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Fragmented Habitats, Fragmented Functions: Unveiling the Role of Habitat Structure in Andean Bird Communities

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Abstract

Understanding the processes that shape biodiversity patterns is an important challenge in ecology. Land-use change is often recognized as a pivotal factor influencing biodiversity at large scales, with habitat heterogeneity being one of the most critical drivers of community composition and diversity. In this study, we evaluate the influence of landscape structure on the functional diversity of bird assemblages in the Upper Magdalena River Valley, Colombia. We used Generalized Linear Models to assess the effects of landscape structure on functional diversity, incorporating landscape metrics such as the number of patches, patch area and shape, and Shannon's diversity and evenness indices. Additionally, we analyzed the influence of landscape structure on functional beta diversity—including its components of functional turnover and nestedness—using a distance-based redundancy analysis. We also examined the relationship between species traits and landscape metrics through a RLQ and fourth-corner analysis. We found a negative effect of habitat loss and fragmentation on functional diversity. Our results show that bird assemblages exhibit higher diversity in non-fragmented landscapes (>75% forest area; <1% urban cover), retaining greater functional richness and functional evenness (FRic > 0.24; FEve > 0.60). Moreover, non-fragmented landscapes seem to support a higher number of nectarivores and forest specialist species. In contrast, bird functional richness decreased with landscape fragmentation (FRic < 0.07). These findings highlight the importance of forest conservation for maintaining species persistence, ecological processes, and ecosystem services provided by birds.

Keywords: bird communities; biodiversity; ecological traits; landscape metrics; Magdalena River Valley

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Academic Editor: José Ramón Arévalo Sierra

Received: 26 April 2025
Revised: 17 June 2025
Accepted: 20 June 2025
Published: 11 July 2025

Citation: Ramos-Mosquera, V.; López-Delgado, E.; Moreno-Palacios, M. Fragmented Habitats, Fragmented Functions: Unveiling the Role of Habitat Structure in Andean Bird Communities. *Ecologies* **2025**, *6*, 52. https://doi.org/10.3390/ecologies6030052

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1. Introduction

Human driven land-use change frequently leads to habitat loss, degradation, and fragmentation [1], disrupting ecosystem functions and altering landscape configurations [2,3]. These impacts are particularly severe in landscapes heavily affected by large-scale monocultures, livestock grazing, and urbanization [4]. In Colombia, extensive areas of native forest have been converted into agricultural matrices [5]. The expansion of these practices reduces suitable habitat areas, decreases habitat connectivity, and creates isolated patches [1,6]. As a result, fragmentation restricts species movement across habitats and negatively impacts

genetic diversity within populations [6], while also diminishing the availability of food and other essential resources for wildlife [7].

Tropical forests offer essential ecosystem services, including carbon storage, climate regulation, and water cycling. They also sustain around 91% of all terrestrial bird species [8]. However, these ecosystems are increasingly threatened as land-use change alters the physical environment and vegetation structure, impacting numerous bird species. In particular, the loss of large and tall trees negatively affects canopy foragers and species that nest in cavities [8,9]. Bird species are valuable indicators for assessing the impacts of fragmentation on biological systems [10]. Research has shown that forest specialist birds are more severely affected by fragmentation compared to species adapted to open habitats [11,12]. Therefore, identifying species particularly vulnerable to habitat fragmentation is pivotal for guiding conservation strategies that aim to preserve biodiversity and maintain ecosystem services [13].

Biodiversity encompasses the variety of life on Earth, including genotypic and phenotypic variation within species [14], and can be assessed through taxonomic, phylogenetic, and functional measures. Taxonomic diversity evaluates species composition and abundance of individuals [15], while phylogenetic diversity considers the evolutionary relationships among species [15]. In contrast, functional diversity measures the diversity of morphological, physiological, and ecological traits within biological communities and holds particular ecological significance, as it provides an accurate assessment of ecosystem functioning [16]. Functional traits provide critical insights into the patterns and processes shaping biological diversity [17,18], including interactions between species and with the environment. Thus, functional diversity emphasizes the species' functional identity rather than its taxonomic classification [15]. Understanding how species' traits influence their responses to landscape changes is essential for assessing the ecological consequences of habitat transformation. The magnitude of these effects is determined by functional diversity and the variability of species' functional traits, such as body size, feeding guild, and dispersal capacity [19]. A reduction in functional trait diversity compromises ecosystem functioning and disrupts the provisioning of ecosystem services essential for human well-being [20]. Consequently, processes like pollination, seed dispersal, and biological pest control decline as a result of forest fragmentation [21].

In recent years, landscape heterogeneity has been recognized as a key determinant of species diversity [22–25]. Heterogeneous landscapes offer diverse ecological niches for species with varying ecological requirements [26]. For instance, landscape heterogeneity provides opportunities for species to access different resources, nesting sites, and shelters, which enhance protection against predators [26]. Consequently, functional traits are closely related to resource availability and habitat conditions [27]. These traits provide valuable insights into how species interact with their environment and how changes in landscape structure influence their persistence and distribution. In Colombia, the Magdalena River Valley is part of a global biodiversity hotspot [28] and harbors a remarkable diversity of native and endemic species, many of which are strongly impacted by habitat loss and fragmentation [29]. Over 85% of the region's native forests and wetlands have been replaced by monocultures and cattle pastures [30]. Despite its ecological significance, research on the impacts of land-use change on the functional diversity of birds in the Upper Magdalena River Valley remains limited [31].

Addressing these knowledge gaps is essential to understanding how human disturbances affect the functioning of bird assemblages. In this study, we examined the influence of landscape structure and configuration on the functional diversity of birds in the Upper Magdalena River Valley, Colombia. Based on the documented negative effects of habitat loss and fragmentation on functional diversity, we hypothesized that (1) areas where

native forest has been significantly reduced or fragmented due to anthropogenic activities would exhibit a decrease in functional groups and, consequently, reduced functional diversity, since habitat alteration limits the availability of ecological niches and microhabitats; (2) highly urbanized areas would negatively correlate with functional diversity, as urban expansion is often associated with the loss of vegetation and homogenization of bird communities; and (3) the effects of habitat loss and fragmentation would differ among trophic niches. Specifically, omnivores would be positively impacted by urbanization due to anthropogenic food sources, while frugivores and nectarivores would be negatively affected.

2. Materials and Methods

2.1. Study Area

This study was conducted at 15 sites in the Upper Magdalena River Valley, Colombia (Figure 1; Table S1), located between the Central and Eastern Cordilleras of the Colombian Andes. These sites are characterized by a tropical climate and elevations ranging from 400 to 2000 m a.s.l., with ecosystems ranging from tropical dry forest to premontane wet forest and lower montane moist forest. The region has an average temperature of 27 °C and an average annual precipitation of 1307 mm [32], with a bimodal rainfall pattern occurring two rainy seasons from March to May and from October to November and two dry seasons from December to February and from June to September [33].

