


Remotely sensed spectral indicators of bird taxonomic, functional and phylogenetic diversity across Afrotropical urban and non-urban habitats

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ABSTRACT

Urban areas are quickly expanding around the world, promoting deep changes in biodiversity. However, certain biogeographic realms, like the Afrotropics, are clearly understudied despite urbanization overlapping with their biodiversity hotspots. A commonly highlighted reason for the lack of information from the Afrotropics has been the logistical problem associated with data collection in the field. Recent advances in satellite remote sensing imagery offer an excellent opportunity to revert this situation, enhancing the understanding of urban impacts on biodiversity. The Normalized Difference Vegetation Index (NDVI) is the most commonly used remotely sensed spectral index (hereafter: indicator) despite several studies showing its limitations and advocating for the use of alternative indicators. Thus, this study identifies the best indicators of bird taxonomic, functional, and phylogenetic diversity in Afrotropical urban and non-urban areas. To do so, we sampled birds at 400 points equally distributed across eight Nigerian areas, two vegetation zones (rainforest vs savannah), and two habitats (urban vs non-urban), and extracted 29 indicators (mean and SD) at 50-m radius of each point (exact area of bird censuses). Random Forest Regressions and Generalized Linear Mixed Effect Models were used to identify the topmost ranked indicator of each avian diversity component, and its variation between urban and non-urban areas. The Modified Chlorophyll Absorption Ratio Index (MCARI) was the best indicator of taxonomic and phylogenetic diversity, while the Normalized Difference Water Index II (NDWI2) and Soil Adjusted Total Vegetation Index (SATVI) got the most support for functional diversity and phylogenetic divergence, respectively. In most cases, NDVI ranks very low (occupying the 25th percentile), not supporting its use for monitoring avian diversity in the Afrotropics. MCARI and NDWI2 showed different associations with taxonomic and functional diversity depending on the habitat, highlighting the need for considering urban areas differently while using these indicators. Our study provides useful tools to remotely monitor Afrotropical avian diversity, particularly in expansive, inaccessible or insecure areas, which could also be more cost-effective.

1. Introduction

Urbanization is a highly ranked human-driven landscape change exerting negative impacts on biodiversity worldwide (Angel et al., 2011; McKinney, 2006; Seto et al., 2012). Coincidentally, this human pressure is expanding more in low-medium income countries of the Global South often characterized with biodiversity hotspots (McDonald et al., 2008; OECD/SWAC, 2020). This overlap, together with an inadequate research capacity (Awoyemi & Ibáñez-Álamo, 2023; Beale, 2018), highlight the urgent need for an efficient monitoring technique that could provide data necessary to safeguard the dwindling biodiversity of

the area (Garzon-Lopez et al., 2024; Schmeller et al., 2017). However, multiple studies conducted in the region have subjectively estimated different urban and vegetation characteristics (e.g., impervious surfaces, water, soil, vegetation and water; hereafter: field-based environmental measures) to examine their effects on the associated biodiversity (e.g., Chamberlain et al., 2017; John & Kagembe, 2022). Despite the relevance of this traditional methodological approach, such a field-based estimation is often laborious, expensive and prone to investigators' errors (Ghosh et al., 1995; Gorrod & Keith, 2009; Morrison, 2016). This is even more challenging when surveys involve repeated coverage of large, inaccessible or insecure sites (Casagli et al., 2017; Negash et al., 2023).

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Thus, harnessing innovative techniques that could provide such information more accurately and at different scales, with minimal costs and time, could enhance biodiversity monitoring and management across different habitats (Benton et al., 2003).

Recent advances in satellite remote sensing imagery with growing resolution and quality have enhanced the capacity to monitor biological diversity and global environmental changes (Pettorelli et al., 2014; Xue & Su, 2017). The multispectral indices extracted from such imagery provide key site-level measures of primary productivity and seasonal variations (e.g., Ghorbani et al., 2020; Harris & Dash, 2011; Peng et al., 2008). This understanding is useful to predict species diversity and distribution across a wide range of habitats (Alabi et al., 2022a; Benedetti et al., 2023; Gaitán et al., 2013; Ghorbani et al., 2020). Among multispectral indices, the Normalized Difference Vegetation Index (NDVI) is still the most frequently used index to obtain vegetation information as a proxy for primary productivity (He et al., 2015; Xu et al., 2022). NDVI exploits the red and near-infrared bands of the electromagnetic spectrum, ensuring that the extracted spectral variability is mainly due to vegetation characteristics (Viña et al., 2011). It is, therefore, hardly surprising that most studies find a positive association between NDVI and species diversity (see Madonsela et al., 2017). However, NDVI shows scaling problems, saturates in areas of high biomass (Gitelson, 2004; Huete et al., 2002; Main et al., 2011), and is affected by soil brightness that lowers its sensitivity to vegetation (Huete & Jackson, 1988). These factors justify the need to incorporate other spectral indicators that have a more comprehensive range for modeling species attributes (Alabi et al., 2022a; Benedetti et al., 2023; Gaitán et al., 2013; Ghorbani et al., 2020). This is crucial, particularly in heterogeneous habitats that offer diverse niches/resources such as urban areas (Cramer & Willig, 2005; Hamm & Drossel, 2017; Pianka, 1966). For example, studies testing the relationships between field-based environmental measures and urban biodiversity show that impervious surfaces and soil can exert differing effects on the various components of animal diversity (e.g., Ibáñez-Álamo et al., 2020; Morelli et al., 2021). This indicates that NDVI alone may not be adequate for the estimation of different biodiversity components (i.e., taxonomic, functional and phylogenetic). This information suggests the need to incorporate additional spectral indicators with the potential to overcome the limitations of NDVI (Benedetti et al., 2023). This approach has been deployed in various plant-based studies. For instance, multispectral indices have been used to investigate primary productivity (Ghorbani et al., 2020), ecosystem structure and functioning (Gaitán et al., 2013), and grain yield (Alabi et al., 2022a). However, the use of multispectral indices to predict animal biodiversity metrics is still scanty (e.g., Bae et al., 2018; Benedetti et al., 2023).

