

Nestedness of snake assemblages on islands of an inundated lake

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Abstract Nestedness is a pattern frequently reported for faunal assemblages in fragmented systems. Although nestedness has been documented for a wide range of taxa, it is rarely tested in snake assemblages. To arrive at robust generalizations about processes and mechanisms structuring island biotas, it is important to examine under-represented taxa such as snakes for the insights they may offer. We tested for the existence of nestedness and underlying causal mechanisms using snake data collected on islands in the Thousand Island Lake, China. We used the line-transect method to survey snake occupancy and abundance on 20 islands during two breeding seasons in 2009 and 2010. We used the recently developed metric WNODF to estimate nestedness. We used Spearman rank correlations to examine the associations of nestedness and habitat variables (area, isolation, and habitat diversity) as well as life-history traits (body size, clutch size, geographical range size and area requirement) related to species extinction and immigration tendencies. Snake assemblages were significantly nested and were shaped by extinction processes mediated through area effects and habitat nestedness. The nestedness of snake assemblages was not due to passive sampling or selective colonization. From a conservation viewpoint, our results indicate that we should protect both the largest island with the most species-rich community and habitat-rich islands to maximize the number of species preserved [*Current Zoology* 58 (6): 828–836, 2012].

Keywords Habitat fragmentation, Habitat nestedness, Nestedness, Selective extinction, Snake, Thousand Island Lake

Nested species subsets, or nestedness, are a pattern frequently reported for faunal assemblages on islands or fragmented systems (Wright et al., 1998). Nestedness occurs when species present at species-poor sites are proper subsets of those present at more species-rich sites (Darlington, 1957; Patterson and Atmar, 1986). Although the pattern was first described nearly 50 years ago (Darlington, 1957), nestedness studies were not popularized until Patterson and Atmar (1986) devised the first community-wide metric to quantify the statistical significance of nestedness. Ever since, nestedness has increasingly become a more part of the theoretical framework of biogeography and biodiversity research (Wright et al., 1998; Whittaker and Fernandez-Palacios, 2007). Although nestedness has been documented for a wide range of taxa (Wright et al., 1998; Mac Nally and Brown, 2001; Fischer and Lindenmayer, 2005; Wang et al., 2010; Hill et al., 2011), it is rarely tested in snake assemblages.

Four general hypotheses have been proposed to account for nestedness: (1) passive sampling, (2) selective extinction, (3) selective colonization, and (4) habitat nestedness. Passive sampling could create nestedness as an artefact of underlying stochastic principles, because

common species are more likely to be sampled in a given area than rare species (Andrén, 1994; Cutler, 1994; Higgins et al., 2006). The selective extinction hypothesis predicts that in systems experiencing species loss or ‘relaxation’, area will be the main factor explaining species nestedness because species with large minimum-area requirements have greater extinction risk (Wright et al., 1998). The selective colonization hypothesis predicts that habitat isolation would generate nestedness through dispersal limitation, as species differ in their ability to colonize distant sites (Darlington, 1957; Patterson, 1987). Finally, the habitat nestedness hypothesis considers the nestedness of species assemblages as a consequence of their reliance on habitats that have a nested distribution (Calmé and Desrochers, 1999; Honnay et al., 1999).

Species life-history traits may also provide useful information for assessing the importance of different processes in generating patterns of nestedness (Meyer and Kalko, 2008; Frick et al., 2009). For instance, if extinction susceptibility is the main driver of nestedness, then life-history traits linked to extinction vulnerability may order species occurrence patterns. In contrast, if dispersal ability is a strong determinant of nestedness

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(Cook and Quinn, 1995; Loo et al., 2002), then eco-morphological characters reflecting relative mobility of species may be important in structuring community composition (Frick et al., 2009). However, although these environmental variables and species traits are intimately linked (Ulrich et al., 2009), few studies have combined them simultaneously to examine their roles in generating nestedness (Wang et al., 2010).

In this study, we examined the distribution of snake species in a fragmented landscape in the Thousand Island Lake, China. The specific objectives are threefold: (1) to assess whether the distribution of snake species across islands follows a nested subset pattern; (2) to determine the mechanisms underlying the nestedness of snake assemblage; and (3) to apply nestedness theory to direct conservation management of snake assemblage in our system.

