ORIGINAL ARTICLE

Turnover of breeding bird communities on islands in an inundated lake

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ABSTRACT

Aim MacArthur and Wilson's theory of island biogeography proposes that the rate at which species colonize an island depends on the island's isolation (distance effect), whereas the local extinction rate depends on its area (area effect). Alternative hypotheses recognize that area can affect the colonization rate (target effect) and that isolation can affect the extinction rate (rescue effect) and, moreover, that these relationships may dominate. We quantify these relationships and associated turnover rates and incidence using long-term counts of breeding bird communities on islands in an inundated lake.

Location Thousand Island Lake, China.

Methods We assessed the occupancy and behaviour of breeding birds on 37 islands from 2007 to 2012. We estimated the effects of area, isolation and other biogeographical parameters on the frequencies of colonization and extinction events using multivariate logistic regression. We then extended these results to derived properties such as species turnover rates and incidence.

Results Extinction rates decreased and colonization rates increased on larger islands. Isolation had no significant effect on colonization or extinction rates. Islands had high species turnover overall, and turnover rates followed the same pattern as extinction rates with different areas and isolations. Pool turnover, which controls for the number of species in the pool, was higher on large islands. Species richness also increased with area. Our study of bird communities supported area and target effects, but not distance and rescue effects.

Main conclusions Island area was a better predictor of colonization and extinction than isolation, probably because of the relatively small scale (*c.* 580 km^2) and homogeneous vegetation structure of our research system, and the strong dispersal ability of birds. We conclude that the differences between our observations and theoretical predictions, or results from other studies that measured colonization and extinction directly, are consistent with the particular biogeography of these islands.

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INTRODUCTION

The island biogeography theory (IBT) of MacArthur & Wilson (1963, 1967) proposes that the number of species on an island is the result of a dynamic equilibrium of colonization and extinction rates that decrease with isolation

(distance effect) and area (area effect), respectively (Manne *et al.*, 1998; Krauss *et al.*, 2003; Husté & Boulinier, 2007). This results in larger and less isolated islands having more species than smaller and more isolated ones (Diamond, 1975; Diamond & Marshall, 1977; Rosenzweig, 1995; Spengler *et al.*, 2011). Central to the theory is that there is

turnover of species on each island (Jones & Diamond, 1976); that is, some species are lost and others gained over time (Whittaker & Fernández-Palacios, 2007). In addition, if distance and area effects govern these relationships, then IBT predicts that large, isolated islands should have slower turnover rates than small, weakly isolated islands (Wright, 1985; Laurance, 2008). Analyses of species turnover are central to testing IBT (Gilbert, 1980; Whittaker, 2000; Burns & Neufeld, 2009) and there is a rich history of such studies (e.g. Diamond, 1969; Terborgh & Faaborg, 1973; Hunt & Hunt, 1974; Reed, 1980; Russell *et al.*, 1995; Foufopoulos & Mayer, 2007; Morrison, 2010).

These familiar ideas produce three sets of testable predictions. The first concerns the relationship of species richness to different areas and isolations. The second concerns the corresponding patterns of species turnover. Finally, there are separate predictions about colonization and extinction rates. Testing these three types of predictions require increasingly demanding data. Moreover, data that conform to the first set of predictions may not necessarily conform to the others. Large islands, for example, may host more species than small ones, but the species may not change over time – we may describe their composition as static, rather than being at a dynamic equilibrium. Species turnover can also have multiple causes, some of them operating at different time-scales (Russell *et al.*, 1995). Indeed, examining the same data on birds on islands off the coasts of Britain and Ireland, Russell *et al.* (2006) found that the largest statistical effect was that island distance determined extinction rate, a result that IBT does not predict.

Besides the processes originally proposed by IBT, colonization rates may also increase with area because of the target effect – larger islands will be easier to find (Johnson, 1980; Lomolino, 1990; Russell *et al.*, 2006; Whittaker & Fernández-Palacios, 2007). Schoereder *et al.* (2004a), however, found no evidence for a target effect in their studies of ants. Brown & Kodric-Brown (1977) also hypothesized a rescue effect related to isolation, in which the higher colonization rates of closer islands will reduce the probability of local extinction, increasing the likelihood that extinction will be followed by recolonizations before the next survey, thereby lowering the observed extinction rates on nearby islands compared with isolated ones (Whittaker & Fernández-Palacios, 2007). Foufopoulos & Mayer (2007) suggested that annual migrants between islands in the Aegean Sea decreased the chances of extinction via a rescue effect. Russell *et al.* (2006), however, not only failed to find a rescue effect for birds on British and Irish islands, but found the opposite: lower extinction rates on more distant islands. They speculated that birds may abandon islands for the nearby mainland from one year to the next, but would be less likely to do so if the mainland were distant. Taken together, these studies suggest that there is no clear agreement as to what mechanisms underlie patterns of species colonization and extinction in island communities (Whittaker & Fernández-Palacios, 2007).

Although species turnover is the direct consequence of colonization and extinction processes, relatively few studies have tested predictions about turnover rates (Schoener, 1983; Vidal *et al.*, 2000; Morrison, 2002). Some studies of birds on islands have revealed that larger islands have lower turnover rates, supporting IBT's predictions (Diamond, 1969; Jones & Diamond, 1976; Russell *et al.*, 1995; Schoereder *et al.*, 2004a; Husté & Boulinier, 2007), whereas Hinsley *et al.* (1995) found no relationship between turnover and island area. Mayer & Chipley (1992) even reported that there was virtually no turnover in their land-bird surveys of Guana Island, British Virgin Islands, spaced over 36 years. The relationship between turnover and isolation is even less clear (Diamond, 1969; Brown & Kodric-Brown, 1977; Nilsson & Nilsson, 1982; Hinsley *et al.*, 1995; Panitsa *et al.*, 2008), and patterns of species turnover are controversial (Schoener, 2010).

Here, we quantify the colonization and extinction dynamics on islands in a large lake in China. We counted the birds present during the breeding season on 37 islands from 2007 to 2012. Our goal is to use these data to test the predictions of the IBT and its extended hypotheses about target and rescue effects. Our paper addresses the following questions: (1) What are the rates of colonization, extinction and species turnover, and the incidence of breeding birds on these islands? (2) Is species composition static or dynamic? (3) Do colonization, extinction and species turnover vary with island area and isolation, and does this variation match the predictions of IBT?

MATERIALS AND METHODS

Study area

Thousand Island Lake (29° 22′–29° 50′ N, 118° 34′–119° 15′ E) is a large artificial reservoir in western Zhejiang Province, China (Fig. 1). It was created in 1959 for hydroelectricity generation by the construction of the Xin'anjiang Dam on the Xin'anjiang River. Flooding an area of approximately 580 km^2, this formed 1078 islands with areas greater than 0.25 ha when the water reached its highest level (108 m) (Wang *et al.*, 2009). Currently, 88.5% of the land area on the islands is covered by forest (Yu *et al.*, 2012), which is a mix of subtropical deciduous and coniferous forest, mainly of *Pinus massoniana*, with many broad-leaved trees and shrub species such as *Cyclobalanopsis glauca*, *Castanopsis sclerophylla*, *Smilax davidiana*, *Grewia biloba* and *Loropetalum chinense*. The climate is a typical subtropical monsoon zone and is strongly seasonal. The average annual temperature is 17.0 °C. Daily temperature ranges from −7.6 °C in January to 41.8 °C in July. The annual precipitation of the region is 1430 mm, mainly concentrated in the rainy season from April to June (Wang *et al.*, 2010).

