

Selective extinction and habitat nestedness are the main drivers of lizard nestedness in the Zhoushan Archipelago

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Abstract

Nested subset pattern (nestedness) is an important part of the theoretical framework of island biogeography and community ecology. However, most previous studies often used nestedness metrics or randomization algorithms that are vulnerable to type I error. In this study, we investigated the nestedness of lizard assemblages on 37 islands in the Zhoushan Archipelago, China. We used the line-transect method to survey species occurrence, abundance, and habitat types of lizards on 37 islands during 2 breeding seasons in 2021 and 2022. We applied the nested metric WNODF and the conservative rc null model to control for type I error and quantify the significance of nestedness. Spearman rank correlations were used to evaluate the role of 4 habitat variables (island area, 2 isolation indices, and habitat diversity) and 4 ecological traits (body size, geographic range size, clutch size, and minimum area requirement) in generating nestedness. The results of WNODF analyses showed that lizard assemblages were significantly nested. The habitat-by-site matrix estimated by the program NODF was also significantly nested, supporting the habitat nestedness hypothesis. The nestedness of lizard assemblages were significantly correlated with island area, habitat diversity, clutch size, and minimum area requirement. Overall, our results suggest that selective extinction and habitat nestedness were the main drivers of lizard nestedness in our system. In contrast, the nestedness of lizard assemblages was not due to passive sampling or selective colonization. To maximize the number of species preserved, our results indicate that we should protect both large islands with diverse habitats and species with large area requirement and clutch size.

Key words: clutch size, habitat nestedness, lizards, minimum area requirement, nestedness, selective extinction, WNODF, Zhoushan Archipelago.

Nested subset pattern (nestedness) is a nonrandom distribution pattern of communities widespread in islands or fragmented systems (Wright et al. 1998; Whittaker and Fernández-Palacios 2007). Nestedness occurs when the species in the species-poor island are an appropriate subset of the species in the species-rich islands (Darlington 1957; Patterson and Atmar 1986). The study of nestedness was popularized by Patterson and Atmar (1986), who conceived the first community-level metric to test for nestedness statistically (Whittaker and Fernández-Palacios 2007; Wang et al. 2012). So far, nestedness has become an important part of the theoretical framework of island biogeography and community ecology (Worthen 1996; Weiher and Keddy 1999; Whittaker and Fernández-Palacios 2007).

Four main hypotheses have been proposed to interpret nestedness, including passive sampling, selective extinction, selective colonization, and habitat nestedness (Table 1; Cutler 1994; Cook and Quinn 1995; Wright et al. 1998). Passive sampling could cause nestedness in that rare species are less likely to be sampled in a given area, compared with common species (Andrén 1994; Higgins et al. 2006). According to the selective extinction hypothesis, in systems experiencing species loss, species with different extinction vulnerability would disappear from sites in a predictable sequence and thus lead to nestedness (Simberloff and Levin

1985; Li et al. 1998). The selective colonization hypothesis posits that island isolation would create nestedness through dispersal limitation because species have distinctive ability to colonize distant sites (Darlington 1957; Cook and Quinn 1995). Finally, the habitat nestedness hypothesis suggests that the species distribution is nested because their habitats are nested (Calmé and Desrochers 1999; Honnay et al. 1999; Wang et al. 2013).

Species life-history traits (ecological traits) may also have important impacts on the formation of nestedness (Table 1; Schouten et al. 2007; Meyer and Kalko 2008; Wang et al. 2010). For instance, if extinction sensitivity is an important factor affecting the distribution structure of species assemblages, then life-history characteristics related to extinction will determine nestedness (Frick et al. 2009; Wang et al. 2012; Chen et al. 2022). However, if dispersal ability is a main driver of nestedness, ecological traits associated with the relative mobility of species may order species occurrence patterns (Cook and Quinn 1995; Meyer and Kalko 2008). In fact, the above processes causing nestedness usually emerge as a result of coupled gradients in site characteristics and species' ecological responses (Ulrich et al. 2009).

To date, relatively few studies have examined the nestedness for the taxon of lizards, particularly in oceanic

Table 1 Four common hypotheses explaining the nestedness pattern of lizard assemblages in the Zhoushan Archipelago, China

Hypotheses	Assumptions	Predictions	References
	Island properties	Species properties	
Selective extinction	Carrying capacities	Extinction sensitivity (e.g., geographic range size, clutch size, and minimum area requirement)	Wright et al. (1998); Wang et al. (2012); Chen et al. (2022)
Selective colonization	Isolation	Dispersal ability (e.g., body size, swimming ability)	Darlington (1957); Cook and Quinn (1995); Meyer and Kalko (2008)
Habitat nestedness	Habitat heterogeneity	Degrees of specialization	Calmé and Desrochers (1999); Honnay et al. (1999); Wang et al. (2013)
Passive sampling	Carrying capacities	Regional abundance (rare species/common species)	Andrén (1994); Cutler (1994); Higgins et al. (2006)

archipelago systems (Perry et al. 1998). The few existing studies on lizard assemblages showed that isolation, habitat diversity, and habitat types were the main external drivers of nestedness (Wang et al. 2010; Rubio and Simonetti 2011; Rocha et al. 2014). Perry et al. (1998) also inferred that certain life-history trait (population density) may be important in generating nestedness. However, except for Wang et al. (2010), other studies did not combine environmental variables and species traits simultaneously to examine their roles in generating nestedness.

