

Taxonomic, phylogenetic, and functional nestedness of mammal assemblages in the Zhoushan Archipelago, China

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Abstract

Nestedness is an important part of the theoretical framework of island biogeography and community ecology. However, most previous studies focused on taxonomic dimension and overlooked functional and phylogenetic nestedness. Here, we simultaneously investigated taxonomic, functional, and phylogenetic nestedness of terrestrial mammals on 39 land-bridge islands in the Zhoushan Archipelago, China. As mammals' response to the environment may depend on their body size, we performed analyses for three mammal assemblages separately: overall species, large and medium-sized species, and small species. The taxonomic nestedness was quantified by organizing the species incidence matrix, while the functional and phylogenetic nestedness were estimated by combining the similarity of their ecological traits and phylogeny. Island characteristics (island area, three isolation indices, land use intensity, and habitat diversity) and species traits (body size, litter size, habitat specificity, geographic range size, and minimum area requirement) were used as predictors of nestedness. Overall and small species were significantly nested in 3 facets of nestedness, and results supported the selective extinction, selective colonization, and habitat nestedness hypotheses. Large and medium-sized species were functionally and phylogenetically nested when matrices were ordered by increasing distance to mainland, supporting the selective colonization hypothesis. Overall, differences in nestedness and its underlying mechanisms were detected not only in 3 facets of nestedness but also in the 3 mammal assemblages. Therefore, frameworks that incorporate taxonomic, phylogenetic, and functional nestedness can contribute to a more comprehensive understanding of nestedness processes. Additionally, it also improves our ability to understand the divergent responses of mammal assemblages to the insular environment.

Key words: body size, functional nestedness, habitat nestedness, mammals, phylogenetic nestedness, selective extinction, selective colonization, Zhoushan Archipelago.

The studies of community structure in island systems using species composition can provide insights into the factors that shape communities in space and time (Worthen 1996). One of the community structures is nestedness, which occurs when the species in the sites with low diversity are proper subsets of the sites with richer diversity (Darlington 1957; Patterson and Atmar 1986). Although Darlington (1957) introduced nestedness to explain the pattern of species distribution on island systems more than 60 years ago, this research field only became popular when Patterson and Atmar (1986) conceived the first community-level metric to analyze nestedness statistically (Whittaker and Fernández Palacios 2007; Wang et al. 2012). Ever since, nestedness has become a crucial part of the theoretical framework of island biogeography and community ecology (Weiher and Keddy 1999; Whittaker and Fernández Palacios 2007; Matthews et al. 2015a; Wang et al. 2023a,b).

Five main hypotheses have been proposed to explain the nested pattern, namely selective colonization, selective extinction, passive sampling, habitat nestedness, and human disturbance (Cook and Quinn 1995; Wright et al. 1998; Fernández-Juricic 2002). The selective colonization hypothesis posits that distance-driven isolation (e.g., distance to the nearest mainland and the nearest larger island)

and species dispersal abilities (e.g., body mass) would generate nestedness patterns via dispersal limitation (Darlington 1957; Patterson 1987). The selective extinction hypothesis postulates some island characteristics (e.g., island area and temporal isolation) and species traits (e.g., litter size, geographic range size, habitat specificity, and minimum area requirement) associated with species extinction risk would also drive nestedness patterns through sequential extinction (Patterson 1987; Bolger et al. 1991). The habitat nestedness hypothesis suggests that the distribution of species is nested in insular systems because their habitats are nested (Calmé and Desrochers 1999; Honnay et al. 1999). Passive sampling model predicts that the regional abundances of species drive their occupancy as rare species in the regional pool have less chance to be found in any patch than more abundant species by chance, thereby influencing the structuring of assemblages (Cutler 1994; Higgins et al. 2006). Finally, human disturbance (e.g., anthropogenic noise pollution and land use intensity) can also promote nestedness because species have different tolerance to disturbance in human-dominated fragmented landscapes (Fernández-Juricic 2002; Gonzalez-Oreja et al. 2012; Wang et al. 2013).

Traditionally, the study of nestedness has been devoted to detecting the drivers that determine community assembly at

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the taxonomic level. However, environmental factors might select species for their functional traits and phylogenetic lineages as well (Melo et al. 2014). When only taxonomic composition is considered, species are treated as functionally and phylogenetically equivalent to each other, which overlooks the phylogenetical or functional nestedness (Forest et al. 2007) and the mechanisms underlying them (Chen et al. 2022). For instance, Chen et al. (2022) found that amphibian communities were phylogenetically and functionally nested with regard to increasing distance to the mainland, reflecting a distance-related selective colonization process overlooked by the traditional taxonomic nestedness analysis. Therefore, considering taxonomic, phylogenetic, and functional aspects simultaneously can provide more refined and comprehensive information for understanding the mechanisms underlying nestedness. Nevertheless, so far, very few studies have investigated all three dimensions of nestedness simultaneously (Chen et al. 2022).

Mammals represent one of the most studied organism groups with readily available data on traits, phylogenies, and species distributions (Benton 2009). This knowledge has been used to study patterns in island biogeography and community ecology (Huang et al. 2012). However, relatively few studies have examined the nestedness of the taxon of mammals, particularly in land-bridge island systems (Palmeirim et al. 2018; Chen et al. 2019). The few existing studies on mammal assemblages typically focus on either large mammal assemblages or small mammal assemblages, overlooking divergent responses of different subsets of mammals to the environment due to their intrinsic characteristics. Mammals can be extremely diverse in the same island system, particularly in body size, ranging from several grams to hundreds of kilograms (Li and Li 1994, 1995; Bao et al. 1995). As such, it is necessary to explore the nested patterns and underlying mechanisms of different mammal assemblages classified by body mass at the same set of sites.

In this study, we tested the taxonomic, functional, and phylogenetic nested patterns of 3 mammal assemblages on 39 land-bridge islands in the Zhoushan Archipelago, China. To do so, we used overall mammal assemblages and 2 size-based subsets: large and medium-sized species (body mass > 1 kg) and small species. We addressed the following 2 questions: (1) Does the distribution of 3 mammal assemblages among islands exhibit taxonomically, functionally, or phylogenetically nested patterns? (2) Do taxonomic, functional, and phylogenetic nestedness follow the same processes among 3 mammal assemblages?

