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Ecomorphological Traits of Bird Communities Along Urbanization Gradient in A Tropical Peri-Urban Landscape of Bogor, Indonesia

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ABSTRACT

In Indonesia, peri-urban landscapes are rapidly developing and characterized by mosaics of natural, agricultural, and developed areas. This study investigated the effects of environmental differences across an urbanization gradient on bird community structure and the composition of ecomorphological traits within the tropical peri-urban landscape of Bogor, Indonesia. Field surveys were carried out between September and February from 2020 to 2023 in five habitats: secondary forest, plantation, riparian, built-up area, and farmland. Habitat conditions were characterized using Leaf Area Index (LAI), Normalized Difference Vegetation Index (NDVI), land-cover composition, and vegetation measurements. Bird communities were evaluated through standardized point-count surveys and the calculation of diversity indices. Relationships between habitat variables and bird ecomorphological traits were assessed using Generalized Linear Mixed Models (GLMMs) and model-based fourth-corner analysis. In total, 19,637 individuals representing 77 species and 35 families were recorded. Species richness was greatest in secondary forest and lowest in farmland, while the Shannon–Wiener index declined from 3.136 to 2.218 along the gradient from less disturbed to more modified habitats. Tree species richness emerged as a key predictor of several ecomorphological traits. Structurally complex habitats favored arboreal, frugivorous, nectarivorous, and cavity-nesting birds, whereas farmland and built-up areas were dominated by generalist, aerial, and omnivorous species. These patterns indicate that vegetation simplification may drive ecological filtering and functional homogenization. Therefore, in tropical urban environments with rapid urbanization, conservation should emphasize the preservation of remnant trees, enhancement of multilayered vegetation, and restoration of riparian corridors to boost habitat variability and connectivity for bird conservation.

Introduction

Urbanization is often identified as a significant driver of global ecosystem change, changing landscapes, and threatening biodiversity at unprecedented threats [1]. Currently, over 50% of the world's population resides inside and near urban areas, and this percentage is steadily rising [2]. Rapid expansion of urban areas, accompanied by large land use conversion, has significant environmental impacts, especially in many tropical regions that host some of the highest levels of biodiversity [3]. Population growth propelled by urbanization exacerbates the loss and degradation of habitats, posing challenges for the conservation of biodiversity [4].

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Cities are becoming larger and are pushing out farther into the peri-urban zones, regions of transition that are interface zones between the urban centers and the rural areas around them [5]. These areas have been more subject to urban impact, sometimes presenting rapid ecological transformation of natural ecosystems from semi-natural to build ecosystems [6]. Nevertheless, peri-urban landscapes are ecologically important due to their varied habitat mosaics, including remaining secondary forests, riparian corridors, agricultural fields, and human settlements, which act as refuges for biodiversity [7,8]. Peri-urban regions are crucial but understudied biodiversity conservation landscapes due to their complexity.

Birds are among the most researched species because they are good bioindicators and have important ecological roles, mobility, and sensitivity to environmental change. They are also among the taxa most vulnerable to habitat changes along the urbanization gradient [9]. Urbanization may alter bird populations by environmental filtering mechanisms, which favor species with certain ecological or morphological traits that make them better able to cope with altered environments [10,11]. Bird persistence is shaped not only by taxonomic diversity but also by functional attributes that determine how species interact with their environment [12]. The ability of species to respond to habitat changes resulting from urban development is highly dependent on a suite of ecomorphological traits, including dietary preference, migratory behavior, disturbance tolerance, and nesting strategy, as well as morphological characteristics [10,11]. Hence, a trait-based approach is useful to understand how birds respond to environmental gradients [13].

Although trait-based avian ecology is well established in temperate regions, research in tropical regions remains uneven in its geographic coverage and ecological contexts, despite recent growth. Trait-based studies at the global scale have shown that urbanization is a functional filter that decreases morphological and dietary variety and favors more generalist species with broader ecological tolerances [10,14–17]. Regional studies across tropical cities in Asia, Africa, and the Americas have shown that frugivores, insectivores, and cavity-nesting birds are consistently less frequent in highly modified urban habitats than in nearby natural areas [13,16,18–22]. Much of this corpus of research inside Indonesia has been created via a lens of land use change rather than urbanization. A study in Jambi, Sumatra revealed the total absence of frugivores in rubber and oil palm monoculture areas, with direct effects on seed dispersion and pest regulation [23]. In North Sumatra, insectivore-frugivores are restricted to forest edges, whereas omnivores dominate residential matrices [24]. In Riau and Central Kalimantan, insectivores and frugivores in oil palm smallholdings depended primarily on spillover from adjacent forest remnants rather than on local plantation habitats, and in Sulawesi, endemic specialists retreated into intact lowland forests as agricultural land expanded [25,26]. Taken together, this body of evidence indicates that the avian functional composition across the Indonesian archipelago is highly sensitive to habitat modification.

However, no published study has examined how ecomorphological traits, including morphological and ecological traits, respond to fine-scale urbanization gradients within a tropical peri-urban landscape in Indonesia. This study aimed to address this gap by examining bird communities across five habitat types along an urbanization gradient in the Ciampea–Dramaga peri-urban landscape of Bogor, West Java. This landscape represents a continuum of habitats with varying levels of urbanization, ranging from remnant secondary forests to farmland and built environments. We hypothesized that bird diversity and functional trait composition vary systematically along the urbanization gradient, with more natural habitats supporting greater functional differentiation than do highly modified habitats. Furthermore, we posited that environmental filtering acts as a dominant ecological mechanism structuring bird trait assemblages along this gradient, where increasing habitat simplification and anthropogenic disturbance selectively favor generalist species while reducing specialists associated with structurally complex vegetation. Therefore, the specific objectives of this study were to (i) analyze habitat characteristics across the urbanization gradient, (ii) assess variations in bird community composition among habitat types, and (iii) model the responses and relationships of ecomorphological traits to differences in habitat characteristics.

Materials and Methods

Study Area

The study was carried out in Ciampea–Dramaga Landscape, which is a peri-urban region in the tropics of Bogor Regency, West Java, Indonesia (6°32’17”–6°33’13” S; 106°41’57”–106°45’33” E) (Figure 1). The study area was approximately 10.1 km^2 in size and was situated at an altitude of 120–190 m a.s.l (above sea level) (https://earth.google.com/ accessed on 27 October 2024), including a lowland mosaic ecosystem that interfaces the rural environment with Bogor City’ urban fringe. The landscape is driven by the rapidly

developing Greater Jakarta metropolitan area (also known as *Jabodetabek*, including Jakarta, Bogor, Depok, Tangerang, and Bekasi). The area is subjected to continuous anthropogenic pressure from agricultural intensification, population growth, and infrastructure development, leading to a distinct urbanization gradient and spatial variations in vegetation structure and land use intensity.

Five representative habitats were selected along the urbanization gradient: secondary forest, plantation, riparian zone, farmland, and built-up area. These habitats differed in canopy structure, vegetation density, and land-cover composition. Secondary forests with a multi-layered canopy and little human disturbance were the least changed habitat cover, whereas built-up regions were mostly residential or infrastructure features. Plantation, riparian, and farmland habitats represent different combinations of vegetation complexity and anthropogenic disturbance. Together, these natural and modified habitats provide an ecologically relevant framework for assessing bird community and functional trait responses to habitat variation and urbanization in tropical peri-urban landscapes.

