

# Richness and composition of plants and birds on land-bridge islands: effects of island attributes and differential responses of species groups

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# ABSTRACT

**Aim** To test relationships between the richness and composition of vascular plants and birds and attributes of habitat fragments using a model land-bridge island system, and to investigate whether the effects of fragmentation differ depending on species natural history traits.

Location Thousand Island Lake, China.

**Methods** We compiled presence/absence data of vascular plant and bird species through exhaustive surveys of 41 islands. Plant species were assigned to two categories: shade-intolerant and shade-tolerant species; bird species were assigned to three categories: edge, interior, and generalist species. We analysed the relationships between island attributes (area, isolation, elevation, shape complexity, and perimeter to area ratio) and species richness using generalized linear models (GLMs). We also investigated patterns of composition in relation to island attributes using ordination (redundancy analysis).

**Results** We found that island area explained a high degree of variation in the species richness of all species groups. The slope of the species–area relationship (z) was 0.16 for all plant species and 0.11 for all bird species. The lowest z-value was for generalist birds (0.04). The species richness of the three plant species groups was associated with island area *per se*, while that of all, generalist, and interior birds was explained mainly by elevation, and that of edge bird species was associated primarily with island shape. Patterns of species composition were most strongly related to elevation, island shape complexity, and perimeter to area ratio rather than to island area *per se*. Species richness had no significant relationship with isolation, but species composition did. We also found differential responses among the species groups to changes in island attributes.

**Main conclusions** Within the Thousand Island Lake system, the effects of fragmentation on both bird and plant species appear to be scale-dependent and taxon-specific. The number of plant species occurring on an island is strongly correlated with island area, and the richness of birds and the species composition of plants and birds are associated with variables related to habitat heterogeneity. We conclude that the effects of fragmentation on species diversity and composition depend not only on the degree of habitat loss but also on the specific patterns of habitat fragmentation.

## **Keywords**

China, habitat heterogeneity, island biogeography theory, land-bridge islands, species-area relationship, species composition, species richness, Thousand Island Lake.

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# INTRODUCTION

Habitat fragmentation is widely considered to be one of the most important and widespread threats to biodiversity (Wilcove et al., 1998; Franklin et al., 2002; Fahrig, 2003; Lindenmayer & Fischer, 2006). Previous studies examining the impacts of fragmentation have shown that species richness and composition in fragmented landscapes are related to a number of attributes of the habitat patches, particularly patch area, isolation, shape, amount of edge habitat, elevation, and nature of the surrounding matrix (Saunders et al., 1991; Murcia, 1995; Hill & Curran, 2003; Ewers & Didham, 2005; Fischer & Lindenmayer, 2007). Of these attributes, area and isolation are generally considered to be the two most important factors affecting species richness in fragments, owing to their influence on extinction and colonization rates, respectively (MacArthur & Wilson, 1963, 1967; Lomolino, 2000; Gardner & Engelhardt, 2008; Keppel et al., 2010).

Fragment area is generally believed to be the single most important factor influencing species richness (Fahrig, 2003). There are many reasons why species richness may increase with area beyond sampling effects and effects on population sizes and viability. For example, perhaps one of the most important consequences of changes in fragment area is an associated change in habitat heterogeneity resulting from changes in topographic complexity, elevational range, fragment orientation, fragment shape and amount of edge habitat (Murcia, 1995; Morrison, 2002; Hill & Curran, 2003; Ries et al., 2004; Ewers & Didham, 2005; Watson et al., 2005; Radford & Bennett, 2007; Laurance, 2008; Hortal et al., 2009). In general, habitat heterogeneity will increase with area, thus creating additional niches and allowing for an increased diversity of species in larger fragments (Hutchinson, 1957; Williams, 1964; Kadmon & Allouche, 2007; Gardner & Engelhardt, 2008).

Different species groups often display different sensitivities to fragmentation and associated changes in habitat diversity or quality (Dettki et al., 1998; Henle et al., 2004; Ewers & Didham, 2005; Cagnolo et al., 2009). Traits that are generally believed to increase a species' vulnerability to fragmentation include low or limited mobility/dispersal, interior habitat requirements, high trophic level, and greater ecological specialization (Henle et al., 2004; Ewers & Didham, 2005; Feeley et al., 2007; Laurance, 2008; Wang et al., 2009). However, relatively few studies have looked simultaneously at patterns of species richness and composition in more than one group in fragmented ecosystems. Instead, comparisons between species groups are generally made by compiling results of disparate studies, a process that may be complicated by discrepancies in methods, choice of fragments, research objectives, etc. (Henle et al., 2004; Ewers & Didham, 2005; Cagnolo et al., 2009). Consequently, the effects of fragment/island attributes on species diversity and on the slope of species-area relationship curves, as well as the responses of different species groups to fragmentation, remain poorly understood.

