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RESEARCH ARTICLE

A landscape-level analysis of bird taxonomic, functional and phylogenetic β-diversity in habitat island systems

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Abstract

Aim: How β-diversity patterns are shaped by landscape-level processes remains unclear across habitat island systems. Here we assessed landscape-level bird β-diversity in habitat island systems and aimed to (1) evaluate the relative contribution of turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) components to multisite β-diversity (β_{SOR}) from taxonomic, functional and phylogenetic dimensions; (2) examine the influence of climate factors and system characteristics in shaping landscape-level patterns of β-diversity measures; and (3) study how β-diversity patterns of bird communities vary with the spatial extents of island systems.

Location: Global.

Taxon: Birds.

Methods: We compiled bird data in 22 habitat island systems from literature and classified these island systems into small and large spatial scales. We partitioned β_{SOR} into β_{SIM} and β_{SNE} from three dimensions for each system and calculated standardized functional and phylogenetic β-diversity measures. We assessed the effects of climate factors and system characteristics on observed and standardized β-diversity measures by multiple linear models for both small and large systems.

Results: We found that the dominant role of β_{SIM} to β_{SOR} in habitat island systems was pervasive. However, the best explanatory variables were not consistent across systems, which depended on the β-diversity components, diversity dimensions and spatial extent of habitat island systems. In general, climate factors acted as the main drivers of bird communities across small and large systems, whereas system characteristics played minor roles.

Main conclusions: Spatial turnover dominated overall bird β-diversity in most habitat island systems. Our results imply the roles of niche-based assembly processes through the interplay among differential functional traits and phylogenetic distances of species, climate factors and system characteristics as well as spatial extent in driving bird communities across multiple habitat island systems at a landscape level. This study offers a better understanding of the processes underlying macroecological patterns of isolated biological communities across habitat island systems.

KEYWORDS
bird, climate, fragmented landscape, niche-based processes, phylogeny, traits, turnover, β-diversity

1 | INTRODUCTION

Island biogeography theory (MacArthur & Wilson, 1967) has inspired fundamental theories and enriched the research of biodiversity maintenance in fragmented landscapes (Haddad et al., 2015). Many spatial attributes (e.g. fragment area and isolation) have been widely associated with biodiversity patterns (Ewers & Didham, 2006). However, most biodiversity studies in fragmented habitats have been restricted to patch-level analyses, which considered individual fragments as the study unit. Landscape-level characteristics (e.g. habitat island characteristics and climate factors) also had important roles in shaping biodiversity distributions in fragmented landscapes (Ewers & Didham, 2006). For example, the importance of landscape-level characteristics (e.g. area scale (AS) and elevational range (ER)) in determining biodiversity patterns has been reported for multiple taxa (e.g. plants, herptiles, mammals and birds) in insular systems (Matthews et al., 2016; Wang et al., 2018). Furthermore, climatic differences creating environmental heterogeneity could act as filters that are associated with biodiversity pattern change along latitudinal environmental gradients (Batista et al., 2021). Thus, it could be challenging to infer landscape-level ecological processes underlying biodiversity patterns from patch-level analyses. Nevertheless, it remains unclear how landscape-level factors, such as climate factors and habitat island characteristics, influence biodiversity patterns across habitat island systems.

β-diversity describes the variation in community composition among sites in response to environmental variation (Whittaker, 1960) and has been used to investigate the rules of community assembly (García-Navas et al., 2020). However, taxonomic β-diversity does not consider the differences in species' functional traits and evolutionary history (Leprieur et al., 2012; Villéger et al., 2013). Functional and phylogenetic β-diversity, which estimate the functional and phylogenetic dissimilarity among communities, can provide additional perspectives by linking ecological and evolutionary processes to biodiversity patterns (Cadotte et al., 2019; Graham et al., 2009). For example, hummingbird assemblages in the northern Andes showed high taxonomic but low functional and phylogenetic β-diversity, indicating geographical barriers played important roles in isolating lineages in similar environments (Weinstein et al., 2014). Moreover, if ecological niches are phylogenetically conserved, closely related species tend to be more similar to each other in their traits than distantly related species, so that phylogenetic distances among species can be used as a proxy for the interspecific dissimilarity at multiple niche aspects (Graham et al., 2009; Swenson, 2013). However, the functional and phylogenetic patterns do not always provide congruent inferences when the selected functional traits do not have a strong phylogenetic signal or conserved traits that cannot be fully accounted for with only a phylogeny (Cadotte et al., 2019; Du et al., 2021; Sobral & Cianciaruso, 2016). Thus, integrated consideration of taxonomic, functional and phylogenetic dimensions of communities would help us better understand the mechanisms in shaping community composition at the landscape level (Sobral & Cianciaruso, 2016; Weinstein et al., 2014).

Recent methodological advances of β-diversity partitioning at multidimensions provide opportunities to unveil the underlying mechanisms of community assembly via two antithetic components (i.e. spatial turnover and nestedness-resultant components), which can reflect different ecological processes (Baselga, 2010; Leprieur et al., 2012; Villéger et al., 2013). Specifically, the spatial turnover accounts for the substitution of species, functional traits or phylogenetic lineages, whereas the nestedness-resultant component represents the degree to which species-poor assemblages are the subsets of species-rich assemblages resulting from ordered extinction, colonization or nested habitats (Baselga, 2010; Leprieur et al., 2012; Ulrich & Gotelli, 2007). This β-diversity partitioning framework allows us to make comparisons of multidimensional β-diversity and offers a unique opportunity to reveal underlying processes structuring communities (Branco et al., 2020). However, this multidimensional β-diversity and its components have been rarely investigated simultaneously across multiple habitat island systems along spatial and environmental gradients.

Functional and phylogenetic β-diversity and their components are positively correlated with their taxonomic equivalents (Carvalho et al., 2019; Swenson, 2014). Therefore, it is complementary to compare functional and phylogenetic β-diversity measures with null expectations. Moreover, the magnitude of deviations between observed values and those expected by chance (i.e. random/neutral sampling) can reflect the strength of the processes acting upon communities (Montaño-Centellas et al., 2019). For example, communities with species that are more similar in functional traits to each other than expected by chance (functional convergence) can be attributed to environmental filtering (Carvalho et al., 2019; Cavender-Bares et al., 2009). On the other hand, communities composed of species that are more functionally dissimilar to each other than expected by chance (functional divergence) can be interpreted as high habitat heterogeneity among habitat fragments (Carvalho et al., 2019; Presley et al., 2018). Furthermore, if ecological niche differences are phylogenetically conserved, communities tend to be phylogenetically convergent when environmental filtering dominates community assembly (Cavender-Bares et al., 2009; Webb et al., 2002), whereas phylogenetical divergence will be resulted from high habitat heterogeneity. A strong relationship between the deviations of functional and phylogenetic β-diversity measures from null expectations and climate factors and system characteristics can indicate the important landscape-level factors driving community assembly processes (Leprieur et al., 2012; Siefert et al., 2013).

