Evaluating functional diversity indices as indicators of bird community responses to forest regeneration, northwest Ecuador

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Abstract

As biodiversity recovery remains a key component of conservation and restoration goals worldwide, conducting accurate community recovery assessments remains a significant challenge for restoration ecology. Community assessments have traditionally relied on taxonomic diversity indices; however, it has been recently suggested that functional diversity indices may provide informative measures of community recovery. Yet, the extent to which these metrics reliably predict community responses during forest regeneration remains uncertain. In this study, we tested the relationship between taxonomic and functional diversity indices in understory bird communities in relation to forest regeneration in the Chocó rainforest of northwest Ecuador. We sampled bird communities across varying forest regeneration classes and utilized LiDAR-derived canopy-level vegetation indices to examine relationships between diversity indices and developing forest structure. Unexpectedly, we observed an inverse relationship between most taxonomic and functional diversity measures as a function of forest regeneration. High species richness, diversity, and functional richness were associated with open-canopy habitats within the early stages of forest regeneration due to a high presence of generalist, disturbance-tolerant species. In contrast, high functional dispersion, functional divergence, and Rao's quadratic entropy were all associated with closed-canopy habitats and later stages of forest regeneration and were mainly driven by differences in beak and wing length. Therefore, not all functional diversity indices indicate the recovery of late-successional

understory bird communities. Unlike functional richness, measures such as functional dispersion, functional divergence, and Rao's quadratic entropy are weighted by species abundances and dominant traits within each community and better explain the shifts in composition between habitats. Thus, these measures could be more useful in assessing faunal community responses to forest regeneration. However, functional diversity measures were only indicative of changes between open and closed canopy habitats, where pairwise comparisons did not show differences between secondary and old-growth forest systems. Lastly, as the observed low levels of species richness in older forests were likely due to lower detection rates from mist-netting, higher levels of functional diversity within these habitats indicate that functional diversity can be assessed with less sampling, offering a more efficient approach to evaluating community responses to forest regeneration.

Keywords: Avian Communities, Chocó Biogeographic Zone, Ecological Restoration, Taxonomic Diversity, LiDAR Drone Imagery, Natural Regeneration

Introduction

Recognizing the regenerative capacity of tropical forests is crucial for addressing climate change and biodiversity loss (Williams et al., 2024). Natural regeneration offers a large-scale, cost-effective solution to forest loss, particularly in areas where forests can recover with minimal human intervention (Bodin et al., 2022; Chazdon & Guariguata, 2016; Williams et al., 2024). Biodiversity measurements of faunal communities within stages of natural regeneration are typically used as indicators of restoration trajectories, as community dynamics can often give insights into the functional recovery of tropical forests (Crouzeilles et al., 2016; Derhé et al., 2018). This is typically done using taxonomic diversity indices (species richness and abundance), which may fail to capture the full range of functional contributions within a community (Acevedo-Charry & Aide, 2019; Crouzeilles et al., 2016; Moreno-Mateos et al., 2020). Thus, functional diversity indices are becoming increasingly popular to evaluate community responses to tropical forest regeneration, as they consider both species richness and abundance in combination with traits relative to species ecological roles (Derhé et al., 2018; O'Brien et al., 2022). However, the extent to which functional diversity indices reliably predict successional patterns, and which measurements are reliably indicative of forest regeneration, are not well understood. Therefore, this study aims to understand the drivers of functional diversity across forest regeneration and to identify which diversity measures might be useful indicators for restoration and conservation initiatives.

Tropical forest regeneration depends on the reassembly of functionally significant species, such as tropical birds (Bello et al., 2024; Carlo & Morales, 2016; Lee, 2018). Many studies have utilized bird communities as a tool to compare stages of forest regeneration and restoration success (Barros et al., 2022; Helms et al., 2018; Latja et al., 2016). Birds play a

critical role in forest regeneration by dispersing seeds for the majority of tropical woody plants (>85%), especially in degraded areas where seed availability limits recovery (Holl, 1999; Howe & Smallwood, 1982; Wunderle, 1997). In addition, nectivorous and insectivorous birds influence energy pathways critical to forest regrowth, as studies have shown that they consume up to 2.5 times more resources in open forests compared to old-growth systems (Malhi et al., 2022). Insectivorous birds are important predators of herbivores, reducing leaf damage on regenerating trees (Morrison & Lindell, 2012). Pollinators also facilitate gene flow of plants, which is important for the long-term viability of plant populations (Kormann et al., 2016). Furthermore, bird communities can rapidly recolonize disturbed areas depending on local environmental conditions such as vegetation structure, resource availability, and remnant vegetation (Helms et al., 2018; Latja et al., 2016; Reid et al., 2012).

Typically, bird communities transition over stages of forest regeneration to become more similar to mature forest communities over time (Owen et al., 2020). However, the functional recovery of bird communities is inconsistent. Some studies report an increase in functional diversity in bird communities in areas with greater vegetation density and canopy structure within early forest regeneration types (Coddington et al., 2023; Remeš et al., 2021), while others have found no variation in functional diversity across stages and types of tropical forest restoration (Barros et al., 2022). Furthermore, a recent study found that both functional diversity and taxonomic diversity decreased as forest recovery progressed (Kortmann et al., 2025). These discrepancies highlight the need to understand what functional diversity indices are useful indicators of forest regeneration, and which might be less helpful in understanding community shifts related to forest succession.

Regenerating vegetation plays a key role in shaping bird distribution and abundance (Cano-Barbacil et al., 2023; Gregory & Gaston, 2000). Regenerating vegetation structure can be assessed using LiDAR (Light Detection and Ranging) imagery. LiDAR imagery is emerging as a transformative tool in restoration ecology, as its ability to capture three-dimensional data makes it particularly valuable for assessing habitat structure and biodiversity within regenerating ecosystems (Viana-Soto et al., 2022). LiDAR is growing particularly important for monitoring structural components of forest regeneration such as vegetation density, complexity, and health (Coops et al., 2021). Functional diversity measures have been shown to strongly associate with vegetation indices (e.g., canopy height, vegetation density, leaf-area density) in tropical secondary and old-growth forests (Coddington et al., 2023; Zahawi et al., 2015). In the initial stages of forest succession, younger forests will have lower basal area, open canopies, and a lack of tall trees (Finegan 1996; Aide et al., 2000). In later stages of succession, mature forests typically consist of larger trees and denser canopies, with a range of vegetation heights and features such as tree cavities, fostering higher species complexity (Remeš et al., 2021; Vesk et al., 2008). The use of LiDAR technology to analyze forest regeneration could enhance our ability to predict which elements of vegetation recovery are crucial for facilitating the recovery of functional diverse animal communities.

In this study, we utilized a regenerating forest gradient and LiDAR-derived vegetation indices to investigate their relationships between the composition, taxonomic diversity, and functional diversity of understory avian communities in the Chocó rainforest of northwest Ecuador. Specifically, we aimed to: (1) investigate the composition, taxonomic diversity, and functional diversity of bird communities in relation to changes in forest regeneration, (2) test for associations between diversity indices and vegetation structure, and (3) determine how functional

traits shift across stages of regeneration, and which traits and environmental variables contribute most to changes in functional diversity. We hypothesized that avian community composition will vary with forest regeneration, where differences in forest structure will act as a filter on avian species composition. Furthermore, we hypothesized that both taxonomic and functional diversity of avian communities will increase with forest regeneration and canopy-level attributes, as older, structurally complex habitats provide a wider range of resources and niches. The increase in avian functional diversity is expected to reflect a more specialized array of foraging behaviors and habitat use in older regenerating forests. Through this research, we aim to a more comprehensive understanding of what diversity indices might be most effective, efficient, and applicable to conservation and restoration strategies as they relate to assessing community responses to tropical forest regeneration.

Methods

Study site

This study was conducted at the Fundación para la Conservación de Los Andes Tropicales (FCAT) Reserve within the greater Mache-Chindul Ecological Reserve (REMACH), a key remnant patch of the Chocó rainforest in northwest Ecuador. The Chocó rainforest is a globally recognized biodiversity hotspot with high levels of endemism (Aguilar Mugica et al., 2009). REMACH encompasses 165,000 hectares (ha) of humid Chocó rainforest, wetlands, and streams within the Rio Esmeraldas drainage, though it is affected by severe rates of deforestation (Durães et al., 2013; Kleemann et al., 2022; Van Der Hoek, 2017).

The FCAT Reserve covered 656 ha during the data collection period and ranged from 350–550 meters (m) above sea level (asl), with a wet season extending from January to June and a dry season from July to December. The research design included 20 plots evenly distributed

across four habitat categories: highly impacted early successional habitat (HIE), low impact early successional habitat (LIE), mid-successional secondary forest (SEC), and old growth Chocó rainforest (OG) (Figure 1). HIE plots were cleared and used as cattle pastures for >20 years until they were abandoned in 2021 when they were purchased by FCAT. LIE plots had lower levels of disturbance, where selective logging and ≤1 year of grazing cattle from 2020–2021 without fire or use of herbicides resulted in less soil compaction and more remnant trees and fruiting vegetation (M Sanchez-Julia, *unpublished data*). SEC areas were predominantly abandoned cocoa plantations that have been naturally regenerating for approximately 25 years. OG represents old growth Chocó rainforest with limited recent human intervention (i.e., low intensity selective logging) that surrounds all other plot categories. Sampling took place in five replicates across each of the five regenerating forest types for a total of 20 plots spaced a minimum of 100 m apart throughout the FCAT Reserve.