1 Materials and Methods

1.1 Study sites

The Thousand Island Lake (29°22'–29°50' N, 118°34'–119°15' E) is a large hydroelectric reservoir created in 1959 by damming of the Xinanjiang River in western Zhejiang Province, China. Construction of the Xinanjiang dam inundated an area of 573 km² when the water reached its final level (108 m), creating 1078 islands

larger than 0.25 ha out of former hilltops. The major vegetation type on the islands is the naturally secondary forests dominated by *Pinus massoniana*. The climate is typical of the subtropical monsoon zone and is highly seasonal, with hot summers and cold winters. The average annual temperature is 17.0 °C, ranging from -7.6 °C in January to 41.8 °C in July. Annual precipitation in the region is 1430 mm. Detailed descriptions of the archipelago can be found elsewhere (Wang et al., 2009a, 2010, 2011, 2012).

Our study system provides an ideal opportunity to study nested subset patterns as it meets the three conditions necessary for the development of nestedness (Patterson and Atmar, 1986; Patterson and Brown, 1991; Wright et al., 1998). First, the islands share an ancestral pool of species prior to fragmentation. Second, the islands have a common biogeographic history. Third, species inhabiting the islands are somewhat hierarchically ordered in terms of their niches and relatively complete species inventories are available (Wang et al., 2009a, 2010, 2011, 2012).

1.2 Sampling methods

1.2.1 Snake sampling We selected a set of 20 islands to represent a range of areas and degrees of isolation (Table 1). To facilitate surveys, we cut transect trails (about 20 cm wide) that traversed the mountain

Table 1 Characteristics of 20 study islands in the Thousand Island Lake, China

Island Code	Island area (ha)	Isolation (m)	Number of habitat types (n)	Species richness (n)	Nested matrix rank	Number of transects (n)	Total length of transects (m)
1	1289.23	897.41	7	11	1	8	3200
2	143.19	1415.09	6	6	3	4	1600
3	55.08	953.95	5	8	2	2	800
4	46.37	729.80	5	4	5	2	800
5	32.29	1936.95	5	5	4	2	800
6	2.90	1785.30	3	2	9	1	275
7	2.83	1238.14	4	2	10	1	150
8	2.29	973.85	4	1	17	1	300
9	1.74	2293.25	3	1	19	1	300
10	1.54	711.04	3	2	11	1	375
11	1.52	2849.99	3	2	12	1	175
12	1.40	1760.34	3	1	16	1	375
13	1.20	2128.52	3	3	8	1	225
14	1.17	2453.37	3	3	7	1	250
15	1.15	847.12	3	1	15	1	275
16	1.01	2437.85	3	3	6	1	250
17	1.01	2103.85	3	2	13	1	250
18	0.86	2321.51	3	1	18	1	225
19	0.83	2298.50	3	2	14	1	275
20	0.80	2097.52	2	1	20	1	300

Island isolation is given as distance to the nearest mainland. Other 3 study islands with no snake species are not listed here.

ridges on all the islands (Wang et al., 2009a, 2010, 2011). To account for the greater habitat diversity associated with larger sites, sampling effort was roughly proportional to island area (\log_{10} transformed) (Schoereder et al., 2004). Accordingly, eight transect trails were sampled on island 1 (the largest study island, area > 1000 ha), four on island 2 (100 < island area < 1000 ha), two on three islands (10 < island area < 100 ha) and one on each of the remaining small islands (island area \approx 1 ha for most islands; Table 1).

We used the line-transect method (Mac Nally and Brown, 2001) to determine snake occupancy and abundance on the study islands during two breeding seasons between April and July in 2009 and 2010. Surveys were conducted both in the daytime (8:00–12:00 AM) and in the night (7:00–12:00 PM) because some species in the region are diurnal while others are nocturnal (Huang, 1990). During the survey, an observer walked each transect trail at a steady pace (10 m min^{-1}) searching the ground and tree boles with SICONG[®] 8×42 roof prism binoculars in the daytime and with a 12V DC lamp at night. Any snakes detected within 10 m of the trails were recorded. Once a snake was detected, the time spent in identification (if necessary) was excluded from the elapsed survey time; only individuals for which confident identifications could be made were included in analyses. We used a global positioning system (GPS) to record the length of each transect (Table 1). Each island was surveyed 15 times. The order in which islands were surveyed and the direction in which the trails were walked were randomized and rotated in order to minimize potential biases (Wang et al., 2010, 2011). Censuses were not conducted during inclement weather such as strong winds or heavy rains.

