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RESEARCH ARTICLE

Nearby large islands diminish biodiversity of the focal island by a negative target effect

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Abstract

1. The Equilibrium Theory of Island Biogeography postulates that larger and closer islands support higher biodiversity through the dynamic balance of colonization and extinction processes. The negative diversity–isolation (i.e. the distance to the mainland) relationship is derived based on the assumption that the mainland is the only source pool for island biotas. However, nearby islands could also act as species sources for focal islands via a source effect. In this study, we move a further step and hypothesize that nearby islands may reduce bird colonizers of the focal island and diminish its biodiversity, resulting in a negative target effect.
2. To test our hypothesis, we assessed the effects of island area and isolation (metrics considering both the mainland and nearby islands) on taxonomic (i.e. species richness), functional and phylogenetic diversity of terrestrial breeding birds on 42 islands in the largest archipelago of China, the Zhoushan Archipelago. Furthermore, we compared the predictive power of the distance to the large island under a set of relative area thresholds and the relative area of nearby islands on species richness under a set of distance thresholds to explore the role of nearby islands as a source and/or target island.
3. We found that island area had a positive effect on species richness, phylogenetic diversity and functional diversity, while the distance to the mainland had a negative effect only on species richness. Species richness on the focal island increased with increasing distance to the nearest larger island, indicating the negative target effect. Furthermore, the negative target effect depended on the area of nearby islands relative to the area of the focal island.
4. Our finding of the negative target effect suggests islands located between the mainland and the focal island can be not only sources or stepping stones, but also colonization targets. This result demonstrates the importance of considering multiple geographical attributes of islands in island biogeographic studies, especially the characteristics related to source and/or target effects.

Duorun Wang and Yuhao Zhao contributed equally to this work and should be considered cofirst authors.

KEYWORDS
bird, functional diversity, island biogeography, phylogenetic diversity, target effect, Zhoushan Archipelago

1 | INTRODUCTION

The Equilibrium Theory of Island Biogeography (ETIB) postulates that island area and isolation are the main determinants of insular biodiversity, yielding the positive diversity–area and negative diversity–isolation relationships (Lomolino & Brown, 2009; MacArthur & Wilson, 1967). The positive diversity–area relationships on islands have been intensively examined (Lomolino, 1982; Matthews et al., 2019). However, the diversity–isolation relationships have been less studied (Carter et al., 2020; Weigelt & Kreft, 2013). The relatively few studies of diversity–isolation relationships may be due to the complexity of choosing biologically meaningful measures of isolation for various insular taxa (Weigelt & Kreft, 2013). In most cases, isolation is calculated as the Euclidean distance between the source (i.e. the mainland) and the focal island, evidenced by the studies of long-distance dispersal events from the mainland to remote islands (Alsos et al., 2007; Harbaugh & Baldwin, 2007).

However, species usually do not follow a straight pathway when they disperse between the mainland and islands or among islands. Instead, islands located between the mainland and the focal islands can act as stepping stones (Gilpin, 1980) to alter dispersal pathways, decrease energy loss and increase the colonization of species (Diaz-Perez et al., 2008; Garb & Gillespie, 2006). This cumulative dispersal distance within a stepping-stone sequence is defined as stepping-stone distance (Gilpin, 1980). Landscape connectivity and geographic barriers have similar roles as stepping stones in influencing dispersal paths, such as the least cost distance (Etherington & Perry, 2016; Zeller et al., 2012), or electrical circuit theory (Chandra et al., 1996; McRae, 2006; McRae & Beier, 2007). Thus, it is necessary to consider the stepping stones in the studies of diversity–isolation relationships.

Apart from their role as stepping stones, islands can also be potential sources for species colonization (Bellemain & Ricklefs, 2008; Carter et al., 2020; Keppel et al., 2009). The rationales are that, on one hand, nearby islands can be closer to the focal island than the mainland, and may reduce the energy cost of species' colonization process. On the other hand, environmental conditions tend to be more similar (i.e. similar climates and/or habitats) between close islands, so well-adapted species on these islands may also persist on the focal island after a dispersal event (Price, 2004; Steinbauer et al., 2012). If islands are extremely isolated from the mainland, the metrices of the distance to the mainland will not be applicable because all islands will have relatively similar measures (Price, 2004). As a result, the distance from focal islands to nearby islands can be a suitable metric for measuring isolation (Bellemain & Ricklefs, 2008; Carter et al., 2020; Keppel et al., 2009). For example, Borges and Hortal (2009) found that the number of single-island endemics of Azorean cavernicolous arthropods shows a strong negative relationship with the distance to nearby islands.

