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Patterns and drivers of avian taxonomic and phylogenetic beta diversity in China vary across geographical backgrounds and dispersal abilities

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ABSTRACT

Geographical background and dispersal ability may strongly influence assemblage dissimilarity; however, these aspects have generally been overlooked in previous large-scale beta diversity studies. Here, we examined whether the patterns and drivers of taxonomic beta diversity (TBD) and phylogenetic beta diversity (PBD) of breeding birds in China vary across (1) regions on both sides of the Hu Line, which demarcates China's topographical, climatic, economic, and social patterns, and (2) species with different dispersal ability. TBD and PBD were calculated and partitioned into turnover and nestedness components using a moving window approach. Variables representing climate, habitat heterogeneity, and habitat quality were employed to evaluate the effects of environmental filtering. Spatial distance was considered to assess the impact of dispersal limitation. Variance partitioning analysis was applied to assess the relative roles of these variables. In general, the values of TBD and PBD were high in mountainous areas and were largely determined by environmental filtering. However, different dominant environmental filters on either side of the Hu Line led to divergent beta diversity patterns. Specifically, climate-driven species turnover and habitat heterogeneity-related species nestedness dominated the regions east and west of the line, respectively. Additionally,

bird species with stronger dispersal ability were more susceptible to environmental filtering, resulting in more homogeneous assemblages. Our results indicated that regions with distinctive geographical backgrounds may present different ecological factors that lead to divergent assemblage dissimilarity patterns, and dispersal ability determines the response of assemblages to these ecological factors. Identifying a single universal explanation for the observed pattern without considering these aspects may lead to simplistic or incomplete conclusions. Consequently, a comprehensive understanding of large-scale beta diversity patterns and effective planning of conservation strategies necessitate the consideration of both geographical background and species dispersal ability.

Keywords: Beta diversity; Environmental filtering; Dispersal limitation; Hu Line; Species dispersal ability; Breeding birds

INTRODUCTION

Understanding how and why species composition varies

spatially is a core area of biogeographic research, given their complex relationships with community assembly (García-Girón et al., 2020; Jiao et al., 2021), biogeographical regionalization (He et al., 2017; Kreft & Jetz, 2010), and biodiversity conservation (Hill et al., 2021; Socolar et al., 2016). Beta diversity, a measure of assemblage dissimilarity among sites, provides a promising approach for addressing these questions. As beta diversity is divided into two distinct and antithetical components, turnover and nestedness, it can provide comprehensive information for assessing assemblage dissimilarity. Turnover signifies the substitution of certain species by others among sites, whereas nestedness denotes differences in species richness caused by species gain or loss among sites (Baselga, 2010, 2012). Generally, turnover can be attributed to factors related to climate or habitat, whereas nestedness can be attributed to factors related to disturbance, productivity, or physical barriers (Alahuhta et al., 2017; Sebastián-González et al., 2020). Therefore, exploring the patterns of beta diversity and its components can provide insights not only into spatial variations in species composition, but also into the mechanisms underlying these variations (Carvalho et al., 2012).

At a broad scale, the mechanisms responsible for beta diversity patterns originate from two ecological processes: environmental filtering and dispersal limitation (König et al., 2017; Qian et al., 2020a; Wang et al., 2012). Environmental filtering implies that environmental factors, such as climate, habitat quality, and habitat heterogeneity, determine species presence or absence; the greater the similarity in the environment between any two sites, the greater the similarity in species assemblages within them (Qian et al., 2020a; Wiescher et al., 2012). In contrast, dispersal limitation proposes that spatial factors, such as geographical distance, influence the probability of species exchange through dispersal; the larger the distance between any two sites, the lower the similarity in species assemblages within them (Nekola & White, 1999). However, as distance increases, species isolation intensifies and environmental dissimilarity increases. Therefore, the challenge in understanding the mechanisms driving beta diversity patterns is to evaluate the relative roles of spatial and environmental factors across different regions (Chase, 2014).

However, growing evidence has indicated that the relative importance of different ecological factors is dependent on both geography and taxonomy (Stuart et al., 2012; Zellweger et al., 2017). Regions with varied geographical characteristics may be influenced by different ecological factors, resulting in diverse beta diversity patterns. For instance, König et al. (2017) reported that vascular plant assemblages in island systems are more influenced by environmental factors than those in mainland systems, resulting in a lower turnover rate among islands globally. Analogously, as the heterogeneous geographical backgrounds of mainland systems are characterized by distinct configurations of environmental conditions, it is reasonable to expect variations in the contributions of both spatial and environmental factors, as well as in the contributions of specific environmental factors across geographical locations. Nevertheless, most large-scale studies on beta diversity have focused on identifying a single universal explanation for the observed patterns, without considering geographical variations in ecological factors (König et al., 2017). Consequently, this has led to simplistic and incomplete conclusions regarding conservation management.

In addition, species with different attributes may respond differently to ecological factors, potentially affecting beta diversity patterns. For example, as species with strong dispersal ability can reach an equilibrium with their environmental niches without being constrained by geographical barriers, they are assumed to form assemblages with homogeneous composition (Nekola & White, 1999). In contrast, species with weak dispersal ability are constrained to a small geographical range due to geographical isolation, and thus tend to form assemblages with heterogeneous composition (Wang et al., 2012). Therefore, comparing species with different dispersal abilities can improve our understanding of broad-scale beta diversity patterns. Although several studies have assessed the influence of dispersal ability on beta diversity, most have relied on comparisons between different taxa (e.g., Peixoto et al., 2017; Zellweger et al., 2017), which may be subjected to bias due to differences in other attributes, such as life history traits or reproductive modes. Therefore, to accurately determine the influence of dispersal ability on beta diversity, it is preferable to assess dispersal-based differences in species within the same taxon.

Additionally, recent developments in beta diversity have emphasized the necessity of incorporating phylogenetic information into the assessment of assemblage dissimilarity (i.e., phylogenetic beta diversity, PBD) (Graham & Fine, 2008). As a supplement to taxonomic beta diversity (TBD), PBD captures the contribution of the evolutionary history of species in assemblages (Jin et al., 2015). Importantly, by facilitating parallel spatial comparisons with TBD, PBD can elucidate the interactions between evolutionary and ecological factors that influence diversity patterns (Peixoto et al., 2017). For instance, PBD may be considerably lower than expected with respect to TBD in regions with strong human disturbance, as heavily modified habitats may favor traits expressed within certain phylogenetic lineages, resulting in phylogenetic clustering between sites (Liang et al., 2019; Weideman et al., 2020).

