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FUNCTIONAL DIVERSITY OF AVIAN MIXED-SPECIES FORAGING FLOCKS ON THE TILARÁN CORDILLERA, COSTA RICA

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Abstract · Avian mixed-species foraging flocks are a well-studied phenomenon that offer a useful system for investigating the distribution of Neotropical avian functional diversity. To characterize the variation in such flocks at different elevations, we studied the species composition of these flocks over a 624 m elevational gradient on both sides of the continental divide that crosses the Tilarán Cordillera in northwest Costa Rica. We characterized the change in the diversity of these flocks across the elevational gradient using several measures of diversity: species richness, trophic guild diversity, functional richness, functional evenness, and functional divergence. We hypothesized that species richness would decline when moving upslope along the elevational gradient, but this pattern would not be mirrored in all measures of functional diversity. Patterns of functional diversity were different and revealed important turnover in species' ecological functions along the elevational gradient. While the lower elevations of the Atlantic side featured higher species richness, the lower elevations of the Pacific side featured the greatest functional richness and greatest functional divergence. Upper elevations showed the lowest species richness and lowest functional evenness. This study highlights the importance of incorporating functional diversity analyses into montane conservation planning that addresses anticipated species altitudinal range shifts with climate change.

Resumen · Las bandadas mixtas de forrajeo en aves son un fenómeno bien estudiado que ofrece un sistema útil para investigar la distribución de la diversidad funcional de las aves neotropicales. Para caracterizar la variación en estas bandadas a diferentes altitudes, estudiamos la riqueza de especies de estas bandadas a lo largo de un gradiente altitudinal de 624 m a ambos lados de la divisoria continental que cruza la Cordillera de Tilarán en el noroeste de Costa Rica. Caracterizamos el cambio en la diversidad de estas bandadas a lo largo del gradiente altitudinal utilizando varias medidas de diversidad: riqueza de especies, diversidad de gremios tróficos, riqueza funcional, uniformidad funcional y divergencia funcional. Planteamos la hipótesis de que la riqueza de especies disminuiría al ascender en el gradiente altitudinal, pero este patrón no se reflejaría en todas las medidas de diversidad funcional. Los patrones de diversidad funcional fueron diferentes y revelaron una importante rotación en las funciones ecológicas de las especies a lo largo del gradiente altitudinal. Mientras que las elevaciones más bajas del lado Atlántico presentaron una mayor riqueza de especies, las elevaciones más bajas del lado Pacífico presentaron la mayor riqueza funcional y la mayor divergencia funcional. Las elevaciones superiores mostraron la menor riqueza de especies y la menor uniformidad funcional. Este estudio destaca la importancia de incorporar análisis de diversidad funcional en la planificación de la conservación de las zonas de montaña que aborde los cambios previstos en los cambios en el rango altitudinal de las especies en respuesta al cambio climático.

Keywords: *altitudinal gradient · functional outliers · Monteverde · Neotropics · tropical montane forest*

INTRODUCTION

Mixed-species foraging flocks are interspecific associations of birds that form due to potential benefits conferred to birds that join the group. These benefits have been well investigated, and may include, but are not limited to, reduced risk of predation and increased foraging efficiency (Sridhar and Shanker 2014, Beauchamp 2021). Many families of birds from terrestrial ecosystems across the world participate in mixed-species flocks, with some families and guilds being common members of such flocks (Thiollay 1999, Sridhar et al. 2009, Colorado and Rodewald 2014).

Avian mixed-species flocks present a convenient system for investigating community assembly and trophic structure of tropical forests (Graves and Gotelli 1993). Consequently, studies have examined the response of these flocks to changes in latitude (Fanjul et al. 2021, Fanjul et al. 2023), elevation (Arbeláez-Cortés and Marín-Gomez 2012, O'Donnell 2017, Montaño-Centellas 2023), and degrees of human disturbance (Mokross et al. 2014, Colorado Zuluaga and Rodewald 2015, Vásquez-Ávila et al. 2021, Coddington et al. 2023). Furthermore, mixed species flocks can be considered conservation targets, especially in the tropics where many threatened species participate in mixed flocks (Zou et al. 2018).

