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Associations between urbanization and avian communities in the Afrotropics: Evidence from taxonomic, functional and phylogenetic diversity

Adewale G. Awoyemi [a,b,c,*], Yahkat Barshep [c], Shiiwua Manu [c], Juan Diego Ibáñez-Álamo [a,*]

[a] *Department of Zoology, Faculty of Sciences, University of Granada, Granada, Spain*
[b] *Forest Center, International Institute of Tropical Agriculture, Ibadan, Nigeria*
[c] *A.P. Leventis Ornithological Research Institute, University of Jos, Nigeria*

A R T I C L E I N F O

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A B S T R A C T

Urbanization negatively affects biodiversity worldwide, with the rapidly urbanizing Afrotropical area being understudied. Furthermore, most previous studies investigating this topic focused on taxonomic diversity while recent findings have highlighted the need to incorporate complementary diversity metrics. Thus, this study investigated how urbanization affects bird taxonomic, functional, and phylogenetic diversity in Nigeria, a country with one of the fastest rates of urbanization in the world. We conducted bird censuses at 400 points organized across eight paired comparisons (urban vs non-urban habitats), vegetation zones (rainforest vs savannah), and seasons (dry vs wet). Of the total 237 bird species recorded, 65 % were never encountered in urban areas, suggesting the negative effect of urbanization that was also supported by our statistical analyses. Taxonomic diversity was significantly higher in non-urban than urban habitats. This contrasted with the result on functional and phylogenetic diversity, which was higher in the urban than non-urban habitat. These relationships were similar across seasons, but more intense in the rainforest, revealing that birds in this vegetation zone are more vulnerable to urbanization than their savannah counterparts. We also found that water cover significantly promoted all avian diversity metrics analyzed during the dry season independently of urbanization. In contrast, canopy and bush cover mediated the effects of urbanization on some diversity components (i.e., functional and phylogenetic diversity). Our results highlight the significance of incorporating spatiotemporal patterns in related studies and provide much needed information for city planners and other urban stakeholders in the Afrotropics.

1. Introduction

The world is experiencing accelerated urban development (United Nations, 2016), which is predicted to increase the urban land cover from 824,200 km^2 in 2020 to 1,145,698 km^2 by 2050 (Angel et al., 2011). This dramatic land-use change mainly occurs in developing countries, such as those in the Afrotropical region (OECD/SWAC, 2020; Seto et al., 2012). Coincidentally, this region holds

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* Correspondence to: Avda. Fuentenueva s/n, Granada 18071, Spain.
E-mail addresses: awoyemi@correo.ugr.es (A.G. Awoyemi), jia@ugr.es (J.D. Ibáñez-Álamo).

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huge but declining biodiversity (Gatti et al., 2015), and is relatively understudied (Ibáñez-Álamo et al., 2017; Magle et al., 2012). Recent studies indicate that the fewer urban studies from the Afrotropics strongly correlate with low levels of local capacity and funding (e.g., Awoyemi and Ibáñez-Álamo, 2023). However, information on effects of urbanization on biodiversity is necessary to prevent or minimize biodiversity loss (e.g., Gaston, 2010; Ives et al., 2016; McKinney, 2006, 2008).

The various components of biodiversity (i.e., taxonomic, functional and phylogenetic diversity) offer complementary information useful in promoting biodiversity conservation (Tucker et al., 2017). Taxonomic diversity reveals the presence of species in an area (Magurran, 2004), while functional diversity shows how the functional traits of species influence ecosystem services and functioning (Mouchet et al., 2010; Reynolds and Howes, 2023). Moreover, phylogenetic diversity provides information on the evolutionary richness or divergence of all species in a given community assemblage (Faith, 1992; Helmus et al., 2007). Thus, recent studies have recommended the simultaneous investigation of taxonomic, functional, and phylogenetic diversity as the same process may affect them in varied ways (Nava-Díaz et al., 2022). In general, urbanization negatively affects bird taxonomic diversity (e.g. Aronson et al., 2014; Ibáñez-Álamo et al., 2017). However, studies investigating the effects of urbanization on bird functional and phylogenetic diversity have found contrasting results across space and time (e.g., La Sorte et al., 2018; Lee et al., 2021; Morelli et al., 2021). These studies also show that urban habitat characteristics (e.g., built surfaces, pedestrians, water, bushes, grasses, or tree canopy) affect biodiversity components differently. Meanwhile, several literature reviews on functional diversity and evolutionary distinctiveness in urban areas have revealed the lack of studies from the Afrotropical region (e.g., Hagen et al., 2017; Ibáñez-Álamo et al., 2017). In fact, a recent review on African urban ecology highlighted that there have been no studies simultaneously investigating the impacts of urbanization on these three components of biodiversity (taxonomic, functional, and phylogenetic diversity) in the continent (Awoyemi and Ibáñez-Álamo, 2023). This lack of information could restrict our ability to tackle the increasing challenge posed by urbanization in the area.

Furthermore, most studies on urban ecology in Africa are city based, with each study conducting research in a single city (Awoyemi and Ibáñez-Álamo, 2023). Thus, if we really want to identify general patterns in the effect of urbanization on African biodiversity, we should consider potential variation between cities. In addition, the Afrotropics has a strong temporal variation associated with climate (e.g., dry or wet season) and vegetation (e.g., rainforest or savannah) that influence biodiversity in the region (Chapin, 1923; Sumasgutner et al., 2023). In Western Africa, for example, bird species richness is higher in the rainforest than in the savannah (Brown et al., 1982; Ezealor, 2001), while food is more abundant in the wet than the dry season (Siegfried, 1972; Sinclair, 1978). However, the influence of this spatiotemporal variation on the taxonomic, functional, and phylogenetic diversity of Afrotropical birds has not been explored in the context of urbanization (Awoyemi and Ibáñez-Álamo, 2023).

In this study, we assessed how urbanization affects the different components of biodiversity (taxonomic, functional and phylogenetic) in Nigeria. This country is a regional representative of the Global South with important biophysical and socioeconomic scenarios different from those of the more commonly studied Global North countries (Shackleton et al., 2021). Nigeria is one of the most densely populated countries in Africa with approximately 226 humans/km^2 (United Nations, 2019). Due to this density and other factors, such as rural-urban migration for a better life (Oyeleye, 2013), Nigeria is projected to experience one of the largest urban expansions globally in the near future (OECD/SWAC, 2020; Seto et al., 2012). This makes it an ideal site to test the effect of urbanization on the continent's biodiversity.

