

## ORIGINAL RESEARCH

# Passive acoustic monitoring reveals the role of habitat affinity in sensitivity of sub-tropical East Asian bats to fragmentation

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## Keywords

AudioMoth, habitat loss, hydroelectric reservoirs, insectivorous bats, island biogeography, land-bridge islands

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## Abstract

Hydropower infrastructure represents a major driver of habitat loss and insular fragmentation worldwide, mostly across the tropics and sub-tropics. Despite growing evidence of dam-induced impacts on biodiversity, the effects of insular habitat fragmentation on species assemblages remain poorly understood, particularly for East Asian vertebrates. Here, we assess how insectivorous bats respond to forest fragmentation in Thousand Island Lake, a mega-hydroelectric dam in East China. Bat assemblages were surveyed across 36 land-bridge islands of different sizes and degrees of isolation, using AudioMoth recorders. Echolocation calls were classified into sonotypes, each corresponding to either single or multiple species, which were further classified according to their habitat affinities into forest or open-space foragers. Based on 22 875 five-min recordings from 108 detector-nights, we recorded 15 bat sonotypes, eight of which we classified as forest sonotypes (2329 bat passes) and seven as open-space sonotypes (52 277 bat passes). Overall, sonotype richness increased with island area, but only above a certain threshold (34 ha). Habitat affinity played an important role in ensemble-level responses to fragmentation; forest sonotype richness increased with island area, whereas open-space sonotype activity was higher in more isolated islands. Our results highlight the relevance of particularly large fragments (>1000 ha) to maintain area-sensitive forest bat species. However, islands below 34 ha in size and those more isolated from the mainland are also of conservation value as they, correspondingly, harbour a variable (but substantial) number of species and concentrate higher activity of open-space foragers. These findings further demonstrate that acoustic sampling methods, as the one presented here, are able to provide key information for evidence-based policies aimed at halting the ongoing wave of dam-induced biodiversity loss.

## Introduction

Anthropogenic habitat loss and fragmentation are key drivers of the ongoing global biodiversity crisis (Haddad et al., 2015; Pfeifer et al., 2017). Although most habitat loss and fragmentation are still associated with the

expansion of agricultural and grazing landscapes (Laurance et al., 2014), increasing amounts of wilderness are falling prey to emerging threats, particularly the one posed by the global boom in hydropower dam construction (Gibson et al., 2017; Zarfl et al., 2015).

In the insular fragmented landscapes created in the aftermath of damming, biological communities are exposed to the effects of island area, degree of isolation and edge effects (Ding et al., 2013; Jones et al., 2016; Yu et al., 2012). Moreover, land-bridge islands—embedded within a uniformly hostile open-water matrix—are at the extreme end of the spectrum of fragment-matrix contrast (Meyer & Kalko, 2008a). Therefore, species assemblages isolated on land-bridge islands are expected to undergo a novel disturbance regime, resulting in drastic shifts in species diversity and community composition through species extinction and turnover (Benchimol & Peres, 2015; Gibson et al., 2013). Yet, despite the considerable ecological impacts associated with hydropower development (Gibson et al., 2017), >3700 dams are under construction or planned, mostly in highly diverse tropical and sub-tropical regions (Zarfl et al., 2015).

Although multiple studies have investigated bat assemblages in fragmented landscapes (reviewed for the tropics in Meyer et al., 2016), generalizations about the effects of fragmentation *sensu lato* remain elusive. For instance, whereas in accordance to MacArthur and Wilson's (1967) island biogeography theory, some studies have found population- and assemblage-level responses to both patch area (Rocha, López-Baucells, et al., 2017; Silva et al., 2020; Struebig et al., 2008) and isolation (Estrada-Villegas et al., 2010; Meyer & Kalko, 2008a), others found either weak or no influence of these metrics (e.g. Pardini et al., 2009). Generalizations are further complicated by idiosyncratic responses, often linked to particular ecological traits such as echolocation (Núñez et al., 2019; Wordley et al., 2017) and wing morphology (Farneda et al., 2015). Furthermore, the scarcity of studies for some key regions—such as East Asia—hinders generalizations about the effects of fragmentation on bats. In fact, there is a remarkable knowledge gap regarding the effects of habitat fragmentation on bats across Asia (Kingston, 2010; Feijó et al., 2019; but see e.g. Struebig et al., 2008) and, to date, no study has used land-bridge islands as a model system to investigate the responses of Asian bats to fragmentation.