Materials and Methods

Study area

We conducted this study in the Zhoushan Archipelago (29°31'–30°04'N, 121°30'–123°25'E), Zhejiang Province, China (Figure 1). The Zhoushan Archipelago is a land-bridge archipelago, which was separated from the continent due to the rising sea levels. The marine transgression inundated this area, creating a total of 1339 islands during the Holocene period (Wang et al. 2009). The climate in this region is strongly seasonal and typical of the monsoon oceanic climate, with rainfall and typhoons occurring from June to October (Wang et al. 2009). Most islands are covered by a dense subtropical evergreen broadleaf forest mixed with secondary coniferous forest, grassland, and shrubs (Wang et al. 2014).

The Zhoushan Archipelago provides an ideal opportunity to investigate the nestedness of mammals for 3 key reasons. First, as land-bridge islands, the Zhoushan Archipelago shares a common ancestral pool of species (Chen et al. 2022). Second, the islands in the archipelago have a common biogeographic history (Wang et al. 2014). Finally, several previous field studies for mammals on large islands have been conducted, which facilitated our identification of mammals (Li and Li 1994, 1995; Bao et al. 1995).

Island characteristics

A cluster of 39 islands was selected according to a broad gradient of island area and isolation from the mainland (Figure 1; Supplementary Table S1). Island area (in km²) was obtained from the officially released data of the Zhoushan Municipal Statistics Bureau (<http://zstj.zhoushan.gov.cn/col/col1229615782/index.html>). Two distance-based isolation metrics, the distance to the nearest mainland and the nearest larger island, were used as proxies of the immigration distance, which were estimated from ArcGIS 10.8 (ESRI 2020). We utilized land use intensity (land under human use/island area) to quantify human disturbance (Xu et al. 2023), which was calculated using the satellite map from the Tianditu Map (<https://zhejiang.tianditu.gov.cn/map>) in ArcGIS 10.8 (ESRI 2020). All the habitats in our study islands can be divided into 9 types: conifer forest, broadleaf forest, coniferous-broad mixed forests, bamboo groves, shrubs, grassland, farmlands, settlement, and stream. Habitat diversity was then calculated as the number of habitat types observed for mammals on each island (Supplementary Table S2). We recorded habitat types for mammals along the transects and extracted additional habitat types through a highly accurate (10-m resolution) habitat digital map (WorldCover 2020, <https://esa-worldcover.org>) to obtain a true number of habitats on each island.

We also introduced temporal isolation, the time since the island separation from the mainland, which is a good predictor of species extinctions on islands (Foufopoulos and Ives 1999). This temporal isolation was estimated according to the minimum ocean depths between an island and the mainland and the rates of sea level rise since the last glacial maximum (Wang et al. 2014). For the minimum ocean depths between an island and the mainland, we combined bathymetric maps with stratigraphy (Liu et al. 2014; Chen et al. 2021). For the rates of sea level rise, we used data describing the rates of sea level rise around the Zhoushan Archipelago since the late Pleistocene (Liu et al. 2014).

Mammal surveys

We used passive infrared camera trapping (O'Brien et al. 2003) to survey the occurrence and abundance of large and medium-sized mammals on the 39 study islands from May 2020 to May 2023. We placed 3–45 Ltl5210 camera traps on each study island, and the distance between 2 nearby camera traps was at least 100 m. Cameras were deployed along trails or at habitats for animal activity to increase the chance of mammal detection on each island (Zungu et al. 2019). Camera traps were placed in the field for 3–6 months. Trapping effort was roughly proportional to log-transformed island areas (Schoereder et al. 2004; Chen et al. 2019), with 8,733 camera days on the largest island and 553 on the smallest island (Supplementary Table S1). Cameras were placed 60–100 cm above the ground and facing north or south to avoid triggering the cameras by sunshine and grass. All cameras were