Here, we used birds as a model group because they experience important community changes between seasons and vegetation zones (e.g., Brown et al., 1982; Morelli et al., 2021) and have a well-validated phylogeny (e.g., Jetz et al., 2012). By incorporating spatial (8 cities in 2 vegetation zones) and temporal (2 seasons) replicates, we (1) investigated differences in the three biodiversity components between habitats (urban vs non-urban), vegetation zones (rainforest vs savannah), and seasons (dry vs wet). Based on previous findings, we expect urban areas to hold significantly lower levels of taxonomic (e.g., Aronson et al., 2014; van Rensburg et al., 2009) and phylogenetic diversity (e.g., Ibáñez-Álamo et al., 2017) than the adjacent non-urban areas, which will contrast with the result on functional diversity (Hagen et al., 2017; Weideman et al., 2020). Given the higher vegetation cover in the rainforest than the savannah (Brown et al., 1982; Ezealor, 2001), we could expect a more intense reduction in biodiversity due to urbanization in the former than in the latter. We also (2) explored how local influential variables, such as pedestrians, bushes, water, and tree canopy affect diversity metrics in the region. The result of our study will provide crucial information for formulating conservation strategies in the Afrotropics and expand our knowledge on the effects of urban development on wild animals.

2. Methods

2.1. Study area and site description

Nigeria has a tropical climate with distinct wet and dry seasons. Annual rainfall and length of wet season generally decrease northwards from the coast (4000 mm–600 mm) (Ezealor, 2001). Variations in daily, monthly, and annual mean temperature are small in coastal and rainforest areas, but become greater further inland; thus, in the savannah part of Nigeria, temperatures over the year range from approximately 8°C to over 40°C (Ezealor, 2001).

The southern Nigerian sites visited for the present study are a typical representative of urban and non-urban rainforest locations. These sites are characterized by dense evergreen forest of tall trees with thick undergrowth and receive a mean annual rainfall of approximately 2000 mm/annum occurring mainly from April to September (Ezealor, 2001). Meanwhile, the northern Nigerian sites are located within the northern Guinea and Sudan savannah vegetation zones, and thus, are classified here as savannah. These sites are characterized by grasses interspersed by small-medium sized trees, and receive annual rainfall of approximately 900 mm/annum occurring mainly between July and September (Ezealor, 2001).

We conducted fieldwork in paired urban and non-urban sites of eight Nigerian cities equally distributed across the rainforest (Auchi, Calabar, Ibadan, Lagos) and savannah (Birnin Kebbi, Dutse, Gombe, Jos) vegetation zones (Fig. 1). Here, we considered an urban area (city) as a contiguous patch of built-up land greater than 1 km^2, and dominated by human-constructed features like buildings (>10 buildings/ha), high human density (>1600 inhabitants/km^2), roads, and vehicles (Marzluff et al., 2001; Niemelä, 1999; Nilon et al., 2003; Schneider et al., 2010). In contrast, we considered the adjacent non-urban areas as places with extensive wilderness/vegetation cover interspersed with agricultural matrix and sparsely settled villages (MacGregor-Fors, 2011; Marzluff et al., 2001). Urban and non-urban sites in this study were situated at least 20 km away from each other to grant the independence of their avian communities following (Liker et al., 2008).

2.2. Estimation of site characteristics and bird data collection

We used the point count method for bird censuses (Bibby et al., 2000). To ensure a widespread distribution of data that could be representative of the study area (Danjuma et al., 2012; Galbraith et al., 2015), we stratified each site (i.e., urban or non-urban site per city) into five areas stationed at the center and its four cardinal points (i.e., west, east, south and, north) similar to Ciski et al. (2019). We then randomly selected five points from each area. The selection of the areas and points were done using the "create random points tool" in ArcGIS. Each point was marked with a GPS to ensure data collection was from the same location.

During the dry season (November 2020-January 2021), we collected data from 50 selected points (i.e., 25 urban vs 25 non-urban) in each of the eight cities (Møller et al., 2012), totaling 400-point count stations across the two vegetation zones (i.e., 200 rainforest vs 200 savannah). Each point was separated from any other by at least 200 m to reduce potential effects of pseudo-replication (Adegbola et al., 2024; Morelli et al., 2017), and visited in the morning, up to 4 h after local sunrise. Point counts lasted 5 min/point during which we recorded the numbers of individuals of each bird species and pedestrians seen or heard at 50-m radius of the point (e.g., Adegbola et al., 2024; Morelli et al., 2021). Thereafter, we estimated the following field-based environmental measures (to the nearest 10 %) at 50 m radius of each point, including canopy cover, bush cover, grass cover, water cover, and built surface. To reduce detection issues related to identification, data on bird species and estimation of the field-based environmental measures were collected only by AGA, an expert ornithologist with more than 10 years of experience working with birds of the region.

To determine the effects of seasonal variation, we repeated the above sampling procedure during the wet season (August-September 2021). However, due to security issues in northern Nigeria at that time, we were only able to perform this second round of point counts in the rainforest sites (i.e., 200 point-count stations).

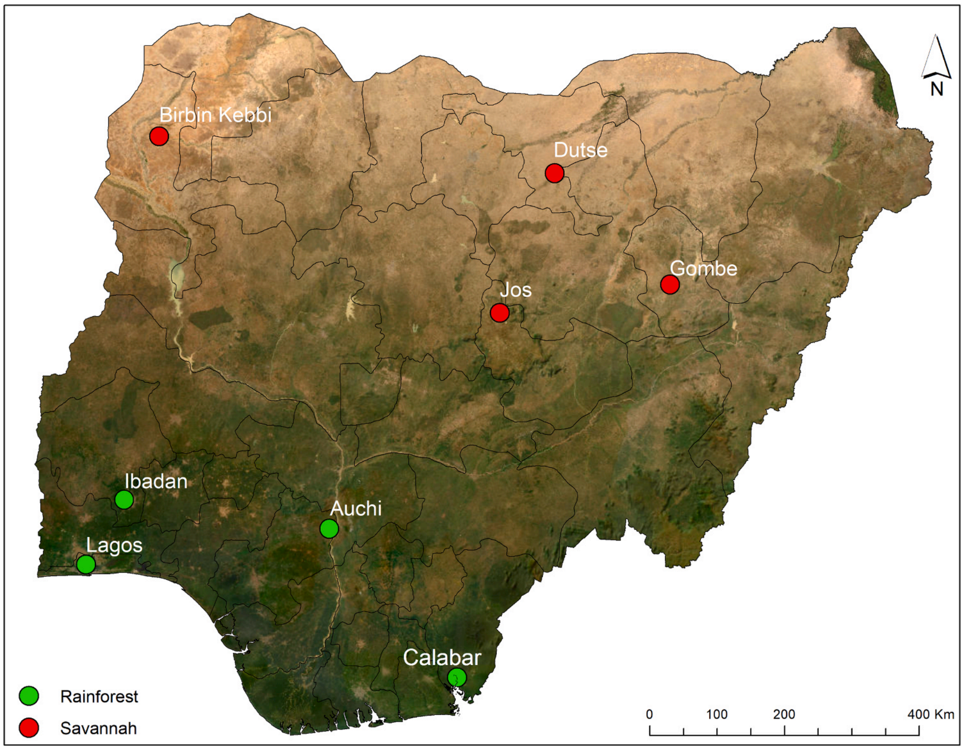


Fig. 1. Distribution of study sites across the savannah and rainforest vegetation zones in Nigeria. At each city, data were collected in paired urban and non-urban sites.

