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Received: 9 August 2023 | Revised: 20 February 2024 | Accepted: 1 March 2024

DOI: 10.1111/geb.13829

RESEARCH ARTICLE

Global Ecology and Biogeography A Journal of Macroecology WILEY

Evolutionary history and environmental variability structure contemporary tropical vertebrate communities

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Funding information
National Science Foundation, Division of Environmental Biology, Grant/Award Number: DEB-2213568; Norges Forskningsråd, Grant/Award Number: NFR301075

Handling Editor: Alejandro Ordonez

Abstract

Aim: Tropical regions harbour over half of the world's mammals and birds, but how their communities have assembled over evolutionary timescales remains unclear. To compare eco-evolutionary assembly processes between tropical mammals and birds, we tested how hypotheses concerning niche conservatism, environmental stability, environmental heterogeneity and time-for-speciation relate to tropical vertebrate community phylogenetic and functional structure.

Location: Tropical rainforests worldwide.

Time period: Present.

Major taxa studied: Ground-dwelling and ground-visiting mammals and birds.

Methods: We used in situ observations of species identified from systematic camera trap sampling as realized communities from 15 protected tropical rainforests in four tropical regions worldwide. We quantified standardized phylogenetic and functional structure for each community and estimated the multi-trait phylogenetic signal (PS) in ecological strategies for the four regional species pools of mammals and birds. Using

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linear regression models, we test three non-mutually exclusive hypotheses by comparing the relative importance of colonization time, palaeo-environmental changes in temperature and land cover since 3.3 Mya, contemporary seasonality in temperature and productivity and environmental heterogeneity for predicting community phylogenetic and functional structure.

Results: Phylogenetic and functional structure showed non-significant yet varying tendencies towards clustering or dispersion in all communities. Mammals had stronger multi-trait PS in ecological strategies than birds (mean PS: mammal = 0.62, bird = 0.43). Distinct dominant processes were identified for mammal and bird communities. For mammals, colonization time and elevation range significantly predicted phylogenetic clustering and functional dispersion tendencies respectively. For birds, elevation range and contemporary temperature seasonality significantly predicted phylogenetic and functional clustering tendencies, respectively, while habitat diversity significantly predicted functional dispersion tendencies.

Main conclusions: Our results reveal different eco-evolutionary assembly processes structuring contemporary tropical mammal and bird communities over evolutionary timescales that have shaped tropical diversity. Our study identified marked differences among taxonomic groups in the relative importance of historical colonization and sensitivity to environmental change.

KEYWORDS
community assembly, ecological strategies, environmental change, functional similarity, niche evolution, phylogenetic relatedness

1 | INTRODUCTION

Tropical forests harbour more than 60% of global mammal and bird species, of which more than 20% are endemic, and many are threatened by extinction (Pillay et al., 2022). Extinction of tropical mammals and birds will lead to the loss of global functional diversity and evolutionary heritage (Brodie et al., 2021; Toussaint et al., 2021). Understanding how broad-scale tropical biodiversity patterns are structured by both evolutionary and ecological assembly processes in local communities is essential to unravelling the formation of tropical diversity (Gerhold et al., 2018; Mittelbach & Schemske, 2015). Contemporary climate and productivity are important macroecological predictors of mammal and bird species richness (Davies et al., 2011; Hawkins et al., 2007) and their functional similarity (i.e. functional redundancy) under niche conservatism (Cooke, Bates, et al., 2019; Hawkins et al., 2006; Romdal et al., 2013). However, the earlier diversification history and fewer unique ecological strategies of tropical birds relative to mammals indicate there were distinct evolutionary trajectories towards the congruent pattern of functional redundancy between these classes as they were subjected to environmental change since the Cretaceous/Eocene (Cooke, Eigenbrod, et al., 2019; Hawkins et al., 2012). Nevertheless, the relative influence of evolutionary and ecological processes on how contemporary tropical mammal and bird communities are structured remains unknown.

Examining community phylogenetic and functional structure can provide insights into the evolutionary and ecological processes underpinning how deterministic assembly processes form local communities (Cavender-Bares et al., 2009; Kraft et al., 2007; Si et al., 2022). Theory suggests that when niche evolution is conserved (i.e. niche conservatism hypothesis (H_1); Losos, 2008), in the absence of anthropogenetic disturbance, functional structure can be strongly coupled with phylogenetic structure due to species' tendency to retain ancestral traits over evolutionary time. Hence, niche-related assembly processes can shape phylogenetic and functional community structure simultaneously. For instance, competitive exclusion between ecologically similar, closely related species can result in phylogenetic and functional dispersion (Webb et al., 2002). On the other hand, differentiated competitive abilities among ecologically similar, closely related species or strong environmental filtering can result in phylogenetic and functional clustering (Beaudrot et al., 2013; Mayfield & Levine, 2010). However, both mammals and birds have shown trophic evolution towards omnivorous diets (Burin et al., 2016; Price et al., 2012) and ecological convergence among distantly related lineages to adapt to environmental dynamics in the tropics (Pigot et al., 2020; Rovero et al., 2020). The evolution of ecological strategies may not necessarily be conserved in these lineages given character displacement among closely related species and convergent evolution among distantly related species. If niche evolution diverges,

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functional structure does not mimic phylogenetic structure (Münkemüller et al., 2020). Consequently, studying phylogenetic and functional community structure simultaneously while considering niche conservatism allows elucidation of the underlying eco-evolutionary assembly processes shaping extant tropical vertebrate communities.

Multiple major macroevolutionary and macroecological assembly processes have been proposed to structure extant tropical vertebrate communities. Tropical regions are hypothesized to support high species richness due to a long geological history of stable, warm climates and productive forest habitats contributing to low extinction rates in comparison to temperate regions (Pianka, 1966). The hypothesized environmental stability in climate, resources and habitats in the tropics over evolutionary time can support the coexistence of closely related lineages in a community without strong environmental filtering removing lineages with intolerant traits (i.e. stability-diversity hypothesis (H_2); Sandel et al., 2011; Pigot et al., 2016). However, previous studies have found that even within tropical regions, areas with more historical climatic change have filtered out cold- or resource-sensitive lineages based on phylogenetic and functional community structures (Pigot et al., 2016; Rowan et al., 2020). In addition, contemporary environmental variability in climate and resources can constrain the range of ecological strategies related to physiology and resource specialization (Barreto et al., 2021; Toszogyova & Storch, 2019). Hence, historical and contemporary environmental variability can be positively associated with phylogenetic and functional clustering as environmental filtering removes species intolerant to climate and resource variability when the phylogenetic and functional structure are coupled under niche conservatism. On the other hand, greater environmental heterogeneity in elevation and habitat types can also support more distantly related lineages with diverse niches due to greater opportunity for ecological specialization along elevational gradients or among habitat types (i.e. heterogeneity-diversity hypothesis (H_3); Stein et al., 2014; Gerhold et al., 2015). Thus, mammal and bird communities in tropical forests with greater elevation gradients and more habitat diversity should have less phylogenetical and functional clustering due to species turnover when niche evolution is conserved.

Independent of environmental stability, the long geological history of tropical lands without glacier coverages provides extended time for in situ speciation (i.e. the time-for-speciation hypothesis (H_4); Stephens & Wiens, 2003; García-Rodríguez et al., 2021) and colonization events among local communities via range expansion after speciation (Pigot & Etienne, 2015). Hence, when niche evolution is conserved and competitive exclusion is weak, the colonization time of a community can be positively associated with phylogenetic and functional clustering along with more potential events of speciation and colonization of closely related lineages.

