

# Functional and phylogenetic structure of island bird communities

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## Summary

1. Biodiversity change in anthropogenically transformed habitats is often nonrandom, yet the nature and importance of the different mechanisms shaping community structure are unclear. Here, we extend the classic Theory of Island Biogeography (TIB) to account for nonrandom processes by incorporating species traits and phylogenetic relationships into a study of faunal relaxation following habitat loss and fragmentation.

2. Two possible mechanisms can create nonrandom community patterns on fragment islands. First, small and isolated islands might consist of similar or closely related species because they are environmentally homogeneous or select for certain shared traits, such as dispersal ability. Alternatively, communities on small islands might contain more dissimilar or distantly related species than on large islands because limited space and resource availability result in greater competitive exclusion among species with high niche overlap.

3. Breeding birds were surveyed on 36 islands and two mainland sites annually from 2010 to 2014 in the Thousand Island Lake region, China. We assessed community structure of breeding birds on these subtropical land-bridge islands by integrating species' trait and evolutionary distances. We additionally analysed habitat heterogeneity and variance in size ratios to distinguish biotic and abiotic processes of community assembly.

4. Results showed that functional–phylogenetic diversity increased with island area, and decreased with isolation. Bird communities on the mainland were more diverse and generally less clustered than island bird communities and not different than randomly assembled communities. Bird communities on islands tend to be functionally similar and phylogenetically clustered, especially on small and isolated islands.

5. The nonrandom decline in species diversity and change in bird community structure with island area and isolation, along with the relatively homogeneous habitats on small islands, support the environmental filtering hypothesis. Our study demonstrates the importance of integrating multiple forms of diversity for understanding the effects of habitat loss and fragmentation, and further reveals that TIB could be extended to community measures by moving beyond assumptions of species equivalency in colonisation rates and extinction susceptibilities.

**Key-words:** biotic homogenisation, competition, deterministic process, environmental filtering, functional trait, habitat fragmentation, null model, phylogenetic structure, selective extinction, stochasticity

## Introduction

Biodiversity change in anthropogenically transformed habitats is often nonrandom, where species are eliminated

from habitats because of selective processes that favour some species over others. This is especially true on small fragment islands, which result in specific or unique local environmental conditions and are more homogeneous than in continuous habitats (Laurance *et al.* 2011), thus potentially increasing the importance of environmental

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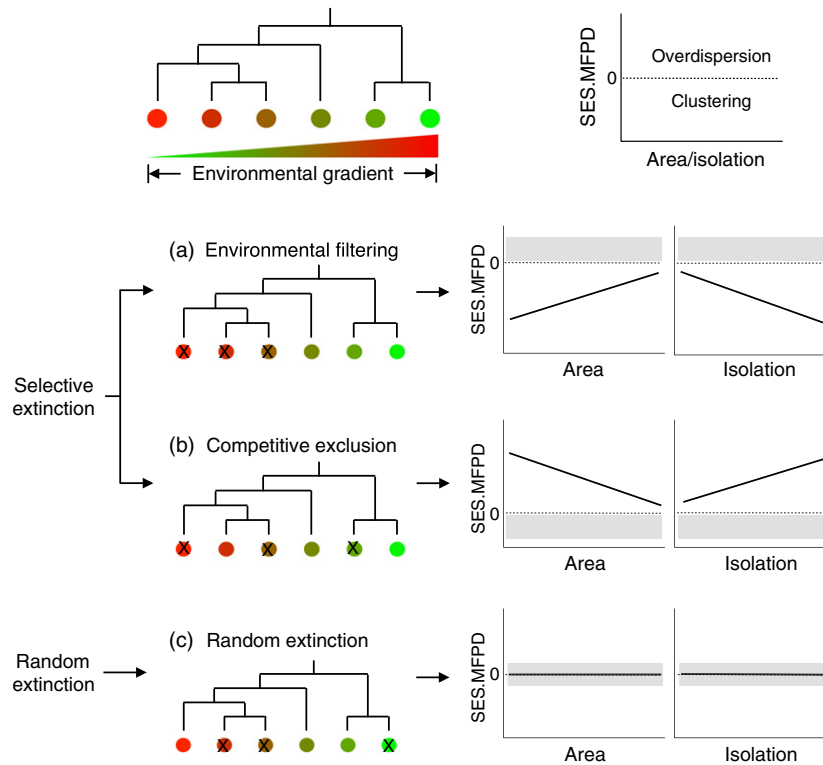
filtering and competitive exclusion (Cavender-Bares *et al.* 2009; Arroyo-Rodríguez *et al.* 2012; Cadotte & Davies 2016). Local communities are structured by a combination of processes that depend on environmental conditions, biotic interactions (e.g. competition) and dispersal, and it is unclear if these processes act independently, interactively or sequentially during community assembly (Cardillo, Gittleman & Purvis 2008; Bregman *et al.* 2015; Wilson *et al.* 2016). Thus, understanding the mechanisms driving species loss in fragment islands can provide much-needed guidance in the design and implementation of conservation strategies and reserve design.