Land-bridge islands (i.e. islands that were once connected to the mainland but were subsequently isolated by rising waters), especially as formed by dam construction and subsequent inundation, are sometimes considered model or 'experimental' systems for researching fragmentation (Gotelli & Graves, 1990; Diamond, 2001; Terborgh *et al.*, 2001; Wu *et al.*, 2003; Terborgh & Feeley, 2008, 2010; Wang *et al.*, 2010a). More specifically, in land-bridge island systems, all fragments are formed within a relatively short period of time as a result of a single known disturbance event. In addition, land-bridge islands, like oceanic islands, are surrounded by a homogeneous and relatively inhospitable matrix (water) and thus have welldelineated boundaries and are more 'closed' than terrestrial habitat fragments, which are often surrounded by a mixture of land covers of variable permeability (Terborgh & Feeley, 2008).



**Figure 1** Location of the Thousand Island Lake, China, and the 41 study islands.

Unlike oceanic islands, man-made land-bridge islands generally occur over spatial scales that are comparable to terrestrial habitat patches and have been formed recently enough that evolution and species adaptation are unlikely to confound results (Terborgh *et al.*, 1997). Despite these advantages, relatively few studies to date have looked at the effects of habitat fragmentation on land-bridge islands.

In this study, we concurrently investigated the diversity and composition of vascular plant and bird species on 41 landbridge islands in the Thousand Island Lake in East China (Fig. 1). Capitalizing on the fact that the formative disturbance, time since isolation, and surrounding matrix - factors that have complicated or confounded previous fragmentation studies - were all controlled for, we examined the relationships between the island attributes and the diversity and composition of the resident bird and plant species. Specifically, we tested the hypotheses that (1) island area and other island attributes related to habitat area and habitat heterogeneity influence the diversity and composition of plant and bird species on land-bridge islands; (2) different factors influence species richness versus species composition; and (3) the factors influencing composition and richness differ between species groups, depending on mobility and habitat requirements.

# MATERIALS AND METHODS

#### Study sites

Thousand Island Lake (TIL) is a large man-made hydroelectric reservoir in western Zhejiang Province, China, located at 29°22'-29°50' N, 118°34'-119°15' E (Fig. 1). TIL was formed by the construction of the Xinanjiang dam on the Xinanjiang River in 1959. An area of 573 km<sup>2</sup> was inundated when the dam was closed, creating 1078 land-bridge islands larger than 0.25 ha when the water reached its highest level (108 m a.s.l.) (Wang et al., 2010b). TIL is within a middle subtropical climatic zone with a monsoon climate (i.e. strongly seasonal with hot, wet summers and cold, dry winters). The mean annual temperature is 17.0 °C, ranging from -7.6 °C in January to 41.8 °C in July. Mean annual precipitation in the TIL region is 1430 mm, with 155 days of precipitation on average per year and with most rain falling during the rainy season between April and June. Currently, 88.5% of land area on the islands is covered by forest, and most forested areas (c. 90%) are unmanaged secondary forests dominated by Masson pine (Pinus massoniana).

## **Field surveys**

We measured bird and plant richness and composition on 41 islands in TIL (Fig. 1; Wang *et al.*, 2010b, 2011). Most of these islands (25) are < 1 ha in area, and only three islands are > 100 ha in area (island area measured at 105 m a.s.l., which generally corresponds to the edge of forest cover). The mean area of the 41 study islands is 37.9 ha, and the median area is 0.8 ha. The smallest study island is 0.16 ha in area with a peak

elevation of 109 m, and the largest island (the largest island in all of TIL) is 1153.9 ha in area with a peak elevation of 299 m. The distance from the study islands to the mainland ranges from 30 to 4075 m (the farthest island from the mainland is 174 in Fig. 1, near the centre of the lake), with a mean distance of 1239 m and a median distance of 973 m. Study islands were selected to (1) cover a wide range of areas and degrees of isolation, (2) have minimum levels of human disturbance, (3) be covered entirely or predominantly by Masson pine forest, and (4) be logistically convenient for fieldwork.