We evaluated snake inventory completeness with randomized (1000×) sample-based species accumulation curve for each island (Colwell, 2005). The estimated number of snake species was calculated using the Chao 2 estimator of species richness (Colwell, 2005). Calculations were made using EstimateS v7.5 software with the default parameters. The species accumulation curve approached an asymptote (Fig. 1), indicating a high level of snake inventory completeness for all study islands.

1.2.2 Habitat variables For each island, we selected three habitat variables (area, isolation and habitat diversity) that were commonly hypothesized to influence nestedness (Patterson and Brown, 1991; Wright et al., 1998; Honnay et al., 1999). Island size was measured by polar planimetry as the total island area in hectares. We

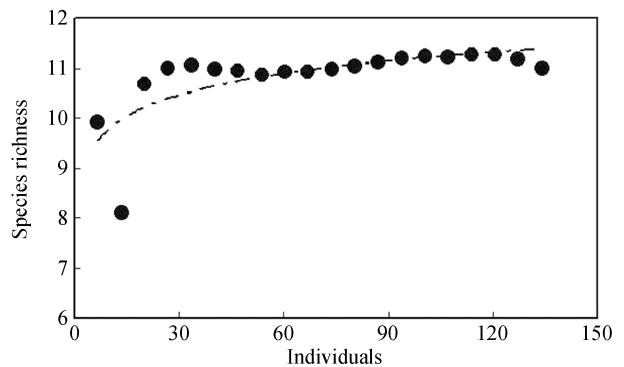


Fig. 1 Species-accumulation curve for snakes in the Thousand Island Lake, China. The sample order was randomized 1000 times.

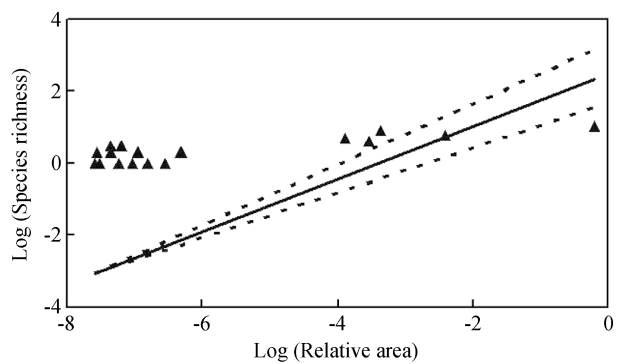


Fig. 2 Comparison of observed data to expected values under the random placement model for snakes in the Thousand Island Lake, China. Expected values (solid line) and associated standard deviations ($\pm 1 \text{ SD}$; dashed lines) are shown. Filled triangles represent observed species richness.

used the distance from the nearest mainland as a measure of isolation (Meyer and Kalko, 2008; Wang et al., 2009b), and estimated it from a map at a scale of 1:10 000.

Habitat diversity was studied by noting the number of habitat types on each island (Table 1). The different habitat types could be easily identified as vegetation composition of the region was relatively simple. Photographs were taken as a record during the intensive surveys between April and November in 2007. Considering the requirements of snakes, all habitat types encountered on each island were identified and classified as: 1) conifer forest, 2) broadleaf forest, 3) coniferous-broad mixed forests, 4) shrubs, 5) bamboo groves, 6) grasses, and 7) farmlands (Wang et al., 2010, 2011).

1.2.3 Life-history traits We selected four commonly cited life-history traits (Table 2), i.e. body size, clutch size, geographical range size, and minimum area requirement, which reflect species extinction and immigration tendencies. Among the life-history traits, clutch

Table 2 Characteristics of snake species detected during sampling on 20 study islands in the Thousand Island Lake, China

Species	Body size (mm)	Clutch size (n)	Geographical range size (km ²)	Area requirement (ha)	Number of islands occupied (n)
<i>Elaphe carinata</i>	1454.06	8.0	3302197	0.80	19
<i>Bungarus multicinctus</i>	1130.81	7.5	2458769	1.20	7
<i>Trimeresurus stejnegeri</i>	720.35	6.5	3320817	1.20	4
<i>Deinagkistrodon acutus</i>	1153.10	20.0	2040812	1.01	4
<i>Naja atra</i>	1049.44	13.0	3663270	1.01	4
<i>Cyclophiops major</i>	753.19	8.5	3336176	32.29	5
<i>Zaocys dhumnades</i>	1682.91	15.0	3105264	0.83	7
<i>Trimeresurus mucrosquamatus</i>	852.12	8.0	2665083	55.08	2
<i>Rhabdophis tigrinus</i>	683.07	18.0	6425370	1.17	6
<i>Ptyas mucosus</i>	1201.58	15.0	3663270	1289.23	1
<i>Oligodon chinensis</i>	598.28	4.5	2018712	55.08	2