Thus, this study investigates the relationships between remotely sensed spectral indices and bird taxonomic, functional and phylogenetic diversity using data collected from eight paired locations in Nigeria (each including urban and non-urban study sites) and from two vegetation zones (i.e., rainforest and savannah). This biodiversity-rich Afrotropical country is among the most impacted by expanding urbanization at the global level (Awoyemi & Ibáñez-Álamo, 2023; Ezealor, 2001; Seto et al., 2012), suggesting the need for an efficient monitoring system to support conservation decisions. Twenty-nine spectral indices (Figure S1) with the potential to capture the positive and negative site features (field-based environmental measures) affecting different components of avian diversity across urban and non-urban habitats (e.g., Chamberlain et al., 2017; Ibáñez-Álamo et al., 2020; Morelli et al., 2021) were extracted for this study (see Alabi et al., 2022a; Benedetti et al., 2023; Ghorbani et al., 2020). This was followed by multistage statistical analyses aimed at investigating the efficient spectral indices that could aid biodiversity monitoring and management given the economic, security and manpower restrictions of the area (Awoyemi & Ibáñez-Álamo, 2023; Garzon-Lopez et al., 2024; Schmeller et al., 2017). The reasons for incorporating multiple spectral indices are threefold. (1) To unravel their suitability for modeling biodiversity metrics across

different habitats. This is particularly important given that previous studies have shown strong variations in the effect of field-based environmental measures on bird taxonomic, functional and phylogenetic diversity across urban and non-urban habitats (e.g., Chamberlain et al., 2017; Hagen et al., 2017; Ibáñez-Álamo et al., 2020). (2) To identify alternative spectral indices that could complement NDVI by overcoming its limitations, particularly in urban habitats, where soil and impervious surfaces are pronounced (e.g., Murgui & Hedblom, 2017). (3) To provide baseline data that could be useful to remotely monitor avian diversity in the Afrotropics. This study focused on birds because they are relatively well-studied across urban and non-urban habitats (Gil & Brumm, 2013; Murgui & Hedblom, 2017). Birds also have a well-validated phylogeny (e.g., Jetz et al., 2012), and experience community changes across seasons and vegetation zones (e.g., Brown et al., 1982; Ezealor, 2001; Hagen et al., 2017; Ibáñez-Álamo et al., 2020; Morelli et al., 2021). Thus, this study can provide an important step toward a better and more efficient monitoring system for avian diversity in Afrotropical environments.

2. Materials and methods

2.1. Study area

Data were collected in eight paired urban and non-urban sites equally distributed across the rainforest (Auchi, Calabar, Ibadan, Lagos) and savannah (Birnin Kebbi, Dutse, Gombe, Jos) vegetation zones in Nigeria (Fig. 1). The rainforest zone is characterized by dense evergreen forests of tall trees with thick undergrowth, and receives a mean annual rainfall of c. 2000 mm/annum (e.g., Ezealor, 2001) occurring mainly from April to September. The savannah is, however, dominated by grasses interspersed by small-medium sized trees and receives an annual rainfall of 600–1200 mm/annum (e.g., Ezealor, 2001), occurring mainly between July and September.

To be considered an urban center, each of the studied cities had a contiguous patch of built-up land greater than 1 km² and dominated by human-constructed features like buildings (>10 buildings/ha), high human density (>1600 inhabitants/km²), roads, and vehicles (Marzluff et al., 2001; Niemelä, 1999; Nilon et al., 2003; Schneider et al., 2010). In contrast, the adjacent non-urban habitats had extensive wilderness/vegetation cover interspersed with agricultural matrix and sparsely settled villages (MacGregor-Fors, 2011; Marzluff et al., 2001). Following Liker et al. (2008), each urban site was at least 20 km from its paired non-urban site to grant the independence of the bird communities.

2.2. Site selection and bird enumeration

Each study site (i.e., urban or non-urban site per city) was stratified into five areas positioned at the center and its four cardinal points (i.e., west, east, south and, north) to guarantee a widespread distribution of data that could be considered representative of the study area (Awoyemi et al. 2024; Giski et al., 2019). Five random points were then selected 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. Each point was separated from any other by at least 200 m to reduce the potential effects of pseudo-replication (Benedetti et al., 2023). During the dry season (November 2020–January 2021), data were collected from 50 points (i.e., 25 urban vs 25 non-urban) in each of the eight paired locations (Møller et al., 2012), totaling 400-point count stations across the two vegetation zones (i.e., 200 rainforest vs 200 savannah).

All birds seen and heard for 5 mins within the 50-m radius of each point were counted (Awoyemi et al., 2024; Sanllorente et al., 2023). These duration and range are ideal for enumerating the optimum number of birds during point count while minimizing potential effects of pseudo-replication (Bibby et al. 2000). The birds were counted in the mornings, up to 4 h after local sunrise (Manu et al. 2007), but only under

