists (Enedino et al. 2018; do Nascimento et al. 2025). Vegetation structure and human disturbance are factors that can modify the spatial and temporal distribution of forest birds (Fernández-Juricic 2004; Minor and Urban 2010), because they are species that select environments with a higher degree of tree cover to ensure food, nesting and protective cover (Bélisle et al. 2001; Fernández-Juricic 2004).

The maintenance and implementation of green areas in both central and suburban urban areas are crucial, as they support the presence of forest species by providing essential resources. Tree cover emerged as a significant predictor of species richness and abundance for forest species, and was strongly related to the turnover component, indicating that sites with greater tree cover share more similar species compositions. This finding highlights the importance of urban tree cover as a key element for guiding bird conservation strategies in cities.

Management Implications and Conclusions

Our results can have several important implications for conservation in urban landscapes. Firstly, tree cover showed a positive relationship with forest species richness and abundance, highlighting the importance of conserving native vegetation patches and other green elements to sustain more sensitive species. For example*, Alipiopsitta xanthops* and *Crax fasciolata*, which are species dependent on forest habitats (Tobias et al. 2022), were found only in areas with high tree cover in the city.

Second, our findings on beta-diversity revealed a replacement (turnover) of species from one location to another (Qian et al. 2005), reinforcing the role of tree cover in shaping community composition. This result was more evident using tree cover in the ordination, suggesting that the retention of forest patches and urban trees can mitigate the effects of urbanization and allow the conservation of birds in urban environments.

Considering that the growth of urban areas is expected to continue in cities around the world, especially in tropical regions (McDonald et al. 2019), efforts should be made to preserve and improve the green spaces still present in these urban environments, especially patches of native vegetation (Aronson et al. 2017). Other studies conducted in the Cerrado highlight the crucial role of urban vegetation in supporting biodiversity. For example, Pena et al. (2017) in Belo Horizonte, Brazil, found that streets with a high proportion and diversity of native trees enhance bird species richness and functional diversity. Similarly, Reis et al. (2012) observed in Palmas, Brazil, that bird species richness declines at different stages of urbanization, significantly impacting trophic guilds and certain bird families. Across urban areas in the Cerrado biome, these studies consistently show a rapid decrease in species richness as natural vegetation is replaced by large urban structures. These findings underscore the importance of landscape heterogeneity, such as the presence of native vegetation and protected areas, in maintaining the high species richness in urban environments. Furthermore, it is important to carry out ecological restoration of large patches of habitat in urban green systems (Lopucki and Kitowski 2017) and urban reforestation (Frigerio et al. 2023), along with increasing housing density (potentially through skyscrapers) elsewhere in the city.

Improving green zones in urban environments should be a goal for more sustainable and biodiversity-friendly urban landscapes in the future.

Finally, although urban planning may be crucial, it should be considered in a broader conservation strategy that acknowledges the limits of urban habitats and the pressing need to manage non-urban landscapes effectively. Although cities are home to most of the human population, they occupy a small percentage of the Earth's surface, estimated at around 0.5-0.7%, underscoring the importance of extending conservation efforts beyond urban areas (Liu et al. 2014; Zhao et al. 2022). Therefore, the management and preservation of adjacent areas become essential for biodiversity conservation within and outside cities. For example, maintaining large areas of habitat intact and avoiding intensive development adjacent to important conservation areas can be strategies for achieving biodiversity-sensitive cities and towns (Ikin et al. 2015).

Supporting information for chapter 1

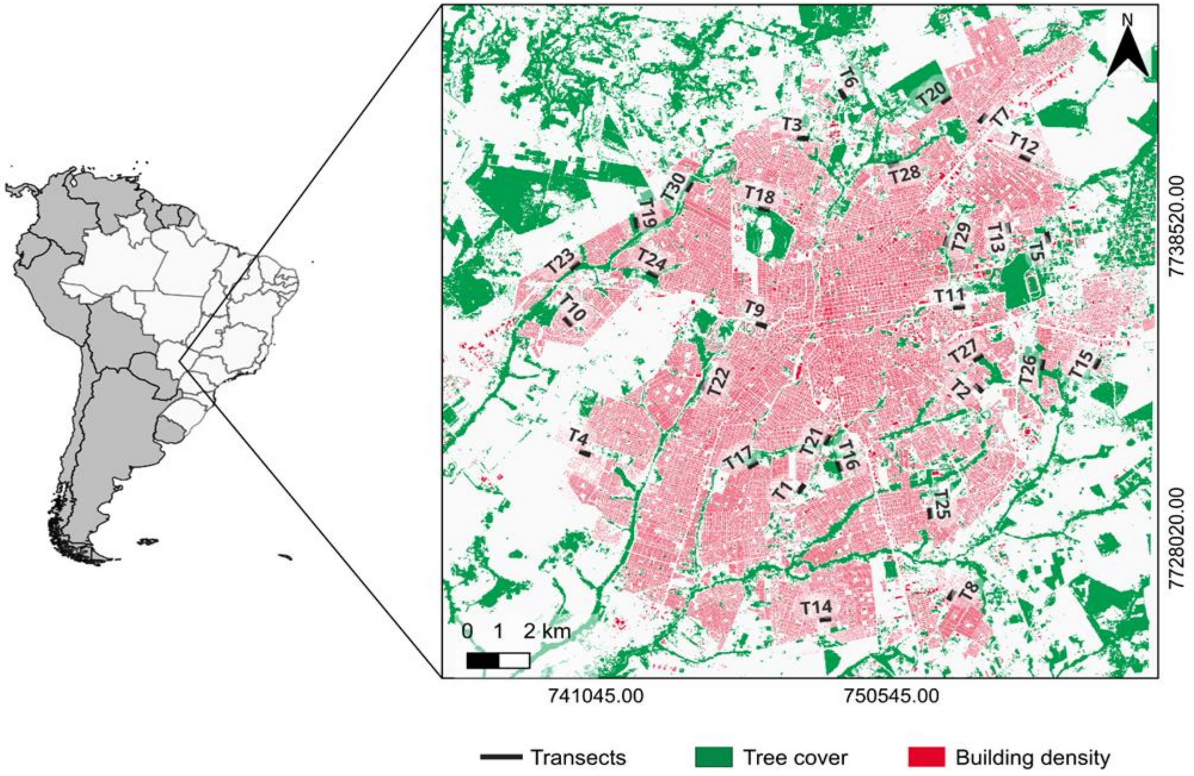

Figure S1. Study area showing the location of the 30 sampling transects in urban areas in Campo Grande, Mato Grosso do Sul, central Brazil.

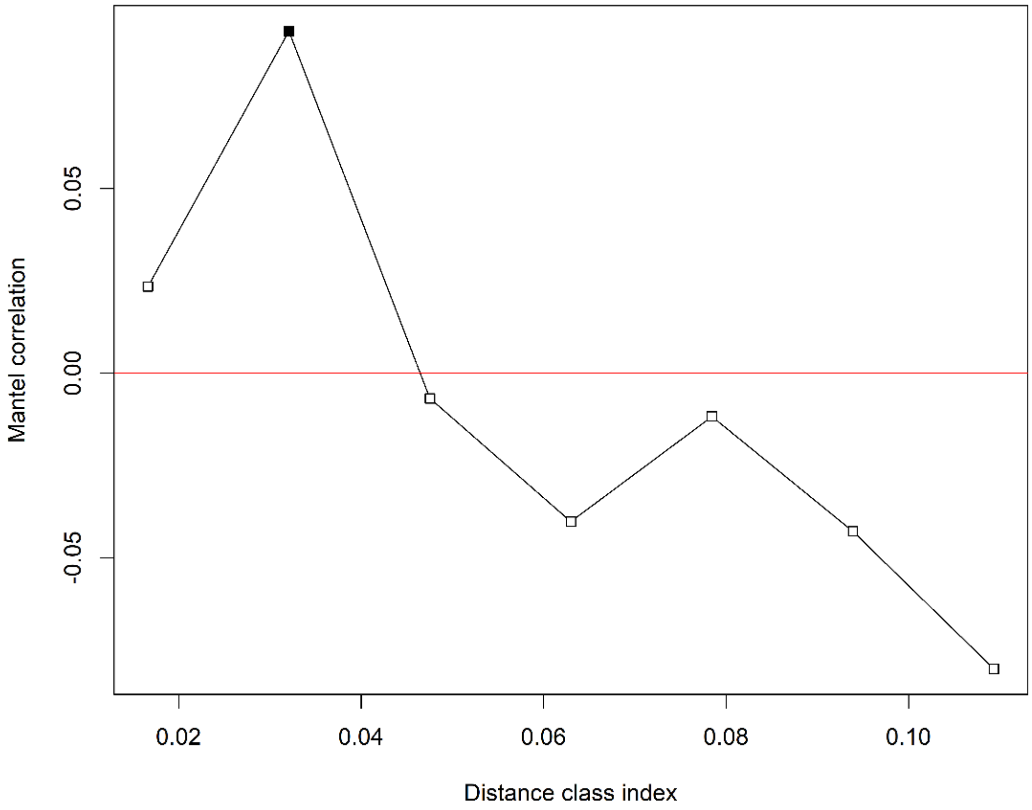

Figure S2. Mantel correlogram to evaluate spatial autocorrelation of data. Significant values are represented by filled squares, and non-significant ones are represented by white blocks. Notice there is only a slightly positive autocorrelation in the second distance class.

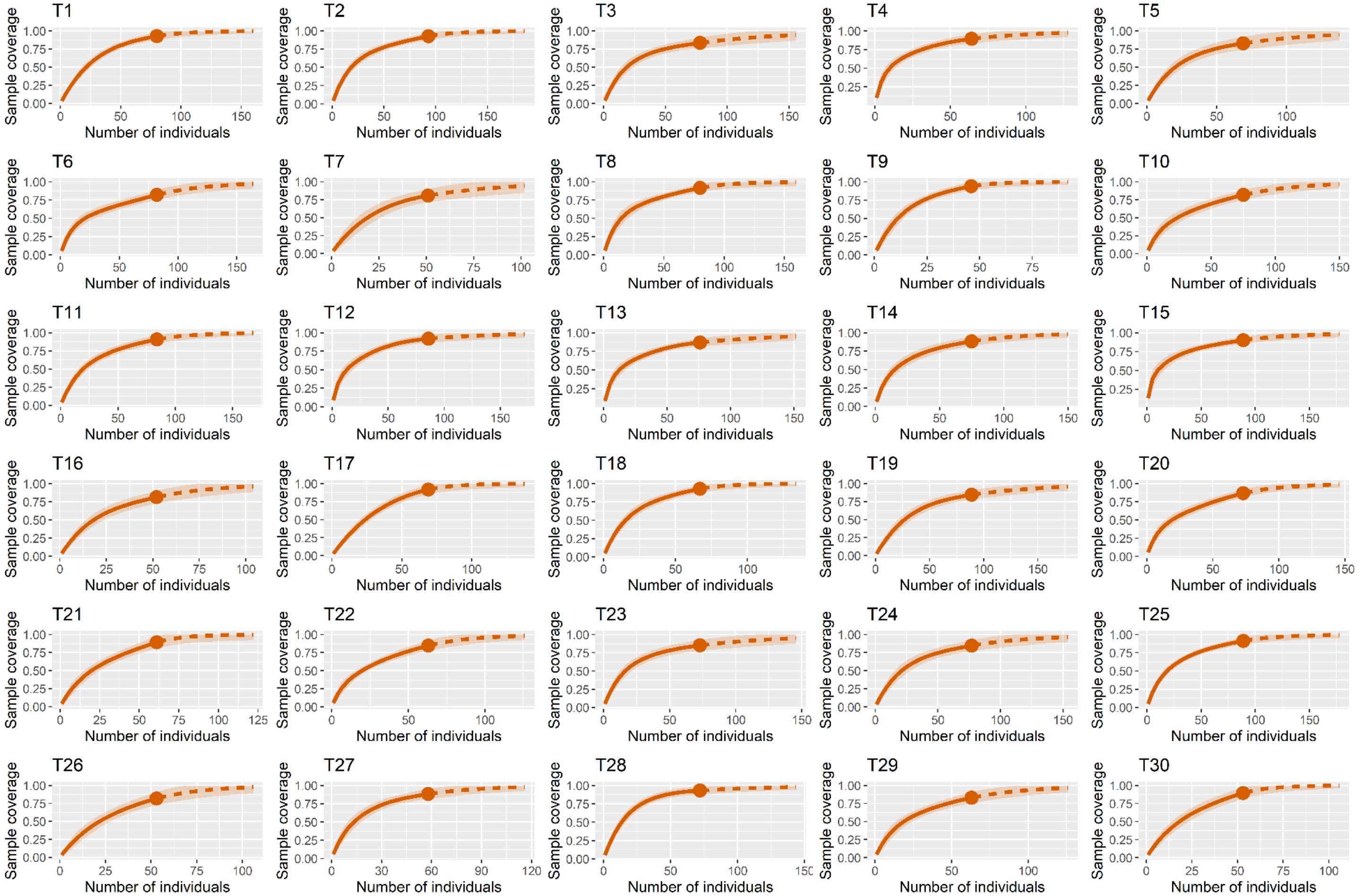

Figure S3. Sample coverage for the 30 sampling transects (T1-T30) by using the iNEXT function and the exponent q = 0 (species richness) for the Hill numbers. Solid symbols refer to the reference samples (the number of individuals found on each sample site).

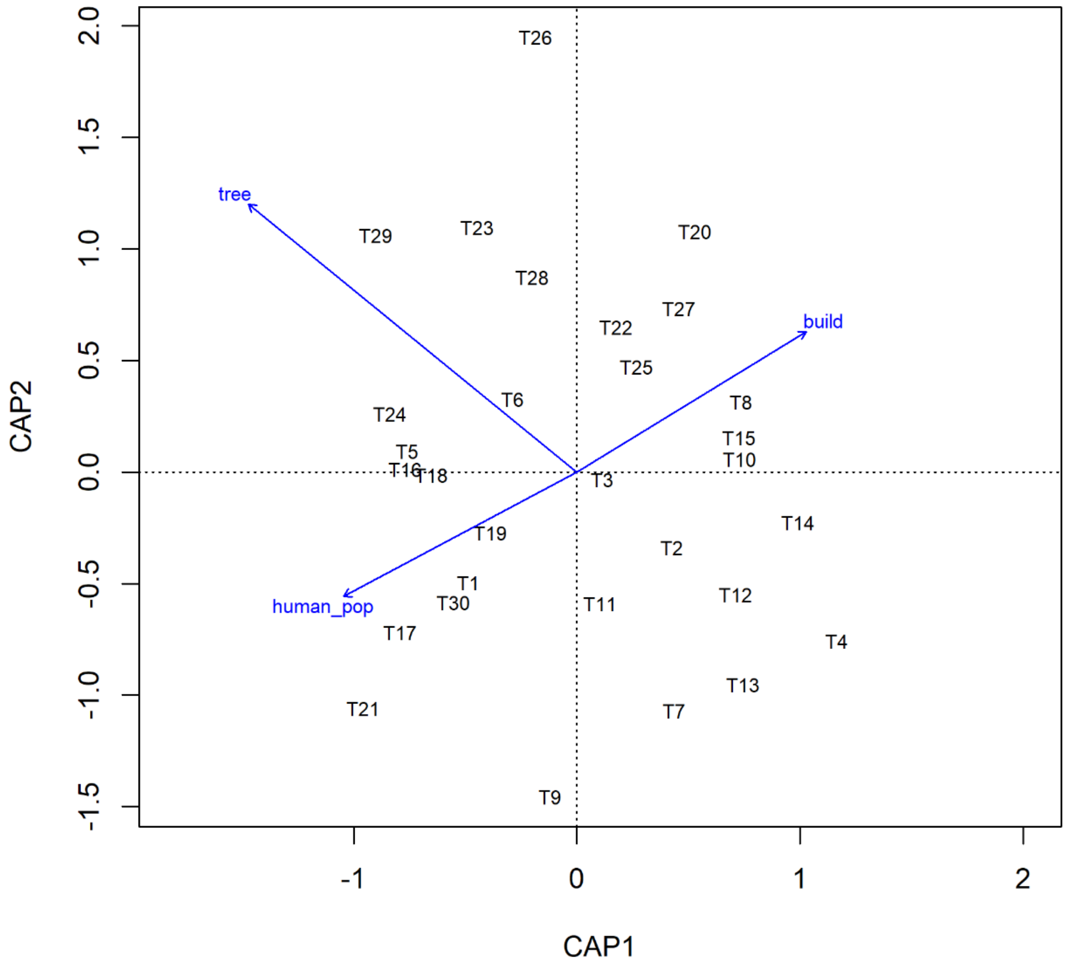

Figure S4. Distance-based redundancy analysis (db-RDA) ordination plot showing the relationship between social and environmental variables — tree cover (tree), human population density (human_pop), and building density (build) and the turnover component of beta-diversity among thirty transects (T1-T30).

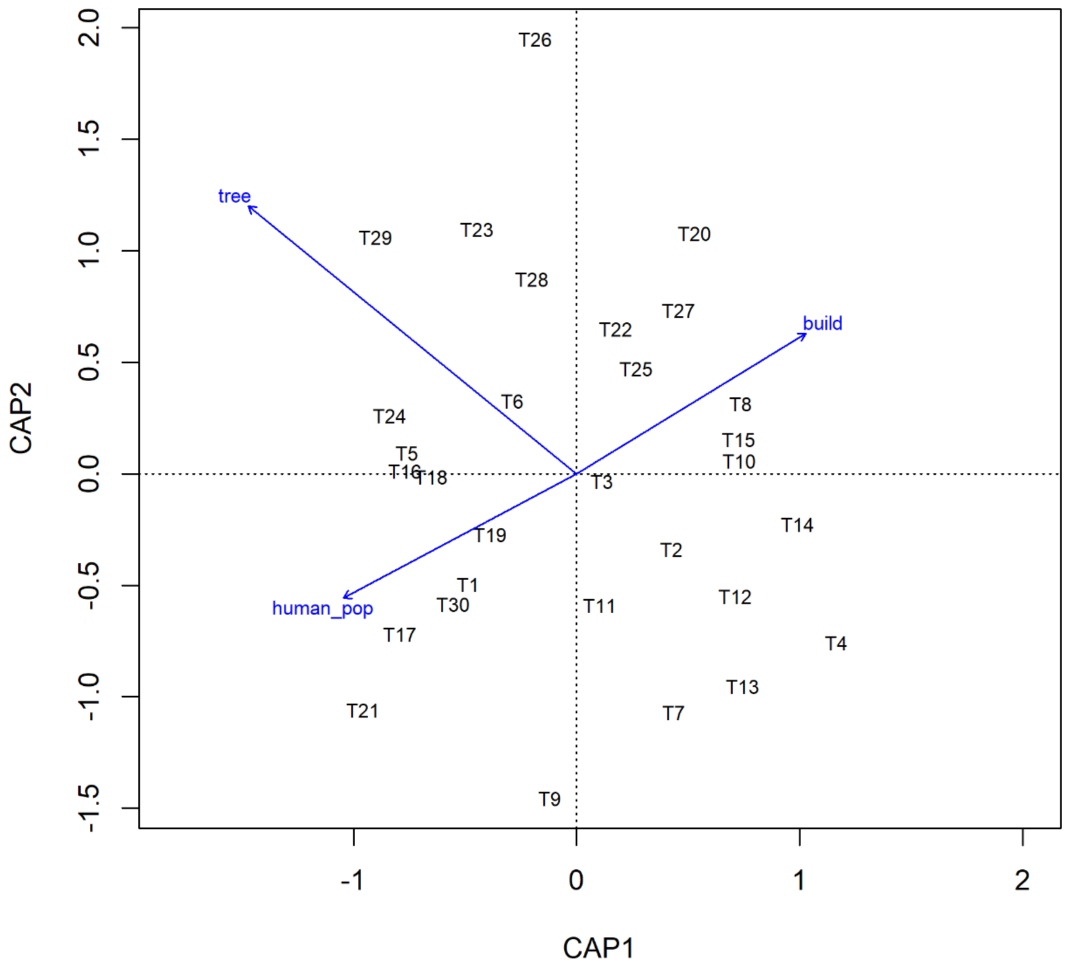

Figure S5. Distance-based redundancy analysis (db-RDA) ordination plot showing the relationship between social and environmental variables — tree cover (tree), human population density (human_pop), and building density (build) and the nestedness component of beta-diversity among thirty transects (T1-T30).