2.3. Avian diversity and community metrics

For each season, we quantified three different components of avian diversity. (1) Taxonomic diversity (TAX) was estimated as bird species richness (BSR); calculated as the total number of bird species recorded at each sampling point (Magurran, 2004). (2) Functional diversity (FUN) was calculated using the Rao's Quadratic Entropy (Rao's Q), which complements the traditional taxonomic approach (de Bello et al., 2010), and is not positively correlated with BSR (Botta-Dukát, 2005). To calculate the Rao's Q, we used the avian niche trait categories provided by Pearman et al. (2014). The calculation was based on bird traits related to their feeding and breeding ecology. We then collected the associated information for each detected bird species from general bird compilations, including the Birds of Africa (Brown et al., 1982; Fry and Keith, 2000; Fry et al., 1988; Fry and Keith Stuart, 2004; Urban et al., 1986; Urban and Fry, 1997), Birds of the World (Pearson, 2020) and Handbook of Avian Body Mass (Dunning, 2007). This compilation resulted in a trait table (Table S1) with 73 variables that describe the ecological niche of each bird species found. The variables included body mass, food types (13 variables), food acquisition behaviors (9 variables), substrate from which food was taken (9 variables), period of day during which a species foraged actively (3 variables), foraging habitats (20 variables) and nesting habitats (18 variables). All variables except the body mass were binomial (scored as either 0 or 1). The Rao's Q of each point was calculated using the function "dbFD" from the "FD" package for R (Laliberté et al., 2015). Finally, (3) Phylogenetic diversity was calculated using two different variables: Faith's phylogenetic diversity (PD; for estimating richness) and phylogenetic species variability (PSV; for estimating divergence) for each community assemblage (Faith, 1992; Helmus et al., 2007). This was based on the recommendation of Tucker et al. (2017) highlighting the significance of integrating complementary information on the total evolutionary history, and the similarity of species within the assemblages. The PD and PSV were estimated by building a phylogenetic tree of the species in each point count. This tree was based on genetic data from all bird species (Jetz et al., 2012) provided in "BirdTree" (www.birdtree.org) and obtained using the "ape" v5.6 package for R (Paradis et al., 2004). Both metrics were estimated (i.e., average values of PD and PSV) using the function "pd'"and "psv" from the "picante" v1.8.2 package for R (Kembel et al., 2010).

2.4. Statistical analyses

Given our inability to collect data in the savannah during the wet season due to security issues, we carried out separate analyses for the dry (rainforest and savannah) and wet seasons (only rainforest). All statistical analyses were conducted with R Version 1.4.1717 (R Core Team, 2022).

Before modeling the diversity metrics, we carried out a series of initial checks in our databases. First, we checked for spatial autocorrelation across sampling points by performing a Mantel test (Legendre and Fortin, 2010; Mantel, 1967) based on a matrix of the geographic distance of the point count stations, and a matrix of differences in BSR, Rao's Q, PD or PSV, and applied the Monte Carlo permutations with 9999 randomizations (Ibáñez-Álamo et al., 2020). Across the dry and wet seasons, there were no significant spatial autocorrelation issues with any estimated diversity metric (all p values > 0.18). Thus, we considered our point counts as statistically independent observations in subsequent analyses. Second, we checked for multicollinearity among the independent variables using the "vif.mer()" function of the "performance" package in R (Bernat-Ponce et al., 2021; Lüdeck et al., 2021), and tested the normality of the dependent variables (Shapiro and Wilk, 1965). During the dry season, built surface, grass cover and the number of pedestrians had high multicollinearity issues (Variance Inflation Factor > 10) in relation to all the diversity metrics, and were thus excluded from subsequent modeling. During the wet season, the interaction of habitat with water cover, built surface and the number of pedestrians (excepting with PSV) had high multicollinearity issues (Variance Inflation Factor > 10) in relation to all the diversity metrics, and were thus excluded from subsequent modeling. Furthermore, we added BSR as an additional predictor while modeling PD (Morelli et al., 2021) as they positively correlated (e.g., for dry season; $r (398) = 0.95$, $p < 0.001$). Third, we standardized all independent numerical variables by using the "scale" function and "optimx" package for scaling and centering (Morelli et al., 2021; Nash, 2017; Revelle, 2022).

We then used Generalized Linear Mixed Models (GLMMs) to determine variations in bird taxonomic (BSR), functional (Rao's Q) and phylogenetic (PD and PSV) diversity in relation to vegetation zones (rainforest vs savannah), habitat types (urban vs non-urban), coverage of canopy, bush, water, and the number of pedestrians, modeled as predictors. The potential interactive effects of habitat types with other independent variables were tested by the corresponding two-way interactions. City ($n = 8$) was included as a random factor to account for possible consistent differences among them. We then used a stepwise backward selection method to simplify the models (Crawley, 2013; Marhuenda et al., 2014). Thus, variables with the highest p values were first removed, and the procedure repeated until the best model (containing significant effects) was selected as the one with the lowest Akaike Information Criterion value (Burnham and Anderson, 2002). We set statistical significance at p value < 0.05, and calculated generalized R2 with the "rsq" package (v. 2.5) as a measure of model fit (Kong et al., 2022; Overs et al., 2023; Zhang, 2022). All candidate models for BSR as the response variable were fitted with Poisson distribution using the "glmer" function of the "lme4" package in R after having explored their distribution (Bates et al., 2015; Shapiro and Wilk, 1965). The models of functional and phylogenetic diversity were fitted using a Gaussian distribution (using the "lmer" function included in the lme4 R package) based on the same initial exploration. Further, we performed Tukey post-hoc tests for pairwise comparisons of the diversity metrics between urban and non-urban habitats using the package "emmeans" (Manley et al., 2015; Yvoz et al., 2020).