Limited in situ observations of elusive and rare vertebrate species in tropical forests have previously hindered our ability to infer assembly processes from realized communities. The in situ communities within protected areas observed by the tropical ecology assessment and monitoring (TEAM) Network provide a great opportunity to elucidate the local assembly processes shaping tropical vertebrate diversity without strong anthropogenetic disturbance. The TEAM Network has conducted standardized camera-trapping to monitor ground-dwelling and ground-visiting mammals and birds in protected tropical rainforests worldwide (Beaudrot et al., 2016; Jansen et al., 2014; Rovero & Ahumada, 2017). Through repeated sampling for up to 7 years, TEAM has extensively surveyed the communities and identified a consistent functional composition among tropical regions (Gorczynski et al., 2021; Rovero et al., 2020).

Here, we aim to unravel the evolutionary trajectories in niche evolution underlying tropical vertebrate phylogenetic and functional structure and identify important evolutionary and ecological processes shaping contemporary tropical mammal and bird communities. Our first objective is to test for niche conservatism (H_1) in driving the degree of niche evolution in ecological strategies underlying the phylogenetic and functional structure of observed tropical mammal and bird communities relative to their regional species pools (objective 1). For objective 1, if niche evolution in ecological strategies has been slow over evolutionary time under niche conservatism, we predict that observed contemporary ecological strategies will derive from earlier speciation in the regional species pools ($P_{1.1}$), and we predict that tropical birds will have stronger imprints of niche conservatism compared to mammals because of the relatively early diversification history of birds compared to mammals ($P_{1.2}$). We also predict a positive link between phylogenetic and functional structure because we expected more closely related lineages to have more similar ecological traits ($P_{1.3}$). Alternatively, if convergent evolution has occurred, we predict that observed contemporary ecological strategies will have been contributed more from recent speciation in the regional species pools, and we predict a negative link between phylogenetic and functional structure ($P_{1.4}$).

Our secondary objective is to test three non-mutually exclusive hypothesized assembly processes in shaping phylogenetic and functional community structure (objective 2): the stability-diversity relationship (H_2), the heterogeneity-diversity relationship (H_3) and time-for-speciation (H_4). We test these assembly processes by comparing the directionality and relative importance of corresponding predictors in explaining phylogenetic and functional structure using regression models separately for tropical mammals and birds. Specifically, when niche evolution of ecological strategies has been slow and the phylogenetic and functional structure is coupled, if the stability-diversity relationship (H_2) is an important assembly process, greater variability of palaeo-environmental changes in temperature and forest loss or contemporary seasonality in temperature and productivity will significantly predict stronger phylogenetic and functional clustering (P_2). If the heterogeneity-diversity relationship (H_3) is an important assembly process, environmental heterogeneity in elevation and habitat will significantly predict lower phylogenetic and functional clustering (P_3). If time-for-speciation (H_4) is an important assembly process, increasing colonization time will relate to greater tip-speciation rates ($P_{4.1}$) and significantly predict stronger phylogenetic and functional clustering among closely related lineages without competitive exclusion ($P_{4.2}$). Important predictors

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shared by tropical mammals and birds indicate congruent evolutionary and ecological processes.

2 | METHODS

2.1 | Community data

Tropical rainforest ground-dwelling and ground-visiting mammal and bird species lists were compiled from in situ observations collected by a standardized camera trapping protocol in 15 protected tropical forests, which were part of the Tropical Ecology Assessment and Monitoring (TEAM) Network (Figure 1a). In each protected tropical forest, the camera traps were deployed at 60 locations 1–2 km apart, with sampling areas estimated by the 2 km convex hull of the camera traps for each TEAM study site spanning 178–369 km2. At each location, a motion-activated camera, Reconyx RM45 or Hyperfire™, was fixed to a tree stem 60 cm above the ground and operated for a minimum of 30 consecutive days per year. The study sites were monitored for at least 2 years and identified by local experts (Jansen et al., 2014). We included the ground-dwelling and ground-visiting species with (1) species-level body mass ≥100 g, (2) spending a large portion of their time on or near ground based on recent functional trait datasets (Soria et al., 2021; Wilman et al., 2014) and (3) located in their native breeding ranges (BirdLife International and Handbook of the Birds of the World, 2018; IUCN, 2014) as the native, residential communities that can be subject to local environmental variability and biotic interactions. Arboreal species detected in five or more photographic events every year in at least one study site were also included (Beaudrot et al., 2016). Mammal communities ranged from 22 species in Manaus to 36 species in Nouabalé Ndoki and bird communities ranged from two species in Bwindi Impenetrable Forest to 17 bird species in Cocha Cashu and Yasuni. The observed species in communities within each tropical region delineated by the phylogenetic relatedness of vertebrates (Holt et al., 2013) were aggregated as each regional species pool to represent the historical dispersers and potential colonizers depending on the biogeographic evolutionary histories (Figure 1a; Figures S1-S8). In total, 170 mammal species from 15 orders (Figure 1b) and 56 bird species from seven orders, mainly non-passerine and non-migratory birds (Figure 1c), were included in this study.