In this study, we investigated the nestedness of lizard assemblages on 37 islands in the Zhoushan Archipelago, China. We addressed the following 3 main questions: (1) Was the distribution of lizard assemblages among islands significantly nested? (2) What are the mechanisms underlying the nestedness of lizard assemblages? (3) How can nestedness theory be applied to direct conservation management of lizard assemblages in our system?

Materials and Methods

Study area

The Zhoushan Archipelago (29°31'~30°04'N, 121°30'~123°25'E), the largest archipelago in China (Li et al. 1998), is located in the northeast of Zhejiang Province, China (Figure 1). There are a total of 1339 islands in the Zhoushan Archipelago, including 58 islands with areas larger than 1 km² (Wang et al. 2009a). It is a land-bridge archipelago that was separated from the continent by the intervention of seawater about 7000–9000 years ago. The climate in this region belongs to the monsoon oceanic climate of the southern margin of the North subtropics, which is overall warm and humid (Li et al. 1998). The archipelago is covered by the dense subtropical evergreen broadleaf forest, which is mixed with secondary coniferous forest, grassland, and shrubs (Chen et al. 2022).

Thirty-seven islands were selected as our study sites, which represent a series of diverse areas, shapes, habitat types, and levels of isolation (Figure 1). Among the islands, the area ranged from 0.68 km² to 476.17 km², the distance from the nearest continent varied from 0.4 km to 77.49 km, and the number of habitat types ranged from 2 to 9 (Table 2). Our sampling effort on each site was roughly proportional to the logarithm of the island area (Schoederer et al. 2004; Chen et al. 2022), and the line transects on each island were set to cover as many habitats as possible (Xu et al. 2017). However, it should be noted that our 37 study islands are not the same of the 37 islands in the amphibian study by Chen et al. (2022). Specifically, 3 islands (#9, #17, #23 in Table 2) in our study were not included in the latter study.

Survey methods

Lizard surveys

We used the line-transect method (Mac Nally and Brown 2001; Wang et al. 2009b) to compile the occurrence and abundance data of lizards on the 37 study islands from May to July in 2021 and 2022 (Supplementary Table 1). Along the line transects on each island, observers searched all the habitat types to find lizards at a steady rate (10 m/min). The survey of lizards was conducted during the daytime when the weather was pleasant from 9:00 AM to 16:00 PM, excluding the hottest period at noon when the activity of lizards

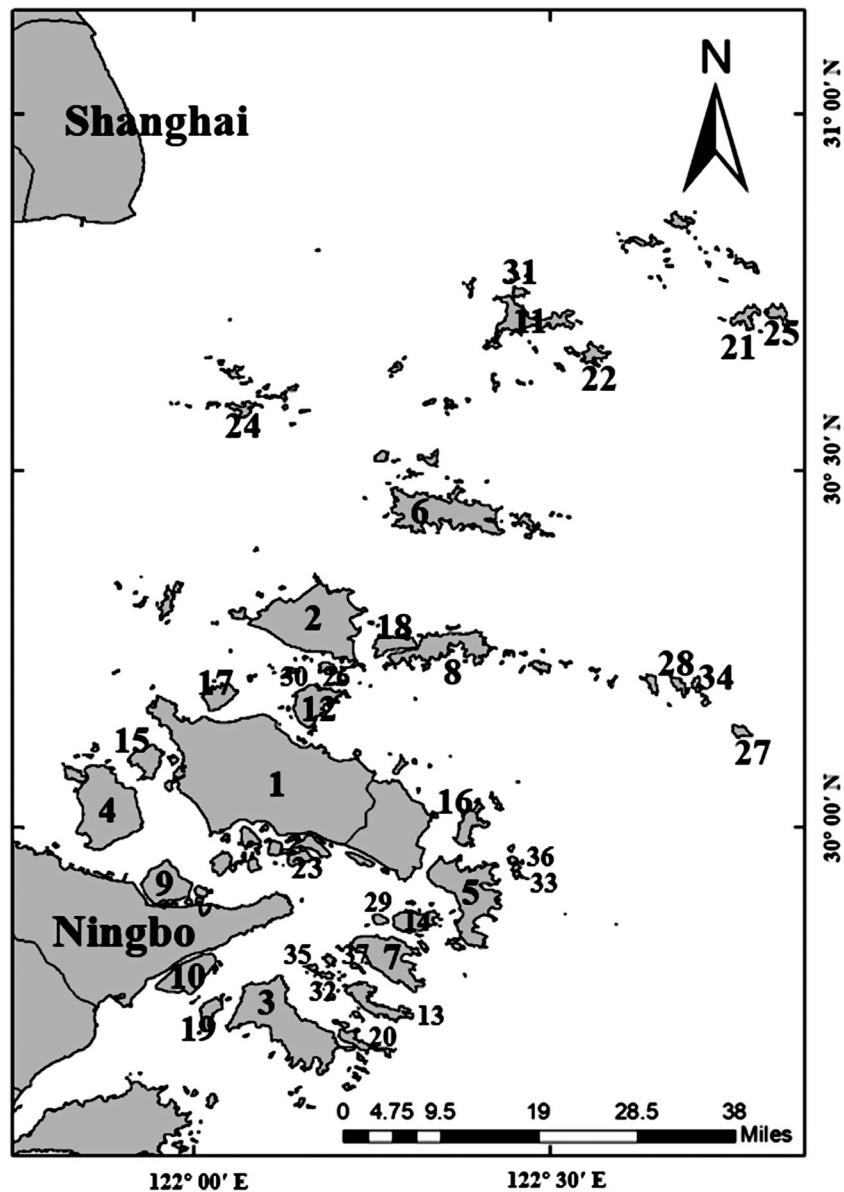


Figure 1 The map of the 37 study islands in the Zhoushan Archipelago, China. The figure was drawn from ArcMap 10.2. The numbers of islands are arranged by area from the largest to the smallest, corresponding to Table 2.

was low (Wang et al. 2009b; Zhong et al. 2022a). Geckos were surveyed from 19:00 PM to 22:00 PM because they are active in nights (Zhao et al. 1999; Meiri 2018). Because lizard activities are susceptible to inclement weather, such as rainstorms and typhoons, all the surveys were conducted on sunny days without rains or fogs (Wang et al. 2009b). Each island was surveyed 3 times to ensure that it was fully sampled.