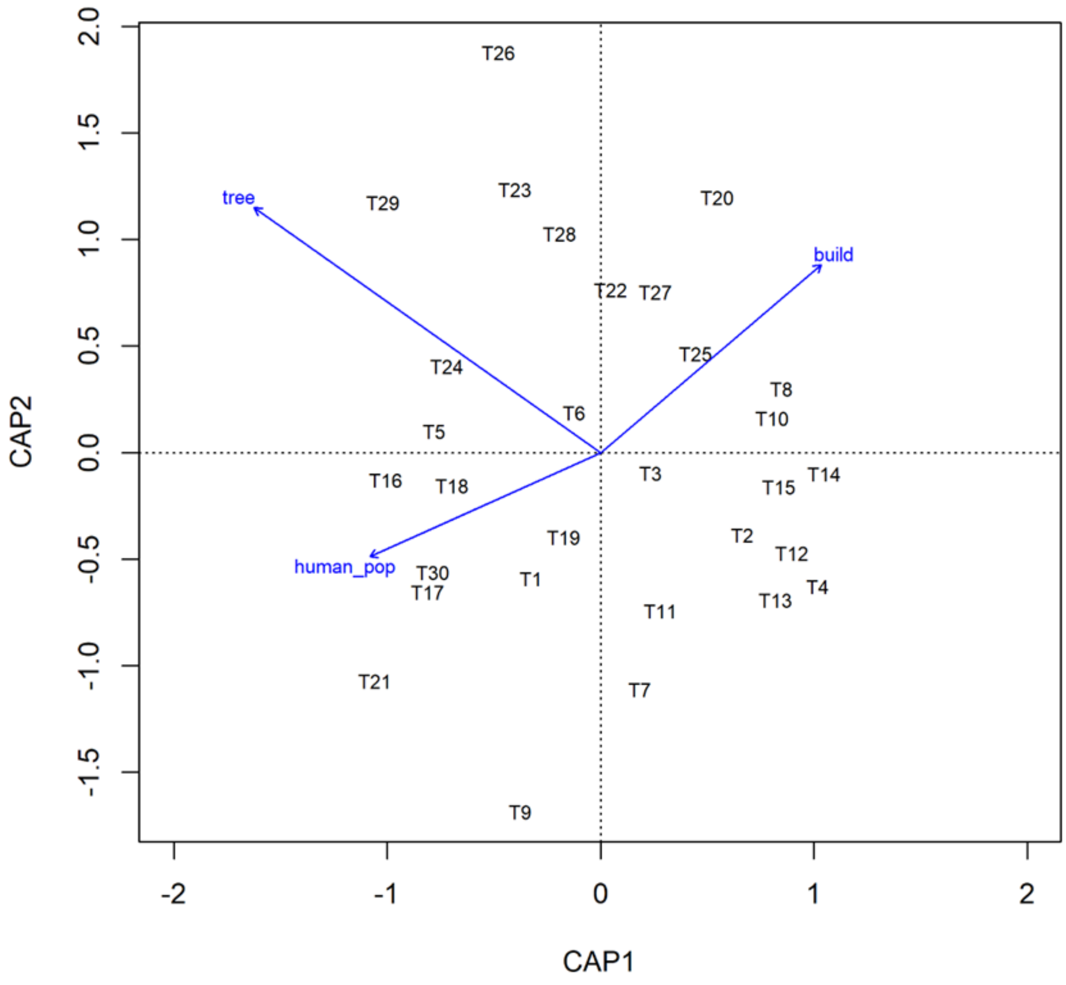

Figure S6. Distance-based redundancy analysis (db-RDA) ordination plot showing the relationship between social and environmental variables — tree cover (tree), human population density (human_pop), and building density (build) and total beta-diversity among thirty transects (T1-T30).

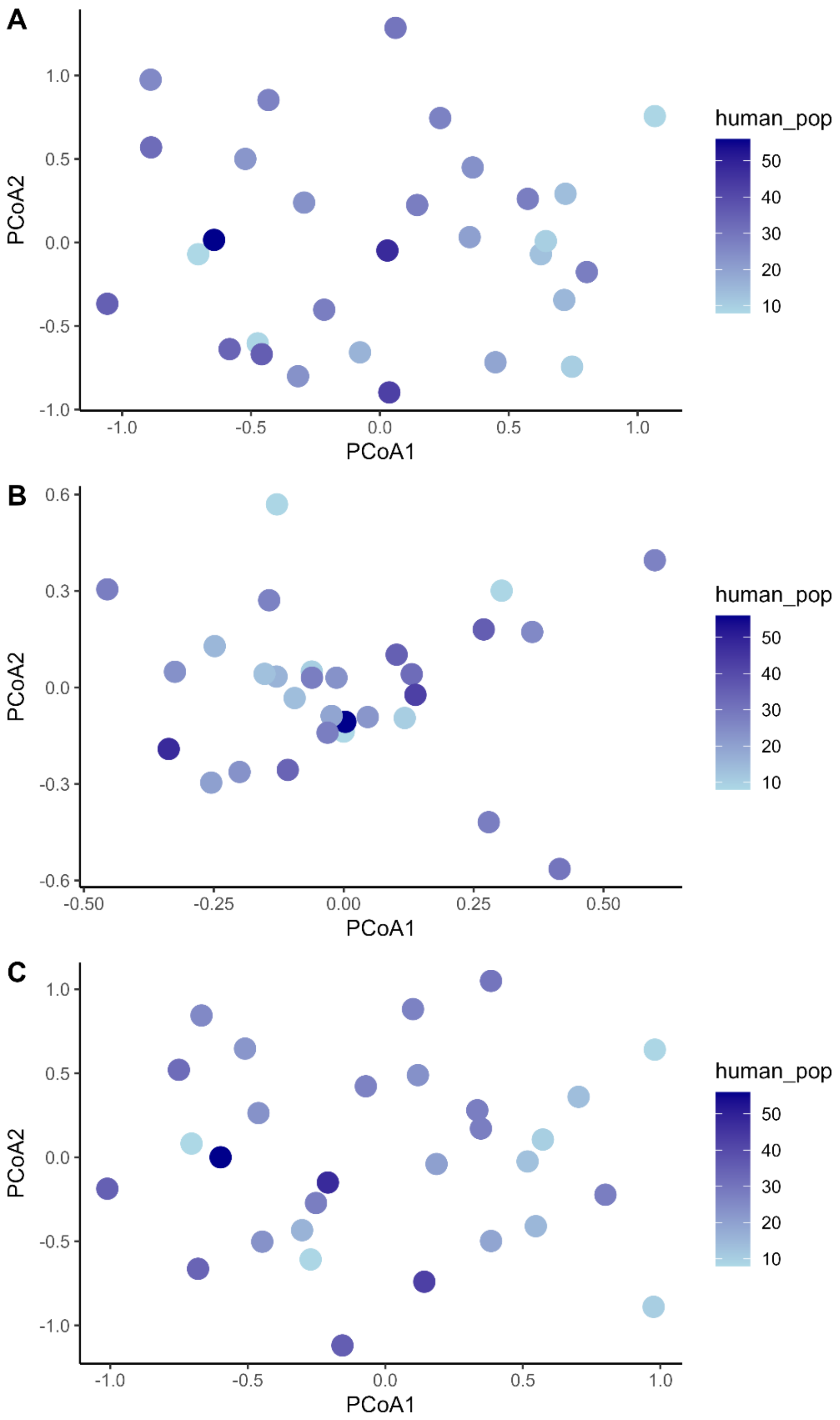

Figure S7. Ordination diagram showing the Principal Coordinates Analysis for total beta-diversity (A), nestedness (B), and turnover (C) based on the Bray-Curtis dissimilarity. The symbols are shaded according to the average human population density (inhabitants per km^2) within a 500 m buffer surrounding each sampled area.

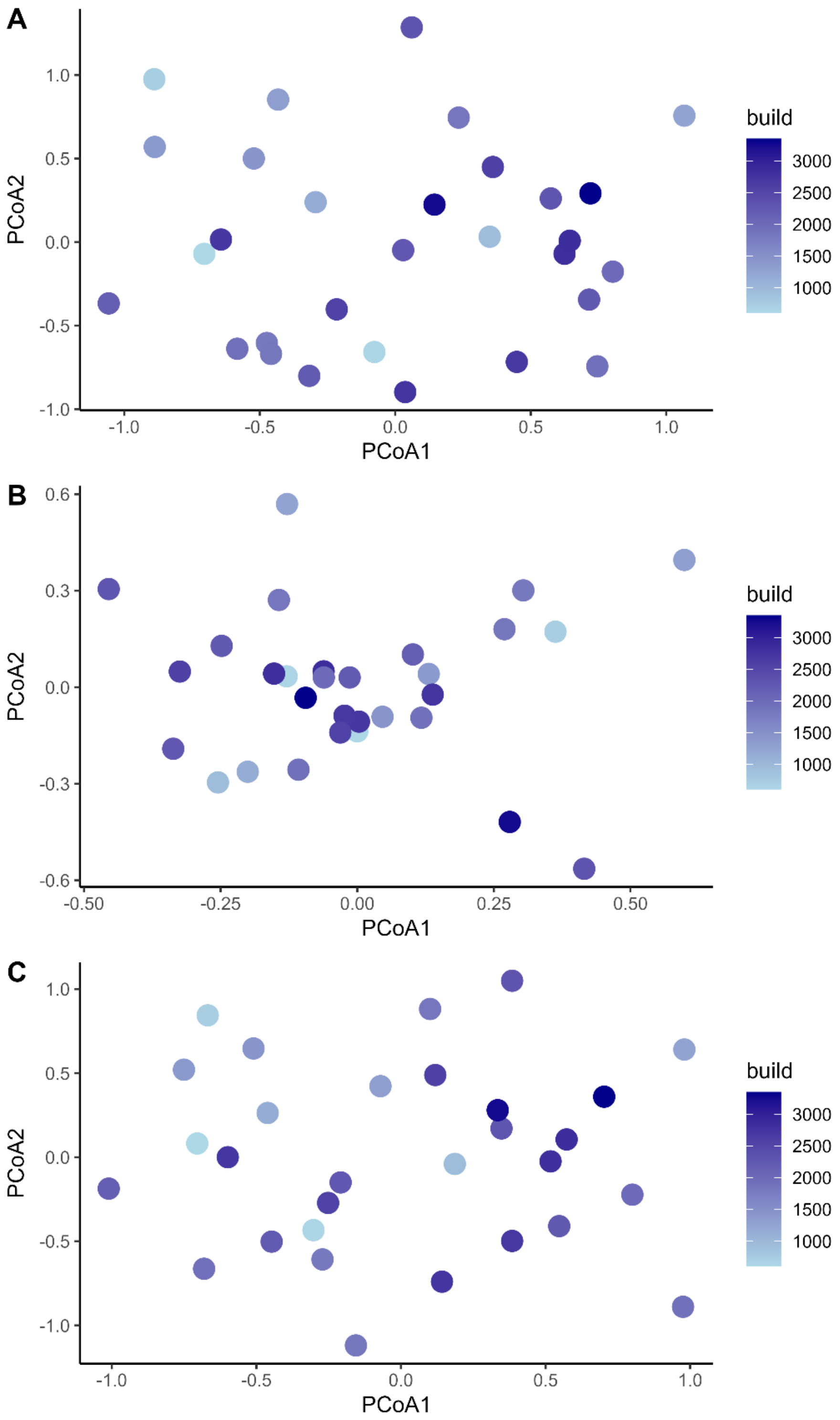

Figure S8. Ordination diagram showing the Principal Coordinates Analysis for total beta-diversity (A), nestedness (B), and turnover (C) based on the Bray-Curtis dissimilarity. The symbols are shaded according to building density (buildings/km²) within a 500 m buffer surrounding each sampled area.

Table S1. Bird species found in the 30 sampled locations in the municipality of Campo Grande, state of Mato Grosso do Sul, Brazil. Relative abundance represents the proportion of individuals of each species in relation to the total number of individuals of all species. Relative frequency (%) indicates the percentage of areas in which the species were found in relation to the total number of areas sampled (N = 30).

Species	**Habitat**	**Trophic Niche**	**Primary Lifestyle**	**Relative Abundance**	**Relative Frequency (%)**
Alipiopsitta xanthops	Forest	Frugivore	Insessorial	0.006	13.333
Amazona aestiva	Shrubland	Frugivore	Insessorial	0.023	30
Amazona amazonica	Forest	Frugivore	Insessorial	0.001	3.333
Ammodramus humeralis	Grassland	Granivore	Terrestrial	0.000	3.333
Ara ararauna	Forest	Omnivore	Insessorial	0.029	83.333
Aramides cajaneus	Forest	Aquatic predator	Terrestrial	0.002	10
Ardea alba	Wetland	Aquatic predator	Terrestrial	0.000	3.333
Athene cunicularia	Grassland	Vertivore	Generalist	0.001	3.333
Basileuterus culicivorus	Forest	Invertivore	Insessorial	0.002	13.333

Brotogeris chiriri	Forest	Omnivore	Insessorial	0.045	86.667
Campylorhamphus trochilirostris	Forest	Invertivore	Insessorial	0.001	6.667
Campylorhynchus turdinus	Forest	Invertivore	Insessorial	0.017	53.333
Caracara plancus	Shrubland	Omnivore	Terrestrial	0.003	20
Cariama cristata	Shrubland	Invertivore	Terrestrial	0.001	6.667
Certhiaxis cinnamomeus	Wetland	Invertivore	Insessorial	0.000	3.333
Chlorostilbon lucidus	Shrubland	Nectarivore	Aerial	0.003	23.333
Coereba flaveola	Shrubland	Nectarivore	Insessorial	0.019	70
Colaptes melanochloros	Forest	Invertivore	Insessorial	0.001	6.667
Colibri serrirostris	Shrubland	Nectarivore	Aerial	0.000	3.333
Columba livia	Human Modified	Granivore	Terrestrial	0.009	30
Columbina picui	Human Modified	Granivore	Terrestrial	0.005	23.333

Columbina squammata	Human Modified	Granivore	Terrestrial	0.005	16.667
Columbina talpacoti	Human Modified	Granivore	Terrestrial	0.026	86.667
Crax fasciolata	Forest	Frugivore	Terrestrial	0.001	6.667
Crotophaga ani	Human Modified	Omnivore	Insessorial	0.005	13.333
Cyanerpes cyaneus	Forest	Omnivore	Terrestrial	0.003	10
Crypturellus undulatus	Forest	Omnivore	Insessorial	0.001	6.667
Cyclarhis gujanensis	Forest	Invertivore	Insessorial	0.008	50
Dacnis cayana	Forest	Frugivore	Insessorial	0.000	3.333
Diopsittaca nobilis	Forest	Omnivore	Insessorial	0.008	20
Elaenia spectabilis	Shrubland	Invertivore	Insessorial	0.000	3.333
Eupetomena macroura	Woodland	Invertivore	Insessorial	0.009	60
Euphonia chlorotica	Shrubland	Nectarivore	Aerial	0.007	43.333

Eupsittula aurea	Forest	Frugivore	Insessorial	0.039	83.333
Empidonomus aurantioatrocristatus	Grassland	Omnivore	Insessorial	0.004	13.333
Furnarius rufus	Shrubland	Invertivore	Terrestrial	0.033	96.667
Guira guira	Human Modified	Invertivore	Terrestrial	0.002	16.667
Heliomaster furcifer	Forest	Nectarivore	Aerial	0.000	3.333
Hylocharis chrysura	Forest	Nectarivore	Aerial	0.004	23.333
Icterus pyrrhopterus	Forest	Invertivore	Insessorial	0.001	6.667
Ictinia plumbea	Forest	Invertivore	Generalist	0.000	3.333
Lepidocolaptes angustirostris	Woodland	Invertivore	Insessorial	0.001	6.667
Mesembrinibis cayennensis	Woodland	Invertivore	Insessorial	0.004	16.667
Megarynchus pitangua	Grassland	Frugivore	Insessorial	0.006	23.333
Melanerpes candidus	Forest	Aquatic predator	Terrestrial	0.003	10

Mimus saturninus	Shrubland	Omnivore	Terrestrial	0.007	30
Molothrus bonariensis	Woodland	Invertivore	Terrestrial	0.021	66.667
Molothrus rufoaxillaris	Human Modified	Invertivore	Terrestrial	0.006	16.667
Momotus momota	Forest	Omnivore	Insessorial	0.000	3.333
Myiarchus ferox	Forest	Invertivore	Insessorial	0.003	16.667
Myiarchus swainsoni	Forest	Invertivore	Insessorial	0.000	3.333
Myiodynastes maculatus	Forest	Invertivore	Insessorial	0.006	30
Myiothlypis flaveola	Woodland	Invertivore	Generalist	0.000	3.333
Myiozetetes cayanensis	Shrubland	Invertivore	Insessorial	0.000	3.333
Nemosia pileata	Forest	Invertivore	Insessorial	0.001	3.333
Nengentus cinereus	Grassland	Invertivore	Insessorial	0.003	20
Orthopsittaca manilatus	Woodland	Frugivore	Insessorial	0.005	10

Passer domesticus	Human Modified	Granivore	Terrestrial	0.110	96.667
Patagioenas picazuro	Forest	Omnivore	Generalist	0.063	100
Pitangus sulphuratus	Human Modified	Omnivore	Insessorial	0.047	100
Progne chalybea	Shrubland	Invertivore	Aerial	0.003	16.667
Progne tapera	Grassland	Invertivore	Aerial	0.026	73.333
Psittacara leucophthalmus	Forest	Omnivore	Insessorial	0.016	43.333
Pyrocephalus rubinus	Woodland	Invertivore	Insessorial	0.001	6.667
Ramphastos toco	Grassland	Frugivore	Insessorial	0.003	16.667
Rupornis magnirostris	Forest	Vertivore	Insessorial	0.003	16.667
Saltator similis	Forest	Invertivore	Insessorial	0.001	6.667
Sicalis flaveola	Shrubland	Granivore	Terrestrial	0.070	96.667
Sporophila caerulescens	Shrubland	Granivore	Generalist	0.001	10

Sporophila lineola	Shrubland	Granivore	Generalist	0.001	3.333
Stilpnia cayana	Forest	Frugivore	Insessorial	0.003	16.667
Syrigma sibilatrix	Wetland	Omnivore	Terrestrial	0.003	13.333
Tersina viridis	Forest	Frugivore	Insessorial	0.002	6.667
Thamnophilus caerulescens	Forest	Invertivore	Insessorial	0.000	3.333
Thamnophilus doliatus	Woodland	Invertivore	Generalist	0.008	46.667
Theristicus caudatus	Grassland	Omnivore	Terrestrial	0.011	36.667
Thraupis palmarum	Forest	Omnivore	Insessorial	0.002	13.333
Thraupis sayaca	Forest	Omnivore	Insessorial	0.045	100
Todirostrum cinereum	Shrubland	Invertivore	Insessorial	0.004	20
Troglodytes musculus	Shrubland	Invertivore	Insessorial	0.001	3.333
Trogon curucui	Forest	Invertivore	Insessorial	0.006	23.333

Turdus amaurochalinus	Forest	Invertivore	Insessorial	0.010	53.333
Turdus leucomelas	Forest	Frugivore	Insessorial	0.002	10
Turdus rufiventris	Forest	Invertivore	Generalist	0.034	96.667
Tyrannus melancholicus	Human Modified	Invertivore	Insessorial	0.032	90
Tyrannus savana	Grassland	Invertivore	Insessorial	0.011	40
Vanellus chilensis	Grassland	Omnivore	Terrestrial	0.019	63.333
Volatinia jacarina	Human Modified	Granivore	Terrestrial	0.009	36.667
Zenaida auriculata	Human Modified	Granivore	Terrestrial	0.054	96.667

Table S2. Results of model selection based on Akaike Information Criterion (AICc) explaining the total bird species richness for all species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***1***	***-87.457***	***177.057***	***0***	***0.415***
Human_pop	**2**	**-87.257**	**178.958**	**1.901**	**0.160**
Build_dens	2	-87.381	179.207	2.150	0.142
Human_pop + Build_dens	2	-87.451	179.347	2.290	0.132
Tree_cover	3	-87.212	181.346	4.289	0.049
Human_pop + Tree_cover	3	-87.223	181.370	4.312	0.048
Buil_dens + Tree_cover	3	-87.381	181.685	4.628	0.041
Build_dens + Human_pop + Tree cover	4	-87.198	183.996	6.938	0.013

Table S3. Results of model selection based on Akaike Information Criterion (AICc) explaining the bird species richness for forest species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights; R^2 - Nagelkerke's R.

