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BIOGEOGRAPHY AND LANDSCAPE PREDICTORS OF SPECIES RICHNESS IN NICARAGUAN DRY FOREST BIRDS

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Abstract · Knowledge of Nicaragua's Pacific slope seasonal tropical dry forest ecosystem and its avifauna remains limited, hindering effective conservation planning. To assess avian community composition and relative abundance, from 2009 to 2018 we conducted standardized monthly surveys in 147 point counts at 29 study sites along Nicaragua's Pacific slope. We also determined the influence of geographic, climatic, and landscape predictors on avian species richness and community similarity among sites. Overall, we documented 257 species at 29 study sites along the Pacific slope, including 17 species that were not previously reported, bringing the cumulative total known from the Pacific slope to 440 species, representing 57% of the country's avifauna. Species distributions exhibited strong geographic heterogeneity: Pacific-exclusive taxa predominated from Chinandega to Managua, whereas Caribbean-affiliated species peaked in Rivas. The geographic variable of elevation did not significantly influence overall species richness, but percent of forest-dependent species increased marginally with elevation, having highest densities in Rivas (70%) and Granada (17%). Landscape variables of tree cover and forest patch size were not associated with overall avian richness, but a larger forest patch size strongly predicted a higher percent of forest-dependent species, underscoring the importance of habitat contiguity. Biogeographic clustering further distinguished the northern and southern assemblages, with unique highland communities above 1000 m. These findings highlight the Pacific slope as a region of exceptional but uneven avian diversity, where the conservation of large, contiguous forest patches, particularly in montane zones, is critical for sustaining forest specialists, maintaining ecological connectivity, and safeguarding ecosystem services.

Resumen · **Biogeografía y predictores del paisaje de la riqueza de especies en las aves del bosque seco de Nicaragua**
El conocimiento sobre el bosque seco tropical estacional de la vertiente del Pacífico de Nicaragua y su avifauna sigue limitado, lo que dificulta una planificación de conservación eficaz. Para evaluar la composición de las comunidades de aves y sus abundancias relativas, durante 2009–2018 realizamos muestreos mensuales estandarizados en 147 puntos de conteo distribuidos en 29 sitios de la vertiente Pacifico de Nicaragua. Evaluamos la influencia de predictores geográficos, climáticos y del paisaje sobre la riqueza de especies y la similitud comunitaria entre localidades. Registramos 257 especies en 29 sitios de estudio, incluidas 17 no documentadas previamente; sumado a los registros previos, el total acumulado de 440 especies conocidas de la vertiente del Pacífico hasta 2018 representa el 57 % de la avifauna nacional. Las distribuciones de las especies mostraron una marcada heterogeneidad espacial: los taxones exclusivos del Pacífico predominaron entre Chinandega y Managua, mientras que las especies con afinidades caribeñas alcanzaron mayor representación en Rivas. La variable geográfica de elevación no influyó significativamente en la riqueza total de especies, pero el porcentaje de especies dependientes de bosque aumentó significativamente con la altitud, con máximos en Rivas (70%) y Granada (17%). A escala de paisaje, la cobertura arbórea y el tamaño de parche no se asociaron con la riqueza aviar, pero un mayor tamaño de parche forestal predijo fuertemente una mayor proporción de especies forestales, subrayando la importancia de la contigüidad del hábitat. El agrupamiento biogeográfico reveló ensamblajes diferenciados entre el norte y el sur, así como comunidades montanas particulares sobre los 1000 m. Estos resultados destacan a la vertiente del Pacífico como una región de diversidad aviar excepcional pero espacialmente desigual, donde conservar parches boscosos extensos y continuos, especialmente en zonas montañosas, es fundamental para sostener a los especialistas de bosque, mantener la conectividad ecológica y salvaguardar los servicios ecosistémicos.

Keywords: *Central American birds · Conservation planning · Forest-dependent species · Patch size · Point counts*

INTRODUCTION

Seasonally dry tropical forests play a fundamental role in modulating Neotropical biogeographic patterns, facilitating evolutionary divergence, and supporting highly endemic avifaunas with specialized physiological and behavioral adaptations to pronounced environmental aridity (Prieto-Torres et al. 2019a, 2019b). Despite their ecological significance, tropical dry forests face intensifying anthropogenic pressures, large-scale deforestation, and land-use conversion (Miles et al. 2006).

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Previous studies have documented patterns of avian richness, rarity, and regional biogeographic structuring in Central American dry forests across Mexico, Guatemala, and El Salvador (Palomera-García et al. 1994, Komar 1998, Gillespie 2000, Peterson and Navarro-Sigüenza 2000, Gillespie and Walter 2001, Ríos-Muñoz and Navarro-Sigüenza 2012, Álvarez-Álvarez et al. 2020, Castillo-Chora et al. 2021, Ramírez-Albores et al. 2021, Aguilar-Jocol et al. 2025). However, Nicaragua's Pacific slope remains comparatively understudied. Prior efforts in Nicaragua's dry forests have largely consisted of regionally restricted checklists and site-based monitoring lacking landscape-level ecological analyses (Esgueva Gómez 1996, Tórrez et al. 2009, 2013, Jarquín and Morales 2017).

