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Bird communities across different levels of human settlement: A comparative analysis from two northern Amazonian ecoregions

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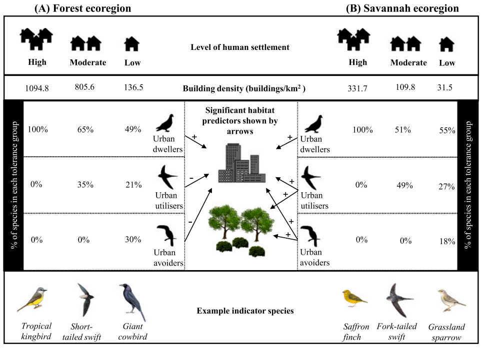
HIGHLIGHTS

- Human settlements impact bird communities in the Neotropics.
- Greater differences in bird community composition observed in human settlements in forest ecoregion vs. savannah region.
- Less urban-tolerant forest species negatively affected by built features in forest ecoregion.
- Built features beneficial to bird species in savannah ecoregion.
- Human settlement has a greater impact on bird communities in forests.

GRAPHICAL ABSTRACT



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ABSTRACT

Urban ecosystems are increasingly dominating landscapes globally, so it is critical to understand the effects of human settlements on biodiversity. Bird communities are effective indicators because they are impacted by the size and expansion of human settlements, exemplified by changes in their habitat use, breeding and foraging behaviours, as well as patterns of richness and abundance. Existing studies on bird community responses to human settlements have mainly focused on single ecoregions and large cities, leaving a gap in comparative research on how differently sized human settlements affect bird communities across various ecoregions. To address this gap, we examine species richness, bird abundances and community composition in human settlements, which exhibit variable sizes, populations, landscape configurations, and overall intensity of settlement in two tropical ecoregions in Guyana, Amazonia: forest and savannah. In each ecoregion we explored how different groupings of urban tolerance in birds responded to human settlements of differing population size and building densities. Overall, we found significant differences in bird communities across the varying levels of human settlement intensity in both ecoregions, with greater differences in bird community composition in the forest ecoregion than the savannah region. In both ecoregions, species richness and abundance were highest at the medium level of settlement of human settlement. Our findings suggest that bird tolerance to human settlements varies based on ecoregion and site-level factors. In the savannah, built features may be benefitting birds from all

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urban tolerance levels, but they have a negative impact on less urban-tolerant species in the forest ecoregion. Our comparative analysis reveals for the first time that the impact of human settlements on avian communities in northern Amazonia varies among ecoregions, indicating that species evolved to live in a savannah may be more tolerant to human settlements than those more evolved to a forest system.

1. Introduction

Human settlements are increasingly dominating landscapes across the globe, with nearly 66 % of all people projected to be living in urban areas by 2050 (Ritchie and Roser, 2018). Urban ecosystems drive land-cover change, which results in irreversible and persistent changes to the landscape (Akubia et al., 2020; Loram et al., 2007). Consequently, it leads to profound impacts on species diversity and distribution by altering, fragmenting, and causing habitat loss for many species (Marzluff, 2001; Melles et al., 2003; Petersen et al., 2022).

Bird communities are particularly impacted by the size and expansion of human settlements, exemplified by changes in their habitat use (Litteral and Shochat, 2017) breeding and foraging behaviours (Croci et al., 2008; Galbraith et al., 2015) and patterns of richness and abundance (Chace and Walsh, 2006). Birds are therefore effective indicators of the impact of human settlements on biodiversity. This is important because wild animal communities, and particularly birds, provide important ecosystem functions such as pest control, seed dispersal and pollination (Anderson et al., 2016; Garcia et al., 2010; García et al., 2018). Additionally, birds have been shown to positively impact the psychological wellbeing of humans (Methorst et al., 2021). Despite the overall negative impacts of human settlements on avifauna, natural and semi-natural habitats (e.g. greenspaces) within urban, peri-urban and rural areas can support diverse communities of birds (Hayes et al., 2020; Litteral and Shochat, 2017).

Human settlements encompass a broad range of variable environments (Faeth et al., 2012). These range from highly developed and modified cities to sparsely populated villages, interspersed with patches of relatively undisturbed natural habitat networks, such as parks and gardens (Aronson et al., 2017; Beninde et al., 2015; Goddard et al., 2010). The wide range of environments and disturbance levels have the potential to support diverse bird communities ranging from native species reliant on undisturbed habitat, to opportunistic and invasive species (both native and introduced) which are tolerant to and in some cases can exploit modified habitats (Blair, 1996). In fact, by accommodating the occurrence of non-native species and introducing novel species, urban development may lead to biotic homogenisation, where the urban centres are dominated by the same few species possessing similar traits, which allow them to thrive in such environments (Croci et al., 2008; Olden et al., 2016). Previous studies have categorised species into three groups based on their tolerance to urban development (Blair, 1996; Fischer et al., 2015) corresponding to a gradient of species' responses to human settlements: urban dwellers range from being solely dependent on urban areas for their survival to having viable populations in both natural and urban ecosystems, urban utilisers range from occasionally using urban resources to breeding in urban areas, and urban avoiders range from non-existent in developed urban areas to self-sustaining populations in natural areas within villages, towns and cities (Fischer et al., 2015).

The Neotropics is the second-most rapidly developing region globally, with high rates of land conversion relative to population growth and over 80 % of the population living in urban areas (Grau and Aide, 2008; Lois-González et al., 2022). However, the majority of studies on human settlements and birds have been conducted in temperate regions (Amaya-Espinel et al., 2019; Ortega-Álvarez and MacGregor-Fors, 2011). Avian tolerance to different intensities of human settlements has not been well explored in the Amazonia, which is the most biologically diverse part of the planet.

Tropical forests harbour the greatest species diversity and vertical complexity of all terrestrial ecosystems (Johnson, 1998; Terborgh, 1985), and Amazonian landscapes are often primarily associated with the "Amazon forest biome", which covers 80 % of Amazonia. However, they also comprise a wider range of ecosystems along climatic, edaphic and hydrological gradients. Another large, and generally understudied, ecosystem in the region is the "Rio Branco-Rupununi savannah" which constitutes open formations of grassland and shrub vegetation, covering an area of 267,000 km^2 in the northern Amazon (de Carvalho and Mustin, 2017; Pires, 1985; Viana et al., 2016).

The Amazonian forest is a complex ecosystem known for its rich faunal and floral diversity and intricate patterns of species density, distribution, and composition. As a result, the potential effects of human settlements on this biome can be far-reaching and potentially detrimental to the delicate balance of its ecosystem (Ferrante et al., 2014; Leveau and Leveau, 2005; Richards and VanWey, 2015). Many Amazonian forest bird species are rare, with small populations adapted specifically to local factors and very sensitive to small changes in their respective forest habitats (Bass et al., 2010; Condit et al., 2000; Terborgh et al., 1990). For example, one study indicated that 250 species of birds can occupy a single square kilometre of Amazonian forest (Vieira et al., 2008). This high biodiversity is due to the fine-scale vertical structuring of forests, which allows more species occupy a unit of area (e.g. per km^2) (Basham et al., 2023; Gouveia et al., 2014; Terborgh, 1985). Although also high in biodiversity (de Carvalho and Mustin, 2017), savannah grassland ecosystems, characterised by openness, are arguably more similar to urban and rural ecosystems as they lack the structural complexity of forests (Herte et al., 1971; Petermann and Buzhdygan, 2021; Dorney et al., 1984). Human settlements in the Amazonian forest biome therefore have the potential to cause a significantly greater impact on biodiversity than those in savannah grasslands. However, avian communities in Amazonian savannah grasslands remain understudied (de Carvalho and Mustin, 2017) and an integrated comparison of how vertebrate communities respond to development in contrasting ecoregions remains scarce (but see Leveau et al., 2017).

Here, we explore avian responses to human settlements across different levels of human settlement intensity in two Amazonian ecoregions in Guyana; A forest system in the north of the country and a savannah system in the south. We examine species richness, bird abundances and community composition in different types of human settlements which exhibit variable sizes, populations, landscape configurations and overall intensity of human settlement. We also explored if building density, the amount of greyspace (gray infrastructure: roads, buildings) and greenspaces (parks, gardens, cropland) explained the richness and abundance of different ways to classify avian species - urban dwellers, urban utilisers and urban avoiders. We do so in our two contrasting study ecoregions, and explore whether the effect of human settlements differed for each bird group, between the two ecoregions. We tested four predictions: 1) bird community composition will show more variation in the forest ecoregion due to the loss of forest structural complexity through human settlement; 2) urban tolerance will be higher in the savannah ecoregion; 3) urban tolerant (dweller) species will have a positive relationship with gray infrastructure; 4) urban avoider species will have a positive relationship with greenspaces.

2. Methods

2.1. Study site and sampling design

Guyana is home to some of the world's most well-preserved oldgrowth tropical rainforest areas, covering an estimated 85 % of the country's land. In addition to these forested regions, Guyana also encompasses savanna grasslands and wetlands (Alder and van Kuijk, 2009). We conducted our research in two parts of Guyana, each representing a different ecoregion; A forest ecoregion in the north of the country and a savannah ecoregion in the south (Fig. 1), part of the 'Rio Branco-Rupununi savannah', which is part of the wider Amazon system (Barbosa et al., 2005; Myers, 1936; Naka et al., 2006; Robbins et al., 2004). In each ecoregion, three sites of human settlements along levels of low to higher intensity of human settlement were surveyed, characterised by different levels of population and corresponding density of buildings (Table 1). Building densities (buildings per square km) and population densities (population per square km) for these locations were calculated in ArcGIS Pro (v2.8.0) using population data from Florczyk et al. (2019) and Guyana Bureau of Statistics (2012) (Imagery source and year: Esri, Maxar, Earthstar Geographics and the GIS User Community 2021).

Study sites from the forest ecoregion were all settlements in areas that historically replaced forests, and are now on the edge of forest (primary and secondary forest). Savannah ecoregion study sites were settlements in areas that were historically grasslands, and are now all bordered by savannah and some 'bush-islands' (isolated, usually small low forest patches) (Fig. 1). Study sites in both ecoregions had differing levels of human settlement, but in each, we sampled their respective largest and smallest human settlements. The forest ecoregion (north) comprised a city, a town and a village while the savannah (south) ecoregion comprised a town, a large village and a small village. This is evidenced by the larger population and building density in the forest (north) than in savannah (south) ecoregion (see below). Therefore, we sampled different relative levels of human settlement within each ecoregion based on building and population densities: 'high', 'medium' and 'low' forest human settlement level and 'high', 'medium' and 'low' savannah human settlement level. Although we acknowledge the differences in population and building density between parallel settlement levels (e.g. high vs high) in the two ecoregions, we do not analyse such comparisons, and, sites were representative of levels of building and population densities in their respective ecoregion. Among our study sites, three were indigenous communities: Karrau located in the forest ecoregion, and Aishalton and Achawib situated in the savannah ecoregion.