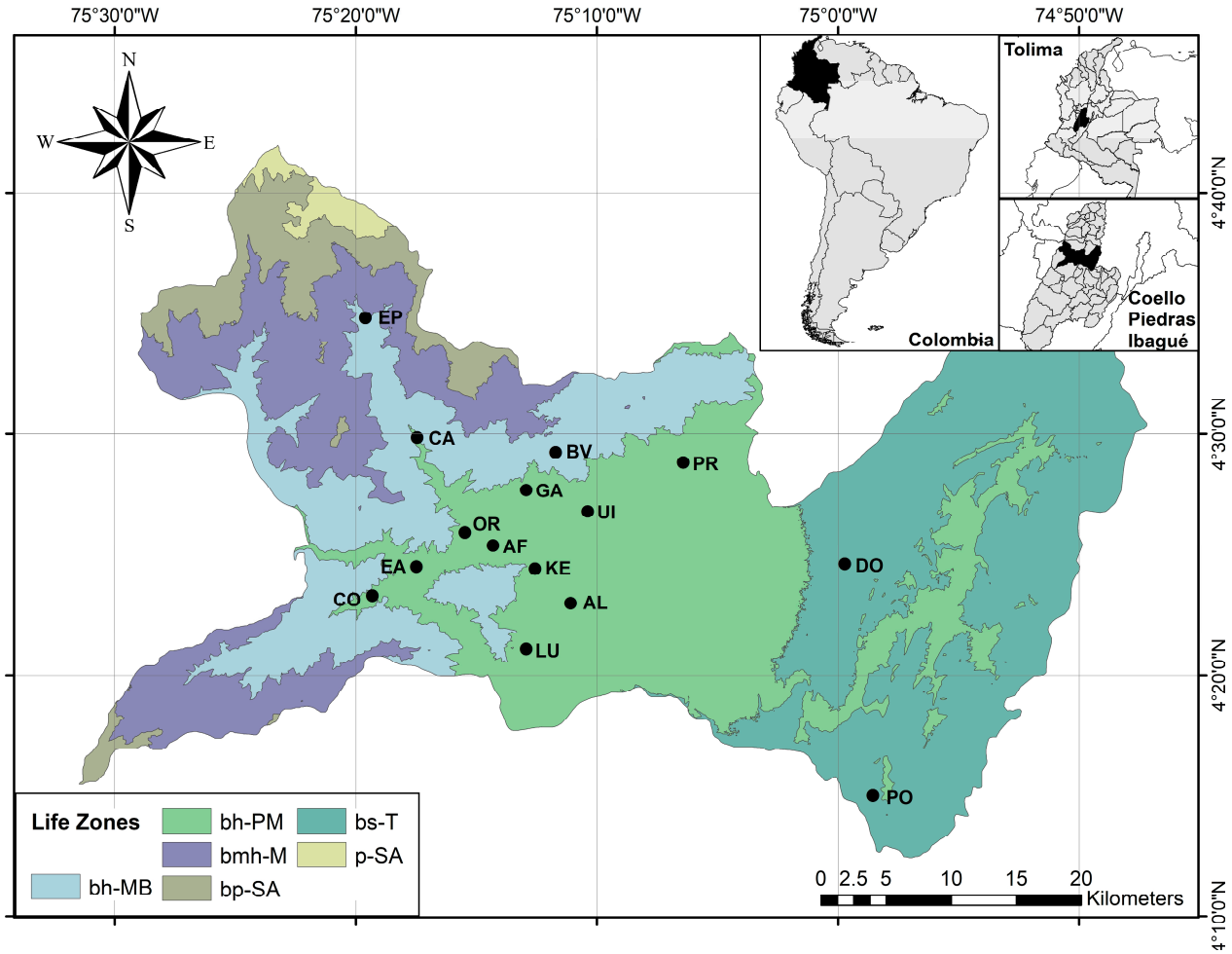

Figure 1. Location map of the 15 study areas in the Upper Magdalena River Valley, Colombia. Life zone codes follow the Holdridge Life Zone (HLZ) classification: bh-MB = lower montane moist forest;

bh-PM = premontane wet forest; bmh-M = montane wet forest; bp-SA = sub-Andean rainforest; bs-T = tropical dry forest; p-SA = sub-alpine paramo. Site abbreviations: AF = Agua Fría; EA = Entre Aguas; GA = Gaia; KE = Kenisha; CA = La Carpintería; AL = Los Alpes; LU = La Lucia; PR = La primavera; OR = Orquídeas del Tolima; CO = Paraíso de Cocora; EP = El Palmar; BV = Bella Vista; DO = Doima; PO = Potrerillo; UI = Universidad de Ibagué.

The Upper Magdalena Valley is subject to high anthropogenic pressure due to land-use change, primarily driven by cattle ranching and agriculture activities [34]. The 15 study sites were selected to encompass a representative range of landscape conditions and varying degrees of habitat fragmentation. These sites capture the region's heterogeneity in terms of elevation, vegetation types, and levels of human disturbance.

2.2. Data Collection

Bird abundance data were compiled from surveys conducted over three years, during the sampling period between June and November 2018, 2019, and 2022. Not all sites were sampled every year, as the data were collected through different research projects carried out over time. Abundance was defined as the number of individuals of each species in an area [35]. Each site was visited two to four times per month by trained and experienced observers. To assess bird community structure, mist nets and visual and audio surveys were employed, following the standardized protocols described by Ralph et al. [36]. Birds were captured using five mist nets (12 × 2.5 m, 36 mm mesh) from 06:00 to 12:00 h and 14:00 to 18:00 h, for a total of 5.110 net-hours. Details of the total effort by site are presented in the Supplementary Material (Table S2). To avoid biases in bird community sampling, we randomized and alternated the positions of mist nets per month. The captures and protocols developed in the present project were conducted under a permit to collect specimens of wild species of biological diversity for non-commercial scientific research purposes, granted by the Corporación Autónoma Regional del Tolima (CORTOLIMA) through Resolution 4188 of 14 December 2016.

Visual point counts were conducted between 14:00 and 15:20 h, concurrently with mist netting. At each site, six observation points were established, spaced 100 m apart to minimize the risk of double counting, resulting in a total of 1.872 h of observation. Observers remained at each point for 10 min, recording only individuals perched, feeding, or nesting within a 50 m radius. Birds flying over the observation points were excluded from the counts.

Additionally, in sites and years where sampling effort was lower, eBird data were used to complement species records and ensure a more comprehensive assessment of bird communities. The eBird platform, a citizen science project, compiles high-quality bird observations, contributed by volunteer observers following semi-structured protocols, and has been widely used in scientific research to study species distributions and abundance [37]. To ensure data consistency, only checklists from the same sampling periods (June to November in 2018, 2019, and 2022) and with a maximum duration of one hour were considered.

We selected data primarily contributed by experienced observers. In those localities where species lists were not contributed by recognized ornithologists, all records were carefully reviewed and compared with the published literature. We excluded unusual records without sufficient evidence for species identification, or those outside the expected species distribution. Furthermore, we excluded records of species prone to over-detection, particularly those that tend to form flocks.

We assessed the effectiveness of three sampling methods using the Chao1 estimator. All records from mist nets, point count surveys, and eBird observations were consolidated into a species-by-site matrix, in which rows represent species, columns correspond to

sampling sites, and each cell contains the abundance (i.e., number of individuals) of a given species [38].

Bird trait data were obtained from the AVONET database [39], which provides functional trait data for all bird species [40]. Since our study did not aim to test hypotheses about specific aspects of avian ecology, we selected traits that encompass a broad range of ecological strategies, such as feeding habits, locomotion, and reproduction. These traits were selected based on the possibility that they would respond to changes in landscape structure [41]. According to Díaz-Cháux et al. [42] these traits reflect species' responses to habitat alteration. Moreover, they have been widely used to evaluate the effects of land-use change on avian diversity [43,44].

We used life history, morphological, and behavioral traits to assess functional diversity. Initially, nine continuous morphological traits, including bill length measured from tip to skull (BLS), bill length measured from tip to the front edge of the nares (BLN), bill width (BW), bill depth (BD), wing chord length (WCL), Kipp's distance (KD), tail length (TAI), tarsus length (TAR), and body mass (MA) (Figure 2), along with two ecological variables (trophic niche and habitat type) were considered. Each species was assigned to one of nine trophic niches (granivore; nectarivore; frugivore; terrestrial herbivore; omnivore; invertivore; vertivore; aquatic predator; and scavenger) and one of eight habitat types (forest; woodland; wetland; grassland; riverine; rock; shrubland; and human-modified) [40].