Land-bridge islands created by construction of dams, such as the islands of the lake, are 'natural experiments' that can be used to test the hypotheses of the IBT (Diamond, 2001; Terborgh & Feeley, 2008). First, the lake was formed by dam
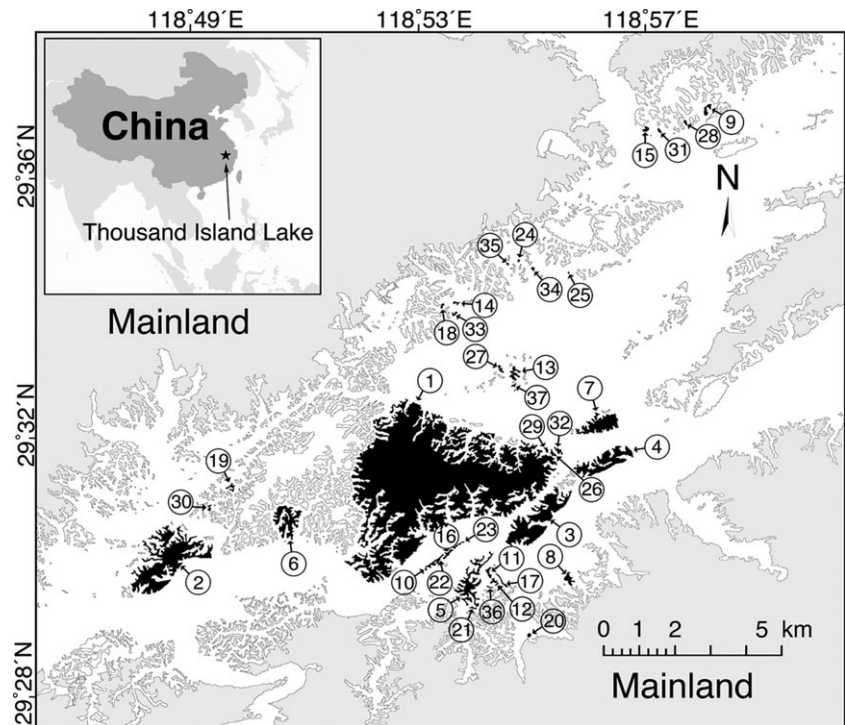
Figure 1 Thousand Island Lake in Zhejiang Province, China, with the 37 study islands numbered in order of decreasing area.

construction and inundated quickly, so that these islands were essentially created simultaneously (Yu *et al.*, 2012). They retain similar vegetation (Hu *et al.*, 2011) and share an ancestral pool of species (Wang *et al.*, 2011). The very similar vegetation structure (see below) minimizes complications from the strong correlation between habitat diversity and area present in most long-isolated islands. Second, we have a relatively complete bird inventory from the area (Wang *et al.*, 2010) and surveyors were familiar with the species. Finally, the islands are relatively small and accessible, so we were able to survey the bird communities thoroughly, several times a year, over a number of breeding seasons.

Field survey

Island attributes

We selected 37 study islands to encompass as much variation in area and isolation as possible (Fig. 1). These islands range from 0.57 ha to approximately 1300 ha, and from about 20 m separation from the mainland to over 3.71 km. For each island, we measured the area in hectares (A), the length of the perimeter in metres (Pe), and the maximum elevation in metres (E). Isolation was measured in multiple ways. The first three were the straight-line distance in metres to the nearest landmass, to the nearest larger landmass and to the nearest mainland. Of these, distance to the mainland provided the best fit to the data. We also calculated two measures based on the presence of land within a 2-km buffer region around a focal island: the total area of all islands intersecting the buffer (mainland not included) and the total area of all land within the buffer (mainland included)

(Moilanen & Nieminen, 2002; Ranius *et al.*, 2010). Because a larger island with a larger perimeter will tend to connect more – i.e. have a higher 'connectivity' – with its surroundings, we recalculated these area-based buffer measures as fractions of the total buffer area. This makes them largely independent of island area. We finally calculated their complements (1 − connectivity) so that they would be measures of isolation, and thus easier to compare with traditional measures. A 2-km buffer size was chosen from a range because it produced the best fit to the data. The second buffer measure – the fraction of buffer that is water – provided the better fit, and this was a better predictor of colonization than the best distance-based measure. We therefore present results using the buffer water fraction as our measure of isolation (I). (See Appendix S1 for a detailed comparison of all the isolation measures.)

We derived the shape index (SI) and perimeter to area ratio (PAR) for each island. SI indicates the relative complexity of each island's shape, and was calculated as $SI = Pe/[2 \times (\pi \times A)^{0.5}]$ (Laurance & Yensen, 1991; Ewers & Didham, 2006; Yu *et al.*, 2012). Finally, after an intensive survey between April and November in 2007, we classified the habitats on each island into seven categories: coniferous forest, broad-leaved forest, mixed coniferous–broad-leaf forests, bamboo groves, shrubs, grasses and farmland (Wang *et al.*, 2010); we defined habitat richness (Hr) as the number of habitat types on each island (see Table S3 in Appendix S2).

Bird survey

Our group surveyed the bird communities on 37 islands (numbered from largest to smallest in Fig. 1) during the

breeding season from 2007 to 2012. The sampling effort on each island was roughly proportional to the logarithm of area (Schoereder *et al.*, 2004b). As a result, eight transects were sampled on Island 1 (the largest study island, area > 1000 ha), four on islands 2 and 3 (island area > 100 ha), two on the next four islands (with areas of 10–100 ha), and one on each of the remaining small islands (island area = c. 1 ha for most islands) (Wang *et al.*, 2009, 2011). We used a global positioning system (GPS) to record the total length of transects on each island (see Table S3 in Appendix S2). Because it was not feasible to make survey effort directly proportional to area, we assessed the completeness of our survey for the largest and proportionally least sampled island (Island 1; see Fig. 1) by creating species accumulation curves for each of the six years. They clearly levelled off before the completion of all surveys (see Fig. S2 in Appendix S3). We concluded that the sampling effort was sufficient on this and the smaller islands to capture the full breeding bird communities.