The dominant habitats in the northern forest ecoregion, outside of human settlements, are rainforest, montane forest, swamp and marsh,

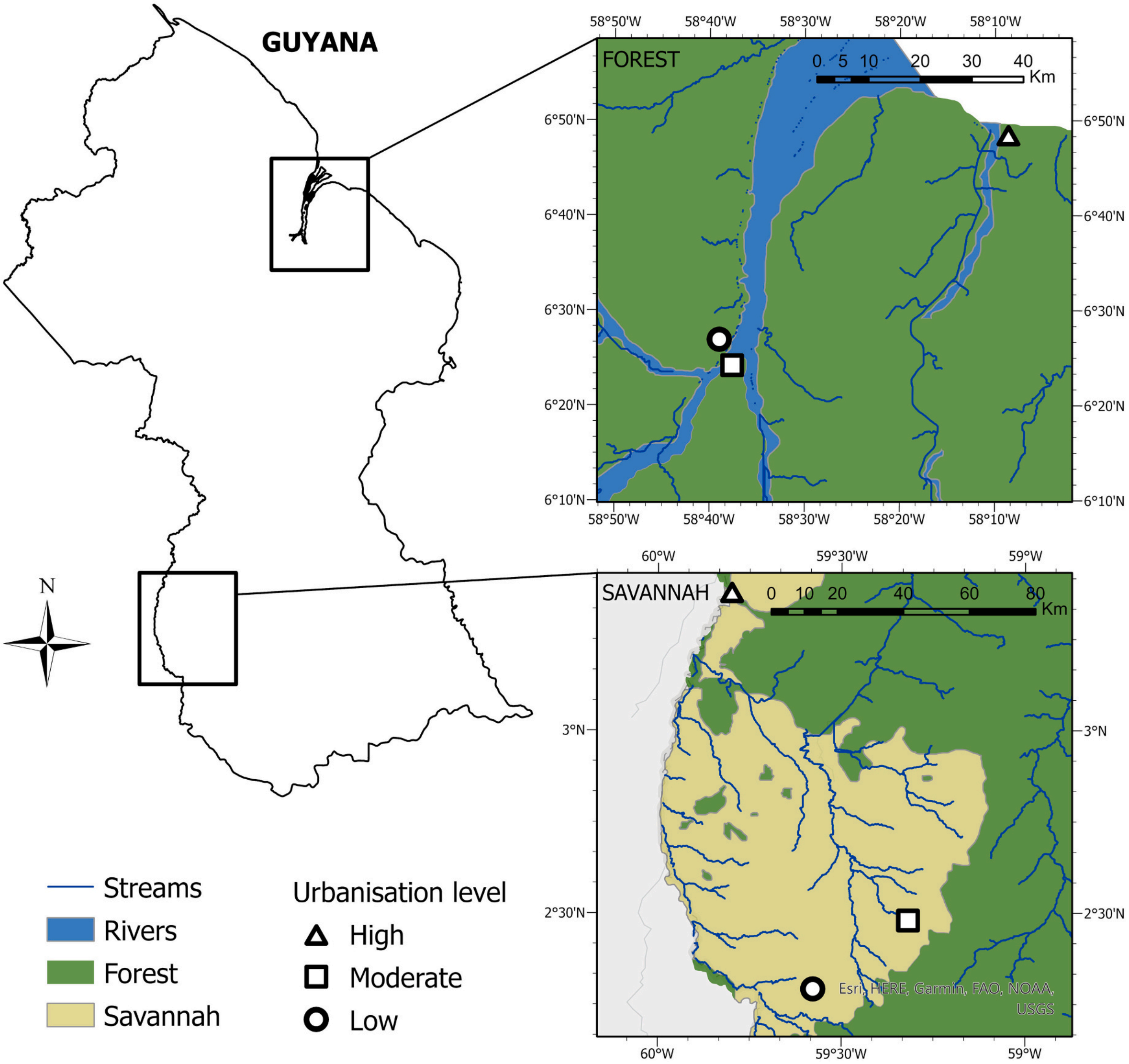

Fig. 1. Study area - Guyana, South America. Location of sample sites in the forest (upper right image) and savannah (lower right image) ecoregions. Shapes indicate sample sites and level of human settlement: triangle (high), medium (square) and low (circle). Rivers (blue areas), forest/secondary forest (dark green areas), and savannah (light olivine) habitats are shaded. Locations of points within each area are shown in Figs. S2 & S3.

Table 1
Characteristics of study settlements sites across the two study ecoregions, along with the building and population density of each settlement in Guyana.

Ecoregion	Settlement	Human settlement level	Number of point counts	Dominant edge habitats	Pop. size	Human pop. Density (/km^2)	Building density (build/km$^{2)}$
Forest (north)	Karrau	Low	18	LF, RI, HU	141	141.0	136.5
	Bartica	Medium	36	LF, RI, HU	7201	2400.1	805.6
	Georgetown	High	76	SF, RI, MA, HU	118,363	3818.2	1094.8
Savannah (south)	Achawib	Low	40	SV, RI, SC, HU	596	85.1	31.5
	Aishalton	Medium	40	SV, RI, SC, HU	1069	267.3	109.8
	Lethem	High	40	SV, RI, SC, HU	7402	2467.3	331.7

LF, lowland forest; SF, secondary forest; RI; riverine habitats (including riparian forest); HU, human altered habitats; MA, marine habitats; SV, savanna grasslands; SC, scrub habitats.

second-growth forest, riverine habitats and human altered habitats such as agricultural areas (including commercial rice and sugarcane) and artisanal gold mines. The southern savannah ecoregion is dominated by natural grasslands, riparian forests, bush islands, wetlands, scrub habitats, cattle ranches and cultivated lands comprising primarily cassava (*Manihot* sp.), sugarcane, peppers and citrus fruits in a rotational multi-crop farming system, most of which is small scale subsistence. Primary habitats in the forest and savannah ecoregions possess differing bird richness and community composition, however, our study concentrated on the avian communities associated with human settlements, rather than primary habitats.

2.2. Bird surveys

We quantified the bird community of each study site via point counts, conducted by two researchers. We quantified the bird community of each study site via point counts, conducted by two researchers. Point-count locations were determined randomly by digitally overlaying a 200 m × 200 m grid over each settlement via GIS, and then using a random number generator to select points. If a point was inaccessible, (e.g., it was private property and permission to survey was not granted, it was covered by a building or fenced off), it was replaced with another from the random sample. All point count locations were at least 200 m apart from one another to ensure independence (Pendleton, 1995). Additionally, to mitigate potential edge effects, all point count locations were situated at least 100 m away from the surrounding natural areas (e.g. forests, rivers, or savannahs). Due to the small size of the majority of settlements surveyed, we were limited in the number of point counts that could be conducted without compromising the independence of point counts (200 m apart). Therefore, the number of point count locations in each settlement was related with the size of the settlement. Forest sites were confined by peripheral habitats, whereas savannah areas were more open, and settlements were of similar size. When trying to get a good estimate of a bird community in small areas, counts should be repeated (Ralph et al., 1995). Therefore, each point count was replicated on a different day no fewer than three days apart, with the exception of one settlement, the 'High' level human settlement in the forest (north) ecoregion (Georgetown), which was much larger than the other five settlements. Therefore, in order to capture an accurate representation of its bird community, point counts were only carried out once, but across more locations than at the other settlements (see summaries in Table 1).

Each point count was conducted on a clear day between 05:30 and 08:30 (Verner and Ritter, 1986). All birds seen or heard within the 50 m radius were recorded during a 15-min interval. Although this duration may introduce the possibility of double counting, as noted in Fuller and Langslow (1984), longer point counts offer several advantages, particularly in highly species rich tropical landscapes (Sutherland, 2006) as in the Guianas. Longer counts can enhance the detection of inconspicuous birds, improve the recording of sensitive species (Fuller and Langslow, 1984), and allow observers more time for careful observation and documentation. Given the high species richness of the region under study, we deemed it crucial to allocate a sufficient duration of 15-min to accurately capture the diverse range of species inhabiting the area. We used limited-radius point counts to ensure that all birds recorded were actively using the surveyed area, and to maintain a consistent sampled area for each point count. If birds were interacting with the habitat, or flying within 25 m of the highest vegetation or built structure within the 50 m radius, they were recorded (Huff, 2000). Any individuals flying above this height threshold were not noted as they were deemed flyovers and not associated with the point being surveyed. Our bird taxonomy follows Remsen Jr et al. (2012).

2.3. Habitat characteristics

At each sample site, we measured habitat characteristics at two local spatial scales: 50 m and 200 m. At the 50 m point level, we measured the percentage (%) ground cover of impervious surface variables and vegetation variables (matching that of each point count survey – see below) by visually estimated ground cover of each variable in bands of 10 % within a 50 m radius of the point count. Impervious surfaces were roads, pavements and buildings and we collectively classified these as 'greyspace' consistent with much of the urban ecology literature, and as in Hayes et al. (2020), which was conducted in Guyana's capital, Georgetown. Vegetation variables included trees, shrubs and grass and we collectively classified these as 'greenspace' (for further details see Table S1). To assess the influence of wider local-scale features we quantified building density surrounding each point count within 200 m (following Amaya-Espinel et al., 2019) of the point, and converted this to km^2. We used satellite imagery and ArcGIS Pro at a 30 m^2 resolution (Imagery source and year: Esri, Maxar, Earthstar Geographics and the GIS User Community 2021). All satellite data coincide with the year of bird sampling.

2.4. Statistical analyses

2.4.1. Species accumulation curves

To investigate whether the level of sampling effort represented the bird communities of each settlement surveyed we made species accumulation curves with 95 % confidence intervals. Error was measured using the CHAO1 function (Chao, 1984) in EstimateS 9.1.0, which calculates true estimated species diversity based on the number of rare species found in a sample (Colwell, 2006).

2.4.2. Effect of human settlements on bird community attributes

Where we surveyed the same point on two occasions, we calculated mean detection for each species across the two counts. In the forest and savannah separately, we plotted box plots of species richness and abundance for each level of settlement, and compared these for statistical differences using non-parametric Kruskal-Wallis tests to explore differences (Rohlf and Sokal, 1981).

To perform a preliminary comparison of bird communities between different levels of human settlement in both ecoregions, we conducted non-metric multi-dimensional scaling (NMDS; Shepard, 1962) from

Bray–Curtis dissimilarity coefficients of the number of detections per species in each point-count location. To conduct the NMDS, we firstly log10 transformed the point count data, as is standard practice when conducting community and ordination analyses (McCune and Grace, 2002; Suarez-Rubio et al., 2011). The NMDS was conducted in PC-ORD v6.0 (McCune and Mefford, 1999). A final ordination of minimum stress on two axes was generated through a random starting configuration of 500 iterations, divided into 250 runs of both randomised and real data for both study ecoregions. To determine if the bird communities were statistically different, we applied a multi-response permutations procedure of Euclidean distances in PC-ORD v6.0 (MRPP; McCune and Grace, 2002) between the number of detections per species in each level. The analysis was repeated three times: initially with the entire assemblage included in the dataset, secondly with species removed if they only occurred once and with species removed if they occurred twice or less. As all three approaches gave consistent results, we report results for the entire assemblage.