We therefore aimed to provide a comprehensive quantitative assessment of landbird communities along the Pacific slope of Nicaragua, with particular emphasis on tropical dry forest ecosystems. By integrating systematic survey data with habitat-based occurrence records, we evaluated species distributions, community composition, and habitat associations within this imperiled landscape. Our primary objectives were to refine our understanding of spatial distribution patterns and identify critical conservation areas using rigorous ecological metrics. Specifically, we investigated how avian species richness, both total and forest-dependent, correlated with elevation, hypothesizing that forest-dependent species richness would increase with elevation due to greater habitat stability. Ultimately, our findings aimed to inform Neotropical biogeography and conservation practice by elucidating the spatial dynamics structuring avian assemblages in seasonally dry tropical forests.

METHODS

Study area. This study was conducted on the Pacific slope of Nicaragua, defined by Stotz et al. (1996) as the western sector of the Central American Isthmus between 13°11'42"N, 86°54'00"W and 11°03'57"N, 85°41'02"W. This region coincides with the Pacific depression of Nicaragua (Funk et al. 2009) and falls within the tropical dry-forest climatic zones as defined by the updated Köppen-Geiger classification (Kottek et al. 2006). The region is characterized by a high human population density (Cincotta et al. 2000). The Pacific slope extends approximately 300 km along the north-south axis and narrows from c. 100 km northwest to c. 20 km near Rivas (Bergoeing 1987). Within Nicaragua, our focal area occurred on the Pacific slope, coinciding with three of the physiographic provinces recognized by Fenzl (1989): the Pacific coastal plain, the volcanic mountain range, and the Nicaraguan depression.

We applied Holdridge's Life Zone scheme (Holdridge 1996) to delineate the bioclimatic zones of the region. Dry forest life zones dominate the western slope of Nicaragua (MARENA 2010, Harvey et al. 2019, Gillman et al. 2026). Based on terrestrial ecoregion frameworks (Dinerstein et al. 2017) and our local mapping data, this biome encompassed approximately 50% of the defined study area. Climatic conditions in the study area were also consistent with the tropical dry forest categories of the Köppen-Geiger system (Kottek et al. 2006), providing a complementary global classification framework. In terms of bird distribution, this area corresponds to the Pacific Slope Biome (Stotz et al. 1996). The Pacific Slope Biome overlaps with Endemic Bird Area 17, which Stattersfield et al. (1998) recognized as globally significant, owing to the occurrence of species with range sizes smaller than 50,000 km².

Avian Survey Protocol. As part of a collaborative initiative under a bilateral agreement between the U.S. Forest Service-International Institute of Tropical Forestry and the U.S. Agency for International Development/Nicaragua, within the framework of the Conservation and Sustainable Tourism in Critical Watersheds project, we implemented a standardized protocol for monitoring avian diversity in seasonally dry tropical ecosystems (Bauer and Arendt 2007, Bauer et al. 2008). To assess avian community composition and relative abundance across a regional landscape, trained observers conducted standardized monthly point counts at 147 permanently marked stations at 29 study sites (Supplementary Material Table S1). This landscape-scale assessment spanned five departments along the Pacific slope of Nicaragua, allowing us to evaluate broad biogeographic patterns rather than strictly local, site-specific densities.

From 2009 to 2018, two trained observers conducted monthly audio-visual point counts at each of the 147 stations, following standard point-count methodology widely applied in avian monitoring (Bibby et al. 1992). Each count lasted 10 min, and the stations were separated by a minimum of 200 m to reduce the likelihood of double-counting individuals. All birds detected visually or aurally were recorded within five radial distance bands (0–5, 6–10, 11–20, 21–40, and >40 m). The >40 m category was included to ensure the detection of vocally conspicuous or wide-ranging species (e.g., parrots, bellbirds, toucans, raptors, scavengers) and aerial foragers such as swifts. Counts were conducted during the first four hours after sunrise and only under suitable weather conditions (no precipitation or wind speeds above established thresholds). Detections were recorded by distance class, but we did not apply distance-sampling models to estimate absolute population densities (Buckland et al. 2015). Instead, our analyses focused on relative abundance, species richness, and community composition across sites and habitats. These metrics emphasize direct characterization of the avian community rather than reliance on surrogate indicator species (Lindenmayer and Likens 2011).

Avifauna Variables.

Avian species richness and abundance. We calculated avian species richness for each site as the total number of distinct species detected during the standardized 10-min point counts and classified the number of forest-dependent species following Stotz et al. (1996). To calculate density, we determined the surveyed area for each of the 147 permanently marked stations using the maximum radial distance band (40 m). We then calculated species density (number of species per hectare) and relative bird density (number of individuals per hectare) by dividing the respective 10-min visual and aural counts by this station area. Because distance sampling modeling was not used to adjust for imperfect detection, we treated these metrics strictly as relative, rather than absolute, densities across the surveyed landscape.

