Received: 29 June 2020 | Revised: 19 May 2021 | Accepted: 24 May 2021

DOI: 10.1111/jbi.14212

RESEARCH ARTICLE

Journal of Biogeography
WILEY

Multiple dimensions of bird beta diversity support that mountains are higher in the tropics

Flavia Montaño-Centellas[1,2] | Bette A. Loiselle[1,3] | Christy McCain[4]

[1]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA

[2]Instituto de Ecología, Facultad de Ciencias Puras y Naturales, Universidad Mayor de San Andres, La Paz, Bolivia

[3]Center of Latin American Studies, University of Florida, Gainesville, FL, USA

[4]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA

Correspondence
Flavia Montaño-Centellas, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA.
Email: flamontano@gmail.com

Funding information
American Philosophical Society; University of Florida; Tropical Conservation and Development Program

Handling Editor: Richard Ladle

Abstract

Aim: We examine latitudinal effects of breeding bird taxonomic, phylogenetic and functional β-diversity (Tβ, Pβ and Fβ, respectively) along elevational gradients to test predictions derived from Janzen's (*The American Naturalist* **101**:233–249, 1967) classic ideas that tropical mountains represent stronger dispersal barriers than temperate mountains.

Location: Global.

Taxon: Birds.

Methods: Using a global dataset from 46 mountains, we examine latitudinal patterns of Tβ, Pβ and Fβ, and their components: β_{rich} and β_{repl}. For each mountain and each dimension of diversity, we calculated (a) total β-diversity, (b) the steepness of distance decay patterns and (c) within-mountain variability in pairwise β-diversity and regressed each one of these response variables against absolute latitude. We predicted that tropical montane biotas would have (a) overall higher Tβ, Pβ and Fβ, (b) faster distance decay patterns and (c) higher within-mountain variability in pairwise β-diversity. Furthermore, we expected the richness component β_{rich} to be more important in temperate mountains, and the replacement component β_{repl} in tropical mountains.

Results: Latitude had a negative effect on total β-diversity for all dimensions of diversity. Similarly, metrics of Tβ and Pβ mostly agree with our expectations, whereas Fβ showed contrasting results with steeper distance decay curves and higher within-mountain variability in temperate mountains. Overall, β_{rich} was a more important component at high elevations in the tropics and across elevations in temperate mountains, and β_{repl} was more important in tropical low and mid-elevations.

Main Conclusions: Our findings are consistent with tropical mountain assemblages containing species with narrow elevational distributions, low dispersal ability and potentially high allopatric speciation, resulting in high β-diversity across elevations. Contrasting results for Fβ indicate high niche packing in tropical assemblages, with most changes in functional diversity among assemblages involving species redundant in trait space.

KEYWORDS
beta diversity partition, distance decay, elevation, functional beta diversity, functional hypervolume, latitude, phylogenetic beta diversity, turnover

1 | INTRODUCTION

Elevational gradients are useful for exploring patterns and mechanisms of biodiversity because of their considerable environmental change over relatively small distances (Graham et al., 2014; Körner, 2007; McCain, 2009a). However, this environmental variation differs with latitude. For instance, temperate mountain systems experience large seasonal temperature variability leading to large thermal overlap between upslope and downslope sites, whereas tropical mountain systems are less variable seasonally leading to reduced thermal overlap elevationally (e.g. Ghalambor et al., 2006; Janzen, 1967). Based on these observations, tropical ecologist Daniel Janzen presented an idea about montane faunas that continues to provoke researchers today (Currie, 2017; Salisbury et al., 2012; Sheldon et al., 2018; Zuloaga & Kerr, 2017). Janzen (1967) proposed that tropical mountains might represent physiologically stronger filters for organisms than temperate mountain systems (i.e. tropical mountains are physiologically 'higher'). Janzen (1967) based his statement on the assumption that, having evolved in less variable environments, montane tropical species might have limited acclimation responses and, therefore, smaller elevational ranges than species in temperate mountains. If Janzen's predictions hold, there should be greater similarity between high- and low-elevation communities in temperate mountains, whereas greater dissimilarity would be expected among tropical montane assemblages as depicted in Figure 1 (Ghalambor et al., 2006; Huey, 1978; McCain, 2009b). Despite the increasing interest in disentangling the causes of elevational diversity gradients and their latitudinal variation (Kraft et al., 2011; Tello et al., 2015), five decades after Janzen's seminal paper many of his predictions remain unresolved.

The concept of β-diversity accounts for the relationship between local and regional diversity and provides information about dissimilarity among communities (Tuomisto, 2010; Whittaker, 1960). Therefore, examining β-diversity patterns can provide insights into the mechanisms driving montane communities (McCain & Beck, 2016), and a way to test predictions derived from Janzen's hypotheses. Several evolutionary and ecological processes interact to shape β-diversity patterns. For instance, β-diversity can be influenced by variation in strength of dispersal limitation (Soininen, Lennon, et al., 2007), species sorting due to environmental heterogeneity (Qian & Ricklefs, 2007) or stochastic processes (Chase & Myers, 2011). Contrasting the phylogenetic dimension of β-biodiversity, which reflects the evolutionary differences among assemblages (Cavender-Bares et al., 2009; Graham & Fine, 2008), with the functional dimension of β-biodiversity, which reflects the variability in ecological attributes (Petchey & Gaston, 2006), may lead to improved understanding of elevational and latitudinal diversity based on niche relationships among species.

Changes in β-diversity among assemblages can be related to two different mechanisms: species replacement (the replacement of one species by another species; β_{repl}) and species loss or gain among assemblages (richness differences; β_{rich}) (Carvalho et al., 2012; Legendre, 2014). The same principle can be applied to different dimensions of diversity by changing the unit of diversity. For example, differences in the number and identity of the functional groups can produce assemblages that differ in functional diversity due to functional richness or replacement, respectively. If β-diversity is mostly explained by changes in β_{rich}, environmental filtering is likely a stronger process limiting the number of species, traits or clades that can exist along a gradient, resulting in a higher number of local and regional extinctions related to harsh environmental conditions (Soininen et al., 2018). On the other hand, if changes are explained by β_{repl}, species interactions resulting in limiting similarity are likely a stronger process shaping assemblages. Alternatively, changes explained by β_{repl} can result from the gradient containing habitats that can sustain similar species richness but require different strategies (i.e. functional traits) (Cardoso et al., 2014; Kluge & Kessler, 2011).

Here, we explore a new approach to disentangle the underlying ecological and evolutionary mechanisms driving β-diversity across elevations. Inspired by Janzen's (1967) seminal work, we test for latitudinal differences in the potential processes driving these patterns (Figure 1). Taxonomic β-diversity (Tβ) along elevational gradients has been found to be highly variable (McCain & Beck, 2016); however, some studies detected decreasing elevational β-diversity with increasing latitude (García-Girón et al., 2020; Kraft et al., 2011; Stevens & Willig, 2002). McCain (2009b) showed that the mean elevational range size of breeding bird species increases with latitude, a pattern that is expected to result in greater taxonomic turnover on tropical mountains. However, how functional (Fβ) and phylogenetic (Pβ) β-diversity changes with elevation and latitude in montane birds remains untested. According to Janzen (1967), tropical species should have lower rates of dispersal and, consequently, higher allopatric speciation rates than temperate mountain species. Thus, we predict tropical montane biotas to have more rapid changes in Pβ across elevations than temperate mountains. We predict greater Fβ within tropical montane assemblages due to the greater climatic stability and productivity towards the tropics, which might allow for more opportunities of specialization and niche partitioning (Jocque et al., 2010; MacArthur, 1984), resulting in faster elevational changes in biodiversity. Furthermore, in a recent study (Montaño-Centellas et al., 2019), we found that the relative role of environmental filtering might change faster across elevations in the tropics, with stronger relevance in the assembly of highland communities. On the contrary, a more homogeneous role of environmental filters was found across elevations in temperate mountains. Based on these findings, we expected β_{rich} to be a more important component of β-diversity at high elevations and β_{repl} to gain importance at low elevations in tropical mountains. In contrast, we expected β_{rich} and β_{repl} to be less variable across elevations in temperate systems, with β_{rich} being consistently more important than β_{repl}. Finally, one potential driver of compositional similarity between two assemblages is the homogenizing effect of dispersal (Leibold et al., 2004). Thus, in tropical mountains, where dispersal is hypothesized to be lower (Janzen, 1967), we expected to have higher replacement of species (Soininen et al., 2018). To test this set of predictions (Figure 1), we simultaneously examine taxonomic, functional and phylogenetic β-diversity