#### Plants

We conducted surveys of all vascular plant species occurring on the 41 study islands during the growing seasons (April to November) of 2007 and 2008. During the surveys, we determined the presence or absence of species (abundance data were not collected) through multiple visits to all study islands, following standard field methods designed to record the highest possible number of species. Islands < 50 ha (38) islands) were circumnavigated and 4-16 transects were established. Each transect was walked a minimum of three times by trained observers. On small islands (< 3 ha, n = 34), 4–8 interior transect surveys were established covering almost the entire island. On each of the medium islands (27.49-47.98 ha, n = 4), 16 transects were established totalling over 10 km in length. On the large islands (> 100 ha, n = 3), surveys were conducted as above but centred on each prominent hill. The total length of transects on each of the large islands was > 20 km and was > 40 km on the largest island. Most plant species encountered during surveys were identified and recorded in the field. We collected voucher specimens for species that could not be identified reliably in the field and identified them according to available literature (Editorial Committee of Flora of Zhejiang, 1993; Zheng, 2005).

## Birds

We censused the presence or absence of birds on the same 41 study islands using a line-transect method. Censuses were conducted during two breeding (April–June) and winter (November–January) seasons from 2007 to 2009 (Wang *et al.*, 2011). We conducted 15 censuses on each island per season (60 repetitions in total). During the censuses, trained observers walked each transect at a constant speed (*c.* 2.0 km h<sup>-1</sup>) and recorded all bird species heard or seen within 50 m of the transect lines (high-flying species passing over the islands were not recorded). The total length of transects (m) on each island was determined relative to island area (Wang *et al.*, 2010b). To avoid possible systematic sampling bias owing to observer fatigue or weather conditions, a restricted random-visitation ordering of survey transects was used.

In order to test if our field surveys were sufficient to capture the true species diversity of the islands, especially on the larger islands, we incorporated plant abundance data that had been collected as part of a separate research project. These data included the abundance of all woody plant species with diameter at breast height  $(d.b.h.) \ge 1$  cm occurring within  $5 \times 5$  m quadrats in 1-ha forest inventory plots on three of the large and medium islands. In addition, we used abundance estimates for each bird species as recorded from multiple repeated transect samplings on the same islands. Rarefaction curves based on these data indicate that the field surveys adequately captured species diversity on these islands (Fig. 2). While we do not have comparable abundance data from other islands, sampling intensity was as great or greater, supporting the contention that field surveys were sufficient to characterize the diversity and composition of plants and birds across all study islands.

#### **Species groups**

Using published data (Editorial Committee of Flora of Zhejiang, 1993) and data collected through our previous studies of the TIL islands, we assigned all recorded plant species to two groups: shade-intolerant and shade-tolerant species. Likewise, but relying especially on our field observations during the past several years of research in TIL, we categorized all recorded bird species into three analogous groups: edge species, interior species, and edge-interior generalist species (Zhuge, 1990; Villard, 1998).

#### **Island attributes**

We measured six spatial attributes characterizing each of the 41 study islands: area in hectares (A), isolation as indicated by the shortest straight-line distance in metres to the mainland (DM) and to the nearest-neighbour island (NND), shape index (SI), perimeter to area ratio (PAR), and peak elevation in metres (E). SI indicates the relative island shape complexity and was calculated as SI =  $P/[2 \times (\pi \times A)^{0.5}]$  (Laurance & Yensen, 1991; Hoffmeister *et al.*, 2005; Ewers & Didham, 2007), where *P* is the perimeter and *A* is the area of the island.

SI is 1 when the shape is a perfect circle, and increases as the shape becomes more irregular and complex. PAR is the relative edge length of an island and provides an indication of the relative amount of edge versus core/interior habitat (McGarigal & Marks, 1995; Wu *et al.*, 2002; Wu, 2004). When calculating these island attributes, we considered the 105 m a.s.l. contour to be the island edge and excluded any beach that forms below this level during periods of low water.

# Data analyses

Using the MMSAR R package (Guilhaumon *et al.*, 2010), we characterized the relationship between the richness of each of the seven species groups (all plants, shade-intolerant plants, shade-tolerant plants, all birds, edge birds, interior birds, and generalist birds) and island area using the log–log power model  $S = cA^z$ , where S is species richness on an island of area A, and c and z are constants (for the bird species groups, species richness was counted as S + 1 owing to some species groups being absent from some islands). z indicates the rate at which species richness changes with area and is commonly used as a measure of a biological community's sensitivity to habitat loss and fragmentation.