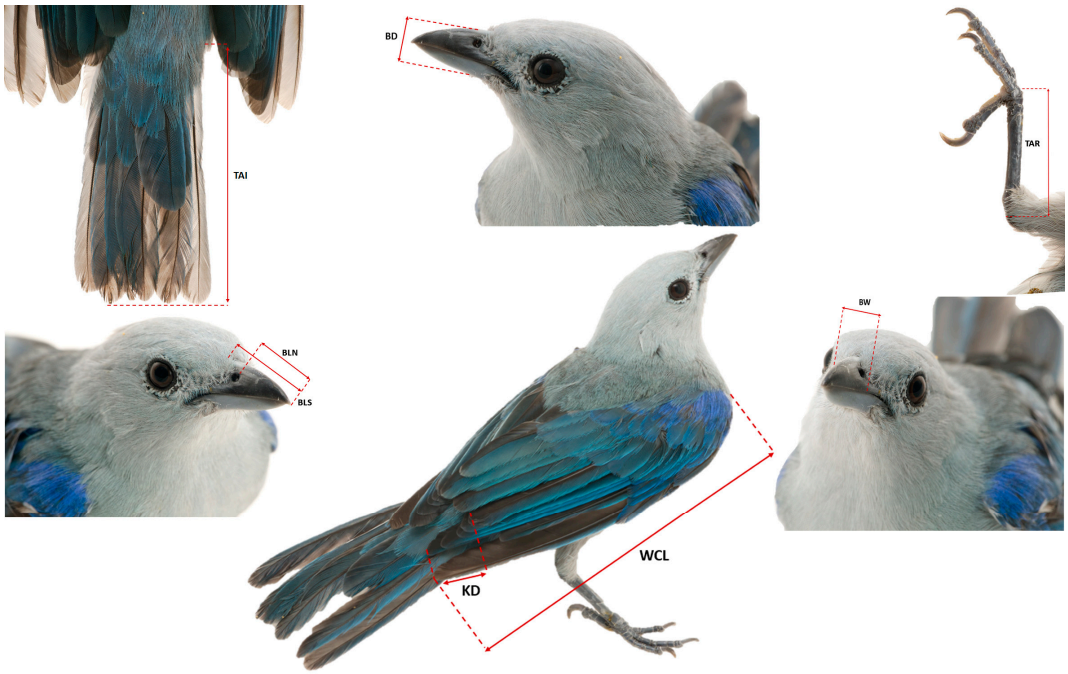

Figure 2. Morphological traits used in the study. Functional trait abbreviations: BLS = bill length measured from tip to skull; BLN = bill length measured from tip to the front edge of the nares; BW = bill width; BD = bill depth; WCL = wing chord length; KD = Kipp's distance; TAI = tail length; TAR = tarsus length.

Among these traits, those related to bill morphology are closely linked to foraging behavior, which in turn influences how species interact with resources in modified landscapes. Additionally, these traits are functionally significant for key ecological processes such as pollination, seed dispersal, and pest control [45]. Other traits, such as wing chord length and Kipp's distance, are associated with flight capacity and dispersal ability—critical aspects of avian ecology in fragmented habitats where connectivity is reduced—[46]. Trophic niche and habitat preference serve as proxies for the degree of ecological specialization,

allowing us to evaluate whether fragmentation disproportionately affects functionally important species with specific trophic roles [47].

2.3. Data Analysis

2.3.1. Landscape Metrics

High-resolution satellite images (0.92 m/pixel) were obtained from Google Earth Pro, selecting images that temporally matched the bird community samplings. These images were manually digitized and georeferenced in the CTM-12 coordinate system through ArcGIS Desktop 10.8. Land-use classification was conducted within a 20 ha area around each sampling site, following the Corine Land Cover methodology adapted for Colombia [48].

To quantify landscape structure and configuration at each site, nine landscape metrics (encompassing patch, class, and landscape levels) (Table 1) were calculated using FRAGSTATS v4.2 software [49]. These metrics were selected, supported by previous evidence of their potential influence on bird communities' responses [50,51]. In particular, patch level metrics related to area and shape have consistently been associated with variation in bird assemblages [51]. Seven land cover categories were identified: forest, secondary vegetation, water bodies, bare soil, burned areas, crops, and built-up areas including roads.

Table 1. Landscape metrics used for investigating the effects of landscape structure on functional diversity of bird assemblages. Modified from McGarigal & Marks [49].

Levels	Metrics	Abbreviation	Units	Description
Patch	Area of forest patches Area of urban cover patches Area of secondary vegetation patches	AREA_F AREA_UC AREA_SV	Hectares	Measures the size of a patch
	Perimeter of forest patches Perimeter of urban patches Perimeter of secondary vegetation patches	PER_F PER_UC PER_SV	Meters	Indicates the patch shape, with a larger perimeter indicating more irregular shapes
Class	Percentage of forest cover within landscape Percentage of urban cover within landscape Percentage of secondary vegetation cover within landscape	PND_F PND_UC PND_SV	Percentage	Quantifies the proportional abundance of each patch type within the landscape
	Number of forest patches Number of urban cover patches Number of secondary vegetation patches	NP_F NP_UC NP_SV	-	Indicates the total number of patches within a particular class
	Shape of forest patches Shape of urban patches Shape of secondary vegetation patches	SHAPE_F SHAPE_UC SHAPE_SV	-	Assesses the complexity of patch shapes within a class
Landscape	Total number of patches	NP	-	Represents the total number of patches within the landscape
	Shannon's diversity index	SHDI	-	Quantifies the diversity within the landscape
	Shannon's evenness index	SHEI	-	Assesses the evenness of patch type distribution across the landscape
	Patch richness	PR	-	Refers to the number of different classes types within the landscape

For patch and class level analyses, only forest, urban areas, and secondary vegetation were considered (Table 1), as the proportion of these land cover types in the landscape can strongly influence bird community structure, particularly for species sensitive to habitat fragmentation [52,53]. Forest cover, often used as a proxy for habitat availability, has been consistently linked to higher bird species richness [54,55].

2.3.2. Functional Diversity

Prior to the functional diversity analysis, we assessed multicollinearity between functional traits using Pearson's correlation coefficient (r). Variables with an $r > 0.75$ and a p-value < 0.05 were considered highly correlated and were excluded from further analysis. This procedure was performed to obtain a reduced set of uncorrelated variables that independently explain the variation in functional traits. The final set of traits used is detailed in the Results Section. Correlations were calculated using the 'cor.mtest' function from the 'corrplot' [56] and 'Hmisc' [57] packages in the R statistical language (Version 4.0) [58].

Following the exclusion of highly correlated traits, all selected traits were standardized to a mean of 0 and standard deviation of 1, using the 'decostand' function of the 'vegan' package [59]. Body mass was log10-transformed for the analyses [60]. Since the dataset included both qualitative and quantitative traits, we constructed a functional distance matrix using Gower's distance [61]. To identify the number of axes that best represented differences in trait composition, we conducted a Principal Coordinate Analysis (PCoA) [62]. We quantified functional alpha diversity using six indices: functional richness (FRic), functional evenness (FEve), functional specialization (FSpe), functional originality (FOri), functional dispersion (FDis), and functional divergence (FDiv).

FRic measures the total volume of the functional space occupied by the species [63]. FEve describes the evenness in the distribution of species abundance within functional space [63]. FSpe quantifies the functional uniqueness of species based on their trait distinctiveness [64]. FDiv quantifies the species abundance with extreme functional traits [63]. FDis is calculated as the mean distance to the centroid of the functional space occupied by the species [65]. FOri is measured as the mean distance to the nearest species within the species pool [66].

Diversity measures were calculated using the 'FD' [67] and 'vegan' [59] packages in R, along with the 'quality_funct_space', 'plot_funct_space', and 'multidimFD' functions [61]. To test for significant differences in functional diversity indices, we conducted a nonparametric rank-based analysis of variance (Kruskal–Wallis) [68,69]. Differences were considered significant at $p < 0.05$.

Functional beta diversity was assessed by measuring the overlap in functional space between two communities [70]. Functional beta diversity was partitioned into functional turnover and functional nestedness as described by Baselga and Villéger et al. [70,71]. Functional beta diversity was calculated using the 'multidimFbetaD' function of the 'betapart' [72] package in R.