China has a rich biodiversity and a heterogeneous geography, providing a "natural laboratory" for exploring large-scale patterns of beta diversity. Notably, China harbors over 1 445 bird species, accounting for one-sixth of the total number of bird species worldwide (Zheng, 2017). However, while the geographical patterns of beta diversity have been thoroughly investigated for plants in China (Qian et al., 2020a, 2020b; Wang et al., 2012), similar studies on avian fauna are lacking. China is also characterized by a diverse geographical landscape and broad environmental gradient (Figure 1). Traditionally, the country can be divided into the eastern and western parts based on the Hu Line (also known as the Heihe-Tengchong Line), a geodemographic demarcation line proposed by the geographer Huan-Yong Hu (Hu, 1935). The eastern regions are characterized by warm and humid plains and accommodate over 90% of the national human population (Yao & Zhang, 2020; Yue et al., 2003). Contrastingly, the western regions are dominated by cold and arid plateaus and are inhabited by a relatively small fraction of the national human population. Additionally, an increasing number of studies have demonstrated that the Hu Line may account for differences not only in geographic and demographic patterns but also in economic, sociological, and ecological patterns in China. For instance, Zhang et al. (2022) reported that potential forestation lands in China are mainly located in the eastern
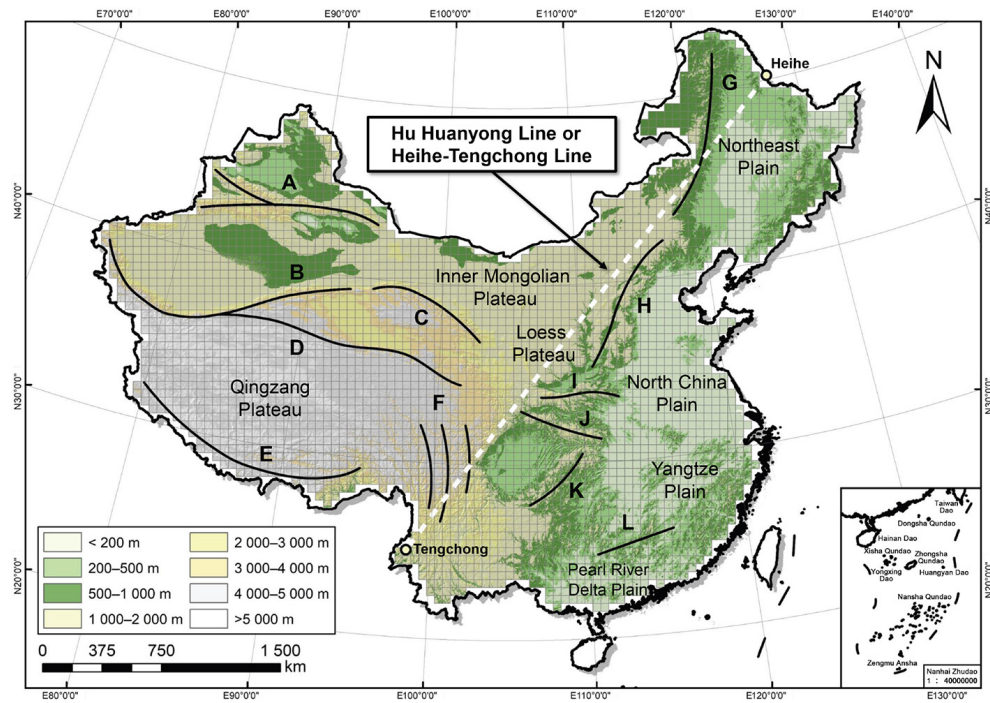
Figure 1 Topographic map of mainland China showing 50 km×50 km equal-area grid system and major mountain ranges
A: Mt. Tianshan; B: Mt. Aerjin; C: Mt. Qilian; D: Mt. Kunlun; E: Mt. Himalyas; F: Mt. Hengduan; G: Mt. Great Khingan; H: Mt. Taihang; I: Mt. Qinling; J: Mt. Daba; K: Mt. Wu; L: Mt. Nanling

regions under both present and future climate scenarios. Kong et al. (2022) found that ecological land changes (e.g., forests, grasslands, lakes) in China from 1995 to 2015 were primarily caused by clustered land degradation in the western regions, but by farmland activities in the eastern regions. Accordingly, it is reasonable to expect that species assemblages will show divergent patterns and mechanisms of compositional dissimilarity on either side of the Hu Line. Previous studies have suggested that assemblages will become more nested and phylogenetically homogeneous in anthropogenic landscapes, owing to increased extinction driven by intense human disturbance (Liang et al., 2019; Wayman et al., 2022; Weideman et al., 2020). However, whether this finding can be applied to the eastern region of the Hu Line, where human disturbance is more intense, remains insufficiently studied.

In the present study, we explored the spatial patterns and determinants of beta diversity in breeding avian assemblages across China, from both a taxonomic and phylogenetic perspective, considering the Hu Line demarcation. We aimed to assess variations in beta diversity and the relative importance of different ecological factors across (1) regions characterized by distinct geographical backgrounds and (2) species delineated by different dispersal abilities. We anticipate that avian assemblage dissimilarity will exhibit divergent patterns and determinants on either side of the Hu Line. Specifically, we predict that in regions east of the Hu Line, nestedness will contribute more substantially to overall dissimilarity, and the divergence between phylogenetic beta diversity and taxonomic beta diversity will be more pronounced. Moreover, we hypothesize that avian assemblages with weak dispersal ability will exhibit higher beta diversity and greater susceptibility to spatial influences, while those with strong dispersal ability will demonstrate lower beta diversity and greater susceptibility to environmental factors.

MATERIALS AND METHODS

Study area
Our study area covered mainland China (hereafter "China", N18°−53° and E73°−134°, Figure 1), covering an area of approximately 9 423 000 km^2. We converted the study area into an equal-area grid system at a spatial resolution of 50 km×50 km, considered an appropriate scale for beta diversity studies in China (e.g., He et al., 2017; Wang et al., 2012; Xu et al., 2014). To assess the robustness of our results in terms of spatial scales, the beta diversity analyses were repeated using 25 km×25 km, 100 km×100 km, and 200 km×200 km spatial resolutions, with the results found to be consistent with those obtained under the 50 km×50 km resolution (Supplementary Figure S1). Therefore, we only reported results obtained using 50 km×50 km resolution. Grids not entirely within the study area were excluded, with 3 486 grids thus retained for subsequent analyses.