Models	K	LL	AICc	ΔAICc	*wi*	R^2
Tree_cover	**2**	**-69.713**	**143.870**	**0**	**0.401**	**0.35**
Human_pop + Tree_cover	**3**	**-69.208**	**145.339**	**1.469**	**0.192**	**0.41**
Buil_dens + Tree_cover	3	-69.658	146.239	2.369	0.123	
Human_pop + Build_dens	1	-72.514	147.170	3.301	0.077	
Null	*4*	*-68.978*	*147.556*	*3.687*	*0.063*	
Human_pop	2	-71.663	147.771	3.901	0.057	
Human_pop + Buil_dens	3	-70.670	148.264	4.394	0.045	
Build_dens	2	-71.963	148.370	4.500	0.042	

Table S4. Results of model selection based on Akaike Information Criterion (AICc) explaining the bird species richness for human-modified species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi*- Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***1***	***-59.380***	***120.903***	***0***	***0.392***
Tree_cover	**2**	**-59.005**	**122.454**	**1.551**	**0.181**
Build_dens	2	-59.272	122.988	2.085	0.138
Human_pop	2	-59.366	123.177	2.274	0.126
Human_pop + Tree_cover	3	-58.957	124.837	3.935	0.055
Build_dens + Tree_cover	3	-58.980	124.882	3.980	0.054
Human_pop + Build_dens	3	-59.269	125.462	4.559	0.040
Build_dens + Human_pop + Tree_cover	4	-58.947	127.493	6.591	0.015

Table S5. Results of model selection based on Akaike Information Criterion (AICc) explaining the bird species richness for granivore species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***1***	***-57.561***	***117.266***	***0***	***0.406***
Tree_cover	**2**	**-57.329**	**119.102**	**1.836**	**0.162**
Human_pop	2	-57.452	119.349	2.083	0.143
Build_dens	2	-57.557	119.559	2.293	0.129
Human_pop + Tree_cover	3	-57.157	121.238	3.972	0.056
Build_dens + Tree_cover	3	-57.322	121.567	4.302	0.047
Human_pop + Build_dens	3	-57.452	121.827	4.562	0.041
Build_dens + Human_pop + Tree_cover	4	-57.116	123.832	6.566	0.015

Table S6. Results of model selection based on Akaike Information Criterion (AICc) explaining the bird species richness for invertivore species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***1***	***-70.859***	***143.860***	***0***	***0.432***
Build_dens	2	-70.769	145.983	2.123	0.149
Tree_cover	2	-70.838	146.121	2.261	0.139
Human_pop	2	-70.849	146.142	2.282	0.138
Build_dens + Tree_cover	3	-70.710	148.344	4.484	0.046
Human_pop + Build_dens	3	-70.768	148.459	4.600	0.043
Human_pop + Tree_cover	3	-70.832	148.587	4.727	0.041
Build_dens + Human_pop + Tree_cover	4	-70.710	151.020	7.160	0.012

Table S7. Results of model selection based on Akaike Information Criterion (AICc) explaining the bird species richness for omnivore species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***1***	***-62.916***	***127.975***	***0***	***0.424***
Human_pop	2	-62.769	129.982	2.007	0.155
Build_dens	2	-62.885	130.215	2.240	0.138
Tree_cover	2	-62.891	130.226	2.251	0.138
Human_pop + Tree_cover	3	-62.758	132.439	4.464	0.045
Human_pop + Build_dens	3	-62.760	132.443	4.469	0.045
Build_dens + Tree_cover	3	-62.837	132.597	4.622	0.042
Build_dens + Human_pop + Tree_cover	4	-62.739	135.078	7.103	0.012

Table S8. Results of model selection based on Akaike Information Criterion (AICc) explaining the bird species richness for insessorial species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***1***	***-62.916***	***127.975***	***0***	***0.424***
Tree_cover	2	-62.769	129.982	2.007	0.155
Human_pop	2	-62.885	130.215	2.240	0.138
Human_pop + Tree_cover	3	-62.891	130.226	2.251	0.138
Build_dens	2	-62.758	132.439	4.464	0.045
Build_dens + Tree_cover	3	-62.760	132.443	4.469	0.045
Human_pop + Build_dens	3	-62.837	132.597	4.622	0.042
Build_dens + Human_pop + Tree_cover	4	-62.739	135.078	7.103	0.012

Table S9. Results of model selection based on Akaike Information Criterion (AICc) explaining the bird species richness for terrestrial species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***1***	***-68.379***	***138.900***	***0***	***0.350***
Tree_cover	**2**	**-67.650**	**139.744**	**0.844**	**0.229**
Human_pop	2	-68.297	141.039	2.139	0.120
Build_dens	2	-68.370	141.184	2.284	0.112
Build_dens + Tree_cover	3	-67.624	142.171	3.271	0.068
Human_pop + Tree_cover	3	-67.626	142.175	3.275	0.068
Human_pop + Build_dens	3	-68.272	143.467	4.567	0.036
Build_dens + Human_pop + Tree_cover	4	-67.611	144.821	5.921	0.018

Table S10. Results of model selection based on Akaike Information Criterion (AICc) explaining the total abundance for all bird species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Tree_cover	**3**	**-117.607**	**242.136**	**0**	**0.321**
Null	***2***	***-119.041***	***242.526***	***0.390***	***0.264***
Human_pop	3	-118.768	244.460	2.323	0.100
Human_pop + Tree_cover	4	-117.486	244.573	2.437	0.095
Build_dens + Tree_cover	4	-117.603	244.806	2.670	0.084
Build_dens	3	-118.966	244.854	2.718	0.082
Human_pop + Build_dens	4	-118.605	246.809	4.673	0.031
Build_dens + Human_pop + Tree_cover	5	-117.485	247.469	5.333	0.022

Table S11. Results of model selection based on Akaike Information Criterion (AICc) explaining the abundance of birds for forest species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights; R^2 - Nagelkerke's R^2.

Models	K	LL	AICc	ΔAICc	*wi*	R^2
Tree_cover	**3**	**-105.267**	**217.458**	**0**	**0.406**	**0.29**
Human_pop + Tree_cover	**4**	**-104.430**	**218.461**	**1.00**	**0.246**	**0.36**
Build_dens + Tree_cover	4	-105.225	220.051	2.59	0.111	
Build_dens + Human_pop + Tree_cover	5	-104.144	220.788	3.33	0.077	
Null	*2*	*-108.534*	*221.512*	*4.05*	*0.054*	
Human_pop	3	-107.480	221.883	4.43	0.044	
Human_pop + Build_dens	4	-106.357	222.314	4.86	0.036	
Build_dens	3	-108.034	222.992	5.53	0.026	

Table S12. Results of model selection based on Akaike Information Criterion (AICc) explaining the abundance of birds for human-modified species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights; R^2 - Nagelkerke's R^2.

Models	K	LL	AICc	ΔAICc	*wi*	R^2
Tree_cover	**3**	**-95.623**	**198.170**	**0**	**0.527**	**0.55**
Build_dens + Tree_cover	**4**	**-95.151**	**199.902**	**1.733**	**0.222**	**0.57**
Human_pop + Tree_cover	4	-95.440	200.479	2.310	0.166	
Build_dens + Human_pop + Tree_cover	5	-94.745	201.991	3.821	0.078	
Build_dens	3	-101.090	209.103	10.933	0.002	
Human_pop + Build_dens	4	-99.831	209.262	11.092	0.002	
Null	*2*	*-102.458*	*209.360*	*11.191*	*0.002*	
Human_pop	3	-101.788	210.500	12.330	0.001	

Table S13. Results of model selection based on Akaike Information Criterion (AICc) explaining the abundance of birds for granivore species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights; R^2 - Nagelkerke's R^2.

Models	K	LL	AICc	ΔAICc	*wi*	R^2
Tree_cover	3	-99.315	205.552	0	0.546	**0.60**
Build_dens + Tree_cover	4	-98.984	207.568	2.016	0.199	
Human_pop + Tree_cover	4	-99.082	207.764	2.212	0.181	
Build_dens + Human_pop + Tree_cover	5	-98.570	209.640	4.088	0.071	
Null	*2*	*-107.155*	*218.755*	*13.203*	*0.001*	
Build_dens	3	-106.051	219.025	13.473	0.001	
Build_dens + Human_pop	4	-104.766	219.131	13.579	0.001	
Human_pop	3	-106.347	219.618	14.065	0.000	

Table S14. Results of model selection based on Akaike Information Criterion (AICc) explaining the abundance of birds for invertivore species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***2***	***-95.991***	***196.427***	***0***	***0.408***
Build_dens	**3**	**-95.467**	**197.858**	**1.431**	**0.199**
Tree_cover	3	-95.948	198.819	2.392	0.123
Human_pop	3	-95.980	198.883	2.456	0.119
Human_pop + Build_dens	4	-95.464	200.528	4.101	0.052
Build_dens + Tree_cover	4	-95.466	200.532	4.105	0.052
Human_pop + Tree_cover	4	-95.926	201.452	5.025	0.033
Build_dens + Human_pop + Tree_cover	5	-95.463	203.427	7.000	0.012

Table S15. Results of model selection based on Akaike Information Criterion (AICc) explaining the abundance of birds for omnivore species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Null	***2***	***-100.376***	***205.197***	***0***	***0.433***
Build_dens	**3**	**-100.087**	**207.097**	**1.901**	**0.167**
Tree_cover	3	-100.277	207.478	2.281	0.138
Human_pop	3	-100.375	207.673	2.477	0.125
Build_dens + Tree_cover	4	-100.067	209.734	4.537	0.045
Human_pop + Build_dens	4	-100.077	209.753	4.557	0.044
Human_pop + Tree_cover	4	-100.272	210.144	4.948	0.036
Build_dens + Human_pop + Tree_cover	5	-100.062	212.624	7.427	0.011

Table 16. Results of model selection based on Akaike Information Criterion (AICc) explaining the abundance of birds for insessorial species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights.

Models	K	LL	AICc	ΔAICc	*wi*
Tree_cover	**3**	**-109.485**	**225.893**	**0**	**0.292**
Null	***2***	***-110.805***	***226.054***	***0.161***	***0.269***
Build_dens	**3**	**-110.416**	**227.755**	**1.862**	**0.115**
Human_pop	3	-110.648	228.218	2.325	0.091
Build_dens + Tree_cover	4	-109.379	228.357	2.464	0.085
Human_pop + Tree_cover	4	-109.417	228.434	2.541	0.082
Human_pop + Build_dens	4	-110.064	229.727	3.835	0.043
Build_dens + Human_pop + Tree_cover	5	-109.229	230.959	5.066	0.023

Table S17. Results of model selection based on Akaike Information Criterion (AICc) explaining the abundance of birds for terrestrial species. We highlight the plausible models (ΔAICc ≤ 2) and the null model in bold and italics, respectively. Human_pop – Human population density; Build_dens – building density; LL – model log likelihood; *wi* - Akaike weights; R^2 - Nagelkerke's R^2.

Models	K	LL	AICc	ΔAICc	*wi*	R^2
Tree_cover	**3**	**-103.008**	**212.940**	**0**	**0.542**	**0.62**
Human_pop + Tree_cover	**4**	**-102.539**	**214.678**	**1.738**	**0.227**	**0.65**
Build_dens + Tree_cover	4	-102.903	215.407	2.467	0.158	
Build_dens + Human_pop + Tree_cover	5	-102.266	217.032	4.093	0.070	
Null	*2*	*-111.085*	*226.614*	*13.674*	*0.001*	
Human_pop + Build_dens	4	-108.658	226.915	13.976	0.001	
Human_pop	3	-110.029	226.982	14.042	0.000	
Build_dens	3	-110.246	227.415	14.475	0.000	

Table S18. Results of distance-based redundancy analysis (db-RDA) testing the effects of social and environmental variables (tree cover, human population density and building density) on the turnover component of beta-diversity among transects.

Variables	**Df**	**SumOfSqs**	**F**	**Pr(>F)**
Tree cover	1	0.19451	1.9602	0.010
Building density	1	0.16242	1.6368	0.031
Human population density	1	0.18184	1.8325	0.014
Residual	26	2.57991	-	-

*Df= Degrees of freedom; SumOfSqs= Variance explained by the variable; F= F-statistic (ratio of explained to unexplained variance); Pr(>F) = P-value (probability of obtaining the observed F under the null hypothesis).

Table S19. Results of distance-based redundancy analysis (db-RDA) testing the effects of social and environmental variables (tree cover, human population density and building density) on the nestedness component of beta-diversity among transects.

Variables	**Df**	**SumOfSqs**	**F**	**Pr(>F)**
Tree cover	1	0.005718	1.0505	0.324
Building density	1	0.001022	0.1877	0.960
Human population density	1	0.001388	0.2550	0.893
Residual	26	0.141531	**-**	**-**

*Df= Degrees of freedom; SumOfSqs= Variance explained by the variable; F= F-statistic (ratio of explained to unexplained variance); Pr(>F) = P-value (probability of obtaining the observed F under the null hypothesis).

Table S20. Results of distance-based redundancy analysis (db-RDA) testing the effects of social and environmental variables (tree cover, human population density and building density) on the total beta-diversity among transects.

Variables	**Df**	**SumOfSqs**	**F**	**Pr(>F)**
Tree cover	1	0.23272	2.0468	0.006
Building density	1	0.17756	1.5617	0.053
Human population density	1	0.19170	1.6860	0.041
Residual	26	2.95616	-	-

*Df= Degrees of freedom; SumOfSqs= Variance explained by the variable; F= F-statistic (ratio of explained to unexplained variance); Pr(>F) = P-value (probability of obtaining the observed F under the null hypothesis).

Chapter 2: Generalist and high-dispersal ability bird species are favored in a tropical urban area*

*This chapter is in the process of publication in Biodiversity and Conservation.

Abstract

Urbanization is one of the main processes driving ecosystem transformation, imposing strong environmental filters that reshape ecological communities. Although urban vegetation can mitigate some of these effects, its effectiveness at supporting functionally rich communities may be limited. We investigated how tree cover, urban area, and human population density at three spatial scales (75 m, 200 m, and 500 m) influence avian functional diversity across thirty urban sites in Campo Grande, Mato Grosso do Sul, Brazil. Our results revealed that functional richness remained stable along the urban gradient. In contrast, functional evenness increased in more urbanized areas and was negatively associated with tree cover, particularly in zones with high human population density. We found no significant relationship between functional divergence or functional dispersion and environmental variables. Using community-weighted means of morphological traits to characterize the functional structure of bird communities, we found that urban area had a positive effect on wing length at 75 m and 200 m scales, a trait associated with increased mobility in fragmented environments. These findings indicate that, even in a spatially heterogeneous tropical city, urban landscapes favor species with greater dispersal capacity and generalist traits. We recommend that urban planning prioritize vegetation structural complexity and green space connectivity to support functionally diverse communities and maintain essential ecosystem services.

Introduction

Urbanization is a complex socio-economic process that has been accelerating worldwide, driving the rapid expansion of cities and reshaping landscapes, with profound consequences for society, the environment, and biodiversity (Seto et al. 2012; United Nations 2018). By 2050, nearly 68% of the global population is expected to reside in urban areas, intensifying pressures on natural ecosystems and the critical services they provide to humanity (Newbold et al. 2015; United Nations 2018). This expansion directly affects biodiversity through habitat loss and fragmentation. The expansion of impermeable surfaces fragments and isolates natural habitats, restricting species mobility and disrupting ecological processes (Newbold et al., 2015; Ding et al., 2025; Simkin et al., 2022). For example, the removal of native vegetation reduces nesting sites for birds (Bhakti et al. 2020). Moreover, the decline of pollinators compromises pollination services and plant reproductive success (Wenzel et al. 2020), and the reduction of frugivorous species alters seed-dispersal patterns and scales, ultimately interrupting gene flow and limiting forest regeneration (Gelmi-Candusso and Hämäläinen 2019). The resulting local extinctions cause a decline in species richness and potentially the loss of essential ecosystem functions in urban environments (Yang et al. 2020).

The loss of species in urban environments is associated with the restructuring of communities, such that only species with greater tolerance to anthropogenic conditions are able to persist (Sol et al. 2013). This process results in ecological filtering, where species are selected based on their functional characteristics (Evans et al. 2011). Factors such as niche overlap and the extinction of lower-tolerance species can lead to an increase in the abundance of species with similar ecological functions, increasing functional redundancy and altering the diversity of functions performed by the remaining species in urban communities (Oliveira Hagen et al. 2017). In a global analysis of urbanization, (Sol et al. 2020) suggest that highly urbanized environments have a distinct functional composition and reduced functional diversity compared to surrounding natural environments. These changes reflect not only shifts in functional diversity but also alterations in key ecosystem functions such as seed dispersion and nutrient cycling (Sekercioglu 2012). One approach to analyzing these changes is to estimate functional diversity based on the understanding that species traits provide valuable information about their functional roles within a given environment, helping to elucidate community patterns and shifts related to land use (Tilman 2001; Cadotte et al. 2011).