Pacific Slope Avifauna. We compiled species accounts for Pacific slope avifauna from online databases (IUCN 2024, AOS 2025, Avibase 2025, Billerman et al. 2025, eBird 2025), global taxonomic authorities (Dickinson et al. 2013-2014), regional and local checklists, field guides, and monographs (Salvin and Godman 1904, Howell 1964, 2010, Belt 2003, Martínez-Sánchez 2007, Salmerón-Belli and Arendt 2007, Morales et al. 2008b, Hernández et al. 2009, Morales et al. 2009, Zolotoff-Pallais et al. 2009, Tórrez et al. 2013, Chavarría-Duriaux et al. 2018, Lezama et al. 2019, Medina and Williams-Guillen 2024, and Paso Pacífico field guides available at https://pasopacifico.org/publications/). We included in quantitative analyses the occurrence records of birds inhabiting Pacific-slope localities surveyed by the authors in the present study and by earlier researchers (Castañeda Mendoza et al. 2004, Zolotoff-Pallais et al. 2006, 2007, Arendt and Tórrez 2008, McCrary et al. 2008, Morales et al. 2008a, Tórrez et al. 2009, 2013, Sandoval and Arendt 2011, Arendt et al. 2013, Lane et al. 2013, Jarquín and Morales 2017). To ensure the reliability of the general occurrence dataset used in our quantitative analyses, we retained only records from Pacific-slope localities documented during at least three independent visits, excluding casual or single-visit observations.

Regional Species Richness. We employed eBird's Data Ex-

plorer (eBird 2025) to quantify total species richness across the Pacific slope ecoregion. For this, we imported the Pacific-slope ecoregion shapefile, partitioned into six political units: Chiapas (MX-CHP-PAC), Guatemala (GT-PAC), El Salvador (SV-PAC), Honduras (HN-PAC), Nicaragua (NI-PAC), and Costa Rica (CR-PAC). For Mexico, we used the Chiapas polygon (southern Mexico) provided in the eBird Pacific-slope shapefile, which corresponds geographically and biogeographically to the Central American Pacific slope, whereas the broader Pacific-slope dry forests of Mexico were fully included in our regional analyses. We then extracted all checklist records whose coordinates fell within each unit polygon and computed the total number of aggregated species per country.

Biogeographical and Landscape Variables.

Ecoregion and bioclimatic zone classification. We used the terrestrial ecoregional framework proposed by Dinerstein et al. (2017) to delineate the study units. We assigned habitat patches to one of five categories based on land use and canopy cover: dense forest, young secondary forest, riparian forest (canopy within 25 m of riverbanks), open areas (e.g., pastures or savannas), and coffee plantations. To focus on native ecosystems, we restricted analyses to sites with continuous forest cover.

Landscape variables. To evaluate landscape-level predictors, we extracted tree-cover percentages from the Hansen et al. (2013) high-resolution global dataset. For these analyses, we defined landscape forest patches as contiguous spatial polygons of tree cover occurring within a predefined 1x1 km² radial buffer centered on each permanently marked survey station. This standardized spatial delineation enabled consistent quantification of local forest extent and facilitated comparisons of habitat structure across survey sites, thereby supporting subsequent analyses of avian species richness, community composition, and forest dependence. We quantified additional landscape-configuration metrics, specifically forest patch size and degree of fragmentation, using the Makurhini package (Godínez-Gómez and Correa Ayram 2020), implementing the spatial-analysis protocols of McGarigal et al. (2002).

Statistical analyses. We evaluated pairwise similarities in avian communities using the Jaccard index, aggregating these presence-absence values across survey points to generate regional similarity matrices and construct community dendrograms. To evaluate the specific relationships among our dependent diversity variables and independent geographic/climatic variables, we utilized generalized linear models (GLMs) and linear mixed-effects models. We modeled two primary response variables: (1) total avian species richness, and (2) the percentage of forest-dependent species. These were tested against continuous predictor variables including geographic factors (latitude, longitude, elevation in m a.s.l.), climatic factors (mean annual precipitation in mm), and landscape metrics (percent tree cover and average forest patch size). The optimal model was selected based on the lowest Akaike Information Criterion (AIC). To assess associations between continuous variables without assuming a normal distribution or being distorted by extreme outliers, Spearman's rank-order correlation and Kendall's tau were performed on the dataset. These tests evaluate the monotonic relationship between the ranks of the variables rather than their raw magnitudes.

Additionally, we used analysis of variance (ANOVA) to test for significant differences in geographic and climatic variables across the discrete biogeographical clusters identified by the Jaccard index matrices. All computations were performed in R (R Core Team 2020), employing the reshape2 package for data restructuring and Jaccard index calculations (Wickham 2007).

RESULTS

Avian species richness. As of 2018, we compiled a list of 440 bird species, including terrestrial, wetland, and aquatic varieties, for the Pacific slope of Nicaragua, representing 57% of the country's avifauna (Chavarría-Duriaux et al. 2018). Of these, 240 species occurred nationwide, 60 occurred on both the Caribbean and Pacific slopes, 60 were shared with the north-central region, and 75 species were exclusive to the Pacific slope. Comparison of tropical dry forest avifauna across Pacific-slope countries yielded a mean species richness of 472 per political unit (excluding Panama), with values ranging from 388 species in Nicaragua to 562 species in Mexico (Table 1).