Dispersal limitation or environmental filtering may increase with not only increasing dispersal distances or environmental gradients among sites but also spatial extent surveyed (Heino et al., 2015; Soininen et al., 2018). A recent meta-analysis has evidenced the positive effects of spatial extent on pairwise β-diversity and turnover component (Soininen et al., 2018). Therefore, considering spatial extent effects is essential for the assessment of climate factors and system characteristics on β-diversity measures across multiple habitat island systems.

Habitat island systems offer an ideal model to understand the causality of processes underlying biodiversity patterns in expanding anthropogenic remnant forests. In addition, birds offer an excellent biological group with diverse species and broad distributions, diverse morphological and ecological traits, and available data of species-level traits and phylogenies (Jarzyna et al., 2021). Here, we provided a comprehensive evaluation of variation in taxonomic, functional and phylogenetic multisite β-diversity of resident birds in 22 habitat island systems along with two kinds of landscape-level characteristics (i.e. climate factors and system characteristics). Because the measurement of β-diversity is affected by the scale of spatial extent (Antão et al., 2019; Heino et al., 2015), we separated habitat island systems into small and large spatial scales. Specifically, we aimed to (1) test whether the relative contribution of turnover and nestedness-resultant components to multidimensional β-diversity exhibit difference between small and large systems, (2) assess the deviations of functional and phylogenetic β-diversity measures that controlled the effects of taxonomic equivalents for habitat island systems and (3) quantify the effects of climate factors and system characteristics in driving multidimensional β-diversity measures, as well as deviations of functional and phylogenetic β-diversity measures from null expectations across small and large systems respectively.

2 | MATERIALS AND METHODS

2.1 | Dataset compilation

We systematically reviewed the literature to compile bird community datasets in fragmented habitat island systems using Web of Science and Google Scholar between January 2018 and December 2019. We searched potential sources using the keyword combination: 'bird' AND 'species' AND 'island' OR 'mountaintop' OR 'hilltop' OR 'patch' OR 'fragment'. Cross-referenced papers derived from the reference lists of sourced papers were also included. Each potential dataset was included if it met the following criteria:

1. Fragments in each habitat island system conformed to discrete habitat islands, that is, natural habitat surrounded by a contrasting matrix (Matthews et al., 2014; Watson, 2002). We also included a few forest fragment systems within a reservoir.
2. Each source provided a complete species list on each fragment.
3. The area and location of each fragment could be obtained from the source.
4. The altitude of each fragment could be obtained from the source or could be derived from satellite images (e.g. Google Earth).
5. Each dataset contained at least six fragments.
6. The description of each dataset was sufficient for evaluating data adequacy.
7. We retained the recently updated version of the dataset for each habitat island system if multiple versions were available.

We also screened the datasets from fragmentation studies such as Matthews et al. (2014, 2015) and Wang, Chen, and Millien (2018). In this step, more than 200 published journal articles were screened. We retained 22 systems that entered our analyses, including eight forest fragments, five reservoirs or lake islands, four mountaintops, three urban parks, one natural reserve and one grassland fragment (Figure 1; the list of data sources is presented in Appendix A; Table S1.2). Each system was classified into two groups based on the spatial extent, that is, small (spatial extent <100 km) and large (spatial extent >200 km) systems (see more details in Table S1.2 in Appendix S2).

We rechecked the species list for each system and discarded all aquatic, nocturnal and aerial bird species. In addition, we also excluded the non-native bird species (i.e. introduced, migratory and uncertain origin species) of each system based on the distribution information of each bird from Birds of the World (BOW, birdsoftheworld.org) and BirdLife International (birdlife.org). Some mismatched names were corrected by checking their synonyms following the species list from the BOW. We also excluded records that were not identified to species (e.g. species identities with 'sp'). Finally, we included 1250 species from 128 families and 24 orders (Table S2.2).

2.2 | Functional traits and phylogenies

Life-history and ecological traits associated with important aspects of the avian niches (Jarzyna et al., 2021; Pearson et al., 2014) were compiled from the BOW, Jetz et al. (2008), Myhrvold et al. (2015) and Wilman et al. (2014). We included (a) body mass, (b) clutch size, (c) generation length, (d) diet, (e) foraging strata and (f) nest location (Table S3.2). We also assessed the degree of a phylogenetic signal of each trait for each system by means of Pagel's λ using the functions of the R package 'phytools' (Revell, 2012). The details of each trait and phylogenetic signal detection are presented in Tables S3.2 and S4.2. While body mass, clutch size, generation length and diet were phylogenetically conserved, foraging strata and nest location were the two most labile traits showing no phylogenetic signal in 8 (36.36%) and 10 (45.45%) of the habitat island systems respectively (Table S4.2).

We calculated the dendrogram-based functional diversity (FD; Petchey & Gaston, 2006) for each community based on our compilation of life-history and ecological traits. Following existing practice (Jarzyna et al., 2021), we calculated a dissimilarity matrix using Gower's distance coefficient (Gower & Legendre, 1986) of the multivariate traits of all 1250 species using the function *gowdis* in the R package 'FD' (Laliberté & Legendre, 2010). Then, a functional dendrogram was built using the unweighted pair group method with arithmetic mean (UPGMA) clustering (Jarzyna et al., 2021; Mouchet et al., 2008) (Figure S1.2). For the functional dendrogram of each system, we pruned the sub-dendrograms of species within each system (i.e. functional sub-dendrogram) and then used the pruned functional sub-dendrogram to estimate the functional β-diversity. Body mass and generation length were ln-transformed before analysis.

To calculate phylogenetic diversity, we constructed a phylogenetic tree with the 1250 species, using the 'Phylogeny subsets' tool from a global bird phylogeny under the option of '*Hackett All*

