



## RESEARCH ARTICLE

# Joint effects of environmental filtering and dispersal limitation on the species assemblage of the Tibetan Plateau

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**Funding information**

Grant/Award Number: National Natural Science Foundation of China and (Grant Number 31900324); Guangdong Basic and Applied Basic Research Foundation, Grant/Award Number: (Grant Number 2020A1515011472)

**Handling Editor:** Hang Sun

**Abstract**

**Aim:** Mountains harbour a rich and non-random cluster of species, yet knowledge of the species' biological attributes that support their coexistence in the montane community is limited. Here, we investigated the association of species occurrence on the Tibetan Plateau with their morphological, ecological or evolutionary constraints.

**Location:** Tibetan Plateau (TP).

**Taxon:** Mammals and birds.

**Methods:** We tested whether species occurrence on the TP correlates with morphological, ecological or evolutionary constraints using the spatial distribution, phylogeny, dispersal ability and thermal niche property data for 1353 terrestrial vertebrates (383 mammals and 970 birds). We used standard (non-phylogenetic) and phylogenetic logistic regressions to elucidate the relative contributions of these attributes of species to explaining their occurrence on the TP. We assessed the geographical patterns of the community structures on the TP and fitted linear mixed models to explore the underlying eco-evolutionary forces.

**Results:** The TP species exhibited a higher cold tolerance, wider thermal niche breadth and higher rate of niche evolution than non-TP species. We supported the assumption that the TP species were not a random subset from the species pool, but were structured jointly by environmental filtering and dispersal limitation. While dispersal and ecological processes underlying species assemblages varied spatially and among taxa, we found that species in stressful environments were limited by environmental filtering, whereas dispersal limitation was more pronounced under favourable climatic conditions.

**Main conclusions:** Our study finds that environmental filtering and dispersal limitation jointly shape the species assemblage on the TP. These findings provide significant insights into community assembly processes on the TP and other montane ecosystems on Earth, especially those that are sensitive to global warming.

**KEYWORDS**

community assembly, dispersal ability, species coexistence, terrestrial vertebrates, thermal niche, Tibetan Plateau

## 1 | INTRODUCTION

Mountains harbour a disproportionate amount of global biodiversity (Rahbek et al., 2019), and have served as ideal systems to address key questions in evolutionary biology and biogeography (Antonelli et al., 2018; Körner, 2007), including elevational/latitudinal diversity gradient (Peters et al., 2016; Quintero & Jetz, 2018), uplift-driven diversification (Badgley et al., 2017; Xing & Ree, 2017) and community assembly (Jarzyna et al., 2020; Qian, Ricklefs, & Thuiller, 2021). Naturalists have observed for centuries that montane communities are not a random combination of species (von Humboldt, 1808), but rather a product of geographical barriers (White, 2016), evolutionary histories (Antonelli, Nylander, Persson, & Sanmartin, 2009; Xing & Ree, 2017) and ecological processes (Graham, Parra, Rahbek, & McGuire, 2009). However, understanding of how these factors interact to structure species assemblages in mountain ecosystems remains largely unexplored (Graham et al., 2014), thereby hindering our projections for effects of global warming on montane biodiversity (La Sorte & Jetz, 2010).

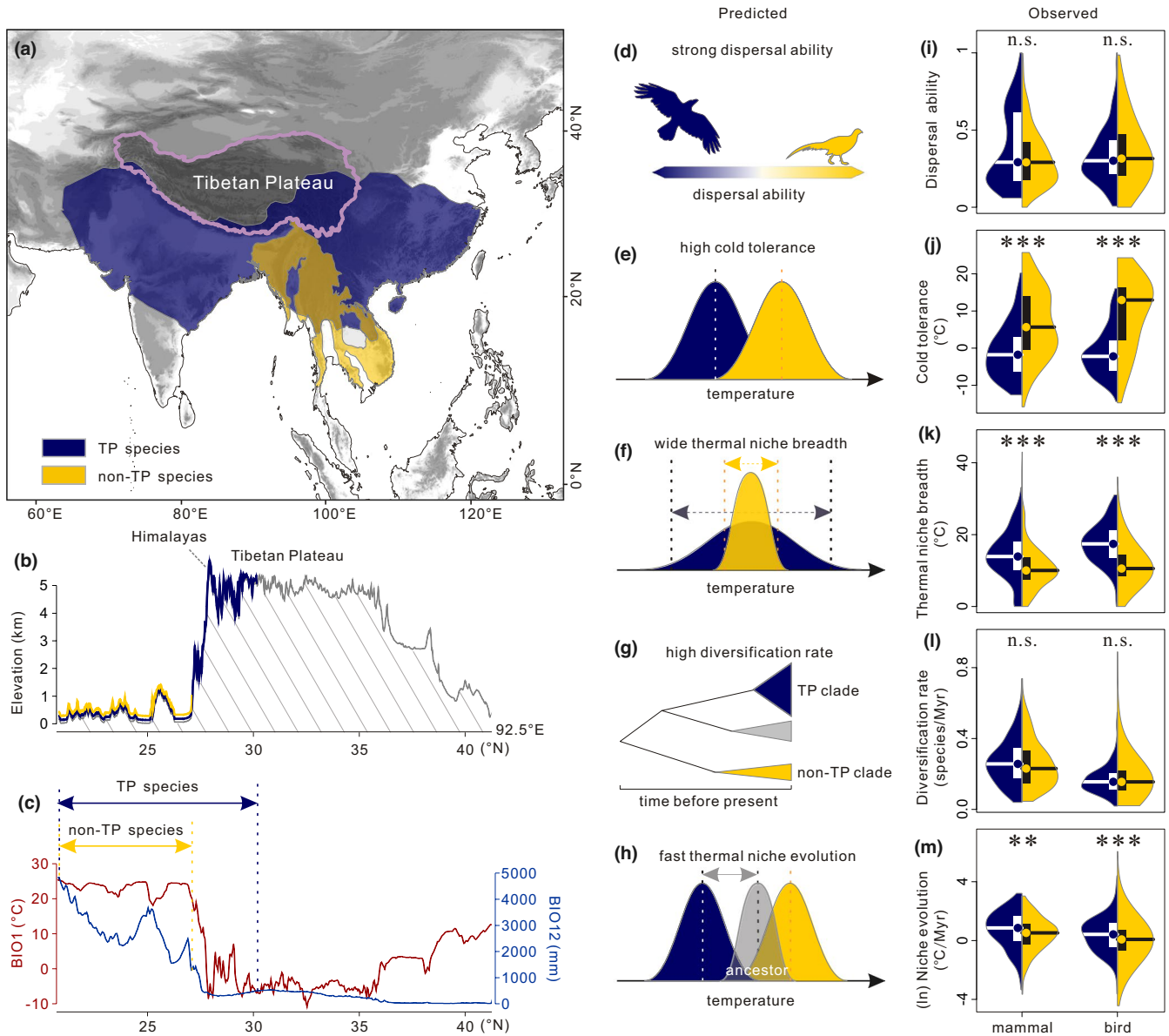
Several hypotheses have been used to explain the montane species assemblages (Figure 1(a–h)). Among these, the dispersal limitation hypothesis proposed that mountains act as geographical barriers to species dispersal (White, 2016), suggesting that species with weak dispersal ability are less likely to access mountain ecosystems (Figure 1d). Furthermore, the environmental filtering hypothesis stated that the occurrence of these species in the mountain ecosystems depends on their ability to sustain beyond these environments (Graham et al., 2014). In general, mountains can sustain species having a high cold tolerance (Figure 1e) or wide thermal breadth (Figure 1f) because these niche properties would increase their ability not only to cross environmental barriers (Faurby & Antonelli, 2018), but will also increase their survivability in highlands characterized by cold temperatures and high climatic variabilities (Khaliq, Hof, Prinzing, Bohning-Gaese, & Pfenninger, 2014). Furthermore, as proposed by the evolutionary history hypothesis, species diversification rate may increase in the mountain ranges (Figure 1g; Hughes & Atchison, 2015; Quintero & Jetz, 2018) because mountain uplift would develop substantial topographical heterogeneity that facilitates niche divergence of lineages, and subsequently leads to reproductive isolation and allopatric speciation (Title & Burns, 2015). In this context, montane species may demonstrate a faster rate of niche evolution than lowland species to adapt quickly to new habitats and climatic conditions (Figure 1h; Wiens & Donoghue, 2004). Accordingly, we predicted that montane species may have strong dispersal ability, high cold tolerance, wide thermal niche breadth, fast diversification rate and increased adaptation to new climatic niches (Figure 1a–h).

