

Article

The small-island effect in amphibian assemblages on subtropical land-bridge islands of an inundated lake

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Abstract

The small-island effect (SIE) has become more and more part of the theoretical framework of island biogeography and biodiversity research. However, previous methods for the detection of SIEs are often flawed in one way or another, including not accounting for model complexity, not comparing all relevant models, and not including islands with no species. Therefore, the existence and the prevalence of the SIE may be dubious. In this study, after controlling for all these methodological shortcomings, we tested for the existence of the SIE in amphibian assemblages on subtropical land-bridge islands created by the inundation of the Thousand Island Lake, China. We used the line transect method to determine the distribution of amphibian assemblages on 23 study islands during 3 breeding seasons from 2009 to 2011. To evaluate whether an SIE exists in amphibian assemblages, we compared the fit of a simple linearized power model with two most widely used breakpoint regression models. The information-theoretic multimodel inference approach based on Akaike's information criterion identified the left-horizontal SIE model as the best single model. Thus, we found strong evidence for the existence of an SIE in our system. The upper limit of the SIE for amphibian assemblages was 39.95 ha. Below this threshold area, amphibian richness varied independently of island size. The SIE in amphibian assemblages may be due to episodic disturbances, stochastic events, and nutrient subsidies from the lake. Our results indicate that all the islands >39.95 ha should be protected for the effective conservation of amphibian assemblages in our system.

Key words: amphibian, breakpoint regression, power function, multimodel inference, small-island effect, species–area relationship, threshold area, Thousand Island Lake.

The species–area relationship (SAR) is one of nature's most general patterns (Lomolino 2000) and often referred to as the closest thing to a rule in ecology (Schoener 1976). Despite its universal recognition, a potentially cryptic and important feature of the SAR—the small-island effect (hereafter SIE)—has been largely neglected by most biogeographers and ecologists (Lomolino 2000; Lomolino and Weiser 2001). The SIE occurs when below a certain threshold

area, species richness varies independently of island size or at least increases at a lesser rate than for larger islands (Lomolino 2000; Triantis et al. 2006; Dengler 2010). The SIE was first described about half a century ago (Niering 1963; MacArthur and Wilson 1967; Whitehead and Jones 1969). However, it was only popularized after Lomolino and Weiser (2001) applied the breakpoint regression method for the first time to identify SIEs statistically.

Ever since, the SIE has become more and more part of the theoretical framework of island biogeography and biodiversity research (Barrett et al. 2003; Gentile and Argano 2005; Panitsa et al. 2006; Whittaker and Fernández-Palacios 2007; Sfenthourakis and Triantis 2009; Dengler 2010; Tjørve and Tjørve 2011; Morrison 2014; Wang et al. 2012a, 2015a, 2016; Gao and Perry 2016).

However, there are still serious debates over the appropriate methodology to identify the SIE (Lomolino and Weiser 2001; Triantis et al. 2006; Burns et al. 2009; Dengler 2010; Triantis and Sfenthourakis 2012). In a critical methodological review, Dengler (2010) argues that previous methods for the detection of SIEs are often flawed in one way or another, including not accounting for model complexity, not comparing all relevant models, not including islands with no species, and not selecting all models in the same *S*-space. Thus, the existence of the SIE may be dubious and the prevalence of the SIE may be less common than previously supposed (Dengler 2010; Tjørve and Tjørve 2011; Morrison 2014). For the unambiguous detection of SIEs, all the above methodological shortcomings should be overcome (Dengler 2010; Morrison 2014; Wang et al. 2012a, 2015a, 2016).

In this study, we tested for the existence of the SIE in amphibian assemblages on subtropical land-bridge islands created by the inundation of the Thousand Island Lake, China. The following 3 questions were addressed: (1) Does evidence exist for an SIE in amphibian assemblages in our system? (2) What mechanisms may underlie the observed SIE patterns? (3) How to apply the SIE theory to direct conservation management of amphibian assemblages in our system?