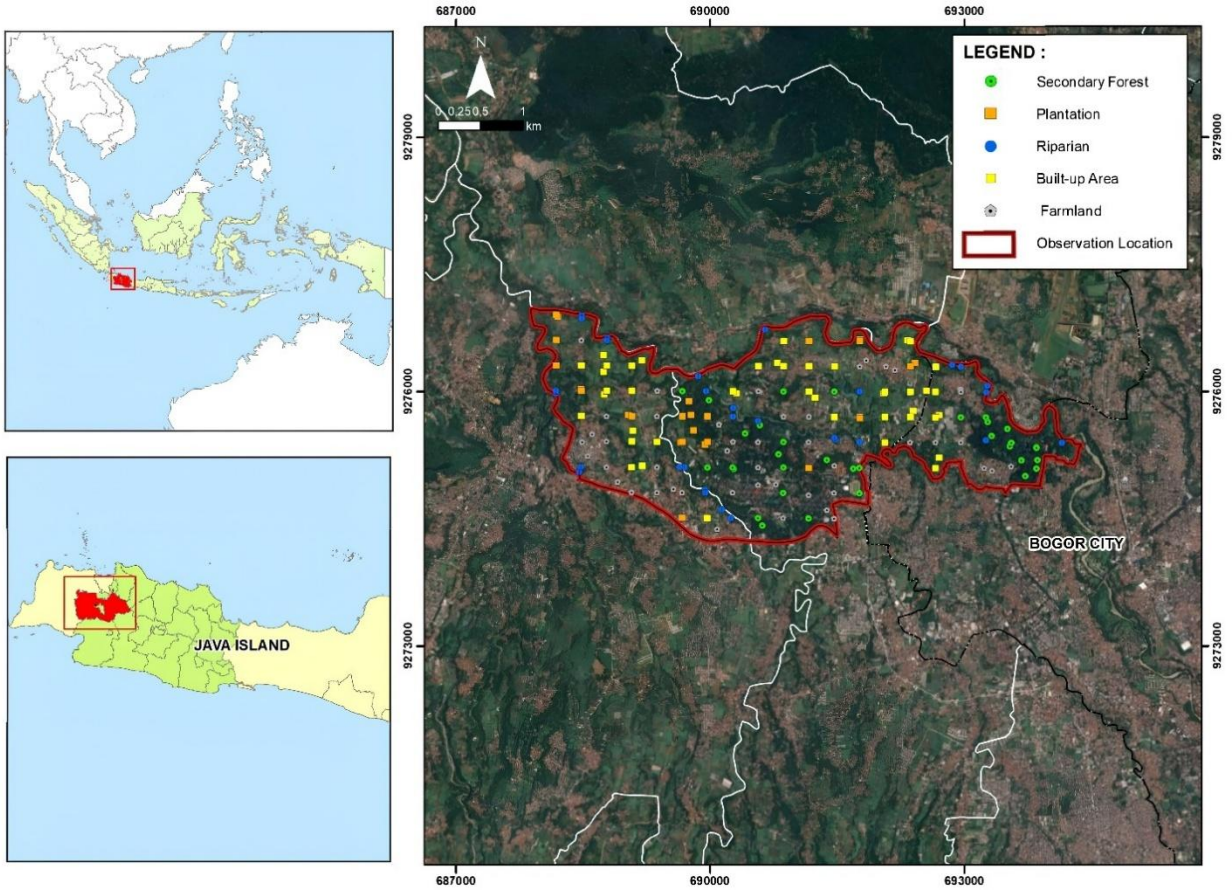


Figure 1. Location and spatial distribution of bird sampling stations in the Ciampea–Dramaga peri-urban landscape, Bogor Regency, West Java, Indonesia. The inset maps locate the study area within Java Island and Indonesia, while the main map shows the study boundary and point-count stations in secondary forest, plantation, riparian, built-up area, and farmland habitats.

Data Collection

Habitat Characteristics

Habitat characteristics were systematically quantified to represent an urbanization gradient across five habitat types, namely, secondary forest, plantation, riparian, built-up area, and farmland, within the Ciampea–Dramaga peri-urban landscape of Bogor, West Java. These habitat types were selected based on contrasting vegetation structures, land-use intensities, and levels of anthropogenic disturbance, forming a continuous gradient from low to high urbanization. Data collection was conducted from September to February during 2020–2023 period. This period was selected because it generally coincides with the late dry-to-wet transition and wet-season period in western Java and overlaps with the migratory season of several species of birds. During this period, vegetation productivity and food resource availability, such as fruits and

insects, are expected to increase, providing suitable conditions for assessing habitat characteristics and improving the detectability of both resident and migratory birds in the study area. As dry-season surveys were not conducted, potential dry-season variation is acknowledged as a limitation of this study.

Vegetation greenness and productivity were assessed using the Normalized Difference Vegetation Index (NDVI), calculated from near-infrared and red reflectance bands in satellite imagery. For each habitat type, NDVI values were obtained from nine spatially independent points aligned with the bird survey locations, allowing the habitat conditions to be directly related to the bird community responses. Canopy cover was quantified using the Leaf Area Index (LAI) from hemispherical canopy photography. Nine plots (20 × 20 m) were established in each habitat type, and hemispherical pictures were obtained at five consistent positions within each plot (four corners and one middle point). Diffuse light images were obtained using a fisheye lens to reduce lighting bias. Mean plot-level LAI values were used to represent canopy structural complexity across habitat types.

Land cover composition was assessed within 50 × 50 m buffers around each sample point based on high-resolution satellite images. Supervised classification was used to distinguish five land cover classes: tree cover, shrubs, agricultural vegetation, open land, and built-up surfaces. The proportional area of each cover object was then calculated to characterize horizontal habitat heterogeneity and land use intensity. Vegetation composition was assessed using nested 20 × 20 m plots covering seedlings, saplings, poles, and trees, following standard survey methods [27]. Vegetation surveys were conducted at five sampling locations per habitat type, each comprising three plots, resulting in a total of 15 plots per habitat type (75 plots in total). Species identity, abundance, diameter at breast height (DBH), and plant height were recorded to quantify the structural and compositional attributes of the vegetation.

Bird Surveys

Bird surveys were conducted during three sampling periods: September 2020–January 2021, September 2021–February 2022, and September 2022–February 2023. These periods covered the late dry-to-wet transition and wet season conditions. Bird communities were surveyed using a standardized point-count method within circular plots with a radius of 50 m [28]. The minimum distance between the point observations was 150 m to reduce spatial overlap and minimize the likelihood of double-counting individuals. During the 2020–2021 and 2021–2022 sampling periods, point observations were established using systematic sampling and were maintained at the same locations during both periods. The number of point observations per habitat was 17 in secondary forests, 15 in plantations, 17 in riparian zones, 33 in built-up areas, and 28 in farmland. In the 2022–2023 sampling period, the sampling effort was standardized to 15 point-count stations per habitat type using stratified sampling; therefore, the point locations differed from those used in the two previous periods.

At each point location, bird surveys were conducted for 15 min during two daily activity periods: morning (6–9 a.m.) and afternoon (3–6 p.m.). Each point was surveyed twice on different days to enhance the detection probability and account for temporal variations in bird activity [29]. Thus, each point received four observation visits per sampling period, consisting of two daily sessions repeated on two separate days, with a total observation duration of 60 min per point. The details of the bird point-count stations, repeat visits, years sampled, and total active observation hours across habitat types are presented in Table 1. The observations were made exclusively in favorable weather. In order to species identification, binoculars, digital cameras and audio recorders were utilized and GPS devices were used to enter the geographical coordinates of each observation site. Species identification was carried out using reputable regional field guides and the latest Indonesian bird checklist was utilized for taxonomic nomenclature [30–32]. Species presence and abundance data were organized into a habitat-by-species matrix to be used for further analysis.

