

Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages

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Summary

1. Taxonomic diversity considers all species being equally different from each other and thus disregards species' different ecological functions. Exploring taxonomic and functional aspects of biodiversity simultaneously can better understand the processes of community assembly.

2. We analysed taxonomic and functional alpha and beta diversities of breeding bird assemblages on land-bridge islands in the Thousand Island Lake, China. Given the high dispersal ability of most birds at this spatial scale (several kilometres), we predicted (i) selective extinction driving alpha and beta diversities after the creation of land-bridge islands of varying area and (ii) low taxonomic and functional beta diversities that were not correlated to spatial distance.

3. Breeding birds were surveyed on 37 islands annually from 2007 to 2014. We decomposed beta diversity of breeding birds into spatial turnover and nestedness-resultant components, and related taxonomic and functional diversities to island area and isolation using power regression models (for alpha diversity) and multiple regression models on distance matrices (for beta diversity). We then ran simulations to assess the strength of the correlations between taxonomic and functional diversities.

4. Results revealed that both taxonomic and functional alpha diversities increased with island area. The taxonomic nestedness-resultant and turnover components increased and decreased with difference in area, respectively, but functional counterparts did not. Isolation played a minor role in explaining alpha- and beta-diversity patterns. By partitioning beta diversity, we found low levels of overall taxonomic and functional beta diversities. The functional nestedness-resultant component dominated overall functional beta diversity, whereas taxonomic turnover was the dominant component for taxonomic beta diversity. The simulation showed that functional alpha and beta diversities were significantly correlated with taxonomic diversities, and the observed values of correlations were significantly different from null expectations of random extinction.

5. Our assessment of island bird assemblages validated the predictions of no distance effects and low beta diversity due to pervasive dispersal events among islands and also suggested that selective extinction drives taxonomic and functional alpha and beta diversities. The contrasting turnover and nestedness-resultant components of taxonomic and functional beta diversities demonstrate the importance of considering the multifaceted nature of biodiversity when examining community assembly.

Key-words: beta diversity, community assembly, dispersal, diversity–area relationship, environmental filtering, functional trait, island biogeography, nestedness, null model, turnover

Introduction

Taxonomic diversity considers all species as being equally different from each other and thus disregards the fact that

species have different ecological functions (Villéger, Grenouillet & Brosse 2013). Functional diversity quantifies the total variation in functional traits across all species within a community (Tilman 2001), which is the key to understand ecosystem processes and its response to environmental stress or disturbance (Chao, Chiu & Jost

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2014). Taking functional traits of taxa into account when exploring the spatial patterns of taxonomic and functional diversities, it can reveal different processes associated with the origin and maintenance of biodiversity (Stegen & Hurlbert 2011). From the perspective of biodiversity conservation, it is also the high priority to protect as much as possible multi-types of biological diversity in a region (Meynard *et al.* 2011).

In addition to investigating the spatial patterns of biological diversity within sites (i.e. alpha diversity), it is also useful to assess the change of species composition between sites in a region (i.e. beta diversity) (Anderson *et al.* 2011). Analogous to taxonomic alpha diversity, taxonomic beta diversity ignores functional dissimilarity between communities (functional beta diversity), and this might hamper our ecological inferences (Swenson, Anglada-Cordero & Barone 2011). Recently, functional-based studies are being increasingly used to improve our inferences about community assembly (McGill *et al.* 2006). However, the broad sense beta-diversity indices are unable to distinguish patterns of species replacement and loss (see Baselga 2010, 2012; Baselga & Leprieur 2015), and this problem also affects functional beta diversity (Villéger, Grenouillet & Brosse 2013).

Decomposing overall beta diversity into turnover and nestedness-resultant components can help understand the processes behind the variation of assemblages in space and time (Baselga 2010). The nestedness-resultant component accounts for differences between assemblages linked to species loss and gain in nested subsets, whereas spatial turnover accounts for differences between assemblages linked to species replacement from one site to another. Both phenomena (species loss and species replacement) can be linked to different processes. Consequently, partitioning beta diversity can provide a potential way to infer the processes behind community assembly (Meynard *et al.* 2011). For example, pervasive dispersal in the absence of selective environmental filtering of species (i.e. neutral dynamics) will result in low taxonomic and functional beta diversities (Weinstein *et al.* 2014). Under these conditions, colonization and extinction are random events; thus, a dominant turnover component relative to nestedness-resultant dissimilarity is expected. In turn, nestedness occurs when colonization and extinction are ordered patterns, which are often linked to deterministic processes of environmental filtering.