Materials and Methods

Study areas

The Thousand Island Lake (29° 22'–29° 50'N, 118° 34'–119° 15'E; Figure 1) is a large hydroelectric reservoir, which was created in 1959 by the damming of the Xinanjiang River in western Zhejiang Province, China (Wang et al. 2009). With the construction of Xinanjiang dam, an area of 573 km² was inundated, creating 1,078 islands >0.25 ha out of former hilltops when the water reached its final level (108 m) (Wang et al. 2010, 2011). The highest peak in the Thousand Island Lake is 405.2 m, whereas the heights of most islands are ranging from 110 to 250 m (Wang et al. 2012a). Forests on the islands were selectively logged before the creation of the dam (Wang et al. 2015a). The major vegetation type on the islands is the naturally secondary forest dominated by *Pinus massoniana* (Wang et al. 2015a). 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 1,430 mm (Wang et al. 2015b).

Our system provides an ideal opportunity to examine the SIE. First, the Thousand Island Lake consists of >1,000 islands and islets (Wang et al. 2009). The vast majority of these islands do not exceed 1 ha in area, which offers an ideal “pool” to select small islands and thus to test for the SIE (Wang et al. 2012a, 2015a). In addition, the islands are located in a relatively small area (Figure 1) and have very similar climates (Wang et al. 2010, 2011), which exclude the impact of extreme climates on the SIE (MacArthur and Wilson 1967). Morrison and Spiller (2008) and Morrison (2014) found that the SIE was more pronounced and the threshold area was higher for archipelagos that had more exposure to disturbance by the hurricanes.

Amphibian survey

The distribution of amphibians in the Thousand Island Lake was surveyed across a set of 23 islands (Figure 1). These islands were selected (1) to represent a range of area and degree of isolation from mainland (Table 1); and (2) to ensure the survey effort on each island was large enough so that all species present could be thoroughly surveyed. Each island was surveyed 15 times, which was sufficient to measure amphibian richness (Wang et al. 2012c). To account for the greater habitat variability associated with larger sites, sampling effort was roughly proportional to island area (log₁₀-transformed) (Schoederer et al. 2004; Wang et al. 2010). Accordingly, 8 transect trails were sampled on island 1 (the largest island, area >1,000 ha), 4 on island 2 (100 < island area < 1,000 ha), 2 on 3 medium-sized islands (10 < island area < 100 ha) and 1 on each of the remaining small islands (island area ≈ 1 ha for most islands) (Table 1; Wang et al. 2012b, 2012c).

We used the line transect method (Jaeger 1994) to determine amphibian occupancy on the study islands during the breeding seasons between July and August from 2009 to 2011. During the survey, an individual observer walked each transect at a steady pace (about 2.0 km h⁻¹). Each transect was situated along accessible edges of the study islands, and 2 m wide and 200–1,000 m long, which depended on the area of the islands (Wang et al. 2012c). Transects were searched for amphibians at night (18:00–24:00 h) with a 12-V DC lamp. Any amphibians detected along the transect trails were recorded. Once an amphibian was detected, the time spent in identification was excluded from the elapsed survey time. All amphibians encountered were identified according to Huang (1990) and Fei (2012). Some amphibians that could not be identified with certainty in the field were captured and taken indoors for further identification. A total of 9 amphibian species was found on the islands (Table 2). We described the habitat and location where each amphibian was captured. Captured amphibians were released at their capture sites the following morning. Surveys were not conducted if there was heavy rain, high wind, or high temperatures (Wang et al. 2009, 2012c). We used a global positioning system (GPS) to record the length of each transect. Each island was surveyed 15 times. To eliminate potential biases owing to observer fatigue or weather conditions, the order in which islands were surveyed and the direction in which the transect lines were walked were randomized and rotated each new census day (MacNally et al. 2002; Wang et al. 2010).

