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Elevational patterns of bird functional and phylogenetic structure in the central Himalaya

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How communities assemble is a central and fundamental question in ecology. However, it has been mired by conflicting conclusions about whether community assembly is driven by environmental filtering, biotic interactions, and/or dispersal processes. Elevational gradients provide an ideal system for exploring the biotic and abiotic forces influencing the processes of community assembly, as these both change dramatically on mountains over short spatial distances. Here, we explored bird taxonomic, functional and phylogenetic diversity, and assessed the role of spatial (area) and environmental factors (temperature, precipitation, plant richness, habitat heterogeneity, the Normalized Difference Vegetation Index (NDVI)) in shaping bird distributions and community structure along a 3600 m elevational gradient in the central Himalayas, China. Our results showed that the three dimensions of diversity consistently showed hump-shaped patterns with similar peaks. Richness-controlled functional diversity decreased with elevation, while richness-controlled phylogenetic diversity showed a Mid Valley pattern. Mean pairwise functional distance decreased linearly with elevation, and mean pairwise phylogenetic distance was nearly constant along the elevation gradient but increased rapidly at higher elevations (above 3900–4200 m a.s.l). The functional structure of bird communities was more clustered relative to source pools (i.e. species more similar to one another) across the elevation gradient, suggesting abiotic or habitat filtering likely governed the assembly processes. However, phylogenetic structure was more clustered relative to source pools at mid-elevations and more overdispersed (i.e. species are less related) at low and high elevations. In addition, primary productivity (NDVI and/or habitat heterogeneity and/or plant richness) was a good predictor of variation for most diversity metrics. Taken together, our study demonstrated contrasting elevational patterns assessed from functional and phylogenetic measures and highlighted the necessity of considering multiple measures of biodiversity when assessing community structure.

Keywords: Community structure, environmental filtering, functional diversity, Himalaya, overdispersion, phylogenetic diversity

Introduction

Understanding how communities assemble is a central and fundamental question in ecology (Götzenberger et al. 2012), which could be driven by environmental filtering (Gleason 1926), biotic interactions (Clements 1916), and/or dispersal processes (Hubbell 2001). Recently, the realization that these mechanisms co-occur simultaneously within communities (Cadotte and Tucker 2017), or sequentially along environmental gradients (Mason et al. 2007) has been shown from studies using evolutionary or functional trait information (Cadotte et al. 2019). Thus, the critical question is no longer to determine which mechanism structures communities, but rather, which mechanism plays a dominant role in community assembly along environmental gradients (Mouchet et al. 2010).

The distribution of biodiversity along elevational gradients, particularly related to species richness, has received extensive attention over the last century, with a rapid increase in recent decades (reviewed by Grytnes and McCain 2007). In these studies, maximal richness at mid-elevations was found to be the most common pattern among vertebrates (45% of all cases, McCain and Grytnes 2010), which was often explained by various spatial (e.g. area, Rahbek 1997) and/or environmental drivers (e.g. climatic variables, productivity, and habitat heterogeneity; Sanders and Rahbek 2012, Pan et al. 2016, Elsen et al. 2017, Srinivasan et al. 2018).

However, a shortcoming of these studies is that analyses of species richness patterns assume all species are ecologically equivalent, resulting in an insufficient and a potentially biased view of biodiversity dynamics, and thus obscuring our understanding of assembly processes (Stevens et al. 2003, Bässler et al. 2016, Si et al. 2016). Functional and phylogenetic diversity both explicitly incorporate species' differences into diversity measures, and which are believed to better reflect the underlying ecological processes than species richness (Cadotte et al. 2011, Mouquet et al. 2012, Srivastava et al. 2012). For example, environmental stress (e.g. cold or dry climate) affects assembly processes and results in functionally and phylogenetically non-random communities (McCain 2009). More generally, communities with high phylogenetic diversity and high trait diversity might indicate that mechanisms supporting heterogeneous niches are prevalent with competition on phylogenetically conserved traits as a commonly cited mechanism, whereas low trait diversity could suggest the existence of environmental filtering on convergent traits (Mayfield and Levine 2010, Pavoine and Bonsall 2011).

Studies of phylogenetic or functional diversity along elevational gradients have emerged in the literature only recently, but most of functional or phylogenetic elevational patterns were not congruent with those from species richness (e.g. Kluge and Kessler 2011, Bässler et al. 2016, Zhang et al. 2020). There could also be fundamental reasons for why various dimensions of diversity measures might differ from one another (e.g. inappropriate phylogenies, use of different and incompatible metrics, skewed distributions of phylogenetic distances, etc. Cadotte et al. 2017; or inclusion of several traits with discrete character states, or dependency on species pools sorting into local communities, etc. Tucker et al. 2018). For example, in a study of bat communities in Peru, Cisneros et al. (2014) found that species richness decreased nonlinearly with increasing elevation, while phylogenetic and functional diversity were, surprisingly, not correlated with elevation. Similarly, passerine bird diversity in the Ailao Mountains, southwest China also showed an inconsistent pattern of species richness and functional/phylogenetic diversity (He et al. 2018). These findings indicate that patterns of functional and/or phylogenetic diversity need not be consistent with patterns of species diversity or one another, demonstrating that one dimension of biodiversity might not be a good surrogate for other dimensions (Devictor et al. 2010, Cisneros et al. 2015, Cadotte et al. 2019). Thus, the conclusions about community assembly and structure along gradients based on taxonomic data only may be misleading or simplistic (Bässler et al. 2014). In addition, the determinants of phylogenetic and functional diversity along environmental gradients are even less clear than for species richness. Recent findings suggest that temperature has the greatest effect on the diversity of bumblebees, grasshoppers and birds (Laiolo et al. 2018), and phylogenetic diversity of soil bacteria, fungi and nitrogen fixers are all better predicted by variation in temperature than pH (Zhou et al. 2016). Taken together, an examination of the determinants of functional and phylogenetic diversity simultaneously can gain additional insights into the relative importance of environmental or biotic drivers in structuring communities (Cadotte et al. 2013, 2019 Monnet et al. 2014, Si et al. 2016).

While there is a substantial amount of work examining biodiversity patterns along elevational gradients, less attention has been paid to understanding how community structure varies with elevation and the mechanisms shaping these patterns. It is generally assumed that competition shapes communities at low elevations where population growth rates and densities are higher (Machac et al. 2011), and communities are subjected to environmental filtering at high elevations where environmental stresses are more pervasive (McCain 2009, Cisneros et al. 2014, He et al. 2018). However, the assembly processes are likely to be even more complex than the expected scenarios because of multiple environmental gradients influenced by elevation resulting in a multitude of ecological processes operating simultaneously (Bässler et al. 2016), and the fact that abiotic influences are never divorced from local biotic interactions (Kraft et al. 2015, Cadotte and Tucker 2017). For example, in a study of pteridophyte assemblages along a tropical elevational gradient, epiphytic fern assemblages tended to be clustered at both low and high elevations, and both appeared to be influenced by environment conditions that select for certain traits (Kluge and Kessler 2011). Similar to this finding, Dehling et al. (2014) also found frugivorous bird assemblages of Tropical Andes in lowlands and highlands were disproportionately influenced by environmental factors. Convergent evolution can also explain trait clustering at low and high elevations if species

traits in different lineages have convergently evolved to cope with environmental pressures (Dehling et al. 2014), or perhaps few lineages have diversified in those environments resulting in assemblages that exhibit both trait and phylogenetic clustering. Thus, these complexities require more studies assessing the relative roles of environmental filtering and biotic competition in structuring communities for better understanding the generality of community assembly along elevational gradients.