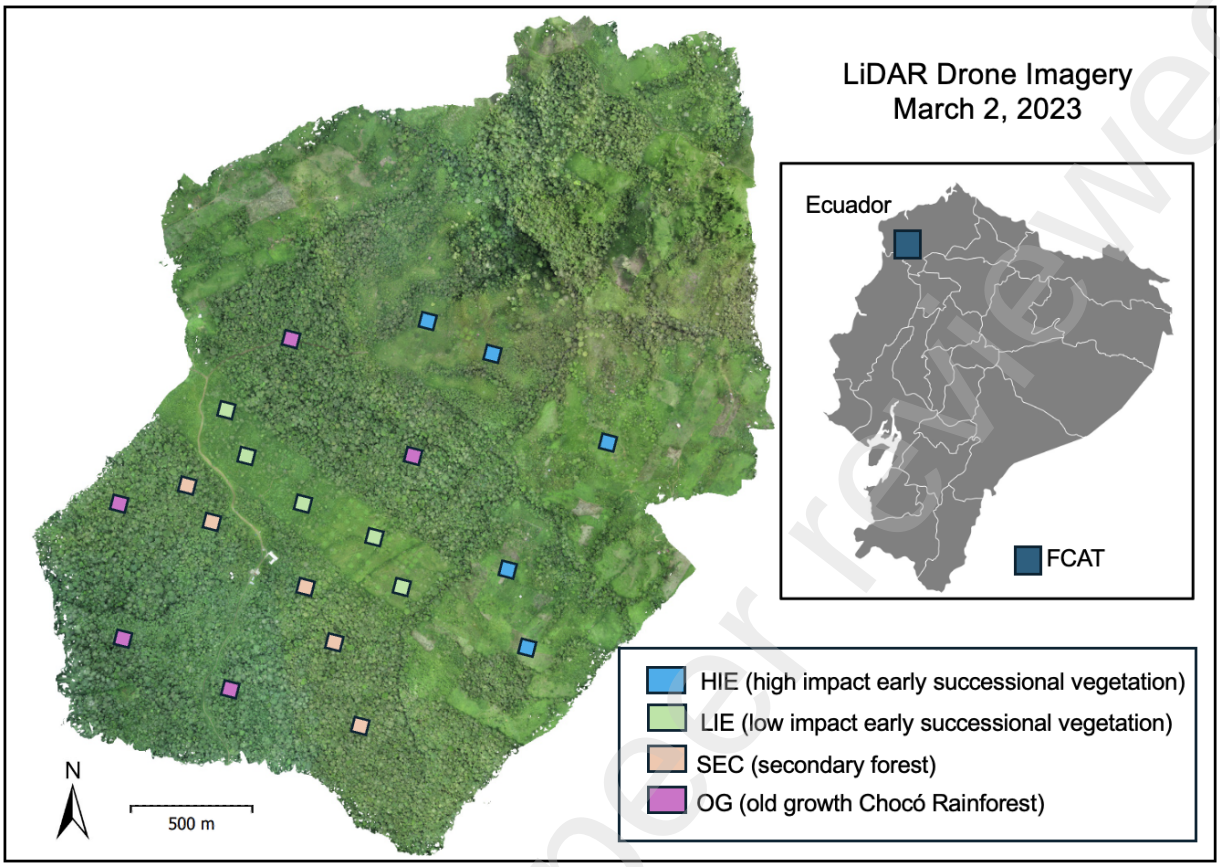

Figure 1: Sampling localities for avian communities within the FCAT Reserve. Sampling took place in 20 plots among four stages of forest regeneration: highly impacted early successional habitat (HIE, blue squares), low impact early successional habitat (LIE, green squares), mid-successional secondary forest (SEC, orange squares), and old growth Chocó rainforest (OG, purple squares).

Sampling for bird communities and functional traits

We conducted bird surveys from May–August in 2022 and 2023 to coincide with the dry season and to include resident species rather than migratory species. In each plot, we used mist-netting to account for abundances of understory bird species. This took place in fair weather from sunrise (~06:30) to 12:30 for two consecutive days at each plot, and then we rotated to a

randomized plot in a different regeneration type. In total, we completed 120 mist-netting hours for each plot (10 nets [120 m per net line] × 6 hours × 2 days), for a total of 2,400 netting hours across all sites. Nets were checked every 20 minutes. Each time a bird was netted, it was placed in a holding bag and brought to a banding station. Individuals were held in bags for no more than 15 minutes. Each bird we captured received a uniquely numbered aluminum band and was identified using *Birds of Ecuador* field guide (Freile & Restall, 2018) before being released at the point of capture. Fieldwork was conducted with MAATE permission (*Ministerio del Ambiente, Agua y Transición Ecológica*) under permit number: MAATE-ARSFC-2022-2589.

Calculating functional diversity indices

To obtain functional traits for each species, we used an open-access dataset that contained morphological, geographical, and behavioral traits for over 12,000 individual species (Tobias et al., 2022). From this data set, we extracted both morphological (beak length (mm), beak width (mm), wing length (mm), mass (g)) and behavioral (primary habitat, trophic niche) functional traits for each observed species (Supplementary Table 1). These traits are relevant to forest regeneration as they influence species foraging strategies, habitat usage, and dispersal abilities. For example, changes in beak morphology may reflect adaptations to specific food resources such as fruiting plant species, and changes in wing morphology may reflect species abilities to maneuver between complex forest vegetation. Categorical traits were numerically coded (e.g., frugivore = 0, granivore = 1). To calculate functional diversity, we took the log transformation of each continuous trait (beak length, wing length, tail length, mass) to normalize the data. We excluded categorical traits (trophic niche, vertical habitat preference, disturbance-tolerance) from functional diversity indices because the inclusion of categorical variables has been shown to reduce the quality of the functional space (Maire et al., 2015).

The resultant trait matrix was paired with weighted abundance data for each regeneration type, where each mist-netting plot was classified as a community. Then, we used the "*dbFD*" function in the *FD* package in R to calculate functional diversity indices (Laliberté et al., 2014). The FD index approach was used, which is the total branch lengths of a functional dendrogram calculated with the Gower distance measure (Podani, 1999). This approach uses a species-trait matrix, which is converted to a distance matrix (Gower distance), and then converted to a dendrogram via the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clustering method. We calculated functional evenness (FEve) and divergence (FDiv) using the convex hull methodology (Villéger et al., 2008), which uses the Gower distance matrix with PCoA analysis to calculate a matrix of transformed coordinates and then uses the PCoA matrices to calculate the functional metrics. High FDiv means species abundances are concentrated towards the extremes of the functional trait space, indicating a high degree of niche differentiation (Sayer et al., 2017). This can occur in communities where a few species have very distinct functional traits that are well-separated from each other. Finally, we calculated functional richness (FRic), Rao's Quadratic Entropy (Rao's Q) and functional dispersion (FDis) using the methodology of Villéger et al. 2008. FRic is the total range or variety of functional traits present among species within a given area or habitat. Rao's Q is a measure of functional diversity that considers both species abundances and their pairwise functional dissimilarities. High Rao's Q indicates high dissimilarity among species, even if the number of species and the total range of functional traits (FRic) are low. FDis quantifies the variability or spread of species trait values within a community where higher FDis indicates greater variability in traits among species, suggesting a community with a wider range of ecological strategies.

Calculating LiDAR-derived vegetation indices

We calculated vegetation indices from LiDAR data captured by drone (EP800, 8.8mm, resolution: 5472 x 3648 pixels) within the FCAT reserve on March 2, 2023. The process involved initial data preprocessing to generate a high-resolution digital elevation model (DEM) from the LiDAR point cloud data (Segurado & Silman, 2023). We utilized QGIS for segmentation and classification techniques to delineate canopy features and estimate height and elevation. Elevation for each point was calculated using the DEM. Elevation among our sites ranged from 416–656 m-asl. To calculate canopy height, the LiDAR data were processed to generate a Digital Surface Model (DSM) and Digital Terrain Model (DTM), and the canopy height was calculated by subtracting the DTM from the DSM using the raster calculator in QGIS. Canopy openness, indicative of light penetration through the canopy, was derived by evaluating gaps in vegetation cover. We calculated canopy openness by setting a threshold value (15 m from ground) to classify pixels based on their height allowing for the determination of open areas within the canopy. The resulting raster layer displayed the percentage of openness across the landscape. Canopy cover, representing the extent of foliage within an area, is quantified by assessing the area occupied by the canopy in relation to the total area. For the canopy cover assessment, we manually classified LiDAR points corresponding to vegetation at a minimum of 15 m from ground level, and the ratio of classified vegetation points to the total area. Finally, we used the density tool to assess distances between canopy points and compute canopy gaps, which allowed us to obtain measures of canopy cover for each plot. We then tested multicollinearity between environmental variables using Spearman's correlation from the *stats* package (Dormann et al., 2013). We found evidence of collinearity between canopy height and canopy openness ($S = 1932$, $p = 0.047$), thus we removed canopy openness from models. Therefore, environmental variables included canopy height, canopy cover, and elevation.

Statistical analyses

All statistical analyses and models were fitted in R (R Core Team, 2022). Abundance data from mist-netting were compiled together into a weighted matrix, where rows represented mist-netting plots (five individual communities per regeneration type), and columns represented individual bird species. Birds observed within mist-netting trials were weighted by their abundance due to our ability to identify individuals from aluminum bands, which allowed us to avoid counting the same individual twice. The resultant weighted adjacency matrix was then used to assess differences in bird communities and taxonomic and functional diversity metrics across each regeneration type. We used these data to calculate Hill numbers using the *iNEXT* package in R (Chao et al., 2014): q = 0 (species richness), Hill q = 1 (exponential of Shannon's diversity index), and Hill q = 2 (inverse of Simpson's index) (Ellison, 2010). Rarefaction and extrapolated curves were generated to determine how taxonomic diversity increases with increasing sampling effort and completeness. Rarefaction and extrapolation of richness, Shannon diversity, and Simpson diversity were calculated for each mist-netting plot (Chao et al., 2014). Sample-based curves evaluated the number of individuals in a sample by plotting diversity estimates in relation to the number of sampling units, while coverage-based curves were plotted against rarefied completeness in relation to sample coverage. Curves were plotted using doubling of sampling size, and 999 bootstrap replicates were used to estimate 95% confidence intervals.