Land-bridge islands created by construction of dams, such as the islands in the Thousand Island Lake (China) in this study, can be viewed as particularly effective systems to explore patterns and mechanisms of community composition variation in fragmented habitats (Wu *et al.* 2003; Terborgh & Feeley 2008). First, because the islands in the lake were created essentially simultaneously due to the quick subsequent inundation after the dam construction, all islands have the same ecological background and clear geological boundaries (Whittaker & Fernández-Palacios 2007). Second, the land-bridge islands are

relatively small and accessible. Species on these islands can be readily sampled and surveyed thoroughly over a number of breeding seasons (Si *et al.* 2014). Finally, given the short history of these islands after lakes formed (e.g. 56 years in our study), the effects of long-term historical and evolutionary processes, such as glacial cycles and speciation, can be excluded (Graham & Fine 2008). In this system, we go beyond taxonomic-based approaches (Si, Baselga & Ding 2015), adding the functional layer to alpha- and beta-diversity analyses. As for the latter, we partitioned overall functional dissimilarity into its spatial turnover and nestedness-resultant components to examine the role of environmental filtering and dispersal processes in shaping community structure and composition, using occupancy data of terrestrial breeding birds on islands in the inundated lake. Based on the classic theory of island biogeography (IBT) (MacArthur & Wilson 1967) and the specific fragmented landscape formed by dam construction, we tested patterns of taxonomic and functional alpha and beta diversities, and formulate the following predictions:

- 1 No distance effects and low taxonomic and functional beta diversities of breeding birds due to pervasive dispersal. According to IBT, the probability of a species colonizing an island depends on its isolation, which means remoter islands receive less species. As the mean distance from a study island to mainland is generally small (1.47 ± 0.86 km) and birds can fly, water surfaces between islands in our system are not the geographical barriers for the vast majority of birds (Si, Baselga & Ding 2015). We thus predict that isolation may play a minor role in driving taxonomic and functional alpha and beta diversities of breeding birds on these land-bridge islands. Furthermore, we also predict that slopes of diversity–area relationships (i.e. z values of power regression models) will be low, as well as taxonomic and functional beta diversities because of pervasive dispersal (Weinstein *et al.* 2014).
- 2 Selective extinction is the driver of breeding bird beta diversity. As the land-bridge islands in our system were formed by dam construction, species on islands will be gradually lost over time, a process known as relaxation (Si *et al.* 2014). Under the relaxation process, extinction is the dominant phenomenon instead of colonization. Particular sets of bird species that are sensitive to high stress intensities or severe environmental conditions of islands will become locally extinct selectively. These effects would likely be linked to particular functional groups of species (e.g. species vulnerable to habitat loss and fragmentation), so we expect functional alpha and beta diversities to be correlated with their taxonomic counterparts. On the contrary, if community structure of breeding birds on islands was simply driven by random extinction as a function of area itself, we would expect taxonomic and functional alpha- and beta-diversity patterns to be decoupled (Fig. 1).

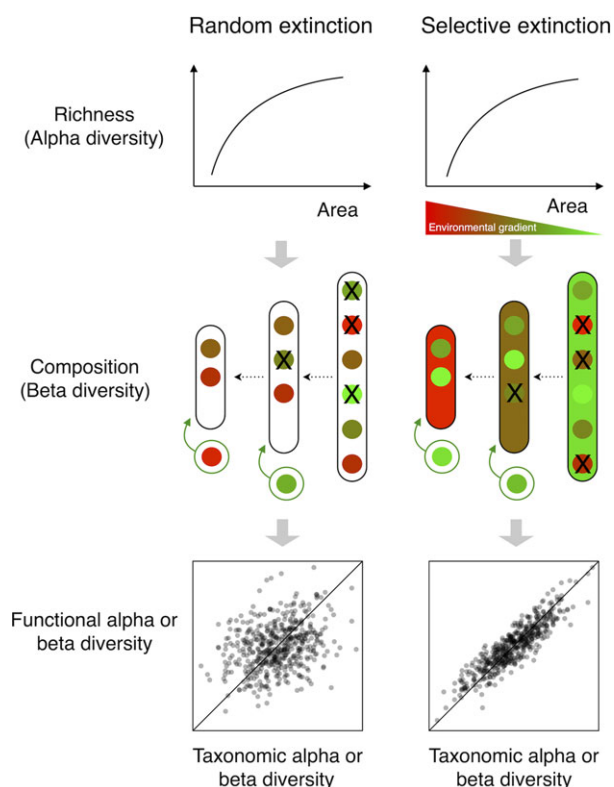


Fig. 1. The hypothetical scheme describing the potential processes of random and selective extinction that drive taxonomic and functional alpha and beta diversities of breeding birds on inundated land-bridge islands. Because of the high vagility of birds and relative short distances from islands to mainland in the inundated lake, we hypothesized less to no dispersal limitation for most birds. Thus, if community structure of birds on islands is driven by random extinction as a function of area, we predict correlations between taxonomic and functional alpha and beta diversities to be decoupled. On the contrary, particular types of birds linked to the particular environmental gradients of islands will extinct selectively, that is the species that are vulnerable to habitat loss and fragmentation on islands with high environmental stress. We thus predict that functional alpha and beta diversities will be correlated with taxonomic diversities. Note that each elliptical bar represents an island, and each colour dot represents a species. Redder elliptical bars indicate islands suffer higher environmental stress than greener ones, and redder dots indicate species have higher vulnerability to environmental stress than greener ones. Colour dots in circles indicate potential colonists.