The Himalayan mountains, which are the highest mountains in the world, with one of the longest elevation gradients, are considered as the one of the world's biodiversity hotspots (Myers et al. 2000). In this region, previous work found hump-shape patterns at mid-elevations for bird, mammal and plant richness (Pan et al. 2016, Hu et al. 2017, Ding et al. 2019, Liang et al. 2020), but the elevational patterns of functional and phylogenetic diversity and structure, and inferred mechanisms influencing these are not well understood. Here, we explored the elevational patterns of bird functional and phylogenetic diversity and assessed the role of spatial (area) and environmental factors (temperature, precipitation, plant richness, habitat heterogeneity, NDVI) in determining the elevational distribution of bird communities. Specifically, we address follow questions: 1) What are the elevational patterns of taxonomic, functional and phylogenetic bird diversity, and how do they differ from one another? 2) Which explanatory variables (spatial or environmental factors) best explain the elevational patterns of three dimensions of biodiversity? 3) What are the functional and phylogenetic structures of bird communities, and the relative importance of ecological processes structuring bird communities along elevational gradients?

Methods

Study sites

Our study sites located at Gyirong Valley (28°15′–29°0′N, 85°6′–85°41′E) of Gyirong County in Tibet, China. This valley lies in the south slope of the central Himalaya, China, and is the longest (running ca 79 km from the bottom of the valley to the summit of Mt Mala) and is the westernmost valley in China' central Himalaya. With the strong influence of the Indian Ocean current, this valley has warmer and moister climate than the other four valleys in Shigatse Region. The Gyirong Valley is characterized by five climate types (the Mountainous Subtropical Zone, the Mountainous Warm Temperate Zone, the Mountainous Cold Temperate Zone, the Subalpine Frigid Zone, and the Alpine Frigid Zone). Human activities are largely concentrated below mid-elevations in the form of tourism, transportation and farming (Liang et al. 2020).

The valley has steep environmental gradients and five distinct vegetation types: evergreen broadleaf forest (1700–2500 m a.s.l.), coniferous and broadleaf mixed forest (2500–3300 m a.s.l.), dark coniferous forest (3300–3900 m a.s.l.), shrub and grass (3900–4700 m a.s.l.), and alpine tundra with sparse grass (4700–5500 m a.s.l.). Our study area has subtropical monsoon climate, with distinct wet (from May to October) and dry seasons (from November to April). At Gyirong Valley, temperature and precipitation decrease with elevation, and the wet season accounts for ca 80% of total amount of annual precipitation in most bands (Ding et al. 2019).

Bird surveys

We used line transects (Bibby et al. 2000) to record bird species richness and abundance across a 3600-m elevational gradient (from 1800 to 5400 m a.s.l.) during the wet season (from May to June in 2012, August in 2012, from September to October in 2012, and from July to August in 2013) in Gyirong Valley. Except the Alpine Frigid Zone, our transects covered all five climate zones. We separated the 3600-m elevational gradient into 12 bands with increments of 300 m. In each band, we set three transects which were chosen based on typical habitats of this band and the logistic accessibility. Specifically, a total of 36 transects were placed across the entire elevation gradient (Fig. 1 for details). The length of each transect within each band was between 2 and 3 km, but the total length of the three transects in each band were restricted to a total of 7.5 km to maintain constant same sampling effort (Rahbek 2005). We repeated each survey four times over a span of two years from 2012 to 2013, and recorded all birds heard and seen when traversing each section of a transect. All surveys were conducted by the same well-trained observers in our research groups (Jingjing Li, Hongfen Cao and Li Xie) along all transects in both years. Bird surveys were conducted between 30 min after dawn and 11:00 and between 15:00 and 30 min before sunset at local times in good weather conditions (i.e. avoiding strong winds or rain). We have tested the sampling effort using individual- and sample-based rarefaction analyses, which showed our survey efforts were sufficient for estimating bird communities along these transects (Hu et al. 2018).

To reduce the potential biases in survey data that can arise with seasonal, long-distance migrants (McCain 2009), we only considered breeding resident birds for subsequent analyses. In this study, migratory statuses were compiled from the local literature (The Comprehensive Scientific Expedition to Qinghai-Xizang Plateau, Chinese Academy of Sciences 1983). We also excluded shorebirds and owls in our analyses due to their specific habitats or nocturnal behavior (Si et al. 2017), resulting in a total of 151 breeding birds in our analyses.

Species trait data

We used commonly measured species-level bird traits linked to resource use to assess functional diversity (Ding et al. 2013, Monnet et al. 2014, Schipper et al. 2016), including one continuous one (i.e. body mass) and three categorical types (i.e. feeding guild, foraging behavior and stratum) (Table 1 and Supporting information). Body mass was estimated as
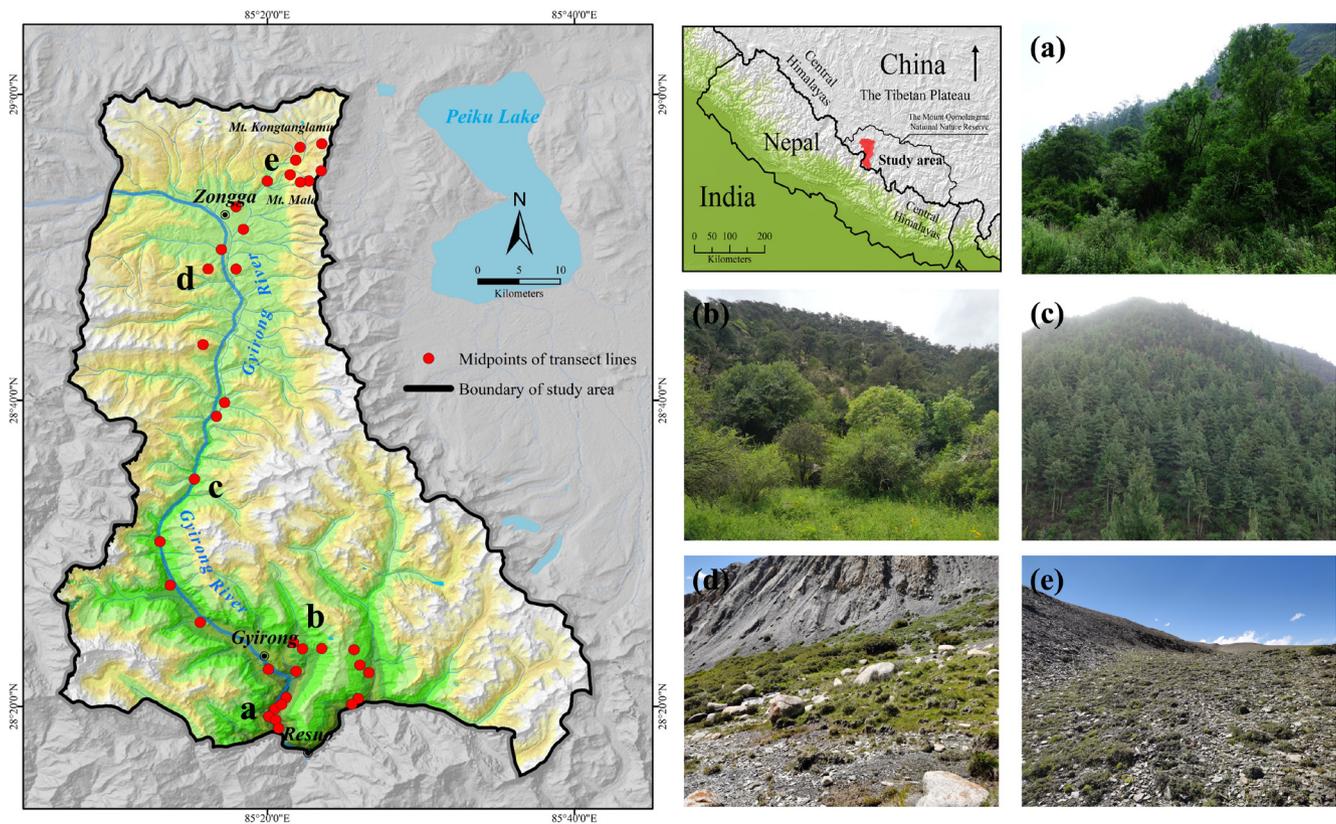
Figure 1. Map of the study area showing the 36 transects distributed in 12 bands with increments of 300 m.

