Landsc Ecol (2026) 41:60
https://doi.org/10.1007/s10980-025-02225-7

RESEARCH ARTICLE

Biotic homogenization and differentiation effects of fragmentation vary with spatial scale for multiple levels of understory bird diversity in northwest Ecuador

Mike Ellis · Luis Carrasco · Fernando Castillo · Juan Rivero de Aguilar · Euan Ferguson · Carmen Azahara Prieto Gil · Elisa Bonaccorso · Jordan Karubian

Received: 13 July 2024 / Accepted: 16 September 2025 / Published online: 4 March 2026
© The Author(s) 2026

Abstract

Context Biotic homogenization and differentiation are two possible outcomes of tropical forest fragmentation with ramifications for biodiversity conservation. The extent of either outcome may vary depending on spatial scale and heterogeneity of climate and habitats, but these relationships remain poorly understood for taxonomic, functional, and phylogenetic metrics of diversity.

Objectives Our goal was to determine the extent to which fragmentation is associated with biotic homogenization and/or differentiation across multiple levels of diversity at landscape versus regional scales.

Methods We examined diversity and similarity of understory bird communities in northwestern Ecuador, an ecoregion characterized by climatic variation, habitat loss and fragmentation, and high levels of biodiversity and endemism.

Results At the landscape level, fragmentation was associated with biotic differentiation of understory bird communities between formerly contiguous intact and fragmented humid forests. At the regional scale, we found taxonomic homogenization across climate zones and forest types: the bird community in the fragmented humid landscape was as similar to the nearby intact humid forest community (mean distance = 3.1 km) as it was to that of drier, seasonal intact forest 60 km away. Patterns of landscape-level differentiation and regional homogenization were present but substantially less pronounced for functional

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-025-02225-7.

M. Ellis (✉) · J. Karubian
Department of Ecology & Evolutionary Biology, Tulane University, 400 Boggs Building, New Orleans, LA 70118, USA
e-mail: msellis10@gmail.com

M. Ellis · E. Ferguson · C. A. P. Gil
Third Millennium Alliance, Quito, Ecuador

L. Carrasco · F. Castillo · J. Karubian
Fundación para la Conservación de los Andes Tropicales, Quito, Ecuador

J. R. de Aguilar
Centro Internacional Cabo de Hornos (CHIC), Puerto Williams, Chile

J. R. de Aguilar
Centro Universitario UMAG, Cabo de Hornos, Chile

E. Bonaccorso
Laboratorio de Biología Evolutiva, Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito, Quito, Ecuador

E. Bonaccorso
Centro de Investigación de la Biodiversidad y Cambio Climático (BIOCAMB), Universidad Tecnológica Indoamérica, Quito, Ecuador

and phylogenetic diversity, indicating functional and phylogenetic redundancy despite turnover and abundance shifts among dominant species.
Conclusions Our results suggest fragmentation of tropical forest (associated with homogenization between humid and drier/seasonal forest) may have similar impacts on communities as climate drying, and while many species may be lost, fragmented communities may retain some functional and evolutionary resilience against environmental stressors.

Keywords Biotic homogenization · Biotic differentiation · Phylogenetic diversity · Functional diversity · Chocó · Tumbes

Introduction

Human-caused habitat loss and fragmentation of natural ecosystems is reshaping biotic communities globally. These changes are particularly impactful at lower latitudes because of the tropics' outsized contribution to biodiversity (Gardner et al. 2009; Gibson et al. 2011). Although the effects of fragmentation on tropical forests vary and may at times increase or have no effect on local α-diversity, it is considered a principal driver of biodiversity loss associated with changes in community composition and β-diversity (Fletcher et al. 2018; Sherry 2021). More specifically, fragmentation can lead to both biotic homogenization, where communities become increasingly similarity over time, or its inverse, biotic differentiation (McKinney and Lockwood 1999; Olden and Rooney 2006). Biotic homogenization and differentiation are thought to be context-dependent (e.g., landscape connectivity levels, regional species pool size, species dispersal traits, type of landcover alteration) and scale-dependent (Arroyo-Rodríguez et al. 2013; Socolar et al. 2016; Rolls et al. 2023). As a result, biotic homogenization and differentiation may not be mutually exclusive across space or time (Socolar et al. 2016; Kramer et al. 2023), and different patterns may emerge for different taxa in different regions (Rolls et al. 2023). Improving our understanding of the ways in which fragmentation alters naturally occurring patterns of β-diversity to create homogenized and/or differentiated communities in the tropics has important implications for conservation and our understanding of basic ecological and evolutionary processes.

Historically, biotic homogenization and fragmentation studies have measured impacts on faunal diversity in terms of species lost and gained, i.e., changes in taxonomic diversity (TD). However, such extirpations and colonizations, with or without turnover, are nonrandom in relation to species traits and evolutionary lineages, meaning homogenization and differentiation may also act on levels of functional (FD) and phylogenetic diversity (PD) (Pielou 1975; Chao et al. 2014). Patterns and eco-evolutionary ramifications of biotic homogenization versus differentiation on FD and PD are less well understood but are important to address because changes in α and β TD may not occur in parallel with changes in FD and PD (Edie et al. 2018; Morelli et al. 2018; Dehling and Dehling 2023). Furthermore, homogenization of FD could cause shifts in ecosystem function and reduced functional redundancy, network robustness, and resilience to environmental stressors (Olden et al. 2004; Biggs et al. 2020; Fricke et al. 2022; Lamperty and Brosi 2022). Homogenization of PD, through extirpation, colonization, replacement, or hybridization of genetically distinct taxa or populations, may erase endemic evolutionary histories and reduce adaptability to environmental stressors that vary in space and time (Olden et al. 2004; Emer et al. 2019). While FD and PD differentiation from fragmentation of tropical forests could lead to greater functional and genetic variability among patches or landscapes, these effects may be relatively short-lived and could precede biotic homogenization, e.g., in cases where biotic differentiation is tied to diminished connectivity among isolated populations with precarious long-term viability (Arroyo-Rodríguez et al. 2013).

Just as patterns of biotic homogenization and differentiation may differ across levels of diversity, they may also differ across spatial scales (Morante-Filho et al. 2016; Soares et al. 2019; Dehling and Dehling 2023). However, the role of scale in shaping homogenizing or differentiating effects of fragmentation is better understood for some taxa than others. These patterns are best documented for plants, and they suggest homogenization is likely across larger areas while differentiation is more likely at smaller scales, although exceptions abound (Arroyo-Rodríguez et al. 2013; Kramer et al. 2023; Rolls et al. 2023). Responses of taxonomic, functional, and phylogenetic β-diversity to fragmentation are less understood for tropical fauna, but birds have been a favored system

for studying TD and FD responses at multiple spatial scales. While birds are known for their motility, the temporal stability and spatial heterogeneity of tropical habitats over many millennia, among other drivers (Pontarp et al. 2019; Sherry et al. 2020), have allowed many bird species occupying forest understories to adapt to narrow environmental niches (Polato et al. 2018; Pontarp et al. 2019; Sherry 2023) and develop reduced dispersal capacity (Moore et al. 2008; Sheard et al. 2020). This combination of reduced motility and increased specialization may make understory tropical bird communities particularly susceptible to both biotic homogenization and differentiation across multiple scales following fragmentation, e.g., by reducing dispersal of forest interior specialists among fragments or facilitating colonization by species associated with drier, more seasonal, or more open habitats (Sherry 2021, 2023).

Traditionally, avian α- and β-diversity responses to tropical fragmentation have been studied at three spatial scales, which we refer to for the remainder of this paper: locally (e.g., within an individual forest fragment), within landscapes (i.e., among forest fragments or among sites from a larger intact forested landscape), or between landscapes (e.g., between landscapes with different levels of fragmentation or between a fragmented landscape and a nearby intact forested landscape with historically similar environmental conditions). At the local level (i.e., within an individual forest fragment), stochasticity and fragment size/shape may contribute to biotic homogenization of bird communities among locations within that fragment relative to those locations' pre-fragmented beta diversity. (DeSouza et al. 2001; Brown et al. 2004; Stratford and Robinson 2005; Visco et al. 2015; Morante-Filho et al. 2016). However, at the within-landscape level, biotic differentiation appears to be more likely among fragments than within intact forest, in part because of mosaic composition factors, area and edge effects, and limited dispersal/colonization across non-forest matrix, among other drivers (Graham and Blake 2001; Laurance et al. 2011a; Morante-Filho et al. 2016; Harrison et al. 2018; Hatfield et al. 2020; Bonfim et al. 2021). Between fragmented and intact landscapes, studies have also pointed to increased differentiation between bird communities, which is most often associated with replacement of specialist species by generalist species (Stratford and Stouffer 1999; Morante-Filho et al. 2016; dos Anjos et al. 2019; Stouffer 2020). In contrast to within- and between-landscape scale studies, regional-level fragmentation studies are conspicuously rare for tropical birds and other fauna, as are studies that simultaneously consider between-landscape and regional patterns. Here, we define "regional-level" studies as those encompassing multiple landscapes *across environmental envelopes or climate gradients within an ecoregion*, and we consider these distinct from traditional "landscape-level" studies comparing, say, intact forested landscapes with fragmented landscapes subject to the same environmental/climatic conditions.

We emphasize this distinction of regional versus landscape scales because within- and between-landscape fragmentation studies have typically focused on before-after comparisons of fragmented forest or juxtaposed intact forested landscapes with formerly contiguous fragments nearby (e.g., Durães et al. 2013; dos Anjos et al. 2019; Stouffer 2020). However, patterns of β diversity across natural landscapes within an ecoregion are, to a large degree, maintained by regional-level variation in climate and habitat heterogeneity (Veech and Crist 2007; Dobrovolski et al. 2012; Astorga et al. 2014; Socolar et al. 2016; Rolls et al. 2023), which may not be captured at the scale of traditional between-landscape studies (Socolar et al. 2016).