Colonization is not only affected by isolation, but also by the area of nearby islands (Taylor, 1987). Accordingly, metrics reflecting the impact of the area of nearby islands have been proposed, such as the neighbour index weighted by the areas (Kalmar & Currie, 2006; Thornton, 1967) and the area of surrounding landmasses within a defined buffer around the focal island (Diver, 2008; Si et al., 2014). The principle of the above metrics has the basis that the potential colonizers increase with the area of the source (Taylor, 1987), known as the *source effect*. Conversely, the nearby island can also act as a colonization target instead of a colonization source if the nearby large island is larger and/or more suitable for the species. Larger islands may potentially receive more colonizers because they are more discoverable, which is known as the *target effect* (Brown & Kodric-Brown, 1977; Johnson, 1980; Lomolino, 1982, 1990). The target effect was proposed based on the focal island and the subsequent researches mainly focused on the target effect of the focal island on its own biodiversity (Carter et al., 2020; Fattorini, 2010; Hauffe et al., 2020; Mendez-Castro et al., 2021; Stracey & Pimm, 2009). However, to the best of our knowledge, no studies have considered the target effect from nearby islands. Here, we propose a new hypothesis that nearby islands would lures away the colonizers from focal islands because of the *negative target effect*, which would reduce biodiversity on focal islands (Figure 1b). The negative target effect (for focal islands) would become stronger with the increasing area of nearby islands and the decreasing distance between the focal island and nearby islands (Figure 1c). Therefore, the impacts of nearby islands on the biodiversity of the focal islands could be either positive or negative, depending on the existence of the nearby large island, and the distance between the focal and nearby islands.

The classic colonization–extinction dynamics from ETIB assumes that all species are ecologically similar with the same probability of colonizing or becoming extinct for a particular island (MacArthur & Wilson, 1967). However, species have distinct functional traits and evolutionary histories (Cadotte et al., 2019). If these functional and phylogenetic differences affect species' extinction or colonization processes, island geographical attributes may influence biodiversity patterns through species traits and/or phylogeny. In fact, isolation could act as a filter where only the species with high dispersal abilities could reach remote islands, leading to a negative relationship between isolation and functional diversity (Carter et al., 2020; Ross et al., 2019; Si et al., 2022). Meanwhile, low extinction rates on large islands and low gene flow to remote islands can both change their phylogenetic diversity (Heaney, 2000; Losos & Schluter, 2000; Tong et al., 2021). Thus, considering species richness, functional diversity and phylogenetic

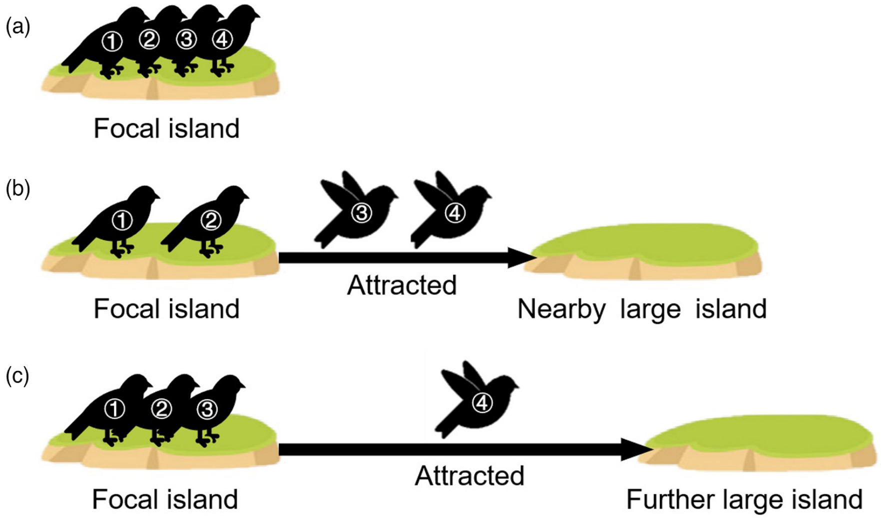

FIGURE 1 Schematic representation of the negative target effect. (a) When there is no larger island around the focal island, all colonizers would stay on the focal island. (b) When there is a nearby large island, colonizers on the focal island may fly to that island, a phenomenon defined as the negative target effect in this study, which can diminish biodiversity of the focal island. (c) When the large island is farther, fewer colonizers will be attracted to this large island. As a result, species richness on the focal island depends on the existence of the nearby large island, and the distance between the focal and nearby islands. The number imbedded in the figure indicates different species.

diversity simultaneously can provide fresh insights in the understanding of the diversity–isolation relationship (Carvajal-Endara et al., 2017; Weigelt et al., 2015).

In this study, we surveyed birds on 42 islands in the largest archipelago of China (Zhoushan Archipelago) to examine the effects of area and isolation on bird diversity. Birds are an ideal taxon for the study of island biogeography due to their relatively high abilities to disperse, and the availability of information on birds' traits and phylogenies (Crouch & Tobias, 2022; Jetz et al., 2012). Specifically, we tested the following questions: (1) How do island attributes (area and isolation) affect species richness, phylogenetic diversity and functional diversity? (2) How do nearby islands affect bird diversity of the focal island, through the source effect or the target effect?

