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Using functional and phylogenetic diversity to infer avian community assembly along elevational gradients

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Abstract

Aim: We present the first global analysis of elevational gradients in functional and phylogenetic diversity of birds and test for signals of deterministic processes (i.e., environmental filtering and limiting similarity) in community assembly. Further, we examine for latitudinal effects in the strength of these processes.

Location: Forty-six elevational gradients across the globe.

Time period: Current (between 1924 and 2016).

Major taxa: Birds.

Methods: We systematically selected, compiled and analysed published data on bird diversity along elevational gradients. For each gradient, we calculated functional and phylogenetic diversity across elevations and described the main patterns for each diversity metric. Then, we calculated standardized effect sizes (SES) of each metric and used these SES values to (a) test the signals of deterministic processes shaping assemblages across elevations and (b) to compare changes in within-mountain diversity, among mountains located at different latitudes.

Results: Birds displayed eight different patterns of functional and phylogenetic diversity across elevations, but no global pattern of increase or decrease was found. There is, however, a consistent global pattern of phylogenetic clustering, with mountain species being more closely related to each other at any given elevation. Latitude had a significant effect on within-mountain changes in functional and phylogenetic diversity across elevations, with more negative slopes (stronger decline in diversity metrics with increasing elevation) in tropical mountains.

Main conclusions: Our findings challenge the idea that the decline of functional and phylogenetic diversity with elevation is a general pattern, emphasizing the uniqueness of each mountain system. In spite of this great variability, we found a latitudinal effect in the patterns of within-mountain functional and phylogenetic dispersion of birds after controlling for effects of species richness. Environmental filtering, thus, may act differently in tropical and temperate mountains, and calls for more comparative studies on the mechanisms driving community assembly at different latitudes.

KEYWORDS

biodiversity, environmental filtering, global analysis, latitude, limiting similarity, niche-based processes

1 | INTRODUCTION

Understanding spatial patterns of biodiversity along environmental gradients and the mechanisms driving them is a main focus in ecology (Hillebrand, 2004; Ricklefs, 2004; Swenson, 2011). Under the classic framework of community assembly, two main niche-based deterministic processes are hypothesized to influence species coexistence within a community: environmental filtering and biological interactions (mainly competition causing limiting similarity; Cavender-Bares, Kozak, Fine, & Kembel, 2009). An examination of the functional and phylogenetic structure of species assemblages, and their comparison with null expectations, can provide insights into the relative importance of these processes in shaping communities (Cavender-Bares et al., 2009; Kraft, Valencia, & Ackerly, 2008; Webb, Ackerly, McPeek, & Donoghue, 2002). Furthermore, the magnitude of the deviations between observed values and those expected by null models can be interpreted as the strength of the processes acting upon assemblages. For instance, assemblages containing species functionally more similar to each other than in null expectations (underdispersion resulting in clustered assemblages) are often attributed to environmental filtering, where environmental conditions related to physiological tolerances, habitat affinities or resource requirements may dominate community assembly (Cavender-Bares et al., 2009; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010; Presley et al., 2018). On the other hand, a pattern of communities with functional overdispersion is often attributed to interspecific competition resulting in either competitive exclusion or character displacement (Kluge & Kessler, 2011; MacArthur & Levins, 1967; Presley et al., 2018). This latter prediction will be valid only if the niche differences among taxa are important for their coexistence (Mayfield & Levine, 2010). If niches are phylogenetically conserved, and close relatives are ecologically more similar to each other than distantly related species, phylogenetic distances between species can be used as a proxy for the evolved ecological differences between them (Cavender-Bares et al., 2009). Thus, competitive exclusion acting upon taxa that overlap in their niche preferences will also result in a community pattern of phylogenetic overdispersion (Cavender-Bares et al., 2009; Mayfield & Levine, 2010). In contrast, phylogenetic underdispersion is consistent with both community assembly driven by environmental filtering or with interclade competition (Mayfield & Levine, 2010). An entire clade may have an advantage over other clades because of superior competitive abilities or because of phylogenetically conserved adaptations to local environmental conditions (Kraft et al., 2008; Lebrija-Trejos et al., 2010).

Environmental conditions change rapidly along elevational gradients, with higher elevations being generally colder and less productive (Graham et al., 2014; Körner, 2007). These changes result in many different habitats and climatic zones within dispersal distances for many species, providing a unique opportunity to test for local drivers of community assembly (Graham et al., 2014). Studies on patterns of taxonomic diversity found that species richness generally decreases with elevation or peaks at mid elevations (Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Graham et al., 2014; McCain, 2009; McCain & Grytnes, 2001; McCain, King, Szewczyk, & Beck, 2018). Decreasing temperature, increasing temperature fluctuation and decreasing habitat complexity and feeding resources are among the most plausible explanations for patterns of decreasing richness (Jankowski et al., 2013; McCain, 2007; Price et al., 2014). Depauperate assemblages at high elevations might result from a loss of species due to strong environmental filtering preventing species from persisting or colonizing these extreme environments (Graham et al., 2014; Hoiss, Krauss, Potts, Roberts, & Steffan-Dewenter, 2012), whereas mid elevation peaks can be caused by wide-ranging species (Quintero & Jetz, 2018) and higher mid-elevation productivity on arid mountains (McCain, 2009), among others. In comparison, fewer studies have explored drivers of elevational patterns of functional or phylogenetic diversity (Cadena et al., 2011; Cisneros et al., 2014; Dehling et al., 2014; Dreiss et al., 2015; Vollstädt et al., 2017). These few studies show a decline in functional and phylogenetic diversity along single elevational gradients (Dehling et al., 2014; Hanz et al., 2019; Vollstädt et al., 2017), with phylogenetic and functional structure changing from overdispersed assemblages at lower elevations towards clustered assemblages at higher elevations (Graham, Parra, Rahbek, & McGuire, 2009; Hanz et al., 2019; Xu et al., 2017). Despite these findings, we still know little about the generality of these patterns and the importance of deterministic processes underlying biodiversity patterns in montane systems (Graham et al., 2014), and how these patterns and processes change across the globe.

Here, we test for signals of deterministic processes driving community assembly along elevational gradients across the globe, to examine the generality of predictions derived from community assembly theory along elevational gradients (Cavender-Bares et al., 2009; Graham et al., 2014; Webb et al., 2002). Specifically, we use a global data set that includes 46 well-sampled elevational gradients of resident birds to address the following questions: (a) are there general patterns of bird functional and phylogenetic diversity along elevational gradients?, (b) do the signals of deterministic processes (i.e., environmental filtering and limiting similarity), as community assembly drivers, change consistently along elevation in all mountain systems?, and (c) is there a latitudinal signal in the strength of environmental filtering and limiting similarity as drivers of community assembly along elevational gradients?