The classic Theory of Island Biogeography (MacArthur & Wilson 1967) (hereafter, TIB) provides a potential basis for assessing the underlying processes of community assembly and species loss in fragment islands. For example, communities on islands created by anthropogenic activities may be largely shaped by local extinctions, with smaller islands exhibiting the highest extinction rates (Laurance *et al.* 2011; Benchimol & Peres 2015), and isolated faunas relax to lower numbers of species, resulting in biodiversity declines (Gibson *et al.* 2013; Si *et al.* 2014; Halley *et al.* 2016). TIB and subsequent metacommunity theories have been used to predict species richness patterns on fragment islands through colonisation–extinction dynamics (Holyoak, Leibold & Holt 2005; Triantis *et al.* 2010), but TIB does not provide the framework to predict how altered assembly mechanisms result in the nonrandom loss of species. This is because classic TIB assumes species are all functionally equivalent with neutral community dynamics. Although the classic TIB briefly discusses the importance of traits, such as dispersal ability (i.e. table 8 on page 81 in MacArthur & Wilson 1967), it still disregards species differences in its core mathematical model that might alter their susceptibility to habitat loss and fragmentation (Püttker *et al.* 2015; Si *et al.* 2016). Despite a half century of research on TIB and its applications to understanding habitat loss and fragmentation (Warren *et al.* 2015), the processes driving community assembly on fragment islands that rely on species' ecological or functional differences have not yet been investigated comprehensively (but see discussions in Cardillo, Gittleman & Purvis 2008; Emerson & Gillespie 2008; Whittaker *et al.* 2014; Jacquet *et al.* 2017). Here, we expand TIB by integrating species' functional and phylogenetic measures, and assess community structure of island avifaunas based on species similarity.

There are two opposing scenarios of community assembly that might explain local extinctions following habitat loss and fragmentation: selective (or nonrandom) and random extinction (Arroyo-Rodríguez *et al.* 2012; Terzopoulou *et al.* 2015; Si *et al.* 2016) (Fig. 1). Selective extinction depends on various nonrandom processes, such as environmental filtering and competitive exclusion that creates distinct community patterns that are different from that expected under random assembly (MacArthur & Levins 1967; Purvis *et al.* 2000; Chase & Leibold 2003;

Götzenberger *et al.* 2012). In addition, these nonrandom processes act on species traits including the influence of local environmental conditions on species' fitness and biotic interactions, including competition, pathogens and other consumptive trophic relationships (Cavender-Bares *et al.* 2009; Gravel *et al.* 2011; Harvey & MacDougall 2014). The environmental influences of small fragments might reflect that local abiotic conditions are more homogenous or stressful, eliminating less fit species (Webb *et al.* 2002; Kraft *et al.* 2015). For example, species requiring large territories or with limited dispersal ability will have a higher probability of local extinction in response to fragmentation (Bregman *et al.* 2015). It is not necessary that species have negative fitness in certain environments (*sensu* Kraft, Godoy & Levine 2015), but rather given the competitive landscape, having lower fitness effectively precludes certain species (Cadotte *et al.* 2015). Consequently, only subsets of species sharing similar functional traits can persist or outcompete other species on small islands (Si *et al.* 2016), resulting in a higher degree of ecological similarity on small islands (i.e. appearing functionally or phylogenetically clustered). Similarly, remote islands might also result in communities comprising more similar species because species with strong dispersal ability are likely to establish populations on isolated islands (Emerson & Gillespie 2008). We can thus predict that communities on smaller, more isolated fragments should appear functionally and phylogenetically clustered, while communities on the mainland, which lack dispersal limitation and provide more environmental opportunities should tend towards being representative of the regional species or overdispersed if competition is important or if there is high habitat heterogeneity (Fig. 1a).

While it may seem to expect intuitively that island area and isolation cause clustering, the alternative scenario is that certain biotic interactions, especially interspecific competition, might limit the coexistence of species with similar niches because resources are more limited in smaller fragments or islands (Diamond 1975; Helmus *et al.* 2007). The importance of competition is thought to increase on small islands because the overall pool of resources is reduced, increasing resource limitation and the potential for interspecific competition (Feeley 2003; Cardillo, Gittleman & Purvis 2008). Consequently, closely related species that share similar traits or resource requirements experience the greatest competition and are more likely to be competitively excluded because of the limited resources (Gómez *et al.* 2010; Sobral & Cianciaruso 2016), or priority effects that inhibit the colonisation of closed related species (Fukami 2015; Klingbeil & Willig 2016), leading to higher degrees of functional and phylogenetic overdispersion on fragment islands (Fig. 1b). Furthermore, we could also expect that isolated communities are overdispersed relative to the mainland if, for example, facilitation increases the probability of colonisation, although this may not be likely if dispersal ability is the limiting factor.



**Fig. 1.** Hypothetical community assembly processes under the scenarios of selective and random extinction, and the predicted patterns within the framework of the Theory of Island Biogeography by integrating species traits and phylogenies. (a) Local environmental condition eliminates vulnerable species, resulting in bird communities more clustered on smaller and remoter islands. (b) Competition eliminates ecologically similar species, leading to higher degree of overdispersion on smaller islands; facilitation might increase the probability of colonisation, resulting in communities on remoter islands more overdispersed. (c) Random extinction assumes species have an equal probability of extinction disregarding species identity and island properties, leading to random functional and phylogenetic patterns. The circles represent species, and red indicates species with a higher vulnerability to environmental stress than the green ones. SES.MFPD is the standardised effect size of the mean functional–phylogenetic distance. Shaded regions indicate the corresponding ranges of expected SES.MFPD of bird communities on the mainland. See more details for SES.MFPD in Materials and methods. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

It should be noted that competition can also eliminate more different and less related species, and can result in community clustering (Mayfield & Levine 2010). Thus, bird communities on small islands may be more ecologically clustered than on large islands because of increased competition, and we can expect similar patterns as the scenario of environmental filtering (Fig. 1a). In reality, abiotic and biotic mechanisms are not easily separable, but by linking patterns of habitat heterogeneity and dominant species traits to island area and isolation, we can better understand the mechanisms driving community assembly on fragment islands.

