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Article

Functional Diversity and Ecosystem Services of Birds in Productive Landscapes of the Colombian Amazon

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Abstract: The expansion of anthropogenic activities drives changes in the composition, structure, and spatial configuration of natural landscapes, influencing both the taxonomic and functional diversity of bird communities. This pattern is evident in the Colombian Amazon, where agricultural and livestock expansion has altered ecological dynamics, avifaunal assemblages, and the provision of regulating ecosystem services. This study analyzed the influence of agroforestry (cocoa-based agroforestry systems – SAFc) and silvopastoral systems (SSP) on the functional diversity of birds and their potential impact on ecosystem services in eight productive landscape mosaics within the Colombian Amazon. Each mosaic consisted of a 1 km² grid, within which seven types of vegetation cover were classified, and seven landscape metrics were calculated. Bird communities were surveyed through visual observations and mist-net captures, during which functional traits were measured. Additionally, functional guilds were assigned to each species based on literature review. Five multidimensional indices of functional diversity were computed, along with community-weighted means per guild. A total of 218 bird species were recorded across both land-use systems. Mean richness and abundance did not show statistically significant differences between SAFc and SSP ($p > 0.05$). However, bird richness, abundance, and functional diversity—as well as the composition of functional guilds—varied according to vegetation cover. Functional diversity increased in mosaics containing closed vegetation patches with symmetrical configurations. Variations in functional guilds were linked to low functional redundancy, which may also lead to differences in the provision of regulating ecosystem services such as biological pest control and seed dispersal—both of which are critical for the regeneration and connectivity of productive rural landscapes.

Keywords: avifauna; functional guilds; agroforestry systems; silvopastoral systems; cocoa; landscape mosaics; patches

1. Introduction

Over the past five decades, more than 17% of the primary forests in the Colombian Amazon have been transformed by processes of colonization involving land grabbing, illicit crop cultivation, and the expansion of agricultural and livestock production in ways that are misaligned with land-use suitability [1,2]. This transformation simplifies the structure and composition of landscapes, reduces vegetation cover heterogeneity, and results in small, isolated patches of remnant vegetation embedded within agricultural matrices [3–5]. The conversion of primary forests leads to significant biodiversity loss [6,7] and to the biotic and functional homogenization of natural communities [8,9]. Several studies have documented the negative effects of fragmentation on biological communities. For instance, Murillo-Sandoval et al. [10] found that habitat patch loss reduces movement capacity

and genetic exchange in mammals, birds, and invertebrates. Similarly, Mena et al. [11] reported that medium- and large-sized terrestrial birds and felids in the Amazon face long-term risks due to the intensification of agricultural activities. Moreover, Negret et al. [12] projected that by 2040, nearly 40% of forest-dependent bird species will lose their habitat as a result of increased forest patch isolation—especially frugivorous and insectivorous species in the Andean-Amazonian foothills.

In this context, and within the framework of nature-based solutions, agroforestry systems (AFS) and silvopastoral systems (SPS) have emerged as key sustainable strategies for mitigating the effects of climate change in the Amazon [13]. In Colombia, the signing of the peace agreement promoted a shift toward sustainable productive practices in the agricultural sector, with the aim of halting deforestation and contributing to peacebuilding efforts [14,15]. However, to achieve the goal of zero deforestation, it is essential to adapt these strategies to local contexts, considering sociocultural, environmental, and productive dimensions [16]. SPS combine forage species with shrubs and perennial trees, optimizing livestock feed while promoting sustainable land use [17]. AFS, in turn, integrate crops of high ecological and economic value—such as cocoa (*Theobroma cacao* L.)—with shade trees and other woody species, including fruit trees, legumes, and native timber species. These practices have been shown to enhance forest restoration and conservation, contributing to the protection of habitats for local flora and fauna [18]. Moreover, the increased structural complexity of these landscapes, along with the agricultural diversification associated with their implementation, enhances the provision of essential ecosystem services [19,20]. In addition, these systems generate both direct and indirect socioeconomic benefits for rural communities, strengthening food security and stimulating regional economies [21–23].

The ecological and functional processes of bird communities are influenced by gradual changes in the composition and configuration of landscapes in productive systems [24,25]. These changes are assessed using landscape metrics that describe the heterogeneity, aggregation, and spatial arrangement of vegetation cover [26,27]. However, the magnitude of their effects depends on functional diversity [7] and on the variability of species' functional traits, such as body size, feeding guild, or dispersal capacity [28–30]. Recent studies have documented divergent responses in birds' functional traits at the patch scale. For instance, the expansion of pasture matrices and the isolation of patches of the same type favor the increase in abundance of small granivores, large vertebrate consumers, and pasture specialists [31,32] but lead to a reduction in pollinator richness [33]. In contrast, greater agricultural diversification—characterized by landscapes with large, symmetrical patches and higher forest heterogeneity—favors the presence of large-bodied frugivores [34–36] and small insectivores [37,38]. Bitani et al. [39] propose that fragmented landscapes with isolated, non-degraded forest patches positively influence insectivore functional richness, whereas Şekercioğlu et al. [40] report that this guild is highly sensitive to human disturbance and land-use change.

Increased structural complexity within the landscape enhances the availability of ecological niches, promotes the coexistence of multiple species, and supports greater functional richness, divergence, and redundancy in bird communities [39,41]. According to Tilman [42], functional diversity is a component of biodiversity that influences ecosystem dynamics, stability, productivity, nutrient balance, and overall functioning. Functional diversity is assessed using multidimensional indices, which offer a robust framework for examining the relationship between biodiversity and ecosystem functioning, based on the value and range of functional traits across species [4,43]. This approach also allows for the evaluation of bird's contributions to regulating ecosystem services such as seed dispersal, pollination, and biological control [44]. These services are critical to enhancing the resilience and sustainability of agroforestry and livestock systems [45–47]. However, the ecosystem services provided by birds in productive systems in the Colombian Amazon re-main largely understudied and undervalued. There is a scarcity of targeted research on the composition and structure of avian diversity within productive systems in the Colombian Amazon [7,12,48–50], and limited understanding of the influence of agroforestry and livestock landscape configuration and composition on these communities [3]. Furthermo-re, the region lacks studies that analyze and explain the causal relationships between avian functional traits, ecological processes, and the

provision of ecosystem services in relation to landscape structure in agroforestry and silvopastoral systems.

Accordingly, this study addressed the following research questions: (1) What are the characteristics of bird community composition and functional diversity across vegetation covers in agroforestry and silvopastoral systems? and (2) What is the relationship between the structure of cocoa-based agroforestry and silvopastoral landscapes and the provision of bird-mediated ecosystem services in the Colombian Amazon? This research examined the relationship between bird provided ecosystem services and the structure and configuration of agroforestry and livestock landscapes undergoing ongoing transformation. It also identified and explained emerging patterns of functional diversity in bird communities within mosaics dominated by agroforestry and silvopastoral matrices. Understanding this dynamic is essential for developing effective conservation and sustainable management strategies, particularly in anthropized landscapes where the interaction between biodiversity and human activities is complex and multifaceted. Through an integrative approach that combines landscape metrics, functional community analysis, and ecosystem service evaluation, this study seeks to provide evidence to guide landscape management practices that foster greater sustainability and biodiversity in productive environments.

2. Materials and Methods

2.1. Study Area

This research was conducted in the northwestern region of the Colombian Amazon, within the department of Caquetá; 01°36'N, 75°36'W (Figure 1). The region is characterized by a dominant geomorphology of rolling hills, piedmont areas, and floodplains, with slopes of less than 12% [51]. The total annual precipitation is 4277 mm, following a unimodal distribution with a peak rainy season occurring on average between April and October. The mean temperature is 28.62°C, and the average relative humidity is 86%.