To address these questions, we first examined patterns of bird functional and phylogenetic biodiversity for each one of the gradients and how they vary among mountain systems. Secondly, on each mountain, we tested for significant deviations of functional and phylogenetic diversity from null expectations (over- or underdispersion) and examined if these patterns hold worldwide. Then, we compared differences in the strength of environmental filtering and limiting similarity among mountain systems to better understand how the assembly processes driving mountain biotas might change with latitude.

Because conditions are generally harsher for organisms at high elevations (i.e., lower temperatures, lower productivity, lower

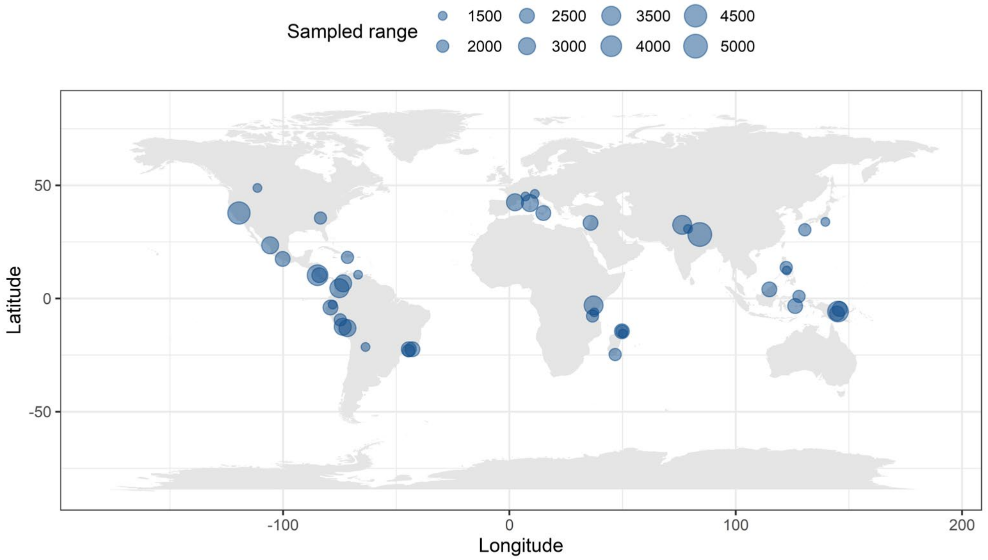

FIGURE 1 Location of the elevational gradients used in our study. Full gradients of bird diversity were obtained for 46 mountain systems ranging from 48.8° N to 24.4° S; each point represents one mountain. Point size represents the upper limit of the elevational range sampled, increasing at 500-m intervals (1,500 represent mountains with ranges lower than 1,500 m, 2,000 represents mountains with sampled ranges between 1,500 and 2,000 m, 2,500 represents mountains with sampled ranges between 2,000 and 2,500, etc.)

vegetation structure), for any given mountain we predicted environmental filtering to be stronger at higher elevations, resulting in functionally clustered assemblages whereas more functionally diverse assemblages were expected at lower elevations (Graham et al., 2014). If niches are conserved, we predicted a similar pattern for phylogenetic diversity (Cavender-Bares et al., 2009). Alternatively, assemblages might be phylogenetically clustered at low elevations if clades differ in competitive abilities and competitive exclusion acts among clades instead of within clades (Mayfield & Levine, 2010).

Based on the seminal work of Janzen (1967) and MacArthur (1984), we further hypothesized that the signal of these deterministic processes would be different for tropical and temperate mountains. Greater temperature stability at tropical latitudes allows for more opportunities for specialization and niche partitioning (Jocque, Field, Brendonck, & De Meester, 2010; MacArthur, 1984), whereas species that experience large temperature changes (at higher latitudes) tend to be physiological and ecological generalists (Dalsgaard et al., 2011; Read et al., 2018). Seasonal conditions in temperate mountains might result in strong environmental filtering across elevations, resulting in lower species richness and less functionally diverse assemblages along the gradient. Thus, the signal of environmental filtering was predicted to be widespread across elevations in temperate mountains, and stronger and more prevalent at high elevations in tropical mountains.

2 | METHODS

2.1 | Bird elevational data

Data on bird assemblages along elevational gradients were extracted from published articles. To do this, we searched the Web of Science using keywords "bird" OR "avian" *and* "elevation" OR "altitude"; the resulting articles were examined and selected largely following McCain's (2009) criteria. First, we pre-selected studies that surveyed all breeding birds, that focused on complete elevational gradients, that sampled at least four elevations and that had adequate sampling effort across elevations (sampled at least 70% of the forested elevational gradient, similar effort across elevations, multiple visits and/or replicates were conducted at each elevation), and that did not have a disproportionately large disturbance at any given elevation [e.g., studies where lower elevations were heavily impacted, McCain (2009)]. We focused on single-gradient data sets (alpha gradients sensu McCain, 2009) because actual coexistence of species within a given assemblage is critical for testing mechanistic processes driving community assembly. After pre-selecting the studies, we either downloaded the species list from the article or its supplementary materials and extracted the information if presented in tables or contacted the main author(s) to have access to these data. After this process, we obtained data from 46 elevational gradients across the globe, located at latitudes between 48.8° N and 24.4° S (Figure 1; Supporting Information Table S1.1). These gradients represent great variability of mountain regions across the globe, ranging in age from very recent uplifts (*c*. 11 Ma in Japan) to the oldest mountain ranges on Earth (*c*. 600 Ma in India). Further, the selected gradients have different evolutionary histories, (Quintero & Jetz, 2018), are located in regions with different climates, on continental landmasses, continental islands or oceanic islands, and range in height from 851 to 8,090 m. Mountain systems included in the analyses varied greatly in recorded species richness, from 22 species in Mikura-Jima, Japan to 577 species in Serrania de Yariguies, Colombia. Altogether, these elevational gradients contained 3,522 breeding bird species (*c*. 35% of the bird species recognized worldwide).