Materials and methods

STUDY AREA

The Thousand Island Lake (29°22'–29°50' N, 118°34'–119°15' E), created in 1959 by the construction of the Xin'anjiang Dam for hydroelectricity, is a large artificial reservoir in Zhejiang Province, eastern China (Fig. 2). Flooding approximately 580 km², the lake formed 1078 islands with areas > 2500 m² when the water reached its highest level (108 m). The dominant vegetation on the islands is a natural secondary forest, mainly of *Pinus massoniana*, with many broad-leaved trees and shrub species such as *Cyclobalanopsis glauca*, *Castanopsis sclerophylla*, *Smilax davidi-*

ana, *Grewia biloba* and *Loropetalum chinense* (Si *et al.* 2014). The lake region has a typical subtropical monsoon climate, with marked seasonality. The average annual temperature is 17.0 °C. Daily temperature ranges from −7.6 °C in January to 41.8 °C in July. The annual precipitation of the region is 1430 mm, mainly concentrated in rainy season between April and June (Wang *et al.* 2010).

ENVIRONMENTAL DATA

We selected 37 study islands to encompass as much variation in area and isolation as possible (Fig. 2). These islands range from 0.57 ha to c. 1300 ha and from about 20 m separation from the nearest shore of the mainland to over 3.71 km. We characterized islands in terms of area and isolation, because these variables are recognized as the key determinants of the probabilities of colonization and extinction processes (MacArthur & Wilson 1967; Losos & Ricklefs 2010), thus being potentially relevant factors behind alpha and beta diversities and their components (Gaston *et al.* 2007). For each island, we measured island area in hectares, and estimated isolation in metres as the shortest shore-to-shore distance from a focal island to the mainland (Table S1, Supporting Information). Accordingly, we measured difference in isolation in metres as the shortest shore-to-shore distance between island pairs (Table S2).

COMMUNITY DATA

We surveyed bird communities on 37 study islands during breeding season (April–June) annually from 2007 to 2014. Sampling effort on each island was roughly proportional to the logarithm of island area. As a result, eight transect trails were sampled on Island 1 (the largest study island, area > 1000 ha), four on Islands 2 and 3 (island area > 100 ha), two on four islands (10 ha < island area < 100 ha) and one on each of the remaining small islands (c. 1 ha for most islands) (Fig. 2; Table S1). We used a global positioning system (GPS) to record the total length of transects on each island (Table S1).

Transects were generally placed along ridge lines, and we cleared narrow census trails (about 20 cm wide) to facilitate surveys (Terborgh, Lopez & Tello 1997). We used stratified random placement to capture all habitat types on study islands and then collected bird occupancy data along these transects (Bibby *et al.* 2000). In each survey, observers walked each transect at a constant speed (c. 2.0 km × h^{−1}), and recorded all the birds seen or heard on the survey island. We excluded high-flying species passing over the islands during surveys, and only confident records were taken for analyses. Over the course of the entire study, we surveyed each transect on these islands 96 times. Surveys ran from after half an hour after dawn to 11:00 h in the morning and from 15:00 h to half an hour before sunset in the afternoon (Wang *et al.* 2010). We did not conduct bird surveys if there was heavy rain, high wind or high temperature. We alternated the direction observer walked on each transect randomly during the 96 surveys to eliminate the potential survey bias (Si *et al.* 2014). In our study, we only considered terrestrial breeding birds, excluding diving birds, ducks, gulls, herons and shorebirds whose habitats extensively rely on water. Nocturnal species, such as owls and owlets, were also excluded in our analyses. During the course of this study, we recorded a total of 63 terrestrial breeding birds on study islands (Table S3).

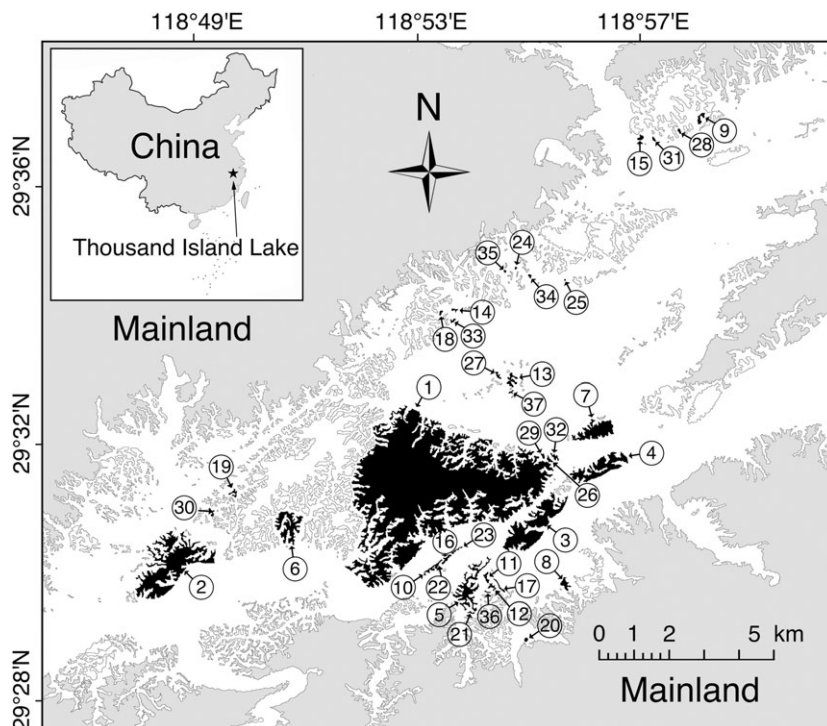


Fig. 2. The 37 study islands of the Thousand Island Lake in Zhejiang Province, eastern China. Study islands were numbered in order of decreasing area.