2.4.3. *Indicator species*

Indicator species analyses (IndVal) in PC-ORD were used to identify species that typify the bird communities associated with different levels of human settlement, following the method described in Dufrêne and Legendre, (1997). An indicator value was assigned to each species as a result of a random reallocation process (4999 permutations), and then these were tested for significance using a Monte Carlo procedure, with species considered indicators if this was significant ($p < 0.05$). High indicator values (%) reflect both high abundance and prevalence within a human settlement level; p-values represent the probability of a similar observation relative to a randomised dataset. To be characteristic of a certain human settlement level, a species has to be found consistently and almost exclusively within that type. Therefore, only bird species with an IndVal value of over 20 % and a p value <0.05 were considered as indicator species for each human settlement level (Della Rocca et al., 2014). Species that occurred in all human settlement levels were excluded from the analysis, as they are considered ubiquitous.

2.4.4. *Urban tolerance analysis*

Considering the spatial and temporal frequency of species observations in both ecoregions, we grouped species into three urban tolerance groups; 'urban dwellers', 'urban utilisers' and 'urban avoiders'. To do so we adopted the classification system proposed by Fischer et al. (2015), which is based on variations in the population dynamics of wildlife in natural and urbanised environments. This categorisation method allowed for the assignment of species to different tolerance groups depending on their ability to cope with the impacts of urban development. Therefore, in our data, the 'urban dweller' group was comprised of species which occurred in high urban areas, 'urban utilisers' were species occurring in medium urban areas, but not observed in high urban areas, and 'urban avoiders' were species observed in low urban areas only.

To assess the influence of habitat variables on our different tolerance groups we used Generalised Additive Models (GAMs) and Zero-Inflated Generalised Additive Models (ZIGAMs) to study associations between the pattern of bird species richness and abundances (response variables) of each tolerance group, with point level environmental and 200 m level characteristics (predictor variables) in both ecoregions. We assessed the relationship of greenspace, greyspace and building density with the richness and abundance of each tolerance group. All three predictor variables were used in each model. GAMs were used to model species dwellers, while ZIGAMs were employed for urban avoiders and utilisers to account for excess zeros in the data. GAMs and ZIGAMs were chosen based on the characteristics of our data and research objectives. GAMs are suitable for capturing nonlinear or complex relationships between variables, while ZIGAMs handle excess zeros commonly observed in species abundance data. A Gamma distribution was used for all models, which is suitable for modelling continuous positive response variables with right-skewed distributions. We also incorporated settlement category, sampling effort (to account for differences in sampling effort in the forest ecoregion), and latitude and longitude (to account for the potential non-independence of sites) as random effects in our models, to control for the potential influence of these variables (see Table S5).

We drew Locally Optimised Scatterplot Smoothing (LOESS) trendlines between group richness and abundance vs greenspace, greyspace and building density. LOESS lines allowed us to capture potential nonlinear associations, as species richness tends to level off. These analyses were repeated two times: first with the entire assemblage included in the dataset, and second with species removed if they only occurred once. Both approaches gave consistent results and, therefore, the results are reported for the entire assemblage. To evaluate the fit of our final models, we used the goodness-of-fit measure according to the lowest Akaike Information Criterion (AIC).

3. Results

3.1. *Bird communities*

Overall, we recorded 6543 birds from 172 species during our surveys in human settlements across Guyana, representing 21 % of the country's total avian species (Braun et al., 2007). In the forest ecoregion, we observed 3730 birds from 117 species across 130 point count locations, while 2813 birds from 121 species across 120 point count locations were recorded in the savannah ecoregion. Overall species accumulation curves for both ecoregions approached an asymptote and observed species richness overlapped with estimated species richness confidence intervals (95 %), indicating our sampling effort was adequate (Fig. A.1). Species richness and abundances of birds varied across levels of human settlement in both ecoregions (Fig. 2).

In the forest ecoregion, bird communities from high and medium levels of human settlement were similar and both had higher mean species richness and abundances than that of the bird community at the low level of human settlement (Fig. 2, Table S2). However, Kruskal-Wallis tests indicated that only medium and low levels differed significantly in abundance ($p = 0.01$), and no communities had significant differences in species richness (Table S3). The bird community from the medium level of human settlement in the savannah ecoregion had the highest mean species richness, significantly larger than the high ($p < 0.005$) and low ($p = 0.021$) levels. The bird community in the highest and medium levels of human settlement had the highest mean bird abundances, both significantly larger than the bird community from the low level of human settlement in the savannah ecoregion ($p < 0.001$).

3.2. *Community differences*

The 2-dimensional NMDS ordination with minimal stress accounted for 85 % (forest ecoregion) and 86 % (savannah ecoregion) of the variability in the bird detection data (Fig. 3). Multi-response permutation procedures (MRPP) showed that differences in overall communities between ecoregions was significant (MRPP, $T = -65.94$, $P < 0.001$). Also, by overall comparison between human settlement levels in both ecoregions, we found significant differences in bird community composition, with greater differences in the forest ecoregion (MRPP, $T = -33.68$, $P < 0.001$) over the savannah (MRPP, $T = -19.27$, $P < 0.001$) (Table S3). By pairwise comparison, all the pairs of human settlement levels showed significant differences (MRPP, $P < 0.001$) in both ecoregions.

3.3. *Indicator species analysis*

The forest ecoregion had a total of 16 indicator species, with six, one and seven species from the low, medium and high levels of human settlement respectively (Table 2). There were 21 in the savannah ecoregion and each level of human settlement had at least four indicator species.

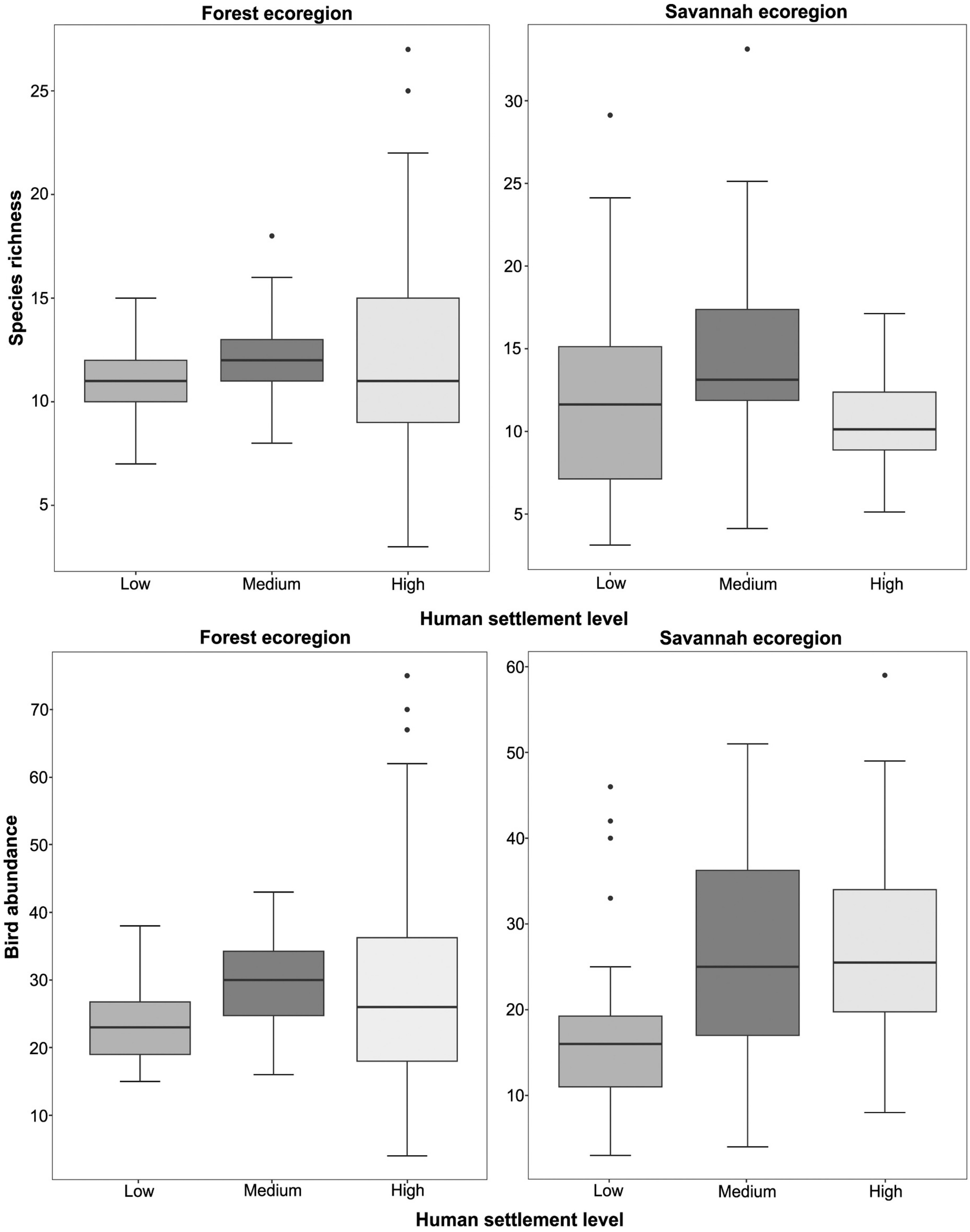

Fig. 2. Boxplots of bird species richness (upper panels) and abundances (lower panels) observed from point count surveys for three levels of human settlement size across two ecoregions (forest – left panels; and savannah – right panels) in Guyana.

Indicators of high human settlement in the savannah ecoregion included the saffron finch (*Sicalis flaveola*), black vulture (*Coragyps atratus*) *and* ruddy ground dove (*Columbina talpacoti*), while the grassland sparrow (*Ammodramus humeralis*) and plumbeous seedeater (*Sporophila plumbea)* were indicators of a low level of human settlement in the region. High levels of human settlement in the forest ecoregion had indicator species including the rock dove (*Columba livia*), carib grackle (*Quiscalus lugubris*) and tropical kingbird (*Tyrannus melancholicus*). Indicator species of a low level of human settlement from the forest ecoregion included the giant cowbird (*Molothrus oryzivorus*), white-throated toucan (*Ramphastos tucanas),* yellow-rumped cacique (*Cacicus cela*) and crested oropendola (*Psarocolius decumanus*).

