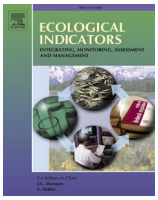
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Original Articles



Habitat niches of bird species along a recovery gradient in the Chocó tropical forest

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ABSTRACT

Conservation programs need improved tools to measure the recovery of animal diversity across restoration gradients. We used soundscapes and expert identifications of bird species to calculate niche position (i.e., mean of environmental conditions across all areas a species occupies) and niche breadth (i.e., the standard deviation of the species distribution) along a recovery gradient; from agriculture to early (up to 20 yrs) and late (up to 38 yrs) recovery, to old-growth forests. Our survey included 323 bird species and was conducted in 66 plots in the lowland Chocoan tropical rainforest in Ecuador where less than 11% of the forest remains intact, and large areas are currently undergoing regeneration post-abandonment. First, we validated our niche metrics by contrasting them against independent global categories of forest density dependency. We then explained the niche metrics of the bird species with different ecological traits, gathered from the literature, reflecting species-specific primary diet, morphology and distribution, and accounting for the phylogenetic relatedness of species. Finally, we explored the phylogenetic signal present in bird species' ecological traits and recovery niche metrics. Niche position and breadth across the recovery gradient closely followed global categories of forest density dependency. However, our approach provided a more fine-scaled sorting of bird species in forest plots categorized as late recovery and old-growth. Granivorous birds occupied niche positions in active cacao and pasture plots and were replaced by frugivorous birds in older regeneration plots. Along the recovery gradient, tail length and handwing index decreased with niche position, supporting previous observations that birds in old-growth forests are less mobile. Birds in old-growth forests had smaller global distribution ranges than birds in agricultural plots. Finally, the latitudinal distribution of birds in the study area averaged south of the equator, with birds in old-growth plots averaging latitudinal centroids in wet forests north of the equator, whereas birds in agriculture plots averaged latitudinal centroids further south of the country, towards the dry and open Tumbesian forest. Frugivores, invertivores and vertivores had broader niche breadths, but these decreased (marginally) with tail length. We suggest these recovery niche metrics as a potentially powerful tool for the rapid assessment of the recovery process, which might support conservation strategies such as biodiversity credits, compensation payments, and strategic land purchases. With the increasing availability of information-intensive models for bird species identification, such as deep learning artificial intelligence, our new niche metrics open the avenue for rapid assessment of tropical biodiversity and new conservation areas at larger scales.

1. Introduction

Forest restoration, one of the United Nations' decadal goals for 2030, is paramount for tropical areas under the current climate crisis (Curtis et al., 2018; Newbold et al., 2020). Birds are conspicuous elements of tropical forests and have been considered indicators of ecosystem integrity (Canterbury et al., 2000; Durant et al., 2009). Despite several studies documenting the effects of tropical forest restoration on bird occurrence (Chazdon, 2003; Karp et al., 2011), we still require cheap and reliable tools to measure how bird species sort themselves across recovery gradients. Since MacArthur's seminal work in the 1960s (MacArthur and MacArthur, 1961), niche theory predicts that forest structure determines bird distribution and abundance (Gregory and Gaston, 2000; Cano-Barbacil et al., 2023). Niche position, i.e., the mean of environmental conditions across all areas a species occupies, is a good indicator of the habitat preferred by individual species. Niche breadth, instead, is the range of conditions where a species is found. As opposed to specialist species, which are disproportionately more threatened with extinction (Şekercioğlu, 2011), generalist species are expected to have wider niche breadths, and previous research has linked generalist bird species to open and disturbed habitats (DeWalt et al., 2003; Mayhew et al., 2019). Here we propose that niche positions and breadths of species co-occurring in a community can indicate the progression achieved by a forest undergoing recovery (MacArthur and MacArthur, 1961; Casas et al., 2016).

Tropical forest conversion results in habitat loss for forest-adapted species (Curtis et al., 2018), reducing species richness and increasing biological homogenization across a wide range of taxonomic groups (Şekercioğlu, 2002; Dent and Wright, 2009; Villeger et al., 2010; Hidasi-Neto et al., 2012; Flynn et al., 2009; Solar et al., 2015). After human intervention, most land is abandoned, and nowadays regrowing secondary forests dominate tropical landscapes (Curtis et al., 2018, Fagua et al., 2019, Nunes et al., 2022). However, the mechanistic understanding of the recovery dynamics of abandoned land is limited, reducing our abilities to manage and conserve these lands (Joyce et al., 2024). Tropical birds play a dominant role in ecosystem restoration by dispersing tree seeds, of as much as 90 % of tropical woody plant species, into degraded lands where seed availability is a major barrier to forest recovery (Holl, 1999; Wijdeven and Kuzee, 2000; Şekercioğlu 2006a; 2012; Wenny et al., 2016; Wijedasa et al., 2020). Tropical birds also play roles in pollination and insect control (Marquis and Whelan, 1994; Van Bael et al., 2003; Şekercioğlu, 2006b), and birds consume as much as 2.5x more resources in logged forests than in old-growth forests (Malhi et al., 2022), shaping the energy pathways necessary for forest recovery. Therefore, developing metrics that assess links between bird community composition and conservation status may aid restoration programs (Alexandrino et al., 2016). Ideally, these metrics should be corrected for artifacts due to phylogenetic relatedness, as sister species are likely to present similar biology (Pagel, 1999).