Habitat sampling

We recorded and classified all habitat types for amphibians on each island during the intensive surveys from April to November in 2007 (Table 3). The different habitat types could be easily identified as vegetation composition of the region was relatively simple (Wang et al. 2010, 2012a). We identified habitat types mainly by examining the substrate and the vegetation cover (Wang et al. 2012b, 2015a). Photographs of all habitat types on each island were taken as a record (Wang et al. 2010, 2012b). Considering the requirements of amphibians (Huang 1990; Fei 2012), all habitat types encountered on the islands were identified and classified as follows: (1) coniferous forest, (2) broadleaf forest, (3) coniferous-broadleaf mixed forest, (4) bamboo grove, (5) shrubland, (6) grassland, and (7) farmland (Table 3) (Wang et al. 2012b, 2015a).

Statistical analyses

To evaluate whether an SIE exists in amphibian assemblages in our system, we compared the fit of a simple linearized power model

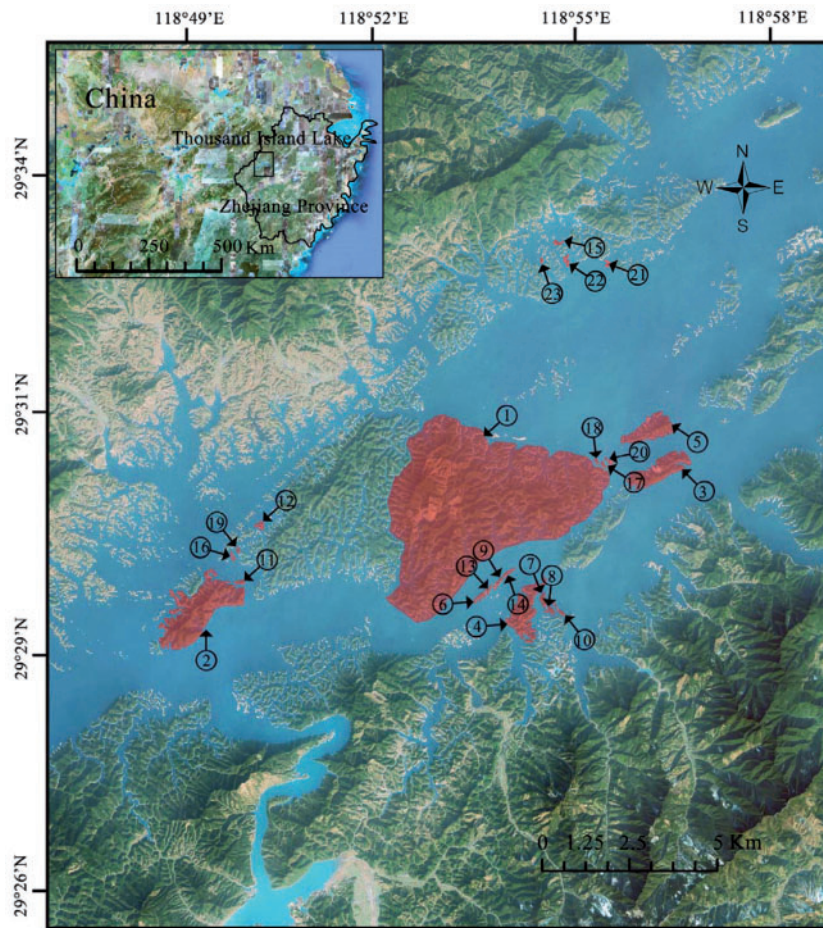


Figure 1. Map showing the 23 study islands (highlighted in red) in the Thousand Island Lake and (inset) the location of the study area in Zhejiang Province, China. See Table 1 for the island codes.

without an SIE (Equation 1) with the following two most widely used SIE models that were proposed by Lomolino and Weiser (2001) (the left-horizontal SIE model; Equation 2) and Dengler (2010) (a continuous two-slope SIE model; Equation 3). If Equation 2 or Equation 3 is supported, the evidence of an SIE is found (Lomolino and Weiser 2001; Dengler 2010). However, datasets fit best by Equation 2 provided stronger evidence for an SIE, while those fit best by Equation 3 provided weaker evidence (Morrison 2014; Wang et al. 2016).

$$\log S = c + z_1 \log A \quad (1)$$

$$\log S = c + (\log A > T)z_1(\log A - T) \quad (2)$$

$$\log S = c + (\log A \leq T)z_1 \log A + (\log A > T) [z_1 T + z_2(\log A - T)] \quad (3)$$

In these equations, S stands for species richness, A for island area, while c_i (intercept), z_i (slopes), and T (breakpoint) are fitted parameters. The logical expression in brackets returns a value of 1 if true and 0 if false (Dengler 2010; Wang et al. 2012a).