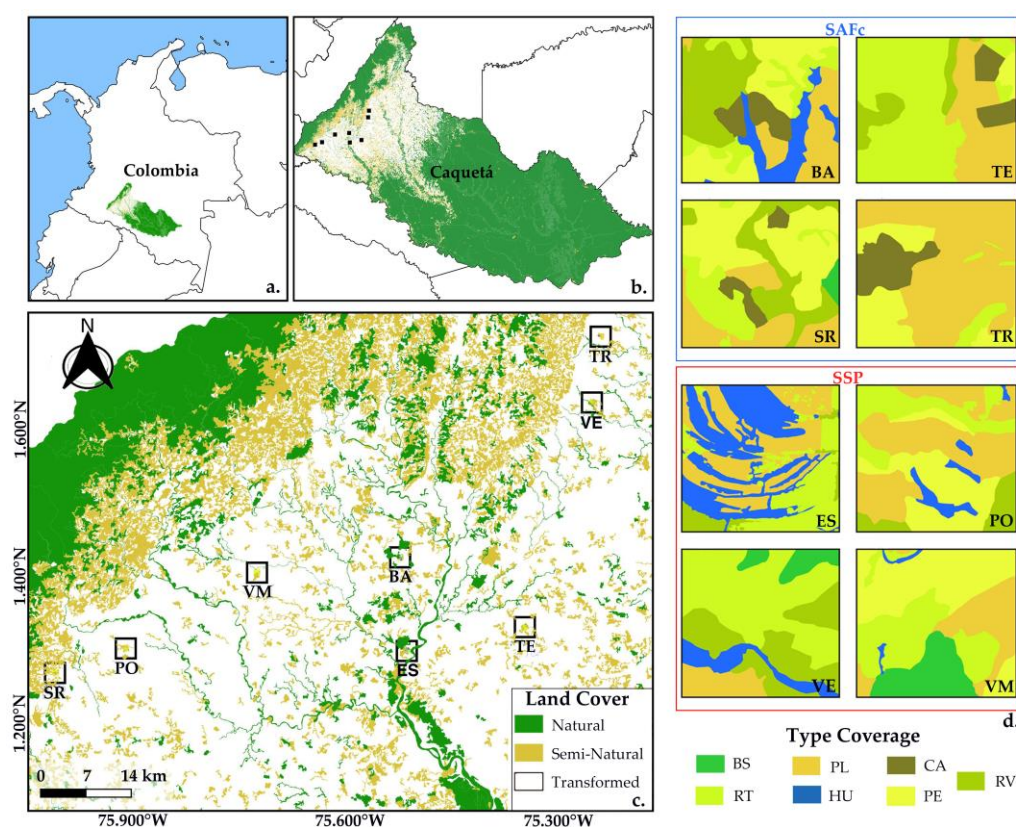


Figure 1. Location of landscape mosaics with cocoa-based agroforestry systems (SAFc) and silvopastoral systems (SSP) in the Colombian Amazon. (a) Location of the department of Caquetá within Colombia; (b) location of the

mosaics in the Caquetá piedmont region; (c) distribution of SAFc and SSP mosaics; (d) thematic land cover map of SAFc mosaics: TR: El Triunfo – El Doncello; BA: Batalla 13 – Florencia; SR: Santa Rosa – San José del Fragua; TE: El Tesoro – La Montañita; and thematic land cover map of SSP mosaics: PO: El Porvenir – Albania; VE: La Vega – El Doncello; VM: Villa Mery – Morelia; ES: Esmeraldas – Milán; BS: secondary forest; CA: cocoa agroforestry crop; HU: wetlands; PE: weedy pastures; PL: clean pastures; RT: early successional fallows; RV: late successional fallows.

The study was conducted across eight landscape mosaics: four dominated by cocoa-based agroforestry systems (SAFc) and four by silvopastoral systems (SSP). Each mosaic covered an area of 1 km² (100 ha), allowing for the inclusion of various types of vegetation cover and landscape elements such as patches, matrix, and corridors [52,53]. Vegetation cover within each mosaic was classified using digital processing of Landsat TM satellite imagery at a 30-meter resolution, with QGIS 3.36 software. This classification followed the guidelines of the CORINE *Land Cover* methodology adapted for Colombia [54]. Ground-truthing and field verification of vegetation cover types were conducted during the fieldwork phase.

The thematic map identified seven categories of vegetation cover across the sampled landscape mosaics (Figure 2): Cocoa agroforestry crops (CA): plantations of *Theobroma cacao* (L.) intercropped with various tree species such as *Hevea brasiliensis* (Müll. Arg.) and *Acacia mangium* (Willd.); Wetlands (HU): natural freshwater bodies located in flood-prone areas of alluvial terraces or between foothill valleys, with aquatic herbaceous vegetation such as *Juncus* L.; Early successional fallows (RT): shrub-herbaceous vegetation between 2–5 m in height, with dominant dbh < 10 cm and species from genera such as *Miconia* (Ruiz & Pav.) and *Spathiphyllum* (H.W. Schott & S.L. Endlicher); Late successional fallows (RV): vegetation older than ten years, primarily arboreal, with heights of 8–12 m, dominant dbh > 10 cm, and an irregular canopy, with species such as *Ochroma pyramidale* (Cav. ex Lam. Urb.) and *Piptocoma discolor* (Kunth Pruski); Clean pastures (PL): areas dominated by *Urochloa* spp. with over 70% ground cover; Secondary forest (BS): arboreal vegetation with pioneer species, height exceeding 12 m, dbh between 15–20 cm, a multi-layered canopy, and tree cover greater than 30%, with species such as *Zygia longifolia* (Willd. Britton & Rose) and *Ormosia coccinea* (Aubl.); Weedy pastures (PE): areas with *Urochloa* spp. mixed with weeds, under 1.5 m in height, including species like *Bellucia pentamera* (Naudin).