The role of ecological and evolutionary processes in shaping community assemblages can be understood by comparing the extent to which phylogenetic structures deviate from expected due to chance (Cavender-Bares, Kozak, Fine, & Kembel, 2009). For example, if a community is primarily driven by environmental filtering,

a phylogenetic clustering (i.e. coexistence of close relatives) can be expected because closely related species often share similar functional traits and environmental requirements under the assumption of phylogenetic niche conservatism (Wiens & Donoghue, 2004). According to the stress dominant hypothesis, communities living at high elevations or in harsh environments are primarily structured by environmental filtering, whereas density-dependent competition is significantly high at lowlands having less stressful environments (Graham et al., 2009). Moreover, a regional phylogenetic structure can result from past climate oscillations (Eiserhardt, Borchsenius, Sandel, Kissling, & Svenning, 2015) and historical biogeography of specific lineages (Qian et al., 2019), thus yielding patterns that deviate from the predictions of the stress dominance hypothesis (Ramm et al., 2018).

The Tibetan Plateau (TP) extends to ca. 2.5 million km<sup>2</sup> with an average elevation exceeding 4500 m, and is characterized by extreme coldness and severe aridity and hypoxia (Wang et al., 2015). Historically, the TP was a part of the Tethys Ocean, and did not emerge above sea level until the Palaeocene/Eocene boundary (ca. 55–50 million years ago) due to the Indo-Asian Collision (Royden, Burchfiel, & van der Hilst, 2008). The subsequent mountain uplift and climatic changes have significantly influenced the historical biogeography of TP's lineages (Ding, Ree, Spicer, & Xing, 2020; Favre et al., 2015), and ultimately altered the biota on the TP over time (He, Lin, Li, Yu, & Jiang, 2020). These contexts indicate that the TP is one of the most challenging and evolutionarily unique regions on Earth (Deng, Wu, Zhou, & Su, 2019), and serves as a good model for testing the eco-evolutionary processes that generate and maintain the diversity patterns (Favre et al., 2015; Yu et al., 2019; Ding et al., 2020). However, despite increased attention on TP's biota, the relative roles of dispersal limitation, abiotic environments and evolutionary history in filtering the TP species from the biogeographical species pool have rarely been investigated.

In this study, we aimed to investigate whether species occurrence on the TP correlates with morphological, ecological or evolutionary constraints using the spatial distribution, phylogeny, dispersal ability and thermal niche property data for 1353 terrestrial vertebrates (383 mammals and 970 birds). Specifically, we first tested the differences in the dispersal ability, thermal niches and evolutionary histories of the TP and non-TP mammal and bird species. We then used standard (non-phylogenetic) and phylogenetic logistic regressions to elucidate the relative contributions of these attributes of species in explaining their occurrence on the TP. Finally, we assessed the geographical patterns of the phylogenetic structures for species communities on the TP and fitted linear mixed models to explore the underlying eco-evolutionary forces. Our results showed that the species on the TP were not only non-randomly assembled, but also structured jointly by environmental filtering and dispersal limitation. Furthermore, the phylogenetic structure patterns of the community assemblages were contrasting for mammals and birds, highlighting the different roles of eco-evolutionary processes in regional assembly among taxonomic groups.



**FIGURE 1** Differences in the dispersal ability, thermal niche properties and evolutionary history between species presence and absence on the Tibetan Plateau (TP). (a–c) an example for different ranges in distributions (a), elevation (b) and climatic conditions (c) between the TP species and non-TP species. (d–h) five species attributes that are hypothesized to determine the presence/absence of TP species. We predicted that the TP species have stronger dispersal ability (d), higher cold tolerance (e), wider thermal niche breadth (f), higher diversification rate (g) or faster rate of niche evolution (h) than the non-TP species. (i–m) violin plots showing the observed difference in species attributes between the TP and non-TP species. The number of species ( $n$ ) per group is 383 for mammals (including 185 TP species and 198 non-TP species) and  $n = 970$  for birds (including 399 TP species and 571 non-TP species). Significant differences were evaluated by the Wilcoxon rank sum test. Asterisks indicate the level of significance (\* $p < 0.05$ , \*\* $p < 0.01$  and \*\*\* $p < 0.001$ )

## 2 | MATERIALS AND METHODS

### 2.1 | Distribution data

We defined the TP species as those with distribution data intersecting with the geographical range of the TP (Figure S1.1), while non-TP species were marked as present in the potential species pool of the TP fauna but absent on the TP. The geographical ranges of the species were obtained from the expert range maps produced by the IUCN Red List database (<http://www.iucnredlist.org>) for mammals,

and BirdLife International and NatureServe (<http://www.birdlife.org>) for birds. We only considered areas wherein a species was extant or probably extant, native and resident, or occurred regularly during the breeding season. Bats were excluded from our analysis. We recognize that the expert range maps often include many deficiencies, such as absence being wrongly declared as presence and varying spatial accuracy among taxa and areas (Jetz, McPherson, et al., 2012). Nevertheless, such expert-based range maps represent one of the best forms of knowledge of a species' possible distribution and have been proven valid in many broad-scale biodiversity

studies (e.g. Howard, Flather, & Stephens, 2020; Loiseau et al., 2020; Harfoot et al., 2021; but see Hurlbert & Jetz, 2007). Here, we gridded the species distribution maps into a  $110 \times 110$  km grid cell to reduce potential errors in the distribution data and improve the accuracy of the results at the cost of spatial precision (Gumbs et al., 2020).