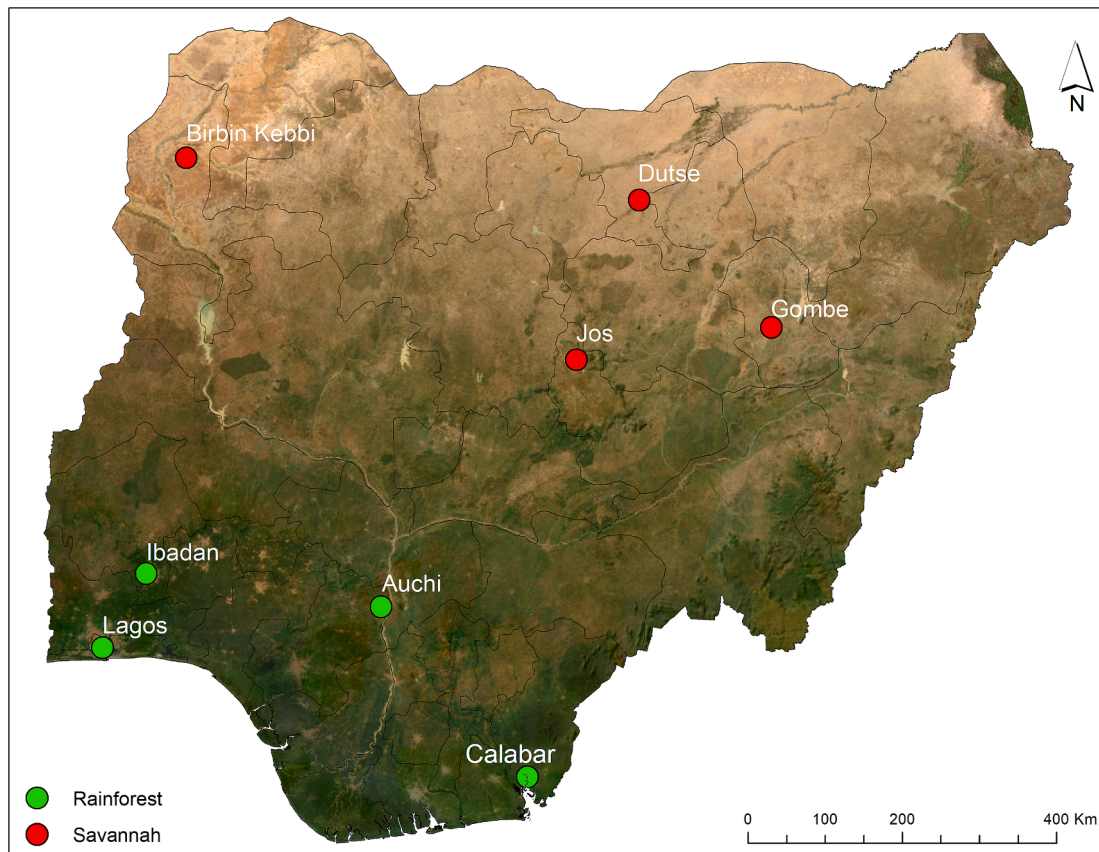


Fig. 1. Distribution of study sites across the savannah and rainforest vegetation zones in Nigeria. At each city, data were collected in paired urban and non-urban sites.

favorable weather conditions estimated with a mobile electronic device that measured weather variables (e.g., temperature and relative humidity). To reduce detection issues related to identification, the birds were counted only by AGA, an expert ornithologist with > 10 years of experience surveying birds in the study area.

2.3. Avian diversity and community metrics

All statistical analyses were performed using the R statistical software (R Core Team, 2024). In each sampling point ($n = 400$), three biodiversity metrics were calculated, including taxonomic, functional and phylogenetic diversity. The taxonomic diversity was quantified as the total number of bird species recorded (bird species richness: BSR) (Magurran, 2004). The Rao's Quadratic Entropy (Rao's Q) was used to estimate functional diversity as the abundance-weighted variance of the dissimilarities between all species pairs (de Bello et al., 2010). The Rao's Q was calculated using the avian niche traits related to their feeding and breeding ecology extracted from Pearman et al. (2014). The trait information of each recorded species was obtained from general bird compilations, including the Birds of Africa (Brown et al., 1982; Fry et al., 1988; Fry & Keith, 2000; Fry and Keith, 2004; Urban et al., 1997; Keith et al., 2014; Urban et al., 1986), Birds of the World (Pearson, 2020) and Handbook of Avian Body Mass (Dunning, 2007). A total of 73 traits were compiled (see Awoyemi et al., 2024) for analyzing the Rao's Q of each point using the 'dbFD' function of the 'FD' package (Laliberté et al., 2015). Thirdly, phylogenetic diversity metrics (Faith, 1992; Helmus et al., 2007), including phylogenetic diversity richness (Faith's phylogenetic diversity; PD), and phylogenetic diversity divergence (phylogenetic species variability, PSV) were calculated given the need to incorporate complementary phylogenetic information of any community assemblage (Tucker et al., 2017). The PD and PSV were calculated

by building 100 phylogenetic trees of the species in each point count station based on genetic data from all bird species (Jetz et al., 2012) available at 'BirdTree' (<https://www.birdtree.org>). We then obtained average values of PD and PSV using functions 'pd' and 'psv' of the 'picante' and 'ape' packages (Kembel et al., 2010; Paradis et al., 2004).

2.4. Extraction of multispectral indices

Cloudless Sentinel 2 Level 1C Images, covering the period of bird censuses (i.e., November 2020-January 2021), were downloaded from the USGS Earth Explorer (<https://earthexplorer.usgs.gov/>). The Sentinel 2 Level 1C is more applicable to this study given its relatively high resolution and the small coverage of data collection points (50-m radius) compared to large-scale studies (Petrosillo et al., 2022; Wang & Atkinson, 2018). These were first preprocessed using the Semi-automatic Classification Plugin within the QGIS to convert raw pixel values to reflectance values and to perform atmospheric correction using the Dark Object Subtraction Correction Technique. The Sentinel allowed us to obtain reflectance images at the 10-m spatial resolution used to derive spectral indices with 'spectralindices' function of the RStoolbox (Alabi et al., 2022a; Avtar & Watanabe, 2020; Leutner et al., 2019). The mean and standard deviation of all available 10-m images/cells/pixels within the 50-m radius of each point count station were taken to estimate the spectral indices (see Figure S1 for a complete list and acronyms) following previous studies using a similar approach (e.g., Benedetti et al., 2023; Morelli et al., 2021). The 50-m radius buffer synchronizes with the exact area of bird censuses, which is commonly used in studies on urban avian diversity (e.g., Ibáñez-Álamo et al., 2020; Sanllorenzo et al., 2023).

2.5. Statistical analyses

Multistage statistical analyses were performed to select and model the most suitable remotely sensed spectral predictors of bird taxonomic, functional and phylogenetic diversity. For modeling, all the continuous variables (spectral indices) were scaled and centered with the 'scale' function of the 'optimx' package to ensure they are within the same range and improve the performance of the algorithm and models (Morelli et al., 2021; Nash, 2017). However, the graphs were plotted using the unscaled variables to infer the significant relationships between the dependent and independent variables similar to other previous studies (e.g., Sanllolente et al., 2023; Schielzeth, 2010). In addition, a Mantel test was performed to check for spatial autocorrelation across the point count stations based on a matrix of the geographic distance of the points and a matrix of differences in BSR, Rao's Q, PD and PSV using the Monte Carlo permutations with 9999 randomizations (Legendre & Fortin, 2010; Mantel, 1967). This test revealed no statistically significant spatial autocorrelation issues (all p values < 0.05), thus, allowing us to consider each point count station as independent observations in subsequent analyses (Dormann et al., 2007; Karlin et al., 1984).