Mixed-species flocks and their ecological structure could provide additional insights into how bird communities vary along elevational gradients. The effects of elevation on species richness have been studied since the origins of biogeography (Lomolino 2001). While high elevations are often less species rich than lower elevations, a monotonic decline in species with elevation is uncommon (Rahbek 1997). In tropical mountains, mid elevations often peak in species richness that correlates with high rainfall (McCain and Grytnes 2010). In some regions this mid elevation peak coincides with the borders of distinct biogeographical regions (Ferro and Morrone

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2014, Hazzi et al. 2018). Elevational changes in tropical latitudes often lead to greater avian species turnover than comparable elevational changes in temperate latitudes (Gaston et al. 2007). Janzen (1967) proposed that this trend was due to environmental stability, specifically the relatively constant temperature at a given elevation in the tropics that allows species to have small tolerance ranges, and consequently, narrow elevational ranges.

As community composition changes with elevation, an accompanying change in functional diversity would be expected. Investigating if the trend in species richness is mirrored by functional diversity enhances our understanding of species' ecological roles along elevational gradients (Cadotte et al. 2011). Functional diversity allows for including species traits to enhance the understanding of a given community's diversity and complements more traditional measures of biodiversity (Villéger et al. 2008). Increasingly, metrics of functional diversity are used to describe and characterize communities beyond species diversity because functional diversity is better able to encapsulate ecosystem functioning (Mcgill et al. 2006, Mammola et al. 2021). These metrics measure species distribution with unique traits, and thus, specific roles in an ecosystem (Cadotte et al. 2011). Functional diversity is useful as a metric because the scope of phenotypic variation present in a given community can be mechanistically tied to its ability to withstand change (Norberg et al. 2001).

Morphological and behavioral traits can be used to measure functional diversity. Mixed species flocks often host invertivorous species, but some members may be partially or entirely frugivorous or nectarivorous (Valburg 1992, Srinivasan et al. 2012). Species that exploit unique resources are irreplaceable, and are likely to play a more important role in ecosystem function than functionally redundant species (Griffin et al. 2009). Thus, investigating how functional diversity changes along gradients provides further insights into the complexity of interactions within flocks. Complex and varied flocks may be an important part of the resilience of the ecosystems in which they participate (Bregman et al. 2016).

We investigated the community structure of mixed-species flocks of birds along elevational gradients in two slopes of the Tilarán Cordillera in Costa Rica by characterizing the species richness, trophic guild diversity and functional diversity in a 624 m elevational gradient. Although the elevational gradient might seem narrow compared to other studies, at 10 degrees of latitude it is enough to produce substantial changes in community assemblages, a trend found in other regions (Gentry 1988, Jankowski et al. 2009, Nguyen and Gómez-Zurita 2016). Besides elevation, rainfall and vegetation differences also contribute to creating unique foraging scenarios on either slope. Differences in vegetation structure have been shown to correlate with flock composition, and varying vegetation complexity may correspond to avian functional diversity differently than to avian species richness (Fanjul et al. 2023). In other studies, a 'decoupling' between patterns of species richness and functional diversity has previously been documented on an elevational gradient in Ecuador (Santillán et al. 2019) informing our hypothesis that the pattern of species richness across this gradient may differ substantially from the pattern of functional diversity. This discrepancy could reveal new priorities in biodiversity conservation that are unique to each slope and elevation belt (Zou et al. 2018). In some locations flocks may be indicators of the composition of the underlying bird community, but often lack many species present in the area (Montaño-Centellas and Jones 2021). Nevertheless, understanding the composition of flocks in their current elevational ranges is an important part of tropical forest conservation because as the elevational ranges of species shift, even to the point of extirpation from montane forests, community functioning may be altered (Sekercioglu et al. 2008, Freeman et al. 2018).

METHODS

Study area. We conducted the study entirely within the contiguous forest that lies mostly northeast of the town of Monteverde, in the Tilarán Cordillera, northwest Costa Rica. The remnant is a mix of primary and secondary rainforest owned and managed by several conservation-minded organizations. Data were collected from four main points of access: trails surrounding the San Gerardo Field Station, the Santa Elena Cloud Forest Road, trails of the Monteverde Biological Station (Estación Biológica Monteverde), and trails within the Bajo del Tigre Reserve (Figure 1).