Recently, chronosequences have become a general framework to explore the progression of forest recovery (Acevedo-Charry and Aide, 2019; Arnold et al., 2021). Using space-for-time substitutions, previous work on chronosequences has found positive effects of patch size, recovery time, and proximity to continuous old-growth forests (Durães et al., 2013; Ausprey et al., 2022) on bird occurrence. In a 20–60 yrs dry forest chronosequence in Costa Rica, bird species richness was highest in early recovery and decreased towards old-growth forests (Hilje et al., 2020). Unexpectedly, bird community composition did not change with recovery age in this dry forest. Moreover, the distribution of ecological traits generally responds to recovery time across chronosequences. For example, in a cloud forest in Peru, Ausprey et al. (2022) found early regeneration habitats with dense understories to host bird species with plant-based (flowers, fruit, and seeds) diets, broad elevational range distributions, and larger habitat breadths, when compared to old-growth forests. Across six tropical chronosequences, bird species in the early stages of recovery had broader latitudinal ranges but not larger distribution areas than birds in old-growth forests (Dunn and Romdal, 2005).

The Chocoan forest in north-western Ecuador is a global hotspot of lowland forest biodiversity (Orme et al., 2005; Devenish et al., 2009). In the last 40 years, the area has been under heavy pressure from the timber industry, large-scale agriculture, and human settlements utilizing the forest as their only economic income; and only a small amount of the old-growth forest (<11 %) is left (Fagua et al., 2019). Previously, we showed that the community composition of vocalizing birds (and other

vertebrates like mammals and amphibians), identified by experts from soundscapes, closely tracked a chronosequence of forest–agricultural habitat mosaic (from cacao plantations and pastures to old-growth forest) in the Ecuadorian Chocó (Müller et al., 2023). Here we expand the database of Müller et al. (2023) to deepen the understanding of birds as a fine-scale tool to indicate forest recovery and habitat characteristics in this important tropical region (Entling et al., 2007). We asked (1) how well bird community composition tracks the recovery gradient. We then (2) calculated niche position and breadth for more than 300 bird species (most of the birds regularly found in the Chocó lowlands) across the recovery gradient. Finally, we (3) aimed to understand which traits drive birds' niche positions and breadths across the gradient. Developing a tool to monitor restoration success is a priority in the current environmental crisis. Birds are well-suited for the task among all available taxa since their high functional trait diversity can reflect forest conditions. Furthermore, birds are sampled relatively easily, and bird ecological and morphological traits are well-documented (Şekercioğlu, 2012; Tobias et al., 2022).

2. Materials and methods

2.1. Study area

This study was conducted at the Reserva Río Canandé (0.5263 N, 79.2129 W) in Ecuador (Esmeraldas Province), as part of the Reassembly Research Unit (https://www.reassembly.de). Sampling was done during the dry season in October-November 2021 and 2022. The research unit design includes 66 plots, located between 128 and 615 m asl in elevation, each encompassing an area of 50 x 50 m, in the following habitat categories: 6 cacao plots, 9 pasture plots, 10 cacao early regeneration plots (≥1 and ≤ 20 yrs old), 6 cacao late regeneration plots (>21, and up to 38 yrs old), 11 pasture early regeneration plots, 7 pasture late

