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RESEARCH PAPER

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Forest canopy height co-determines taxonomic and functional richness, but not functional dispersion of mammals and birds globally

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Abstract

Aims: Taller forest canopies may harbour higher biodiversity by providing more and varied resources. No previous studies have assessed whether forest canopy height shapes the taxonomic and functional diversity of terrestrial vertebrates at global and regional scales. Here, we examine the roles of forest canopy height and other environmental variables in shaping global and regional patterns of species richness and functional diversity of mammals and birds.

Location: Global.

Time period: Present day.

Major taxa studied: Terrestrial mammals and birds.

Methods: Global forest canopy height data at 1 km spatial resolution were used to measure forest vertical structure. Species richness, functional richness and functional dispersion of mammals and birds were calculated using range maps and trait data. Spatial simultaneous autoregressive error models were used to evaluate associations between species richness and functional diversity and their predictors, including mean canopy height, standard deviation of canopy height, net primary productivity, current climate and historical climate stability, topography and human activities.

Results: The mean canopy height emerged as one of two predictors most associated with the species richness and functional richness of mammal. However, mean canopy height had little explanatory power for functional dispersion. Mean annual temperature and net primary productivity contributed most to explain global-scale mammal and bird functional dispersion. At the regional scale, mean canopy height, net primary productivity and mean annual temperature were the variables most associated with the species richness and functional diversity of mammals and birds.

Main conclusions: Forest canopy height is an important predictor of species richness and functional diversity of terrestrial vertebrates at both global and regional scales, at a similar overall level to productivity and temperature. Our study highlights the crucial role of the complex vertical structure in shaping the global and regional patterns of vertebrate diversity.

Gang Feng and Jian Zhang contributed equally to this study.

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KEYWORDS
forest vertical structure, functional biogeography, functional dispersion, functional richness, niche packing, vertical niche differentiation

1 | INTRODUCTION

Forest vertical structure, as represented by forest canopy height and its variability, is thought to play a crucial role in determining biodiversity across varying spatial scales, notably by taller forest canopy providing more available niches and thereby promoting species coexistence (MacArthur & MacArthur, 1961; Roll, Geffen, & Yom-Tov, 2015; Zhang, Kissling, & He, 2013). In addition, the diverse microclimate and habitats provided by complex forest vertical structure may benefit species through greater buffering against climatic instability and habitat change (Oliveira & Scheffers, 2019; Scheffers et al., 2013). The greater niche space provided by taller forest canopies may also increase functional diversity of biotic assemblages by harbouring species characterized by more divergent sets of traits (Aguirre-Gutiérrez et al., 2017; Bae et al., 2018). Positive relationships between canopy height and vertebrate species richness at regional and global scales have been reported (Culbert et al., 2013; Ilsøe, Kissling, Fjeldså, Sandel, & Svenning, 2017; Jiménez-Alfaro, Chytrý, Mucina, Grace, & Rejmánek, 2016; Roll et al., 2015). However, no studies have tested whether vertebrate functional diversity is also associated with canopy height at a global scale.

A broad range of environmental factors beyond canopy height, such as energy availability, historical climate stability, environmental heterogeneity and human activities, have been associated with large-scale biodiversity patterns (Evans, Warren, & Gaston, 2005; Jarzyna & Jetz, 2017; Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015). Specifically, the energy availability hypothesis suggests that temperature affects species diversity directly, by affecting the numbers of individuals, and indirectly, by controlling resource availability, which would constrain functional diversity through its effect on the population viability of niche specialists (Evans et al., 2005). Regions with higher productivity could harbour more species by sustaining more individuals and viable populations and could also have higher functional diversity by affording a greater diversity of niches (Currie et al., 2004; Evans et al., 2005). Palaeoclimate may also affect current taxonomic and functional diversity through its effect on speciation, extinction and migration (Svenning et al., 2015). Besides these climate-based hypotheses, higher environmental heterogeneity provides greater habitat diversity and better climate change buffering, which are also likely to promote higher species richness and functional diversity (Stein, Gerstner, & Kreft, 2014). Lastly, biodiversity loss, in terms of both taxonomic and functional diversity, is widely linked with human activities (Jarzyna & Jetz, 2017; Liang et al., 2019).

Functional diversity, broadly defined as trait variation in a community, is directly linked with environmental conditions and biotic interactions and is assumed to be a better predictor of ecosystem functioning and services than species richness (Swenson, 2013; Violle, Reich, Pacala, Enquist, & Kattge, 2014). Species richness is not always related consistently to functional diversity. A biotic assemblage may have low functional diversity, while harbouring high species richness; for example, reflecting functional homogenization caused by structurally homogeneous vegetation (Aguirre-Gutiérrez et al., 2017). Furthermore, the underlying mechanisms that limit geographical distribution of species richness and functional diversity may differ (Oliveira et al., 2016; Seymour, Simmons, Joseph, & Slingsby, 2015); for example, one study found global mammal species richness to be related closely to actual evapotranspiration (a measure of productivity), but that functional diversity was explained better by regional evolutionary history (Oliveira et al., 2016).