Thereafter, the spectral indices (mean and SD separately at 50-m radius) were ranked based on their potential to predict each avian diversity metric by carrying out a feature importance analysis using the 'Boruta' package (Kursa & Rudnicki, 2010). The Boruta package is an advanced technique built upon the random forest regression model that removes statistically irrelevant variables and is one of the most accurate and robust feature selection methods (Degenhardt et al., 2019; Sanchez-Pinto et al., 2018; Speiser et al., 2019). This machine-learning algorithm constructs various independent decision trees for model fitting, and selects the model with the maximum votes for a specific class or value (Breiman, 2001). From each node, inputted variables are selected randomly, after which the subsets are used to calculate the best model output (Alabi et al., 2022a; Herrero-Huerta et al., 2020).

The result of the random forest regression showing the ranking of the 29 spectral indices is presented in Figure S1. Regarding SD analysis, MTCI was rejected as a potential predictor of Rao's Q and PSV, MCARI and REIP were rejected because they were unable to potentially predict PSV. Although this reveals that the remaining spectral indices could be potentially useful in modeling the biodiversity metrics, they differ in their predictive power (Figure S1), and are highly correlated (i.e., VIF > 5) based on the multicollinearity test performed with the 'vif.mer ()' function of the 'performance' package (Bernat-Ponce et al., 2021; Lüdeck et al., 2021). Because of this multicollinearity issue, and to avoid overparameterization of models and enhance the interpretation of results (Baranyi et al., 1996; Marhuenda et al., 2014; Ortega-Álvarez et al., 2022; Seibert et al., 2019), only the topmost ranked spectral indices were incorporated in subsequent analyses based on their predictive power (Table 1).

Subsequently, Generalized Linear Mixed Models (GLMMs) were employed. BSR was included as the response variable modeled assuming Poisson distribution (using 'glmer' function from 'lme4' package), while the remaining response variables (i.e., Rao's Q, PD, and PSV) were

modeled assuming Gaussian distribution based on the 'lmer' function of 'lme4' package (Bates et al., 2015). In addition, because BSR strongly correlates with PD (Tucker et al., 2017), BSR was included as a control independent variable while modeling this phylogenetic diversity metric following previous procedures (e.g., Morelli et al., 2021; Tucker et al., 2017). City (n = 8) was included as a random factor to account for possible consistent differences among paired locations. Habitat (urban vs non-urban) and vegetation zone (rainforest vs savannah) were included as fixed factors, while the topmost spectral indices corresponding to each biodiversity metric (see Table 1) were modeled as predictors. However, the vegetation zone strongly correlated with the topmost ranked spectral indices in almost all cases (i.e., VIF > 10), and was therefore removed from the analysis based on the same reasons stated above. The two-way interaction between habitat and the corresponding spectral index was also incorporated in the models. Meanwhile, the Akaike Information Criterion value (Burnham & Anderson, 2002) and generalized R² with the 'rsq' package were calculated as a measure of model fit (Kong et al., 2022; Overs et al., 2023; Zhang, 2022). The statistical significance was set at p value < 0.05. Finally, the magnitude of effect sizes (< 0.2 = negligible, < 0.5 = small, < 0.8 = medium, otherwise = large) of all the variables retained in the final models (Cohen, 1992) were calculated. This incorporation of the magnitude of effect size statistics has been recommended in biological sciences as it enhances the assessment of the relationships within data than the sole use of p-values (e.g., Nakagawa & Cuthill, 2007). This approach has been applied in many biological and social sciences research (e.g., Díaz et al., 2013; Jungmann & Witthöft, 2020; Strelan et al., 2020).

To determine the strength of the GLMMs, a 10-fold cross-validation was also performed with the 'caret' package (Kuhn et al., 2023). This involved dividing the entire dataset into training and testing subsets using 70/30 proportions known to give the best result based on an evaluation of different machine learning techniques (Alabi et al., 2022; Nguyen et al., 2021). The Mean Absolute Error, Mean Squared Error, Root Mean Squared Error, Normalized Root Mean Squared Error, and R-squared (as squared Pearson's r) were computed (Table S1) to assess the quantitative performance of the GLMMs (Kuhn et al., 2023). The whole methodological procedure is summarized in Figure 2.

3. Results

In this study, a total of 6,477 birds of 207 species were recorded from the 400-point count stations equally distributed across the study sites, habitats and vegetation zones in Nigeria. In general, more birds were recorded in the non-urban (50.3 ± 17.4 SD) than the urban habitat (21.9 ± 4.8 SD). The differences in the bird species richness recorded across the studied habitats and cities are presented in Table 2.

3.1. Ranking of multispectral predictors of avian diversity metrics

The random forest regression reveals the topmost ranked spectral indicators of each avian diversity component (Table 1; Fig. S1). This

Table 1

Topmost ranked spectral indices (mean and SD) with the best predictive power of bird taxonomic (BSR), functional (Rao's Q), phylogenetic diversity richness (PD) and phylogenetic divergence (PSV) across habitats (urban and non-urban) and vegetation zones (rainforest and savannah) in Nigeria. The full ranking of all the spectral indices is presented in Figure S1.

	Mean (50-m radius)				Standard Deviation (50-m radius)			
	BSR	Rao's Q	PD	PSV	BSR	Rao's Q	PD	PSV
MCARI	1st		1st		MCARI			
SR					SR	1st		
NDWI2		1st			NDWI2			
NBRI					NBRI		1st	
SATVI				1st	SATVI			1st
CLG					CLG			1st