A complete species list for each island is the foundation of any measure of nestedness (Cam et al. 2000; Wang et al. 2012; Xu et al. 2017). To evaluate the inventory completeness of lizards, we randomized (1000×) sample-based and site-based species accumulation curve for each island (Colwell 2013). We calculated the estimated number of lizard species on the study islands using the Chao 2 estimator of species richness (Table 2). Calculations were conducted using the EstimateS version 9.2 software with the default parameters (Colwell 2013).

Habitat variable surveys

For each island, we collected data on 3 types of habitat variables (area, isolation, and habitat diversity), which are generally thought to influence nestedness (Wright et al. 1998; Calmé and Desrochers 1999; Wang et al. 2012). Area of each island (in km²) was obtained from the officially published data of the Zhoushan Municipal Statistics Bureau (<http://zstj.zhoushan.gov.cn/col/col1229615782/index.html>). Two isolation indices were used as a measure of isolation, including isolation1 (the distance from the nearest mainland) and isolation2 (the distance from the nearest larger island), which were estimated from the ArcGIS 10.7 (ESRI, Redlands, CA). Considering that the habitats of lizards and geckos are quite different (Meiri 2018; Zhong et al. 2022b), all the habitat types in our system were mainly divided into 9 types: forest, shrub, grassland, farmland, reservoir, settlement, stream, mountain bare rock, and mountain road facilities (Supplementary Table 2). Habitat diversity was then

Table 2 Characteristics of 37 study islands in the Zhoushan Archipelago, China. Isolation1 is given as distance to the nearest continent; Isolation2 is the distance to the nearest larger island

Island code	Island area (km ²)	Isolation1 (km)	Isolation2 (km)	Number of habitat types (<i>n</i>)	Species richness (<i>n</i>)	Expected richness (Chao2)	Survey completeness	Nested matrix rank
1	476.17	9.10	9.10	9	8	8.5	0.94	1
2	104.97	59.42	11.38	9	7	10	0.70	4
3	93.66	6.97	6.97	9	7	15	0.47	3
4	77.35	3.50	3.50	8	7	13	0.54	2
5	61.82	19.02	0.89	9	5	5.5	0.91	12
6	59.79	55.83	11.38	9	4	4	1.00	17
7	40.37	9.44	5.98	9	5	6	0.83	7
8	33.56	40.23	4.62	9	3	3	1.00	29
9	28.37	0.40	0.40	6	3	4	0.75	30
10	26.90	0.45	0.45	6	2	2	1.00	35
11	24.44	46.07	25.27	6	5	5.5	0.91	11
12	22.88	26.69	2.71	8	3	3	1.00	22
13	17.01	13.89	2.08	7	5	8	0.63	9
14	14.51	13.87	1.21	8	5	5	1.00	8
15	14.20	16.53	1.82	6	4	4	1.00	16
16	11.85	24.88	2.92	7	6	14	0.43	6
17	11.10	30.38	1.75	7	4	6	0.67	15
18	10.92	39.18	0.28	8	3	4	0.75	27
19	7.28	7.23	1.75	7	4	5	0.80	18
20	6.92	19.50	0.50	7	5	5	1.00	14
21	5.74	77.49	20.71	7	3	3	1.00	24
22	5.21	61.00	3.54	7	2	2	1.00	34
23	5.15	4.73	0.47	6	4	4.5	0.89	21
24	4.92	32.71	22.33	7	3	3.5	0.86	28
25	4.08	81.26	0.73	7	2	2	1.00	36
26	3.14	34.82	1.19	8	5	8	0.63	10
27	2.95	65.94	34.74	5	3	3.5	0.86	31
28	2.64	62.36	7.92	6	3	3	1.00	25
29	2.22	10.98	1.05	5	3	3	1.00	26
30	1.94	33.67	2.65	6	4	6	0.67	20
31	1.72	47.70	0.28	6	3	3.5	0.86	32
32	1.51	9.73	2.40	6	4	5	0.80	19
33	1.44	30.40	2.45	5	6	6	1.00	5
34	1.41	63.80	0.94	4	2	2	1.00	33
35	0.93	8.17	3.60	2	2	2	1.00	37
36	0.88	30.50	0.36	5	5	6	0.83	13
37	0.68	11.74	1.31	6	3	3	1.00	23

calculated as the number of habitat types observed for lizards on each island (6.81 ± 1.60 ; Mean \pm SD; Table 2; Wang et al. 2012).