Owing to differences in climate, geological and evolutionary history among continents and regions, biodiversity patterns and their underlying drivers might not be the same in different regions (Coops, Rickbeil, Bolton, Andrew, & Brouwers, 2018; Davies, Buckley, Grenyer, & Gittleman, 2011; Ilsøe et al., 2017). For example, the effects of tree canopy cover and human influence on woodpecker species richness vary among biogeographical regions; for example, effects of tree canopy cover are especially pronounced in Nearctic, Palaearctic and Saharo-Arabian regions (Ilsøe et al., 2017). Vertebrate richness in Australia at the continental scale is strongly related to energy availability, whereas at the regional scale it is more strongly coupled to forest structure and productivity (Coops et al., 2018). Differences in energy availability, climate seasonality and biotic pressure might cause the divergent patterns of functional structure of mammals between tropical and temperate regions, that is, functional clustering in the tropics and functional overdispersion in temperate regions (Safi et al., 2011). In addition to such regional effects, taxonomic groups with divergent dispersal ability may also be affected differently by these factors (Sandel et al., 2011).

In this study, for the first time, we evaluated the relative influence of forest canopy height and other environmental variables in determining global- and regional-scale patterns of both species richness and functional diversity for terrestrial mammals and breeding birds. Specifically, we predicted that by providing greater niche space and by buffering changes in climate and habitat, taller forest canopies should harbour greater species richness, greater functional richness and overdispersed functional structure (Aguirre-Gutiérrez et al., 2017; Bae et al., 2018; MacArthur & MacArthur, 1961; Scheffers et al., 2013). To investigate this hypothesis, we used global-scale species distribution data for nearly all terrestrial mammals and breeding birds to map taxonomic and functional diversity. We applied spatial simultaneous autoregressive error models to evaluate the relative importance of canopy height and other environmental predictors in determining the patterns of vertebrate diversity globally and across regions.

2 | MATERIALS AND METHODS

2.1 | Vertebrate data on species distributions and traits

Distribution data for terrestrial mammals (limited to forest regions only) were obtained from the International Union for Conservation of Nature (https://www.iucn.org). Distribution data for birds (also limited to forest regions only) were compiled from the Birdlife International data-zone (https://www.birdlife.org). The data were available as geographical information system polygons, covering known or inferred areas of occurrence. The polygons were converted into rasters to match the canopy height layer exactly. A species was counted as present if any part of the 110 km grid cells (Molleweide equal-area projection) was covered by the species range polygon. Grid cells with < 50% land area were excluded. For mammals, we used all 4,924 terrestrial mammal species. For birds, we used breeding distributions of all terrestrial bird species, resulting in 8,708 bird species for the present work.

Functional trait data for mammals and birds were extracted from a comprehensive database, EltonTraits v.1.0 (Wilman et al., 2014). Some mismatched species names in EltonTraits were corrected by checking their synonyms at the Red List Website of the International Union for Conservation of Nature. We used 15 traits for mammals and 19 traits for birds that measured body mass, diet, foraging habitat preference and activity period (Supporting Information Table S1). These traits represent many aspects of resource use and have been widely used in other investigations of mammal and bird functional diversity (e.g., Belmaker & Jetz, 2013; Girardello et al., 2019). We $\log_{10}$-transformed body mass before all the analyses.

2.2 | Measures of functional diversity

Given that both continuous and categorical traits were included, a dendrogram-based approach for the measures of functional diversity was taken (Podani & Schmera, 2006). First, we calculated a distance matrix using Gower's distance coefficient, which allows for different types of variables while standardizing them (Gower & Legendre, 1986). Second, we used hierarchical clustering to build separate functional dendrograms for mammals and birds, using an average agglomeration method, which provides a better goodness-of-fit to dissimilarities than single and complete linkage classification (UPGMA; Mouchet et al., 2008; Podani & Schmera, 2006). Third, we used the functional dendrogram to calculate two common properties of functional diversity, namely functional richness and functional dispersion. Functional richness was calculated as the total branch length of the functional tree containing the coexisting species in a given grid cell (Petchey & Gaston, 2002). Functional dispersion was calculated as the mean pairwise functional distance between all species within a given assemblage in a given grid cell (Weiher, Clarke, & Keddy, 1998). These two metrics are complementary; functional richness measures the utilization or volume of trait space occupied within a given community, whereas functional dispersion measures the degree of clustering or overdispersion of species in trait space. To control for the effects of species richness on functional diversity measures, we computed standardized effect sizes (SESs) for both measures using the functions "pd.moments" and "mpd.moments" in the R package PhyloMeasures (Tsirogiannis & Sandel, 2015), which could provide an efficient solution by calculating the mean and standard deviation without randomization processes compared with slow and inexact randomization approaches (Kembel et al., 2010; Webb, Ackerly, & Kembel, 2008). Grid cells with fewer than three species were excluded from all the analyses because such species-poor assemblages might have extreme values for functional diversity.

