

# Forest structure predicts species richness and functional diversity in Amazonian mixed-species bird flocks

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## Abstract

Secondary forest has the potential to act as an important habitat for biodiversity and restoring ecological benefits. Functional diversity, which includes morphological and behavioral traits that mediate species interactions with the surrounding environment, relates to the resilience of ecosystems. To assess the relationship between habitat structural differences in primary and secondary forest and the resultant differences in functional diversity of avian species, we followed 11 mixed-species flocks at the Biological Dynamics of Forest Fragments Project, near Manaus, Brazil. We used remote sensing LiDAR to assess which three-dimensional forest structural features are most closely associated with variation in species richness and functional diversity in secondary and primary tropical forest flocks. The species richness of flocks in primary forest increased in areas with higher elevation and higher leaf area density in the understory and subcanopy but was not correlated with habitat structure in secondary forest. Functional diversity increased at lower elevations and with a denser subcanopy in both primary forest and secondary forest but only increased with greater understory leaf area density in primary forest. Together, these results indicate that a dense subcanopy and understory can be important for mixed-species flocks and that flock richness and functional diversity can be predicted by vegetation structure.

Abstract in Portuguese is available with online material.

## KEYWORDS

bird, Brazil, forest fragmentation, functional traits, leaf area density, light detection and ranging, secondary forests, vegetation structure

## 1 | INTRODUCTION

Fragmentation of tropical rainforests is one of the main drivers of global biodiversity loss (Barlow et al., 2018; Betts et al., 2019), and more fragmentation is expected in the coming decades (Fischer

et al., 2021; Taubert et al., 2018). Forest fragmentation threatens forest biodiversity and diminishes the ecosystem services that forests offer, such as their contribution to biogeochemical cycles, water quality, and global air quality (Foley et al., 2005; Grantham et al., 2020). Deforested sites are often abandoned, and the regenerating matrix

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between forest fragments can influence the dynamics and species composition of animal communities in forest fragments and can facilitate the recolonization of fragments after they are isolated from continuous forest (Gascon et al., 1999; Wolfe et al., 2015). Naturally regenerating secondary forests that grow between fragments often become important reservoirs for biodiversity as the forests gain age and structural complexity (Chazdon et al., 2009; Gilroy et al., 2014; Lennox et al., 2018; Poorter et al., 2021; Queiroz et al., 2014). However, biodiversity itself, which only accounts for species richness and abundance but not how species interact with their environments, may not be the best metric for measuring the functional aspects of an ecosystem (e.g., pollination, seed dispersal, pest control, and nutrient cycling), and functional diversity may be more appropriate (Cadotte et al., 2011; Gagic et al., 2015).

Functional diversity combines species richness, abundance, and morphological, behavioral, and ecological traits of species to assess how species interact with their environment and influence ecological processes within their community (Cadotte et al., 2011; Cooke et al., 2019; Violle et al., 2007). Functional diversity also carries important implications for the functionality of an ecosystem and the services that it offers, as higher measures of functional diversity indicate greater productivity and resilience of ecosystems while lower measures can indicate ecosystem degradation (Bregman et al., 2016; Cadotte et al., 2011; Grantham et al., 2020). Therefore, functional diversity may be a more informative metric than species diversity or richness for measuring the recovery of ecosystem function and stability after deforestation or biodiversity loss (Cadotte et al., 2011; Gagic et al., 2015; Mouillot et al., 2013). However, little is known about the relationship between vegetative characteristics and functional diversity in regenerating secondary forests.

Naturally regenerating secondary forests have the capacity to regain a substantial proportion of the biomass and biodiversity that exists in undisturbed primary forests (Bregman et al., 2016; Lennox et al., 2018; Poorter et al., 2021). In addition, forest structural complexity—consisting of diverse vertical vegetation layers and a closed canopy—is known to positively associate with species biomass among most taxonomic groups at local scales by providing a greater diversity of resources and niches for species to utilize (Carrasco et al., 2019; Goetz et al., 2007; Lennox et al., 2018; Tews et al., 2004). Birds may be an ideal taxon to study the return of species and functional diversity to recovering secondary forests, as they have a high probability of occurring in low biomass forests and exhibit a strong and well documented connection between functional traits and ecosystem processes (Ikin et al., 2019; Lennox et al., 2018; Pigot et al., 2020). Among birds, understory mixed-species flocks provide an excellent system to study which vegetative characteristics are most important to the return of functional diversity to the recovering forest.

Understory Amazonian mixed-species flocks are large interspecific groups of insectivorous birds that forage together in a shared home range (Munn, 1985; Munn & Terborgh, 1979). The core flock obligate species (generally 5–10 species) are frequently joined by other facultative species from the larger forest bird community and

can contain as many as 65 species throughout the course of a single day (Martínez & Gomez, 2013). These flocks are known to associate with over 100 species, representing ~36% of the core forest avifauna in central Amazonia (Rutt & Stouffer, 2021). Flock movement is conspicuous, flocks can be easily followed and observed (Mokross et al., 2014), flocks associate with a large percentage of forest avifauna (Rutt & Stouffer, 2021), and they are sensitive to forest disturbance as flock size and diversity significantly decrease in small forest fragments and early successional forest (Maldonado-Coelho & Marini, 2004; Mokross et al., 2014; Stouffer, 2020; Zou et al., 2018). Mixed-species flocking species are known to recolonize secondary forests that have regenerated to a certain threshold—at least 4–7 m tall (Rutt et al., 2020)—and even breed in them (Rutt et al., 2021). Yet, evidence suggests that secondary forests are suboptimal habitat for mixed-species flocks as flock size and network associations decrease in disturbed forests (Mokross et al., 2014; Mokross et al., 2018; Powell et al., 2013). Yet, little is known about which structural characteristics facilitate the return of mixed-species flocks to secondary forest.