FUNCTIONAL TRAIT DATA

We selected body mass, main feeding guild, main feeding stratum and main feeding behaviour for breeding birds on study islands as their functional traits (Table S4). Presence or absence was scored for main feeding guild (carnivore, granivore, insectivore, omnivore and nectivore), main feeding stratum (ground, understorey, midstorey, canopy and air) and main feeding behaviour (glean, probe, leap and sally) (Ding *et al.* 2013). All of selected bird traits are related to resource use, energy requirements and trophic levels that have been commonly measured and used in functional diversity studies (Petchey *et al.* 2007; Flynn *et al.* 2009). Trait data were collected from field surveys and from the literatures (Zhuge 1990; Zhao 2001).

DIVERSITY MEASURES

We assessed both alpha and beta diversities of breeding bird communities. In our study, taxonomic alpha diversity is the number of species on each island. Functional alpha diversity is the multidimensional functional space (the convex hull hypervolume) occupied by a species community (Villéger, Mason & Mouillot 2008). On the estimation of functional alpha diversity, we used the Gower's distance (Gower 1966) to compute the functional distances between all species pairs because our original trait matrix (Table S4) includes mixed binary and continuous variables. We then performed a principal co-ordinates analysis (PCoA) based on this functional distance matrix, and used the first three PCoA axes (93.20% of total inertia) to quantify functional alpha diversity (Villéger, Mason & Mouillot 2008; Laliberté & Legendre 2010) (Table S5).

For beta diversity, we used dissimilarity indices methodologically linked to the aforementioned measures of alpha diversity, that is dissimilarity measures based on the proportion of shared and unique fractions of species counts, and overlap and distinct-

tive parts of multidimensional functional spaces, for taxonomic and functional beta diversities, respectively. In our study, overall dissimilarity was always partitioned into its turnover and nestedness-resultant components (Baselga 2010). The general framework of beta-diversity partitioning is that the Simpson dissimilarity index describes species turnover without the influence of richness gradients (Lennon *et al.* 2001). As Sørensen dissimilarity and Simpson dissimilarity are equal in the absence of nestedness, their difference is a net measure of the nestedness-resultant component of beta diversity (Baselga 2010; Leprieux *et al.* 2011). We used beta-diversity ratio to represent the relative contribution of nestedness-resultant component to overall beta diversity. For example, if beta-diversity ratio > 0.5, beta diversity is determined dominantly by the nestedness-resultant component, or the spatial turnover is the dominant one (Dobrovolski *et al.* 2012). Likewise, we additively partitioned functional beta diversity into its spatial turnover and nestedness-resultant components in the same framework of Sørensen dissimilarity (Villéger, Grenouillet & Brosse 2013). Due to computational constraints of the high number of species, it was not possible to compute multiple-site dissimilarity for functional beta diversity. Therefore, we estimated multiple-site taxonomic and functional beta diversities and its two components as the mean of 666 pairwise Sørensen dissimilarities of bird communities on 37 study islands, respectively.

STATISTICAL ANALYSES

We tested the associations between island variables using Pearson's correlation and found island area was uncorrelated to isolation ($r = -0.13$, $P = 0.46$). Regarding taxonomic and functional alpha diversities, we set up a power regression models with two predictors (island area and isolation), respectively. As for beta-diversity patterns, we used multiple regression models for distance matrices (MRM) (Lichstein 2007) to examine the relationships between dissimilarity matrices (overall beta diversity,

and its turnover and nestedness-resultant components) and the Euclidean distance matrices of environmental variables (difference in area and difference in isolation). Compared to multiple regressions, all variables in MRM are distance matrices and P -values are estimated by permutation test (9999 runs) to remove the effect of non-independence between cases on P -values (Legendre, Lapointe & Casgrain 1994).

To test the strength of the correlations between functional and taxonomic alpha and beta diversities, we simulated bird assemblages on these islands under the assembly processes of random and selective extinction following the procedure of Mouchet *et al.* (2010). The random assembly algorithm randomly subsampled species without replacement from the regional pool by maintaining the observed species richness on each island (i.e. fixed-row random-column algorithm, or r0 algorithm; rows are islands and columns are species, hereafter). For comparison, we also simulated another two null models under the process of random extinction on each island: (i) maintaining species occupancy but randomizing species richness (i.e. random-row fixed-column algorithm, or c0 algorithm) and (ii) both maintaining species occupancy and species richness (i.e. fixed-row fixed-column algorithm, or quasiswap algorithm) (Jonsson 2001; Miklós & Podani 2004). Selective extinction, the deterministic process of environmental filtering, was simulated by randomly choosing an 'optimal' species, and then selected nearest species (e.g. species with lowest Gower's distance) to this optimal species until target local species richness reached on each island (Maire *et al.* 2015). Each simulation was run 100 times. If selective extinction is the major process driving community assembly of bird assemblages in our study system, we expect the observed correlation coefficients (Pearson's r) to be outside the ninety-fifth quantiles of the null distributions obtained under the random extinction scenario. We also expect the observed correlation coefficients to be in the fifth and ninety-fifth quantiles of the null distributions obtained under the selective extinction scenario. On the contrary, if random extinction

majorly drives the process of community assembly, we expect the observed correlation coefficients to be in the fifth and ninety-fifth quantiles of the null distributions obtained under the random extinction scenario, but to be outside the fifth quantiles of the null distributions obtained under the selective extinction scenario.