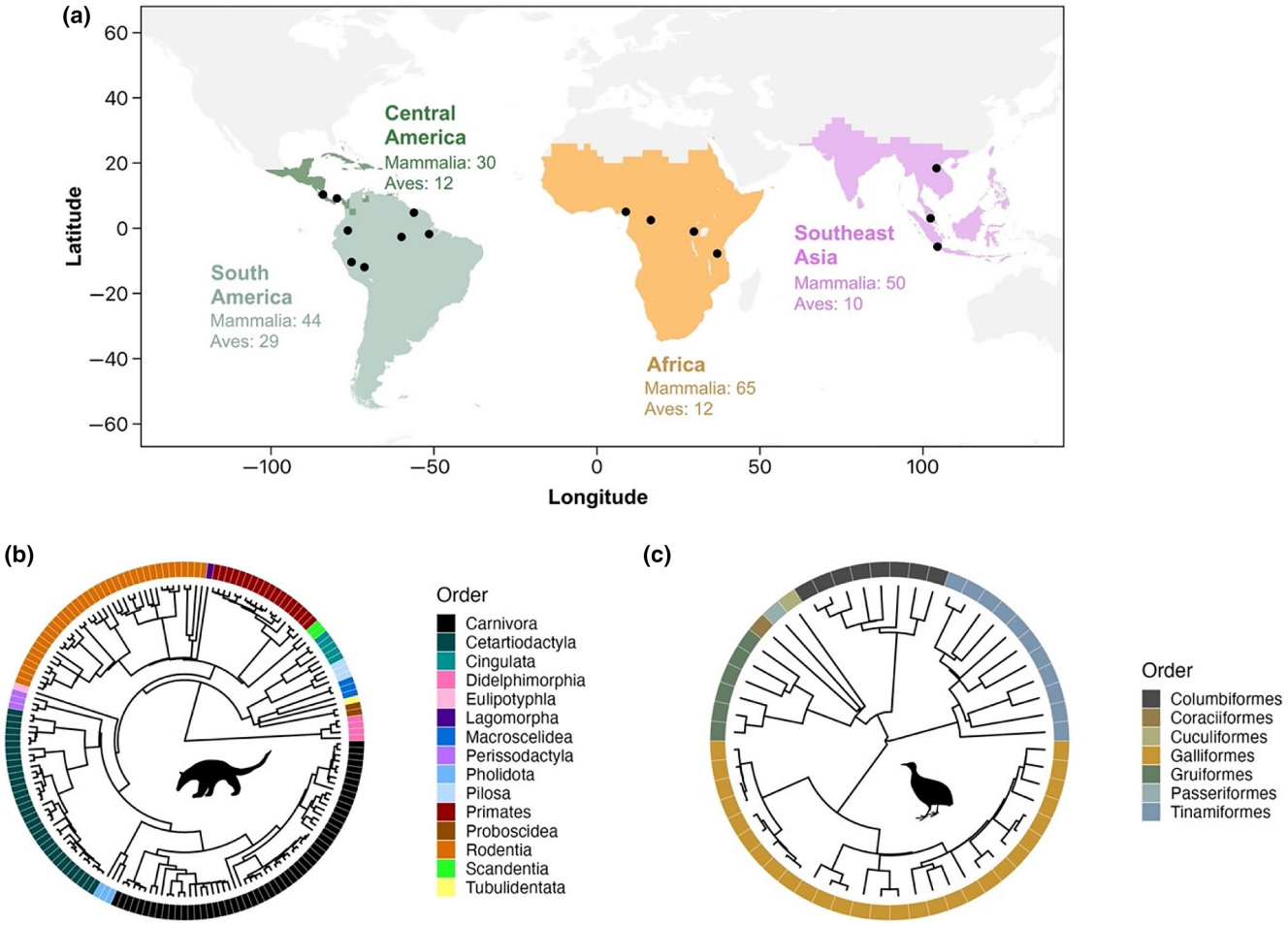

FIGURE 1 (a) Locations of the 15 TEAM study sites from four tropical regions as designated by Holt et al. (2013) with species richness of each regional species pool, and species-level phylogenies of (b) the 170 mammal species and (c) 56 bird species observed in the 15 TEAM study sites. Mammal species consisted of 15 orders and bird species consisted of seven orders.

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2.2 | Phylogenetic signal of niche evolution

For objective 1, we first estimated the degree of niche evolution within regional species pools ($P_{1.1}$). We then ran a Student's *t*-test to test for differences in niche evolution for the regional species pools of birds compared to mammals ($P_{1.2}$). When niches have slowly evolved in the regional species pool under niche conservatism (H_1), the observed ecological strategies across communities in the region would evolve from early speciation and the ecological similarity would be coupled with phylogenetic relatedness in the descending lineages. To quantify the degree of niche evolution, we implemented a recently developed test of phylogenetic signal in multiple traits (i.e. the S3 statistic in Pavoine et al., 2010) to measure the relative contrition of early speciation and later speciation to the ecological strategies of observed tropical mammal and bird communities. Instead of testing the phylogenetic signal of individual traits (e.g. using Blomberg's *K*; Blomberg et al., 2003; or Pagel's λ Freckleton et al., 2002), the S3 statistic applies Rao's *Q* diversity index (Botta-Dukát, 2005) to multiple traits and can accommodate heterogeneous data types. Specifically, multi-trait diversity is decomposed along nodes (i.e. speciation events) as node weights. The node weights are calculated using functional dissimilarity among the descending lineages on the bifurcating phylogenetic trees for each regional species pool. Functional dissimilarity was measured with Rao's *Q* diversity index based on the functional distance of ecological strategies between species in the regional species pool. The S3 statistic quantifies the root/tip skewness of node weights by measuring the summed node weights weighted by their order from the root towards tips on the phylogenetic tree, and it is scaled by the total number of nodes. We applied the modified S3 statistic, scaled to be bounded between zero and one (Prinzing et al., 2021), to calculate multi-trait phylogenetic signal in ecological strategies. Values closer to one indicate a stronger phylogenetic signal under slow niche evolution.

We collected the phylogeny of the regional species pool by trimming the species-level, time-calibrated phylogeny of extant species separately for mammals and birds (hereafter referred to as the complete tree; Jetz et al., 2012; Upham et al., 2019). We used six traits associated with physiology and ecological strategies for resource acquisition: body mass, trophic level, activity cycle, foraging stratum, diet breadth and habitat breadth. Species-level traits were acquired from the latest trait data compilations for mammals (Soria et al., 2021) and birds (Wilman et al., 2014), where the habitat breadth of all missing values for mammals ($N = 2$) and birds ($N = 56$) was acquired from the number of habitat types on IUCN Redlist (https://www.iucnredlist.org) (Table S1). We then measured node weights for the S3 statistics using the R package 'adiv' v2.2 (Pavoine, 2022) for each regional species pool. To account for the uncertainty in tree topology and divergence times, we estimated the means of S3 statistics for each regional species pool over 100 complete trees sampled from the 10-k credible set (Nakagawa & De Villemereuil, 2019).

We assessed potential differences between the degree of niche evolution in the studied regional species pools and the global species pool (Vamosi et al., 2009). Specifically, we compared the estimated multi-trait phylogenetic signals between regional species pools and the global species pool using mammals as an example. The same methods used for the regional species pools were applied to estimate the multi-trait phylogenetic signal in the global mammal species pool ($N = 5257$ mammal species; Table S2) based on 10 complete trees sampled from the 10-k credible set due to the computational time required for each complete tree.

2.3 | Phylogenetic and functional community structure

For objective 1, we next quantified each observed community's phylogenetic and functional structure relative to the null expectation of random composition from its regional species pool using two pairwise distance-based measures of phylogenetic structure and two pairwise distance-based measures of functional structure. We then conducted linear regression models to test for niche conservatism and convergence based on the relationship between phylogenetic and functional structure ($P_{1.3}$).

With the same phylogeny of the regional species pool used in estimating the degree of niche evolution in ecological strategies, we measured the regional pairwise phylogenetic distance based on branch length for all species in the regional species pool separately for mammals and birds. For each community, we extracted the pairwise phylogenetic distance in the regional species pool based on species occurrence. The phylogenetic structure was then first measured by the mean pairwise phylogenetic distance among all species pairs (MPD) from the root across the community phylogeny to represent phylogenetic relatedness shaped by historical speciation and colonization events and local environmental change over deep time. Second, we measured mean phylogenetic distance only among the nearest species pairs (MNPD) to represent the phylogenetic relatedness shaped by recent speciation and colonization events, contemporary environmental variability and biotic interactions (Webb et al., 2002).

The functional structure was quantified in a comparable way to the phylogenetic structure by measuring the mean distance first among all species pairs (MFD) to represent the overall ecological similarity and second only among the nearest species pairs (MNFD) to indicate the ecological similarity among the most ecologically similar species pairs. With the same traits used in estimating the degree of niche evolution in ecological strategies, we measured the pairwise Gower's distance for all species in the regional species pool. For each community, we extracted the pairwise Gower's distance in the regional species pool based on species occurrence.

We measured the standardized effect sizes of the four distance-based indices to quantify comparable community structure independent of species richness and regional biogeographic histories. The standardized effect sizes (SESs) of MPD, MNPD, MFD and MNFD for each community were measured as (observed mean distance − $\text{mean}_{\text{null values}}$)/$\text{SD}_{\text{null values}}$, which is analogous to normalized

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Z-scores. The null values were generated by shuffling each community's taxa labels across its regional pairwise distance matrix of phylogeny or functional positions 10,000 times to randomize the evolutionary relatedness and functional similarity while maintaining the spatial occurrence and species richness (Swenson, 2014). The SESs will reflect the relative structure of communities after accounting for species richness and biogeographic histories and allow for comparing relationships with local evolutionary and environmental predictors across tropical regions. Negative SESs indicate the tendency for clustering of more closely related or functionally similar species within a local community for phylogenetic or functional measurements respectively. Positive SESs show the tendency for dispersion of more distantly related or functionally dissimilar species in a local community. For the nominal significance level of 0.05, SESs > 1.96 indicate significantly overdispersed and SESs < −1.96 indicate significantly clustered community structure relative to random composition from regional species pools.