We used the power function (log–log model) as the basic function to detect the SIE for 3 main reasons. First, it usually fits the (island) SAR well (Dengler 2009; Triantis et al. 2012). Second, it is one of the few functions for which biological significance has been assigned to model parameters (Martin and Goldenfeld 2006;

Triantis et al. 2012). Finally, it is widely used in SIE studies (e.g., Barrett et al. 2003; Gentile and Argano 2005; Panitsa et al. 2006; Morrison and Spiller 2008; Sfenthourakis and Triantis 2009; Qie et al. 2011; Wang et al. 2012a; Gao and Perry 2016), which allows comparisons with previous literature.

We fitted all the equations with the non-linear regression module of STATISTICA 8.0 (StatSoft Inc. 2008). We used the default settings of the program (loss function = $(\text{OBS} - \text{PRED})^2$; estimation method = quasi-Newton; convergence criterion = 0.0001; starting values for all parameters = 0.1; step-width for all parameters = 0.5) (Dengler 2010; Wang et al. 2012a, 2015a, 2016). The program obtained an optimal solution for model parameters by an iterative process (StatSoft Inc. 2008). If the iterative process did not converge, we altered the starting values until the program found a minimum (Dengler 2010).

An information-theoretic multimodel inference approach was used for model selection (Burnham and Anderson 2002). We compared the performance of the above 3 SAR models using the Akaike information criterion (AIC) corrected for small sample size ($\text{AIC}_c = \text{AIC} + 2K(K+1)/(n-K-1)$, where K is the number of model parameters and n is the number of observations). For model selection, we calculated the difference in AIC_c values (Δ_i) and Akaike weights (ω_i) for each model among a set of candidate models. Akaike weights (ω_i) are the probability that the model is the best model in the set of candidate models, given the data (Burnham and

Table 1. Characteristics of the 23 study islands in the Thousand Island Lake, China

Island code	Latitude	Longitude	Area (ha)	Isolation (m)	Number of habitats	Number of transects	Amphibian richness
1	29°31'11.4"N	118°52'25.9"E	1289.23	897.41	7	8	9
2	29°30'30.2"N	118°49'09.3"E	143.19	1,415.09	6	4	5
3	29°31'51.5"N	118°56'24.5"E	55.08	953.95	5	2	1
4	29°29'40.0"N	118°53'39.1"E	46.37	729.80	5	2	1
5	29°32'06.8"N	118°56'13.8"E	32.29	1,936.95	5	2	1
6	29°30'01.9"N	118°53'09.0"E	2.90	1,785.30	3	1	1
7	29°29'54.9"N	118°54'13.9"E	2.83	1,238.14	4	1	2
8	29°29'45.8"N	118°54'22.5"E	2.29	973.85	4	1	1
9	29°30'12.5"N	118°53'31.1"E	1.74	2,293.25	3	1	1
10	29°29'43.4"N	118°54'33.4"E	1.54	711.04	3	1	1
11	29°30'28.1"N	118°49'24.5"E	1.52	2,849.99	3	1	1
12	29°31'14.6"N	118°49'38.7"E	1.40	1,760.34	3	1	1
13	29°30'11.3"N	118°53'25.4"E	1.20	2,128.52	3	1	1
14	29°30'19.2"N	118°53'38.7"E	1.17	2,453.37	3	1	1
15	29°34'47.6"N	118°54'43.2"E	1.15	847.12	3	1	1
16	29°34'36.8"N	118°55'38.5"E	1.03	1,458.81	3	1	1
17	29°30'49.1"N	118°49'17.2"E	1.01	2,437.85	3	1	1
18	29°31'45.5"N	118°55'21.6"E	1.01	2,103.85	3	1	1
19	29°31'48.4"N	118°55'18.1"E	0.86	2,321.51	3	1	1
20	29°30'54.6"N	118°49'21.1"E	0.83	2,298.50	3	1	1
21	29°29'34.7"N	118°55'09.9"E	0.80	2,097.52	3	1	1
22	29°34'38.6"N	118°54'57.8"E	0.67	1,139.87	3	1	2
23	29°34'40.2"N	118°54'34.2"E	0.59	640.53	2	1	1