Species data of each gradient were carefully inspected, nomenclature standardized and taxonomy updated when necessary to match that of Jetz, Thomas, Joy, Hartmann, and Mooers (2012). For each data set, we assumed that a species was present between its highest and lowest reported elevation (range interpolation) and created distributional ranges for each species. Following earlier global analyses of taxonomic diversity, each gradient was then subdivided into 100-m-wide elevational bands (McCain, 2009; McCain & Grytnes, 2001), and all species occurring in each band were considered as a bird assemblage for analyses. We calculated species richness in each assemblage within each mountain. The width of the elevational band was chosen to have the maximum possible resolution (minimum width) that balances the resolution of empirical records while being biologically meaningful (McCain, 2009; McCain & Grytnes, 2001). To examine if our decision to use 100-m bands affected our results we also conducted the analyses for bird assemblages with 200-m and 400-m elevational subdivisions. Similarly, to examine our decision to include all 46 gradients, we conducted our analysis including only those mountains with sampled gradients of 2,000 m or more. Overall patterns of functional and phylogenetic diversity did not change with these divisions. However, wider elevational subdivisions resulted in the exclusion of one mountain (with 200-m bands) and 14 mountains (with 400-m bands) for our main analysis, as regressions were conducted with a minimum of five points in all cases. We present results for 100-m subdivisions in the main text, but trends for 200-m and 400-m elevational bands and for gradients larger than 2,000 m are presented in Supporting Information Appendix S1.

2.2 | Patterns of functional and phylogenetic diversity along elevational gradients

We calculated functional and phylogenetic diversity for each assemblage in each mountain system. To fully capture the information contained in functional traits and phylogenetic distances, we used one metric to denote richness [functional richness (FRis) or phylogenetic richness] and one metric of dispersion [functional dispersion (FDis) or phylogenetic dispersion]. Richness metrics are better for detecting differences within assemblages (differences in the size of trait space occupied by an assemblage, or in the aggregated quantity of phylogenetic differences contained in the assemblage), whereas dispersion metrics more accurately measure the signal of deterministic processes by highlighting the extent of variation among traits or tips in a phylogeny within assemblages (i.e., the distribution of units within assemblages; Swenson, 2014; Tucker et al., 2017), while controlling for effects of species richness (Chao, Chiu, & Jost, 2014). We assessed correlations among species richness and functional and phylogenetic metrics with Pearson moment correlations.

We used the updated version of the bird phylogeny (available at birdtree.org, revised July 2018) of Jetz et al. (2012), based on the backbone tree by Hackett et al. (2008) to summarize phylogenetic relationships among species for each gradient. Jetz et al.'s (2012) phylogeny results from a Markov chain Monte Carlo (MCMC) process, and is, therefore, composed of 10,000 trees derived from the posterior distribution rather than of a single consensus tree. For any given calculation of phylogenetic diversity (n = 1,000 per gradient, see null models below), we randomly selected one of the 10,000 trees and pruned to the subset of bird species found at that gradient. Phylogenetic diversity was then calculated for each assemblage with Faith's index (PD) and with mean pairwise distance (MPD). PD relates to phylogenetic richness and sums the quantity of phylogenetic differences present in the assemblage, whereas MPD is a divergence-based phylogenetic dispersion metric (Tucker et al., 2017; Webb et al., 2002). Phylogenetic diversity metrics were calculated with functions of the "picante" package (Kembel et al., 2010) in R (R Core Team, 2018).

Functional traits for all bird species were compiled from the Wilman et al. (2014) global data set. We included (a) diet, (b) vertical foraging strata, and (c) body mass. In Wilman et al. (2014), diet and foraging strata are presented as percentages in multiple columns that add up to 100 for each species (categories for diet: invertebrates, vertebrates, fish, fruit, nectar, seed, other plant; categories for foraging: ground, understorey, mid-high, canopy, aerial), thus they represent non-independent variables. To account for this non-independence and to reduce dimensionality of these variables, we ran two separate principal component analyses (one for diet and one for foraging strata) and kept the first axis to describe each of these two functional traits. The resulting three traits (diet, foraging strata and body mass) were then standardized to a mean of 0 and a variation from −1 to 1 and used to create a *species* × *trait* matrix for each bird assemblage (for each elevational band within each gradient). Functional diversity was calculated for each assemblage as FRic and FDis. FRic represents the minimum volume occupied by the community in multivariate functional space (Villéger, Mason, & Mouillot, 2008) and FDis represents the mean distance of individual species to the community centroid in trait space (Laliberté & Legendre, 2010). FRic and FDis were calculated with functions of the "FD" package in R (Laliberté, Legendre, Shipley, & Laliberté, 2014). We tested for phylogenetic signal of each trait for each mountain system by means of Pagel's λ using functions of the "phytools" package in R (Revell, 2012). Whereas diet and body mass were phylogenetically conserved, foraging strata was the most labile trait showing no phylogenetic signal in seven of the mountain gradients in our data set (15%) (Supporting Information Table S1.2).

To examine the patterns of functional and phylogenetic diversity across elevations, we fitted quadratic regressions for each biodiversity metric (FRic, FDis, PD and MPD) as a function of elevation. Based on the overall shape of the polynomial, the signs and significances of the coefficients (positive or negative) and the relative magnitudes of the coefficients, we assigned diversity patterns for each mountain to a category (see Supporting Information Appendix S2 for a detailed explanation of this process). Following McCain's (2009) approach, we used names that could be ecologically interpreted instead of mathematical names for the diversity curves' shapes. Patterns were classified as Increasing or Decreasing (if the increase or decrease was monotonic, following a linear trend); Mid Peak or Mid Valley if the highest or lowest values of the diversity metric occurred at mid