Table 1. Bird survey effort across five habitat types in the Ciampea–Dramaga landscape during three sampling periods from 2020 to 2023. The table reports the number of point-count stations, four repeat visits per station, and total active observation hours; each station contributed 60 min of observation per sampling period.

Type of habitat	Bird points by sampling period			Repeat visits	Total observation hours
	2020–2021	2021–2022	2022–2023		
Secondary forest	17	17	15	4	49
Plantation	15	15	15	4	45
Riparian	17	17	15	4	49
Built-up area	33	33	15	4	81
Farmland	28	28	15	4	71

Ecomorphological Traits-Habitat Characteristics

The ecomorphological traits of all recorded bird species were compiled to assess functional responses to habitat variation along the urbanization gradient. The traits were categorized into ecological and morphological dimensions, indicating behavioral, life history, and structural adaptations to environmental conditions. Ecological traits comprised feeding guild, primary lifestyle, reproductive strategy, migratory status, nest type, and nesting substrate. Morphological traits included body mass, bill proportions (length, width, and depth), hand-wing index, tarsus length, and tail length.

Trait data were collected by direct measurement of adult individuals from the ornithological collections at the Museum Zoologicum Bogoriense (MZB), supplemented with secondary data from worldwide trait databases and published literature [33,34]. Measurements were standardized among data sources, and adult trait values were averaged to derive species-level means. This procedure minimized individual variation and improved consistency in community-level analyses.

Feeding guilds (insectivore, granivore, frugivore, nectarivore, piscivore, carnivore, and omnivore) represent trophic specialization [20], whereas primary lifestyle categories (aerial, terrestrial, insessorial, and generalist) describe mobility and foraging strata [33]. Reproductive strategy was classified as brood-parasitism or non-brood-parasitism [35], while species were categorized as resident or migratory based on their migratory status [36]. Nesting-related traits included nest type (no nest, cavity, open, domed, or nest parasitism) [35] and substrate (the structure in which they place their eggs, i.e., in the ground, tree, non-tree vegetation, or cliff-bank) [34]. This integrated trait framework provides a comprehensive assessment of bird functional strategies across habitat types.

Data Analysis

Habitat Characteristics

Habitat characteristics were assessed by combining remote-sensing indices with field vegetation data to capture multidimensional environmental variation. NDVI values were calculated using standardized red and near-infrared spectral bands on ArcMap software version 10.8 and averaged each sample point within each habitat type [37]. LAI was estimated from hemispherical photographs processed in HemiView software version 2.1, with plot-level values averaged across five images.

Land cover composition was quantified within 50 × 50 m plots using supervised classification of high-resolution satellite imagery. Vegetation composition at each growth stage was evaluated using the Importance Value Index (IVI), which combines relative density, frequency, and dominance to identify dominant plant species [38]. Together, these metrics characterized horizontal and vertical habitat heterogeneity along the urbanization gradient.

Bird Communities

Bird community structure was compared among habitat types based on taxonomic diversity, evenness, dominance, and species composition. Species diversity was measured using the Shannon–Wiener Diversity Index, Pielou´s Evenness Index, and Berger–Parker Dominance Index [39]. Community similarity among habitats was quantified using the Bray–Curtis Similarity Index and visualized with the unweighted pair group method with arithmetic mean (UPGMA) hierarchical clustering. All diversity and similarity analyses were done in RStudio software version 4.2.3 using the package 'BiodiversityR'. Hierarchical clustering was performed using the PAST software version 4.03. These complementary metrics permitted a more direct interpretation of species diversity, community dominance, and compositional similarity along the urbanization gradient.

Ecomorphological Traits-Habitat Characteristics

Ecomorphological trait–habitat characteristic relationships were examined using three matrices: environmental variables (R), species abundance (L), and species traits (Q). Environmental predictors included NDVI, LAI, proportionate land cover classes, vegetation density, tree species richness, and mean DBH and height. All predictors were standardized before to analysis and pairwise correlations were used to check for multicollinearity, with predictors with an absolute value of r greater than 0.75 removed to avoid redundancy [40].

Generalized Linear Mixed Models (GLMMs) were used to analyze the responses of individual ecomorphological traits to habitat characteristics. The previously performed multicollinearity check resulted in keeping the environmental variables as fixed predictors and include the sample location as a random intercept to account for the non-independence of the observations belonging to the same sampling unit.

Binary ecological traits (feeding guild, primary lifestyle, reproductive strategy, migratory status, nest type, and nesting substrate) were modeled using a binomial distribution with a logit link. Continuous morphological traits, including body mass, bill proportions, hand-wing index, tarsus length, and tail length, were modeled with Gaussian distributions after residual diagnostics. In particular, the general model structures are:

Ecological trait response ~ environmental predictors + (1 | sampling location) (1)

Morphological trait response ~ environmental predictors + (1 | sampling location) (2)

Model selection was based on the Bayesian Information Criterion (BIC), and statistical significance was assessed using Wald tests [41]. Model diagnostics were assessed using simulated residuals to detect overdispersion, zero inflation, and deviations from residual uniformity. These diagnostic checks were used to evaluate whether the fitted models adequately represented the observed data structure prior to ecological interpretation.

Multivariate relationships between bird ecomorphological traits and habitat characteristics were further examined using a model-based fourth-corner approach. Before this analysis, principal component analysis (PCA) was applied to the trait matrix to reduce dimensionality, simplify covariance among traits, and minimize redundancy among correlated ecological and morphological variables. The retained principal components were selected based on explained variance, ecological interpretability, and relevance to the fourth-corner results. These components represented the major functional dimensions of bird species and were interpreted using the strongest positive and negative trait loadings.

Model-based fourth-corner analysis was conducted with a least absolute shrinkage and selection operator (LASSO) penalty to identify the most relevant trait–environment associations while reducing model complexity and minimizing the risk of overfitting [42]. Although model-based fourthcorner analysis can be applied directly to standardized trait variables, PCA was used in this study as a dimension-reduction step to simplify the trait structure before evaluating multivariate trait– environment relationships [43]. All statistical analyses were conducted in RStudio version 4.2.3 using the 'lme4', 'glmmTMB', 'mvabund', 'ecoCopula', 'MuMIn', 'dplyr', and 'ggplot2' packages.

Results and Discussion

Results

Habitat Characteristics

Distinct variations in vegetation indices and land cover composition were observed along the urbanization gradient. Both NDVI and LAI were highest in the secondary forest, moderate in plantation and riparian habitats, and lowest in built-up and farmland areas, indicating a decline in vegetation productivity and canopy complexity with increasing urbanization (Table 2). Land cover composition also varied markedly among habitats. Forest areas were dominated by tree vegetation (88.81%), whereas plantations were primarily covered by cultivated crops (72.29%), such as oil palm, coffee, and citrus. Riparian zones were characterized by mixed tree and agricultural cover (55.83%), whereas built-up areas were dominated by impervious surfaces (70.72%) with sparse vegetation. Farmland habitats consisted mainly of croplands (79.57%) interspersed with open land and scattered trees (Figure 2).