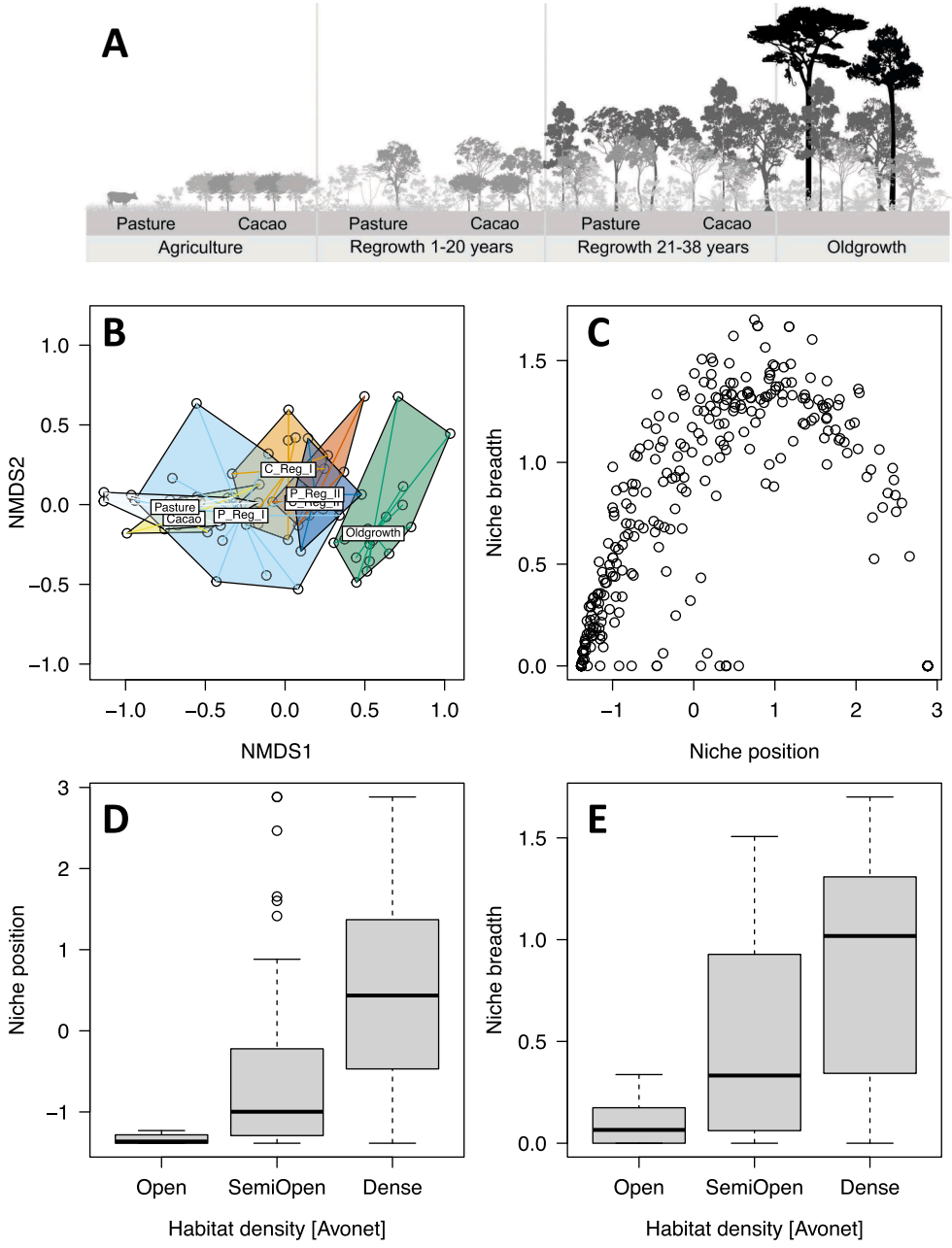


Fig. 1. **(A)** Schematic outline of the forest regeneration gradient in Canandé. **(B)** NMDS-Ordination of 323 bird species across 66 plots collected with soundscapes in our study site; Stress = 0.15. **(C)** Niche position vs. breadth. Validation of our niche position **(D)** and breadth **(E)** with global information on forest dependency.

regeneration plots, and 17 old-growth forest plots, without known age since last disturbance (Fig. 1A). Agricultural and recovery plots were near forest, and on average cacao and pasture plots were located ~ 58 m from the nearest forest edge within ~ 10.1 ha patches except for regenerating cacao plots which were in smaller 2.0 ± 0.4 ha cacao plantations. Old-growth plots averaged 388 m to the nearest forest edge and, within a 1 km radius, were surrounded by ~ 87 % forest, an 18 % increase compared to agricultural plots at ~ 69 %; please see Escobar et al. (2024) for further details. Agricultural areas, namely cacao plantations and pastures, were selected from active farms close to the study area and defined as zero years since regeneration. The regenerating areas are under natural succession with negligible human interference. In our study site, old-growth plots are structurally complex and have large hardwood trees. An expanded description of the study site and design of the chronosequence can be found in Escobar et al. (2024).

2.2. Sampling bird communities via sound recording

We characterized bird communities with sound recorders. In brief, we deployed one Bioacoustic Recorder (BAR-LT, Frontier Labs, Meanjin, Australia) with one omnidirectional microphone facing down at a height of ~ 1.70 m above ground in the center of each of the 66 plots. While species-specific detection probabilities in Canandé are unknown and beyond the scope of our work, we expect recorders to detect most species in tropical areas, with denser forest than their temperate counterparts (Winiarska et al., 2024), within a 100-m radius, with a decreasing detection function with forest density, distance and altitude. Average forested areas within 100-m radii of plot centers were about 10 % for agriculture plots, and the amount of primary forest increased with time since abandonment. The recorders were programmed to record 2 min every 15 min throughout the day for two weeks concurrently, with a sampling rate of 44.1 kHz. Each soundscape recording was digitized and labeled with the site name, location number, and date. Two of us (RG and JF) identified birds independently by listening to different sets of seven 2-minute spectrogram files in two days, for a total of 56 min per plot. These files were selected from 06:00 h, 06:15 h, 06:30 h, 06:45 h, 07:00 h, 07:15 h, 12:00 h, 12:15 h, 16:00 h, 16:15 h, 17:00 h, 17:15 h, 18:00 h and 18:15 h on days without heavy rain, covering the high activity phases of birds around dusk and dawn, as well as few minutes during the day to cover flock activities. Experts were blinded to the audio file's spatial location and habitat type. As a measure of abundance, we used the metric 'frequency per plot,' calculated by counting files containing a positive recording of a species. Further details can be found in Müller et al. (2023).