Through our surveys over a nine-year period, we confirmed 257 species at 29 study sites along the Pacific slope, including 17 species not previously reported (Supplementary Material Tables S2 and S3). The Department of Rivas supported the highest proportion of species (70%), followed by Granada (17%), Chinandega (11%), and Managua (2%). Generalized linear modeling indicated a significant latitudinal increase in Pacific-exclusive species from Managua northward to Chinandega, adjacent to the Honduran border (R^2 = 0.30, P = 0.03), whereas Caribbean taxa were nearly absent in these northwestern departments but peaked in Rivas, bordering Costa Rica.

Antbirds (Thamnophilidae) were most abundant between Rivas and Managua, except for the widely distributed Barred Antshrike *Thamnophilus doliatus* (Tórrez et al. 2009). Cardinalid tanagers *Habia rubica* and *H. fuscicauda* were detected in 91% of the surveys at 200–800 m a.s.l. Humid-forest furnariids (ovenbirds and woodcreepers) also peaked from Managua to Rivas, although less than 60% of regularly recorded species occurred across all elevations and were mostly concentrated below 300 m in Rivas. Conversely, dry-ecosystem specialists such as Carolina Wren *Thryothorus ludovicianus*, White-bellied Chachalaca *Ortalis leucogastra*, Pacific Parakeet *Psittacara strenuus*, and Fan-tailed Warbler *Basileuterus lachrymosus* predominated from Chinandega to Managua and were effectively restricted to Pacific-slope habitats.

Based on Jaccard similarity indices, the Pacific slope avian communities exhibited discrete similarity clusters across elevational bands (Figure 1). Clusters revealed three distinct elevational groupings: lowlands (0–200 m a.s.l.), mid-elevations (201–800 m a.s.l.), and highlands (801–1300 m a.s.l.), with the

Table 1. Country-level species richness in seasonally dry tropical forests along the Pacific slope of Mexico and Mesoamerica. Panama is included solely to denote its similarity to Costa Rica (Chesser et al. 2024, Bird Conservancy 2025, Lepage 2025).

Country	Tropical dry forest species count
Mexico	562
Guatemala	431
El Salvador	545
Honduras	395
Nicaragua	388
Costa Rica	512
Panama	514

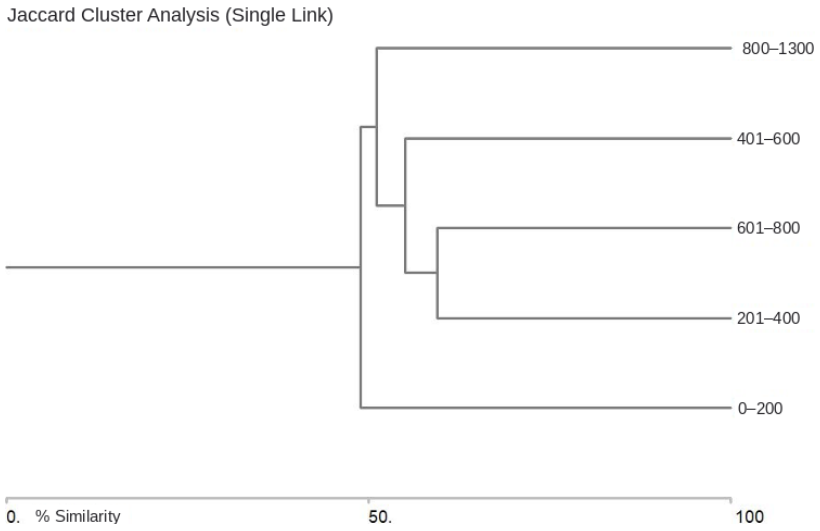

Figure 1. Dendrogram of Jaccard index avian community similarity across survey sites grouped by elevation gradient.

most pronounced compositional dissimilarity observed between the lowest and highest elevational bands (Figure 1). Among these, low-elevation communities below 200 m were the most compositionally distinct (Figure 1). Within the mid-elevation band, the 400–600 m a.s.l. cluster largely corresponded to Carazo (Figure 2). At the high elevation band, sites exceeding 1000 m were concentrated in the Maderas Volcano Natural Reserve, Ometepe Island (Site 2), Mombacho Volcano Natural Reserve, Granada (Site 1), and El Bajo Reserve, El Crucero, Managua (Site 29) at c. 930 m a.s.l. (Figure 2).

Linear modeling of total species richness against elevation revealed no significant relationship (Figure 3A). However, when restricted to forest-dependent taxa, generalized linear models demonstrated that percent of forest-dependent species in communities increased with elevation (t = 1.88, df = 8,27, P = 0.07; Figure 3B). The highest densities of forest-dependent species, based on relative abundance and richness metrics, were found in Rivas (70%) and Granada (17%).

Biogeographical zonation. Jaccard index clustering partitioned the survey sites into five principal assemblages grouped by the distinct semi-transparent, colored background polygons in Figure 2, and three outliers (distinguished by white circular markers: Sites 1, 2, and 29), with a latitudinal break near 12°N (Figure 2). Spatially, these communities could be classified into three distinct macro-geographical groups: (1) a northern zone (>12°N) encompassing lowland sites; (2) a southern zone (11.1°–12.4°N) comprising lowland and mid-elevation assemblages; and (3) a compositionally unique group of highland outliers (>900 m a.s.l.), such as the Mombacho Volcano Natural Reserve (Granada) and Maderas Volcano Natural Reserve, Ometepe Island (Rivas) (Sites 1 and 2, Figure 2), that did not cluster with the other the regional lowland matrices (Figure 2). Four sites, Natura, Managua (Site 12), La Mákina, Carazo (Site 28), Xiloá, Lake Managua (Site 15), and Finca El Tigüilote, Managua (Site 27), clustered within the convergence zone (Figure 2), whereas three remained compositionally dissimilar.