3.4. Urban tolerance analysis

Based on the classification employed in this study, the urban

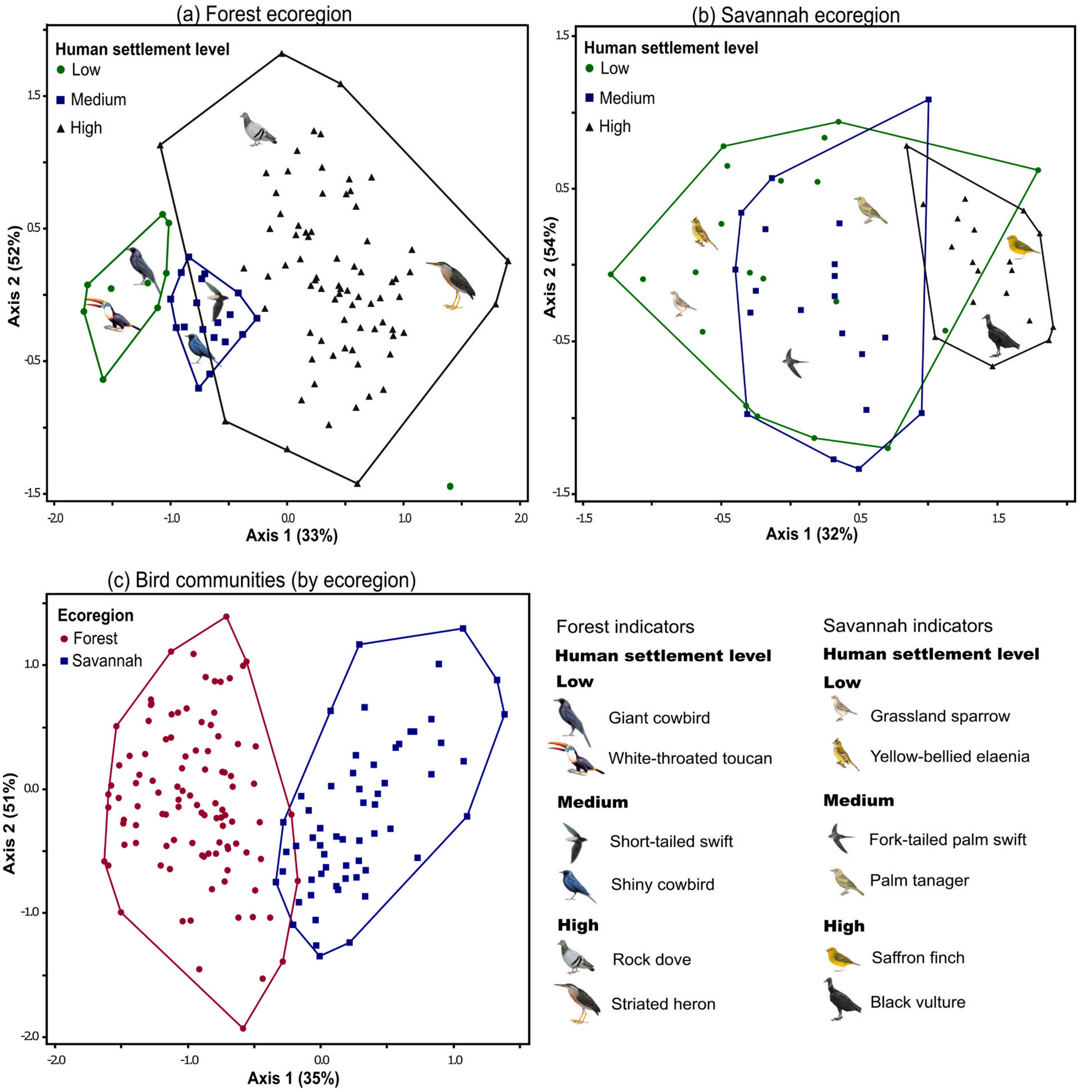

Fig. 3. Non-metric multi-dimensional scaling (NMDS) ordination of bird species community composition based on all 117 species from a forest ecoregion (a) and 121 species from a savannah ecoregion (b) detected across three levels or human settlement intensity in Guyana, South America. NMDS of total bird communities from two ecoregions based on 172 species (c). All bird communities were significantly different (MRPP $p < 0.001$; Table S3). In (a) and (b) bird images show the species with the highest indicator values (IndVal) within each human settlement level.

tolerance of birds exhibited similarities in both ecoregions while also showing variations across tolerance categories and levels of human settlement intensity (Fig. 4). In the forest ecoregion, the bird community at the low level of human settlement had a lower proportion of urban dwellers and a higher proportion of urban avoiders than the low urban bird community of the savannah ecoregion. However, in medium sized settlements, urban dweller and urban utiliser species in the savannah ecoregion were almost equal in species richness, while urban dwellers were more common at the medium level in the forest ecoregion.

After accounting for the potential random effects of survey effort, point location and settlement level, local habitat variables were important for some subsets of bird richness and abundance (Figs. 5 & 6, Table S4 & S5). Across the whole forest ecoregion bird community (all species in all tolerance groups combined), we found a significant negative effect of building density and greyspace on the richness and abundance, while in the savannah, only building density was positively related only to abundance.

When breaking down by tolerance groups, in the forest ecoregion, we found a significant negative effect of building density on abundance of urban avoiders ($n = 15$) and utilisers ($n = 19$), as well as utiliser richness indicating that higher building densities have negative impacts on these populations (Figs. 5 & 6, Table S4). While, building density had a positive effect on urban dweller ($n = 81$) abundance. Greyspace also had a negative relationship with utiliser richness and abundance. In contrast, in the savannah ecoregion, building density had a positive effect on avoider ($n = 15$) species richness, and utiliser ($n = 44$) and dweller ($n = 62$) abundance, and increasing amounts of greenspace had a positive impact on the richness of utiliser and avoider species, while greyspace had a negative effect on the abundances and richness of avoiders (Figs. 5 & 6, Table S4).

Table 2
Indicator species for different levels of human settlement forest ecoregion and a savannah ecoregion determined using IndVal (Dufrêne and Legendre, 1997).

Species	English name	Human settlement level	Indicator value	p-value
Forest				
Molothrus oryzivorus	Giant cowbird	Low	62.3	0.0002
Ramphastos tucanus	White-throated toucan	Low	44.4	0.0002
Ramphocelus carbo	Silver-beaked tanager	Low	44.1	0.0108
Cacicus cela	Yellow rumped cacique	Low	34.1	0.0116
Psarocolius decumanus	Crested oropendola	Low	33.3	0.0002
Tachornis squamata	Fork-tailed palm swift	Low	28.2	0.0106
Euphonia violacea	Violaceous euphonia	Low	24.1	0.0038
Molothrus bonariensis	Shiny cowbird	Medium	76.1	0.0002
Chaetura brachyura	Short-tailed swift	Medium	47.8	0.002
Thraupis episcopus	Blue-gray tanager	Medium	43	0.01
Troglodytes aedon	House wren	Medium	42.6	0.006
Pitangus sulphuratus	Great kiskadee	Medium	38.8	0.0322
Butorides striata	Striated heron	High	53	0.0002
Colomba livia	Rock dove	High	51.5	0.0002
Tyrannus melancholicus	Tropical kingbird	High	35.3	0.0024
Quiscalus lugubris	Carib grackle	High	31.6	0.0012
Savannah				
Ammodramus humeralis	Grassland sparrow	Low	46.5	0.0002
Elaenia flavogaster	Yellow-bellied elaenia	Low	37.7	0.0108
Sturnella magna	Eastern meadowlark	Low	34.2	0.0032
Sporophila plumbea	Plumbeous seedeater	Low	33.6	0.0036
Zenaida auriculata	Eared dove	Low	30.5	0.0264
Pyrocephalus obscurus	Vermilion flycatcher	Low	25	0.0106
Tachornis squamata	Fork-tailed palm swift	Medium	63.2	0.0002
Thraupis palmarum	Palm tanager	Medium	42.7	0.0062
Troglodytes aedon	House wren	Medium	40.5	0.0024
Vireo olivaceus	Red-eyed vireo	Medium	35.1	0.0018
Ramphocelus carbo	Silver-beaked tanager	Medium	30	0.012
Sicalis flaveola	Saffron finch	High	70.1	0.0002
Coragyps atratus	Black vulture	High	57.6	0.0002
Cathartes burrovianus	Lesser yellow-headed vulture	High	48.5	0.0002
Tyrannus melancholicus	Tropical kingbird	High	44.1	0.0028
Pitangus sulphuratus	Great kiskadee	High	41.9	0.008
Columbina talpacoti	Ruddy ground dove	High	41.6	0.0002
Thraupis episcopus	Blue-gray tanager	High	40.5	0.012
Rupornis magnirostris	Roadside hawk	High	28	0.0082
Cathartes melambrotus	Greater yellow-headed vulture	High	26	0.0132
Columba livia	Rock dove	High	25	0.0072

4. Discussion

In the absence of urban type disturbance, structurally complex forest systems may intrinsically have higher species richness compared to savannah systems. However, our comparative study in northern Amazonia shows that the impact of human settlements on avian communities varies among ecoregions, indicating that species evolved to live in a savannah may be more tolerant to human settlements than those more evolved to a forest system. In the savannah ecoregion, many species seem to benefit from urban development, while in the forest ecoregion, the most urban-tolerant species may still benefit, but less tolerant species face negative impacts from urban development.

4.1. Changes in avian community structure

Most of our knowledge on the impacts of human settlements on avian communities derives from single ecoregion studies (Leveau et al., 2017). However, because we sampled two regions, we were able to reveal that, as expected, in the forest ecoregion, variation in bird communities between human settlement levels was greater. This suggests the loss of habitat heterogeneity in forest ecoregions due to human settlement may be steeper than in savannah grasslands, where intermediate levels of urbanisation may be composed by more vegetation layers (lawn, shrubs, and trees) than grassland (Leveau and Leveau, 2005). However, despite this difference, the results of our study confirm that the composition of species can undergo significant changes during the human settlement process in both forest and savannah ecoregions (Blair, 1996; Sol et al., 2014; Symes et al., 2017).

Driving changes in community composition between levels of human settlement in the savannah ecoregion, as revealed by indicator value analysis, native grassland specialists such as grassland sparrow (*Ammodramus humeralis*) and eastern meadowlark (*Sturnella magna)* become more dominant at the low level of human settlement. Both ground-nesters, higher predation may prevent this species from adapting to more developed areas (Colombo et al., 2021; Hovick and Miller, 2016). Unsurprisingly, generalist birds such as the native ruddy-ground dove, saffron finch and non-native rock dove (*Colomba livia*) were indicative of high levels of human settlement in the savannah ecoregion (Abilhoa and Amorin, 2017; de Toledo et al., 2012). Additionally, human settlements can provide optimal environments for large scavengers that exploit refuse (Chamberlain et al., 2017). Our data confirms this, identifying the lesser yellow-headed vulture (*Cathartes burrovianus),* black vulture *(Coragyps atratus)* and greater yellow-headed vulture *(Cathartes melambrotus)* as an indicator species for high levels of human settlement in the savannah.