To test for differences in the composition of understory bird communities across the regeneration gradient, we used abundance data from the adjacency matrix to calculate dissimilarity between plots using the Bray-Curtis dissimilarity index and the "*vegdist*" function in the *vegan* package in R (Oksanen et al., 2022). The Bray-Curtis index accounts for differences in species composition and abundance between plots, providing a measure of dissimilarity that

ranges from 0 (identical communities) to 1 (completely different communities with no overlapping species). To evaluate statistical support for differences in avian communities across regenerating stages, we performed a Permutational Multivariate Analysis of Variance (permanova) using the "*adonis*" function in the *vegan* package. Then, to assess the relationship between bird community composition and environmental variables, we used a Redundancy Analysis (RDA). First, the abundance matrix was normalized using the Hellinger transformation (Legendre & Gallagher, 2001). We plotted the RDA using the "*rda"* function in the *vegan* package in R and fitted relative environmental variables to the model using the "*anova.cca*" function with 1000 null model iterations. To determine if specific trophic niches (e.g., frugivores) within communities differed across regeneration types, we used categorical data to perform a chi-squared test using the "*chisq.test*" function in the *stats* package in R.

When considering differences in taxonomic and functional diversity indices, we first tested for spatial autocorrelation using the *spdep* package in R. We created a distance matrix from the UTM Northing and Easting coordinates of each sampling location. Next, we used the *spdep* package to construct a neighborhood structure based on this distance matrix, converting the neighbor list into spatial weights. This allowed us to assess spatial autocorrelation through Moran's I test. We found evidence of spatial autocorrelation for several of our response variables. Therefore, we performed Generalized Least Squares (GLS) analyses incorporating a Gaussian correlation structure. We chose Gaussian correlations because they allow for a continuous decay of spatial autocorrelation over distance, which is more appropriate for modeling the gradual environmental gradients and the spatial structure in our dataset compared to alternative correlation structures that may assume more abrupt changes. The Gaussian correlation structure was defined using plot coordinates (easting and northing).

For diversity metrics that exhibited significant spatial autocorrelation, we applied GLS regression to account for spatial dependence in model residuals. To evaluate differences in taxonomic and functional diversity across sites, we then modeled taxonomic and functional diversity metrics first as functions of regeneration type, then as functions of environmental variables. Both sets of models retained the Gaussian spatial correlation structure to account for spatial dependence. We used Type II Wald chi-square tests for response variables as a function of regeneration type. We used Type III tests for response variables as a function of environmental variables due to the interaction between canopy cover and canopy height, which was included in models. We then plotted all relationships using the *ggplot2* package (Wickham et al., 2016).

Finally, to determine how functional traits shift across stages of regeneration, and which traits contribute most to changes in functional diversity, we ran a redundancy analysis (RDA) between species abundances across regeneration types, with functional traits as explanatory variables. We tested the significance of each explanatory variable using ANOVA-like permutation tests under the "*anova.cca"* function with 1,000 permutations applied to evaluate individual variable contributions. The "*envfit"* function was again used to fit explanatory variables onto the RDA ordination, and p-values were extracted to determine which variables significantly influenced community structure. Variables with $p < 0.05$ were classified as significant. To examine correlations among explanatory variables, a Pearson correlation matrix was computed using the "*cor*" function in the vegan package for each diversity measure and functional trait.

Results

Avian community composition differed as a function of forest regeneration

We recorded a total of 940 individual birds representing 111 different species across all study sites (Supplementary Table 1). Among these, the most frequently observed species were *Phaethornis yaruqui* (White-whiskered Hermit, n = 98), *Asemospiza obscura* (Dull-colored Grassquit, n = 64), and *Sporophila funerea* (Thick-billed Seed Finch, n = 48). Rarefaction analysis showed that our sampling effort captured 83–90% of total species richness, 89% of species diversity, and 95% of community evenness (Supplementary Figure 1). Understory bird communities differed as a function of regeneration type ($r^2 = 0.47$, $F = 4.68$, $p \leq 0.01$) (Figure 2). Species richness also varied among regeneration type ($r^2 = 0.64$, $F = 12.40$, $p \leq 0.01$), where low-impacted plots (LIE) had the highest species richness observed (mean = 27.6, variance = 7.8), followed by high-impact early successional (HIE) plots (mean = 25.4, variance = 41.3). Furthermore, bird abundances varied significantly across sites ($r^2 = 0.43$, $F = 5.70$, $p \leq 0.01$), where the highest bird abundances were recorded in HIE (mean = 56.8, variance = 796) and LIE plots (mean = 66.6, variance = 134.3), while SEC and OG plots had comparatively lower bird numbers (SEC: mean = 37.8, variance = 123.7; OG: mean = 26.8, variance = 83.7).

Both canopy cover and canopy height were higher in older forests (SEC and OG) than in younger sites (HIE and LIE) (cover: $r^2 = 0.83$, $p \leq 0.01$, height: $r^2 = 0.83$, $p \leq 0.01$) (Table 1). Elevation was also different across regenerating stages, where younger sites (HIE and LIE) were lower in elevation than older sites (SEC and OG) ($r^2 = 0.63$, $p \leq 0.01$). Considering communities of understory birds across regeneration types, canopy height was the biggest predictor of community differences in terms of environmental variables (variance = 0.16, $F = 5.82$, $p \leq 0.01$). Canopy height demonstrated strong associations with RDA 1 (0.98), whereas canopy cover

exhibited a weaker and non-significant positive relationship with RDA 1 (0.98) and RDA 2 (0.05) (variance = 0.02, F = 0.92, p = 0.47). Elevation also had a non-significant relationship (variance = 0.03, F = 0.98, p = 0.36) with RDA 1 (0.53) and RDA 2 (-0.85) suggesting a lesser influence on the observed variation in the dataset. Constrained variables explained about 35.4% of the total variance in our RDA.

Taxonomic and functional diversity differed across forest regeneration stages

Both taxonomic and functional diversity of understory bird communities differed as a function of regeneration stage (Supplementary Table 3). Expected species richness (Q_0) and species diversity (Q_1) were highest in high-impact early successional sites and declined in mature forests (Figure 3). In contract, when minimizing the influence rarer species using Inverse Simpson Index (Q_2), we observed that older forests (SEC and OG) had higher diversity than younger successional sites. While changes in species richness (Q_0) and the Inverse Simpson Index (Q_2) were not associated with any environmental predictor, Shannon entropy (Q_1) was driven by changes in canopy height and decreased with increasing canopy (chi-squared = 4.92, p = 0.03) (Table 3). Functional diversity indices exhibited a similar trend as Q_2; functional dispersion, functional divergence, and RaoQ were all greater in mature forests (SEC and OG) than in early successional ones (HIE and LIE) (Figure 3). Pairwise tests showed that functional divergence of bird communities differed between high impact sites and secondary forests (p = 0.05), high impact sites and old growth forests (p = 0.02), and low-impact sites and old growth forests (p = 0.03). Functional divergence was strongly influenced by both canopy height (chi-squared = 11.46, p < 0.001) and the interaction between canopy cover and height (chi-squared = 12.53, p < 0.001) (Table 2). Functional dispersion followed similar patterns and was higher in later successional forests, with differences between early successional stages (HIE) and both

intermediate and mature forests (SEC, p = 0.008; OG, p = 0.002), and between LIE and later stages (SEC, p = 0.007; OG, p = 0.002). Functional dispersion was also associated with both canopy height (chi-squared = 5.63, p = 0.02,) and the interaction between canopy cover and height (chi-squared = 5.64, p = 0.02). Rao's Quadratic Entropy also varied between highly impacted sites and old growth forests (p = 0.02), and low impacted sites with both secondary forests (p = 0.04), and old growth forests (p = 0.01). Like dispersion and divergence, Rao's Quadratic Entropy was also associated with both canopy height (chi-squared = 6.19, p = 0.01) and the interaction between canopy cover and height (chi-squared = 6.87, p = 0.01). In contrast, the functional richness of understory bird communities was lowest in the more mature forests and highest in early successional areas (p = 0.03), and pairwise comparisons revealed that functional richness only differed between early successional stages (HIE) and mature forests (OG) (p = 0.03). Both functional richness and functional evenness were not driven by any environmental predictor variables.

Both younger sites (HIE and LIE) clustered together on the RDA, indicating greater functional similarity compared to mature forest plots (SEC and OG) (Figure 4). The RDA model explained 64.73% of total variation in functional diversity (constrained inertia = 0.4122). Functional richness was associated with open-canopy habitats (HIE and LIE), mainly driven by variations in beak width and tarsus length. Both beak width and tarsus length were positively associated with functional richness, yet were negatively associated with functional dispersion, functional divergence, and Rao's Q (Figure 5). Functional dispersion, functional divergence, Rao's Quadratic Entropy, and functional evenness were all indicators of closed canopy habitats and associated with both SEC and OG. OG and SEC forests clustered together on the RDA but exhibited distinct trait shifts. Specifically, changes in tail length, mass, and wing length were

associated with old growth forests, whereas changes in beak length were more strongly associated to both OG and SEC habitats. Beak length was strongly correlated with differences in functional dispersion (0.85), functional divergence (0.79), and Rao's Q (0.81), whereas wing length was positively correlated with functional dispersion (0.55) and Rao's Q (0.67).