Research on the impact of urbanization on functional diversity (FD) has highlighted significant shifts in ecosystem functioning due to increasing urban density. For instance, (Weeks et al. 2025) conducted a global analysis of bird species and found that land-use changes, particularly those associated with urbanization and agricultural expansion, undermine the stability of avian functional diversity. These declines are most pronounced in regions with low species richness and high human impact, where the loss of functionally unique species leads to reduced ecosystem resilience (Oliver et al. 2015; Tscharntke and Batáry 2023). In the Cerrado biome, Brazil, where increasing urbanization leads to declines in both functional richness of bird communities and in the cultural ecosystem services that urban residents derive from birds, suggesting a potential loss of nature-based benefits in highly urbanized areas (Souza et al. 2019). Historical land-use changes may also play a crucial role in shaping biodiversity patterns. Almeida-Gomes, et al. (2025) found evidence of a taxonomic extinction debt in Campo Grande, Brazil, where bird species richness was influenced by past urban expansion, yet this taxonomic debt was not reflected by a functional extinction debt, suggesting that although species loss occurs, key functional traits may be retained within urban bird assemblages. Moreover, parks, riparian zones, and urban protected areas expand habitat and resource availability, promote species movement across urban landscapes, and supporting biodiversity conservation (Aronson et al. 2014; Lynch 2019).

While urbanization has led to significant biodiversity shifts, certain elements in the landscape can help to mitigate these impacts. Vegetative attributes of street trees can facilitate species movement between urban parks and habitat patches, while also mitigating the negative effects of noise exposure on urban bird communities (Pena et al. 2017). Additionally, homes with gardens and heterogeneous landscapes play a crucial role in supporting bird biodiversity, helping to counterbalance the impact of impervious surfaces (Souza et al. 2019). Larger areas of native forest favor sensitive bird groups (Dale 2018), while the density and height of trees and shrubs contribute to greater species richness (Ciach and Fröhlich 2017).

A key question is how landscape features within urban environments contribute to maintaining functional diversity and, consequently, ecosystem functioning. In this study, we investigate the impact of urbanization and tree cover on the functional diversity of birds in Campo Grande, Mato Grosso do Sul, Brazil, within the Cerrado biome. Birds were chosen as the focal group because they have been widely studied and serve as excellent indicators of urban ecosystem changes, including noise pollution and landscape modification (Sekercioglu 2006; Bonier et al. 2007; Fontana et al. 2011; Pena et al. 2017; Souza et al. 2019). To address this gap, we explore two key questions: (1) How do avian functional diversity and community structure respond to gradients in tree cover, urban area, and human population density? and (2) do species' functional traits influence their presence along a tree cover gradient and urbanization? Our goal is to identify which landscape features are most strongly associated with the maintenance of functional diversity, providing insights that can inform urban planning and biodiversity-friendly city design.

Material and Methods

Study area

We conducted this study in the urban perimeter of the municipality of Campo Grande (20° 28′ 13″S, 54° 37′ 25″W), state of Mato Grosso do Sul, Brazil (Fig. S1). The study area was formerly entirely covered by Cerrado, including dry forests, grasslands, wetlands, shrublands, and savannahs (Ribeiro and Walter 1998). However, most of the native vegetation (~80%) has been replaced by pastures, crops, and urban areas (MapBiomas 2024). There is a strong dry season (from April to September) and a rainy season (October to March), with an average annual precipitation of 1,530 mm and an average annual temperature ranging from 18°C to 29°C (Ferreira et al. 2017). The city has nearly 954,000 inhabitants and an average population density of 111.11 inhabitants/km2 (IBGE 2024).

Sampling design

We established 30 line transects each of 200 meters for sampling birds in the urban area of Campo Grande, ranging in tree cover (0 to 50.69%) and urban area (41.35 to 100%). Most transects (N = 28) were a minimum distance of 1 km apart (range: 0.81 to 17.7 km) to maximize the independence of sampling units. To evaluate if our dataset presents spatial autocorrelation (Oden 1984), we used a Mantel correlogram and found no evidence of spatial autocorrelation in species composition.

Landscape and demographic metrics

To analyze landscape and demographic metrics, we created buffers with a radius of 75, 200, and 500 meters around each of the thirty sampled locations. Using land-use and land-cover maps from the MapBiomas Project (collection 9.0), we calculated the percentage of tree cover (including forest and savanna formations) and urban area within each buffer. These calculations were performed in ArcGIS 10.6.1. First, we determined the area (ha) occupied by native vegetation and urban area within each buffer. We then divided these values by the total buffer area and multiplied by 100 to obtain percentage values. The MapBiomas classification uses the term “forest formation”, but throughout the text we adopt the more general term “tree cover” to refer to forest and savannah vegetation types.

Population density (number of inhabitants per hectare) was extracted for each of the three buffer sizes (75 m, 200 m, and 500 m) using data obtained from the SiSGRAN, a system managed by the Municipality of Campo Grande. It allows the population to access data, information, and indicators on various city themes, including maps and geographical data. These density data are available per neighborhood and represent the number of inhabitants per hectare. To extract population density information for each sample, we utilized an intersection algorithm. However, when our samples overlapped in multiple neighborhoods, we employed arithmetic means to represent the population density of the sample.

Before model construction, we assessed the correlation between the three landscape variables (tree cover, urban area, and population density) using Pearson’s correlation test (function cor.test) to identify potential collinearity among predictors at three spatial buffer scales. Variables with strong pairwise correlations ($|r| > 0.7$) were not included together in the same additive models to avoid inflated parameter estimates. In addition, to better visualize the relationship between variables, we applied Pearson’s correlation tests with the function ggpairs from the R package GGally (v2.2.1) (Schloerke et al. 2021) and displayed the results in pairwise correlation plots (Fig. S2). Based on these results, we built linear models to evaluate the relationship between landscape structure and functional diversity metrics.

Bird sampling

Bird sampling was conducted between July and November 2022, from 06:00 to 10:00, when most species in the region are most active (Souza et al. 2019). To minimize detection bias, we avoided sampling on days with adverse weather conditions (e.g., rain). Two observers systematically walked each transect, recording bird species through both visual and acoustic identification, with each transect surveyed for 12 minutes. This method allows for a larger sampling area to be covered in the same period compared to point sampling (Bibby 2000; Gregory et al. 2004; Pejchar et al. 2008; Karp et al. 2011). Each transect was sampled three times, resulting in a total sampling effort of 18 km of line transects and 45 hours of observation.

To assess sampling completeness, we calculated sample coverage for each transect using the iNEXT package (Hsieh et al. 2016) with q = 0 for Hill numbers (species richness). Sample coverage estimates the proportion of total individuals belonging to species detected in the sample (Hsieh et al. 2016). Our analysis indicated that transects were well-sampled, with a mean sample coverage of 0.94 (range: 0.89–0.97).

Functional diversity metrics

We used the AVONET dataset (Tobias et al. 2022) to select the functional traits for the observed species. We selected four quantitative morphological traits: beak length, tail length, wing length, and body mass. These traits were chosen because they are key proxies for ecological functions related to resource use, foraging strategies, and species' mobility. All traits were standardized before analysis. We computed the pairwise functional distance among species using Gower distance (de Bello et al. 2021). A Principal Coordinates Analysis (PCoA) was then applied to reduce dimensionality and construct a multidimensional functional space, following Palacio et al. (2022). We evaluated the quality of the space based on the mean absolute deviation (MAD) and root mean square deviation (RMSD) between the original and reduced distances (Konno and Yamazaki 1991). Based on these metrics, we retained four axes in the final analysis as a balance to reduce dimensionality and improve the result interpretation.

Using the resulting functional space, we calculated four functional diversity indices for each site. Functional Richness (Fric): represents the volume of functional space occupied by a species assemblage, reflecting the range of ecological roles present in the community. Functional Evenness (FEve): describes how regularly species abundances are distributed within this functional space, indicating how evenly ecological functions are represented. Functional Divergence (FDiv): quantifies how far high species abundances are from the centre of the functional space, highlighting the dominance of functionally distinct species. Functional Dispersion (FDis): measures the abundance-weighted mean distance of species' trait values from the centroid of the functional space, providing an index of overall trait dispersion within the assemblage. We also calculated standardized effect sizes (SES) for each index using a null model approach, in which SES was computed as (observed value - mean of null distribution) divided by the standard deviation of the null distribution, based on 999 randomly generated communities (Ulrich and Gotelli 2010).

To examine how different components of urbanization influence functional diversity, we fitted a set of linear models, including both simple and additive formulations. Our goal was to test whether the inclusion of demographic features and tree cover improves the explanation of functional diversity patterns. We first fitted simple linear models, relating each functional diversity metric to a single predictor (tree cover, urban area or human population density) at different buffer scales (75 m, 200 m, and 500 m). To test whether population density added explanatory value beyond landscape structure alone, we then constructed additive models combining two predictors: (1) tree cover + population density; or (2) urban area + population density. We hypothesize the inclusion of population density would respond to additional pressures related to anthropogenic disturbances, not captured by one variable alone. Due to collinearity, models combining tree cover and urban area were excluded. To assess whether the inclusion of additional explanatory variables improves model fit, we compared nested models using tests via ANOVA.

We computed community-weighted means (CWMs) for each morphological trait. We then assessed the association of CWMs with tree cover and urban area at each of the three spatial scales.

Results

Response of Avian Functional Diversity and community structure

A total of 89 species and 3434 individuals were recorded (Table S1). The most abundant species were *Passer domesticus* (479 individuals), *Patagioenas picazuro* (273), and *Sicalis flaveola* (260). Tree cover varied considerably between the points sampled, from 0 to 59.79% in the 75-metre buffer, from 0 to 44.60% in the 200-metre buffer, and from 0 to 42.69% in the 500-metre buffer. The proportion of urban area was high at most of the points, ranging from 43 to 100% in the 75-metre buffer, 48 to 100% in the 200-metre buffer and 41 to 100% in the 500-metre buffer. There was a variation of 8 to 56 inhabitants/ha between the three buffers analyzed.

Functional Evenness (FEve) showed a negative and significant relationship with tree cover at all the spatial scales analyzed: 75 m (-0.004854 ± 0.001879 SE, $t= -2.499$, $p= 0.018$, $R^2= 0.18$), 200 m (-0.005235 ± 0.001960 SE, $t= -2.479$, $p= 0.019$, $R^2= 0.18$), and 500 m (-0.006787 ± 0.003008 SE, $t= -2.061$, $p= 0.048$, $R^2= 0.13$). Standardized values of Functional Evenness (SES.FEve) also showed a negative and significant relationship with tree cover at the the 75 m (-0.022291 ± 0.008922 SE, $t= -2.499$, $p= 0.019$, $R^2= 0.18$), 200 m (-0.023239 ±

0.009373 SE, t= -2.479, p= 0.019, R^2= 0.18), and 500 m (-0.02971 ± 0.01441 SE, t= -2.061, p= 0.049, R^2= 0.13) (Fig. 1; a-f) spatial scales, indicating values becoming slightly more underdispersed than expected. A positive and significant relationship was observed between FEve and urban area at the 75 m (0.004769 ± 0.001705 SE, t= 2.436, p= 0.021, R^2= 0.17) and 200 m (0.005466 ± 0.001707 SE, t= 2.414, p= 0.022, R^2= 0.17) scales. An opposite trend was found when relating SES.FEve to urban area, with a significant and positive relationship at the 75 m (0.020062 ± 0.008235 SE, t-value= 2.436, p= 0.021, R^2= 0.17) and 200 m (0.020498 ± 0.008491 SE, t-value= 2.414, p= 0.022, R^2= 0.17) buffer scales (Fig. 1; g-l).

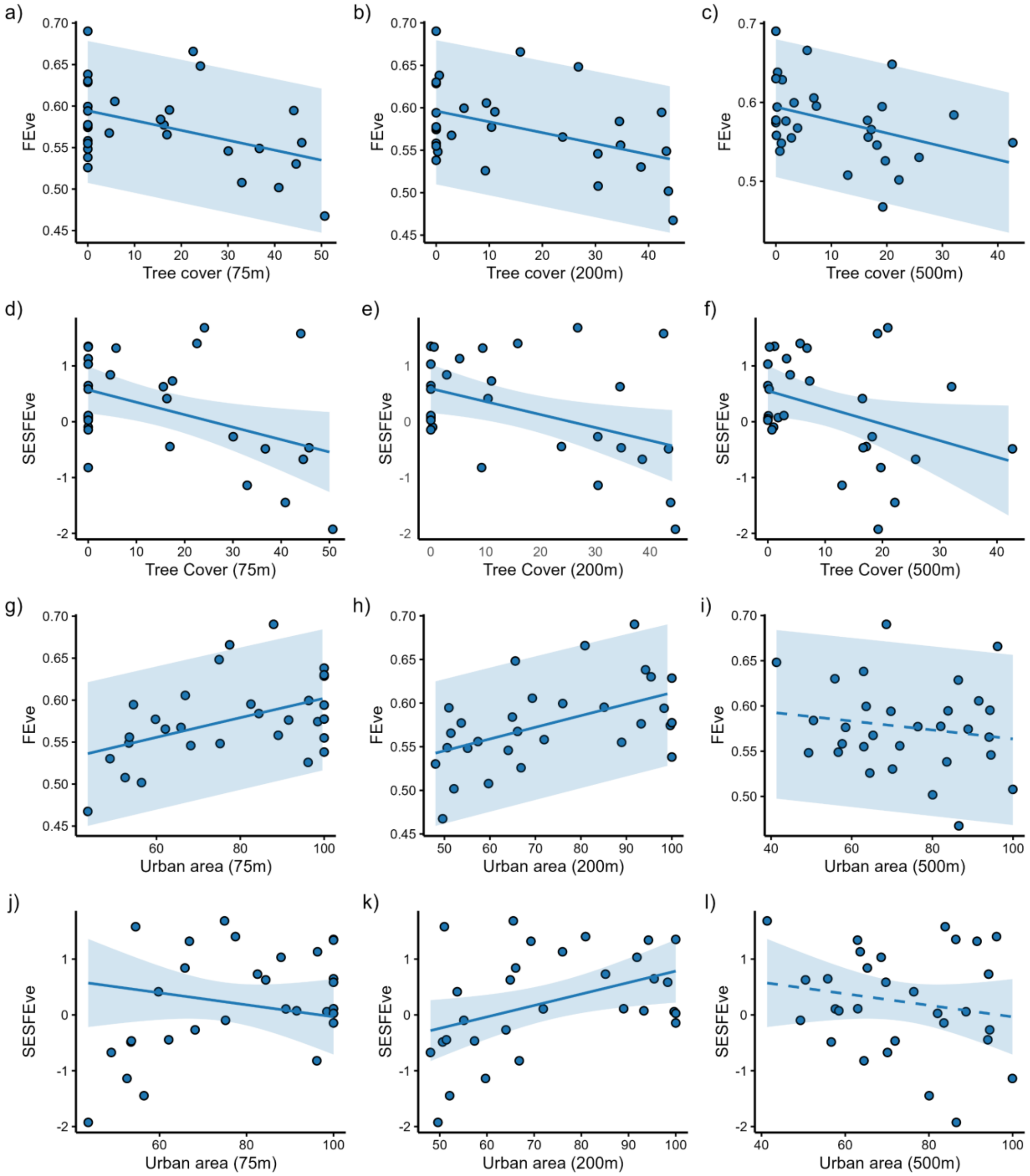

Figure 1. Linear relationship between Functional Evenness (FEve) and Standardized Effect Size of Functional Evenness (SESFEve) as a function of tree cover (a-f) and urban area (g-l) at three spatial scales (75 m, 200 m, and 500 m). 95% confidence intervals. Solid lines represent significant relationships, while dashed lines show the non-significant trends.

Functional richness (FRic) did not show a significant relationship with tree cover or urban area at any special scale (75 m, 200 m, and 500 m). Likewise, we did not detect a significant relationship between SES.FRic and tree cover or urban area (Fig. S3). Similarly, the Functional dispersion (FDis) and Functional divergence (FDiv) metrics and their standardized values (SES.FDis and SES.FDiv), did not show statistically significant relationships with tree cover or urban area (Fig. S4 and S5) at any of the scales.

Among the additive models, the inclusion of human population density along with tree cover or urban area resulted in models that remained statistically significant in relation to FEve at the 75 m and 200 m buffer scales (Fig. S6). However, ANOVA comparisons revealed that the addition of population density did not significantly improve model fit ($p > 0.05$, Table S2). These results indicate that tree cover or urban alone are the main drivers of functional uniformity, with population density contributing little to model performance.

Influence of Functional traits on species

The linear models fitted using Community Weighted Means (CWMs) showed that urban area had a positive and significant effect on Wing length in 75 m ($\beta = 0.227$, $p = 0.039$, $R^2 = 0.12$) and 200 m ($\beta = 0.257$, $p = 0.023$, $R^2 = 0.15$) (Fig. 2) buffers. For the other traits, there were no significant effects of urban area detected at any of the buffer scales analyzed. Likewise, across buffer scales (75 m, 200 m, and 500 m) we detected no significant association between the weighted average values of the birds’ morphological traits (Beak Length, Tail Length, Wing Length and Mass) and tree cover (Fig. S7).

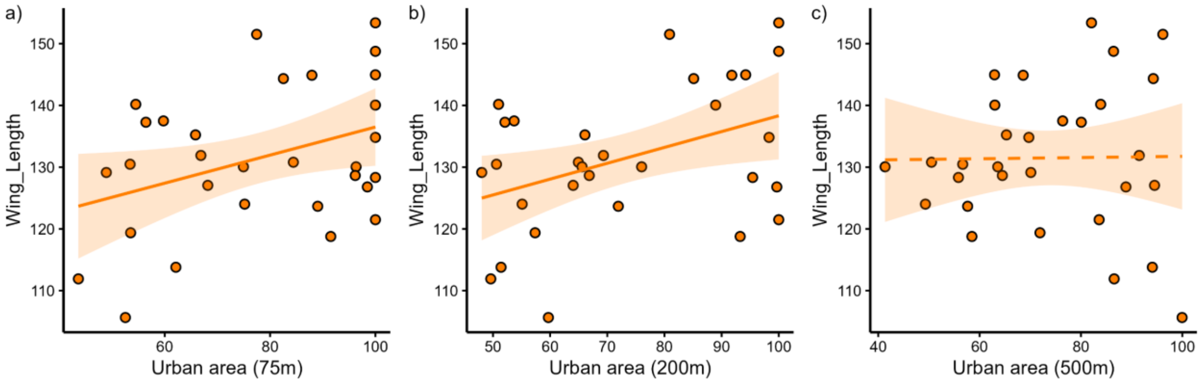

Figure 2. Relationships between community-weighted means (CWMs) of wing length and urban area across at three spatial scales (75 m, 200 m, and 500 m). 95% confidence intervals. Solid lines represent significant relationships, while dashed lines indicate non-significant trends.

Discussion

Urbanization acts as a strong environmental filter that restructures biological communities, including birds and favoring species with traits adapted to human-dominated landscape. In this study, we found that the functional richness of urban birds remained unchanged across gradients of tree cover and urban area. This functional stability indicates that the urban context, marked by air and noise pollution, and high fragmentation of the native vegetation, limits the colonization and persistence of functionally distinct species, restricting ecological diversification, even in apparently more favorable locations.