ANOVA revealed significant inter-cluster differences in latitude ($F_{3,37}$ = 6.38, P < 0.001), longitude ($F_{3,37}$ = 9.68, P < 0.001), and elevation ($F_{3,37}$ = 4.45, P = 0.002), driven largely by contrasts between lowland (<300 m a.s.l.) and highland (>1000 m a.s.l.) sites. Mean annual precipitation did not differ significantly among clusters. The northern zone (>12°N) encompassed Chinandega, León, and Managua (11.9°N–13°N), with elevations spanning 10–1200 m a.s.l. and rainfall between 1500 and 1800 mm, e.g., Cosigüina Volcano Natural Reserve, Chinandega (Site 9). The southern zone (11.1°–12.4°N) included Managua, Masaya, Carazo, Nandaime, Granada, and Rivas. Despite the higher mean annual precipitation (1400–2100 mm), the elevations were restricted to 0–600 m, with the Carazo Plateau hosting the upper limits. Notably, the sites of Mombacho Volcano Natural Reserve, Granada (Site 1) and Maderas Volcano Natural Reserve, Ometepe Island, Rivas (Site 2), plus El Bajo Reserve, El Crucero, Managua (Site 29), did not align closely with other clusters (Figure 2), underscoring their unique avifaunal composition.

Tree cover and species richness patterns. Vegetative cover across the Pacific slope was heterogeneous, with the southwestern region (11°–12°N) exhibiting greater tree cover than the northwestern region (12°–13°N). The spatial extent of these forest patches was significantly linked to topography; robust non-parametric analyses across 29 surveyed sites demonstrated that forest patches were marginally larger at higher elevations (Spearman's ρ = 0.466, P = 0.0108; Kendall's τ = 0.349, P = 0.0085). At the landscape level, generalized linear models indicated that avian species richness was not significantly associated with tree cover. Considering the percent of forest-dependent species, tree cover showed no significant relationship, but average forest patch size was a significant positive predictor of forest-dependent species (R^2 = 0.64, t = 5.43, df = 8,16, P < 0.001), with higher percentages of forest-dwelling species at sites with larger forest patches (Figure 4). Degree of fragmentation did not yield a statistically significant effect.

DISCUSSION

Biogeographical context. Our field surveys from the Pacific slope of Nicaragua provide the first comprehensive and systematic assessment of avian diversity in this region. Through standardized audiovisual surveys conducted between 2009 and 2018, we directly confirmed 257 species at 29 study sites, including 17 species not previously reported on the Pacific slope. When these survey results were combined with additional records from authoritative checklists, field guides, and databases (e.g., Chavarría-Duriaux et al. 2018, Avibase 2025, eBird 2025), the total number of species known from the Pacific slope reached 440 by 2018, representing 57% of Nicaragua's national avifauna. This comprehensive tally demonstrates that, although tropical dry forests in Nicaragua have often been considered species-poor relative to other Pacific-slope ecoregions (Komar 1998, Tórrez et al. 2013, Saldívar and Vammen 2024), the Pacific slope nonetheless supports a remarkably rich avifauna. When placed in a broader Mesoamerican context, this richness