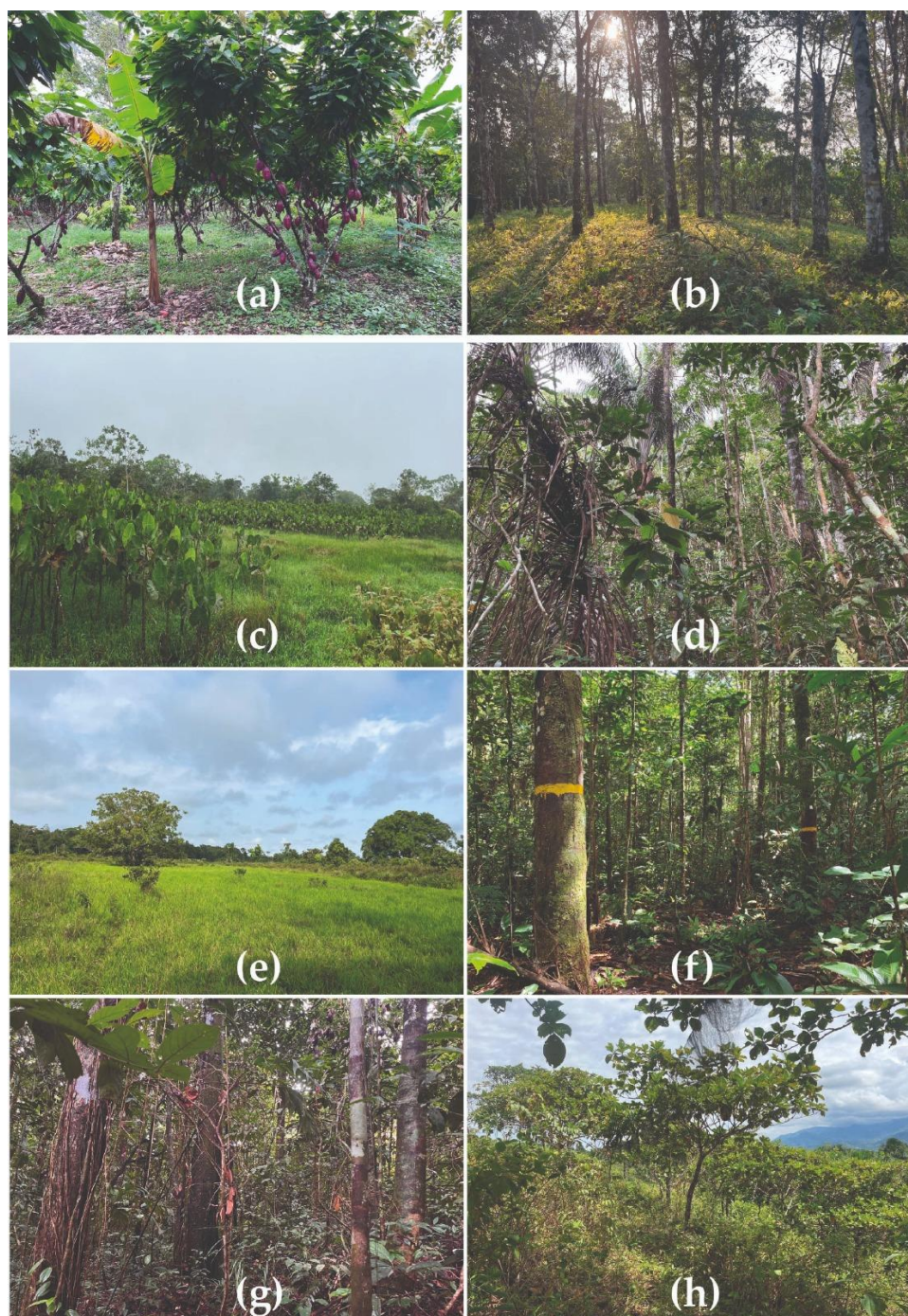


Figure 2. Vegetation cover types classified within landscape mosaics of cocoa-based agroforestry systems (SAFc) and silvopastoral systems (SSP) in the Colombian Amazon. (a) cocoa agroforestry crops – CA; (b) shade tree species in cocoa cultivation; (c) wetlands – HU; (d) early successional fallows – RT; (e) late successional fallows – RV; (f) clean pastures – PL; (g) secondary forest – BS; (h) weedy pastures – PE.

The analysis of landscape structure for each mosaic followed the methodology proposed by Velásquez-Valencia and Bonilla-Gomez [3], who used FragStat software version 4.2 [55] to calculate seven landscape metrics that describe the heterogeneity, aggregation, and spatial configuration of vegetation cover types [41]. Landscape heterogeneity was assessed using the mean fractal dimension index (FRAC); aggregation was measured using the contagion index (CONTIG); and spatial configuration was evaluated using the mean shape index (SHAPE), patch area (AREA), circularity index (CIRCLE), perimeter–area ratio (PERIM), and mean perimeter–area ratio (PARA). The average values of these landscape metrics per vegetation cover type across the classified mosaics are presented in Table S1 of the supplementary material.

2.2. Bird Census and Functional Traits

Bird community censuses were conducted in each landscape mosaic from January to November 2023, using observation methods (point counts) and mist netting. For bird observations, a 5×5 grid was established across each 1-km² mosaic, consisting of 25-point count stations spaced 250 meters apart. This design allowed for the inclusion of different vegetation cover types within each mosaic. Each point was sampled by a single observer between 06:00 and 10:00 hours using 10×42 mm binoculars. All species observed and/or heard within a fixed 50-meter radius at each point were recorded during a 25-minute period, totaling 83.33 person-hours of observation.

For mist netting, five 1-km longitudinal transects spaced 250 meters apart were established in each mosaic. On each transect, nine mist nets (12×2.5 m; 20 mm mesh) were deployed once, totaling 45 nets per mosaic and 360 nets throughout the study. The nets were strategically placed to intercept bird movement between vegetation types [56]. Nets were active for five hours each morning (06:00–11:00) and monitored every 20 minutes. The netting effort per mosaic totaled 225 net-hours, for a grand total of 1800 net-hours across the study. A total of 350 individuals were captured across the eight mosaics. Each bird was measured using a digital caliper (0.01 mm precision), weighed using a digital scale (0.20 g precision), and released at the capture site. All collections were conducted under the framework of Resolution 1015 of 2016, authorizing the non-commercial scientific collection of wildlife specimens by the University of the Amazon.

Seven morphological traits were selected to assess the functional diversity of bird communities in the selected mosaics: total body length (LTO), tarsus length (LTA), extended wing length (AEX), gape width (COM), bill height (ALT), total culmen length (CTO), and body weight (PES). According to Coddington et al. [57], these traits reflect species' responses to changes in landscape structure and their contributions to ecosystem functioning. For observed species that were not captured, trait values were obtained from the average measurements of five individuals per species housed in the Ornithological Collection of the Natural History Museum at the University of the Amazon (UAM) and from the global AVONET database of avian morphological, ecological, and geographic traits [58]. Species taxonomy followed the nomenclature of the South American Classification Committee (SACC) [59], with verification from bird field guides for Colombia [60–62].

Identified species were categorized into seven dietary guilds based on literature review: frugivores (FRU), insectivores (INS), nectarivores (NEC), granivores (GRA), folivores (FOL), scavengers (CAR), and vertebrate consumers (VER). These traits provide qualitative ecological information on species, indicating how birds act as mobile links that transfer matter and energy within and between elements of productive landscapes. In doing so, they contribute to ecosystem adaptability, resilience, and long-term functioning [63–65]. The complete matrix of functional traits for bird species in SAFc and SSP systems is presented in Table S2 of the supplementary material.

2.3. Statistical Analysis

A generalized linear mixed model (GLMM) analysis of variance was performed to test for differences in bird species richness and abundance among vegetation cover types classified within SAFc and SSP mosaics. Vegetation cover was treated as a fixed effect, while farms were treated as a random effect. A Poisson distribution was used for the error term; if overdispersion was detected, a Negative Binomial distribution was applied [66]. These analyses were conducted using InfoStat statistical software, version 2020 [67].

To analyze the functional diversity of bird communities by vegetation cover type in SAFc and SSP systems, a species–trait matrix (E species \times R traits) was constructed using InfoStat version 2020 [67]. From this matrix, five multidimensional indices were calculated: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and Rao's quadratic entropy (RaoQ). The use of these complementary indices is recommended by Bonfim et al. [68], as they explain the interactions between biodiversity, ecosystem functioning, and the provision of ecosystem services [69,70]. FRic represents the volume of functional space occupied by a community, independent of species abundances. FEve reflects the evenness of abundance

distribution across functional space, and FDiv measures the functional dissimilarity among dominant species [71]. FDis is the mean distance of individual species from the community centroid and is influenced by dominant species [72]. According to Pla et al. [73], RaoQ is a quadratic form that integrates the distance matrix among species and their relative abundances. Functional diversity analyses were performed in R version 4.2 [74] using the FD package [75].

To determine average variation in species morphology by guild and identify dominant functional traits within vegetation cover types, community weighted means (CWM) were estimated [76]. CWM values were calculated using the FDiversity package [77].