Species distribution data
We accessed the previous avian checklists for China compiled by Zheng (2017), MacKinnon et al. (2003), and China Bird Report Checklist of Birds of China v.7.0. We also retrieved avian distribution data from the BirdLife Data Zone (BirdLife International, www.datazone.birdlife.org/). The distribution range of each bird species was categorized into resident, breeding season, non-breeding season, passage, and uncertain. We concentrated on breeding birds, as they exhibit more stable distributions than non-breeding birds, thus yielding more consistent responses to environmental factors. Using GIS software, we extracted the resident and breeding season ranges for each bird species and overlaid these onto the previously established grids covering China. Bird species whose resident and breeding season ranges intersected with any of these grids were considered as breeding birds in China. Conversely, birds whose resident and breeding season ranges

did not intersect with any grid were excluded from the study. Consequently, data for 1 146 species were obtained for subsequent analyses.

Phylogenetic reconstruction

We generated a phylogenetic tree for the 1 146 breeding birds using the "Phylogeny subsets" tool from a global bird phylogeny under the tree option "Hackett All Species: a set of 10 000 trees with 9 993 OTUs each" (Jetz et al., 2012). Subsequently, we sampled 5 000 trees from the pseudo-posterior distributions and calculated a maximum-clade credibility tree based on mean node heights using TreeAnnotator v.1.8.2 in the BEAST package (Drummond & Rambaut, 2007; Si et al., 2017). The resulting consensus tree was used for subsequent calculations of PBD (Supplementary Figure S2).

Environmental variables

Three groups of variables, i.e., climate, habitat heterogeneity, and habitat quality, were used to characterize environmental conditions for each grid (Supplementary Figure S3).

Climate is considered a strong environmental filter for assemblage dissimilarity due to differences in energy availability, physiological tolerance, and speciation (Wayman et al., 2022). For this study, climate variables included mean annual temperature, mean annual precipitation, potential evapotranspiration, mean annual temperature range, temperature seasonality, and precipitation seasonality, which were retrieved from the WorldClim database v.2.0 (www.worldclim.org) at a spatial resolution of 1 km×1 km. The value of each 50 km×50 km grid for all climate variables was calculated as the average of values of all 1 km×1 km grids within it.

Habitat heterogeneity is another important environmental driver of assemblage dissimilarity because the absence or presence of certain habitats may cause the loss or gain of their specialists (Calmé & Desrochers, 1999; Wang et al., 2010). Here, we used habitat diversity and elevational range to represent habitat heterogeneity for each grid. Habitat diversity was calculated by applying the Simpson's diversity index on the percentage values of different land cover categories for 2020 (obtained from the GlobalLand30 database; www.globallandcover.com) within each grid (Meynard et al., 2011). Elevational range was calculated as the difference between maximum and minimum elevations in each grid, thus representing topographic heterogeneity (Kerr & Packer, 1997). Elevation data were derived from the International Scientific & Technical Data Mirror Site, Computer Network Information Center, Chinese Academy of Sciences (www.gscloud.cn).

Both human disturbance and productivity can strongly impact assemblage dissimilarity (Sebastián-González et al., 2020). Here, we grouped human disturbance and productivity into a habitat quality variable group, with the assumption that habitat quality is higher under less human disturbance and/or higher productivity. We used the normalized difference vegetation index (NDVI) as a proxy of primary productivity (Ding et al., 2021; Pettorelli et al., 2011), with the associated data downloaded from the Resource and Environment Science and Data Center, Chinese Academy of Sciences (www.resdc.cn) at a spatial resolution of 1 km×1 km. Average NDVI values from July and October 2019 and January and April 2020 were used. The value for each 50 km×50 km grid was calculated as the average of values for all 1 km×1 km

grids within it. We used the area of anthropogenic land cover, including farmlands, residential areas, and construction lands, to represent human disturbance (Zhang et al., 2013). Anthropogenic land cover data were extracted from the GlobalLand30 database and calculated using zonal statistics in GIS for each grid.

Beta diversity calculations

Beta diversity was calculated and partitioned following Baselga (2010) and included three dissimilarity matrices: (1) Sørensen's dissimilarity index (β_{sor}), accounting for the total compositional dissimilarity between assemblages; (2) Simpson's dissimilarity index (β_{sim}), capturing only compositional dissimilarity due to species turnover; and (3) nestedness-resultant dissimilarity, representing the difference between β_{sor} and β_{sim} (β_{sne}). These matrices are defined as follows (Baselga, 2010):

$$\beta_{sor} = \frac{b+c}{2a+b+c} \tag{1}$$

$$\beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)} \tag{2}$$

$$\beta_{sne} = \beta_{sor} - \beta_{sim} = \frac{\max(b,c)-\min(b,c)}{2a+b+c} \times \frac{a}{a+\min(b,c)} \tag{3}$$

When these matrices are applied for TBD analysis, a represents the number of species shared by the two grids, b represents the number of species unique to one grid, and c represents the number of species unique to the other grid (Baselga, 2010). However, when applied for PBD analysis, shared and unique species are replaced with shared and unique branch lengths in the phylogenetic tree, respectively (Leprieur et al., 2012). Total beta diversity and its two components were referred to as $\beta_{tax.sor}$, $\beta_{tax.sim}$, and $\beta_{tax.sne}$ for TBD, and were referred to as $\beta_{phy.sor}$, $\beta_{phy.sim}$, and $\beta_{phy.sne}$ for PBD. The matrices were calculated using the "betapart" package in R v.4.0.5 (Baselga & Orme, 2012).

We applied a moving window approach (Peixoto et al., 2017; Pinto-Ledezma et al., 2018; Qian et al., 2020a; Wang et al., 2012) to estimate the geographical patterns of beta diversity. Specifically, for each focal grid, a moving window, i.e., circle with a specific radius, was generated with its center placed at the centroid of the focal grid (Supplementary Figure S4). The above beta diversity matrices were calculated between the focal grid and each surrounding grid within this moving window, with their average values then assigned to the focal grid. Three different moving window radii, i.e., 100 km, 200 km, and 300 km, were used, which produced consistent results. Thus, we only reported results obtained using the 200 km radius.