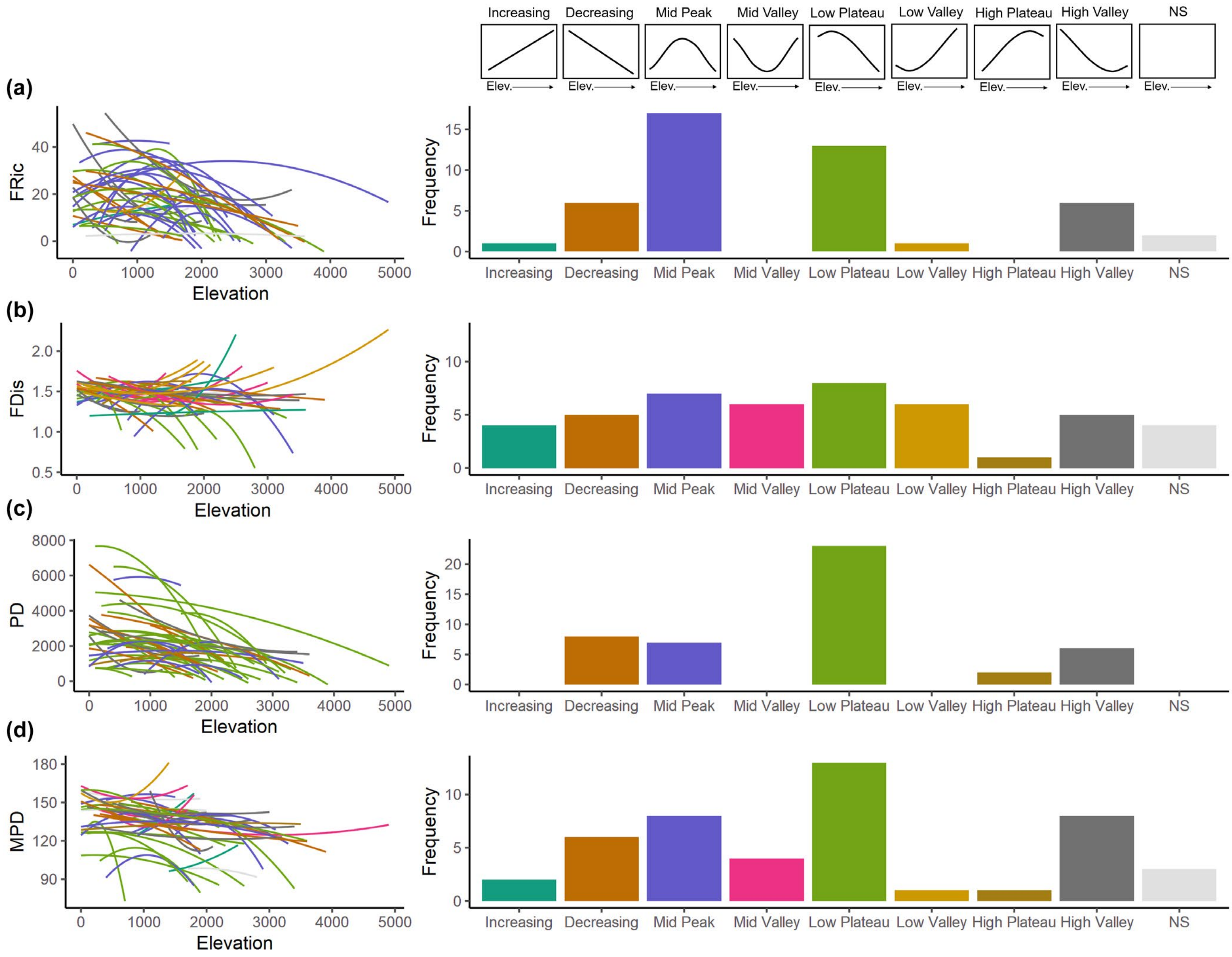

FIGURE 2 Patterns of bird functional and phylogenetic diversity along elevational gradients: (a) functional richness (FRic); (b) functional dispersion (FDis); (c) phylogenetic richness, Faith's index (PD); (d) phylogenetic dispersion, mean pairwise distance (MPD). Each curve represents one of the 46 mountains included in the analysis. Patterns can follow one of eight possible trends (curve shapes) represented on top of frequency bars or show no significant relationship with elevation (NS). Colours of lines correspond to the best fitted quadratic regression model to describe its pattern (see Supporting Information Appendix S2)

elevations, respectively; Low Plateau or High Plateau, if there is a peak of diversity metrics that occurs in more than three consecutive elevational bins towards low or high elevations, respectively; Low Valley or High Valley, if the lowest values of diversity occurs in more than three consecutive elevation bins towards low or high elevations, respectively. Non-significant associations were categorized as "NS". Shapes of these curves are shown in the top panel of Figure 2.

2.3 | Deterministic processes driving community assembly

We were interested in searching for signals of environmental filtering and limiting similarity as potential processes determining assemblages across elevations. To do this, we tested if observed functional and phylogenetic diversities were different than expected given random assembly. For each mountain separately, we constructed null models created by randomizing trait and phylogeny tip labels (1,000 runs) while fixing rows and columns of the observed community data matrix (Swenson, 2014). We tested for clustering or overdispersion by examining the deviation of each observed biodiversity metric from the average of the null model (Swenson, 2014; Ulrich & Gotelli, 2013), and standardizing these values to allow comparisons among assemblages (hereafter standardized effect size, SES). The direction of SES (higher or lower than the expected null) was interpreted as overdispersion or underdispersion, and the magnitude of SES was interpreted as the strength of the signal of deterministic processes on the assemblage (Swenson, 2014).

We tested for a global trend in the magnitude and direction of these effect sizes with linear mixed-effect models for each one of our diversity metrics (SES FRic, SES FDis, SES PD and SES MPD) as a function of normalized elevation (scaled between −1 and 1). Our