2.3 | Canopy height data

Global forest canopy height data at 1 km spatial resolution were used (Simard, Pinto, Fisher, & Baccini, 2011). This map was produced from data acquired by the Geoscience Laser Altimeter System onboard the Ice, Cloud and land Elevation Satellite. In this study, we aggregated 1 km grid cells of global canopy height data into 110 km grid cells with an equal-area Molleweide projection (nearly 1° at the equator) by calculating the mean and standard deviation of the 1 km cell canopy heights within its extent. Finally, we generated two canopy height-related raster layers at 110 km resolution, including the mean height (htMean) and the standard deviation of height (htSD) (Supporting Information Figure S1). We also considered the coefficient of variation of the heights as one measure, but it had a high correlation (Pearson correlation coefficient of .91) with mean height. For this reason, we did not include it in the further analyses. Grid cells with < 50% land area were excluded. For each layer, the total number of 110 km grid cells was 10,031.

2.4 | Environmental data

To disentangle the relative importance of canopy height versus other environmental variables for vertebrate diversity, we extracted current climate and topographical variables from the WorldClim database at 10 arc-min resolution (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), productivity-related variables from the Moderate Resolution Imaging Spectrometer global terrestrial data at 30 arc-s resolution (Mu, Zhao, & Running, 2011; Running et al., 2004), human influence from the Global Human Influence Index Dataset v.2 at 1 km resolution (WCS & CIESIN, 2005), and glacial–interglacial climate stability variables at 2.5 arc-min resolution (Sandel et al., 2011). Climate stability variables included the velocity and anomaly for mean annual temperature (MAT) and annual precipitation (MAP) between the Last Glacial Maximum (LGM; ~21,000 years ago) and the present (1950–2000) to represent the amplitude of late Quaternary glacial–interglacial climate change (Sandel et al., 2011). All these environmental layers were resampled to the 110 km equal-area grid used for the canopy height data.

Among these variables, some were highly correlated (Table S2). To reduce multicollinearity, we removed variables causing high correlations (Pearson's correlation, $r > |.7|$), retaining those with the clearest biological meaning. Finally, we selected seven environmental variables for the present analysis, namely net primary productivity (NPP), MAT, precipitation seasonality (precSeason), LGM-to-present velocity for MAT (tempVelo), LGM-to-present anomaly for MAP (prepAnomaly), elevation range (elevRange) and human influence index (HUMAN). To improve the normality and linearity of these variables, we $\log_{10}$-transformed MAT, percSeason, elevRange and tempVelo and square root-transformed NPP, precAnomaly and HUMAN.

2.5 | Statistical analysis

Spatial simultaneous autoregressive error models, which account for residual spatial autocorrelation in the data, were used to evaluate the relative importance of each predictor in determining the patterns of vertebrate diversity (Kissling & Carl, 2008). We then used the "LMG" approach to evaluate the role of each predictor in the global patterns of vertebrate diversity. The "LMG" approach, named after Lindeman, Merenda, and Gold (1980), yields "natural" decompositions of the model r^2 in linear regression models. This computer-intensive approach has been recommended after comparison with other importance metrics, because it clearly identifies the contribution of a variable by itself and in combination with all other predictors (Johnson & Lebreton, 2004). The "LMG" approach was calculated using the function "calc.relimp" in the R package "relaimpo" (Grömping & Lehrkamp, 2018). Although htMean, htSD and NPP showed relatively strong pairwise correlations, values of the variance inflation factor for these three predictors relative to each other and to all other predictors were always lower than four, suggesting that collinearity among explanatory variables should not greatly affect our results. Therefore, we included all the predictors in one model for the analyses. We note that our estimates of relative importance are statistical estimates that might still be influenced somewhat by the correlations between the predictors included.

To test the differences in potential drivers for diversity patterns among zoogeographical regions, we used the classification by Holt et al. (2013). We assigned all the 110 km grid cells into seven zoogeographical realms, that is, the Nearctic, Neotropical and Panamanian, Palaearctic and Sino-Japanese, Oriental and Oceanian, Afrotropical and Saharo-Arabian, Madagascan, and Australian realms. Among these realms, the number of 110 km grid cells ranged from 46 (Madagascan) to 3,272 (Palaearctic and Sino-Japanese). The seven realms were defined according to the UPGMA clustering of global phylobeta diversity values for species assemblages of amphibian, bird and non-marine mammalian species (Holt et al., 2013). All statistical analyses were conducted in R (R Core Team, 2017). We used the "errorsarlm" function in the R package *spdep* to run the spatial simultaneous autoregressive error models (Bivand et al., 2015).

3 | RESULTS

3.1 | Spatial patterns of vertebrate species richness and functional diversity

Species richness of mammals and birds at the global scale showed similar patterns, with the highest values in northern South America, Central Africa and Southeast Asia (Figure 1a,b; Supporting Information Figure S2). Standardized bird functional richness showed similar patterns to species richness, whereas standardized mammalian functional richness displayed different patterns relative to species richness, with functional richness peaking in northern North America, central South America, the western coast of Africa and South Asia (Figure 1c,d; Supporting Information Figure S3). The patterns of standardized functional dispersion in mammals and birds differed, with mammals exhibiting functional clustering in many regions (central America, northern South America, central Africa, South Europe and Southeast Asia), whereas birds were functionally overdispersed in nearly all tropical and subtropical regions and in Northern Eurasia (Figure 1e,f; Supporting Information Figure S2).