Species life-history traits

For each species, we selected 4 life-history traits, including body size, geographic range size, clutch size, and minimum area requirement, which could reflect species extinction and immigration tendencies (Li et al. 1998; Tingley et al. 2013; Zhong et al. 2022a). Among the traits, geographic range size, clutch size, and minimum area requirement were closely related to extinction proneness (Li et al. 1998; Siliceo and Díaz 2010; Wang et al. 2012). We used body length (mm) to represent body size, which is usually linked to dispersal

ability (Jenkins et al. 2007; Wang et al. 2012). Average clutch size was used as an index of reproductive potential (Wang et al. 2009b). The data on body size, geographic range size, and clutch size were obtained from published literature (Zhao et al. 1999; Zhong et al. 2022b). The minimum area requirement of each species was based on our field survey and estimated as the area of the smallest island occupied by each species (Li et al. 1998; Wang et al. 2010; Xu et al. 2017).

Statistical analyses

Quantification of nestedness

We used the recently developed nestedness metric WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill) to assess the nestedness of lizard assemblages.

WNODF is a simple modification of the nestedness metric NODF that incorporates species abundance data (Almeida-Neto and Ulrich 2011). Compared with other nestedness metrics, WNODF has several unique advantages. First, both presence–absence data and abundance data can be used to assess the nestedness by WNODF. Second, not only the whole incidence matrix (WNODF), but also species (WNODF_R) and sites (WNODF_C) can be calculated separately (Wang et al. 2013). Finally, the WNODF metric is less sensitive to matrix size and shape, and less prone to Type I error, than other commonly used metrics (Almeida-Neto and Ulrich 2011). We used the *rc* randomization algorithm to randomly generate 1000 matrices and estimated the statistical results within the 95% confidence interval. Among the algorithms, the *rc* null model is the most conservative to Type I error by maintaining the original matrix size and the original abundance in both rows and columns (Almeida-Neto and Ulrich 2011). All the above calculations were performed using the program NODF version 2.0 (Almeida-Neto and Ulrich 2011).

Determinants of nestedness

We used the random placement model (Coleman 1981) to determine whether passive sampling from species abundance distributions played a major role in generating the nestedness of lizard assemblages (Higgins et al. 2006; Wang et al. 2010). Based on the random placement model, the expected species richness $S_{(\alpha)}$ ($S_{(\alpha)} = S - \sum_{i=1}^S (1 - \alpha)^{n_i}$) depends on the region's relative area α ($\alpha = a_k / \sum_{k=1}^k a_k$) and the abundance (n_i) of each species in the region. In the above model, S is the sum of the species richness at all locations, and a_k is the area of a certain location. The variance σ^2 of $S_{(\alpha)}$ is determined as $\sigma_{(\alpha)}^2 = \sum_{i=1}^S (1 - \alpha)^{n_i} - \sum_{i=1}^S (1 - \alpha)^{2n_i}$. The random placement model should be rejected if more than one-third of the points lie outside 1 standard deviation (± 1 SD) of the expected species-area curve (Coleman et al. 1982).

We used the nestedness metric NODF in the program NODF version 2.0 (Almeida-Neto et al. 2008) to evaluate whether the habitat-by-site matrix (Supplementary Table 3) was significantly nested. If the habitat-by-site matrix was nested, then the nestedness of lizard assemblages in our system can be interpreted by the habitat nestedness hypothesis (Calmé and Desrochers 1999; Wang et al. 2013).

The order in which sites and species are sorted by WNODF can be compared with numerous independent variables to assess their roles in generating nestedness (Patterson and Atmar 2000; Xu et al. 2017). We performed Spearman rank correlations between the island ranks in the maximally

packed matrix and ranked island attributes (island area, 2 isolation indices, and habitat diversity; Table 2). Similarly, we calculated Spearman rank correlations between the species ranks in the maximally packed matrix and ranked species traits (body size, geographic range size, clutch size, and minimum area requirement; Table 3). All the above analyses were performed in R 4.2.1 (R Core Team 2021).

Results

General survey results

A total of 2126 individuals of lizards belonging to 8 species, 5 genera, and 3 families were detected during the 2-year study period. Among all species, the 3 geckos species were the most abundant, whereas *Plestiodon chinensis* and *Scincella modesta* were the rarest species (Table 3). The observed species richness on each island varied from 2 to 8 (4.11 ± 1.58 ; Mean \pm SD; Table 2). Survey completeness of lizard assemblages for the 37 study islands was very high 0.86 ± 0.17 (Mean \pm SD; Table 2). The species accumulation curve using individuals or islands as surveying units both approached an asymptote (Supplementary Figure 1), which also indicated a high level of lizard inventory completeness for the study islands.

Nestedness of lizard assemblages

Based on the species-by-site abundance or presence–absence matrix (Supplementary Table 1), the results of WNODF verified that lizard assemblages in the Zhoushan Archipelago were significantly nested (Table 4). Additionally, both species composition (WNODF_C = 29.33, $P < 0.001$) and species incidence (WNODF_R = 38.48, $P < 0.001$) were significantly nested (Table 4).

Determinants of nestedness

The nestedness of lizard assemblages was significantly and negatively correlated with the island area (Table 5). Nestedness was also significantly and positively related to the species traits linked to extinction tendencies (clutch size and minimum area requirement; Table 5).

The habitat-by-site matrix estimated by the program NODF was significantly nested (NODF_{obs} = 79.22 > NODF_{exp} = 48.92, $P < 0.001$; Table 4), supporting the habitat nestedness hypothesis. In addition, species nestedness was significantly and negatively correlated with habitat diversity (Table 5).