Statistical analyses

To assess the contribution of turnover and nestedness components to total beta diversity across China, we divided β_{sne} by β_{sor} to yield the β_{ratio} ($\beta_{tax.ratio}$ and $\beta_{phy.ratio}$ for TBD and PBD, respectively) for each grid. A β_{ratio} value greater than 0.5 indicates that total beta diversity is largely driven by nestedness, whereas a value less than 0.5 indicates that total beta diversity is mainly determined by turnover (Pinto-Ledezma et al., 2018).

To assess the spatial relationship between taxonomic and phylogenetic dissimilarity, we calculated the deviation of PBD from TBD (hereafter β_{dev}) for each grid using the formula:

$$\beta_{dev} = 1(\beta_{phy}/\beta_{tax}) \qquad (4)$$

where a greater value of β_{dev} indicates less variation in phylogenetic composition with respect to variations in taxonomic composition between sites, and vice versa (Peixoto et al., 2017; Qian et al., 2020a).

Furthermore, to assess the effects of different ecological factors on the beta diversity of breeding birds, we conducted variance partitioning analysis (VPA) for each grid based on a 200 km radius moving window. In the VPA, the beta diversity matrices between the focal grid and each surrounding grid within the window served as response variables, while spatial and environmental distances between the corresponding grid pair served as predictors. Spatial distance was calculated as the Euclidean distance of each pair of grid centers in a three-dimensional (i.e., latitude, longitude, and altitude) geographic space. Environmental distance was calculated as the Euclidean distance of each pair of grids in a multi-dimensional environmental space with environmental variables as coordinates, and was calculated for the three groups of environmental variables (climate, habitat heterogeneity, and habitat quality), respectively. The VPA results were averaged for all grids across China to yield a universal assessment of the effects of different ecological factors on the beta diversity of breeding birds. Additionally, to explore spatial variation in the relative importance of different ecological factors across China, the predictor with the highest adjusted R^2 value based on VPA for each grid was assigned as the primary determinant. VPA was conducted using the "vegan" package in R v.4.0.5 (Dixon, 2003).

To assess the differences in beta diversity and its determinants among regions with distinct geographical backgrounds, we divided grids into eastern and western regions along the Hu Line, resulting in 1 521 and 1 965 grids, respectively. Subsequently, we counted the proportion of grids dominated by turnover and nestedness components and the proportion of grids dominated by different ecological factors on either side of the line.

To estimate the influence of species dispersal ability on beta diversity and its determinants, we calculated a dispersal ratio for each species by dividing its mean wing length (mm) by the cube root of its mean mass (g), adopted as a proxy for dispersal ability in birds according to previous studies (Fischer & Lindenmayer, 2005; Woinarski, 1989; Zhang et al., 2020). The mass and wing length data were derived based on life history and ecological traits of Chinese birds in Wang et al. (2021). Subsequently, all species were sorted in ascending order based on their dispersal ratio values and trisected into weak, medium, and strong dispersal groups. We repeated beta diversity calculations and VPA for each dispersal group and performed Wilcoxon signed-rank tests to determine any significant differences in beta diversity and its determinants between different groups (Supplementary Figure S5). In addition, to compare the contributions of different dispersal groups to overall patterns, we used the simultaneous autoregressive model to correlate the beta diversity of each group with that of all species, while accounting for spatial autocorrelation (Wang et al., 2012). The Wilcoxon signed-rank test and simultaneous autoregressive model were conducted using the "stats" and "spatialreg" packages in R v.4.0.5.

RESULTS

The spatial patterns of TBD and PBD for breeding birds were highly consistent across China (Figure 2). Areas with high total TBD and PBD, along with their respective turnover and nestedness components, were primarily observed in the mountainous regions, including the Tianshan, Kunlun, Aerjin, Himalaya, Great Khingan, Taihang, and Hengduan mountains (Figure 2).

Contrary to expectations, the turnover component exhibited a much higher contribution than the nestedness component in the eastern regions of China, with $\beta_{tax.ratio}<0.5$ and $\beta_{phy.ratio}<0.5$ grids accounting for 89.2% and 83.8% of the total, respectively. Conversely, nestedness exhibited a higher contribution in the western regions, with $\beta_{tax.ratio}>0.5$ and $\beta_{phy.ratio}>0.5$ grids accounting for 60.8% and 64.2% of the total, respectively (Figure 3; Supplementary Figure S6). Furthermore, across both the eastern and western regions, PBD was markedly lower than the values predicted by TBD, as evidenced by β_{dev} exceeding 0.3 (Figure 2). Similar trends were observed for their turnover and nestedness components.

The VPA results revealed that for both TBD and PBD and their respective turnover and nestedness components, environmental distance alone explained the variations more clearly than spatial distance alone, with independent explained variation range of 0.29−0.37 and 0.03−0.05 and a shared explained variation range of 0.08−0.18 for environmental distance and spatial distance, respectively, (Supplementary Figure S7). In terms of environmental distance, climate and habitat heterogeneity were the predominant explanatory factors in the eastern (Figure 4A) and western (Figure 4B) regions of China, respectively. Comparatively, habitat quality dominated in only a few grids across China. Notably, grids with higher spatial distance explanatory power were mostly located in mountainous regions, such as the Kunlun and Taihang mountains. These trends were observed for both TBD and PBD.

As predicted, species with weaker dispersal abilities exhibited significantly higher levels of TBD, PBD, and their respective components ($P<0.01$), whereas those with stronger dispersal abilities showed significantly lower levels (Figure 5). Moreover, the independent explanatory power of spatial distance increased significantly with decreasing species dispersal ability, while the independent explanatory power of environmental distance and shared explanatory power of spatial and environmental distances decreased significantly with decreasing species dispersal ability (Figure 6). Furthermore, TBD, PBD, and their respective components, when considered across all species, demonstrated the strongest correlations with species possessing strong dispersal capabilities and the weakest correlations with species exhibiting weak dispersal abilities (Supplementary Table S1).