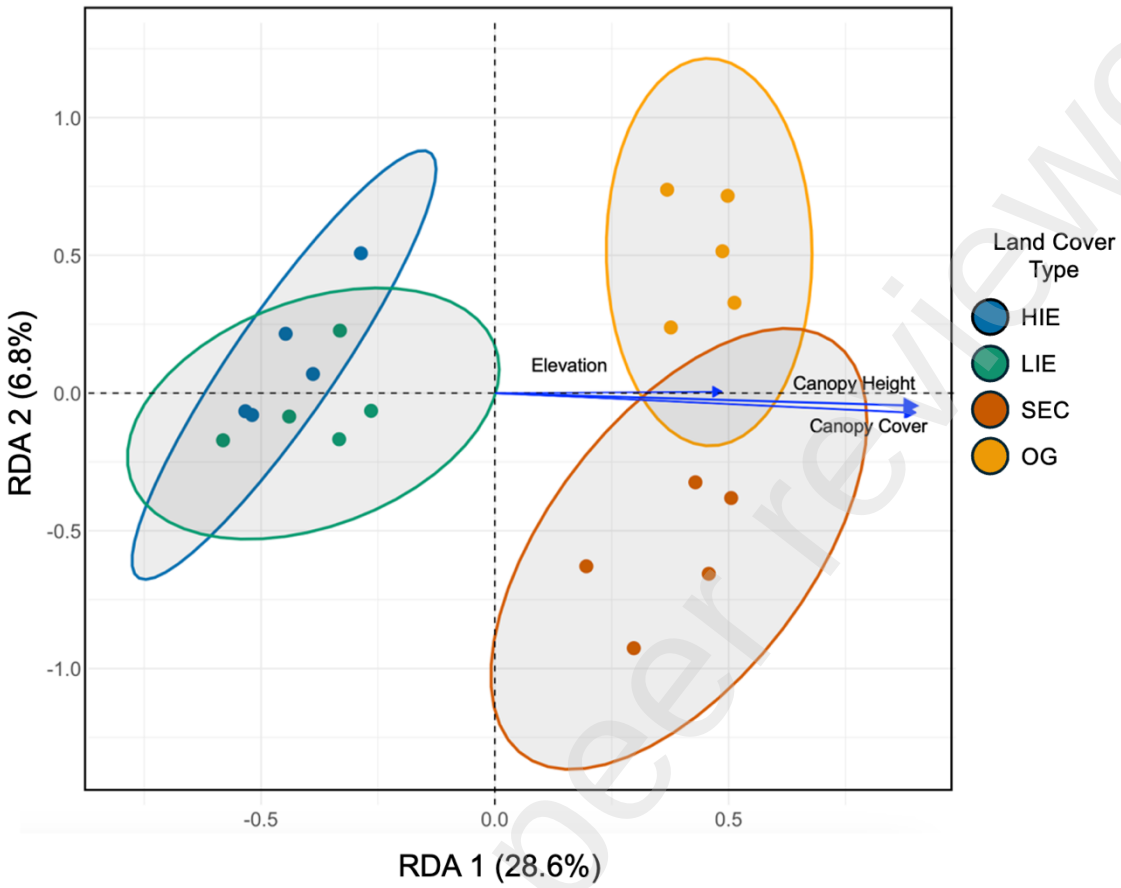

Figure 2: Redundancy Analysis (RDA) biplot of bird community composition constrained by selected environmental variables (canopy cover, canopy height, and elevation), and grouped by regeneration type (highly impacted early successional habitat (HIE, blue), low impact early successional habitat (LIE, green), mid-successional secondary forest (SEC, orange), and old growth Chocó rainforest (OG, yellow). Points in the plot represent communities or individual plots and blue arrows represent environmental variables. The x-axis (RDA1) explains 28.6% of the variation in bird community composition. The y-axis (RDA2) explains 6.8% of the variation. The direction and length of the arrows indicate the strength and direction of the relationship between each environmental variable and the ordination axes. Samples located in the same direction as an arrow are positively associated with that environmental variable.

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Table 1: Vegetation indices calculated from LiDAR data captured by drone within the FCAT Reserve. This included canopy height (m), canopy cover (%), canopy openness (%), and elevation (m-asl). "Stage" represents the four regenerating forest categories: highly impacted early successional habitat (HIE), low impact early successional habitat (LIE), mid-successional secondary forest (SEC), and old growth Chocó rainforest (OG).

Regeneration Type	Value	Canopy Height (m)	Canopy Cover (%)	Canopy Openness (%)	Elevation (m-asl)
HIE	Mean	6.84 (± 3.11)	7.59 (± 4.56)	12.22 (± 1.04)	466.76 (± 1876.79)
LIE	Mean	4.93 (± 0.33)	11.31 (± 18.87)	14.12 (± 0.11)	539.94 (± 157.50)
SEC	Mean	27.22 (± 13.76)	26.42 (± 14.41)	12.86 (± 0.23)	533.54 (± 432.5)
OG	Mean	26.76 (± 94.98)	25.53 (± 33.07)	12.89 (± 0.11)	533.76 (± 140.65)

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Table 2: Type III Wald chi-square tests assessing the effects of canopy cover, canopy height, elevation, and their interaction on taxonomic and functional diversity metrics. Generalized least squares (GLS) regression was used to account for spatial dependence in model residuals, with a Gaussian spatial correlation structure applied. Relationships are highlighted by + or – symbols, where + indicates a positive correlation between variables, and a – indicates a negative correlation between variables. Significant relationships ($p < 0.05$) are highlighted in bold with an asterisk (*).

Response Variable	Predictor	Relation (+ or -)	Chi Squared	P-value
Species Richness (Q_0)	Canopy Cover	-	0.20	0.66
	Canopy Height	-	1.48	0.22
	Elevation	-	1.33	0.25
	Canopy Cover * Canopy Height	-	0.25	0.62
Shannon Entropy (Q_1)	Canopy Cover	-	0.06	0.81
	Canopy Height	**-**	**4.92**	**0.03***
	Elevation	-	0.76	0.38
	Canopy Cover * Canopy Height	-	1.96	0.16
Inverse Simpson Index (Q_2)	Canopy Cover	+	0.07	0.79
	Canopy Height	+	4.36	0.04
	Elevation	+	0.38	0.54
	Canopy Cover * Canopy Height	+	2.41	0.12
Functional Richness (FRic)	Canopy Cover	-	0.00	0.98
	Canopy Height	-	0.05	0.82
	Elevation	-	1.72	0.19
	Canopy Cover * Canopy Height	-	0.01	0.93
Functional Divergence (FDiv)	Canopy Cover	+	1.18	0.28
	Canopy Height	**+**	**11.46**	**< 0.001 ***
	Elevation	+	3.28	0.07
	Canopy Cover * Canopy Height	**+**	**12.53**	**< 0.001 ***
Functional Evenness (FEve)	Canopy Cover	+	0.56	0.45
	Canopy Height	+	2.22	0.14
	Elevation	+	1.07	0.30
	Canopy Cover * Canopy Height	+	2.64	0.10
Functional Dispersion (FDis)	Canopy Cover	+	2.06	0.15
	Canopy Height	**+**	**5.63**	**0.02 ***
	Elevation	+	0.50	0.48
	Canopy Cover * Canopy Height	**+**	**5.64**	**0.02 ***
Rao's Quadratic Entropy (RaoQ)	Canopy Cover	+	2.67	0.10
	Canopy Height	**+**	**6.19**	**0.01 ***
	Elevation	+	0.47	0.49
	Canopy Cover * Canopy Height	**+**	**6.87**	**0.01 ***