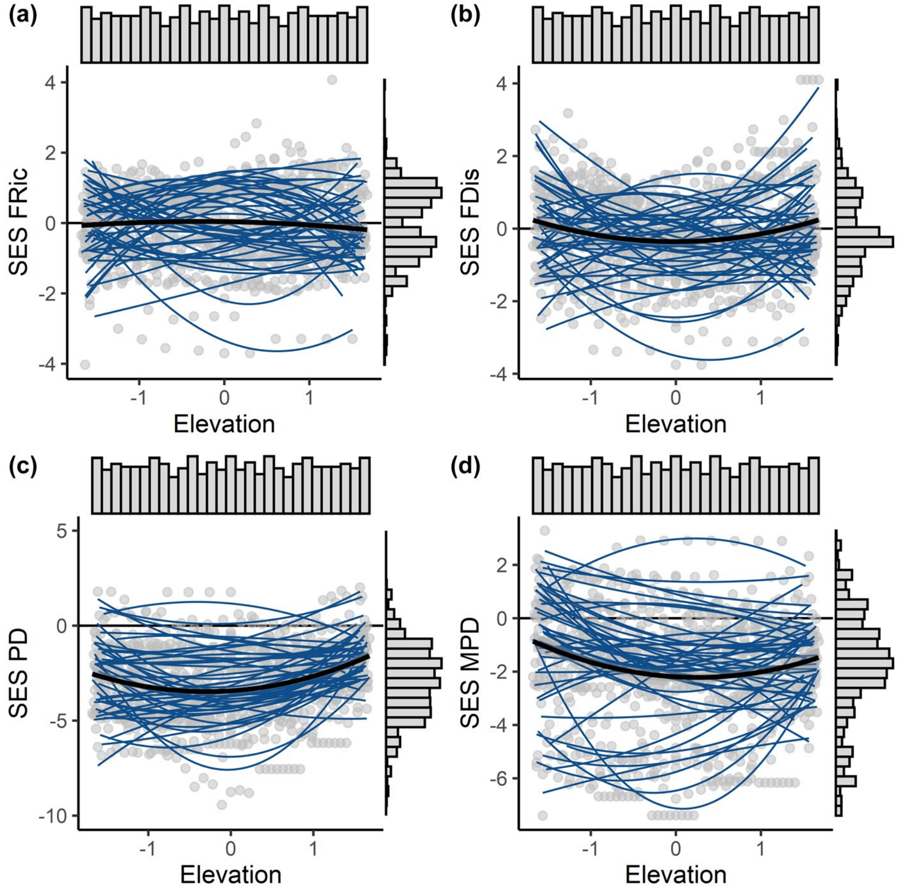

FIGURE 3 Global trends of functional and phylogenetic diversity after controlling for effects of species richness. Each panel shows the standardized effect size (SES) of the diversity metric (deviations from null expectations, grey dots) across elevations. Lines at $y = 0$ represent the expected values if assembly was random across elevations. (a) Functional richness (FRic); (b) functional dispersion (FDis); (c) phylogenetic richness, Faith's index (PD); (d) phylogenetic dispersion, mean pairwise difference (MPD). Elevation has been normalized (scaled and centred at 0) to allow comparisons among mountains. Quadratic polynomial regressions for diversity metrics against elevation for each mountain (blue lines) and for all mountains together (black line) are presented. Grey bars show the frequency distributions of observed SES values for bird assemblages

models followed a quadratic form, with elevation and elevation^2 as fixed factors and mountain system as a random factor. Significances of the model and the predictors were obtained by means of the likelihood ratio test (Bolker et al., 2009; Burnham & Anderson, 2002).

Finally, to test for the latitudinal effect on the magnitude and direction of the SES we contrasted the differences in SES for each diversity metric among mountains at different latitudes, with a two-stage mixed-effect model (Viechtbauer, 2010) for each metric, separately. Two-stage mixed-effect models are a type of multivariate meta-regression performed in two hierarchical steps. First, we fitted a linear model of SES as a function of elevation for each mountain and extracted the slope of elevation and the variance associated with this slope. Then, we used these two new variables (slopes and their variances) to calculate weighted values of the slope and used these new values as response variables for a multivariate meta-regression with absolute latitude as predictor and hemisphere as covariate (Koricheva, Gurevitch, & Mengersen, 2013). Meta-regression models were performed with the package "metafor" in R (Viechtbauer, 2010).

3 | RESULTS

3.1 | Patterns of diversity along elevational gradients

Most gradients showed either a decrease in FRic with elevation, following linear decreasing, low plateau or high valley patterns, or a mid-elevation peak (Figure 2a). Two mountains show no elevational pattern of FRic. FDis varied more, with roughly half of the mountains showing increasing patterns of FDis with elevation, and half showing decreasing patterns (Figure 2b). Four mountains show no elevational pattern in FDis. PD showed mostly a decreasing pattern with a low elevation plateau (Figure 2c), whereas MPD was more variable. Although most mountains followed a pattern of low plateau, mid-elevation peak or high valley; a few mountains increased in MPD at higher elevations (Figure 2d). Three mountains show no elevational pattern of MPD (see Supporting Information Appendix S2 for coefficients and predicted shapes of quadratic regressions for each mountain). Richness metrics (FRic and PD) were overall positively

TABLE 1 Parameter estimates (± *SE*) of mixed-effect models of functional and phylogenetic diversity of bird assemblages across elevations in 46 mountain systems worldwide. Separate models were performed for the standardized effect size (SES) of functional richness (SES FRic), functional dispersion (SES FDis), phylogenetic richness [SES Faith's index (PD)] and phylogenetic dispersion [SES mean pairwise distance (MPD)]. Each metric was modelled with quadratic linear mixed-effect models, with elevation and elevation^2 as predictor variables. For all models, we included one random factor to control for the mountain system (allowing for random intercepts)

Fixed effects	SES FRic	SES FDis	SES PD	SES MPD
Intercept	−0.009 ± 0.11	−0.44 ± 0.12	−3.21 ± 0.22	−2.02 ± 0.27
Elevation	−0.035 ± 0.027	0.002 ± 0.03	−0.28 ± 0.04**	−0.18 ± 0.034**
Elevation^2	−0.064 ± 0.031*	0.205 ± 0.03**	0.49 ± 0.041**	0.37 ± 0.04**
Random effects (variance)				
Mountain ID	0.486	0.555	2.18	3.26

$^{*}p$ < .05; $^{**}p$ < .001.

correlated with species richness, whereas correlations with dispersal metrics (FDis and MPD) varied greatly (see Supporting Information Appendix S3). There was no latitudinal variation in the coupling or decoupling of functional and phylogenetic metrics (Supporting Information Figure S3.8).

3.2 | Deterministic processes driving community assembly

We found no consistent global pattern in the increase or decrease in SES of functional and phylogenetic metrics across elevations (Figure 3, Table 1). Although elevation and elevation^2 were significant predictors, overall model fit was poor and patterns across mountains varied greatly. We found, however, that phylogenetic diversity was overall underdispersed, with values of SES PD and SES MPD of most assemblages below null expectations (Figure 3c,d). Furthermore, these trends remained when we used different grains of analysis (200-m and 400-m elevational bands, see Supporting Information Figures S1.1 and S1.2).

There was a significant yet weak effect of latitude on the variation of SES of FRic, SES FDis and SES MPD across elevations, with more negative slopes towards tropical latitudes (Table 2, Figure 4; mixed-effect models test of moderators QM$_1$ = 5.80, p = .016 for SES FRic; QM$_1$ = 4.47, p = .03 for FDis and QM$_1$ = 7.94, p = .005 for MPD). Changes in SES PD across elevations were explained by hemisphere but not by latitude (Table 2, QM$_1$ = 5.29, p = .07), with Southern Hemisphere mountains having more negative slopes (see Supporting Information Table S1.3 for full models). Although we cannot completely rule out that this result is driven by the nature of the available data, that is, most extra-tropical mountains were in the Northern Hemisphere (Figure 1), we did not find an effect of latitude when examining only mountains between 0 and 25° of latitude (Supporting Information Figure S1.4). Latitudinal patterns did not change when calculated for 200-m and 400-m elevational bands (Supporting Information Figures S1.4 and S1.5) or when calculated for mountains with sampled gradients of 2,000 m or more (Supporting Information Figure S1.6).