The nestedness of lizard assemblages did not appear to result from selective colonization (Table 5). Nestedness of

Table 3 Ecological traits of lizard species on 37 study islands in the Zhoushan Archipelago, China

Species	Body size (mm)	Geographic range size (km ²)	Clutch size (<i>n</i>)	Minimum area requirement (km ²)	Population abundance (<i>n</i>)	Mean abundance (SD)	Nested matrix rank
<i>Takydromus septentrionalis</i>	64.00	2347321.80	3.5	0.69	136	3.68 (5.91)	1
<i>Plestiodon elegans</i>	79.00	2520261.88	6.5	0.88	53	1.43 (2.75)	7
<i>Plestiodon chinensis</i>	105.00	2438373.56	21.0	1.94	8	0.22 (0.42)	8
<i>Scincella modesta</i>	48.00	1171199.92	9.0	1.51	21	0.57 (0.87)	6
<i>Sphenomorphus indicus</i>	76.00	3284468.81	6.0	0.88	35	0.95 (1.35)	4
<i>Gekko japonicus</i>	64.00	1918348.55	2.0	1.44	376	10.16 (19.07)	5
<i>Gekko hokouensis</i>	65.00	1256464.85	2.0	0.69	677	18.30 (21.24)	2
<i>Gekko subpalmatus</i>	61.00	1027502.31	2.0	0.69	820	22.16 (38.11)	3

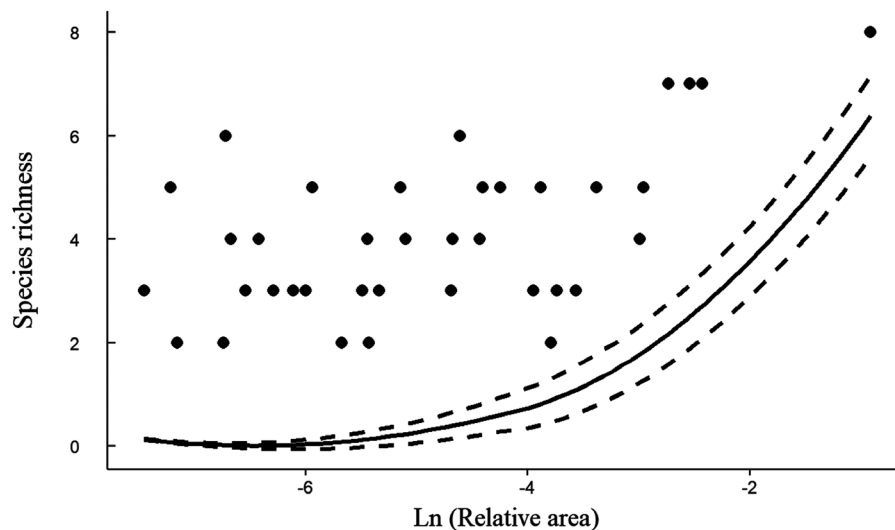
Table 4 Results of nestedness analyses using the program NODF conducted on the abundance matrix (WNODF) or presence–absence matrix (NODF) for lizard assemblages and their habitats on 37 study islands in the Zhoushan Archipelago, China

		WNODF			NODF		
		Observed	Expected	<i>P</i>	Observed	Expected	<i>P</i>
Species	All matrix	30.09	50.13	< 0.001	65.78	40.86	< 0.001
	Sites	29.81	49.24	< 0.001	65.65	40.76	< 0.001
	Species	36.75	74.02	< 0.001	68.91	43.19	< 0.001
Habitats	All matrix				79.22	48.92	< 0.001
	Sites				79.01	48.57	< 0.001
	Species				83.09	55.51	< 0.001

Table 5 Spearman rank correlations between rank orders of sites and species in the maximally nested matrix and orders of sites and species after rearranging the matrix according to each explanatory variable

	Island biogeographic variables				Species life-history traits			
	Island area (km ²)	Isolation1 (km)	Isolation2 (km)	Number of habitat types (<i>n</i>)	Body size (mm)	Geographic range size (km ²)	Clutch size (<i>n</i>)	Minimum area requirement (km ²)
<i>r_s</i>	-0.475	0.284	-0.231	-0.478	0.431	0.310	0.732	0.872
<i>P</i>	0.003	0.088	0.168	0.003	0.286	0.462	0.039	0.005

Significant results are shown in bold.

**Figure 2** The random placement model for lizards on 37 study islands in the Zhoushan Archipelago, China. Observed species richness (filled circles), expected values (solid line), and associated standard deviations (± 1 SD; dashed lines) are shown, respectively.

lizard assemblages was not correlated with the 2 isolation indices or body size as a proxy for dispersal ability ($P > 0.05$; Table 5).

The results of the random placement model showed that none of the observed points was within 1 standard deviation (± 1 SD) of the predicted species–area curve (Figure 2), rejecting the passive sampling hypothesis.

Discussion

In this study, we investigated the nestedness of lizard assemblages in the Zhoushan Archipelago, China. Our study differs from previous nestedness studies in several ways. First, although nestedness has been documented for a variety

of taxa (Wright et al. 1998; Watling and Donnelly 2006; Dondina et al. 2022), it is rarely examined in lizard assemblages from oceanic archipelago systems (Perry et al. 1998). Our study on lizards thus fills in a significant gap and contributes to the ecological generality of nestedness across a wide range of taxa. Second, few studies have explicitly tested the sampling effect or habitat nestedness hypothesis due to the difficulties in collecting species abundance or habitat data (Li et al. 1998; Wright et al. 1998; Xu et al. 2017). In contrast, we tested the 4 hypotheses underlying nestedness simultaneously in our study. Finally, most previous studies used nestedness metrics (e.g., temperature metric) or random fill algorithms that are vulnerable to type I error (Atmar and Patterson 1993; Fischer and Lindenmayer 2002; Ulrich and Gotelli 2007).