Canopy height is known to be positively correlated with mixed-species flock richness (Lee et al., 2005; McDermott et al., 2014; Colorado Zuluaga & Rodewald, 2015; Jones & Robinson, 2020), and the presence of old-growth large-diameter trees is associated with functional diversity (Jones & Robinson, 2020). Yet, many forest layers exist between the canopy and forest floor, especially in the tropics, and the impact these layers may have on species richness and functional diversity in mixed-species flocks is unknown. Other structural characteristics may rival or exceed the relevance of canopy height in predicting species richness and functional diversity of mixed-species flocks. If these vegetative features are identified, they may help conservation efforts to accelerate the return of functionally important bird species to human-disturbed habitats through reforestation efforts.

In this paper, we use light detection and ranging (LiDAR) technology to assess forest floor to canopy vegetation structure to determine which aspects of forest structure are positively correlated with species richness and functional diversity in mixed-species flocks in primary forest and secondary tropical rainforest in the Brazilian Amazon. We aim to answer the following questions: (a) What vegetative structural features predict species richness and functional diversity in mixed-species flocks? (b) Do the vegetative structural features that predict species richness and functional diversity in mixed-species flocks differ in primary forest and secondary forest?

## 2 | METHODS

### 2.1 | Study site

Our study took place at the Biological Dynamics of Forest Fragments Project (BDFFP) in central Amazonia, ~80 km north of Manaus, Brazil in both disturbed and continuous forest. Initial forest fragment isolation began in the 1980s to make space for cattle ranches

(Bierregaard, 2001; Stouffer et al., 2011). The cattle ranches are now abandoned and occupied by regenerating secondary forest. The BDFFP now has 90% or greater forest cover and is composed of a collection of forest fragments of various sizes and adjoining secondary forest of different ages and structures, all surrounded by continuous undisturbed *terra firme* forest (Rutt et al., 2017; Stouffer, 2020). Bierregaard (2001) provides a complete overview and description of this field site.

## 2.2 | Data collection

### 2.2.1 | Flock following

KM followed 11 mixed-species flocks during three consecutive dry seasons between June 2009 and August 2011, eight in continuous primary forest (mean canopy height = 21.0 m) and three in 23-year-old secondary forest (mean canopy height = 17.2 m), for an average of 31 h each (range = 17–86 h), totaling 343 h. Flock locations were recorded every 30 s using a Garmin eTrex Vista HCx GPS unit (~10 m resolution). We recorded the species composition of the flock in 30 min time blocks. A species was considered to be part of the flock if it foraged within 15 m of the flock core for more than 30 min. Based on our experience with this flocking system, we only recorded the presence of species known to participate in mixed-species flocks and excluded all other species encountered incidentally. Twenty-nine species (24%) that occurred in fewer than five 30 min time-blocks were removed from analysis in an effort to focus on regular flock participants.

To reduce spatial autocorrelation and follow other flock studies from this system, GPS data were thinned to mark a flock location every 2 min (Mokross et al., 2018; Rutt et al., 2020). To diminish the influence of roosting sites (Jullien & Thiollay, 1998; Martínez & Gomez, 2013), we only used spatial data between 0630 h and 1730 h local time, which allowed flocks time to disperse away from permanent gathering areas. Home range size (95%) was analyzed with autocorrelated kernel density estimation (AKDE) using the "ctmm" package (Calabrese et al., 2016). This method selects the best-fit continuous time movement model to account for the autocorrelation structure intrinsically found in the data. For a full description of flock-following methods, see Mokross et al. (2018).

### 2.2.2 | Functional diversity

Functional diversity metrics were composed of morphological measurements and dietary components for each species. Morphological measurements were taken from local species mist netted at the BDFFP (Johnson & Wolfe, 2017) to avoid variance from samples at other locations that may be adapted to different ecosystems. When local measurements were not available or the sample size for local species was too small (<4 individuals), we used measurements from the AVONET dataset (Tobias et al., 2022). The following

morphological measurements were included for each species that KM detected in mixed flocks: bill length (mm), bill width (mm), bill depth (mm), tarsus length (mm), tail length (mm), wing length (mm), hand wing index (mm), Kipp's distance (mm), and mass (g).

Dietary information was extracted from Elton-Traits 1.0 (Wilman et al., 2014). For each diet category, Wilman et al. (2014) estimated the percent diet in 10% increments for each species. In this study, we combined the diet categories of vertebrate endotherms (vend), vertebrate ectotherms (vect), and general vertebrates, or unknown vertebrates, (vunk) into a single category "vertebrate"; fish (vfish) and scavenge, carcasses, carrion, etc. (vscav) were omitted from our combined "vertebrate" category as these categories did not contribute to the diet of any species in our study. As a result, we used six diet traits in our study (invertebrate, vertebrate, fruit, nectar, seed, and plant) which added to 100% for each species.