Island isolation is given as distance to the nearest mainland.

Table 2. The species by site matrix for amphibian assemblages on 23 study islands in the Thousand Island Lake, China

Species	Islands																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Odorrana schmackeri</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Bufo gargarizans</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Rhacophorus megacephalus</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Microhyla ornata</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hyla chinensis</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Fejervarya limnocharis</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pelophylax nigromaculatus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pelophylax plancyi</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rana zhenhaiensis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3. The habitat by site matrix for amphibian assemblages on 23 study islands in the Thousand Island Lake, China

Habitats	Islands																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Coniferous forest	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Broadleaf forest	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Coniferous-broadleaf mixed forest	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bamboo grove	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Shrubland	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Grassland	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Farmland	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Anderson 2002). Models for which $\Delta_i \leq 2$ are considered to have substantial support, values of 4–7 have considerably less support, whereas those with $\Delta_i \geq 10$ essentially have no empirical support and can be ignored (Burnham and Anderson 2002).

Results

We found strong evidence for the existence of an SIE in amphibian assemblages in the Thousand Island Lake, China (Figure 2, Table 4). Based on the information-theoretic multimodel inference approach,

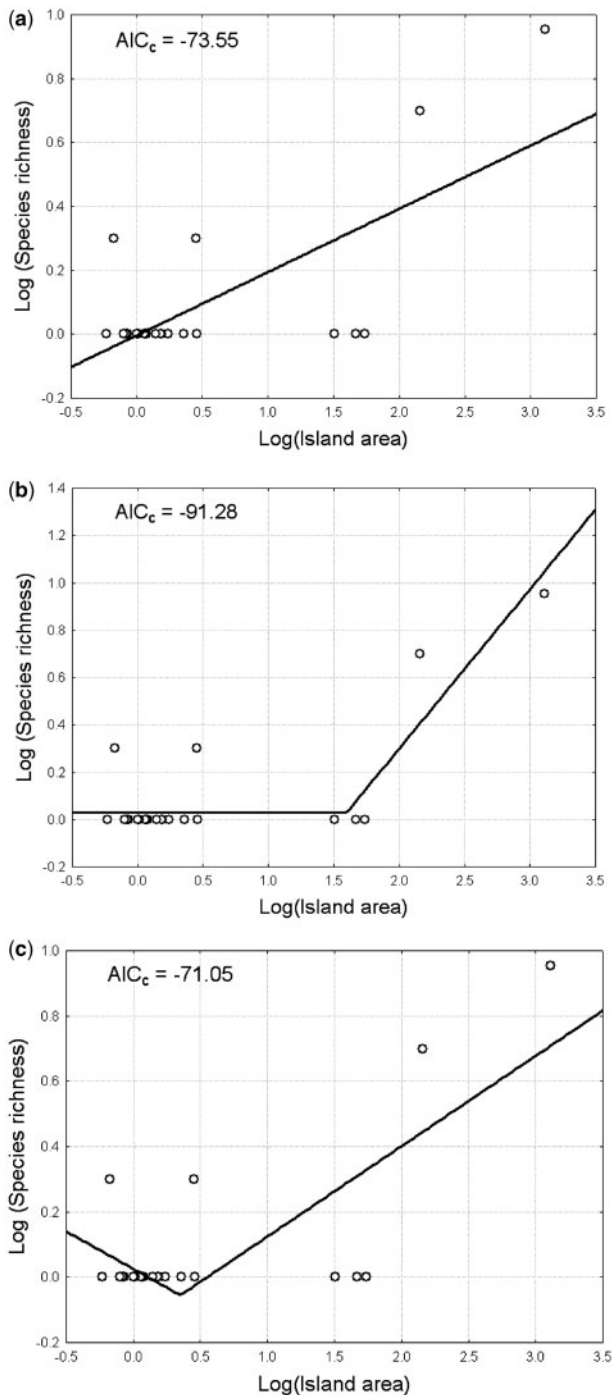


Figure 2. The 3 regression models of SAR for amphibians on 23 study islands in the Thousand Island Lake, China. Two breakpoint regression models (b)–(c) were compared with the simple linearized power model (a) to detect the SIE. The AIC_c values are shown (the lowest value denotes the best model).

the left-horizontal SIE model (Equation 2) was identified as the best single SAR model ($\Delta\text{AIC}_c = 0$, $w_i = 0.9998$) (Table 4). In contrast, the other two SAR models received no empirical evidence of support ($\Delta\text{AIC}_c \geq 17.73$) (Table 4).