TABLE 2 Coefficients of the best two-stage mixed-effect models (meta-regression) explaining patterns of variation in functional diversity and phylogenetic diversity along elevational gradients as a function of latitude and hemisphere. Separate models were performed for functional richness (FRic), functional dispersion (FDis), phylogenetic richness, Faith's index (PD) and phylogenetic dispersion, mean pairwise distance (MPD). Hemisphere only contributed to the model for standardized effect size (SES) PD. Model fit and significance, as indicated by the test of moderators (QM), for SES FRic were QM$_1$ = 5.80, p = .016, for SES FDis QM$_1$ = 4.47, p = .034, for SES PD QM$_1$ = 5.29, p = .07 and for SES MPD QM$_1$ = 7.94, p = .005). Full models are presented in Table S1.2 in Supporting Information Appendix S1

Model	Coefficient	*SE*	*z* value	*p*
β SES FRic ~ Latitude				
Intercept	−.249	.112	−2.236	.025
Latitude	.012	.005	2.409	.016
β SES FDis ~ Latitude				
Intercept	−.230	.137	−1.676	.094
Latitude	.012	.006	2.115	.034
β SES PD ~ Hemisphere				
Intercept	.485	.112	4.326	.001
Hemisphere (South)	−.380	.165	−2.307	.021
β SES MPD ~ Latitude				
Intercept	−.501	.147	−3.401	.001
Latitude	.018	.007	2.818	.005

4 | DISCUSSION

Our study constitutes the first global analysis of elevational gradients in functional and phylogenetic diversity of birds for signals of deterministic processes in community assembly. We took advantage of the replicated settings provided by mountains and focused on two facets of diversity for bird assemblages across elevations using data from well-sampled mountains around the globe. Local-scale data were important as they reflect the scale where species can interact in space and time either directly or indirectly (Graham et al., 2014). In elevational gradient studies, empirical data are sensitive to sample

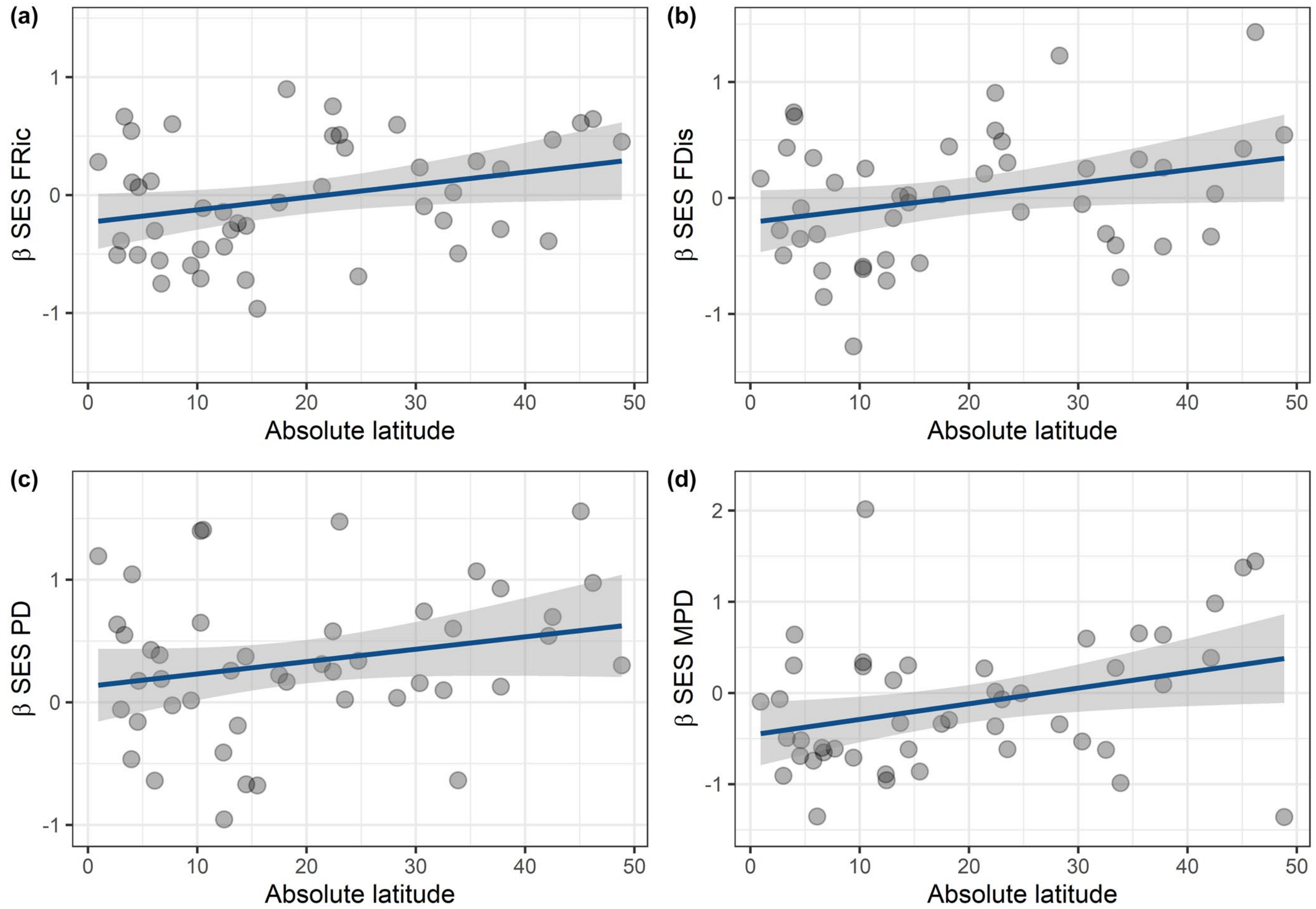

FIGURE 4 Effect of latitude on the patterns of elevational change in standardized effect size (SES) of (a) functional richness, FRic; (b) functional dispersion, FDis; (c) phylogenetic richness, Faith's index (PD); (d) phylogenetic dispersion, mean pairwise difference (MPD), across elevations. For each mountain, the pattern of change in SES across elevations is represented by the slope of a linear regression (β; grey dots), where more negative values represent decrease in diversity metrics with elevation and positive values represent increases. The magnitude of β represents the strength of the changes in diversity patterns across elevations; higher magnitudes of β would correspond to strong changes across elevations, whereas lower magnitudes would be found in mountains where patterns of underdispersion, or overdispersion are homogeneous across elevations

size, differences in human impact along elevation, and sampling effort (McCain, 2004, 2009; McCain & Grytnes, 2001). Furthermore, problems with scale and data non-independence among elevational bands have also been discussed in several studies (Nogues-Bravo, Araujo, Romdal, & Rahbek, 2008). Although we are aware that all these biases might affect the data sets included in this study, we have no reason to believe that they do so in a systematic fashion across data sets, making it unlikely that they affect our main findings. Thus, our analyses and conclusions are rooted in robust global data.