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in the Zhoushan Archipelago, Zhejiang Province, China (29°31′–31°04′N, 121°30′–123°25′E) (Figure 2). We selected this region because Zhoushan Archipelago comprises 1390 inshore islands and islets (hereafter 'islands' for simplicity) of varying area and isolation, which is the largest archipelago of China. Among these islands, 58 islands have an area larger than 1 km^2, representing ca. 10% of the total island area in this region.

The Zhoushan archipelago was formed during the late Pleistocene, separating from the Tiantai Mountains of Zhejiang Province 7000–9000 years ago (Li et al., 1998). This region belongs

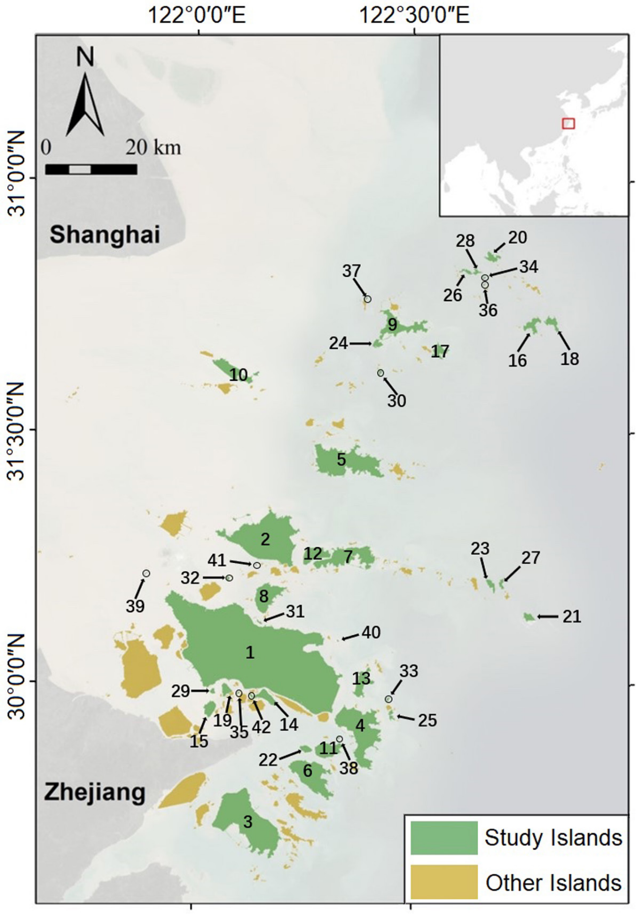

FIGURE 2 The 42 study islands (in green) in the Zhoushan Archipelago, Zhejiang, China. Islands are labelled according to the decreasing order of areas from Island 1 to Island 42.

to the subtropical ocean monsoon zone and has strong seasonal climate (Zhang et al., 2016). Subtropical evergreen broad leaf forest dominates the natural vegetation (Yu et al., 2019). Although the climate of the archipelago is similar to the mainland, species richness of fauna and flora is lower on the islands, with no endemic animal species (Huang, 1990; Li et al., 1998; Zhou, 1987; Zhuge & Gu, 1990).

We selected 42 islands encompassing as much variations in area and isolation as possible (Table S1). Islands are labelled in order of decreasing areas from Island 1 to Island 42. For each island, we measured 12 island geographical attributes by considering various sources, stepping stones and surrounding landmass (Table S1). The area of study islands in the Zhoushan Archipelago ranges from 0.05 to 515.37 km^2, and the distance to continental shores ranges from 4.2 to 81.2 km (Figure 2, Table S2).

2.2 | Bird survey

We surveyed bird assemblages on the study islands in the breeding season of 2020 (from April to June). We set up transects on each island to cover various habitat types for birds except highly urbanized regions (i.e. cities and towns). For the largest island (Island 1: Zhoushan Island), we set eight transects. For the rest of the study islands, we set one, two or four transects, where the number of transects was based on island area and land-use types (Table S2). We used Global Positioning System (GPS) to record the position and the length of each transect. The transect length was 2 km on most study islands. However, the transect length was restricted to 1 km for several small islands, as the steep terrain (e.g. cliffs near the edges) did not allow us to set a 2-km transect.

For bird surveys, at least two well-trained surveyors walked at a constant speed (ca. 1.5 km/h) along transects and recorded the identities and abundance of all birds heard and seen. Bird surveys were conducted 2 h after sunrise and 1 h before sunset, and the overall surveying time was restricted to 1.5 h in each survey. We only conducted bird surveys on days with good weather conditions, excluding heavy raining or strong windy days. All transects were surveyed twice, which is the maximum survey effort we could afford due to the large region of the Zhoushan Archipelago, the limited transportations in this region, and the relatively short period of the breeding season (April–June). Surveyors walked the transects in a random order by inversing the starting point to avoid survey biases. Our study did not require ethical approval because we did not catch birds during the survey.