### 2.2.3 | Vegetation structure

We used airborne LiDAR data (June 2008), to measure three-dimensional vegetation profiles for each forest type studied. A full description of the airborne LiDAR data collection methods can be found in Stark et al. (2012) and Lefsky et al. (2017). Almeida et al. (2019) compared the vegetation profile of different forest types at this site and found that secondary forests contained denser vegetation in the understory and midstory, and lower canopy heights when compared to primary forest. Elevation (m) was calculated by building a digital elevation model using classified ground points. Mean canopy height (m) was normalized by subtracting classified ground point elevation from the height of the canopy. Leaf area density (LAD) was also derived from the LiDAR data and is described as the one-sided leaf area within a given vertical stratum ( $\text{m}^2/\text{m}^3$ ). LAD describes variance in vertical and horizontal vegetative structures across different height intervals (Bouvier et al., 2015). Mean LAD was further divided into three separate vertical bins to characterize forest structure: understory (0–5 m), midstory (6–15 m), and subcanopy (16–25 m). Canopy LAD (>25 m) was omitted from our models as it is tightly correlated with mean canopy height (Coddington et al., *In Review*). All vegetation covariates were derived using the package "lidR" (Roussel et al., 2020) in R version 4.1.2 (R Core Team, 2021). All metrics were calculated using a 1 m resolution and averaged to 10 m resolution to match flock data.

Flock home ranges were aligned to their corresponding LiDAR forest structure footprint using ArcGIS Pro (version 2.8.0). All LiDAR pixels outside the flock home range (95%) were removed to ensure that no superfluous pixels were analyzed. LiDAR raster footprints were loaded with all aforementioned vegetative structural characteristics and subdivided into 10 m × 10 m pixels to match the resolution of the GPS units during flock following efforts. The average species richness of each individual 100 m<sup>2</sup> pixel within each flock's territory was calculated and rounded to the nearest whole integer. Flock territories were distinct and did not overlap. We only calculated unique species present in the flock when measuring species

richness and did not account for the number of individual birds present.

### 2.3 | Statistical data analysis

We used a principal component analysis (PCA) on all measured morphological and dietary traits to normalize all variables and reduce correlation. Of the 15 principal components (PCs), the first four explained 67.21% of the variation in the morphological traits (Table 1). PC1 explained 33.35% of the variation and was loaded with traits associated with body size and diet, positively with mass, tarsus length, bill size, and vertebrate diet, and negatively with invertebrate diet. PC2 explained 18.14% of the variation and was loaded with traits associated with mobility and diet, positively with tarsus length, invertebrate diet, vertebrate diet and bill length, and negatively with hand wing index, Kipp's distance, fruit diet, plant diet, and nectar diet. PC's 3 and 4 accounted for a combined 15.72% of the variation and were both loaded with a mix of physical and dietary traits. The functional trait space of PCs 1–4 was used to calculate the 50%, 95%, and 99% probability contours of the multivariate kernel densities.

Functional richness and functional evenness were calculated for each 100m<sup>2</sup> pixel based on species composition time blocks in each flock territory using the *dbFD* function in the R package *FD* (Laliberté et al., 2014). Functional richness was estimated as the volume of trait space occupied by the species in a flock. Functional evenness estimates a measure of the regularity of the distribution

of species trait dissimilarities away from the centroid in functional space. Functional evenness is highest when all nearest neighbor distance pairs show an even spread between species in trait space. In addition, we calculated the functional distinctiveness (*D<sub>i</sub>*) of each species detected in our study to determine which species were the most functionally unique with the “*funrar*” package in R (Grenié et al., 2017). Functional distinctiveness is a measure of how unusual a species' trait value is compared to that of other species in the community, ranging from 0 to 1. Lower functional distinctiveness values indicate functional redundancy while higher values indicate more functionally distinct species.

To explore how flock species richness and functional diversity are predicted by forest structure, we ran six generalized linear mixed models (GLMM). We ran two separate groups of three GLMMs in each forest type, secondary or primary forest, to avoid describing vegetative differences between distinct habitat types. The response variables for each group of three models were species richness, functional richness, and functional evenness, respectively, with elevation, understory LAD, midstory LAD, subcanopy LAD, and mean canopy height as predictor variables, and individual flock as a random effect (Table 3). One secondary forest flock home range was outside the area covered by LiDAR and omitted from the GLMM analyses, which left only two secondary forest flocks in our analysis. Because most 100 m<sup>2</sup> pixels were never visited by the flock, even inside the outlined home range, the dataset contains an excess of zeros (70%). Therefore, we modeled species richness and functional richness with zero-inflated negative binomial distributions to