Given that TIB assumes that extinction and colonisation rates are essentially independent of species identity and that extinctions are functionally and phylogenetically random (Emerson & Gillespie 2008; Whittaker *et al.* 2014), we can use TIB as a null model for changes in functional or phylogenetic patterns with fragmentation. Thus, the null expectation is that there should be no difference in the community patterns from mainland and island observations since all species have an equal probability of extinction regardless of species traits and island properties (Fig. 1c).

Islands created by dam construction, such as the Thousand Island Lake in China, which is the focus of this study, can be viewed as a particularly effective and unique system to explore the functional/phylogenetic community structure and underlying mechanisms in community assembly at local scales (Whittaker & Fernández-Palacios 2007; Warren *et al.* 2015). Because of the clear ecological background and relatively short history (57 years) of the lake, the evolutionary processes, such as *in situ* speciation and character displacement, can be excluded in our analyses (Cardillo, Gittleman & Purvis 2008; Graham & Fine 2008). In this study, we examined breeding bird communities across 36 islands that differ in area and isolation. The goal of this study is to place functional–phylogenetic analyses of community structure of island birds within the framework of TIB, with the broader goal of potentially extending TIB to examining community assembly by accounting for species' ecological nonequivalence (Fig. 1). Here, we test the following questions: (i) Do patterns of functional–phylogenetic diversity (FPD) of island birds show similar patterns to taxonomic diversity, or does accounting for bird species' similarity provide new

insights into TIB? Specifically, (ii) are the bird communities clustered or overdispersed on study islands? And (iii) do bird community structures vary with island area and isolation?

## Materials and methods

### STUDY AREA AND ISLANDS

The Thousand Island Lake, China (29°22'–29°50'N, 118°34'–119°15'E) was created in 1959 by the construction of the Xin'anjiang Dam for hydroelectric production that resulted in the flooding of an area of approximately 580 km<sup>2</sup> (Fig. 2). The lake created 1078 islands with areas >2500 m<sup>2</sup> when the water, which fluctuates annually, reaches 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 davidiana*, *Grewia biloba* and *Loropetalum chinense* (Si *et al.* 2014). The lake region has a typical subtropical monsoon climate, with marked seasonality. The annual precipitation of the region is 1430 mm, mainly concentrated in rainy season between April and June. The average annual temperature is 17.0 °C, and the daily temperature ranges from –7.6 °C in January to 41.8 °C in July (Wang, Chen & Ding 2011; Si, Baselga & Ding 2015).

We selected 36 study islands that encompass as much variation in area and isolation as possible (Fig. 2). The gradient of island area ranges from 0.57 ha to c. 1300 ha, and their isolation ranges from about a 20-m separation from the nearest shore of the mainland to over 3.71 km. We characterised islands in terms of area and isolation (Fig. 3c), because these variables are recognised as the key determinants of the colonisation and extinction probabilities in the framework of TIB (MacArthur & Wilson 1967; Losos & Ricklefs 2010). 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). Compared with the distance-based isolation, we also estimated the buffer-based isolation that measures the influence of neighbouring islands as the fraction of buffer area that is water within a 2-km buffer region around a focal island (Si *et al.* 2014). We found that results based on both isolation measures were largely identical, so we used the straightforward island-to-mainland distance as the isolation measure in this study (Appendix S1). Between April and November in 2007, we intensively surveyed habitat types on study islands, and classified the habitats on each island into seven categories: coniferous forest, broad-leaved forest, mixed coniferous broad-leaf forests, bamboo groves, shrubs, grasses and farmland (Wang, Chen & Ding 2011) (Table S2).

### BIRD COMMUNITY DATA

We surveyed the bird communities on these 36 study islands during breeding seasons (April–June) annually from 2010 to 2014. Sampling effort on each island was roughly proportional to the logarithm of island area (Schoereder *et al.* 2004). As a result, eight transect trails were sampled on the largest study island (area >1000 ha), four on the two islands between 100 and 1000 ha, two on the four islands between 10 and 100 ha, and one on each of the remaining small islands (c. 1 ha for most islands) (Wang, Chen & Ding 2011) (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 a Global Positioning System to record the total length of transects on each island, and used stratified random placement to capture all habitat types on study islands, and then collected bird occupancy data along these transects. In each survey, observers walked each transect at a constant speed (c. 2.0 km × h<sup>-1</sup>), and recorded all the birds seen or heard on the survey islands. We excluded high-flying species passing over the islands during