We recorded 89 species of birds, which represents approximately 24% of the avifauna recorded for the municipality of Campo Grande (404 spp) and 14.6% of the species known for the state of Mato Grosso do Sul (610 spp.; www.wikiaves.com.br). These results indicate that there is ecological filtering exerted by urbanization, in which only a fraction of the regional species richness is present in the areas sampled. The most abundant species (*Passer domesticus*, *Patagioneas picazuro*, and *Sicalis flaveola*) are generalist species that are highly adaptable to different gradients in urban areas, which reinforces patterns already found in other cities in the Cerrado biome (Pena et al. 2017; Souza et al. 2019; Santos et al. 2024).

Functional richness (FRic) remained constant along the urban areas, with no significant variation in response to tree cover or the proportion of urban area, regardless of the spatial scale analyzed, even after standardization (SESFRic). This stability suggests a strong environmental filtering effect imposed by urbanization, which limits the occurrence of species with functionally distinct traits, leading to communities composed of a reduced set of ecological strategies capable of persisting in urban environments (Sol et al. 2014; Aronson et al. 2016). One possible explanation is compensatory dynamics, in which the loss of sensitive or specialized species is compensated by generalist species that have similar ecological functions (Laliberté et al. 2010; Marcacci et al. 2021). This process can keep functional metrics stable, even with substantial changes in community composition (Banks-Leite et al. 2014; Matuoka et al. 2020). Thus, the apparent constancy of FRic along the urban gradient may be due to the ecological transformations that have occurred over time with increasing urbanization and loss of tree cover.

Functional evenness (FEve) showed a positive relationship with the proportion of urbanized area at the 75 m and 200 m scales, indicating that more urbanized environments favor communities composed of tolerant and functionally complementary species, resulting in a more uniform functional distribution. The observed pattern aligns with Melo and Piratelli (2023), who reported increased functional evenness in areas with higher vehicle traffic in São Paulo, Brazil. This was interpreted as a consequence of filtering species, where only those tolerant to urban stressors persist. Similarly, our results suggest that highly urbanized environments promote the coexistence of functionally similar yet complementary species, likely due to adaptive traits that confer resilience to disturbance (Evans et al. 2011; Sol et al. 2014).

In contrast, functional evenness (FEve) exhibited a negative relationship with tree cover across all spatial scales analyzed. This suggests that as vegetation increases, the functional space becomes less evenly occupied, likely due to the dominance of specific functional groups, such as insectivores and frugivores, that share similar traits (Mason et al. 2005; Villéger et al. 2008; Oliveira Hagen et al. 2017; Melo and Piratelli 2023). This trend may reflect reduced niche complementarity in areas with higher vegetation, where a few dominant functional strategies prevail. Although we did not sample within large urban parks in Campo Grande, previous studies comparing interior and exterior zones of urban green spaces suggest that these areas may function as refuges for specialist species (Schütz and Schulze 2015; Melo and Piratelli 2023). Concepción et al. (2015) found that urbanization filters out functionally distinct specialist species of beetles and spiders, leading to functional convergence driven by the persistence of mobile and generalist taxa. Likewise, Callaghan et al. (2019) showed that generalist birds are the most urban-tolerant, thriving in highly modified environments due to their ecological flexibility. These findings reinforce the idea that tree cover and urban structure independently shape the functional structure of bird assemblages, with vegetation favoring trait redundancy and urban area promoting evenness through functional complementarity among urban tolerant species.

Functional divergence (FDiv) and functional dispersion (FDis) showed no significant relationships with tree cover or urban area across any of the spatial scales analyzed, a pattern that persisted even after standardization (SES). These results suggest that, despite environmental heterogeneity in vegetation and urbanization levels among the 30 sites, this variation was insufficient to influence the distribution or spread of functional traits within bird assemblages. A likely explanation is the dominance of urban-tolerant, generalist species (i.e. *Passer domesticus*, *Patagioenas picazuro*, and *Sicalis flaveola*) which were consistently abundant across the gradient, as observed in other studies (e.g. Abilhoa and Amorin 2017).

These species share intermediate functional traits and are highly adapted to urban conditions, including elevated noise (Proppe et al. 2013; Perillo et al. 2017), nesting opportunities provided by building structures (James Reynolds et al. 2019), and access to anthropogenic food sources and human-altered habitats (Sol et al. 2014; Leveau and Leveau 2016). Their widespread occurrence results in communities that are functionally redundant and constrained around a narrow set of trait combinations. Consequently, FDis and FDiv remain stable, reflecting a homogenized functional structure shaped by strong environmental filtering that excludes functionally distinct specialist species (do Nascimento et al. 2025). This pattern is supported by the very low detection rates of forest-associated species, including *Momotus momota* and *Ictinia plumbea* (Lopez et al. 2023; www.wikiaves.com.br), species found in the middle and upperstory of tropical forests and along forest edges and gallery forests.

Finally, community weighted means (CWMs) revealed that urban areas had a positive and significant effect on bird wing length, especially at the 75 m and 200 m spatial scales. This trait is associated with greater flight efficiency and enhanced mobility, which are advantageous in fragmented landscapes with high levels of noise, physical barriers (e.g., roads and buildings), and sparse vegetation (Fernández-Juricic 2000; Croci et al. 2008; Santos et al. 2024). Although few studies have explicitly reported increases in wing length in urban birds, evidence suggests that urbanization can selectively shape morphological traits related to movement and habitat use. For instance, Santos et al. (2024) found that tail length was greater in birds from more urbanized areas in Brasília, Brazil, reinforcing the idea that mobility-related traits are filtered by urban environments. Together, these findings support the interpretation that functionally homogeneous bird communities in cities are dominated by species with high mobility and generalist strategies. This is consistent with do Nascimento et al. (2025) who demonstrated that urbanization acts as a strong functional filter, excluding small-bodied, diet-specialist, and colorful species, while promoting those with greater dispersal capacity and ecological plasticity.

Conclusion

In conclusion, our study shows that urbanization exerts strong functional filters on bird communities, favoring generalist and functionally similar species across the urban gradient. Despite variation in tree cover, functional diversity remained low and structurally unchanged, suggesting a limited ecological benefit of isolated vegetation in highly urbanized contexts. In contrast, functional evenness (FEve) increased with the proportion of urbanized area and decreased with tree cover across spatial scales suggesting that urban environments promote the coexistence of functionally complementary generalist species, while more vegetated areas are dominated by a few functionally redundant groups. Additionally, wing length, a trait linked to mobility, was positively associated with urban area, indicating that structurally complex and noisy environments select species with greater dispersal capacity. These patterns highlight the predominance of species adapted to fragmented and anthropogenic landscapes.

We recommend that urban conservation strategies prioritize the connectivity of green spaces and increase the structural complexity of vegetation to support functionally diverse assemblages. Maintaining functional diversity is fundamental not only for ecological processes, but also for guaranteeing ecosystem services in tropical cities such as Campo Grande, a national reference for birdwatching ecotourism

Supporting information for chapter 2

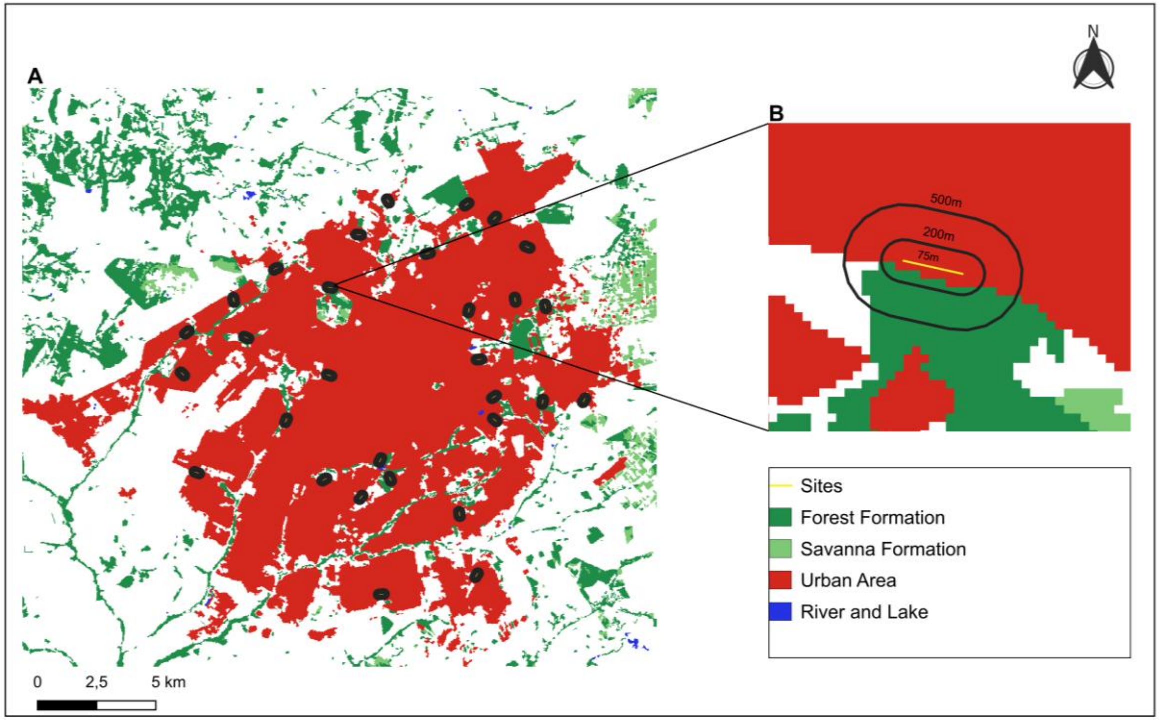

Figure S1. Study area in Campo Grande, Mato Grosso do Sul, Brazil. (A) Map of the municipality of Campo Grande with the location of the 30 sampling points represented by black circles. (B) Detail of one of the sampling points, highlighting the 75 m, 200 m, and 500 m buffers used to extract environmental data, including urban area and tree cover (forest and savannah formations).

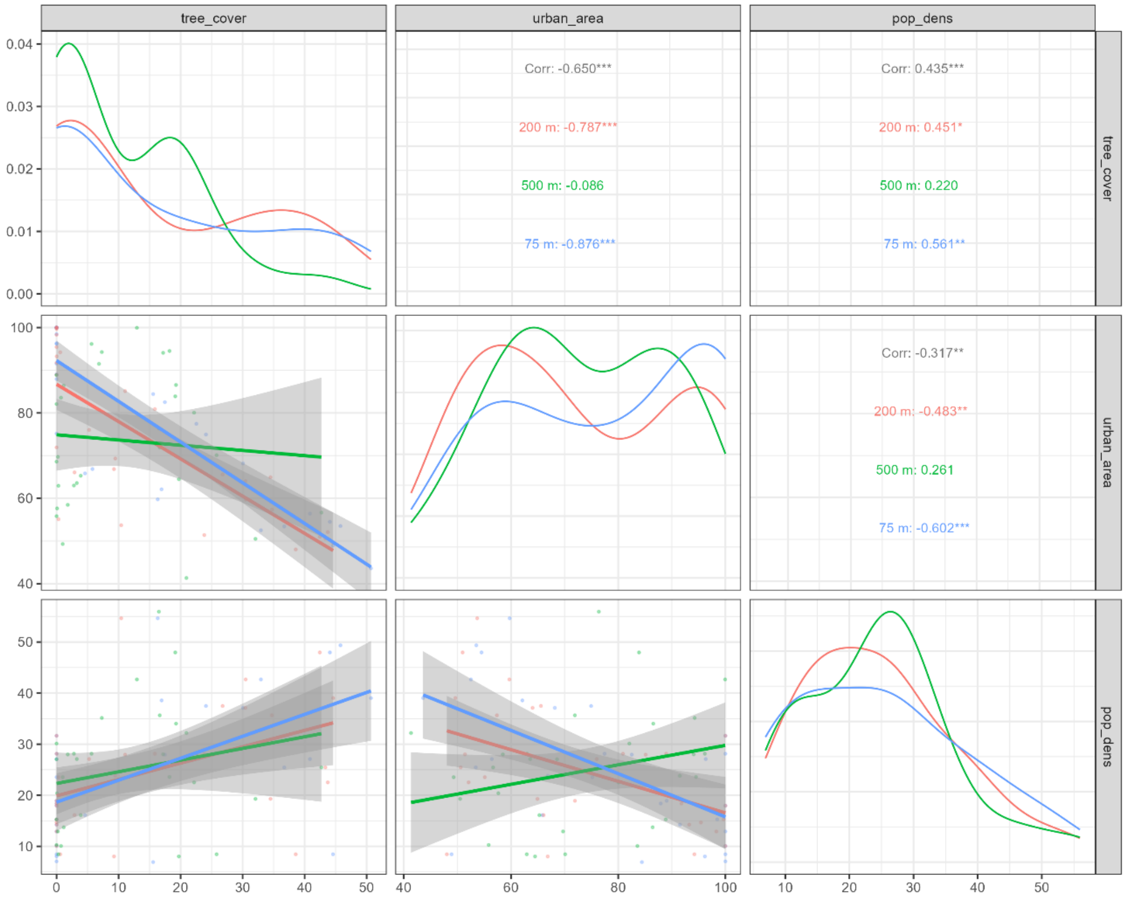

Figure S2. Correlation plot showing the results for Pearson's correlation test between Tree cover, Urban area and Human population density for the three scales of buffers (75, 200 and 500 m). Significant results are shown with an asterisk (*).

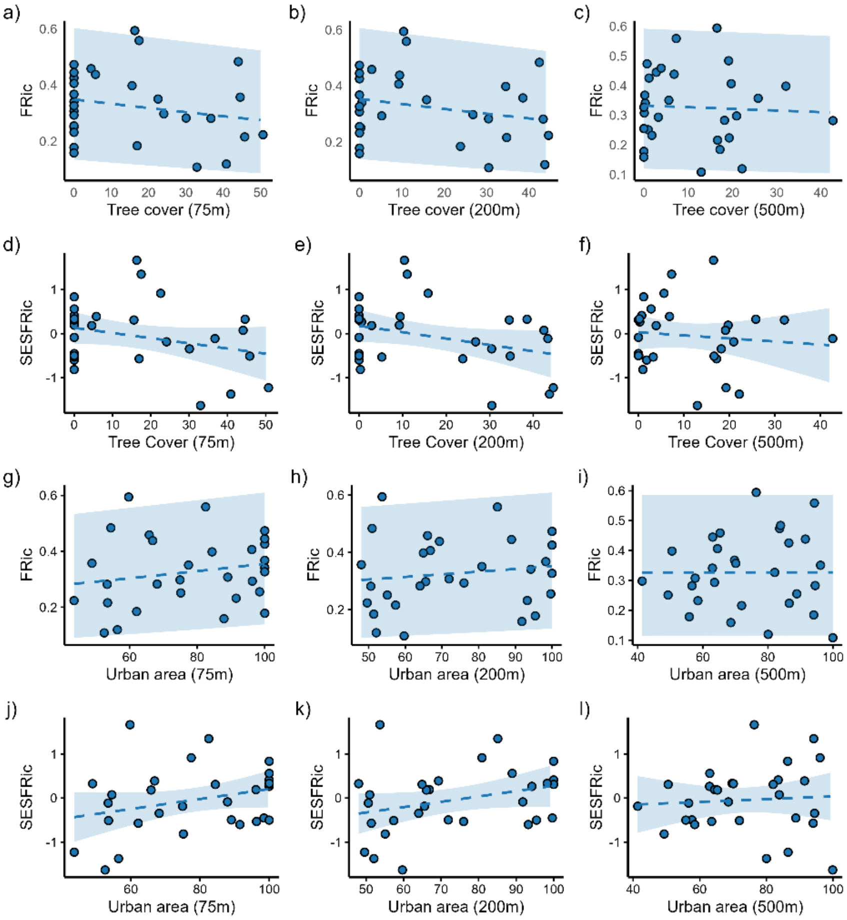

Figure S3. Linear relationship between Functional Richness and Standardized values (SESFRic) with tree cover (a-f) and urban area (g-l) measured at three spatial scales (75 m, 200 m and 500 m). 95% confidence interval. The dashed line showed the non-significant trends (p>0.05).

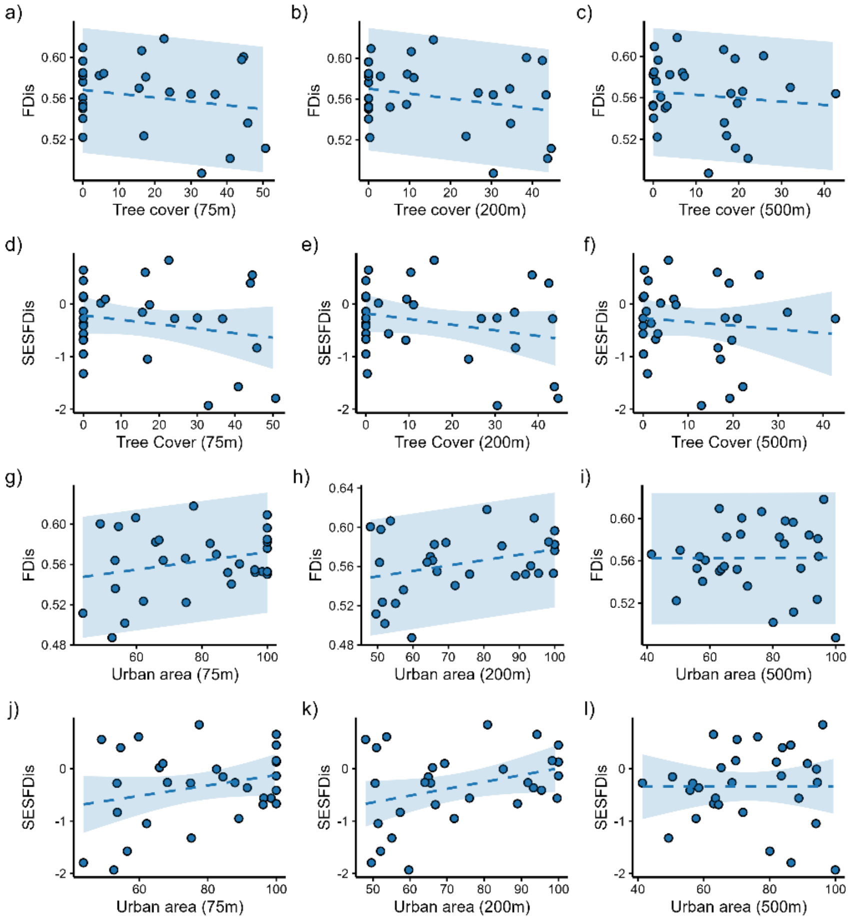

Figure S4. Linear relationship between Functional Dispersion and Standardized values (SESFDis) with tree cover (a-f) and urban area (g-l) measured at three spatial scales (75 m, 200 m and 500 m). 95% confidence interval. The dashed line showed the non-significant trends (p>0.05).