We used R packages 'ape' v5.7–1 (Paradis et al., 2023) and 'mFD' v1.0.6 (Magneville et al., 2023) to measure pairwise phylogenetic distance and Gower's distance respectively. The SESs of the four indexes were quantified by R package 'picante' v1.8.2 (Kembel et al., 2020) with null values generated by the randomization method of taxa label shuffling over 10,00 times. To account for the uncertainty in tree topology and divergence times, we also estimated the means of each community's SES.MPD and SES.MNPD over the 100 complete trees sampled from the 10-k credible set.

To assess potential differences in community phylogenetic structure based on the studied regional species pools compared to the global species pool (Vamosi et al., 2009), we compared the estimated community phylogenetic structure relative to the regional species pools and the global species pool using mammals as an example. We applied the same methods for the regional species pools to estimate the standardized effect sizes of the two phylogenetic structures relative to the global mammal species pool ($N = 5257$ mammal species; Table S2) based on 10 complete trees sampled from the 10-k credible set.

2.4 | Evolutionary and environmental predictors

For our second objective, we used linear regression to test the relative importance of the stability-diversity relationship (H_2), the heterogeneity-diversity relationship (H_3) and time-for-speciation (H_4) in assembling vertebrate communities.

To test the hypothesized stability-diversity relationship (H_2), we quantified palaeoenvironmental changes in temperature and historical forest loss, and contemporary variability in temperature and productivity. To test the hypothesized heterogeneity-diversity relationship (H_3), we measured environmental heterogeneity based on topography and habitat diversity. These environmental predictors were extracted by overlaying global maps with a two-km convex hull around the periphery of the camera trap array for each TEAM study site. Palaeoenvironmental changes in temperature over geological time were measured as the temperature variability (i.e. coefficient of variation, CV) in annual mean temperature over 12 time periods since 3.3 Mya (Figure S9) using the bioclimatic map from PaleoClim.org at 2.5 arcmins (Brown et al., 2018). Palaeoenvironmental changes in forest cover were measured as differences in land-cover rank between 2015 and prehistorical time 10,000 BC (i.e. Holocene) from the reconstructed land-use maps from HYDE 3.2 (Klein Goldewijk et al., 2017) at 5 arcmins. We reclassified the land-cover types as the rank defined by Rowan et al. (2020): one for natural forests, two for semi-natural forests, three for range lands, four for croplands, five for villages and six for urban and dense settlements. Lower difference values since prehistorical time represent less disturbance in forest coverage.

Contemporary environmental variability was estimated from the mean and seasonality of annual temperature and productivity. We collected the seasonality of annual temperature from the bioclimatic map for 1979–2013 (Karger et al., 2017) at 2.5 arcmins. For productivity, we estimated the mean and seasonality as the CV from the monthly mean values with the vegetation index of enhanced vegetation index (EVI), which were compiled from the 16-day products of the Terra Moderate Resolution Imaging Spectroradiometer at 250 m from 2000 to 2015 (Didan, 2015). EVI has been broadly used to estimate ecosystem productivity (Huete et al., 2002) and better detects seasonality in dense tropical forests than the normalized difference vegetation index (NDVI; Figueira Branco et al., 2019; Sarmah et al., 2018).

Elevational range and habitat diversity have been recognized as important environmental predictors for community assembly. We measured elevational ranges with the digital elevation map from the Shuttle Radar Topography Mission dataset at 3 arcseconds (Jarvis et al., 2008). We estimated the habitat diversity as the Shannon index of habitat types from the IUCN level 2 habitat map (Jung et al., 2020), generated by the global land-cover map in 2015 at ~100 m resolution. The habitat types include human-altered habitats, such as arable lands, rural and urban areas. Greater Shannon index values of habitat diversity thus represent more habitat types other than tropical rainforests. The environmental predictors of EVI and elevation range were extracted through Google Earth Engine and the others with the R package 'terra' v 1.7–46 (Hijmans et al., 2023).

To test the time-for-speciation hypothesis (H_4), we quantified the maximum time for the niche evolution of endemic lineages and colonizers by estimating colonization time as the stem age of each community (Benício et al., 2021; García-Rodríguez et al., 2021). To investigate whether the colonization time was positively related to in situ speciation events at local communities, we further estimated the tip speciation rate for each community by averaging the species-level lineage speciation rate of all species in a community (i.e. the DR metric in Jetz et al., 2012) as a proxy for the recent speciation rate (Title & Rabosky, 2019). The DR metric was measured by the branch lengths and the number of speciation events from the tip towards the root of the complete tree for a focal species, with more weights distributed to branches close to the tip. Hence, a greater value of the mean tip speciation rate of a community suggests

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the potential for greater speciation rates in the local area (García-Rodríguez et al., 2021). We measured the colonization time and the mean tip speciation rate for each community over 100 sampled trees and tested their relationships using linear regression models. Summary statistics for the evolutionary and environmental predictors can be found in the Table S3.

2.5 | Regression modelling

For objective 2, we applied a global linear regression model with model selection on all possible combinations of evolutionary and environmental predictors of community structure. We separately modelled the four measures of community structure for mammals and birds as response variables for a total of eight global regression models. The predictors included temperature variability since 3.3 Mya, forest cover change since the Holocene, contemporary temperature seasonality, mean contemporary productivity, contemporary productivity seasonality, elevation range, contemporary habitat diversity and colonization time. None of the predictors were strongly co-linear (i.e. correlation coefficient ≤0.7; Dormann et al., 2013; Figure S10). We standardized the predictors in models and compared models using Akaike's Information Criterion corrected for a small sample size (AICc). When the model weight of the best model with the lowest AICc was smaller than 0.9 and there were multiple candidate models with delta AICc <2, we applied a model-averaging approach to the model set containing the top 95% of model weights (Burnham & Anderson, 2002). Model averaging allowed us to measure the relative effect sizes of predictors weighted by the summed model weights of the models in which the predictor was included. The relative importance of predictors was then assessed based on their significance and the summed model weights of each predictor. All model selection and averaging were conducted with the R package 'MuMIn' v1.47.5 (Bartoń, 2022). All visualizations were done using the R packages 'ggplot2' v3.4.3 (Wickham et al., 2023) and 'ggtree' v 3.8.2 (Yu et al., 2017) when related to phylogeny.

3 | RESULTS

3.1 | The degree of niche evolution underlying regional species pools and community structure

Our first objective was to test for niche conservatism (H_1) in the ecological strategies underlying the phylogenetic and functional structure of observed tropical mammal and bird communities relative to their regional species pools. None of the multi-trait phylogenetic signal values were near one ($P_{1.1}$). In contrast to our expectations ($P_{1.2}$), we did not identify a significant difference between mammals and birds in the multi-trait phylogenetic signals of observed ecological strategies ($t = 2.65$, $p = 0.063$; Figure 2a). Furthermore, the regional