Our study used the most recent and appropriate nestedness metric (WNODF) and the best-performing fixed-fixed algorithm, which can successfully avoid the type I error (Ulrich and Gotelli 2007; Almeida-Neto and Ulrich 2011; Wang et al. 2012).

The nestedness of lizard assemblages was consistent with the selective extinction hypothesis because the nestedness was significantly correlated with island area and the species trait linked to extinction tendencies (minimum area requirement). Selective extinction is widely considered as a pivotal driver of nestedness, particularly in land-bridge archipelagos and in habitat fragments that are experiencing species loss or “faunal relaxation” (Patterson 1987; Bolger et al. 1991; Wang et al. 2012). As the Zhoushan Archipelago has been isolated from the mainland for 7000–9000 years (Wang et al. 2009a), it is highly likely that faunal relaxation has already occurred. Previous studies in the same system found that selective extinction is the main driver of nestedness for amphibians and butterflies (Li et al. 1998; Xu et al. 2017; Chen et al. 2022). In our study, selective extinction may cause nestedness because lizard species with large area requirement have higher extinction risks and thus will go extinct first (Li et al. 1998; Xu et al. 2017).

However, we found a positive correlation between species rank in the maximally nested matrix and clutch size, which is contrary to the selective extinction hypothesis. According to the selective extinction hypothesis, lizard species with lower reproductive potential (small clutch size) are more prone to extinction (Siliceo and Díaz 2010) and should thus be found on a small subset of islands. By contrast, in our study, lizard species with small clutch size are widespread and abundant in most of the islands, whereas species with large clutch size can be found only in a nested subset of islands. One possible explanation for the result is that lizard species with large clutch size in our system are also those with large minimum area requirement that are more prone to extinction (Spearman $\rho = 0.717$, $P = 0.045$). Our result thus suggests that we should pay prior attention to lizard species with large clutch size (e.g., *P. chinensis*, *S. modesta*).

The nestedness of lizard assemblages was also in accord with the habitat nestedness hypothesis as the habitats of lizards in our system were significantly nested. Habitat nestedness is considered as the most parsimonious process to explain species nestedness (Calmé and Desrochers 1999). However, so far, few studies have explicitly tested the habitat nestedness hypothesis probably because of the difficulty in collecting habitat data. For example, the 2 previous studies in the Zhoushan Archipelago did not collect habitat data for amphibians and butterflies to test the habitat nestedness hypothesis (Li et al. 1998; Xu et al. 2017). Consistent with previous findings (Calmé and Desrochers 1999; Honnay et al. 1999; Wang et al. 2013; Tan et al. 2021), our study provides further evidence for the role of habitat nestedness in generating species nestedness.

There was no evidence that the nestedness of lizard assemblages resulted from passive sampling. Several studies have shown that nestedness could arise from random sampling of species differing in their relative abundances (Andrén 1994; Cutler 1994; Higgins et al. 2006). Although it is stressed that the data should be tested for passive sampling prior to other hypotheses, the sampling effect has rarely been examined probably because of the difficulties involved in collecting species abundance data (Andrén 1994; Wright et al. 1998).

Our results indicate that passive sampling plays little role in the development of nestedness, which is consistent with the results of several previous studies (Worthen et al. 1998; Wang et al. 2010; Xu et al. 2017; Chen et al. 2022).

The nestedness of lizard assemblages was also not in accord with the selective colonization hypothesis. The nestedness was not correlated with the 2 island isolation indices and species body size as a proxy for dispersal ability. At least 3 reasons may explain why the correlations are weak. First, compared with other vagile taxa (e.g., birds or bats), colonization probably has rarely occurred in our system due to the poor dispersal ability of lizards, which may greatly reduce the impact of selective colonization on nestedness (McAbendroth et al. 2005; Wang et al. 2010). Second, the stepping stone effect of some small islands may dilute the effect of isolation by distance (Xu et al. 2017; Uezu et al. 2008). Finally, the lack of a significant effect of isolation on nestedness is because the biologically meaningful quantification of isolation is notoriously difficult (Lomolino 1996). In fact, we know very little about the relative dispersal ability of most lizards, which precludes strong inferences on the impact of selective colonization on nestedness.

Chen et al. (2022) recently investigated the nestedness of amphibians in the Zhoushan Archipelago. The results of the nestedness in amphibians are general consistent with our study on lizard nestedness. Overall, the nestedness of amphibians and lizards are both consistent with the selective extinction and habitat nestedness hypotheses, but not caused by passive sampling and selective colonization. Specifically, the nestedness of amphibians and lizards are correlated with island area, habitat diversity, clutch size, and minimum area requirement. However, clutch size is negatively correlated with the nestedness of amphibians, which is opposite to our result. In addition, geographic range size also affects the nestedness in amphibians, but not in lizards. Therefore, although the general processes determining the nestedness of amphibians and lizards are largely congruent, their specific responses in life-history traits to the long-term insular isolation are quite different.

So far, Spearman rank correlation has been widely used to determine the drivers of nestedness. Because the ordering of the sites or species by the nestedness software (e.g., NODF) is only relative, Spearman rank correlation is particularly suitable for analyzing such variables (Patterson and Atmar 2000). By contrast, the multiple linear regression analysis cannot be used because the dependent variable (rank values of the sites or species) often does not meet the assumption of normal distribution (Zar 2010). However, it is often hard to quantify the relative role of multiple significant drivers of nestedness due to the use of the univariate rank-correlation approach.