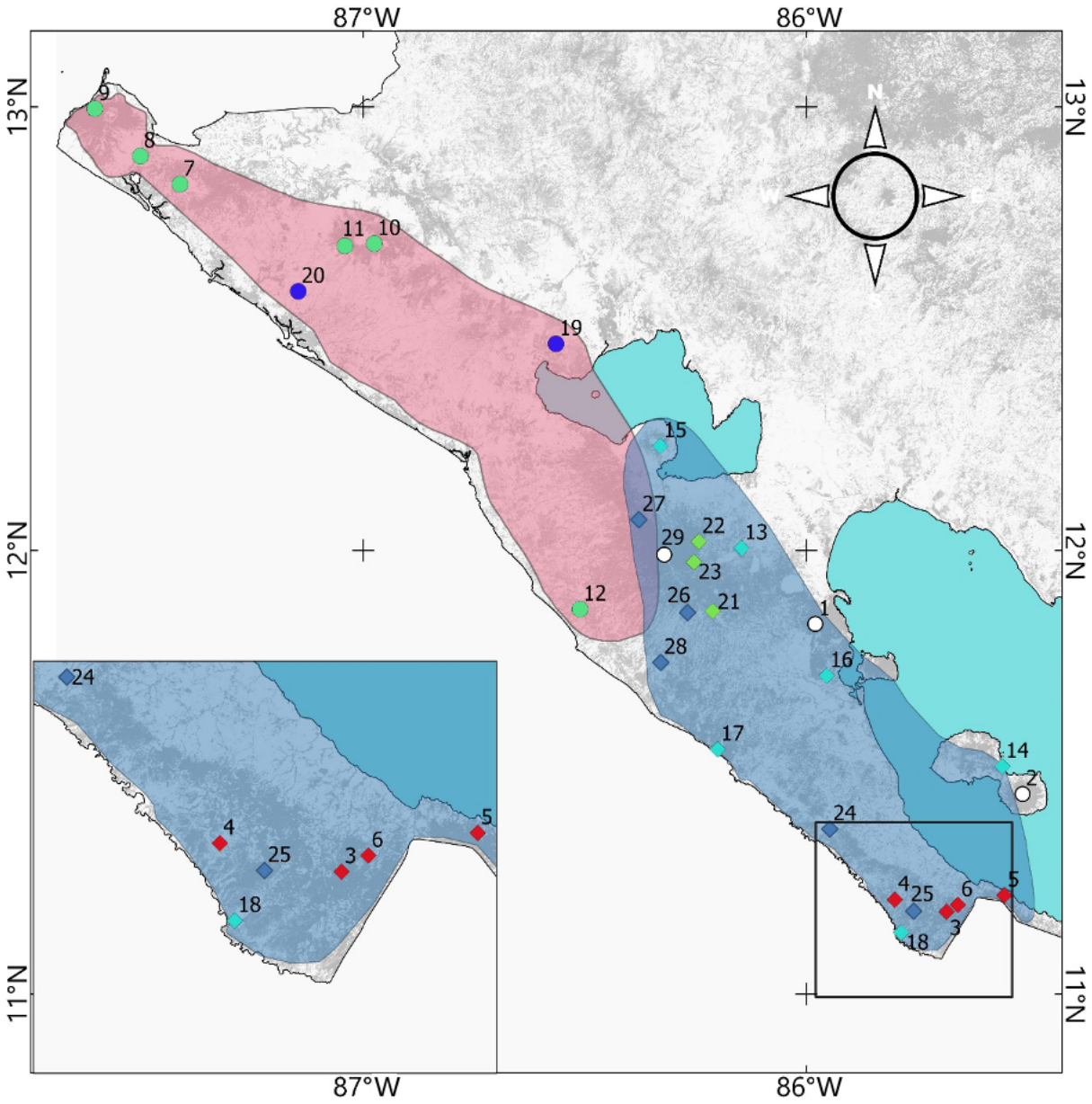

Figure 2. Dry forest site delineation based on the average Jaccard similarity index. Site classification, derived from the clustering of average Jaccard values, identifies distinct biogeographical assemblage areas, indicated by the light, semi-transparent background polygons. The 29 survey sites are plotted using various colored markers and shapes with numbers corresponding to the site list below. The overlapping boundaries of the northern and southern zones form a convergence zone near the major latitudinal discontinuity at 12°N. The 29 survey sites were: 1. Mombacho Volcano Natural Reserve (Granada); 2. Maderas Volcano (Ometepe Island) (Rivas); 3. Finca Guadalupe (Rivas); 4. Las Fincas Nica Dev (Rivas) (no new species); 5. Finca Isla Vista (Rivas); 6. Mono Bayo Private Reserve (Rivas); 7. Hato Nuevo (Chinandega); 8. Cabaña Los Pozo (Chinandega); 9. Cosigüina Volcano Natural Reserve (Chinandega) (no new species); 10. San Cristóbal−Casita Volcano Natural Reserve (Chinandega) (no new species); 11. Finca El Porvenir(Chinandega); 12. Natura Reserve (Managua); 13. Masaya Volcano National Park (Masaya) (no new species); 14. Isthmus of Istían, Ometepe Island (Rivas) (no new species); 15. Xiloá (Lake Managua) (Managua); 16. Domitila Private Wildlife Reserve; 17. Chacocente Wildlife Refuge; 18. La Flor Wildlife Refuge; 19. Momotombo Volcano Natural Reserve (León) (no new species); 20. Finca El Ensayo; 21. Concepción María Private Reserve (Carazo) (no new species); 22. Montibelli Private Wildlife Reserve (Managua) (no new species); 23. Chocoyero-El Brujo Natural Reserve (Masaya) (no new species); 24. Brito (Rivas); 25. Escameca Grande Wildlife Reserve (Rivas); 26. Gaia Forests, Granada (no new species); 27. Finca El Tigüilote, Managua (no new species); 28. La Mákina Natural Reserve (Diriamba); 29. El Bajo Reserve, El Crucero (Managua).

aligned closely with regional patterns. Comparable national-scale assessments, such as Komar's (1998) study of El Salvador, further underscore the importance of country-level analyses for understanding regional avian diversity patterns. Although our compilation of avifauna lists registered the fewest tropical dry forest species for Nicaragua, our surveys documented 440 species by 2018, which is equivalent to 93% of the regional average across Mexico and Central America. Ongoing additions are expected, given the inherent fluidity of bird distributions (Chesser et al. 2024, IUCN 2024, Bird Conservancy 2025, Lepage 2025).