2.3.3. Effect of Landscape Structure on Bird Functional Diversity

The initial dataset included 19 landscape variables, many of which were highly correlated. To reduce the dimensionality and identify key landscape metrics, we applied a Principal Component Analysis (PCA), selecting variables with correlation coefficients above 0.5 [73]. These variables were transformed and standardized (mean = 0; standard deviation = 1) prior to analysis. The PCA was conducted in R [58] using the 'FactoMineR' [74] and 'factoextra' [75] packages.

To assess the influence of landscape variables on functional alpha diversity indices, we fitted a Generalized Linear Model (GLM). For each index, multiple models were constructed with different combinations of landscape variables as predictors. We began with a full model including all landscape variables selected through Principal Component Analysis (PCA) and then generated a series of simplified models through stepwise removal of variables to identify the most parsimonious explanatory set.

GLMs were fitted using a gamma distribution, which is suitable for continuous explanatory variables [76]. We selected the best model based on the Akaike Information

Criterion (AIC), considering the model with the lowest AIC value as the best fit. The AIC is widely used in ecological modeling to compare multiple models and identify the model that best represents the biological process of interest [77]. Additionally, we evaluated the statistical significance of explanatory variables within the models, considering variables significant at $p < 0.05$. This analysis was conducted using the 'Metrics' [78] and 'DescTools' [79] packages in R. To assess model fit, we examined the residual value distribution using quantile–quantile (Q-Q) plots, which included a dispersion test and Kolmogorov–Smirnov test. These analyses were calculated using the 'DHARMa' [80] package.

To assess whether variation in bird assemblage composition (beta functional diversity) was related to landscape structure, we applied a Distance-Based Redundancy Analysis (db-RDA) [81]. This analysis quantifies the relationship between each landscape metric and beta diversity, as well as its components (functional turnover and functional nestedness) [82]. All variables were standardized and centered (mean = 0; standard deviation = 1). We used the 'forward.sel' function from the 'adespatial' [83] package in R, with 999 permutations and a significance level of <0.05.

Finally, to test trait–landscape metric relationships we used a RLQ and fourth-corner analysis as proposed by Dray et al. [84]. Both analyses are based on the ordination of three data matrices, which crosses environmental variables (R), species distribution (L), and species traits (Q) [85]. RLQ analysis is a multivariate technique that examines all variables simultaneously and integrates several analyses. First, we conducted a correspondence analysis (CA) on the species occurrence data (matrix L), which is appropriate for datasets with multiple zero values [86], followed by a principal component analysis (PCA) on the environmental matrix (R) and a Hill–Smith test on the trait matrix (Q), which works with both quantitative and qualitative variables [85]. RLQ analysis integrates these analyses to maximize the covariance between traits and environmental ordinations, resulting in a co-structure among the matrices represented by the RLQ axes. Variables with the highest positive or negative scores on the RLQ axes are the main contributors to the observed patterns, while those with scores close to zero do not contribute to the trait–environment relationships [87].

Fourth-corner analysis evaluates bivariate associations between landscape metrics and functional traits (one functional trait and one landscape variable at a time) [88]. Monte Carlo permutation tests with 10,000 permutations were applied to test for significant variables ($\alpha = 0.05$). This analysis employs two statistical models to test the null hypothesis: model 2 tests whether the environment has no significant effect on species distribution with fixed traits [84], while model 4 tests whether species traits are not associated with the species distribution with fixed environmental variables [89]. We used permutation model 2 to assess the significance of trait–environmental associations. These analyses were conducted using the 'ade4' [90] package in R.

3. Results

3.1. Landscape Metrics

Landscape fragmentation was classified primarily based on the proportion of urban land cover: low fragmentation (<1% urban cover), medium fragmentation (2–7%), and high fragmentation (>7%). In addition, other landscape features were considered for site classification, including the reduction in continuous native forest (low fragmentation: >75% forest cover; medium fragmentation: 30–75%; high fragmentation: <30%) and increased landscape heterogeneity due to human intervention (low fragmentation: <0.70; medium fragmentation: 0.71–1.30; high fragmentation: >1.30).

Universidad de Ibagué (UI), Los Alpes (AL), Agua Fria (AF), Potrerillo (PO), and Doima (DO) were classified as highly fragmented, characterized by the highest landscape

diversity. These areas also exhibited a greater percentage of urban land cover and the lowest forest cover. In contrast, Bella Vista (BV) and El Palmar (EP) were identified as the least fragmented sites, with a higher percentage of forest cover and minimal urban land cover (Table S3; Figure S1).

3.2. Functional Diversity

A total of 17.565 individuals, representing 402 species, 52 families, and 22 orders were registered during the study (Table S4). The most abundant species were the Crimson-Backed Tanager (*Ramphocelus dimidiatus*; n = 464), followed by the Black-Billed Thrush (*Turdus ignobilis*; n = 418) and Blue-gray Tanager (*Thraupis episcopus*; n = 410). The families with the highest abundance were Thraupidae (27%) and Tyrannidae (15%). The most abundant order was Passeriformes (45%). Species richness and abundance varied among methods: mist nets captured 175 species (n = 3.904); visual and audio observations recorded 356 species (n = 12.171); and eBird checklists recorded 175 species (n = 1.490). Rarefaction curves to assess eBird data completeness are provided in the Supplementary Material (Figure S2). Additionally, overall sampling completeness, as estimated using the Chao1 richness estimator, ranged from 76% to 99% (Figure S3).

To estimate functional diversity indices, we included all recorded individuals and excluded bill length (BLN), bill depth (BD), wing chord length (WCL), and tail length (TAI) from the analyses to reduce multicollinearity. Functional originality (FOri) was the only index that did not show significant differences between bird assemblages (p = 0.092) (Figure 3F). The highest values for functional richness (FRic) and functional evenness (FEve) were observed in non-fragmented landscapes, particularly in BV and EP (Figure 3A,B). In contrast, fragmented landscapes such as DO, PO, and UI exhibited the lowest FRic value (Figure 3A). Functional beta diversity was low (40%), with functional turnover contributing 11%, while functional nestedness accounted for the majority of variation (29%) in functional beta diversity.

3.3. Effect of Landscape Structure on Bird Functional Diversity

We selected the first two principal components from the PCA of the landscape metrics. These two explained 61% of the total variation (PC1: 37.2%; PC2: 24%). The variables selected for inclusion in the GMLs were mainly related to the area and perimeter of forest and secondary vegetation patches, as well as to landscape diversity and evenness (Figure S4).

According to best-fit GLMs selected based on the lowest AIC values and the significance of landscape variables, all models showed an adequate fit to the gamma distribution assumptions ($p > 0.05$) (Figure S5). Some functional alpha diversity indices (FRic, FDiv, FEve, and FSpe) were significantly related to landscape variables (Table 2). The landscape variables with the greatest influence on functional alpha diversity indices were landscape diversity (SHDI) and the percentage of forest area within landscapes (PND_F) (Table 2). We found that greater forest area within landscapes was associated with higher functional richness in bird assemblages, while greater landscape heterogeneity (SHDI) corresponded to increased functional specialization (Table 2). A complete list of all models tested for each of the functional diversity indices are presented in the Supplementary Material (Table S5).