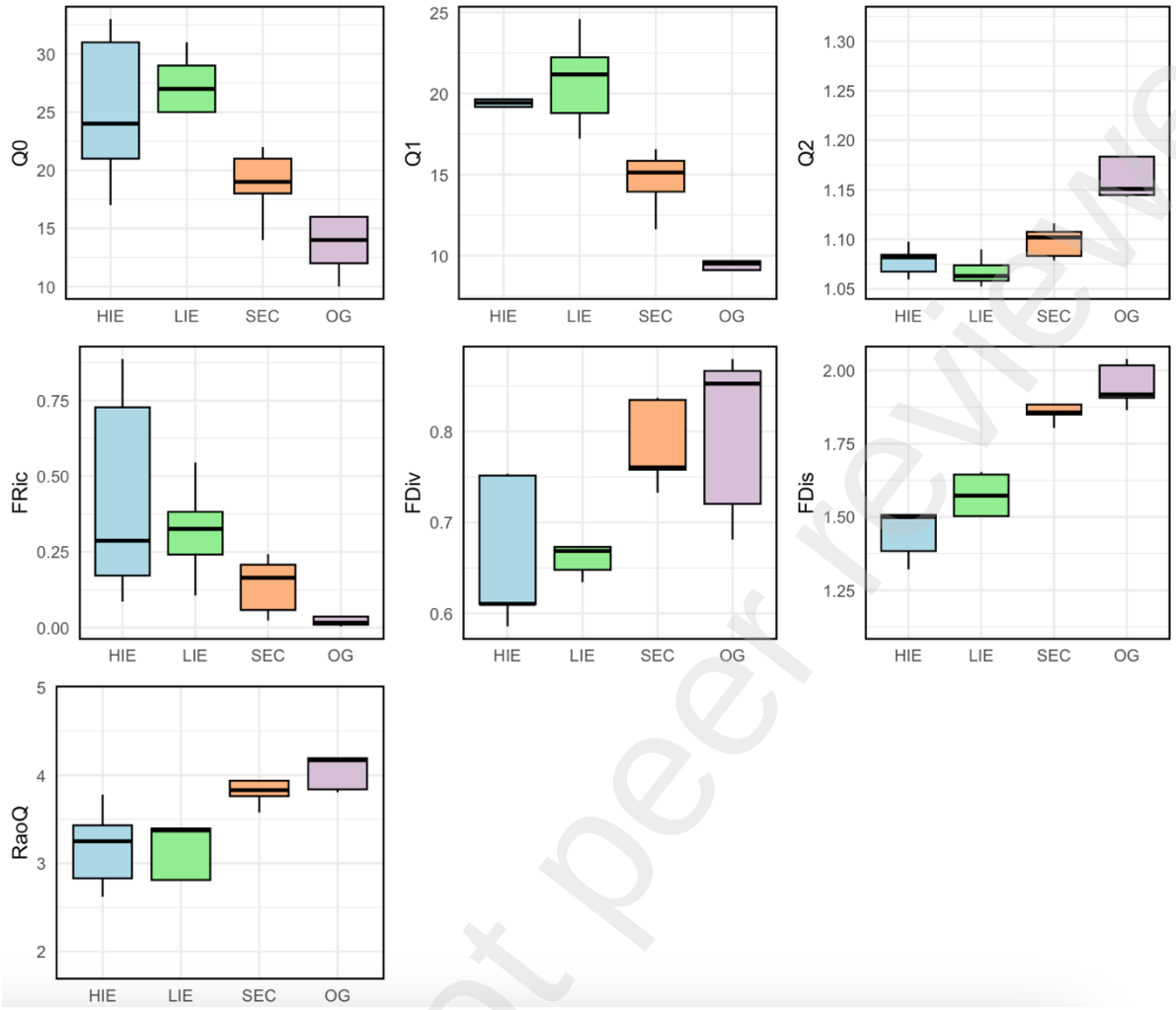

Figure 3: Differences in Hill numbers (Q_0 = species richness, Q_1 = exponential of Shannon Entropy, Q_2 = Inverse Simpson Index) and functional diversity metrics (FDiv = functional divergence, FDis = functional dispersion, FRic = functional richness, RaoQ = Rao's Quadratic Entropy) across a regenerating forest gradient. Plots include highly impacted early successional habitat (HIE, blue), low impact early successional habitat (LIE, green), mid-successional secondary forest (SEC, orange), and old growth Chocó rainforest (OG, purple).

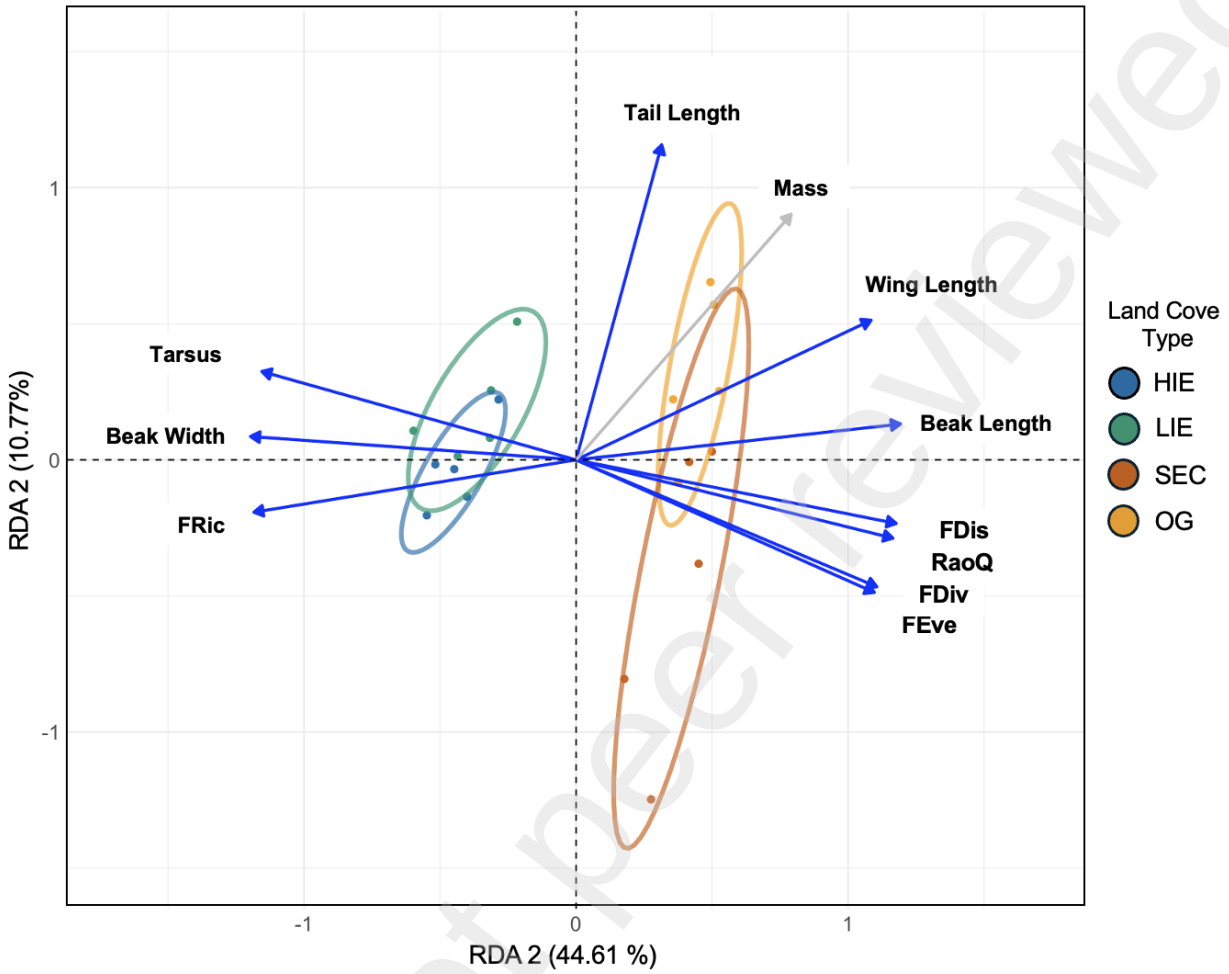

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Figure 4: Redundancy Analysis (RDA) biplot illustrating the relationships between functional diversity indices, morphological traits, and community composition. Individual sample plots are represented by points corresponding to their regeneration type (HIE = blue, LIE = green, SEC = red, and OG = yellow). Arrows represent exploratory vectors, with blue arrows indicating variables that significantly ($p < 0.05$) explain variation in community composition, and gray arrows representing non-significant predictors. The x-axis (RDA1) explains 44.61% of the constrained variation, while the y-axis (RDA2) explains 10.77%. Functional diversity indices (FDis: Functional Dispersion, FDiv: Functional Divergence, FRic: Functional Richness, RaoQ: Rao's Quadratic Entropy) and

morphological traits were used as explanatory variables. Sites and species positioned closer together share more similar trait compositions. The direction and length of arrows indicate the strength and influence of each predictor on community structure.

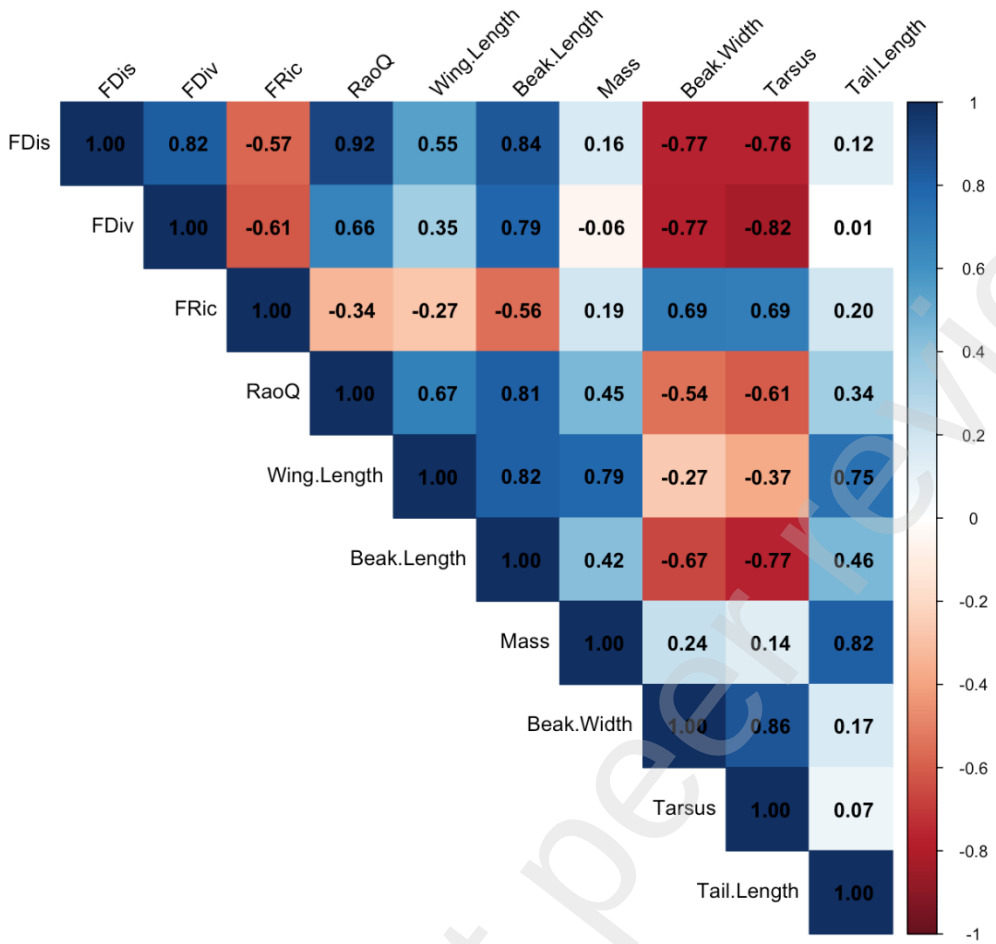

Figure 5: Pearson correlation matrix illustrating the relationships between functional diversity indices (FDis: Functional Dispersion, FDiv: Functional Divergence, FRic: Functional Richness, RaoQ: Rao's Quadratic Entropy) and morphological traits (Wing Length, Beak Length, Mass, Beak Width, Tarsus, Tail Length). The color intensity and shading represent the strength and direction of the correlations, with warmer colors (red) indicating strong positive correlations and cooler colors (blue) representing strong negative correlations. Correlation coefficients are displayed within the matrix, with significant relationships highlighted.