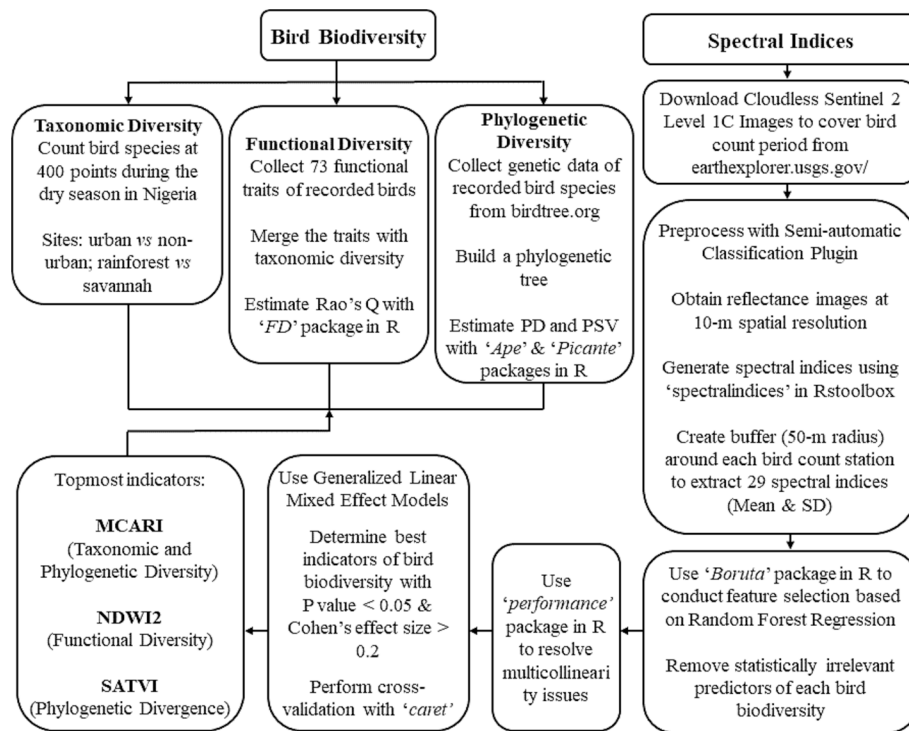


Fig. 2. Flow diagram summarizing the study methodology.

Table 2

Total bird species richness recorded across habitats (urban vs non-urban) in Nigeria, November 2020–January 2021. The size of each city was obtained from Google Earth (accessed October 2020).

City	City size (km ²)	Bird Count (Urban)	Bird Count (Non-urban)
Auchi	35	20	66
Calabar	406	17	45
Ibadan	3,080	24	80
Lagos	1171	16	56
Birnin Kebbi	35	20	32
Dutse	45	24	48
Gombe	90	23	26
Jos	260	31	49
Mean	640.25	21.88	50.25
Standard Deviation	1,057.17	4.76	17.41

procedure also discarded several indicators for the mean and SD approach. The results for the mean dataset indicate that MTCI cannot be used to predict phylogenetic divergence. Regarding SD values, MTCI, MCARI, and REIP were rejected as potential predictors of PSV. In addition, MTCI and MCARI were also rejected and selected tentatively as predictors of Rao's Q, respectively. The ranking of spectral indicators shows MCARI as the most highly ranked index capable of potentially predicting both BSR and PD, simultaneously. The analyses also show the potential of SATVI by ranking it first to simultaneously predict PSV (mean) and PD (SD). In most cases (i.e., mean and SD across all diversity metrics), the commonly modeled NDVI ranks very low (occupying the 25th percentile) based on its predictive power (Fig. S1).

3.2. Relationships between avian diversity metrics and the mean of spectral indices across habitats

A significantly higher BSR was found in the non-urban (Estimate ± SE = 1.83 ± 0.05, Z = 36.32, p < 0.001; Fig. 3; Table S2) than the urban habitat (Estimate ± SE = -0.58 ± 0.05, Z = -11.99, p < 0.001, effect size = -0.58; Table S2). This result contrasts with those obtained for the

remaining metrics as the urban habitat holds significantly higher levels of Rao's Q (Estimate ± SE = 8.18 ± 3.25, t = 2.52, p = 0.01, effect size = 0.24; Fig. 3; Table S2) and PD (Estimate ± SE = 14.44 ± 5.90, t = 2.45, p = 0.02, effect size = 0.08; Fig. 3; Table S2) than the non-urban habitat (Fig. 3; Table S2). Although not statistically significant, PSV values were also higher in the urban habitat (Estimate ± SE = 9.42E-04 ± 1.44E-03, t = 0.66, p = 0.51; Fig. 3; Table S2) compared to the more natural habitat (Fig. 3; Table S2). In all cases, variations in the values of BSR, Rao's Q, PD and PSV here were similar to those obtained by a previous study using the same dataset focused on investigating the influence of urbanization on avian diversity components in the Afrotropics (Awoyemi et al., 2024).

Regarding spectral indices, the main focus of this study, a significant interaction effect of MCARI with habitat was found on BSR (Estimate ± SE = -0.29 ± 0.08, Z = -3.64, p < 0.001, effect size = -0.29; Table S2), showing an increase in the BSR value as MCARI increases in the non-urban habitat compared with the adjacent urban habitat (Fig. 4a). Further, the significant interaction effect of MCARI with habitat on PD (Estimate ± SE = 28.71 ± 7.39, t = 3.88, p < 0.001, effect size = 0.16; Table S2) showed an opposite pattern to that obtained for BSR: in this case, PD values increases in the urban habitat as MCARI increases in comparison with the adjacent urban habitat (Fig. 4b). Furthermore, NDWI2 mediated the effect of urbanization on Rao's Q as this significant interaction effect (Estimate ± SE = 10.18 ± 3.68, t = 2.76, p = 0.006, effect size = 0.30; Table S2) revealed an increasing Rao's Q values as NDWI2 increases in the urban habitat compared with the non-urban habitat (Fig. 4c). Meanwhile, the interaction effect of habitat and SATVI on PSV showed a marginal statistical significance (Estimate ± SE = 2.81E-03 ± 1.52E-03, t = 1.85, p = 0.07; Table S2). Overall, these results (Table S2) compare with those validated through machine learning approach as revealed by the R-squared values (Table S1).

3.3. Relationships between avian diversity metrics and the standard deviation of spectral indices across habitats

The analyses using the SD approach represent the variation in the

Estimate	Mean (50-m radius)			
	BSR	Rao's Q	PD	PSV
Urban	-0.58	0.24	0.08	
MCARI	0.24		-0.07	
NDWI2		-0.19		
SATVI				
Urban x MCARI	-0.29		0.16	
Urban x NDWI2		0.30		
Urban x SATVI				
Estimate	Standard Deviation (50-m radius)			
	BSR	Rao's Q	PD	PSV
Urban	-0.60	0.23	0.08	
CLG				
NBRI				
SATVI			-0.07	
SR	0.10			
Urban x CLG				
Urban x NBRI				
Urban x SATVI				
Urban x SR	-0.12			