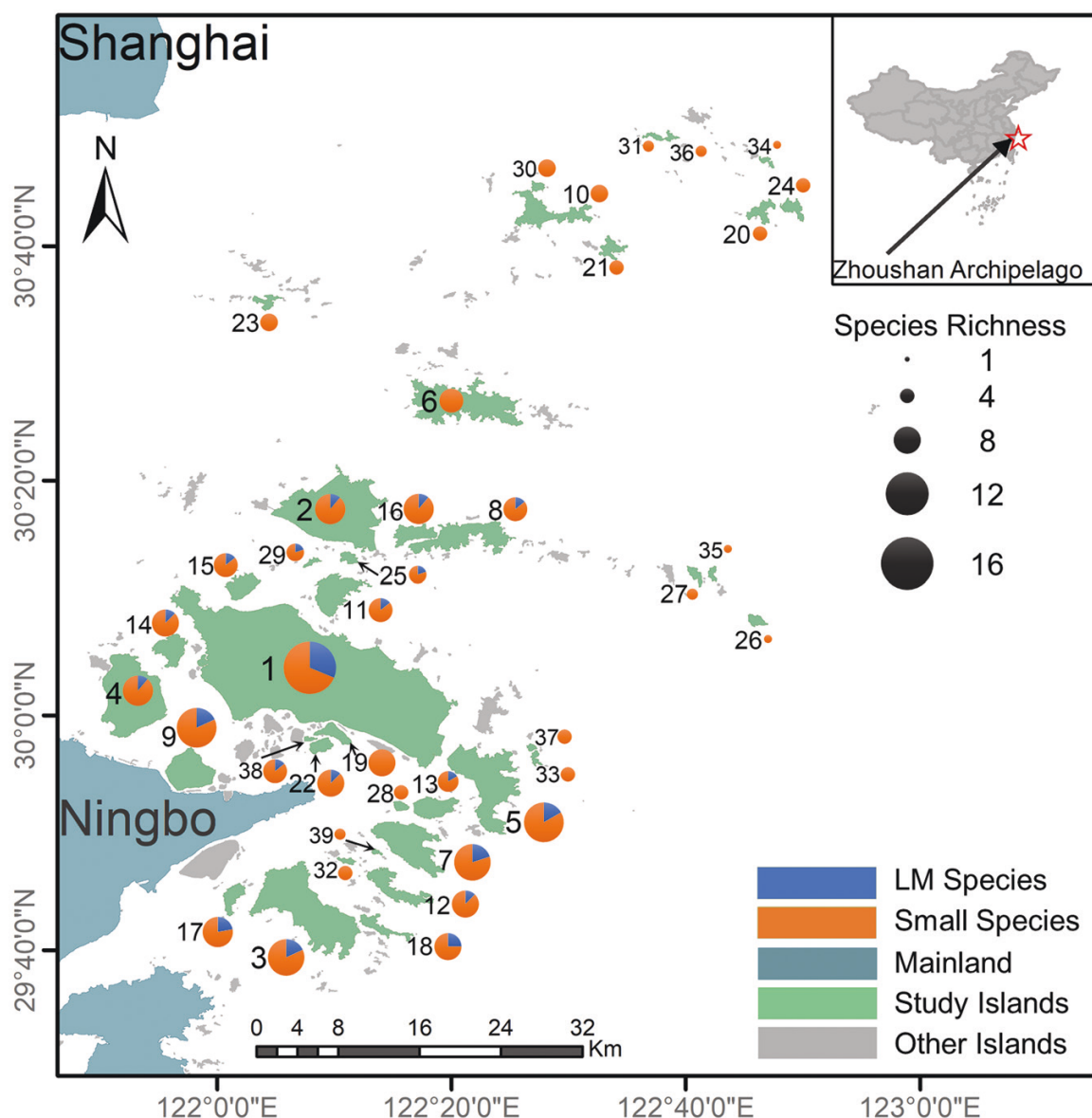


Figure 1. The map of the 39 study islands in the Zhoushan Archipelago, China. The numbers of islands are arranged by area from the largest to the smallest. Species richness of each study island was presented by the size of the dot behind its island number. LM Species: Large and Medium-sized Species.

set to take 3 photographs and a 10-s video after each trigger with a 60-s photographic delay between 2 captures. We then identified large terrestrial mammals using these photographs. Individuals sometimes trigger the camera multiple times in a row as one moves slowly at a camera site, resulting in continuous photographs of the same species (Kauffman et al. 2007; Zungu et al. 2019). Therefore, consecutive photographs of individuals of the same species are taken for at least 30 min (O'Brien et al. 2003; Zungu et al. 2019).

We used the live-trapping method (Lynam and Billick 1999; Wang et al. 2010) to survey the occurrence and abundance of small mammals. Small mammals were captured with wire-mesh cage traps (22.5 cm × 8.75 cm × 7.5 cm) baited with a mixture of peanut butter, sesame oil, and honey wrapped in bread in the summer and autumn of 2021 and 2022. The distance between 2 traps was greater than 20 m, and each site was sampled for only one night to ensure that more heterogeneous habitats could be investigated. Captured individuals

were identified and released immediately after measuring their body size. The line-transect method was used as a supplemental measure to survey the occurrence of mammals. We excluded the domestic species (e.g., cats, dogs, goats, and rabbits), aquatic species (e.g., Eurasian Otter), and flying mammals (e.g., bats) from analyses.

To test the sampling efforts for each island, we assessed the completeness of the mammalian survey using the species accumulation curve based on the random sample for each island (Wang et al. 2012; Colwell et al. 2014). We analyzed the sampling completeness in the vegan package in R v4.2.2 using raw data (Oksanen et al. 2013).

Ecological traits of mammals

For each species, we selected 2 life-history traits (body size and litter size) and 3 ecological traits (minimum area requirement, habitat specificity, and geographic range size) as predictors of nestedness (Supplementary Table S3). We used body

mass (g) and average annual litter size (n) to represent body size and litter size respectively. Following Wang et al. (2010), geographic range size (km^2) was calculated by using the minimum land area convex polygon of published point data. The data on body size, litter size, and geographic range size were obtained from published literature (Smith and Xie 2009; Jiang et al. 2017). The habitat specificity was calculated as the number of habitats used by a given species (Feeley et al. 2007; Chen et al. 2022), ranging from 2 (greatly specialized) to 7 (highly generalized). The minimum area requirement was estimated as the area of the smallest island occupied by each species (Wang et al. 2010; Xu et al. 2017). The habitat specificity and the minimum area requirement were based on our field surveys.

Statistical analyses

Taxonomic nestedness

We used the NODF metric, the most commonly used metric that is independent of the size and shape of the matrix, to assess the taxonomic nestedness of the 3 mammal assemblages across the 39 islands. We also applied the NODF metric to evaluate the nestedness of the habitat-by-site matrix, which is frequently used to infer the habitat nestedness hypothesis (Calmé and Desrochers, 1999). The NODF metric can quantify nestedness not only for the whole matrix (Figure 2) but also independently for contributions by matrix rows (nestedness among sites, NODFr) and matrix columns (nestedness among species incidences, NODFc) (Ulrich et al. 2009). The “proportional-proportional” (PP) randomization algorithm was used to determine the significance of nestedness, which proportionally resamples the matrix incidence according to row and column totals (Matthews et al. 2015b; Chen et al. 2022). We generated 1,000 matrices randomly and used the 95% confidence interval to assess the significance of nestedness. We finally obtained observed NODF, stimulated mean NODF (simulated NODF), standard deviation (SD), and Z-values ((observed NODF – simulated NODF)/SD) from the default output.txt document produced by the NODF version 2.0 (Ulrich and Almeida-Neto 2012).