Transects were generally placed along ridge-lines, and narrow census trails (about 20 cm wide) were cleared to facilitate surveys (Terborgh *et al.*, 1997; Wang *et al.*, 2011). Where islands had more than one habitat type, a stratified random placement was used to capture all the types. We recorded bird occupancy along these transects (Bibby *et al.*, 2000) during the breeding season (April–June) annually from 2007 to 2012. In each survey, observers walked each transect at a constant speed (c. 2.0 km h^{-1}). We recorded all the birds seen or heard, excluding high-flying individuals passing over the islands. We also recorded behaviours – such as carrying nesting materials, strong territorial singing and fighting – that are considered compelling evidence of breeding (Bibby *et al.*, 2000), as well as direct evidence in the form of observed nests and juveniles. Species were entered as 'present' in an island only if at least one of these kinds of evidence of breeding was recorded. We surveyed each transect 78 times over the course of the entire study. Surveys ran from half an hour after sunrise to 11:00 h in the mornings and from 15:00 h to half an hour before sunset in the afternoons. We did not conduct surveys if there was heavy rain, high wind or high temperatures. We varied the direction the observer walked on each transect randomly, to eliminate a potential source of survey bias (Mac Nally *et al.*, 2002; Wang *et al.*, 2010).

Species pool

We only considered terrestrial birds, excluding diving birds, ducks, gulls and shorebirds. In addition, both year-round residents and summer visitors are potential breeding birds, but over the course of three nest surveys from April to July in 2011, all observed nesting species were residents. We therefore also excluded summer visitors.

We assumed that all islands receive colonists from the same species pool (Wang *et al.*, 2011) and considered two possible pools. The first was the complete set of resident species that were detected on one or more islands during the study (71 species). The second added breeding resident species from the nearby mainland (93 species, based on amateur reports and our own surveys over the study period). We found no significant differences in our results except for a constant scaling of colonization estimates (because pool size appears in the denominator; see Fig. S3 in Appendix S3). Hereafter, we present results based on the larger species pool.

Island biogeographical parameters

Fundamental parameters

Following Russell *et al.* (2006), we considered these parameters:

Species pool size, P: the number of terrestrial bird species that are candidates for breeding on a given island.

Colonization rate, λ: the probability of a species being present on an island in year $t + 1$, when it was absent in year t.

Extinction rate, μ: the probability that none of the individuals of a species present on an island in year t are present in year $t + 1$.

Higher-order parameters

From these fundamental parameters, we can calculate the following:

Observed extinction rate, δ: the probability of a species' presence on an island one year followed by an absence in the next year. This happens when the disappearance of all individuals of a species is not rescued by the colonization of new individuals (Rosenzweig & Clark, 1994). So, $\delta = \mu \times (1 - \lambda)$.

Incidence, j: the probability that a breeding species is present on an island in a given year. At a community level, we calculate incidence as S/P, where S is the species richness. So, $j = \lambda/(\lambda + \delta)$.

Species richness, S: the number of species on an island in a given year. We estimate species richness as incidence multiplied by the number of species (pool size): $S = P \times j = P \times \lambda/(\lambda + \delta)$.

Island turnover, T: the number of species that change through colonization and extinction from one year to the next, divided by the number of species present on an island in both years. We calculated T as $(C_{t,t+1} + E_{t,t+1})/(S_t + S_{t+1})$, where $C_{t,t+1}$ and $E_{t,t+1}$ are the number of colonization and observed extinction events from one year to the next. In a state of dynamic equilibrium, $T = \delta$ (Russell *et al.*, 1995).

Pool turnover, τ: the number of species on an island that change through colonization and extinction from one year to the next, divided by the number of species in the pool. We calculated τ as $(C_{t,t+1} + E_{t,t+1})/P$. Russell *et al.* (2006) showed that $\tau = 2 \times \lambda \times \delta/(\lambda + \delta)$.

More detailed descriptions of these parameters are given in Russell *et al.* (2006).

Data analyses

We surveyed four island attributes – A, Pe, Hr and E – and derived three attributes – I, PAR and SI (see earlier definitions for details). We log-transformed all island attributes to normalize their distributions (Morrison, 2002). As shown by the correlation matrix for the island attributes (see Table S4 in Appendix S2), A, Pe, PAR, SI, Hr and E are significantly correlated with each other (Pearson correlation coefficients from 0.79 to 0.99). Based on these findings, we used A and I as the candidate island attributes.

During two consecutive years, there are four possible transitions from the first year to the next – AA, AP, PA and PP – where A is absence and P is presence. The maximum number of turnover events a species can have on an island during our 6-year survey is five (APAPAP or PAPAPA). The probabilities of the transitions are $1 − \lambda$, λ, δ and $1 − \delta$, respectively. Because of the rescue effect, however, $\delta = \mu \times (1 − \lambda)$ (Rosenzweig & Clark, 1994). This makes the probabilities of the different transitions non-independent, so we model them simultaneously. We thus set up a multivariate logistic regression model with two predictors (A and I) and six parameters (α_0, α_1, α_2, β_0, β_1 and β_2) to be estimated. For island i,

$$Pr(AP) = \lambda_i = \frac{1}{1 + e^{-(\alpha_0 + \alpha_1 A_i + \alpha_2 I_i)}},$$

$$Pr(AA) = 1 − \lambda_i,$$

$$Pr(PA) = \delta_i = \mu_i(1 − \lambda_i) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 A_i + \beta_2 I_i)}} \times (1 − \lambda_i),$$

and

$$Pr(PP) = 1 − \delta_i.$$

If a_i, b_i, c_i and d_i are counts of the four transitions (AA, AP, PA and PP) for all bird species on island i, then the likelihood of the whole dataset is

$$L = \prod_i (1 − \lambda_i)^{a_i} \lambda_i^{b_i} \delta_i^{c_i} (1 − \delta_i)^{d_i}.$$

We used the method of maximum likelihood to fit this model to the data for all the islands.

With four regression parameters (in addition to two constants), we had $2^4 = 16$ candidate models. We used Akaike's information criterion (AIC) for model selection, weighting and averaging to incorporate uncertainty. (The version corrected for small sample size, AIC_c, was not necessary here because our observations were the individual transitions, of which there were 17,020 in the dataset.) We considered model weight w_i as a measure of the relative plausibility of a model given the data (Anderson, 2008). We calculated w_i as $w_i = \frac{e^{-0.5\Delta_i}}{\sum e^{-0.5\Delta_i}}$, where $\Delta_i = AIC_i − AIC_{min}$, AIC_i is the AIC value for model i, and AIC_{min} is minimum AIC value in the model set. Because basing inference on only the 'best' model can ignore models that are also quite plausible, we made the following four sets of inferences using model weights to capture variation across the whole set of models (Anderson, 2008).

1. Confidence set of models. This is the set of models, in descending order of plausibility, for which the cumulative sum of models weights w_i first exceeds 0.95. An alternative way to generate a confidence set is all those models where $\Delta AIC < 2$ compared with the best model, as this indicates that the compared models are fairly similar (Anderson, 2008).
2. Examining the relative importance of predictors. We measured the relative importance of predictors A and I by summing w_i for every model in which that predictor appeared.
3. Estimating biogeographical parameters. Our predicted colonization and extinction rates for each island were the w_i-weighted averages of the predictions across all candidate models. From these basic rates, we then calculated island turnover, pool turnover and incidence as described above.
4. Estimating the predictor parameters. We calculated the model-averaged estimate of a parameter as the w_i-weighted average of the estimates for that parameter in every model in which it occurs (Anderson, 2008). We also calculated the unconditional variance estimate as the sampling variance, given a model g_i, plus the variance due to the model selection uncertainty:

$$\text{var}\left(\hat{\bar{\theta}}\right) = \sum w_i \left[\text{var}\left(\hat{\theta}_i | g_i\right) + (\hat{\theta}_i − \hat{\bar{\theta}})^2\right],$$

where $\hat{\bar{\theta}}$ is the model-averaged estimate of a parameter, $\hat{\theta}_i$ is the parameter and w_i is the model weight for g_i.