To identify the potential species pool of the TP fauna, we generated a possibility map of the species pool using a similarity index (SI) calculated by the proportion of the TP species in each grid cell (Carvajal-Endara, Hendry, Emery, & Davies, 2017). We used different SI value thresholds to define three potential species pools as small, medium or large (SI = 0.8, 0.7 and 0.6, respectively), which included 898, 1110 and 1364 species, respectively. In this study, we showed the results of only the large species pool (SI  $\geq 0.6$ ) because it represented the most likely species pools for the TP fauna considering the geographical distance (Figure S1.2). After combining the currently available attributes of the species (see below), our database included 1353 species ( $n = 383$  mammals and  $n = 970$  birds) for downstream analyses.

## 2.2 | Dispersal ability

We obtained species wing morphology, which is described by the hand-wing index (HWI), from Sheard et al. (2020) to represent the dispersal ability of birds. High HWI values reflect more elongated wings and higher flight performance, while low HWI values indicate shorter and broader wings that are associated with weak flight performance (Sheard et al., 2020). For species for which HWI data were unavailable, the average HWI of the species from the same genus was used. We estimated the home range size as a surrogate proxy for the dispersal ability of mammals (Whitmee & Orme, 2013) following the methods provided by Tucker, Ord, and Rogers (2014). We compiled empirical data of the body mass and diet of mammals from several sources (Jones et al., 2009; Tucker et al., 2014; Wilman et al., 2014), and fitted linear models separately for carnivores, herbivores and omnivores. Subsequently, we interpolated the home range sizes of the remaining mammals (Figure S1.3). We assigned all species to one of the following three trophic groups based on the data obtained from Wilman et al. (2014): (i) carnivores (species with diets comprising at least 90% vertebrate and/or invertebrate prey), (ii) herbivores (species with at least 90% vegetation diets) and (iii) omnivores (species with diets comprising 10–90% vegetation). The home range and body mass data were log<sub>10</sub>-transformed prior to analysis. To maximize comparison between mammals and birds, we normalized the dispersal ability for each species (values ranging from 0 to 1, with small values indicating low dispersal ability).

## 2.3 | Thermal niche properties

We calculated species-specific thermal niches using climate data derived from the WorldClim dataset (version 2.0; 2.5 arc min spatial

resolution; Fick & Hijmans, 2017). We measured the cold tolerance per species using the minimum values for mean annual temperature (BIO1) across every  $110 \times 110$  km grid cell within a species range. Furthermore, we used the difference between the minimum and maximum values of BIO1 for estimating the thermal niche breadth (Rolland & Salamin, 2016; Varzinczak, Moura, & Passos, 2020). The minimum and maximum values were measured using the 10th and 90th percentiles to avoid extreme values extracted from the geographical range of any species, respectively (Liu, Ye, & Wiens, 2020). We also measured cold tolerance using the minimum values for the minimum temperature of the coldest month (BIO6) and calculated the thermal niche breadth from the difference between the minimum BIO6 temperature and maximum temperature of the warmest month (BIO5). We used the original estimations of the thermal niches (i.e. minimum BIO1 and the range of BIO1) for further analyses because these two estimations were strongly correlated (Pearson's  $r = 0.94$  and  $0.77$  for cold tolerance and niche breadth, respectively).

## 2.4 | Diversification rate

We calculated the species-level diversification rate based on the equal-splits metric following Jetz, Thomas, et al. (2012). This method calculates the per-species estimates of expected pure birth diversification rates for the immediate present moment (e.g. tree tips; Upham, Esselstyn, & Jetz, 2019). Species with a higher diversification rate have shorter branches shared with other species towards the present, whereas those with a lower diversification rate are subtended by long unshared branches, suggesting that they are evolutionarily distinct (Upham et al., 2019). We obtained a random sample of 1000 phylogenetic trees from published phylogenies for mammals (Upham et al., 2019) and birds (the 'Hackett' backbone; Jetz, Thomas, et al., 2012) and estimated the species diversification rate on the full species-level phylogeny for each taxonomic group ( $n = 5804$  for mammals and  $n = 9993$  for birds). Median diversification rate values for each species calculated from a posterior distribution of 1000 time-calibrated trees were used.

## 2.5 | Rate of thermal niche evolution

Prior to estimating the rates of thermal niche evolution, we assessed the likelihood of niche evolution for each clade under four models, including white noise, Brownian Motion, Ornstein-Uhlenbeck and estimated lambda, using the 'ape' (Paradis & Schliep, 2019) and 'geiger' (Pennell et al., 2014) packages in R version 4.0.4 (R Development Core Team, 2021). As the Brownian motion models were preferred for most clades based on the Akaike information criterion (AIC) score (Table S1.1), we transformed the phylogenies based only on the Brownian motion model and reconstructed ancestral values for each node using the phylogenetic generalized least-squares approach (Liu et al., 2020). Furthermore, we calculated the rates of thermal niche evolution based on the



phylogeny of species within each clade (i.e. genus or family) using the cold tolerance (i.e. minimum BIO1 values) per species. Eight clades that included fewer than four species in the phylogeny and that might fail to estimate the rates of thermal niche evolution were excluded (Kozak & Wiens, 2013); consequently, our dataset included 121 clades (66 families and 55 genera; Table S1.1). The thermal niche evolution rates of each species were calculated as the absolute difference between the observed value of a species and the estimated value for its most recent ancestor divided by the branch length (Quintero & Wiens, 2013). Moreover, we calculated the median thermal niche evolution rate for each species using a posterior distribution of 1000 time-calibrated trees to account for phylogenetic uncertainty.

## 2.6 | Statistical analyses

To quantify the relative importance of different species attributes (i.e. dispersal, thermal niche and evolutionary history) in explaining the occurrence of the TP species, we implemented logistic regressions, in which species presence/absence on the TP was the binary response variable, and the species dispersal ability (DP), thermal niche properties (cold tolerance, CT, and thermal niche breadth, TB) and evolutionary histories (diversification rate, DR, and rate of niche evolution, NE) were the predictor variables.

$$O/1 \sim DP + CT + TB + DR + NE$$

Niche evolution was ln-transformed to improve linearity, and all predictors were standardized (mean = 0, SD = 1) to allow comparison between the model coefficients. The collinearity among variables was low in the full models (i.e. including all five predictors) as assessed by variance inflation factors (all VIFs <4). Thus, we used a multimodel approach based on the sample-size corrected AIC (AICc) to evaluate model-averaged parameter estimates in a likelihood-based framework. We ran 31 models for every possible combination of the five predictor variables and estimated the relative importance of each variable as the sum of the AICc weights ( $\sum w_i$ ) of all models that included the variable (Burnham & Anderson, 2002).