TABLE 1 Variable loadings in each principal component

	PC1	PC2	PC3	PC4
Eigenvalue	5.002	2.722	1.298	1.059
Variance	33.349	18.144	8.654	7.061
Cumulative Variance	33.349	51.492	60.146	67.208
Trait	PC1	PC2	PC3	PC4
Average Bill Depth	<b>4.068</b>	0.095	-0.723	<b>-1.054</b>
Average Bill Width	<b>3.992</b>	0.180	-0.557	-0.883
Average Bill Length	<b>3.509</b>	<b>1.970</b>	0.918	-0.537
Average Tail	<b>3.661</b>	0.526	<b>1.483</b>	0.020
Average Tarsus	<b>2.646</b>	<b>3.264</b>	<b>-3.559</b>	-0.565
Average Wing	0.051	0.226	<b>4.449</b>	-0.288
Hand Wing Index	<b>1.599</b>	<b>-4.378</b>	<b>3.950</b>	0.209
Kipps Distance	<b>3.497</b>	<b>-2.087</b>	<b>3.064</b>	0.987
Average Mass	<b>3.892</b>	<b>1.060</b>	0.199	<b>1.216</b>
Diet Fruit	0.804	<b>-5.088</b>	<b>-2.799</b>	<b>-1.192</b>
Diet Invertebrate	<b>-1.283</b>	<b>4.934</b>	<b>3.831</b>	-0.278
Diet Nectar	0.285	<b>-1.992</b>	-0.034	<b>-3.430</b>
Diet Plant	-0.245	<b>-1.881</b>	<b>-1.951</b>	<b>1.377</b>
Diet Seed	0.84	-0.067	<b>-1.391</b>	<b>8.681</b>
Diet Vertebrate	<b>1.314</b>	<b>1.645</b>	<b>-3.222</b>	<b>-2.099</b>

Note: PCs are labeled with eigenvalue and % of variance explained. Significant loadings are in bold.

account for both excess zeros and overdispersion in the data using the “glmmTMB” package (Brooks et al., 2017). Because functional evenness is not represented as a whole integer, it was modeled with zero-inflated beta-distributions instead of zero-inflated negative binomial distributions. For each forest type, we used likelihood ratio tests to compare the fit of full models with null models using the R package “performance” (Lüdtke et al., 2021). Parameters were estimated by maximizing likelihood using the “glmmTMB” package (Brooks et al., 2017), and all plots were generated with “ggplot2” (Wickham, 2011).

### 3 | RESULTS

We detected a combined 90 species participating in mixed-species flocks with 84 occurring in primary forest and 63 occurring in secondary forest. Additionally, 28 species were detected only in primary forest compared to 6 species only detected in secondary forest. The average number of species present in a flock at one time was 9 ( $SD = 1.9$ ) in primary forest, compared to 7 ( $SD = 2.1$ ) species in secondary forest. The most functionally distinct species in the two forest types often had a large body size with a semi-frugivorous diet (e.g., *Selenidera piperivora*, *Trogon* spp.; Table 2).

The total volume of functional trait space occupied by all species that attended primary forest flocks (856.6) was slightly smaller than the trait space occupied by species in secondary forest flocks (910.6; Figure 1). This was largely due to two of the top five most functionally distinct species in our study (*Trogon violaceus* and *Cacicus haemorrhous*) being detected only in secondary forest flocks, though these two species are known to be common in primary forest at our site. While the trait space occupied by the total secondary forest flock species pool was slightly larger, the average functional trait space occupied by individual secondary forest flocks (413.1) amounted to 81% of what was found in primary forest flocks (509.9). Mean functional evenness was slightly higher in secondary forest flocks (0.724) when compared to primary forest flocks (0.701).

Several vegetative covariates emerged as predictors of mean species richness and functional diversity in mixed-species flocks in the GLMMs (Table 3), and no vegetative covariates were significant in secondary forest. Species richness in primary forest increased in areas of high elevation ( $p < .001$ ,  $EST = 0.006$ ,  $S.E. = 0.001$ ), high understory LAD ( $p < .001$ ,  $EST = 0.045$ ,  $S.E. = 0.012$ ), high subcanopy LAD ( $p = .018$ ,  $EST = 0.121$ ,  $S.E. = 0.051$ ), and lower mean canopy height ( $p = .024$ ,  $EST = -0.004$ ,  $S.E. = 0.002$ ) (see Table 3 for model results). Functional richness, the volume of the functional trait space, was significantly correlated with multiple vegetative metrics that were shared across both primary and secondary forest types. Elevation was significant and negative in primary forest ( $p < .001$ ,  $EST = -0.004$ ,  $S.E. = 0.002$ ) and secondary forest ( $p < .001$ ,  $EST = -0.017$ ,  $S.E. = 0.003$ ) as lower elevations predicted greater functional richness. Subcanopy LAD was also important for functional richness in primary forest ( $p = .007$ ,  $EST = 0.311$ ,  $S.E. = 0.115$ ) and secondary forest ( $p = .037$ ,  $EST = 0.439$ ,  $S.E. = 0.211$ ), as areas

with a denser subcanopy showed increased levels of functional richness in both forest types. Understory LAD was a significant positive predictor of functional richness in primary forest only ( $p = .008$ ,  $EST = 0.068$ ,  $S.E. = 0.025$ ), as areas with a dense understory were correlated with increased levels of functional richness. Functional evenness, the regularity of the distribution of species trait dissimilarities in functional space, was significant and correlated negatively with elevation ( $p = .038$ ,  $EST = -0.004$ ,  $S.E. = 0.002$ ) and positively with subcanopy LAD in secondary forest ( $p = .003$ ,  $EST = 0.388$ ,  $S.E. = 0.003$ ), due to increased measures of functional evenness at lower elevations, and in areas with a denser subcanopy. Functional evenness was not correlated with any covariates in primary forest.