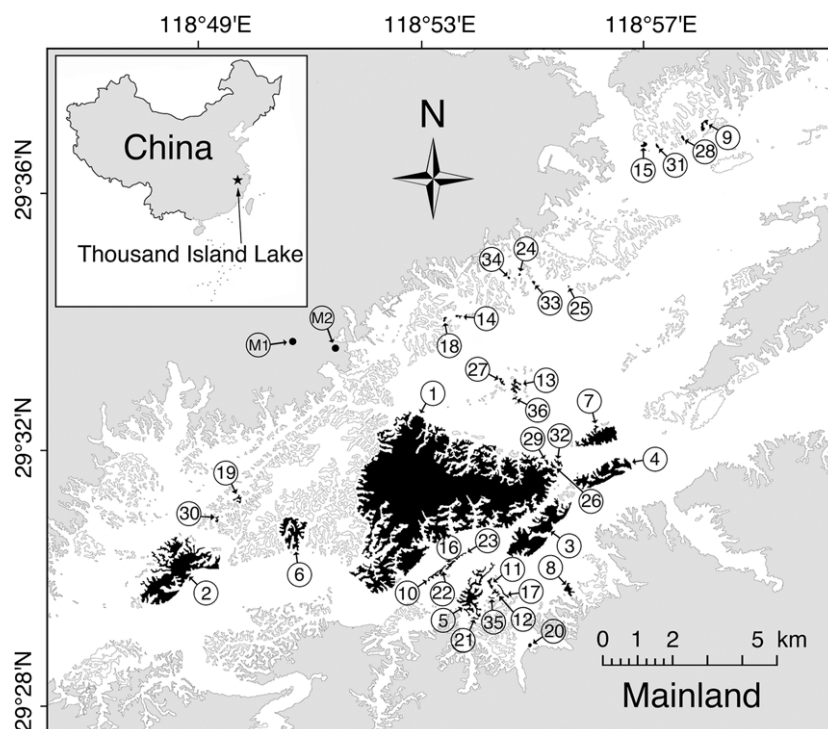
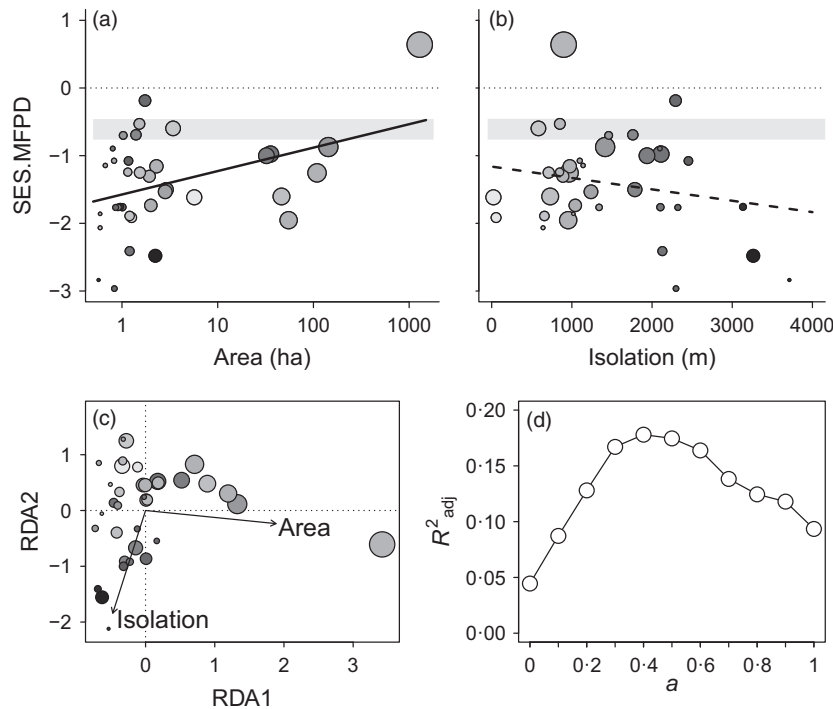


Fig. 2. The research sites (36 study islands and two mainland sites) in the Thousand Island Lake region, Zhejiang Province, eastern China. Study islands were numbered in order of decreasing area.





**Fig. 3.** Bird communities and the standardised effect size of the mean functional–phylogenetic distance (SES.MFPD). (a, b) The relationships between SES.MFPD and island variables [area (log-transformed, ha) and isolation (m)] using linear regression models, compared with bird communities from the mainland. (c) Redundancy analysis (RDA) of 57 species on 36 study islands with island variables fitted into the ordination. (d) Adjusted  $R^2$  values of the regressions between SES.MFPD and island variables across the range of  $a$  (the phylogenetic weighting parameter). The black lines show the predicted values of SES.MFPD for each island variable that were obtained by holding another island variable constant at their means. Shaded regions indicate the corresponding ranges of observed SES.MFPD of bird communities on the mainland. The larger size of the dots indicates the island with larger area, and darker shaded dots indicate the more isolated islands and vice versa.

surveys, and only included confident records. We also recorded species' behaviours on each island in field surveys, such as those carrying nesting materials, strong territorial singing and fighting (i.e. indirect evidence), as well as direct evidence in the form of observed nests and juveniles. We entered the species as 'present' in an island only if at least one of these kinds of breeding evidence was recorded (Si *et al.* 2014). Over the course of the entire study, we surveyed each transect on these islands 51 times. Surveys ran from half an hour after dawn to 11:00 h in the mornings and from 15:00 h to half an hour before sunset in the afternoon. We did not conduct bird surveys if there was heavy rain, high wind or high temperature. We changed the direction the observer walked on each transect randomly, aiming to remove the potential survey bias (Wang, Chen & Ding 2011; Si *et al.* 2014).