the mean of the male and female individuals, and the three-dimensional foraging strategies were based on the primary food habits, foraging stratum and foraging behavior of birds. Body mass is widely considered as one of the single most informative traits of animal species (Brown 1995) because, for example, large birds require more resources, are from higher trophic levels, and are more vulnerable to extinction than smaller bodied birds (Gaston and Blackburn 1995, Cohen et al. 2003). Feeding guild, foraging behavior and stratum also measure various aspects of resource use, mainly reflecting how birds search for and use food (Devictor et al. 2010, Calba et al. 2014, Schipper et al. 2016, Sitters et al. 2016). All trait data were compiled from the local literature: The Avifauna of Xizang (Zheng et al. 1983).

To understand how bird functional traits varied with elevation and whether abiotic or biotic filtering is occurring (as clustering could be a result of biotic and abiotic processes, Goberna et al. 2014, Zhang et al. 2020), we additionally analyzed dispersion metrics for the continuous traits (i.e. body

mass in this study) to evaluate the role of filtering (see the section of 'Diversity indices' below for the estimation of multivariate trait distance). The rationale is that environmental filtering would lead to a decrease in trait range or variance (narrower ranges of trait values within communities when filtering has a dominant role in structuring communities, Graham et al. 2012, Fortunel et al. 2014, Zhang et al. 2020). We quantified the range, variance and community-weighted mean (CWM) of body mass using the R script provided by Kraft and Ackerly (2010) and 'dbFD' function in the 'FD' R package (Laliberté et al. 2014), respectively.

Explanatory variables

Given the potential importance of spatial and environmental factors in determining bird distributions (McCain 2009, Pan et al. 2016, Elsen et al. 2017, Srinivasan et al. 2018), we assessed the explanatory power of six factors in determining taxonomic, functional and phylogenetic diversity along

Table 1 Traits used to measure functional diversity and phylogenetic signals of breeding birds in the Gyirong Valley of central Himalaya, China.

Trait type	Trait	Range or categories	Blomberg's K	p
Resource quantity	Body mass (ln, g)	Continuous, 1.50–9.21	3.19	0.001
Feeding guild	Carnivore, granivore, insectivore, omnivore	Binary	/	< 0.001
Foraging behavior	Glean, probe, leap, sally	Binary	/	< 0.001
Foraging stratum	Ground, understorey, midstorey, canopy, air	Binary	/	< 0.001

elevational gradients. These factors include area, mean annual precipitation (precipitation), mean annual temperature (temperature), plant species richness (plant richness), habitat heterogeneity, and the Normalized Difference Vegetation Index (NDVI). We estimated the area of each elevation band of the Gyirong valley using 30-m digital elevation model (DEM) (CNIC-CAS, <http://www.gscloud.cn>). Precipitation and temperature were obtained from WordClim database (<http://www.worldclim.org>, 1950–2000) at 30 arc-sec resolution, and the value for each elevational band was calculated as the average of all grid cells within it. Plant richness was collected in the field from three quadrats per elevational band in September 2015. During the course of the field survey, we identified plant species following the nomenclature of Wu (1983–1987).

For the estimation of habitat heterogeneity, we first obtain the types of land cover in each 300-m elevational band from the 300-m GlobCover land cover data from CNIC, CAS (<http://www.gscloud.cn/>, accessed on 25 Oct 2015), and recorded 22 land-cover types following the United Nations Land Cover Classification System (LCCS) which primarily reflect the different types of forest, woodland, shrubland, and herbaceous communities. Then we estimated habitat heterogeneity by Shannon diversity index as follows: Habitat het-

$$\text{erogeneity} = \frac{\sum_{j=1}^{s} p_j \cdot \ln(p_j)}{\ln(s)}$$, where s represents the total

number of land-cover types in each band, and p_j is the proportion of areas in jth land-cover type.

NDVI measures ecosystem energy (Tucker and Sellers 1986, Mittelbach et al. 2001, Levin et al. 2007), which is often used as a surrogate for ecosystem primary productivity, vegetation height and structural complexity (Gordo 2007, Verschuyl et al. 2008). We obtained NDVI data for Gyirong Valley at 1 km resolution over a period of 4 years (2011–2014) from the Ministry of Environment Protection of the People's Republic of China <http://www.zhb.gov.cn>. We found the temporal variation of NDVI data changed little since 2011–2014. We thus averaged this four-year data for each elevational band by ERDAS IMAGINE 9.2 (ERDAS, Inc., Atlanta, GA, USA). All environmental variables were cropped and, if necessary, resampled to the same extent and spatial resolution (30 × 30 m).

Diversity indices

We estimated taxonomic, absolute functional and phylogenetic diversity of birds at each elevation band along the elevational gradient. Taxonomic diversity was calculated as observed species richness (SR), which is the number of bird species recorded within each elevation band. Absolute functional diversity was estimated as functional richness (FRic) (Villéger et al. 2008), and FD (Petchey and Gaston 2002). Absolute phylogenetic diversity was estimated as Faith's phylogenetic diversity index (PD) (Faith 1992).

FRic represents the multidimensional volume of functional space (i.e. convex hull volume) occupied by the species within a community (Villéger et al. 2008). To estimate FRic,

we first used Gower's distance (Gower 1966) to compute the pairwise functional distance between all birds. We then reduced the dimensions of functional distance matrix using PCoA, and estimated convex hull volume of functional spaces for species within a community in R using the package *FD* (Laliberté and Legendre 2010). FD is the sum of the branch lengths of the functional dendrogram for species within a community (Petchey and Gaston 2002). We constructed the functional dendrogram of bird species using UPGMA clustering methods based on the functional distance matrix, and calculated dendrogram-based FD in R using the function 'pd' in R package *picante* (Kembel et al. 2010). Higher value of FRic or FD indicates species within a community have more trait differences.