We conducted all analyses in R 3.0.0 (R Core Team, 2013) and MATHEMATICA 9.0 (Wolfram Research, 2012).

RESULTS

The mean turnover rate for islands in Thousand Island Lake was 30.5% year^{-1}, indicating that species composition was dynamic, not static, and therefore that IBT is a valid model to consider.

Confidence set and predictor importance

There were four models in the confidence set for simultaneously predicting colonization and extinction rates, whether the criterion was summed model weight ≥ 0.95 or $\Delta AIC < 2$. These were the four models in which area was a predictor of both extinction and colonization, and included all possible combinations of isolation as a predictor. All models outside this set had essentially zero plausibility (Table 1). This ranking gave area an importance of 1.0 for both colonization and extinction, and isolation importances of 0.41 (colonization) and 0.64 (extinction) (Table 2). Isolation did not appear in the best or third-best models for colonization in the confidence set, or in the third-best or fourth-best models for extinction (Table 1).

Biogeographical parameters

Using weighted model averaging, we predicted fundamental and higher-order biogeographical parameters for 37 islands

Table 1 All candidate models for simultaneously predicting colonization and extinction rates according to ΔAIC of breeding birds on 37 islands in Thousand Island Lake (China) surveyed from 2007 to 2012. Abbreviations: AIC, Akaike's information criterion; log(L), likelihood; k, number of parameters in the model; w, model weight; A, area (ha); I, isolation; $α_0$–$α_2$, logistic regression parameters for colonization; $β_0$–$β_2$, logistic parameters for extinction; SE, standard error; the subscripts 'c' and 'e' after the predictor variables in column 1 represent predictors of colonization and extinction rates, respectively.

Model components	log(L)	k	AIC	ΔAIC	w	$α_0$	SE($α_0$)	$α_1$	SE($α_1$)	$α_2$	SE($α_2$)	$β_0$	SE($β_0$)	$β_1$	SE($β_1$)	$β_2$	SE($β_2$)
A_c A_e I_e	−4502.96	5	9015.92	0.00	0.387	−3.0074	0.0440	0.1017	0.0188	—	—	−0.4346	0.1176	−0.1422	0.0227	0.5484	0.3127
A_c I_c A_e I_e	−4502.38	6	9016.75	0.83	0.256	−3.0950	0.0906	0.1040	0.0190	−0.2680	0.2400	−0.4413	0.1269	−0.1420	0.0228	0.5279	0.3408
A_c A_e	−4504.61	4	9017.21	1.29	0.204	−3.0074	0.0441	0.1017	0.0188	—	—	−0.6192	0.0542	−0.1358	0.0224	—	—
A_c I_c A_e	−4503.89	5	9017.78	1.85	0.153	−3.1041	0.0878	0.1042	0.0190	−0.2963	0.2306	−0.6187	0.0542	−0.1359	0.0224	—	—
A_e I_e	−4516.46	4	9040.92	24.99	0.000	−2.8946	0.0370	—	—	—	—	−0.4260	0.1185	−0.1503	0.0225	0.5481	0.3144
A_e	−4518.10	3	9042.19	26.27	0.000	−2.8946	0.0371	—	—	—	—	−0.6105	0.0543	−0.1439	0.0223	—	—
I_c A_e I_e	−4516.26	5	9042.53	26.60	0.000	−2.9431	0.0842	—	—	−0.1530	0.2375	−0.4297	0.1121	−0.1503	0.0225	0.5362	0.2910
I_c A_e	−4517.82	4	9043.64	27.72	0.000	−2.9520	0.0811	—	—	−0.1812	0.2276	−0.6101	0.0543	−0.1441	0.0223	—	—
A_c	−4524.17	3	9054.34	38.42	0.000	−3.0179	0.0441	0.1129	0.0188	—	—	−0.8146	0.0451	—	—	—	—
A_c I_c	−4523.51	4	9055.01	39.09	0.000	−3.1112	0.0984	0.1154	0.0190	−0.2856	0.2656	−0.8144	0.0451	—	—	—	—
A_c I_e	−4523.92	4	9055.84	39.91	0.000	−3.0182	0.0441	0.1132	0.0188	—	—	−0.7469	0.1137	—	—	0.2123	0.3262
A_c I_c I_e	−4523.30	5	9056.60	40.68	0.000	−3.1081	0.0902	0.1156	0.0189	−0.2753	0.2405	−0.7535	0.1025	—	—	0.1912	0.2901
—	−4540.67	2	9085.34	69.41	0.000	−2.8946	0.0371	—	—	—	—	−0.8235	0.0449	—	—	—	—
I_c	−4540.45	3	9086.90	70.97	0.000	−2.9457	0.0858	—	—	−0.1614	0.2432	−0.8234	0.0449	—	—	—	—
I_e	−4540.49	3	9086.99	71.06	0.000	−2.8946	0.0370	—	—	—	—	−0.7674	0.1070	—	—	0.1759	0.3059
I_c I_e	−4540.30	4	9088.60	72.67	0.000	−2.9430	0.0880	—	—	−0.1528	0.2494	−0.7711	0.1042	—	—	0.1642	0.2954

(Table 3). As the islands were ranked from largest to smallest, the signs of the relationships between each parameter and area were immediately obvious (see below).

Predictor parameters

See Fig. 2 for the relationships between the island characteristics of area and isolation and the model-weighted biogeographical predictions from Table 3. See Table 2 for the corresponding parameters relating to the fundamental processes of colonization and extinction, and their associated unconditional variances. Our results showed:

1. As expected by IBT, extinction rates were lower on islands with larger area. Colonization also increased with area; this was a demonstration of the target effect. Thus, other things being equal, larger islands will support more species. A difference in area of three orders of magnitude led to slightly more than a twofold difference in extinction rate.

2. The relative importance of isolation was much less than that of area for predicting colonization and extinction rates. The confidence intervals for both relationships included zero (Table 2). The expected relationship had the expected sign – the colonization rate was lower on more isolated islands – and the sign of the other relationship was positive: the extinction rate was slightly higher on more isolated islands.

Because colonization rates, and therefore 'rescues', were low (< 0.1), the observed extinction rates (and therefore island turnover) essentially followed actual extinction, being lower on larger islands (see Fig. 2). Incidence (a proxy for species richness) was dramatically larger on larger islands, given that they had a higher colonization rate as well as a lower extinction rate. Pool turnover, unlike island turnover, was higher on large islands (because it was divided by a constant, rather than by each island's species richness). The effects of isolation on all of these measures were weak to non-existent.