2.3. Bird traits and phylogeny

We compiled a list of bird traits reflecting primary diet, morphology, and distribution from the AVONET database (Tobias et al., 2022). We selected five **morphological** traits important for birds' foraging behavior, dispersal, and diet (Şekercioğlu, 2006, Ausprey et al., 2022). *Body Mass* was included as a species average, incorporating male and female measures. *Handwing Index* (HWI, 100*Kipp's distance/wing length, where Kipp's distance is the length from the tip of the first secondary feather to the tip of the longest primary and wing length) is Kipp's distance corrected for wing size. A high HWI indicates a bird species with elongated wings needed for long-distance flights (Sheard et al., 2020). *Beak Length* (Culmen) is the length from the tip of the beak to the base of the skull. *Tarsus Length* was measured from the posterior notch between the tibia and tarsus to the end of the last scale of acrotarsium (at the foot bend). Finally, *Tail Length* was measured as the distance between the tip of the longest rectrix and the point at which the two central rectrices protrude from the skin, typically measured using a ruler inserted between the two central rectrices. Longer tarsus and tails are characteristic of birds from open areas. Wing length was excluded because of collinearity with other traits. All morphological traits are highly correlated to bird mass; therefore, for analyses, we use the residuals of a linear model on mass [log(traitX) ~ log(body mass)]. We also included one trait representing the **primary diet**. For this, birds were sorted according to eight trophic niche categories: Granivore, Scavenger, Aquatic Predator, Nectarivore, Frugivore, Omnivore, Invertivore, Vertivore. Finally, we used three **distribution** traits reflecting birds' forest and global distribution. The first one, *Migration status*, has three categories: 1 = Sedentary; 2 = Partially migratory, i.e., when a minority of the population migrates long distances, or most of the population undergoes short-distance migration, nomadic movements, distinct altitudinal migration, etc.; and 3 = Migratory, i.e., when the majority of the population undertakes long-distance migration. The *centroid of the known latitudinal distribution* is the geometric center of the species range. Lastly, *Range Size*, on a logarithmic scale, is the total area of the mapped range (global distribution area) of the species. We extracted the phylogeny for our bird species using the recently published megaphylogeny for all birds (Fig. 2**)** in Jin and Qian, 2023.

2.4. Community-level analyses

All analyses were conducted in R Statistical Software (v. 4.2.2, R Core Team, 2023). We visualized community composition across the chronosequence using a non-metric multidimensional scaling method (NMDS; Clarke and Warwick, 2001) in *vegan* (Oksanen et al., 2017). The NMDS is an ordination technique that projects the multivariate representation of communities matrices to points in a low-dimensional space, such that the relative dissimilarity among communities is represented by the relative distances separating them. The Bray-Curtis distance between matrices constituted by species frequencies (as proxy for abundance) was used as a measure of similarity. We assume that an ordination accurately represents the dissimilarity among plots when the stress value after configuration optimization is < 0.2.

2.5. Niche analyses

To quantify habitat preferences and distributions of bird species' in Canandé across the restoration gradient, we fitted a Canonical Correspondence Analysis (CCA) with plot age as an independent variable. For this analysis, we set the age of old-growth forest plots at 50 yrs. This number follows the visual progression of bird community composition in our NMDS analyses (see below), and it is within previous calculations of the time needed to recover insect communities (30 yrs, Hönle et al., 2022), and plant diversity (55yrs) and biomass (100 yrs, Escobar et al., 2024) in this forest. For each bird species, we calculated niche position along the recovery gradient as the score of the first axis of the CCA (Ter Braack and Šmilauer, 2002). Then, we calculated niche breadth as the standard deviation of species distribution using the function *tolerance* (Ter Braack and Šmilauer, 2002), as implemented in *vegan*. Species recorded in only one plot (n = 43) had a niche breadth value of zero, and were not included in further analyses. Niche metrics of bird species across the gradient were validated by plotting them against the **Habitat Density Index (HDI)** for birds in AVONET. Briefly, the index divides species into those that inhabit i) dense habitats: bird species primarily living in the lower or middle storey of the forest or dense thickets and dense shrubland, ii) semi-open habitats: bird species primarily living in open shrubland, scattered bushes, parkland, low dry or deciduous forest, and thorn forest, and iii) open habitats: bird species primarily living in deserts, grassland, open water, low shrubs, rocky habitats, seashores, cities, or on top of the forest canopy (Tobias et al., 2022). HDI therefore provides an independent proxy of the recovery gradient in our study site.