For phylogenetic diversity, we first downloaded 5000 pseudo-posterior distributions of bird phylogenies from birdtree.org using the source of tree 'Hackett All Species' (Jetz et al. 2012) and estimated the Maximum Clade Credibility tree using mean node heights by the software TreeAnnonator v1.8.2 of the BEAST package (Drummond and Rambaut 2007, Si et al. 2017). Faith's phylogenetic diversity index was thus estimated as the sum of all branch lengths of the phylogeny connecting all species of an elevational band using the function 'pd' in R package *picante* (Kembel et al. 2010). Branch lengths represent evolutionary time, with higher PD indicating species in a community accumulate more evolutionary time (Tucker et al. 2019).

Because SR, FRic, FD and PD are all types of richness metrics, they are comparable and conceptually analogous (Tucker et al. 2017, 2018). Furthermore, FD has been frequently used to compare with PD because they are both tree-based metrics (Safi et al. 2011, Albouy et al. 2015, Chapman et al. 2018, Dias et al. 2020, Zhao et al. 2020). However, FRic, FD and PD are all correlated with SR -since they sum across species, so we also calculated the standardized effect size (SES) of FRic, FD and PD using null models to control for the effects of species richness (i.e. richness-controlled metrics). Null model was run by randomly selecting species 999 times from all the species recorded across the entire elevation gradient, keeping species richness constant in each band (Jarzyna et al. 2021). Because SES. FRic showed no clear patterns along elevational gradient (Supporting information), indicating that elevational patterns of FRic may be mainly driven by the variations of species richness. We thus only considered the results of FD in this study.

We tested the phylogenetic signal of continuous trait (body mass) using Blomberg's K (Blomberg et al. 2003) and Pagel's λ (Pagel, 1999). A lower phylogenetic signal and less trait conservatism than expected from random evolution could be indicated by the values of $K \approx 1$ or $K < 1$, whereas a high degree of phylogenetic signal and stronger phylogenetic signals in trait data than expected from a Brownian motion of trait evolution could be indicated by the value of $K > 1$ (Ackerly 2009). Further, we performed a significance test for differences between the observed patterns of trait data and the expected by randomly shuffling

species at the tips of the phylogeny (Blomberg et al. 2003). Similarly, we tested the phylogenetic signal of body mass using the Pagel's λ that is compared with Brownian model as well as Blomberg's *K*. When trait values are randomly distributed across species, λ is close to zero, indicating a very weak signal, and a strong signal when λ is close to 1 (Molina-Venegas and Rodríguez 2017). We also test the phylogenetic signal of three groups of categorical traits (i.e. feeding guild, foraging behavior and stratum) using 'Fixed tree, character randomly reshuffled' model proposed by Maddison and Slatkin (1991). In this study, Blomberg's K and Pagel's λ showed similar results: all functional traits have significant phylogenetic signals (p < 0.05), with body mass having the strongest signal ($K > 3$ and $\lambda = 1$) (Table 1 and not shown results).

Functional and phylogenetic assemblage structure

Mean pairwise functional distance (MFD) and mean pairwise phylogenetic distance (MPD) were calculated to evaluate the elevational changes in the functional and phylogenetic relatedness of bird species, respectively (Webb et al. 2002). Specifically, MFD (or MPD) refer to the average functional (or phylogenetic) distance between all pairs of species in each elevation band, and is calculated as:

$$MFD \, or \, MPD = \frac{\sum_i^n \sum_j^n \delta_{i,j}}{n} (i \neq j)$$

where n is species richness in each band, $\delta_{i,j}$ is the pairwise functional (or phylogenetic) distance (Euclidean distance) between species i and species j.

Further, these indices were compared to 999 randomized communities to test whether the functional and phylogenetic community structures differed from random expectations. Specifically, random communities were generated by tip-shuffling across all taxa included in the distance matrix across the entire elevational gradient, which assumes that all species could colonize habitats across the whole gradient but are excluded due to local biotic and abiotic factors. In each randomization run, species richness was kept constant for communities within each band but tip labels in functional or phylogenetic distance matrix were shuffled. These randomizations were performed using the function *ses.mpd* in R package *picante* (Kembel et al. 2010). We then calculated the standardized effect size (SES) of MFD and MPD for each band as SES = (Obs − Exp)/SDexp, where Obs is the observed MFD or MPD, Exp is the mean of the 999 null communities and SDexp is the standard deviation of the 999 simulated values. We can use SES values to infer community assembly processes (i.e. environmental filtering or competition) when traits were conserved (i.e. with phylogenetic signals): if SES values < 0, it indicates environmental filtering may drive community clustering; if SES > 0, competitive exclusion may drive community overdispersion (Webb et al. 2002).

Data analyses

We employed first, second and third-order polynomial regression analyses to assess the linear, quadratic or cubic elevational distributions of different dimensions of bird diversity, respectively. The best-fitting models were selected based on the values of AICc (the corrected Akaike Information Criterion) (Anderson 2008) using the package *MuMIn* (Bartoń 2020).

We conducted single-variable ordinary least squares (OLS) models to explore the associations between taxonomic, functional and phylogenetic diversity and each explanatory variable. To make direct comparison of regression coefficients or improve normality, we standardized all dependent and independent variables (Standard Deviation = 1 and Mean = 0) before the OLS regression analysis and hierarchical partitioning. Moreover, we applied spatial autoregressive error models to control for the spatial autocorrelation using R function 'errorsarlm' in *spdep* package (Bivand et al. 2015).

Hierarchical partitioning (Chevan and Sutherland 1991) was applied to identify the explanatory variables that best accounted for variation in each of the three dimensions of bird diversity, because this method can effectively alleviate collinearity problems, and was commonly used in identifying the most likely causal factors (Olea et al. 2010). Further, to reduce collinearity, we also selected models with high explanatory power but low values of the Variance Inflation Factor (VIF), which is a measure of collinearity among independent variables in the multiple linear regression model. We dropped explanatory variables with the values > 10 (Dormann et al. 2013) and performed a hierarchical partitioning analysis to reveal the relative importance of the selected variables. Results from hierarchical analyses of the selected variables were generally similar to that with the six variables used in the above analysis (Supporting information).

For all analyses, area and MAP were log-transformed to improve normality. All calculations and analyses were performed in R 3.6.1 (<https://www.r-project.org>) and SAM 4.0 (Rangel et al. 2010, <http://www.ecoevol.ufg.br/sam>).

Results

A total of 151 breeding resident birds were recorded in this study, ranging from 13 to 65 species at each elevation band. Species richness, FD and PD all showed hump-shaped patterns, however, the elevation bands where they peaked were almost similar (Fig. 2, Table 2): the predicted species richness peaked at the fifth elevation band (i.e. 3000–3300 m a.s.l.), FD peaked at the fourth elevation band (2700–3000 m a.s.l.), and PD peaked the fifth elevation band (3000–3300 m a.s.l.). Richness-controlled functional diversity (indicated by SES.FD) decreased with increasing elevation, whereas richness-controlled phylogenetic diversity (indicated by SES. PD) showed Mid Valley patterns (lowest values of the diversity metric occurred at mid elevations).