4.1 | Patterns of functional and phylogenetic diversity along individual elevational gradients

Bird assemblages at higher elevations often represent a smaller subset of the overall mountain species pool than lowland assemblages. Thus we expected functional and phylogenetic diversity to decrease with elevation, as only a subset of traits and clades would remain in high elevation assemblages (Dehling et al., 2014; Graham et al., 2009; Hanz et al., 2019; Vollstädt et al., 2017). We found great variation in the elevational patterns of functional and phylogenetic diversity among mountains. On most mountains functional and phylogenetic richness decreased with elevations, although not necessarily following a linear trend, or showed a mid-elevation peak, resembling the main trends of bird species richness (McCain, 2009). Elevational patterns for dispersion metrics, however, were more variable. FDis showed contrasting patterns, with roughly the same number of mountains following decreasing patterns and increasing patterns of FDis with elevation. A decay in FDis with increasing elevation might result from the loss of distinctive functional traits with elevation. For instance, families of large insectivores (e.g., Bucconidae, Motacillidae, Formicaridae, Thamnophilidae) and large frugivores (e.g., Psittacidae, Lybiidae) are often restricted to mid and low elevations, potentially increasing trait dispersion in low elevation assemblages. In contrast, higher FDis in high elevations may result from two mechanisms: (a) species that are lost towards high elevations are redundant in traits and therefore, species in the extremes of the trait space remain but the average of distances between species increases. For example, in the Andes of Peru, Pigot, Trisos, and Tobias (2016) found that less productive habitats in higher elevations supported fewer species but all functional guilds were present; most additional species at lower elevations occurred within the range of trait space occupied by high elevation species, suggesting high niche packing in lowland assemblages. Alternatively, higher FDis at high elevations may also result from (b) few species added towards high elevations presenting extreme traits, increasing the overall distance among species pairs. For example, waterfowl (e.g., geese and ducks), a high elevation clade with large body sizes, were present in high elevation assemblages in our data set, potentially increasing overall trait space at these elevations. These mechanisms need not be mutually exclusive, potentially acting in different mountain systems and even within the same mountain.

On most mountains, phylogenetic dispersion (MPD) decreased with elevation, a pattern expected by the gradual loss of lineages with increasing elevation. Consistent with previous studies in tropical mountains (Dehling et al., 2014; Hanz et al., 2019), lower MPD can result from lower temperatures or productivity preventing species persistence or colonization, increasing extinction rates and lowering rates of speciation at high elevations (Graham et al., 2014; Price et al., 2014). Alternatively, if highland assemblages are mostly composed of lowland immigrants, as in the Himalayas (Päckert et al., 2012), a decay of MPD with elevation can also result from differences in the time of lineage arrival and priority effects (Fjeldså, Bowie, & Rahbek, 2012). Contrary to our expectations, some mountains with decreasing patterns of PD showed patterns of increase in MPD with elevation, suggesting sister taxa being lost towards high elevations but not entire clades, that is, within-clade competition (Mayfield & Levine, 2010). For instance, resource limitation at higher elevations can drive competitive exclusion of close relatives that overlap in diet or body mass (two highly conserved traits in our data sets) reducing overall phylogenetic richness, but increasing phylogenetic distances among species in highland assemblages (Graham et al., 2014). Alternatively, high MPD values could result from different diversification rates between lowland and highland assemblages. The isolation and heterogeneity of higher elevation landscapes may facilitate the rapid radiation of immigrant clades. If these immigrants are more closely related to taxa from distant regions with similar climates than to other taxa at other elevations in the same mountain range, as suggested by Quintero and Jetz (2018), then the mean phylogenetic distances among species would increase.

4.2 | Deterministic processes driving community assembly along elevation

Our findings challenge the idea that signals of deterministic processes are consistent across mountains. Within mountain gradients, we predicted a gradient from overdispersed bird assemblages at lower elevations to clustered assemblages at higher elevations (Dreiss et al., 2015; Graham et al., 2009; Hanz et al., 2019). Functional underdispersion was expected to occur predominantly at higher elevations where community assembly should be dominated by environmental filtering, driven by gradients in temperature, resource availability and vegetation structure (Dehling et al., 2014; Dreiss et al., 2015; Hanz et al., 2019; Kraft et al., 2008; Lebrija-Trejos et al., 2010; Trisos, Petchey, & Tobias, 2014). On the contrary, species similarity was expected to be lower in lowland communities resulting in functionally overdispersed assemblages potentially due to a higher relative importance of interspecific competition and niche partitioning (Cavender-Bares et al., 2009; Price et al., 2014). As niches are conserved, we expected similar trends for phylogenetic diversity (Webb et al., 2002). After controlling for effects of species richness, we found no consistent elevational patterns in the SES of functional and phylogenetic diversity across mountains, suggesting that ecological and historical factors shaping functional and phylogenetic diversity in montane avifaunas are distinct for each system. Mountains in our data set are characterized by unique combinations of characteristics (i.e., mountain age, size, biogeographical history, current climate and past climatic stability) that can ultimately determine the rates of speciation, extinction and colonization, across elevations (Fjeldså et al., 2012; Janzen, 1967; Jetz & Fine, 2012; Price et al., 2014), driving various patterns of functional and phylogenetic diversity (Cavender-Bares et al., 2009). In fact, mountain ID explained a great amount of variation in our models and no consistent rules were detected on how SES of functional and phylogenetic diversity vary across elevations.