3.2 | Drivers of species richness and functional diversity at the global scale

At the global scale, mean canopy height (htMean) and NPP were the two variables most closely associated with the species richness of mammals and birds (Figure 2). The functional richness of mammals showed similar patterns to those of mammalian species richness, that is, the two variables with the highest importance values were again htMean and NPP, although the values were not high (Figure 2). For bird functional richness, NPP and MAT were the two most important variables. Mammal and bird functional dispersion was also most closely associated with MAT and NPP. The standard deviation of canopy height was also associated with the species richness of mammals and birds, but had no associations with functional diversity.

3.3 | Drivers of species richness and functional diversity at the regional scale

Vertebrate species richness was strongly associated with htMean and NPP in most biogeographical regions (Figures 3 and 4). Among all predictors, htMean, NPP and MAT had the highest frequency as the two most closely associated variables for vertebrate functional diversity in each region. Notably, vertebrate functional dispersion had strong relationships to htMean within some regions, in contrast to the global scale, with a negative relationship in the Neotropical and Panamanian region and positive relationships in in the Afrotropical and Saharo-Arabian and the Madagascan regions, whereas bird functional dispersion was negatively correlated with htMean in the

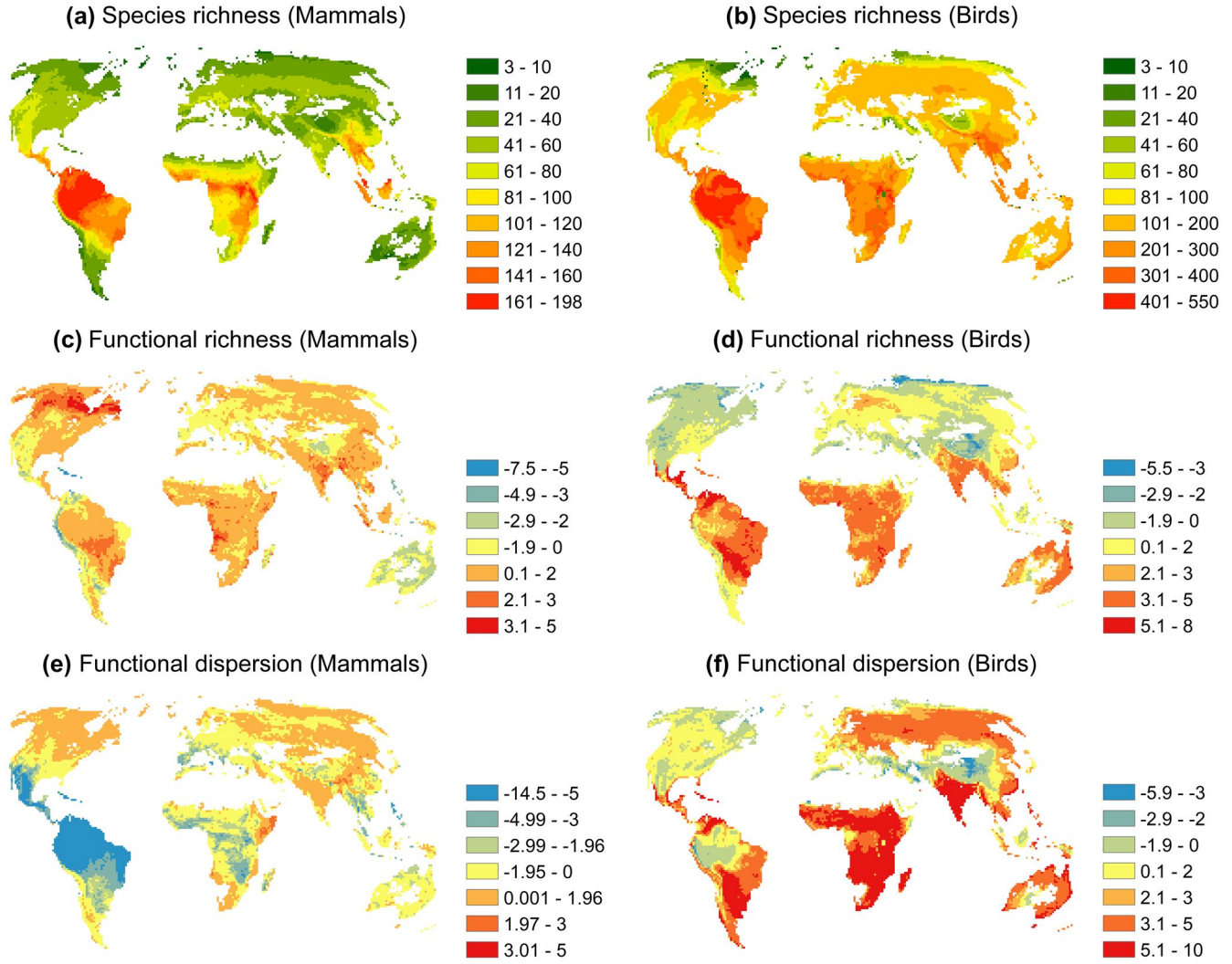

FIGURE 1 Spatial patterns of species richness and standardized functional diversity measures for mammals and breeding birds. Maps are in the Mollweide equal-area projection

Neotropical and Panamanian and the Oriental and Oceanian regions (Figures 3 and 4).