In conclusion, both island characteristics and species ecological traits influenced the nestedness of lizard assemblages in the Zhoushan Archipelago. Understanding the nestedness pattern and its mechanistic basis has important implications for biodiversity conservation and can be used to direct management efforts (Patterson 1987; Fleishman et al. 2002; Xu et al. 2017). Our results have 3 general conservation implications. First, to maximize the number of species preserved, large islands should be the focus of conservation because the nestedness of lizard assemblages was correlated with the island area and all the 8 lizard species occurred on the largest island (Zhoushan Island; Supplementary Table 1). Second, as habitat diversity and habitat nestedness played important

roles in structuring the nestedness of lizard assemblages, habitat-rich islands also should receive more attention in lizard diversity conservation. Finally, as minimum area requirement and clutch size were positively correlated with lizard nestedness and species with larger area requirement and clutch size have higher extinction risk, those species should be given conservation priority to prevent their local extinction.

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Conflict of interests

The authors declare no competing interests.

Author contributions

YW conceived the study. MZ, CT, QZ, CZ, and CC collected the data. MZ performed the analyses and wrote the first draft of the manuscript. YW contributed substantially to the writing of the manuscript.

Supplementary Material

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

References

- Almeida-Neto M, Guimarães P, Guimarães PRJ, Loyola RD, Ulrich W, 2008. A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. *Oikos* 117:1227–1239.
- Almeida-Neto M, Ulrich W, 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. *Environ Model Softw* 26:173–178.
- Andrén H, 1994. Can one use nested subset pattern to reject the random sample hypothesis? Examples from boreal bird communities. *Oikos* 70:489–491.
- Atmar W, Patterson BD, 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–382.
- Bolger DT, Alberts A, Soulé ME, 1991. Occurrence patterns of bird species in habitat fragments: Sampling, extinction, and nested species subsets. *Am Nat* 137:155–166.
- Calmé S, Desrochers A, 1999. Nested bird and micro-habitat assemblages in a peatland archipelago. *Oecologia* 118:361–370.
- Cam E, Nichols JD, Hines JE, Sauer JR, 2000. Inferences about nested subsets structure when not all species are detected. *Oikos* 91:428–434.
- Chen C, Zhan C, Wang Y, 2022. Do functional and phylogenetic nestedness follow the same mechanisms as taxonomic nestedness? Evidence from amphibians in the largest archipelago of China. *J Anim Ecol* 91:2424–2436.
- Coleman BD, 1981. On random placement and species-area relations. *Math Biosci* 54:191–215.
- Coleman BD, Mares M, Willig MR, Hsieh Y-H, 1982. Randomness, area, and species richness. *Ecology* 63:1121–1133.
- Colwell RK, 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9.2. User's Guide and application. Available from: <http://purl.oclc.org/estimates>.
- Cook RR, Quinn JF, 1995. The influence of colonization in nested species subsets. *Oecologia* 102:413–424.
- Cutler AH, 1994. Nested biotas and biological conservation: Metrics, mechanisms, and meaning of nestedness. *Landscape Urban Plann* 28:73–82.
- Darlington PJ, 1957. *Zoography*. New York: John Wiley and Sons.
- Dondina O, Orioli V, Tirozzi P, Bani L, 2022. Long-term dynamic of nestedness in bird assemblages inhabiting fragmented landscapes. *Landscape Ecol* 37:1543–1558.
- Fischer J, Lindenmayer DB, 2002. Treating the nestedness temperature calculator as a “black box” can lead to false conclusions. *Oikos* 99:193–199.
- Fleishman E, Betrus CJ, Blair RB, Mac NR, Murphy DD, 2002. Nestedness analysis and conservation planning: The importance of place, environment, and life history across taxonomic groups. *Oecologia* 133:78–89.
- Frick WF, Hayes JP, Heady PA, 2009. Nestedness of desert bat assemblages: Species composition patterns in insular and terrestrial landscapes. *Oecologia* 158:687–697.
- Higgins CL, Willig MR, Strauss RE, 2006. The role of stochastic processes in producing nested patterns of species distributions. *Oikos* 114:159–167.
- Honnay O, Hermy M, Coppin P, 1999. Nested plant communities in deciduous forest fragments: Species relaxation or nested habitats? *Oikos* 84:119–129.
- Jenkins DG, Brescacin CR, Duxbury CV, Elliott JA, Evans JA et al., 2007. Does size matter for dispersal distance? *Global Ecol Biogeogr* 16:415–425.
- Li Y, Niemelä J, Li D, 1998. Nested distribution of amphibians in the Zhoushan archipelago, China: Can selective extinction cause nested subsets of species? *Oecologia* 113:557–564.
- Lomolino MV, 1996. Investigating causality of nestedness of insular communities: Selective immigrations or extinctions? *J Biogeogr* 23:699–703.
- Mac Nally R, Brown GW, 2001. Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: Predictions, compositional change and faunal nestedness. *Oecologia* 128:116–125.
- McAbendroth L, Foggo A, Rundle SD, Bilton DT, 2005. Unravelling nestedness and spatial pattern in pond assemblages. *J Anim Ecol* 74:41–49.
- Meiri S, 2018. Traits of lizards of the world: Variation around a successful evolutionary design. *Global Ecol Biogeogr* 27:1168–1172.
- Meyer CFJ, Kalko EKV, 2008. Bat assemblages on Neotropical land-bridge islands: Nested subsets and null model analyses of species co-occurrence patterns. *Divers Distrib* 14:644–654.
- Patterson BD, 1987. The principle of nested subsets and its implications for biological conservation. *Conserv Biol* 1:323–334.
- Patterson BD, Atmar W, 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol J Linn Soc* 28:65–82.
- Patterson BD, Atmar W, 2000. Analyzing species composition in fragments. In: Rheinwald G, editor. *Isolated Vertebrate Communities in the Tropics*. Bonn Zoological Monographs 46. Bonn: Alexander Koenig Zoological Research Institute and Zoological Museum. 9–24.
- Perry G, Rodda G, Fritts T, Sharp T, 1998. The lizard fauna of Guam's fringing islets: Island biogeography, phylogenetic history, and conservation implications. *Global Ecol Biogeogr Lett* 7:353–365.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: <https://www.R-project.org/>
- Rocha CFD, Vrcibradic D, Kiefer MC, Menezes VA, Fontes AF et al., 2014. Species composition, richness and nestedness of lizard assemblages from Restinga habitats along the Brazilian coast. *Braz J Biol* 74:349–354.
- Rubio AV, Simonetti JA, 2011. Lizard assemblages in a fragmented landscape of central Chile. *Eur J Wildl Res* 57:195–199.