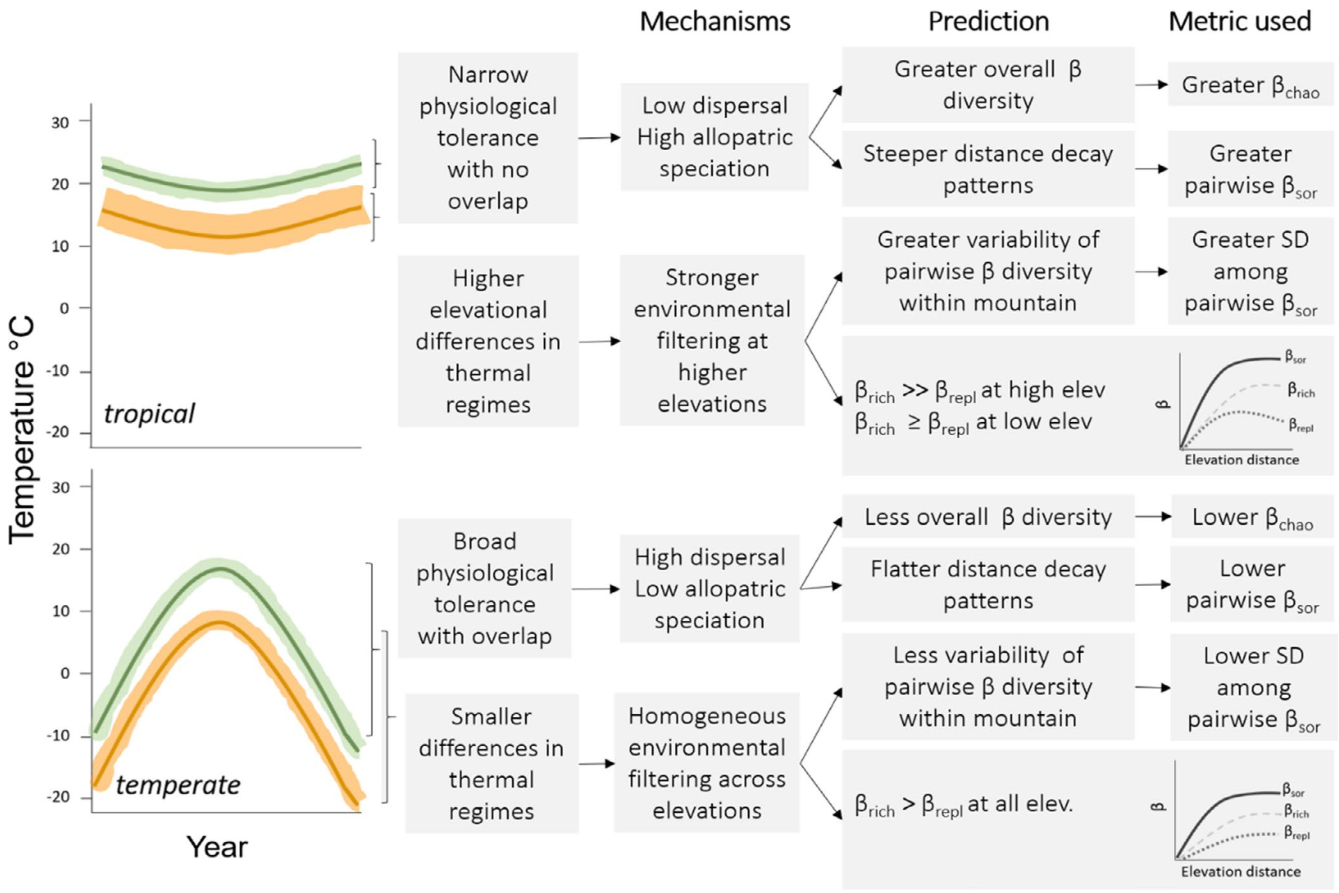

FIGURE 1 Schematic representation of the expected patterns of β-diversity along elevational gradients. Our scheme is derived from ideas by Janzen (1967) and Ghalambor et al. (2006) for taxonomic diversity and extended for predictions of functional diversity and phylogenetic diversity. Seasonal changes in air temperature experienced by a low-elevation species (in green) and a high-elevation species (in orange) in temperate and tropical mountains. Seasonality in temperate mountains results in broad physiological tolerance and consequently, greater thermal overlap between high- and low-elevation species. On the contrary, narrow physiological tolerances results in reduced thermal overlap between high- and low-elevation species in the tropical mountain system. The greater overlap in thermal distributions of species in temperate mountains results in reduced functional β-diversity, whereas the narrow thermal distributional ranges in tropical mountains will result in greater species and trait replacement. Furthermore, because of these differences in annual thermal regimes at different elevations, between tropical and temperate mountains, we expect the relative role of environmental filtering in driving community assembly to vary more across elevations in tropical mountains with a more homogeneous role across elevation with increasing latitude. This would lead to greater variation in pairwise β values between consecutive elevational bands and to greater differences in the relative importance of β_{rich} and β_{repl} as components of functional β-diversity in tropical mountains. Finally, if traits are conserved, we expect the same responses for metrics of phylogenetic β-diversity

of breeding bird assemblages, and their partition into β_{rich} and β_{repl}, across 46 well-sampled elevational gradients worldwide.

2 | MATERIALS AND METHODS

2.1 | Bird elevational data

Elevational data for bird assemblages were extracted from published articles; for details, see Montaño-Centellas et al. (2019). Briefly, we searched Web of Science using 'bird' OR 'avian' and 'elevation' OR 'altitude' and the resulting articles were examined and pre-selected following McCain (2009a). Studies were selected only if they surveyed all breeding birds, focused on complete elevational gradients, sampled at least four elevations and 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 did not have a disproportionately large disturbance at any given elevation (Montaño-Centellas et al., 2019). To homogenize the spatial scale of data collection among studies, we focused on single-gradient datasets (alpha gradients *sensu* McCain, 2009a). We extracted information from the manuscript itself, supplementary materials or contacted the main author for access to the data. We considered only breeding species, but herein we will refer to them simply as species. This process resulted in 46 elevational gradients located between 50°N and 24.4°S of latitude (30 located in tropical latitudes and 16 in temperate latitudes). A list of the data sources is found in

Appendix A. Altogether, these gradients contained 3522 breeding bird species, with species richness ranging from 22 to 577 species (Montaño-Centellas et al., 2019). For each mountain, we assumed that a species was present between its highest and lowest reported elevation (range interpolation) and used that range for each species in the analyses. Each gradient was then partitioned into 200 m wide elevational bands and all species occurring in each band were considered as an assemblage. The elevational band (200 m) width was chosen to balance resolution of empirical records, amount of collection effort in each interval, and to include a minimum of four assemblages in any given mountain. To further evaluate our choice of band width, we also performed analyses with elevational band widths of 100 and 400 m. Latitudinal patterns for all three band widths resulted in unchanged conclusions, thus we only present the 200 m resolution (see Appendix S1).

Finally, although we included only gradients that sampled at least 70% of the mountain height, it is possible that the length of the sampled gradient or the starting point of the gradient (e.g. if it includes 'lowlands' or not) might further affect our results. To assess these potential biases, we performed our analyses including only mountains that have more than 2000 m of sampled gradient ($N = 27$) and including only mountains that have at least one elevational band below 500 m (mountains that include 'lowlands', $N = 27$). These elevational sampling subsets also resulted in unchanged conclusions; thus, all datasets are presented (Appendix S1).

2.2 | Functional and phylogenetic data

We used the updated version of the avian phylogeny (Jetz et al., 2012), based on the backbone tree by Hackett et al. (2008) to summarize phylogenetic relationships among species. Using 5000 trees derived from posterior distribution of this phylogeny, which included all bird species in our dataset, we constructed a maximum credibility tree using function *maxCladeCred* in package 'phangorn' (Schliep et al., 2019). For each mountain, we cropped the tips of this phylogeny to match the species present and use these phylogenies for calculations of phylogenetic beta diversity (Pβ). All analyses were conducted within RStudio (RStudio, 2018) an environment for R (R Development Core Team, 2009).

Functional traits were compiled from Wilman et al. (2014). We used three subsets of traits. Two subsets describe specific ecological strategies thought to be important in mediating biotic interactions: diet and foraging strata (Marra & Remsen, 1997; Naoki & Stouffer, 2007), and one, body mass, considered to be a surrogate of environmental tolerance and caloric requirements. Data on diet and foraging strata consist of seven axes each; axes refer to proportional use of different categories of food (invertebrates, vertebrate endotherms, vertebrate ectotherms, fish, carcasses, fruits, nectar, seeds, other plant materials) and stratum for feeding (water, water surface, ground, understorey, mid-storey, canopy, aerial), respectively. Body mass is the average weight of an individual, in grams. For all 3522 species, we created a multivariate pairwise trait dissimilarity matrix including all three functional traits (diet, foraging and body mass) using Gower's distance (function *gowdis*, in package 'FD') (Laliberté et al., 2014). For these calculations, we weighted each category within each subset equally (each diet and foraging category weighted 1/7 and body mass weighted 1). Following Mammola and Cardoso (2020), we performed a principal coordinate analysis (PCoA) with function *cmdscale* (package 'stats') on the pairwise trait dissimilarity matrix and selected the first two axes to describe a two-dimensional trait space for each species (hereafter referred as trait space). Adding more dimensions to the trait spaces was computationally unfeasible. Together the two first axes explained 55% of the inertia. The resulting trait space was used for calculations of functional beta diversity (Fβ). Finally, to further examine individual components of trait diversity, we performed additional calculations for Fβ with each subset of traits (diet, foraging strata and body mass), separately (see Appendix S2).

2.3 | Effects of latitude on mountain β-diversity

We were interested in examining how latitude relates to (a) overall values of Tβ, Pβ and Fβ in each mountain, to (b) the relationship between assemblage dissimilarity (Tβ, Pβ and Fβ) and elevational distance between two elevational bands (i.e. distance decay patterns) and to (c) variability of pairwise Tβ, Pβ and Fβ within each mountain (Figure 1). To do this, we regressed three different response variables against latitude as described below.

First, we used the framework proposed by Chao et al. (2014) and extended by Chiu and Chao (2014) and Chiu et al. (2014) to calculate Tβ, Pβ and Fβ. This framework takes advantage of the relationship between local diversity (alpha diversity, α), diversity turnover among localities (beta diversity, β) and regional diversity (gamma diversity, γ), and results in one single value of β-diversity per mountain (as opposed to a set of pairwise values across elevations) (Hill, 1973; Jost, 2007). Specifically, we calculated β-diversity for each mountain based on the multiplicative partitioning of diversity proposed by Jost (2007) where beta diversity is the ratio of gamma diversity and alpha diversity. These metrics are normalized and range between 0 and 1, and thus, are directly comparable across communities. We present these values as $T\beta_{chao}$, $F\beta_{chao}$ and $P\beta_{chao}$, respectively. Calculations utilized packages 'hillR' (Li, 2018) and 'adiv' (Pavoine, 2020).

Second, we examined whether tropical mountains had 'faster' changes in diversity than temperate mountains (i.e. if distance decay patterns were steeper) (Soininen, McDonald, et al., 2007). For each mountain separately, we calculated pairwise Tβ, Fβ and Pβ among all pairs of assemblages with Sorensen-family indices using the frameworks proposed by Podani and Schmera (2011) and Carvalho et al. (2012). This resulted in one dissimilarity matrix for each dimension of diversity per mountain (hereafter referred as $T\beta_{sor}$, $F\beta_{sor}$ and $P\beta_{sor}$). Pairwise $T\beta_{sor}$ was calculated on site x species matrix using incidence data, where site referred to a 200 m elevational band. $P\beta_{sor}$ was calculated based on the phylogenetic tree, with path to the root included in the calculations. $F\beta_{sor}$ was calculated as pairwise difference in kernel n-dimensional hypervolumes between bird assemblages (Blonder et al., 2014). $T\beta_{sor}$ and $P\beta_{sor}$ were calculated with function *beta* (Cardoso et al., 2014) and $F\beta_{sor}$ with function *kernel.beta* (Mammola & Cardoso, 2020) in package 'BAT' (Cardoso et al., 2020).