Multi-scale studies simultaneously comparing between-landscape and regional-level effects of fragmentation on diversity are therefore uniquely suited to improve our understanding of and ability to predict patterns of biotic homogenization and differentiation (Socolar et al. 2016). The propensity of anthropogenic impacts to alter naturally occurring patterns of habitat and climate heterogeneity between landscapes and across entire regions also suggests these are important scales at which to test for evidence of fragmentation-induced biotic homogenization and differentiation (Gardner et al. 2009; Karp et al. 2012). Recent research on amphibians and birds in agricultural and urban landscapes, for example, shows anthropogenic landscape change may erase β-diversity patterns driven by regional heterogeneity in climate and habitat (Vallejos et al. 2016; Karp et al. 2018; Liang et al. 2019; Dehling and Dehling 2023). To date, however, it appears most studies on regional-scale impacts of fragmentation on avian communities have focused on population and metapopulation

dynamics of temperate species rather than β-diversity (e.g., Rolstad 1991; Boulinier et al. 2001; Stephens et al. 2004). To the best of our knowledge, no study has yet sought to compare bird communities in tropical forest fragments with those from heterogeneous intact forest types across a wider region to determine how fragmentation shapes patterns of taxonomic, functional, and phylogenetic homogenization and differentiation at both landscape and regional scales.

Here we use mist netting surveys in NW Ecuador to characterize understory bird communities in three broad forest types within the region: humid forest fragments, adjacent intact humid forest, and intact semi-humid seasonal forest located 60 km away (Table 1). Our goals were to (1) estimate and compare α TD, FD, and PD among the three forest types; (2) document the extent of biotic homogenization and differentiation of β TD, FD, and PD at between-landscape and regional levels; and (3) describe differences in the relationships between community composition and understory bird habitat measures. We hypothesized that increased environmental heterogeneity associated with fragmentation of humid forests, combined with stochasticity, would lead to greater α-diversity within the fragmented landscape as well as biotic differentiation at the between-landscape scale comparing fragmented and intact humid forest bird communities. Because fragmentation may directly or indirectly make humid forest less suitable for species adapted to cooler, darker, wetter conditions and, conversely, more suitable for species adapted to warmer, brighter, drier conditions (Stratford and Stouffer 1999; Stratford and Robinson 2005; Sherry 2021), we also hypothesized that fragmentation of humid forest would lead to biotic homogenization at the regional scale by driving bird communities in humid forest fragments to more closely resemble those in semi-humid intact forest. Given that tropical forest bird communities are known for substantial levels of functional and phylogenetic redundancy (Sayer et al. 2017; Monge-González et al. 2021; Monge et al. 2023; Calsavara et al. 2023), we predicted that hypothesized changes in α and β diversity at all scales would be lower for FD and PD than for changes seen in TD.

Methods

Study area

We sampled birds and their habitats across $n = 41$ total sites in three distinct forest types in northwestern Ecuador: intact humid forest, fragmented humid forest, and intact semi-humid forest (Table 1). Deforestation is ubiquitous throughout the region, and large tracts of forest (i.e., our intact sites) are now restricted to higher elevations (300–800 m.a.s.l.) with steep slopes. Because all forest in the region has experienced anthropogenic alteration, we use the term "intact" loosely to describe large tracts of continuous forest (> 4000 ha) in contrast with our sampled fragments (< 50 ha). All intact humid sites were within the Bilsa Biological Reserve (Bilsa) on the eastern side of Reserva Ecológica Mache-Chindul (REMACH), and all intact semi-humid sites were in the Jama-Coaque Reserve 60 km south-south-west of Bilsa on the same coastal cordillera mountain range. All humid fragment sites were formerly contiguous with Bilsa ≤ 60 years ago and are just within or just outside the boundaries of REMACH (Fig. 1). Most of our sampling sites within Bilsa and the fragments were previously sampled between 2004 and 2011 by Durães et al. (2013), who provide additional information on the study area. While all

Table 1 Forest type descriptions and sampling effort in terms of sites, sampling periods (i.e. three consecutive days of mist-netting at the same site) and total net hours

Forest	Intactness	Moisture	Lat, Long	Mean elevation (min–max)	Sites	Sampling periods	Total net hours
Bilsa	Intact	Humid	0.342600, − 79.729115	523 (390–638)	16	18	2980
Jama-Coaque	Intact	Semi-Humid	− 0.116902, − 80.120859	491 (365–664)	8	23	3455
Fragments	Fragmented	Humid	0.365477, − 79.678381	482 (365–627)	17	21	3140

All elevations in meters above sea level; coordinates provided for each forest are centroids of sampled sites

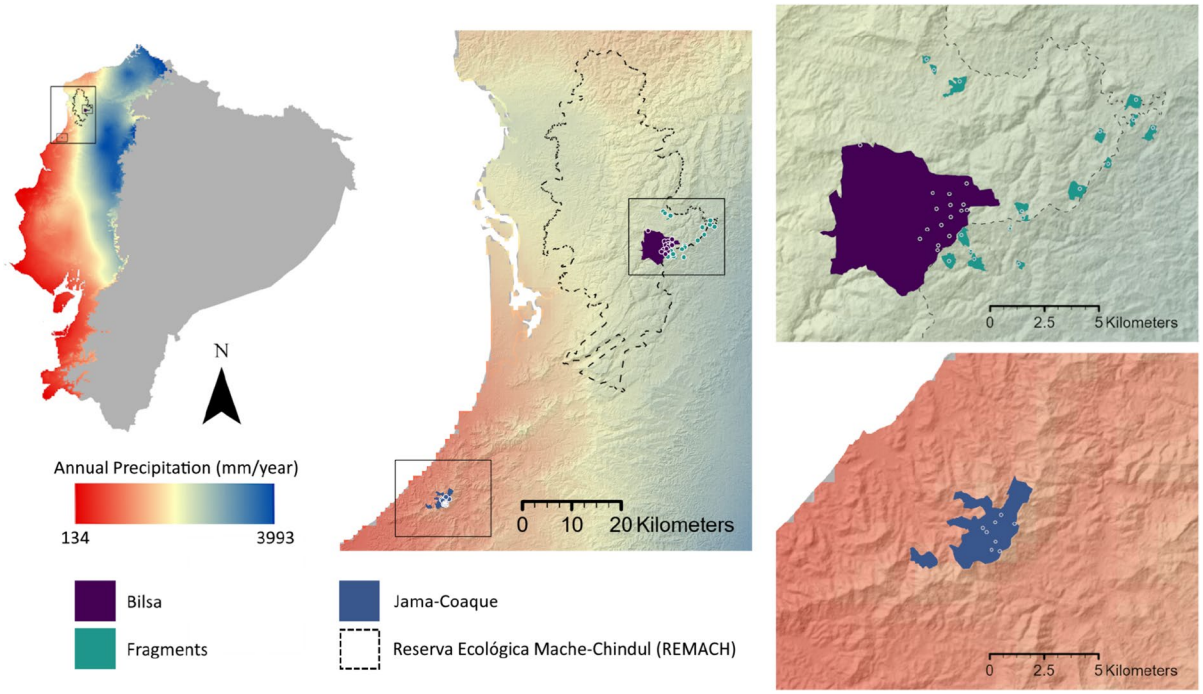

Fig. 1 Study area showing annual precipitation gradient in lowland western Ecuador (≤1000 m.a.s.l.). Insets show progressively zoomed in scales from left to right; sampling locations are shown with white dots inside each forest type. Precipitation data from WorldClim (Fick & Hijmans 2017)

three forest types are part of the Chocó biodiversity hotspot, Jama-Coaque, the southernmost forest, is in the transition zone between the wet Chocó and the dry Tumbes biodiversity hotspots. At the Jama-Coaque sites, seasonal variation between wet and dry periods is more extreme, annual rainfall is 23% lower, and temperatures average 1 °C warmer than in Bilsa (Fundación para la Conservación de los Andes Tropicales, Third Millennium Alliance; unpublished data). In all forest types, higher elevations are considerably wetter than lower elevations due to greater prevalence of *garúa*, or cold mist/drizzle, during much of the year. Humid forest fragments ranged in size from 2.7 to 47.9 ha (mean 20.7 ha, SD = 14.2 ha) and in distance to Bilsa from 0.01 to 7.2 km (mean 3.1 km, SD = 2.5 km). Because elevation is a key driver of differences in compositional similarity of birds, we chose intact and fragmented forest sampling sites within the same elevational range (Table 1) to ensure we compared "apples to apples."

Avian and habitat sampling

We used 30-mm mist nets to sample avian communities between 2013 and 2018 in our three forest types during both wet and dry seasons. Sampling periods consisted of three consecutive days of mist-netting (mean = 155.1 total net hours, SD = 15.5 net hours) from 30 min after sunrise to roughly 5 h after sunrise. At each site, we placed n = 8–10 mist nets (12 m × 3 m) along linear transects measuring ~ 250 m dependent upon terrain constraints. In fragments, transects began at the interior forest edge and continued toward the fragment centroid. Because standard-height mist nets are inadequate tools for sampling canopy birds, we considered these species bycatch and removed them from analyses (MacArthur and MacArthur 1974; Blake and Loiselle 2001) a decision supported by preliminary tests in which inclusion of under-represented canopy species drastically diminished explanatory power of habitat models. We identified species

as canopy birds based on local expert knowledge and foraging strata information from the Birds of the World database (Birds of the World 2024). All non-hummingbird species were banded with unique identification numbers. Hummingbirds at Jama-Coaque were similarly banded in most instances. In cases when the correct band size was unavailable for hummingbirds, individuals were identified by snipping the tip of a unique rectrix or combination of rectrices.