### 4 | DISCUSSION

Avian mixed species flock richness and functional diversity were associated with different vegetation characteristics in primary and secondary forests. Specifically, areas with denser and more complex understory and subcanopy vegetation were associated with greater flock species richness and functional richness in primary forest, and elevation and denser subcanopy vegetation were associated with functional richness and functional evenness in secondary forest. Our results indicate that these vegetative characteristics may help facilitate the return of species and functionally diverse mixed-species flocks to previously disturbed habitats that are now secondary forest.

Vegetation structural characteristics, such as canopy height, are known to be associated with tropical mixed species flock richness (Colorado Zuluaga & Rodewald, 2015; Jones & Robinson, 2020; Lee et al., 2005; McDermott et al., 2014); however, our study uses LiDAR data to offer a finer degree of precision on the association between flock species richness and functional diversity and below-canopy vegetation structure. Here, we find that a denser understory and subcanopy are stronger predictors of flock species richness in primary forest than canopy height, as higher canopy height led to lower species richness. However, our findings that a higher canopy led to lower species richness was largely driven by outlier species counts in areas with a low canopy. Our study does not disagree with the importance of canopy height in predicting avian species richness, as canopy height and subcanopy LAD are positively correlated (Coddington et al., In Review). Rather, our study suggests that subcanopy LAD may be a more appropriate predictor of species richness in our subset of flocking species or is simply correlated with some other unmeasured aspect of forest structure that is attractive to flocks. A dense subcanopy may open more foraging niches that allows flocks to support a greater number of species with higher vertical foraging strategies (Montaño-Centellas & Jones, 2021), or they may be more prone to overlap with canopy flocks (Munn, 1985), both of which would increase species richness.

Functional richness was also associated with a denser subcanopy in primary and secondary forests. Potentially, as a result of the more functionally unique species that join flocks which tend to forage



**TABLE 2** List of all mixed-species flock participants, in order of functional distinctness (Di)

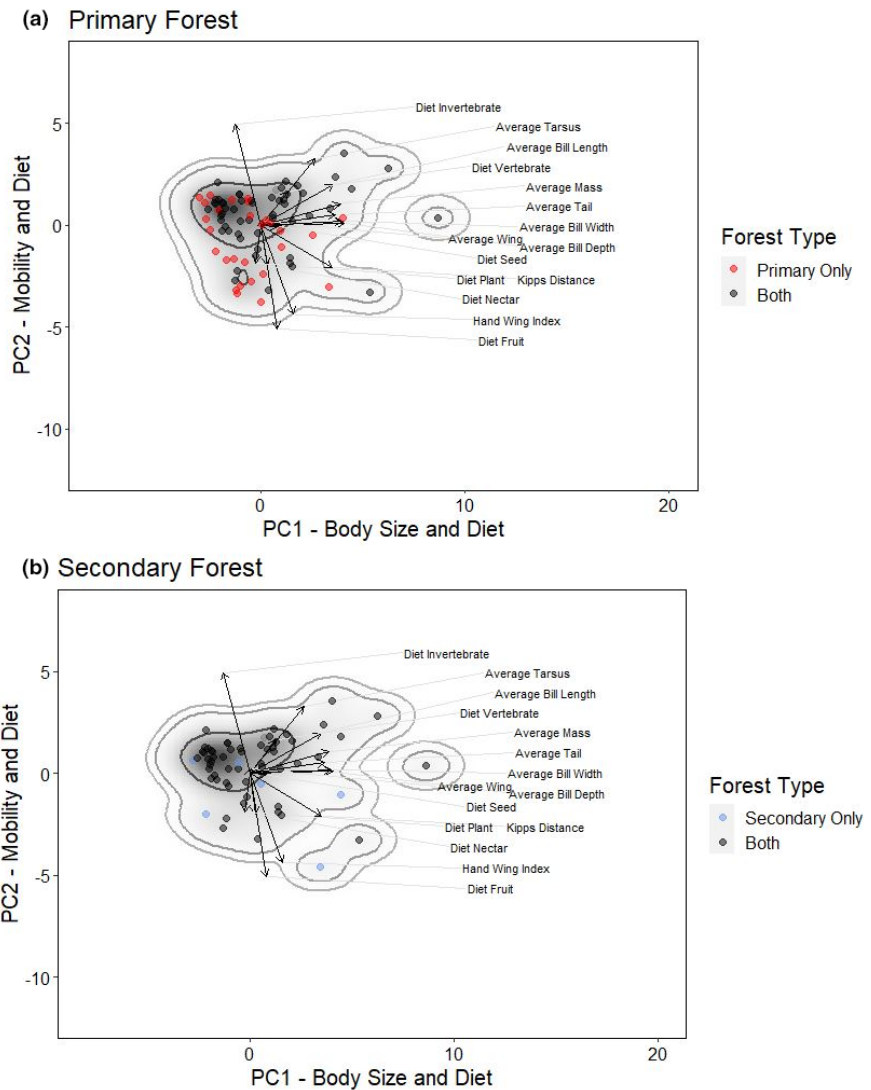
No.	Species	Di
1	<i>Selenidera piperivora</i>	0.349
2	<i>Trogon viridis</i>	0.311
3	<i>Trogon violaceus</i>	0.283
4	<i>Campephilus rubricollis</i>	0.278
5	<i>Cacicus haemorrhous</i>	0.262
6	<i>Celeus torquatus</i>	0.256
7	<i>Chlorophanes spiza</i>	0.253
8	<i>Piaya melanogaster</i>	0.248
9	<i>Monasa atra</i>	0.235
10	<i>Trogon rufus</i>	0.234
11	<i>Dendrocolaptes certhia</i>	0.225
12	<i>Loriotus cristatus</i>	0.224
13	<i>Cyanerpes caeruleus</i>	0.217
14	<i>Attila spadiceus</i>	0.212
15	<i>Dacnis cayana</i>	0.204
16	<i>Caryothraustes canadensis</i>	0.198
17	<i>Cyanerpes cyaneus</i>	0.197
18	<i>Capito niger</i>	0.197
19	<i>Galbula dea</i>	0.196
20	<i>Dacnis lineata</i>	0.196
21	<i>Lamprospiza melanoleuca</i>	0.194
22	<i>Cymbilaimus lineatus</i>	0.194
23	<i>Saltator grossus</i>	0.188
24	<i>Nonnula rubecula</i>	0.187
25	<i>Tersina viridis</i>	0.187
26	<i>Celeus elegans</i>	0.186
27	<i>Dendrocincla fuliginosa</i>	0.184
28	<i>Tangara chilensis</i>	0.181
29	<i>Sittasomus griseicapillus</i>	0.180
30	<i>Tangara punctata</i>	0.168
31	<i>Automolus ochrolaemus</i>	0.166
32	<i>Cyanerpes nitidus</i>	0.165
33	<i>Celeus undatus</i>	0.163
34	<i>Dendrexetastes rufigula</i>	0.160
35	<i>Pheugopedius coraya</i>	0.156
36	<i>Campylorhamphus procurvoides</i>	0.153
37	<i>Myrmotherula brachyura</i>	0.153
38	<i>Ramphocaenus melanurus</i>	0.152
39	<i>Tyrannulus elatus</i>	0.150
40	<i>Tangara varia</i>	0.150
41	<i>Ramphocelus carbo</i>	0.149
42	<i>Picumnus exilis</i>	0.149
43	<i>Pachyramphus minor</i>	0.149
44	<i>Zimmerius gracilipes</i>	0.148
45	<i>Euphonia cayennensis</i>	0.147
46	<i>Galbula albirostris</i>	0.146