DISCUSSION

General patterns of beta diversity for breeding bird assemblages in China

Elevated TBD and PBD values were identified in mountainous areas, consistent with global trends observed across a wide range of taxa (Melo et al., 2009; Peixoto et al., 2017; Wang et al., 2012). Mountainous areas are typically characterized by strong geographic barriers and environmental gradients, which likely contribute to increased assemblage dissimilarity compared to plains (Graham et al., 2009). Furthermore, China is partitioned into various biogeographical regions by broad
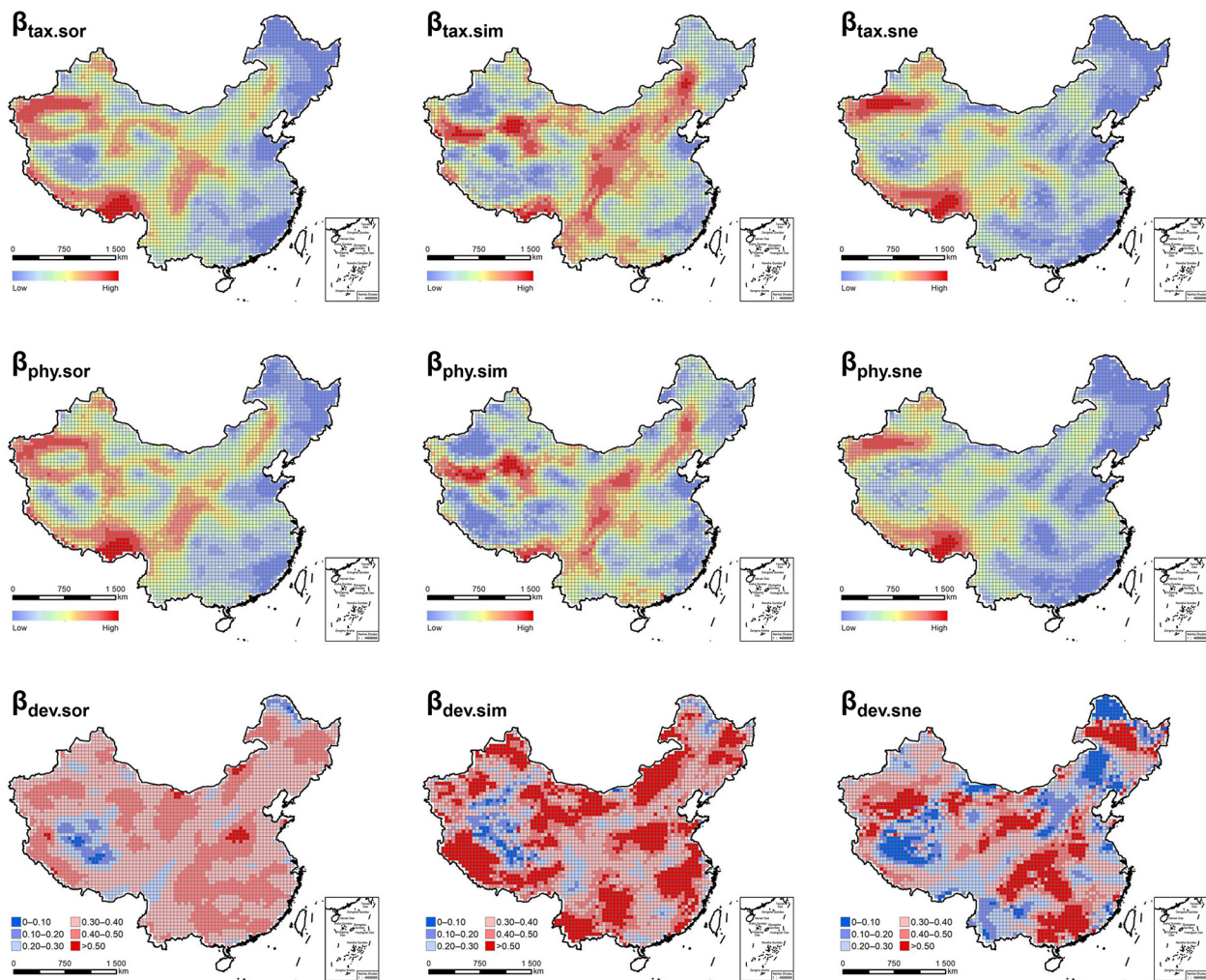
Figure 2 Patterns of taxonomic beta diversity (β$_{tax}$), phylogenetic beta diversity (β$_{phy}$), and deviations of β$_{phy}$ from β$_{tax}$ (β$_{dev}$, calculated as β$_{dev}$=1−(β$_{phy}$/β$_{tax}$) for breeding birds in mainland China
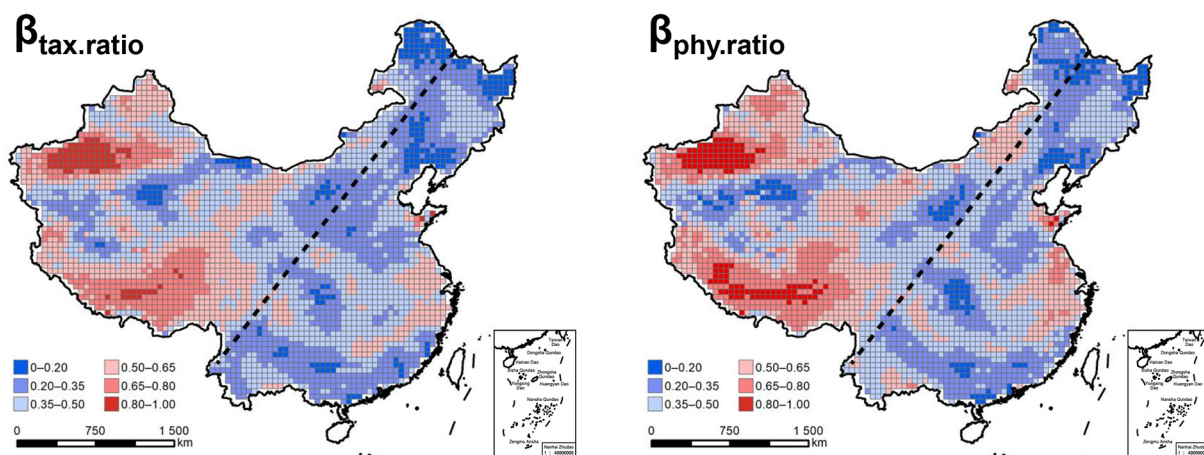

Figure 3 Contribution patterns of turnover and nestedness components to total beta diversity of taxonomic and phylogenetic beta diversity (β$_{tax.ratio}$ and β$_{phy.ratio}$) for breeding birds in mainland China
β$_{ratio}$ was determined as the ratio of β$_{sne}$ to β$_{sor}$. Black dashed line represents Hu Line.