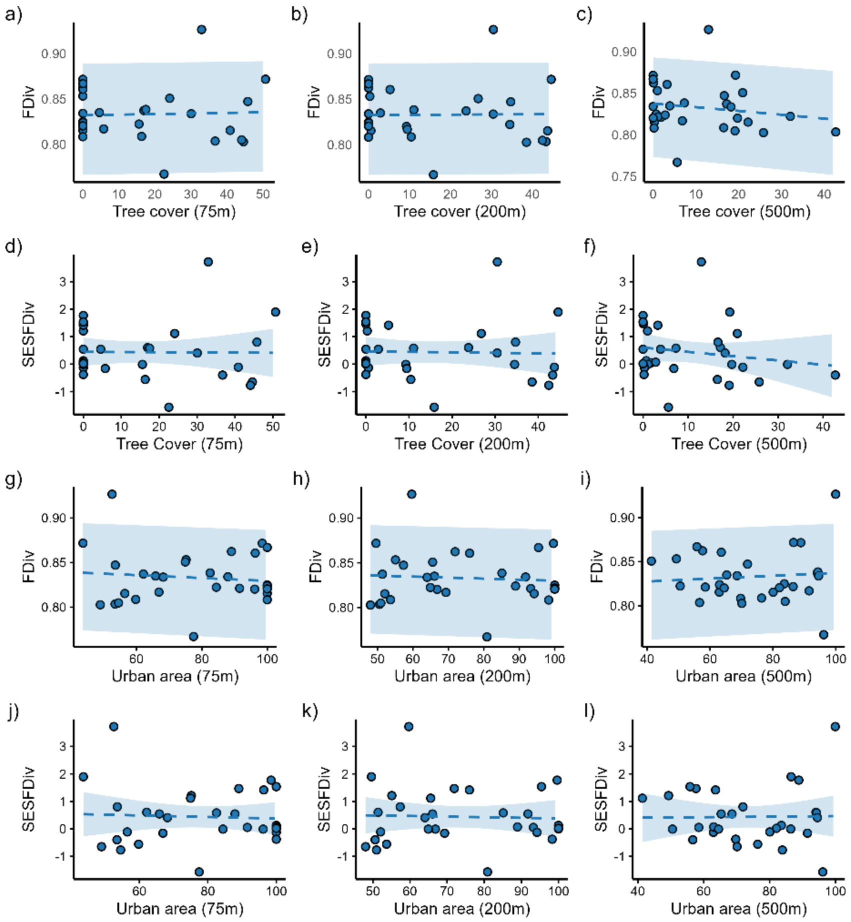

Figure. S5. Linear relationship between Functional Divergence and Standardized values (SESFDiv) with tree cover (a-f) and urban area (g-l) measured at three spatial scales (75 m, 200 m and 500 m). 95% confidence interval. The dashed line showed the non-significant trends (p>0.05).

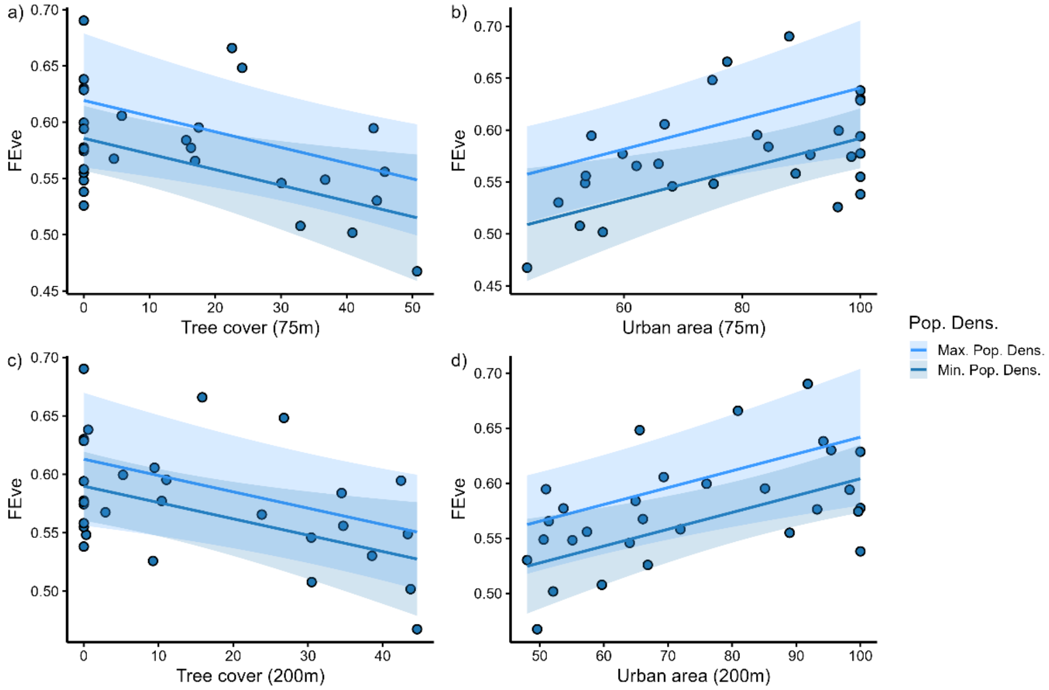

Figure S6. Relationship between additive models, the first column represents functional evenness with tree cover + population density in the 75 and 200 m buffers (a and c). In the second column the relationship of functional evenness with urban + population density in the 75 and 200 m buffers (b and d). Solid lines represent significant relationships.

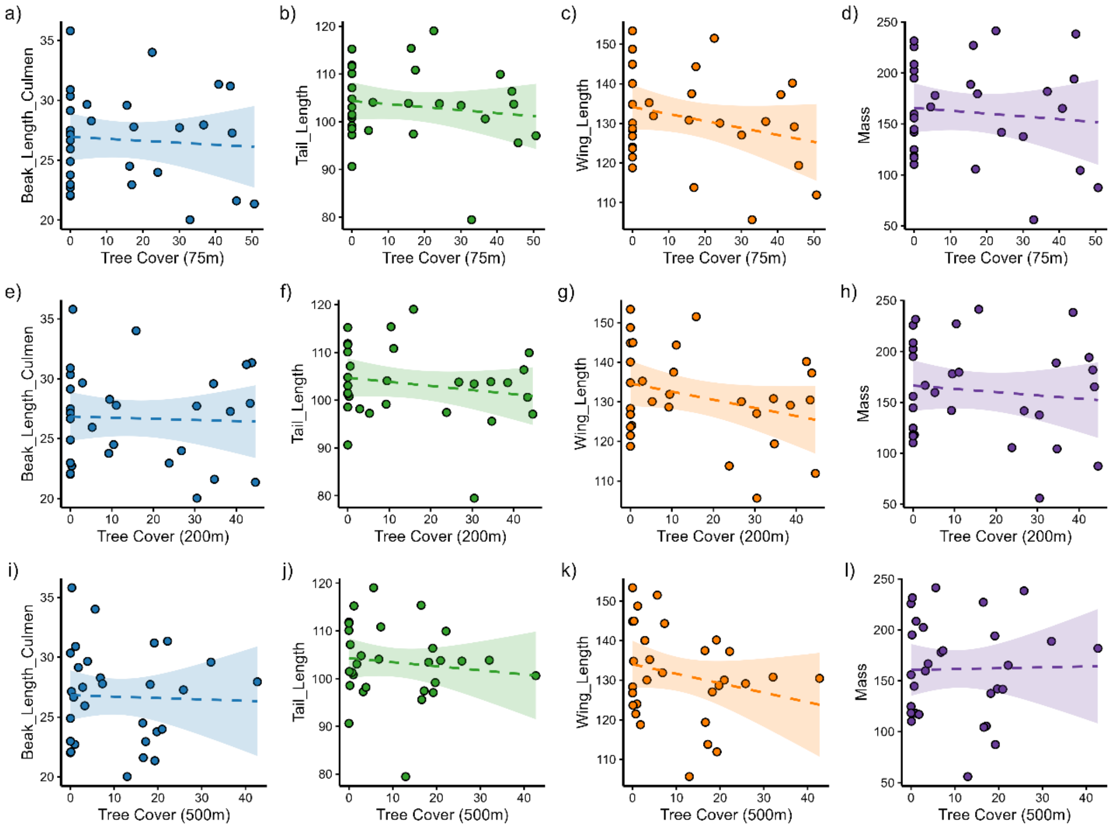

Figure S7. Relationships between community-weighted means (CWMs) of four bird traits and tree cover across three spatial scales (75 m, 200 m, and 500 m). 95% confidence interval. Dashed lines indicate non-significant trends ($p>0.05$).

Table S1. List of species present by family in thirty areas in the city of Campo Grande, Mato Grosso do Sul, Brazil.

Family	Species
Accipitridae	*Ictinia plumbea*
Accipitridae	*Rupornis magnirostris*
Ardeidae	*Ardea alba*
Ardeidae	*Syrigma sibilatrix*
Caracarinae	*Caracara plancus*
Cariamidae	*Cariama cristata*
Charadriidae	*Vanellus chilensis*
Columbidae	*Columba livia*
Columbidae	*Columbina picui*
Columbidae	*Columbina squammata*
Columbidae	*Columbina talpacoti*
Columbidae	*Patagioenas picazuro*
Columbidae	*Zenaida auriculata*
Cracidae	*Crax fasciolata*
Cuculidae	*Crotophaga ani*
Cuculidae	*Guira guira*
Dendrocolaptidae	*Campylorhamphus trochilirostris*
Dendrocolaptidae	*Lepidocolaptes angustirostris*
Fringillidae	*Euphonia chlorotica*
Furnariidae	*Certhiaxis cinnamomeus*
Furnariidae	*Furnarius rufus*
Hirundinidae	*Progne chalybea*
Hirundinidae	*Progne tapera*
Icteridae	*Icterus pyrrhopterus*

Icteridae	*Molothrus bonariensis*
Icteridae	*Molothrus rufoaxillaris*
Mimidae	*Mimus saturninus*
Momotidae	*Momotus momota*
Parulidae	*Basileuterus culicivorus*
Parulidae	*Myiothlypis flaveola*
Passerellidae	*Ammodramus humeralis*
Passeridae	*Passer domesticus*
Picidae	*Colaptes melanochloros*
Picidae	*Melanerpes candidus*
Psittacidae	*Alipiopsitta xanthops*
Psittacidae	*Amazona aestiva*
Psittacidae	*Amazona amazonica*
Psittacidae	*Ara ararauna*
Psittacidae	*Brotogeris chiriri*
Psittacidae	*Diopsittaca nobilis*
Psittacidae	*Eupsittula aurea*
Psittacidae	*Orthopsittaca manilatus*
Psittacidae	*Psittacara leucophthalmus*
Rallidae	*Aramides cajaneus*
Ramphastidae	*Ramphastos toco*
Rhynchocyclidae	*Todirostrum cinereum*
Strigidae	*Athene cunicularia*
Thamnophilidae	*Thamnophilus caerulescens*
Thamnophilidae	*Thamnophilus doliatus*
Thraupidae	*Coereba flaveola*
Thraupidae	*Cyanerpes cyaneus*

Thraupidae	*Dacnis cayana*
Thraupidae	*Nemosia pileata*
Thraupidae	*Saltator similis*
Thraupidae	*Sicalis flaveola*
Thraupidae	*Sporophila caerulescens*
Thraupidae	*Sporophila lineola*
Thraupidae	*Stilpnia cayana*
Thraupidae	*Tersina viridis*
Thraupidae	*Thraupis palmarum*
Thraupidae	*Thraupis sayaca*
Thraupidae	*Volatinia jacarina*
Threskiornithidae	*Mesembrinibis cayennensis*
Threskiornithidae	*Theristicus caudatus*
Tinamidae	*Crypturellus undulatus*
Trochilidae	*Chlorostilbon lucidus*
Trochilidae	*Colibri serrirostris*
Trochilidae	*Eupetomena macroura*
Trochilidae	*Heliomaster furcifer*
Trochilidae	*Hylocharis chrysura*
Troglodytidae	*Campylorhynchus turdinus*
Troglodytidae	*Troglodytes musculus*
Trogonidae	*Trogon curucui*
Turdidae	*Turdus amaurochalinus*
Turdidae	*Turdus leucomelas*
Turdidae	*Turdus rufiventris*
Tyrannidae	*Elaenia spectabilis*
Tyrannidae	*Empidonomus aurantioatrocristatus*

Tyrannidae	*Megarynchus pitangua*
Tyrannidae	*Myiarchus ferox*
Tyrannidae	*Myiarchus swainsoni*
Tyrannidae	*Myiodynastes maculatus*
Tyrannidae	*Myiozetetes cayanensis*
Tyrannidae	*Nengetus cinereus*
Tyrannidae	*Pitangus sulphuratus*
Tyrannidae	*Pyrocephalus rubinus*
Tyrannidae	*Tyrannus melancholicus*
Tyrannidae	*Tyrannus savana*
Vireonidae	*Cyclarhis gujanensis*

Table S2. Comparison between simple and additive models using ANOVA to analyze functional evenness (FEve) of urban birds at different spatial scales. Df = degrees of freedom; RSS = Sum of the squares of the residuals of the complete model; F = F test statistic; p = significance level of the test.

Comparison Models	Buffer (m)	Df	RSS	F	p-value
Tree vs Tree + Pop	75 m	1	0.0557	0.78	0.386
Build vs Build + Pop	75 m	1	0.0525	1.57	0.221
Tree vs Tree + Pop	200 m	1	0.0558	0.4	0.534
Build vs Build + Pop	200 m	1	0.0502	1.11	0.301

Chapter 3: Urbanization reduces alpha, beta, and gamma diversity of bird communities in urban road verges*

*This chapter is under consideration for submission to the journal Biological Conservation.

Abstract

Changes in land use driven by urbanization represent a serious threat to biodiversity conservation worldwide, affecting community composition and ecosystem functioning. Urban road verges may represent valuable habitats within cities, contributing to biodiversity conservation and the provision of ecosystem services that benefit human well-being. We evaluated the potential of urban road verges to maintain and conserve bird communities across different levels of urbanization in Campo Grande, a Brazilian city embedded in the Cerrado biodiversity hotspot. We compared the alpha, beta, and gamma diversity of bird communities in 30 urban road verges distributed in three urbanization classes (low: <50%; intermediate: 50–90%; or high: >90%). A total of 2,629 individuals from 100 bird species were recorded. Alpha and gamma diversity were higher in less urbanized areas. Beta diversity was dominated by species turnover across all urbanization classes, with turnover being especially pronounced in the low urbanization class. Our results highlight the importance of urban road verges in maintaining avian diversity within cities, particularly in regions where native vegetation cover is still preserved. We recommend maintaining structural heterogeneity within road verges as well as native vegetation remnants in its surroundings. These management practices may enhance the contribution of road verges to biodiversity conservation and ecosystem services provisioning in urban environments.

Introduction

Biodiversity conservation faces multiple challenges in urban areas. As cities expand, species living in these areas must deal with several negative impacts of urbanization (Grimm et al. 2008; Sushinsky et al. 2013). For example, the loss of tree cover in cities reduces resource availability (e.g., habitat and food) for some species (Tee et al. 2018) and makes the microclimate warmer and unsuitable for other species (Melaas et al. 2016; Piano et al. 2017; Cabon et al. 2024). Moreover, habitat fragmentation resulting from urbanization can lead to genetic and demographic isolation, potentially disrupting ecological processes, such as dispersal or migration (Bierwagen 2007; Güneralp and Seto 2013).

Several studies have shown that urbanization leads to a loss of local (alpha) and regional (gamma) diversity (Socolar et al. 2016; Banville et al. 2017; Spooner et al. 2018; Allen et al. 2019). In addition, urbanization can also cause a reduction in beta diversity, contributing to the process of biotic homogenization (McKinney 2006; Ferenc et al. 2014). Homogenization in dense urban areas can occur both through a decrease in turnover (i.e., species replacement between sites), and through an increase in nestedness resulting from species loss (Socolar et al. 2016). Urbanization can increase nestedness, indicating that urban communities become impoverished subsets of natural communities, reflecting the low heterogeneity of available habitats (Vallejos et al., 2016; Kale et al., 2018; Sidemo-Holm et al., 2022; Fu et al., 2025). However, turnover is often the predominant component of beta diversity for different groups of organisms, both in urban and non-urban environments, suggesting that species replacement, rather than loss, is a key driver of community differentiation across landscapes (Filgueiras et al. 2016; Hill et al. 2018; Salomão et al. 2019; Ganci et al. 2022).

To mitigate the impacts of urbanization on biodiversity, green elements including native forest remnants, urban parks, isolated trees, green roofs, and gardens play an essential role (LaMontagne et al. 2015; Dale 2018; Partridge and Clark 2018; de Groot et al. 2021). However, other less-studied green elements embedded within the urban matrix may also play an important role. Among them, road-associated habitats (herein 'urban road verges') represent a potentially valuable but still underexplored habitat, with the potential to contribute to biodiversity conservation and provision of ecosystem services that positively affect human health and well-being (Weber et al. 2014). For instance, road verges may enhance local climate regulation by the presence of street trees (Ligtermoet et al. 2022). In addition, road verges can provide nesting and foraging habitats for birds (White et al. 2005) and habitat for bees and butterflies (White et al. 2005; Brown et al. 2024). However, few studies have quantified community-level patterns in urban road verges (Suhonen et al. 2017; Brown et al. 2024; Bichi et al. 2024).

Most community studies have focused on alpha diversity and local variables (e.g., verge size and vegetation type), while beta and gamma diversity remain unexplored in urban road verge habitats. Existing studies have also concentrated mainly on plants and insects, particularly pollinators such as bees and butterflies (Cilliers and Bredenkamp 2000; Vakhlamova et al. 2016; Priyadarshana et al. 2025), often emphasizing the importance of structural attributes of the road verges (Säumel et al. 2016; Marshall et al. 2019; Ligtermoet et al. 2022). To our knowledge, no study has assessed communities in urban road verges considering simultaneously the three dimensions of diversity (alpha, beta, and gamma). In addition, studies adopting a landscape perspective, in which land use and cover surrounding road verges are quantified, also remain scarce, despite their importance. A landscape perspective allows, for instance, evaluation of how the amount of urbanized area in the landscape influences local communities within urban road verges, thereby providing a stronger basis for conservation and management strategies in urban areas.

To assess the impact of urbanization on bird communities inhabiting road verges, we sampled 30 road verges distributed across a gradient of urbanization. Birds are suitable models for assessing the ecological importance of urban road verges for several reasons. Birds can serve as indicators of a healthy urban environment (Evans et al. 2011; Campbell et al. 2022; Díaz et al. 2022). Moreover, evidence shows that these linear habitats can positively affect bird diversity in some human-dominated landscapes, providing habitat, serving as corridors for dispersal, and offering stepping stones that facilitate movement across urban matrices (Morelli et al. 2014; O'Sullivan et al. 2017; Bernes et al. 2017; Ligtermoet et al. 2022). To quantify the impacts of urbanization on bird communities of road verges, we compared the alpha, beta, and gamma diversity of bird communities among three levels of urbanization (low, medium, and high). We hypothesized that alpha and gamma diversity will be lower in areas with high urbanization, especially when compared to areas with low urbanization. Furthermore, we expected to find more homogeneous communities (reduced beta-diversity) in these highly urbanized areas, due to the process of biotic homogenization.

Material and Methods

Study area

We conducted this study in the urban perimeter of the municipality of Campo Grande (20°25′43" - 20°34'40"S; 54°33'24" - 54°39'49"W), state of Mato Grosso do Sul, Brazil. The study area was formerly entirely covered by Cerrado, including dry forests, grasslands, wetlands, shrublands, and savannahs (Ribeiro and Walter 1998). However, most (~80%) of the native vegetation has been replaced by pastures, crops, and urban areas (Ganci et al., 2022). There is a dry season (from April to September) and a rainy season (October to March), with an average annual precipitation of 1,530 mm and an average temperature of 23.3°C (Mendonça and Danni-Oliveira 2017; Ferreira et al. 2017). The degree of urbanization in Campo Grande varies spatially across administrative regions, with population densities ranging from 26.5 to 42.6 inhabitants per hectare (Planurb, 2024).