DISCUSSION

Our analysis of breeding bird communities in Thousand Island Lake, China, tested the classic island biogeography theory of MacArthur and Wilson, as well as the target effect and the rescue effect, by examining the determinants of colonization and extinction rates. We also considered the patterns of species richness and species turnover that arise from these fundamental processes. Some predictions of the theory did hold: larger islands had lower extinction rates (area effect) and turnover rates, and higher colonization rates (target effect), and therefore more species overall. Other predictions were not supported: island isolation was relatively unimportant. Neither the distance effect nor the rescue effect was detected.

Why isolation is relatively unimportant

IBT predicts that larger and less isolated islands should have more bird species. We found that species richness increased strongly with area, but was not significantly affected by

Table 2 Relative importance and weighted average parameter estimates for area and isolation as predictors of colonization and extinction rates for breeding birds on 37 islands in Thousand Island Lake (China) surveyed from 2007 to 2012. An asterisk (*) indicates that the confidence interval of the weighted parameter estimate excludes zero.

Parameter	Colonization rate		Extinction rate	
	Importance	α	Importance	β
Area	1.00	0.103 ± 0.037*	1.00	-0.140 ± 0.045*
Isolation	0.41	-0.279 ± 0.464	0.64	0.540 ± 0.635

Table 3 Predicted biogeographical parameters for breeding bird communities on 37 islands in Thousand Island Lake (China) surveyed from 2007 to 2012. Fundamental parameters were estimated from the data, and higher-order parameters calculated from these. Island numbering follows Fig. 1. Abbreviations: λ, colonization rate; μ, extinction rate; δ, observed extinction rate; T, island turnover; j, incidence; S, species richness; τ, pool turnover.

| Island	Fundamental parameters		Higher-order parameters			
	λ	μ	δ, T	j	S	τ
1	0.0927	0.1693	0.154	0.377	35.02	0.116
2	0.0745	0.2245	0.208	0.264	24.54	0.110
3	0.0740	0.2198	0.204	0.267	24.79	0.109
4	0.0688	0.2411	0.225	0.235	21.81	0.105
5	0.0687	0.2362	0.220	0.238	22.14	0.105
6	0.0676	0.2384	0.222	0.233	21.68	0.104
7	0.0646	0.2629	0.246	0.208	19.34	0.102
8	0.0573	0.2808	0.265	0.178	16.54	0.094
9	0.0534	0.3089	0.292	0.154	14.36	0.090
10	0.0527	0.3120	0.296	0.151	14.07	0.089
11	0.0517	0.3238	0.307	0.144	13.41	0.089
12	0.0507	0.3303	0.314	0.139	12.94	0.087
13	0.0493	0.3495	0.332	0.129	12.02	0.086
14	0.0502	0.3314	0.315	0.138	12.80	0.087
15	0.0502	0.3307	0.314	0.138	12.81	0.087
16	0.0502	0.3262	0.310	0.140	12.97	0.086
17	0.0489	0.3410	0.324	0.131	12.18	0.085
18	0.0491	0.3365	0.320	0.133	12.38	0.085
19	0.0490	0.3350	0.319	0.133	12.40	0.085
20	0.0513	0.3025	0.287	0.152	14.09	0.087
21	0.0483	0.3393	0.323	0.130	12.11	0.084
22	0.0484	0.3388	0.322	0.130	12.13	0.084
23	0.0485	0.3354	0.319	0.132	12.28	0.084
24	0.0481	0.3403	0.324	0.129	12.03	0.084
25	0.0467	0.3578	0.341	0.120	11.20	0.082
26	0.0472	0.3499	0.333	0.124	11.53	0.083
27	0.0454	0.3767	0.360	0.112	10.43	0.081
28	0.0465	0.3561	0.340	0.120	11.20	0.082
29	0.0466	0.3532	0.337	0.121	11.30	0.082
30	0.0461	0.3592	0.343	0.119	11.03	0.081
31	0.0460	0.3604	0.344	0.118	10.98	0.081
32	0.0459	0.3604	0.344	0.118	10.96	0.081
33	0.0452	0.3688	0.352	0.114	10.58	0.080
34	0.0451	0.3672	0.351	0.114	10.59	0.080
35	0.0450	0.3625	0.346	0.115	10.71	0.080
36	0.0444	0.3739	0.357	0.110	10.27	0.079
37	0.0433	0.3918	0.375	0.103	9.62	0.078
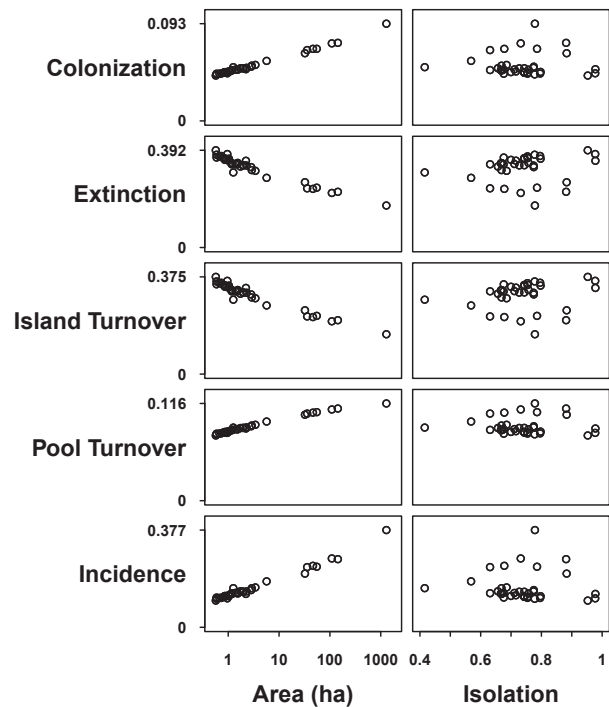
Figure 2 The relationships between island variables and predicted biogeographical parameters for all breeding birds on 37 islands in Thousand Island Lake (China) surveyed from 2007 to 2012. The colonization and extinction rates were model-weighted averages, and the higher-order parameters were derived from these. Isolation was estimated as buffer water fraction of the total area of all land within a 2-km buffer (mainland included). See more details for these measures in the Materials and Methods.

isolation. Previous studies on birds and plants in the lake have found similar patterns (Wang *et al.*, 2010, 2011; Hu *et al.*, 2011; Yu *et al.*, 2012). For birds at least, one reason may simply be that the islands are not sufficiently isolated. The most isolated island was less than 4 km from the mainland, and many were much closer. Studies confirm that long-distance dispersal events are reasonably common, even among species thought to be poor dispersers (e.g. Van Houtan *et al.*, 2007). The distances in this study might not be great enough to significantly affect dispersal probability for birds. By comparison, the isolations in Russell *et al.* (2006) ranged from 0.2 to 119.5 km.