For each site, we sampled habitat characteristics at the beginning, middle, and end of mist netting transects and used the averages of the three measurements per characteristic for analyses. As a proxy for forest successional stage, we counted the number of large trees (DBH ≥ 50 cm) and small to mid-sized trees (10 cm ≤ DBH < 50 cm) in 20-m and 10-m circular plots, respectively, at the three sampling points per transect. We counted the number of *Cecropia* spp. trees, a genus of early successional species, in the same 10-m circular plots as an index of past disturbance (Durães et al. 2013; Lamperty et al. 2021). At each of these circular plots, we used a densiometer to estimate canopy openness in the four cardinal directions 10-m from the plot center and averaged these estimates. We measured canopy height using hypsometers and laser rangefinders but exclude these data from analyses due to strong correlation with canopy openness and abundance of large trees. Fragment area was measured by walking the boundary of each fragment with a GPS. We used the updated Hansen et al. Global Forest Change (Hansen et al. 2013) dataset to estimate the amount of surrounding forest cover in 500-m, 1-km, and 2-km circular areas around the centroid of each mist netting transect during the year in which it was sampled. Surrounding forest cover within these distances has been found to shape abundance, diversity, and/or community composition of terrestrial and understory tropical birds (Kormann et al. 2018; Cook et al. 2020). We found forest cover estimates within these different distances were highly correlated with one another and report only on the best performing cover variable for each forest type. Although the Hansen et al. (2013) dataset does not distinguish between plantation and natural forest, and while oil palm, teak, cacao, and balsa plantations are common in NW Ecuador, at the time of sampling, our remote fragments were embedded in a matrix of cattle pasture.

Spatial scale

We conducted our analyses at two spatial scales discussed in the introduction. We define "between-landscape" comparisons as those between Bilsa (intact humid forest) and our humid fragments because of their shared environmental conditions and former contiguity but contrasting land cover composition over a relatively large area (~ 120 km^2). Due to their differences in environmental conditions – principally habitat type, precipitation, and seasonality – we consider our Jama-Coaque sites distinct from the humid intact and fragmented landscapes in and around REMACH. We therefore define "regional-level" comparisons as those incorporating this regional environmental heterogeneity, i.e., comparisons of humid fragments or Bilsa vs. drier, more seasonal Jama-Coaque.

Statistical analyses

We used the Hill-Chao attribute diversity framework and package *iNEXT.3D* (Chao et al. 2021) in R (R Core Team 2023) to estimate and compare α taxonomic (TD), functional (FD), and phylogenetic diversity (PD) for each forest type (Jost et al. 2010; Chao et al. 2021). Under this unifying framework, attribute diversity – whether of species, functional groups, or phylogenetic tree branch length – can be weighted by abundance through the exponent q to yield attribute richness ($q = 0$), the effective number of intermediately abundant attributes ($q = 1$), or the effective number of common/dominant attributes ($q = 2$) (Chao et al. 2021). When $q = 0$, TD is species richness and gives rare and common species equal weight; when $q = 1$, it is a transformation of Shannon's index and weights all species by their relative abundance. When $q = 2$, TD is a transformation of the Gini-Simpson index and conveys more information about common species in a community, i.e., those responsible for the majority of ecological interactions (Jost et al. 2010). Similarly, PD extensions of the framework, when dividing total branch length by tree depth (i.e., mean-PD), are abundance-weighted transformations of Faith's phylogenetic diversity divided by tree depth (q = 0), phylogenetic entropy (q = 1), and Rao's quadratic entropy (q = 2) (Chao et al. 2021). FD extensions are derived from distance-based pairwise comparisons of species functional traits used to define

functionally distinct species beyond a certain threshold (Chao et al. 2019, 2021). Here, we use quadratic entropy, i.e., "the mean distance between any two individuals randomly selected from the pooled dataset" as our threshold (Chao et al. 2021). These Hill-Chao attribute diversity equivalencies improve upon earlier indices of diversity by utilizing standardized scales and comparable units (TD: "effective number of species", FD: "effective number of virtual functional groups", mean-PD: "effective number of lineages"), providing insight into richness and evenness simultaneously, following intuitive additive and multiplicative rules, abiding by rules of density and replication invariance, and maintaining independence between α and β diversity (Jost et al. 2010; Chao et al. 2014).

For all Hill-Chao diversity and composition analyses, we use abundance data and include only unique captures, excluding any subsequent recaptures of the same individual within or across combined sampling periods. Because we were limited to one to two sampling periods at each site, we were unable to determine detectability using mark-recapture approaches. We minimized differences in detection biases across forest types as much as possible by standardizing mist-netting materials and protocols across forest types and excluding all species for which our survey methodology was not designed, i.e., those not regularly found in the understory.

To test for significant differences in community composition among forest types, we first ran a bias-adjusted betadispersion ANOVA to check for equal variance among groups followed by a PERMANOVA (*betadisper* and *adonis2*, respectively, in package *vegan*) (Oksanen et al. 2007). We then used package *iNEXT.beta3D* in R to estimate and compare pairwise taxonomic, functional, and phylogenetic β-diversity at the between-landscape and regional scales (Jost et al. 2011; Socolar et al. 2016; Chao et al. 2019, 2023). We sourced functional trait data related to morphology (nares-to-tip beak length, width, and depth; tarsus, wing, and tail length; mass), dispersal ability (Hand-wing index, Kipp's distance), trophic niche, and primary foraging style from the AVONET database (Tobias et al. 2022) and combined these with local expert knowledge on foraging strata. For mean-PD analyses with *iNEXT.beta3D* (Chao et al. 2023), we averaged estimates of α- and β-diversity and their 95% confidence intervals using branch lengths from 1000 random subtrees of the updated Jetz et al. (2012) supertree based on the Hackett et al. (2008) distribution (Jetz et al. 2012).

To test for TD, FD, and mean-PD homogenization and differentiation at the between-landscape level (between combined fragments and Bilsa) and regionally (between Bilsa, fragments, and Jama-Coaque), we report pairwise comparisons of the *CqN* (similarity) index, which is a Sørensen-type estimate of percent overlap (Chao et al. 2014, 2019; Chao & Chiu 2016; Jost et al. 2011). Like the Chao-Hill attribute diversities from which it is drawn, *CqN* boasts the benefits described above and can be reduced to more limited, conventional indices of compositional (dis) similarity. When $q=0$, *CqN* reduces to the richness-based Sørensen index; when $q=1$, it reduces to the Horn index; when $q=2$, it reduces to the Morisita-Horn index (Jost et al. 2011). For all α and β diversity analyses, we used 50 bootstraps to generate *CqN* point estimates and 95% confidence intervals after verifying that estimates did not differ when using 200 and 2000 bootstraps for a subset of the data (TD, $q=2$). By convention, Hill-Chao α and β diversity are considered significantly different when confidence intervals do not overlap or when proportion overlap is $<50\%$ of the average margin of error between two diversity or similarity estimates (Cumming and Finch 2005; Jost et al. 2011).

Because we had an unequal distribution of sites among forest types (Table 1), and because we were limited to one sampling period in most but not all sites, we controlled for unequal sampling effort using rarefaction and extrapolation with the *iNEXT.3D* and *iNEXT.beta3D* packages in R (Chao et al. 2021, 2023). Additionally, we ran initial α diversity analyses three times: (1) using all available data; (2) while truncating Bilsa and fragment data sets to 16 sites sampled once apiece and Jama-Coaque to 8 sites sampled twice apiece, and (3) using just 8 sites from all forest types sampled once apiece to verify the efficacy of a time-for-space substitution of effort in our 8 Jama-Coaque sites (Figures S1, S2). In all cases, we were able to rarefy or extrapolate forest diversity and compositional similarity to a sample coverage of 96–99% at the forest level without a doubling in reference sample size. We found our Hill-Chao diversity and similarity estimates to be robust in the face of unequal sampling effort when $q=1$ and $q=2$, therefore, we report only results of analyses using all

available data, which increased estimate confidence for all analyses. Because TD, FD, and mean-PD compositional similarity patterns for $q=1$ and 2 were nearly identical, we report only on $q=2$ here but provide $q=1$ in supplementary materials (Figure S3).

We used a principal components analysis (PCA) to visualize overlap in environmental space and environmental heterogeneity among our three forest types. To visualize compositional similarity of forest types, we calculated *CqN* between sites using the *hilldiv* package in R and overlaid environmental vectors for shared, non-colinear habitat variables on a non-metric multidimensional scaling (NMDS) ordination with the *vegan* package in R (Oksanen et al. 2007; Alberdi and Gilbert 2019; R Core Team 2023). We present NMDS for $q=2$ here. To model the relationship between community composition and environment in each forest type, we used the *adonis2* function in R's *vegan* package to run PERMANOVAs with marginal effects and a step-wise removal method after first removing significantly colinear variables with Pearson's correlation coefficients above 0.5. Models weighted for abundant species ($q=2$) outperformed those for other orders of q, and we present the former here.

Results

Captures and α diversity

Across all sites ($n=41$) and sampling periods ($n=62$), we captured 3,523 birds of 148 species. We identified 64 of these captures (1.8%) from 28 species (18.9%) as canopy bycatch and removed them from all subsequent analyses. Of the 120 remaining understory species, 47 (39.2%) were found in all three forest types. Eleven species (9.2%) were unique to humid forest fragments, 11 (9.2%) were unique to Bilsa, and 19 (15.8%) were unique to Jama-Coaque. Sixteen species (13.3%) were captured in both fragments and Bilsa but not Jama-Coaque, 12 species (10.0%) were captured in both fragments and Jama-Coaque but not Bilsa, and 4 species (3.3%) were captured in both Jama-Coaque and Bilsa but not fragments.

Within-landscape α taxonomic diversity (TD) of understory birds was significantly higher in Jama-Coaque than Bilsa, and estimates for fragments fell between the two for both $q=1$ (intermediately abundant species) and 2 (dominant species; Fig. 2). Fragments were significantly more diverse than Bilsa for both orders of q and significantly less diverse than Jama-Coaque for $q=2$. Wide confidence intervals around $q=0$ (species richness) in Bilsa and fragments suggest we lacked adequate sampling to detect a substantial portion of rare species present, limiting inferences about species richness ($q=0$). Patterns of evenness, i.e., the spread between q estimates, were similar across forest types for $q=1$ and $q=2$. For the same orders of q, slightly overlapping confidence intervals suggest Jama-Coaque had significantly more functional diversity (FD) than both Bilsa and fragments, which did not differ significantly from one another (Fig. 2). Phylogenetic diversity was again significantly higher for $q=1$ and 2 in Jama-Coaque than in fragments and when compared to Bilsa for $q=1$ based on proportional overlap <0.50 in 95% CIs (Cumming and Finch 2005).