Discussion

The degree to which natural regeneration promotes functional and resilient communities is a key question for ecological and conservation research. To address this question, expanding diversity assessments, which have traditionally been taxonomically based, to incorporate functional diversity indices will be an important step forward for understanding forest regeneration as well as the field of conservation and restoration ecology (Chazdon, 2008, 2013; Lamb, 2018; Nabhan et al., 2020). However, we found that different functional or taxonomic diversity indices provided drastically different results, and that not all measures were equally good indicators of forest regeneration. The strongest differences in bird functional and taxonomic composition were between open and closed canopy environments, where most taxonomic indices were highest in open canopy environments and most functional diversity measures were highest in closed canopy environments. Functional richness was associated with open-canopy habitats in early stages of regeneration, and functional evenness showed no changes between regeneration stages. Inversely, functional divergence, functional dispersion, and Rao's quadratic entropy increased as a function of canopy cover and height and were indicative of forest communities. Therefore, functional divergence, functional dispersion, and Rao's quadratic entropy might be more valuable to consider in community assessments within tropical forest restoration.

The strongest differences in bird functional and taxonomic composition were associated with vegetation changes between open and closed canopy environments. Functional dispersion, functional divergence, and Rao's Q increased with canopy height and density independently of bird species richness, indicating as forests grow taller and more structurally complex, the species that persist have more distinct ecological roles (Remeš et al., 2021). This result is not surprising,

as functional diversity measures reflect deeper ecological processes that take longer to recover compared to simpler metrics like species richness and abundance (Acevedo-Charry & Aide, 2019). Resources provided by taller vegetation might allow the coexistence of species with diverse ecological strategies by providing more niche space (Aguirre-Gutiérrez et al., 2017; Oliveira & Scheffers, 2019). Other work has found similar trends, where increased tree cover positively correlated with increased guild richness and a greater distribution of functional traits (Ikin et al., 2019). However, canopy attributes only explained 35% of the variance in bird communities. Thus, other variables are important to consider, as factors such as food availability can also influence functional diversity by filtering trait assemblages (Flynn et al., 2011; Pena et al., 2023; Quitian et al., 2019). For instance, in a Peruvian cloud forest, early regeneration habitats with dense understories supported more bird species with plant-based diets (flowers, fruits, and seeds), broader elevational ranges, and wider habitat breadths compared to old-growth forests (Ausprey et al., 2022). Furthermore, dispersal ability and historical contingency also contribute to changes in community assembly (Gao et al., 2024), therefore could also contribute to changes in functional diversity.

Species richness and Shannon's entropy were highest in early stages of forest regeneration, likely due to the high abundance of generalist disturbance-tolerant species. Generalist species adapted to fast population growth in resource-rich environments dominate earlier successional stages, while species with higher competitive ability in resource-limited environments, or those that depend on resources such as higher structural vegetation complexity, dominate older-growth forests (Pinotti et al., 2012). However, functional richness was also associated with open-canopy habitats, in contrast to functional dispersion, functional divergence, and Rao's quadratic entropy). Functional richness is simply defined as the proportion of the total number of traits

available that are occupied by at least one individual, and may correlate with species richness (Villéger et al., 2008). Therefore, functional richness is independent of species abundances (Karadimou et al., 2016), and similar to species richness, will increase as the number of species present increases regardless of species rarity. Thus, high species richness in early successional plots could result in a wider range of functional traits present within a community, but not necessarily equate to a more functionally diverse community overall. Differences in functional richness across regeneration stages was explained by changes in beak width and tarsus length. In this system, open canopy habitats were dominated by a high diversity of small, wide beaked granivorous species including *Oryzoborus funereus*, *Sporophila corvina,* and *Sporophila nigricollis.* Therefore, early successional habitats likely maintain a mix of open-area specialists (e.g., ground-foraging species) and habitat-edge opportunists, but lack the ecological specialization seen in forests (Ausprey et al., 2022). Thus, functional richness may not be a good indicator of forest regeneration, similar to species richness, as it could lead to a biased interpretation of recovery if the dominant species present are not functionally diverse.

Functional dispersion, functional divergence, and Rao's quadratic entropy were all associated with closed canopy habitats and thus may serve as more accurate indicators of forest recovery. The observed increase in functional dispersion in mature forests could indicate higher degrees of niche differentiation, where lower rates of competition in older sites may enhance species co-occurrences and complementarity (O'Brien et al., 2022). Studies have suggested that communities with higher functional dispersion may be better able to respond to environmental changes (Flynn et al., 2011; Kuebbing et al., 2018). Similarly, the increase in functional divergence in mature forests could suggest that the distribution of traits becomes more varied and

specialized in later stages of regeneration, allowing for greater resource partitioning and reduced competition among species (Sayer et al., 2017).

Functional dispersion was driven by changes in both beak and wing length, whereas changes in functional divergence were more strongly associated with in beak length. Longer beaks may facilitate access to a wider range of food resources, including specialized foraging niches such as probing into tree bark or nectar. Increased wing length in closed-canopy environments could provide enhanced flight efficiency, enabling birds to navigate more complex environments. Landscapes with higher tree cover facilitate the movement of species, where birds with larger wings might have higher mobility across patches of degraded landscapes if the surrounding forest has higher levels of canopy cover (Remeš et al., 2021). Furthermore, high Rao's quadratic entropy values in mature forests signifies greater functional diversity overall, meaning the species within a community have more distinct functional traits and are less functionally redundant (Sayer et al., 2017). Changes in Rao's quadratic entropy were also driven by beak and wing length and additionally included mass. Mass being associated with few functional diversity indices indicates that body size influences resource use and habitat specialization independently of other morphological traits. In structurally complex environments, larger-bodied species may exploit different foraging strata or require larger territories, whereas smaller species may have increased maneuverability in dense vegetation.

Other systems have also found contrasting patterns of taxonomic and functional diversity indices in relation to forest regeneration. Some have found that regeneration time increases both functional diversity and species diversity of bird communities (Ikin et al., 2019; Remeš et al., 2021), however both studies only utilized one measure of functional or taxonomic diversity. Ikin et al. (2019) found that species richness correlated with functional richness and, contrasting to

our findings, increased with forest cover. Another study observed an increase in functional diversity as a function of forest regeneration in mammalian communities, however found no differences in taxonomic diversity across regeneration stages (Derhé et al., 2018). In contrast, others have found that regeneration did not significantly increase either functional or taxonomic diversity (Barros et al., 2022). When focusing on individual functional diversity measures, one study found that functional divergence, functional richness, and functional evenness of plant communities changed independently of one another (Pakeman, 2011), similar to what we observed in avian communities. These contrasting findings highlight the complexity of biodiversity recovery, suggesting that taxonomic and functional diversity may respond differently to forest regeneration depending on the taxa studied, the metrics used, and the specific environmental conditions of the system.

The observed low rates of taxonomic diversity in closed-canopy forests could be due to low detection rates from mist-net sampling. Therefore, substantial effort would be needed to saturate a species accumulation curve and accurately account for a high proportion of the species residing within these dense, biodiverse habitats. Since functional diversity indices were indicative of closed-canopy habitat, these measures could potentially be a faster and more efficient way of assessing community responses to forest regeneration as they require less sampling effort than taxonomic assessments. However, not all functional diversity indices were characteristic of regeneration, and some functional diversity indices are sensitive to under sampling (Kortmann et al., 2025; Van Der Plas et al., 2017). It has been observed that functional evenness is highly sensitive to under sampling, and functional richness is intermediately sensitive to under sampling, making them potentially less useful in biodiversity surveys (Van Der Plas et al., 2017). Functional divergence, function dispersion, and Rao's quadratic entropy were all less sensitive to

under sampling (Van Der Plas et al., 2017), and were strongly associated with closed-canopy habitats might, making them more useful when aiming to understand the functional recovery of communities across forest regeneration.

Despite its distinction between open and closed canopy habitats, functional diversity measures did not elucidate differences between secondary and old-growth communities. This could be due to the fact that we did not capture the full set of functional traits or environmental gradients associated with changes in bird communities across regenerating forests. For example, one study found that bird functional divergence increased with increasing variability in tree diameter (Schuldt et al., 2022). Therefore, considering foraging behaviors such as cavity nesting, bark gleaning, and sit-and-wait foraging might have explained the variation between secondary and old growth habitats. However, another study found that avian functional dispersion and functional divergence was comparable among secondary and old growth tropical forests (Sayer et al., 2017), therefore this lack of differentiation between the two regeneration classes could be a feature of closed-canopy forests. Future research should try to cover the scope of the drivers of functional diversity bird community recovery, including varying environmental parameters and behavioral traits.

Overall, our study contributes to the growing use of functional diversity indices as a means of assessing biodiversity responses to forest regeneration. Our findings underscore the importance of selecting robust functional diversity indices that are both ecologically meaningful and resilient to sampling limitations when evaluating community responses to forest regeneration. By prioritizing indices like functional divergence, functional dispersion, and Rao's quadratic entropy, restoration practitioners can more reliably assess community functional recovery, ultimately improving the effectiveness of biodiversity monitoring in regenerating forests.

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Supplementary Table 1: Description of each functional trait obtained for each bird species, including its variable type, measurement metric, and functional importance.