3. Results

We recorded a total of 8738 birds of 237 species across the eight paired urban and non-urban habitats and seasons (dry season =

400-point counts and wet season = 200-point counts) throughout the surveys (Table 1; see Table S1 for the list of bird species and their functional traits). Of the eight studied cities, Jos recorded the highest number of bird species in the urban habitat during the dry season, while Ibadan registered the highest number of bird species during the wet season (Table 1). The urban habitat was dominated by laughing dove (*Streptopelia senegalensis*; present in 41 % of all urban point counts studied), common bulbul (*Pycnonotus barbatus*; 32 %), speckled pigeon (*Columba guinea*; 28 %), yellow-billed kite (*Milvus aegyptius*; 25 %) and red-eyed dove (*Streptopelia semitorquata*; 20 %). Meanwhile, common bulbul (39 %), green-backed camaroptera (*Camaroptera brachyura*; 25 %), vinaceous dove (*Streptopelia vinacea*; 23 %), green crombec (*Sylvietta virens*; 23 %), and little greenbul (*Andropadus virens*; 16 %) were the most commonly recorded species in the adjacent non-urban habitat. We found that 65 % (n = 154) of all species recorded were never encountered in urban areas (e.g., cassin's hawk-eagle *Aquila africana*, black-shouldered nightjar *Caprimulgus nigriscapularis*, ahanta francolin *Francolinus ahantensis*, oriole warbler *Hypergerus atriceps*, and chestnut wattle-eye *Platysteira castanea*).

3.1. *Avian biodiversity during the dry season*

We found significant interaction effects of habitat (urban *vs* non-urban), vegetation zone (rainforest *vs* savannah), and site-level indices on BSR, Rao's Q, PD, and PSV (Fig. 2; Table S2). Specifically, BSR was significantly lower in the urban than non-urban habitat across vegetation zones (habitat × vegetation zone interaction: Estimate $\pm$ SE $= 0.44 \pm 0.10$, $Z = 4.55$, $p < 0.001$), although more intensely in the rainforest than the savannah (Fig. 3a). We also found significant differences between rainforest and savannah for non-urban areas (higher BSR in the former) but not for urban habitats (Fig. 3a). In general, the higher Rao's Q values in the urban than non-urban habitat (Table S2) were not significantly different across the vegetation zones (habitat × vegetation zone interaction: Estimate $\pm$ SE $= -0.07 \pm 8.34$, $t = -0.008$, $p = 0.99$; Fig. 3b). Meanwhile, PD revealed contrasting results as this metric was significantly higher in the urban than non-urban habitat only in the rainforest (habitat × vegetation zone interaction: Estimate $\pm$ SE $= -34.72 \pm 12.45$, $t = -2.79$, $p = 0.006$; Fig. 3c; Table S2). In contrast, we found no significant differences between urban and non-urban habitats for PSV (Estimate $\pm$ SE $= 0.002 \pm 0.002$, $t = 1.16$, $p = 0.25$; Fig. 3d).

Our results also show contrasting effects of local influential predictors (Fig. 2; Table S2). With the exception of PSV (Estimate $\pm$ SE $= 1.12 \pm 6.58$, $t = 1.707$, $p < 0.089$; Fig. 2), water cover was in general, significantly (positively) associated with all the diversity metrics during the dry season (BSR: Estimate $\pm$ SE $= 0.05 \pm 0.02$, $Z = 2.139$, $p = 0.032$; Rao's Q: Estimate $\pm$ SE $= 4.70 \pm 1.82$, $t = 2.58$, $p = 0.011$; PD: Estimate $\pm$ SE $= 5.99 \pm 2.83$, $t = 2.12$, $p = 0.035$; Fig. 2). On the contrary and also during this season, the number of pedestrians did not significantly influence PSV values as this variable was not retained in the final model (Table S2). PSV was the only diversity metric for which we could test this predictor during the dry season as it was excluded from the others due to multicollinearity issues. Furthermore, we found that habitat (i.e., urbanization) mediated the effect of some local variables during this season (Fig. 2). In this respect, bush cover significantly promoted Rao's Q (Estimate $\pm$ SE $= 27.12 \pm 6.85$, $t = 3.96$, $p < 0.001$; Fig. 4a) while canopy cover did the same for PD values (Estimate $\pm$ SE $= 21.23 \pm 10.02$, $t = 2.12$, $p = 0.035$; Fig. 4b) in urban habitats compared to more natural habitats.

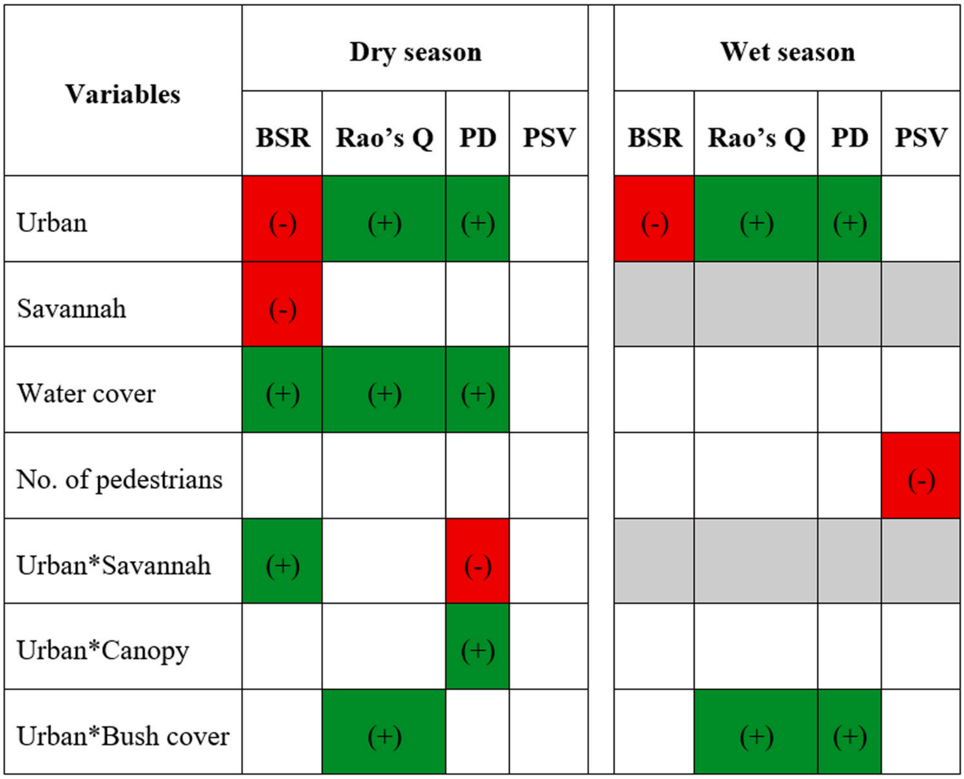
3.2. *Avian biodiversity during the wet season*

BSR was significantly higher in the non-urban than urban habitat (Estimate $\pm$ SE $= -0.65 \pm 0.11$, $Z = -6.14$, $p < 0.001$; Table S3; Fig. 5a). This contrasts with the results of Rao's Q (Estimate $\pm$ SE $= 26.13 \pm 7.85$, $t = 3.33$, $p = 0.001$; Table S3; Fig. 5b) and PD (Estimate $\pm$ SE $= 50.24 \pm 12.85$, $t = 3.91$, $p < 0.001$; Table S3; Fig. 5c) that were significantly higher in the urban than non-urban habitat. We found no significant differences for PSV during this season (Estimate $\pm$ SE $= 3.96 \pm 2.85$, $t = 1.39$, $p = 0.17$; Table S3; Fig. 5d).