We modeled niche position and breadth against ecological traits using two Generalized Least Squares models (gls, Zuur et al., 2009) in the *nlme* package (Pinheiro et al., 2023). However, in gls analysis, data points (individual bird species) might not be independent (Felsenstein, 1985; Garland et al., 1992), which inflates the degrees of freedom. Therefore, we corrected the phylogenetic relatedness of bird species by

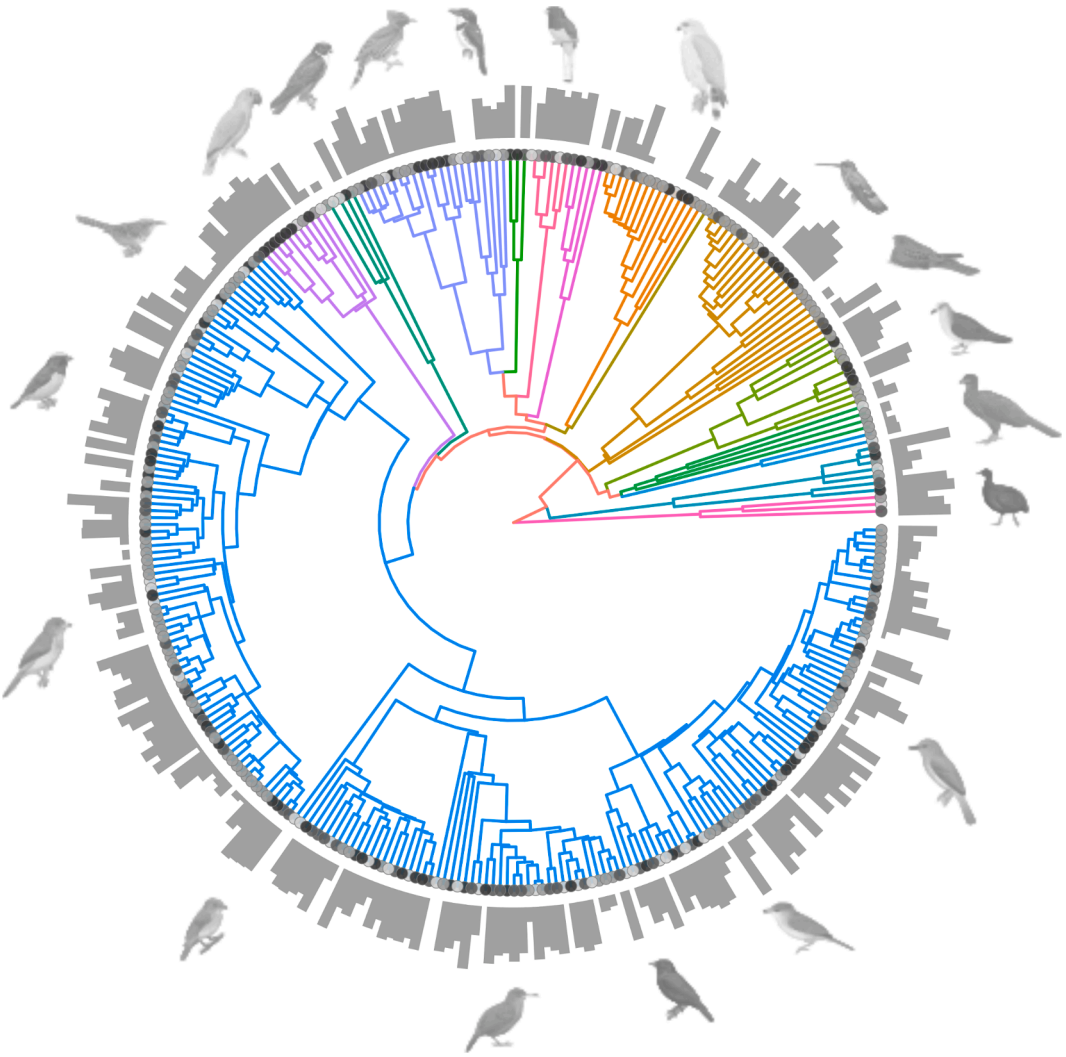


Fig. 2. A phylogeny of 323 bird species included in this study. Colors depict different bird Orders. Dots on the tips of the tree represent the niche position on a grey scale (darker colors towards old-growth forests). Bars are measures of niche breadth (from narrow to wide).

including a correlation structure in the GLS. The correlation structure was derived from the phylogenetic tree of birds using Pagel's λ (Pagel, 1999). Pagel's λ measures the phylogenetic dependence of trait data under a Brownian model of evolution (Pagel, 1999). Finally, we explored the phylogenetic signal of trait and niche measures using Pagel's λ. In this analysis, values closer to 0 indicate phylogenetic independence in trait values and values closer to 1 indicate trait values as expected by Brownian motion.