To assess the phylogenetic relatedness among species, we also combined the data with dated phylogenies to build a phylogenetic logistic regression (Ives & Garland, 2010) in the R package 'phyloim' (Ho & Ané, 2014). This method was similar to that of standard (non-phylogenetic) logistic regression, except a measure of the phylogenetic signal (i.e. alpha) was added to the model. Alpha ( $\alpha$ ) is a parameter derived from the Ornstein–Uhlenbeck model of evolution, in which an  $\alpha$  value close to zero indicates a strong phylogenetic signal (Ives & Garland, 2010). To account for phylogenetic uncertainty, we ran phylogenetic logistic regressions over a set of 1000 phylogenetic trees and reported the median value and an inference interval as the 2.5th–97.5th percentiles for model coefficients. The variance ( $R^2$ ) explained by each model was estimated using the R package 'rr2' (Ives & Li, 2018).

To investigate whether differences exist among factors that determine species occurrence on the TP, we repeated the logistic regression analysis procedures described above for each species assemblage separately within 110 × 110 km grid cells. In this analysis, the presence/absence of TP species in each grid cell was the binary response variable. Furthermore, we evaluated the goodness-of-model fit of models for each grid by calculating the proportion of variance explained by the five variables, and elucidated the relative independent effect of each predictor with a hierarchical partitioning in the R package 'hier.part' (Mac Nally & Walsh, 2004). We performed these analyses based on the results of standard (non-phylogenetic) logistic regression because obtaining the variance explained by each factor for phylogenetic models was not currently possible.

## 2.7 | Phylogenetic structure analyses

We quantified the phylogenetic structure of the TP fauna and tested whether species on the TP were phylogenetically clustered or overdispersed using the net relatedness index (NRI). Compared to other indices (e.g. the nearest taxon index; Faith's phylogenetic diversity), the NRI provided more information on the basal structure of the phylogenetic tree (i.e. deeper evolutionary dynamics; Webb, Ackerly, McPeck, & Donoghue, 2002), which makes it better suited for inferring the assembly processes on the TP as its fauna underwent a striking change during the Cenozoic period (He et al., 2020). The NRI tests the significance of the observed pattern and calculates the standardized effect size of the mean pairwise phylogenetic distance (MPD) between all species with respect to null expectations generated by randomly selecting species across the tips of the phylogeny (999 runs).

$$NRI_{\text{sample}} = -1 \times \frac{MPD_{\text{sample}} - MPD_{\text{rnsample}}}{sd(MPD_{\text{rnsample}})}$$

Positive NRI values indicate phylogenetic clustering, whereas negative values indicate phylogenetic overdispersion. As NRI approximates the Z distribution, a value greater than 1.96 (or less than -1.96) is equivalent to the significance at  $p < 0.05$ . We calculated the NRI with 1000 phylogenetic trees and reported the consequent results as medians. We calculated the NRI of (i) the entire TP fauna and (ii) each grid-based community to evaluate the spatial patterns of the phylogenetic structure of TP fauna. To evaluate the effect of abiotic factors on the phylogenetic structure of fauna, we first fitted generalized least square models with the grid-based NRI as response variables, and the mean annual temperature, mean annual precipitation, elevation range and climate change velocity as predictors. Climate change velocity data were acquired from the study by Sandel et al. (2011). The elevation range was measured as the difference between the maximum and minimum elevations based on the digital elevation model derived from the National Centres for Environmental Information (<https://www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/data/>). We evaluated the potential for spatial autocorrelation in the residuals using the Moran's



I statistic (Dormann et al., 2007). Given significant levels of spatial autocorrelation in the residuals of linear regression models (Moran's  $I = 0.145$  for mammals and  $0.142$  for birds, both  $p \leq 0.01$ ), we corrected for the spatial autocorrelation by creating a correlation structure that incorporates the latitude and longitude of each cell. We compared five spatial correlation structures (i.e. corExp, corGaus, corLin, corRatio and corSpher) in the R package 'nlme' (Pinheiro et al., 2021), and chose the 'corExp' structure as it always achieved the best performance based on the AIC. In addition, we included the TP subregions as a random effect and fitted linear mixed-effects models to disentangle the relative effect of each predictor. The TP subregions were defined according to Xing and Ree (2017). Collinearity among these predictors was tested using VIFs.

### 3 | RESULTS

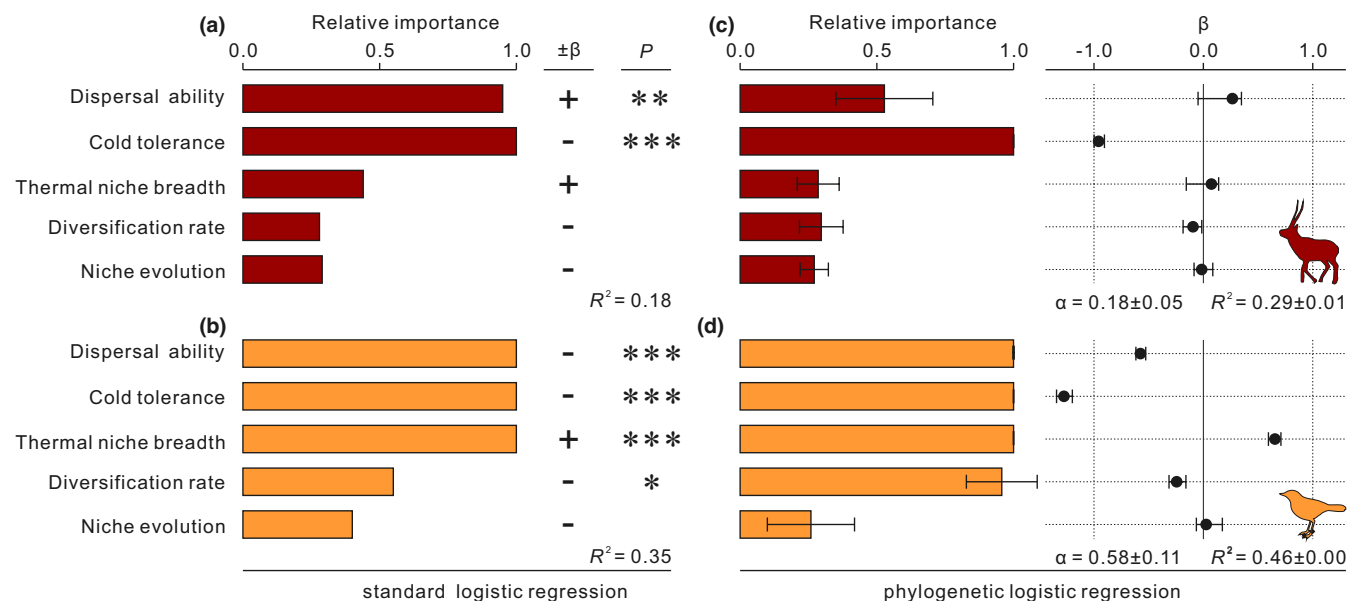
#### 3.1 | Differences in species attributes between the TP and non-TP species