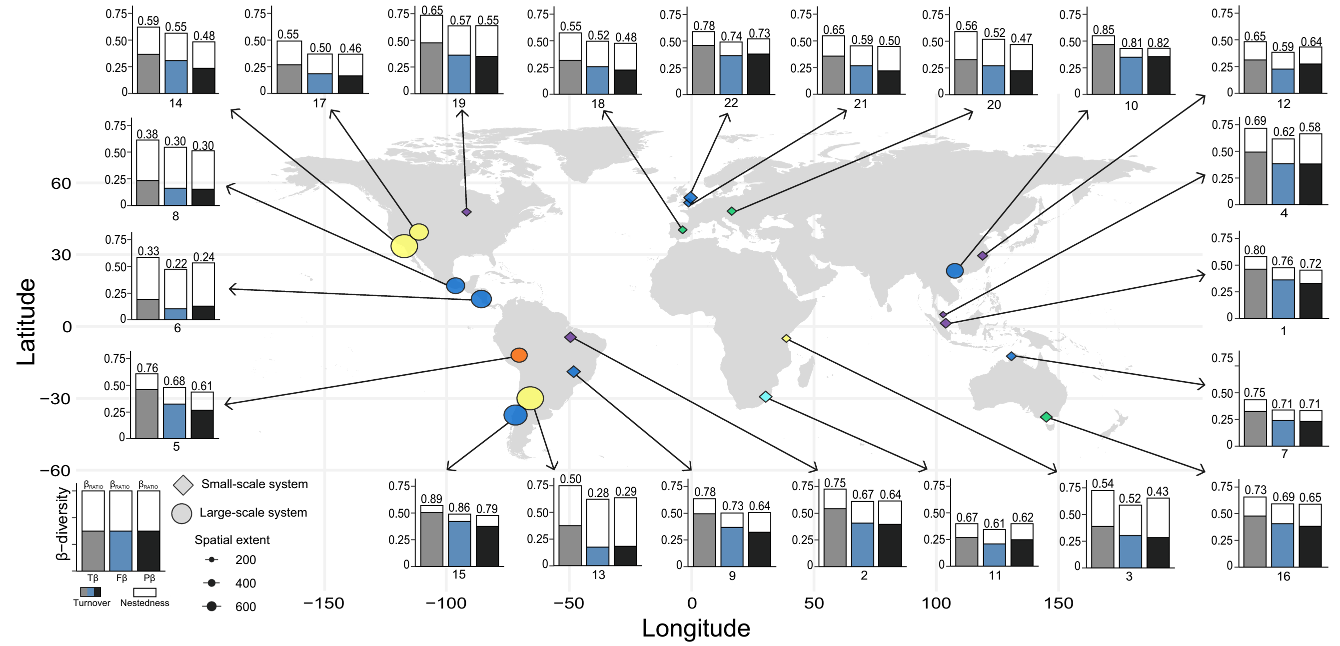

FIGURE 1 Location of the 22 habitat island systems (54° N to 38° S). The point size represents the spatial extent of the habitat island systems. Lozenge represents small habitat island systems (spatial extent <100 km); cycle represents large habitat island systems (spatial extent >200 km); spatial extent, the geographical distance (km) between the localities situated farthest from each other within the habitat island systems. Different colours show different types of habitat island system: dark blue, forest fragments; purple, reservoir and lake islands; yellow, mountaintop islands; green, urban parks; orange, natural reserves; light blue, grassland fragments. For each histogram, left bar represents taxonomic β-diversity (Tβ); middle bar represents functional β-diversity (Fβ); and right bar represents phylogenetic β-diversity (Pβ). The number on each bar represents β_{RATIO}, the relative contribution of spatial turnover to β-diversity (calculated as $\beta_{RATIO} = \beta_{SIM} / \beta_{SOR}$). For definitions of 1–22, see Appendix A, and more details for each habitat island system are presented in Table S1.2 in Appendix S2

Species: a set of 10000 trees with 9993 OUTs each' (Jetz et al., 2014). We sampled 5000 trees from the pseudo-posterior distributions and calculated a maximum clade credibility tree using mean node heights in the software TreeAnnotator (version 2.6.3) of the 'BEAST 2' package (Bouckaert et al., 2014). We used this resulting consensus tree for all subsequent phylogenetic analyses (Figure S2.2). The same procedure applied to the functional dendrogram for each system was also employed in the phylogenetic tree.

2.3 | Taxonomic, functional and phylogenetic β-diversity measures

We calculated observed multisite taxonomic, functional and phylogenetic overall β-diversity for each system because multisite metrics may be more reliable than average pairwise metrics for estimating overall community heterogeneity within a pool (Baselga, 2013). The multisite taxonomic overall dissimilarity was calculated based on presence–absence community data for each system using the Sørensen dissimilarity index (Sørensen, 1948) and its functional and phylogenetic equivalents. Following Baselga (2010, 2012), overall dissimilarity (β_{SOR}) was partitioned into spatial turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) components. As the multisite measures are strongly affected by the number of sites (Baselga, 2010), we computed the averaged β-values using a resampling procedure for 20 systems, taking 1000 random samples of six inventories (the minimum number of fragments, in the datasets 4 and 9). We calculated β-diversity measures using the R package 'betapart' (Baselga & Orme, 2012). We further calculated the ratio between β_{SIM} and β_{SOR} ($\beta_{RATIO} = \beta_{SIM}/\beta_{SOR}$) to evaluate the relative contribution of the turnover component to β-diversity from taxonomic, functional and phylogenetic dimensions (i.e. $T\beta_{RATIO}$, $F\beta_{RATIO}$ and $P\beta_{RATIO}$) for each system.

2.4 | Standardized functional and phylogenetic β-diversity measures

We used a null model procedure to determine whether functional and phylogenetic β-diversity measures were greater than or less than expected given the observed level of taxonomic β-diversity. The null model procedure was generated by randomizing the names of species across the tips (i.e. 'shuffling tip' approach) 1000 times but retained the structure of the functional sub-dendrograms and phylogenetic subtrees (Swenson, 2014). The null model procedure was conducted in the R package 'picante' (Kembel et al., 2010). The standardized β-diversity measures (SES.β) were calculated using the observed value of β-diversity measures (Obs) and the mean ($Mean_{null}$) and standard deviation (SD_{null}) of the null expectations of functional and phylogenetic compositions as follows:

$$\mathrm{SES}.\beta = (\mathrm{Obs} - \mathrm{Mean}_{\mathrm{null}}) / \mathrm{SD}_{\mathrm{null}}.$$

The departure from null expectations indicates that species community within a system is non-random with respect to functional traits and phylogenetic lineages, providing evidence of deterministic community assembly processes (Webb et al., 2002). If the observed β-value is significantly lower than that expected by chance ($\mathrm{SES} < -1.96$), environmental filtering ought to prevent dissimilarity across assemblages. On the contrary ($\mathrm{SES} > 1.96$), habitat heterogeneity among fragments is expected to enhance assemblage dissimilarity. If observed β-diversity does not significantly differ from expected by chance ($-1.96 < \mathrm{SES} < 1.96$), stochastic processes and/or the balance of opposite niche-based processes dominate the dissimilarity of bird assemblages (Du et al., 2021; Siefert et al., 2013).

2.5 | System characteristics and climate factors

Drawing on previous work, we selected ER, AS (the ratio between the area of the largest and smallest fragments), the total area of habitat fragments of each habitat island system (AT) and mean inter-fragment distance (MID) to represent the system characteristics. To explore the potential drivers of landscape-level patterns of bird β-diversity in habitat island systems, we included the system characteristics and five climate factors (mean annual temperature, MAT; annual precipitation, AP; precipitation of the driest quarter, PDQ; temperature and precipitation seasonality, TS and PS) for each system (more details about these drivers can be seen in Table S5.2).