3. Results

In our soundscapes, we found 323 bird species from 50 families, i.e., about 95 % of known bird species from the study area. A list of species, traits and habitat characteristics and plot information is included in Supplementary Tables S1-3.

3.1. Community-level analyses

According to the NMDS plot, bird communities in different recovery categories clustered together, and organized along the recovery gradient (Fig. 1B). Compared to pasture plots, succession trajectories were faster for cacao plots.

3.2. Niche position and breadth across the recovery gradient

We extracted niche position for all 323 species and niche breadth for 280 species, e.g., those that occurred in more than one plot. Niche position followed the recovery gradient from agriculture (negative values, left on the X axis of the CCA plot) to old-growth forests (positive values, right on the X axis of the plot) (Fig. 1C). When plotting against niche position, niche breadth presented a concave shape and was highest in intermediate levels of niche position (Fig. 1C). Recovery niche position followed well the HDI for birds in AVONET (Fig. 1D). Instead, niche breadth increased from birds inhabiting open forests to birds inhabiting dense forests, according to the HDI (Fig. 1E).

3.3. Traits

Recovery niche position was not affected by bird frequency or the number of plots where species occurred. Similarly, niche breadth was not affected by bird frequency although, as expected, it increased with the number of plots where species occurred (Table 1). Our phylogenetically corrected generalized least squares (gls) analysis found niche position and breadth, in part, explained by ecological traits (Table 1). Niche positions indicative of agricultural habitats (found in the left, negative, margin of the ordination, Fig. 1) were dominated by granivorous birds (**Supplementary** Figure 1). In contrast, other feeding

Table 1
Phylogenetically corrected generalized least squares (gls) models with recovery niche position (323 spp.) and breadth (280 spp.) of bird species against diet, morphology and distribution variables.

	Niche Position			Niche Breadth			Pagel's λ
	Coef.	t		Coef.	t		
(Intercept)	2.05	2.55	*	1.44	4.73	***	
Frequency	−0.004	−1.44		−0.002	−1.90	^	
Occurrence	−0.004	−0.86		0.011	5.43	***	
Diet							
Nectarivore	1.017	1.39		0.036	0.14		
Frugivore	1.021	2.87	**	0.351	2.43	*	
Omnivore	0.771	2.04	*	0.244	1.60		
Invertivore	0.917	2.56	*	0.296	2.03	*	
Vertivore	1.128	1.97	*	0.597	2.54	*	
Morphology							
Body Mass	0.007	0.08		−0.041	−1.27		0.98
Beak Length	0.183	0.85		0.130	1.65		0.99
Tarsus Length	−0.494	−1.06		−0.255	−1.43		0.97
Tail Length	−0.489	−2.08	*	−0.166	−1.80	^	0.99
HandWing Index	−0.022	−1.88	^	−0.001	−0.26		0.97
Habitat							
Migration	−0.311	−1.62		−0.143	−1.83	^	0.65
Latitudinal Centroid	0.016	2.18	*	0.001	0.45		0.7
Range Size	−0.119	−2.83	***	−0.049	−2.84		0.15
Succession Niche Breadth							0.34
Succession Niche Position							0.25

p-value:^= marginally significant, * < 0.05, ** < 0.01, *** < 0.001.
Diet categories Aquatic Predator and Scavenger were included in the model but removed from table due to low sample size. p- and t-values are presented relative to the granivorous birds. For beak, tail and tarsus length, the analysis was done on residuals from a regresion with body mass. We also present a summary of the phylogenetic signal, measured by Pagel's λ, of niche position and breadth, and a suite of ecological traits included in this study. Values closer to 0 indicate phylogenetic independence in trait values and values closer to 1 indicate trait values as expected by Brownian motion.

strategies, except nectarivores, were more common with increasing niche positions (toward the right axis of the ordination in Fig. 1, indicative of old-growth forests). Morphologically, birds with short tails and low handwing index tended towards positive niche positions. Finally, birds with lower latitudinal centroids (those species whose distributions are closer to the equator) and smaller global distribution ranges were associated positively with niche position. Frugivores, invertivores and vertivores had broader niche breadths, as well as species with shorter tails (Table 1). Niche metrics presented low phylogenetic signal (low niche conservatism,) as opposed to ecological traits which presented high phylogenetic signal (Table 1).