MFD decreased linearly with elevation, whereas MPD kept nearly constant along the elevation gradient until
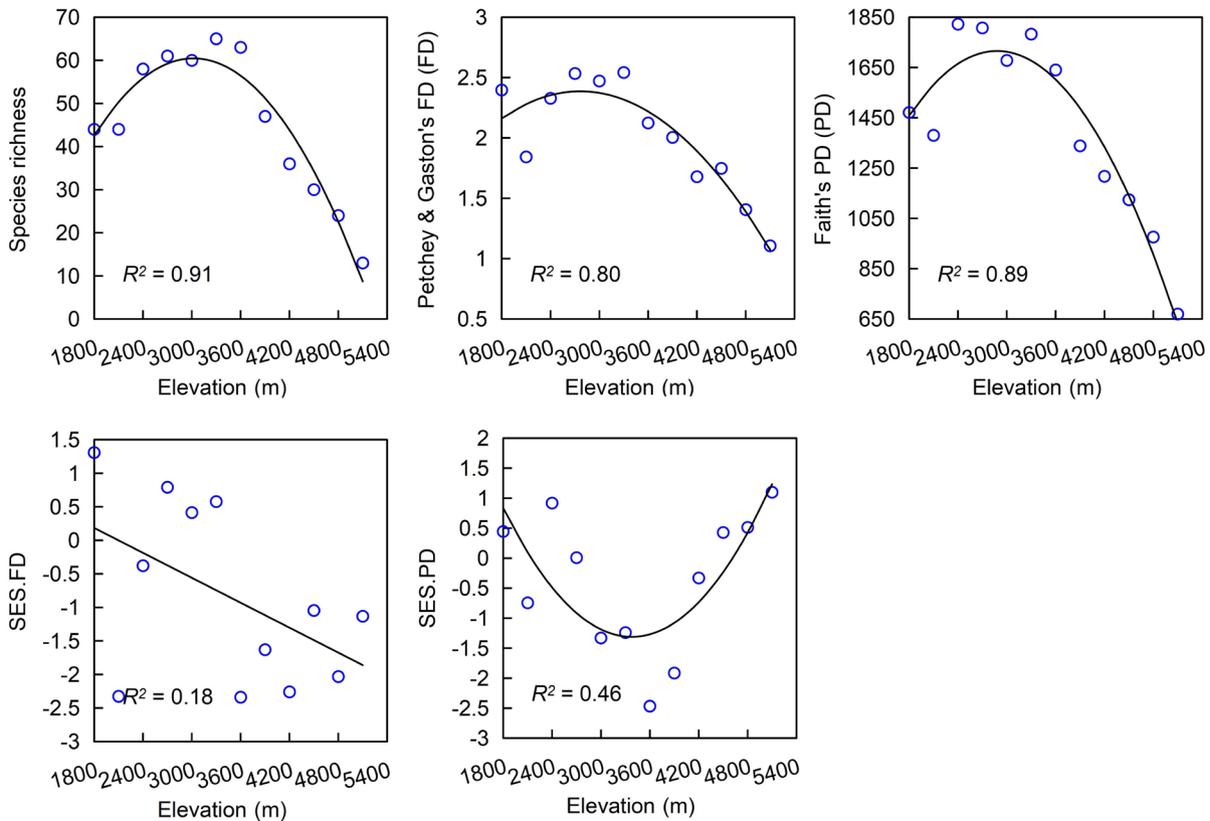
Figure 2. Elevational patterns of bird species richness, functional diversity (FD), phylogenetic diversity (PD) and its standardized effect size (SES.FD and SES. PD) along a 3600 m elevational gradient in the central Himalaya, China.

the eighth elevation band (3900–4200 m a.s.l.), and then increased steeply (Fig. 3). SES.MFD was generally negative, indicating bird communities were functionally clustered across most of the gradient, except at first and mid-elevation bands. In contrast, SES.MPD showed a clear and opposite pattern compared with SES.MFD: positive values at low or high elevations, but smaller values at mid-elevations. This indicates that bird communities were phylogenetically over-dispersed at low or high elevations but clustered at mid-elevations (Fig. 3). In addition, the range of body mass showed a hump-shaped pattern, whereas community-weighted mean of body mass increased with increasing elevation (Supporting

information). Surprisingly, variance of body mass showed no clear patterns in this study.

The single-variable ordinary linear squares models and spatial autoregressive error models showed similar patterns for taxonomic, functional and phylogenetic diversity and each explanatory variable (Table 3). As indicated by hierarchical partitioning (Fig. 4), species richness was best explained by NDVI (27.72%, the percentage of independent explained variance for NDVI, the same below) and habitat heterogeneity (24.05%), FD was best explained by NDVI (21.17%) and plant species richness (20.93%), and PD was best explained by NDVI (23.95%) and habitat heterogeneity (19.67%). In

Table 2 Best-fitted models from polynomial regression analyses of the effect of elevation on different measures of diversity.

	Best-fitted models	R^2	F	p
SR	$SR = 0.072 \times ele - 0.000012 \times ele^2 - 48.58$	0.91	54.52	< 0.001
FD	$FD = 0.0013 \times ele - 0.00000024 \times ele^2 + 0.55$	0.80	22.97	< 0.001
PD	$PD = 1.27 \times ele - 0.00022 \times ele^2 - 106.2$	0.89	45.54	< 0.001
SES.FD	$SES.FD = -0.00062 \times ele + 1.30$	0.18	3.35	0.097
SES.PD	$SES.PD = -0.0058 \times ele + 0.00000086 \times ele^2 + 8.51$	0.46	5.70	< 0.05
MFD	$MFD = -0.0000084 \times ele + 0.31$	0.38	7.74	< 0.05
MPD	$MPD = 0.091 \times ele - 0.000034 \times ele^2 + 0.0000000039 \times ele^3 + 42.17$	0.82	17.63	< 0.001
SES.MFD	-	-	-	-
SES.MPD	$SES.MPD = -0.0049 \times ele + 0.00000072 \times ele^2 + 7.52$	0.51	6.69	< 0.05