As predicted, the TP species exhibited a higher cold tolerance, wider thermal niche breadth and higher rate of niche evolution than the non-TP species (Wilcoxon rank sum test,  $p < 0.05$ ; Figure 1). However, no differences were observed in the dispersal ability and diversification rate between the TP and non-TP species ( $P > 0.05$ , Figure 1). These findings were broadly similar for mammals and

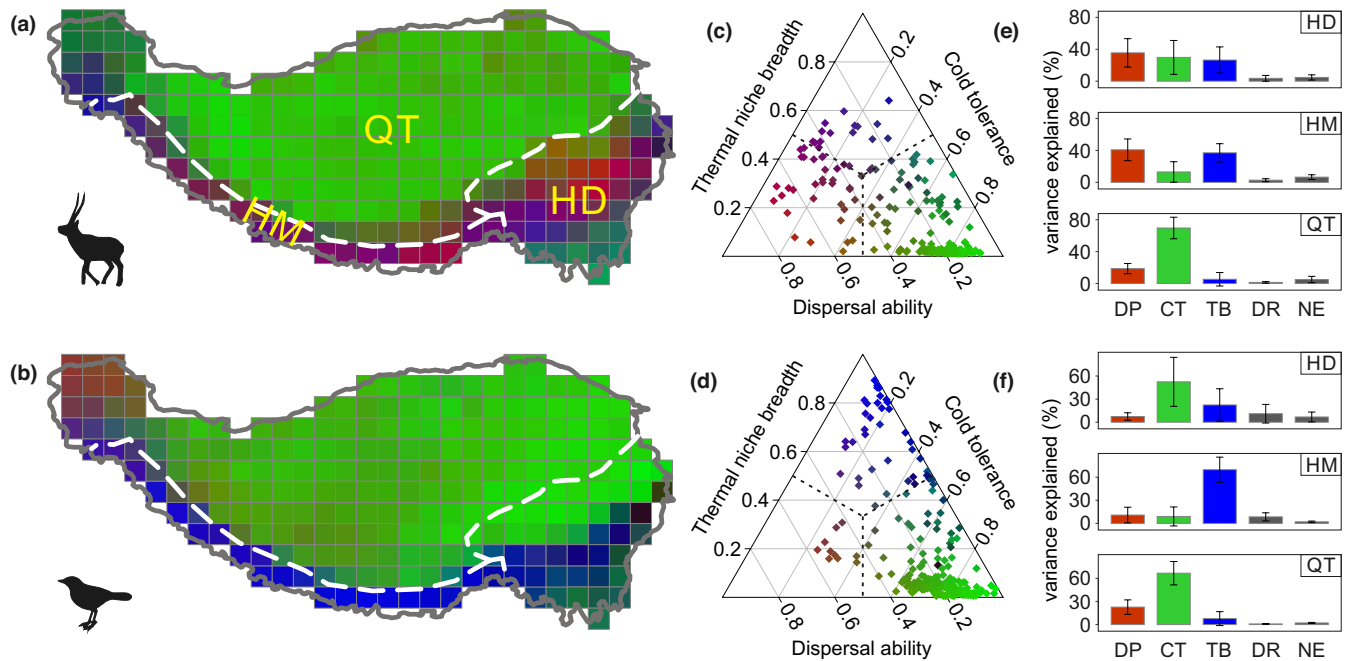
birds, and among different sizes of species pools, with the only exception that the differences in the niche evolution rate between the TP and non-TP species were significant ( $p < 0.05$ ) with increasing sizes of species pool (compare Figure 1 with Figure S1.4).

#### 3.2 | Predictors explaining the occurrence of TP species

Among all the possible combinations of standard (non-phylogenetic) logistic regression models for mammals, the highest ranked model based on the AICc included dispersal ability and cold tolerance as explanatory variables (Table S1.2) and explained 18% of the total variance (Figure 2(a)). Sum of the Akaike weights ( $\Sigma wi$ ) indicated that cold tolerance ( $\Sigma wi = 1.00$ ) was the most important attribute, followed by dispersal ability ( $\Sigma wi = 0.95$ ) and niche breadth ( $\Sigma wi = 0.44$ ), while diversification rate ( $\Sigma wi = 0.29$ ) and rate of niche evolution ( $\Sigma wi = 0.28$ ) had marginal explanatory power (Figure 2a; Table S1.2). The best-fitting model for birds explained 35% of the total variance (Figure 2(b)) and included all variables except the rate of niche evolution (Table S1.3). Furthermore, dispersal ability, cold tolerance and niche breadth were the most important attributes ( $\Sigma wi = 1$ ; Figure 2b), followed by diversification rate ( $\Sigma wi = 0.91$ ) and rate of niche evolution ( $\Sigma wi = 0.29$ ). Phylogenetic logistic regression models identified important variables that were similar to those identified by standard logistic



**FIGURE 2** Regression coefficients of predictors and model diagnostics for logistic regression models explaining the presence of species on the Tibetan Plateau. Results of logistic regression for mammals (a) and birds (b). Bar lengths show the relative importance value of each variable, which are calculated by the sum of the Akaike weight of models including them. Plus and minus symbols indicate the sign of model-averaged logistic regression coefficient estimates ( $\beta$ ). Asterisks indicate the level of significance of variables in logistic regression analyses ( $*p < 0.05$ ,  $**p < 0.01$  and  $***p < 0.001$ ).  $R^2$  indicates the variance explained by the best model. Results of phylogenetic logistic regression for mammals (c) and birds (d). Bar lengths show the mean relative importance values with a vertical bar representing standard deviations based on the calculations of 1000 phylogenetic trees. Filled dots represent the median values of regression coefficient ( $\beta$ ) estimates for phylogenetic models with an inference interval as the 2.5th–97.5th percentiles for 1000 phylogenetic trees. The phylogenetic correlation ( $\alpha$ ) and the variance ( $R^2$ ) explained by a model are shown as the mean values and standard deviation of the best models among 1000 repetitions