mountain ranges (He et al., 2017). These mountain ranges act as ecotones between disparate faunal habitats, thereby facilitating in intense biotic turnover (Lomolino, 2001). For instance, high TBD and PBD turnover rates were observed in the Great Khingan, Taihang, Hengduan mountain ranges, which generally run along the Hu Line. Moreover, certain mountain ranges, such as Himalaya and Tianshan mountains in western China, host multiple endemic species, and thus serve as regional or even global biodiversity hotspots (Wang et al., 2016). Such differences in species richness between mountains and their surrounding habitats may drive the dominance of the nestedness component. These findings
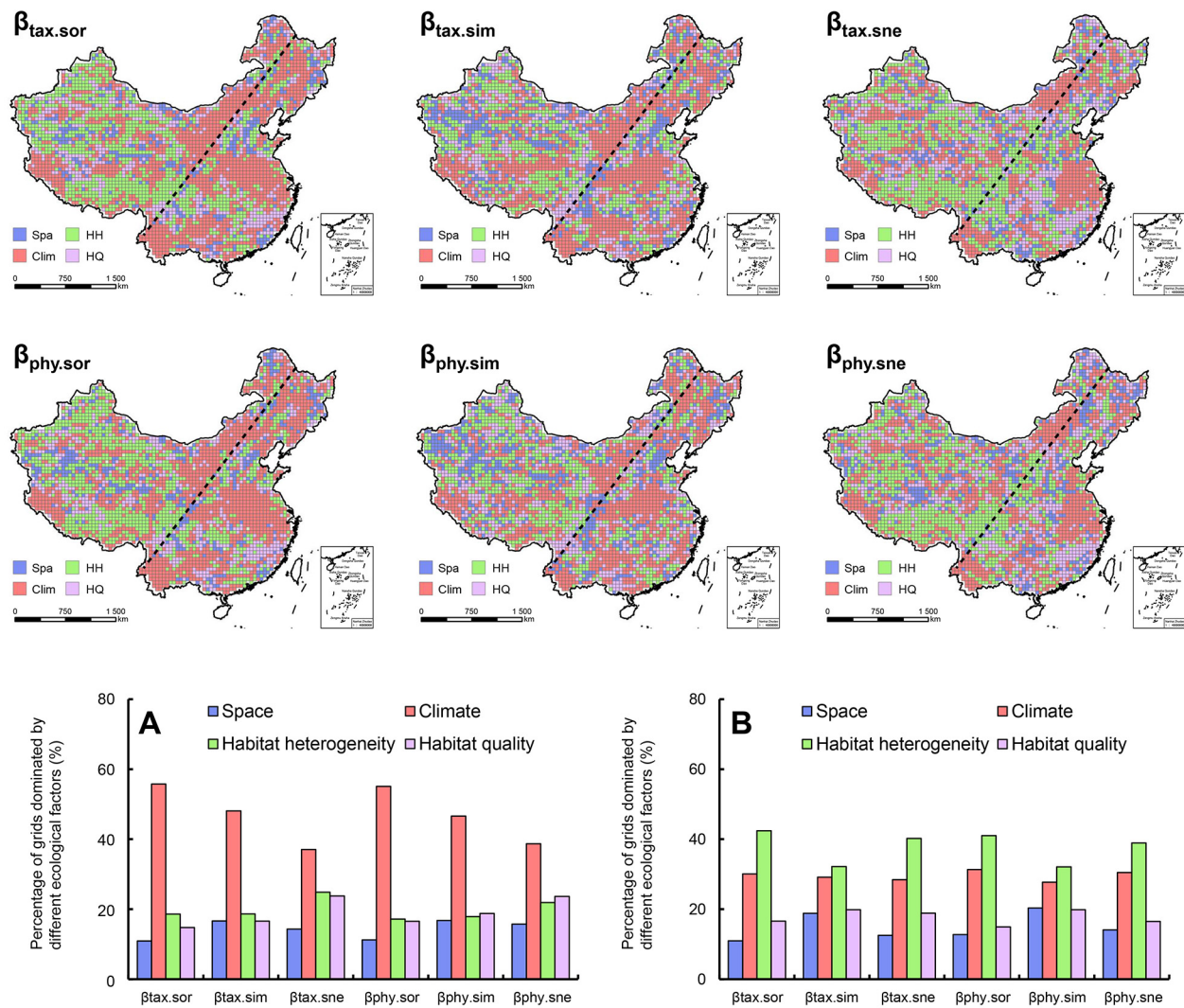
Figure 4 Dominant explanatory factor patterns for breeding birds for taxonomic and phylogenetic beta diversity ($\beta_{tax.sor}$ and $\beta_{phy.sor}$, respectively) and their respective turnover ($\beta_{tax.sim}$ and $\beta_{phy.sim}$) and nestedness ($\beta_{tax.sne}$ and $\beta_{phy.sne}$) components, and proportion of grids dominated by different ecological factors in eastern (a) and western (b) regions of mainland China

Spa: Spatial distance; Clim: Climate distance; HH: Habitat heterogeneity distance; HQ: Habitat quality distance. The black dashed line represents the Hu Line.

suggest that mountain ranges are hotspots not only for alpha diversity but also for beta diversity, thus warranting urgent consideration in the planning and design of large-scale conservation initiatives.

Although the patterns of TBD and PBD were highly consistent, the latter was considerably lower than the former for most regions, irrespective of their geographical location in the eastern or western regions on either side of the Hu Line. These findings suggest that compositional variations in breeding bird assemblages may be more likely to occur in phylogenetically proximate species rather than distant ones. Considering that both TBD and PBD exhibited strong associations with environmental distances, our results support the notion that environmental conditions, whether related to climate or habitat heterogeneity, may selectively favor species with certain niches, leading to phylogenetically homogeneous assemblages according to the phylogenetic niche conservatism hypothesis (Jin et al., 2015).