4. Discussion

4.1. Why do bird communities follow the forest recovery gradient so closely

Assessing bird communities with autonomous soundscape samples, expert identification, and simple recovery niche measures allowed us to determine the recovery success of functionally diverse taxa in a tropical lowland Chocó Forest in Ecuador. Our recovery chronosequence, including two common land uses (cacao plantations and pastures) and old-growth forests with complex forest structure, provided ample opportunities for bird species to sort themselves by their ecological niches (DeWalt et al., 2003; Zahawi et al., 2015). As expected, bird communities were good indicators of the gradient (Müller et al., 2023) and sorted distinctly well (i.e., continuously) into habitat niches across the chronosequence. Our measures of niche breadth were narrower towards both ends of the axis, e.g., open habitats and old-growth forests. However, when we sorted birds according to the HDI, birds in dense forests had broader niche breadths, meaning that forest birds can use multiple stages of the recovery chronosequence but also that birds inhabiting open areas are restricted in their habitat use. Niche measures extracted from the survey were good fits for independent categories of the HDI. Still, they indicated forest use (especially for those birds in dense forests) at a much finer scale, refining the indicators in BirdLife International (2023). This was unexpected and suggested a larger conservation value of birds occurring in closed habitats and most likely dispersing seeds from old-growth plants into recovering areas. Nonetheless, how well forest bird species can fly into open areas at our study site remains an open question.

4.2. Traits across the recovery gradient

Different authors have addressed how specific avian traits are favored in the different habitats along a recovery gradient (Şekercioğlu, 2006; Reid et al., 2008). We found that active agricultural habitats benefit finch-like granivorous birds feeding on grass seeds. This is similar to the results from Şekercioğlu (2012) in his worldwide review and Barlow et al. (2006) for terrestrial granivores in Amazonian forests. Reid et al. (2012) found granivore abundance negatively correlated with canopy cover in Costa Rica. In contrast, in our study, frugivores were more often found in old-growth forests, in line with Şekercioğlu (2012) and Bregman et al. (2016). This is also in accordance with previous research showing that the quality and diversity of resources for frugivores are higher in mature forests (Wenny et al., 2016; Pessoa et al., 2017a; Pessoa et al., 2017b). Bird species in old-growth forests had longer beaks and shorter tails, suggesting a more specialized diet on resources that are mainly found in mature forests (Pessoa et al., 2017a; Pessoa et al., 2017b; Sherry et al., 2020). Low hand wing index (rounded wings) indicated birds inhabiting old-growth forests have reduced dispersal ability and are more sedentary (Bregman et al., 2016; Sheard et al., 2020). We also found that, in our study site, birds in old-growth forests have distributions centered more towards the Northern Hemisphere, but birds from open habitats are centered towards the Southern Hemisphere, which is in accordance with the distribution of lowland rainforests and dry forests in Ecuador (Banda et al., 2016). Birds in old-growth forests have smaller global distribution ranges, typical for endemic tropical forest birds, and are thereby more threatened by forest loss, whereas open-forest birds can survive in the natural dry forest and in agriculture (Karp et al., 2018). Importantly, our gls analysis ensured that the relationship between recovery niche metrics and traits was independent from the phylogenetic history of species, a pattern similar to that found for British birds by Gregory and Gaston (2000).

Forest recovery niche position and breadth showed a low phylogenetic signal. Other studies on birds (Brändle et al., 2002, Böhning-Gaese and Oberrath, 1999), spiders (Entling et al., 2007), and plants (Prinzing et al., 2001) have also found low phylogenetic signal in niche measures. This suggests that forest recovery niches are flexible, and that adaptation to forests with closed canopies (such as those found in our study site in late succession) evolved independently many times in tropical birds.

4.3. Caveats

Recording and analyzing environmental audio recordings have become common for monitoring birds (Sethi et al., 2022; De Araújo et al., 2023; Müller et al., 2023) as well as other taxa (Müller et al., 2023, Do Nascimento et al., 2024). This methodology has several advantages over other approaches, such as 1) reducing costs by not requiring experts to be present in the field, 2) simultaneous standardized sampling of a