We estimated Pearson's correlation coefficients between taxonomic and functional alpha and beta diversities. Significance of correlations between taxonomic and functional beta diversities and its two components was estimated by Mantel test (9999 runs) (Legendre & Legendre 2012). All calculations and statistical analyses in this study were performed in R (R Core Team 2015) using packages BETAPART (Baselga & Orme 2012), ECODIST (Goslee & Urban 2007), FD (Laliberté & Legendre 2010) and VEGAN (Oksanen *et al.* 2013). Annotated R scripts for randomization tests simulating the processes of random and selective extinction are given in Appendix S1.

Results

RELATIONSHIPS BETWEEN TAXONOMIC AND FUNCTIONAL DIVERSITIES

We recorded a total of 63 terrestrial breeding bird species on 37 study islands with a mean taxonomic diversity of 27 species on each island (\pm SD 5, range 20–47). As shown in Fig. 3a, functional alpha diversity was positively correlated with taxonomic alpha diversity ($r = 0.64$, $P < 0.001$). Taxonomic beta diversity ranged from 0.05 to 0.42 with a mean value of 0.21 (± 0.06) (Table 2). On average, the taxonomic nestedness-resultant component (0.08 ± 0.08) was lower than the taxonomic turnover (0.13 ± 0.07), and contributed to 37% ($\pm 30\%$) to taxonomic beta diversity (Table 2). Functional and taxonomic beta diversities were

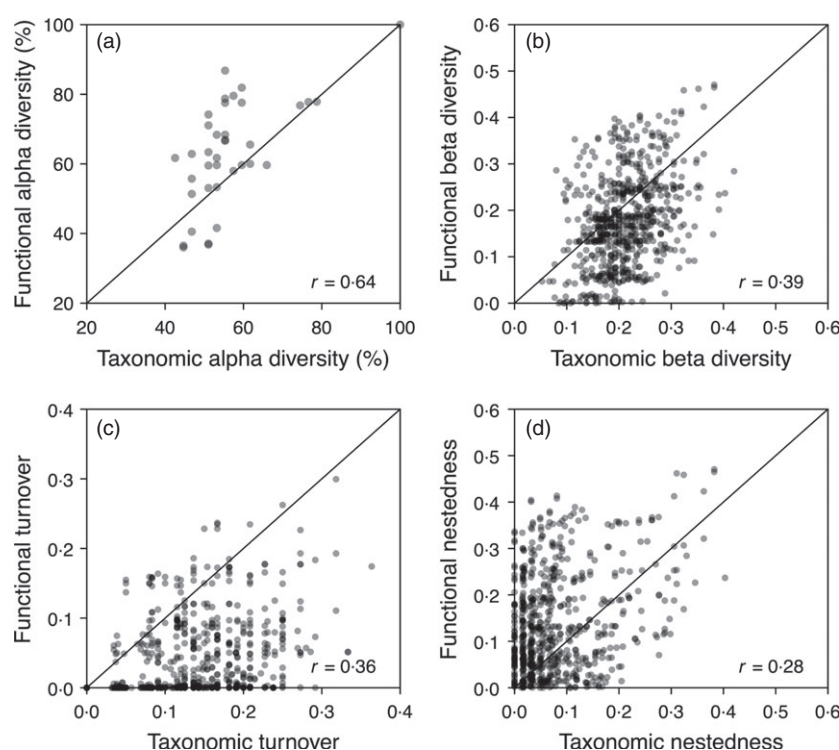


Fig. 3. Correlation coefficients (Pearson's r) between taxonomic and functional alpha (a) and beta (b) diversities, including its turnover (c) and nestedness-resultant (d) components, of breeding bird communities on 37 study islands in the Thousand Island Lake, China. Significance of correlations between taxonomic and functional beta diversities and its two components was estimated by Mantel test. All correlations were significant ($P < 0.05$).

positively correlated ($r = 0.39$, $P < 0.001$, Fig. 3b). Functional beta diversity had a similar average value as taxonomic beta diversity (0.18 ± 0.10 vs. 0.21 ± 0.06) (Table 2). Functional and taxonomic nestedness-resultant components were positively correlated ($r = 0.28$, $P = 0.01$, Fig. 3d). The functional nestedness-resultant component was almost twice higher than taxonomic nestedness-resultant component (0.14 ± 0.11 vs. 0.08 ± 0.08) (Table 2). In contrast, the functional turnover component was three times lower than taxonomic turnover (0.04 ± 0.05 vs. 0.13 ± 0.07) (Table 2). Functional and taxonomic turnover were also positively correlated ($r = 0.36$, $P < 0.001$, Fig. 3c). Functional nestedness-resultant component contributed on average to 75% ($\pm 31\%$) of functional beta diversity (Table 2).