We used pairwise Pearson correlation coefficients to analyse the relationships among island attributes, with the significance level adjusted by Bonferroni correction. Global Moran's *I* (Moran, 1950) was used to test the spatial autocorrelation of island attributes and species richness, and the Mantel test (Mantel, 1967) was used to test the effect of the spatial structure of islands on species richness. We fitted generalized linear models (GLMs) with a Poisson link function to predict the species richness of all seven species groups based on the six island attributes. A backward stepwise regression was then used to identify the best-fit models [variable selection and model evaluation were both based on Akaike information criterion (AIC) values]. A significant contribution of each effect to model fit was assessed using a two-tailed chi-square



**Figure 2** Rarefaction curves of three large or medium study islands in the Thousand Island Lake, China, for (a) woody plants with d.b.h.  $\geq 1$  cm in 1-ha monitoring plots, and (b) birds from transect samplings.

distribution. The contribution of each island attribute to predicting species richness was determined by calculating the proportion of the deviance explained, similar to  $R^2$ .

Finally, we used redundancy analysis (RDA) to analyse patterns of species composition and the contributions of the island attributes (Legendre & Gallagher, 2001). All analyses were conducted in R 2.10.1 (R Development Core Team, 2009).

# RESULTS

# **Correlations among island attributes**

For the 41 study islands, A, SI and E are significantly positively correlated (R = 0.72-0.90, P < 0.001; Table 1), indicating that larger islands have more complex shapes and higher elevations. SI and PAR are significantly negatively correlated (R = -0.51, P < 0.05), as are PAR and E (R = -0.73, P < 0.001). There are no significant correlations between A, SI, PAR or E and either measure of isolation (DM or NND).

# Plant and bird species richness and classification

We recorded a total of 376 vascular plant species belonging to 256 genera and 96 families (see Appendix S1 in Supporting Information). Of these species, 198 were classified as shade-intolerant and 178 as shade-tolerant. We recorded a total of 96 bird species, belonging to 61 genera and 29 families (Appendix S2). Eighteen species were classified as edge species, 48 were classified as interior species, and 30 were classified as edge–interior generalist species.

## Species-area relationships

All fits of the power-function species–area relationship  $(S = cA^z)$  were highly significant, and the correlations were all positive, with area explaining a high proportion of variation in the richness of all species groups. The fitted *z*-values for all, shade-intolerant and shade-tolerant plants were 0.16, 0.14 and 0.18, respectively. These values are comparable to results from a separate study looking at plant communities across 154 TIL islands (Hu *et al.*, 2011). The fitted *z*-values for all, edge,

**Table 1** Pearson correlation coefficients among attributes of 41islands in the Thousand Island Lake, China.

Pearson correlation	DM	NND	SI	PAR	E
A	-0.07	-0.12	0.86***	-0.35	0.72***
DM		0.29	-0.06	0.21	-0.20
NND			-0.07	0.06	-0.04
SI				-0.51*	0.90***
PAR					-0.73***

A, area; DM, nearest distance to the mainland; NND, nearest-neighbour distance; SI, shape index; PAR, perimeter/area ratio; E, elevation. \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001 (significance levels adjusted by Bonferroni correction).

interior and generalist birds were 0.11, 0.09, 0.18 and 0.04, respectively (Fig. 3).

# Species richness and spatial attributes

The global Moran's I showed that only DM had significant spatial autocorrelation (Moran's I = 0.45, Z-score = 5.17, P < 0.01). However, there was no effect of the spatial structure of islands on plant and bird richness as indicated by the Mantel test (plant: R = -0.05, P = 0.577; bird: R = -0.05, P = 0.651). The GLMs and stepwise analysis indicated that the richnesses of the three plant species groups all increased with island area, but the richnesses of the bird species groups were not related to area (Table 2). Elevation had a significant positive effect on the richness of all plants, shade-intolerant plants, all birds, generalist birds and interior bird species. For plants, island attributes explained 65-86% of the variation in species richness; for birds, island attributes explained 45-76% of the variation (Table 2). Island area was the variable that explained the most variation in the species richness of all plant species groups. The richness of shade-tolerant plant species was also significantly associated with PAR. For all bird species, generalist and interior bird species, E was the only significant explanatory variable. SI was the only significant factor in explaining the richness of edge bird species.