Our choice of Podani and Schmera (2011) and Carvalho et al. (2012) metrics relied on their mathematical properties, which allow partitioning $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$ into its two additive components (β_{rich} and β_{repl}), with these components scaled in the same way. Relativized values of β-diversity components are comparable across communities and most importantly, ecologically interpretable. An extended discussion on benefits of this partition method can be found in Cardoso et al. (2014) and Ensing and Pither (2015). The Baselga metrics were unused for these reasons but also due to smaller capacities for sites comparisons (≤10; Baselga, 2010, 2013) and trait comparisons (≤4; Baselga et al., 2018) than we needed. We present further details on our choice of metrics in Appendix S3.

We assessed whether dissimilarity between elevations in terms of $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$ is mostly explained by replacement (β_{repl}) or richness differences (loss or gain of species, clades or functional groups; β_{rich}) using functions by Cardoso et al. (2020). This analysis resulted in two dissimilarity matrices, one for β_{repl} and one for β_{rich} for each dimension of diversity ($T\beta_{repl}$, $P\beta_{repl}$ and $F\beta_{repl}$, and $T\beta_{rich}$, $P\beta_{rich}$ and $F\beta_{rich}$, respectively). Then, we used our computed values of $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$, and their components, and fitted power-law models with dissimilarity (pairwise β-diversity) as response variable and elevational distance between two elevations as predictor, for each mountain separately. Power-law functions have been suggested to be appropriate to model distance decay patterns at our study scale (single gradients), where potential stochastic sampling effects might affect occurrence (Nekola & McGill, 2014). Goodness of fit of each curve is calculated as a pseudo-r^2, and significance calculated by randomizing elevational distances 1000 times and computing the proportion of times model deviance is smaller than the exponential model (Gómez-Rodríguez & Baselga, 2018). Distance decay models were calculated with function *decay.model* in package 'betapart' (Baselga et al., 2018). In these models, higher slopes represent curves with faster rates of change in diversity. We extracted the slope, its significance and overall model fit (pseudo r^2) for each distance decay model fitted (see Appendix S4). Slopes that were statistically significant were used as a surrogate of the 'steepness' of the distance decay of each mountain system.

Third, to describe variability of pairwise Tβ, Pβ and Fβ within each mountain, we again used our calculated pairwise $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$ matrices and extracted only pairwise distances between consecutive elevational bands to represent change in diversity for a 200 m increase in elevation. For each mountain, we summarized overall variability in every 200 m increase in elevation as the SD of Tβ, Pβ and Fβ values.

We used generalized linear models (GLMs) to test for the effect of latitude on our three response variables: (a) overall beta diversity ($T\beta_{chao}$, $P\beta_{chao}$ and $F\beta_{chao}$), (b) the steepness of the distance decay patterns of $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$ (slopes of distance decay models and their components) and (c) within mountain variability in pairwise β-diversity (SD of $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$). For β_{chao}, we used beta distributed GLMs performed in 'betareg' package (Zeileis et al., 2016), as our response variable was constrained between 0 and 1 but did not include exact values of 0 or 1. For the steepness of distance decay models and $SD\beta_{sor}$ models, we use Gamma distribution GLMs with link identity, as response variables were positive and included values of 0 and 1. In all cases, we used the absolute value of latitude to describe the geographical position relative to the Equator. After preliminary examination, we decided on including a quadratic term for latitude for steepness of distance decay models. Furthermore, because Northern and Southern hemispheres do not follow the same seasonality patterns, we included a categorical variable hemisphere (two levels: North or South) as a covariate.

3 | RESULTS

We examined latitudinal effects on (a) overall values of $T\beta_{chao}$, $P\beta_{chao}$ and $F\beta_{chao}$ in each mountain, (b) steepness of distance decay patterns of similarity and (c) variability of pairwise $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$ within each mountain (Figure 1). As expected, latitude had a negative effect on overall taxonomic and functional β-diversity ($T\beta_{chao}$ and $F\beta_{chao}$), with tropical mountains having higher beta diversity (Figure 2, Table 1). A similar negative trend was observed for phylogenetic β-diversity ($P\beta_{chao}$), but the effect was not significant ($p = 0.054$). Effect sizes were weak in all cases, likely due to high variability among mountains. Hemisphere was not significant for any dimension of β-diversity. These negative latitudinal trends are consistent with narrow physiological tolerance in tropical species resulting in narrower elevational distributions, and low dispersal and potentially high allopatric speciation in mountain assemblages, resulting in greater β-diversity (see Figure 1). Furthermore, results were consistent when using only a subset of traits to calculate $F\beta_{chao}$ (Table S2.7, Figure S2.5 in Appendix S2), suggesting greater turnover in functional traits related to physiological tolerance (i.e. body mass) and biotic interactions (i.e. diet and foraging), across elevations.

When examining the relationship between the steepness of distance decay patterns and latitude (Figure 3), we found partial support for our predictions. The linear predictor of latitude had a negative effect on the steepness of distance decay patterns of dissimilarity for all three dimensions of diversity with steeper curves in tropical mountains closer to the Equator (Table 2, Figure 3b). However, the quadratic predictor of latitude had a positive, yet weaker effect, resulting in an increase in steepness in mountains located in the temperate region (above ~23°; Figure 3b). A detailed examination of distance decay curves shows that, for Tβ and Pβ, mountains across latitudes showed variable patterns, with lower values at mid-latitudes (Figure 3a). Contrary to our expectations, a few temperate mountains showed faster accumulation of functional dissimilarity ($F\beta_{sor}$) than tropical mountains (Figure 3a). The steeper values of Fβ distance decay patterns in temperate mountains were mostly explained by the β_{rich} component (Figure 4). Our analyses of separate sets of traits further indicate that this result might be

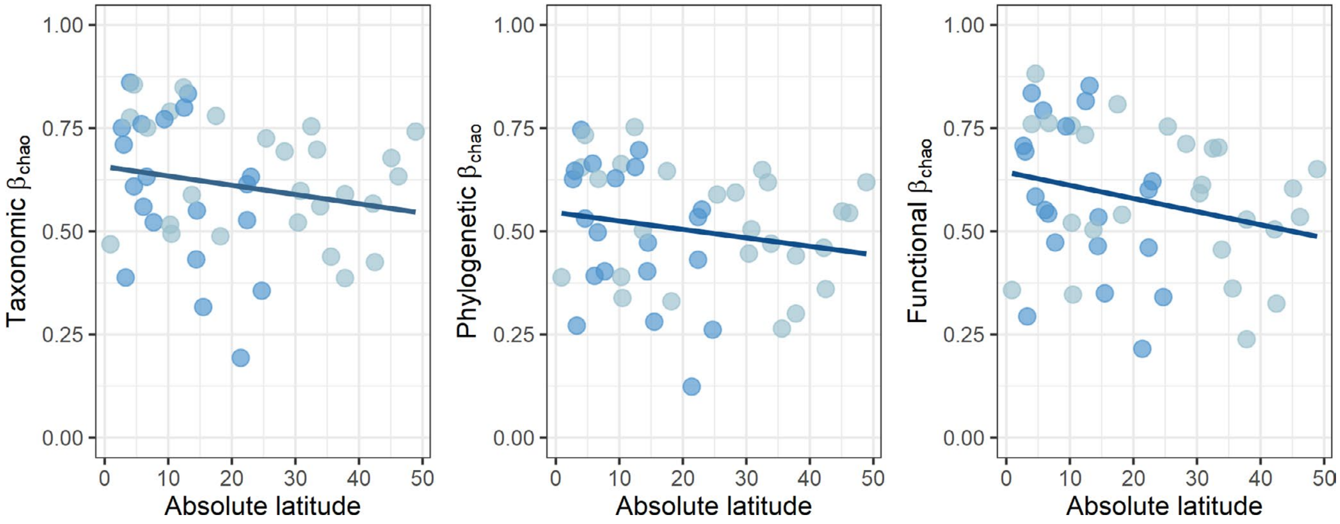

FIGURE 2 Patterns of taxonomic beta diversity ($T\beta_{chao}$), phylogenetic beta diversity ($P\beta_{chao}$) and functional beta diversity ($F\beta_{chao}$) for 46 mountain systems across latitude. Lines correspond to the multiple regression of β-diversity against absolute latitude, and hemisphere (North or South) as a covariate. Results of regressions are presented in Table 1. Dark blue points represent mountains in the Southern hemisphere and light blue points mountains in the Northern hemisphere. Latitude had a significant negative effect on $T\beta_{chao}$ and $P\beta_{chao}$ (p = 0.025 and 0.019, respectively) and a negative but not significant effect for $F\beta_{chao}$ (p = 0.054); hemisphere was not significant in any model

TABLE 1 General linear models with beta distribution for taxonomic ($T\beta_{chao}$), phylogenetic ($P\beta_{chao}$) and functional ($F\beta_{chao}$) beta diversity as a function of absolute latitude (Lat) and hemisphere (North or South) as a covariate

Model	Parameter	Estimate	SE	z-value	p value
$T\beta_{chao}$~Lat+Hem	Intercept	0.959	0.233	4.106	<0.0001
	Latitude	−0.017	0.007	−2.238	0.025
	Hemisphere (South)	−0.387	0.212	−1.828	0.068
$P\beta_{chao}$~ Lat+Hem	Intercept	0.407	0.211	1.927	0.054
	Latitude	−0.013	0.007	−1.919	0.054
	Hemisphere (South)	−0.300	0.195	−1.539	0.124
$F\beta_{chao}$~ Lat+Hem	Intercept	0.835	0.249	3.352	<0.001
	Latitude	−0.019	0.008	−2.345	0.019
	Hemisphere (South)	−0.304	0.227	−1.339	0.181

driven by the loss of functional space related with foraging strata (Figures S2.6 and S2.7 in Appendix S2).