The study area straddled the continental divide just north of Cerro Amigos, one of the tallest mountains in the Tilarán Cordillera. Water to the southwest of this ridge flows into the Pacific Ocean, whereas water to the northeast of the ridge flows into the Gulf of Mexico and the Atlantic Ocean. The study area covered an elevational gradient of 624 m. These two slopes exhibited notably distinct rainfall patterns that lead to substantial differences in vegetation. The Atlantic slope was characterized by relatively large amounts of consistent rainfall throughout the year, while the Pacific slope experienced a dry season from December through April that became less pronounced at higher elevations (Arciniega-Esparza et al. 2022). The lower elevations of the study area featured several vegetative differences that became less apparent as elevations approached the continental divide. The Atlantic slope forest featured a dense understory and large amounts of epiphytic growth. In contrast, the understory of the Pacific slope forest was less dense and the trees held fewer epiphytes, but the understory became denser with elevation gain (Nadkarni et al. 1995). These vegetative differences created different foraging landscapes for birds between the two slopes. The forest on the Pacific slope was also situated in remanent forest of the Bajo del Tigre Reserve that is split from the continuous forest by the small towns of Monteverde and Santa Elena and a road (Figure 1), and as a result the lower reaches of the Pacific zone were slightly disconnected from the rest of the study area, even though the town of Monteverde is somewhat forested. Consequently, bird species that are sensitive to fragmentation, such as some insectivores and large frugivores (Bregman et al. 2014), may be underrepresented in the Pacific zone.

Data collection. To avoid inconsistency in data collection due to different observers, all data was collected by a single observer (SBE) during the timeframe 15 November to 9 December 2022. During this timeframe, flock searches took place between 0600 and 1500 h local time, but observation times were not standardized further due to the unpredictable nature of locating flocks. Data was recorded for each mixed-species foraging flock encountered in the study area. We defined a mixed-species foraging flock as two or more species of birds moving in the same direction within 15 m of the closest individual for at least five min (Stotz 1993). Importantly, this definition stipulates that a flock must not be the result of a unique resource such as an army ant swarm or fruiting tree.

Searching for flocks involved quietly walking trails and dirt roads in the forested areas of the study area, moving around a given flock slowly in order to better evaluate the composition, following the flock off the trail when possible, but avoiding influencing the movement of the flock. Upon encountering a unique flock, a timer was started, and then the number of individuals of each species in the flock was noted using 8 x 42 binoculars. Birds that kept pace with the flock were considered members, while birds that only briefly interacted with the flock were disregarded. The data was considered complete and usable only after the flock had been observed for a span of at least five minutes without seeing a previously unnoticed member of the flock. After concluding the observation of a flock, the GPS coordinates and elevation were noted for the midpoint of where the