Vegetation composition showed distinct variations across habitat types along the urbanization gradient. The secondary forest exhibited the highest species richness across all growth stages, dominated by *Khaya grandifoliola*, *Macaranga gigantea*, and *Hevea brasiliensis*. Species richness declined in plantations, where dominance shifted from *Macaranga gigantea* and *Citrus aurantiifolia* to *Artocarpus altilis* and *Ceiba pentandra*. In contrast, riparian habitats exhibited moderate diversity, with *Ficus septica*, *Hevea brasiliensis*, and *Swietenia macrophylla* as the dominant species. Built-up areas were characterized by disturbance-tolerant and cultivated species, such as *Ficus septica*, *Psidium guajava*, and *Mangifera indica*. In contrast, farmlands were dominated by managed vegetation, primarily *Gliricidia sepium* and *Artocarpus heterophyllus*. Overall, the habitats followed a gradient from least to most urbanized, progressing from secondary forest, plantation, riparian, built-up, to farmland, reflecting a progressive decline in vegetation productivity, structural heterogeneity, and floristic diversity. These patterns indicate an increase in ecological simplification with intensified anthropogenic disturbances.

Table 2. Mean NDVI and LAI values across five habitat types along the Ciampea–Dramaga urbanization gradient. Values were averaged from nine sampling locations or plots per habitat; NDVI indicates vegetation greenness, whereas LAI quantifies leaf area per unit ground area and serves as an indicator of canopy density.

Type of habitat	Mean of NDVI and LAIv Value	
	NDVI	LAI
Secondary forest	0.511	2.129
Plantation	0.439	0.967
Riparian	0.414	0.810
Built-up area	0.336	0.357
Farmland	0.301	0.257

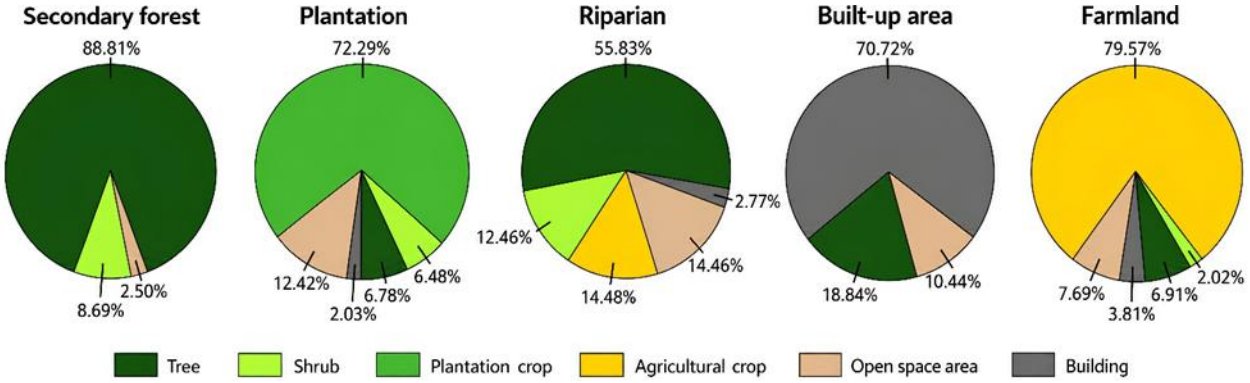


Figure 2. Proportional land-cover composition within 50 × 50 m areas centered on sampling points in five habitat types in the Ciampea–Dramaga peri-urban landscape. The pie charts show the percentages of tree, shrub, plantation crop, agricultural crop, open-space, and building cover.

Bird Communities

A total of 77 bird species from 35 families, comprising 19,637 individuals, were recorded across five habitat types along the urbanization gradient between 2020 and 2023. Species richness peaked in the secondary forest and declined progressively toward farmland, reflecting a reduction in vegetation complexity with increasing urbanization (Table 3). The Chao1 estimator predicted potential species richness of 69 in secondary forests, 55 in plantations, 45 in riparian habitats, and 40 in farmland. Diversity indices (Margalef and Shannon–Wiener) showed consistent gradients, with the highest diversity in secondary forests and lower in farmland. Pielou's evenness index remained relatively stable. However, it was slightly higher in riparian habitats, whereas dominance (Berger–Parker index) increased towards highly urbanized environments, being greatest in farmland and built-up areas and lowest in secondary forests, indicating greater ecological homogenization under anthropogenic pressure. At a 0.50 similarity cut-off, the Bray–Curtis analysis clustered secondary forest, plantation and riparian habitats. In contrast, built-up and farmland habitats formed a separate cluster indicative of more similar compositions of more urbanized communities (Figure 3).

Table 3. Bird community diversity, abundance, evenness, and dominance across five habitat types in the Ciampea–Dramaga landscape during surveys from 2020 to 2023. The table presents observed and Chao1-estimated species richness, family richness, pooled bird detections, Margalef and Shannon–Wiener diversity, Pielou evenness, and Berger–Parker dominance.

Parameters	Type of habitat				
	Secondary forest	Plantation	Riparian	Built-up area	Farmland
Species richness	60	52	42	44	38
Chao1 index	69	55	45	44	40
Family	30	24	22	23	18
Abundance	2,460	2,841	2,159	5,608	6,569
Margalef index	7.358	5.890	5.068	4.470	3.728
Shannon-Wiener index	3.136	2.797	2.774	2.390	2.218
Pielou index	0.801	0.751	0.785	0.675	0.654
Berger-Parker index	0.178	0.263	0.215	0.307	0.355

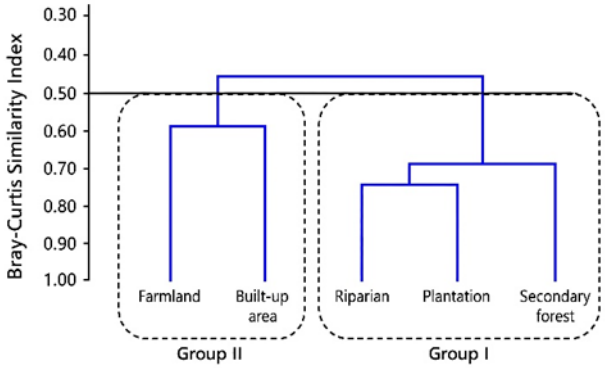


Figure 3. Unweighted Pair Group Method with Arithmetic Mean (UPGMA) dendrogram based on Bray–Curtis similarity in bird species composition among five habitat types in the Ciampea–Dramaga landscape. At the 0.50 similarity cut-off, secondary forest, plantation, and riparian habitats form Group I, while built-up area and farmland form Group II.

Responses and Relationships of Ecomorphological Traits with Habitat Characteristics

Selection of habitat variables

Pearson's correlation was used to analyze linear connections between environmental predictors, and significant correlations were defined as $r > 0.75$ to determine multicollinearity. The LAI showed strong correlations with the NDVI ($r = 0.95$), tree density ($r = 0.97$), pole density ($r = 0.92$), and seedling density ($r = 0.93$) (Figure 4). Similarly, NDVI was strongly associated with tree density ($r = 0.90$), tree height ($r = 0.78$), and tree diameter ($r = 0.82$). Canopy cover was positively correlated with pole density ($r = 0.91$) and tree density ($r = 0.94$), and tree height and diameter were also highly correlated ($r = 0.93$). These high correlation values indicate potential multicollinearity if the variables are included simultaneously in subsequent models. Based on these results, seven independent variables were retained for GLMMs and fourth-corner analyses: NDVI, tree height, tree species richness, pole density, shrub cover, non-vegetated cover, and agricultural cover.