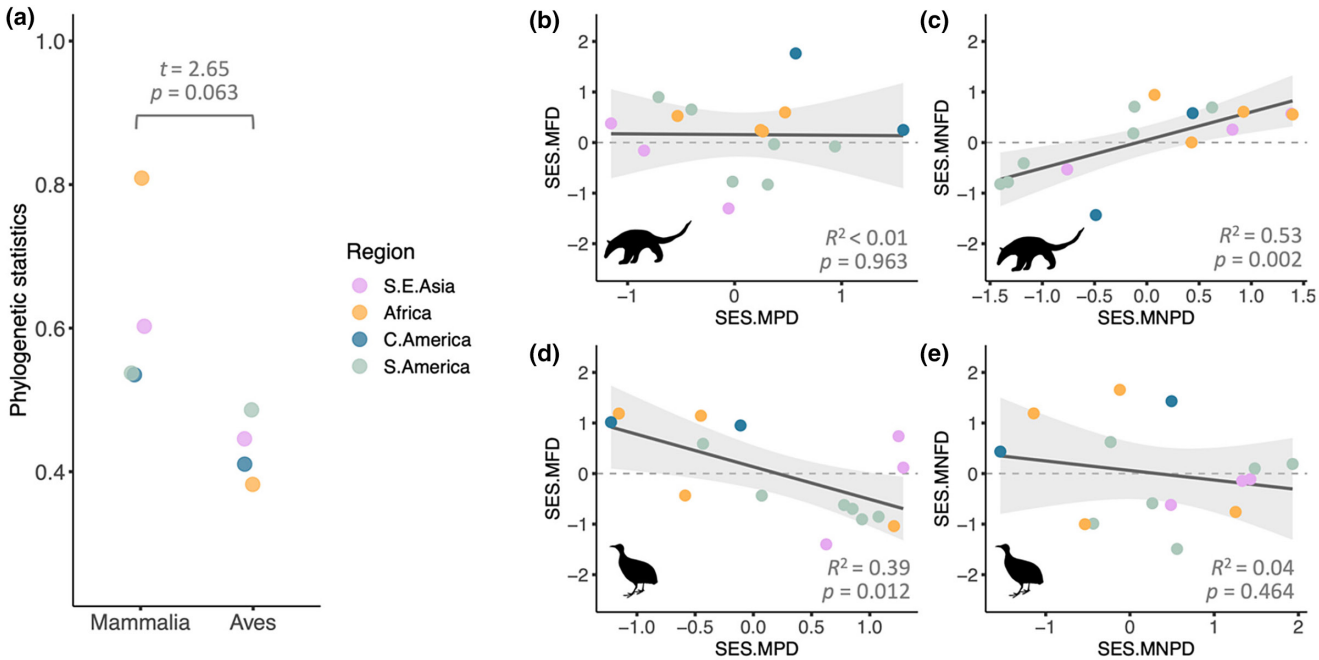

FIGURE 2 The degree of niche conservatism within regional species pools and in mammal and bird communities. Panel (a) shows values of the multi-trait phylogenetic signal of the regional species pools, with the *t*-value and *p*-value from the Student's *t*-test for differences in regional multi-trait phylogenetic signals between mammals and birds. Multi-trait phylogenetic signal values near one suggest slow niche evolution and therefore niche conservatism, whereas values near zero suggest rapid niche evolution. The relationship between standardized effect sizes of the root-level functional structure (SES.MFD) and phylogenetic structure (SES.MPD) (b, d) and the tip-level functional structure (SES.MNFD) and phylogenetic structure (SES.MNPD) (c, e) for (b, c) mammal and (d) bird communities, which display linear regression estimates with 95% confidence intervals, *R*-squared values and *p*-values.

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species pools for mammals generally had higher multi-trait phylogenetic signals (mean = 0.62, ranging from 0.53 to 0.81) than birds (mean = 0.43, ranging from 0.39 to 0.49). The multi-trait phylogenetic signal values of the regional mammal species pools were also higher compared to their global species pool (Figure S1).

Both mammal and bird communities showed highly variable, non-significant tendencies towards clustering and dispersion in phylogenetic and functional structure at both the root level and the tip level relative to the regional species pools (Figure S12). The root-level standardized effect sizes (SESs) of phylogenetic structure (SES.MPD) ranged from −1.16 to 1.58 for mammals and from −1.22 to 1.29 for birds. The tip-level SESs of phylogenetic structure (SES.MNPD) ranged from −1.40 to 1.39 for mammals and from −1.54 to 1.93 for birds. The phylogenetic structure values for SES.MPD and SES.MNPD relative to the regional species pool showed weaker clustering tendencies than those relative to the global species pool of mammals (Figure S13). The root-level SESs of functional structure (SES.MFD) ranged from −1.30 to 1.76 for mammals and from −1.40 to 1.19 for birds. The tip-level SESs of functional structure (SES.MNFD) ranged from −1.43 to 0.94 for mammals and from −1.49 to 1.66 for birds.

Mammal communities did not have a significant relationship between root-level phylogenetic and functional structure (est. = −0.01, SE = 0.29, $p = 0.963$; Figure 2b) but showed a significant positive relationship between tip-level phylogenetic and functional structure (est. = 0.56, SE = 0.14, $p = 0.002$; Figure 2c; $P_{1.3}$). On the other hand, bird communities had a significant negative relationship between the root-level phylogenetic and functional structure (est. = −0.64, SE = 0.22, $p = 0.012$) (Figure 2d; $P_{1.4}$) but did not have a significant relationship between the tip-level phylogenetic and functional structure (est. = −0.19, SE = 0.25, $p = 0.464$; Figure 2e).

3.2 | Eco-evolutionary predictors of tropical vertebrate community structures

For objective 2, we tested three non-mutually exclusive assembly processes (i.e. stability-diversity (H_2), heterogeneity-diversity (H_3) and time-for-speciation (H_4)) in shaping the phylogenetic and functional structure of tropical mammal and bird communities separately using linear regression models. Among our study sites, we did not identify significant associations between colonization time and tip speciation rates for either mammal or bird communities (est. = 0.0003, SE = 0.0002, $p = 0.16$ for mammals; est. = −0.001, SE = 0.0008, $p = 0.15$ for birds; Figure S14; $P_{4.1}$). For tropical mammal communities, model-averaged results showed that only colonization time significantly predicted phylogenetic structure and only elevation range significantly predicted functional structure (Figure 3; Table S4). Coloniztion time was positively associated with a tendency for tip-level phylogenetic clustering (est. = −0.55, 95% CI of −1.04 and −0.05; Figure 3b; $P_{4.2}$), while elevation range was positively associated with a tendency for root-level functional dispersion (est. = 0.46, 95% CI of 0.12 and 0.80; Figure 3c; P_3).

For tropical bird communities, the model-averaged results show that only elevation range significantly predicted phylogenetic structure, while contemporary temperature seasonality and habitat diversity significantly predicted functional structure (Figure 4; Table S5). Specifically, elevation range was positively associated with a tendency for tip-level phylogenetic clustering (est. = −0.60, 95% CI of −1.13 and −0.07; Figure 4b; P_3). For functional structure, temperature seasonality was positively related to a tendency for root-level clustering (est. = −0.43, 95% CI of −0.75 and −0.10; Figure 4c; P_2). Habitat diversity was positively associated with a tendency for functional dispersion at both the root level (est. = 0.64, 95% CI of 0.27 and 1.02; Figure 4c) and the tip level (est. = 0.61, 95% CI of 0.13 and 1.10; Figure 4d; P_3).

For both mammals and birds, all predictors had summed model weights larger than zero, and significant predictors had the greatest importance based on their summed model weights (Figure 5; Table S6). We further identified non-significant predictors with high importance as those with summed model weights (sw) greater than 0.5 and we consider these to be secondary predictors of community structure. For tropical mammals (Figure 5a), productivity means and colonization time were secondary predictors of the root-level phylogenetic structure (sw = 0.62 and 0.56 respectively). Mean productivity was positively associated with a tendency for root-level phylogenetic clustering (est. = −0.44, 95% CI of −0.88 and 0.004; P_2), whereas colonization time was positively related to a tendency for root-level phylogenetic dispersion (est. = 0.38, 95% CI of −0.01 and 0.77; $P_{4.2}$). Temperature variability since 3.3 Mya was a secondary predictor of tip-level phylogenetic structure (sw = 0.53) associated with a tendency for clustering (est. = −0.42, 95% CI of −0.88 and 0.04; P_2). Land cover change since the Holocene was a secondary predictor of the root-level functional structure (sw = 0.72) associated with a tendency for clustering (est. = −0.40, 95% CI of −0.81 and 0.005; P_2). Contemporary seasonality in temperature and productivity, as well as habitat diversity, had low importance in assembling mammal community structure.