Sampling design

We established 30 line transects for sampling, each 200 meters long, located in 30 different urban median strips (hereafter urban road verges) across Campo Grande (Figure 1). The urban road verges were selected based on the level of urbanization in their surroundings, to encompass areas with low, intermediate and high levels of urbanization (see below). To maximize the independence among sampling units, all transects were spaced at least 1 km.

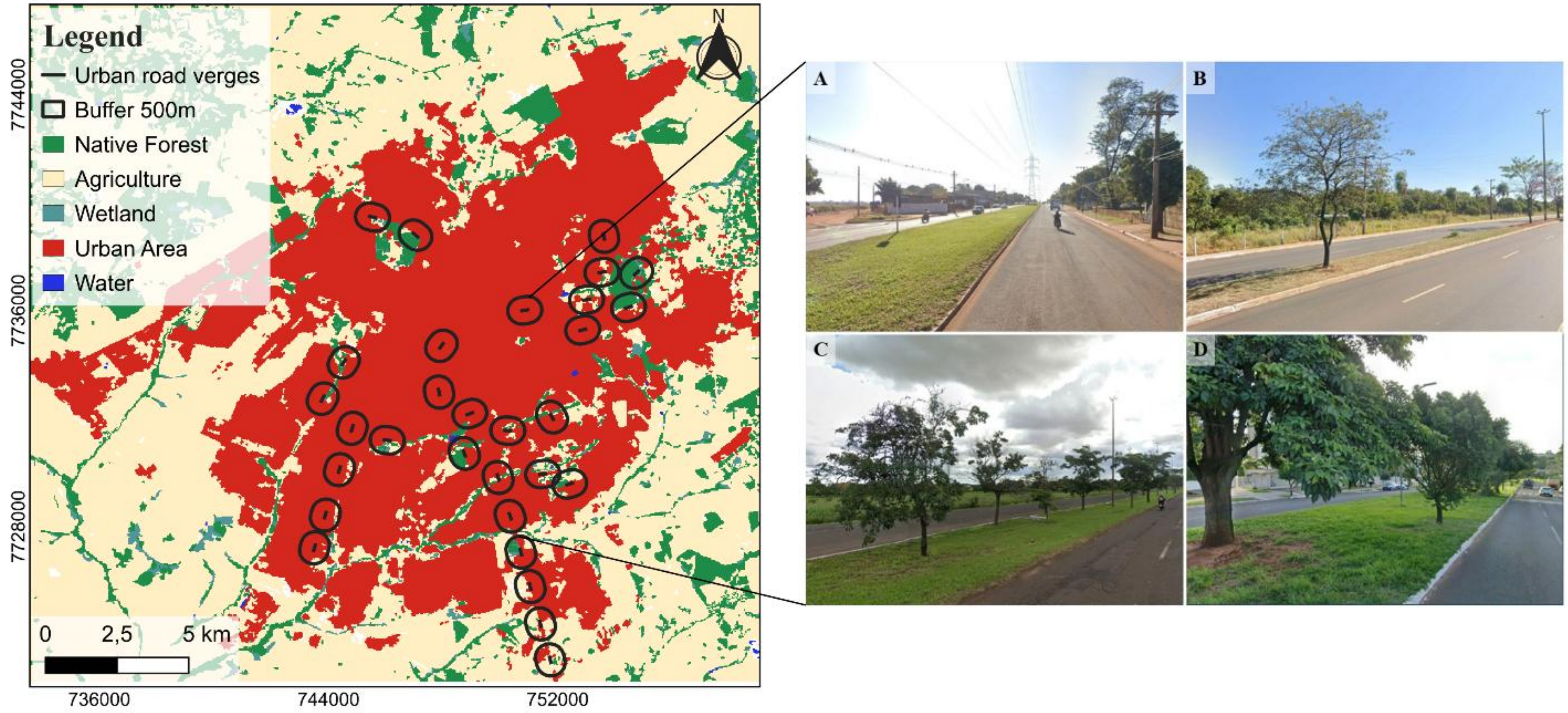

Figure 1. Study area showing the distribution of the 30 sampled urban road verges, in the city of Campo Grande, Brazil. Photos of four sampled urban road verges (A-D)

Bird sampling

Bird sampling was conducted between October and December 2022, coinciding with the nesting period in the Cerrado biome (Marini et al. 2012). Sampling took place between 06:00 and 10:00 am, when most species in the region are active (Souza et al. 2019). Surveys were not carried out on days with adverse weather conditions (e.g. rainy days) to reduce potential biases in detectability. Each transect (N = 30) was surveyed three times on different days. During each survey, two observers simultaneously walked the 200-m transect in one direction (unidirectional sampling) at a speed of approximately 1 km/h, resulting in a duration of 12 minutes per transect. Birds were recorded through visual and acoustic identification, totaling 18h of sampling effort across all transects. This approach allows broader spatial coverage compared with point count sampling (Bibby 2000; Gregory et al. 2004; Pejchar et al. 2008; Karp et al. 2011), and our sampling effort was consistent with previous studies with birds in urban areas (Xie et al. 2016; Guo et al. 2019; Leveau and Leveau 2020).

Local and landscape variables

For each transect, we measured the following local variables: the number of trees; the number of tree species; and the average width of the urban road verge. To quantify the number of trees and number of tree species, we conducted a field survey to record all woody plants over 1.5 meters tall. The identification of tree species was performed by a researcher with experience in plant taxonomy. The average width (in meters) of each urban road verge was calculated as the average of measurements taken at the beginning, middle and end of the transect. The number of trees per urban road verge varied from 0 to 92 trees, while the number of tree species varied from 0 to 29 species. Finally, the average road verge width ranged from 3.3 to 33.7 meters.

To characterize the landscape composition surrounding the 30 sampled urban road verges (local landscapes), we first created a buffer of a 500-meter radius around each sampled transect. Land use and land cover data for the sampling year (2022) was obtained from the MapBiomas project (collection 9.0, at 10-m resolution). We calculated the percentage of native forest cover (including forest and savanna formations) and urban area within each buffer using ArcGIS 10.6.1. Initially, we determined the area (ha) occupied by native vegetation and urban area within each buffer. These values were then divided by the total buffer area and multiplied by 100 to obtain percentage values. Forest cover and urban area cover varied from 0 to 62.6% and 6.6 to 99.5%, respectively, and they were highly negatively correlated (Pearson's correlation: $r = -0.63$; $p < 0.001$).

Since different levels of urbanization can have different impacts on bird diversity, with higher levels potentially associated with lower bird species richness (Reis et al. 2012), we classified local landscapes in three urbanization classes for the analyses, based on the percentage of urban area within a 500-m buffer: low (< 50%), intermediate (50-90%) and high (>90%) urbanization. To ensure that our sampling design was adequate, we first tested differences in forest cover, number of trees, number of tree species, and road verge width among different classes. To do so, we fitted generalized linear models (GLMs) with Gaussian error distribution. Post-hoc pairwise comparisons were performed using estimated marginal means (EMMeans) with Tukey adjustment. We found variation in forest cover among the urbanization classes ($\chi^2 = 18.48$, $df = 2$, $p < 0.001$, $R^2 = 0.41$; Figure S1), with pairwise comparisons revealing significant differences between the high and low levels of urbanization ($p < 0.001$), and between the intermediate and low levels of urbanization ($p=0.02$), but no differences between the high and intermediate levels of urbanization ($p=0.17$). There was no difference among the three treatments (urbanization classes) in terms of number of trees ($\chi^2 = 0.76$, $df = 2$, $p = 0.68$, $R^2 = 0.03$; Figure S2), number of tree species ($\chi^2 = 1.14$, $df = 2$,

$p = 0.57$, $R^2 = 0.04$; Figure S3), and average verge width ($\chi^2 = 0.03$, df = 2, $p = 0.98$, $R^2 = 0.001$; Figure S4). For forest cover, which is expected to be negatively correlated with urban areas, the absence of differences among treatments for all these local variables indicates that our sampling design was appropriate and that possible differences in bird communities may be attributed to the treatment effect (urbanization classes), rather than other potentially confounding local factors.

Analysis of alpha, beta and gamma diversity

Alpha diversity was quantified as the number of species recorded at each of the 30 local landscapes. Gamma diversity was quantified as the total number of species recorded across a similarly sample sized combination of local landscapes within each urbanization level (details in the next section). We followed Baselga (2010) to calculate the multiple-site total beta diversity (ßSOR), and their components of nestedness (ßNES) and spatial turnover (ßSIM). Beta diversity is the sum of the turnover and the nestedness components and may vary from 0 to 1. To calculate total beta diversity and its two components, we used the betapart R package (Baselga et al. 2025). We used a species-by-site incidence matrix as in Delciellos et al. (2025), rather than abundance data, for two reasons. First, we were interested in the impacts of urbanization on the number of species and their identities, rather than their abundance. Second, as we did not mark the individuals, and several birds in tropical areas present high site fidelity (Feng et al. 2019; Turella et al. 2022; Paxton and Paxton 2025), there would be a high risk of double-counting individuals.

Randomization approach for diversity comparison

Alpha, beta, and gamma diversity were quantified using a resampling procedure (following Baselga et al. 2010), because the number of local landscapes varied across the three urbanization classes (low = 7 local landscapes; intermediate = 14; high = 9). The resampling approach allowed us to standardize the number of local landscapes considered among the three urbanization classes. For each urbanization class, we randomly sampled five local landscapes 9999 times. Thus, we obtained 9999 estimates of alpha, beta and gamma diversity for each urbanization class. We used five local landscapes as the number of samples to allow variation in the landscapes selected across interactions, even in the urbanization class with fewer replicates (low class; 7 local landscapes).

To compare alpha, beta and gamma diversity among urbanization levels, we evaluated the overlap among the 95% confidence intervals, assuming that the absence of overlap indicates ecologically significant differences. We did not use statistical significance tests because they are not recommended for interpreting randomization results (White et al. 2014), considering that our sample sizes (i.e., the number of iterations) are arbitrarily high.

Results

A total of 100 bird species were recorded across the 30 urban road verges. Alpha diversity varied across the urbanization classes, with urban road verges in the low urbanization class presenting higher mean species richness (CI 95%: 24.2-26.6 species) than local landscapes in intermediate (CI 95%: 16.6-25.8 species) and high (CI 95%: 16.6-20.4 species) urbanization classes (Fig. 2a). Similar results were observed for the total number of species in each urbanization class (i.e., gamma diversity). Urban road verges in landscapes with low urbanization harbored higher total species richness (CI 95%: 57-66 species) than landscapes with intermediate (CI 95%: 41–57 species) or high (CI 95%: 32-40 species) levels of urbanization (Fig. 2b).

We found higher values of total beta diversity (βSOR) in low (CI 95%: 0.62–0.68) and intermediate (CI 95%: 0.60–0.68) urbanization classes compared to the high (CI 95%: 0.49-0.59) class (Fig. 3c). There was a higher turnover (βSIM) in low (CI 95% 0.60-0.65) than intermediate (CI 95% 0.51-0.63) and, especially, high (CI 95% 0.40-0.53) urbanization classes (Fig. 3a). On the other hand, there was a higher nestedness (βNES) in intermediate (CI 95% 0.03-0.12) and high (CI 95% 0.04-0.09) than in low (CI 95% 0.01-0.03) levels of urbanization (Fig. 3b). For all urbanization classes, the turnover component explained most of the variation in beta diversity (Fig. 3d).

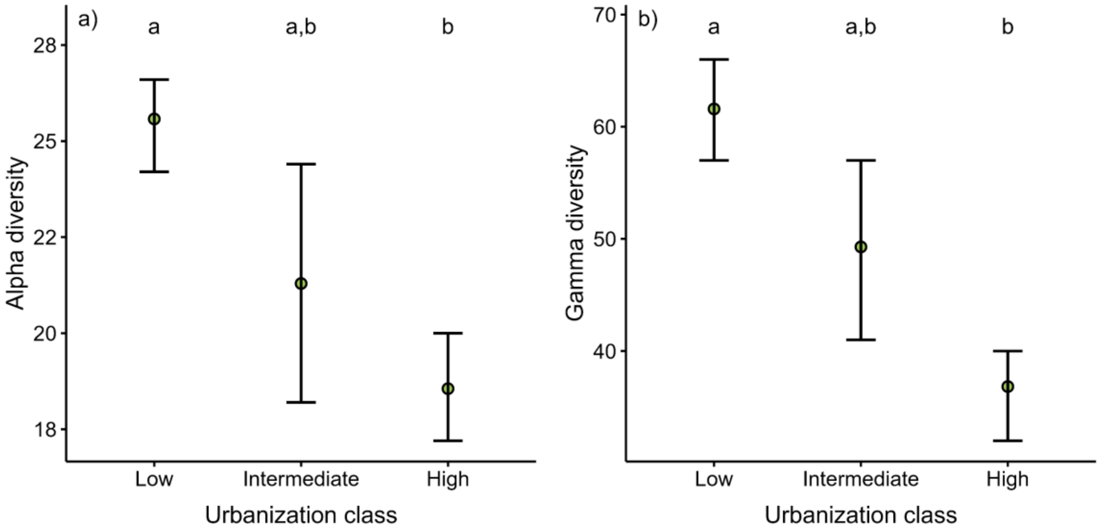

Figure 2. Variation in alpha diversity (α) and gamma diversity across urbanization classes (low <50%, intermediate 50–90%, high >90%). Points represent mean values, and error bars indicate 95% confidence intervals. Different letters denote significant differences between pairs of urbanization classes.

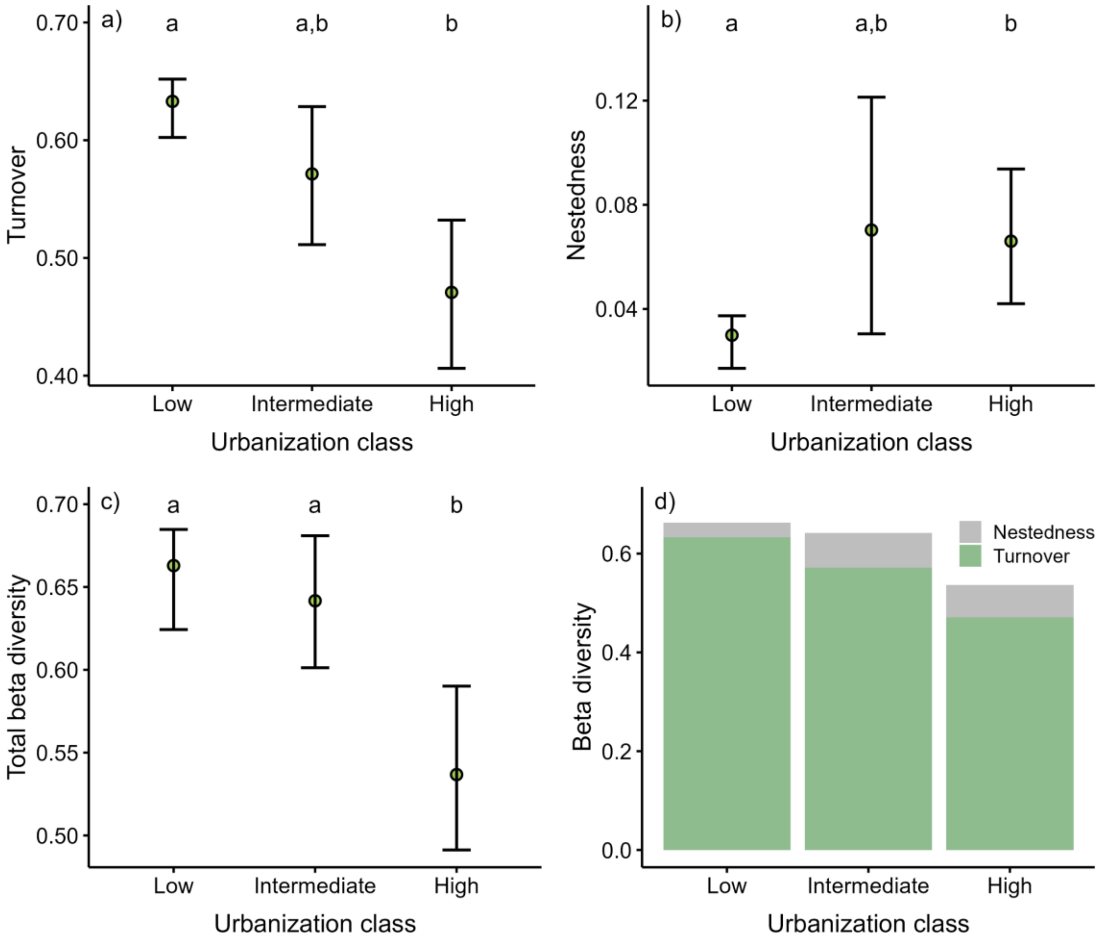

Figure 3. Patterns of beta diversity components (turnover, βSIM; nestedness, βNES; and total beta diversity, βSOR) across three classes of urbanization (low <50%, intermediate 50–90%, high >90%). Points represent mean values and error bars indicate 95% confidence intervals. Different letters denote significant differences between urbanization classes. The stacked bars show the relative contribution of turnover and nestedness to total beta diversity.

Discussion

Our study highlights the importance of road verges for maintaining birdlife in urban environments in Brazil. We found that bird communities of urban road verges embedded in areas with low levels of urbanization present higher alpha, gamma and beta diversity. Moreover, the turnover component of beta diversity was higher in the low urbanization class, and this component explained most of the variation in beta diversity for all urbanization classes. These results corroborate the hypothesis that urbanization leads to impoverished and more homogeneous biological communities (Clergeau et al. 2006; Devictor et al. 2007; Filloy et al. 2015; Morelli et al. 2016; Batáry et al. 2018).

As expected, alpha diversity decreased with increasing urbanization, reflecting the negative impact of urban development on bird richness. Some urban road verges with intermediate urbanization maintained similar local richness to those of less urbanized areas; however, others showed values closer to those of highly urbanized areas, suggesting a possible threshold of habitat change beyond which alpha diversity declines drastically (Aronson et al. 2014; Callaghan et al. 2024). This pattern has also been observed in other studies comparing urbanization gradients, indicating a consistent and negative response of bird communities to urban intensification (Cam et al., 2000; Ferenc et al., 2014; Reis et al., 2012; Sidemo-Holm et al., 2022). For gamma diversity, which represents the total number of species within each urbanization class, the pattern was similar to that observed for alpha diversity. The highest total richness occurred in areas with low levels of urbanization, while increasing urbanization was associated with a gradual loss of species. This decline became more pronounced in highly urbanized sites, where gamma diversity was markedly lower. Similar patterns have been reported in other urban bird studies, where species richness and overall diversity decrease along the urbanization gradient due to habitat simplification and reduced availability of resources (McKinney 2006; Carvajal-Castro et al. 2019; Callaghan et al. 2024). Less urbanized areas, which maintain larger and more structurally complex vegetation patches, act as refuges for a greater number of species. Similarly, Korányi et al. (2021) found that bird richness in urban green spaces was strongly associated with vegetation structure and tree cover, emphasizing the importance of heterogeneous and well-vegetated areas for maintaining urban biodiversity.