Finally, our assessment of latitudinal effects on within mountain variability in pairwise β-diversity (SD β_{sor}) also supported our prediction of higher variability in $T\beta_{sor}$ and $P\beta_{sor}$ in mountains towards the tropics (Figure 5, Table 3). This finding is consistent with different mechanisms acting at different elevations in tropical mountains, whereas more homogeneous environmental filtering might drive less variable pairwise β-diversity in temperate mountains (Montaño-Centellas et al., 2019). Furthermore, hemisphere also had a negative effect on SD $T\beta_{sor}$ and SD $P\beta_{sor}$, with mountains in the Southern hemisphere having less within mountain variability than mountains in the more seasonal Northern hemisphere (Table 3). In both cases, the effect of latitude was also significant for the β_{repl} component (Table S2.10 in Appendix S2). In contrast, within mountain variability in functional β-diversity (SD $F\beta_{sor}$) increased towards higher latitudes (Figure 5), a pattern likely driven by higher variability in functional β-diversity for foraging space (Figure S2.9 in Appendix S2). Although not statistically significant (Table 3), this trend is consistent with our finding of steeper distance decay patterns of Fβ at higher latitudes (Figure 3b).

4 | DISCUSSION

We examined latitudinal effects on multiple dimensions of bird β-diversity across elevations (Graham et al., 2014) and their partition into β_{rich} and β_{repl} components (Legendre, 2014). We based our expectations on Janzen (1967) who proposed that mountains represent stronger barriers to dispersal (are 'higher') in the tropics because of species' narrower physiological tolerances. Wider tolerances at higher latitudes result in part because stronger seasonality in temperate regions selects for broader tolerances (Ghalambor et al., 2006). Our results are consistent with tropical mountain assemblages containing species with narrow elevational distributions, low dispersal abilities and potentially high probabilities of allopatric speciation, resulting in higher β-diversity across elevations.

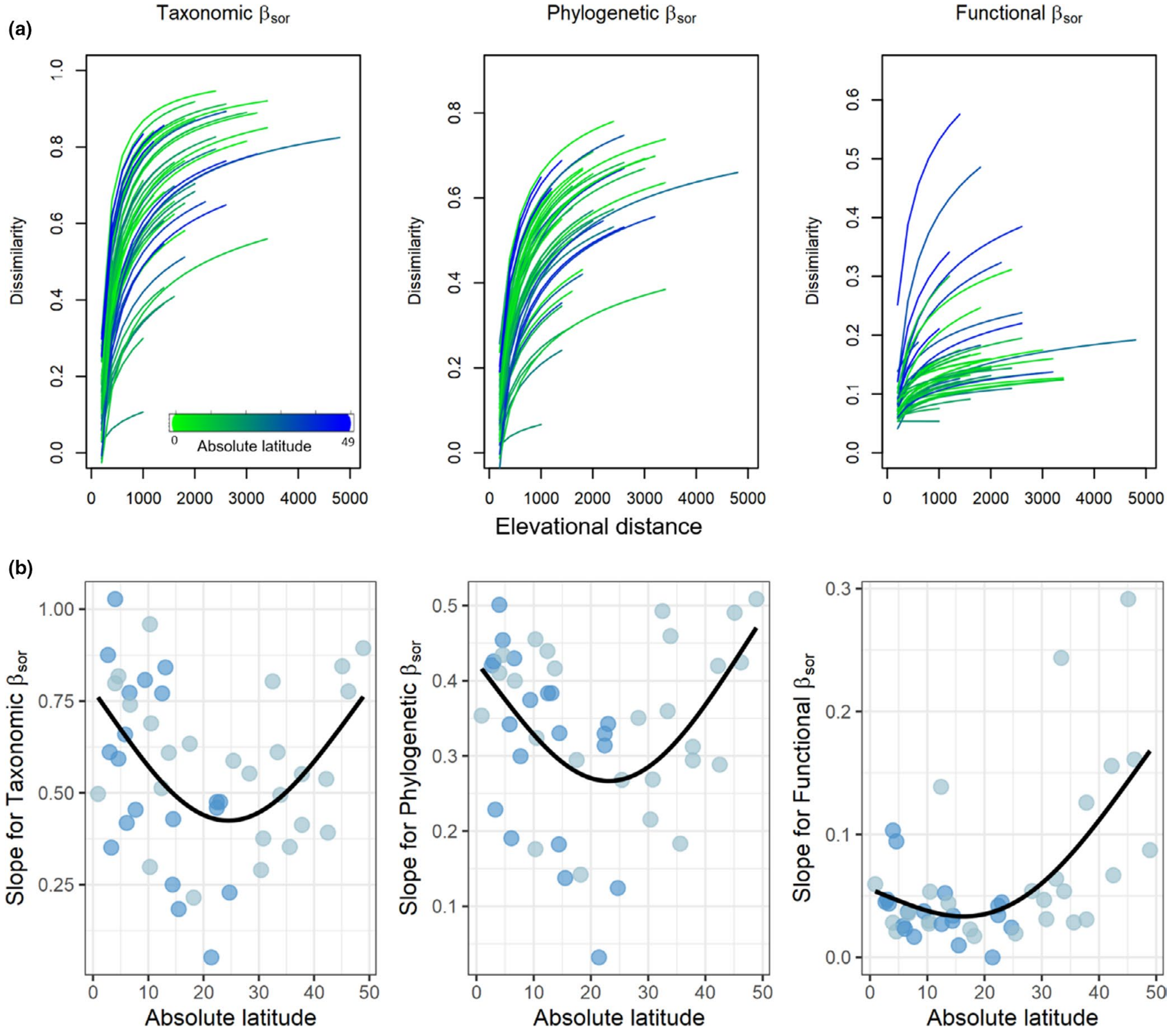

FIGURE 3 (a) Distance decay patterns for taxonomic ($T\beta_{sor}$), phylogenetic ($P\beta_{sor}$) and functional ($F\beta_{sor}$) beta diversity for avian assemblages along elevation for 46 mountains across the globe, and (b) the latitudinal effects on the steepness of these distance decay patterns (slope of $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$). In (a) mountains are colour coded with a continuous palette that ranges from green (latitude 0) to blue (latitude 49). Mountains located towards the Equator are closer to the green extreme, and those located towards higher latitudes are closer to the blue extreme. Latitude had a significant effect on the slope of distance decay patterns for all three dimensions of diversity. Regression results for (b) are presented in Table 2

Building on Janzen's early hypotheses regarding differences in thermal regimes as potential mechanisms driving latitudinal changes, we predicted higher values of β-diversity in tropical mountains and tested our hypotheses with well-sampled observational data in mountains across the globe. Mountains included in our dataset are characterized by distinctive combinations of features (i.e. mountain size, biogeographical history, age), characteristics that determine different rates of speciation, extinction and colonization across elevations in each mountain system (Fjeldså et al., 2012; Janzen, 1967; Jetz & Fine, 2012; Price et al., 2014), and ultimately different patterns of functional and phylogenetic β-diversity. We found a mostly consistent negative relationship between latitude and β-diversity, most effect sizes are, however, weak due to the natural variability contained in our dataset. Local empirical data are important as they reflect which species co-occur and likely interact in space and time (Graham et al., 2014); however, it has been suggested that inferring processes from patterns of observational data could be problematic when using observational data (Cadotte & Tucker, 2017; Kraft et al., 2015). Although we do discuss potential mechanisms driving our results, our aim in this study is not to test for these mechanisms, but to examine whether beta diversity patterns are consistent with predictions derived from Janzen's (1967) article.

Our findings for $T\beta_{chao}$, $F\beta_{chao}$ and $P\beta_{chao}$ agree with our expectations, with a negative, albeit relatively weak, relationship between

TABLE 2 Coefficients for absolute latitude (linear and quadratic terms) and hemisphere (North and South) as predictors of the steepness (slope) of distance decay patterns of beta diversity (β_{sor}) across elevations. Coefficients were extracted from GLMs with Gamma errors for taxonomic ($T\beta_{sor}$), phylogenetic ($P\beta_{sor}$) and functional ($F\beta_{sor}$), separately. Models for the separated components (β_{rich} and β_{repl}) for each dimension of diversity, and models for functional β-diversity calculated for subsets of traits are presented in Tables S2.8 and S2.9 in Appendix S2, respectively

Models	Parameter	Estimate	SE	*t*-value	*p* value
$T\beta_{sor}$~ Lat+Hem	Latitude	−0.032	0.008	−3.768	0.001
	Latitude^2	0.001	0.000	3.476	0.001
	Hemisphere (South)	−0.071	0.069	−1.033	0.308
$P\beta_{sor}$~ Lat+Hem	Latitude	−0.016	0.004	−3.657	0.001
	Latitude^2	0.0003	0.000	3.609	0.001
	Hemisphere (South)	−0.039	0.035	−1.115	0.271
$F\beta_{sor}$~ Lat+Hem	Latitude	−0.004	0.002	−2.023	0.049
	Latitude^2	0.0001	0.000	3.030	0.004
	Hemisphere (South)	−0.006	0.016	−0.378	0.707