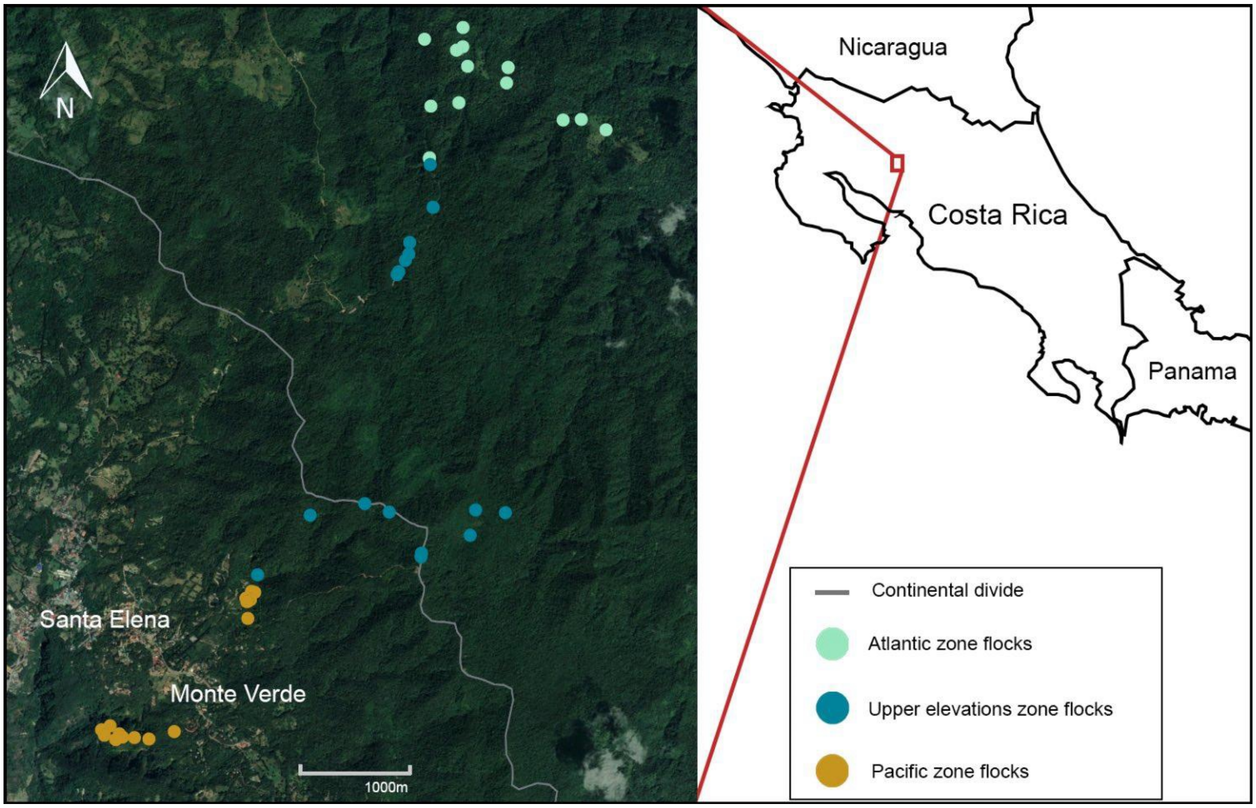

Figure 1. Map of study area in the Tilarán Cordillera, Costa Rica, showing flock locations with color indicating zone. Pacific zone flocks (1200–1512 m) indicated in gold. Upper Elevations zone flocks (1512–1824 m) indicated in blue. Atlantic zone flocks (1200–1512 m) indicated in green. The continental divide is marked in gray. The towns of Santa Elena and Monte Verde are labeled.

flock was observed (Gaia GPS). Most flocks were observed for over 15 min, and some for up to an hour. To keep observations independent, flocks observed at the same location (within 50 m of each other) were ignored, even on separate days. While following each flock, the number of each species observed in that flock was recorded. We used the taxonomy from the AOS Checklist of North and Middle American Birds (Chesser et al. 2023).

Flocks were divided into three separate zones depending on elevation and side of the continental divide. This created an 'Upper Elevation' zone and two lower elevation zones named 'Atlantic' and 'Pacific' depending on which slope they were from. The Upper Elevation zone encompassed 1824–1512 meters a.s.l., while the lower elevation Atlantic and Pacific zones both occurred between 1512–1200 m a.s.l. All three zones span an equal elevation gradient of 312 m. Due to uneven numbers of flocks encountered in the three zones, a random number generator was used to eliminate eight flocks from the 'Upper Elevations' and two flocks from the 'Pacific' group. This resulted in 16 flocks for each zone, allowing these zones to be directly compared in cumulative measures and functional diversity metrics.

Data analysis. We calculated both a mean number of species and a mean number of individuals per flock for the three zones. The standard deviations associated with those means were also calculated along with an ANOVA. We used the *vegan* R package to compute the Jaccard similarity between the three groups in terms of total species abundance for each zone (Oksanen et al. 2025).

To further characterize and contrast the mixed species flocks from the different zones, we used functional diversity metrics to characterize the layout of species on a multidimensional trait space (Petchey and Gaston 2006). We used three indices proposed by Villéger et al. (2008): functional richness, functional evenness and functional divergence. Functional richness is defined as the extent to which a community fills the trait space, more specifically it is the volume inside a convex hull defined by the species in the trait space (Cornwell et al. 2006). Accordingly, higher values of functional richness are a result of species with extreme trait values stretching the volume. Functional evenness encapsulates both the regularity of spacing of species in the trait space and how the abundance of those species is distributed (Villéger et al. 2008). The index approaches 1 when species and their abundances are linked by branches of a minimum spanning tree with equal branch lengths, and approaches 0 when a subset of species and their abundance are clumped together in a small portion of the tree (Villéger et al. 2008). Functional divergence explains where in the trait space species, and their abundances are grouped (Mason et al. 2005). Villéger et al. (2008) propose a novel way to calculate this index which involves using the abundance-weighted divergences of species from the center of gravity of the previously mentioned convex hull of the trait space. Values of this index approach 1 when species with trait values far from the center of gravity of the trait space are abundant, while conversely, this index approaches 0 when species with traits close to the center of gravity are the most abundant.

Trait data for all bird species in this study were obtained from the Avonet database (Tobias et al. 2022). All numerical variables (beak length, beak width, hand-wing index, and body mass) were scaled and centered to have 0 mean and unit variance. The *fundiversity* R package (Grenié & Gruson 2023) was used to calculate three functional diversity indices as defined in Villéger et al. (2008). The functional richness, evenness and divergence indices were calculated with the cumulative species seen in flocks of each zone. To showcase morphological functional diversity, we performed separate principal component analyses for each zone (R Core Team 2022, Wickham 2016). These PCAs utilized the same four morphological functional traits listed above to illustrate the trait spaces of the zones in a two-dimensional way. The 'trophic niche' variable of the Avonet Database was used to illustrate the foraging guilds composition of the birds in each of the three study zones (Wickham 2016, Tobias et al. 2022).