Another explanation might be history. As these are land-bridge islands, they are assumed to have started with essentially a full 'mainland' complement of species, and gradually lost them over time, a process known as relaxation. They therefore approach the MacArthur and Wilson equilibrium from 'above'. In the initial stages of this process, extinction is the dominant phenomenon and, in 'classic' IBT, extinction is not affected by isolation. The question is therefore: have these islands reached equilibrium, or are they still in an earlier stage of relaxation? The first survey took place 48 years after the islands were created. Ferraz *et al.* (2003) found that isolated patches of 100 ha take about 10 years to lose 50% of their bird species. All but the largest island in this study have a similar or smaller area, suggesting that 48 years is more than sufficient to have approached a new, post-isolation equilibrium. If relaxation were still occurring, we would also expect to see a decrease in the extinction rate and an increase in the colonization rate over time. Whereas six consecutive years of data do not provide much power to discover temporal trends, we looked for evidence of continued relaxation in our data, and found none.

Species turnover

One of the main goals in our study was to test the turnover patterns in the lake. Our results showed that smaller islands had higher island turnover rates, as predicted by IBT, whereas they had lower pool turnover rates. In other words, larger islands experienced more absolute numbers of colonization events and observed extinction events than smaller islands, but fewer relative to their species richness, which increased even more with area.

The mean turnover rate for islands in the lake was 30.5% year^{-1}. This estimate was higher than for other studies, which found mostly 1–10% year^{-1} in terrestrial vertebrates and vascular plants (Diamond & May, 1977; Schoener, 1983; Mayer & Chipley, 1992; Panitsa *et al.*, 2008). The contributing processes of colonization and extinction were both considerably higher than at least one other study of birds on islands (Russell *et al.*, 2006). There are a number of possible reasons for variation between studies. Tropical birds may be expected to have lower turnover rates because they are more sedentary, more likely to be resident, and have lower adult mortality (Mayer & Chipley, 1992). The lake is a subtropical system, and may have higher turnover. Another possible explanation is not having reached relaxation equilibrium, which would elevate extinction rates and thus turnover. As described earlier, however, there was no evidence for that in our system (and nor would it explain the high colonization rates).

More plausibly, the vast majority of islands in the lake are less than 1 ha in area (Wang *et al.*, 2012). Their bird populations are therefore small, and vulnerable to local extinction because of the death or movements of a few individuals (Gaston & Blackburn, 2000). Much of the turnover in this system may simply be a result of such stochastic processes (Rosenzweig, 1995; Gotelli & Graves, 1996; Boulinier *et al.*,

2001). A related possibility is the hypothesis proposed by Russell *et al.* (2006) that, at the smallest distances, extinction is elevated because birds can easily choose to leave an island if conditions are not ideal (a foraging-based model). In our study, most of the islands fall into the 'very close' category, such that 'leaving by choice' extinctions may be elevated in general. We note that the islands have unusually low vegetation diversity, being dominated by a single species (*Pinus massoniana*), which may make them less than ideal resource clusters for some species.

The target effect

Two of the key predictions of IBT are that area determines extinction (area effect), and that isolation determines colonization (distance effect). Of these two, our results showed only the area effect, but they also showed a very strong target effect, in which colonization increases with larger island sizes (Johnson, 1980; Lomolino, 1990; Russell *et al.*, 2006). We propose that the target effect is magnified when distances are small, as here (Fig. 1); the closer islands are to a source, the more likely they are to be 'visible' from that source, and the more their relative visibility is likely to matter (size is of course also a key determinant of visibility), whereas a bird that spots an isolated island in a large expanse of ocean is likely to be drawn to it, no matter what its size is. This again speaks to a need to improve upon current models of dispersal between isolated and less isolated patches. These in turn will require studies that gather detailed information on the movement trajectories of real animals in fragmented systems.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Comparison of distance-based and buffer-based measures of isolation.
Appendix S2 Island attributes and the correlation matrix of the study islands.
Appendix S3 Species accumulation curves for the largest island and comparison of two species pools.

BIOSKETCH

Xingfeng Si is a PhD candidate at Zhejiang University, China. He conducted this work as a part of his PhD project when visiting the Pimm Group at Duke University, USA. His research interest lies in biogeography, community ecology, conservation biology and biodiversity monitoring using camera traps.

Author contributions: X-F.S., S.L.P. and P.D. conceived the ideas; X-F.S. and P.D. collected the data; X-F.S., G.J.R. and S.L.P. analysed the data; X-F.S. wrote the first version of the manuscript, and all authors contributed substantially to revisions.

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SUPPORTING INFORMATION

Turnover of breeding bird communities on islands in an inundated lake

Xingfeng Si, Stuart L. Pimm, Gareth J. Russell and Ping Ding

Appendix S1 Comparison of distance-based and buffer-based measures of isolation.

We compared five types of isolation measures for breeding bird communities in Thousand Island Lake (Table S1; see main paper for more details on these measures). Because the island with the largest straight-line distance to mainland in the lake is 3.71 km, we artificially selected nine buffers within a radius of 0.1 km, 0.5 km, 1 km, 1.5 km, 2 km, 2.5 km, 3 km, 3.5 km and 4 km, respectively. We ran the logistic regression analyses based on the measure of BUF2 (buffer water fraction of the total buffer area within the buffer including the mainland; Table S1) to explain the probability of colonization (λ) for breeding bird communities with different buffer distances, respectively: $\text{logit}(\lambda_i) = \alpha + \beta I_i$, where I_i is the isolation of island i, λ_i is the colonization rate of island i, β is the coefficient, and α is the constant coefficient (Moilanen & Nieminen, 2002).

Table S2 shows the results of model selection based on AIC for each buffer distance. The measure with a radius of 2 km had the smallest AIC (ΔAIC > 2), so we considered the first model with the smallest AIC as the best-fitted model. We therefore used the buffer measure of distance at a radius of 2 km (r = 2 km) in our analyses. We then ran the analyses for each measure of isolation.

Figure S1 shows the relationships between island variables and predicted biogeographical parameters for all breeding bird species on 37 islands based on distance-based and buffer-based measures of isolation (see main paper for detailed calculations). These results produced almost identical patterns of these relationships.

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Table S1 Comparison of distance-based and buffer-based isolation measures of breeding bird communities on 37 islands in Thousand Island Lake (China) from 2007 to 2012 (see main paper for details of the calculations of the relative importance of isolation). Abbreviations: I, isolation; S, connectivity; A, land area; $BUFA$, the total buffer area for a focal island within the buffer; d, distance between two land masses; r, buffer radius.

| Measure	Description	Equation	Relative importance of isolation[§] Colonization	Extinction
Distance-based measures				
DIS1	Straight-line distance to the nearest land mass (m)	—	0.28	0.27
DIS2	Straight-line distance to the nearest larger land mass (m)	—	0.27	0.42
DIS3[*]	Straight-line distance to the nearest mainland (m)	—	0.45	0.41
Buffer-based measures				
BUF1	Buffer water fraction of the total buffer area (mainland not included)	For island i, $I_i = 1 - S_i$, where $S_i = \frac{\sum_{j=1}^{n} A_j}{BUFA_i}$, for all $j \neq i$ and $d_{ij} < r$.	0.27	0.34
BUF2[*]	Buffer water fraction of the total buffer area (mainland included)	For land i, $I_i = 1 - S_i/BUFA_i$, where $S_i = \frac{\sum_{j=1}^{n} A_j}{BUFA_i}$, for all $j \neq i$ and $d_{ij} < r$.	0.41	0.64

[*]DIS3 provided the best fit to the data of breeding bird communities among distance-based measures according to the relative importances; BUF2 was a better fit than BUF1.
[§]All unconditional confidence intervals of the weighted parameter estimates for isolations included zero (data not shown).