- Schoederer JH, Galbiati C, Ribas CR, Sobrinho TG, Sperber CF et al., 2004. Should we use proportional sampling for species–area studies? *J Biogeogr* 31:1219–1226.
- Schouten MA, Verweij PA, Barendregt A, Kleukers RJM, de Ruiter PC, 2007. Nested assemblages of Orthoptera species in the Netherlands: The importance of habitat features and life-history traits. *J Biogeogr* 34:1938–1946.
- Siliceo I, Díaz JA, 2010. A comparative study of clutch size, range size, and the conservation status of island vs. mainland lacertid lizards. *Biol Conserv* 143:2601–2608.
- Simberloff D, Levin B, 1985. Predictable sequences of species loss with decreasing island area—land birds in two archipelagos. *New Zealand J Ecol* 8:11–20.
- Tan X, Yang X, Chen C, Wang Y, 2021. Nestedness and underlying processes of bird assemblages in Nanjing urban parks. *Curr Zool* 67:383–392.
- Tingley R, Hitchmough RA, Chapple DG, 2013. Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. *Biol Conserv* 165:62–68.
- Uezu A, Beyer DD, Metzger JP, 2008. Can agroforest woodlots work as stepping stones for birds in the Atlantic forest region? *Biodivers Conserv* 17:1907–1922.
- Ulrich W, Gotelli NJ, 2007. Null model analysis of species nestedness patterns. *Ecology* 88:1824–1831.
- Ulrich W, Almeida-Neto M, Gotelli NJ, 2009. A consumer's guide to nestedness analysis. *Oikos* 118:3–17.
- Wang Y, Bao Y, Yu M, Xu G, Ping D, 2010. Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. *Divers Distrib* 16:862–873.
- Wang Y, Ding P, Chen S, Zheng G, 2013. Nestedness of bird assemblages on urban woodlots: Implications for conservation. *Landscape Urban Plann* 111:59–67.
- Wang Y, Li Y, Wu Z, Murray BR, 2009a. Insular shifts and trade-offs in life-history traits in pond frogs in the Zhoushan Archipelago, China. *J Zool* 278:65–73.
- Wang Y, Xi W, Ping D, 2012. Nestedness of snake assemblages on islands of an inundated lake. *Curr Zool* 58:828–836.
- Wang Y, Zhang J, Feeley KJ, Jiang P, Ding P, 2009b. Life-history traits associated with fragmentation vulnerability of lizards in the Thousand Island Lake, China. *Anim Conserv* 12:329–337.
- Watling JI, Donnelly MA, 2006. Fragments as islands: A synthesis of faunal responses to habitat patchiness. *Conserv Biol* 20:1016–1025.
- Weiher E, Keddy P, 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge: Cambridge University Press.
- Whittaker RJ, Fernández-Palacios JM, 2007. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford: Oxford University Press.
- Worthen WB, 1996. Community composition and nested-subset analyses: Basic descriptors for community ecology. *Oikos* 76:417–426.
- Worthen WB, Jones MT, Jetton RM, 1998. Community structure and environmental stress: Desiccation promotes nestedness in mycophagous fly communities. *Oikos* 81:45–54.
- Wright DH, Patterson BD, Mikkelsen GM, Cutler A, Atmar W, 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia* 113:1–20.
- Xu A, Han X, Zhang X, Millien V, Wang Y, 2017. Nestedness of butterfly assemblages in the Zhoushan Archipelago, China: Area effects, life-history traits and conservation implications. *Biodivers Conserv* 26:1375–1392.
- Zar JH, 2010. *Biostatistical Analysis*. Upper Saddle River, New Jersey: Prentice Hall.
- Zhao EM, Jiang YM, Huang QY, Zhao H, Zhao KT et al., 1999. *Fauna Sinica•Reptilia (Vol. 2): Squamata•Lacertilia*. Beijing: Science Press.
- Zhong YX, Chen CW, Wang YP, 2022a. Biological and extrinsic correlates of extinction risk in Chinese lizards. *Curr Zool* 68:285–293.
- Zhong YX, Chen CW, Wang YP, 2022b. A dataset on the life-history and ecological traits of Chinese lizards. *Biodivers Sci* 30:22071.