In this study, we only considered terrestrial birds, so we excluded water birds, such as diving birds, shorebirds and seagulls, whose habitats are associated with water. To test the sampling efforts for each island, we calculated the sampling completeness using the *iNEXT* function in the 'iNEXT' package in R (Hsieh et al., 2016). The sampling completeness curves showed that the survey effort was sufficient (Figure S1, Table S3).

2.3 | Island geographical attributes

We used ArcGIS Desktop v9.4.1 to calculate island area and isolation metrices. Landmass polygons were extracted from the GADM database of global administrative areas (https://gadm.org/), which were used to calculate the island area (Area) of the 42 study islands. The distance metrics were then calculated based on the Universal Transverse Mercator map (UTM map) for all islands in the Zhoushan Archipelago, including 42 study islands. We considered a landmass as a life-supporting island when the area of a landmass was larger than 0.05 km^2 (Russell & Clout, 2004).

We also calculated 10 additional isolation metrics (Table S1), but we only kept five of them, because the removed metrics were highly correlated with the chosen ones (Spearman $\rho \geq 0.60$, Figure S2). These chosen isolation metrics are the distance to the mainland (DM), the mean distance to the five nearest islands (DN5), the distance to the nearest large island (DNL), the neighbour index of all islands (NI) and the proportion of landmass within 1 km (B1) (see the summary of isolation metrics in Table 1 and Table S1).

To estimate these metrics, we first calculated the shortest shore-to-shore distance between each pair of all islands (i.e. a total of 847,320 pairs for all islands) and the shortest shore-to-shore distance between each island and the nearest mainland using 'Generate Near Table' tool in ArcGIS. Based on the above data, we calculated the first three isolation metrices (DM, DN5 and DNL) for each study island. The neighbour index (NI) was calculated as the sum of the area of all nearby islands that are closer than the nearest continental shores, and weighted by the squared distances of each pair of focal islands and nearby islands (Kalmar & Currie, 2006). Additionally, we used the buffer-based distance metrices to reflect the proportion of landmass (B1). We calculated the surrounding area around the focal island by 'Buffer' tool in ArcGIS. The optimal buffer radius for measuring isolation depends on the spatial scale of the study (i.e. 1 km in our study region) (Weigelt & Kreft, 2013). NI and B1 thus reflect the effect of surrounding landmasses on the focal island (Kalmar & Currie, 2006).

In consideration of that the negative target effect is also a function of the area of the nearby islands, we calculated the relative area of nearby islands (RAD). This index was estimated as the area of nearby islands divided by that of the focal island. We used distance thresholds to separate nearby islands and the focal island by a specific distance value.

2.4 | Diversity indices

For phylogenetic data, we obtained the phylogenetic tree by pruning the recorded terrestrial species in this study from the global phylogenetic tree of birds from Bird Tree (http://birdtree.org) under the option of '*Hackett All Species: a set of 10000 trees with 9993 OTUs each*'. We then sampled 9999 pseudo-posterior distributions and constructed the Maximum Clade Credibility tree using the mean

TABLE 1 The definitions and abbreviations of isolation measures and the relative area of nearby islands for the focal island

Island geographical attribute	Abbreviation	Definition
Island area	Area	The area of the focal island
The distance to the mainland	DM	The shortest Euclidean distance to continental shores
The mean distance to nearby islands	DN5	The mean distance to a fixed number (five in the analysis) of nearest islands
The distance to the nearest large island	DNL	The distance to the nearest island larger than the relative area of the focal island (i.e. relative area threshold, 100% in the analysis)
Neighbour index	NI	The sum of nearby islands' area weighted by the squared distances of each pair of the focal and nearby island. Those islands were all islands closer to the continental shores
Proportion of landmass	B1	Proportion of surrounding landmass in the buffers for the focal island. Buffer radius was applied in 1 km
Relative area of nearby islands	RAD	The area of the nearby islands divided by that of the focal island. The nearby islands were less than 1 km distance from the focal island (i.e. distance threshold, 1 km in the analysis)

node heights by the software Tree Annonator v1.8.2 of the BEAST package (Drummond & Rambaut, 2007). We used this phylogenetic tree for further analyses (Figure S3a).

For functional traits, we chose body mass, wing length and tail length to calculate functional diversity. Body mass is widely considered as one of the single most informative traits of animal species (Cadotte & Tucker, 2017), while morphological differences in wings and tails are related to the dispersal ability of birds (Cooney et al., 2017). Because of the significant correlation among these traits (Figure S4a), wing length and tail length were divided by body length to correct for species body size (i.e. relative wing and tail length) (Diaz et al., 2016). Body mass, relative wing length and relative tail length were $\log_{10}$-transformed before analyses to reduce heteroscedasticity (Figure S4b,c). All trait data were extracted from a published trait dataset of all birds in China (Wang et al., 2021).