Table S2 Logistic regression with buffer-based measures of isolation within different buffer radii explaining the probability of colonization for breeding bird communities on 37 islands in Thousand Island Lake (China) surveyed from 2007 to 2012. Abbreviations: I_i, isolation for island i; d.f., degrees of freedom; log(L), log-likelihood; AIC, Akaike's information criterion; r, buffer radius.

Measures	d.f.	log(L)	AIC	ΔAIC	Model weight
I_i, r = 2 km	2	−3008.37	6020.75	0	0.63
I_i, r = 1 km	2	−3009.41	6022.82	2.07	0.23
I_i, r = 1.5 km	2	−3010.45	6024.91	4.16	0.08
I_i, r = 0.5 km	2	−3010.86	6025.73	4.98	0.05
I_i, r = 0.1 km	2	−3013.53	6031.05	10.30	0.00
I_i, r = 2.5 km	2	−3013.95	6031.89	11.15	0.00
I_i, r = 3 km	2	−3014.85	6033.69	12.94	0.00
I_i, r = 3.5 km	2	−3015.10	6034.20	13.45	0.00
I_i, r = 4 km	2	−3015.11	6034.23	13.48	0.00

Figure S1 Relationships between island variables and predicted biogeographical parameters for all breeding bird species on 37 islands in Thousand Island Lake (China) surveyed from 2007 to 2012, based on distance-based and buffer-based measures of isolation. The distance-based measures are the straight-line distance in metres to the nearest nearby land mass (DIS1; green triangle), straight-line distance to the nearest larger land mass (DIS2; red triangle) and straight-line distance to the nearest mainland (DIS3; black triangle). We also calculated two buffer-based measures based on the presence of land within a 2-km buffer around a focal island: the buffer water fraction of the total area of all islands intersecting the buffer, excluding the mainland (BUF1; red circle), and the buffer water fraction of the total area of all land intersecting the buffer, including the mainland (BUF2; black circle). The colonization and extinction rates were model-weighted averages, and the higher-order parameters were derived from these.
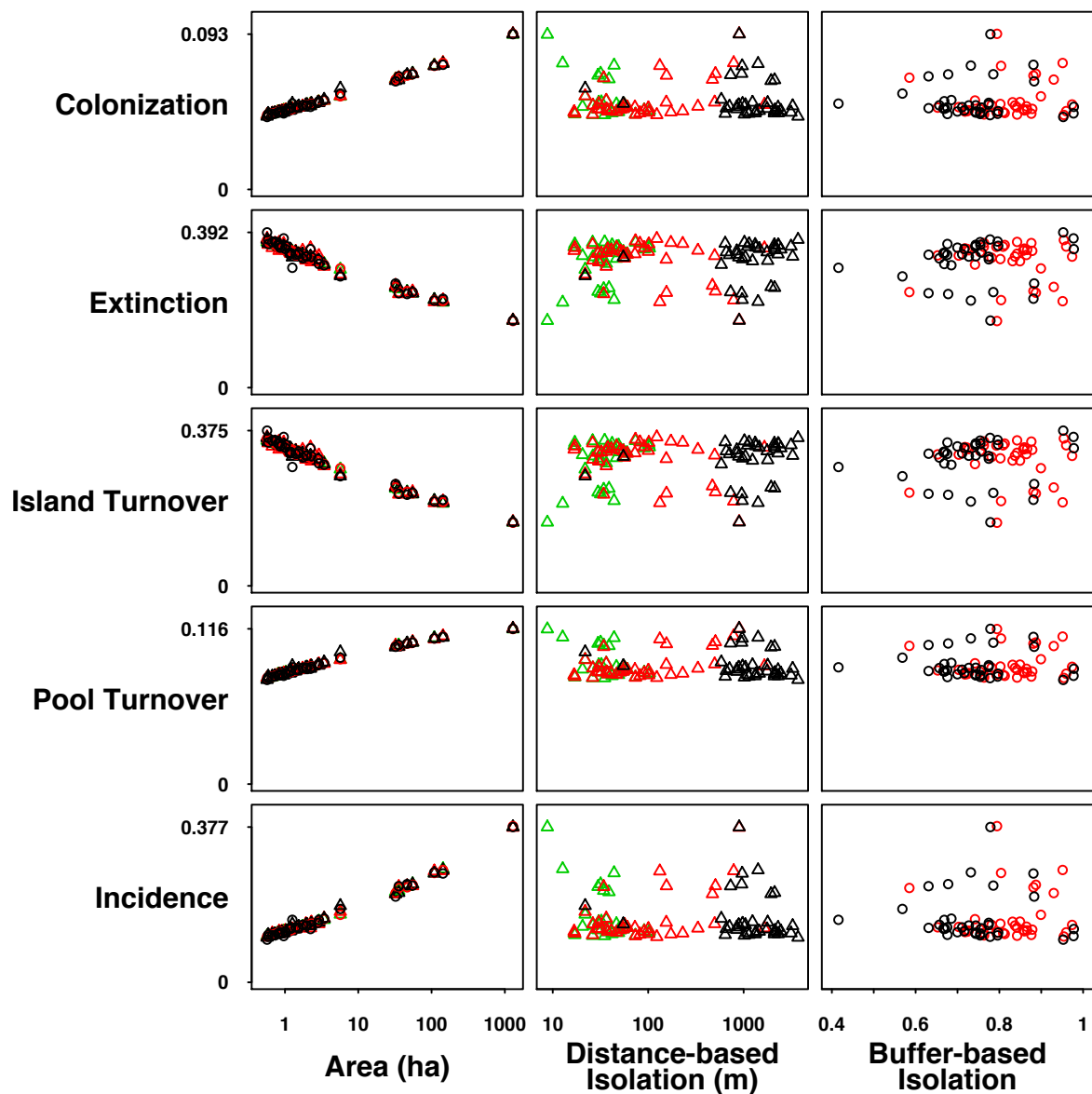
Appendix S2 Island attributes and the correlation matrix of the study islands.

Table S3 Characteristics of 37 study islands in Thousand Island Lake, China. Abbreviations: A, area (ha); I, isolation; Pe, perimeter (m); PAR, perimeter to area ratio; SI, shape index; Hr, habitat richness; E, maximum elevation (m).