Swifts were indicators of medium levels of human settlement in both ecoregions, potentially taking advantage of increased nesting opportunities provided through building construction (short-tailed swift; forest ecoregion) and planting of trees (fork-tailed palm swift; savannah ecoregion) typical of emerging urban development (Biancalana, 2018; Collins and Thomas, 2012). Indicators of low human settlement intensity in the forest ecoregion were species such as the giant cowbird (*Molothrus oryzivorus*), crested oropendola (*Psarocolius decumanus*), and white-throated toucan (*Ramphastos tucanus*). These species feed on a wide range of insects, fruits, seeds, and flowers of large canopy trees, and our results suggest low levels of urban encroachment and proximity to native forest may meet their habitat requirements in forested areas (Fahrig, 2003; Zapata and Robledano, 2014).

Several urban avian studies have demonstrated the impact of human settlement on bird richness and abundance (McKinney, 2008; Ortega-Álvarez and MacGregor-Fors, 2011). Generally, settlements have fewer bird species, but higher abundances compared to surrounding ecosystems. Consistent with the consensus in previous research, we found that bird abundance was greatest at medium and high levels of human settlement in both ecoregions (Chace and Walsh, 2006; Faeth et al., 2012; Njoroge, 2014).

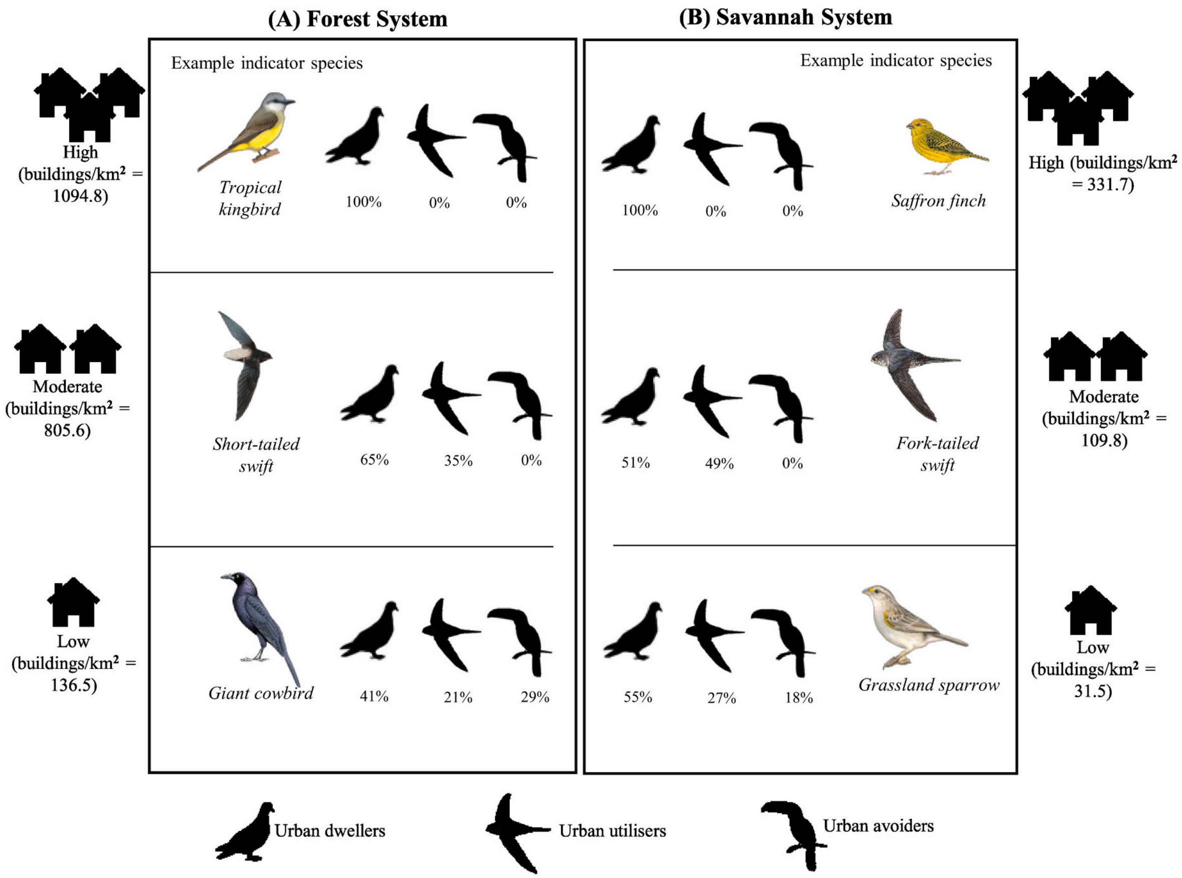

Fig. 4. The proportion of avian urban dwellers, utilisers and avoiders in two northern Amazonia ecoregions; forest ecoregion (A.) and savannah ecoregion (B.) for three levels of human settlement surveyed in Guyana. Indicator species were present for all levels of human settlement in both ecoregions.

Bird species richness is influenced by vegetation abundance and habitat heterogeneity, and the highest diversity of species is typically found in moderately disturbed habitats, rather than in the most natural habitats (Blair, 1996; Marzluff, 2001; McKinney, 2002; Natuhara and Imai, 1996; Reynaud and Thioulouse, 2000; Tratalos et al., 2007b). Our findings demonstrate a similar trend in both ecoregions, with areas of medium human settlement showing statistically higher species richness, particularly in the savannah ecoregion. Although species richness was highest in the medium level of human settlement in the forest ecoregion, this difference was not significant. Our findings support the idea that avian richness peaks in areas with intermediate levels of human settlement, which differs from previous studies that suggest urban intensity has a negative relationship with bird richness (Blair, 1996; Lepczyk et al., 2008; Tratalos et al., 2007a). The mechanisms that may cause these patterns are diverse. Landscape changes that occur during moderate levels of development can increase the diversity and abundance of resources available for birds by altering the plant community through crop cultivation and introducing ornamentals, changing vegetation structure (Smith et al., 2010). Moderate urban development can also increase the structural diversity of the ecosystem making them more heterogeneous in form. This occurs through the introduction of infrastructure such as buildings and electricity poles, which may provide sites for nesting and perching. Consequently, this can benefit various groups of birds, including habitat generalist species and native habitat specialist species (Blair, 1996; Mainwaring, 2015; Marzluff, 2001).

4.2. *The effects of site-level and landscape variables on urban tolerance groups*

We assessed several environmental variables with regard to bird abundance, species richness and urban tolerance. It is known that urban habitat features affect urban avian species both positively and negatively (Chace and Walsh, 2006; Evans et al., 2009; Ortega-Álvarez and MacGregor-Fors, 2009) and according to our study this differs depending on the surrounding ecoregion and, according to the classification used in this study, the urban tolerance of a species.

Species' responses to environmental changes can be complex, species-specific, and locality dependent. Our prediction of a positive relationship between urban tolerant bird species and built structures was upheld in the forest ecoregion, as we observed a positive effect of building density on urban dwellers. Notably, building density also had a positive impact on all tolerance groups in the savannah ecoregion. However, in the forest ecoregion, we observed a negative effect of building density on utilisers and avoiders, likely attributed to the loss of structural complexity and shelter provided by the forest as a result of urban development. Additionally, negative impacts on these less urban tolerant birds could be attributed to pollution, anthropogenic disturbance, lack of resources, and unsuitable habitat conditions, as well as higher predation risk in built-up areas (Alberti, 2005; Fischer et al., 2015; Sorace, 2002).

In the savannah ecoregion our data suggests all tolerance groups are potentially benefiting from new breeding sites and food resources provided by built environments, such as the construction of new houses in human settlements (Blair, 1996; Chace and Walsh, 2006; Luniak, 2004; Sushinsky et al., 2013; Tomasevic and Marzluff, 2017; Tryjanowski et al., 2020), while negatively impacting avoiders and utilisers in the forest ecoregion, supporting our prediction that urban tolerance is potentially higher in the savannah ecoregion. However, less urban adapted species may also depend on greenspaces in urban areas for shelter and foraging opportunities (Fernández-Juricic and Jokimäki,

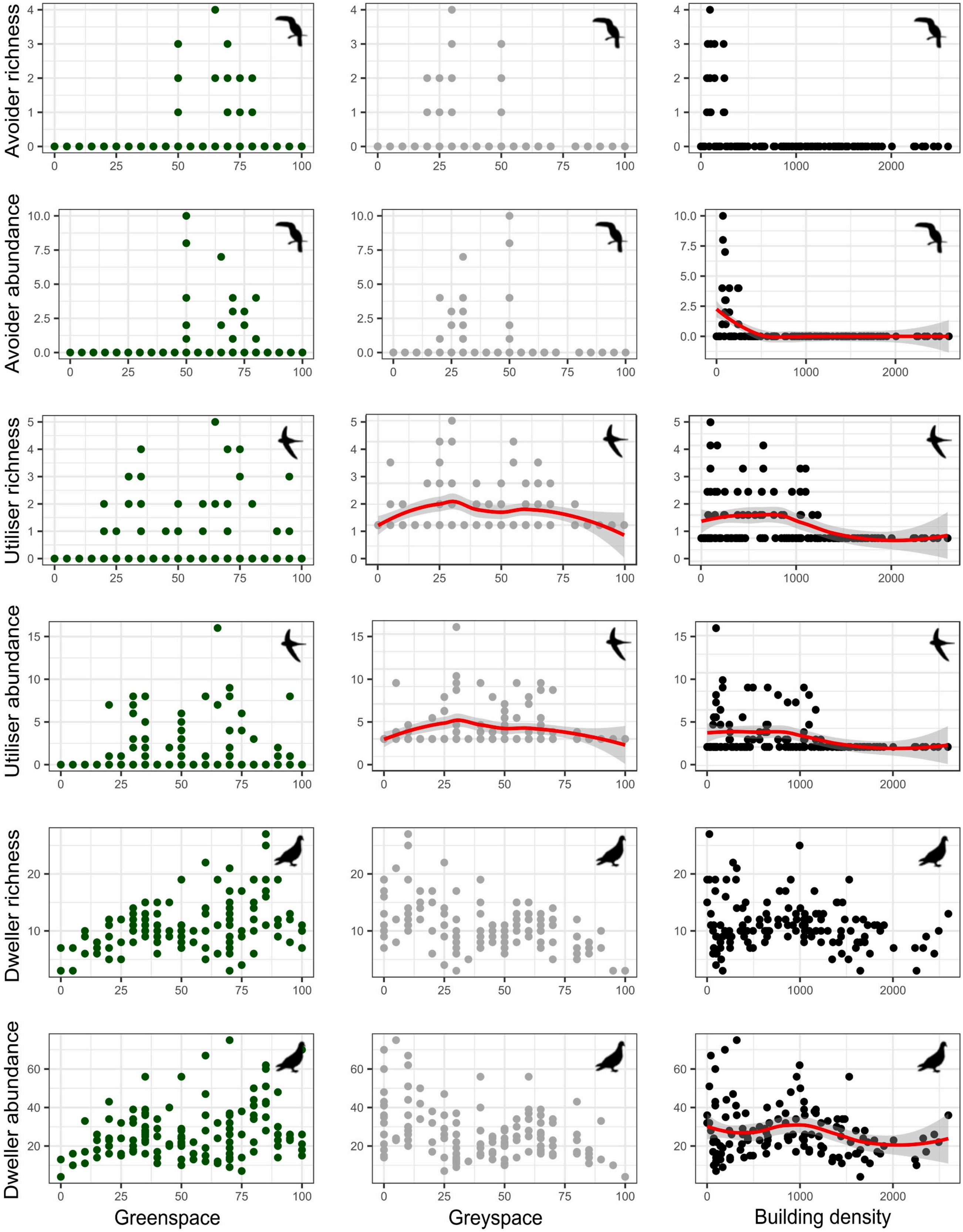

Fig. 5. Forest Ecoregion. Multiple bivariate scatter plots and LOESS lines between urban dweller, utiliser and avoider species richness or bird abundance and the point level habitat characteristics within 50 m (greyspace and greenspace ground cover) and 200 m width buffers (building density) in a forest ecoregion in Guyana, South America. Points represent the number of point count locations in each ecoregion. Red lines represent statistically significant relationships. Shaded areas represent confidence intervals.