We calculated species richness (SR; the number of species on an island), richness-controlled Faith's phylogenetic diversity (PD) and richness-controlled Petchey and Gaston's functional diversity (FD) as taxonomic, phylogenetic and functional diversity respectively. Faith's phylogenetic diversity is the sum of the branch length of species within a community (Faith, 1992), and Petchey and Gaston's functional diversity is the total branch length of the functional dendrogram where species are clustered based on selected traits (Petchey & Gaston, 2002). However, the raw phylogenetic diversity and functional diversity are all correlated with SR, so we used null models to control for the effects of species richness (Ding et al., 2021). Null model was run 999 times by randomly selecting species from all the birds on the study islands, keeping species richness constant (Jarzyna et al., 2021).

We calculated PD using the function 'ses.pd' in the 'PICANTE' package (Kembel et al., 2010), with 'null.model' argument setting as 'richness'. We calculated the FD following the same way of PD, where the trait-based dendrogram was used instead of the phylogenetic tree (Ding et al., 2021). The trait-based dendrogram (Figure S3b) was generated with a Gower dissimilarity distance matrix from trait values, using the algorithm of the unweighted pair group method with arithmetic mean (UPGMA) (Kembel et al., 2010).

2.5 | Data analyses

We used model averaging methods to compare the effects of island area (Area) and five isolation metrics (DM, DN5, DNL, NI and B1) on bird diversity (SR, PD and FD). We first used linear models with all combinations of multiple predictors to test whether SR, PD and FD were related to island area and isolation metrics. RAD was highly correlated with DNL (Spearman $|\rho|>0.70$, Figure S2). In addition, the full model incorporating RAD ($R^2_{adj}=0.68$) had a lower adjusted R^2 than the full model with DNL ($R^2_{adj} = 0.74$). We thus included DNL in the model averaging. We selected all models and performed model averaging with ΔAICc <2 using the function 'model.avg' in the 'MuMIn' package (Gross et al., 2017). Area was $\log_{10}$-transformed to improve the normality. To reduce the effect of collinearity, isolation metrics were standardized by calculating the regression residuals between them and area. Both island geographical attributes and diversity indices were scaled by the mean centring and divided by the standard deviation prior to the analysis to make the standardized regression coefficients comparable.

The predictive power (R^2) of DNL is affected by the area of islands because larger islands are frequently known to have a stronger target effect (Johnson, 1980; Lomolino, 1990). If the nearby island is too small, they would have limited effects on the focal island, indicating that these islands could be ignored if their area was smaller than a certain relative area threshold. If DNL had significant effects on any diversity metrics, we would further use linear models to test R^2 of DNL with different relative area thresholds on diversity metrices.

Considering that the negative target effect may not only be due to a certain island, we also tested the predictive power of the relative area of the nearby islands (RAD) with a set of distance thresholds. RAD was $\log_{10}$-transformed to improve the normality before analysis. All the analyses were performed in R software v4.1.1 (https://www.R-project.org).

3 | RESULTS

A total of 119 terrestrial bird species were recorded on 42 study islands with a mean of 23.9 species per island, belonging to eight orders and 34 families. The most widely distributed species was *Pycnonotus sinensis*, which was found on all 42 islands. *Zosterops japonicus* (on 38 islands), *Hirundo rustica* (on 38 islands) and *Cettia fortipes* (on 37 islands) were also common in our study region.

3.1 | The effects of area and isolation on bird diversity

Island area had a positive effect on species richness (SR), phylogenetic diversity (PD: richness-controlled Faith's phylogenetic diversity) and functional diversity (FD: richness-controlled Petchey and Gaston's functional diversity) (Figure 3, Table S4). It indicated that larger islands would harbour more bird species and these species on larger islands would have more varied functional traits and evolutionary histories. Species richness was mainly affected by distance to the mainland (DM) and distance to the nearest large island (DNL, Figure 3a, Table S4). The impact of DNL was positive, indicating the focal island that was farther away from the nearest large island supported more bird species. The impact of DM was negative, indicating fewer species on islands that were more isolated from the mainland. Phylogenetic diversity and functional diversity had no relationships with any of the isolation metrics (Figure 3b,c, Table S4).

3.2 | The negative target effect on bird richness

DNL had a significant effect on SR, so we further tested its predictive power (R^2) on SR under a set of relative area thresholds. The predictive power of DNL increased with the relative area threshold of nearby islands at first, then reaching the peak when the threshold was 50% ($R^2 = 0.374$, $p < 0.001$) (Figure 4a, Table S5). After that it decreased and tended to be stable after the threshold exceeded 120%. This result indicated that the focal islands would have lower species richness when the relative area of the nearest large island is larger. The relative area of the nearby islands (RAD) had a negative effect on SR, and its predictive power increased with the distance threshold (Figure 4b, Table S6), reaching the peak at 9.0 km ($R^2 = 0.474$, $p < 0.001$).