Fig. 3. Schematic presentation of main associations between values of taxonomic diversity estimated from bird species richness (BSR), functional diversity estimated from Rao's Quadratic Entropy (Rao's Q) and phylogenetic diversity estimated from Faith's phylogenetic diversity (PD) and phylogenetic species variability (PSV), calculated for avian communities across urban and non-urban habitats in Nigeria, and spectral indices. Positive associations are indicated in green color (light green for effect sizes < 0.2), negative ones are highlighted in red (light red for effect sizes < 0.2), grey color indicates indices not incorporated in the model regarding each response variable, while white color denotes tested variables not statistically significant. The magnitude of effect sizes (< 0.2 = negligible, < 0.5 = small, < 0.8 = medium, otherwise = large; Cohen, 1992) of all the significant variables are inserted in each cell. These results are simplified to reflect only significant variables from the final models shown in detail in Table S2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

investigated spectral indices during the entire period of data collection (November 2020-January 2021). Regarding this measure, findings for the predictor habitat (urban vs non-urban) were very similar to those obtained in the analyses using mean values for the spectral indices. BSR was significantly higher in the non-urban (Estimate ± SE = 1.82 ± 0.10, Z = 18.16, p < 0.001; Fig. 3; Table S2) than the urban habitat (Estimate ± SE = -0.60 ± 0.05, Z = -12.22, p < 0.001, effect size = -0.6; Table S2). Although showing a similar pattern, the higher value of PSV recorded in the non-urban (Estimate ± SE = 3.19E-02 ± 1.26E-03, t = 25.31, p < 0.001; Fig. 3; Table S2) than the urban habitat was not statistically significant (Estimate ± SE = -4.53E-04 ± 1.19E-03, t = -0.38, p = 0.70; Table S2). In contrast, urban habitat supported significantly higher levels of Rao's Q (Estimate ± SE = 7.64 ± 3.29, t = 2.32, p = 0.02, effect size = 0.23; Fig. 3; Table S2) and PD values (Estimate ± SE = 14.17 ± 6.42, t = 2.21, p = 0.03, effect size = 0.08; Fig. 3; Table S2) than the nearby non-urban habitat: Rao's Q non-urban habitat (Estimate ± SE = 38.36 ± 3.21, t = 11.94, p < 0.001, effect size = -0.12; Fig. 3; Table S2); PD non-urban habitat (Estimate ± SE = 332.90 ± 6.30, t = 52.86, p < 0.001, effect size = -0.05; Fig. 3; Table S2).

In general, no significant interaction effects between the SD of spectral indices and habitat were found on any of the diversity metrics considered (Table S2). However, results show that SR significantly increased BSR values (Estimate ± SE = 0.10 ± 0.03, Z = 3.64, p < 0.001, effect size = 0.10; Fig. 3; Table S2), while SATVI significantly decreased PD (Estimate ± SE = -12.44 ± 5.89, t = -2.11, p = 0.04, effect size = -0.07; Fig. 3; Table S2). Finally, neither NBRI nor CLG had any statistically significant effect on Rao's Q (Estimate ± SE = 1.51 ± 2.34, t =

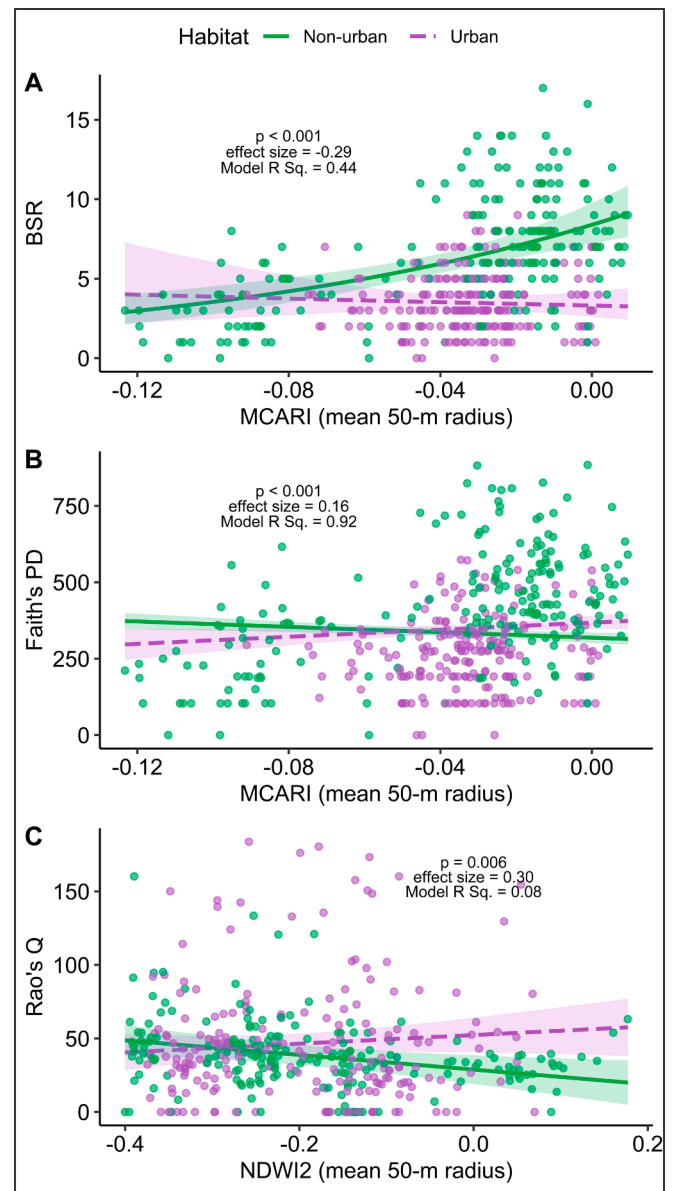


Fig. 4. (A) Association of the Modified Chlorophyll Absorption Ratio Index (MCARI) and taxonomic diversity (BSR) by habitat (urban vs non-urban), (B) association of MCARI and phylogenetic diversity (Faith's PD) by habitat (urban vs non-urban), and (C) association of the Normalized Difference Water Index II (NDWI2) and functional diversity (Rao's Q) by habitat (urban vs non-urban). Please, note that the plots are based on unscaled independent variables (i.e., spectral indices) and might not completely match the predicted effect based on the models (e.g. MCARI x habitat for Faith's PD). The p-value, effect size and R² of the significant effects are inserted in the corresponding panel above (see Table S2 for the full model output).

0.64, p = 0.52, effect size = 0.04; Fig. 3; Table S2) and PSV (Estimate ± SE = -1.13E-05 ± 8.40E-04, t = -0.01, p = 0.989; Fig. 3; Table S2), respectively, even if they were the topmost ranked spectral indices selected by the Boruta model.