# Species composition and spatial attributes

The correlation between the Jaccard dissimilarity indices of plant and bird species composition and distance between island pairs was not significant (R = 0.04, P = 0.59 for plants; R = -0.06, P = 0.09 for birds), indicating an absence of spatial autocorrelations in composition.

The results of the RDA ordinations of species composition are shown in Fig. 4. Island attributes explained 17–20% of variation in composition, and were significant explanatory factors for all sets but edge and generalist bird species (P < 0.05 for interior birds and < 0.01 for the other four species groups). For the five species groups, E, PAR and SI were more strongly associated than area with axis 1 (RDA1). The isolation index DM (and NND for edge birds) had higher explanatory power along axis 2 (RDA2) than other island attributes, indicating the important contribution of isolation to explaining patterns of species composition of the five species groups across the 41 islands.

# DISCUSSION

In previous studies looking at patterns of species richness across fragments or islands, *z*-values of fitted species–area relationships were typically found to be between 0.20 and 0.35 (Rosenzweig, 1995, 2004; May & Stumpf, 2000; Panitsa *et al.*, 2006; Santos *et al.*, 2010). Here we found *z* to be only 0.16 for all plants and 0.11 for all birds, indicating a relatively slow change in richness with change in island area at TIL. The low



**Figure 3** Species–area relationships of six plant and bird species groups on 41 study islands in the Thousand Island Lake, China, based on the log–log power models  $\ln(S) = z \times \ln(A) + c$  for plants, and  $\ln(S + 1) = z \times \ln(A) + c$  for birds, where *S* is species richness, *A* is area, and *z* and *c* are constants. Figures show richness of (a) all plants and all birds, (b) shade-intolerant plants and shade-tolerant plants, (c) edge birds, interior birds, and generalist birds.

**Table 2** Results from generalized linearmodels (GLMs) with Poisson link functionand stepwise regression of island attributesfor predicting the richness of plant and birdspecies groups in the Thousand Island Lake,China. Only attributes retained in the best-fitmodels are shown. Variable selection andmodel estimation were based on the Akaikeinformation criterion (AIC). The abbrevia-tions are as in Table 1.

Richness of species groups	Island attributes	Estimate	SE	<i>P</i> -value	Deviance explained (%)
All plants	Area	$1.15 \times 10^{-3}$	$1.04 \times 10^{-4}$	< 0.001	70.31
1	Elevation	$3.10 \times 10^{-3}$	$5.89 \times 10^{-4}$	< 0.001	3.98
	PAR	-1.68	1.14	0.14	0.89
	SI	$-7.98 \times 10^{-2}$	$4.96 \times 10^{-2}$	0.11	0.54
Shade-intolerant	Area	$1.40 \times 10^{-3}$	$2.53 \times 10^{-4}$	< 0.001	63.72
	SI	$-1.21 \times 10^{-1}$	$6.48 \times 10^{-2}$	0.06	1.35
	Elevation	$3.25 \times 10^{-3}$	$1.46 \times 10^{-3}$	< 0.05	0.54
Shade-tolerant	Area	$9.85 \times 10^{-4}$	$9.41 \times 10^{-5}$	< 0.001	65.68
	PAR	-6.34	1.12	< 0.001	13.88
	DM	$-5.06 \times 10^{-5}$	$3.44 \times 10^{-5}$	0.14	0.81
All birds	Elevation	$4.67 \times 10^{-3}$	$5.25 \times 10^{-4}$	< 0.001	75.51
Edge birds	SI	$1.56 \times 10^{-1}$	$4.00 \times 10^{-2}$	< 0.001	47.06
Generalist birds	Elevation	$2.08 \times 10^{-3}$	$7.89 \times 10^{-4}$	< 0.01	45.72
Interior birds	Elevation	$8.26 \times 10^{-3}$	$8.20 \times 10^{-4}$	< 0.001	72.46

DM, nearest distance to the mainland; PAR, perimeter/area ratio; SI, shape index.



**Figure 4** Species composition of plants and birds on 41 study islands in the Thousand Island Lake, China, in relation to five island attributes as characterized by redundancy analyses (RDA). Figures show species composition of (a) all plant species, (b) shade-intolerant plants, (c) shade-tolerant plants, (d) all bird species, (e) edge birds, (f) interior birds, (g) generalist birds. Each point represents a single study island. The size of the points varies in relation to log island size. The lengths and angles of the arrows represent the explanatory power of the island attributes along each axis; that is, the explanatory power is higher when the length is longer and the angle is smaller. The abbreviations are as in Table 1.