4 | DISCUSSION

Our study explored the effects of island geographical attributes on bird diversity on islands in the Zhoushan Archipelago, China. We found positive diversity–area relationships for species richness (SR), richness-controlled phylogenetic diversity (PD) and richness-controlled Faith's phylogenetic diversity (FD), as well as a negative relationship between distance to the mainland (DM) and SR, which are consistent with the Equilibrium Theory of Island Biogeography. We also found that the nearest large island could reduce bird richness on focal islands through the negative target effect (Figure 4). In contrast, bird richness on the focal islands was lower when the relative area of nearby islands was larger (Figure 4). Our results thus illustrated the importance to consider the effects of island geographical attributes, especially that related to nearby islands, to better understand the biodiversity patterns on oceanic islands.

4.1 | The effects of area and isolation on bird diversity

SR, PD and FD of bird assemblages on study islands increased with island area (Figure 3). This positive relationship between area and SR has been recognized since the 19th century that is widely acknowledged today, termed as the species–area relationship (Lomolino, 1982; Matthews et al., 2019). This pattern could be explained by the ETIB (MacArthur & Wilson, 1967): extinction rates decrease with island area, resulting in higher species richness on larger islands. In addition to species richness, there is also a similar phylogenetic diversity–area pattern based on extinction and speciation processes (Eme et al., 2020; Matthew & Anthony, 2012). However, speciation should be negligible in the Zhoushan Archipelago, because the archipelago separated from the mainland only *ca*. 9000 years ago and has no endemic animal species on the islands (Li et al., 1998). As a result, low extinction rates on large islands would lead to high phylogenetic diversity. Larger islands also tend to have richer resources, higher ecosystem productivities and more diverse habitat types (Wardle et al., 2003), so larger islands could support diverse species with distinct functional traits and evolutionary histories.

We also found that distance to the mainland (DM, standardized by area) had a negative impact on bird richness (Figure 3a, Table S4). Many empirical studies have verified this negative species–distance relationship (Kalmar & Currie, 2006; Kreft et al., 2008; Lomolino, 2000; Whitehead & Jones, 1969). This pattern could be explained by the lower colonization rate on remoter islands (MacArthur & Wilson, 1967). However, unlike the prevailing species–area relationship, the significant effects of DM on SR were rarely reported (Abbott, 1978; Price, 2004). Indeed, previous