For each guild, a separate analysis of variance was performed using linear mixed models (LMMs) to assess differences in functional diversity and community-weighted means (CWMs) across the vegetation cover types classified in the SAFc and SSP systems. The response variables included the functional diversity indices—FRic, FEve, FDiv, FDis, and RaoQ—as well as the CWMs for each of the seven morphometric traits. Vegetation cover was modeled as a fixed effect and farms as random effects. The same analysis was repeated independently for each of the seven bird guilds. Model assumptions were evaluated through graphical inspection of residuals. Differences between means were tested using Fisher's LSD test ($\alpha = 0.05$). To evaluate bird species richness and abundance, generalized linear mixed models (GLMMs) were used, with vegetation cover as a fixed effect and farms as a random effect. A Poisson distribution was applied for the error term. When differences between means were tested, Fisher's LSD test ($\alpha = 0.05$) was again employed. All analyses were carried out using InfoStat statistical software, version 2020 [67]. This analytical approach allowed testing whether habitat heterogeneity influences bird richness and abundance [78].

To explore the relationship between functional diversity indices, guild-specific CWMs, vegetation cover types, and landscape structure metrics, a partial least squares (PLS) regression was performed to generate a triplot visualization [79]. This analysis was conducted separately to examine relationships among landscape metrics, vegetation cover types, overall functional diversity indices, guild-specific diversity indices, and the community-weighted means (CWMs) of bird traits per guild. Analyses were performed using InfoStat version 2020 [67].

3. Results

A total of 5498 individual birds were recorded, representing 218 species, 48 families, and 23 orders. Forty percent of all sampled individuals belonged to eleven species from seven families. The family Tyrannidae exhibited the highest species richness and abundance, with 38 species and 1012 individuals recorded. The most abundant and widespread species across all mosaics and vegetation cover types were *Crotophaga ani* (Linnaeus, 1758), *Thraupis episcopus* (Linnaeus, 1766), and *Ramphocelus carbo* (Pallas, 1764), with 316, 260, and 258 individuals, respectively. No statistically significant differences ($p > 0.05$) were found in mean richness or abundance between the SAFc and SSP systems. In cocoa-based agroforestry systems (SAFc), 184 species and 3089 individuals were recorded, compared to 168 species and 2409 individuals in the silvopastoral systems (SSP). However, vegetation cover types showed significant differences in mean species richness ($p = 0.0061$) and abundance ($p = 0.0094$). Early successional fallows, weedy pastures, and cocoa agroforestry crops supported the highest levels of species richness and abundance (Figure 3). Early successional fallows and clean pastures exhibited the highest number of exclusive species, with 20 and 15 species respectively.

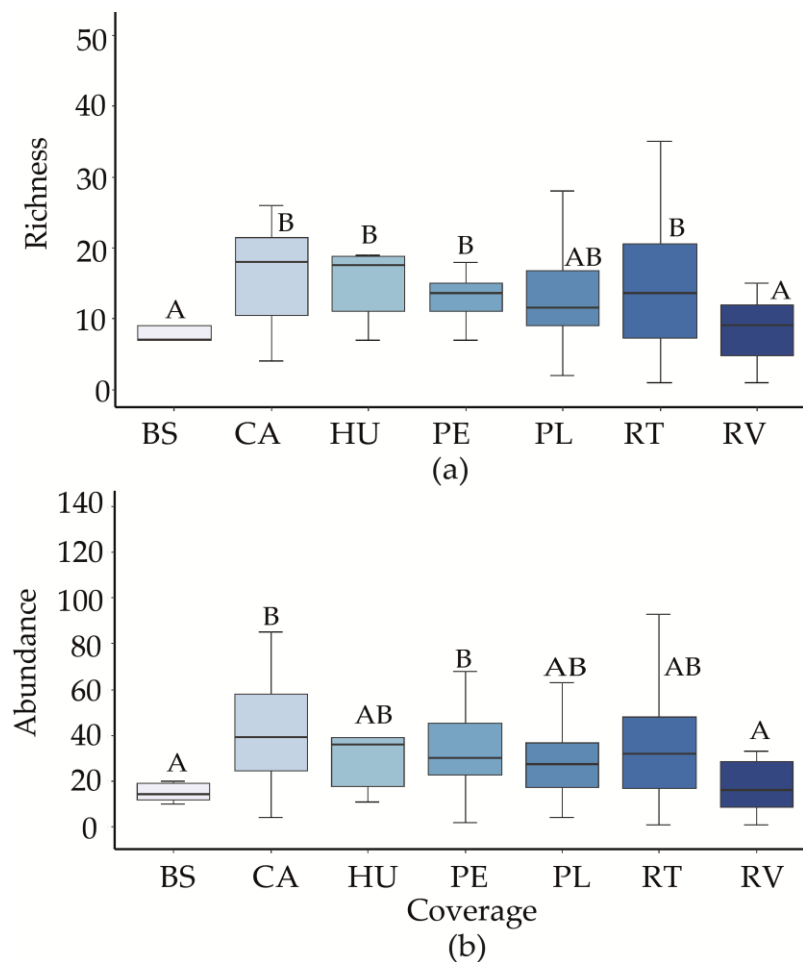


Figure 3. Boxplot of mean species richness (a) and abundance (b) of birds across vegetation cover types in cocoa-based agroforestry systems (SAFc) and silvopastoral systems (SSP) in the Colombian Amazon. BS: secondary forest; CA: cocoa agroforestry crop; HU: wetlands; PE: weedy pastures; PL: clean pastures; RT: early successional fallows; RV: late successional fallows. Values sharing a common letter indicate means that are not significantly different ($p > 0.05$).

3.1. Functional Diversity of the Bird Community by Vegetation Cover Types and Systems

All functional diversity indices, with the exception of functional richness (FRic), showed significant differences among vegetation cover types ($p < 0.05$). Early successional fallows exhibited the highest values for FDiv, FDis, and RaoQ, while secondary forest had the highest value for FEve. Late successional fallows recorded the lowest values across all indices. Within the SAFc systems, no significant differences were found among vegetation cover types for FRic, FEve, or FDiv. In contrast, in the SSP systems, early and late successional fallows and wetlands recorded the highest values for FEve, FDis, and RaoQ, respectively ($p < 0.05$). The lowest values for these three indices were found in secondary forest. The complete results of the linear mixed model (LMM) analysis for functional diversity indices by vegetation cover type and system are provided in Table S3 of the supplementary material.

3.2. Functional Diversity of the Bird Community by Guilds, Vegetation Cover Types, and Systems

The functional diversity indices FDis and RaoQ for frugivorous, insectivorous, and granivorous guilds showed significant differences across vegetation cover types within both systems ($p < 0.05$) (Figure 4). Specifically, the highest values of these indices were recorded in weedy pastures for frugivores, in cocoa agroforestry crops for insectivores, and in wetlands for granivores. Among the vegetation cover types present in both systems, only the RaoQ index showed significant differences within the insectivorous guild. In this guild, cocoa agroforestry crops in SAFc exhibited the highest

values for both indices, while clean pastures showed the highest values in SSP. The full results of the generalized linear mixed model (GLMM) analysis for functional diversity indices by guild, cover type, and system are presented in Table S4 of the supplementary material.