4 | DISCUSSION

By linking forest canopy height and other environmental predictors with global patterns of vertebrate species richness and functional diversity based on certain traits, our results showed that forest canopy height was consistently an important predictor of vertebrate species richness after accounting for the effects of NPP, climate and other variables, whereas its effects on functional diversity were weaker and more variable, with stronger coupling to functional richness than functional dispersion, with the latter often having negative relationships to canopy height in highly species-rich tropical realms. These findings suggest that canopy height promotes species richness only in part via an expansion of functional niche space, but also via greater ecological packing, leading to co-existence of functionally similar species.

4.1 | Species richness and functional diversity

Although species richness is the most common measure of biodiversity in ecology and biogeography, it does not capture the ecological differences among species (Swenson, 2013; Violle et al., 2014). Both global and regional studies have indicated that species richness and functional diversity often show divergent patterns and are affected by different drivers (Aguirre-Gutiérrez et al., 2017; Oliveira et al., 2016). For example, butterfly species richness and functional dispersion in the Netherlands are not consistently correlated; for example, high functional dispersion may occur in regions with low species diversity (Aguirre-Gutiérrez et al., 2017). Temporal trends of taxonomic and functional diversity of birds in France are also

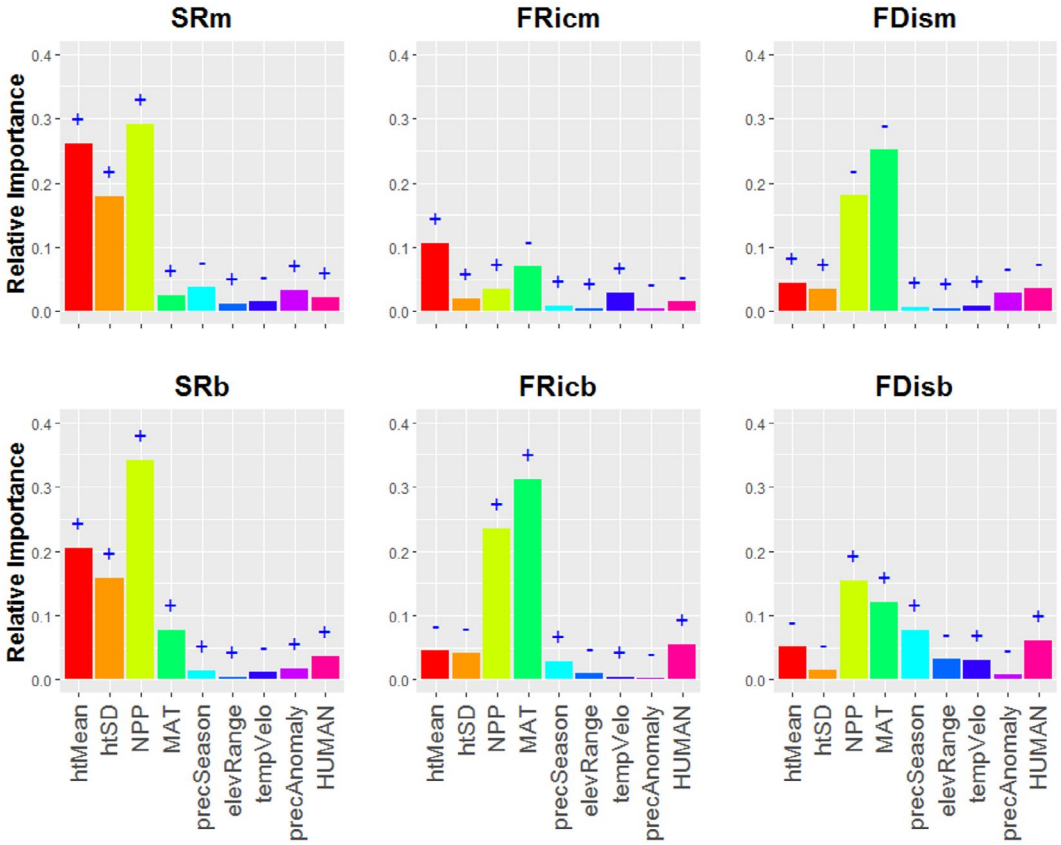

FIGURE 2 Statistical relative importance of canopy height and other predictors for species richness (SR), standardized functional richness (FRic) and functional dispersion (FDis) at a global scale ("m" and "b" refer to mammals and birds, respectively). Abbreviations: the signs "+" and "−" at the top of each bar represent positive and negative effects; elevRange = elevational range; htMean and htSD = mean height and the standard deviation of height; HUMAN = human influence index; MAT = mean annual temperature; NPP = net primary productivity; precSeason = precipitation seasonality; prepAnomaly = Last Glacial Maximum-to-present anomaly for mean annual precipitation; tempVelo = Last Glacial Maximum-to-present velocity for MAT

not consistent (Monnet et al., 2014). Furthermore, a global study of mammals shows that patterns of functional diversity and species richness are decoupled because of different drivers; that is, environmental factors for species richness and evolutionary history for functional diversity (Oliveira et al., 2016).