We then obtained the site ranks and species ranks in the maximally packed nested matrix (Figure 2) from the default output.txt file (Tan et al. 2021). When sites were significantly nested, we performed Spearman rank correlations to identify the most important predictors by calculating the correlations between the site ranks in the maximally packed matrix and ranked island characteristics (island area, 3 isolation indices, land use intensity, and habitat diversity) (Zhang et al. 2022). Likewise, Spearman rank correlations were used to examine which ecological traits (body size, litter size, habitat specificity, geographic range size, and minimum area requirement) would affect nestedness (Wang et al. 2010, 2012; Xu et al. 2017). However, we did not perform partial Spearman rank correlation because the sample size ($n = 18$) in our study might be too small to perform multi-predictor partial correlation tests (Supplementary Tables S4–S6; Chen et al. 2022; Zhang et al. 2022).

The random placement model (Coleman 1981) is often used to test the passive sampling hypothesis (Calmé and Desrochers 1999; Wang et al. 2013; Xu et al. 2017). For the random placement model, the expected species richness $S_{(\alpha)}$, $S_{(\alpha)} = S - \sum_{i=1}^S (1 - \alpha)^{n_i}$, depends on the relative area of the island α , $\alpha = a_k / \sum_{k=1}^K a_k$, and the abundance (n_i) of each

species in the region, where the parameter of S is the sum of the species richness at all locations and the variable of a_k is the area of the island k . The variance of standard deviation (σ^2) of $S(\alpha)$ is calculated as $\sigma^2 = \sum_{i=1}^S (1 - \alpha)^{n_i} - \sum_{i=1}^S (1 - \alpha)^{2n_i}$ (Coleman 1981). The random placement model should be rejected when more than one-third of the observed data points fall outside one standard deviation (± 1 SD) of the expected species–area curve (Coleman 1981).

Functional and phylogenetic nestedness

We used treeNODF to calculate phylogenetic (phyloNODF) and functional (traitNODF) nestedness (Melo et al. 2014). The treeNODF is an extension of the NODF index, which computes the percentage of the phylogenetic or functional diversity that occurs in phylogenetically or functionally poorer sites also present in functionally or phylogenetically richer sites (Melo et al. 2014; Almeida-Gomes et al. 2019; Carvalho 2021). The treeNODF is a composite metric that can be decomposed in compositional (S.Fraction) and resemblance components (topoNODF, topoNODF = treeNODF – S.Fraction). The compositional components represent the treeNODF fraction expected if all species are equally related (Melo et al. 2014). The resemblance components are the treeNODF fraction that cannot be accounted for by compositional components deriving from particular tree topologies (Melo et al. 2014). The analysis of both compositional and resemblance components can distinguish whether the observed nestedness is determined primarily by tree topology or compositional nestedness (Melo et al. 2014).

We carried out the analyses in 2 steps. In the first step, to avoid possible wrong a priori prediction, we arranged the rows in the incidence matrix (Figure 2) according to both increasing and decreasing all island characteristics, resulting in 2 inverted incidence matrices for each island characteristic. In the second step, we employed the function “treeNodfTest” and the null model permRows to calculate phylogenetic and functional nestedness by linking the ordered species incidence matrices to phylogenetic and functional dendrogram, respectively, using package CommEcol (Melo et al. 2014). The phylogenetic tree (Supplementary Figure S1a) was constructed based on a species-level phylogeny of global mammals in the R package ape (Paradis and Schliep 2019; Upham et al. 2019). The functional dendrogram (Supplementary Figure S1b) was generated with a Gower dissimilarity distance matrix from values of ecological traits mentioned above, using UPGMA (unweighted pair group method with arithmetic mean) clustering algorithm in the package FD and ape (Paradis and Schliep 2019; Upham et al. 2019). To assess whether the observed values and their components differed from those expected by chance, permRows permutation tests (999 replications) were performed (Matthews et al. 2015b; Chen et al. 2022).

In addition, envNODF, one of treeNODF, can be used to judge whether species with a particular trait occur in a limited range of environmental conditions (e.g., rare species) present in a subset of the conditions occupied by species occupying a wide range of conditions (e.g., common species) (Melo et al. 2014; Chen et al. 2022). We used the 6 island characteristics mentioned above to generate a dendrogram as producing functional dendrograms (Melo et al. 2014). We also ordered the presence–absence matrix following a priori hypothesis for each species trait (increasing or decreasing order). We used the permRows test on all matrices to evaluate the nestedness

among species (Melo et al. 2014). All the above analyses were carried out in R v4.2.2 (R Core Team, 2022).

Results

General survey results

Based on 50,225 trap nights with camera-trapping methods and 6,398 trap nights using live-trapping methods, we identified and recorded a total of 18 mammal species, including 7 large and medium-sized mammals and 11 small mammals (Figure 2, Supplementary Figure S2 and Table S1). Among the species, *Crocridura shantungensis* (sp18) was the most wide-spread, occurring on 38 of the 39 study islands. The recorded mammal richness on each island ranged from 1 to 16 (Figure 2, Supplementary Table S1), and the most species-rich assemblages were on the largest island (Figure 2, Supplementary Table

S1). When using the 2 mammal subsets for analysis, islands on average harbored 0–5 large and medium-sized mammal species and 1–11 small mammal species (Supplementary Figure S2 and Table S1). The species accumulation curve for each island using individuals as surveying units approached an asymptote, and 36 study islands had sampling completeness higher than 90% and 3 study islands had sampling completeness higher than 80%, which suggested a high level of inventory completeness for the study islands (Supplementary Figure S3, Table S1).

Taxonomic nestedness of mammal assemblages

Based on the species-by-site matrices, the results of taxonomic nestedness showed that overall species (NODF = 83.01, $P < 0.01$) and small mammals (NODF = 83.06, $P < 0.01$) were significantly nested, but large and medium-sized species was not nested (NODF = 12.2, $P > 0.05$) (Table 1).