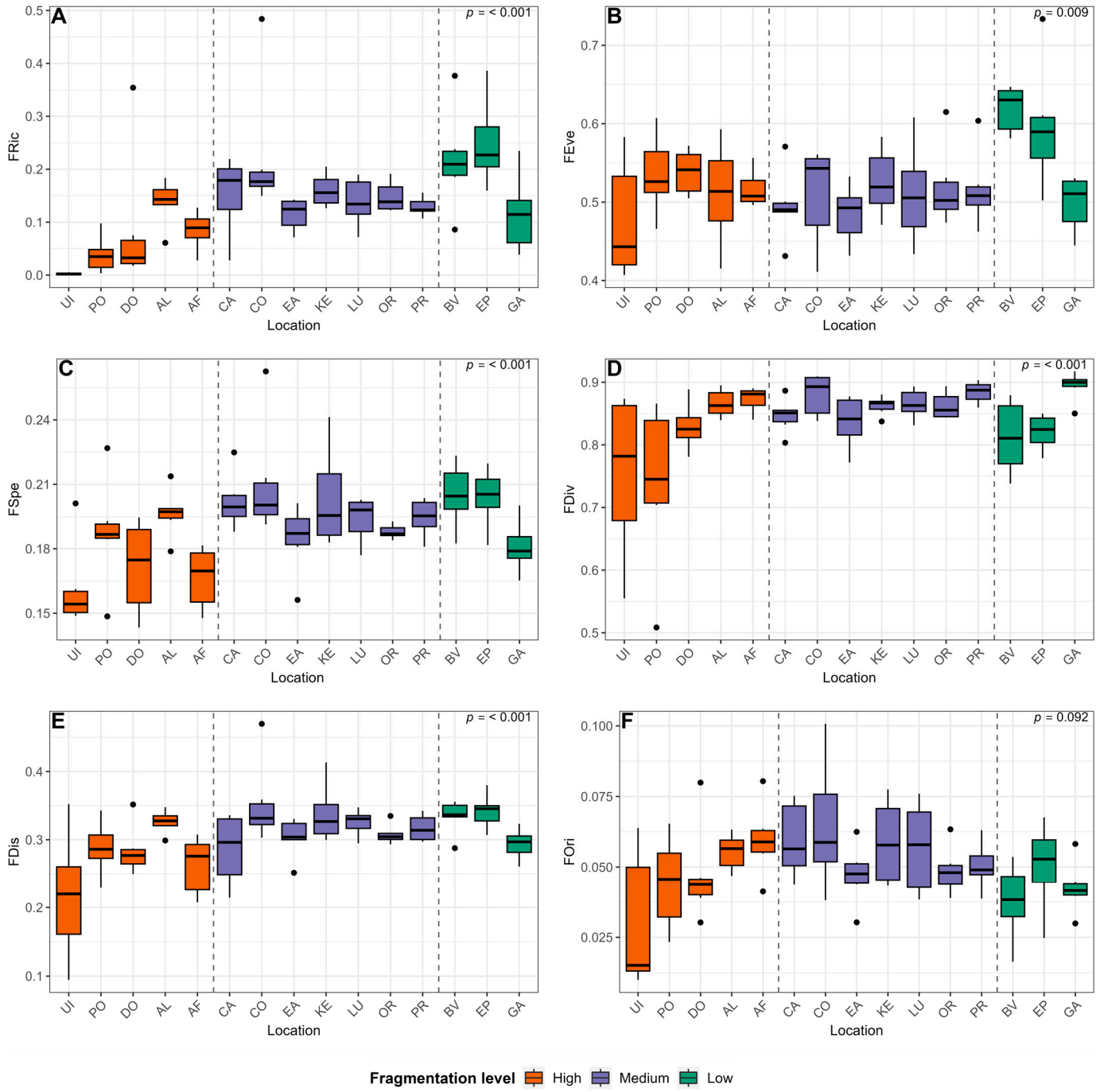

Figure 3. Comparison of functional alpha diversity indices bird assemblages: (**A**) functional richness (FRic), (**B**) functional evenness (FEve), (**C**) functional specialization (FSpe), (**D**) functional divergence (FDiv), (**E**) functional dispersion (FDis), and (**F**) functional originality (FOri). Black dots represent outliers. Site abbreviations: UI = Universidad de Ibagué; PO = Potrerillo; DO = Doima; AL = Los Alpes; AF = Agua Fría; CA = La Carpintería; CO = Paraíso de Cocora; EA = Entre Aguas; KE = Kenisha; LU = La Lucia; OR = Orquídeas del Tolima; PR = La primavera; BV = Bella Vista; EP = El Palmar; GA = Gaia.

Regarding db-RDA analysis, landscape structure explained a high proportion of total beta diversity variation (R^2 = 0.63; p = 0.028). The landscape diversity index (R^2 = 0.22), the percentage of forest area within landscapes (R^2 = 0.27), and the number of secondary vegetation patches (R^2 = 0.14) all contributed significantly to total beta diversity variation.

Similarly, the percentage of variation explained by the functional turnover component was high (R^2 = 0.52; p = 0.001) and was predominantly influenced by the even distribution of diversity within communities (R^2 = 0.52). In contrast, no landscape variables were found to significantly influence functional nestedness.

Table 2. Comparison of best-fit Generalized Linear Models (GLMs) to test the influence of landscape variables on functional diversity indices. The *p*-values indicate the statistical significance of each parameter estimated in the selected models. Diversity indices abbreviations: FRic = functional richness; FDiv = functional divergence; FEve = functional evenness; FSpe = functional specialization. Landscape metric abbreviations: AREA_F = area of forest patches; PND_F = percentage of forest cover within landscapes; SHDI = shannon's diversity index; SHEI = shannon's evenness index; NP_SV = number of secondary vegetation patches; PER_F = perimeter of forest patches; AREA_SV = area of secondary vegetation patches; PER_SV = perimeter of secondary vegetation patches.

Model	Landscape Variables	Parameter Estimated	*p*-Value	AIC
FRic	AREA_F	−0.009	0.032	0.6
	PND_F	0.021	0.015	
FDiv	SHDI	0.219	0.005	−22.8
	SHEI	−0.342	0.024	
	NP_SV	−0.005	0.016	
	PER_F	5.349×10^{-6}	0.004	
	AREA_SV	2.505×10^{-5}	0.001	
	PER_SV	−0.003	0.003	
FEve	PND_F	−0.001	0.007	−30.5
FSpe	SHDI	0.106	0.025	−49.1

The first two axes in the RLQ analysis accounted for 94% of the total variation between landscape variables and species traits. The ordinations revealed distinct patterns in bird functional diversity based on habitat characteristics. Forest specialist birds (H.f) and nectarivorous birds (T.n) were predominantly found in sites with the largest forest areas (AREA_F), such as Gaia (GA) and BV (Figure 4A,C,D). In contrast, omnivorous birds (T.o) were associated with more heterogeneous landscapes (SHDI) (e.g., PO, DO, and AF). Species with greater body mass (MA) were present in sites with fewer secondary vegetation patches (NP_SV) (e.g., UI) (Figure 4C,D). Granivore birds (T.g), however, were more common in sites with extensive secondary vegetation patches (NP_SV, AREA_SV) such as Kenisha (KE) and AL (Figure 4A,C). Additionally, fruit-dependent species (T.f) were less frequent in urban areas like UI, while nectarivorous birds (T.n) were less abundant in fragmented landscapes, including PO, DO, and AF (Figure 4A,D).

Functional traits were significantly influenced by environmental variables (fourth corner: p value = 0.019). A total of 41 environment–trait links were significant, with 19 positive relationships and 22 negative relationships (Figure 5). Insectivorous birds (T.i) were negatively associated with greater landscape heterogeneity (SHDI) but positively linked to sites with larger forest areas (AREA_F). Birds with an omnivorous diet (T.o) and wider bill width (BW) were strongly positively correlated with landscape heterogeneity, while forest bird species (H.f) showed a negative association with it (SHDI). Additionally, the presence of shrubland birds (H.s) was positively associated with increasing landscape heterogeneity (SHDI) (Figure 5).