In support of these studies, our results also showed that global patterns of mammal species richness and functional diversity (as represented by the traits used in this study), including functional richness and functional dispersion, were different. For example, northern North America had high functional richness and functional dispersion but low species richness. In contrast, the high species richness but low functional diversity in the tropics suggests that these species are functionally redundant and exhibit relatively close packing in ecological space (Oliveira et al., 2016; Safi et al., 2011). However, species richness and functional diversity of birds showed consistent patterns at the global scale. For example, most tropical regions (except for the Amazon Basin and Andean regions) have great species richness and high functional diversity, suggesting that expansion of niche space might be dominant for birds in these regions. The divergent patterns of functional diversity between mammals and birds indicate that different processes are shaping the functional diversity of these two groups.

4.2 | The role of forest canopy height in determining vertebrate diversity

Taller forest canopy height and the associated complex vertical vegetation structure should provide greater niche space and thus promote greater species richness (MacArthur & MacArthur, 1961; Oliveira & Scheffers, 2019; Roll et al., 2015). For example, a recent global study showed that tree canopy height was significantly associated with bird and mammal species richness, although not as strongly as productivity (Roll et al., 2015). Furthermore, tree cover was more closely associated with global woodpecker (Picidae) species richness than other variables, such as temperature, past climate, topographical heterogeneity and human influence (Ilsøe et al., 2017). At regional scales, animal assemblage diversity in Europe has been found to be explained better by vegetation diversity than by climate and elevational range (Jiménez-Alfaro et al., 2016). Likewise, vertebrate species richness in the Neotropical region has been found to be coupled jointly to variation of forest canopy height and climate (Moura, Villalobos, Costa, & Garcia, 2016). Consistent with these studies, our results showed that forest canopy height was an important driver of bird and mammalian species richness at both global