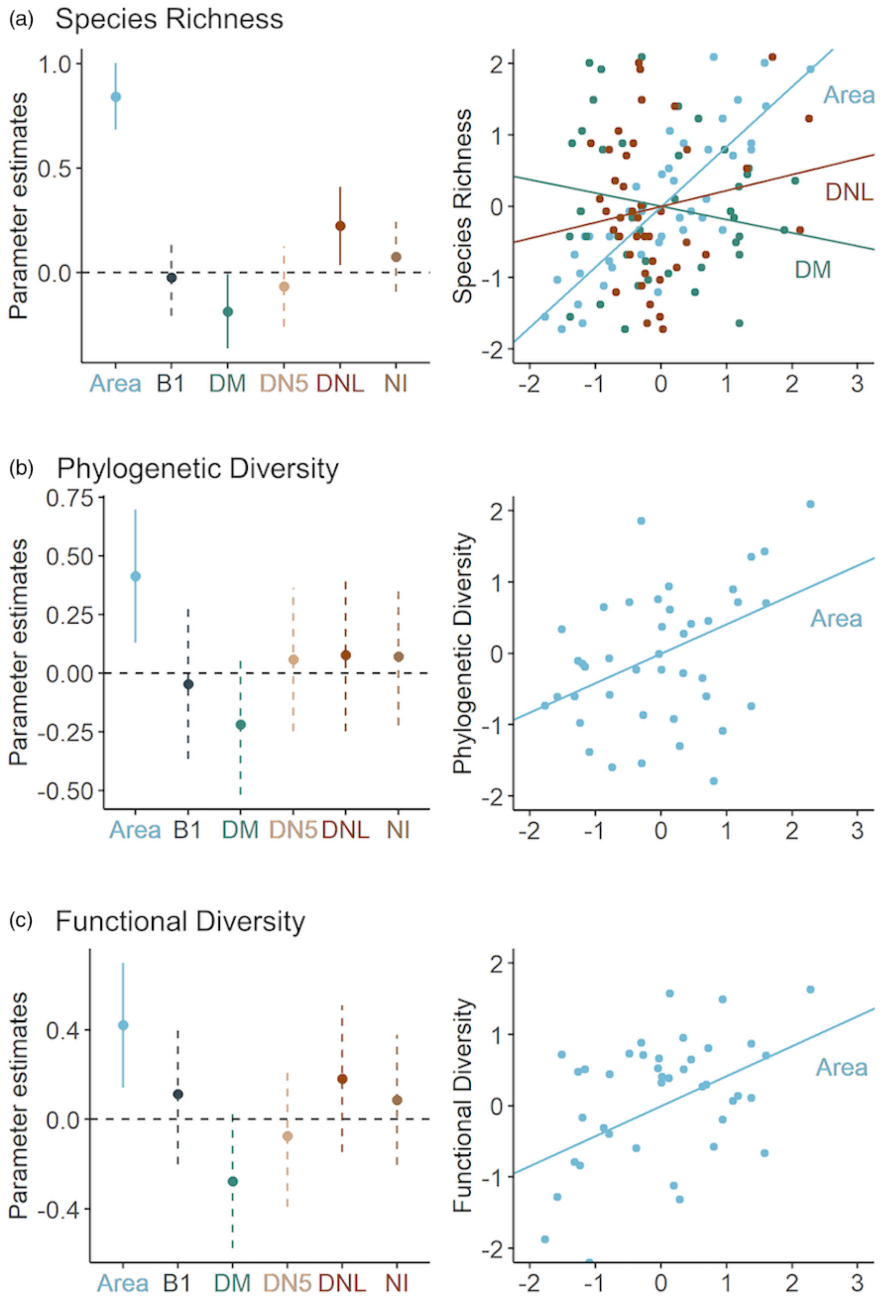

FIGURE 3 The parameter estimates (standardized regression coefficients) of island area (Area), the proportion of landmass within 1 km (B1), the distance to the mainland (DM), the mean distance to the five nearest islands (DN5), the distance to the nearest large island (DNL) and the neighbour index of all islands (NI) on (a) species richness (SR), (b) richness-controlled Faith's phylogenetic diversity (PD) and (c) richness-controlled Petchey and Gaston's functional diversity (FD) of bird assemblages on 42 islands in the Zhoushan Archipelago, China. The isolation metrics were standardized by area. A predictor is considered statistically significant when the 95% confidence interval does not cross zero. The scatter plots on the right indicate the significant relationships. Bird diversity indices are shown on the *y*-axis, while predictors are shown on the *x*-axis.

studies on other taxa revealed that DM had limited effects on species richness, such as amphibians (Li et al., 1998), butterflies (Zhang et al., 2016), and bryophytes (Liu et al., 2019; Yu et al., 2019) in the Zhoushan Archipelago. We speculated that some species of these taxa may have limited abilities to disperse from the mainland directly to remote islands, but species with relatively better dispersal abilities made the dispersal events from the mainland directly to remote islands, which may be more common in birds.

The isolation metrics considering the nearby island (e.g. DN5, DNL, NI and B1) had no significant negative impacts on bird diversity, compared with distance to the mainland. This finding suggested that the nearby island, instead of the mainland, might be the direct source pool for a focal island. Many studies have considered the nearby island as the source (Carter et al., 2020; Mendez-Castro et al., 2021; Weigelt & Kreft, 2013), which could be a typical case in island systems that are far from the continent, such as the Hawaiian Islands (Cardoso et al., 2010; Price, 2004; Weigelt & Kreft, 2013). However, the Zhoushan Archipelago is close to the mainland (the farthest study island is 81.2 km from the mainland, Table S2). Taken together, our results indicated that the mainland acted as the source of birds in our study region as predicted by ETIB (MacArthur & Wilson, 1967).

4.2 | The target effect of the nearby islands

The positive impact of DNL on SR indicated that these islands might have a target effect rather than a source effect on the bird diversity