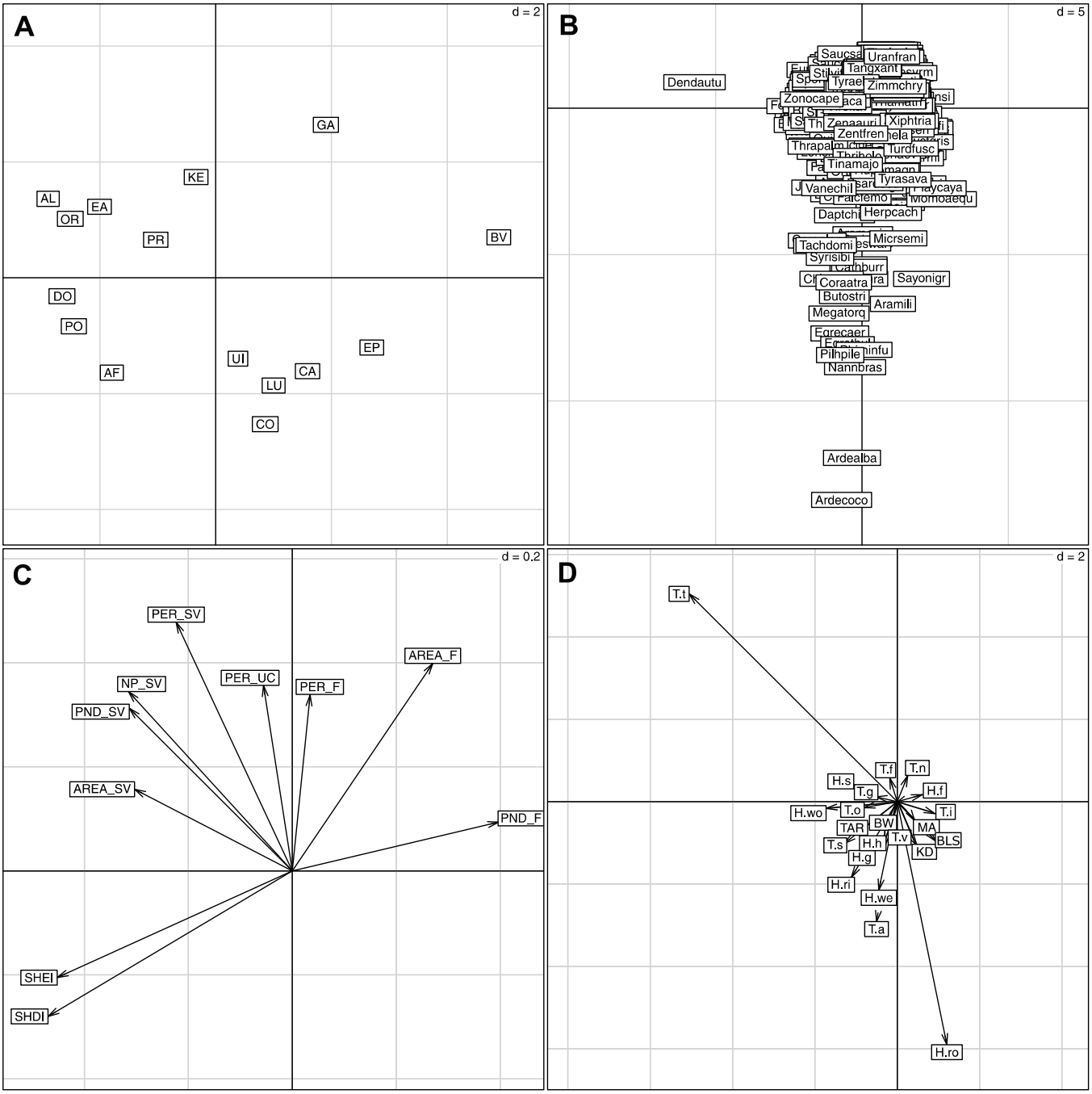

Figure 4. Results of the RLQ analysis from the bird assemblage data. The ordination plots show the scores of (**A**) study sites, (**B**) species distribution (matrix L), (**C**) landscape metrics (matrix R), and (**D**) species traits (matrix Q). Site abbreviations: UI = Universidad de Ibagué; PO = Potrerillo; DO = Doima; AL = Los Alpes; AF = Agua Fría; CA = La Carpintería; CO = Paraíso de Cocora; EA = Entre Aguas; KE = Kenisha; LU = La Lucia; OR = Orquídeas del Tolima; PR = La primavera; BV = Bella Vista; EP = El Palmar; GA = Gaia. Landscape metric abbreviations: SHDI = shannon's diversity index; SHEI = shannon's evenness index; PND_SV = percentage of secondary vegetation within landscapes; PER_SV = perimeter of secondary vegetation patches; AREA_SV = area of secondary vegetation patches; AREA_F = area of forest patches; NP_SV = number of secondary vegetation patches; PER_F = perimeter of forest patches; PND_F = percentage of forest cover within landscapes; PER_UC = perimeter of urban patches. Functional trait abbreviations: H.f = forest-dependent species; H.g = grassland species; H.h = human-modified species; H.ri = riverine species; H.ro = rocky habitats species; H.s = shrubland species; H.we = wetland species; H.wo = woodland

species; T.a = aquatic predator; T.f = frugivorous species; T.g = granivorous species; T.i = invertivorous species; T.n = nectarivorous species; T.o = omnivorous species; T.s = scavenger species; T.t = terrestrial herbivorous species; T.v = vertivorous species; BLS = bill length measured from tip to skull; BW = bill width; KD = Kipp's distance; TAR = tarsus length; MA = body mass.