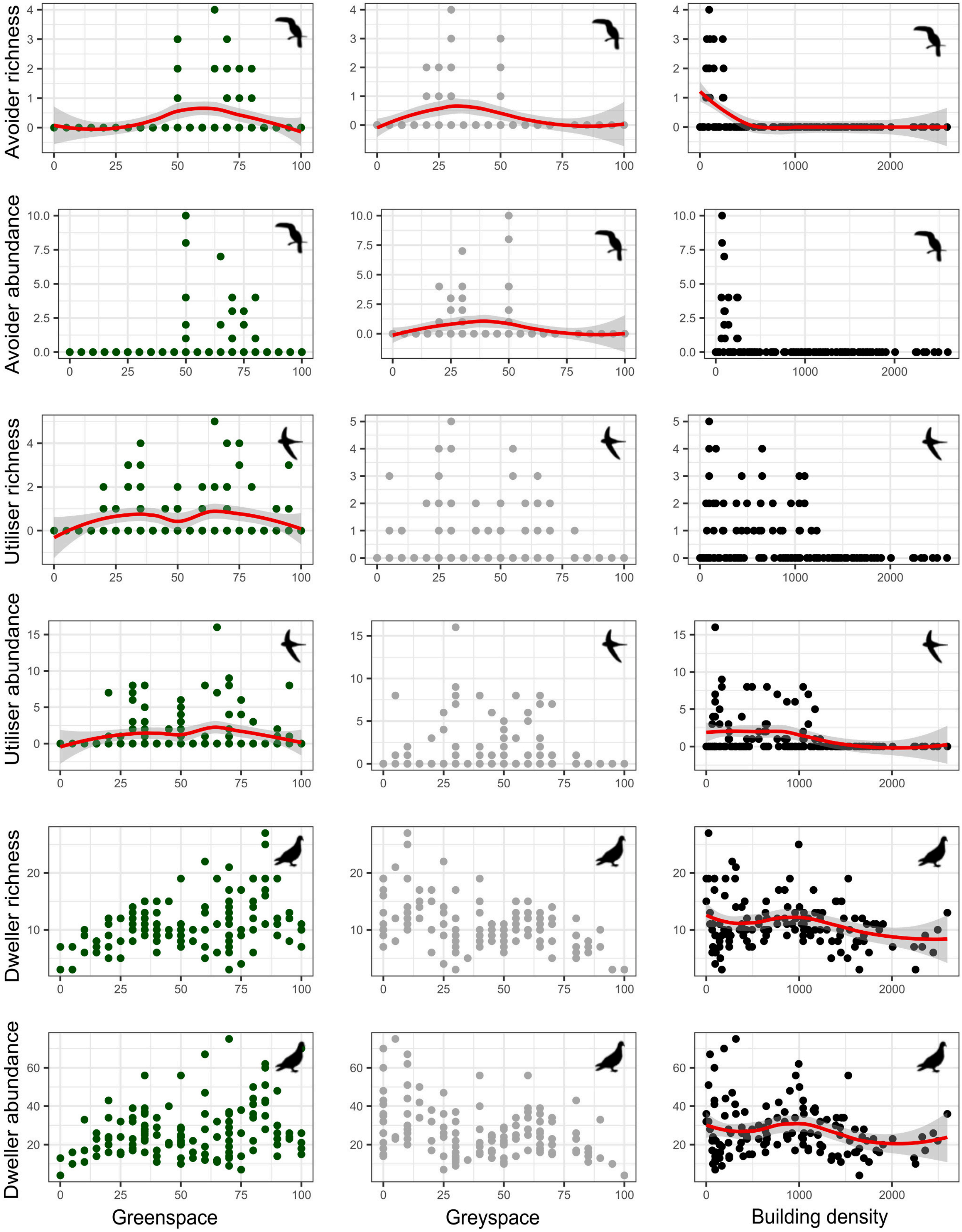

Fig. 6. Savannah Ecoregion. Multiple bivariate scatter plots and LOESS lines between urban dweller, utiliser and avoider species richness or bird abundance and the point level habitat characteristics within 50 m (greyspace and greenspace ground cover) and 200 m width buffers (building density) in a savannah ecoregion in Guyana, South America. Points represent the number of point count locations in each ecoregion. Red lines represent statistically significant relationships. Shaded areas represent confidence intervals.

2001; Máthé and Batáry, 2015). Our study confirms this in savannah grasslands, as urban avoider and utiliser communities in had a positive relationship with greenspace coverage, suggesting that greenspaces act as a refuge for some less tolerant species in urban areas, emphasising the importance of a heterogeneous landscape with areas of native vegetation for their survival in human landscapes (McKinney, 2002). Other studies have reported similar patterns for urban bird species worldwide (Chamberlain et al., 2007; Chang et al., 2017; Chang and Lee, 2016; Ferenc et al., 2016; Imai and Nakashizuka, 2010; Jokimäki, 1999).

4.3. Concepts and methodological considerations

Native species exhibit varying degrees of flexibility in their tolerance to human activity in urban environments, which may differ geographically (Litteral and Shochat, 2017). Although species typically show consistency in their response to human settlements, some species can be classified as urban tolerant in one area and urban intolerant in another (Sol et al., 2014). For instance, in our study, some species previously categorised as urban intolerant in Brazil (Abilhoa and Amorin, 2017) were found to be abundant in one or both of our highly urbanised settlements, and thus classified as urban dwellers in this study. The difference is likely due to the density of each species in the surrounding region, as some species may be too scarce to generate propagules. However, bird sampling over large regions is time-consuming and costly, resulting in scarce information on avian urban tolerance in the northern Amazon (Sol et al., 2020). Therefore, a more general measure of urban tolerance may enhance our comprehension of avian responses to human settlement in the Neotropics such as flight initiation distance, as highlighted by Mikula et al. (2023).

In this study, we applied the urban tolerance categories proposed by Fischer et al. (2015). The lowest levels of human settlement intensity in both ecoregions were characterised by predominantly natural habitats, surrounded by extensive undisturbed areas. This setting allowed us to include bird species classified as “avoiders,” which show a preference for undisturbed environments and are less likely to occur in moderately or highly urbanised areas. Our classification of bird species as “urban avoiders” aligns with Fischer et al.’s (2015) definition, as they are typically absent in developed areas but may persist in natural patches within urban landscapes. Fischer et al. (2015) emphasise that conserving urban avoiders in human settlements depends on factors like the size, shape, number, configuration, quality, and connectivity of natural areas within the urban matrix. Our study aimed to assess the significance of various habitat features for urban avoiders in our study systems, providing valuable insights into this aspect of urban bird conservation.

Our study focused on the intensity of human settlement relative to the ecoregion under investigation. However, the potential effect of varying characteristics between the forested and savannah regions on our results merits consideration. Higher population and building density in the forested area may contribute to increased human activities and urban development, leading to more pronounced habitat alterations, pollution, and disturbances that could impact bird communities. In contrast, the lower population density in the savannah region may result in comparatively fewer human-induced disturbances and lower settlement levels, potentially influencing bird species’ responses and displaying higher tolerance towards human settlements, as our data suggests.

Our study design could introduce potential bias when comparing multiple points from one settlement in each category, per ecoregion. To address the potential confounding factors that this approach brings, we employed statistical methods that account for spatial dependencies. Additionally, detectability bias is a concern when analysing bird abundance, influenced by habitat-specific factors, as well as sampling methods (Anderson et al., 2015; Moore et al., 2004). To address this, we used standardised protocols with two experienced surveyors present at all point count stations.

4.4. Implications for conservation and urban planning

Despite limited published studies on urban bird communities in Guyana (Fisher et al., 2021; Hayes et al., 2020), our study provides clear evidence that urban greenspaces, in particular the savannah ecoregion, are vital habitats for a range of species. This is an important finding as there is a lack of studies on how greenspaces can benefit local avifauna in this rapidly developing part of Amazonia (Chace and Walsh, 2006; Myers, 2021). In order to maintain or improve wildlife communities in urban ecosystems urban planning can use this knowledge to consider the needs of wildlife communities in human settlements (Hostetler et al., 2011; Nilon et al., 2017). This would entail maintaining natural vegetation and interconnected green spaces linked via habitat corridors that may even be able to provide essential resources for species of conservation concern. Indeed, in our study notable species inhabiting greenspaces included the endemic blood-coloured woodpecker (*Veniliornis sanguineus*), and the IUCN Near Threatened bearded tachuri (*Polystictus pectoralis*) and eastern meadowlark (*Sturnella magna*) (IUCN, 2022; Rodrigues et al., 2018).

4.5. Conclusion

Comparative research, such as ours, is essential for recognising generalisable response patterns that help to define a broader ecology of human settlements in the Neotropics, and across the world. The larger variation in bird community composition in the forest ecoregion suggests human settlement is having a greater impact in the region, with some less tolerant species negatively affected by building density and built infrastructure. In contrast building density benefited almost all species in the savannah ecoregion. Our findings also indicate that the most abundant and common bird species in all settlements were native, accounting for over 20 % of Guyana’s total bird species. This highlights the potential for Neotropical human settlements to provide suitable habitats for high native bird diversity if managed effectively (Beninde et al., 2015).

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CRediT authorship contribution statement

William M. Hayes: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Brian J. O’Shea:** Conceptualization, Writing – review & editing. **Meshach A. Pierre:** Investigation. **Asaph Wilson:** Investigation. **Jake E. Bicknell:** Conceptualization, Methodology, Writing – review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.166535.