Complementing our results for the dry season, the number of pedestrians significantly reduced PSV values during the wet season (Estimate $\pm$ SE $= -2.28 \pm 9.47$, $t = -2.411$, $p = 0.018$). In this same context, habitat (i.e., urbanization) mediated the effect of only bush cover among local variables, significantly promoting Rao's Q (Estimate $\pm$ SE $= 21.84 \pm 10.12$, $t = 2.16$, $p = 0.032$; Fig. 6a), and

Table 1
Variation in bird species richness recorded across cities, seasons, and habitats in Nigeria, November 2020—September 2021. Note: Wet season surveys were conducted only in the four rainforest sites due to security issues in the savannah sites. The size of each city was obtained from Google Earth (accessed October 2020).

		Dry season		Wet season	
City	Size km^2	Urban	Non-urban	Urban	Non-urban
Auchi	35	20	66	21	80
Calabar	406	17	45	17	52
Ibadan	3080	24	80	30	73
Lagos	1171	16	56	16	41
Birnin Kebbi	35	20	32	NA	NA
Dutse	45	24	48	NA	NA
Gombe	90	23	26	NA	NA
Jos	260	31	49	NA	NA
Mean	640.25	21.875	50.25	21	61.5
Standard Deviation	1057.17	4.76	17.41	6.38	18.12



Variables	Dry season				Wet season			
	BSR	Rao's Q	PD	PSV	BSR	Rao's Q	PD	PSV
Urban	(-)	(+)	(+)		(-)	(+)	(+)	
Savannah	(-)				▨	▨	▨	▨
Water cover	(+)	(+)	(+)					
No. of pedestrians								(-)
Urban*Savannah	(+)		(-)		▨	▨	▨	▨
Urban*Canopy			(+)					
Urban*Bush cover		(+)				(+)	(+)	

Fig. 2. Schematic presentation of main associations (from final models) between values of taxonomic diversity (estimated from bird species richness), functional diversity (estimated from Rao's Quadratic Entropy), phylogenetic diversity (estimated from Faith's Phylogenetic Diversity and phylogenetic species variability) calculated for avian communities across habitats (urban and non-urban) and seasons (dry and wet) in Nigeria, and different characteristics of the sites. Positive significant associations are indicated in green (+), while negative ones are highlighted in red (-). The grey color indicates untested associations because of our inability to collect data in the savannah during the wet season due to important security issues in the area. These results were simplified to reflect only significant variables from the final models shown in detail in Tables S2-S3.

PD (Estimate ± SE = 40.44 ± 15.23, T = 2.655, p = 0.009; Fig. 6b) compared with non-urban habitats. No additional predictor significantly influenced avian diversity indices for the wet season (Table S3).

4. Discussion

Our study showed that urbanization has a complex and multifaceted effect on avian diversity. This is because not all biodiversity components were similarly affected by this human-induced landscape change. This finding matches previous studies from other regions of the world (Devictor et al., 2010; Morelli et al., 2017), and suggests the need for the simultaneous study of multiple diversity components.

4.1. Variations in avian diversity across urbanization, seasons, and vegetation zones

We found that urbanization severely reduced avian taxonomic diversity, with the urban habitat supporting less than half the number of bird species recorded in the adjacent non-urban habitat. This is consistent with previous findings from other regions of the world, and based on other Afrotropical (e.g., Chamberlain et al., 2017) and Pantropical studies (e.g., Alexandrino et al., 2022). In addition, the similar numbers of bird species we recorded across the surveyed cities may have been due to their habitat similarities. Several authors (e.g., Clergeau et al., 2001; McKinney, 2006; Savard et al., 2000) have argued that human activities produce similar ecological structures, functions, and constraints that affect the associated biodiversity in urban areas worldwide (i.e., biotic homogenization).

Our results revealed that rainforest birds seem to be more affected by urbanization than their savannah counterparts. Urban habitats in the rainforest hold a much smaller proportion of their corresponding non-urban habitats than the urban vs. non-urban savannah comparison. This finding is critical for conservation prioritization. Although the rainforest is more productive than the savannah (Brown et al., 1982; Ezealor, 2001), it also concentrates a larger proportion of urban development in the area (OECD/SWAC, 2020; Seto et al., 2012). The rainforest sites investigated in our study are part of the "Western African Forests", one of the 25 global biodiversity hotspots (Myers et al., 2000), highlighting the relevance of potential ecological alteration in this region. The extent of