For tropical birds (Figure 5b), elevation range was the only secondary predictor of root-level phylogenetic structure (sw = 0.63) and was associated with a tendency for clustering (est. = −0.47, 95% CI of −0.94 and 0.003; P_3). Palaeoenvironmental changes, contemporary productivity means and seasonality and colonization time had low importance in assembling bird community structure.

4 | DISCUSSION

We aimed to identify the ecological and evolutionary processes that have structured contemporary mammal and bird diversity from local communities in the wet tropics. By incorporating in situ observations, we are the first to quantify the mammal and bird phylogenetic and functional structure of realized communities throughout the tropics. To circumvent the potential pitfalls of inferring eco-evolutionary processes from phylogenetic and functional community structure, we comprehensively examined the degree of niche evolution underlying

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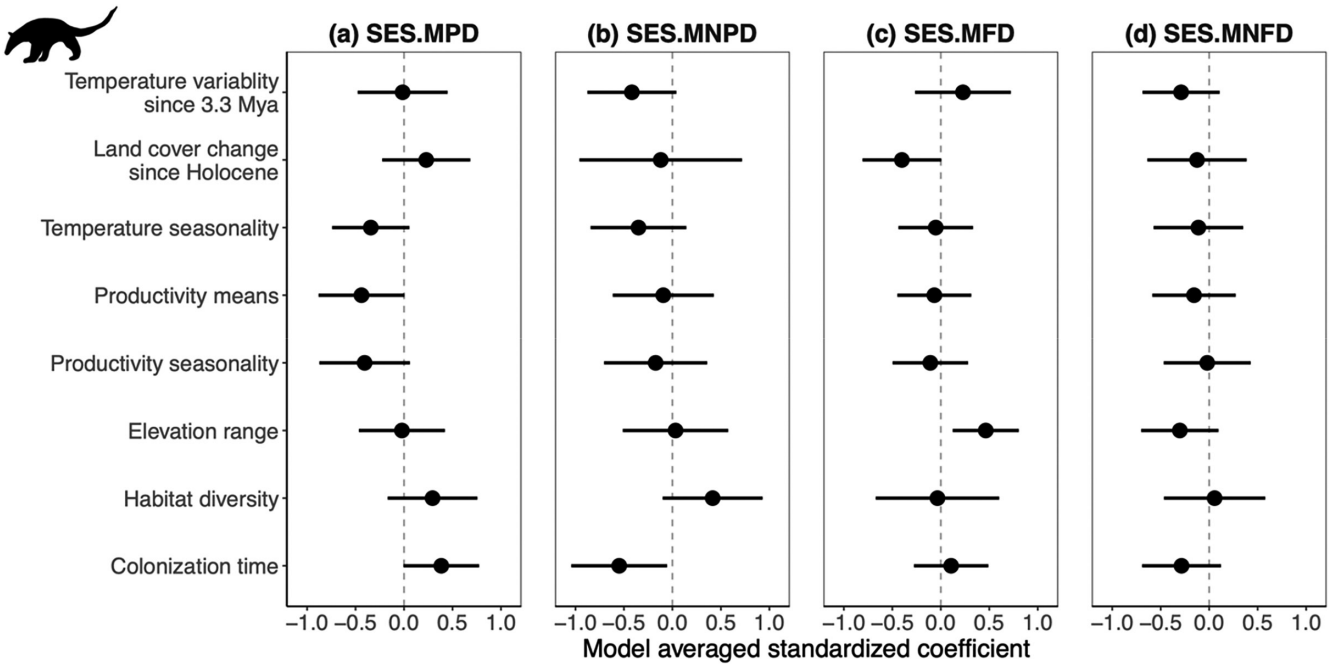

FIGURE 3 Standardized coefficient plots for tropical mammal phylogenetic structure (a) at the root level (SES.MPD) and (b) at the tip level (SES.MNPD) and functional structure (c) at the root level (SES.MFD) and (d) at the tip level (SES.MNFD). Estimates are averaged based on the 95% confidence set of models for the standardized effect sizes for each measure of community structure. The points represent the coefficient estimates with 95% confidence intervals. Silhouette of *Tamandua mexicana* acquired from PHYLOPIC http://phylopic.org/ under the Public Domain Mark 1.0 licence.

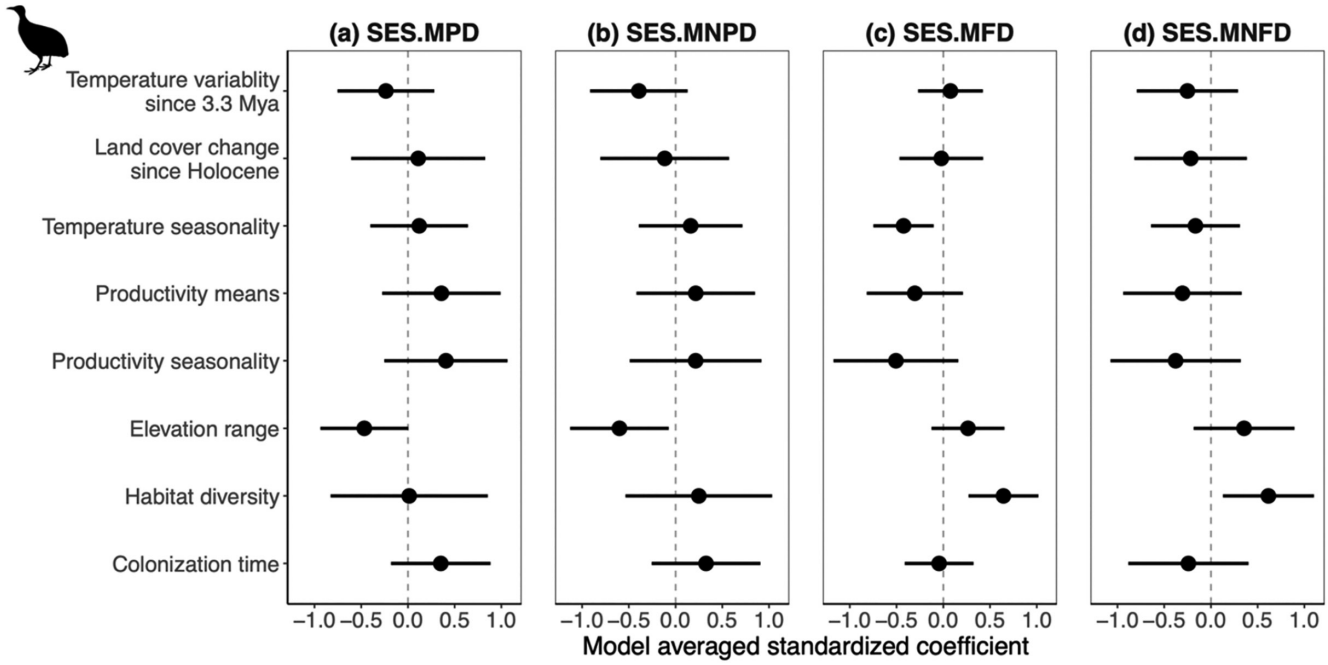

FIGURE 4 Standardized coefficient plots for tropical bird phylogenetic structure (a) at the root level (SES.MPD) and (b) at the tip level (SES.MNPD) and functional structure (c) at the root level (SES.MFD) and (d) at the tip level (SES.MNFD). Estimates are averaged based on the 95% confidence set of models for the standardized effect sizes for each measure of community structure. Silhouette of *Tinamus major* acquired from PHYLOPIC http://phylopic.org/ under the Public Domain Mark 1.0 licence.