We found, however, an overall global pattern of phylogenetic underdispersion, with most mountains having phylogenetically clustered assemblages across elevations (Figure 3). At any given elevation, phylogenetic underdispersion can result from either environmental filtering preventing lineages from establishing and persisting, or from among clade competition, where a few clades have stronger competitive abilities and exclude other lineages (Swenson & Enquist, 2009; Webb et al., 2002). Our findings, however, suggest that evolutionary and historical processes, which act over long time scales might predominate, thus driving phylogenetic underdispersion in mountain systems (Jetz et al., 2012). When a mountain uplifts, it provides new habitats for avian clades to colonize, either from adjacent lowlands or from distant areas with similar conditions (Fjeldså et al., 2012; Quintero & Jetz, 2018). Rapid in situ diversification of these immigrant clades increases local species richness (Cadena et al., 2011; Fjeldså et al., 2012) and drives strong phylogenetic turnover across elevations, particularly if the immigrant clades are distant relatives, increasing the overall pool of species and lineages (Swenson, Enquist, Pither, Thompson, & Zimmerman, 2006).

Building on seminal studies by Janzen (1967) and MacArthur (1984), we hypothesized that patterns of underdispersion would be widespread in temperate mountains and stronger towards high elevations in tropical mountains (Graham et al., 2014; Hoiss et al., 2012). Greater climatic stability and productivity at tropical latitudes might allow more opportunities for specialization and niche partitioning (Jocque et al., 2010; MacArthur, 1984). Thus tropical mountains are predicted to contain more specialists and species with smaller niches (Fjeldså et al., 2012), whereas more seasonal and less productive areas at higher latitudes are expected to contain more physiological and ecological generalist species (Dalsgaard et al., 2011; Read et al., 2018). Thus, we expected to find differences in the responses to environmental filtering, measured as within-mountain patterns of underdispersion, among mountains at different latitudes. As predicted, we found a significant effect of latitude on the pattern of change in functional diversity (i.e., the slope of the regression of SES against elevation, Figure 4). Functional diversity generally declined more quickly with elevation on mountains located at lower latitudes compared to those in temperate regions. This result implies that the relative role of environmental filtering changes faster across elevations in the tropics, with stronger relevance in the assembly of highland assemblages. Studies in tropical mountains have found similar results, with the loss of food resources and vegetation structure suggested as plausible mechanisms driving functional underdispersion in high elevation bird assemblages (Dehling et al., 2014; Hanz et al., 2019), and niche partitioning and interspecific competition potentially driving functional overdispersion in lowland assemblages (Pigot et al., 2016; Price et al., 2014). On the contrary, less negative slopes for functional underdispersion at higher latitudes suggests that environmental filters are relatively homogeneous across elevations, regardless of their importance. This may be a result of the strong seasonality and low productivity experienced across elevations in temperate mountains.

Latitudinal patterns of within-mountain changes in phylogenetic dispersion (i.e., the slope of the regression of SES MPD against elevation, Figure 4) resembled those of functional diversity. Mountains towards the tropics had stronger patterns of decay in SES MPD with elevation, further supporting our conclusion of stronger signals of environmental filtering at high and mid elevations in mountains at lower latitudes and more even environmental filtering effects along temperate gradients. Of course, as discussed above, phylogenetic structure in local assemblages can also result from competitive exclusion among clades. Within temperate mountains, abiotic filters may play dominant roles structuring local assemblages (Swenson et al., 2012). If species differ in traits that confer upon them different competitive abilities and that allow them to persist under harsh conditions (i.e., low and less stable temperatures), then competitive exclusion can drive phylogenetic clustering where these conditions are more extreme (i.e., higher elevations).

We found no effect of latitude in within-mountain changes of phylogenetic richness, but an effect of hemisphere, with southern mountains having stronger within-mountain variation in SES PD (Table 2). Unfortunately, we cannot completely rule out that the significance of hemisphere in this relationship is a confounding factor erasing the signal of latitudinal effects as most of the temperate mountains in our data set are located in the north. However, when only mountains between 0 and 25° were included, the effect of hemisphere weakened (Supporting Information Figure S1.3), but the lack of latitudinal effects persisted. Differences in diversity patterns between the Northern and Southern Hemispheres have long been recognized (Gentry, 1988; Rabosky, Title, & Huang, 2015). Differences in continental landmasses and in annual temperature fluctuations (reduced in the Southern Hemisphere), result in distinct current and past climate histories in the Northern and Southern Hemispheres (Jetz & Fine, 2012), as well as differences in primary productivity. These differences likely explain latitudinal gradients in tree diversity between hemispheres (Burns, 2007), with southern forests being denser and more diverse (Burns, 2007). If bird functional and phylogenetic diversity patterns within elevational gradients are mostly driven by environmental filtering through abiotic conditions, resource availability or vegetation structure (Cadena et al., 2011; Graham et al., 2014; Hanz et al., 2019), it is plausible that differences between hemispheres can arise. For instance, denser and more diverse southern montane forests might provide a wider range of resources available for birds, as well as more complex habitat structure, two main characteristics found to be key in driving bird functional and phylogenetic diversity in single elevational gradients (Hanz et al., 2019).

Altogether, our findings challenge the idea that the decline of functional and phylogenetic diversity with elevation is a general pattern (Hanz et al., 2019). On the contrary, our results highlight the fact that global-scale diversity gradients in mountain systems can arise from combinations of species responses to contemporary and past climates (Jetz & Fine, 2012), geographical variation in the origin of clades (Cadena et al., 2011; Fjeldså et al., 2012) and variable diversification rates (Hawkins et al., 2012; Quintero & Jetz, 2018). However, in spite of this great variability, we found a latitudinal effect in the patterns of within-mountain functional and phylogenetic dispersion of birds after controlling for effects of species richness. This finding suggests that environmental filtering may act differently in tropical and temperate mountains and calls for more comparative studies testing for specific mechanisms shaping functional and phylogenetic diversity in tropical and temperate mountain systems.

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DATA AVAILABILITY STATEMENT

Bird diversity data used for all analyses have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.tqjq2bvtc). Bird raw data were extracted from published sources detailed in the Appendix and are available from the original source or from upon request from the correspondence authors of these articles.

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BIOSKETCHES

Flavia A. Montaño-Centellas has a background in tropical ecology and conservation, particularly of mountain systems. She is an ecologist focusing on the drivers of diversity patterns across environmental gradients, and conducts research on both large- and local-scale ecological patterns. In her studies, Flavia has explored community level questions, using birds and bats as model systems. She has recently received her PhD from the University of Florida.

Christy McCain is an Assistant Professor at the University of Colorado Boulder. She is broadly interested in the theoretical and empirical aspects that cause and maintain species biodiversity.

Bette A. Loiselle is a Professor at University of Florida. Her research interests include understanding the ecological consequences of seed dispersal and population and behavioral ecology of tropical birds.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX: DATA SOURCES

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