Between-landscape and regional compositional similarity

We found no significant difference in multivariate homogeneity of forest type variances ($F=2.87$, $p=0.07$), so we proceeded with PERMANOVA analyses and found community composition significantly differed among the three forest types ($F=3.5$, $R^2=0.16$, $p=0.002$). We defined the between-landscape level comparison as the comparison between fragmented and intact humid forest landscapes in and around REMACH. At this level, we found an estimated 27.5% difference in taxonomic composition between intact and fragmented humid forest understory bird communities (i.e., 100% similarity minus the Bilsa × Fragments point estimate) for *CqN* $q=2$ (common species, Fig. 3). FD and PD exhibited differentiation of ~ 5% and ~ 2%, respectively (Fig. 3). Diversity estimates for $q=1$ (intermediately abundant attributes, Figure S3) followed similar patterns.

At the regional level, *CqN* $q=2$ compositional similarity (β diversity) analyses showed varying degrees of biotic homogenization for taxonomic (TD) versus functional (FD) and mean phylogenetic diversity (mean-PD). Regionally, in the absence of either biotic homogenization or differentiation– a null hypothesis scenario – the understory bird community in forest fragments should be identical to that of Bilsa (i.e., *CqN* similarity = 100%) and have

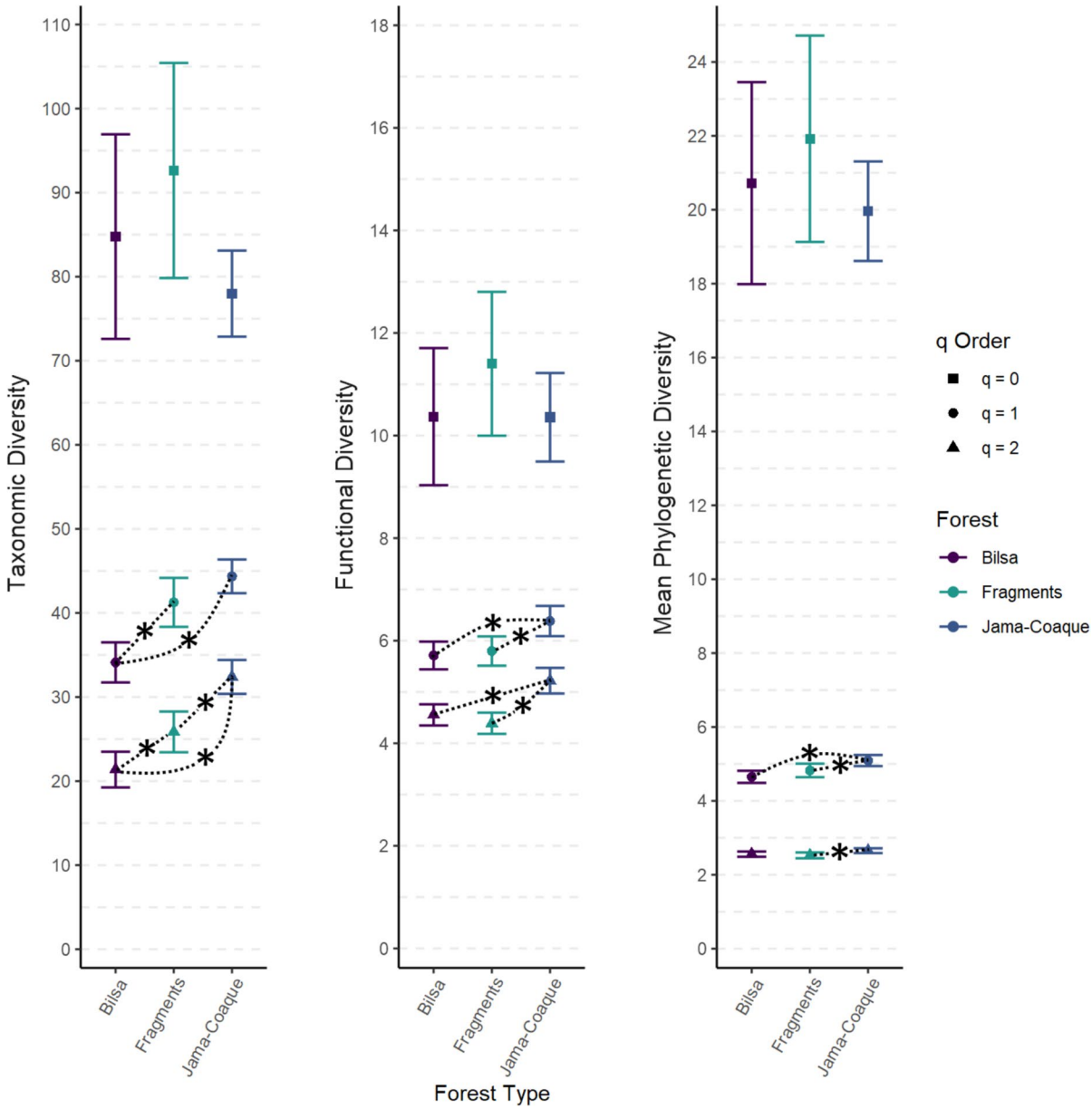

Fig. 2 Taxonomic, functional, and phylogenetic alpha diversity by forest type with 95% confidence intervals. Dashed lines with asterisks indicate significant differences based on confidence interval overlap. Hill-Chao q order determines relative abundance weighting (i.e., 0 = species richness, 1 = species neither common nor rare, 2 = dominant species). All orders of q are equal in a perfectly even community; less even communities demonstrate more spread between q estimates

the same amount of overlap with Jama-Coaque that the Bilsa community has – roughly 61% TD, 87% FD, 89% mean-PD (i.e., CqN similarity point estimates from Fig. 3). Instead, in addition to the estimated 27.5% between-landscape differentiation, we found an estimated 12% increase in compositional similarity between the humid forest fragments community and the Jama-Coaque community. Moreover, we found no significant difference in β TD between Fragment × Bilsa and Fragment × Jama-Coaque comparisons, meaning fragmented humid forests appear to be as taxonomically similar to

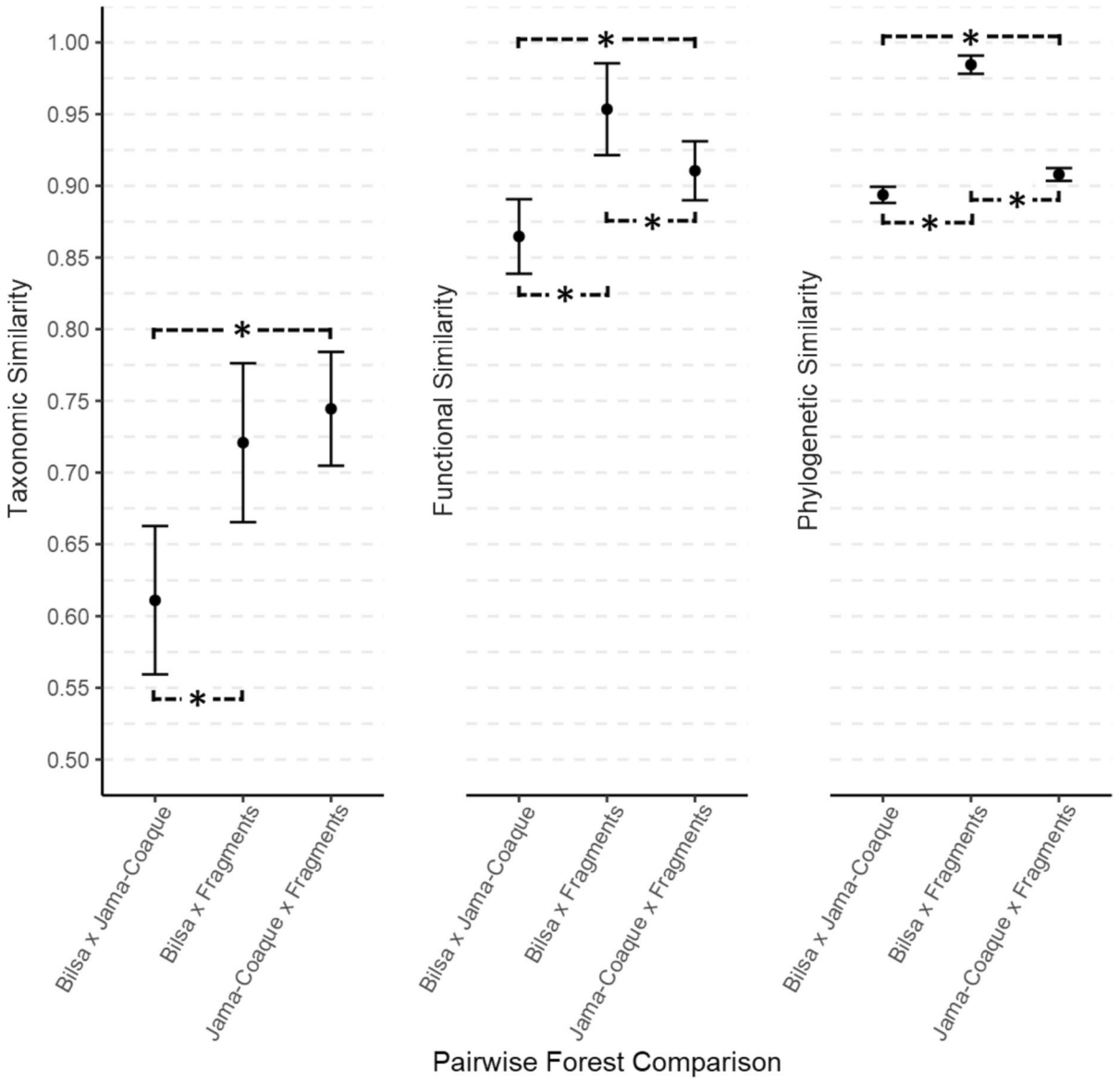

Fig. 3 Regional homogenization (Jama-Coaque x Fragments) and landscape-level differentiation (Bilsa x Fragments) of taxonomic, functional, and phylogenetic diversity between forest types expressed as pairwise CqN similarity of understory bird communities for $q = 2$ (dominant species). Error bars show 95% confidence intervals. Point estimates are colored with first forest type in pairwise comparison, error bars with color of second forest type. Significant differences denoted with dashed brackets and asterisks

Jama-Coaque (60 km away) as they are to Bilsa (mean distance = 3.1 km). This finding suggests fragmentation of humid forest causes homogenization in understory avian communities at the regional scale, with communities in the region's wetter climatic zones becoming more similar to those from drier/more seasonal climate zones (Fig. 3). In terms of FD and mean-PD, while there was a significant increase in homogenization with semi-humid intact forest, the understory bird community in fragments remained significantly more similar to Bilsa than Jama-Coaque (Fig. 3). Estimates for $q = 1$ followed qualitatively similar patterns (Figure S3), but intervals for similarity estimates of $q = 0$ were too wide

to make inferences about biological differences in species richness or functional overlap.