regional species pools and community structure (objective 1). In contrast to previous work that has investigated niche evolution on ecological traits separately (e.g. Olalla-Tárraga et al., 2017), this is the first study to examine niche evolution in the diversity of ecological strategies based on multiple ecological traits and to identify the distinct macroevolutionary trajectories of ecological strategies

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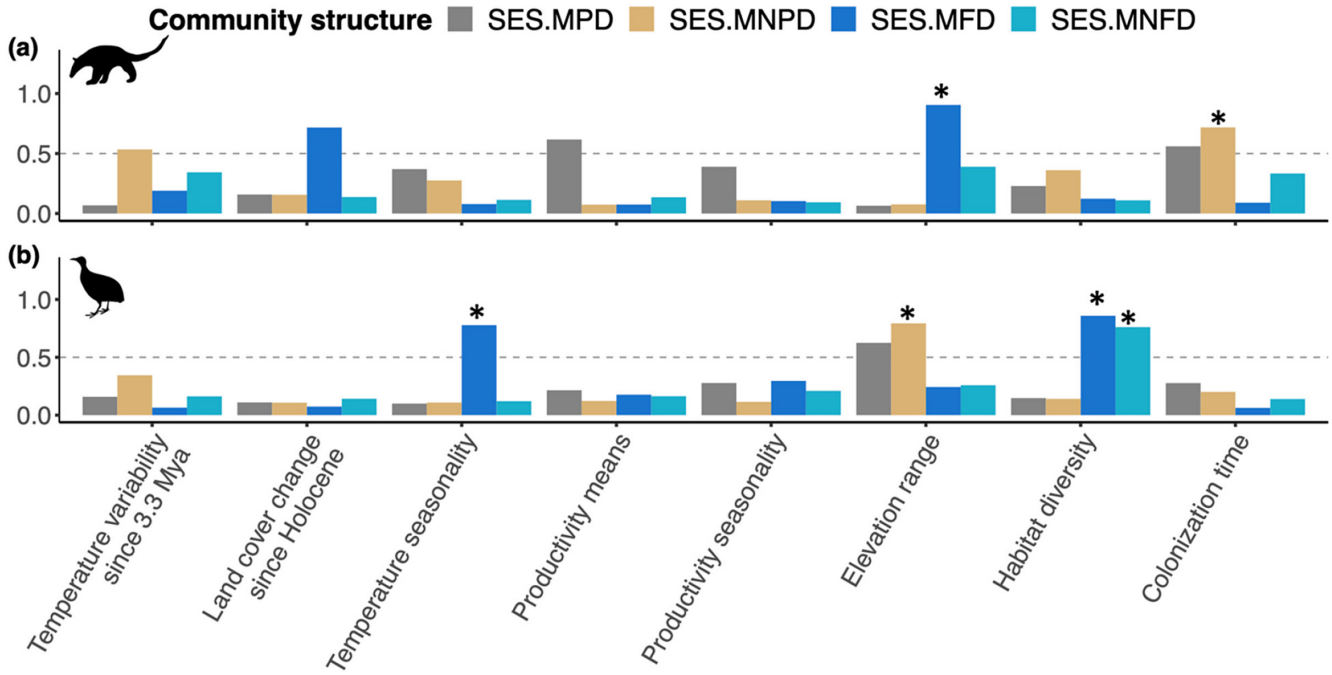

FIGURE 5 Relative importance of the eight evolutionary, palaeo-environmental and contemporary environmental predictors in the averaged models of phylogenetic structure at the root level (SES.MPD) and the tip level (SES.MNPD) and functional structure at the root level (SES.MFD) and the tip level (SES.MNFD) for tropical ground-dwelling and ground-visiting (a) mammals and (b) birds. Asterisks indicate significant predictors with *p*-value less than 0.05. Silhouettes of *Tamandua Mexicana* and *Tinamus major* acquired from PHYLOPIC http://phylopic.org/ under the Public Domain Mark 1.0 licence.

underlying community structure between mammals and birds. We further broaden the depth of major macroecological hypotheses into deeper time by integrating reconstructed environmental data for palaeo-environmental changes in climate and human-altered land cover while accounting for macroevolutionary processes (objective 2). Our findings provide evidence that contemporary assemblages of tropical vertebrates have imprints of historical assembly processes over evolutionary scales, with distinct eco-evolutionary processes assembling contemporary tropical mammals versus birds.

4.1 | Distinct evolutionary histories underlying tropical mammal and bird communities

In testing the degree of niche evolution underlying regional species pools, we did not find that observed ecological strategies were derived from ancient speciation, given that the multi-trait phylogenetic signal values were not close to one for either mammals or birds (Figure 2a). In contrast to our prediction ($P_{1.1}$), these results suggest the diversity of observed ecological strategies in each regional species pool has not been predominately retained from ancient lineages for mammals or birds. Furthermore, in contrast to our expectations that birds would exhibit stronger niche conservativism than mammals given their relatively earlier diversification history ($P_{1.2}$), birds tended to have lower multi-trait phylogenetic signal values than mammals, suggesting that their avian ecological strategies have evolved from even more recently descended lineages.

Opposite relationships between phylogenetic and functional structure for mammals and birds further document distinct evolutionary histories of niche evolution for these taxa (Figure 2b–e). For mammals, the positive association between tip-level phylogenetic and functional structure supports the prediction for niche conservatism ($P_{1.3}$) that niche evolution has been slow among the closely related descending lineages of the ancient lineages, leading to the coupled phylogenetic and functional structure at the tip level. For birds, the negative relationship between the root-level phylogenetic and functional structure and the relatively lower multi-trait phylogenetic signal values suggests convergent evolution in the ancient lineages, leading to the decoupled phylogenetic and functional structure. Unlike the potentially conserved climatic niches of vertebrates associated with stable climate in the tropics (Khaliq et al., 2015, but see Bennett et al., 2021; Rolland et al., 2018), our findings suggest that different taxonomic groups that co-exist in species-rich tropical regions have diverged along dietary and foraging strategy axes with varying evolutionary rates. For instance, the ground-dwelling and -visiting non-passerine birds in our study convergently evolved towards omnivorous diets (Figures S5-S8) to coexist in the communities (Burin et al., 2016).

We found higher estimates of multi-trait phylogenetic signal in the regional species pools with pruned phylogenetic trees than in the global species pool with the complete phylogenetic tree of mammals (Figure S11). This study focused on ground-dwelling and ground-visiting mammals and birds larger than 100 g and their ecological strategies related to dietary and habitat breadth. However,

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using mammals as an example, the complete phylogenetic tree encompasses more variation in ecological strategies than the focal species have, such as unique strategies found outside of tropical forests and additional variation in foraging strata (e.g. fossorial, arboreal and volant mammals; Cooke, Eigenbrod, & Bates, 2019). The higher multi-trait phylogenetic signal value in the regional species pools compared to the global species pool of mammals suggests that the ecological strategies of ground-dwelling and ground-visiting mammals are more conserved with a lower degree of niche evolution than the global species pool.