The species distribution along the Pacific slope of Nicaragua was heterogeneous. Pacific-exclusive taxa predominated from Chinandega to Managua, whereas the number of Caribbean-affiliated species peaked in Rivas. Four tropical dry-forest specialists, Carolina Wren, White-bellied Chachalaca, Pacific Parakeet, and Fan-tailed Warbler, dominated from Chinandega to Managua within vegetation associations subject to seasonal moisture deficits (Murphy and Lugo 1986). Their ecological requirements illustrate why these species are particularly vulnerable to habitat loss: the Carolina Wren thrives in dense understory and riparian scrub; the chachalaca inhabits gallery and swamp forests, woodlands as well as urban parks; and the warbler specializes in evergreen and semi-deciduous ecotones and ravine edges (Stattersfield et al. 1998, IUCN 2024, Avibase 2025). Integrating regional checklists with the eBird (2025) Basic Dataset, eBird Science (2025) Status and Trends, GBIF

(2025), and Lepage (2025) underscores that these species have critical habitat requirements, and that their persistence depends on conserving specific forest types across the Pacific slope. This finding directly supports our results, showing their local dominance and restricted distribution, and highlights the necessity of transboundary conservation planning.

Ant-tanagers of the genus *Habia* (Family Cardinalidae) were detected in 91% of the surveys between Managua and Rivas at 200−800 m a.s.l. Their abundance in Nicaragua complements regional patterns, where *Habia* species exploit a wide range of habitats from Mexico to Costa Rica, with a mean elevation centered at c. 320 m (Palomera-García et al. 1994, Stotz et al. 1996, Gillespie and Walter 2001, Ríos-Muñoz and Navarro-Sigüenza 2012). Understanding these associations is vital for landscape-scale conservation, particularly in fragmented or regenerating areas.

Role of elevation in structuring communities. Our analysis revealed a marginal positive correlation between the percent of forest-dependent species in avian communities and elevation. This observed concentration at higher elevations, particularly within the montane refugia of Rivas and Granada, diverged from classical models and findings from Mexico (McCain 2009, Vázquez-Reyes et al. 2017, Neate-Clegg et al. 2018) that frequently report unimodal mid-elevational richness peaks (McCain 2009). Worldwide, these gradients are shaped by interactions between temperature and water availability (McCain 2009), although recent analyses have suggested accelerated lineage diversification at higher elevations (Quintero and Jetz 2018).

This positive scaling of percent forest-specialists with elevation in our study aligns with emerging Neotropical research demonstrating that lowland avian communities are disproportionately vulnerable to landscape-scale habitat degradation (Quintero and Jetz 2018). Recent studies assessing elevational gradients have quantified that forest-dependent bird populations at lower elevations exhibit a significantly higher sensitivity to surrounding forest loss than their highland counterparts. This anthropogenic filtering in the lowlands likely amplifies the profound compositional dissimilarity we recorded between lowland (<200 m a.s.l.) and highland (>800 m a.s.l.) assemblages.

Recent assessments of Neotropical human-modified landscapes further confirm that agricultural conversion homogenizes lowland ecosystems by favoring non-forest generalists, subsequently restricting structurally dependent taxa to higher

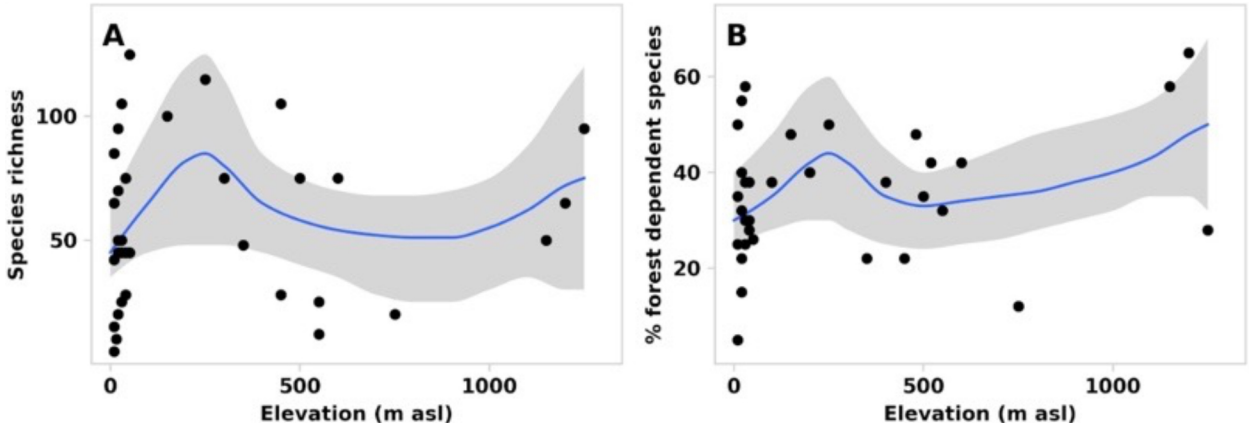

Figure 3. Relationships between elevation (m a.s.l.) and (A) total avian species richness, and (B) the percentage of forest-dependent species across survey sites on the Pacific slope of Nicaragua. Each data point represents a distinct, permanently marked point-count station, plotting site-specific elevation against its corresponding calculated avian diversity metric. Blue lines represent fitted values with 95% confidence intervals indicated by gray shading.