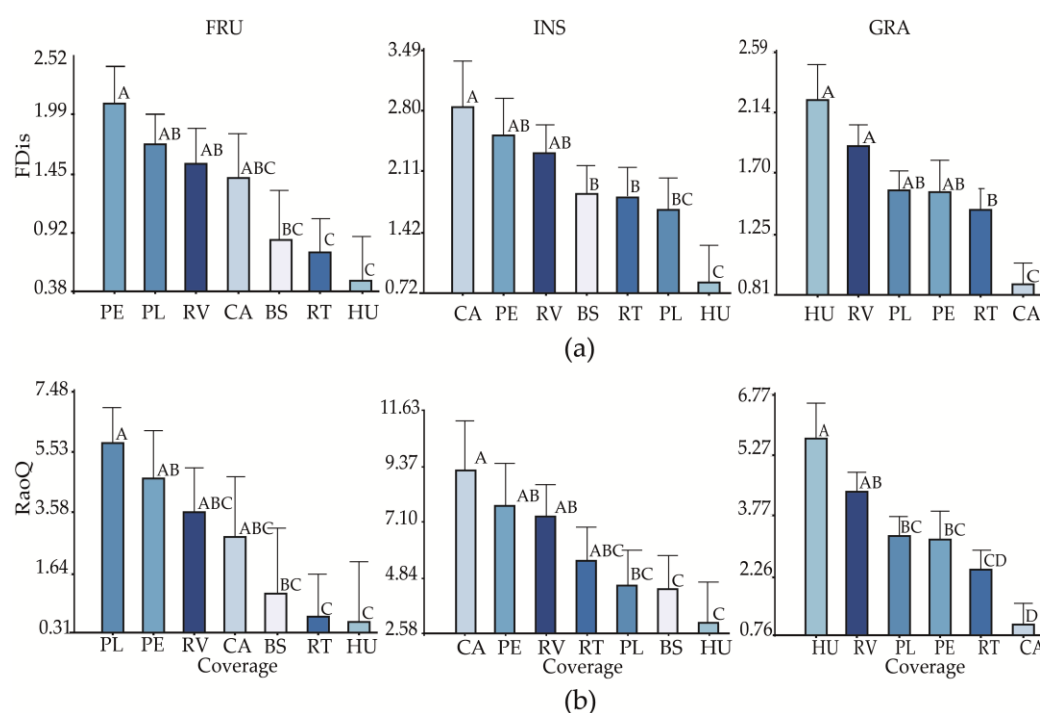


Figure 4. Values of the functional diversity indices (a) FDis and (b) RaoQ for bird guilds across vegetation cover types in cocoa-based agroforestry and silvopastoral systems in the Colombian Amazon. FRU: frugivores; INS: insectivores; GRA: granivores; BS: secondary forest; CA: cocoa agroforestry crop; HU: wetlands; PE: weedy pastures; PL: clean pastures; RT: early successional fallows; RV: late successional fallows. Pairwise mean comparisons were performed using Fisher's LSD test ($\alpha = 0.05$). Values sharing a common letter indicate means that are not significantly different ($p > 0.05$).

3.3. Functional Composition of the Bird Community by Vegetation Cover Types and Systems

Community-weighted means (CWMs) of bird morphological traits differed significantly across vegetation cover types present in both SAFc and SSP systems ($p < 0.05$). The highest mean total body length was observed in secondary forest, while extended wing length and body weight peaked in weedy pastures, and total culmen length was greatest in early successional fallows. Birds inhabiting late successional fallows exhibited the lowest CWM values across all traits. Within both systems, significant differences in CWMs among vegetation cover types were detected (SAFc: $p < 0.0001$; SSP: $p < 0.0001$). In SAFc, birds from secondary forests showed the highest CWMs, whereas in SSP, birds in secondary forests exhibited the lowest values. In contrast, within the SSP system, bird communities in late successional fallows recorded the highest CWM values. The complete matrix of generalized linear mixed model (GLMM) results for CWMs of morphological traits by cover type and system is provided in Table S3 of the supplementary material.

3.4. Functional Composition of the Bird Community by Guilds, Vegetation Cover Types, and Systems

Significant differences were found in the community-weighted means (CWMs) of bird morphometric traits ($p < 0.05$) within guilds across vegetation cover types in both systems (Figure 5). Among frugivores, CWMs were highest in weedy pastures; among granivores, in late successional fallows, wetlands, and secondary forests; among insectivores, in early successional fallows and wetlands; and among nectarivores, in weedy pastures and wetlands. Within the vertebrate consumer guild, only the gape width trait showed significant differences among cover types ($p < 0.05$).

Differences in CWMs among cover types were also observed between the SAFc and SSP systems ($p < 0.05$). In SAFc, frugivores, granivores, insectivores, and nectarivores showed their highest total body length values in cocoa agroforestry crops, while vertebrate consumers showed their highest values in late successional fallows. In SSP, frugivores and granivores had the greatest body size in late successional fallows, and insectivores and nectarivores in early successional fallows. Morphometric traits within the vertebrate consumer guild did not vary significantly among cover types in this system. The full results of the generalized linear mixed model (GLMM) analysis of community-weighted means for bird morphometric traits by guild, vegetation cover, and system are provided in Table S5 of the supplementary material.