Contrasting origins and drivers of beta diversity on either side of the Hu Line
Environmental distance predominantly accounted for the

patterns in both TBD and PBD, as well as their respective turnover and nestedness components, signifying the crucial role of environmental filtering in shaping breeding bird assemblages in China. However, when geographical variations in ecological factors were considered, different dominant environmental filters and beta diversity components were observed on either side of the Hu Line. In the eastern regions, climate and turnover emerged as the primary drivers and components for both TBD and PBD, suggesting that compositional variations in breeding bird assemblages in these regions are largely driven by species turnover along climatic gradients. This observation contradicts prior assumptions that regions experiencing high levels of human disturbance would display lower assemblage turnover and higher nestedness (Wayman et al., 2022). Conversely, in the western regions, where anthropogenic influence is comparatively weaker, habitat heterogeneity and nestedness became the principal determinants and components of beta diversity, although climate and turnover still showed significant influence. These findings imply that in these regions, sites with fewer habitat types contain only a subset of species present in
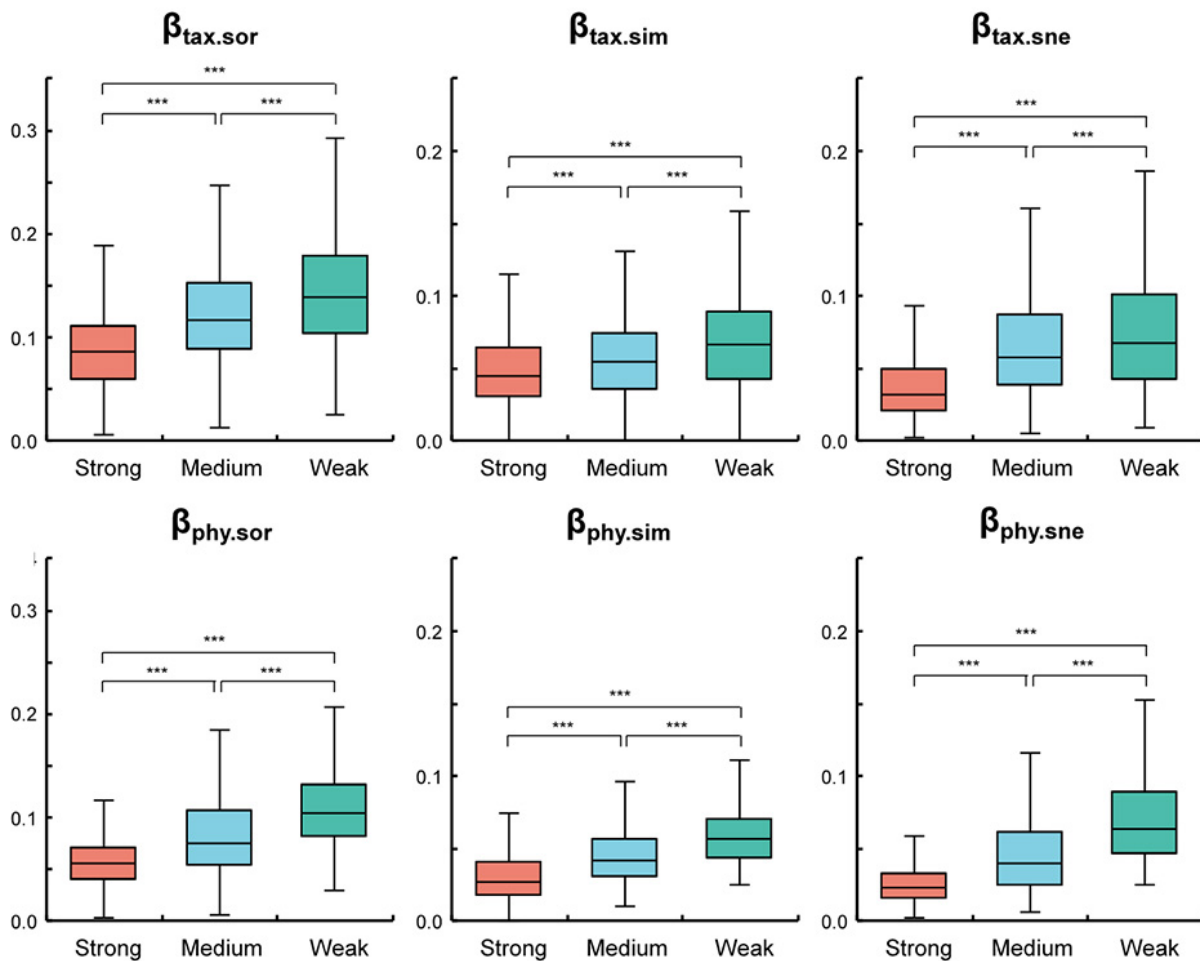
Figure 5 Taxonomic and phylogenetic beta diversity and their components for species with strong, medium, and weak dispersal ability
Significant differences were determined using Wilcoxon signed-rank tests. ***: *P*<0.001.

sites with greater habitat diversity, leading to a pattern of nestedness in species community composition, as posited by the habitat nestedness hypothesis (Calmé & Desrochers, 1999; Honnay et al., 1999). The harsh environmental conditions present in the western region likely limits the range of available habitat types, thereby promoting a nestedness pattern of species distribution. Moreover, the western region bird assemblages were characterized by species with robust dispersal capabilities (Supplementary Figure S8), which are more adept at adapting to variations in habitat, thereby facilitating nestedness (Cook & Quinn, 1995; de Siqueira Neves et al., 2021).

Our findings broadly illustrated that regions with different geographical backgrounds are subject to different ecological factors, which may lead to divergent patterns of assemblage dissimilarity. Thus, emphasizing a single explanatory factor for the observed patterns (such as climate, in our case) could result in the oversight of other crucial ecological determinants that are closely associated with certain regional properties (such as habitat heterogeneity, in our case). Such bias may not only hinder a comprehensive understanding of the mechanisms underlying large-scale community assemblages, but also misdirect the development of appropriate conservation and management strategies, given that different ecological processes may have divergent management and conservation implications (Angeler, 2013). For instance, our results suggest that prioritizing sites with high habitat

heterogeneity could ensure biodiversity conservation in western China, where nestedness is the dominant pattern. Conversely, in eastern regions where turnover is predominant, focusing on multiple sites with diverse climatic environments may be more important, albeit administratively and financially challenging (Socolar et al., 2016).