potentially large area. However, our approach comes with a few caveats. First, there are challenges associated with bird sampling, namely the high diversity and strong temporal diurnal niches (e.g., some woodcreepers have a very narrow temporal niche of vocalization) of birds in tropical forests. Even though recordings allow us to cover different times of the day in contrast to traditional observations where a plot is visited once per day at a specific time, we still cannot sufficiently detect species with extremely narrow dial or temporal niches. A second bias lies in the distance to the source and canopy openness when using microphones, with birds in open habitats and closer to the microphone being more easily detected. While we acknowledge that our dataset likely incorporated this bias (e.g., agricultural plots were embedded in a forested matrix, and old-growth plots were usually far from agricultural land, Escobar et al., 2024), we found compartmentalization of birds across the gradient and reduced variability in niche breadth in birds occurring in open habitats, suggesting that habitat type, not distance, determined the likelihood of finding a species in a recording. In particular, the niche breadths of birds recorded in more open habitats (lower recovery niche positions) were reduced. However, niche measures for birds inhabiting open areas in Canandé likely do not represent the whole spectrum of habitats these species use, as some species might occur in additional habitats such as settlements or dry areas common in the coastal areas in southern Ecuador, as suggested by Hatfield et al. (2018). By the same token, our measures were reduced in species inhabiting old-growth forests since our old-growth forests represent the end of the recovery gradient. Third, recovery in Canandé was faster than that reported from other ecosystems, and it was likely facilitated by low-intensity farming in agricultural sites and their proximity to the matrix of old-growth forest remnants. Our chronosequence comprises small and relatively young disturbance events embedded in a landscape of old-growth forest. To date, it is difficult to disentangle the role of the matrix in shaping the patterns in our chronosequence. Still, studies looking at the recovery of forest plots embedded in old-growth forests usually find important effects of the matrix in regenerating areas (Mayhew et al., 2019).

4.4. Conclusions and management implications

There is a broader recognition that conservation programs need quantitative data for the selection and/or recognition of forests most in need of conservation (Brown et al., 2013). In the past, these efforts concentrated on monitoring keystone species or populations of endangered species (Mills et al., 1993). These approaches are difficult to implement in species-rich ecosystems of high conservation value, like tropical forests, where they are most needed. Moreover, poor accessibility and maintenance costs make conservation efforts little scalable in space and time. Currently, biodiversity credits (biocredits) and strategic land purchases are increasing as alternatives to managing land and its biodiversity. These initiatives differ from carbon credit schemes, which are more interested in offsets of carbon emissions by industries. Biocredits are units of biodiversity that can be bought by interested parties. Biocredits bring funds to local managers, custodians, and monitoring programs created for their restoration or preservation (Ducros and Steele, 2022). Together with other strategies, such as strategic land purchases and compensation payments, they emphasize the need for informed decision-making in the selection of land purchases for conservation, as well as for evaluating and adapting existing management strategies (Chazdon et al., 2009; Hardy et al., 2018). Different ways have been proposed to quantify and monitor biodiversity within conservation schemes. Information-intensive and high-tech approaches (including, but not limited to soundscape recordings identified by deep learning artificial intelligence models, metabarcoding and eDNA, social network platforms such as iNaturalist, etc.) have been proposed to automatize or speed up the survey of specific species (Sethi et al., 2022; De Araújo et al., 2023; Basset et al., 2023) or whole assemblages (Müller et al., 2023). Here, we advance the development of metrics that use field-based data and are less prone to biases. Niche metrics and bird communities obtained with semi-automated audio recordings can be valuable to stakeholders and decision-makers and can aid programs interested in quantifying forest integrity and measuring restoration success. For example, local managers can sample birds along gradients and use our niche position metrics to calculate progress in recovery. Similarly, the niche metrics presented here can help managers to sort forest patches of different conservation value, e.g., when assigning age categories to forests across the landscape (Barlow et al., 2007a, Barlow et al., 2007b) of unknown history, and thus complement conservation efforts based on biodiversity credits, compensation payments, and strategic land purchases (Mills et al., 1993, Brown et al., 2013, Ducros and Steele, 2022). Furthermore, with the increasing availability of deep learning AI models for bird species identification, our new niche metrics open the avenue for rapid assessment of tropical biodiversity and new conservation areas at larger scales (Sethi et al., 2022).

CRediT authorship contribution statement

Ana Falconí-López: Writing – original draft, Investigation. **Oliver Mitesser:** Writing – review & editing, Investigation, Formal analysis. **H. Martin Schaefer:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Nico Blüthgen:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Annika Busse:** Writing – review & editing, Investigation, Formal analysis. **Heike Feldhaar:** Writing – review & editing, Project administration, Funding acquisition. **Juan Freile:** Writing – review & editing, Data curation. **Rudy Gelis:** Writing – review & editing, Data curation. **Nina Grella:** Writing – review & editing, Investigation. **Christoph Heibl:** Writing – review & editing, Investigation, Formal analysis. **Mareike Kortmann:** Writing – review & editing, Visualization, Investigation, Formal analysis. **Felicity L. Newell:** Writing – review & editing, Investigation. **Dominik Rabl:** Writing – review & editing, Investigation, Formal analysis. **Matthias Schleuning:** Writing – review & editing, Investigation, Funding acquisition, Data curation. **Sebastian Seibold:** Writing – review & editing, Investigation, Formal analysis. **Çağan H. Şekercioğlu:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Boris A. Tinoco:** Writing – review & editing, Writing – original draft, Investigation. **Constance J. Tremlett:** Writing – review & editing, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **Jörg Müller:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **David A. Donoso:** Writing – review & editing, Project administration, Investigation, Formal analysis, Conceptualization, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data is available as supplementary materials

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Appendix A. Supplementary data

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