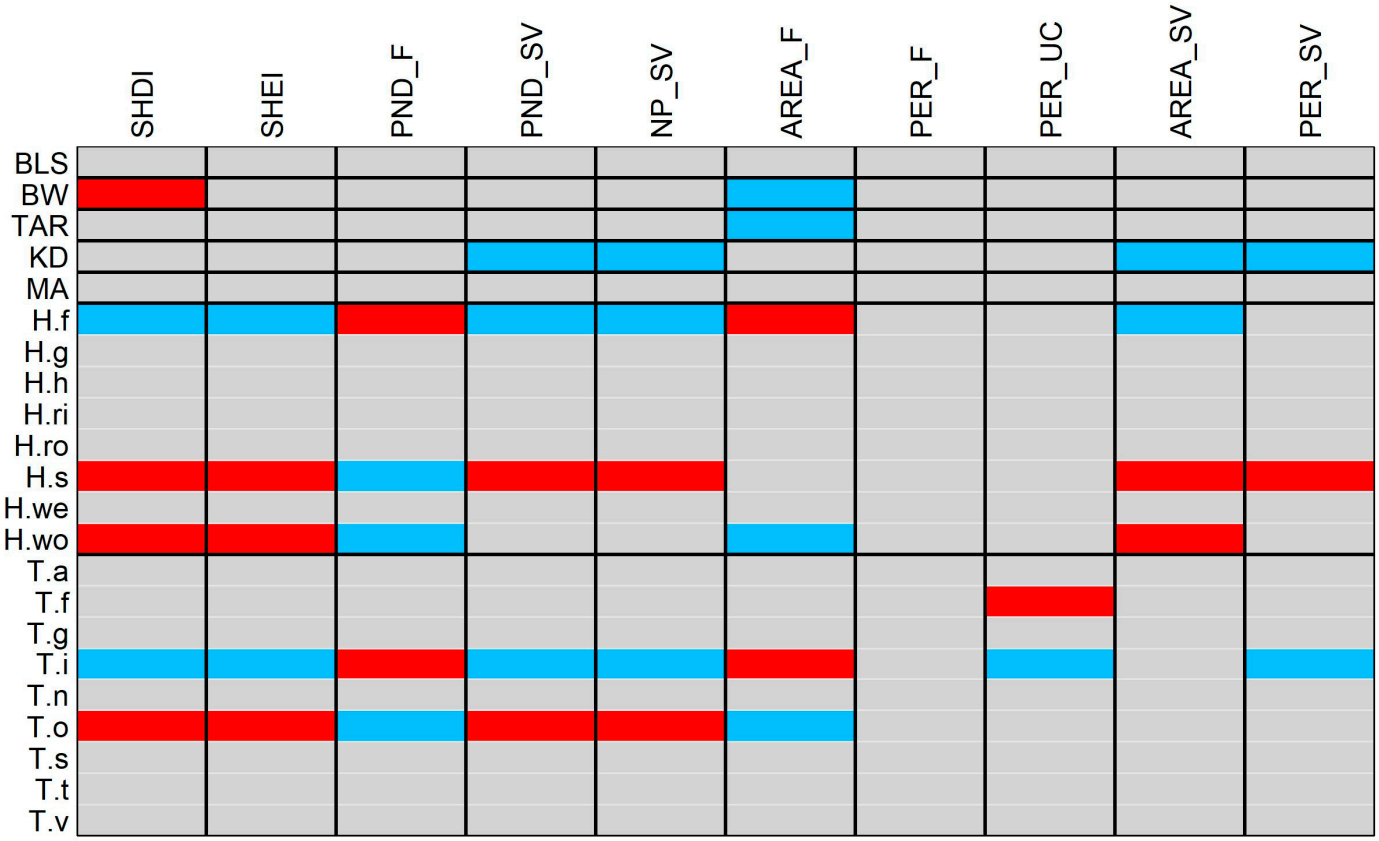

Figure 5. Results of the fourth-corner tests. Significant positive associations ($p < 0.05$) are indicated by red cells and significant negative associations are represented by blue cells. Non-significant associations are represented by gray cells. Functional trait abbreviations: BLS = bill length measured from tip to skull; BW = bill width; TAR = tarsus length; KD = Kipp's distance; MA = body mass; H.f = forest-dependent species; H.g = grassland species; H.h = human-modified species; H.ri = riverine species; H.ro = rocky habitats species; H.s = shrubland species; H.we = wetland species; H.wo = woodland species; T.a = aquatic predator; T.f = frugivorous species; T.g = granivorous species; T.i = invertivorous species; T.n = nectarivorous species; T.o = omnivorous species; T.s = scavenger species; T.t = terrestrial herbivorous species; T.v = vertivorous species. Landscape metric abbreviations: SHDI = shannon's diversity index; SHEI = shannon's evenness index; PND_F = percentage of forest cover within landscapes; PND_SV = percentage of secondary vegetation within landscapes; NP_SV = number of secondary vegetation patches; AREA_F = area of forest patches; PER_F = perimeter of forest patches; PER_UC = perimeter of urban patches; AREA_SV = area of secondary vegetation; PER_SV = perimeter of secondary vegetation patches.

4. Discussion

In this study, we investigated the effects of landscape structure and configuration on birds' functional diversity in the Upper Magdalena River Valley, Colombia. Our findings reveal that both functional richness and functional evenness are significantly influenced by landscape fragmentation. As we hypothesized, fragmented landscapes (i.e., areas with the highest urban cover) showed the lowest values of functional richness and evenness, suggesting that habitat structure plays a crucial role in driving an environmental filtering process. In fragmented areas, bird communities were dominated by generalist species with larger body sizes, broader bill widths, and large tarsi. In contrast, more conserved

areas supported species with narrower bill widths and small tarsi, associated with more specialized ecological requirements. This process tends to exclude species with narrow habitat requirements [91] and selects species with functional traits that enable them to persist and tolerate habitat changes [92,93].

4.1. Landscape Metrics

The reduction in native forest cover is considered one of the main indicators of landscape fragmentation [94]. The lowest level of fragmentation was recorded in BV and EP, with more than 75% forest area and less than 1% urban cover. In contrast, UI, AL, AF, PO, and DO were classified as highly fragmented areas, with less than 32% forest cover (Table S3). These sites also exhibited the highest percentage of urbanized landscape (>10% urban cover) and greater landscape heterogeneity (SHDI) (Table S3), indicating a more fragmented landscape structure, primarily driven by human-induced transformations such as deforestation, urban expansion, and agricultural activities.

4.2. Functional Alpha Diversity

Our findings indicate that bird functional alpha diversity varied significantly among study sites. As expected, intensely urbanized areas had a negative impact on bird assemblages. We observed a declining trend in functional richness and evenness in response to urban intensification, with the most urbanized areas exhibiting the lowest values (e.g., UI). This pattern aligns with previous studies showing that bird functional diversity tends to be lower in fragmented landscapes compared to continuous habitats [95,96]. Urban areas have recently undergone extensive land clearing and fragmentation, leading to a loss of forest cover [97]. These changes can reduce the abundance of specialist bird species and alter the composition of functional groups, ultimately increasing functional similarity among bird communities [98].

Our findings indicate that urban areas support a higher number of generalist species with large body sizes and high dispersal capacities, such as the Cattle Egret (*Ardea ibis*), Bare-Faced Ibis (*Phimosus infuscatus*), and Black Vulture (*Coragyps atratus*). These species tend to exploit the upper layers of vegetation for nesting, foraging, and perching. The prevalence of these traits may be explained by the fact that larger species are better adapted to cope with anthropogenic disturbances, including high levels of human activity and vehicle traffic, which are characteristic of urban environments [99,100]. Additionally, large-bodied species appear to be more tolerant of human presence, as evidenced by their shorter flight initiation distances [99]. Similar patterns have been reported by Ikin et al. [101] and Pena et al. [100], who found a positive correlation between urbanization levels and increased body mass in birds.

Functional richness values were higher in less fragmented sites, such as EP and BV. This increased functional diversity is likely associated with a more complex vertical vegetation structure, which is typically found in areas with greater forest cover [102]. Such structural complexity provides a greater abundance of food resources for bird species [103]. Studies suggest that landscapes with a high percentage of vegetation cover enhance the availability of ecological niches and microhabitats, promoting the presence of specialized species and facilitating the coexistence of functionally distinct species within ecosystems [104,105]. These findings underscore the importance of well-preserved landscapes in maintaining key functional groups and essential ecosystem services, including pollination, seed dispersal, scavenging, and pest control [106].

Our findings align with those of Santillán et al. [107] who examined the effects of landscape fragmentation along an elevational gradient on the functional diversity of bird communities in southern Ecuador. They reported significantly reduced functional richness

in fragmented forests at lower elevations. Low functional richness may indicate that some community resources remain unused [16], suggesting that birds perform fewer ecological roles within the ecosystem [106]. Conversely, ecosystems with high functional diversity tend to support species that fulfill a wide range of ecological roles, thereby enhancing overall ecosystem functioning, stability, and resilience [108].

In our study, the functional evenness of bird assemblages increased with greater forest cover in the landscape, as observed in sites like BV. High functional evenness has been associated with more efficient resource utilization by birds. This metric reflects whether the abundance of bird species is evenly distributed within the functional space [109]. In contrast, UI exhibited the lowest functional evenness, which may suggest that certain resources used by birds are being over-utilized. This imbalance could make the community more vulnerable to habitat alterations, such as biological invasions [110,111].

Interestingly, the abundance of insectivorous birds, particularly tyrant flycatchers (Tyrannidae), was notably higher in urban areas. Previous studies have shown that tropical insectivorous birds may possess a greater capacity to adapt to fragmented habitats [112].

4.3. Functional Beta Diversity

The results revealed low functional beta diversity, primarily driven by functional nestedness. This component reflects the gain or loss of functional traits within bird assemblages, suggesting that the species pool and functional traits in less diverse communities are subsets of those found in more diverse sites [113]. In our study, we found that highly fragmented sites represented subsets of the functional space observed in sites with lower levels of fragmentation. These shifts in functional traits may be driven by reduced landscape connectivity and resource availability [114,115]. Our findings align with those of Matthews et al. [116] and Yang et al. [117], who suggested that habitat loss and fragmentation are key drivers of functional nestedness, suggesting that communities in more altered areas are represented by a narrower range of functional traits, resulting in functionally less diverse communities.

Total beta diversity was significantly associated with the percentage of forest area within landscapes. Previous studies have demonstrated that vegetation structure and composition play a pivotal role in shaping bird assemblages [118,119]. These results may indicate that resources were not evenly distributed across all study sites. Variation in community composition reflects differences in resource availability, as species with diverse traits occupy specific ecological niches shaped by habitat structure and resource distribution [120]. As a result, the presence or absence of particular species or functional groups within a given environment can significantly influence changes in the community's functional composition.