**FIGURE 3** Spatial non-stationarity in the relative importance of species dispersal ability, thermal niche properties and evolutionary history in explaining the occurrence of Tibetan Plateau (TP) mammal and bird species within each grid cell. (a) and (b) maps showing the distribution of proportion of variance explained by the top three predictors. Three TP subregions are delineated and labelled. Abbreviations: HD, Hengduan Mountains, HM, Himalayas, and QT, Qiangtang Plateau (c) and (d) triangle plots show the proportion of variance explained by the top three predictors: dispersal ability, cold tolerance and niche breadth. Each dot in the triangle scatter plots represents a grid cell assemblage with identical colours. (e) and (f) Proportion of variance explained by each predictor was calculated as the average value across all grid cells for each subregion with a vertical bar representing standard deviation. Abbreviations: DP, dispersal ability; CT, cold tolerance, TB, thermal niche breadth, DR, diversification rate and NE, niche evolution

regression (Figure 2c, d). The phylogenetic alpha coefficient ( $\alpha$ ) was almost zero for mammals ( $\alpha = 0.18 \pm 0.05$ ), suggesting that phylogenetic signals existed in the community assembly of species on the TP; however, the phylogenetic signals for birds were relatively weak ( $\alpha = 0.58 \pm 0.11$ ). These results were significant for different sizes of the species pools, both for standard logistic regression (Figure S1.5) and phylogenetic logistic regression (Figure S1.6) models.

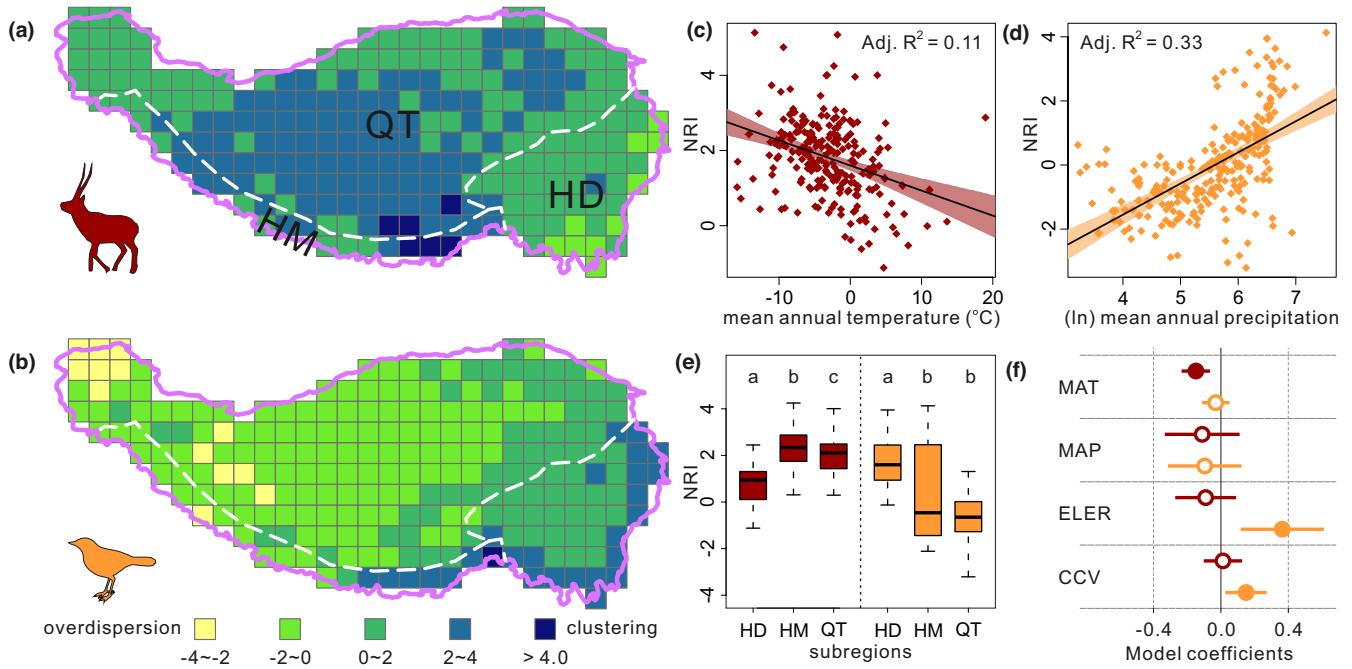
### 3.3 | Effect of spatial variations on determinants

We performed standard logistic regressions and hierarchical partitioning analysis separately for each grid-based assemblage within the TP. We emphasized more on the top three variables (dispersal ability, cold tolerance and niche breadth; Figure 3a–d) because the evolutionary history (rate of niche evolution and diversification rate) explained a minimally observed variance ( $10.2 \pm 4.1\%$  for mammals and  $4.9 \pm 1.9\%$  for birds; Figure 3e, f). Furthermore, substantial spatial variations in the relative role of predictors were observed in explaining the occurrence of the TP species within each assemblage (Figure 3a–d). For example, dispersal ability and niche breadth contributed the most in structuring the mammal assemblages of the Himalayas and Hengduan Mountains, whereas cold tolerance was important in the inner TP region (i.e. Qiangtang Plateau; Figure 3a,b).

For birds, most grid cells were on the right edge of the triangle (Figure 3d), suggesting that cold tolerance and niche breadth were more significant than dispersal ability. Despite the spatial variations in the relative importance of predictors between mammals and birds, cold tolerance was consistently observed to significantly influence species assemblages within the Qiangtang Plateau (Figure 3; Figure S1.7).

### 3.4 | Phylogenetic structure of the TP fauna

All TP birds showed closer phylogenetic relationships than expected ( $\text{NRI} = 3.67 \pm 0.26$ ; all 1000 randomized phylogenies were significantly clustered,  $p < 0.05$ ), whereas the mammal community represented a phylogenetic subset of species randomly drawn from the regional species pool ( $\text{NRI} = -0.88 \pm 0.70$ ; 946 out of 1000 trees were not significant,  $p > 0.05$ ). Notably, the phylogenetic structure for the grid-based species assemblages was non-random within the TP and showed a significantly contrasting pattern between mammals and birds (Pearson's  $r = -0.29$ ,  $p < 0.05$ ; Figure 4a, b). The phylogenetic structure for mammals showed a positive NRI throughout the TP, excluding the eastern edge of the plateau (Figure 4a). Conversely, the NRI for birds was positive in the eastern region of the TP, but negative in the western region (Figure 4b). Significantly clustered communities ( $\text{NRI} > 2$ ) for mammals occurred in the inner TP region



**FIGURE 4** Phylogenetic community assemblage structure on the Tibetan Plateau (TP). (a) and (b) Maps showing the geographical distribution of the net relatedness index (NRI) values for mammals and birds. Three TP subregions are delineated and labelled. Abbreviations: HD, Hengduan Mountains, HM, Himalayas and QT, Qiangtang Plateau. (c) and (d) Scatterplots showing the correlations between the phylogenetic structures and the highest related variables (mean annual temperature for mammals and mean annual precipitation for birds; see Figure S1.8 for details). The solid lines represent the fitted linear models and the shaded areas are the 95% confidence intervals of these models. Adj.  $R^2$  refers to the adjusted  $R^2$  of the linear regression. Both relationships are significantly different from zero ( $p < 0.05$ ). (e) Boxplots showing the NRI distributions among three subregions with letters indicating significant differences (Wilcoxon rank sum test,  $p < 0.05$ ). (f) Coefficient estimates and 95% confidence intervals for predictors from linear mixed models explaining the spatial variations in the NRI of mammals and birds. Filled dots represent statistically significant relationships ( $p < 0.05$ ). Abbreviations: MAT, mean annual temperature, MAP, mean annual precipitation, ELER, elevation range and CCV, climate change velocity

(i.e. Qiangtang Plateau; Figure 4a), whereas significantly clustered communities for birds emerged in the southeast edge of the plateau (i.e. the East Himalayas and Hengduan Mountains; Figure 4b).