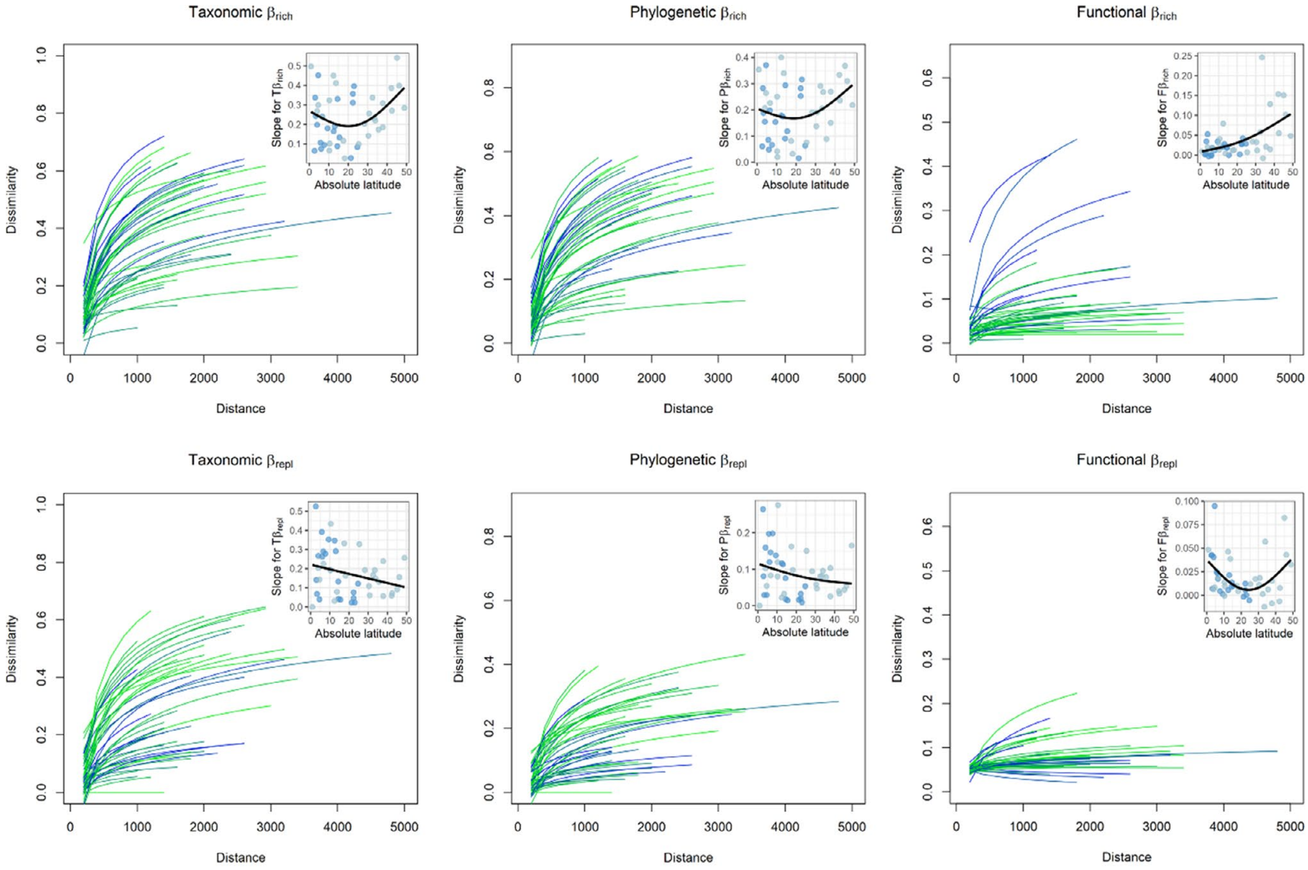

FIGURE 4 Distance decay patterns for the two components (β_{rich} and β_{repl}) of taxonomic, phylogenetic and functional β-diversity of bird assemblages in 46 elevational gradients. Mountains are colour coded with a continuous palette that ranges from green (latitude 0) to blue (latitude 49). Mountains located towards the Equator are closer to the green extreme, and those located towards higher latitudes are closer to the blue extreme. Boxes within each panel show the latitudinal effects on the steepness of these distance decay patterns (slope of $T\beta_{sor}$, $P\beta_{sor}$ and $F\beta_{sor}$)

β-diversity and latitude (see also García-Girón et al., 2020; Soininen, McDonald, et al., 2007 for similar results with other taxa). Tropical assemblages might contain more specialists and species with smaller niches and narrower distributions (Fjeldså et al., 2012; Janzen, 1967; McCain, 2009b), driving faster changes of species, traits and lineages across elevations. On the contrary, temperate assemblages might contain more physiological and ecological generalist species (Dalsgaard et al., 2011) with wider elevational distributions (McCain, 2009b), resulting in smaller changes in diversity across elevations. Within-mountain variability in Tβ and Pβ (SD β_{sor}) further support our predictions, with higher variability within tropical mountain assemblages. High within-mountain variability suggests that the rate of change in species composition and lineages is not constant with elevation; fast and slow rates of change (high and low dissimilarities

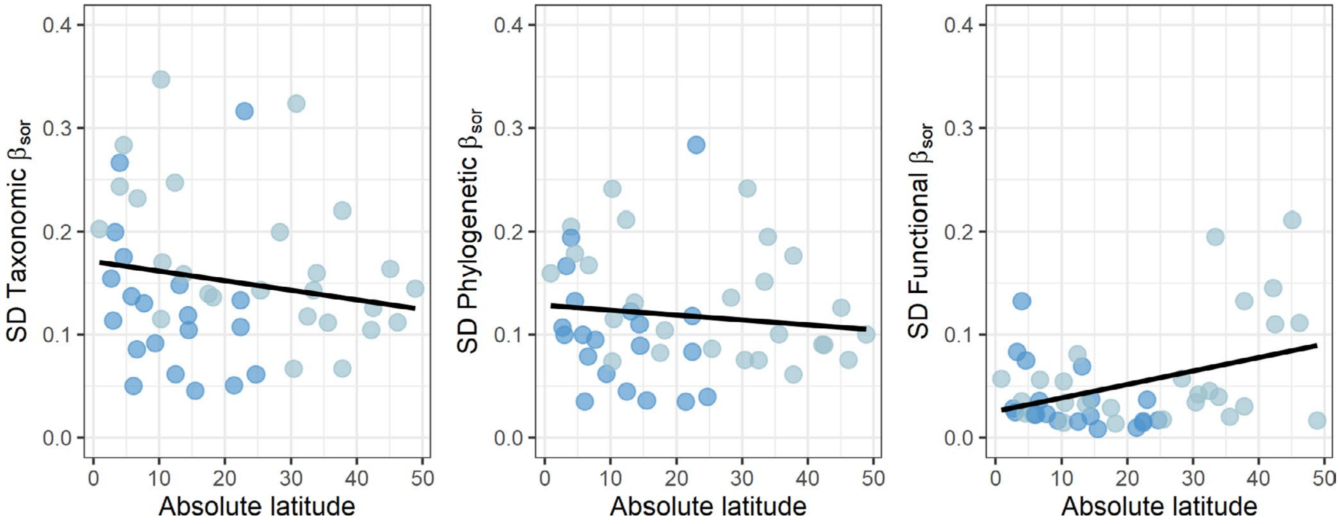

FIGURE 5 Variability in within-mountain taxonomic, functional and phylogenetic β-diversity across elevations, measured as the standard deviation of Sorensen dissimilarity (SD β_{sor}) between neighbour elevational bands, for 46 mountain systems worldwide. Black lines correspond to the multiple beta regression of β against absolute latitude with hemisphere (North or South) as a covariate. Results of regressions are presented in Table 3. Dark blue points represent mountains in the Southern hemisphere and light blue points mountains in the Northern hemisphere. Latitude had a significant negative effect on SD Tβ_{sor} but no significant effect on either SD Fβ_{sor} or SD Pβ_{sor}

TABLE 3 General linear models with beta distribution for the variability of taxonomic (SD Tβ_{sor}), functional (SD Fβ_{sor}) and phylogenetic (SD Pβ_{sor}) beta diversity, as a function of absolute latitude (Lat) and hemisphere (North or South) as a covariate. Models for the separated components (β_{rich} and β_{repl}) for each dimension of diversity, and models for functional β-diversity calculated for subsets of traits are presented in Tables S2.10 and S2.11 in Appendix S2, respectively

Models	Parameter	Estimate	SE	*z*-value	*p* value
SDTβ_{sor}~ Lat+Hem	Intercept	−1.152	0.156	−7.366	<0.0001
	Latitude	−0.016	0.005	−3.004	0.009
	Hemisphere (South)	−0.596	0.157	−3.802	<0.001
SDPβ_{sor}~ Lat+Hem	Intercept	−1.545	0.160	−9.622	<0.0001
	Latitude	−0.013	0.005	−2.267	0.023
	Hemisphere (South)	−0.515	0.160	−3.219	0.001
SDFβ_{sor}~ Lat+Hem	Intercept	−3.008	0.255	−11.798	<0.001
	Latitude	0.010	0.008	1.303	0.193
	Hemisphere (South)	−0.325	0.237	−1.365	0.172

between neighbour elevational bins) can be found along the same elevational gradient. At any given elevation, species-specific bird responses to abiotic stress and/or species interactions interplay to structure avifaunas (Srinivasan et al., 2018). Differences in physical complexity, tree composition, feeding resources and abiotic factors have all been found to drive species composition across elevations in tropical mountains, with varying relative importance in different elevational zones (Hanz et al., 2019; Montaño-Centellas et al., 2021). Our finding of higher within-mountain variability in tropical mountains is consistent with greater elevational differences in the relative role of environmental and biotic filtering acting upon species and lineages in tropical than temperate mountains (Montaño-Centellas et al., 2019).

In contrast, we found mixed results in our analyses of Fβ. Although total functional β-diversity (Fβ_{chao}) did decrease with latitude, the rate of change (steepness of distance decay patterns) and within-mountain variability in Fβ (SD Fβ) were higher in temperate mountains. For any given mountain, we expected low Fβ when comparing neighbour elevational bands at higher elevations, due to a more restricted community formed by a harsher abiotic environment, whereas higher values of Fβ were predicted among neighbour bands at lower elevations, likely resulting from competitive interactions and niche partition (Fontana et al., 2017, 2020). These changes in the speed of change in different elevational zones would result in high within-mountain variability in Fβ (SD Fβ). However, because the relative role of environmental filtering might change faster within tropical mountains, with greater importance at high elevations (Montaño-Centellas et al., 2019), we expected higher within-mountain variability in Fβ (SD Fβ) towards the tropics. On the contrary, a more homogeneous role of environmental filters across elevations characterizes temperate mountains (Montaño-Centellas et al., 2019); thus, we predicted lower within-mountain variability in Fβ (SD Fβ) in mountains at higher latitudes. Contrary to our expectations, within-mountain variability in Fβ (SD Fβ) was lower in mountains at lower latitudes. We argue that these patterns might result from stronger niche packing in tropical avifaunas (Pigot et al.,

2016) especially from low to mid-elevations. Here the loss of species and/or lineages with elevation largely involve redundant species, causing only small reductions in overlap of functional hypervolumes between assemblages. This would result in less steep distance decay curves in tropical mountains, whereas in less packed temperate assemblages, each species that is lost with increasing elevation might have a stronger impact in the size and overlap of functional space resulting in steeper distance decay curves.