Environmental drivers of community composition

Substantial overlap in a PCA plot of environmental variables with a focus on elevation, vegetation structure, and forest cover suggest the three forest types are structurally quite similar for the metrics we quantified but that the fragmented humid forest landscape appears to be substantially more homogenous, occupying a smaller environmental space, than either intact forest type (Fig. 4A). An NMDS CqN plot for $q=2$ shows substantial community overlap between fragments and both intact forest types – again suggestive of homogenization – although forest fragments also appear to support understory birds with a large, novel ecological space despite the fragments' evidently more homogenous habitats (Fig. 4B). Bilsa and Jama-Coaque communities overlapped to a much smaller extent. After removing colinear terms, the *envfit* model of all forest types for $q=2$ had a 67% correlation between environmental variables and ordination vectors (Table 2). Environmental variables did not follow the same patterns of collinearity among forest types, resulting in unique combinations of terms included in $q=2$ PERMANOVA models for each forest type (Table 2). In models for each forest type, elevation was a nearly significant or highly significant driver of community composition and explained a large portion of the observed variation. In Bilsa, the number of large trees (> 50 cm DBH) was the only significant driver. Large trees were a significant driver of community composition in fragments as well but to a lesser extent, and number of smaller to mid-sized trees (10–49 cm DBH) played a significant role in shaping community composition, as did fragment size. Number of cecropias was identified as a significant driver of community composition overall and in Jama-Coaque, highlighting the importance of disturbance in shaping understory bird communities, but it was excluded from Bilsa and Fragment models due to its collinearity with other variables.

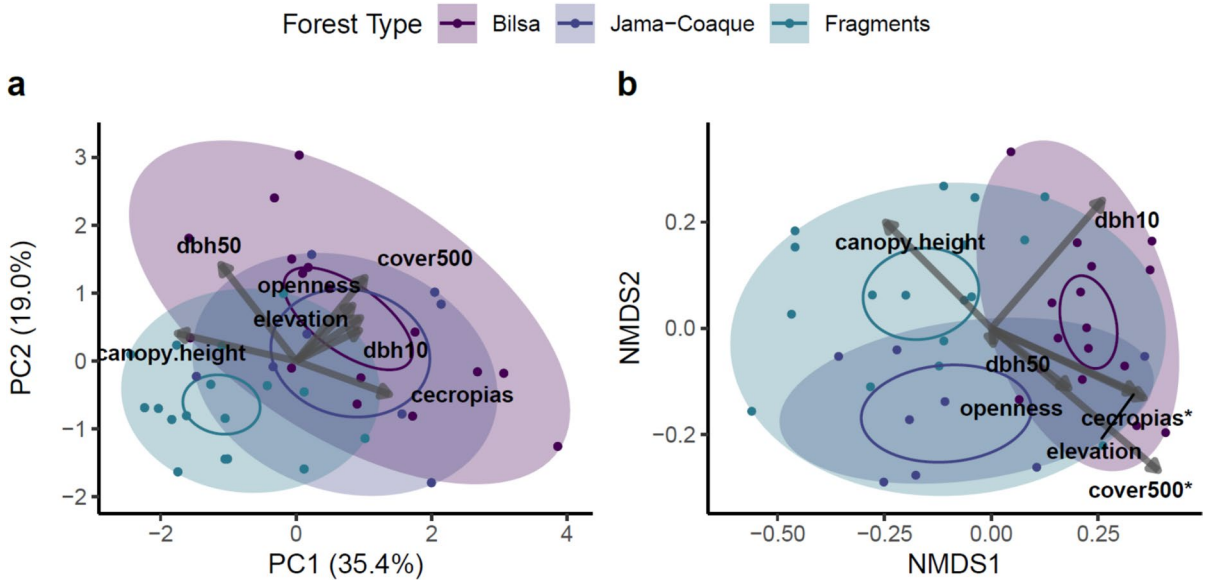

Fig. 4 Environmental and understory bird ecological spaces by forest type. **a** PCA plot of environmental variables measured in each forest type. Local measures of elevation and forest structure suggest substantial overlap among forest types but reduced environmental heterogeneity in fragments. **b** Taxonomic *CqN* compositional similarity NMDS for $q=2$; statistically significant environmental drivers shown with an asterisk ($p<0.05$). Outer ellipses are based on site scores (points); inner rings show 95% confidence intervals of forest type centroids. Cover500 = % forest cover within 500 m of sampling site, openness = % canopy openness, cecropias = number of cecropias, dbh10 = number of trees between 10 and 50 cm DBH, dbh50 = number of trees > 50 cm DBH

Table 2 Community composition NMDS and PERMANOVA model results by forest type for $q=2$ with R^2 and p-value (in parentheses) for each environmental variable

Variables denoted by "–" were excluded from models due to significant collinearity with other model terms or absence of area measures in intact forest; significant model terms ($\alpha=0.05$) are bolded

	NMDS envfit	Bilsa	Jama-Coaque	Fragments
Elevation	0.13 (0.10)	0.12 (0.07)	**0.45 (0.001)**	**0.26 (0.001)**
DBH > 50 cm	–	**0.24 (0.008)**	–	**0.18 (0.001)**
DBH > 10 cm	0.13 (0.08)	0.03 (0.59)	0.06 (0.18)	**0.10 (0.03)**
500 m Cover (%)	**0.22 (0.01)**	0.07 (0.25)	–	–
2 km Cover (%)	–	–	–	0.06 (0.13)
Cecropias	**0.15 (0.05)**	–	**0.13 (0.04)**	–
Openness	0.05 (0.42)	0.10 (0.14)	0.08 (0.13)	0.07 (0.10)
Area	–	–	–	**0.14 (0.01)**
Model R^2	0.61	0.58	0.92	0.75
Model p-value	–	**0.018**	**0.006**	**0.001**

Discussion

Impacts of anthropogenic landscape change on biotic communities are well documented. Still, little is known about fragmentation's role in shaping patterns of β diversity among tropical faunal communities across spatial scales or climate gradients – an important knowledge gap given the roles of heterogeneous climates and habitats in maintaining β diversity (Veech and Crist 2007). We present a novel comparison of understory bird communities of fragmented and intact forests from distinct climate zones in a single ecoregion. Specifically, we investigated patterns of local differentiation and regional homogenization across taxonomic (TD), functional (FD) and phylogenetic diversity (PD), and we assessed environmental correlates of community composition. We found support for each of our hypotheses. First, at the between-landscape scale, we found strong signals of biotic differentiation associated with fragmentation: humid forest fragments had significantly higher α-diversity and a ~ 27.5% difference in composition of dominant understory bird communities compared to the intact humid forest with which they were formerly contiguous ≤ 60 years ago. Second, at the regional scale, and in contrast to landscape-level differentiation, we found strong evidence of biotic homogenization between opposite ends of a climate gradient: the understory bird community in forest fragments was as taxonomically similar to that of adjoining intact humid forest (0.01 to 7.2 km away) as it was to that of intact semi-humid seasonal forest 60 km away. As predicted, while both biotic differentiation and homogenization occurred across taxonomic (TD), functional (FD), and phylogenetic diversity (PD), FD and PD were significantly less impacted than TD, providing strong evidence of functional and phylogenetic redundancy within the region's humid understory bird communities. Within all forest types, local habitat characteristics explained a large portion of understory bird community composition, and while there was substantial overlap in habitat among forest types, reduced heterogeneity in forest structure measures among fragments point to other environmental forces not measured here as important drivers reshaping fragment bird communities across spatial scales.

At the 'between-landscape' scale, we found humid forest fragments overall held more understory bird species (α TD) than the intact forest with which they were formerly contiguous, but only when considering common species ($q=2$) and species neither common nor rare ($q=1$). Increases in α TD were accompanied by significant differentiation of β TD between fragmented forest and adjacent intact forest at the between-landscape scale. These patterns of differentiation occurred even though major environmental correlates of community composition (i.e., elevation, forest structure measures) were more homogenous among forest fragments than they were among sites in adjacent intact humid forest (as well as drier and more seasonal intact forest 60-km away). Despite this homogeneity among fragments, environmental drivers of understory bird community composition were similar to those found for diversity of other bird groups reported from our Bilsa and fragment sampling sites: hummingbirds (elevation, surrounding forest cover, canopy openness, Huh et al. 2023), nocturnal birds (fragment area and elevation, Walter et al. 2017a, b), large-bodied frugivores (surrounding forest cover, Walter, Browne, Freile, Olivo, et al., 2017a,

2017b), terrestrial birds (elevation, Cook et al. 2020), and overall species richness (large trees, Durães et al. 2013). Our models and PCA plots suggest environmental filtering of between-landscape differentiation largely reflects changes in landscape composition, which is consistent with principles of island biogeography often applied to forest fragments (e.g., vicariance, colonization and extinction trade-offs related to fragment size and isolation, amount of surrounding forest cover) and the role of stochasticity in shaping fragment communities (Graham and Blake 2001; Tscharntke et al. 2012; Cook et al. 2020; Bonfim et al. 2021).