4. Discussion

This study revealed suitable remotely sensed spectral indicators of bird taxonomic, functional and phylogenetic diversity across Afro-tropical environments. It complements the growing body of literature demonstrating the relevance of these indices for monitoring biodiversity over the use of traditional field-based environmental measures that are

potentially less accurate, laborious, expensive and prone to investigators' errors (Ghosh et al., 1995; Gorrod & Keith, 2009; Morrison, 2016). By performing multistage statistical analyses, this study sheds light on the effectiveness of using remotely sensed spectral indices for monitoring biodiversity over space and time. Furthermore, the association between some of these spectral indices and different avian diversity components can change between urban and non-urban habitats, providing useful directions for researchers and conservationists. This study does not aim to discuss differences in avian diversity between urban and non-urban habitats in the region as it has been done in a previous study using the same dataset (Awoyemi et al., 2024). In contrast, it discussed the effectiveness of using the spectral indices as proxies for monitoring changes in multifaceted avian diversity across Afrotropical urban and non-urban habitats.

4.1. Predictive power of spectral indices across multifaceted avian diversity

To our knowledge, this study is the first to simultaneously investigate the predictive associations between multispectral indices (29) and avian taxonomic, functional and phylogenetic diversity across Afrotropical urban and non-urban environments (see Awoyemi & Ibáñez-Álamo, 2023). In this respect, the result of this study revealed that spectral indices do not only differ in their capacity to potentially predict avian diversity, but are also strongly influenced by the specific biodiversity component investigated, supporting the need to simultaneously use diverse spectral indices. Considering the mean, for example, while MCARI was the topmost ranked index capable of potentially predicting BSR and PD, NDWI2 and SATVI had the most capability of predicting Rao's Q and PSV, respectively. It is on this backdrop that we argue against the "universal" use of a single index like the NDVI as a proxy for investigating multiple facets of biodiversity (e.g., Bae et al., 2018; Lev-*eau* et al., 2020). The NDVI ranks below average in most cases here (Fig. S1), a pattern found by other plant-based studies (e.g., Alabi et al., 2022a; Alabi et al., 2022b). While this study did not invalidate the use of NDVI, it showed that other spectral indices outperform it. Interestingly, MCARI, NDWI2 and SATVI have been reported that they overcome some of the limitations attributed to NDVI (Gitelson, 2004; A. Huete et al., 2002; Huete & Jackson, 1988; Main et al., 2011; McFeeters, 1996; Wu et al., 2008), and are rated first in this study. In addition, MCARI ranks as the topmost predictor of both BSR and PD, supporting the consistency of the overall results as these two measures of biodiversity are known to be strongly correlated (e.g., Morelli et al., 2021; Sanllorente et al., 2023). Given that Rao's Q is not correlated with BSR (Botta-Dukát, 2005), it is not surprising that a different spectral index (NDWI2) rather than MCARI ranks as the strongest predictor of functional diversity. This finding also highlights the significance of "non-vegetation" variables on biodiversity (NDWI2 is associated with water; McFeeters, 1996), and strengthening the initial argument revolving around the need to test the efficiency of multispectral indices while investigating biodiversity metrics (Bae et al., 2018; Benedetti et al., 2023). MTCI was the most commonly rejected predictor of avian diversity in this study, which recommends against its use in this context. This index also measures chlorophyll concentration, and has been employed for related measures such as leaf defoliation (e.g., Hawryło et al., 2018). Its rejection here could be attributed to the better performance of MCARI (related index) at predicting avian diversity in the Afrotropical region. This study thus provides a clear direction for future studies aiming to investigate the relationships between spectral indices and multiple facets of biodiversity in Afrotropical environments. Additionally, it opens up this remote sensing research line so that future studies can test the validity and applicability of the ranking result across other taxa, regions and habitats.

4.2. Relationships between spectral indices and multifaceted avian diversity across habitats

The GLMM results suggested that using the mean of spectral indices as a proxy for biodiversity performs relatively better than the SD. This conclusion is based on the higher number of significant associations using the mean in comparison with the SD (6 vs 3). In fact, all the three significant interaction for SD data indicated negligible effect sizes (0.07–0.12), rather supporting the use of mean data. This result compares with those from other studies (e.g., Benedetti et al., 2023; Hobi et al., 2021), and suggests that the mean of spectral indices better reflects the different avian diversity components than their variations estimated through the SD. Alternatively, environmental variations during the 3-month period of data collection may not be enough to trigger statistically significant associations with the investigated biodiversity metrics. Future studies could consider longer periods (within or between years) to explore the influence of environmental variations further.

Unlike other studies from temperate regions mainly using NDVI and EVI to evaluate avian diversity (e.g., Bae et al., 2018; Benedetti et al., 2023; He et al., 2015; Xu et al., 2022), this study proposes the use of MCARI, NDWI2 or SATVI to simultaneously model multiple avian diversity components across urban and non-urban habitats. Regarding the mean, MCARI was positively associated with higher avian taxonomic diversity in the non-urban habitat. This index measures leaf chlorophyll content, a good indicator of photosynthetic ability required for various plant metabolic activities, particularly growth and food production (Daughtry et al., 2000; Wu et al., 2008). Increasing photosynthetic ability is closely associated with luxuriant vegetation growth and yield (Long et al., 2006; Makino, 2011), which are key to the persistence of birds due to the provision of food and nesting habitats (Ferber et al., 2014; Moorcroft et al., 2002; Narango et al., 2017). This may partly explain why MCARI was positively associated with bird taxonomic diversity in the non-urban habitat. In contrast, increasing MCARI was negatively correlated with bird taxonomic diversity in the urban habitat. Although initially surprising, this result suggests that a combination of different factors (e.g., habitat richness, vegetation structure...) rather than photosynthetic ability of vegetation alone determines bird taxonomic diversity in the urban habitat (e.g., Beninde et al., 2015). This position is consistent with the intermediate disturbance hypothesis, showing that bird taxonomic diversity peaks in urban areas with intermediate levels of disturbance (Callaghan et al., 2019; Tratalos et al., 2007). As noted during our survey, a high MCARI value in the urban habitat could be disproportionately influenced by certain gardens or parks dominated by few or exotic plant species which cannot hold high bird taxonomic diversity. Supporting this view, studies conducted in Canberra (Australia) and multiple Spanish cities showed that the replacement of native vegetation with exotics significantly reduced bird taxonomic diversity in urban areas (Ikin et al., 2013; Sánchez-Sotomayor et al., 2022). Since bird taxonomic diversity in urban areas is, in general, positively associated with higher and native plant species (e.g., Narango et al., 2017), this result suggests that maintaining a mosaic of habitats (including vegetation dominated by native species) within urban areas could be more important for birds than only the amount of vegetation vis-à-vis MCARI in the area.