Our partition of β-diversity into its components β_{repl} and β_{rich} provided further support for our hypotheses. Species replacement (the change of species identity between communities while retaining species richness invariable) has been suggested to reflect species sorting by environment or dispersal processes, whereas changes in the number of species are likely related with ordered extinction–colonization dynamics (Carlos Carvalho & Cardoso, 2018; Carvalho et al., 2012). In most gradients, $T\beta_{rich}$ and $P\beta_{rich}$ values were higher than $T\beta_{repl}$ and $P\beta_{repl}$ suggesting changes in β-diversity with elevational distance resulted mostly from the loss (or gain) of species and lineages. β-diversity patterns mostly explained by changes in β_{rich} are consistent with environmental filtering having a dominant role in the assembly of montane assemblages worldwide (Montaño-Centellas et al., 2019), limiting the number of species and clades that can exist along a gradient and resulting in local and regional extinctions related to harsh environmental conditions (Soininen et al., 2018). The relevance of $T\beta_{repl}$ and $P\beta_{repl}$ was, however, consistently higher for mountains at lower latitudes (Figure 4). A higher importance in $P\beta_{repl}$ in tropical mountains suggests that there is a strong replacement of lineages among assemblages without a notable difference in the amount of phylogenetic information encompassed by the different communities (Kluge & Kessler, 2011). This could happen, for instance, if different elevations have radiation or speciation events, if biological interactions result in the local exclusion of closely related taxa and/or if there are low rates of dispersal (Soininen et al., 2018). An example of such mechanisms is found in the Neotropical genus of tapaculo *Scytalopus*, which shows particularly rapid non-adaptive diversification resulting in major lineages occupying distinct elevational zones in the tropical Andes (Cadena & Cespedes, 2020). Fast replacement of lineages in tropical mountains can also be explained by niche conservatism. Lineages that evolved in warm stable environments might be unable to colonize higher elevations as they lack adaptations to survive in cooler environments (Wiens & Graham, 2005). Thus, many lineages occupying tropical high elevations are closely related with lineages from temperate latitudes that tracked favourable conditions and were able to colonize these new habitats following mountain uplifts (Quintero & Jetz, 2018).

The steeper values of Fβ distance decay patterns in temperate mountains were mostly explained by the β_{rich} component. This is consistent with environmental filtering favouring only certain traits along the gradient and filtering out many others (Cardoso et al., 2014; Kluge & Kessler, 2011). Our results suggest that the fast decrease in functional space overlap among temperate assemblages results from a faster loss of functional groups with elevational distance, reducing the overlap of assemblages' functional space. Furthermore, we found a negative effect of latitude on the steepness of distance decay patterns of $F\beta_{repl}$, implying a faster replacement (instead of reduction) of functional traits with elevational distance in tropical mountains than in temperate mountains.

This study highlights the importance of examining multiple dimensions of diversity, as different patterns might contain non-redundant information about the drivers of diversity patterns. Altogether, our results agree with predictions derived from Janzen's original ideas of tropical mountains representing stronger barriers to dispersal for biotas than temperate mountains. Greater climatic stability and productivity in tropical latitudes might allow more opportunities for specialization and fine niche partitioning within functional space (i.e. niche filling) (Jocque et al., 2010; MacArthur, 1984; Pigot et al., 2016). In consequence, tropical montane assemblages might contain more specialists and species with smaller niches and narrower elevational distributions (Fjeldså et al., 2012; McCain, 2009b), resulting in overall higher β-diversity patterns and greater relevance of the replacement component driving these patterns. On the other hand, mountains in more seasonal and less productive areas at higher latitudes where a more restricted pool of clades is found will contain less speciose assemblages, composed mostly of physiological and ecological generalists with wider elevational distributions (Dalsgaard et al., 2011; Read et al., 2018), resulting in overall lower values of β-diversity. In temperate mountains, dissimilarity in functional space among assemblages accumulates faster, as a result of decreases in species richness and the consequent loss of functional space (β_{rich} component). In tropical mountains, niche packed assemblages accumulate functional dissimilarity less rapidly than temperate mountains likely because decreases in species richness with elevation result in less densely packed functional space but not in marked reductions in functional space overlap, at least from mid- to low elevations. Fifty years after Janzen's (1967) seminal paper, data across the globe and new analytical approaches allow for unravelling the processes underlying how latitude impacts various components of diversity.

ACKNOWLEDGEMENTS

We are thankful to all researchers who contributed their unpublished raw data: H. B. Katuwal, D. Horak, M. Brambilla, P. Pedrini, D. Chamberlain, as well as others that shared their data from elevational gradients in published materials. We are also grateful to E. Bruna, J. Blake, B. Scheffers and S. Robinson for early discussions about the project idea. The project was conducted with support of a Graduate School Fellowship Award from the University of Florida and grants from the Tropical Conservation and Development Program at UF and the American Philosophical Society, all granted to FMC. No permits were required to conduct this research.

DATA AVAILABILITY STATEMENT

Bird raw data were extracted from published sources listed in Appendix A. Bird species per elevation and bird beta diversity data used for analyses are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.r4xgxd2cj).

ORCID

Flavia Montaño-Centellas https://orcid.org/0000-0003-3115-3950
Bette A. Loiselle https://orcid.org/0000-0003-1434-4173
Christy McCain https://orcid.org/0000-0002-6416-0703

REFERENCES

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A. (2013). Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, *36*(2), 124–128. https://doi.org/10.1111/j.1600-0587.2012.00124.x.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., & Leprieur, F. (2018). Package 'betapart'. Partitioning beta diversity into turnover and nestedness components. Version 1.5.1.

Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography*, *23*(5), 595–609. https://doi.org/10.1111/geb.12146

Cadena, C. D., & Cespedes, L. N. (2020). Origin of elevational replacements in a clade of nearly flightless birds: Most diversity in tropical mountains accumulates via secondary contact following allopatric speciation. In V. Rull, & A. Corolina (Eds.), *Neotropical diversification: Patterns and processes* (pp. 635–659). Springer.

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology & Evolution*, *32*(6), 429–437. https://doi.org/10.1016/j.tree.2017.03.004

Cardoso, P., Mammola, S., Rigal, F., & Carvalho, J. C. (2020). Package BAT: Biodiversity assessment tools. Version 2.0.0.

Cardoso, P., Rigal, F., Carvalho, J. C., Fortelius, M., Borges, P. A. V., Podani, J., & Veech, J. (2014). Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. *Journal of Biogeography*, *41*(4), 749–761. https://doi.org/10.1111/jbi.12239

Carlos Carvalho, J., & Cardoso, P. (2018). Decomposing the causes for Niche differentiation between species using hypervolumes. *bioRxiv*. https://doi.org/10.1101/485920.485920

Carvalho, J. C., Cardoso, P., & Gomes, P. (2012). Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, *21*(7), 760–771. https://doi.org/10.1111/j.1466-8238.2011.00694.x

Cavender-Bares, J., Kozak, K. H., Fine, P. V., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*(7), 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Chao, A., Chiu, C. H., & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2351–2363. https://doi.org/10.1098/rstb.2011.0063

Chiu, C. H., & Chao, A. (2014). Distance-based functional diversity measures and their decomposition: A framework based on Hill numbers. *PLoS One*, *9*(7), e100014. https://doi.org/10.1371/journal.pone.0100014

Chiu, C. H., Jost, L., & Chao, A. (2014). Phylogenetic beta diversity, similarity, and differentiation measures based on Hill numbers. *Ecological Monographs*, *84*(1), 21–44. https://doi.org/10.1890/12-0960.1

Currie, D. J. (2017). Mountain passes are higher not only in the tropics. *Ecography*, *40*(4), 459–460. https://doi.org/10.1111/ecog.02695

Dalsgaard, B. O., Magård, E., Fjeldså, J., Martín González, A. M., Rahbek, C., Olesen, J. M., Ollerton, J., Alarcón, R., Cardoso Araujo, A., Cotton, P. A., Lara, C., Machado, C. G., Sazima, I., Sazima, M., Timmermann, A., Watts, S., Sandel, B., Sutherland, W. J., & Svenning, J.-C. (2011). Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and Quaternary climate-change velocity. *PLoS One*, *6*(10), e25891. https://doi.org/10.1371/journal.pone.0025891.

Ensing, D. J., & Pither, J. (2015). A novel multiple-site extension to pairwise partitioned taxonomic beta diversity. *Ecological Complexity*, *21*, 62–69. https://doi.org/10.1016/j.ecocom.2014.11.008.

Fjeldså, J., Bowie, R. C. K., & Rahbek, C. (2012). The role of mountain ranges in the diversification of birds. *Annual Review of Ecology, Evolution, and Systematics*, *43*(1), 249–265. https://doi.org/10.1146/annurev-ecolsys-102710-145113.

Fontana, V., Guariento, E., Hilpold, A., Niedrist, G., Steinwandter, M., Spitale, D., Nascimbene, J., Tappeiner, U., & Seeber, J. (2020). Species richness and beta diversity patterns of multiple taxa along an elevational gradient in pastured grasslands in the European Alps. *Scientific Reports*, *10*(1), 12516. https://doi.org/10.1038/s41598-020-69569-9.