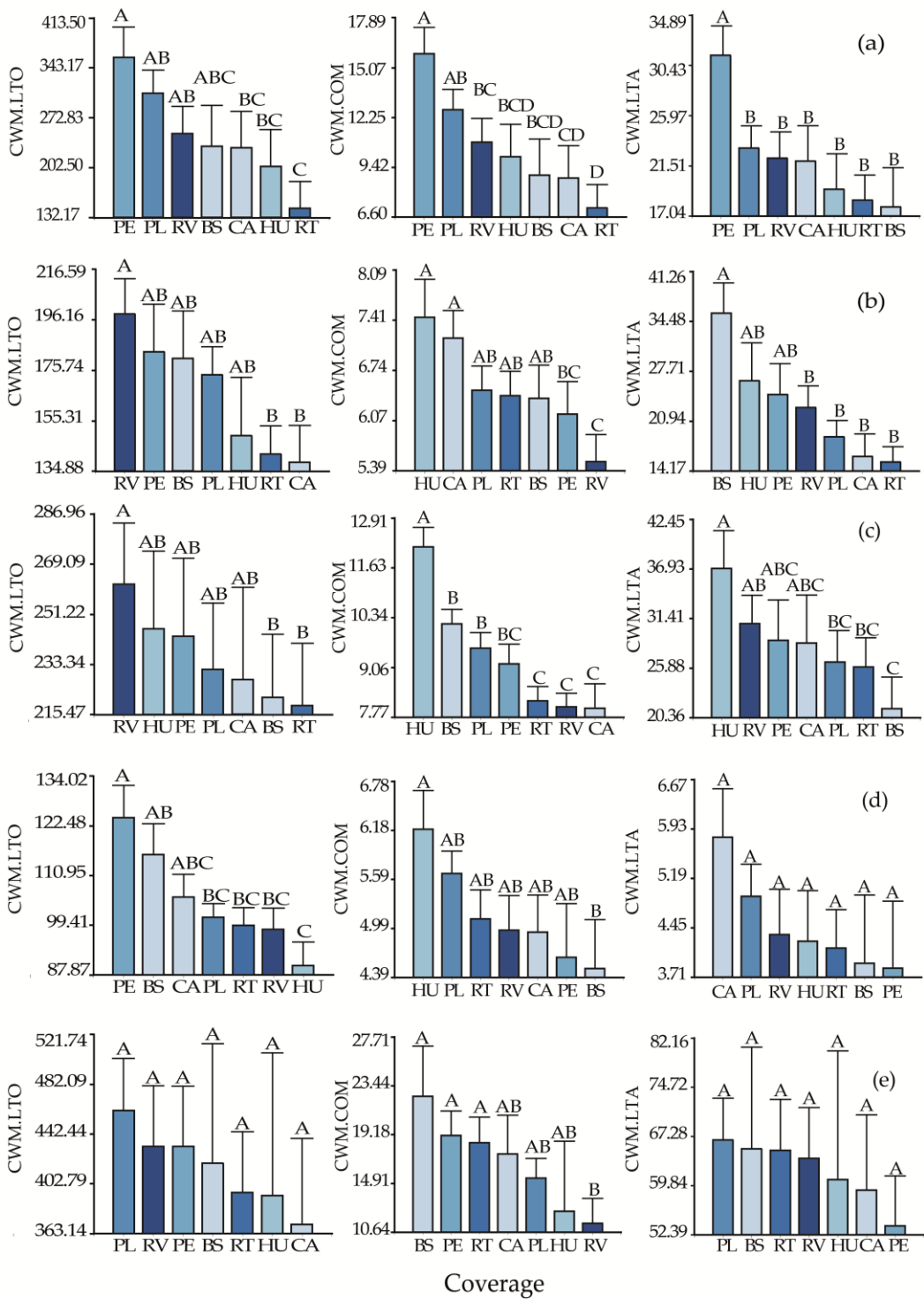


Figure 5. Community-weighted means (CWMs) of bird morphometric traits by guilds across vegetation cover types classified within cocoa-based agroforestry and silvopastoral systems in the Colombian Amazon. (a) frugivores; (b) granivores; (c) insectivores; (d) nectarivores; (e) vertebrate consumers. BS: secondary forest; CA: cocoa agroforestry crop; HU: wetlands; PE: weedy pastures; PL: clean pastures; RT: early successional fallows; RV: late successional fallows. LTO: total body length; COM: gape width; LTA: tarsus length. Pairwise mean comparisons were performed using Fisher's LSD test ($\alpha = 0.05$). Values sharing a common letter indicate that their means are not significantly different ($p > 0.05$).

3.5. Relationship Between Functional Diversity and Composition and Landscape Structure

Partial least squares (PLS) regression analysis between landscape metrics, guild-level functional diversity, and vegetation cover types revealed that Factors 1 and 2 explained 52.3% of the variation (Figure 6). On the positive end of Factor 1, a relationship was found between large patch areas, symmetrical shapes, and shorter inter-patch distances—particularly in cocoa agroforestry crops and late successional fallows—with higher FDis and RaoQ values for granivores, nectarivores, and frugivores, as well as FDis for vertebrate consumers. Conversely, on the negative end, patch types with reticulated and asymmetrical edges were associated with FDis and RaoQ values of insectivores and RaoQ of vertebrate consumers. This suggests that higher functional diversity values in most guilds are positively associated with larger, more regularly shaped patches. However, insectivore functional diversity increased in smaller and more spatially dispersed patches.

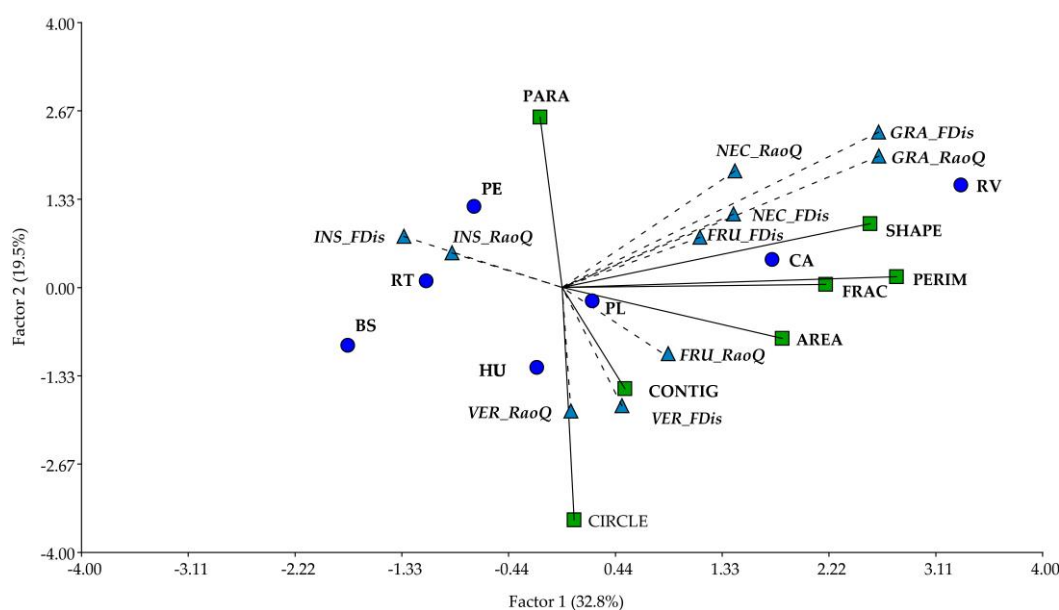


Figure 6. Triplot generated through partial least squares (PLS) regression showing the relationship between landscape metrics (squares), functional diversity indices by guild (triangles), and vegetation cover types (circles) in cocoa-based agroforestry and silvopastoral systems of the Colombian Amazon. FRU: frugivores; NEC: nectarivores; GRA: granivores; INS: insectivores; VER: vertebrate consumers; BS: secondary forest; CA: cocoa agroforestry crop; HU: wetlands; PE: weedy pastures; PL: clean pastures; RT: early successional fallows; RV: late successional fallows.

In the PLS regression between the CWMs of bird guild traits, landscape metrics, and vegetation cover types, Factors 1 and 2 explained 79.9% of the variation (Figure 7). On the positive end of Factor 1, a relationship was observed between patches with greater structural complexity—characterized by smaller areas and more reticulated shapes (PARA)—and bird guilds composed of individuals with greater body weight, larger body size, and extended wing length. These traits were predominantly associated with early successional fallows, secondary forests, and weedy pastures. On the negative end, smaller-bodied insectivores and nectarivores with shorter culmen lengths were associated with more homogeneous vegetation patches—those with larger size, symmetrical shapes, and greater

contiguity—such as clean pastures and wetlands. Thus, larger-bodied frugivores, granivores, and vertebrate consumers with longer bills and greater mass tend to be associated with smaller, more circular, and less contiguous patches with asymmetric edges.

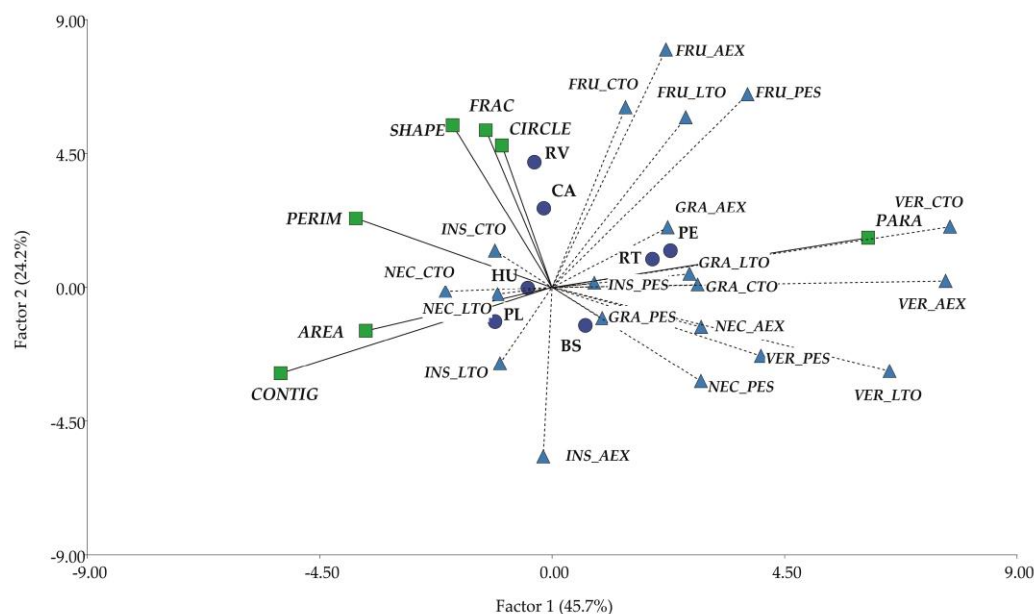


Figure 7. Triplot generated through partial least squares (PLS) regression showing the relationship between landscape metrics (squares), community-weighted means (CWMs) of bird traits by guild (triangles), and vegetation cover types (circles) in cocoa-based agroforestry and silvopastoral systems in the Colombian Amazon. FRU: frugivores; NEC: nectarivores; GRA: granivores; INS: insectivores; VER: vertebrate consumers; BS: secondary forest; CA: cocoa agroforestry crop; HU: wetlands; PE: weedy pastures; PL: clean pastures; RT: early successional fallows; RV: late successional fallows; LTO: total body length; AEX: extended wing length; CTO: total culmen length; PES: weight.