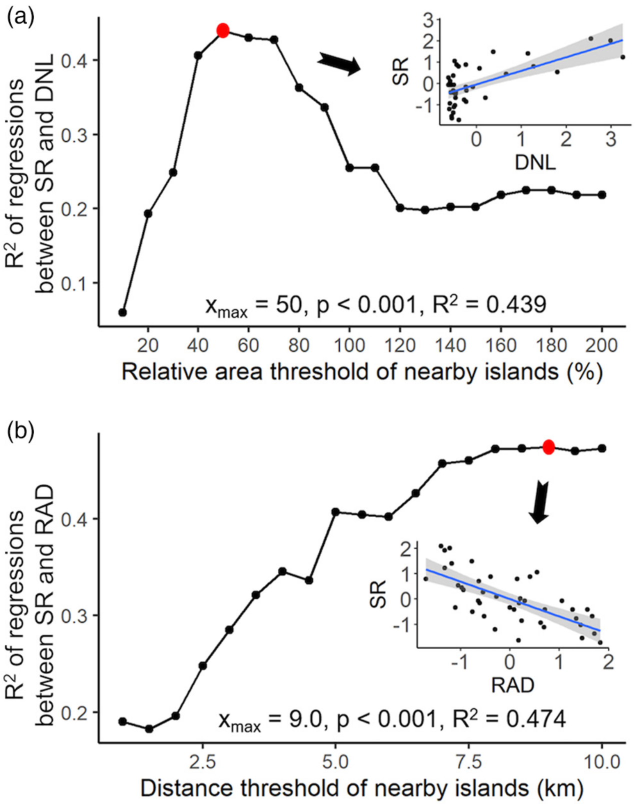

FIGURE 4 The coefficients of determination (R^2) of simple regressions between species richness (SR) and (a) distance to the nearest large island (DNL), and (b) the relative area of a fixed number of nearby islands (RAD). The R^2 measures the predictive power of the model with different settings of parameters that are shown on the *x*-axis: (a) the relative area threshold represents the minimum area of the nearest large island used for calculating DNL; (b) the distance threshold represents the maximum distance between the focal island and nearby islands used for calculating RAD. The imbedded figures indicate the relationship with the highest R^2 value, respectively.

of the focal island. Large islands could be a better target for birds to arrive (Gilpin & Diamond, 1976; Lomolino, 1990; Whitehead & Jones, 1969). As mentioned above, the mainland acted as the source of birds in our study region, so we predicted that nearby islands could attract colonizers and reduce the colonization rate of the focal island, like the dilution effect (Delm, 1990).

The strength of the impact of DNL on SR first increased and then stabilized with the increasing relative area threshold of the nearest large island (Figure 4a, Table S5). The predictive power of DNL on SR increased at first because target effect is also affected by island area (Carter et al., 2020; Johnson, 1980; Lomolino, 1990; Mendez-Castro et al., 2021). The predictive power was highest when the area threshold was 50%. This phenomenon suggested birds might be attracted by islands smaller than the focal island in our study region. The negative target effect will be strongest when the area threshold reaches 50%. That suggested the islands with half area of focal islands seem to be a prior choice for birds in our study region. On one hand, predators frequently require large territories. So, they may be absent on the relatively smaller nearby island, leading to lower predation pressures (Hanski & Gilpin, 1991; Woodroffe, 2000). For example, we only found species from Accipitriformes on larger study islands. On the other hand, larger islands usually have longer history of human activities, leading to resource constraints and high competition (McKinney, 2002, 2006). As a result, birds might favour the smaller nearby islands because of lower predation risks and competition pressures. Notably, when the area threshold was higher than 120% (the nearest large island is 1.2 times large than the focal island), the predictive power tended to be stable because the nearest large island would not change with the increase in the area threshold. For example, the DNL of islands near Island 1 would become the distance to Island 1 in our study system. However, further studies are needed to test the generality of our findings on the area threshold for DNL.

DNL only represents the target effect of the nearest large island. Target effect is only affected by the area of the focal islands (Carter et al., 2020; Johnson, 1980; Lomolino, 1990; Mendez-Castro et al., 2021), while the negative target effect should be affected by the relative area of all nearby islands. As a result, we also tested the predictive power of the relative area of the nearby islands (RAD), which estimated the negative target effect of all nearby islands. RAD had a negative impact on SR and had a higher R^2 than DNL (Figure 4, Tables S5 and S6), further supporting the negative target effect. We also found the predictive power of RAD increased with the distance threshold, which meant that the negative target effect would be stronger with more nearby islands. Although we speculated that the predictive power would keep increasing, there were more than a quarter of the study islands within a radius of 10 km from the mainland. Further studies are needed to test the generality of our findings beyond our study region. This result also supported our hypothesis of the negative target effect that this effect resulted from multiple islands, not from a certain island.

5 | CONCLUSIONS

In this study, we found the positive effect of island area on taxonomic (i.e. species richness), functional and phylogenetic diversity of terrestrial birds, as well as the negative effect of distance to the mainland on bird richness. Following our hypothesis, this study detected the negative target effect that nearby islands will reduce bird colonizers of the focal island and diminish its diversity. Our results thus expanded the traditional target effect and provided a new insight into the species distribution patterns across oceanic islands by explicitly considering both target and source effects of nearby islands. We believe more similar studies would aid to unravel the generalization or idiosyncrasy of our observation, and to further enrich the theories in island biogeography.

AUTHOR CONTRIBUTIONS

Xingfeng Si designed and supervised the study. Duorun Wang, Yuhao Zhao and Xingfeng Si conceived the ideas. Duorun Wang, Yuhao Zhao, Shupei Tang, Xiangxu Liu, Wande Li, Peng Han, Di Zeng, Yangheshan Yang, Guangpeng Wei, Yi Kang and Xingfeng Si collected the data. Duorun Wang analysed the data and led the writing of the manuscript with contributions from Yuhao Zhao and Xingfeng Si. All other authors contributed to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Figshare https://doi.org/10.6084/m9.figshare.21078148.v1 (Wang et al., 2022).

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