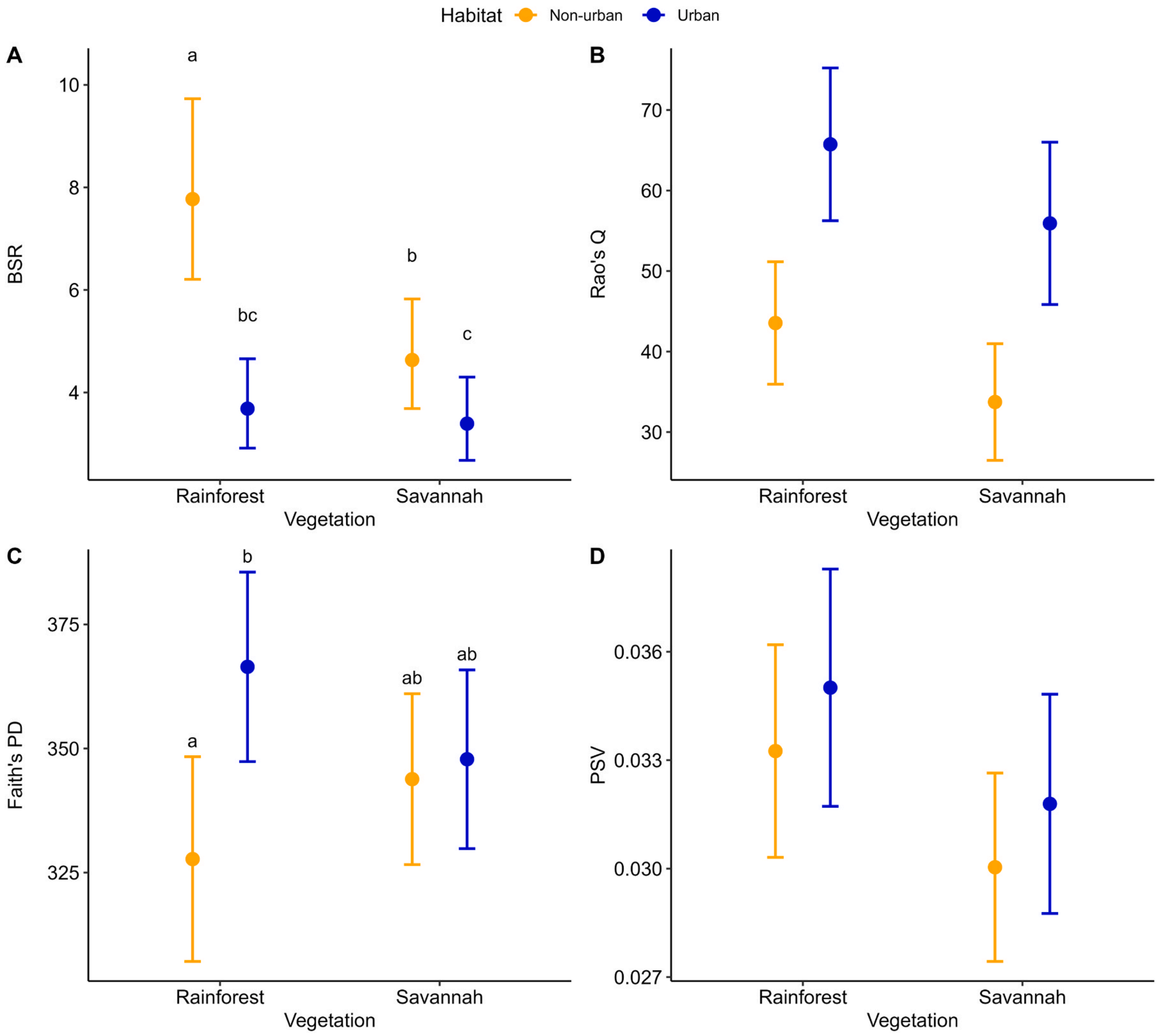


Fig. 3. Mean ± 95 % Confidence Interval across vegetation zones (rainforest *vs* savannah) and habitats (urban *vs* non-urban) for four avian diversity components estimated from across eight Nigerian cities during the dry season: (A) taxonomic diversity (bird species richness, BSR); (B) functional diversity (Rao's Q); (C) phylogenetic diversity (Faith's PD) and phylogenetic divergence (PSV). Significant associations ($P < 0.01$) are indicated with asterisks. For those diversity variables showing significant differences for the interaction habitat x vegetation zone (BSR and PD), different letters indicate significant differences according to Tukey post-hoc tests using the package "emmeans". The plots are based on model predictions.

primary vegetation of the Western African Forests has been reduced to approximately 10 % of its original size (1,265,000 km^2), and urbanization is a leading threat in the area (Myers et al., 2000; OECD/SWAC, 2020; Seto et al., 2012). If the current urban expansion continues unabated, a greater number of bird species could be threatened.

Furthermore, the consistently lower taxonomic diversity we recorded in the urban than in the non-urban site during both the dry and wet seasons corroborates previous studies revealing that anthropogenic features (e.g., built surface, human density) rather than non-anthropogenic factors (e.g., climate, geography) are better predictors of the loss of taxonomic diversity in urban habitats (e.g., Aronson et al., 2014). However, this does not imply that future urban studies should not consider other variations as we found that they could be important in tropical regions (e.g., different reduction in BSR associated with urbanization between vegetation zones). Studies investigating taxonomic diversity of birds in urban areas have been previously conducted in Africa (Adegbola et al., 2024; Afrifa et al., 2022; Aouissi et al., 2017; Njoroge et al., 2014), but those comparing taxonomic diversity between urban and non-urban habitats are still scarce (Chamberlain et al., 2019; Lee et al., 2021). Thus, our study provides much-needed information to fill this important knowledge gap.

In general, functional diversity was higher in the urban than non-urban habitat independently of vegetation zone or season. Urban areas could offer more ecological niches than non-urban areas (Lokatis and Jeschke, 2022; Palacio, 2020), which could explain our findings as additional niches could enhance avian FD (Petchey and Gaston, 2002). For instance, the non-urban sites of the rainforest visited for this study comprised mainly of forest vegetation compared with the urban sites that included a mosaic of habitats, including parks, gardens, cemeteries, sanitary landfills, residential areas, and offices. Our result showing a higher phylogenetic diversity in urban

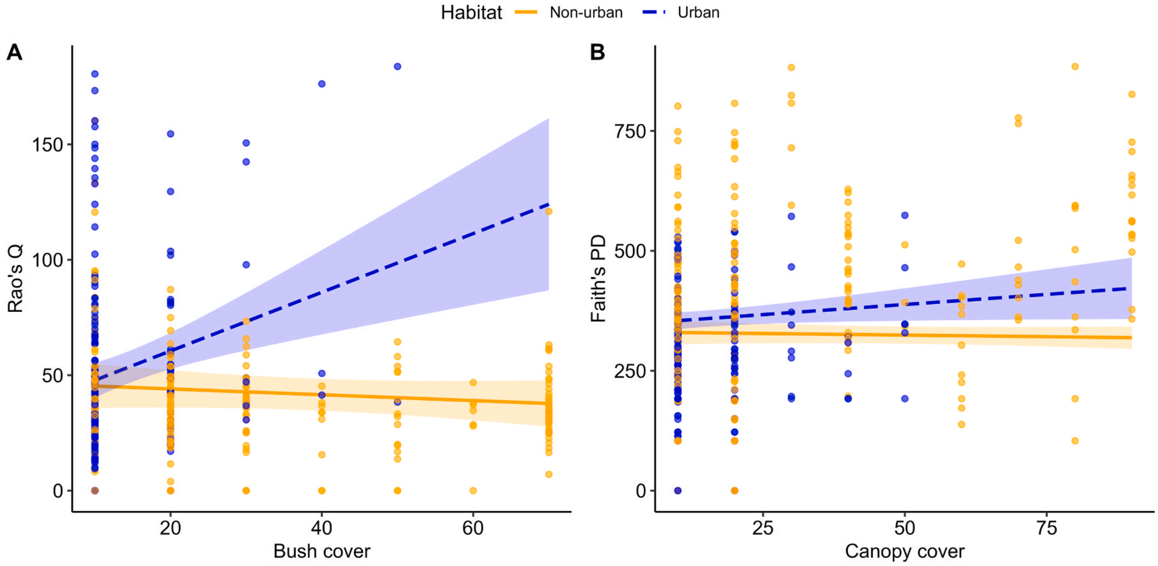


Fig. 4. (A) The effect of bush cover by habitat (urban *vs* non-urban) on functional diversity (Rao's Q) during the dry season, and (B) the effect of canopy cover by habitat (urban *vs* non-urban) on phylogenetic diversity (Faith's PD) during the dry season. The plots are based on model predictions.

than non-urban habitat supports this position. Moreover, generalist birds (e.g., urban exploiters) capable of exploiting diverse habitat niches are more abundant in urban than non-urban areas that supports more specialist birds (Lee et al., 2021). Thus, this study pinpoints the need for additional studies investigating the specific urban attributes promoting avian functional diversity in the region.