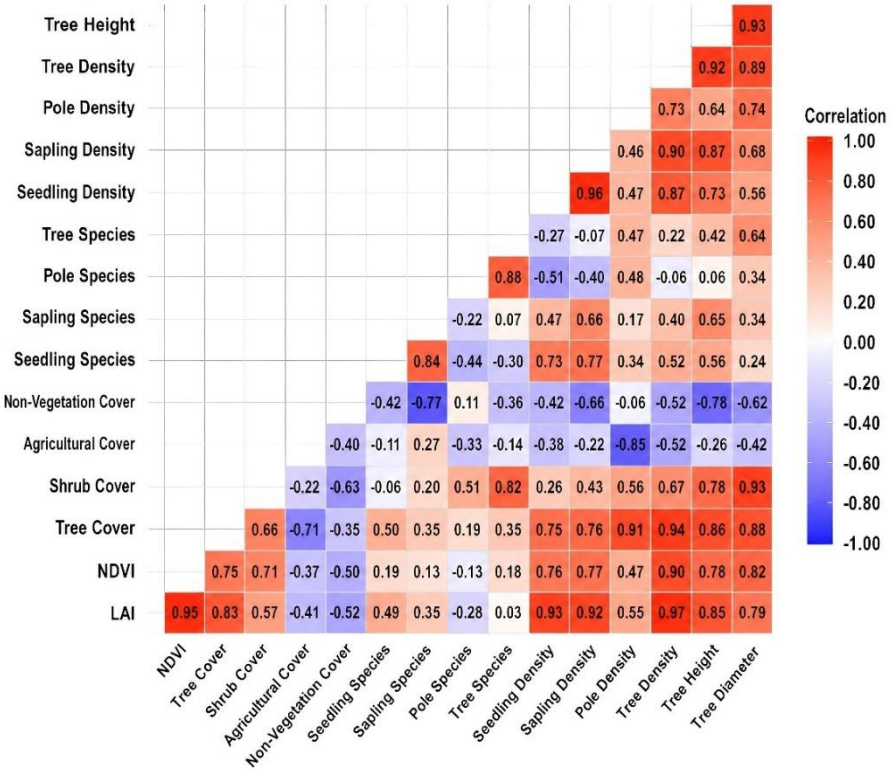


Figure 4. Pairwise pearson correlation matrix for environmental variables measured across the five habitat types in the Ciampea–Dramaga landscape. Cell values represent Pearson's correlation coefficients (r), with red and blue indicating positive and negative correlations, respectively. Absolute correlation coefficients greater than 0.75 were considered evidence of multicollinearity and used to guide predictor selection before model fitting.

Modelling prediction of ecomorphological trait response to habitat characteristics

GLMMs and BIC model selection identified tree species richness (env5) as the dominant environmental predictor of bird ecomorphological traits along the urbanization gradient (Table 4). Across feeding guilds, tree richness had significant positive effects on insectivore, frugivore, nectarivore, and omnivore guilds but a significant negative effect on carnivores. Although the association with granivore abundance was best supported by the BIC, it was not statistically significant. Tree richness was the strongest predictor of primary lifestyle variation, showing a significant negative association with aerial species and significant positive associations with insessorial and generalist birds, confirming its central role in structuring foraging strategies across the urbanization gradient.

Table 4. Best-supported binomial GLMMs relating ecological bird traits to habitat variables across the Ciampea–Dramaga urbanization gradient. For each trait, the table reports the top-ranked model (ΔBIC = 0.00), BIC, standardized predictor, logit-scale estimate with standard error, and Wald-test p-value. Predictor codes are env2 = shrub cover, env3 = agricultural cover, env4 = non-vegetated cover, env5 = tree species richness, and env7 = tree height, while ns, *, **, and *** denote p ≥ 0.05, p < 0.05, p < 0.01, and p < 0.001.

Trait	Best model	BIC	Predictor	Estimate (SE)	p-value
A. Feeding Guild					
Insectivore	Insectivore ~ env5	310.05	env5	+0.332 (0.162)	0.041*
Frugivore	Frugivore ~ env5	287.25	env5	+0.634 (0.175)	< 0.001***
Granivore	Granivore ~ env5	305.39	env5	−0.275 (0.158)	0.082 ns
Nectarivore	Nectarivore ~ env5	305.46	env5	+0.516 (0.164)	0.001**
Carnivore	Carnivore ~ env5	297.54	env5	−0.703 (0.178)	< 0.001***
Omnivore	Omnivore ~ env5	288.51	env5	+0.817 (0.196)	< 0.001***
B. Primary Lifestyle					
Aerial	Aerial ~ env5	286.28	env5	−0.679 (0.173)	< 0.001***
Terrestrial	Terrestrial ~ env7	307.56	env7	+0.111 (0.154)	0.468 ns
Insessorial	Insessorial ~ env5	288.59	env5	+0.449 (0.165)	0.006**
Generalist	Generalist ~ env5	270.76	env5	+0.612 (0.172)	< 0.001***
C. Reproductive Strategy					
Brood parasitism	Brood_Parasitism ~ env5	287.01	env5	+0.786 (0.177)	< 0.001***
Non-brood parasitism	Non_Brood_Parasitism ~ env5	297.78	env5	+0.368 (0.168)	0.028*
D. Migratory Status					
Migrant	Migrant ~ env5	291.75	env5	+ 0.821 (0.187)	< 0.001***
Non-migrant	Non_Migrant ~ env5	309.72	env5	+ 0.344 (0.157)	0.028*
E. Nest Type					
No nest	No_Nest ~ env2	310.74	env2	−0.316 (0.166)	0.056 ns
Cavity nest	Cavity_Nest ~ env5	276.29	env5	−0.306 (0.165)	0.064 ns
Open nest	Open_Nest ~ env2 + env3	276.66	env2; env3	−1.023 (0.244); −0.532 (0.209)	< 0.001***; 0.011*
Domed nest	Domed_Nest ~ env2 + env5	290.67	env2; env5	−0.753 (0.295); −0.943 (0.295)	< 0.001***; 0.001**
Nest parasitism	Nest_Parasitism ~ env5	305.86	env5	−0.377 (0.159)	0.018*
F. Nest Substrate					
Ground	Ground_Nest ~ env4	292.47	env4	+0.503 (0.203)	0.013*
Tree	Tree_Nest ~ env5	289.23	env5	−0.602 (0.164)	< 0.001***
Non-tree vegetation	Non_Tree_Nest ~ env5	292.85	env5	−0.605 (0.168)	< 0.001***
Cliff-bank	Cliff_Bank_Nest ~ env5	295.02	env5	−0.463 (0.166)	0.005**

Tree species richness further dominated the models explaining reproductive strategy and migratory status. Positive associations were observed for both brood-parasitic and non-brood-parasitic species, and for migrants, non-migrants were jointly associated with tree richness and shrub cover (env2), indicating that resident species respond to a broader vegetation gradient. Nesting strategies were primarily structured by vegetation composition: shrub cover (env2) negatively affected no-nest, open-nest, and domed-nest species, whereas agricultural cover (env3) additionally reduced open-nest species occurrence. Tree richness (env5) negatively influenced cavity and domed nesters, suggesting that structurally complex canopies may limit the availability or detectability of suitable nesting sites. Nesting substrate preferences followed a similar pattern; non-vegetated cover (env4) was positively associated with ground nesting, whereas shrub cover and tree richness negatively predicted tree substrate, non-tree, and cliff-bank nesting.