RESULTS

We observed a total of 62 species in the 48 flocks included in this analysis. The mean flock size was 8.6 ± 4.55 individuals; the smallest flock contained three individuals and the largest flock contained 24 individuals. There was a mean 5.3 ± 2.92 species per flock; one flock was composed of just two species, while the flock that boasted the most individuals also contained the most species, a total of 16 species.

Jaccard similarity in species abundance among the three zones showed that the lower elevation (Atlantic and Pacific) flocks were more similar in terms of species composition than the Upper Elevation flocks. The Jaccard index of the Atlantic and Pacific flocks was 0.33, while the Upper Elevations flocks formed an outlier with 0.18 Jaccard similarity.

Species richness varied among the three zones, with the lowest number of 23 species recorded in the Upper Elevations zone (Table 1). Similarly, the most species-rich flock in the Upper Elevations zone (11 species) had fewer species than the species-rich flocks in the Pacific and Atlantic zones, 14 and 16 species respectively. The flock with the greatest number of individuals from each zone also contained the highest number of species. The mean number of species per flock was relatively similar among zones, with an ANOVA yielding a *P* value of 0.63. Similarly, zones did not differ significantly in the average number of individuals per flock, with an ANOVA *P* value of 0.47.

Measures of functional diversity revealed different trends among the three zones. Functional richness was highest in the Pacific zone. Functional evenness displayed a new dimension to the data, showing that the Upper Elevations had large gaps between unique species in the trait space. Functional divergence showed that the most functionally rich zone, the Pacific, also displayed the most divergence (Table 1).

Morphological differences in the birds found in flocks of each zone produced trait spaces with unique patterns of outlier species. Principal component analyses effectively mapped four continuous morphological functional traits (beak length, beak width, hand-wing index, and body mass) onto a two-dimensional space that explained most of the trait variation (Figure 2). The sum of principal components 1 (PC1) and 2 (PC2) explained 85.3%, 80.6%, and 88% of the variation in traits of the species found in the Atlantic, Upper Elevations and Pacific zones, respectively.

The morphological trait spaces of all three zones displayed similar patterns (Figure 2). PC1 mainly captured variation in body mass and bill morphology, while PC2 explained most variation in hand-wing index, a proxy for dispersal ability (Sheard et al. 2020, Claramunt et al. 2022). Many species were clumped together, while species with larger mass, bill morphology and hand-wing indices radiated away from the main cluster (Figure 2). The Upper Elevations exhibited only four species that were morphologically distinct enough to be differentiated from the main grouping of species (Figure 2b).

Most species observed in flocks throughout the study were primarily invertivorous (Table 1). However, all zones contained three or more species classified as frugivorous (Table 1). Two of the three species classified as omnivorous: Sooty-capped Chlorospingus *Chlorospingus pileatus* and Spangle-cheeked Tanager *Tangara dowii* were exclusively members of Upper Elevations flocks. One individual of the third omnivorous species, Black-thighed Grosbeak *Pheucticus tibialis*, was only recorded in an Atlantic flock. The only nectarivore species seen participating in flocks was the Bananaquit *Coereba flaveola*; which was seen participating singly in two Atlantic flocks.

DISCUSSION

Our results show a distinct community structure of mixed-species flocks across the Tilarán Cordillera with changes in species richness, functional diversity, and trophic guild composition. We documented how a decent on either side of the continental divide can cause notable change in each of these measures of diversity, revealing trends in the diversity of mixed-species flocks of the Tilarán Cordillera that may apply to other elevational gradients in the Neotropics. Furthermore, while our study area spanned a relatively small elevational gradient of 624 vertical meters, compared to gradients of other studies that often exceed 1500 vertical meters (Muñoz 2016, Montaño-Centellas 2020, Muñoz and Jankowski 2023). This comparably small vertical change was enough to produce notable changes in the community assemblages.

The species richness of flocks in our study area followed an expected trend: the higher elevation zone had fewer species per flock, and cumulatively, both lower elevation zones had greater species counts compared to the Upper Elevations zone. In contrast, the average number of individuals per flock remained relatively constant across the gradient, perhaps suggesting that while there may be a decline in species richness, the abundance of birds may be fairly stable across the gradient.