2.6 | Data analysis

We performed multiple linear models to quantify the effects of putative five climate factors and four system characteristics on three dimensions of β-diversity and their components as well as standardized functional (SES.Fβs) and phylogenetic (SES.Pβs) β-diversity measures for small and large systems. All explanatory variables were ln-transformed and Z-standardized to obtain standardized regression coefficients. We built all possible combinations of explanatory variables to determine the final optimal combined model for each β-diversity measure. The minimum number of parameters was set at zero (i.e. a model containing only the intercept) and the maximum to nine (the subsets of possible combinations of nine explanatory variables). We thus examined all 512 possible combinations of nine explanatory variables for each β-diversity measure. The variance inflation factors (VIFs) were also calculated for each model to evaluate its multicollinearity. Then we dropped the models in which VIF values of explanatory variables were >5, resulting in 494 and 243 combined models for each β-diversity measure of small and large systems respectively. We used the Akaike information criterion (AIC) to rank models and calculated Akaike weights to indicate the best-fit models (Burnham & Anderson, 2002). For each β-diversity measure, we selected the best set of predictors (i.e. the model with the minimum AIC value, thereafter inferred as best model). The direction and magnitude of predictors contained in the best model were assessed from the sign and value of standardized coefficients. These analyses we conducted using the R package 'stats' and the function *AIC* and *Akaike.weights* in the R package 'qpcR' (Ritz & Spiess, 2008). Competing models were presented in Tables S8.3 and S9.3 in Appendix S3. Model residuals were checked for normality and homogeneity of variance to verify that all model assumptions were met.

All analyses were conducted in the R environment, version 4.0.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Taxonomic, functional and phylogenetic β-diversity measures in habitat island systems

Patterns of taxonomic, functional and phylogenetic multisite β-diversity (β_{SOR}) and their turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) components for bird communities were congruent across both small and large systems (Figure 1). The observed β-diversity measures showed no difference between small and large systems (Figure 2). For both small and large systems, $T\beta_{SOR}$ were significantly higher than $F\beta_{SOR}$ (small systems: $t = 2.420$, $p = 0.023$; large systems: $t = 2.962$, $p = 0.009$) and $P\beta_{SOR}$ (small systems: $t = 2.117$, $p = 0.044$; large systems: $t = 3.145$, $p = 0.006$). $T\beta_{SIM}$ for small systems was significantly higher than $F\beta_{SIM}$ ($t = 2.420$, $p = 0.023$) and $P\beta_{SIM}$ ($t = 3.453$, $p = 0.002$), whereas $T\beta_{SIM}$ for large systems showed no difference with $F\beta_{SIM}$ ($t = 1.964$, $p = 0.067$) but higher than $P\beta_{SIM}$ ($t = 2.396$, $p = 0.029$). In addition, no difference was found among β_{SNE} at three dimensions across both small ($T\beta_{SNE}$ versus $F\beta_{SNE}$: $t = 0.200$, $p = 0.843$; $T\beta_{SNE}$ versus $P\beta_{SNE}$: $t = -0.688$, $p = 0.498$; $F\beta_{SNE}$ versus $P\beta_{SNE}$: $t = -0.903$, $p = 0.375$) and large systems ($T\beta_{SNE}$ versus $F\beta_{SNE}$: $t = -0.052$, $p = 0.959$; $T\beta_{SNE}$ versus $P\beta_{SNE}$: $t = -0.186$, $p = 0.855$; $F\beta_{SNE}$ versus $P\beta_{SNE}$: $t = -0.129$, $p = 0.900$) (Figure 2).

All pairs of dissimilarities were strongly correlated (Table S6.3). Although we found strong correlations between $T\beta_{RATIO}$ and $F\beta_{RATIO}$, and between $T\beta_{RATIO}$ and $P\beta_{RATIO}$ for bird communities across both small and large systems, the relative contributions of the turnover to β-diversity differed among three dimensions (Figure 1; Figure S3.3). For small systems, all datasets had $T\beta_{RATIO}$ and $F\beta_{RATIO}$ values higher than 0.5, while nine datasets (64.3%, 9 out of 14) had $P\beta_{RATIO}$ values higher than 0.5. For large systems, most datasets (75%, 6 out of 8) had $T\beta_{RATIO}$ values higher than 0.5, whereas only 50.0% and 37.5% of the datasets were found to have $F\beta_{RATIO}$ and $P\beta_{RATIO}$ values higher than 0.5 respectively.

3.2 | Standardized functional and phylogenetic β-diversity measures in habitat island systems

Standardized functional ($\mathrm{SES}.F\beta_{SOR}$) and phylogenetic ($\mathrm{SES}.P\beta_{SOR}$) β-diversity showed no difference between small and large systems

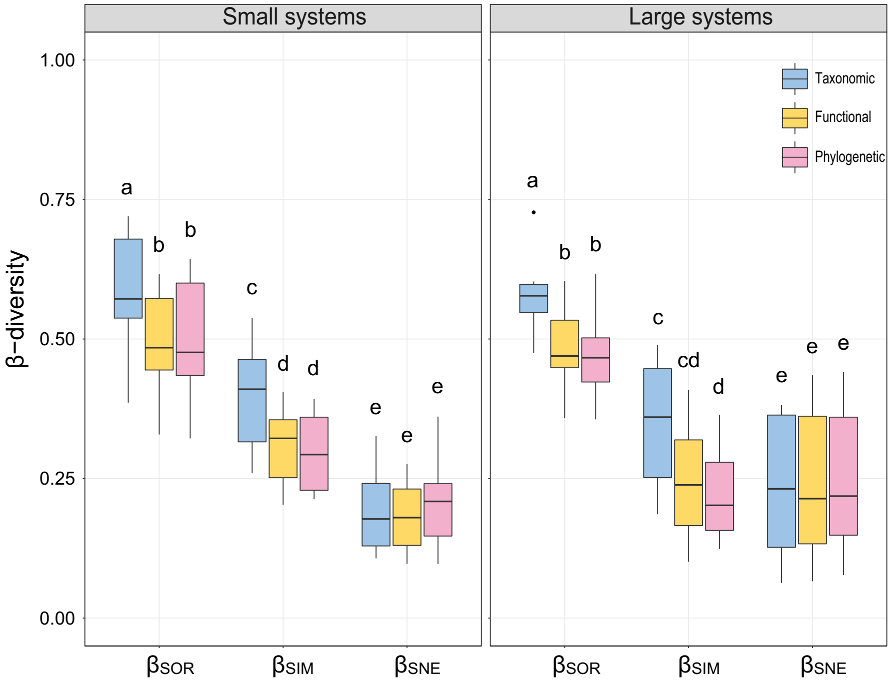

FIGURE 2 Comparisons of mean β-diversity measures at taxonomic, functional and phylogenetic dimensions for small and large habitat island systems. Small systems (spatial extent <100 km); large habitat island systems (spatial extent >200 km); spatial extent, the geographical distance (km) between the localities situated farthest from each other within the habitat island systems. Boxplots with different letters indicate significant difference (two-sided *t*-test, $p < 0.05$); top and bottom of the box indicate the first and third quartiles; and the whiskers indicate the minimum and maximum values

(SES.Pβ_{SOR}: $t = -0.989$, $p = 0.334$; $t = 1.840$, $p = 0.080$) respectively. Similar trends were found for standardized turnover (SES.Fβ_{SIM}: $t = -0.256$, $p = 0.801$; SES.Pβ_{SIM}: $t = 0.565$, $p = 0.578$) and nestedness-resultant components (SES.Fβ_{SNE}: $t = 0.110$, $p = 0.913$; SES.Pβ_{SNE}: $t = 0.947$, $p = 0.354$). For small and large systems, Fβ_{SOR} and its components did not differ from null expectations (Table S7.3). We found significant divergence with three and two datasets of small systems that SES.Pβ_{SOR} and SES.Pβ_{SNE} values were significantly higher than those expected by chance (Table S7.3).