References

Abilhoa, V., Amorin, R., 2017. Effects of urbanization on the avian community in a southern Brazilian city. Rev. Bras. Ornitol. 25, 31–39.

Akubia, J.E., Ahmed, A., Bruns, A., 2020. Assessing how land-cover change associated with urbanisation affects ecological sustainability in the greater Accra metropolitan area, Ghana. Land 9, 182.

Alberti, M., 2005. The effects of urban patterns on ecosystem function. Int. Reg. Sci. Rev. 28, 168–192.

Alder, D., van Kuijk, M., 2009. A Baseline Assessment of Forest Carbon in Guyana. Unpublished Guyana Forestry Commission Report. www.bio-met.co.uk/pdf/gybasass09.pdf?PHPSESSID=96bf1c0f71526544339a4086ae77fa89.

Amaya-Espinel, J.D., Hostetler, M., Henriquez, C., Bonacic, C., 2019. The influence of building density on Neotropical bird communities found in small urban parks. Landsc. Urban Plan. 190, 103578.

Anderson, A.S., Marques, T.A., Shoo, L.P., Williams, S.E., 2015. Detectability in audio-visual surveys of tropical rainforest birds: the influence of species, weather and habitat characteristics. PLoS One 10, 0128464.

Anderson, S.H., Kelly, D., Robertson, A.W., Ladley, J.J., 2016. Pollination by Birds. Why Birds Matter Avian Ecol. Funct. Ecosyst, Serv, p. 73.

Aronson, M.F., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S., Nilon, C.H., Vargo, T., 2017. Biodiversity in the city: key challenges for urban green space management. Front. Ecol. Environ. 15, 189–196.

Barbosa, R.I., Souza, J.M.C., Xaud, H.A.M., 2005. Savanas de Roraima: referencial geográfico e histórico. Savanas Roraima Etnoecologia Biodiversidade E Potencialidades Agrosilvipastoris 11–19.

Basham, E.W., Baecher, J.A., Klinges, D.H., Scheffers, B.R., 2023. Vertical stratification patterns of tropical forest vertebrates: a meta-analysis. Biol. Rev. 98, 99–114.

Bass, M.S., Finer, M., Jenkins, C.N., Kreft, H., Cisneros-Heredia, D.F., McCracken, S.F., Pitman, N.C.A., English, P.H., Swing, K., Villa, G., Fiore, A.D., Voigt, C.C., Kunz, T. H., 2010. Global conservation significance of Ecuador's Yasuní National Park. PLoS One 5, 8767.

Beninde, J., Veith, M., Hochkirch, A., 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol. Lett. 18, 581–592.

Biancalana, R.N., 2018. Nesting association of swifts (Apodidae) and wasps in Brazil. Wilson J. Ornithol. 130, 992–996.

Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6, 506–519.

Braun, M.J., Finch, D.W., Robbins, M.B., 2007. A Field Checklist of the Birds of Guyana. Smithsonian Institution, Washington, DC, USA.

de Carvalho, W.D., Mustin, K., 2017. The highly threatened and little known Amazonian savannahs. Nat. Ecol. Evol. 1, 100.

Chace, J.F., Walsh, J.J., 2006. Urban effects on native avifauna: a review. Landsc. Urban Plan. 74, 46–69.

Chamberlain, D., Kibuule, M., Skeen, R., Pomeroy, D., 2017. Trends in bird species richness, abundance and biomass along a tropical urbanization gradient. Urban Ecosyst. 20, 629–638.

Chamberlain, D.E., Gough, S., Vaughan, H., Vickery, J.A., Appleton, G.F., 2007. Determinants of bird species richness in public green spaces. Bird Study 54, 87–97.

Chang, C.-R., Chien, H.-F., Shiu, H.-J., Ko, C.-J., Lee, P.-F., 2017. Multiscale heterogeneity within and beyond Taipei city greenspaces and their relationship with avian biodiversity. Landsc. Urban Plan. 157, 138–150.

Chang, H.-Y., Lee, Y.-F., 2016. Effects of area size, heterogeneity, isolation, and disturbances on urban park avifauna in a highly populated tropical city. Urban Ecosyst. 19, 257–274.

Chao, A., 1984. Nonparametric estimation of the number of classes in a population. Scand. J. Stat. 11, 265–270.

Collins, C.T., Thomas, B.T., 2012. Food habits of two fork-tailed swifts in Venezuela. Wilson J. Ornithol. 124, 152–157.

Colombo, M.A., Jauregui, A., Gonzalez, E., Segura, L.N., 2021. Nesting biology and nest survival of the grassland sparrow (Ammodramus humeralis) in grazed grasslands of Central-Eastern Argentina. Neotropical Biodivers. 7, 67–74.

Colwell, R.K., 2006. EstimateS: statistical estimation of species richness and shared species from simples, version 8.0. http://viceroy.eeb.uconn.edu/EstimateS.

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., 2000. Spatial patterns in the distribution of tropical tree species. Science 288, 1414–1418.

Croci, S., Butet, A., Clergeau, P., 2008. Does urbanization filter birds on the basis of their biological traits. Condor 110, 223–240.

Della Rocca, F., Stefanelli, S., Pasquaretta, C., Campanaro, A., Bogliani, G., 2014. Effect of deadwood management on saproxylic beetle richness in the floodplain forests of northern Italy: some measures for deadwood sustainable use. J. Insect Conserv. 18, 121–136.

Dorney, J.R., Guntenspergen, G.R., Keough, J.R., Stearns, F., 1984. Composition and structure of an urban woody plant community. Urban Ecol. 8, 69–90.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Evans, K.L., Newson, S.E., Gaston, K.J., 2009. Habitat influences on urban avian assemblages. Ibis 151, 19–39.

Faeth, S.H., Saari, S., Bang, C., July 2012. Urban Biodiversity: Patterns, Processes and Implications for Conservation. John Wiley & Sons, Ltd, Chichester, 10.1002/9780470015902.a0023572.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Ferenc, M., Sedláček, O., Mourková, J., Exnerová, A., Škopek, J., Formánek, J., Fuchs, R., 2016. Disentangling the influences of habitat availability, heterogeneity and spatial position on the species richness and rarity of urban bird communities in a central European city. Urban Ecosyst. 19, 1265–1281.

Fernández-Juricic, E., Jokimäki, J., 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. Biodivers. Conserv. 10, 2023–2043.

Ferrante, M., Lo Cacciato, A., Lövei, G.L., 2014. Quantifying Predation Pressure along an Urbanisation Gradient in Denmark Using Artificial Caterpillars. Eur. J, Entomol, p. 111.

Fischer, J.D., Schneider, S.C., Ahlers, A.A., Miller, J.R., 2015. Categorizing wildlife responses to urbanization and conservation implications of terminology. Conserv. Biol. 29, 1246–1248.

Fisher, J.C., Bicknell, J.E., Irvine, K.N., Hayes, W.M., Fernandes, D., Mistry, J., Davies, Z. G., 2021. Bird diversity and psychological wellbeing: a comparison of green and coastal blue space in a neotropical city. Sci. Total Environ. 793, 148653.

Florczyk, A.J., Corbane, C., Ehrlich, D., Freire, S., Kemper, T., Maffenini, L., Melchiorri, M., Pesaresi, M., Politis, P., Schiavina, M. and Sabo, F., 2019. GHSL data package 2019. Luxembourg, EUR, 29788, 290498.

Fuller, R.J., Langslow, D.R., 1984. Estimating numbers of birds by point counts: how long should counts last? Bird study. 31, 195–202.

Galbraith, J.A., Beggs, J.R., Jones, D.N., Stanley, M.C., 2015. Supplementary feeding restructures urban bird communities. Proc. Natl. Acad. Sci. 112, 2648–2657.

Garcia, D., Zamora, R., Amico, G.C., 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. Conserv. Biol. 24, 1070–1079.

García, D., Miñarro, M., Martínez-Sastre, R., 2018. Birds as suppliers of pest control in cider apple orchards: avian biodiversity drivers and insectivory effect. Agric. Ecosyst. Environ. 254, 233–243.

Goddard, M.A., Dougill, A.J., Benton, T.G., 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends Ecol. Evol. 25, 90–98.

Gouveia, S.F., Villalobos, F., Dobrovolski, R., Beltrão-Mendes, R., Ferrari, S.F., 2014. Forest structure drives global diversity of primates. J. Anim. Ecol. 83, 1523–1530.

Grau, H.R., Aide, M., 2008. Globalization and land-use transitions in Latin America. Ecol. Soc. 13, 16.

Guyana Bureau of Statistics (2012) Demography, Vital & Social statistics – Population & Housing Census, www.statisticsguyana.gov.gy/, accessed 18 January 2023.

Hayes, W.M., Fisher, J.C., Pierre, M.A., Bicknell, J.E., Davies, Z.G., 2020. Bird communities across varying landcover types in a Neotropical city. Biotropica 52, 151–164.

Herte, M., Kobriger, N., Stearns, F., 1971. Productivity of an urban park. University of Wisconsin Field Station Bulletin 4, 14–18.

Hostetler, M., Allen, W., Meurk, C., 2011. Conserving urban biodiversity? Creating green infrastructure is only the first step. Landsc. Urban Plan. 100, 369–371.

Hovick, T.J., Miller, J.R., 2016. Patch-burn grazing moderates eastern meadowlark nest survival in Midwestern grasslands. Am. Midl. Nat. 176, 72–80.

Huff, M.H., 2000. A Habitat-Based Point-Count Protocol for Terrestrial Birds, Emphasizing Washington and Oregon. Gen. Tech. Rep. PNW-GTR-501,. U.S. Department of Agriculture, pp. 1–39.

Imai, H., Nakashizuka, T., 2010. Environmental factors affecting the composition and diversity of avian community in mid-to late breeding season in urban parks and green spaces. Landsc. Urban Plan. 96, 183–194.

IUCN. 2022. The IUCN red list of threatened species. Version 2022-2. https://www.iucnredlist.org. Accessed on 10 January 2023.

Johnson, C.N., 1998. Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. J. Anim. Ecol. 67, 689–698.

Jokimäki, J., 1999. Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. Urban Ecosyst. 3, 21–34.

Lepczyk, C.A., Flather, C.H., Radeloff, V.C., Pidgeon, A.M., Hammer, R.B., Liu, J., 2008. Human impacts on regional avian diversity and abundance. Conserv. Biol. 22, 405–416.

Leveau, C.M., Leveau, L.M., 2005. Avian community response to urbanization in the Pampean region, Argentina. Ornitol Neotrop 16, 503–510.

Leveau, L.M., Leveau, C.M., Villegas, M., Cursach, J.A., Suazo, C.G., 2017. Bird communities along urbanization gradients: a comparative analysis among three Neotropical cities. Ornitol. Neotrop. 28, 77–87.