The left-horizontal SIE model showed that the threshold area (T) of the SIE for amphibian assemblages was 39.95 ha (Table 4). Below this threshold area, amphibian richness varied independently of island size (Figure 2b). However, amphibian richness increased

quickly with island size beyond the threshold area (Figure 2b). Compared with the other two SAR models, the slope of the left-horizontal SIE model was much steeper beyond the threshold area (Figure 2, Table 4).

Discussion

In this study, we tested for the existence of the SIE in amphibian assemblages on subtropical land-bridge islands created by the inundation of the Thousand Island Lake, China. We found strong evidence for the existence of an SIE in our system. The threshold area (T) identified by the left-horizontal SIE model was 39.95 ha for amphibian assemblages.

Dengler (2010) suggested that 4 criteria are necessary for the robust detection of an SIE: (1) the goodness-of-fit measure employed should account for varying model complexity; (2) at least 3 models (linear, the left-horizontal SIE model, and breakpoint with 2 different slopes) should be evaluated; (3) model selection should be carried out in the same S -space for all models; and (4) islands with no target species that fall within the range size limit of the study should be included in the analyses (also see Wang et al. 2015a, 2016). Except for the criterion 4 of including empty islands, which is not applicable in our system (Table 1), our analyses meet all the criteria listed above (Dengler 2010). Thus, our detection of the SIE in amphibian communities is robust and creditable.

The threshold area identified by the left-horizontal SIE model for amphibian assemblages in our system was 39.95 ha, which is different from that of Lake Erie and West Indies in the study of Lomolino and Weiser (2001). The upper limit of the SIE is overall highest for species groups with relatively high resource requirements and low dispersal abilities, and for biotas of more isolated archipelagos (Lomolino and Weiser 2001). The threshold area of SIEs thus tends to depend on the taxon studied and mainly on the general characteristics of the archipelagos (Lomolino and Weiser 2001; Triantis et al. 2006; Wang et al. 2016). Future studies should determine how the threshold area of SIEs varies among multiple taxa and archipelagos, and attempt to elucidate the mechanisms underlying the variation of the threshold area.