In addition to the field surveys on islands, we selected two mainland sites (M1 and M2; Fig. 2) that have similar habitats as on islands (Table S1). We also surveyed each transect 51 times on the mainland using the same sampling protocol as on study islands during breeding seasons annually from 2010 to 2014. In this study, the mainland dataset was independent of island datasets that was used as a baseline for comparison only. For both datasets, we considered only terrestrial breeding birds, excluding diving birds, ducks, gulls, herons and shorebirds whose habitats extensively rely on water. The rationale of considering only breeding birds in our study is that during breeding seasons, breeding birds have fixed territories, intensively compete for nesting and other resources, and potentially reduce the frequency of movements among islands. During the course of our study, we

recorded a total of 57 terrestrial breeding birds on study islands, and 55 terrestrial breeding birds on the mainland (Table S3).

#### COMMUNITY PHYLOGENY AND FUNCTIONAL TRAITS

To obtain the phylogenetic tree, we pruned the global phylogenetic tree of birds from *BirdTree* (<http://birdtree.org>) under the option of 'Hackett All Species: a set of 10 000 trees with 9993 OTUs each' (Jetz *et al.* 2012) to include only 57 island birds from this study. We then sampled 5000 pseudo-posterior distributions and constructed the Maximum Clade Credibility tree using mean node heights by the software *TreeAnnotator* v1.8.2 of the BEAST package (Drummond & Rambaut 2007; Ricklefs & Jønsen 2014). We used this resulting tree for all subsequent analyses on phylogenetic analyses (Fig. S1). Similar to the procedures for island birds' tree, we also constructed the phylogenetic tree of 55 mainland birds for further analyses (Fig. S2).

We chose body mass, main feeding guild and main feeding stratum for breeding birds in this study as their functional traits (Table S4). Presence or absence was scored for main feeding guild (carnivore, granivore, insectivore, omnivore and nectivore), and main feeding stratum (ground, understorey, midstorey, canopy and air). Body mass is widely considered as the single most informative trait of animal species because it is directly related to individuals' resource utilisation, trophic level and extinction vulnerability (Ding *et al.* 2013). The traits of feeding guild and stratum are also related to resource requirements and sensitivity

to habitat change that have been commonly used in the studies of bird functional diversity (e.g. Petchey *et al.* 2007; Si *et al.* 2016). Trait data were collected from field surveys and the literature (Zhuge 1990; Zhao 2001).

## DIVERSITY MEASURES

To estimate multiple facets of bird diversity, we integrated species traits and phylogenies using a method recently proposed by Cadotte, Albert & Walker (2013). We calculated the functional distance (Gower distance) (Gower 1966) of all traits using the function *gowdis* in R package *FD* (Laliberté & Legendre 2010), and the phylogenetic distance (patristic distance) using the function *cophenetic* in R package *stats*. We then combined functional and phylogenetic distances into a single measure, the functional–phylogenetic distance matrix (Cadotte, Albert & Walker 2013) using the function *funct.phylo.dist* in R package *pez* (Pearse *et al.* 2015). The calculated functional–phylogenetic distance matrix measures the distance between different species, and includes a phylogenetic weighting parameter,  $a$ , which scales the relative contribution of functional and phylogenetic distances to the functional–phylogenetic distance matrix. For example, when  $a = 0$ , only functional distance contributes to the functional–phylogenetic distance matrix, and only phylogenetic distance when  $a = 1$ . Otherwise, at an intermediate value of  $a$ , both of functional and phylogenetic distances contribute to the resulting functional–phylogenetic distance matrix. In this study, we varied  $a$  from 0 to 1 (in intervals of 0.1), and the best  $a$  was determined by the highest adjusted  $R^2$  values of the regression model (described below). By integrating species traits and phylogenies, this combined method could overcome the shortcomings of approaches that are based exclusively on functional or phylogenetic distance (Mayfield & Levine 2010; Cadotte, Albert & Walker 2013).

To compare diversity patterns with taxonomic diversity (measured as species richness), we calculated the distance-based FPD using the function *dbFD* in R package *FD*, following the method of calculating the distance-based functional diversity by replacing the original functional distance (e.g. Gower distance) as the functional–phylogenetic distance matrix (Villéger, Mason & Mouillot 2008; Cadotte, Albert & Walker 2013). To infer community assembly mechanisms (i.e. environmental filtering vs. competitive exclusion) of breeding birds on each island, we calculated the standardised effect size (SES) of the mean functional–phylogenetic pairwise distance (MFPD) (SES.MFPD) using the function *ses.mpd* in R package *picante* (Kembel *et al.* 2010). SES.MFPD compared the observed MFPD with 999 randomised communities using tip shuffling null models that was calculated as:  $SES.MFPD = (X_{obs} - X_{null})/SD_{null}$ , where  $X_{obs}$  is the observed value of MFPD,  $X_{null}$  is the mean of the simulated values from 999 randomised communities, and  $SD_{null}$  is the standardised deviation of the simulated values. SES.MFPD could thus be interpreted in terms of community assembly patterns: the negative values of SES.MFPD indicate community clustering, and positive values indicate community overdispersion (Webb *et al.* 2002; Fig. 1).