The lower PD found in the non-urban than the urban habitat of the rainforest implies an increase in evolutionary richness due to urbanization. This result did not meet our expectations, particularly given the higher levels of taxonomic diversity (BSR) we recorded in the non-urban habitat independently of season. However, higher levels of BSR may not directly translate into higher PD for birds if the different species that dominate the community share similar evolutionary relationships (i.e., closely related species), leading to phylogenetic redundancy, a pattern found by other urban studies (e.g., Sanllorente et al., 2023). This is clearly represented with the example of the family Lybiidae for which we found six species in the non-urban habitat (*Lubius leucocephalus, Lybius vieilloti, Pogoniulus bilineatus, Pogoniulus chrysoconus, Pogoniulus scolopaceus,* and *Pogoniulus subsulphureus*), of which only two were registered in the urban habitat (*P. bilineatus* and *P. chrysoconus*). Additionally, some urban features (e.g., buildings, vehicles or pedestrians) could provide opportunities for some evolutionarily unique groups of species to colonize urban environments. In this sense, our study revealed nine distantly related species that could have boosted PD values in the urban habitat (*Accipiter badius, Apus affinis, Colius striatus, Euplectus hordeaceus, Falco alopex, Hirundo fuligula, Lagonosticta larvata, Necrosyrtes monachus,* and *Phoeniculus purpureus*), which were never recorded in the non-urban habitat during our survey. Meanwhile, the lack of significant differences in PD values between urban and non-urban habitats in the savannah contrasts with those obtained for the rainforest (dry season) and reinforces the importance of considering the vegetation zone in this kind of studies.

The results of our PSV indicated that urban birds in Nigeria are no more closely related to each other than non-urban birds independently of the vegetation zone. This finding contradicts those obtained by Morelli et al. (2021), highlighting the relevance of our study that focused on the understudied Afrotropics.

4.2. Effects of local influential features on avian diversity across urbanization, seasons, and vegetation zones

During the dry season, water cover was the crucial local variable promoting all the diversity metrics considered across habitats and vegetation zones. The positive associations we found between water cover and the three biodiversity metrics during this season could be due to enhanced availability of the diverse resources linked to water. For instance, water availability could attract bird species (e.g., waterbirds) seeking access to this restricted resource during the dry season. This is plausible given that this effect was lost during the wet season, when water or associated resources (e.g., seeds, flowers, leaves) were more readily available in Afrotropical environments. In addition, food becomes scarcer in Afrotropical environments during dry weather conditions (Siegfried, 1972; Sinclair, 1978), and water availability could ameliorate this situation.

Bush cover in the urban habitat significantly enhanced both functional (dry and wet seasons) and phylogenetic diversity (wet season) compared with more natural habitats. This contrast between habitats highlights the importance of bushes in Afrotropical cities, providing a clear conservation action that city planners and urban conservationists could implement. In fact, Clergeau et al. (2006) found that the functional group of bush-dwelling birds significantly decreased with increasing urbanization, further supporting our recommendation in this respect. Bushes in cities could provide additional nesting and feeding opportunities (e.g., Daniels and Kirkpatrick, 2006; Grant et al., 2006) that could also partially explain the observed positive association between urbanization and bird

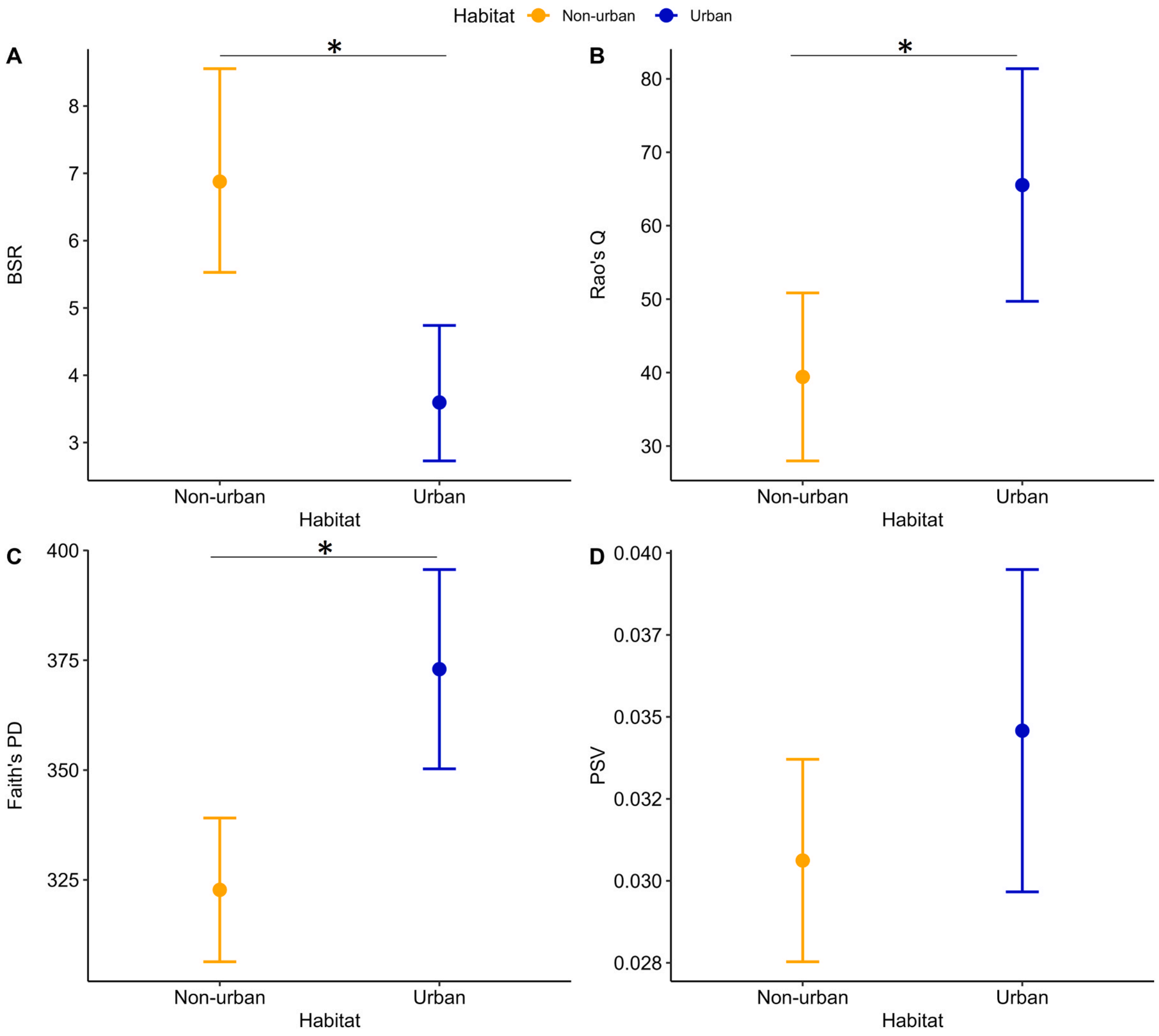


Fig. 5. Mean ± 95 % Confidence Interval for four avian diversity components estimated from across four Nigerian cities during the wet season: (A) taxonomic diversity (bird species richness, BSR); (B) functional diversity (Rao's Q); (C) phylogenetic diversity (Faith's PD); and (D) phylogenetic divergence (PSV). Significant associations ($P < 0.01$) are indicated with asterisks. The plots are based on model predictions.