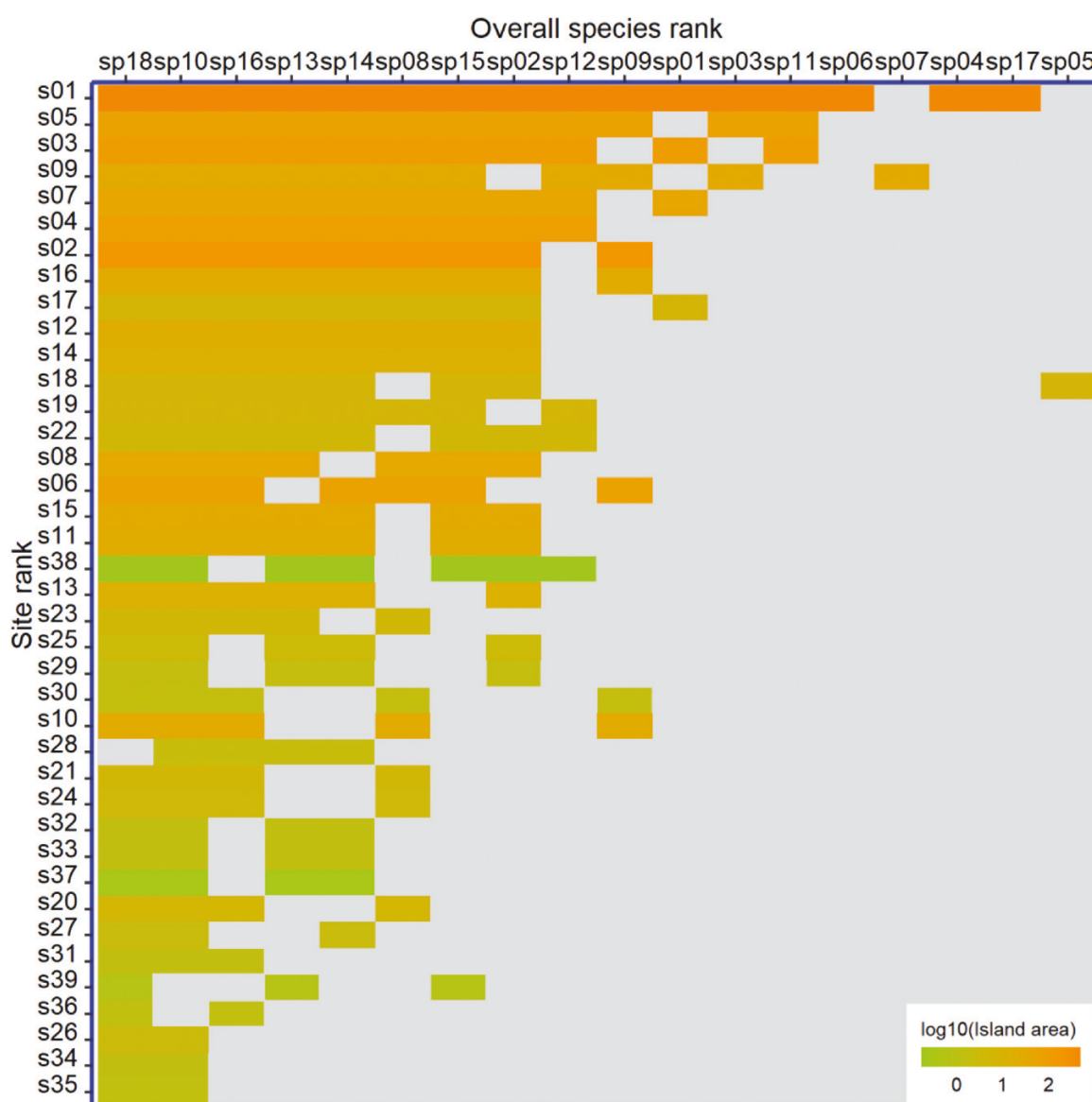


Figure 2. Maximally packed nested presence-absence matrix for overall species on the 39 study islands in the Zhoushan Archipelago, China. Species code from sp01 to sp18 are *Sus scrofa*, *Hydropotes inermis*, *Muntiacus reevesi*, *Prionailurus bengalensis*, *Viverricula indica*, *Rhizomys sinensis*, *Melogale moschata*, *Mustela sibirica*, *Erinaceus amurensis*, *Rattus norvegicus*, *Callosciurus erythraeus*, *Niviventer confucianus*, *Rattus losea*, *Suncus murinus*, *Apodemus agrarius*, *Mus musculus*, *Crocridura attenuata*, *Crocridura shantungensis*. Rows are colored by the log-transformed island area of the respective row.

Additionally, species composition and species incidence for overall species and small mammals also were highly significantly nested (Table 1).

The nestedness of overall species and small mammals was significantly and negatively correlated with island area and positively related to temporal isolation (Table 2), supporting the selective extinction hypothesis. Species nestedness ranks of these 2 mammal assemblages were significantly correlated with the species traits (litter size and minimum area requirement) linked to extinction risk (Table 2).

The nestedness of overall species and small mammals was also significantly and positively related to distance to the nearest mainland (Table 2), supporting the selective colonization hypothesis. The habitat-by-site matrix was highly and significantly nested (NODF = 85.27, $P < 0.01$) (Table 1), which was consistent with the habitat nestedness hypothesis. Meanwhile, Spearman rank correlations revealed that the nested patterns of the 2 mammal assemblages were significantly and negatively correlated with habitat diversity (Table 2).

In contrast, the results of random placement models indicated that the nestedness of mammal assemblages was not

attributed to passive sampling. None of the observed species richness was within one standard deviation (± 1 SD) of the predicted species-area curve for all three mammal assemblages (Figure 3, Supplementary Figure S4). Similarly, when large and medium-sized mammals and small mammals were analyzed separately according to 2 main survey methods, none of the observed species richness by using live-trapping methods and 4 of the 28 observed data points with camera-trapping methods were within one standard deviation (± 1 SD) of the predicted species-area curve (Supplementary Figure S4).