Morphological traits were primarily driven by tree species richness (env5) (Table 5). Tree richness had significant positive effects on body mass, bill proportion, and tarsus length, and a significant negative effect on the hand-wing index, indicating reduced wing elongation in structurally complex, densely vegetated habitats that select for greater maneuverability in these habitats. Tail length was best explained by non-vegetation cover (env4), although the association was not statistically significant. Agricultural cover (env3) was significantly negatively associated with tail length, suggesting that species in open, managed landscapes tend toward shorter tails adapted for rapid, energy-efficient flight.

Table 5. Best-supported GLMMs relating bird morphological traits to habitat variables across the Ciampea–Dramaga urbanization gradient. For each trait, the table reports the top-ranked model (ΔBIC = 0.00), BIC, standardized predictor, coefficient estimate with standard error, and Wald-test p-value. Predictor codes are env4 = non-vegetated cover and env5 = tree species richness, while ns and *** denote p ≥ 0.05 and p < 0.001, respectively.

Trait	Best model	BIC	Predictor	Estimate (SE)	p-value
Body mass	Body_Mass ~ env5	720.48	env5	+0.561 (0.075)	< 0.001***
Bill proportion	Bill_Proportion ~ env5	715.56	env5	+0.624 (0.071)	< 0.001***
Hand-wing index	Hand_Wing_Index ~ env5	754.00	env5	−0.500 (0.079)	< 0.001***
Tarsus length	Tarsus_Length ~ env5	749.29	env5	+0.619 (0.080)	< 0.001***
Tail length	Tail_Length ~ env4	705.37	env4	+0.059 (0.079)	0.452 ns

Ecomorphological trait – habitat characteristic relationship

The model-based fourth-corner analysis with the LASSO penalty identified the second principal component (PC2) as the primary ecomorphological axis associated with forest habitats, showing the strongest negative coefficient (r = –0.14) (Figure 5). PC2 captured significant variation in bird trait–habitat relationships. Traits with negative loadings, including tree, insessorial, frugivore, and cavity_nest, were dominant in forest habitats, whereas traits with positive loadings, such as aerial, insectivore, and non-tree_vegetation, were more characteristic of open environments. Similarly, plantation habitats exhibited the strongest association with PC2 (r = –0.10) (Figure 6), indicating that this axis best explains ecomorphological variation within partially modified landscapes. Traits such as open_nest, domed_nest, generalist, body_mass, and non-tree_vegetation had high negative loadings, whereas migrant and brood_parasitism traits showed weaker and opposite associations.

Riparian habitats were negatively associated with PC1 (r = −0.12) (Figure 7), the main ecomorphological axis describing trait–environment variation in these semi-natural systems. Negative PC1 loadings indicated greater representation of body mass, carnivory, hand-wing index, and cliff-bank nesting, whereas positive loadings for bill proportion, tarsus length, domed nests, and non-tree vegetation reflected more open and structurally heterogeneous conditions. Built-up areas were positively associated with PC1 (r = 0.24) and PC2 (r = 0.22) (Figure 8), indicating trait shifts under urban conditions. Domed nesting and non-tree vegetation loaded positively on PC1, while body mass, bill proportion, and hand-wing index loaded negatively. Along PC2, aerial, insectivorous, and terrestrial traits contrasted with tree-associated, insessorial, frugivorous, and cavity-nesting traits, suggesting a transition from vegetation-dependent strategies toward traits favored in open and urbanized habitats.

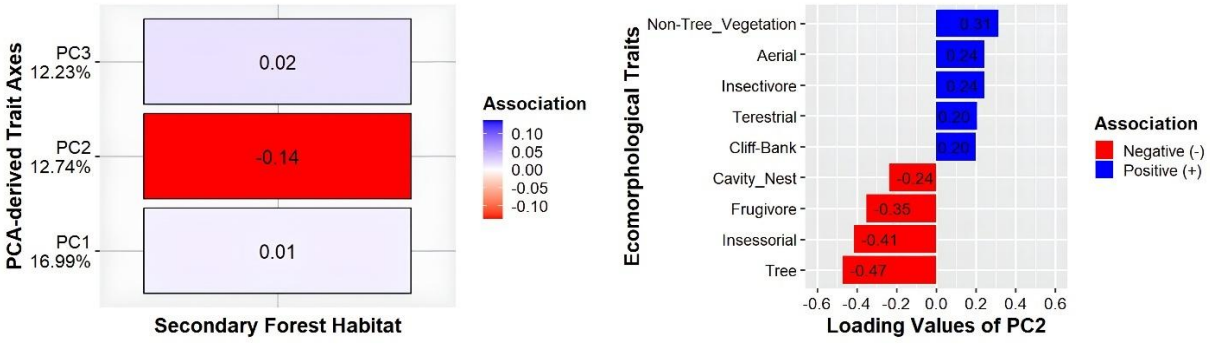
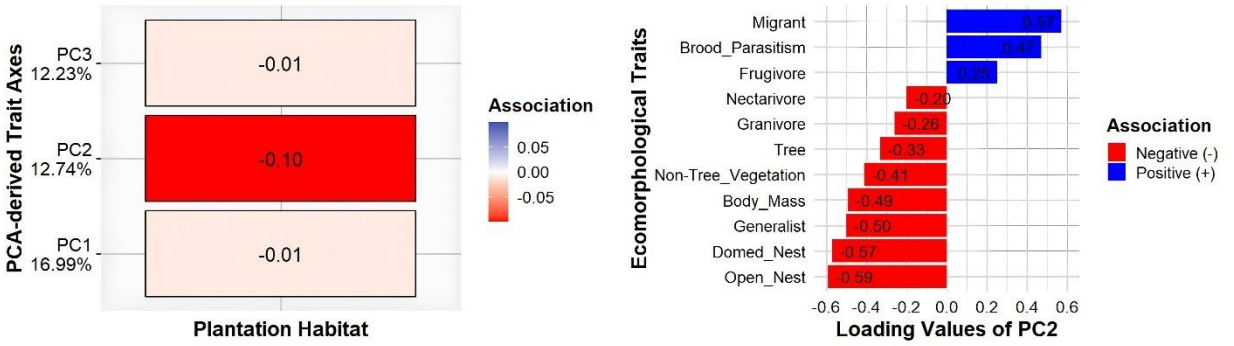
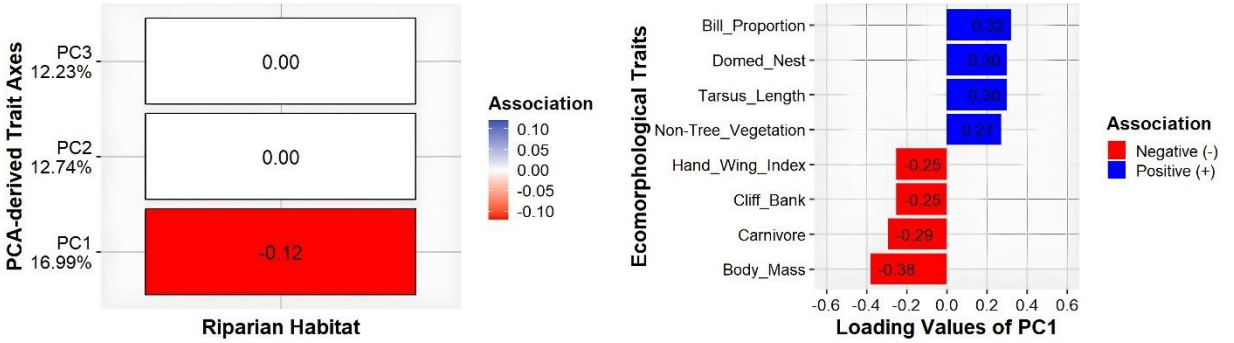


Figure 5. LASSO-penalized model-based fourth-corner associations between secondary forest habitat and PCA-derived ecomorphological trait axes in the Ciampea–Dramaga landscape. Panel A shows habitat–axis coefficients for PC1, PC2, and PC3, which explain 16.99%, 12.74%, and 12.23% of total trait variation, respectively, with red and blue indicating negative and positive coefficients; Panel B displays the largest loadings on PC2.