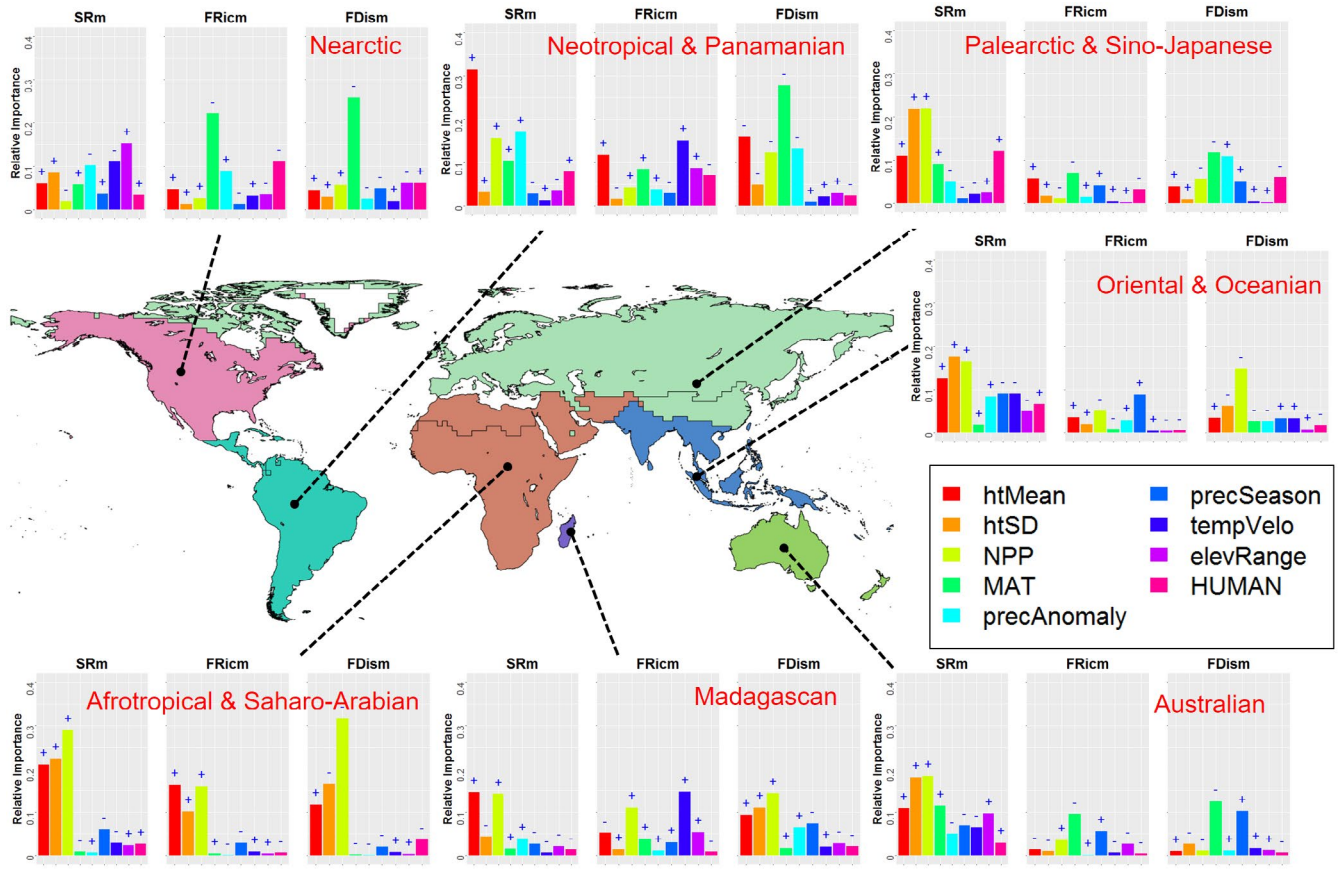

FIGURE 3 Statistical relative importance of canopy height and other predictors for mammal species richness (SRm) and standardized functional richness (FRicm) and functional dispersion (FDism) in the seven zoogeographical realms using the LMG approach. For definitions of abbreviations, see legend to Figure 2

and regional scales, especially for birds in the Nearctic region and for mammals in the Neotropical and Panamanian regions.

The greater niche space provided by taller forest canopy height should not only promote species richness but also increase functional diversity (Bae et al., 2018). Studies on the association between animal functional diversity and remote sensing-derived vegetation structure are imperative and missing (Davies & Asner, 2014). Several studies on the relationships between them have provided mixed results (Aguirre-Gutiérrez et al., 2017; Remeš & Harmáčková, 2018). For example, canopy height in Australia is poorly linked with bird functional diversity, although it could predict species richness well (Remeš & Harmáčková, 2018). In contrast, functional diversity of butterflies in the Netherlands is positively correlated with average vegetation height (Aguirre-Gutiérrez et al., 2017). Here, we found that the functional richness of birds and mammals was significantly associated with forest canopy height, especially for mammals, providing strong evidence for the role of forest canopy height in promoting vertebrate functional diversity. Notably, the somewhat weaker associations between forest canopy height and vertebrate functional richness (as described by the traits used in the present study) compared with vertebrate species richness suggest that canopy height promotes species richness only in part via a simple expansion of niche space, but must also include processes allowing greater ecological packing; that is, coexistence of functionally similar species (Ricklefs, 2012; Safi et al., 2011). Notably, although forest canopy height was not associated with vertebrate functional dispersion at the global scale, we found a strong negative association between forest canopy height and vertebrate functional dispersion in the Neotropical and Panamanian regions, suggesting that high forest canopy promotes the packing of functionally similar species in species-rich tropical regions.

4.3 | The roles of other environmental variables in determining vertebrate diversity

Our analyses showed positive relationships between NPP and vertebrate species richness, consistent with previous studies and supporting the hypothesis that regions with higher NPP offer more resources, allowing more individuals and greater potential for species to coexist (Coops et al., 2018; Oliveira et al., 2016; Roll et al., 2015). Previous studies on the associations between NPP and vertebrate functional diversity have shown mixed results (Gómez-Ortiz, Dominguez-Vega, & Moreno, 2017; Oliveira et al., 2016). For example, in Mexico NPP was associated only with mammal species richness, but not with functional diversity (Gómez-Ortiz et al., 2017). In contrast, a global study