4. Discussion

The method used to document bird records enabled the analysis of functional traits for 218 bird species present in cocoa-based agroforestry systems (SAFc) and silvopastoral systems (SSP). This study represents the first effort to explore the relationship between the structure and spatial configuration of productive landscapes and the functional diversity of bird communities in SAFc and SSP systems in the Colombian Amazon, providing a comprehensive perspective on ecological dynamics within these systems. Although no significant differences were observed in bird species richness or abundance between the two systems, SAFc supported the highest total number of species and individuals. However, species richness, abundance, functional diversity, and the composition of bird guilds varied depending on vegetation cover types within both systems. The findings of this study partially support the proposed hypothesis, which stated that bird functional diversity is greater in mosaics with closed-canopy patches featuring symmetrical configurations in SAFc and SSP landscapes of the Colombian Amazon.

4.1. Functional Diversity and Composition of Bird Communities by Vegetation Cover and System

Vegetation cover types with greater structural complexity in SAFc systems—such as secondary forests and fallows—favored higher functional diversity and evenness within bird communities. According to Davis et al. [19], this complexity promotes habitat niche diversity and facilitates the presence and dispersion of functional traits across communities. In contrast, functional diversity was reduced in homogeneous cover types, which were dominated by functionally similar species and showed less trait dispersion. As noted by Jacoboski and Hartz [31], vegetative homogeneity limits

the availability of key microhabitats and resources, thereby constraining niche partitioning within bird communities.

In SSP systems, cover types in transitional stages or with intermediate succession provided critical refuge and food resources for birds, supporting the coexistence of species with divergent functional traits and diverse adaptations [80]. This was evident in the fallows and weedy pastures of the SSP system, which recorded the highest functional diversity and evenness. Giraldo et al. [7] suggest that the presence of structurally complex vegetation patches within grassland-dominated matrices benefits functional diversity.

The structure and composition of different vegetation cover types influenced the distribution of functional diversity and traits within bird communities. Larger-bodied bird species were associated with closed-canopy vegetation in both SAFc and SSP mosaics, such as secondary forests and cocoa agroforestry crops. In contrast, smaller-bodied birds predominated in open habitats such as pastures and wetlands. These results are consistent with findings by Landázuri et al. [35] and Velásquez-Trujillo et al. [81], who reported that larger species respond positively to increased structural heterogeneity and have more specific habitat requirements. Accordingly, the CWM for total body length decreased in communities associated with structurally simpler vegetation.

Functional traits related to mobility and dispersal capacity—such as extended wing length and body weight—were influenced by environmental filters linked to the contrast of the surrounding matrix. These traits reached their highest values in bird communities found in pastures and wetlands. This pattern reflects the tolerance, dispersal capacity, and adaptability of these species to traverse highly contrasting matrices in SAFc and SSP systems [82]. Conversely, traits associated with resource exploitation, such as total culmen length, were greater in bird communities of early successional fallows. This vegetation type was dominated by species with long, straight bills from the order Pelecaniformes (*Mesembrinibis cayennensis* (Gmelin, 1789) and *Phimosus infuscatus* (Lichtenstein, 1823)). Early fallows offer a mosaic of shrub and herbaceous microhabitats in open areas with low percolation rates, creating high availability of food resources such as fruits, insects, and small vertebrates from both soil and aquatic environments. These conditions make such habitats particularly attractive to ground and aquatic insectivores [9].

Overall, the functional traits of bird communities respond to improvements in connectivity and variations in vegetation structure within productive systems. These traits vary predictably according to local-scale production characteristics and the basic structural features of vegetation formations in the landscape [3]. A gradual decline in morphometric trait sizes was observed when moving from closed to open cover types. In mosaics with high vegetation heterogeneity, such as those in SAFc systems, the broad range of available resources supports larger-bodied species and greater functional diversity [83,84]. In contrast, SSP systems include more disturbed areas at different successional stages and offer limited resources that favor smaller, highly mobile species such as *R. carbo*, *T. episcopus*, and *Manacus manacus* (Linnaeus, 1766).

4.2. Functional Diversity of Bird Communities by Guilds, Vegetation Cover Types, and Systems

In weedy pastures and wetlands, frugivorous and granivorous birds exhibited greater functional diversity. According to Xu et al. [41], these guilds benefit from the presence of trees embedded within a pasture matrix, where the availability of fruits, grains, and seeds is high. This favors large frugivores such as *Psarocolius decumanus* (Pallas, 1769), *P. angustifrons* (Spix, 1824), and *Pteroglossus castanotis* (Gould, 1834), which in turn play a key role in seed dispersal [57]. Likewise, large granivores such as *Crypturellus cinereus* (Gmelin, 1789), *C. undulatus* (Temminck, 1815), and *Tinamus guttatus* (Pelzeln, 1863) were associated with secondary forests, likely in response to the higher structural complexity of vegetation that may offer both food resources and shelter from predators. This aligns with the findings of Alvarez-Alvarez et al. [45], who suggest that functional groups of specialist birds are more strongly associated with less disturbed forest patches. These cover types offer higher canopy density, a greater diversity of fruiting trees, floral structures, and a rich variety of arthropods [85].

The insectivorous bird community exhibited higher functional dispersion in cocoa agroforestry crops, a condition likely related to the vertical structure of these cover types. This vertical stratification is shaped by forest management practices such as shade regulation, tree species diversification, pruning, and the management of organic residues [86,87]. Bennett et al. [88] similarly suggest that such practices enhance canopy density, define mid-level strata, and increase organic matter accumulation on the forest floor. These conditions raise insect availability across various vegetation layers [6], promoting the presence of large-bodied and abundant insectivores, such as *Crotophaga ani* and *C. major* (Gmelin, 1788). In early successional fallows, vegetation succession and the diversification of shade trees contributed to greater functional diversity in nectarivorous birds. These cover types are characterized by the presence of flowering plants that provide nectar and shelter for this guild [33,41]. The presence of nectarivorous species supports the provision of pollination as an ecosystem service, contributing to the regeneration of native flora in productive systems. Furthermore, they may help improve fruit production and quality in economically important crops [89].

Regarding vertebrate consumers, secondary forests stood out as the cover type with the highest functional diversity. The complex structure of these habitats facilitates the coexistence of species with diverse hunting and foraging strategies [90]. For example, large predators such as *Rupornis magnirostris* and *Milvago chimachima* showed a positive association with dense vegetation and large trees, which offer vantage points for locating prey. This pattern supports previous findings suggesting that the ecosystem functions performed by predator guilds are influenced by structural heterogeneity and resource availability across the landscape [34,91].