The observed values of correlation coefficients were all outside the ninety-fifth quantiles of the null distributions, indicating that observed patterns were significant different from the null expectations of random extinction using r0 algorithm (Fig. 4a). Analogous to r0 algorithm, observed values of correlation coefficients were also significant different from null expectations using c0 (Fig. S1a) and quasiswap (Fig. S1b) algorithms, excepting for the correlations of alpha diversity and nestedness-resultant component using quasiswap algorithm (Fig. S1b). None of observed values of correlation coefficients were within the fifth and ninety-fifth quantiles of the null distributions of selective extinction (Fig. 4b).

CORRELATES OF ALPHA AND BETA DIVERSITIES

As shown in Table 1, taxonomic alpha diversity increased with island area ($t = 12.28$, $P < 0.001$), but was not significantly related to isolation ($t = -1.97$, $P = 0.06$). Similar

results were observed for functional alpha diversity (island area: $t = 2.66$, $P = 0.01$; isolation: $t = -1.31$, $P = 0.20$) (Table 1). However, the strength of the relationship was much higher for taxonomic than for functional alpha diversity ($R^2 = 0.82$, $F_{2,34} = 80.84$, $P < 0.001$ and $R^2 = 0.17$, $F_{2,34} = 4.81$, $P = 0.01$, respectively) (Table 1). The parameter estimates of island area in this study (z values of the fitted power functions of diversity-area relationships) were both < 0.100 (taxonomic, 0.082; functional, 0.057) (Table 1). As shown in Table 3, taxonomic turnover decreased with difference in area ($P < 0.001$), whereas taxonomic beta diversity and its nestedness-resultant component increased with difference in area ($P = 0.003$ and $P < 0.001$, respectively). Functional beta diversity and its components were not significantly related to difference in area (all P -values > 0.05) (Table 3). Taxonomic and functional dissimilarities and their components were also not significantly related to isolation (all P -values > 0.05) (Table 3).

Discussion

Our results showed that, in our research system, both taxonomic and functional alpha diversities increased with island area. Taxonomic nestedness-resultant and turnover components of dissimilarity had positive and negative relationships with difference in area, respectively, but there were no significant relationships for functional counterparts. Isolation played a minor role in shaping bird community structure given the relative small separations between islands, compared to the strong dispersal ability of the vast majority of birds. We validated the predictions of (i) low taxonomic and functional beta diversities due to pervasive dispersal in these close-connected contemporary

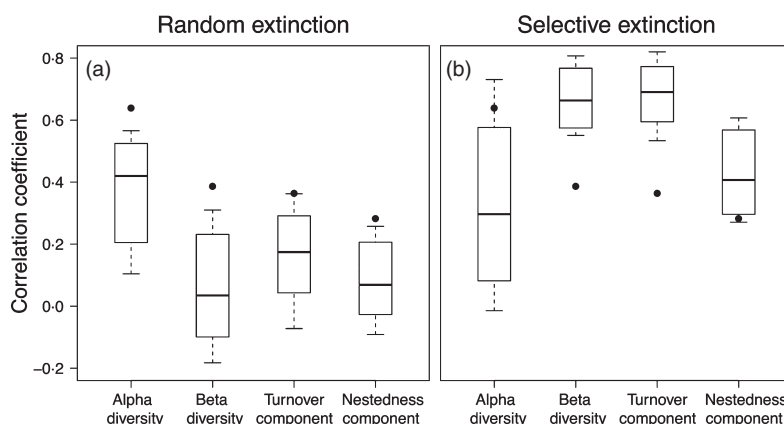


Fig. 4. Results of randomization tests simulating the processes of random and selective extinction in breeding bird communities on 37 study islands in the Thousand Island Lake, China. The random assembly algorithm randomly subsampled species without replacement from the regional pool by maintaining the observed species richness on each island. Selective extinction process was simulated by randomly choosing an 'optimal' species, and then selected species with lowest functional distance to this optimal species until target local species richness reached. We ran 100 randomization tests following the processes of random and selective extinction, respectively. The black dots are the observed correlation coefficients between taxonomic and functional diversities. The middle lines of boxes are the median values of the null distributions. The lower and upper hinges (boundaries of boxes) are the fifth and ninety-fifth quantiles of the null distributions. The lower and upper adjacent values (whiskers below and above box plots) are the minimums and maximums of the null distributions.

Table 1. Results of power regression models for taxonomic and functional alpha diversities against island area (ha) and isolation (m) for breeding birds on 37 islands in the Thousand Island Lake, China

	Coefficient		Intercept	R^2	F
	Area	Isolation			
Taxonomic alpha diversity	0.082***	-0.025	1.45***	0.82	80.84***
Functional alpha diversity	0.057*	-0.053	1.14***	0.17	4.81*

Significant levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

islands, and (ii) significant correlations, and higher than predicted from a null model of random extinction, between taxonomic and functional alpha and beta diversities, thus suggesting the existence of a process of selective extinction. Moreover, by partitioning beta diversity, our results showed that functional nestedness-resultant component dominated overall functional beta diversity due to the loss of species that were vulnerable to habitat loss and fragmentation, whereas turnover component was the dominant component of overall taxonomic beta diversity.