Litteral, J., Shochat, E., 2017. The role of landscape-scale factors in shaping urban bird communities. Ecol. Conserv. Birds Urban Environ. 135–159.

Lois-González, R.C., González-Pérez, J.M., Irazábal, C., 2022. The study of Latin American and Caribbean cities in the 21st century. In: The Routledge Handbook of Urban Studies in Latin America and the Caribbean. Routledge.

Loram, A., Tratalos, J., Warren, P.H., Gaston, K.J., 2007. Urban domestic gardens (X): the extent & structure of the resource in five major cities. Landsc. Ecol. 22, 601–615.

Luniak, M., 2004. Synurbization - adaptation of animal wildlife to urban development. Proceedings of the 4th international symposium on urban wildlife conservation. Tucson, 50–55.

Mainwaring, M.C., 2015. The use of man-made structures as nesting sites by birds: a review of the costs and benefits. J. Nat. Conserv. 25, 17–22.

Marzluff, J.M., 2001. Worldwide urbanization and its effects on birds. Avian Ecol. Conserv. Urban. World 19–47.

Máthé, O., Batáry, P., 2015. Insectivorous and open-cup nester bird species suffer the most from urbanization. Bird Study 62, 78–86.

McCune, B., Grace, J.B., 2002. Urban DL Analysis of Ecological Communities. Glenden Beach Or. MjM Softw, Des.

McCune, B., Mefford, M.J., 1999. Multivariate analysis of ecological data, version 4.17. MjM Software Design. https://books.google.co.uk/books/about/PC_ORD.html?id=pZPQOwAACAAJ&redir_esc=y.

McKinney, M.L., 2002. Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. Bioscience 52, 883–890.

McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst. 11, 161–176.

Melles, S., Glenn, S., Martin, K., 2003. Urban Bird Diversity and Landscape Complexity: Species–Environment Associations along a Multiscale Habitat Gradient. Conserv, Ecol, p. 7.

Methorst, J., Rehdanz, K., Mueller, T., Hansjürgens, B., Bonn, A., Böhning-Gaese, K., 2021. The importance of species diversity for human well-being in Europe. Ecol. Econ. 181, 106917.

Mikula, P., Tomášek, O., Romportl, D., Aikins, T.K., Avendaño, J.E., Braimoh-Azaki, B.D., Chaskda, A., Cresswell, W., Cunningham, S.J., Dale, S., Favoretto, G.R., 2023. Bird tolerance to humans in open tropical ecosystems. Nat. Commun. 14, 2146.

Moore, J.E., Scheiman, D.M., Swihart, R.K., 2004. Field comparison of removal and modified double-observer modeling for estimating detectability and abundance of birds. Auk 121, 865–876.

Myers, G., 2021. Urbanisation in the global south. Urban Ecol. Glob. South 27–49.

Myers, J.G., 1936. Savannah and forest vegetation of the interior Guiana plateau. J. Ecol. 162–184.

Naka, L.N., Cohn-Haft, M., Mallet-Rodrigues, F., Santos, M.P.D., de Fátima Torres, M., 2006. The avifauna of the Brazilian state of Roraima: bird distribution and biogeography in the Rio Branco basin. 14, 197–238.

Natuhara, Y., Imai, C., 1996. Spatial structure of avifauna along urban-rural gradients. Ecol. Res. 11, 1–9.

Nilon, C.H., Aronson, M.F.J., Cilliers, S.S., Dobbs, C., Frazee, L.J., Goddard, M.A., O'Neill, K.M., Roberts, D., Stander, E.K., Werner, P., Winter, M., Yocom, K.P., 2017. Planning for the future of urban biodiversity: a global review of City-scale initiatives. BioScience 67, 332–342.

Njoroge, J.B., NdaNg'ang'a, P.K., Natuhara, Y., 2014. The pattern of distribution and diversity of avifauna over an urbanizing tropical landscape. Urban Ecosyst. 17, 61–75.

Olden, J.D., Comte, L., Giam, X., 2016. Biotic homogenisation. eLS 1–8.

Ortega-Álvarez, R., MacGregor-Fors, I., 2009. Living in the big city: effects of urban land-use on bird community structure, diversity, and composition. Landsc. Urban Plan. 90, 189–195.

Ortega-Álvarez, R., MacGregor-Fors, I., 2011. Dusting-off the file: a review of knowledge on urban ornithology in Latin America. Landsc. Urban Plan. 101, 1–10.

Pendleton, G.W., 1995. Effects of sampling strategy, detection probability, and independence of counts on the use of point counts. Monit. Bird Popul. Point Counts USDA For. Serv. Gen. 131–133. Tech. Rep. PSW-GTR-149,.

Petermann, J.S., Buzhdygan, O.Y., 2021. Grassland biodiversity. Curr. Biol. 31, 1195–1201.

Petersen, T.K., Speed, J.D., Grøtan, V., Frøyen, Y.K., Austrheim, G., 2022. Urbanisation and land-cover change affect functional, but not compositional turnover of bird communities. Urban Ecosyst. 1–20.

Pires, J.M., 1985. The Vegetation Types of the Brazilian Amazon. Amazonia, GT Prance.

Ralph, C.J., Droege, S., Sauer, J.R., 1995. Managing and monitoring birds using point counts: standards and applications. Ralph C John Sauer John R Droege Sam tech. Ed. 1995 Monit. Bird Popul. Point counts gen tech rep PSW-GTR-149 Albany CA US dep. Agric. For. Serv. Pac. Southwest res. Stn. 149, 161–168.

Remsen Jr., J.V., Cadena, C.D., Jaramillo, A., Nores, M., Pacheco, J.F., Pérez-Emán, J., Robbins, M.B., Stiles, F.G., Stotz, D.F., Zimmer, K.J., 2012. A Classification of the Bird Species of South America. Am. Ornithol. Union, Recuperado.

Reynaud, P.A., Thioulouse, J., 2000. Identification of birds as biological markers along a neotropical urban–rural gradient (Cayenne, French Guiana), using co-inertia analysis. J. Environ. Manag. 59, 121–140.

Richards, P., VanWey, L., 2015. Where deforestation leads to urbanization: how resource extraction is leading to urban growth in the Brazilian Amazon. Ann. Assoc. Am. Geogr. 105, 806–823.

Ritchie, H., Roser, M., 2018. Urbanization. Our World Data. https://ourworldindata.org/urbanization?source=content_type%3Areact%7Cfirst_level_url%3Aarticle%7Csection%3Amain_content%7Cbutton%3Abody_link.

Robbins, M.B., Braun, M.J., Finch, D.W., 2004. Avifauna of the Guyana Southern Rupununi, with Comparisons to Other Savannas of Northern South America. Ornitol, Neotropical.

Rodrigues, A.G., Borges-Martins, M., Zilio, F., 2018. Bird diversity in an urban ecosystem: the role of local habitats in understanding the effects of urbanization. Iheringia Sér. Zool. 108, 2018017.

Rohlf, F.J., Sokal, R.R., 1981. Comparing numerical taxonomic studies. Syst. Biol. 30, 459–490.

Shepard, R.N., 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. II. Psychometrika 27, 219–246.

Smith, H.G., Dänhardt, J., Lindström, Å., Rundlöf, M., 2010. Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. Oecologia 162, 1071–1079.

Sol, D., González-Lagos, C., Moreira, D., Maspons, J., Lapiedra, O., 2014. Urbanisation tolerance and the loss of avian diversity. Ecol. Lett. 17, 942–950.

Sol, D., Trisos, C., Múrria, C., Jeliazkov, A., González-Lagos, C., Pigot, A.L., Ricotta, C., Swan, C.M., Tobias, J.A., Pavoine, S., 2020. The worldwide impact of urbanisation on avian functional diversity. Ecol. Lett. 23, 962–972.

Sorace, A., 2002. High density of bird and pest species in urban habitats and the role of predator abundance. Ornis Fenn. 79, 60–71.

Suarez-Rubio, M., Leimgruber, P., Renner, S.C., 2011. Influence of exurban development on bird species richness and diversity. J. Ornithol. 152, 461–471.

Sushinsky, J.R., Rhodes, J.R., Possingham, H.P., Gill, T.K., Fuller, R.A., 2013. How should we grow cities to minimize their biodiversity impacts? Glob. Change Biol. 19, 401–410.

Sutherland, W.J. (Ed.), 2006. Ecological Census Techniques: A Handbook, 2nd ed. Cambridge University Press, Cambridge.

Symes, C.T., Roller, K., Howes, C., Lockwood, G., van Rensburg, B.J., 2017. Grassland to urban forest in 150 years: avifaunal response in an African metropolis. Ecol. Conserv. Birds Urban Environ. 309–341.

Terborgh, J., 1985. The vertical component of plant species diversity in temperate and tropical forests. Am. Nat. 126, 760–776.

Terborgh, J., Robinson, S.K., Parker III, T.A., Munn, C.A., Pierpont, N., 1990. Structure and organization of an Amazonian forest bird community. Ecol. Monogr. 60, 213–238.

de Toledo, M.C.B., Donatelli, R.J., Batista, G.T., 2012. Relation between green spaces and bird community structure in an urban area in Southeast Brazil. Urban Ecosyst. 15, 111–131.

Tomasevic, J.A., Marzluff, J.M., 2017. Cavity nesting birds along an urban-wildland gradient: is human facilitation structuring the bird community? Urban Ecosyst. 20, 435–448.

Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J., Gaston, K.J., 2007a. Bird densities are associated with household densities. Glob. Change Biol. 13, 1685–1695.

Tratalos, J., Fuller, R.A., Warren, P.H., Davies, R.G., Gaston, K.J., 2007b. Urban form, biodiversity potential and ecosystem services. Landsc. Urban Plan. 83, 308–317.

Tryjanowski, P., Morelli, F., Møller, A.P., 2020. Urban birds: Urban avoiders, urban adapters, and urban exploiters. In: The Routledge Handbook of Urban Ecology. Routledge, pp. 399–411.

Verner, J., Ritter, L.V., 1986. Hourly variation in morning point counts of birds. Auk 103, 117–124.

Viana, P.L., de Mota, N.F.O., dos Gil, A.S.B., Salino, A., Zappi, D.C., Harley, R.M., Ilkiu-Borges, A.L., de Secco, R.S., Almeida, T.E., Watanabe, M.T.C., 2016. Flora das cangas da Serra dos Carajás, Pará, Brasil: história, área de estudos e metodologia. Rodriguésia 67, 1107–1124.

Vieira, I.C.G., de Toledo, P., da Silva, J., Higuchi, H., 2008. Deforestation and threats to the biodiversity of Amazonia. Braz. J. Biol. 68, 949–956.

Zapata, V.M., Robledano, F., 2014. Assessing biodiversity and conservation value of forest patches secondarily fragmented by urbanisation in semiarid southeastern Spain. J. Nat. Conserv. 22, 166–175.