4.2 | Eco-evolutionary processes assembling mammal communities

By using a null model approach to quantify community structure and taking account of each regional species pool, we identified highly variable phylogenetic and functional community structure with tendencies spanning dispersion and clustering for both mammals and birds within each tropical region. Vamosi et al. (2009) previously documented that stronger clustering is more likely to be observed when local community structure is compared to global phylogenetic structure. Similarly, we found stronger tendencies in phylogenetic clustering relative to the global species pool compared to those relative to the regional species pools (Figure S13). Within each region, the inconsistent phylogenetic and functional community structure suggests varying evolutionary and ecological processes assembling communities differently among locations relative to its regional evolutionary history. For tropical mammal communities, we found that the dominant eco-evolutionary assembly processes were related to colonization time for the tip-level phylogenetic structure and elevation range for the root-level functional structure. In our study, colonization times were not significantly associated with the estimated tip speciation rates among mammal communities as predicted ($P_{4.1}$), suggesting that colonization time can be related to the chance of speciation and colonization events in the regional species pools (i.e. speciation in the regional species pool and range expansion towards communities) rather than the potential of in situ speciation in communities over evolutionary time (i.e. in situ speciation and range restriction in the community; Pigot & Etienne, 2015). Partially supporting the time-for-speciation hypothesis ($P_{4.2}$), the significant positive association of colonization time with the tendency for clustering in the tip-level phylogenetic structure suggests more colonization events for closely related species to colonize local communities after the speciation of ancient lineages in the regional species pools. The significant positive association of elevation range with the tendency for root-level functional dispersion supports the heterogeneity-diversity relationship (P_3) in supporting more ecologically diverse species along a greater elevational gradient of the ancient lineages. This can be related to functional turnover, which has been observed in small mammals and passerine birds (Presley et al., 2012), or the coexistence of ecologically diverse species without elevational specialization (Laurance et al., 2011).

We also identified secondary predictors (i.e. non-significant but of high importance) for the root-level phylogenetic structure, with mean productivity associated with the tendency for clustering and colonization time associated with the tendency for dispersion. Partially supporting the stability-diversity hypothesis (P_2), mean productivity was positively associated with the tendency for root-level phylogenetic clustering but not functional clustering, which suggests a minor contribution of resource availability to the persistence of closely related lineages. The positive effects of colonization time on root-level phylogenetic dispersion tendencies, rather than clustering tendencies ($P_{4.2}$), may relate to the persistence of ancient lineages and distantly related colonizers over colonization time. For instance, the mammal communities in this study included ancient lineages of Marsupials in America and Placentalia that diverged in the Cretaceous (~160 Mya) and lineages that radiated after the Palaeogene (~66 Mya) (Davies & Buckley, 2011; Grossnickle et al., 2019; O'Leary et al., 2013).

Temperature variability since 3.3 Mya was a secondary predictor for tip-level phylogenetic structure and was positively related to the tendency for clustering. Supporting the stability-diversity hypothesis (P_2), temperature variability since 3.3 Mya indicates a minor contribution of historical environmental filtering for lineages tolerant to temperature fluctuations over evolutionary time. As predicted for the stability-diversity hypothesis (P_2), land cover change since the Holocene was a secondary predictor for the tendency for root-level functional clustering, suggesting there has been filtering for species tolerant to forest loss.

4.3 | Eco-evolutionary processes assembling bird communities

The important eco-evolutionary assembly processes for tropical bird communities were distinct from those of mammal communities. We found that the dominant predictors for bird community structure were elevation range for the tendency for tip-level and root-level phylogenetic clustering, temperature seasonality for the tendency for root-level functional clustering and habitat diversity for the tendency for functional dispersion. In contrast to the heterogeneity-diversity relationship (P_3), elevation range was positively associated with the tendency for tip-level phylogenetic clustering, suggesting filtering for non-passerine, ground-dwelling birds, which differs from what has been observed in passerine birds. Specifically, phylogenetic and functional turnover and rapid in situ diversification of immigrant lineages across climatic zones have been observed in passerine birds in tropical mountains (Fjeldså et al., 2012; Jarzyna et al., 2021). Instead, our findings of a greater degree of niche evolution and convergent evolution underlying the phylogenetic and functional structure of non-passerine birds suggest colonization of early immigrant non-passerine birds that adapted to broad niches along elevational gradients. Hence, elevational gradients played a different role in shaping the functional structure of bird communities than mammal communities.

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For functional structure, temperature seasonality was associated with the tendency for root-level functional clustering, which supports the stability-diversity hypothesis (P_2) that contemporary climatic variability filters for tolerant species. These tolerant species can be from lineages with varying phylogenetic relatedness under convergent evolution, consistent with the observed greater degree of climatic niche evolution (Rolland et al., 2018). Furthermore, the contemporary climatic stability filter on bird functional structure suggests greater sensitivity to climatic changes compared to mammals. On the other hand, habitat diversity associated with the tendency for functional dispersion at both the root and tip levels supports the heterogeneity-diversity relationship (P_3). More ecologically dissimilar bird species can be supported by diverse habitat types given their narrower habitat breadth relative to mammals in our study. This finding indicates that habitat homogenization may be a stronger filter for birds. The documented climatic stability filter and habitat diversity effects on bird functional structure suggest that ongoing deforestation and climate change may interrupt the processes maintaining tropical vertebrate diversity (Barlow et al., 2018; Hoang & Kanemoto, 2021).

5 | CONCLUSION

Our study has revealed distinct ecological and evolutionary processes that have shaped tropical forest mammal and bird communities. We identified differing niche evolution trajectories for tropical mammals and birds based on opposing associations between their phylogenetic and functional structure. We then documented distinct evo-ecological processes assembling mammal and bird communities. For tropical mammals with slower niche evolution in ecological strategies, the important assembly processes were time for speciation and colonization in regional species pools, palaeoenvironmental variability, contemporary resource availability supporting more lineages and elevation gradients supporting functional turnover. In contrast, for non-passerine birds with convergently evolved lineages, elevation, temperature variability and habitat diversity acted as environmental filters. Our findings provide insight into the distinct evolutionary histories of niche evolution and eco-evolutionary assembly processes for tropical mammals and birds. Future studies should consider the evolutionary histories underlying community structure and eco-evolutionary assembly processes for assessing vertebrate communities' responses to ongoing environmental changes.

AUTHOR CONTRIBUTIONS

CH conceptualized the study, collected environmental and phylogenetic data and led the data analysis and manuscript writing. DG supervised the functional data collection and analysis and provided feedback on the manuscript. RB, SE, SJ, MGML, FR, JS, FS and DS provided data curation and management and provided feedback on the manuscript. LB advised the project and contributed to the writing.

ACKNOWLEDGEMENTS

All camera-trapping data were collected by the Tropical Ecology Assessment and Monitoring Network, previously a collaboration between Conservation International, the Smithsonian Institute and the Wildlife Conservation Society. We gratefully thank all TEAM funders, staff and contributors. We thank Dr. Amy Dunham, Dr. Kory Evans, Dr. Santiago Segarra and Dr. Tom Miller for feedback and discussion. This work was supported by the National Science Foundation grant (DEB-2213568 to L.B.) and the Research Council of Norway (project NFR301075 to D.S. and L.B.).

CONFLICT OF INTEREST STATEMENT

We have no competing interests to declare.

DATA AVAILABILITY STATEMENT

Raw camera-trap data from the TEAM Network are available at Wildlife Insights (https://www.wildlifeinsights.org). The data produced from this study and the R code to reproduce the analyses and figures are archived onthe Dryad Digital Repository at https://doi.org/10.5061/dryad.ht76hdrpm.

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BIOSKETCH

The author team is a group of ecologists who are interested in large-scale patterns of tropical vertebrate diversity under environmental changes.

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How to cite this article: Hsieh, C., Gorczynski, D., Bitariho, R., Espinosa, S., Johnson, S., Lima, M. G. M., Rovero, F., Salvador, J., Santos, F., Sheil, D., & Beaudrot, L. (2024). Evolutionary history and environmental variability structure contemporary tropical vertebrate communities. *Global Ecology and Biogeography*, *00*, e13829. https://doi.org/10.1111/geb.13829

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