**TABLE 2** (Continued)

No.	Species	Di
47	<i>Automolus infuscatus</i>	0.145
48	<i>Euchrepomis spodioptila</i>	0.145
49	<i>Cyphorhinus arada</i>	0.144
50	<i>Tachyphonus surinamus</i>	0.143
51	<i>Tangara mexicana</i>	0.143
52	<i>Isleria guttata</i>	0.142
53	<i>Xiphorhynchus pardalotus</i>	0.142
54	<i>Ornithion inerme</i>	0.142
55	<i>Piculus chrysochloros</i>	0.141
56	<i>Lanio fulvus</i>	0.141
57	<i>Deconychura longicauda</i>	0.140
58	<i>Pachyramphus marginatus</i>	0.140
59	<i>Terentriacus erythrurus</i>	0.136
60	<i>Laniocera hypopyrra</i>	0.134
61	<i>Piculus flavigula</i>	0.133
62	<i>Epinecrophylla gutturalis</i>	0.132
63	<i>Myrmotherula menetriesii</i>	0.132
64	<i>Veniliornis cassini</i>	0.131
65	<i>Herpsilochmus dorsimaculatus</i>	0.129
66	<i>Tunchiornis ochraceiceps</i>	0.129
67	<i>Myrmotherula axillaris</i>	0.129
68	<i>Mionectes macconnelli</i>	0.127
69	<i>Lepidocolaptes albolineatus</i>	0.127
70	<i>Rhytipterna simplex</i>	0.127
71	<i>Microxenops milleri</i>	0.126
72	<i>Myiopagis caniceps</i>	0.126
73	<i>Tolmomyias poliocephalus</i>	0.125
74	<i>Rhynchocyclus olivaceus</i>	0.125
75	<i>Phylloscartes virescens</i>	0.125
76	<i>Piprites chloris</i>	0.124
77	<i>Thamnomanes caesius</i>	0.124
78	<i>Pachysylvia muscipapina</i>	0.124
79	<i>Myrmotherula longipennis</i>	0.124
80	<i>Myiopagis gaimardii</i>	0.123
81	<i>Xenops minutus</i>	0.122
82	<i>Onychorhynchus coronatus</i>	0.121
83	<i>Tolmomyias assimilis</i>	0.121
84	<i>Vireolanius leucotis</i>	0.121
85	<i>Glyphorhynchus spirurus</i>	0.121
86	<i>Pachyramphus surinamus</i>	0.121
87	<i>Myiobius barbatus</i>	0.120
88	<i>Certhiasomus stictolaemus</i>	0.120
89	<i>Philydor erythrocerum</i>	0.120
90	<i>Thamnomanes ardesiacus</i>	0.118

Note: Species in red were detected in primary forest only, and species in blue were detected in secondary forest only, while species in black we detected in both forest types. No. indicates the species distinctiveness rank; lower Di numbers indicate less distinct species.