4.4. Effect of Landscape Structure on Bird Functional Diversity

A significant relationship was observed between functional alpha diversity indices and landscape variables. GLMs showed that the percentage of forest cover was the most influential habitat factor affecting functional diversity of Andean bird assemblages. These results are similar to those reported by Tinoco et al. [121], who reported a significant relationship between native vegetation coverage and functional diversity of hummingbirds in Ecuador's Andes Mountains. The positive correlation between functional diversity and native vegetation cover underscores the critical role of forest cover in shaping bird functional diversity, emphasizing that changes in forest cover within landscapes can substantially impact ecosystem functionality.

Moreover, we found that an abundance of omnivorous birds was negatively correlated with the percentage of forest cover within landscapes and positively associated with

landscape heterogeneity. One possible reason for these findings is that these species tend to be more tolerant to disturbed areas and less affected by habitat urbanization [122]. Omnivorous species exhibit the ability to utilize a broad range of food resources, resulting in increased abundance in areas with higher levels of anthropization and greater food availability [123]. This trend is consistent with findings from other studies [100,122,124], which reported that omnivore bird abundance tends to rise in more urbanized areas.

Finally, landscape heterogeneity—resulting from fragmentation processes at a local scale—appears to favor the presence of omnivorous species. However, a negative effect was observed in frugivorous and nectarivorous species. In highly urbanized areas, frugivorous birds became less frequent, likely due to a reduction in the availability of flowers and fruits, which are often less abundant in urban environments [122]. These findings underscore the contrasting responses of bird functional groups to urbanization and habitat fragmentation, highlighting the need to preserve diverse landscapes to support specialized species.

Our findings demonstrate that bird functional diversity and the composition of functional guilds are closely associated with landscape structure, particularly vegetation and urban cover. Landscapes with continuous forest patches supported higher functional diversity and a broader range of functional traits, including nectarivorous and frugivorous species, which are key for maintaining ecosystem functions such as pollination and seed dispersal. In contrast, fragmented areas were dominated by generalist species with larger body sizes, broader bill widths, and higher dispersal capacities—traits that are typically associated with greater ecological tolerance. The low functional beta diversity observed, mainly driven by nestedness, suggests a loss of functional traits within bird assemblages, likely as a consequence of reduced landscape connectivity and resource availability. Therefore, maintaining landscapes with sufficient native forest cover is essential to support functionally diverse bird communities and ensure the provision of critical regulating ecosystem services.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ecologies6030052/s1, Table S1: Characteristics of the study areas in the Upper Magdalena River Valley, Colombia. Life zone codes follow the Holdridge Life Zone (HLZ) classification: bh-PM = premontane wet forest; bs-T = tropical dry forest; bh-MB = lower montane moist forest. Table S2: Summary of sampling effort by site. Table S3: Results of landscape metrics at patch, class, and landscape level. Land cover types: F = forest cover, UC = urban cover, and SV = secondary vegetation cover. Site codes: AF = Agua Fría; BV = Bella Vista; DO = Doima; EP = El Palmar; EA = Entre Aguas; GA = Gaia; KE = Kenisha; CA = La Carpintería; LU = La Lucia; AL = Los Alpes; OR = Orquídeas del Tolima; CO = Paraíso de Cocora; PO = Potrerillo; PR = La Primavera; UI = Universidad de Ibagué. Figure S1: Location and land cover types of the sampling sites. Site codes: AF = Agua Fría; BV = Bella Vista; DO = Doima; EP = El Palmar; EA = Entre Aguas; GA = Gaia; KE = Kenisha; CA = La Carpintería; LU = La Lucia; AL = Los Alpes; OR = Orquídeas del Tolima; CO = Paraíso de Cocora; PO = Potrerillo; PR = La Primavera; UI = Universidad de Ibagué. Table S4: Structure of bird assemblages in the 15 study areas. Site abbreviations: AF = Agua Fría; EA = Entre Aguas; GA = Gaia; KE = Kenisha; CA = La Carpintería; AL = Los Alpes; LU = La Lucia; PR = La primavera; OR = Orquídeas del Tolima; CO = Paraíso de Cocora; EP = El Palmar; BV = Bella Vista; DO = Doima; PO = Potrerillo; UI = Universidad de Ibagué. Figure S2: Rarefaction curves for the study areas. Site codes: AF = Agua Fría; BV = Bella Vista; DO = Doima; EP = El Palmar; LU = La Lucia; AL = Los Alpes; CO = Paraíso de Cocora; PO = Potrerillo; PR = La Primavera; UI = Universidad de Ibagué. Figure S3: Species accumulation curve for the study sites. Site codes: AF = Agua Fría; BV = Bella Vista; DO = Doima; EP = El Palmar; EA = Entre Aguas; GA = Gaia; KE = Kenisha; CA = La Carpintería; LU = La Lucia; AL = Los Alpes; OR = Orquídeas del Tolima; CO = Paraíso de Cocora; PO = Potrerillo; PR = La Primavera; UI = Universidad de Ibagué. Figure S4: Contribution of landscape variables to the first two PCA axes. The red dashed line indicates variables with correlation coefficients > 0.5. Landscape metric abbreviations: PND_SV = percentage of secondary vegetation within landscapes; SHEI = shannon's evenness index; PER_SV = perimeter of secondary vegetation patches;

AREA_SV = area of secondary vegetation patches; AREA_F = area of forest patches; NP_SV = number of secondary vegetation patches; PER_F = perimeter of forest patches; SHDI = shannon's diversity index; PND_F = percentage of forest cover within landscapes; PER_UC = perimeter of urban patches; PND_UC = percentage of urban cover within landscapes; NP = total number of patches; NP_UC = number of urban cover patches; AREA_UC = area of urban patches; SHAPE_F = shape of forest patches; SHAPE_SV = shape of secondary vegetation patches; SHAPE_UC = shape of urban patches; PR = patch richness; NP_F = number of forest patches. Figure S5: Distribution of the residuals in a Q-Q plot for the best model selected. KS test = Kolmogorov–Smirnov. Table S5: Results of Generalized Linear Models (GLMs). Landscape metric abbreviations: SHDI = shannon's diversity index; SHEI = shannon's evenness index; PND_SV = percentage of secondary vegetation within landscapes; PER_SV = perimeter of secondary vegetation patches; AREA_SV = area of secondary vegetation patches; AREA_F = area of forest patches; NP_SV = number of secondary vegetation patches; PER_F = perimeter of forest patches; PND_F = percentage of forest cover within landscapes; PER_UC = perimeter of urban patches; AIC = Akaike Information Criterion; wi = Akaike weights; * = p-value < 0.05.

Author Contributions: Conceptualization: V.R.-M., methodology: V.R.-M., E.L.-D. and M.M.-P.; software: V.R.-M. and E.L.-D.; formal analysis: V.R.-M. and E.L.-D.; investigation: V.R.-M., E.L.-D. and M.M.-P.; data curation: V.R.-M.; writing—original draft preparation: V.R.-M.; writing—review and editing: E.L.-D. and M.M.-P.; supervision: E.L.-D. and M.M.-P. All authors have read and agreed to the published version of the manuscript.

Funding: The article processing charge (APC) was partially supported by Universidad de Ibagué through its "Divulgación Científica" cost center (No. 300500), under internal authorization Act No. 301/3001.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Code in R and data are openly available in FigShare at https://doi.org/10.6084/m9.figshare.28377053.v1 (accessed on 24 April 2025).

Acknowledgments: The authors thank Jorge E. García-Melo for his valuable assistance in photographing the avian functional traits presented in Figure 2, as well as the editor and four anonymous reviewers on the manuscript for their valuable comments.

Conflicts of Interest: The authors declare no conflicts of interest.

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