While sample sizes (16 flocks per zone) are not large enough to confidently conclude that the flocking birds of the Atlantic zone are a more species-rich group than their counter-

Table 1. Cumulative and average measures of mixed-species foraging flock diversity across the three zones: upper elevations, and lower Atlantic and Pacific slopes of the Tilarán Cordillera, Costa Rica. For cumulative measures N =16 flocks per zone, for means ± standard deviation all flocks were included N = 16, 24, 18 flocks for Atlantic, Upper Elevations, and Pacific, respectively.

Diversity Measure	Atlantic 1200–1512 m	Upper Elevations 1512–1824 m	Pacific 1200–1512 m
Species richness	37	23	33
Functional richness	7.319	8.923	11.864
Functional evenness	0.563	0.365	0.444
Functional divergence	0.597	0.488	0.679
Mean number of species	5.69 ± 3.2	4.71 ± 2.1	5.17 ± 3.0
Mean number of individuals	8.88 ± 4.7	8.92 ± 4.3	7.39 ± 4.0
Max number of species	16	11	14
Max number of individuals	24	21	19
Invertivore species	30	18	29
Frugivore species	5	3	4
Omnivore species	1	2	0
Nectarivore species	1	0	0

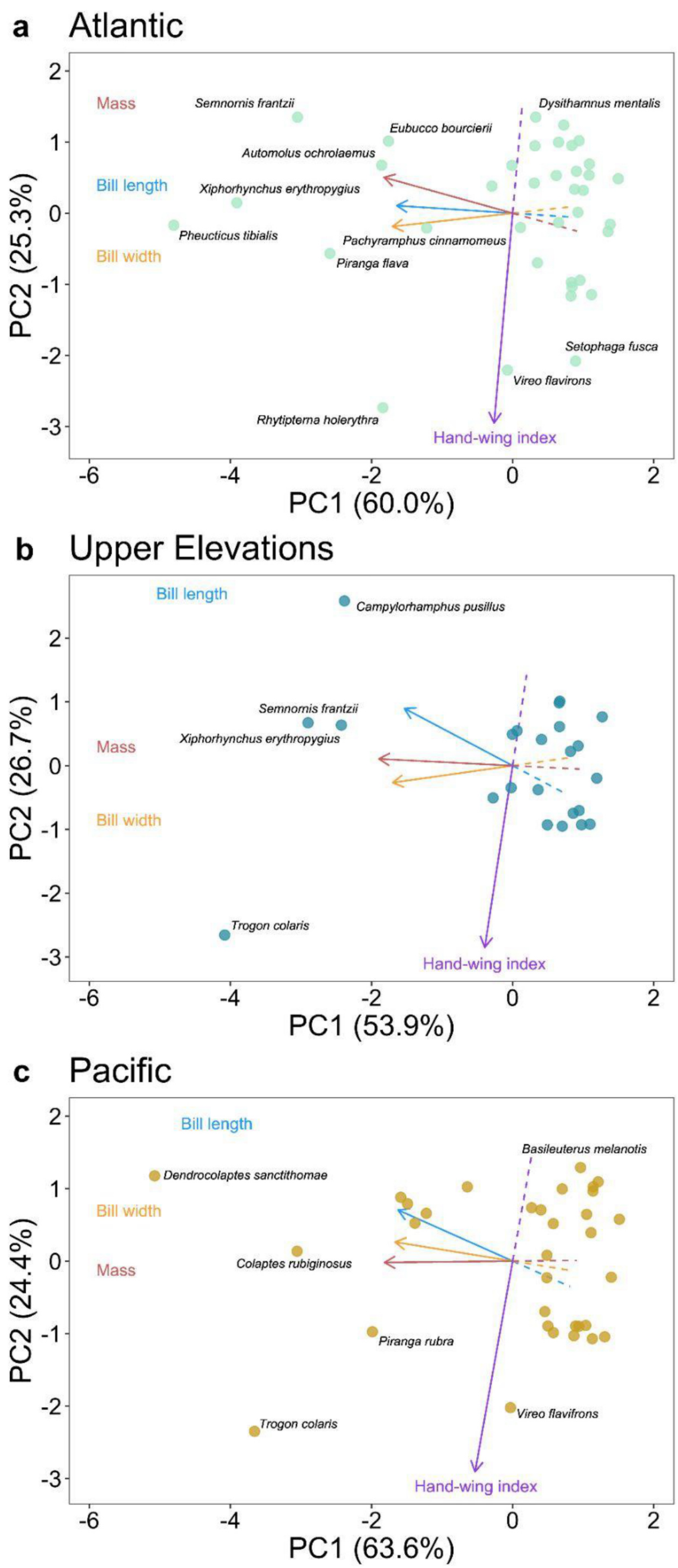

Figure 2. Principal component analyses of 4 morphological traits of species (dots) that composed the flocks of the Atlantic, Pacific and Upper Elevations zones in the Tilarán Cordillera, Costa Rica. The percentage of variation captured by PC1 and PC2 is indicated in parentheses. Solid arrows indicate the direction and scale of vectors representing each trait.