Phylogenetic and functional nestedness

Considering overall mammal assemblages, the observed values of functional and phylogenetic nestedness were all significantly larger than expected for matrices ranked by decreasing island area and habitat diversity and increasing distance to the nearest mainland and temporal isolation ($Z = 3.43$ – 6.15 , $P < 0.01$, Table 3; Supplementary Table S7). For the large and medium-sized mammal assemblages, the functional and phylogenetic nestedness emerged for incidences sorted by increasing distance to the nearest mainland ($Z = 2.09$ and 2.02 ,

Table 1. Results of nestedness analyses using the program NODF conducted on the presence–absence matrix for 3 mammal assemblages and their habitats on 39 study islands in the Zhoushan Archipelago, China

	NODF _{obs}	NODF _{exp}	SD	Z	P
Overall species					
NODF	83.01	76.99	2.00	3.01	0.002
NODFc	83.39	78.04	1.99	2.69	0.004
NODFr	81.19	71.94	3.35	2.76	0.003
Large and medium-sized species					
NODF	12.20	12.79	2.03	−0.29	0.348
NODFc	11.20	12.03	2.02	−0.41	0.317
NODFr	47.62	39.61	7.73	1.03	0.163
Small species					
NODF	83.06	78.92	2.00	2.07	0.010
NODFc	82.47	78.68	1.99	1.91	0.020
NODFr	91.03	82.12	3.43	3.43	0.003
Habitats					
NODF	84.54	80.04	1.96	2.29	0.001
NODFc	84.05	79.58	2.00	2.23	0.001
NODFr	94.80	89.54	3.04	1.73	0.018

NODF, nestedness values for the whole matrix; NODFr, nestedness values for nestedness among sites; NODFc, nestedness values for nestedness among species incidences; NODF_{obs}, observed NODF; NODF_{exp}, stimulated mean NODF; SD, standard deviation; Z, Z-value; P, P-value.

Table 2. Spearman rank correlations (r_s) between rank orders of sites and species in the maximally nested matrices and orders of sites and species after rearranging the matrix according to each explanatory variable

	Island characteristics						Species ecological traits				
	Area	DTNM	DTNI	HD	LUI	TISM	BM	LS	HS	GRS	MAR
r_s (overall species)	−0.824	0.663	0.044	−0.866	−0.133	0.785	0.470	−0.806	−0.392	−0.218	0.805
P (overall species)	<0.001	<0.001	0.789	<0.001	0.418	<0.001	0.051	<0.001	0.108	0.384	<0.001
r_s (small species)	−0.841	0.619	0.015	−0.880	−0.221	0.774	0.209	−0.815	−0.090	−0.345	0.673
P (small species)	<0.001	<0.001	0.929	<0.001	0.175	<0.001	0.539	0.002	0.793	0.299	0.023

Area, Island area (km²); DTNM, distance to nearest mainland (km); DTNI, distance to nearest larger island (km); HD, habitat diversity (n); LUI, land use intensity (land under human use/island area); TISM, time since island separation from mainland (years); BM, body mass (g); LS, litter size (n); HS, habitat specificity (n); GRS, geographic range size (km²); MAR, minimum area requirement (km²).

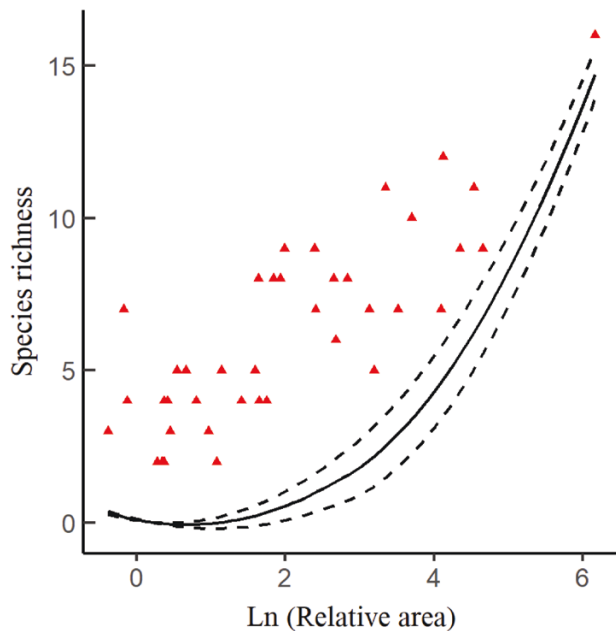


Figure 3. The random placement model for overall species on the 39 study islands in the Zhoushan Archipelago, China. Observed species richness (filled triangles), expected values (solid line), and associated standard deviations ($\pm 1SD$; dashed lines) are shown, respectively.

$P < 0.05$; Table 3; Supplementary Table S8), while the phylogenetic nestedness was mainly due to the resemblance components ($P < 0.05$) rather than the species compositions ($P > 0.05$; Table 3; Supplementary Table S8). For small mammals, the calculative outcomes of the functional and phylogenetic nestedness indicated that they were all nested for matrices arranged by increasing distance to the nearest mainland and temporal isolation and decreasing island area and habitat diversity ($Z = 2.74\text{--}5.85$, $P < 0.01$; Table 3; Supplementary Table S9).

Interestingly, the observed values of resemblance components were only phylogenetically nested for incidence ordered by decreasing distance to the nearest island for large and medium-sized mammal assemblages (Table 3; Supplementary Table S8). Moreover, observed functional nestedness and phylogenetic nestedness values were mainly represented by the species compositions rather than the resemblance components (Table 3).

Similarly, when linking species ecological traits to the environment dendrogram for all three mammal assemblages, slight differences were discovered. For overall species, the highly nested patterns emerged for incidences sorted by increasing body size and minimum area requirement and decreasing litter size (envNODE, $Z = 2.11\text{--}3.80$, $P < 0.05$; Supplementary Table S7). For large and medium-sized mammals, the observed envNODE values ordered by increasing minimum area requirement and decreasing body size as well as habitat specificity were significantly higher than expected by chance (envNODE, $Z = 2.07\text{--}2.17$, Supplementary Table S8). For small mammals, significant nestedness was observed for incidences ranked by increasing minimum area requirement and decreasing litter size (envNODE, $Z = 2.34$ and 2.88 , $P < 0.05$; Supplementary Table S9).

Discussion

In this study, we simultaneously investigated the presence of taxonomic, functional, and phylogenetic nestedness and

underlying causal mechanisms in 3 mammal assemblages in the Zhoushan Archipelago, China. Results showed that the selective extinction hypothesis, selective colonization hypothesis, and habitat nestedness hypothesis were supported in overall and small mammal metacommunities, but the selective colonization hypothesis was only supported in large and medium-sized mammal assemblages when performing phylogenetic and functional nestedness analysis.