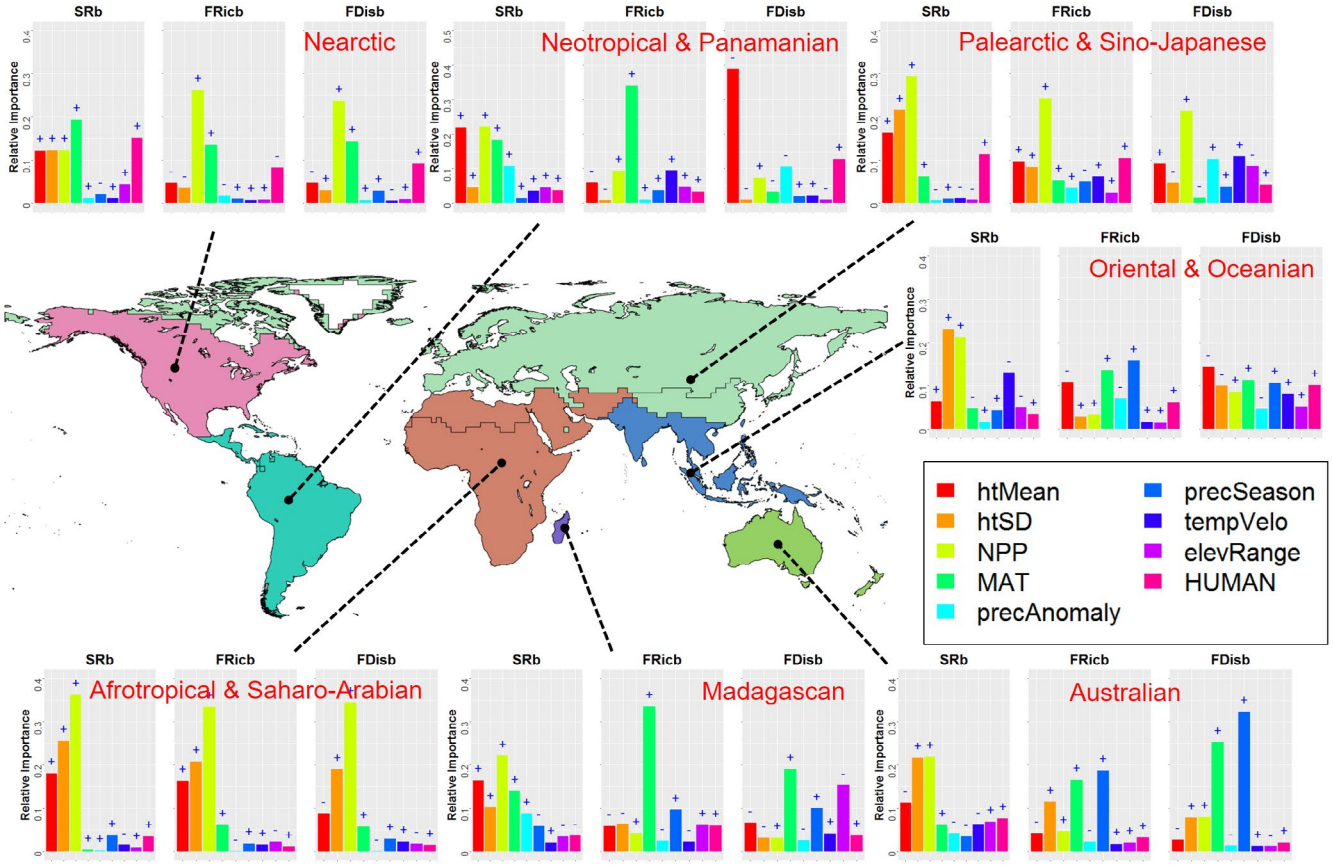

FIGURE 4 Statistical relative importance of canopy height and other predictors for bird species richness (SRb) and standardized functional richness (FRicb) and functional dispersion (FDisb) in the seven zoogeographical realms using the LMG approach. For definitions of abbreviations, see legend to Figure 2

found the functional diversity of mammals to be linked to actual evapotranspiration, an indicator of NPP (Oliveira et al., 2016). Consistent with that study, our results showed NPP to be associated with vertebrate functional diversity at both global and regional scales, although the associations tended to be weaker than with species richness.

The energy availability hypothesis proposes that temperature could constrain functional diversity through its effect on the population viability of niche position specialists (Evans et al., 2005). Supporting this hypothesis, our results showed that temperature was positively correlated with bird functional richness at the global scale and in several biogeographical realms. However, we note that the NPP relationships might also capture well the effects related to forest vertical structural complexity.

4.4 | Conclusions

Overall, our results indicate that forest canopy height plays an important role in explaining taxonomic and functional diversity of vertebrates at both global and regional scales, although complementary to other drivers, such as NPP and temperature. As a fundamental property of forest ecosystems, canopy vertical structure has important implications for maintenance of biodiversity and ecosystem functioning (MacArthur & MacArthur, 1961; Zhang, Nielsen, Mao, Chen, & Svenning, 2016). Although earlier studies have assessed the links between canopy structure and functional diversity at local and regional scales (Aguirre-Gutiérrez et al., 2017; Remeš & Harmáčková, 2018), our study has provided the first quantification of this potential linkage globally and across biogeographical realms, providing evidence for the importance of the complex vertical structure of forests in shaping the global and regional patterns of terrestrial vertebrate taxonomic and functional diversity. Our study supports the importance of protecting old-growth forests, often characterized by taller canopies and complex vertical structure (Frey et al., 2016; Lindenmayer, Lauranc & Franklin, 2012), suggesting that these forests provide crucial refugia against climatic and anthropogenic disturbances for the conservation of taxonomic and functional diversity. Hereby, the present study serves as an important basis for building a comprehensive understanding of the importance of vegetation structure for biodiversity conservation in this epoch of human-induced global change.

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DATA AVAILABILITY STATEMENT

The data we used are provided as the Supporting Information.

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BIOSKETCHES

Gang Feng and **Jian Zhang** are interested in combining community ecology with macroecology and biogeography to assess the relative roles of local, regional and historical factors in shaping biodiversity patterns.

SUPPORTING INFORMATION

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

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