Univariate linear regression models showed that the NRI of species was significantly correlated with all the tested variables (adjusted  $R^2 = 0.04 \sim 0.33$ ,  $p < 0.05$ ; Figure S1.8), with mean annual temperature and precipitation having the highest correlations among mammals (adjusted  $R^2 = 0.11$ ; Figure 4c) and birds (adjusted  $R^2 = 0.33$ ; Figure 4d), respectively. NRI values per cell in the Hengduan Mountains for mammals were significantly lower than those in the Himalayas and Qiangtang Plateau, while NRI values for birds were significantly higher in the Hengduan Mountains (Wilcoxon rank sum test,  $p < 0.05$ ; Figure 4e). However, the rank of importance of these variables changed in the linear mixed models that accounted for the spatial autocorrelation (Table S1.4). The mean annual temperature (relative importance, RI = 0.93) had significant negative effects on the NRI of mammal assemblages, while the elevation range (RI = 0.97) and climate change velocity (RI = 0.48) had significant positive effects on the NRI of bird assemblages (Figure 4f; Table S1.4). Despite the relatively strong positive correlation between elevation range and climate change velocity ( $r = 0.79$ ; Figure S1.9), our results were not affected by collinearity because the VIFs were less than 2 in all the models.

## 4 | DISCUSSION

### 4.1 | Thermal niches explain the occurrence of TP species

The community assemblages on the TP are not a random combination of species, but comprise species with various specific attributes that enable them to sustain in highland environments. Consistent with our predictions, high cold tolerance of species was a key predictor in explaining species occurrence on the TP (Figure 2), thus supporting the assumption that severe climatic conditions in mountain ranges exhibit a strong filtering effect on the species assemblages (Graham et al., 2014; Qian et al., 2021). Additionally, thermal niche breadth plays an important role. Previous studies have frequently described the associations between climatic niche breadth and species geographical range (Varzinczak et al., 2020). Sexton, Montiel, Shay, Stephens, and Slatyer (2017) summarized that species with wider niche breadths most probably exhibited high ecological plasticity and adaptability to different climatic conditions, thus reducing extinction risk and increasing their ability to utilize new habitats. Together, the stressful environment on the TP may promote the filtering out of species with a weak cold tolerance and narrow thermal niche breadth. This supports our initial predictions





and highlights the effect of environmental filtering on montane species assemblages.

## 4.2 | Dispersal ability explains the occurrence of TP species

Our results confirmed that the occurrence of species on the TP was strongly correlated with the strength of dispersal ability (Figure 2), although no significant differences in the dispersal ability were observed between the TP and non-TP species (Figure 1i). Species native to the TP were assumed to have colonized from surrounding regions (He, Lin, Ding, Yu, & Jiang, 2021; Wen, Zhang, Nie, Zhong, & Sun, 2014), because the TP did not emerge above sea level until the Indo-Asian collision (Royden et al., 2008). Mammals with strong dispersal ability were proposed to conveniently overcome the topographical barriers and colonize the TP by migrating long distances (He et al., 2021; Li & Wang, 2015). Furthermore, stressful environments and low resource availability on the TP may force species to migrate farther for food resources (Teitelbaum et al., 2015), thus enhancing the dispersal ability (quantified as home range size) of the species on the TP. Surprisingly, dispersal ability (quantified as HWI) negatively affected the occurrence of birds on the TP (Figure 2b, d), indicating that birds living on the TP exhibited lower dispersal ability than those living outside of the TP. This result differed from our prediction, possibly because the decreased partial pressure of oxygen at high altitudes considerably increases the energy costs of flights and limits the flight performance of birds (Senner et al., 2018). Alternatively, the southeastern TP region (i.e. the Hengduan Mountains and Himalayas) fundamentally supports the diversity of many ground-dwelling birds or birds, such as parrotbills (Liu et al., 2016) and pheasants (Cai et al., 2018) having limited volant abilities. Therefore, the positive effect of dispersal ability on the occurrence of bird species on the TP may have been overshadowed by the negative effects of various weak-dispersing lineages.

## 4.3 | Spatial variations in the contributions of environmental filtering and dispersal limitation

Notably, the relative roles of environmental filtering and dispersal limitation in explaining the species occurrence on the TP varied spatially (Figure 3). Cold tolerance consistently had a strong effect on the occurrence of mammal and bird species on the Qiangtang Plateau (Figure 3), supporting a general mechanism driven by niche-related processes (i.e. environmental filtering). This was expected because the Qiangtang Plateau has a more stressful environment than the Hengduan Mountains and Himalayas (Xing & Ree, 2017). Additionally, uplift-driven changes in climatic conditions during the Cenozoic could have probably promoted the increased rate of species extinction on the Qiangtang Plateau, and its present-day biota was subsequently recolonized and assembled by species adapted

to cold conditions (Ding et al., 2021). Contrastingly, the Hengduan Mountains and Himalayas probably served as shelters for the TP species during the Quaternary glacial period (Yu et al., 2019) because these regions show high topographical and temperature variations. In these regions, species could track their climatic niche by moving short distances uphill or downslope as a response to climatic fluctuations. Alternatively, the Hengduan Mountains and Himalayas comprise more generalist species across the neighbouring lowlands than the Qiangtang Plateau; thus, species with wider thermal niche breadth inhabit these regions. Therefore, different ecological conditions and evolutionary contexts within the TP have resulted in spatial variations in the relative influences of environmental filtering and dispersal limitation.