**FIGURE 1** Two-dimensional functional trait space represented by PC scores of functional traits of species observed in (a) primary forest and (b) secondary forest. PC1 axis reflects variation in body size and diet while PC2 reflects variation in traits associated with mobility and diet. Species in red were detected in primary forest only, and species in blue were detected in secondary forest only



above the midstory (e.g., *Piaya melanogaster*, *Chlorophanes spiza*), thus denser vegetation in the subcanopy increases the available foraging niches for facultative species to exploit (Goetz et al., 2014). It is somewhat surprising that higher subcanopy LAD predicted higher levels of functional evenness, but only in secondary forest, as they also predicted functional richness in this forest type. This may be a result of some of the most functionally unique species in our study being detected in secondary forest only (e.g., *Trogon violaceus*, *Cacicus haemorrhous*), even though they are also known to exist nearby in primary forest. Niche theory suggests that a species might need to broaden their niche in secondary forest, leading to reduced resource overlap and competition (MacArthur & Levins, 1967). Alternatively, a decrease in the number of primary forest species from secondary forest flocks could reduce competition between flock obligates, opening more niches for non-flocking species to exploit. Flocks that are found in forest types with less structural complexity are also less stable (Mokross et al., 2014; Jones & Robinson, 2020), which may further reduce competition between flock obligates. When more species join secondary forest flocks, the heightened values of functional evenness suggest that species are less similar in their niche

space. Greater functional richness and evenness associated with subcanopy vegetation complexity in secondary forests indicates that a larger and wider volume of niches that are evenly spaced out occupy these forests, but that functionally similar species are not present.

Denser understory vegetation also led to increases in flock species richness and functional richness in primary forest, but not secondary forest, which can be partially explained by the increased likelihood of terrestrial and near-ground foragers to join flocks in areas with a denser understory. Terrestrial and near-ground insectivores move along the forest floor and utilize specific foraging strategies that closely tie them to certain microhabitats (Stouffer & Bierregaard, 1995; Lees & Peres, 2008; Stratford & Stouffer, 2013, 2015). As a result of their specific habitat requirements, near-ground and terrestrial foragers are known to be extremely vulnerable to forest fragmentation (Stouffer & Bierregaard, 1995; Stouffer & Bierregaard Jr, 2007; Stratford & Stouffer, 1999) and several near-ground foragers were only detected in primary forest in our study (e.g., *Cyphorhinus arada*, *Iserlia guttata*). This is not surprising given that near-ground and terrestrial foragers are among the most

TABLE 3 Estimated coefficients of species richness, functional richness, and functional evenness from GLMMs for primary forest and secondary forest, with Likelihood Ratio Test results

Primary Forest	Species richness				Functional richness				Functional evenness			
	Estimate	Std. error	z value	p-value	Estimate	Std. error	z value	p-value	Estimate	Std. error	z value	p-value
Intercept	1.561	0.132	11.855	<.001	1.298	0.254	5.106	<.001	1.021	0.122	8.343	<.001
Elevation	0.006	0.001	6.199	<.001	-0.004	0.002	-2.037	.042	0.001	0.001	0.508	.612
Understory LAD	0.045	0.012	3.755	<.001	0.068	0.025	2.671	.008	0.007	0.014	0.466	.641
Midstory LAD	-0.004	0.020	-0.215	.593	-0.038	0.042	-0.915	.360	0.010	0.024	0.415	.678
Subcanopy LAD	0.121	0.051	2.363	.018	0.311	0.115	2.700	.007	-0.003	0.060	-0.047	.963
Mean Canopy Height	-0.004	0.002	-2.252	.024	-0.002	0.004	-0.463	.643	-0.003	0.002	-1.472	.141
LR-Test Results	$\chi^2 = 60.02$	df = 5	p-value =	<.001	$\chi^2 = 17.37$	df = 5	p-value =	.004	$\chi^2 = 4.04$	df = 5	p-value =	.544
Secondary Forest	Species Richness				Functional Richness				Functional Evenness			
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
Intercept	1.895	0.294	6.443	<.001	1.762	0.326	5.401	<.001	0.594	0.200	2.964	.003
Elevation	-0.001	0.003	-0.558	.577	-0.017	0.003	-5.542	<.001	-0.004	0.002	-2.072	.038
Understory LAD	0.010	0.037	0.271	.786	0.127	0.076	1.669	.095	-0.044	0.046	-0.937	.349
Midstory LAD	0.100	0.134	0.751	.452	0.132	0.274	0.481	.631	0.171	0.154	1.113	.266
Subcanopy LAD	-0.015	0.116	-0.130	.897	0.439	0.211	2.083	.037	0.388	0.130	2.999	.003
Mean Canopy Height	-0.003	0.007	-0.440	.660	0.007	0.015	0.501	.616	0.001	0.010	0.100	.920
LR-Test Results	$\chi^2 = 1.22$	df = 5	p-value =	.942	$\chi^2 = 17.94$	df = 5	p-value =	.003	$\chi^2 = 19.18$	df = 5	p-value =	.002

Note: Significant ( $p < .05$ )  $p$  values for vegetation covariates are in bold.



vulnerable to habitat fragmentation (Stouffer & Bierregaard, 1995; Stratford & Stouffer, 1999; Powell et al., 2013) and are often absent from secondary forests that are younger than 25 years of age (Wolfe et al., 2015). It is also possible that increased levels of understory LAD allow core flock obligates to spend more time foraging in the understory, opening more foraging niches in the midstory and subcanopy for higher foraging species to exploit. Alternatively, increased structural complexity in the understory may open more specialized foraging microhabitats (Michel et al., 2015) or provide cooler microclimates for understory species (Jirinec et al., 2022).