RELATIONSHIPS BETWEEN TAXONOMIC AND FUNCTIONAL DIVERSITIES

In our study, taxonomic and functional alpha and beta diversities were all significantly correlated (Fig. 3). More importantly, the observed correlation coefficients were all larger than those predicted by null expectations of random extinction (Fig. 4a). As shown in Fig. 4b, observed correlation coefficient between taxonomic and functional alpha diversities was higher than the expectation under the process of selective extinction, but observed values for beta diversity and its components were all lower. This could imply the process of selective extinction we simulated in this study are not exactly the one operating in reality. Alternatively, another possible explanation may be that there was still a component of random extinction in our island system. Considering the nature of the islands in the lake, most islands are relative small with area < 2 ha (Fig. 2; Table S1). Bird populations on small islands are generally small. These small populations are therefore vulnerable to local extinction that may be a result of stochastic processes (Si *et al.* 2014). However, the fact that the observed correlations are always larger than predicted from random extinction reinforces the conclusion that the deterministic process of selective extinction operate in this system. In other words, birds that are sensitive to particular environmental conditions, such as habitat loss and fragmentation in this study, disappeared

gradually on particular islands after the lake formed during the process of species relaxation.

ALPHA DIVERSITY–AREA RELATIONSHIPS

Taxonomic and functional alpha diversities both increased with island area, but were not significantly related to isolation (Table 1). The pattern of species richness increasing with island area is well-known as the species–area relationship (SAR) (Rosenzweig 1995), or taxonomic diversity–area relationship (TDAR) used in this study. Functional diversity–area relationship (FDAR) was also proposed recently in the studies of functional diversity (e.g. Mazel *et al.* 2014; Whittaker *et al.* 2014). Generally, the z values of the fitted power functions of diversity–area relationships are between 0.2 and 0.3 across a plethora of studies worldwide as reviewed in Rosenzweig (1995). In this study, the z values of the taxonomic and functional alpha diversities were both below 0.1 (Table 1). The relative low z values indicated that taxonomic and functional alpha diversities of breeding birds were weakly affected by habitat loss compared to other systems (see also plant studies in the same system; Hu *et al.* 2011). One possible reason might be the relatively homogeneous vegetation dominated by *P. massoniana* on the study islands. It could be expected that species loss rates with decreasing area were relative lower in systems with less habitat diversity that supports less richness of niches (Rosenzweig 1995). Another explanation could be that for birds at least (e.g. Great tit, *Parus major*), an individual not only can actively abandon an island that failed to provide enough resources or refugia, but also can use several nearby islands to search food (as we noticed on islands in the field survey). This may mitigate the effects of habitat loss and fragmentation on breeding bird communities, and hence, the TDAR and FDAR relationships are not steep (i.e. low z values).

TURNOVER AND NESTEDNESS-RESULTANT COMPONENTS

Although overall taxonomic and functional beta diversities were both generally low in our study, they differed in

Table 2. Summary of taxonomic and functional beta diversities and its turnover and nestedness-resultant components of breeding birds on 37 study islands in the Thousand Island Lake, China. Each tablet represents mean \pm standard deviation and range of pairwise beta diversity and its two components. Beta-diversity ratio is the relative contribution of nestedness-resultant component to overall beta diversity

	Taxonomic	Functional
Beta diversity	0.21 \pm 0.06 (0.05–0.42)	0.18 \pm 0.10 (0.00–0.47)
Turnover	0.13 \pm 0.07 (0.00–0.36)	0.04 \pm 0.05 (0.00–0.30)
Nestedness	0.08 \pm 0.08 (0.00–0.40)	0.14 \pm 0.11 (0.00–0.47)
Beta-diversity ratio	0.37 \pm 0.30 (0.00–1.00)	0.75 \pm 0.31 (0.01–1.00)

the relative preponderance of the turnover or nestedness-resultant components (Table 2). In this study, the turnover component contributed more to taxonomic beta diversity (beta-diversity ratio < 0.5), whereas the nestedness-resultant component was the dominant component of functional beta diversity (ratio > 0.5) (Table 2). The possible explanation should be related to the biogeography of the lake. In our system, the vast majority of islands in the lake are small islands (*c.* < 2 ha). Bird populations on small islands generally suffer higher stress than on islands with larger size. Consequently, only a portion of birds with certain traits can occur on these small islands (discussed below). It is also the evidence that functionally similar species can still be taxonomically different, so that species composition changes among islands in the lake are mostly because of species replacement, leading to the dominance of turnover pattern in taxonomic dissimilarity.