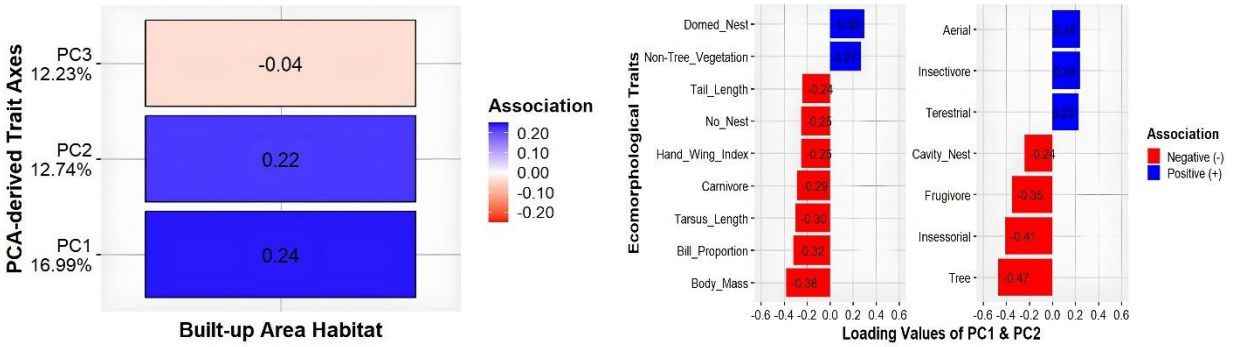
(A) (B)

Figure 6. LASSO-penalized model-based fourth-corner associations between plantation habitat and PCA-derived ecomorphological trait axes in the Ciampea–Dramaga landscape. Panel A shows habitat–axis coefficients for PC1, PC2, and PC3, which explain 16.99%, 12.74%, and 12.23% of total trait variation, respectively, with red and blue indicating negative and positive coefficients; Panel B displays the largest loadings on PC2.



(A) (B)

Figure 7. LASSO-penalized model-based fourth-corner associations between riparian habitat and PCA-derived ecomorphological trait axes in the Ciampea–Dramaga landscape. Panel A shows habitat–axis coefficients for PC1, PC2, and PC3, which explain 16.99%, 12.74%, and 12.23% of total trait variation, respectively, with red and blue indicating negative and positive coefficients; Panel B displays the largest loadings on PC1.



(A) (B)

Figure 8. LASSO-penalized model-based fourth-corner associations between built-up area habitat and PCA-derived ecomorphological trait axes in the Ciampea–Dramaga landscape. Panel A shows habitat–axis coefficients for PC1, PC2, and PC3, which explain 16.99%, 12.74%, and 12.23% of total trait variation, respectively, with red and blue indicating negative and positive coefficients; Panel B displays the dominant loadings on PC1 and PC2.

Farmland habitats were most strongly negatively association with PC2 (r = –0.14) (Figure 9), and thus this axis accounted for the most ecomorphological variation in cultivated landscapes. Traits with high negative loadings on PC2, including open_nest, omnivore, ground, and terrestrial, were dominant in the farmlands. In contrast, generalist, nectarivore, broodparasitism, and insessorial traits had positive loadings and showed

opposite ecological associations. The negative direction of PC2 indicated that traits adapted to open and disturbed environments were more prevalent in agricultural habitats, whereas forest-associated traits declined with increasing habitat simplification.

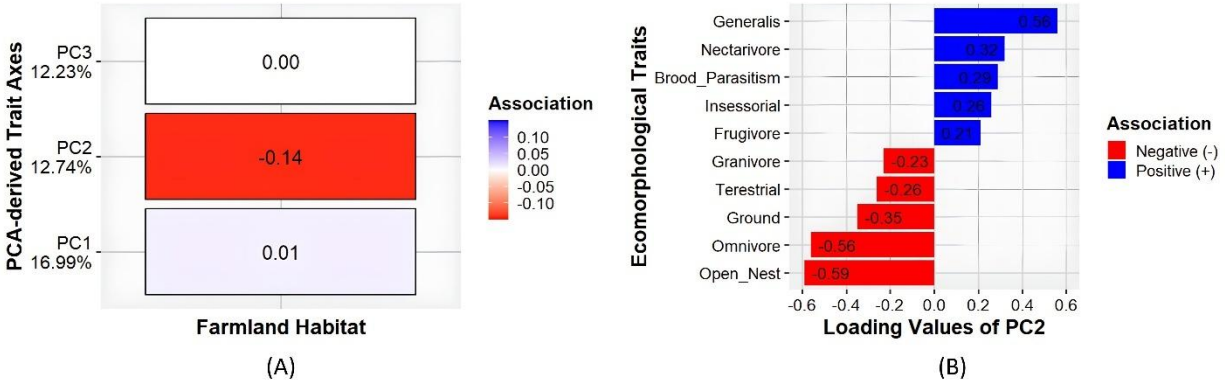


Figure 9. LASSO-penalized model-based fourth-corner associations between farmland habitat and PCA-derived ecomorphological trait axes in the Ciampea–Dramaga landscape. Panel A shows habitat–axis coefficients for PC1, PC2, and PC3, which explain 16.99%, 12.74%, and 12.23% of total trait variation, respectively, with red and blue indicating negative and positive coefficients; Panel B displays the largest loadings on PC2.

Discussion

Habitat characteristics along the Ciampea–Dramaga urbanization gradient were evaluated using four ecological parameters: LAI, NDVI, land cover composition, and vegetation structure. LAI represents the cumulative leaf surface area per unit of ground, reflecting canopy density and productivity [44]. Remote-sensing-derived NDVI quantifies vegetation greenness and condition from differences in near-infrared and red reflectance [37], with higher values representing denser, healthier vegetation [45]. Land-cover proportions and vegetation composition further describe plant dominance and habitat heterogeneity along the urbanization gradient [46].

LAI and NDVI were highest in secondary forests dominated by *Hevea brasiliensis*, *Khaya* spp., and *Macaranga gigantea*, with dense canopy cover and high primary productivity. *H. brasiliensis* presence is consistent with anthropogenic legacies of former plantation systems in this region [47]. On the other hand, farmland habitats had overall the lowest LAI and NDVI values, with only annual crops (such as maize, cassava, and rice) prevailing to make up simplified vegetation structures. Plantations and riparian areas showed intermediate plant structural diversity, whereas built-up settlements, such as the green campus of the IPB Dramaga, retained moderate greenness with ornamental or remnant trees [48]. In summary, these results demonstrate a gradient between forested and agricultural habitats that is consistent with global patterns of vegetation simplification associated with urban growth.