We found that overall species and small species were taxonomically nested in our system, but not for large and medium-sized species, suggesting that whether the nested pattern is significant, even within the same island system, may depend on which mammal assemblages were selected for analysis. A recent study detected taxonomic nestedness of large and medium-sized mammals in land-bridge islands, and it was greatly affected by island area (Chen et al. 2019). Indeed, large islands harbored richer large and medium-sized species in our study, but they account for a relatively small proportion of selected islands and the whole archipelago (Figure 1, Supplementary Table S1). Meantime, large and medium-sized species were detected on 20 of the 39 study islands, while *Hydropotes inermis* (sp02) was the only large and medium-sized species occurring on 13 of these 20 study islands.

The results of functional and phylogenetic nestedness for overall species and small species generally mirrored the patterns as revealed in the taxonomic nestedness, indicating that island area, distance to nearest mainland, habitat diversity, and temporal isolation determined the functional and phylogenetic nestedness of these 2 mammal assemblages. We also found that the species-site matrix of large and medium-sized species arranged by increasing distance to mainland was significantly nested in both phylogenetic nestedness and functional nestedness, indicating that islands with short-distance from the nearest mainland harbored higher phylogenetic and functional diversity (Chen et al. 2022). However, the analysis of taxonomic nestedness did not detect a significantly nested pattern, indicating that the distance-driven selective colonization process was overlooked entirely by taxonomic nestedness analyses. The reasons may be attributed to 2 important aspects. First, the inapparent nested pattern of taxonomic nestedness prevents measuring the correlation between maximally packed matrix and island characteristics or species ecological traits. In addition, island mammal assemblages may tend to be phylogenetically and functionally clustered (Si et al. 2022), resulting in a disproportionate influence in phylogenetic and functional diversities with taxonomic diversity.

The phylogenetic and functional nestedness for the 3 mammal assemblages was driven mainly by compositional nestedness, as the compositional components always comprised a major proportion of functional nestedness rather than the resemblance component. Some previous studies also discovered more contributions of compositional component on 18 area-ordered bird matrices and 37 islands-ordered amphibian matrices (Matthews et al. 2015b; Chen et al. 2022). However, several studies found relatively higher contributions of resemblance components in their systems (Melo et al. 2014; Jacoboski et al. 2016). When relating to previous studies (Melo et al. 2014; Matthews et al. 2015b; Almeida-Gomes et al. 2019; Chen et al. 2022), we considered the reason can be attributed to the fact that generalist mammal species not only occurred on most islands but also were the only species on a majority of islets, which magnifies the values of compositional

Table 3. The phylogenetic (phyloNODF) and functional (traitNODF) nestedness values for 3 mammal assemblages in the Zhoushan Archipelago, China

Mammal assemblages	treeNODF	Metric	Island characteristics					
			Area	DTNM	DTNI	HD	LUI	TISM
Overall species	phyloNODF	phyloNODF	79.07**	64.65**	47.72	79.61**	51.31	74.00**
		S.Fraction	74.81**	62.57**	44.42	75.88**	48.39	71.05**
		topoNODF	4.27**	2.07	3.30	3.72*	2.92	2.94
		topo Prop.	5.39	3.21	6.92	4.68	5.70	3.98
	traitNODF	traitNODF	77.26**	68.30**	46.58	78.93**	50.34	76.18**
		S.Fraction	73.71**	65.10**	44.07	75.47**	47.87	72.52**
		topoNODF	3.55**	3.20*	2.51	3.46**	2.47	3.66**
		topo Prop.	4.60	4.69	5.38	4.39	4.90	4.80
Large and medium-sized species	phyloNODF	phyloNODF	37.65	41.18*	28.51	37.45	33.17	34.96
		S.Fraction	31.84	32.89	27.11	31.58	31.58	27.63
		topoNODF	5.81	8.28*	1.40	5.87	1.59	7.32
		topo Prop.	15.44	20.11	4.92	15.67	4.80	20.95
	traitNODF	traitNODF	37.29	39.33*	29.75	36.43	32.50	36.27
		S.Fraction	32.63	33.68*	27.89	31.84	30.79	31.05
		topoNODF	4.65	5.64*	1.86	4.58	1.71	5.22
		topo Prop.	12.48	14.35	6.24	12.58	5.26	14.38
Small species	phyloNODF	phyloNODF	76.77**	61.60**	49.47	76.02**	55.44	71.26**
		S.Fraction	71.99**	60.03**	44.54	71.56**	51.12	68.31**
		topoNODF	4.78*	1.57*	4.93*	4.46	4.32	2.95
		topo Prop.	6.23	2.55	9.97	5.87	7.80	4.13
	traitNODF	traitNODF	77.21**	68.03**	46.24	77.08**	53.03	75.58**
		S.Fraction	74.04**	66.11**	44.54	74.09**	50.80	72.81**
		topoNODF	3.17**	1.92	1.70	3.00**	2.24	2.77**
		topo Prop.	4.11	2.82	3.67	3.89	4.22	3.66

We reported phylogenetic and functional nestedness and their 2 components (S. Fraction and topoNODF). For each island characteristic, we only reported the results with the better fit (smaller P values of phylogenetic or functional nestedness). The proportion of treeNODF represented by topoNODF (topo Prop.) is also presented. * $P < 0.05$, ** $P < 0.01$. See variable abbreviations in Table 2.

components and leads to a lower proportion of resemblance components in our system.