For beta diversity, our results showed that total beta diversity (βSOR) was higher in low and intermediate urbanization classes compared to highly urbanized areas. Similar results were found by Callaghan et al. (2024) across the continental United States. This pattern indicates that different sites in less urbanized areas harbor distinct bird assemblages, likely reflecting greater habitat and resource heterogeneity. The observed pattern was mainly driven by species turnover (βSIM), rather than nestedness (βNES), suggesting that differences in composition arise from species replacement rather than simple species loss (Sidemo-Holm et al., 2022). This outcome suggests that the more heterogeneous habitats in low urbanized sites support distinct species sets, reinforcing the importance of forest cover in maintaining habitat-specialist species, which tend to decline with increasing urbanization (Luck and Smallbone 2011). In contrast, reduced turnover in highly urbanized areas suggests biotic homogenization and dominance of generalist species, as found in other studies (Chace and Walsh 2006; Clergeau et al. 2006; McKinney 2006; Callaghan et al. 2019).

The occurrence of biotic homogenization in highly urbanized areas highlights the importance of maintaining landscape heterogeneity and forest cover to prevent species loss and enhance biodiversity within cities. Distinct bird assemblages can provide multiple and complementary ecological functions across space and time, due to differences in species composition and functional traits (Pagani-Núñez et al. 2019; Marcacci et al. 2021). In this context, urban road verges play a crucial role as linear green infrastructures that can improve air quality, contribute to carbon sequestration, mitigate noise, and provide a variety of ecosystem services (Säumel et al. 2016; O'Sullivan et al. 2017; Phillips et al. 2019). In addition, these vegetated corridors increase connectivity between other green areas or isolated trees within urban and peri-urban matrices, serving as habitat and movement routes for various taxa, such as butterflies (Saarinen et al. 2005), arthropods (Schaffers et al. 2012), birds (Young et al. 2007), and pollinators (Phillips et al. 2019). Therefore, urban road verges embedded in landscapes with greater forest cover tend to host more heterogeneous communities, while those in highly urbanized environments tend house impoverished and homogeneous communities.

Conclusion

Our study highlights how urbanization level can determine the importance of urban road verges for bird conservation. However, their presence does not replace the need to preserve forest remnants, which remain irreplaceable for the conservation of specialized and forest-dependent species (Paton et al. 2019; Thaweepworadej and Evans 2022). Decision-makers should prioritize the restoration of forest remnants surrounding urban road verges, to conserve bird diversity and to improve the provision of ecosystem services in urban environments. However, the conservation of biodiversity and the provision of ecosystem services in road verges may also depend on appropriate management practices (O'Sullivan et al. 2017). For example, adjusting mowing frequency, reducing excessive pruning, and selecting suitable native tree species can enhance habitat quality and structural complexity. Similarly, a study conducted in Brazil emphasized that strengthening legislation and promoting immediate and practical strategies are essential to safeguard native vegetation and pollinator diversity in road verges (Altomare et al. 2025). In this sense, tree planting and the restoration of urban road verges can represent effective and viable measures to improve habitat availability, increase ecological connectivity, and mitigate the effects of pollution and noise on bird communities.

Supporting information for chapter 3

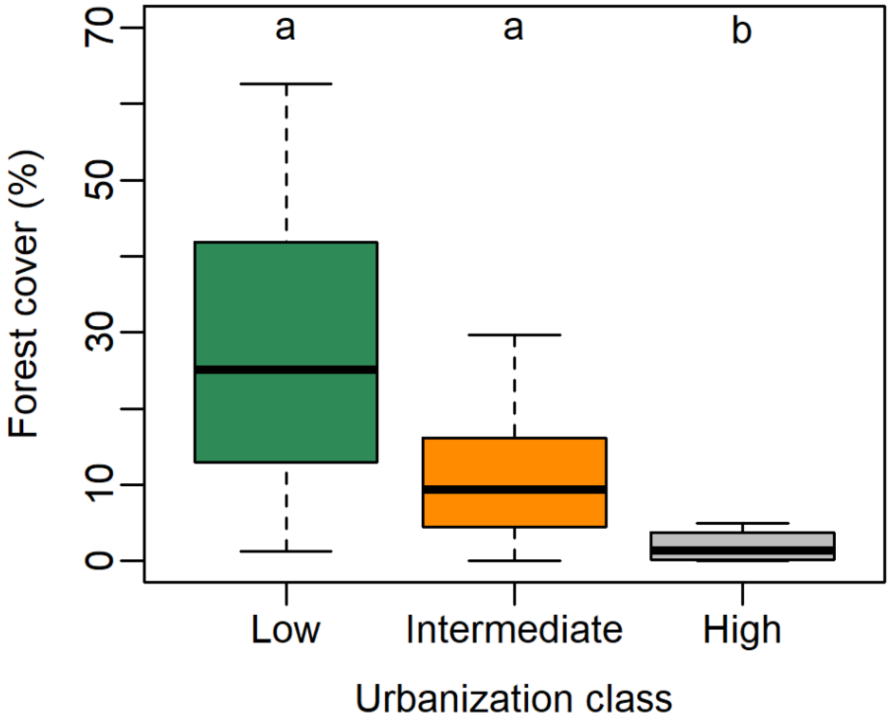

Figure S1. Variation in forest cover across three urbanization classes (Low <50%, Intermediate 50–90%, and High >90%). Each boxplot shows the median (bold horizontal bars), quartiles (boxes), maximum and minimum excluding outliers (bars) and outliers (circles). The different letters above the boxplots indicate statistically significant differences between treatments ($P \leq 0.05$) based on post-hoc pairwise tests.

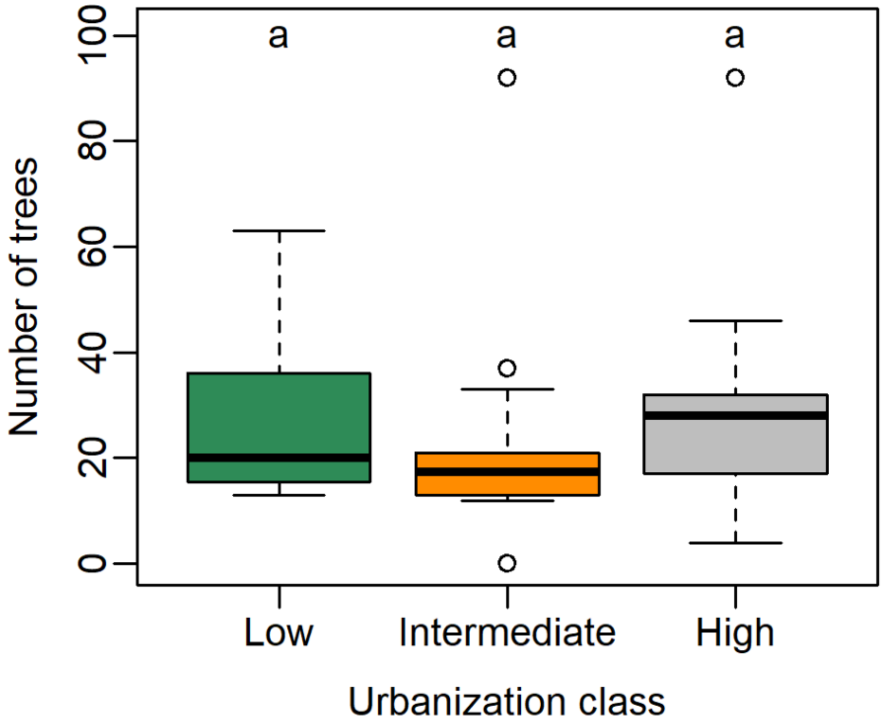

Figure S2. Variation in the number of trees across three urbanization classes (Low <50%, Intermediate 50–90%, and High >90%). Each boxplot shows the median (bold horizontal bars), quartiles (boxes), maximum and minimum excluding outliers (bars) and outliers (circles). The different letters above the boxplots indicate statistically significant differences between treatments ($P \leq 0.05$) based on post-hoc pairwise tests.

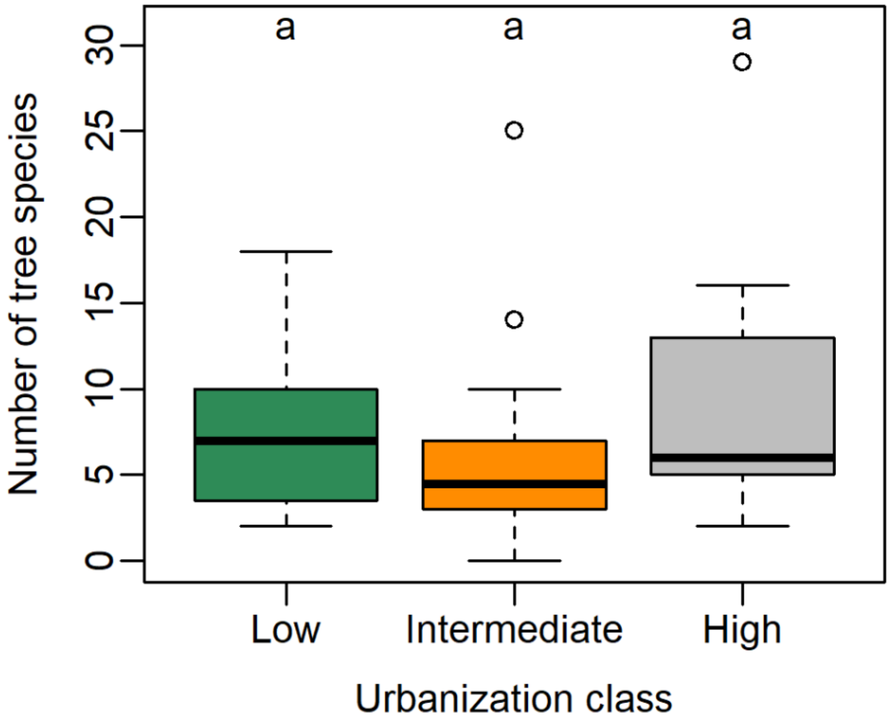

Figure S3. Variation in the number of tree species across three urbanization classes (Low <50%, Intermediate 50–90%, and High >90%). Each boxplot shows the median (bold horizontal bars), quartiles (boxes), maximum and minimum excluding outliers (bars) and outliers (circles). The different letters above the boxplots indicate statistically significant differences between treatments ($P \leq 0.05$) based on post-hoc pairwise tests.

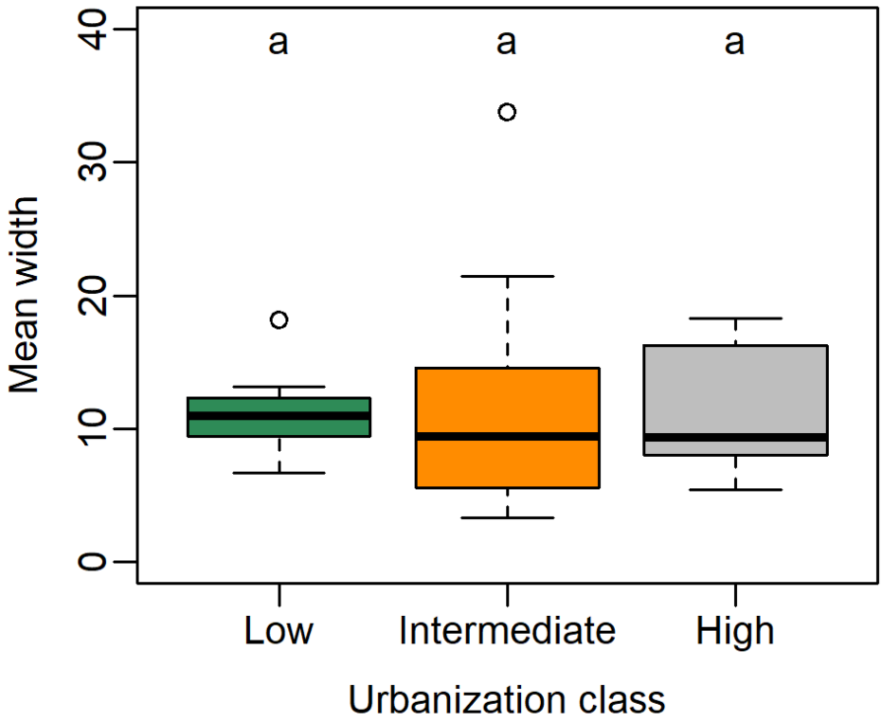

Figure S4. Variation in mean width of urban road verges across three urbanization classes (Low <50%, Intermediate 50–90%, and High >90%). Each boxplot shows the median (bold horizontal bars), quartiles (boxes), maximum and minimum excluding outliers (bars) and outliers (circles). The different letters above the boxplots indicate statistically significant differences between treatments (P ≤ 0.05) based on post-hoc pairwise tests.

Table S1. List of bird species recorded in the three urbanization classes in Campo Grande, MS, Brazil.

Species	Low	Intermediate	High
Accipitridae			
Elanus leucurus	X		
Ictinia plumbea	X	X	X
Rupornis magnirostris		X	X
Spizaetus tyrannus	X		
Megaceryle torquata		X	
Apodidae			
Apodidae sp.		X	

Ardeidae			
Ardea alba		X	X
Butorides striata		X	
Syrigma sibilatrix	X		X
Coragyps atratus	X		X
Charadriidae			
Vanellus chilensis	X	X	X
Columbidae			
Columba livia	X	X	X
Columbina picui	X	X	X
Columbina squammata		X	
Columbina talpacoti	X	X	X
Leptotila verreauxi		X	
Patagioenas cayennensis		X	X
Patagioenas picazuro	X	X	X
Zenaida auriculata	X	X	X
Cracidae			
Crax fasciolata	X		
Cuculidae			
Crotophaga ani	X	X	
Guira guira	X	X	
Piaya cayana	X		
Dendrocolaptidae			
Lepidocolaptes angustirostris	X	X	
Falconidae			
Caracara plancus	X	X	X
Falco sparverius		X	X
Euphonia chlorotica		X	
Furnariidae			
Furnarius rufus	X	X	X
Phacellodomus rufifrons		X	
Synallaxis frontalis	X		
Galbulidae			
Galbula ruficauda	X		
Hirundinidae			

Progne chalybea		X	
Progne tapera	X	X	X
Icteridae			
Gnorimopsar chopi	X	X	
Icterus pyrrhopterus	X		
Molothrus bonariensis	X	X	X
Mimidae			
Mimus saturninus		X	X
Parulidae			
Basileuterus culicivorus	X		
Geothlypis aequinoctialis		X	
Myiothlypis flaveola	X		
Passeridae			
Passer domesticus	X	X	X
Picidae			
Colaptes melanochloros	X		
Melanerpes candidus	X	X	
Pipridae			
Antilophia galeata	X		
Polioptilidae			
Polioptila dumicola		X	
Psittacidae			
Alipiopsitta xanthops	X	X	
Amazona aestiva		X	
Ara arauana	X	X	X
Brotogeris chiriri	X	X	X
Diopsittaca nobilis	X	X	X
Eupsittula aurea	X	X	X
Forpus xanthopterygius		X	
Aratinga sp.		X	
Orthopsittaca manilatus	X	X	
Psittacara leucophthalmus	X	X	X
Ramphastidae			
Ramphastos toco	X	X	X
Rhynchocyclidae			

Todirostrum cinereum	X	X	
Tolmomyias sulphurescens	X		
Strigidae			
Athene cunicularia	X	X	X
Thamnophilidae			
Herpsilochmus longirostris		X	
Thraupidae			
Coereba flaveola	X	X	X
Cyanerpes cyaneus		X	
Sicalis flaveola	X	X	X
Sporophila caerulescens			X
Sporophila leucoptera	X	X	
Sporophila lineola	X	X	
Sporophila sp.			X
Stilpnia cayana	X	X	
Thraupis palmarum	X	X	X
Thraupis sayaca	X	X	X
Volatinia jacarina	X	X	X
Threskiornithidae			
Mesembrinibis cayennensis	X	X	
Theristicus caudatus	X	X	X
Trochilidae			
Chlorostilbon lucidus	X		X
Eupetomena macroura	X	X	X
Hylocharis chrysura	X		
Troglodytidae			
Campylorhynchus turdinus		X	
Troglodytes musculus	X		X
Turdidae			
Turdus leucomelas	X	X	X
Turdus rufiventris	X	X	X
Turdus sp.		X	
Tyrannidae			
Camptostoma obsoletum	X		
Elaenia flavogaster		X	

Elaenia spectabilis	X	X	
Empidonomus varius		X	X
Griseotyrannus aurantioatrocristatus	X	X	
Machetornis rixosa	X	X	X
Megarynchus pitangua	X	X	
Myiarchus ferox		X	
Myiarchus swainsoni		X	
Myiodynastes maculatus	X	X	
Myiozetetes cayanensis	X		
Nengetus cinereus	X	X	X
Pitangus sulphuratus	X	X	X
Pyrocephalus rubinus	X		
Tyrannidae sp.	X		X
Tyrannus melancholicus	X	X	X
Tyrannus savana	X	X	X
Vireonidae			
Cyclarhis gujanensis		X	
Vireo chivi	X		

General conclusion

In this thesis, we investigated the effects of urbanization, including building density, human population density, and tree cover on bird assemblages. Urbanization represents one of the most pervasive drivers of biodiversity loss, yet its effects on species composition and ecological functions can vary depending on the structure and quality of urban green spaces. Across the three chapters of this thesis, we demonstrate that the maintenance of native vegetation, tree cover, and structural heterogeneity within cities are key determinant of taxonomic and functional diversity in tropical urban environments.

In the first chapter, we showed that tree cover plays a crucial role in sustaining forest-dependent bird species in urban landscapes, emphasizing that the retention and restoration of native vegetation patches can mitigate the negative impacts of urbanization. The patterns of beta diversity were primarily driven by species turnover, reinforcing that urban green areas contribute to maintaining spatial heterogeneity and community differentiation across the city.

In the second chapter, we found that urbanization acts as a strong functional filter, promoting the dominance of generalist and functionally similar species. Despite local variation in tree cover, functional diversity remained relatively low in highly urbanized areas, while functional evenness increased with urban intensity. These patterns suggest that urban environments favor the coexistence of adaptable species but limit the ecological functions provided by more specialized taxa. Traits associated with mobility, such as wing length, were positively related to urban areas, indicating that species with higher dispersal capacity are more capable of persisting in fragmented and disturbed landscapes.

The third chapter highlighted the complementary role of urban road verges for biodiversity conservation. Although these habitats can provide resources and connectivity for some bird species, they cannot substitute forest remnants. The conservation and restoration of surrounding vegetation, coupled with adequate management practices such as reduced mowing and the use of native tree species, are essential to enhance habitat quality and the delivery of ecosystem services in urban areas.

Taken together, our findings demonstrate that urbanization filters bird communities both taxonomically and functionally, but that its negative effects can be mitigated through strategic planning and habitat management. Preserving and connecting native vegetation patches, increasing tree cover, and promoting heterogeneous green spaces are fundamental actions to sustain ecological processes and ecosystem services in tropical cities. These results reinforce that biodiversity-sensitive urban design can reconcile human development with nature conservation, contributing to more resilient, sustainable, and functionally diverse urban ecosystems.

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