3.3 | Drivers of β-diversity measures across habitat island systems

Model performance was higher for explaining the three dimensions of β-diversity (β_{SOR}) and turnover components (β_{SIM}) for large systems than that for small systems, whereas the nestedness-resultant components showed opposite patterns (Figure 3). The deviance reduction tests conducted on explanatory variables in the best models (minimum AIC value) indicated that most of them had a significant ($p < 0.05$) effect on the considered β-diversity measure for both small and large systems (Figure 3; Table S8.3). For small systems, MAT and TS were strongly and negatively related to taxonomic and functional β_{SOR} and β_{SIM}, whereas Pβ_{SOR} was positively related to the PDQ (Figure 3a–c). All precipitation-related variables (AP, PDQ and PS) were the main determinants of Fβ_{SNE} and the only significant determinants of Pβ_{SNE}. Mean inter-fragment distance also negatively influenced Tβ_{SNE} and Fβ_{SNE} (Figure 3b). For large systems, MAT and system characteristics were the main determinants explaining the increases of Tβ_{SOR} (MAT and MID), Fβ_{SOR} (MAT, AT and MID) and Pβ_{SOR} (ER and MID) (Figure 3d–f; Table S8.3). For β_{SIM}, we found TS, AP and PDQ were positively related to Tβ_{SIM}, PS had the greatest effect on Fβ_{SIM}, while PDQ, PS and AT showed a positive effect on Pβ_{SIM} (Figure 3d–f). The three dimensions of β_{SNE} appeared no significant relationships with climate factors and system characteristics, except a negative influence of AT on Tβ_{SNE} (Figure 3d–f).

3.4 | Drivers of standardized functional and phylogenetic β-diversity measures across habitat island systems

For small systems, the best model of the effects of climate factors and system characteristics on SES.Fβ_{SOR} was a null model (Figure 4a; Table S9.3). SES.Fβ_{SIM} was explained by AP and PS, exhibiting positive and negative effects respectively. Climate factors were the important explanatory variables for SES.Pβ_{SOR} (TS and AP), SES.Pβ_{SIM} (MAT, AP, PDQ and PS) and SES.Pβ_{SNE} (TS, AP and PDQ), while two system characteristics showed significant effects on SES.Pβ_{SIM} (ER and MID) and SES.Pβ_{SNE} (ER) (Figure 4b). For large systems, AS and MID were the important explanatory variables for SES.Fβ_{SOR}, whereas SES.Fβ_{SIM} and SES.Fβ_{SNE} were not significantly affected by climate factors and system characteristics (Figure 4c). TS and AT best explained SES.Pβ_{SOR}, while SES.Fβ_{SNE} was best explained by TS and PS (Figure 4d). Additionally, AS and MID were positively related to SES.Pβ_{SNE} (Figure 4d).

4 | DISCUSSION

This study focused on three dimensions of β-diversity and two spatial extents of landscapes for bird assemblages across landscape-level characteristics using data from well-sampled habitat island systems around the globe. Our findings confirm that landscape-level