Nomenclature follows Huang (1990).

size, geographical range size and minimum area requirements are three key traits associated with extinction-proneness (Davidar et al., 2002; Henle et al., 2004), while body size is usually linked to dispersal ability (Jenkins et al., 2007). Body size has been shown to be positively correlated with flotation and swimming endurance in reptiles and mammals (Schoener and Schoener, 1984; Cook and Quinn, 1995; Jenkins et al., 2007). We used body length (mm) to represent body size, and used clutch size as an index of reproductive potential, and the data were obtained from Huang (1990). If a range instead of the mean SVL or clutch size was provided in the literature, we used the arithmetic mean of the limits (Gaston and Blackburn, 1995). Following Jones et al. (2003), geographic range size (km²) was obtained from the most recent available published species range maps by digitizing the area into a Geographic Information System (ArcView 3.2). Where no range maps were available, the minimum area convex polygon of published point data was calculated excluding areas of water. The data on geographic range size were obtained from Huang (1990). The minimum area requirement of each species was estimated as the area of the smallest island occupied by each species (Li et al., 1998; Davidar et al., 2002; Wang et al., 2010).

1.3 Statistical analyses

1.3.1 Quantification of nestedness To estimate nestedness, we used the recently developed metric WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill), which is a simple modification of the NODF (Almeida-Neto and Ulrich, 2011). The most advantage of WNODF, compared with other metrics, is that it can quantify nestedness using quantitative

(abundance) instead of presence-absence data (Almeida-Neto and Ulrich, 2011). Like NODF, WNODF is directly based on two major properties of nestedness currently not correctly quantified by alternative nestedness metrics: (1) whether marginal totals (i.e. fills) differ among columns and/or among rows, and (2) whether presences (1's) in less-filled columns and rows coincide, respectively, with those found in more-filled columns and rows. Thus, unlike other metrics, nestedness may not only be calculated for the whole incidence matrix (WNODF), but for species (WNODF_R) and sites (WNODF_C) individually as well. We used the program NODF version 2.0 (Almeida-Neto and Ulrich, 2011) to calculate the above indices and compared them with those of 1000 randomly assembled communities. Statistical inference was made using the lower and upper 95% confidence intervals. The WNODF metric is also less sensitive to matrix size and shape, and less prone to Type I error, than other commonly used metrics (Almeida-Neto et al., 2008; Almeida-Neto and Ulrich, 2011).

To ensure that our results were not biased owing to metric choice, we also examined the nestedness of assemblages using the various nestedness metrics in the program NESTEDNESS (Ulrich, 2006) and the popular metric BINMATNEST (Rodríguez-Gironés and Santamaría, 2006). The results were qualitatively similar regardless of the choice of metric, so here we only report the results using WNODF.

1.3.2 Determinants of nestedness The order in which sites and species are sorted by WNODF independently can be compared with numerous possible independent variables to evaluate their role in genera-

1.3.3 Idiosyncratic species analysis Atmar and Patterson (1993) termed species that decrease the matrix-wide nestedness “idiosyncratic”. One goal of nestedness analysis was to identify such idiosyncratic species that run counter to the ecological and geographic gradients of species occurrences and cause a nested subset pattern (Ulrich et al., 2009). We used the program NODF version 2.0 (Almeida-Neto and Ulrich, 2011) to calculate idiosyncrasy values and the respective 95% confidence limits. Idiosyncratic species were those with idiosyncrasy values (WNODF) outside the lower and upper 95% confidence limits (Almeida-Neto and Ulrich, 2011).

2 Results

2.1 Nestedness of snake assemblages in the Thousand Island Lake

The snake assemblages in the Thousand Island Lake were significantly nested (Table 5). The whole snake-by-island incidence matrix (Table 3) exhibited a stronger degree of nestedness than expected by chance (WNODF = 40.58, $P < 0.05$) (Table 5). Species (WNODF_R = 40.17, $P < 0.05$) and sites (WNODF_C = 40.70, $P < 0.05$) also were significantly nested (Table 5), respectively.