SR, species richness; FD, functional diversity; PD, phylogenetic diversity; SES.FD, the standardized effect size of FD; SES.PD, the standardized effect size of PD; MFD, mean pairwise functional distances; MPD, mean pairwise phylogenetic distance; SES.MFD, the standardized effect size of MFD; SES.MPD, the standardized effect size of MPD; ele, elevation.
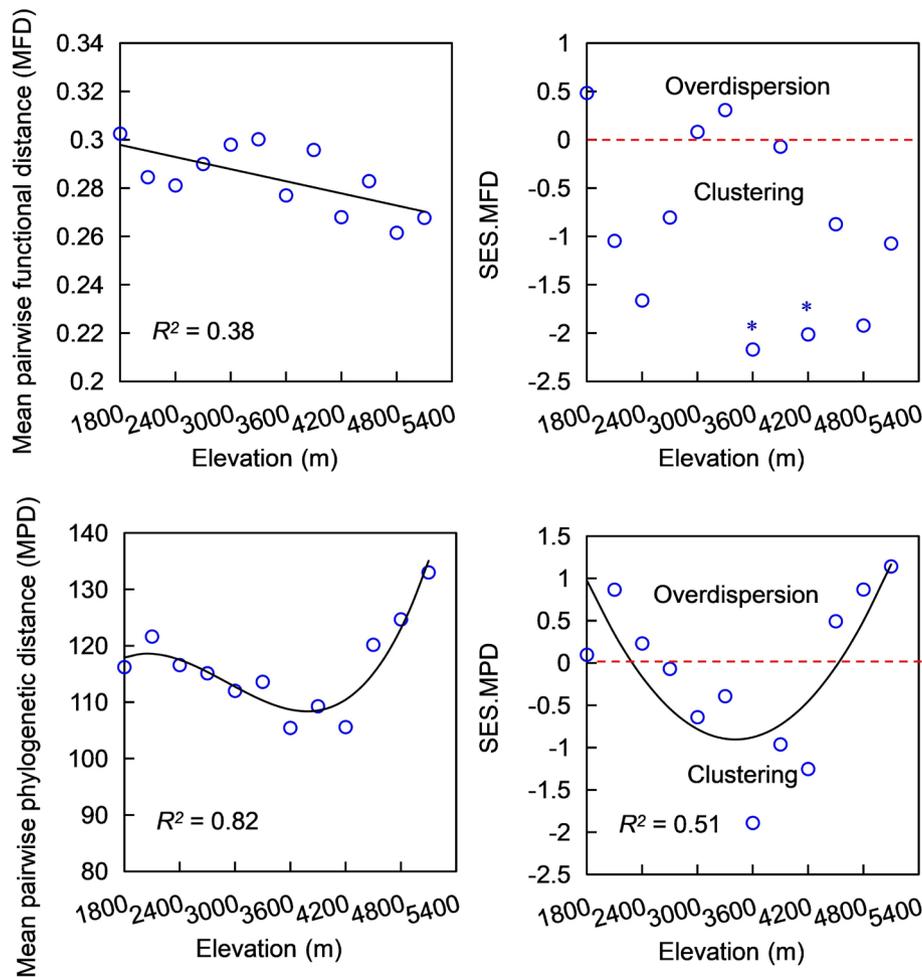
Figure 3. Elevational patterns of the observed mean pairwise functional distance (MFD), mean pairwise phylogenetic distance (MPD), the standardized effect size (SES) of MFD (SES.MFD) and MPD (SES.MPD) of breeding birds along a 3600-m elevational gradient in the central Himalaya, China.

addition, SES.FD was best explained by plant species richness (24.18%), and SES.PD was best explained by HH (18.87%) and NDVI (18.60%). MFD was best explained by temperature (15.97%) and precipitation (14.24%), and MPD was best explained by habitat heterogeneity (33.57%).

Discussion

Elevational patterns of bird diversity

Bird species richness, absolute functional and phylogenetic diversity both showed unimodal patterns peaked at similar elevation bands. Specifically, the predicted species richness peaked at the fifth elevation band (3000–3300 m a.s.l.) (Fig. 2), though high elevation locations had substantially lower diversity than lower elevation sites. Indeed, various hypotheses including single factors such as climate, space, evolutionary history and biotic processes (reviewed by McCain and Grytnes 2010), as well as the combinations and/or interactions of these factors (Pan et al. 2016,

Hu et al. 2017, Ding et al. 2019), have been proposed to explain elevational richness patterns. The mid-elevation peak in bird communities of Gyirong Valley likely reflects the fact that this area covers various combinations of benign and heterogeneous conditions, and thus promotes species richness (Ding et al. 2019). For example, habitat heterogeneity, NDVI, and plant richness approximately peaked at mid-elevations, which could support more bird species by supply more diverse niches (Allouche et al. 2012) or supporting a productivity-species richness relationship (discussed below).

Similar to species richness, absolute FD and PD also showed a hump-shaped relationship with elevation, peaked at the fourth elevation band (2700–3000 m a.s.l.) and the fifth elevation band (3000–3300 m a.s.l.), respectively. The unimodal patterns of absolute FD and PD are likely to be driven by species richness since they are not independent on species richness. After controlling for effects of species richness, functional diversity (indicated by SES.FD) decreased with elevation. This suggests that bird assemblages in high elevations have had functional differences filter out and only a subset of traits remain (Dehling et al. 2014, Vollstädt et al.

Table 3. Results of the single-variable OLS regression and spatial auto regressive models of bird species richness, functional diversity, phylogenetic diversity and each predictor.

		Area	MAP	MAT	HH	NDVI	PSR
Species richness	$Coef_{OLS}$	−0.44	0.54	0.64*	0.65*	0.82**	0.75**
	r^2_{OLS}	0.11	0.22	0.34	0.36	0.64	0.51
	$Coef_{SAR}$	−0.26	0.44	0.53	0.23	0.85	0.37
	AIC_{SAR}	26.50	25.59	23.87	19.04	19.78	22.24
FD	$Coef_{OLS}$	−0.59*	0.65*	0.75**	0.46	0.86***	0.86***
	r^2_{OLS}	0.28	0.37	0.52	0.13	0.72	0.72
	$Coef_{SAR}$	−0.82	0.78	1.22	0.17	1.24	0.83
	AIC_{SAR}	33.22	33.78	28.58	34.94	25.30	25.30
PD	$Coef_{OLS}$	−0.54	0.65*	0.73**	0.57	0.87***	0.82***
	r^2_{OLS}	0.22	0.36	0.48	0.25	0.73	0.65
	$Coef_{SAR}$	−0.43	0.67	0.72	0.22	0.95	0.57
	AIC_{SAR}	30.20	28.85	26.95	27.30	22.67	23.80
SES.FD	$Coef_{OLS}$	−0.50	0.48	0.51	−0.044	0.54	0.67*
	r^2_{OLS}	0.17	0.15	0.19	-	0.22	0.40
	$Coef_{SAR}$	−0.69	0.38	0.66	−0.14	0.66	0.81
	AIC_{SAR}	38.42	38.41	37.94	42.11	36.05	31.06
SES.PD	$Coef_{OLS}$	−0.06	0.034	−0.089	−0.60*	−0.26	−0.12
	r^2_{OLS}	-	-	-	0.30	-	-
	$Coef_{SAR}$	−0.17	0.074	−0.044	−0.49	−0.24	−0.057
	AIC_{SAR}	41.47	41.60	41.63	36.99	41.16	41.62
MFD	$Coef_{OLS}$	−0.58*	0.57	0.67*	0.19	0.69*	0.68*
	r^2_{OLS}	0.27	0.25	0.40	-	0.42	0.41
	$Coef_{SAR}$	−0.82	0.69	1.06	0.12	1.03	0.84
	AIC_{SAR}	37.33	37.74	33.24	42.30	31.28	33.70
MPD	$Coef_{OLS}$	0.061	−0.10	−0.25	−0.70*	−0.33	−0.27
	r^2_{OLS}	-	-	-	0.44	0.02	-
	$Coef_{SAR}$	0.11	−0.093	−0.20	−0.46	−0.23	−0.22
	AIC_{SAR}	39.36	39.38	38.81	33.96	38.52	38.68

Notes: The two (or one) highest r² and two (or one) lowest AIC in each column were in green shaded areas.
*p < 0.05.
**p < 0.01.
***p < 0.001.
FD, functional diversity; PD, phylogenetic diversity; MFD, mean pairwise functional distance; MPD, mean pairwise phylogenetic distance; MAP, mean annual precipitation; HH, habitat heterogeneity; NDVI, Normalized Difference Vegetation Index, MAT, mean annual temperature.