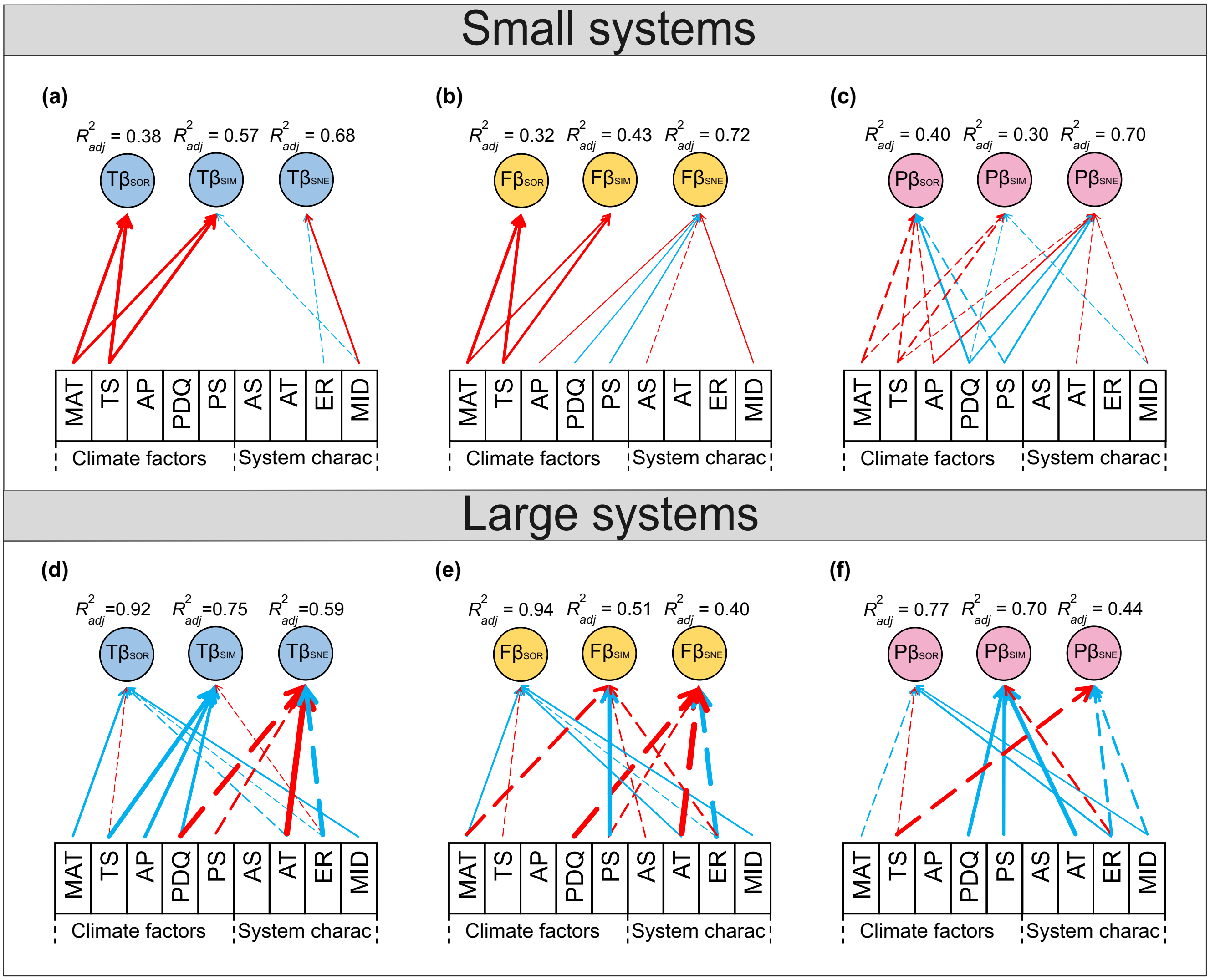

FIGURE 3 Effect of climate factors and system characteristics on β-diversity measures at taxonomic ($T\beta_{SOR}$, $T\beta_{SIM}$ and $T\beta_{SNE}$), functional ($F\beta_{SOR}$, $F\beta_{SIM}$ and $F\beta_{SNE}$) and phylogenetic ($P\beta_{SOR}$, $P\beta_{SIM}$ and $P\beta_{SNE}$) dimensions across multiple habitat island systems. Small systems (spatial extent <100 km); large habitat island systems (spatial extent >200 km); spatial extent, the geographical distance (km) between the localities situated farthest from each other within the habitat island systems. System charac, system characteristics. MAT, mean annual temperature (°C); TS, temperature seasonality (standard deviation × 100); AP, annual precipitation (mm); PDQ, precipitation of the driest quarter (mm); PS, precipitation seasonality (coefficient of variation); AS, area scale, the ratio between the area of the largest and smallest fragments; AT, the total area of habitat islands of a habitat island system (km^2); ER, elevational range (m); MID, mean inter-fragment distance (km). Arrows represent the influence of predictors retained by the AIC-based selection procedure with $p < 0.05$ (full line) and $p > 0.05$ (dashed line) for the β-diversity measures. Blue and red indicate positive and negative relationships respectively. Arrow width is proportional to the effect size given by the standardized coefficients of the best model from multi-model inference. The R^2_{adj} are provided on top of the response variables. The full lists of competing models (ΔAIC ≤2) are presented in Table S8.3 in Appendix S3

β-diversity patterns and their best landscape-level characteristics varied across β-diversity components, dimensions and spatial extent. Except for the differences between small and large systems, we found substantial incongruent responses of standardized functional and phylogenetic β-diversity to our landscape-level characteristics.

4.1 | β-diversity measures in habitat island systems

Overall, a dominant role of the taxonomic turnover in determining dissimilarities among bird communities held for most habitat island systems (20 out of 22), regardless of the spatial extent of systems (Figure 1). This result suggested that species replacement rather than species loss/gain was the main process in changing community composition among bird assemblages in habitat island systems, which were consistent with results from other systems and organisms (Antão et al., 2019; Soininen et al., 2018; Wang, Wiegand, et al., 2018). Our finding thus further verified the turnover-dominant pattern in the partitioned components of taxonomic β-diversity in habitat island systems.

When concerning the spatial extent of these systems, the differences emerged. For small systems, they all had values of $T\beta_{RATIO}$ and

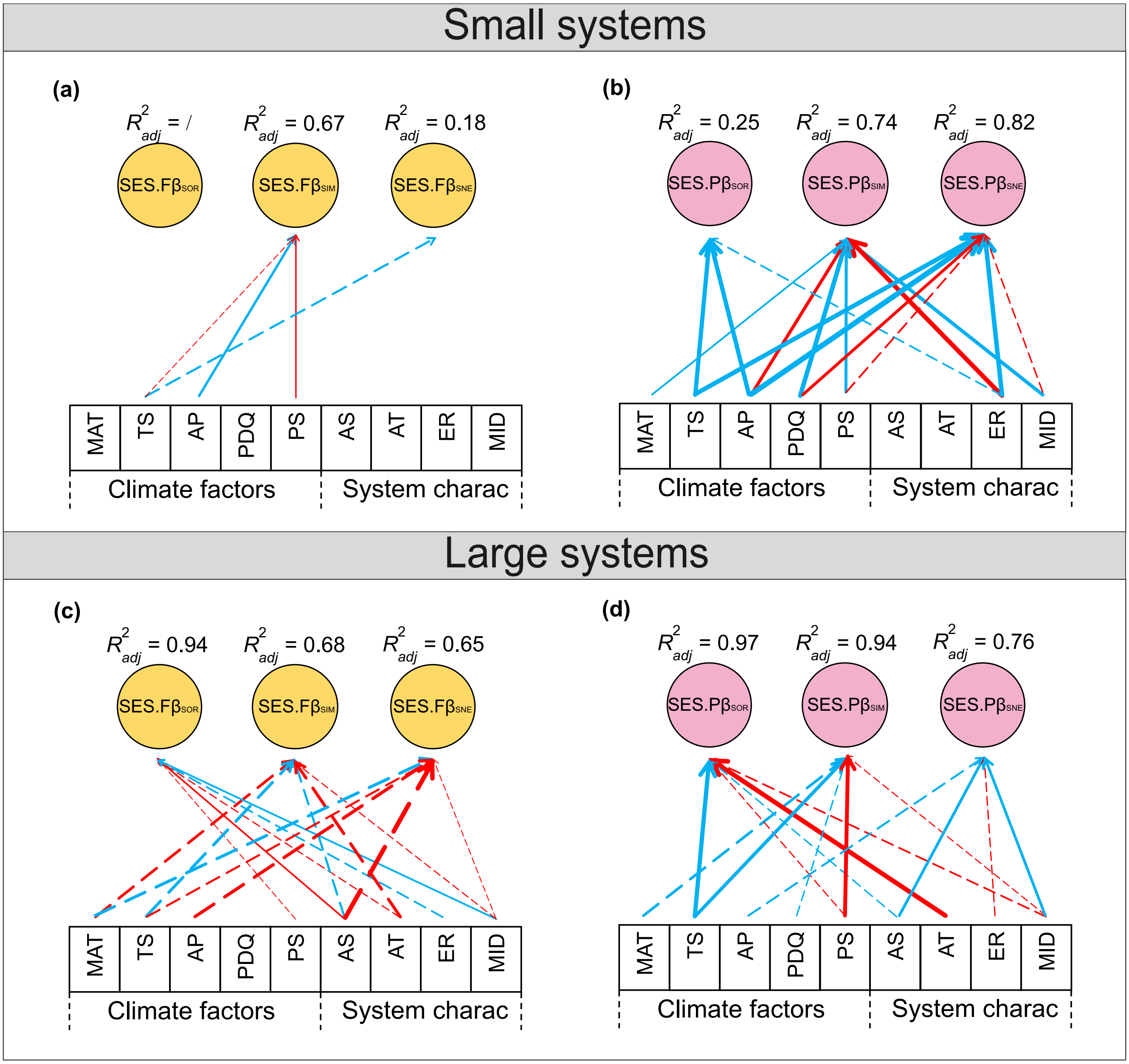

FIGURE 4 Effect of climate factors and system characteristics on the standardized β-diversity measures at functional (SES.Fβ_{SOR}, SES.Fβ_{SIM} and SES.Fβ_{SNE}) and phylogenetic (SES.Pβ_{SOR}, SES.Pβ_{SIM} and SES.Pβ_{SNE}) dimensions across multiple habitat island systems. Small systems (spatial extent <100 km); large habitat island systems (spatial extent >200 km); spatial extent, the geographical distance (km) between the localities situated farthest from each other within the habitat island systems. Arrows represent the influence of predictors retained by the AIC-based selection procedure with $p < 0.05$ (full line) and $p > 0.05$ (dashed line) for the β-diversity measures. Blue and red indicate positive and negative relationships respectively. Arrow width is proportional to the effect size given by the standardized coefficients of the best model from multi-model inference. The R^2_{adj} are provided on top of the response variables. /, no explanatory variable in the best model. The definitions of abbreviations of explanatory variables are in Figure 3. The full lists of competing models (ΔAIC ≤2) are presented in S9.3 in Appendix S3