Though we address overall patterns of diversity without a focus on species identities in this paper, our findings at the between-landscape scale are also consistent with previously reported patterns of biotic differentiation at relatively fine spatial scales driven by declines in interior forest specialist species and increases in generalist, edge, and open-area species (Stratford and Stouffer 1999; Morante-Filho et al. 2016; dos Anjos et al. 2019). Previous work on bird communities within- and between-landscapes in fragmented forests of Brazil found β-diversity was shaped by both environmental filtering and dispersal limitation (Morante-Filho et al. 2016). Fragmentation may also modify the stable microclimates and microhabitats – including foraging substrates and prey – to which these species have adapted (Stratford and Robinson 2005; Visco et al. 2015; Ausprey et al. 2021; Sherry 2023). These shifts purportedly impact physiology, resource availability, and foraging success. For example, understory insectivores may not see or forage optimally in bright conditions or may find themselves in an increasingly inhospitable "arthropod desert" (Stratford and Robinson 2005; Sherry et al. 2020; Ausprey et al. 2021; Sherry 2021). If this is the case, and fragmentation is making tropical forest microclimates and microhabitats less suitable for a suite of understory birds adapted to cool, humid, and dark conditions and their corresponding resources, then conversely, fragmentation could be improving conditions for species adapted to hotter, drier, and brighter habitats and the fruits, seeds, insects, and other resources found therein.

The regional homogenization of common ($q=1$) and dominant ($q=2$) species between humid forest fragments and intact semi-humid seasonal forest is consistent with the idea that fragmentation of humid forest creates or improves habitat for birds associated with drier regions. Specifically, our results indicate fragmentation of humid forests is associated with regional homogenization that increased community overlap between humid and drier, more seasonal landscapes from ~ 61% to ~ 72%–a 12% increase in understory bird species associated with the drier Jama-Coaque reserve in a humid forest system 60 km away. Similar regional homogenization in response to anthropogenic landscape modification likely benefited dry forest birds in agricultural landscapes in Costa Rica and may have been due partly to greater similarity between agricultural vegetation structure and dry forest structure than wet forest structure (Karp et al. 2018). Our models also suggest increased density of small to mid-sized trees is associated with community structure in these homogenized fragment communities with drier/seasonal forest species. The apparent homogeneity of fragment forest structure we observed, in contrast with the larger ecological space occupied by the fragment bird community, suggests there are several habitat variables we did not measure (e.g., micro-climate, leaf litter, food resource availability) or include in analyses that may be important for understanding how fragmentation shapes bird communities. Other aspects of anthropogenic landscape change associated with fragmentation that we did not quantify, for example selective logging and edge effects, may also be as important in shaping fragment communities as fragment area and isolation (Laurance et al. 2011a; Tscharntke et al. 2012; Durães et al. 2013; Kormann et al. 2018).

Simultaneous comparisons of landscape-level and regional-level patterns of biotic homogenization and differentiation provide new insight into eco-evolutionary ramifications of fragmentation across spatial scales. The regional homogenization we documented, on top of the 27.5% increase in differentiation at the between-landscape level, could reshape food chains, pollination services, seed dispersal, and other functions, potentially leading to cascading trophic effects and further biotic homogenization with drier climate zones among rare and non-dominant birds, as well as other taxa, over time (Park and Razafindratsima 2019; Bonfim et al. 2021; Li et al. 2022; Lamperty and Brosi 2022). Our findings highlight the need for continued work to better predict how regional homogenization and landscape-level differentiation will affect ecosystem function and the erosion or safeguarding

of biodiversity. This work should aim to compare networks, functions, and services of homogenizing and differentiating species in intact habitats across climatic gradients. Though we are just beginning to understand understory bird interaction networks in the tropics, there is evidence that understory birds play key roles in tropical plant-animal interaction networks (Carreira et al. 2020; da Silva et al. 2021), that fragmentation can cause deterioration of these networks (Marjakangas et al. 2020; Menezes Pinto et al. 2021), and that differences in scale dependence of plant-animal interactions may lead to demographic consequences for some species but not others (García et al. 2011; Emer et al. 2018).

Biological traits vary in the ways in which they affect ecosystem function at every scale, and studies documenting the distribution of those traits across multiple scales of environmental heterogeneity are therefore necessary to predict ecosystem responses (Suárez-Castro et al. 2018). We found only about 20% as many effective functional groups (FD) as effective species (TD) for $q = 1$ and 2 and even fewer effective lineages (PD) in our three forest types. These results suggest the region's high diversity of understory birds harbors substantial functional and phylogenetic redundancy, and lost or declining species were replaced with functionally/phylogenetically similar species. Such functional redundancy may provide network and ecosystem resiliency even in the face of substantial TD change (Hooper et al. 2005; Ramos-Robles et al. 2018; Hiraiwa and Ushimaru 2024). Given the lower-than-expected β FD and PD between Jama-Coaque and fragments relative to β TD, it appears functionally and phylogenetically distinct species were less likely to colonize fragments, or demonstrate large changes in abundance (Online Appendix 2), than functionally redundant species (Online Appendix 4). The absence of these unique functional groups and lineages from fragments raises questions about several aspects of fragment community structuring. These include dispersal ability of different families and functional groups in a fragmented landscape, the roles of competition and resource availability in shaping communities (Sherry et al. 2020; Sherry 2021), whether niches for semi-humid seasonal forest specialists exist in humid fragments, and regional to local species pool filtering. Environmental filters are thought to limit which functional traits and phylogenetic lineages present in a region may occur locally (Emerson and Gillespie 2008; Kraft and Ackerly 2010; Belmaker and Jetz 2013). While our findings suggest anthropogenic fragmentation may override naturally occurring environmental filters, allowing semi-humid species to dominate where humid species once reigned, changes in dominant understory bird species identity may bring little change in dominant functional traits or lineages.

Analyzing patterns of biotic homogenization and differentiation at both landscape and regional scales simultaneously may provide new insight into the conservation of tropical biodiversity threatened by anthropogenic landscape and climate change For example, Socolar et al. (2016) highlight the importance of spatial scale when using β-diversity to plan protected areas and corridors. While the between-landscape differentiation we observed might suggest fragments are worth protecting because they harbor unique diversity not found in intact humid forest, our regional comparison reveals much of the "novel" fragment diversity in this system is actually closely associated with intact semi-humid seasonal forest, and the remaining component of unique fragment diversity may be driven by open-habitat and generalist species already benefitting from conversion of forest to urban and agricultural areas. The evidence we found that fragmentation benefits species from hotter, drier, more seasonal forests suggests humid forest fragmentation, like agricultural conversion, could exacerbate the drying effects of climate change in the region (Karp et al. 2018; Senior et al. 2019). While sparse data coverage and disagreement between models place some ambiguity on climate change predictions for the area over the next 100 years, it is predicted that mean and extreme temperatures in the area will increase, as will precipitation extremes and variability, particularly between El Niño and La Niña years (Chou et al. 2014; Dereczynski et al. 2020; Castellanos et al. 2022). In such a scenario, humid forest fragments may not provide adequate habitat for interior forest species regardless of patch connectivity, but our results suggest they may provide refuge for bird communities from semi-humid seasonal forest if these habitats themselves become less habitable due to anthropogenic climate or landscape change, though it is unclear how they might respond to increased precipitation. Conservationists may therefore wish to consider increasing connectivity between drier parts of the ecoregion and fragmented humid landscapes to

facilitate range-shifts in response to climate change, particularly for dispersal-limited species (Pearson 2006; Krosby et al. 2010; Laurance et al. 2011b; Beier et al. 2012; Senior et al. 2019).

Biotic homogenization and differentiation are processes that occur over time, and studies of these patterns across both time and space are rare due to logistical trade-offs between spatial vs. temporal replication (Kramer et al. 2023; Rolls et al. 2023). In this study, we were limited to one three-day sampling period for many of our sites, and some sites were sampled in different years. While this was sufficient to document patterns arising among common and dominant species, it limited our ability to detect all species present and prevented analysis of species richness ($q = 0$). As a result, we were unable to make inferences about homogenization and differentiation of rare species, which may contribute unique phylogenetic lineages and functionality to their communities (Leitão et al. 2016; dos Anjos and de Almeida 2020; dos Anjos et al. 2023). This also limited our ability to document temporal changes in patterns of homogenization and differentiation as well as possible bias arising from undetected interannual variation in communities. Still, tropical lowland understory bird communities are largely sedentary, and homogenization/differentiation trends may increase over time. Indeed, in the years since we collected our field data, all 19 species we found only in Jama-Coaque have been documented on eBird in one of the largest fragments we sampled in the humid REMACH area (eBird 2025), highlighting the importance of both sampling effort and longitudinal studies and suggesting long-term sampling could reveal even stronger patterns of homogenization and differentiation. These sightings also suggest local and landscape-level species pools do draw from the full complement of humid and semi-humid forest species present in the regional pool (Ricklefs 1987; Morton and Law 1997; Lessard et al. 2012), which provides additional hope for successful range shifts in the face of climate change. Additionally, it raises important questions that future longitudinal studies may better answer: does low abundance of rarer non-humid forest species limit their ability to persist in and colonize fragments (Tellería et al. 2003)? Or could recent evidence that birds from drier, more seasonal habitats are better dispersers than humid forest species (Sheard et al. 2019, 2020; Weeks et al. 2023) indicate these fragments are still being colonized and still homogenizing with the semi-humid seasonal forest, in some cases 60 years after their formation? Turnover and extinction dynamics in fragments are more fluid than in intact forest (Boulinier et al. 2001) and may lead to ecosystem decay driven by decreases in humid forest specialist species and increases in generalist species over time (Lovejoy et al. 1984; Laurance et al. 2011a; Blandón et al. 2016). However, additional studies are needed to determine if this extinction debt has been paid (Vellend et al. 2006; Kuussaari et al. 2009; Durães et al. 2013), if redundant and unique semi-humid seasonal forest specialists will continue to colonize humid fragments over time, and if these newcomers will be able to rescue ecosystem function in the long-term.