Table 5 Results of nestedness analyses with program NODF conducted on the species-by-site matrix for snake assemblages on 20 islands in the Thousand Island Lake, China

WN_{obs}	$WN_{exp}(SD)$	P	Rank correlation with habitat variables						Rank correlation with species life-history traits							
			Area (ha)		Isolation (m)		Number of habitat types (n)		Body length (mm)		Clutch size (n)		Geographical range size (km ²)		Area requirement (ha)	
			r_s	P	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P
WNODF	40.58	26.52 (3.83)	< 0.05													
WNODF _C	40.70	25.25 (4.00)	< 0.05	-0.616	0.004	0.156	0.511	-0.671	0.001							
WNODF _R	40.17	31.46 (5.07)	< 0.05						-0.400	0.223	-0.142	0.678	0.005	0.989	0.773	0.005

Given are observed WNODF (WN_{obs}), expected WNODF (WN_{exp}), and Monte Carlo-derived probabilities that the matrix was randomly generated 1000 times. Also indicated are the relationships 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.

2.2 Mechanisms determining nestedness

Nestedness of snake assemblages was significantly negatively correlated with island area (Table 5). Nestedness also was significantly positively correlated with species traits linked to extinction tendencies (i.e. area requirement) (Table 5).

The habitat-by-site matrix estimated by program NODF was significantly nested (NODF_{obs} = 66.35 > NODF_{exp} = 44.30, $P < 0.05$) (Table 4). Furthermore, species nestedness was significantly negatively correlated with habitat diversity (Table 5), which provided further support for the habitat nestedness hypothesis.

Only one of the observed data points lay within ± 1 SD of the expected species-area curve (Fig. 2), which did not follow expectations from the random placement model.

Nestedness of snake assemblages was not significantly correlated with either island isolation or species body size as a measure of dispersal ability (Table 5).

2.3 Idiosyncratic species

Among the 11 snake species occurred on islands, *Elaphe carinata*, *Rhabdophis tigrinus* and *Cyclophiops major* were determined as idiosyncratic species (Table 6). These three species had idiosyncrasy values (WNODF) that were outside the lower and upper 95%

confidence limits (Table 6).

3 Discussion

In this study, we systematically tested for the existence of the nestedness and underlying influencing mechanisms in snake assemblages in the Thousand Island Lake. To date, although nestedness has been documented for a wide range of taxa (Wright et al., 1998; Fischer and Lindenmayer, 2005; Wang et al., 2010; Hill et al., 2011), it is rarely tested in snake assemblages (Mac Nally and Brown, 2001; Hecnar et al., 2002; Watling et al., 2009). Our study on snakes thus fills in a significant gap, and contributes to the ecological generality of nestedness across a range of taxa.

3.1 Mechanisms determining nestedness

The nestedness of snake assemblages was consistent with the selective extinction hypothesis because nestedness was significantly correlated with island area and species traits that are linked to extinction tendencies (i.e. area requirement). Selective extinction is widely considered as a key driver of nestedness, particularly in land-bridge archipelagos and in habitat fragments that are experiencing species loss or ‘relaxation’ (Patterson, 1987; Bolger et al., 1991; Li et al., 1998; Wang et al., 2011). The rate of relaxation depends largely on the

Table 6 Results of idiosyncrasy species analysis with program NODF conducted on the species-by-site matrix for snake assemblages on 20 islands in the Thousand Island Lake, China

Species	WNODF	L5%CL	U5%CL	Occurrence (n)
<i>Elaphe carinata</i>	0.2105	0.3636	2.1538	19
<i>Zaocys dhumnades</i>	2.5714	0.4286	3.4286	7
<i>Bungarus multicinctus</i>	1.2857	0.3333	3.6250	7
<i>Rhabdophis tigrinus</i>	0.0000	0.3333	3.8333	6
<i>Cyclophiops major</i>	0.0000	0.2000	3.8333	5
<i>Deinagkistrodon acutus</i>	1.2500	0.0000	3.7143	4
<i>Trimeresurus stejnegeri</i>	2.0000	0.0000	4.2000	4
<i>Naja atra</i>	3.0000	0.0000	5.3333	4
<i>Trimeresurus mucrosquamatus</i>	0.0000	0.0000	7.3333	2
<i>Oligodon chinensis</i>	0.0000	0.0000	6.3333	2
<i>Ptyas mucosus</i>	0.0000	0.0000	6.3333	1

Given are idiosyncrasy values (WNODF), the lower and upper 95% confidence limits, and species occurrences.

fragment area, fragment isolation and generation time of the study organism (Brooks et al., 1999). For certain vertebrate taxon such as birds, community relaxation approximates an exponential decay with a half-life of 50 years for fragments of roughly 1000 ha (Brooks et al., 1999). Considering the short isolation time (about 50 years) of the Thousand Island Lake, it is highly possible that the islands are still in the process of faunal relaxation. In our system, selective extinction may cause nestedness because snake species with large area requirements have higher extinction risks and thus will go extinct first (Wang et al., 2010).