Fβ_{RATIO} larger than 0.5, whereas almost half of cases with β_{RATIO} <0.5 at the phylogenetic dimension. This result means that taxonomic and functional turnover tended to occur in lineages with relatively close phylogenies (Du et al., 2021). The turnover components dominated taxonomic and functional β-diversity, indicating that species turnover occurs in bird species possessing unique traits, and suggesting the possibility that taxonomically and functionally dissimilar species occupy different islands. Considering the small mean areas of fragments (ranging from 0.02 to 1.80 km^2) and short MIDs (ranging from 2.35 to 28.64 km) within small systems, it is plausible that stochastic extinction (e.g. leaving by choice and death of a few individuals) coupled with stochastic colonization may result in random local community compositions among fragments and thus elevate the taxonomic and functional β-diversity and turnover among bird assemblages.

Therefore, we speculate stochastic processes resulted in the preponderance of the turnover component over the nestedness-resultant component of taxonomic and functional in these small systems. In contrast, high $T\beta_{RATIO}$ but low $F\beta_{RATIO}$ and $P\beta_{RATIO}$ within large systems may imply a phenomenon of functional and phylogenetic redundancy that taxonomically distinct species occurring on fragments are derived from species pools with similar combinations of functional traits and evolutionary histories (Devictor et al., 2010; Ricotta et al., 2020). Thus, environmental filtering seems to be the determining process shaping trait pools and phylogenetic structure in large systems.

4.2 | Standardized functional and phylogenetic β-diversity measures in habitat island systems

Regardless of the spatial extent of habitat island systems, SES.βs at functional and phylogenetic dimensions for all systems were between −1.96 and 1.96 except three small systems (Table S7.3). This may be routinely interpreted as evidence for the neutral process in the assembly of communities for the majority of systems, independently of bird trait and phylogenetic relatedness compositions (Swenson et al., 2012). It is likely to be a consequence of the high dispersal rates of birds among habitat fragments. Under a scenario that pervasive dispersal in the absence of selective environmental filtering of species, community assembly is largely stochastic and dictated by the species dispersal (Si et al., 2016; Sobral & Cianciaruso, 2016). Therefore, birds within habitat island systems might be less subject to local ecological restrictions and historical legacies on fragments, preventing the emergence of non-random patterns of functional and phylogenetic β-diversity.

However, some recent studies have considered that random levels of functional and phylogenetic SES.βs may not necessarily indicate an absence of niche-based processes (e.g. Carvalho et al., 2019; Du et al., 2021; Siefert et al., 2013; see also Sobral & Cianciaruso, 2016). For example, Siefert et al. (2013) proposed that the null model procedure was not a purely 'neutral' model and should be considered as a conservative test of niche-based processes, because the null expectations were based on observed patterns of taxonomic β-diversity, which were probably driven in part by niche-based processes. Another potential explanation for our random-level functional and phylogenetic SES.βs is that two contrasting niche-based processes (e.g. environmental filtering and habitat heterogeneity) might be balanced and show no clear patterns compared with null expectations.

4.3 | Drivers of β-diversity measures across habitat island systems

Regardless of the spatial extent of habitat island systems, climate factors acted as the main drivers of bird communities rather than system characteristics chosen. Although the best explanatory variables varied according to the β-diversity components, diversity dimensions and spatial extent of habitat island systems, temperature- and precipitation-related factors exhibited the most widespread effects in explaining the patterns of β-diversity measures. For small systems, our results indicated lower temperature and temperature stability drove higher taxonomic and functional β-diversity and turnover. Being endotherms and having a high surface-to-mass ratio, lower ambient temperature would induce birds to elevate the metabolic energy that must be expended to maintain their body temperatures (Bicudo et al., 2010). In addition, lower temperatures will influence plant phenology, limiting the resource availability on fragments (Hanz et al., 2019; Newton, 2003). In this case, one may expect that higher energy demands coupled with lower resource availability will be a strong limiting filter for species with similar ecological roles, promoting the species composition variation through differentiation of species niches for birds inhabiting small systems with low MAT. Also, high TS could filter out the species that have a low tolerance for severe temperature change or a specialized set of traits (Hanz et al., 2019; Huntley et al., 2016). This could lead to taxonomic compositional similarity and functional redundancy (i.e. different islands contain species with similar ecological roles) among bird assemblages (Bicudo et al., 2010; Ferger et al., 2014), preventing taxonomic and functional dissimilarity in the systems with high TS.

We also found functional and phylogenetic nestedness-resultant dissimilarities decreased with AP and increased with PDQ and PS. Different from temperature, precipitation-related water limitation may act as an indirect driver for an ordered loss of functional traits that are conserved across lineages (e.g. functional traits exhibited strong phylogenetic signals; see Table S4.2) (Bicudo et al., 2010; Hanz et al., 2019). For example, fragmented habitats are expected to be environmentally homogeneous (Sobral & Cianciaruso, 2016). Lower AP and higher PS could further trigger destructions of forest complexity on fragments (Hanz et al., 2019; Newton, 2003). These attributes together reduced the availability of habitat shelters, nesting sites or foraging substrate for birds (Hanz et al., 2019). Where this occurs, most tree-dwelling (e.g. Bucconidae, Cuculidae and Picidae), ground-dwelling (e.g. Formicariidae, Thamnophilidae and Motacillidae) insectivorous and large frugivorous (e.g. Bucerotidae and Psittacidae) birds that rely on specific foraging substrates or high fruit crop requirements would be often restricted to larger fragments. Meanwhile, bird assemblages tended to be homogeneous on smaller fragments by maintaining generalist species (e.g. species with small body sizes, omnivores and flying insectivores) that respond adaptively to hostile environmental conditions. These together resulted in higher functional and phylogenetical nestedness-resultant dissimilarities across bird assemblages (e.g. Si et al., 2016). In addition, the possible reason for the positive relationships between PDQ and the nestedness-resultant dissimilarities at the functional and phylogenetic dimensions is the existence of rare species on different fragments due to scarce water availability in the driest quarter, causally lowering functional and phylogenetic nestedness-resultant dissimilarities across bird assemblages. Taken together, these results indirectly reflect deterministic processes based on thermal filtering and resource availability that have played major roles in structuring bird assemblages across small systems.

For large systems, we found that a higher taxonomic turnover was associated with higher TS, AP and PDQ, while functional and phylogenetic turnover were positively associated with PS and PDQ. Compared with small systems, these results indicated that changes in species identities, functional traits and evolutionary histories of species would exhibit dissimilar patterns along with major climate factors across large systems. This finding partly upholds the view that for given changes in species turnover, climate factors may independently affect the functional and phylogenetic turnover, depending on the strength of environmental filtering, the particular functional traits and the phylogenetic relatedness of the species considered (Webb et al., 2002). We also found that taxonomic and phylogenetic turnover were significantly related to the gradient of PDQ, while functional and phylogenetic turnover were significantly related to the gradient of PS across large systems. In this context, while species turnover changes rapidly along with major climate factors, the variation of their functional traits is mostly driven by the tendency of species to retain ancestral ecological characteristics (i.e. phylogenetic niche conservatism; Wiens & Graham, 2005). The corollary of this pattern is that bird communities inhabited in large-scale systems with high PS or high water availability may display large variations in species composition while these different assemblages may possess similar functions and/or share similar evolutionary histories.