Island	A	I	Pe	PAR	SI	Hr	E	Number of transects	Total length of transects (m)
1	1289.23	0.78	105,965	82	832	7	298.5	8	3200
2	143.19	0.88	17,465	122	412	6	251.1	4	1600
3	109.03	0.73	12,022	110	325	6	226.9	4	1600
4	55.08	0.79	7570	137	288	5	198.0	2	800
5	46.37	0.68	10,444	225	433	5	174.0	2	800
6	35.64	0.63	7318	205	346	5	175.2	2	800
7	32.29	0.88	5892	182	292	5	196.7	2	800
8	5.69	0.57	1489	262	176	3	109.0	1	375
9	3.42	0.69	1164	340	178	4	131.1	1	300
10	2.90	0.67	1242	428	206	3	126.3	1	275
11	2.83	0.77	901	318	151	4	125.5	1	150
12	2.29	0.77	957	418	178	4	130.5	1	300
13	2.23	0.98	1341	601	253	3	113.5	1	400
14	2.00	0.74	795	397	158	3	126.0	1	300
15	1.93	0.73	658	341	134	4	125.3	1	250
16	1.74	0.66	604	347	129	3	126.2	1	300
17	1.54	0.76	706	459	161	3	125.5	1	375
18	1.52	0.71	604	398	138	3	123.5	1	250
19	1.40	0.68	723	516	172	3	115.9	1	375
20	1.26	0.42	427	339	107	3	138.5	1	200
21	1.20	0.67	506	421	130	3	125.1	1	225
22	1.20	0.67	552	460	142	3	116.7	1	225
23	1.17	0.63	609	520	159	3	116.6	1	250
24	1.15	0.67	503	437	132	3	121.0	1	275
25	1.03	0.80	488	474	136	3	115.6	1	250
26	1.01	0.72	492	487	138	3	124.0	1	250
27	0.96	0.98	595	620	171	3	115.0	1	250
28	0.91	0.74	412	453	122	4	122.2	1	275
29	0.86	0.70	429	498	130	3	119.5	1	225
30	0.83	0.74	432	521	134	3	123.0	1	275
31	0.83	0.75	398	479	123	4	120.7	1	250
32	0.80	0.74	451	563	142	2	117.8	1	300
33	0.73	0.80	527	722	174	3	106.7	1	300
34	0.67	0.75	420	626	145	3	109.8	1	325
35	0.59	0.68	314	532	115	3	113.0	1	225
36	0.59	0.78	408	691	150	3	110.0	1	250
37	0.57	0.95	346	607	129	3	113.0	1	200

Table S4 The Pearson correlation matrix for the island attributes of the 37 study islands in Thousand Island Lake, China. Abbreviations: *A*, area (ha); *I*, isolation; *Pe*, perimeter (m); *PAR*, perimeter to area ratio; *SI*, shape index; *Hr*, habitat richness; *E*, maximum elevation (m).

	A	*I*	*Pe*	*PAR*	*SI*	*Hr*
I	0.09					
Pe	0.99***	0.14				
PAR	−0.96***	0.06	−0.91***			
SI	0.94***	0.25	0.97***	−0.79***		
Hr	0.88***	0.16	0.86***	−0.87***	0.79***	
E	0.95***	0.10	0.94***	−0.94***	0.86***	0.88***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Appendix S3 Species accumulation curves for the largest island and comparison of two species pools**.**

Figure S2 Species accumulation curves for the largest, and proportionally least-sampled, island (Island 1 in Fig. 1) in Thousand Island Lake, China. Each curve represented the cumulative count of species recorded against the number of samples in each year from 2007 to 2012.
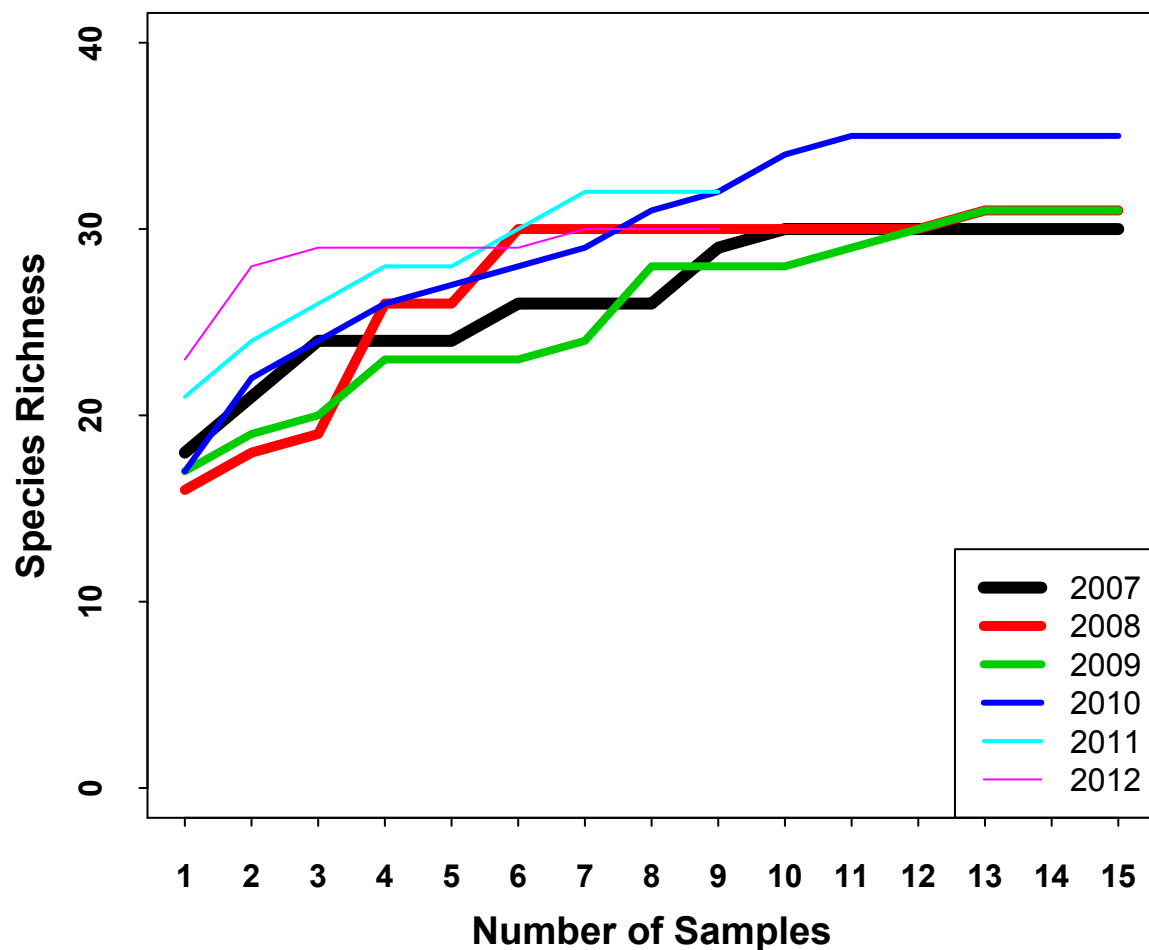
Figure S3 Comparison of the colonization and extinction rates between two species pools across areas and isolations of breeding bird communities in Thousand Island Lake region, China. Abbreviations: RI, residents with evidence of breeding recorded only on islands (71 species); RIM, residents with evidence of breeding recorded on both islands and the nearby mainland (93 species).