Bird species richness and diversity showed a clear declining pattern along the urbanization gradient, being highest in secondary forest habitats and lowest in built-up areas and farmland. This pattern supports the increasing disturbance hypothesis, predicting a negative relationship between the intensity of disturbance and biodiversity [49,50]. Forests with complex multistrata vegetation structure provide various foraging resources, nesting sites, and microhabitats that support specialist species, while those in more simplified habitats favor generalist and disturbance-tolerant taxa [51,52]. Increased human modification promotes ecological divergence and the homogenization of communities as evidenced by the unique clustering of bird assemblages between forests, plantations, and riparian areas, forming a separate cluster from built-up and farmland areas [53,54].

Multicollinearity analysis indicated strong correlations among vegetation variables, particularly LAI, NDVI, and density measures across the tree, sapling, and seedling strata. Seven independent variables were retained to reduce multicollinearity: NDVI, tree height, tree species richness, pole density, shrub cover, non-vegetated cover, and agricultural area. GLMMs have shown that, out of all the environmental variables tested, variation in bird ecomorphological traits is ultimately best explained by tree species richness, demonstrating the key role of vegetation diversity as a driver of both the taxonomic and functional structuring of the bird community [55]. For insectivorous, frugivorous, nectarivorous, and omnivorous guilds,

there were positive associations with tree richness, highlighting that structurally complex habitats offer greater resource heterogeneity and foraging opportunities [56]. Conversely, carnivorous species are negatively associated with the complexity of the vegetation, preferring habitats without cover to maximize hunting efficiency [57]. Finally, tree richness also supported insessorial and generalist species, consistent with the vertical niche diversification concept [58], whereas aerial foragers declined as canopy density increased [59].

Morphological adaptations further illustrate the effects of environmental filtering along this gradient. Tree species richness was positively associated with body mass, bill proportions, and tarsus length, indicating that structurally complex habitats may support birds capable of using multiple foraging strata and diverse food resources [60]. The negative association between tree richness and the hand-wing index reveals a selection for species with increased maneuverability in vegetation-dense habitats [61,62]. Agricultural cover and tail length were negatively correlated, suggesting that open habitats may favor short-tailed species that are suited to rapid, energy-efficient flight [63,64]. Together, these results demonstrate that environmental filtering driven by vegetation structure and composition determines the distribution of functional and morphological traits [65], favoring species whose ecological and anatomical characteristics match the local habitat conditions.

Model-based fourth-corner analysis indicated that variations in bird–environment relationships were primarily driven by habitat structural heterogeneity along the urbanization gradient. Trait associations revealed an ecological transition from forest habitats with complex vertical structures to open agricultural and urban systems characterized by simplified vegetation. This pattern reflects environmental filtering, where only species with traits adapted to specific habitat conditions persist [66,67]. Forest habitats are dominated by arboreal, insessorial, frugivorous, and cavity-nesting species that are dependent on large trees and multilayered vegetation, contributing to key ecological functions such as seed dispersal and insect regulation [68,69]. As vegetation complexity declined in plantations, generalist species with open- or dome-nesting traits became dominant, reflecting functional replacement, where disturbance-tolerant species maintain basic ecosystem functions but with reduced functional diversity. This pattern reflects functional replacement, in which specialist species are replaced by species with broad ecological tolerances that can adapt to variations in substrates and resources [70].

Further along the urbanization gradient, riparian habitats supported small-bodied, highly mobile carnivorous species with elevated hand-wing indices, reflecting morphological and behavioral adaptations for open-water foraging and cliff-bank nesting on vertical substrates. These aerodynamic and foraging traits are consistent with the findings from tropical river ecosystems, where morpho-functional adaptations play a key role in structuring riparian bird assemblages [71]. Built-up areas were dominated by dome-nesting and non-tree vegetation users that exploit artificial substrates and low vegetation, whereas aerial and insectivorous species benefited from open spaces and abundant insect prey. In contrast, arboreal, frugivorous, and cavity-nesting species have declined because of reduced tree cover and the loss of natural nesting sites [17].

In farmlands, open-nesting, omnivorous, ground-dwelling, and terrestrial species predominated, reflecting their high ecological flexibility and tolerance to anthropogenic disturbances [72]. In contrast, nectarivorous and brood-parasitic species were negatively associated with agricultural habitats, suggesting that specialized feeding and reproductive strategies may limit persistence in open, fragmented landscapes [73]. Together, these trends reveal an apparent ecological gradient from specialist-dominated forest communities to generalist-dominated urban and agricultural assemblages. This shift suggests functional homogenization, in which increasing anthropogenic pressure and habitat simplification reduce trait diversity within bird communities [74]. In this sense, the loss of structurally complex habitats (e.g., forests) decreases not only the richness of species, but also the functional dimensions of bird assemblages vital to ecosystem stability and long-term ecological resilience [75].

The peri-urban landscape of Ciampea-Dramaga is nevertheless of important conservation value for the maintenance of numerous species of protected bird. Adopting urban wildering, which relies on preserving and restoring natural processes and allowing for spontaneous vegetation growth, rather than just ornamental landscaping, may improve habitat quality and resilience. Multi-species planting, protection of remnant trees and restoration of riparian corridors may enhance ecological connectedness and preserve biodiversity [76,77]. Integrating semi-natural rewilding into urban planning, reinforcing local conservation policies, promoting community stewardship, and implementing long-term monitoring are crucial for limiting functional homogenization and maintaining ecosystem stability in rapidly urbanizing tropical landscapes.

Conclusions

Habitat variation along the urbanization gradient strongly shaped bird community structure and ecomorphological traits in the Ciampea–Dramaga peri-urban landscape. Species richness and functional diversity were highest in forest habitats and gradually decreased in more urbanized regions, indicating that human disturbance favors ecological simplicity in the studied area. Habitat complexity acts as an environmental filter that favors specialist birds, particularly arboreal, frugivorous, and cavity-nesting species. In contrast, simpler agricultural and built-up environments were dominated by generalist, aerial, and omnivorous species. These findings are in line with the increasing disturbance hypothesis, highlighting biodiversity loss as a consequence of increased habitat change. Urban wildering initiatives should be deliberately targeted via conservation methods that promote habitat variability, retain remaining trees, and improve riparian corridor restoration for greater ecological connectedness and ecosystem resilience. Finally, strengthening local conservation governance, fostering community stewardship, and long-term monitoring of ecological results are measures to mitigate homogenization and conserve biodiversity in rapidly urbanizing tropical settings.

Author Contributions

SPA: Conceptualization, Methodology, Investigation, Software, Writing - Review & Editing; **AMD**: Conceptualization, Methodology, Writing - Review & Editing, Supervision; **YAM**: Conceptualization, Methodology, Writing - Review & Editing, Supervision; **DAR**: Conceptualization, Methodology, Writing - Review & Editing, Supervision; **ABD**: Writing - Review & Editing; and **YHN**: Writing - Review & Editing.

AI Writing Statement

During the preparation of this work the authors used Paperpal in order to assist in correcting grammar, spelling, and language fluency. After using this tool/service, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

Conflicts of Interest

There are no conflicts to declare.

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