## STATISTICAL ANALYSES

We log-transformed island area to normalise model residuals, and found that there was no significant correlation between

island area and isolation (Pearson's  $r = -0.21$ ,  $P = 0.21$ ). We accordingly used redundancy analysis to assess the patterns of species composition and the contributions of island area and isolation (Legendre & Legendre 2012).

We calculated the values of SES.MFPD across the range of  $a$  values. We then estimated the adjusted  $R^2$  values of the regressions between derived SES.MFPD and island variables (area and isolation) using linear regressions. The adjusted  $R^2$  value in this study reached its maximum (0.18) when  $a = 0.4$  (Fig. 3d). We therefore calculated FPD at  $a = 0.4$ , and regressed FPD on each island against island variables using linear regression models respectively. Additionally, we tested the spatial autocorrelation of richness, FPD and SES.MFPD using the global Moran's  $I$  (Legendre & Legendre 2012) using the function *Moran.I* in R package *ape*. We found no evidence of significant spatial autocorrelation (i.e.  $P > 0.05$ ; Table S5), so we did not consider it in our analyses.

Because both biotic and abiotic processes can produce clustering (i.e. Fig. 1a), we additionally analysed habitat heterogeneity and variance in size ratios (VSR) as an attempt to detect potential drivers. First of all, we defined habitat richness as the number of habitat types on each island (Table S2). Because habitat richness significantly increased with island area in this study ( $R^2 = 0.84$ ,  $P < 0.001$ ; Fig. S3a), we used a new predictor, habitat heterogeneity, which was the regression residuals of habitat richness on island area. We then regressed habitat heterogeneity against diversity and community measures. If smaller islands exhibit both clustered communities and lower habitat heterogeneity, we can infer that the environment has a disproportionate influence on community assembly. Alternatively, to test whether community assembly is driven by competition, we evaluated the evenness in the spacing between the log-transformed ranked trait values (i.e. VSR) for species within a community (Cadotte & Davies 2016). If competition is the main driver of community assembly on the islands, traits will be evenly spaced (low VSR). To compare the observed VSR with sampled VSR, we generated null communities by randomly selecting species from the island species pool and maintaining species richness on each island with 999 runs. We can thus expect observed VSR of each island would be significantly lower than the 95% confident intervals of sampled VSR from null communities. In addition, we examined the effect of competition in a finer extent at the guild level. Bird guilds are defined as groups of bird species that exploit the same class of environmental resources in a similar way (Simberloff & Dayan 1991; Ding *et al.* 2015). We thus classified breeding birds based on their dietary categories and foraging strata, and included only bird guilds on each island with more than three species to guarantee the statistical requirement. In our analysis, we used four guild groups (insectivores, omnivores, canopy and understorey guilds). We generated null distributions for each guild by randomly sampling species in the same guild from the island species pool and maintaining species richness of each guild on each island with 999 runs. Finally, we regressed SES.MFPD of each guild on each island against island area and isolation, and also ran VSR analyses for each guild to examine the effect of competition (see more details about the guild-level analyses of SES.MFPD and VSR in Appendix S1).

## Results

A total of 57 terrestrial breeding birds were recorded on 36 study islands with a mean of 23 species per island

( $\pm$ SD 6, range 16–44; Table S1). As shown in Fig. S4a,b, richness increased with island area ( $t = 10.88$ ,  $P < 0.001$ ), but did not significantly decrease with isolation ( $t = -0.35$ ,  $P = 0.73$ ; Table S6). However, FPD increased with island area ( $t = 5.85$ ,  $P < 0.001$ ) and decreased with island isolation ( $t = -4.31$ ,  $P < 0.001$ ; Fig. 4). Additionally, the ordination of redundancy analysis showed that island area and isolation were both significant explanatory variables of community compositional differences ( $R^2 = 0.15$ ,  $P < 0.001$ ; Fig. 3c), indicating their important contributions to explaining the community structure of island birds.

SES.MFPD of bird communities on study islands ranged from  $-2.96$  to  $0.64$  with a mean value of  $-1.41$  ( $\pm$ SD  $0.72$ ), indicating that clustering was most commonly observed, except for the largest island (Island 1: SES.MFPD =  $0.64$ ), which was overdispersed (Fig. 3a,b). SES.MFPD increased with island area ( $t = 2.47$ ,  $P = 0.02$ ), and did not significantly decrease with isolation ( $t = -1.29$ ,  $P = 0.21$ ; Fig. 3a,b; Table S6). For the guild-level analyses, SES.MFPD showed generally clustering patterns as similar as those from the island-level analyses (Table S7; Fig. S5).

Species richness, FD, PD and FPD significantly increased with habitat heterogeneity, respectively (Table S8). However, none of SES.MFPD, SES.MFD and SES.MPD had significant relationships with habitat heterogeneity (Table S8). The analyses of VSR of body mass showed that observed values were not significantly lower than sampled values from null communities, neither for all species (Fig. S6) nor each guild (Fig. S7) on each island. Instead, the observed VSR on two islands (Islands 17 and 35) for all species, as well as the observed VSR on Island 17 for omnivores were significantly higher than sampled VSR (Figs S6 and S7b).