Trait	Variable	Description	Functional Importance
Beak Length (mm)	Continuous	Length from the tip of the beak to the base of the skull	Refers to different feeding strategies relating to functional role of species (e.g., seed-dispersers, pollinators).
Beak Width (mm)	Continuous	Width of the beak at the anterior edge of the nostrils	Refers to different feeding strategies relating to functional role of species (e.g., seed-dispersers, pollinators).
Wing Length (mm)	Continuous	Length from the carpal joint (bend of the wing) to the tip of the longest primary feather on the flattened wing	Flight performance, migration, feeding ability. Birds with shorter wings are typically suited for denser vegetation, while birds with larger wings can cover more range and aid in habitat connectivity.
Mass (g)	Continuous	Body mass given as species average (incorporating both male and female body mass)	Energy requirements, activity levels, environmental conditions. Larger-bodied birds require more food to maintain energy and, thus, may play important environmental roles such as dispersing large seeds across landscapes.
Primary Habitat	Categorical	Primary habitat species are found in, including human-modified, shrubland, and forests	Refers to species' ability to perform functional roles across multiple landscapes. Species adapted to human-modified landscapes may be important in connecting disturbed areas to non-disturbed areas.
Trophic Niche/Diet Type	Categorical	Species are put into certain categories if over 60% of their diet is made up of one food source (e.g., frugivore, nectarivore)	Refers to different feeding strategies relating to the functional role of species (e.g., seed-dispersers, pollinators).

685 **Supplementary Information**

Supplementary Table 2: Bird community data for species surveyed across the entire FCAT Reserve. Species codes represent 4-digit codes based on each species' common name. Trait data, including trophic niches, habitat associations, and morphological traits for each species were collected using an open access data set provided by Tobias et al., 2022. Morphological traits include average mass (g), beak length (mm), beak width (mm), wing length (mm), and tail length (mm). Abundance represents the total number of individuals observed during the study.

Code	Scientific Name	Trophic Niche	Habitat	Abundance	Mass	BeakLength	BeakWidth	WingLength	Tail Length
AMHB	Amazilia amazilia	Nectarivore	Shrubland	2	4.3	20.7	2.9	61.8	37.6
BABW	Campylorhynchus zonatus	Invertivore	Forest	1	34.6	24	3.9	78.4	82
BANA	Coereba flaveola	Nectarivore	Shrubland	24	10	13.2	3.6	54.6	34.1
BAWS	Pygochelidon cyanoleuca	Invertivore	Human Modified	1	9.7	8.6	3.6	92.3	48.8
BAYW	Cantorchilus nigricapillus	Invertivore	Forest	4	23.9	19.2	4.2	65.8	54.3
BBSC	Campylorhamphus pusillus	Invertivore	Forest	1	40.5	55	4.2	95.6	95
BCAS	Thamnophilus atrinucha	Invertivore	Forest	5	23.6	19.4	5.4	67.9	56.1
BCHH	Amazilia amabilis	Nectarivore	Forest	20	4.3	21.3	2	52.3	29.2
BCOF	Myiophobus fasciatus	Invertivore	Shrubland	7	9.9	13.5	5	58.9	54.1
BCRM	Lepidothrix coronata	Frugivore	Forest	16	8.3	10.9	3.7	56.8	26.6
BFDA	Dacnis lineata	Frugivore	Forest	2	11	13	3.5	58	40.6
BGRA	Volatinia jacarina	Granivore	Human Modified	4	9.9	10.4	4.3	47.8	42.8
BGRO	Cyanoloxia cyanoides	Granivore	Forest	3	32.5	19.6	10.2	79.6	66.8
BGTA	Tangara episcopus	Omnivore	Forest	7	35	14.2	6.4	87.3	64
BHTA	Tangara gyrola	Frugivore	Forest	2	21	12.7	4.8	73.5	51.4

BIAN	Gymnopithys bicolor	Invertivore	Forest	7	31.1	18.5	5.1	75.3	46.6
BNTA	Tangara cyanicollis	Frugivore	Forest	9	17	12.3	4.5	66.1	46.5
BRAT	Attila spadiceus	Invertivore	Forest	2	39.1	22.3	7.3	85.6	67.8
BTBA	Threnetes ruckeri	Nectarivore	Forest	34	5.2	33.4	3	56.6	36.3
BTFG	Automolus ochrolaemus	Invertivore	Forest	2	40.2	22.7	4.8	87.1	74.8
BTSA	Saltator maximus	Frugivore	Shrubland	8	47.6	20.7	8.9	96.1	88.9
BURW	Myiothlypis fulvicauda	Invertivore	Forest	6	14.9	14.3	4.5	63.3	49.7
CBAN	Poliocrania exsul	Invertivore	Forest	4	26.5	21.1	5	66.6	47.3
CHTY	Zimmerius albigularis	Invertivore	Forest	16	10.4	9	3.2	49.6	44.5
CHWA	Myiothlypis chlorophrys	Invertivore	Forest	3	16.2	12.9	4.6	61	48.1
CIMB	Pachyramphus cinnamomeus	Invertivore	Forest	3	20.3	16.8	7.6	77	59.4
CIVI	Vireo chivi	Invertivore	Forest	14	16.1	14	4.4	68	52.1
COAR	Pteroglossus torquatus	Frugivore	Forest	2	219.1	104	22.9	146.9	150.5
COTF	Todirostrum cinereum	Invertivore	Shrubland	10	6.3	14.8	4.8	42.5	33.8
CRWO	Thalurania colombica	Nectarivore	Forest	12	4.5	20.4	2.3	52.3	33.1
CTST	Epinecrophylla fulviventris	Invertivore	Forest	6	10.4	15	4.1	50.9	33.2
DCGQ	Asemospiza obscura	Granivore	Shrubland	64	11.2	10.4	4.8	52.4	42.3
DUAN	Cercomacroides tyrannina	Invertivore	Forest	1	16.3	18.2	4.9	62.7	60.4
DUPI	Patagioenas goodsoni	Frugivore	Forest	1	176	17	4	148.7	99.6
DWAN	Microrhopias quixensis	Invertivore	Forest	2	7.9	15.6	4.1	53	52.7
ECTR	Turdus maculirostris	Omnivore	Forest	4	69.6	22.5	4.9	112.6	97.7
FRTA	Ramphocelus flammigerus	Frugivore	Forest	15	33	18.4	8.2	88.6	74.8
GAGW	Myiothlypis fraseri	Invertivore	Woodland	1	11.6	13.5	5	65	55.7
GANT	Taraba major	Invertivore	Forest	1	59.2	26.3	7	90.6	81
GBAN	Crotophaga sulcirostris	Invertivore	Human Modified	1	82	26.9	9.5	129.3	162.7
GCBR	Heliodoxa jacula	Nectarivore	Forest	5	8.1	26.4	2.5	70.3	44.2
GMAK	Cryptopipo litae	Frugivore	Forest	8	14.9	13.3	4.3	69.2	46.8
GOWO	Colaptes rubiginosus	Invertivore	Forest	1	55.8	27	7.1	123.7	76.3
GRET	Discosura conversii	Nectarivore	Forest	3	3	14.4	1.3	42.2	42
GRHO	Chlorophanes spiza	Frugivore	Forest	6	19	15.9	4.5	68.3	48.2
GYBM	Progne chalybea	Invertivore	Shrubland	1	50	15.3	5.6	130.6	66.4

HOWR	Troglodytes aedon	Invertivore	Shrubland	19	10.9	15.9	3	51.4	41.1
LBST	Heliomaster longirostris	Nectarivore	Forest	1	6.6	35	2.7	58.4	30.7
MUTO	Ciccaba virgata	Omnivore	Forest	1	284	33	9	240.6	149.1
NOSC	Schiffornis veraepacis	Omnivore	Forest	6	31.1	21.2	5.3	87.3	70.2
OBEE	Euphonia xanthogaster	Frugivore	Forest	22	13	10.7	4.8	61.4	36
OBFL	Mionectes oleagineus	Frugivore	Forest	21	11.2	11.8	4.2	60.5	48.2
OBSP	Arremon aurantiirostris	Omnivore	Forest	4	34.5	16	6.6	72.7	66.4
OCEE	Euphonia saturata	Frugivore	Forest	2	13.3	10	3.9	57.7	32.3
OCYE	Geothlypis semiflava	Invertivore	Shrubland	4	17.2	14.7	3.3	59.7	52.7
ORFC	Myiotriccus ornatus	Invertivore	Forest	2	10.6	10.3	3.6	52.4	26.5
OLPI	Picumnus olivaceus	Invertivore	Forest	5	10.6	10.3	3.6	52.4	26.5
OLWO	Sittasomus griseicapillus	Invertivore	Forest	4	13.1	16.1	4	76.7	76.5
ORFL	Myiotriccus ornatus	Invertivore	Forest	5	9.9	13.2	5.4	59.6	41.2
OSFT	Mionectes olivaceus	Frugivore	Forest	26	15.3	13.7	4.1	69	40
PAAN	Myrmotherula pacifica	Invertivore	Shrubland	6	10.1	15.3	3.6	50.6	28
PAPA	Forpus coelestis	Omnivore	Shrubland	1	26.1	16.6	9.4	76.8	39.4
PATA	Tangara palmarum	Omnivore	Forest	1	39	15	5.9	92.5	70.4
PBRW	Dendrocincla fuliginosa	Invertivore	Forest	5	38.7	29.9	6.4	104.9	86.7
PCFA	Heliothryx barroti	Nectarivore	Forest	3	5.5	21.9	2.2	63.8	57
PCHU	Amazilia rosenbergi	Nectarivore	Forest	4	3.7	23.9	2.2	52.8	30
PLXE	Xenops minutus	Invertivore	Forest	2	10.6	13.1	2.8	55.7	43.6
PVTH	Turdus obsoletus	Omnivore	Forest	2	74.8	22.2	5	116	86.1
RCMA	Ceratopipra mentalis	Frugivore	Forest	15	15	12.1	4.4	58.5	28
RFSP	Cranioleuca erythrops	Invertivore	Forest	1	16.9	14.6	3.2	64.8	71.4
RMFL	Myiozetetes cayanensis	Invertivore	Shrubland	1	25.9	14.4	5.4	84.1	71.4
RTAH	Amazilia tzacatl	Nectarivore	Forest	22	4.8	21.9	3.1	56.4	34.2
RUFP	Lipaugus unirufus	Frugivore	Forest	1	82.1	24	7.2	132.4	112
SBAN	Crotophaga ani	Omnivore	Human Modified	2	110.1	30.6	9.9	144	180.6
SCBW	Microcerculus marginatus	Invertivore	Forest	2	18.2	19.2	3.4	58.7	24.2
SCFC	Myiarchus phaeocephalus	Invertivore	Woodland	1	26.3	22.5	7.1	93	89.8
SCPT	Lophotriccus pileatus	Invertivore	Forest	2	7.5	13.2	3.6	48.9	39.3