By comparison, a striking feature of our results is that increasing MID negatively affected taxonomic and functional nestedness-resultant dissimilarities across small systems, while increasing AT negatively and positively affected taxonomic nestedness-resultant dissimilarity and phylogenetic turnover, respectively, across large systems (Figure 2). The former indicates that for given small systems, decreasing MID tended to induce nested species losses that lead to high nestedness-resultant dissimilarity among bird assemblages. Russell et al. (2006), for example, proposed that local extinction tends to increase at the smallest distances because birds can actively abandon hostile islands and stay on those with suitable habitats/resources (i.e. optimal foraging theory). In this context, we speculate that decreasing MID would induce a higher probability of 'leaving by choice' extinction on smaller fragments (see also Si et al., 2014), resulting in more-common assemblage members (e.g. generalist) becoming non-random subsets of the larger biota and thus higher values of nestedness-resultant dissimilarity in small systems. The latter indicates that for given large systems, an increasing AT was more likely to prevent the nested species losses and to promote phylogenetic turnover. When the total area of a system increases, it could provide new habitats for distant clades to colonize from adjacent areas with similar conditions. Rapid in situ diversification of these immigrant clades increases the overall species pool (Montaño-Centellas et al., 2019) drives strong phylogenetic turnover and causally lowers unique species in the richer assemblages.

4.4 | Drivers of standardized functional and phylogenetic β-diversity measures across habitat island systems

A major finding of this study is that climate factors and system characteristics played important roles in driving the (potentially niche-based) community assembly across fragmented landscapes. As our results show, some variables related to temperature, precipitation and habitat heterogeneity (e.g. AS and ER) may jointly regulate the SESβs in both small and large systems (Figure 4). Considering the water–energy dynamic (O'Brien, 1998) and climate stability hypotheses (Stevens, 1989), climatic factors affect aboveground plant biomass, vegetation structure and habitat heterogeneity (e.g. more vegetation strata and niches with increasing vegetation structure). Under the assumption that habitat heterogeneity is positively correlated with climate, AS and ER, the link between habitat heterogeneity and assembly patterns is reasonable as habitat heterogeneity has been demonstrated to be an influential factor affecting community assembly, especially in habitat island systems (Carvalho & Cardoso, 2014; Ohyama et al., 2021; Rosenzweig, 1995). In this light, for example, the negative effects of AP and ER on SES.Pβ_{SIM} across small systems reveal that, as habitat heterogeneity increased, the magnitude of phylogenetical divergence among bird assemblages gradually decreased (i.e. positive SES.Pβ_{SIM} tended to 0), while phylogenetical convergence consistently increased (i.e. negative SES.Pβ_{SIM} away from 0). We can find the mechanism of such results from the area–heterogeneity trade-off (Allouche et al., 2012). The area–heterogeneity trade-off suggested that any increase in environmental heterogeneity within a fixed space would result in a reduction in the averaged amount of effective area available for individual species and thus increases the likelihood of stochastic extinctions of species with narrower niche widths. In our case, high habitat heterogeneity within habitat island systems may create high niche diversity with smaller niche sizes compared to the amount of suitable area for bird species, which results in decreasing number of specialized species (i.e. those phylogenetically distinct lineages) but increasing the number of generalized species that possess very broad niches. Similarly, climate seasonality (i.e. TS and PS) could influence the niche-based processes contributing to SES.Pβ_{SIM} across large systems. In addition, our results highlight that the effects of landscape-level characteristics on ecological processes of community assembly could be mediated by the spatial extent. Specifically, by comparison, we found that SES.Pβ_{SIM} and SES.Pβ_{SNE} for small systems were more prone to be strongly affected by all chosen variables, whereas SES.Pβ_{SIM} and SES.Pβ_{SNE} for large systems were less associated with these variables (Figure 4b,d). One possible reason is that within small systems, the spatially close bird assemblages could experience more overlaying processes such as competitive coexistence and facilitation (Cadotte et al., 2019), while the spatial structure of sampling scale also exhibits strong effects on these ecological processes (Perronne et al., 2017).

Finally, our explanatory variables explained a greater proportion of variance in SES.Pβs than what we did for functional equivalents (see R^2_{adj} in Figure 3a–d). We also found SES.Fβs and SES.Pβs exhibit incongruent responses to the landscape-level explanatory variables across both small and large systems. A possible explanation of these incongruencies is that the phylogenies reflect a comprehensive estimate of multivariate traits that were measured and not measured (Cadotte et al., 2019), which appears to better capture complex ecological processes at the landscape level. On the other hand, previous studies have demonstrated that the outcome of the analysis of functional diversity could depend on the choice and numbers of functional traits (Cadotte et al., 2019; Meynard et al., 2011). However, we are often limited in the choice of functional attributes and lack knowledge about which traits reflect efficient local adaptations for analyses across multiple systems at the landscape level (Meynard et al., 2011; Petchey & Gaston, 2006). Even though we included body mass which is known to affect the physiology of species (Bicudo et al., 2010), as well as ecological traits representing major aspects of birds' requirements, we might still miss some relevant information that potentially influenced community assembly (Cadotte et al., 2019; Tucker et al., 2018). Altogether, our findings support the idea that taking into account phylogenetic relatedness composition together with functional composition could provide a more integrated and complementary picture of assembly processes at the landscape level. Furthermore, our findings echo the previous proposal of Tucker et al. (2018) that a multi-aspect combination of traits are needed for assessing the underlying mechanisms of community assembly.

5 | CONCLUSIONS

This study showed turnover was the dominant component in overall β-diversity of bird assemblages. Climate factors and system characteristics exhibited important influence on the niche-based processes in community assembly at the landscape level. We concluded that the effects of landscape-level characteristics on ecological mechanisms of community assembly could be mediated by the spatial extent of habitat island systems. This study offers a better understanding of the processes underlying macroecological patterns of isolated biological communities across habitat island systems.

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CONFLICT OF INTEREST

All authors contributed throughout the manuscript and declared no conflict of interest.

DATA AVAILABILITY STATEMENT

The data we used are provided as the Supporting Information.

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BIOSKETCH

Chi Zeng is interested in the structure of ecological communities and factors responsible for animal species distributions on fragmented islands.

Author contributions: C.Z., X.S. and L.W. conceived the study. C.Z. and L.W. compiled the data. C.Z. and W.L. rechecked the lists of birds. C.Z. performed data analysis with the assistance of X.S. and L.W. C.Z. and L.W. led the writing.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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APPENDIX A

DATA SOURCES FOR DATASET 1–22

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