Conclusion

New statistical tools are opening doors for researchers to expand upon decades of tropical fragmentation studies by combining taxonomic diversity analyses with functional and phylogenetic diversity analyses in unifying frameworks. This approach provides greater insight into impacts of anthropogenic landscape change and patterns of biotic homogenization and differentiation across spatial scales. The increased diversity and biotic differentiation in fragments that we documented belied regional loss of diversity and homogenization of understory bird communities across a climate and forest type gradient. Fortunately, it appears functional and phylogenetic redundancy are prevalent among understory birds of the Chocó and suggest these communities may offer some ecological resiliency in fragmented forests, at least over the course of ~ 60 years (the maximum age of fragments in the region). However, the long-term ramifications of species loss are unclear and beyond the scope of this study. We also found some evidence that homogenization between semi-humid seasonal forest and humid fragments is related to similarity in vegetation structure that could be associated with other aspects of anthropogenic landscape change like selective logging, but homogeneity of fragment vegetation structure and importance of landscape composition suggest other factors may be contributing to community homogenization across regional gradients of climate and habitat heterogeneity. Together, these findings

serve to further highlight the importance of conserving intact forests to prevent biotic homogenization and associated species loss, especially across environmental gradients, but they offer some hope that avian communities may continue to provide the majority of their ecological services and retain major phylogenetic histories in the face of fragmentation.

Acknowledgement We thank Third Millennium Alliance (TMA) team members R. Lynch, D. Murillo, and E. Márquez for their support and assistance organizing and maintaining this project, as well as the many interns who helped with data collection. We similarly thank Fundación para la Conservación de los Andes Tropicales team members M. Gonzalez, M. Baquero, C. Aulestia, and J. Bermingham. We thank TMA, Fundación Jatun Sacha, and the private landowners around Bilsa for access to their properties for sampling. Thank you to D. Karp, T. Sherry, and the Karubian lab for their valuable feedback on this manuscript and to S. Albert and the Institute for Bird Populations for equipment donations. Data were collected under permits MAE-DNB-CM-2015-0017 from the Ministerio de Ambiente del Ecuador granted to Universidad Technológica Indoamérica and MAE-UAF-DPAM-2018-1395-E granted to the Corporación Grupo Ecológico Jama-Coaque.

Author contributions ME and JK: were involved in conceptualization, resources, and methodology. All authors were involved in data curation, investigation, and project administration. ME, JK, EB, and JRA: contributed to writing—review and editing. ME: performed formal analysis, visualization, and writing—original draft.

Funding This work was supported by funding from Third Millennium Alliance, Tulane University, the Disney Conservation Fund, the US Fish & Wildlife Service, and the Conservation, Food & Health Foundation.

Data availability Supporting data for this study to be made available in the Dryad Digital Repository: link and citation.

Declarations

Conflict of interest The authors have no competing interests to declare.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by-nc-nd/4.0/.

References

Alberdi A, Gilbert MTP (2019) hilldiv: an R package for the integral analysis of diversity based on Hill numbers. Biorxiv 545665

Arroyo-Rodríguez V, Rös M, Escobar F et al (2013) Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. J Ecol 101:1449–1458

Astorga A, Death R, Death F et al (2014) Habitat heterogeneity drives the geographical distribution of beta diversity: the case of New Zealand stream invertebrates. Ecol Evol 4:2693–2702

Ausprey IJ, Newell FL, Robinson SK (2021) Adaptations to light predict the foraging niche and disassembly of avian communities in tropical countrysides. Ecology 102:e03213

Beier C, Beierkuhnlein C, Wohlgemuth T et al (2012) Precipitation manipulation experiments–challenges and recommendations for the future. Ecol Lett 15:899–911

Belmaker J, Jetz W (2013) Spatial scaling of functional structure in bird and mammal assemblages. Am Nat 181:464–478

Biggs CR, Yeager LA, Bolser DG et al (2020) Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11:e03184

Birds of the World (2024) Comprehensive life histories for all bird species and families. https://birdsoftheworld.org. Accessed 2 Mar 2024

Blake JG, Loiselle BA (2001) Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. Auk 118:304–326

Blandón AC, Perelman SB, Ramírez M et al (2016) Temporal bird community dynamics are strongly affected by landscape fragmentation in a Central American tropical forest region. Biodivers Conserv 25:311–330

Bonfim FCG, Dodonov P, Cazetta E (2021) Landscape composition is the major driver of the taxonomic and functional diversity of tropical frugivorous birds. Landsc Ecol 36:2535–2547

Boulinier T, Nichols JD, Hines JE et al (2001) Forest fragmentation and bird community dynamics: inference at regional scales. Ecology 82:1159–1169

Brown LM, Ramey RR, Tamburini B, Gavin TA (2004) Population structure and mitochondrial DNA variation in sedentary Neotropical birds isolated by forest fragmentation. Conserv Genet 5:743–757

Calsavara LC, Lima MR, Bochio GM et al (2023) Bird communities are more functionally redundant in less disturbed Araucaria forest. Ornithol Res. https://doi.org/10.1007/s43388-023-00142-4

Carreira DC, Dáttilo W, Bruno DL et al (2020) Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. Sci Rep 10(1):10594

Castellanos E, Lemos MF, Astigarraga L et al (2022) Central and South America. In: Portner H-O, Roberts DC, Tignor M et al (eds) Climate change 2022: Impacts, adaptation and vulnerability. Cambridge University Press, Cambridge, pp 1689–1816

Chao A, Chiu C (2016) Bridging the variance and diversity decomposition approaches to beta diversity via similarity and differentiation measures. Methods Ecol Evol 7:919–928

Chao A, Chiu C-H, Jost L (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. Annu Rev Ecol Evol Syst 45:297–324

Chao A, Chiu C, Villéger S et al (2019) An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. Ecol Monogr 89:e01343

Chao A, Henderson PA, Chiu C et al (2021) Measuring temporal change in alpha diversity: a framework integrating taxonomic, phylogenetic and functional diversity and the *iNEXT.3D* standardization. Methods Ecol Evol 12:1926–1940

Chao A, Thorn S, Chiu C et al (2023) Rarefaction and extrapolation with beta diversity under a framework of H ill numbers: the iNEXT. beta3D standardization. Ecol Monogr 93:e1588

Chou SC, Lyra A, Mourão C et al (2014) Assessment of climate change over South America under RCP 4.5 and 8.5 downscaling scenarios. Am J Clim Change 03:512–527

Cook RN, Ramirez-Parada T, Browne L et al (2020) Environmental correlates of richness, community composition, and functional traits of terrestrial birds and mammals in a fragmented tropical landscape. Landsc Ecol 35:2825–2841

Cumming G, Finch S (2005) Inference by eye: confidence intervals and how to read pictures of data. Am Psychol 60:170–180

da Silva LB, da Silva JB, Souza CS et al (2021) Plant–animal interactions of understory species in an area of tropical rainforest, north-eastern Brazil. Austral Ecol 46:561–573

Dehling DM, Dehling JM (2023) Elevated alpha diversity in disturbed sites obscures regional decline and homogenization of amphibian taxonomic, functional and phylogenetic diversity. Sci Rep 13:1710

Dereczynski C, Chan Chou S, Lyra A et al (2020) Downscaling of climate extremes over South America – Part I: model evaluation in the reference climate. Weather Clim Extremes 29:100273

DeSouza O, Schoereder JH, Brown V, Bierregaard Jr RO (2001) A theoretical overview of the processes determining species richness in forest fragments. Lessons from Amazonia: the ecology and conservation of a fragmented forest, pp 13–21

Dobrovolski R, Melo AS, Cassemiro FA, Diniz-Filho JAF (2012) Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 21:191–197

dos Anjos L, de Almeida BA (2020) On the importance of niche packing for local species richness in taxonomic bird groups of the Neotropical region. J Ornithol 161:1083–1092

dos Anjos L, Bochio GM, Medeiros HR et al (2019) Insights on the functional composition of specialist and generalist birds throughout continuous and fragmented forests. Ecol Evol 9:6318–6328

dos Anjos L, Ragassi Urbano M, Simões Oliveira H, Laerte Natti P (2023) The functional importance of rare and dominant species in a Neotropical forest bird community. J Nat Conserv 72:126361

Durães R, Carrasco L, Smith TB, Karubian J (2013) Effects of forest disturbance and habitat loss on avian communities in a Neotropical biodiversity hotspot. Biol Conserv 166:203–211

eBird (2025) Reserva FCAT. https://ebird.org/hotspot/L9726728. Accessed 31 Aug 2025

Edie SM, Jablonski D, Valentine JW (2018) Contrasting responses of functional diversity to major losses in taxonomic diversity. Proc Natl Acad Sci 115:732–737

Emer C, Galetti M, Pizo MA et al (2018) Seed-dispersal interactions in fragmented landscapes – a metanetwork approach. Ecol Lett 21:484–493

Emer C, Galetti M, Pizo MA et al (2019) Defaunation precipitates the extinction of evolutionarily distinct interactions in the Anthropocene. Sci Adv 5:eaav6699

Emerson BC, Gillespie RG (2008) Phylogenetic analysis of community assembly and structure over space and time. Trends Ecol Evol 23:619–630

Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315

Fletcher RJ, Didham RK, Banks-Leite C et al (2018) Is habitat fragmentation good for biodiversity? Biol Conserv 226:9–15

Fricke EC, Ordonez A, Rogers HS, Svenning J-C (2022) The effects of defaunation on plants' capacity to track climate change. Science 375:210–214

García D, Zamora R, Amico GC (2011) The spatial scale of plant–animal interactions: effects of resource availability and habitat structure. Ecol Monogr 81:103–121

Gardner TA, Barlow J, Chazdon R et al (2009) Prospects for tropical forest biodiversity in a human-modified world. Ecol Lett 12:561–582

Gibson L, Lee TM, Koh LP et al (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:378–381

Graham CH, Blake JG (2001) Influence of patch- and landscape-level factors on bird assemblages in a fragmented tropical landscape. Ecol Appl 11:1709–1721

Hackett SJ, Kimball RT, Reddy S et al (2008) A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768

Hansen MC, Potapov PV, Moore R et al (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Harrison XA, Donaldson L, Correa-Cano ME et al (2018) A brief introduction to mixed effects modelling and multimodel inference in ecology. PeerJ 6:e4794

Hatfield JH, Barlow J, Joly CA et al (2020) Mediation of area and edge effects in forest fragments by adjacent land use. Conserv Biol 34:395–404