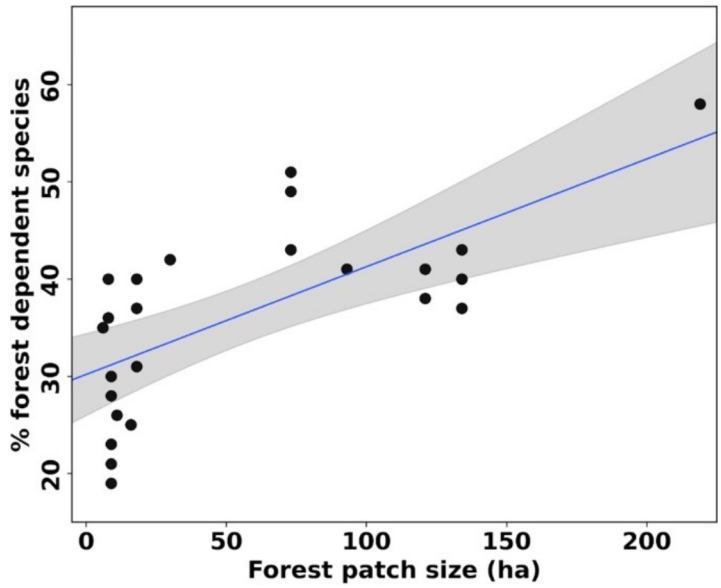

Figure 4. Relationship between the percentage of forest-dependent avian species and the mean size of surrounding landscape forest patches (ha), delineated within a 1x1 km² spatial buffer around each survey site along the Pacific slope of Nicaragua. Each data point represents a distinct, permanently marked point-count station. The solid blue line denotes the regression fit, with gray shading indicating 95% confidence intervals.

elevations (Karp et al. 2012, Vázquez-Reyes et al. 2017, Menezes Pinto et al. 2021). Such discrete community turnover and the role of elevation as a barrier to faunal exchange remains a subject of debate. However, studies such as Ghalambor et al. (2006) reinforce Janzen's (1967) hypothesis that tropical mountains restrict the elevational range of species and impede population interchange. While higher latitudes exhibit greater taxonomic exchange, tropical regions foster stronger vicariance isolation (allopatric speciation) and climatic fluctuations (Janzen 1967, Núñez-Zapata et al. 2016).

Our analyses demonstrated a significant positive relationship between forest-patch extent and elevation. Fertile lowland areas of tropical dry forest were largely restricted to small, highly fragmented remnants, e.g., Brito (Rivas), Las Fincas Nica Dev (Rivas), Gaia Forests (Granada), Xiloá - Lake Managua (Managua). In contrast, steep, higher-elevation volcanic slopes harbored expansive, continuous tracts of dense forest. These elevated regions, such as Momotombo Volcano Natural Reserve (León), Cosigüina Volcano Natural Reserve (Chinandega), San Cristóbal−Casita Volcano Natural Reserve (Chinandega), and Maderas Volcano Natural Reserve, Ometepe Island, function as biological islands, sustaining contiguous habitats that span thousands of hectares. Because our models identified average forest patch size as a robust positive predictor of forest-dependent species, this topographic constraint on habitat retention likely explains the higher proportion of sensitive taxa at higher elevations, thereby reinforcing the observed patterns of biogeographic partitioning. These findings underscore the importance of tropical highlands and indicate that the conservation and restoration of montane forests, specifically Nicaraguan elevations such as El Crucero (c. 930 m) and the Mombacho Volcano Natural Reserve, Granada, Maderas Volcano Natural Reserve, Ometepe Island, and San Cristóbal−Casita Volcano Natural Reserve, Chinandega (>1000 m a.s.l.), will bolster avian diversity while reinforcing vital watershed services.

Conservation implications for Nicaragua's Pacific-slope avifauna: Our findings demonstrated marked geographic heterogeneity in species richness across the Pacific slope of Nicaragua, consistent with prior regional observations (Martínez-Sánchez et al. 2001). Highland ecosystems (>700 m a.s.l.) emerged as critical refugia for forest-dependent taxa, with percent of forest dependent species in communities strongly correlated with forest patch size. At both low and high elevations, larger forest patches functioned as strongholds, whereas the degree of fragmentation did not yield a statistically significant effect. Globally, tropical dry forests are recognized as highly threatened ecosystems with limited formal protection (Miles et al. 2006), and Nicaragua has the same vulnerabilities. The effective protection of avian biodiversity is complicated by the patchy distribution of dry-forest remnants, which often follow simple latitudinal or elevational patterns. Therefore, conservation strategies must transcend reserve designation and prioritize landscape connectivity, restoration of native vegetation, and protection of large (>50 ha) forest patches across administrative boundaries. Such strategies are strengthened by basing conservation planning on direct measures of species richness and community composition rather than surrogate indicators alone (Lindenmayer and Likens 2011).

Sustained and expanded research across Nicaragua's Pacific watershed is essential for diagnosing both the natural and anthropogenic drivers of avian decline. Regional analyses have shown that areas of high species richness and endemism across Mesoamerica are disproportionately important for conservation (Ramírez-Albores et al. 2021), emphasizing the urgent need to develop a comprehensive understanding of these biodiversity-rich regions to underpin informed conservation planning, support environmental education, and foster ecotourism initiatives. Collaborative, data-driven approaches that integrate habitat restoration, connectivity enhancement, and community engagement are pivotal for securing the long-term persistence of Pacific-slope bird assemblages.

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