parts in the Pacific zone, mountain ranges with different rainfall patterns on opposing slopes may show differences in the species richness of their mixed-species flocks. Seasonal rainfall patterns result in varying availability of food such as arthropods and fruits, and this variation has been shown to affect composition and behavior of mixed-species flocks (Develey and Peres 2000, Mangini et al. 2022). The Atlantic slope of the Tilarán Cordillera receives more rainfall than the Pacific slope (Waylen et al. 1998) and high levels of rainfall are often correlated with high floral and avian diversity (Rompré et al. 2007).

Forest connectivity is also a factor that could influence the diversity of flocks encountered in this study. While both the Upper Elevations and Atlantic zones were situated in unfragmented forest, the flocks of the Pacific zone were observed in a smaller remnant of forest that is split from the continuous forest by a road and two small towns.

Functional diversity of flocks. The functional diversity indices used in this analysis provide an important perspective on how elevation affects the morphological diversity of birds participating in mixed-species flocks. Functional richness is an index that seeks to describe the amount of functional space filled by a community (Villéger et al. 2008). Thus, this index is influenced by species with traits at the extremes. The Pacific zone had the highest functional richness, followed by the Upper Elevation zone. The Pacific functional richness score was largely increased by two species: Collared Trogon *Trogon collaris* and Northern Barred-Woodcreeper *Dendrocolaptes sanctithomae.* Both species have a relatively wide bill and high body mass with differing extremes in hand-wing index —trait combinations which stretch the amount of functional space taken up by the species of this zone. Similarly, the Upper Elevation's functional richness score was largely increased by two species, each seen individually participating in separate flocks just once, the Collared Trogon *Trogon collaris* and the Brown-billed Scythebill *Campylorhamphus pusillus,* a large woodcreeper with a very long decurved bill. The Atlantic zone's flocks did not contain morphological outliers that were as distinct.

Functional evenness is a metric that captures the regularity and abundance of species plotted on a trait space for a given community (Mason et al. 2005). This metric varied substantially between the Upper Elevations and the lower zones because, although the Upper Elevations had two morphological outlier species, there were only two other species that fell outside a main concentration of species in the trait space of that zone. Both lower elevation zones featured species that effectively bridged the gap between the most morphologically distinct species and the main cluster.

Functional divergence explains how species and their abundance are distributed relative to the center of the trait space (Villéger et al. 2008). The three zones scored similarly on this index. All zones featured a similar pattern with small bodied, small billed species such as warblers (Parulidae) and vireos (Vireonidae) forming a main cluster, and larger species spreading away. The lack of even smaller species such as hummingbirds (Trochilidae) meant that these relatively abundant species could drive up the functional divergence metric along with birds on the other end of the trait spectrum. Species with morphological traits that fall in the middle of the spectrum like tanagers (Thraupidae) were also abundant members of flocks, but only in the Upper Elevations zone were they abundant enough to push the index under 0.5. While we believe that the functional diversity indices reported here capture more about community complexity than species richness, we acknowledge that they do not encapsulate the entire scope of each community's structure since we only focused on species that joined mixed flocks.

Morphologically extreme species. We also found interesting trends captured by examining the functional traits of the species involved in mixed-species flocks. All three zones featured morphological outliers that differed from the relatively small-bodied, small-billed birds that composed the majority of flocks. These morphological outliers account for much of the functional variation captured in this study, yet were never abundant members of flocks. Black-thighed Grosbeak *Pheucticus tibialis,* Rufous Mourner *Rhytipterna holerythra,* and Buff-throated Foliage-gleaner *Automolus ochrolaemus* were all unique to the Atlantic zone. Black-thighed Grosbeak *Pheucticus tibialis* is a restricted-range species, and potentially of conservation concern given the vast habitat loss in Central America (Ocampo-Peñuela et al. 2016), although it is only classified as Least Concern by the International Union for the Conservation of Nature (Birdlife International 2020). The Rufous Mourner is a cavity nester and, as such, is vulnerable to habitat loss and degradation (Snow et al. 2017, Van Der Hoek et al. 2017), with its populations declining at La Selva in Costa Rica over 40 years (1960–1999; Sigel et al. 2006). Both these species indicate that lower elevations of the Atlantic slope still support flocks used by species vulnerable to habitat loss and degradation.