2017, Hanz et al. 2019). For example, more than half of species were ground foragers, and understory and midstory birds were observed less frequently in higher elevations, compared to species at mid and low elevations. In contrast, phylogenetic diversity (indicated by SES.PD) showed a Mid Valley pattern along the elevation gradient (i.e. lowest values of the phylogenetic diversity occurred at mid elevations, as defined by Montaño-Centellas et al. 2020). This indicated that greater lineage diversity emerged at either ends of the elevation gradient, though these elevations contain more depauperate assemblages than mid elevations. The Mid Valley pattern observed here supported previous findings that birds in the lowland tend to represent older groups (Päckert et al. 2012, Wu et al. 2014), and is also consistent with previous findings that forest communities in high elevations were more distinct and species were not closely related in eastern Himalaya as filtering may operating on certain species with shared traits but with distinct evolutionary lineages (Shooner et al. 2018, Rana et al. 2019).

The contrasting patterns of MFD and MPD provided additional insights into bird community structure. The decline of MFD across elevational gradient indicated bird species were more functionally similar at high elevations, but at the same time these assemblages were also comprised of phylogenetically dissimilar species. These contrasting patterns can be explained by the phylogeny of bird species in the central Himalaya (Supporting information) and the fact that these highland species belonged to different clades that have converged on the same traits for ground foraging like *Columba rupestris*, *Leucosticte brandti* and *Eremophila alpestris*. This incongruent pattern between functional and phylogenetic results might seem surprising but it actually frequently emerges in other studies, despite the fact that significant phylogenetic signals are commonly detected (reviewed by Cadotte et al. 2019). Indeed, Cadotte et al. (2019) found that nearly half of 99 comparative studies showed incongruencies between functional and phylogenetic diversity, with phylogenetic overdispersion and functional underdispersion being the most common. The primary reason for such incongruencies is that traits and phylogeny, because of how they are measured and synthesized, might capture different ecological processes. For example, functional traits could better reflect
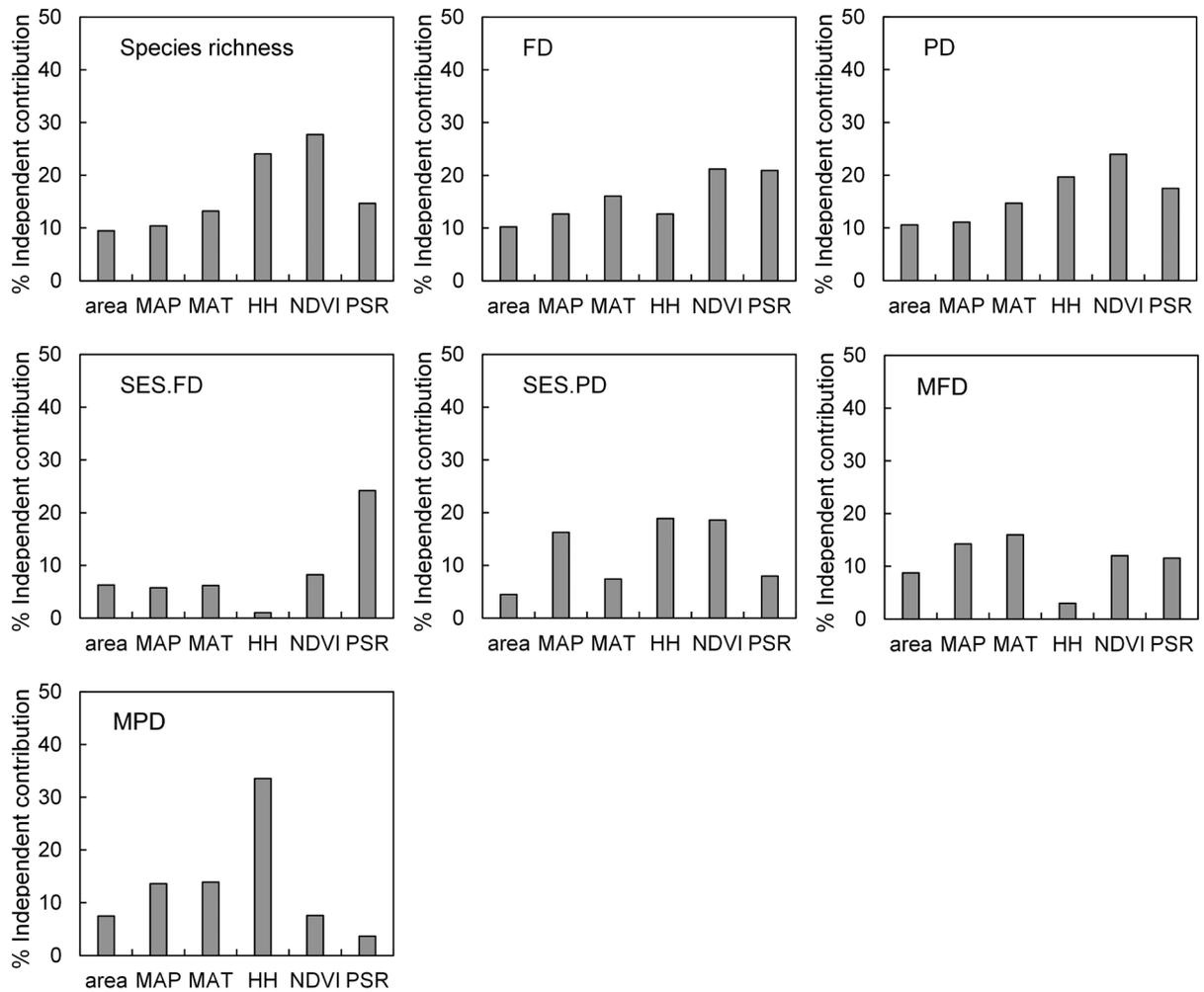
Figure 4. The percentage of independent contribution of each variable derived by hierarchical partitioning on each dimension of biodiversity of breeding birds along a 3600-m elevational gradient in the central Himalaya, China. Abbreviations: FD, functional diversity; PD, phylogenetic diversity; SES.FD, the standardized effect size of FD; SES.PD, the standardized effect size of PD; MFD, mean pairwise functional distance; MPD, mean pairwise phylogenetic distance; MAP, mean annual precipitation; MAT, mean annual temperature; HH, habitat heterogeneity; NDVI, Normalized Difference Vegetation Index, PSR, plant species richness.

the extent of competition whereas phylogenetic information likely better captures the multivariate niche (Cadotte et al. 2019, Huang et al. 2020, Zhao et al. 2020). Secondly, decisions about which and how to combine traits influence phylogenetic and trait congruence (Cadotte et al. 2017). Finally, both the functional trait and phylogenic approaches have several inherent weaknesses, for instance, the functional trait approach tends to ignore within-species (population) variation in trait values, whereas phylogenetic approach likely overestimates the information relevant to one or a few traits of species (Zhao et al. 2020). This finding highlights the importance of considering multiple dimensions of biodiversity simultaneously when assessing the assembly process.