The taxonomic, phylogenetic, and functional nestedness of all 3 mammal assemblages were consistent with the selective colonization hypothesis, as the 3 dimensions of nested patterns for them were significantly correlated with distance to the nearest mainland. However, we found that the taxonomic nestedness was not correlated with body size, a proxy of dispersal ability. One possibility for this unexpected result is that small species' colonization and extinction were unrelated to body size (Lima et al. 1996). The alternative possible explanation is that several small mammals, such as *Rattus norvegicus* (sp10), *Mustela sibirica* (sp08), and *Mus musculus* (sp16), were mainly found in human settlements, harboring more opportunities to migrate to remote islands through human activities. Interestingly, we observed opposite results between overall species and large and medium-sized species when relating body size to the environment dendrogram. For overall species, the observed envNODF value was significantly nested for the matrix arranged by increasing body size among species. For large and medium-sized species, however, the observed envNODF was significantly nested for the matrix arranged by decreasing body size among species. The dominant reason is likely that mammals from these 2 assemblages immigrated to remote islands through different approaches, that is, some small-bodied mammals have more

opportunities to immigrate via human activities, but some large-bodied mammals have more abilities to immigrate via their dispersal capacity.

The taxonomic, phylogenetic, and functional nestedness of overall species and small mammals were all consistent with the selective extinction hypothesis for 3 reasons. First, the nested patterns of overall and small mammal assemblages were significantly correlated with island area. In fact, island area is typically a crucial predictor of the nested pattern in faunal assemblages on land-bridge islands or habitat island systems (Patterson and Atmar 1986; Hecnar et al. 2002; Louzada et al. 2010). Second, the nested patterns of overall and small mammal assemblages were significantly related to temporal isolation. As the 39 islands separated from the mainland, ranging from 8,400 to 10,700 years, faunal relaxation of mammal assemblages has already occurred. Finally, the taxonomic nestedness for overall species and small mammals was correlated with the species traits linked to extinction risk (litter size and minimum area requirement). For instance, *Crocidura shantungensis* (sp18) and *Rattus norvegicus* (sp10), with larger litter sizes and smaller area requirements, were found on most islands in our system.

The taxonomic, phylogenetic, and functional nestedness of overall species and small species also aligned with the habitat nestedness hypothesis because the habitat-by-site matrix

estimated by the program NODF was significantly nested. In addition, habitat diversity was correlated with their taxonomic nestedness. The habitat nestedness hypothesis is the most parsimonious process to account for nestedness (Calmé and Desochers 1999), but previous studies often have overlooked the test of habitat nestedness hypothesis. Consistent with previous findings (Calmé and Desochers 1999; Honnay et al. 1999; Wang et al. 2013), our study verified the significance of habitat nestedness in generating taxonomic nested patterns.

We found that the taxonomic, phylogenetic, and functional nestedness of 3 mammal assemblages did not correlate with land use intensity, rejecting the human disturbance hypothesis. At least 2 reasons can explain why these correlations are weak. On the one hand, several generalist species with higher tolerances to human disturbance (e.g., rodents and shrews) were widely distributed across the archipelago, which may weaken the correlations. On the other hand, the land use intensity reflects current conditions of human disturbance rather than the long-term effects, as ancient residents have dwelled in this region for over 5,000 years (Li and Li 1994; He et al. 2019).

We also found that the taxonomic nestedness of overall species and small species was not attributable to passive sampling because the random placement models were rejected, which is consistent with the results of several previous studies in this archipelago (Xu et al. 2017; Chen et al. 2022; Zhang et al. 2022). Empirical studies have reported that nested patterns could arise from random sampling of species differing in their relative abundances (Cutler 1994; Higgins et al. 2006). Hence, it is emphasized that the data should be tested for passive sampling prior to other hypotheses, while the sampling effect has rarely been tested probably due to the difficulties of collecting species abundance data (Wright et al. 1998). In our study, camera-trapping methods and live-trapping methods were used to survey large and medium-sized species and small species respectively. These different sampling methods have different estimates of abundance data, which may affect the results of the passive sampling.

Surprisingly, we observed consistent results for both the nested pattern and underlying processes between overall species and small species, regardless of which dimensions in nestedness were measured. Similarly, Almeida-Gomes et al. (2015) also found that the observed functional nestedness value ordered by the amount of habitat was significantly higher than expected by chance for overall species and forest-dependent species but not for generalist species of amphibian communities in an Atlantic Forest fragmented landscape, but the reason behind this result has not been explained. In our study, the reasons underlying such a pattern might be twofold. First, small species account for a greater proportion of overall species in all study islands, ranging from 69% to 100%. Second, the species richness of small species and overall species were significantly positively correlated (Spearman's $r = 0.98$, $P < 0.001$), with the same distribution range on study islands.

As collinearities often exist among island variables or species traits, partial Spearman rank correlations are widely used to separate out the independent effect of these variables on nestedness (Frick et al. 2009; Wang et al. 2010, 2012, 2023). However, like several previous studies (Chen et al. 2022; Zhang et al. 2022), we did not perform partial Spearman rank correlation because the sample size ($n = 18$) in our study might be too small to perform multi-predictor partial

correlation tests. Hence, when the sample size is small, it is often hard to quantify the relative role of multiple significant drivers of nestedness using the univariate rank-correlation approach (Chen et al. 2022; Zhang et al. 2022). For example, a strong correlation between island area and habitat diversity was found in our study (Spearman's $r = 0.87$, $P < 0.001$; Supplementary Table S4), but we cannot determine whether island area or habitat diversity is more important in determining nestedness.

In conclusion, we found the differences of nestedness and underlying mechanisms not only in 3 dimensions of the nested pattern but also in 3 mammal assemblages. Therefore, we highlight that a framework that incorporates taxonomic, phylogenetic, and functional nestedness can contribute to a more comprehensive understanding of nestedness processes. In addition, large and medium-sized species and small species show contrasting responses to nestedness due to the intrinsic characteristics. Thus, it is necessary to explore the nested pattern and other patterns of island biogeography and community ecology for different subsets of species separately. Our results advance the understanding of community structure patterns and underlying mechanisms of mammal assemblages on the land-bridge island ecosystems.

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Conflict of Interests

The authors have no conflicts of interest to declare.

Authors' Contributions

Y.W. and C.C. conceived the ideas; C.Z. and L.B. conducted fieldwork; C.Z. analyzed the data and performed the statistical analyses; C.Z. led the writing of the manuscript with critical inputs from Y.W.; Y.W. supervised the work.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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