SHTY	Phyllomyias griseiceps	Invertivore	Forest	1	7.2	9	3.7	51.6	45.2
SHWO	Lepidocolaptes souleyetii	Invertivore	Woodland	3	25.7	32.7	4.1	92.3	84.5
SLAN	Myrmotherula schisticolor	Invertivore	Forest	3	9.6	15.5	3.3	54.9	36.9
SLSP	Synallaxis brachyura	Invertivore	Shrubland	28	18.3	16.3	3.4	57.9	76.7
SOBT	Camptostoma obsoletum	Invertivore	Shrubland	5	8.1	9.8	3.2	52.3	40.9
SPWO	Xiphorhynchus erythropygius	Invertivore	Forest	3	46.8	34.8	5.4	115.6	108.1
SQCU	Piaya cayana	Invertivore	Forest	1	102	32	8.8	145.5	278.6
SRFL	Myiobius sulphureipygius	Invertivore	Forest	6	11.6	14.6	4.2	66.4	56.2
SRWS	Stelgidopteryx serripennis	Invertivore	Shrubland	3	15.7	10.5	3.4	107.5	47.8
STFL	Mionectes olivaceus	Frugivore	Forest	2	15.3	13.7	4.1	69	40
STHR	Phaethornis striigularis	Nectarivore	Forest	6	3	23.7	2.4	39.1	36.4
STTA	Tangara icterocephala	Frugivore	Forest	4	22	12.6	5.1	70.5	45
STXE	Xenops rutilus	Invertivore	Forest	1	11.2	13.3	2.9	65.8	49
TBEU	Euphonia laniirostris	Frugivore	Forest	28	15	10.1	5.6	61	37.1
TBSF	Sporophila funerea	Granivore	Human Modified	48	13	12.6	6.9	55	48.7
TCTA	Chrysocorypha delatrii	Invertivore	Forest	1	18	15.2	4.9	71.4	58.1
VASE	Sporophila corvina	Granivore	Human Modified	40	10.6	10.7	5.3	52.9	42.8
VBHU	Amazilia julie	Nectarivore	Forest	14	3.3	16	1.2	43.1	26
WBMA	Manacus manacus	Frugivore	Forest	26	16.7	11.5	4.4	52.2	32.8
WBWO	Glyphorynchus spirurus	Invertivore	Forest	3	14.6	13.7	4.4	68.7	66
WFLA	Myrmotherula axillaris	Invertivore	Forest	3	8.1	15	3.4	50.9	36.5
WSTA	Tachyphonus rufus	Invertivore	Shrubland	1	34.4	18.7	6.1	83	77.2
WTGS	Atticora tibialis	Invertivore	Forest	1	10.6	7.4	3.4	88.2	53
WTRS	Platyrinchus mystaceus	Invertivore	Forest	4	9.7	13.1	7.3	55	29.9
WTSI	Eutoxeres aquila	Nectarivore	Forest	13	10.6	27.5	3.6	70.5	54
WWHE	Phaethornis yaruqui	Nectarivore	Forest	98	5.4	45.6	2.6	59.5	53.8
WWPU	Malacoptila panamensis	Invertivore	Forest	6	42.6	29.3	9.5	87.4	71.8
YBEL	Elaenia flavogaster	Invertivore	Woodland	3	24.8	12.7	5	77.4	70.6
YBSE	Sporophila nigricollis	Granivore	Shrubland	35	9.6	9.1	5	52.4	43

YBSI	Spinus xanthogastrus	Granivore	Forest	2	12.7	10.5	4.3	65.2	40.5
YCTY	Tyrannulus elatus	Invertivore	Shrubland	3	7	8.3	3.2	48.2	40.7
YOFL	Tolmomyias sulphurescens	Invertivore	Forest	1	14.3	13.4	5.4	63	55.5

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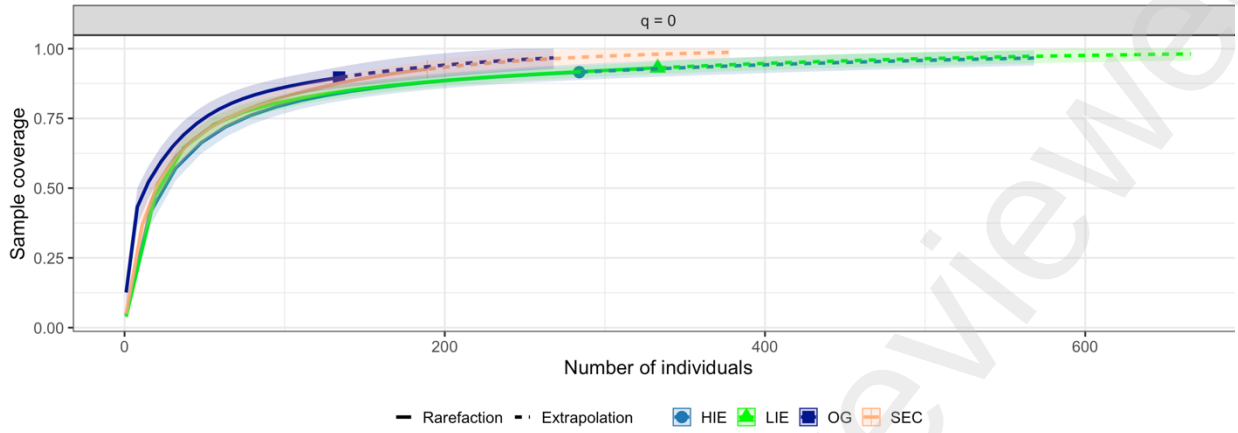
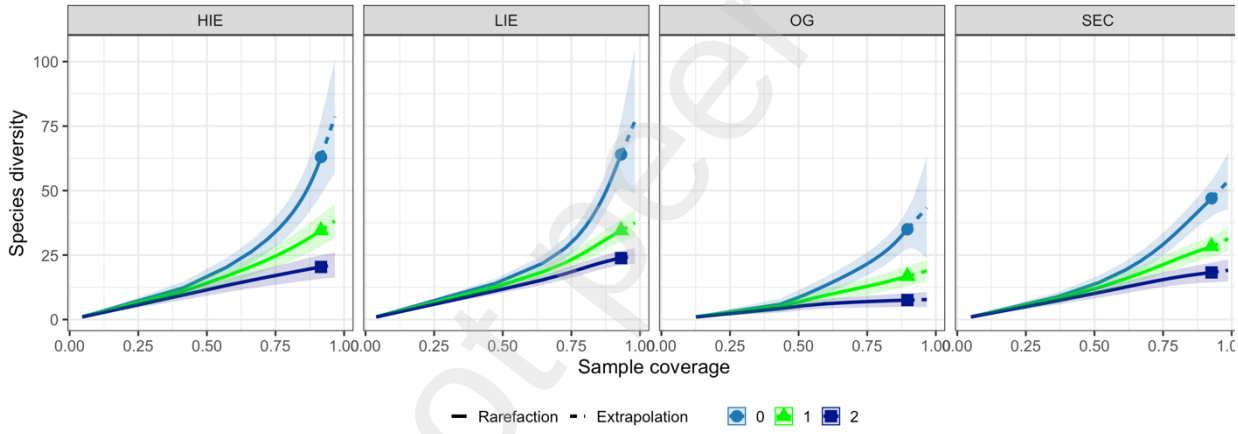
A)



B)



Supplementary Figure 1: Sampling completeness curves across four habitat types, representing different stages of regeneration and old-growth forest. The curves are color-coded: blue for HIE plots, green for LIE plots, pink for SEC plots, and purple for OG plots. A) Displays the overall sample coverage between sites where all plots within each habitat type are aggregated together, while B) examines the hill numbers/species diversity within each plot, where q = 0 (species richness), q = 1 (Shannon Diversity), and q = 2 (inverse Simpson).

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Supplementary Table 3: Type II Wald chi-square tests assessing diversity indices as a function of regeneration stage (HIE, LIE, SEC, OG). Generalized least squares (GLS) regression was used to account for spatial dependence in model residuals, with a Gaussian spatial correlation structure applied. Significant relationships ($p < 0.05$) are highlighted in bold.

Response Variable	Chi Squared	P- Value
Species Richness (Q0)	34.44	**< 0.001**
Shannon Entropy (Q1)	79.32	**< 0.001**
Inverse Simpson Index (Q2)	25.66	**< 0.001**
Functional Richness (FRic)	11.46	**0.001**
Functional Divergence (FDiv)	14.27	**0.002**
Functional Evenness (FEve)	4.42	0.22
Functional Dispersion (FDis)	35.60	**< 0.001**
Rao's Quadratic Entropy (RaoQ)	20.98	**< 0.001**

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