## 4.4 | Weak effect of evolutionary history on the occurrence of TP species

Many studies have documented rapid clade radiations occurring in mountain ranges (Hughes & Atchison, 2015 and the references therein) due to the increasing probabilities of allopatric divergence and high rates of niche evolution (Kozak & Wiens, 2010; Figure 1). However, our results did not indicate a significant difference in the diversification rate between the TP and non-TP species (Figure 1m). Additionally, we observed that the evolutionary history had a relatively weak impact on the occurring TP species (Figure 2). Moreover, the relative influence of evolutionary history was also negligible in the Hengduan Mountains and Himalayas (Figure 3), which have been frequently regarded as the biological diversification centres (Ding et al., 2020; Hu et al., 2021). This indicated that the TP species do not necessarily have a faster rate of niche evolution or a higher diversification rate than the non-TP species. This pattern may occur when specific montane clades underwent allopatric speciation via phylogenetic niche conservatism, which limits species dispersal in unsuitable habitats or climatic niches (Hua & Wiens, 2013). This speciation mode is widely documented in the Hengduan Mountains and Himalayas (e.g. Hu et al., 2016; Wan et al., 2018) particularly for small-ranged lineages that are specialized to a particular climatic niche. Moreover, niche filling in these regions has been observed to slow the species diversification rate (Price et al., 2014). Nevertheless, the weak effect of evolutionary history on the species assemblage of the TP was unexpected, and implies that processes, such as environmental filtering or dispersal limitation, are strong enough to override the influence of evolutionary history.

## 4.5 | Different phylogenetic structure patterns between mammals and birds

Due to the highly selective pressure by cold temperatures on the species occurrence on the Qiangtang Plateau (Figure 3a), we



expected phylogenetically clustered structures of species assemblages based on the stress dominance hypothesis (Coyle et al., 2014; Graham et al., 2009). Species assemblages for mammals changed from phylogenetic clustering on the Qiangtang Plateau to overdispersion in the Hengduan Mountains (Figure 4(a)). This observed pattern was consistent with our predictions and coincided with the previously assessed spatial patterns of phylogenetic structure for vascular plants on the TP (Yan, Yang, & Tang, 2013). Moreover, the phylogenetic logistic regression models identified strong phylogenetic signals in the mammal communities of the TP (phylogenetic alpha coefficient =  $0.18 \pm 0.05$ ; Figure 2c), suggesting that mammal communities are more likely to be clustered in the tree of life during stressful environments on the TP and tend to share evolutionary adaptations to survive and sustain under cold and low-oxygen conditions. This result was consistent with the observations by Qian et al. (2021), who found that phylogenetic clustering of global alpine flora results from strong environmental filtering and phylogenetic niche conservatism.

In contrast, the species assemblages of birds distributed in the Hengduan Mountains and Eastern Himalayas exhibited significant phylogenetic clustering (Figure 4b). We suggest that this pattern cannot be simply attributed to environment filtering, because the climatic conditions in these regions are favourable for most species. Indeed, our result found a significant positive effect of elevation range on the NRI of bird assemblages (Figure 4f), implying that such a phylogenetically clustered pattern possibly involves the uplift-driven diversification of birds. Strong evidence for in situ speciation has been demonstrated in the Hengduan Mountains and Himalayas for many avian clades, such as parrotbills (Liu et al., 2016), pheasants (Cai et al., 2018) and babblers (Cai et al., 2020). Contrastingly, the avian communities on the Qiangtang Plateau were strongly shaped by climatic constraints (Figure 3b) and showed a general phylogenetic overdispersion (Figure 4b). Due to the relatively weak phylogenetic signals for bird communities on the TP (phylogenetic alpha coefficient =  $0.58 \pm 0.11$ ; Figure 3), we suggested that the functional traits of birds on the Qiangtang Plateau most probably converged to tolerate stressful environments despite having split from distinct lineages over millions of years. Evidence from genetic expression (Hao et al., 2019), protein function (Zhu et al., 2018) and phenotypic traits (Barve, Ramesh, Dotterer, & Dove, 2021) have shown that several distinct clades of birds that are native to the TP have evolved similar adaptations in response to cold environments, thus corroborating our findings.

#### 4.6 | Potential limitations

Several potential limitations of our analyses deserve mention. First, our findings may be biased by the different species pool sizes. It is vital to determine the region from which the species pool is accurately selected to test the differences in species-level attributes between the TP and non-TP species or capture the signature of the assembly

process on the community phylogenetic structure, but is often challenging (Graham et al., 2014). Different delineations of species pools may also affect the outputs of null models (Cornell & Harrison, 2014). Second, the dispersal ability of mammals was not directly measured, but was estimated by linear models with body mass and dietary guild inputs. However, this relationship may be more complicated than expected, not only due to possible nonlinearities between dispersal and life-history traits (Stevens et al., 2014), but also due to interdependence between spatial and temporal dispersal (Buoro & Carlson, 2014). Finally, we did not use the physiological tolerance of species (i.e. fundamental climatic niches), but instead estimated the realized climatic niche based on their geographical range. Although this method has been proven valid at large spatial scales by numerous studies (Gómez-Rodríguez, Baselga, & Wiens, 2015; Varzinczak et al., 2020), the physiological tolerance data of species should ideally be compiled from experimentally derived measures (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014). Therefore, better simulation of species' biological attributes that integrate more complexity with high-quality life-history data for more species (Buoro & Carlson, 2014; Stevens et al., 2014) is promising to better understand the forces underlying the regional assembly of the TP.

## 5 | CONCLUSION

This work quantified the relative roles of the ecological and evolutionary processes in structuring the species assemblages of mammals and birds on the TP, one of the most stressful highlands of the world, using the spatial distribution, phylogeny, dispersal ability and thermal niche data of species. To our best knowledge, the TP fauna has been demonstrated, for the first time, not as a random combination of species, but as a result of interplay between environmental filtering and dispersal limitation. However, substantial spatial variations in the relative contributions of these factors, along with the differences in the phylogenetic structures of the community assemblages between mammals and birds, highlight the different roles of eco-evolutionary processes in generating regional community assemblages across space and among taxonomic groups. This study provides significant insights into the underlying processes, which structure species assemblages, by moving from testing community assembly to directly assessing mechanistic links between the occurrence of the montane species and their morphological, ecological or evolutionary constraints.

## ACKNOWLEDGEMENTS

We are grateful to the Chief Editor C. N. Meynard, Associate Editor H. Sun and two anonymous reviewers for their constructive comments on the manuscript. This work was supported by grants from the National Natural Science Foundation of China (grant no. 31900324) and Guangdong Basic and Applied Basic Research Foundation (grant no. 2020A1515011472). No permit was needed to carry out the present work.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.qrfj6q5hk>. This dataset includes: (a) species-level data that indicates species' biological attributes (dispersal ability, thermal niche properties, and evolutionary history) of all species included in logistic regressions; (b) grid-based data that indicates the phylogenetic structure metrics and all predictors for each species community.

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#### SUPPORTING INFORMATION

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**How to cite this article:** He, J., Lin, H., Wang, R., Dai, C., Yu, H., Tu, J., Yu, J. & Jiang, H. (2022). Joint effects of environmental filtering and dispersal limitation on the species assemblage of the Tibetan Plateau. *Journal of Biogeography*, 00, 1–14. <https://doi.org/10.1111/jbi.14328>