Fontana, V., Kohler, M., Niedrist, G., Bahn, M., Tappeiner, U., & Frenck, G. (2017). Decomposing the land-use specific response of plant functional traits along environmental gradients. *Science of the Total Environment*, *599–600*, 750–759. https://doi.org/10.1016/j.scitotenv.2017.04.245

García-Girón, J., Heino, J., Baastrup-Spohr, L., Bove, C. P., Clayton, J., de Winton, M., Feldmann, T., Fernández-Aláez, M., Ecke, F., Grillas, P., Hoyer, M. V., Kolada, A., Kosten, S., Lukács, B. A., Mjelde, M., Mormul, R. P., Rhazi, L., Rhazi, M., Sass, L., … Alahuhta, J. (2020). Global patterns and determinants of lake macrophyte taxonomic, functional and phylogenetic beta diversity. *Science of the Total Environment*, *723*, 138021. https://doi.org/10.1016/j.scitotenv.2020.138021

Ghalambor, C. K., Huey, R. B., Martin, P. R., Tewksbury, J. J., & Wang, G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, *46*(1), 5–17. https://doi.org/10.1093/icb/icj003.

Gómez-Rodríguez, C., & Baselga, A. (2018). Variation among European beetle taxa in patterns of distance decay of similarity suggests a major role of dispersal processes. *Ecography*, *41*(11), 1825–1834. https://doi.org/10.1111/ecog.03693.

Graham, C. H., Carnaval, A. C., Cadena, C. D., Zamudio, K. R., Roberts, T. E., Parra, J. L., McCain, C. M., Bowie, R. C. K., Moritz, C., Baines, S. B., Schneider, C. J., VanDer Wal, J., Rahbek, C., Kozak, K. H., & Sanders, N. J. (2014). The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. *Ecography*, *37*(8), 711–719. https://doi.org/10.1111/ecog.00578.

Graham, C. H., & Fine, P. V. A. (2008). Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. *Ecology Letters*, *11*(12), 1265–1277. https://doi.org/10.1111/j.1461-0248.2008.01256.x.

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K.-L., Harshman, J., Huddleston, C. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, C. C., & Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, *320*(5884), 1763–1768. https://doi.org/10.1126/science.1157704

Hanz, D. M., Böhning-Gaese, K., Ferger, S. W., Fritz, S. A., Neuschulz, E. L., Quitián, M., Santillán, V., Töpfer, T., & Schleuning, M. (2019). Functional and phylogenetic diversity of bird assemblages are filtered by different biotic factors on tropical mountains. *Journal of Biogeography*, *46*(2), 291–303. https://doi.org/10.1111/jbi.13489.

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, *54*(2), 427–432. https://doi.org/10.2307/1934352.

Huey, R. B. (1978). Latitudinal pattern of between-altitude faunal similarity: Mountains might be "higher" in the tropics. *The American Naturalist*, *112*(983), 225–229. https://doi.org/10.1086/283262.

Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *The American Naturalist*, *101*(919), 233–249. https://doi.org/10.1086/282487.

Jetz, W., & Fine, P. V. A. (2012). Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLOS Biology*, *10*(3), e1001292. https://doi.org/10.1371/journal.pbio.1001292.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448.

Jocque, M., Field, R., Brendonck, L., & De Meester, L. (2010). Climatic control of dispersal–ecological specialization trade-offs: A metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography*, *19*(2), 244–252. https://doi.org/10.1111/j.1466-8238.2009.00510.x

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*(10), 2427–2439. https://doi.org/10.1890/06-1736.1

Kluge, J., & Kessler, M. (2011). Phylogenetic diversity, trait diversity and niches: Species assembly of ferns along a tropical elevational gradient. *Journal of Biogeography*, *38*(2), 394–405. https://doi.org/10.1111/j.1365-2699.2010.02433.x

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, *22*(11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006.

Kraft, N., Adler, P. B., Godoy, O., James, E., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*(5), 592–599. https://doi.org/10.1111/1365-2435.12345.

Kraft, N., Comita, L. S., Chase, J. M., Sanders, N. J., Crist, T. O., Stegen, J. C., Vellend, M., Boyle, B., Anderson, M. J., Cornell, H. V., Davies, K. F., Freestone, A. L., Inouye, B. D., Harrison, S. P., & Myers, J. A. (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, *333*(6050), 1755–1758.

Laliberté, E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). Package 'FD'. Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. (Version 1.0-12). https://CRAN.R-project.org/package=FD

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, *23*(11), 1324–1334. https://doi.org/10.1111/geb.12207.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Li, D. (2018). hillR: Taxonomic, functional, and phylogenetic diversity and similarity through Hill numbers. *Journal of Open Source Software*, *3*(1), 1041. https://doi.org/10.21105/joss.01041

MacArthur, R. H. (1984). *Geographical ecology: Patterns in the distribution of species*. Princeton University Press.

Mammola, S., & Cardoso, P. (2020). Functional diversity metrics using kernel density n-dimensional hypervolumes. *Methods in Ecology and Evolution*, 1–10. https://doi.org/10.1111/2041-210x.13424

Marra, P. P., & Remsen, J. V. (1997). Insights into the maintenance of high species diversity in the neotropics: Habitat selection and foraging behavior in understory birds of tropical and temperate forests. *Ornithological Monographs*, *48*, 445–483. https://doi.org/10.2307/40157547

McCain, C. M. (2009a). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, *18*(3), 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x

McCain, C. M. (2009b). Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecology Letters*, *12*(6), 550–560. https://doi.org/10.1111/j.1461-0248.2009.01308.x

McCain, C. M., & Beck, J. (2016). Species turnover in vertebrate communities along elevational gradients is idiosyncratic and unrelated to species richness. *Global Ecology and Biogeography*, *25*(3), 299–310. https://doi.org/10.1111/geb.12410

Montaño-Centellas, F. A., Loiselle, B. A., & Tingley, M. W. (2021). Ecological drivers of avian community assembly along a tropical elevation gradient. *Ecography*, *44*, 1–15. https://doi.org/10.1111/ecog.05379

Montaño-Centellas, F. A., McCain, C., & Loiselle, B. A. (2019). Using functional and phylogenetic diversity to infer avian community assembly along elevational gradients. *Global Ecology and Biogeography*, *29*(2), 232–245. https://doi.org/10.1111/geb.13021

Naoki, K., & Stouffer, P. C. (2007). Arthropod resource partitioning among omnivorous tanagers (Tangara spp.) in Western Ecuador. *The Auk*, *124*(1), 197–209.

Nekola, J. C., & McGill, B. J. (2014). Scale dependency in the functional form of the distance decay relationship. *Ecography*, *37*(4), 309–320. https://doi.org/10.1111/j.1600-0587.2013.00407.x

Pavoine, S. (2020). Adiv: Analysis of diversity. Version 2.0.

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, *9*(6), 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x.

Pigot, A. L., Trisos, C. H., & Tobias, J. A. (2016). Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1822), 20152013. https://doi.org/10.1098/rspb.2015.2013

Podani, J., & Schmera, D. (2011). A new conceptual and methodological framework for exploring and explaining pattern in presence – Absence data. *Oikos*, *120*(11), 1625–1638. https://doi.org/10.1111/j.1600-0706.2011.19451.x

Price, T. D., Hooper, D. M., Buchanan, C. D., Johansson, U. S., Tietze, D. T., Alström, P., Olsson, U., Ghosh-Harihar, M., Ishtiaq, F., Gupta, S. K., Martens, J., Harr, B., Singh, P., & Mohan, D. (2014). Niche filling slows the diversification of Himalayan songbirds. *Nature*, *509*, 222. https://doi.org/10.1038/nature13272

Qian, H., & Ricklefs, R. E. (2007). A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters*, *10*(8), 737–744. https://doi.org/10.1111/j.1461-0248.2007.01066.x

Quintero, I., & Jetz, W. (2018). Global elevational diversity and diversification of birds. *Nature*, *555*, 246. https://doi.org/10.1038/nature25794

R Development Core Team. (2009). R version 2.9. 2. R Project for Statistical Computing, Vienna, Austria.

Read, Q. D., Baiser, B., Grady, J. M., Zarnetske, P. L., Record, S., & Belmaker, J. (2018). Tropical bird species have less variable body sizes. *Biology Letters*, *14*(1), 20170453. https://doi.org/10.1098/rsbl.2017.0453

RStudio. (2018). RStudio: Integrated development environment for R. Version 1.1.442. Boston, MA, USA.

Salisbury, C. L., Seddon, N., Cooney, C. R., & Tobias, J. A. (2012). The latitudinal gradient in dispersal constraints: Ecological specialisation drives diversification in tropical birds. *Ecology Letters*, *15*(8), 847–855. https://doi.org/10.1111/j.1461-0248.2012.01806.x

Schliep, K., Paradis, E., de Oliveira Martins, L., Potts, A., White, T. W., Stachniss, C., & Kendall, M. (2019). Package 'phangorn': Phylogenetic reconstruction and analysis. v. 2.5.5.

Sheldon, K. S., Huey, R. B., Kaspari, M., & Sanders, N. J. (2018). Fifty years of mountain passes: A perspective on Dan Janzen's classic article. *The American Naturalist*, *191*(5), 553–565. https://doi.org/10.1086/697046

Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, *27*(1), 96–109. https://doi.org/10.1111/geb.12660

Soininen, J., Lennon, J. J., & Hillebrand, H. (2007). A multivariate analysis of beta diversity across organisms and environments. *Ecology*, *88*(11), 2830–2838. https://doi.org/10.1890/06-1730.1

Soininen, J., McDonald, R., & Hillebrand, H. (2007). The distance decay of similarity in ecological communities. *Ecography*, *30*(1), 3–12. https://doi.org/10.1111/j.0906-7590.2007.04817.x

Srinivasan, U., Elsen, P. R., Tingley, M. W., & Wilcove, D. S. (2018). Temperature and competition interact to structure Himalayan bird communities. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1874), 20172593. https://doi.org/10.1098/rspb.2017.2593

Stevens, R. D., & Willig, M. R. (2002). Geographical ecology at the community level: Perspectives on the diversity of New World bats. *Ecology*, *83*(2), 545–560. 10.1890/0012-9658(2002)083[0545:GEATCL]2.0.CO;2

Tello, J. S., Myers, J. A., Macía, M. J., Fuentes, A. F., Cayola, L., Arellano, G., Loza, M. I., Torrez, V., Cornejo, M., Miranda, T. B., & Jørgensen, P. M. (2015). Elevational gradients in β-diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. *PLoS One*, *10*(3), e0121458. https://doi.org/10.1371/journal.pone.0121458

Tuomisto, H. (2010). A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, *33*(1), 2–22. https://doi.org/10.1111/j.1600-0587.2009.05880.x

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*(7), 2027. https://doi.org/10.1890/13-1917.1

Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A. B., Rocha, A. V., & Zeileis, M. A. (2016). Package 'betareg'. Version 3.3. https://CRAN.R-project.org/package=betareg

Zuloaga, J., & Kerr, J. T. (2017). Over the top: Do thermal barriers along elevation gradients limit biotic similarity? *Ecography*, *40*(4), 478–486. https://doi.org/10.1111/ecog.01764

BIOSKETCHES

Flavia A. Montaño-Centellas has a background in tropical ecology and conservation, particularly of mountain systems. Her research focuses on the drivers of diversity patterns both at large scale and local scales, with emphasis in the role of species interactions in community assembly. In her studies, Flavia has explored community-level questions, using birds and bats as model systems. She is currently an Associate Researcher at the Instituto de Ecología, Universidad Mayor de San Andres, in Bolivia. **Bette A. Loiselle** is a Professor at University of Florida. Her research interests include understanding the ecological consequences of seed dispersal and population and behavioural ecology of tropical birds. **Christy McCain** is an Associate Professor at the University of Colorado Boulder. She is broadly interested in the theoretical and empirical aspects that cause and maintain species biodiversity as well as how biodiversity is modified by anthropogenic change.