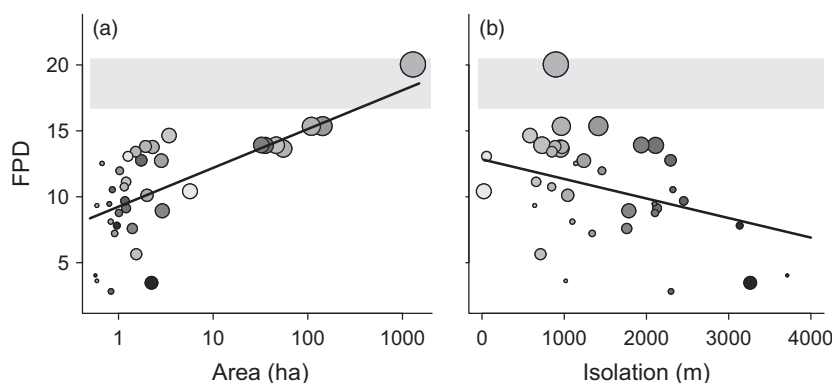
Bird communities on the mainland had higher values of richness, FPD and SES.MFPD (richness: mean 45, range 38–52; FPD: mean 18.59, range 16.67–20.50; SES.MFPD:

mean  $-0.52$ , range  $-0.73$  to  $-0.31$ ; Figs 3a,b; 4a,b and S4a,b). In other words, bird communities on the mainland were more diverse and generally less clustered than island bird communities and not much different than randomly assembled communities.

## Discussion

In this study, our results showed that richness and SES.MFPD show similar responses to island size and isolation: significantly increasing with island area, and decreasing with isolation non-significantly. However, FPD increased with island area, and decreased with isolation both significantly; this relationship might provide some evidence of the distance effect expected by TIB, which has not been detected in our previous studies when analysing bird diversity without incorporating species traits and phylogenies (see Si *et al.* 2014). In this study, bird communities on islands were all more clustered than null communities, except for the largest island, supporting the overriding importance of environmental filtering in influencing bird community assembly, and perhaps following by competitive or trophic interactions. Additionally, bird communities on smaller islands, which had fewer habitat types, were more clustered than on larger islands. While the decline of species richness on small and isolated islands is expected by TIB, our results reveal that this decline is nonrandom and that community structure changes with island area and isolation.

Integrating functional traits and phylogenies (Cadotte, Albert & Walker 2013) demonstrates a potentially powerful approach for revealing underlying mechanisms in shaping community structure on fragment islands. In this study, adjusted  $R^2$  values of the relationships between SES.MFPD and island variables peaked at an intermediate value of the phylogenetic weighting parameter ( $a = 0.4$ ), indicating that both functional and phylogenetic information contribute to explaining island community



**Fig. 4.** The relationships between functional–phylogenetic diversity (FPD) and island variables [area (log-transformed, ha; a) and isolation (m; b)] using linear regressions. The black lines show the predicted values of FPD for each island variable that were obtained by holding another island variable constant at their means. Shaded regions indicate the corresponding ranges of observed FPD of bird communities on the mainland. The larger size of the dots indicates the island with larger area, and darker shaded dots indicate the more isolated islands and vice versa.

structure. More interestingly, when combining species traits and phylogenies, we found that FPD significantly decreased with isolation, suggesting that bird communities on remoter islands tended to be more clustered and more over dispersed on closer islands (Fig. 3b). However, none of richness, FD or PD alone showed a significant relationship with isolation (Fig. S4). Accordingly, we observed that SES.MFPD significantly increased with island area even though neither the pure functional nor phylogenetic components (SES.MFD and SES.MPD respectively) showed significant relationships with area (Fig. S8). It suggests that the integrated measure is more ecologically meaningful than either component, separately, because they both capture some degree of meaningful ecological differences, but are not synonymous measures.

Our results revealed that bird communities on islands were all more clustered than null communities, except the largest island, and we further support the inference of environmental filtering as the main driver of community assembly. Consequently, only birds with their niches represented on more homogeneous islands (i.e. smaller islands; Fig. S3a), or with the ability to tolerate higher environmental stress were selected over others (Kluge & Kessler 2011), resulting in these persisting species becoming nonrandom subsets of the larger biota. For example, top predators that have relatively large body mass and require large territories, were absent on small islands (Table S3). In addition, trophic constraints on small islands may also explain the absence of species as small islands support less available food types (i.e. insects) (Gravel *et al.* 2011; Harvey & MacDougall 2014). In contrast to these species, omnivores and canopy birds (i.e. generalist/resistant species) are distributed widely on our study islands and are not very sensitive to habitat loss and fragmentation (Ding *et al.* 2013; Si *et al.* 2016). This inequality leads to mostly generalist or resistant species persisting on the islands, and thus bird communities became homogenised and clustered on smaller islands (Boyer & Jetz 2014; Harvey & MacDougall 2014).