The nestedness of snake assemblages was also in accord with the habitat nestedness hypothesis because the habitats in our system have a nested distribution. The habitat nestedness is considered as the most parsimonious process to explain species nestedness because it points directly to associations between species and their habitats, but rather ignores population dynamics or life history of species (Calmé and Desrochers, 1999). However, despite its theoretical and practical interest, very few studies have explicitly examined the relationship between habitat nestedness and species nestedness. Consistent with previous findings (Calmé and Desrochers, 1999; Azeria et al., 2009; Wang et al., 2010), our study provides further evidence for the role of habitat nestedness in generating species nestedness.

The nestedness of snake assemblages did not appear to result from passive sampling. Although it is stressed that the passive sampling hypothesis should be tested prior to other hypotheses (Andrén, 1994; Cutler, 1994), the sampling effect has rarely been examined perhaps because of the difficulties involved in collecting species abundance data (Andrén, 1994; Cutler, 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 Worthen et al. (1998) and Wang et al. (2010, 2011).

The nestedness of snake assemblages was also not attributable to selective colonization because nestedness was not correlated with island isolation or species body size as a measure of dispersal ability. Three main factors may explain why this correlation is weak. First, colonizations probably have rarely occurred in our system due to the poor dispersal ability of snakes (Mac Nally and Brown, 2001). Second, the lack of a significant effect of isolation on nestedness is probably because the biologically meaningful quantification of isolation is notoriously difficult (Lomolino, 1996). We know little, if anything, about the relative dispersal ability of most snakes, which precludes strong inferences about selective colonization. Finally, our use of body size to estimate dispersal ability (Cook and Quinn, 1995; Andrews and Gibbons, 2005) may inadvertently include signals of extinction risk. Gaston and Blackburn (1995) and Cardillo and Bromham (2001) have demonstrated body size-extinction effects in birds and mammals, respectively.

Two potential caveats may exist for our estimate of nestedness and testing of the passive sampling hypothesis. First, estimate of nestedness is sensitive to the inventory completeness of the species list (Cam et al., 2000). In our study, the species accumulation curve approached an asymptote (Fig. 1), indicating a high level of snake inventory completeness for all study islands. Thus, inventory completeness probably would not bias our estimate of nestedness. Second, the differences in detection probabilities among species (Bailey et al.,

2004; MacKenzie et al., 2006) would probably confound our estimate of abundance, which in turn may bias our test of the passive sampling hypothesis. In our case, the numbers of snakes reported seem very low, indicating that our estimate of abundance may be biased. However, to what contents the relative abundance recorded may differ from true abundance needs more detailed studies and warrants further evaluations.

3.2 Conservation implications

In the context of habitat fragmentation, understanding the nestedness pattern and its mechanistic basis has important implications for conservation and can be used to direct management efforts (Wang et al., 2010, 2011). In our system, the snake assemblages were shaped by extinction processes mediated through area effects and habitat nestedness. Our results have four general conservation implications. First, as all snake species occurred on the largest island (Table 3), we should thus protect the largest island with the most species-rich community to maximize the number of species preserved. In contrast, a combine of 15 small islands with areas smaller than 2.90 ha could only support 7 snake species (Table 3). Therefore, small islands will have less conservation value as they have a large degree of overlap in species composition with large islands (Patterson, 1987). Second, as area requirement is correlated with nestedness and species with large area requirements have higher extinction risks, these species should be given conservation priority. Specifically, *Ptyas mucosus* only occurs on the largest island (1289.23 ha), and *Trimeresurus mucrosquamatus* and *Oligodon chinensis* only occur on islands larger than 55.08 ha. Considering their large area requirements, these three species are most vulnerable to extinction and thus should be focused on for conservation. Furthermore, *Elaphe carinata*, *Rhabdophis tigrinus* and *Cyclophiops major* deviated considerably from perfect nestedness. These three idiosyncratic species, although all occurred on the largest island, should be given additional conservation efforts. Finally, as habitat nestedness plays an important role in structuring community composition, we should pay more attention to islands with diverse habitats.

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