The Brown-billed Scythebill was one of the few morphological outlier species that was seen in an Upper Elevations flock. This species sparsely inhabits an extensive geographic range (Birdlife International 2020). Records indicate that it is mostly found in large continuous montane forests (Marantz et al. 2020). As a result of its extremely small hand-wing ratio, it is unlikely to disperse effectively over large distances (Claramunt et al. 2022). Given this species' sensitivity to fragmentation and limited dispersal ability, there is danger of losing morphological, and by extension functional, diversity in these forests and their associated mixed-species flocks. The Brown-billed Scythebill is morphologically distinct and likely has no avian counterparts that can exploit the foraging niche it is able to access with its long decurved bill. With no other species to fulfill its ecological role, loss of this species is likely to have greater ecosystem functioning implications than a functionally redundant species (Cadotte et al. 2011).

The Collared Trogon *Trogon collaris* was a functional outlier in both the Pacific and Upper elevations zones likely due to its size, bill morphology and low dispersal ability. Though this trogon is widely distributed and not threatened (Birdlife International 2022), it expands the functional diversity for both of these zones. Large-bodied frugivores such as the Collared Trogon are vulnerable to habitat degradation (Kattan et al. 1994, Velho et al. 2012), and play important roles in ecosystem functioning through seed dispersal (Coates-Estrada and Estrada 1988).

The Pacific slope has fewer outlier species with the Northern Barred-Woodcreeper *Dendrocolaptes sanctithomae* being one of them; this species is thought to need large home ranges and is considered sensitive to forest disturbance (Marantz et al. 2020). All three studied zones had unique and specialized species, indicating that these forests are contributing to regional species richness and conserving important functional diversity within Costa Rican rainforests.

The species that were more common members of flocks in this study were often less functionally unique than the functional outliers highlighted above. Common Chlorospingus *Chlorospingus flavopectus* was the most abundant species observed in this study and was seen in all but one of the Upper Elevations flocks. This species is omnivorous and intermediate in bill and body size between many of the smaller invertivores, and larger functional outliers previously discussed. While this species may not increase the functional richness of flocks, its abundance and social nature seem to make it an important species for flock formation (Powell 1979, Valburg 1992, Slifkin 2019).

The morphological trait spaces generated in this study are a starting point for examining the breadth of foraging niches that flocks exploit, which can be complemented with data on foraging guild (Supplementary Material Table S1). Bill length and width for example, have long been seen as correlates with foraging options for frugivorous, granivorous, and invertivorous birds (Lederer 1975, Grant 1981, Moermond et al. 1986, Rojas et al. 2021, González-Varo et al. 2023). Yet it is hard to find a continuous variable that correlates with bird foraging strata and behavior —if it creeps up trunks or gleans invertebrates from leaves. Due to this challenge, we were unable to add a dimension to the trait space that captured these important foraging dynamics. However, our results showed a marked dominance of invertivorous birds on mixed-species flocks in all three zones. Frugivorous birds followed in number of species, reflecting a common trend of mixed-species flocks being composed of species dependent on seasonal and dynamic food sources (Develey and Peres 2000). With only one nectarivore species observed in our study it seems that these species do not regularly participate in mixed species flocks in the area, yet nectarivores are important in abundance and diversity in tropical forests (Newbold et al. 2014).

Conclusion. We found that the Pacific and Atlantic lower elevations of the Tilarán Cordillera had higher species richness than upper elevations, but differed in their patterns of functional richness and trophic niche composition. Our study provides an initial overview of how elevation and Atlantic/Pacific slope dynamics are correlated with differences in mixed-species flock composition. Larger sample sizes and a larger elevational gradient would allow to draw broader conclusions on how elevation affects flock diversity. This type of more comprehensive and detailed study would have important implications for increasing our knowledge of tropical community ecology and conservation, as climate change continues to shift the elevational ranges of avian species (Freeman et al. 2018, Neate-Clegg et al. 2021). Mixed-species flocks are important elements of Neotropical montane forests and provide a convenient system for understanding how abiotic changes will affect community composition in the future. While this study lacks the scope necessary for informing policy, examining existing abiotic gradients through the lens of functional diversity has the potential to predict and address particularly impactful biodiversity loss.

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