Elevation was also an important predictor of species richness and functional richness in both forest types. However, the range in elevation within a territory is not usually very large (35–40 m). Mixed-species flocks in lowland tropical rainforests favor lower elevations within their territory as these areas have reduced effects of wind turbulence and sunlight (Coddington et al., *In Review*; Ewers & Banks-Leite, 2013; Potts et al., 2014), which increases both moisture and arthropod abundance (Williams-Linera & Herrera, 2003; Chan et al., 2008). However, the results of our study suggest that flock species richness decreases at lower elevations, as core flock obligates favor these areas (Coddington et al., *In Review*). Species richness decreases in lower elevations potentially because measures of species richness in these flocks are often driven by the presence of higher canopy foraging species (e.g., *Tangara sp.*, *Cyanerpes sp.*) that may not follow flock obligates to lower elevation areas where their specific foraging niches are too far from the core of the flock. Despite the tendency for fewer species to join flocks at lower elevations in primary forest, functional richness was also positively associated with lower elevations in both forest types, which indicates that the species that are joining flocks in these low-lying areas are maintaining a high degree of functional richness. It is worth noting that flock following took place in the dry season and perhaps more species gravitate to the lower elevations which are cooler and moister at this time of year (Jirinec et al., 2022).

Many studies have emphasized the importance of below-canopy structure for estimating avian diversity (Zellweger et al., 2016; Bae et al., 2018; Carrasco et al., 2019; Cooper et al., 2020). Our study found that LAD in the subcanopy and understory are especially important vegetative metrics for maintaining or attracting functional richness in Amazonian mixed-species flocks in both disturbed and undisturbed habitats, which has important implications for forest restoration efforts that aim to attract biodiversity. It is also noteworthy that in secondary forest, functional richness returns to level that are similar to primary forest before species richness returns to similar levels. Several studies have shown that regenerating forests can attain similar species richness, structure, and function of primary forests after approximately 20 years (Basham et al., 2016; Dunn, 2004; Letcher & Chazdon, 2009). Functional richness likely returns faster than species richness in hyper diverse ecosystems, like the Amazon, due to their high degrees of functional dissimilarity and redundancy (Safi et al., 2011; Cooke et al., 2019). Elevated levels of species richness result in a denser occupation of overlapping trait space (Pigot et al., 2016), which implies that a large percentage of available trait

space may be occupied without a full complement of avian species that were present pre-disturbance. Functional richness measures the convex hull of the trait space of the community but does not inform about the interior relationships and similarity or dissimilarity of species within the community. Thus, functional richness tells us that in both primary and secondary forest the overall trait space occupied by mixed species flocks is similar. However, the functional evenness result of greater evenness in secondary forest informs us that the species are less similar in trait space in secondary forest than the community of species in primary forest and there is less functional redundancy, a trait associated with more highly resilient ecosystems. Reduced functional evenness in primary forest flocks may also result from shared territoriality that diminishes insectivore densities and may allow for more functionally similar species to co-exist (Powell, 1989). Additionally, primary forest flocks that exhibit more stability may also have stronger costs associated with “activity matching” (Sridhar & Guttal, 2018), resulting in flock compositions with core members that are more similar in morphology or function. Therefore, it is not surprising that functional richness is predicted by vegetative structure before species richness in secondary forests, as flocks in these habitats exhibit diminished species richness and have fewer network associations (Mokross et al., 2014; Rutt et al., 2020) as they are less similar to each other in trait space than species in primary forest. These results underscore the important role that regenerating secondary forests play in maintaining the functional diversity of birds in disturbed tropical forests, and the ecological services the birds provide, such as pollination, pest control, scavenging, and seed dispersal to continue succession in secondary forests (Michel et al., 2020).

Our results agree with previous work which suggests that naturally regenerating secondary forests demonstrate impressive flexibility by recovering a diminished, yet substantial subset of avian biodiversity and functional diversity (Bregman et al., 2016; Lennox et al., 2018). These results are consistent with a larger body of work that demonstrates that overall functional trait space can be resilient in the face of declines in species richness (Bregman et al., 2016; Oliveira et al., 2020; Oliveira & dos Anjos, 2022). However, we acknowledge that this study only focuses on the functional diversity of a subset of bird species, those that participate in mixed-species flocks, and does not account for the overall functional diversity of the forest to which all its inhabitants contribute.

In summary, our results agree with previous work that disturbed forests can host a substantial, but lesser degree of avian functional diversity when compared to primary forest (Bregman et al., 2016; Gómez et al., 2020; Oliveira & dos Anjos, 2022). In addition, denser vegetation in the understory and subcanopy are important predictors of species richness and functional diversity, which if incorporated in future forest restoration projects could facilitate the rapid return of functionally diverse avian species in tropical habitats. Our study provides further evidence that regenerating secondary forests are a valuable resource for preserving both biodiversity and ecosystem services in disturbed landscapes and highlights which aspects of

forest vegetation structure are most important for enhanced species richness and functional diversity in lowland tropical forests.

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## CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in work reported or in the conclusions, implications, or opinions stated.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in George Mason University Dataverse at <https://doi.org/10.13021/orc2020/JUM6RX>.

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