The possible reason of the dominant nestedness-resultant component in functional beta diversity is that selective extinction, the deterministic process of environmental filtering, played an important role in shaping the patterns of bird functional diversity. Because environmental filtering favours certain traits over others, only birds with abilities to tolerate the abiotic conditions (e.g. generalists or resistant birds) can potentially colonize islands with high stress (Kluge & Kessler 2011), resulting in assemblages on smaller islands are functional subsets of assemblages on larger islands (Fig. 1). For example, we noticed insectivores and understorey birds were very sensitive to island area and most of these birds were absent on small islands. In our research system, the habitats on study islands are relatively homogeneous dominated by *P. massoniana*. Thus, the main factor of the environmental stress was island size. On small islands in the lake, the trophic constraints may explain the absence of insectivores and understorey birds that are sensitive to habitat loss and fragmentation because the lack of required food (i.e. insects) or the lack of specific habitats (Ding *et al.* 2013). Instead, omnivores and canopy birds were not very sensitive to island size (e.g. generalist/resistant species) that distributed widely on islands regard-

less of island size in the lake (Ding *et al.* 2015). As a result, birds with certain traits that are sensitive to habitat loss and fragmentation locally disappeared on smaller islands, but generalist/resistant species can still exist on the vast majority of islands after the lake was formed, leading to the dominant nestedness-resultant component in functional beta diversity.

BETA-DIVERSITY CORRELATES

In this study, taxonomic turnover and nestedness-resultant components significantly decreased and increased with difference in area, respectively, whereas there were no effects on difference in isolation from taxonomic and functional aspects of dissimilarities (Table 3). The relative short distances between islands in our system (see Fig. 2) might explain the lack of distance effects on taxonomic and functional dissimilarities. At least for most birds, this range of distances among islands should not act as dispersal barriers in any case, resulting in no relationships between dissimilarities and difference in isolation. In other words, birds can actively choose to abandon hostile islands and stay on islands with suitable habitats/resources.

The effect of difference in area can be explained by the mechanism of selective extinction. It is obvious that species with larger area requirement are more prone to local extinction on small islands. The rationale is that at least in our study, larger islands generally have weaker environmental stress, and potentially support higher habitat richness, resulting in more richness of niches. Alternatively, small islands support less species richness, which tend to be subsets of larger islands, resulting in the positive relationship between difference in area and taxonomic nestedness-resultant component (Si, Baselga & Ding 2015). Regarding the turnover component, bird communities can still have high replacement from island to island (including the replacement of species sensitive to habitat loss and fragmentation). However, our results suggest that these different species are functionally similar because taxonomic turnover decreased with difference in island area, but functional turnover did not.

Table 3. Results of the multiple regression models between dissimilarity indices and differences in island variables of breeding bird communities on 37 study islands in the Thousand Island Lake, China. Dissimilarity indices include taxonomic and functional beta diversities and its turnover and nestedness-resultant components. Island variables include difference in area (ha) and difference in isolation (m)

	Coefficient				
	Difference in area	Difference in isolation	Intercept	R ²	F
Taxonomic dissimilarity					
Beta diversity	0.0001**	0.0000	0.20	0.18	72.07**
Turnover	−0.0001***	0.0000	0.13	0.17	68.13***
Nestedness	0.0002***	−0.0000	0.06	0.49	314.21***
Functional dissimilarity					
Beta diversity	0.0000	−0.0000	0.19	0.03	11.43
Turnover	−0.0000	0.0000	0.04	0.03	11.23
Nestedness	0.0001	0.0000	0.15	0.06	21.77

Significant levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

CONSERVATION IMPLEMENTATION AND FUTURE PERSPECTIVES

Comparing with taxonomic beta diversity, studies on functional beta diversity are scarcer (Swenson, Anglada-Cordero & Barone 2011). Assessing whether patterns of functional beta diversity and its components are paired with taxonomic beta diversity could help policy-makers set priority areas for protection (Villéger, Grenouillet & Brosse 2013; Mazel *et al.* 2014). For example, larger islands have priority to be protected when nestedness-resultant component dominates overall beta diversity, whereas all island should be considered for protection when turnover contributed more (Baselga 2010). In our study, the contrasting turnover and nestedness-resultant components of taxonomic and functional beta diversities provide a challenge for biodiversity conservation in our system (Table 3), i.e. from the taxonomic point of view, all islands should be protected due to its high turnover component, whereas from a functional perspective, priority efforts should be put on larger islands because of the dominant nestedness-resultant functional component. Additionally, exploring species distributions from multifaceted perspectives in large spatial scale can also provide substantial ecological information to develop an integrative approach for biodiversity conservation, instead of using any one diversity measure as a surrogate for other one (Devictor *et al.* 2010). Further insights could be gained by analysing other taxa with lower dispersal ability, such as small mammals, reptiles and arthropods in this island system, so that we can move a further step to examine the processes of random and selective colonization in community assembly.

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Data accessibility

Data associated this paper are archived in the online Supporting Information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Characteristics of study islands.

Table S2. Paired distances of study islands.

Table S3. Occupancy data of breeding birds.

Table S4. Trait data of breeding birds.

Table S5. Eigenvalues of PCoA axes.

Figure S1. Results of randomization tests.

Appendix S1. R scripts for randomization tests.