functional diversity found in this study. In addition, we could speculate that the species attracted by bushes are of different evolutionary lineages (e.g., *Corvus albus, Passer griseus*), which could explain the increase in phylogenetic richness during the wet season.

Similar to urban bush cover, tree canopy in Afrotropical cities could attract canopy-loving species from distantly related evolutionary lineages (e.g., *Poicephalus senegalus or Necrosyrtes monachus*), consequently explaining its positive association with the phylogenetic richness obtained during the dry season. Parrots and other species could look for feeding resources in the urban canopy as the dry season corresponds with the peak of fruiting in the region (Brugiere et al., 1999; Polansky and Boesch, 2013). In addition, urbanization selects against ground nesters (Croci et al., 2008; Jokimäki and Huhta, 2000), but urban trees could act as safe nest sites for other groups of birds. For example, during data collection, we observed some critically endangered hooded vultures *Nerosyrtes monachus* nesting at an urban park in Lagos. Hooded vultures are persecuted and traded for traditional belief-based practices (Williams et al., 2021), and urban sites could be a haven for this and related species due to relatively low perceived predation pressure. This adaptation to urban life has also been found in European birds (Møller, 2008).

Surprisingly, the number of pedestrians was not significantly associated with BSR, Rao's Q or PD (for those models incorporating the variable; see Tables S2 and S3). Studies conducted in other regions of the world, such as Europe or South America, have shown that increasing the number of pedestrians has negative impacts on bird taxonomic and functional diversity (Curzel et al., 2021; Ibáñez-Álamo et al., 2020; Sanllorente et al., 2023). This contradictory finding could be explained by the fact that birds from our study area deal better with humans. It could also suggest that other aspects beyond human activities (e.g., landscape organization) play a more important role for Afrotropical birds. Supporting these positions, our wet season result revealed that the number of pedestrians rather significantly decreased phylogenetic relatedness (i.e., PSV) independently of habitat. Thus, bird communities with more pedestrians seem to hold less closely related species as the fear of humans could exert a filtering effect on certain species (Braimoh et al.,

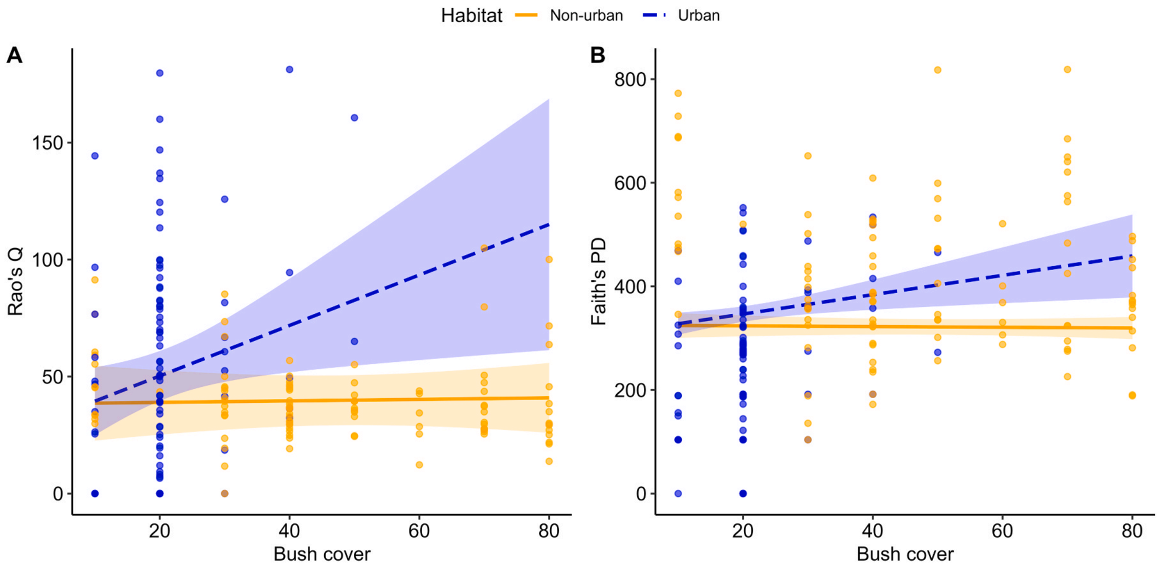


Fig. 6. (A) The effect of bush cover by habitat (urban *vs* non-urban) on functional diversity (Rao's Q) during the wet season, and (B) the effect of bush cover by habitat (urban *vs* non-urban) on phylogenetic diversity (Faith's PD) during the wet season. The plots are based on model predictions.

2018).

5. Conclusions and recommendations

This study revealed that Nigerian urban areas hold a significantly lower bird species richness compared with non-urban ones. This effect is more severe in the rainforest than in the savannah, highlighting the vulnerability of birds in this vegetation zone to the urbanization process. We also found contrasting results among biodiversity components, suggesting the need to investigate urban effects beyond BSR (see also Ibáñez-Álamo et al., 2020; Morelli et al., 2021). Despite our limitations, our findings indicate between-season consistency in the associations between urbanization and these different biodiversity indices.

Our study highlights the need to minimize the impacts of urbanization on biodiversity and recommends the following: (1) Replication of our study in other Afrotropical areas and with other taxa to test the generality of our findings; (2) The need for city planners to integrate a combination of features that could promote biodiversity-friendly cities. In this context, our study showed that the integration of a mosaic of water bodies, bushes, and trees could boost avian diversity in Afrotropical urban centers, particularly during the dry season; (3) The use of alternatives for field-based predictors of avian diversity. A recent review on African urban ecology (Awoyemi and Ibáñez-Álamo, 2023) recommends the use of remotely sensed vegetation variables (e.g., Normalized Difference Vegetation Index) to overcome accessibility issues. We hope that our study and recommendations will promote sustainable urban development in the Afrotropics.

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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03108.

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