Even though the relatively small distances between islands might not be a barrier for most birds (Si *et al.* 2014), we found that island isolation also resulted in lower diversity (measured by FPD). This result reveals that species with particular traits were unlikely to colonise more distant islands, or simply due to fear of overwater dispersal (Diamond 1981). For example, we found Silver pheasant (*Lophura nycthemera*) and Chinese bamboo partridge (*Bambusicola thoracicus*) were absent on the three most isolated islands (Islands 13, 27 and 36; Table S3) in our system. Although *L. nycthemera* or *B. thoracicus* could have the opportunity to fly over the water surface between two islands, they might still fail to reach relatively remote islands due to the limited dispersal abilities or willingness. On the contrary, we found Streak-breasted scimitar babbler (*Pomatorhinus ruficollis*), a common passerine bird in our system, was also absent on these three remotest islands (Table S3). It might be simply

explained that although they might have the ability to reach remote islands, they are likely unwilling to fly over open water. As a result, only birds with better dispersal capacities without psychological fear have the ability to reach remote islands separated by relatively wider water surface, resulting in lower diversity and more clustered bird communities on more isolated islands.

In addition to the nonrandom processes (e.g. environmental filtering as we detected in our system), other processes such as competition and stochasticity might still play roles in shaping bird community structure in our island system, given the relatively low amount of variations explained (i.e.  $R^2 = 0.18$ ). For natural experiments, it is always difficult to infer mechanisms from patterns (McIntire & Fajardo 2009). Although we did not detect the effect of competition at both island and guild levels (Figs S5–S7), competition might still exist in our system. For example, it is possible that groups of similar species coexisting on islands might be just superior competitors but weaker dispersers (e.g. Levins & Culver 1971). However, we did not see the direct evidence of competition from our results. To detect the effect of competition directly, additional studies or controlled experiments are needed (e.g. Schoener 1983; Mayfield & Levine 2010). Moreover, it is widely recognised that island bird communities undergo stochastic colonisation and extinction events, and local environmental contingency could result in the appearance of stochasticity (Cardillo, Gittleman & Purvis 2008; Emerson & Gillespie 2008; Klingbeil & Willig 2016). We should expect that bird communities on small islands have a higher degree of stochasticity in their assemblages (Fig. S9c). However, it is challenging to simply assign the variation to stochasticity in this study because: (i) we might have not measured important traits; (ii) other physical aspects of islands or other large-scale features could also influence community structure; and (iii) despite our attempts to combine traits and phylogeny, the relevant community structure could be an inherently multivariate problem requiring more sophisticated analyses. Regardless, further studies are required to explore the relative contributions of stochasticity (e.g. chance colonisation and ecological drift) and determinism (e.g. environmental filtering and interspecific competition) in structuring community assembly, and to determine the generality of our findings in other fragmented landscapes, as well as on oceanic islands by incorporating species' evolutionary processes (Strong, Szyska & Simberloff 1979; Travis & Ricklefs 1983; Losos *et al.* 1998; Schluter 2000; Emerson & Gillespie 2008).

In conclusion, our study used island biogeography as the backdrop to test hypotheses about the effects of island area and isolation on community structure. We show that bird communities on islands tend to be functionally similar and phylogenetically clustered, especially on small and isolated islands. Furthermore, the nonrandom decline in species diversity and change in bird community structure with island area and isolation following habitat loss and



fragmentation support the environmental filtering hypothesis. Our study demonstrates the importance of integrating multiple forms of diversity for understanding the effects of habitat loss and fragmentation. Perhaps more importantly, we show that TIB offers predictions and insights into the mechanisms of community assembly by moving beyond assumptions of species equivalency in colonisation rates and extinction susceptibilities.

### Authors' contributions

X.S., M.W.C., A.B. and P.D. conceived the ideas; X.S. and P.D. designed the study; X.S., D.Z., Y.Z., J.L., Y.W., S.W. and P.D. collected field data; X.S. analysed the data; X.S. and M.W.C. led the writing, and all authors contributed critically to the drafts and gave final approval for publication.

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### Data accessibility

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

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Table S1.** Characteristics of study islands and mainland sites.

**Table S2.** Habitat types on study islands.

**Table S3.** Occupancy data of breeding birds on islands and the mainland.

**Table S4.** Trait data of breeding birds on islands and the mainland.

**Table S5.** Results of spatial autocorrelation test for island birds.

**Table S6.** Results of linear regressions between diversity/community measures and island variables.

**Table S7.** Results of linear regressions between SES.MFPD for each guild and island variables.

**Table S8.** Results of simple linear regressions between diversity/community measures and habitat heterogeneity.

**Table S9.** Species richness of each guild on study islands.

**Fig. S1.** Phylogenetic tree of island birds.

**Fig. S2.** Phylogenetic tree of mainland birds.

**Fig. S3.** Relationship between island variables and habitat heterogeneity.

**Fig. S4.** Relationships between diversity measures and island variables.

**Fig. S5.** Relationships between SES.MFPD and island variables for each guild.

**Fig. S6.** VSR distributions of body mass for island birds.

**Fig. S7.** VSR distributions of body mass for each guild of island birds.

**Fig. S8.** Functional and phylogenetic community structure.

**Fig. S9.** Relationships between mean functional–phylogenetic distance and island variables.

**Fig. S10.** Bird diversity and community structure that incorporate species similarity.

**Appendix S1.** Supporting methods on isolation measures, randomisation tests, and guild-level analyses of SES.MFPD and VSR.