*z*-values found at TIL may reflect the fact that the habitats on the study islands are relatively homogeneous, as the forests on all islands are dominated by Masson pine. Thus few additional niches are provided as island area increases, resulting in a slow increase in species numbers with increasing area. Indeed on small islands, the increase in edge habitat and edge-tolerant species may partially compensate for the loss of interior species. Furthermore, the low isolation of most of the islands may allow for frequent movement or dispersal among islands or between the islands and mainland, especially for birds. This last point is supported by the absence of significant isolation effects. Also supporting this last point are the differences in *z*-values for all birds versus all plants, as well as between the different species groups within both plants and birds. *z*-values were lower for bird species than for the analogous plant species groups as well. These patterns suggest that for the species groups with higher mobility, the islands are not closed but represent a network of interconnected habitat patches, and that the influence of area is scale-dependent, varying in relation to species mobility (Whittaker & Fernández-Palacios, 2007). In addition, *z* was lower for the generalist and edge bird species and for shade-intolerant plant species and was higher for shade-tolerant plants and interior bird species, suggesting that the area effect is also taxon-specific (Henle *et al.*, 2004).

Island area *per se* was the primary explanatory factor for species richness of the three plant species groups when analysing the integrated effects of all island attributes by GLMs and stepwise analysis. However, elevation (E) was the only significant explanatory factor associated with the richness of all birds, generalist birds and interior bird species, and SI

was the only attribute associated with the richness of edge birds. The richness of all plants and shade-intolerant plants was related to elevation, and that of shade-tolerant plant richness to PAR. In addition, E, SI and PAR were the factors most strongly associated with the species composition of most species groups, as indicated through RDA ordinations, rather than island area per se. Considering the positive relationship among area, elevation and SI, and the negative relationships between PAR and elevation/SI, we assume that species richness and composition on the land-bridge islands at TIL is driven not only by area per se, but also by differences in island elevation, shape and relative edge length. The effects of these attributes on species richness and composition may reflect their positive correlation with habitat heterogeneity. These phenomena echo the conclusions of previous studies, namely that species diversity within a region increases with area as a result of decreasing extinction rate and increasing habitat heterogeneity (Williams, 1964; MacArthur & Wilson, 1967; Johnson & Simberloff, 1974; Ries et al., 2004; Watson et al., 2005; Kadmon & Allouche, 2007; Gardner & Engelhardt, 2008; Hortal et al., 2009), and species groups with different habitat requirements and mobility respond differently to changes in habitat (Henle et al., 2004; Ewers & Didham, 2005; Feeley et al., 2007; Laurance, 2008; Wang et al., 2009; Hu et al., 2011).

It is somewhat surprising that elevation was the dominant variable correlated with the richness of most bird species groups at TIL, because most previous studies of oceanic archipelagos and habitat islands have found fragment area to be the primary factor in models of avian species diversity (Rosenzweig, 1995; Ricklefs & Lovette, 1999; Watling & Donnelly, 2006). One possible explanation is that of the island attributes used in this study: elevation is the only factor representing vertical habitat heterogeneity, and hence greater elevation may allow for increased numbers of available habitat types in an otherwise fairly homogeneous forest. Further studies incorporating detailed data on topography, soil features and habitat use, etc. are required to test this hypothesis.

At TIL, we found no significant correlations between measures of island isolation and species richness. This may also be attributable to the relatively short distance between islands or to scale-dependent effects (Whittaker & Fernández-Palacios, 2007). However, the species composition of most plant and bird species groups was associated with distance to mainland (DM), and the composition of edge bird species was associated with nearest-neighbour island distance (NND), as characterized by RDA ordinations.

Based on the observations in this study, we conclude that the effects of habitat fragmentation at the Thousand Island Lake, China, appear to be scale-dependent and taxon-specific, and are associated primarily with various island attributes related to habitat diversity. The number of plant species is strongly associated with island area, but the richness of birds and the composition of plants and birds are more strongly associated with other island attributes. Additional studies will be required to reveal the influences of other habitat factors such as microclimate, topography, community structure and soil, as well as the effects of habitat fragmentation on species interactions.

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# SUPPORTING INFORMATION

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

**Appendix S1** List of plant species occurring on the Thousand Island Lake study islands.

**Appendix S2** List of bird species occurring on the Thousand Island Lake study islands.

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# BIOSKETCH

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