Hiraiwa MK, Ushimaru A (2024) Loss of functional diversity rather than species diversity of pollinators decreases

community-wide trait matching and pollination function. Funct Ecol. https://doi.org/10.1111/1365-2435.14527
Hooper DU, Chapin FS III, Ewel JJ et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35
Huh KM, Ellis M, Castillo F et al (2023) Hummingbird diversity in a fragmented tropical landscape in the Chocó biogeographic zone. Biotropica 55:418–429
Jetz W, Thomas GH, Joy JB et al (2012) The global diversity of birds in space and time. Nature 491:444–448
Jost L, DeVries P, Walla T et al (2010) Partitioning diversity for conservation analyses. Divers Distrib 16:65–76
Jost L, Chao A, Chazdon RL (2011) Compositional similarity and β (beta) diversity. Biological diversity: frontiers in measurement and assessment, pp 66–84
Karp DS, Rominger AJ, Zook J et al (2012) Intensive agriculture erodes β-diversity at large scales. Ecol Lett 15:963–970
Karp DS, Frishkoff LO, Echeverri A et al (2018) Agriculture erases climate-driven β-diversity in Neotropical bird communities. Glob Change Biol 24:338–349
Kormann UG, Hadley AS, Tscharntke T et al (2018) Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization. J Appl Ecol 55:1288–1298
Kraft NJB, Ackerly DD (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecol Monogr 80:401–422
Kramer JMF, Zwiener VP, Müller SC (2023) Biotic homogenization and differentiation of plant communities in tropical and subtropical forests. Conserv Biol 37:e14025
Krosby M, Tewksbury J, Haddad NM, Hoekstra J (2010) Ecological connectivity for a changing climate. Conserv Biol 24:1686–1689
Kuussaari M, Bommarco R, Heikkinen RK et al (2009) Extinction debt: a challenge for biodiversity conservation. Trends Ecol Evol 24:564–571
Lamperty T, Brosi BJ (2022) Loss of endangered frugivores from seed dispersal networks generates severe mutualism disruption. Proc R Soc Lond B Biol Sci 289:20220887
Lamperty T, Karubian J, Dunham AE (2021) Ecological drivers of intraspecific variation in seed dispersal services of a common neotropical palm. Biotropica 53:1226–1237. https://doi.org/10.1111/btp.12966
Laurance WF, Camargo JLC, Luizão RCC et al (2011a) The fate of Amazonian forest fragments: a 32-year investigation. Biol Conserv 144:56–67
Laurance WF, Carolina Useche D, Shoo LP et al (2011b) Global warming, elevational ranges and the vulnerability of tropical biota. Biol Conserv 144:548–557
Leitão RP, Zuanon J, Villéger S et al (2016) Rare species contribute disproportionately to the functional structure of species assemblages. Proc R Soc B Biol Sci 283:20160084
Lessard J-P, Borregaard MK, Fordyce JA et al (2012) Strong influence of regional species pools on continent-wide structuring of local communities. Proc R Soc B Biol Sci 279:266–274
Li W, Zhu C, Grass I et al (2022) Plant-frugivore network simplification under habitat fragmentation leaves a small core of interacting generalists. Commun Biol 5:1214
Liang C, Yang G, Wang N et al (2019) Taxonomic, phylogenetic and functional homogenization of bird communities due to land use change. Biol Conserv 236:37–43
Lovejoy TE, Rankin JM, Bierregaard RO Jr et al (1984) Ecosystem decay of Amazon forest remnants. Extinctions Univ Chic Press Chic 111:295–325
MacArthur RH, MacArthur AT (1974) On the use of mist nets for population studies of birds. Proc Natl Acad Sci 71:3230–3233
Marjakangas E-L, Abrego N, Grøtan V et al (2020) Fragmented tropical forests lose mutualistic plant–animal interactions. Divers Distrib 26:154–168
McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453
Menezes Pinto Í, Emer C, Cazetta E, Morante-Filho JC (2021) Deforestation simplifies understory bird seed-dispersal networks in human-modified landscapes. Front Ecol Evol. https://doi.org/10.3389/fevo.2021.640210
Monge O, Maggini I, Schulze CH et al (2023) Physiologically vulnerable or resilient? Tropical birds, global warming, and redistributions. Ecol Evol 13:e9985
Monge-González ML, Guerrero-Ramírez N, Krömer T et al (2021) Functional diversity and redundancy of tropical forests shift with elevation and forest-use intensity. J Appl Ecol 58:1827–1837
Moore RP, Robinson WD, Lovette IJ, Robinson TR (2008) Experimental evidence for extreme dispersal limitation in tropical forest birds. Ecol Lett 11:960–968
Morante-Filho JC, Arroyo-Rodríguez V, Faria D (2016) Patterns and predictors of β-diversity in the fragmented Brazilian Atlantic forest: a multiscale analysis of forest specialist and generalist birds. J Anim Ecol 85:240–250
Morelli F, Benedetti Y, Perna P, Santolini R (2018) Associations among taxonomic diversity, functional diversity and evolutionary distinctiveness vary among environments. Ecol Indic 88:8–16
Morton RD, Law R (1997) Regional species pools and the assembly of local ecological communities. J Theor Biol 187:321–331
Oksanen J, Kindt R, Legendre P et al (2007) The Vegan Package. Commun Ecol Package 10:719
Olden JD, Rooney TP (2006) On defining and quantifying biotic homogenization. Glob Ecol Biogeogr 15:113–120
Olden JD, LeRoy Poff N, Douglas MR et al (2004) Ecological and evolutionary consequences of biotic homogenization. Trends Ecol Evol 19:18–24
Park DS, Razafindratsima OH (2019) Anthropogenic threats can have cascading homogenizing effects on the phylogenetic and functional diversity of tropical ecosystems. Ecography 42:148–161
Pearson RG (2006) Climate change and the migration capacity of species. Trends Ecol Evol 21:111–113
Pielou EC (1975) Ecological diversity. No Title
Polato NR, Gill BA, Shah AA et al (2018) Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. Proc Natl Acad Sci 115:12471–12476
Pontarp M, Bunnefeld L, Cabral JS et al (2019) The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. Trends Ecol Evol 34:211–223

R Core Team (2023) R: A Language and Environment for Statistical Computing.
Ramos-Robles M, Andresen E, Díaz-Castelazo C (2018) Modularity and robustness of a plant-frugivore interaction network in a disturbed tropical forest. Ecoscience 25:209–222
Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. Science 235:167–171
Rolls RJ, Deane DC, Johnson SE et al (2023) Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems. Biol Rev 98:1388–1423
Rolstad J (1991) Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biol J Linn Soc 42:149–163
Sayer CA, Bullock JM, Martin PA (2017) Dynamics of avian species and functional diversity in secondary tropical forests. Biol Conserv 211:1–9
Senior RA, Hill JK, Edwards DP (2019) Global loss of climate connectivity in tropical forests. Nat Clim Change 9:623–626
Sheard C, Neate-Clegg MHC, Alioravainen N et al (2019) The latitudinal gradient in hand-wing-index: global patterns and predictors of wing morphology in birds. Evol Biol. https://doi.org/10.1101/816603
Sheard C, Neate-Clegg MHC, Alioravainen N et al (2020) Ecological drivers of global gradients in avian dispersal inferred from wing morphology. Nat Commun 11:2463
Sherry TW (2021) Sensitivity of tropical insectivorous birds to the anthropocene: a review of multiple mechanisms and conservation implications. Front Ecol Evol 9:662873
Sherry TW (2023) Niche concept scale in space and time: evolutionary perspectives from tropical insectivorous birds. Front Ecol Evol 11:1197920
Sherry TW, Kent CM, Sánchez NV, Şekercioğlu ÇH (2020) Insectivorous birds in the Neotropics: ecological radiations, specialization, and coexistence in species-rich communities. Auk 137:ukaa049
Soares CJRS, Sampaio MB, Santos-Filho FS et al (2019) Patterns of species diversity in different spatial scales and spatial heterogeneity on beta diversity. Acta Bot Bras 34:9–16
Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? Trends Ecol Evol 31:67–80
Stephens SE, Koons DN, Rotella JJ, Willey DW (2004) Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biol Conserv 115:101–110
Stouffer PC (2020) Birds in fragmented Amazonian rainforest: lessons from 40 years at the biological dynamics of forest fragments project. Condor 122:duaa005
Stratford JA, Robinson WD (2005) Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. Front Ecol Environ 3:85–92
Stratford JA, Stouffer PC (1999) Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. Conserv Biol 13:1416–1423
Suárez-Castro AF, Simmonds JS, Mitchell MG et al (2018) The scale-dependent role of biological traits in landscape ecology: a review. Curr Landsc Ecol Rep 3:12–22
Tellería JL, Baquero R, Santos T (2003) Effects of forest fragmentation on European birds: implications of regional differences in species richness. J Biogeogr 30:621–628
Tobias JA, Sheard C, Pigot AL et al (2022) AVONET: morphological, ecological and geographical data for all birds. Ecol Lett 25:581–597
Tscharntke T, Tylianakis JM, Rand TA et al (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87:661–685
Vallejos MAV, Padial AA, Vitule JRS (2016) Human-induced landscape changes homogenize Atlantic forest bird assemblages through nested species loss. PLoS ONE 11:e0147058
Veech JA, Crist TO (2007) Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. Glob Ecol Biogeogr 16:650–656
Vellend M, Verheyen K, Jacquemyn H et al (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87:542–548
Visco DM, Michel NL, Boyle WA et al (2015) Patterns and causes of understory bird declines in human-disturbed tropical forest landscapes: a case study from Central America. Biol Conserv 191:117–129
Walter ST, Browne L, Freile J et al (2017a) Nocturnal bird diversity in forest fragments in north-west Ecuador. J Trop Ecol 33:357–364
Walter ST, Browne L, Freile J et al (2017b) Landscape-level tree cover predicts species richness of large-bodied frugivorous birds in forest fragments. Biotropica 49:838–847
Weeks TL, Betts MG, Pfeifer M et al (2023) Climate-driven variation in dispersal ability predicts responses to forest fragmentation in birds. Nat Ecol Evol 7:1079–1091

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.