4.3. Relationship Between Landscape Structure and Functional Diversity and Composition

According to Davis et al. [19], diet plays a key role in the distribution of birds across different environments and in their capacity to provide ecosystem services. In this study, the functional diversity of bird guilds showed a positive relationship with patch size and shape in the analyzed landscape mosaics. Circular patches with lower structural complexity exhibited greater functional diversity among guilds—except in the case of insectivores. In this context, functional diversity (RaoQ) increased with connectivity among large fragments [78]. This trend was evident in cocoa crop and late fallow patches, where functional heterogeneity rose with patch contiguity but decreased in mosaics with higher habitat contrast. Granivores, nectarivores, frugivores, and vertebrate consumers showed a decline in functional diversity in fragmented landscapes. These results align with Landázuri et al. [35], who emphasized the sensitivity of frugivores to agricultural land expansion, although they contrast with Šekercioğlu [92], who suggests that the high primary productivity of agroforestry systems in tropical regions attracts more fruit- and nectar-feeding birds compared to other groups.

In contrast, insectivores exhibited divergent responses to patch metrics. Their functional diversity increased in heterogeneous cover types with asymmetric shapes and reticulated edges, and was not negatively affected by fragmentation or isolation. Bitani et al. [39] noted that insectivore functional richness tends to be higher in disturbed forest patches. However, these findings diverge from those of Šekercioğlu et al. [40], who reported that tropical insectivorous birds are more sensitive to human disturbance.

Large-bodied frugivores and small, short-winged insectivores were associated with isolated, structurally complex patches of dense, heterogeneous vegetation. Increased area and contiguity of pasture-dominated patches reduced the expression of functional traits in frugivores but favored large insectivores with robust wings and bills. Similar patterns were observed by Landázuri et al. [35], who indicated that larger-bodied species are more sensitive to land-use changes.

Granivorous and vertebrate-consuming guilds with greater body length showed a positive relationship with open pastures of complex shapes, consistent with Lisón et al. [32], who suggested that landscapes containing large, less reticulated agricultural patches favor raptor and seed-eating bird richness. Finally, nectarivores with larger wings and higher body weight were associated with

the area and shape of secondary forest patches. However, both total body length and culmen length in this guild increased in pastures with complex shapes. According to Mayani-Parás et al. [93], body size may influence trophic niche differentiation. As such, smaller nectarivorous species are more affected by forest openness, while larger species may be more tolerant to these changes [94].

4.4. Implications for Ecosystem Service Provision

Functional traits within bird guilds promote niche segregation, minimizing interspecific competition and reflecting each species' capacity to exploit specific resources. In this context, the concept of functional guilds (FG) is introduced to describe groups of species that, although performing similar roles within the ecosystem, display high variability in their functional traits—resulting in low functional redundancy [6]. This attribute is closely linked to species coexistence and their contribution to key ecosystem services, underscoring the importance of functional diversity in maintaining ecological resilience [95]. These findings are consistent with previous studies [45,84,94] that emphasize the role of heterogeneity in vegetation composition and landscape configuration in the provision of ecosystem services associated with avian functional diversity in agroforestry and silvopastoral systems. Alvarez-Alvarez et al. [45] suggest that forest-dwelling granivorous birds, as well as small-bodied insectivores and nectarivores, benefit from greater structural complexity in vegetation within productive landscapes. Complementarily, Smith et al. [94] and Pérez-Cabral et al. [84] conclude that more complex agroforestry landscapes support greater functional diversity and evenness in bird communities, which in turn enhances the temporal stability of the ecosystem services they provide—such as pest control and pollination.

According to Michel et al. [64] and Adelino et al. [96], regulatory services such as seed dispersal, biological pest control, and pollination are among the primary benefits provided by Neotropical birds. Seed dispersal is facilitated by frugivorous and granivorous functional guilds (FG), including both large and small species [97]. Large frugivores play a crucial role in the genetic flow of tree species used as shade in agroforestry systems such as cacao plantations. This function supports regeneration and sustainability in these productive systems. In contrast, small frugivores and granivores, despite having lower dispersal capacities, can contribute to vegetation recovery in degraded lands and help maintain biological corridors, thereby enhancing connectivity across fragmented landscapes [45,92]. The insectivorous FG is particularly important for biological pest control, consuming a wide range of arthropods, including herbivorous and frugivorous insects that reduce agricultural productivity [98]. In this study, areas with high vegetation heterogeneity, such as early successional stages and cacao crops, were predominantly inhabited by small insectivorous birds, which are especially relevant for managing pests in cacao plantations—a crop vulnerable to numerous herbivores [64,99]. In contrast, large insectivorous birds, which are commonly associated with pastures and livestock, likely contribute to controlling larger and more mobile arthropod populations, including species that affect livestock production [8,80].

The nectarivorous FG, composed primarily of hummingbirds (Trochilidae), contributes to the ecosystem service of pollination [33]. Although this service has received less attention compared to insect-mediated pollination, birds represent a reliable alternative due to their consistent year-round activity and tolerance to various climatic conditions [64,97]. This service deserves greater attention in agroecosystems, as its effectiveness can vary depending on landscape characteristics and vegetation configuration [28,100,101]. Overall, knowledge regarding the contribution of birds to ecosystem services in the Colombian Amazon—particularly in productive contexts—remains limited. This study highlights how attributes such as diversity, body size, and morphological traits determine birds' functional roles through their mobility and specialization. Further research is recommended across different spatial and temporal scales to evaluate patterns of resource use and interspecific dynamics under changing landscape structures and configurations. These investigations are essential for designing management strategies that promote both ecological and economic sustainability in the region.

Birds respond not only to land-use changes, but also to the composition, structure, and spatial configuration of patches within rural landscapes. Thus, to support bird conservation and sustain critical ecosystem services in cacao agroforestry (SAFc) and silvopastoral systems (SSP) in the Colombian Amazon, it is essential to implement integrated landscape management. This involves planning and designing landscapes with higher structural heterogeneity, including mosaics with circular-shaped patches, lower structural complexity, and greater spatial contiguity. Such designs enhance connectivity among natural vegetation patches and facilitate the movement and dispersal of bird species from different FGs across the landscape. A greater diversity of habitats increases birds' functional heterogeneity and strengthens the ecosystem services they provide, such as pest control and seed dispersal [64,97,102–104]. Implementing these management approaches helps maintain ecological balance and ensures the sustainability of productive systems.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org. Associated with the publication of the scientific article Table S1: Mean values of landscape metrics by class in the vegetation covers classified in the thematic map in landscape mosaics with cocoa agroforestry systems (SAFc) and silvopastoral systems (SSP) of the Colombian Amazon; Table S2: List of the 218 bird species observed and captured; Table S3. Analysis of variance with Generalized Linear Mixed Models (GLMM) for the functional diversity indices and CWM for the vegetation covers; Table S4. Analysis of variance with GLMM for the functional diversity indices for each guild in the vegetation covers; Table S5. Analysis of variance with GLMM of the community-weighted means of morphometric traits for each guild in the vegetation covers.

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Abbreviations

The following abbreviations are used in this manuscript:

SAFc	Agroforestry Systems with Cacao
SSP	Silvopastoral Systems
FRU	Frugivores

INS	Insectivores
GRA	Granivores
NEC	Nectarivores
VER	Vertebrate Consumers
BS	Secondary Forests
CA	Cacao Agroforestry Crops
HU	Wetlands
PE	Weedy Pastures
PL	Clean Pastures
RT	Early Successional Shrubs
RV	Late Successional Shrubs
FRAC	Mean Fractal Index
CONTIG	Contiguity Index
SHAPE	Shape Index
AREA	Total Area
CIRCLE	Circularity Index
PERIM	Perimeter–Area Ratio
PARA	Mean Perimeter–Area Ratio
LTO	Total Body Length
LTA	Tarsus Length
AEX	Extended Wing
COM	Commissure
ALT	Beak Height
CTO	Total Culmen Length
PES	Weight

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