Although with a small effect size (0.16), the significant interaction between MCARI and habitat on phylogenetic diversity contrasted with the result on taxonomic diversity. It showed that while taxonomic diversity reduces with higher MCARI value in the urban habitat, phylogenetic diversity increases. This result suggests that evolutionarily unique groups of distantly related birds are attracted to urban areas with high MCARI values. In this sense, avian assemblages showing a preference for various vegetation compositions associated with MCARI, such as flowers (sunbirds), fruits (hornbills), tree canopy (vultures) or grasses (firefinches) recorded during the study, could have enriched phylogenetic diversity in the urban habitat. This would have added to the

phylogenetic diversity values already contributed by birds (e.g., swifts, sparrows or crows) that are more associated with urban features (e.g., built surfaces and telecommunication platforms) than vegetation (MCARI) in comparison with the non-urban habitat. In general, this study showed that Afrotropical urban areas with high productivity levels indicated by high MCARI values are rich in bird phylogenetic diversity. This is probably because urban areas with high MCARI values support evolutionarily unique groups of birds even while the species richness is low relative to the non-urban habitat.

The NDWI2 delineates water resources while eliminating soil and terrestrial vegetation features (McFeeters, 1996), which is useful for assessing bird habitat suitability (e.g., Teng et al., 2021). Interestingly, this study showed that the functional diversity of birds significantly increases as NDWI2 increases in the urban habitat in comparison with the non-urban habitat. This interaction has the highest effect size (0.30) among all the indices investigated in this study, clearly showcasing the significance of water resources to birds in the Afrotropical urban habitat. This study was conducted during the dry season, when water and food resources are scarce in the area (Siegfried, 1972; Sinclair, 1978). Thus, the feeding and breeding opportunities provided by water during these harsh conditions could attract birds with diverse traits, invariably promoting the functional diversity obtained in this study. In addition, this higher functional diversity may not have been contributed by waterbirds alone. For instance, the observation of luxuriantly growing bushes and grasses near urban puddles during the fieldwork could provide feeding and breeding opportunities for other functionally different groups of birds like nectarivores and granivores. Corroborating this finding, a study conducted across Europe showed that the proportion of water coverage in the urban habitat is significantly associated with higher values of avian functional diversity in both the breeding and wintering seasons (Ibáñez-Álamo et al., 2020). During our survey, we observed that the coverage of water permeates extensive building density, and contributes to the mosaic of habitats available for different groups of birds in the urban habitat, further supporting the finding. Regarding the contracting result showing that increasing NDWI2 reduces functional diversity in the non-urban habitat, it could be speculated that the effect of water coverage on functional diversity is mediated by landscape organization shaping bird traits in these two habitats (e.g., Ibáñez-Álamo et al., 2024). Although with a marginal statistical significance ($p = 0.07$), increasing SATVI tends to increase the degree of phylogenetic relatedness of birds in the urban habitat. With this, urban areas with a high vegetation cover indicated by higher SATVI seem to hold more closely related bird species.

5. Conclusions

This study provides an evidence base supporting the use of remotely sensed spectral indicators as proxies for monitoring avian diversity in Afrotropical environments, which is crucial given the manpower and socioeconomic restrictions of the region (Awoyemi & Ibáñez-Álamo, 2023). We tested the relevance of this methodological approach using a relatively large dataset from Nigeria (8 paired urban and non-urban sites across rainforest and savannah), one of the most rapidly urbanizing countries at the global level, and a typical representative of the Afrotropical region (Awoyemi & Ibáñez-Álamo, 2023; OECD/SWAC, 2020; Seto et al., 2012).

Bird taxonomic, functional and phylogenetic diversity are not similarly affected by urbanization in the Afrotropics (e.g., Awoyemi et al., 2024) and other regions (e.g., Hagen et al., 2017; Ibáñez-Álamo et al., 2020; Morelli et al., 2021). Thus, one remotely sensed spectral indicator may not be appropriate to monitor all components of avian diversity in tandem, in which case this study recommends the use of several indicators, including MCARI, NDWI2 and SATVI. This study also showed that using the mean of spectral indices outperforms SD while investigating multiple avian diversity metrics. By being the topmost ranked indicator simultaneously predicting taxonomic and phylogenetic

diversity, this study identifies MCARI as the best indicator of avian diversity in Afrotropical environments, and recommends its use as such. MCARI estimates the photosynthetic ability of vegetation, a measure of primary productivity, while accounting for shadow, soil reflectance and nonphotosynthetic materials (Daughtry et al., 2000; Wu et al., 2008). Thus, it can overcome some of the limitations of the NDVI, a more commonly used index in this respect that ranks very low among the spectral indices investigated here. This study also showed that high MCARI values in the urban habitat are associated with low bird taxonomic diversity but high phylogenetic diversity. Furthermore, NDWI2, the topmost predictor of functional diversity in the region, exhibits a positive significant effect in the urban habitat. From an applied perspective, these combined indicators could be used to remotely monitor the different bird diversity metrics in certain Afrotropical urban and non-urban areas (e.g., expansive, inaccessible or insecure sites), which could even be more cost-effective. This insight could be useful for certain governmental and non-governmental agencies responsible for monitoring biodiversity in the region, such as the BirdLife International, represented in the study area by the Nigerian Conservation Foundation. To encourage biodiversity-friendly cities in the Afrotropics, this study showed that maintaining a mosaic of habitats high in photosynthetic ability (MCARI) and water (NDWI2) could boost bird phylogenetic and functional diversity in urban areas, thereby providing a clear applied recommendation for city planners and other urban stakeholders in the area. We recommend future studies to test the validity of our findings across other taxa, regions, and habitats.

CRedit authorship contribution statement

Adewale G. Awoyemi: Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data analysis, Conceptualization. **Tunrayo R. Alabi:** Writing – review & editing, Validation, Software, Formal analysis, Data curation. **Juan Diego Ibáñez-Álamo:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112966>.

Data availability

Data will be made available on request.

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