A variety of hypotheses have been proposed to explain the SIE. First, MacArthur and Wilson (1967) hypothesized that extinction rates on small islands could be area-independent, which may result in the SIE. Contrary to the area-independent extinction hypothesis, our previous studies on the same set of 23 study islands indicate that amphibian assemblages in our system are highly nested and are shaped largely by extinction processes mediated through area effects (Wang et al. 2012c). Second, the habitat quality hypothesis states that on small islands there is a threshold area below which the presence or the absence of certain habitat types is the major driver of species richness (Wiens 1962; Niering 1963; Whitehead and Jones 1969). However, there seems no such threshold area for the occurrence of key habitat types in our system and all our study islands have at least 2 habitat types for amphibians (Table 3). Moreover, the subsidized island biogeography hypothesis indicates that small islands often receive greater amounts of nutrient influxes per unit area from the surrounding system than large islands, so that island area is no longer an accurate predictor of species richness (Anderson and Wait 2001; Barrett et al. 2003). The unique annual fluctuating cycle of water level in our system does bring some nutrient subsidies from the lake to islands (Wang et al. 2012a). Such nutrient subsidies on small islands may override the effect of island area on amphibian richness (Anderson and Wait 2001; Barrett et al. 2003). Finally, episodic disturbances and other stochastic events may play a major role

Table 4. Results of the non-linear regression analyses of species–area data of amphibians on 23 islands in the Thousand Island Lake, China

Model	Parameter estimate				Model selection				
	c	z_1	z_2	T	K	$\log(L)$	AIC_c	Δ_i	ω_i
$\log S = c + z_1 \log A$	−0.0036	0.1981			3	40.41	−73.55	17.73	0.00014
$\log S = c + (\log A > T) z_1 (\log A - T)$	0.0317	0.6732		1.6015	4	50.75	−91.28	0	0.99982
$\log S = c + (\log A \leq T) z_1 \log A + (\log A > T) [z_1 T + z_2 (\log A - T)]$	0.0253	−0.2297	0.2768	0.3502	5	42.29	−71.05	20.23	4.10×10^{-5}

Model performance is assessed using AIC-based model selection among a set of candidate models. For each model, the fitted parameters (c , z , and T), the log-likelihood ($\log L$), number of estimable parameters (K), sample-size adjusted AIC (AIC_c), akaike differences (Δ_i) and akaike weights (ω_i) are presented. T is \log_{10} of the area in ha of the breakpoint.

in determining amphibian richness on small islands within the range of the SIE (Lomolino 2000; Lomolino and Weiser 2001).

The breakpoint species–area model and the SIE have important implications for conservation and can be used to direct management efforts (Lomolino and Weiser 2001; Whittaker and Fernández-Palacios 2007). First, we found that the slope of the left-horizontal SIE model was actually much steeper beyond the threshold area than those estimated by traditional SAR models (Figure 2). Thus, species extinctions estimated by the left-horizontal SIE model would be more accurate and exceed estimates based on those traditional SAR models (Lomolino and Weiser 2001). In addition, the threshold area of the SIE for amphibian assemblages in our system was 39.95 ha. Below this threshold area, amphibian richness varied independently of island size (Figure 2). Thus, for effective conservation of amphibian assemblages in our system, all the islands larger than 39.95 ha should be protected. Such a conservation recommendation is also supported by the nested distribution of amphibian assemblages (Wang et al. 2012c), in which the amphibian species present on the smaller islands also present on the larger ones (Table 2). In contrast, for islands that fall within the range of the SIE, alternative conservation efforts may be more effective by optimizing habitat quality and managing amphibian populations within those islands (Lomolino and Weiser 2001). For these small and highly fragmented islands, improving habitat quality by avoiding or decreasing the influences of edge effect, human disturbance, and invasive species are important for the conservation management of amphibian populations (Todd and Rothermel, 2006; Pilliod and Wind 2008).

We provided a case study to test for the existence of the SIE in a subtropical land-bridge archipelago. However, the more interesting and important question is to determine the overall prevalence of the SIE. Wang et al. (2016) found that SIEs were quite prevalent for both all the islands (104 cases, 49.3%) and the datasets excluding empty islands (73 cases, 34.6%) in 211 global island datasets. Nevertheless, these datasets are focused on islands without species and are not gathered specifically to directly evaluate the prevalence of SIEs (Wang et al. 2016). Thus, future study should collect all island datasets worldwide across a broad diversity of taxa and archipelago types and conducts a meta-analysis with the appropriate methods to determine the overall prevalence of the SIE.

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