Effects of species dispersal ability
In addition to geographical background, species dispersal ability also played a profound role in shaping the beta diversity of breeding bird assemblages in China. Generally, species with weak dispersal ability exhibited higher beta diversity, consistent with the findings of Wang et al. (2012), who observed higher beta diversity for woody plants with restricted range sizes within China. Species with weak dispersal ability tend to have narrower geographical ranges compared to those with strong dispersal ability (Nekola & White, 1999; Stevens, 1989). Consequently, they may be less likely to occur uniformly across different assemblages, leading to more dissimilar species composition among assemblages. Nevertheless, our analysis revealed that overall beta diversity (all species combined) was largely driven by species with strong dispersal ability. These results are congruent with previous observations on global turnover patterns in bird assemblages (Buckley & Jetz, 2008) and analogous with the previous finding that species richness patterns are mainly determined by species with wider ranges (Kreft et al. 2006; Lennon et al. 2004). Such evidence implies that loss of
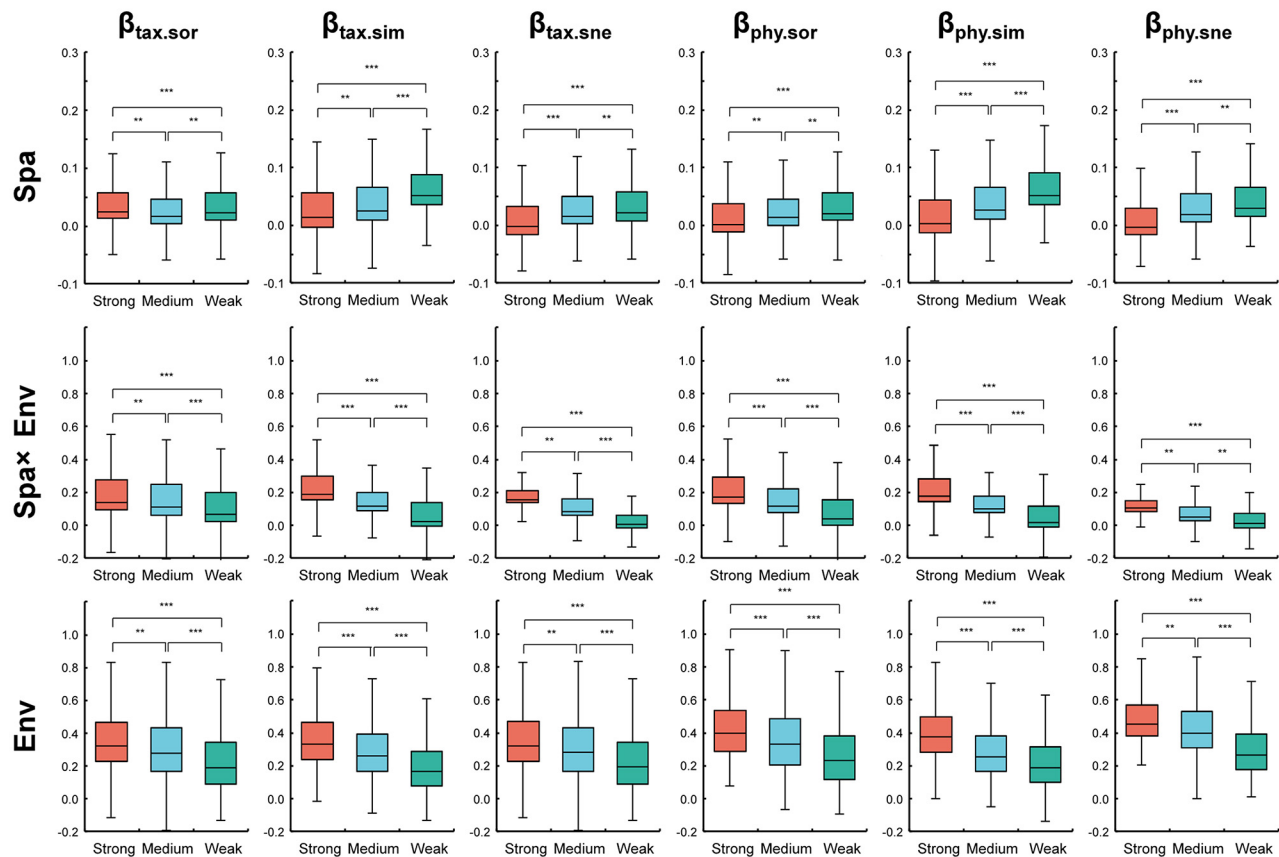
Figure 6 Independent and shared explanatory powers of spatial and environmental distances for taxonomic and phylogenetic beta diversity of species with strong, medium, and weak dispersal ability

Significant differences were determined using Wilcoxon signed-rank tests. [**]: $P<0.01$; [***]: $P<0.001$.

species with strong dispersal ability could have profound impact on both alpha and beta diversity, and they should be considered equally important for biodiversity conservation as those with weak dispersal ability, although the latter generally receive greater attention due to their rarity.

The influence of dispersal ability on beta diversity has frequently been attributed to the differential responses of species to different ecological factors (Linares-Palomino & Kessler, 2009; Qian, 2009). It is widely posited that species with strong dispersal ability can access and inhabit most, if not all, environmentally suitable areas, thereby forming more homogeneous assemblages. In contrast, species with weak dispersal ability are restricted to fewer suitable sites, thereby forming more heterogeneous assemblages (Nekola & White, 1999; Wang et al., 2012). In the present study, we found that spatial factors held greater importance for bird species with weaker dispersal abilities. Conversely, both environmental factors alone and the effects of spatial and environmental factors combined were significantly more important for bird species with strong dispersal ability. Given that environmental variables at large scales often exhibit spatial structure, these combined effects are typically considered indirect environmental influences (Mazel et al., 2017; Qian et al., 2020a). Therefore, these results provide strong evidence for the aforementioned hypotheses. Conservation strategies targeting species with strong dispersal ability should focus on maintaining the suitability of available habitats through various measures, such as closely monitoring the impacts of global change. In contrast, conservation efforts targeting species with weak dispersal ability should prioritize the availability of

suitable habitats by undertaking measures such as the establishment of ecological corridors.

CONCLUSIONS

Although geographical background and species attributes are important for understanding the mechanisms driving beta diversity patterns, they are frequently neglected in large-scale beta diversity studies. Here, we explored the spatial patterns of beta diversity and its determinants across different geographical regions in mainland China, focusing on breeding birds with different dispersal capabilities. Different components and drivers of beta diversity were prevalent on the two sides of the Hu Line. Moreover, species exhibiting stronger dispersal ability were more susceptible to environmental factors and formed more homogeneous assemblages. These findings underscore the importance of considering both geographical background variation and species dispersal abilities to achieve a comprehensive understanding of the mechanisms underlying large-scale beta diversity. Future research should rigorously examine the potential interactive effects of these factors to provide a suitable reference for implementing conservation strategies tailored to specific local conditions.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHOR'S CONTRIBUTION

J.C.L. conceived and designed the study with the help of Z.F.D.; J.C.L., G.W.L., X.N.N., and W.B.H. collected and compiled the data; J.C.L., Y.M.H., and Z.X.Z. analyzed the data; J.C.L. led the writing, which Z.F.D. revised; H.J.H., X.F.S., and C.L.L reviewed the manuscript. All authors read and approved the final version of the manuscript.

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