Community assembly mechanisms

Overall, SES.MFD values were negative, except for three elevation bands with values greater than zero (the first, fifth,

and sixth elevation bands, Fig. 3). In this study, all traits had significant phylogenetic signals (Table 1) so that we can infer bird communities should be functionally or phylogenetically clustered when SES.MFD or SES.MPD were < 0. Following this, the negative SES.MFD at low or high elevations indicated bird communities were functionally clustered (the communities at 7th and 9th bands were even significantly clustered; see circles with asterisk in Fig. 3). It indicates that abiotic or biotic filtering might play a dominant role in structuring the bird assemblages, such as harsher environment, or greater stress that selects against bird species that cannot persist at low or high elevations. Narrower range of body mass at both low and high elevations further confirmed that filtering probably plays a central role in structuring bird communities (Supporting information). This is a relatively rare observation but has been reported by Kluge and Kessler (2011), who found environmental filtering structured epiphytic fern assemblages at both low and high elevations due to drought

at low elevations or frost at high elevations. For birds at high elevations, harsh environments (e.g. cold and dry) is often considered as an ecological filter favoring species with specific traits that can tolerant harsh conditions (Graham et al. 2009, Dehling et al. 2014, He et al. 2018, Zhang et al. 2020). Specifically, colder and drier environments favor relatively large-sized species. In this study, large species appear to better survive in these particular conditions, such as *Leucosticte brandti*, *Eremophila alpestris* and *Columba rupestris*, which mainly forage on the ground searching for seeds. For birds at low elevations, either disturbance regimes or biotic interactions have been suggested as the main factor filtering species that lack appropriate traits for persistence under particular conditions (Nogués-Bravo et al. 2008, Bernard-Verdier et al. 2012, Vollstädt et al. 2017). However, we need more studies to evaluate the relative roles of different filters (e.g. human activities) in shaping clustered structure of bird assemblages at low elevations. Interestingly, functional overdispersion was observed at mid-elevations (e.g. the fifth and sixth elevation bands), possibly indicating competition still played a role in these communities, or that there was a greater heterogeneity of resources or habitat types, or even that mid ranges contain representatives of both high and low elevation assemblages, which are distinct from one another.

Compared to SES.MFD, elevational trends of SES. MPD showed a contrasting pattern, which tended towards clustering at mid-elevations (SES values < 0) and overdispersion towards low and high elevations (SES values > 0). This indicated that co-occurring species are more phylogenetically related at mid-elevations than at low or high elevations (Pavoine et al. 2010, Montaño-Centellas et al. 2020). Phylogenetic overdispersion in high and low elevations can be the result of competition for limiting resources in stressful environments (after accounting for convergent traits), which tend to be maximized with distantly related species (Valiente-Banuet and Verdu 2007). Conversely, these overdispersed regions might contain higher habitat heterogeneity or very distinct niches. However, either phylogenetic or functional approach alone may be insufficient to disentangle specific processes shaping community structure, requiring us to use complementary analyses by including both approaches (Cadotte et al. 2017). Taken together, the contrasting patterns of functional and phylogenetic community structure (i.e. SES.MFD and SES.MPD) along the elevational gradient indicated that other unmeasured traits might also be essential in structuring the assemblage and again, highlighted the importance of considering multiple dimensions of biodiversity.

Driving factors

Primary productivity (NDVI and/or habitat heterogeneity and/or plant richness as a proxy), and climate were found to be good predictors of variation in species richness, absolute functional and phylogenetic diversity (FD and PD), richness-controlled functional and phylogenetic diversity (SES.FD and SES.PD), MFD and MPD along the elevation

gradient. Our findings are partially consistent with the previous research showing that temperature and habitat could structure species' distributions in the western Himalayas (Elsen et al. 2017), and that temperature had significant control over the distributions of species in eastern Himalayas (Srinivasan et al. 2018).

In this study, NDVI and habitat heterogeneity explained most variance in overall bird richness. NDVI often explains variation in species richness among sites (reviewed by Pettorelli et al. 2011). For example, averaged NDVI had a positive linear effect on bird species richness and is generally considered as a key factor shaping bird communities in east Asia (Ding et al. 2006). St-Louis et al. (2009) also found that bird species richness was best predicted by the variation of NDVI (accounted for 82.3% of the variability). These positive relationships might attribute to higher resource abundance for birds (Gordo 2007), as high NDVI is likely to reflect not only the abundance of invertebrate food (e.g. insects and arthropods) for insectivores and omnivores, but also the quantity and quality of plant foods for granivores and omnivores (reviewed by Pettorelli et al. 2011), and/or higher habitat variability, as NDVI could be an indication of high variability in habitat types (St-Louis et al. 2009), and likely confirms the presence of a positive species richness–productivity relationship. The prominent association between habitat heterogeneity and overall bird richness could be simply explained by the habitat heterogeneity hypothesis – more complex habitats provide more niches and diverse ways for birds to exploit environmental resources and thus increase species diversity, especially if species are relatively specialized to different habitat types (Kerr et al. 2001, reviewed by Tews et al. 2004).

Richness-controlled functional diversity (indicated by SES.FD) was best explained by plant richness. This is because higher plant species likely reflects greater food resources, or supplies more complex vegetation structure (Kissling et al. 2008, Zhang et al. 2013, Wang et al. 2020). Thus, the diverse traits of species within communities lead to a higher value of FD. Temperature was the best predictor of MFD, probably because temperature is considered as a broad indicator of energy available to organisms and a strong determinant of nutrient dynamics in mountain food cycles (Laiolo et al. 2015). Taken together, our results reconfirmed that functional diversity and species relatedness were dependent on climatic and energetic variables. In this study, richness-controlled phylogenetic diversity (indicated by SES.PD) was best explained by habitat heterogeneity and NDVI, whereas MPD was also best explained by habitat heterogeneity. Surprisingly, both habitat heterogeneity and NDVI have negative effects on PD. Although the negative association between species' phylogenetic diversity and habitat heterogeneity were contradictory to our expectation, it might be partially explained by species with distinct evolutionary histories but with similar traits in high elevations being affected more by environmental filtering. These cold-adapted species might be the relict lineages that were widely distributed at the last glaciation in the high elevations of the Himalayas (Shooner et al. 2018,

Rana et al. 2019). However, this negative relationship is open to discussion and needs further studies to test the generality of our findings from other mountain systems.

Conclusions

In this study, we found taxonomic, functional and phylogenetic diversity consistently exhibited a hump-shaped pattern, peaking at similar elevation bands. Richness-controlled functional diversity decreased with increasing elevation, while richness-controlled phylogenetic diversity showed a Mid Valley pattern. The incongruencies among the dimensions of diversity in elevation gradients provide complementary insights into community structure and assembly. At low and high elevations, it is likely that abiotic filtering governed the assembly processes as indicated by the negative SES.MFD and narrower range of body mass. Further, our results confirm the predictive power of primary productivity (NDVI and/or habitat heterogeneity and/or plant richness as a proxy) and climate in explaining species richness, absolute functional and phylogenetic diversity variation along the elevational gradient likely provides evidence that productivity-biodiversity relationships (NDVI is positively correlated with species richness in this study) are applicable to functional and/or phylogenetic diversity.

Author contributions

Zhifeng Ding: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Huijian Hu**: Data curation (supporting); Funding acquisition (equal); Investigation (supporting); Project administration (lead); Supervision (lead); Writing – review and editing (supporting). **Marc Cadotte**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **Jianchao Liang**: Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (supporting). **Yiming Hu**: Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (supporting). **Xingfeng Si**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Methodology (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Data accessibility statement

Data used in this study are uploaded in Supporting Information.

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