Author contributions: FMC and BAL conceived the study, FMC and CM compiled the data and conceived the analyses, FMC compiled the dataset, performed the analyses, and wrote the manuscript. All authors provided critical comments to the analyses and the manuscript.

SUPPORTING INFORMATION

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

How to cite this article: Montaño-Centellas, F., Loiselle, B. A., & McCain, C. (2021). Multiple dimensions of bird beta diversity support that mountains are higher in the tropics. *Journal of Biogeography*, 48, 2455–2468. https://doi.org/10.1111/jbi.14212

APPENDIX A

DATA SOURCES

Blake, J. G. & Loiselle, B. A. (2000). Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *The Auk*, 117, 663–686.

Burner, R. C., Chua, V. L., Brady, M. L., Van Els, P., Steinhoff, P. O., Rahman, M. A. & Sheldon, F. H. (2016). An ornithological survey of Gunung Mulu National Park, Sarawak, Malaysian Borneo. *The Wilson Journal of Ornithology*, 128, 242–254.

Chamberlain, D., Brambilla, M., Caprio, E., Pedrini, P. & Rolando, A. (2016). Alpine bird distributions along elevation gradients: The consistency of climate and habitat effects across geographic regions. *Oecologia*, 181, 1139–1150.

Cordeiro, N. (1994). Forest birds on Mt. Kilimanjaro, Tanzania. Scopus, 17, 65–112.

Diamond, J. M. (1972). Avifauna of the Eastern Highlands of New Guinea. Cambridge, MA: Nuttall Ornithological Club, Harvard.

Diamond, J. M. & Lecroy, M. (1979). Birds of Karkar and Bagabag islands, New Guinea. *Bulletin of the American Museum of Natural History*, 164, 467–532.

Dixit, S., Joshi, V. & Barve, S. (2016). Bird diversity of the Amrutganga Valley, Kedarnath, Uttarakhand, India with an emphasis on the elevational distribution of species. *Check List*, 12, 1–11.

Donegan, T. M., Avendaño, J. E., Briceño-L. E., Luna, J. C., Roa, C., Parra, R., Turner, C., Sharp, M. & Huertas, B. (2010). Aves de la Serranía de los Yariguíes y tierras bajas circundantes, Santander, Colombia. *Cotinga*, 32, 72–89.

Eguchi, K., Takeishi, M., Nagata, H., Henmi, Y. & Kawaji, N. (1989). Altitudinal distribution of forest birds in the Yaku-shima Island,

Kagoshima prefecture, Japan, 1: Breeding season. *Japanese Journal of Ecology*, 39, 53–65.

Goodman, S., Hawkins, A. & Razafimahaimodison, J.-C. (2000). Birds of the Parc National de Marojejy, Madagascar: With reference to elevational distribution. *Fieldiana Zoology*, 175–200.

Goodman, S. M. (1990). The birds of Mt. Isarog National Park, southern Luzon, Philippines, with particular reference to altitudinal distribution. *Fieldiana. Zoology* (USA). no. 60.

Goodman, S. M., Willard, D. E. & Gonzales, P. C. (1995). The birds of Sibuyan Island, Romblon Province, Philippines, with particular reference to elevational distribution and biogeographic affinities. *Fieldiana. Zoology*, 82, 1–57.

Grinnell, J. & Storer, T. I. (1924). Animal life in the Yosemite: An account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. Berkeley, CA: University of California Press.

Hawkins, A. F. A. (1999). Altitudinal and latitudinal distribution of east Malagasy forest bird communities. *Journal of Biogeography*, 26, 447–458.

Jankowski, J. E., Ciecka, A. L., Meyer, N. Y. & Rabenold, K. N. (2009). Beta diversity along environmental gradients: Implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology*, 78, 315–327.

Jankowski, J. E., Merkord, C. L., Rios, W. F., Cabrera, K. G., Revilla, N. S. & Silman, M. R. (2013). The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. *Journal of Biogeography*, 40, 950–962.

Kendeigh, S. C. & Fawver, B. J. (1981). Breeding bird populations in the Great Smoky Mountains, Tennessee and North Carolina. *The Wilson Bulletin*, 93, 218–242.

Latta, S. C., Rimmer, C. C. & McFarland, K. P. (2003). Winter bird communities in four habitats along an elevational gradient on Hispaniola. Condor, 179–197.

Mahabal, A. & Sharma, T. (1992). Distribution patterns of birds of Kangra Valley (Himachal Pradesh). *Himalayan Journal of Environment and Zoology*, 6, 85–96.

Mallet-Rodrigues, F., Parrini, R. & Rennó, B. (2015). Bird species richness and composition along three elevational gradients in southeastern Brazil. *Atualidades Ornitológicas*, 188, 39–58.

Martínez, O., Maillard, O., Vedia-Kennedy, J., Herrera, M., Mesili, T. & Rojas, A. (2011). Riqueza específica y especies de interés para la conservación de la avifauna del área protegida Serranía del Aguaragüe (Sur de Bolivia). *El hornero*, 26, 111–128.

Massa, B., Lo Valvo, M. & Catalisano, A. (1989). Bird communities on Mount Etna (Sicily, Italy). *Italian Journal of Zoology*, 56, 349–356.

McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18, 346–360.

Medina-Macías, M. N., González-Bernal, M. A. & Navarro-Sigüenza, A. G. (2010). Distribución altitudinal de las aves en una zona prioritaria en Sinaloa y Durango, México. *Revista mexicana de biodiversidad*, 81, 487–503.

Molina Martinez, Y. G. (2014). Birds of the Totare River Basin, Colombia. *Check List*, 10, 269–286.

Nathan, R. & Werner, Y. L. (1999) Reptiles and breeding birds on Mt. Hermon: Patterns of altitudinal distribution and species richness. *Israel Journal of Zoology*, 45, 1–33.

Navarro, A. G. (1992). Altitudinal distribution of birds in the Sierra Madre Del Sur, Guerrero, Mexico. *The Condor: Ornithological Applications*, 94, 29–39.

Nishiumi, I. (2002). Vertical distribution of birds in Mikurajima. *National Museum of Science Japan*, 38, 239–247 [text in Japanese].

Paulsch, D. (2008). Aves. Provisional checklist of flora and fauna of the San Francisco valley and its surroundings (Reserva Biológica San Francisco, Province Zamora-Chinchipe, southern Ecuador). *Ecotropical Monographs*, 4

Poulsen, M. K. & Lambert, F. R. (2000). Altitudinal distribution and habitat preferences of forest birds on Halmahera and Buru, Indonesia: Implications for conservation of Moluccan avifaunas. *Ibis*, 142, 566–586.

Prodon, R., Thibault, J. C. & Dejaifve, P. A. (2002). Expansion vs. compression of bird altitudinal ranges on a Mediterranean island. *Ecology*, 83, 1294–1306.

Robbins, M. B., Ridgely, R. S., Schulenberg, T. S. & Gill, F. B. (1987). The avifauna of the Cordillera de Cutucu, Ecuador, with comparisons to other Andean localities. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 139, 243–259.

Romdal, T. S. (2001). Altitudinal distribution and abundance patterns of bird species in the Eastern Arc Mountains, Tanzania. *Scopus*, 35–54.

Romdal, T. S. & Rahbek, C. (2009). Elevational zonation of afrotropical forest bird communities along a homogeneous forest gradient. *Journal of Biogeography*, 36, 327–336.

Safford, R. J. & Duckworth, J. W. (1990). A Wildlife survey of Marojejy Nature Reserve, Madagascar. Cambridge, UK: International Council for Bird Preservation. ICBP Study Report, 40.

Sainz-Borgo, C. (2012). Composición de la avifauna en un sector del Parque Nacional El Ávila, Venezuela. *Revista Venezolana de Ornitologia*, 2, 16–25.

Socolar, S. J., González, Ó. & Forero-Medina, G. (2012). Noteworthy bird records from the northern Cerros del Sira, Peru. *Cotinga*, 35, 24–36.

Terborgh, J. (1977). Bird species diversity on an Andean elevational gradient. *Ecology*, 58, 1007–1019.

Thiollay, J.-M. (1980). L'évolution des peuplements d'oiseaux le long d'un gradient altitudinal dans l'Himalaya central. *Revue d'écologie*, 2.

Thompson, L. S. (1978). Species abundance and habitat relations of an insular montane avifauna. *The Condor*, 80, 1–14.

Thorstrom, R. & Watson, R. (1997). Avian inventory and key species of the Masoala Peninsula, Madagascar. *Bird Conservation International*, 7, 99–115.

Tvardikova, K. (2013). Trophic relationships between insectivorous birds and insect in Papua New Guinea. Thesis Series, No 9. University of South Bohemia, Czech Republic.