The recent increase in the availability of affordable autonomous recorders is making Passive Acoustic Monitoring a useful technique to undertake biodiversity surveys, allowing higher spatial and temporal replication (Hill et al., 2018; López-Baucells et al., 2021). This is especially relevant for surveys of aerial insectivorous bats that commonly evade capture (Gibb et al., 2019), further allowing us to improve our understanding of the impacts of habitat loss and fragmentation on this diverse group of mammals.

Thousand Island Lake in sub-tropical East China was formed in 1959 by a mega-hydroelectric dam. The

reservoir covers 573 km<sup>2</sup> and contains over 1000 variable-size islands. Due to its great potential for the study of fragmentation detached from the blurring influence of the surrounding matrix, it has been used as a model system to investigate consequences on a wide array of taxa, including plants (Yu et al., 2012), arthropods (Zhao et al., 2020), reptiles (Wang et al., 2015) and birds (Ding et al., 2013; Si et al., 2016). Here, we use acoustic recorders to examine assemblage, ensemble- and sonotype-level responses of aerial insectivorous bats to the joint effects of habitat loss and fragmentation. Specifically, we address the following questions:

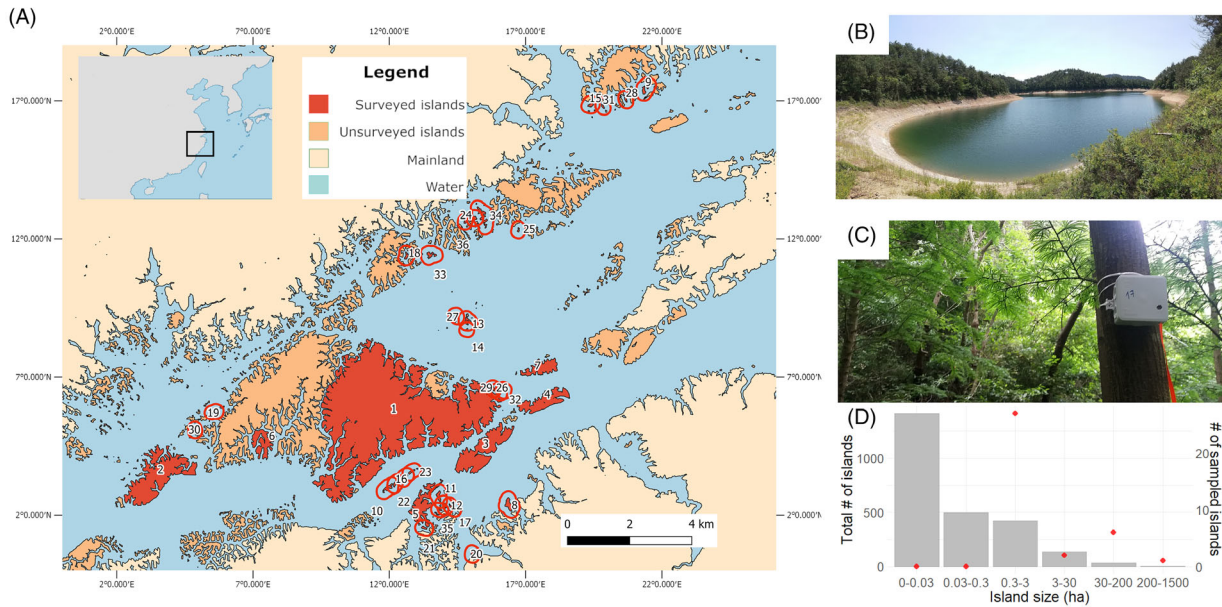
i) What are the patterns of bat sonotype richness, activity (proxy of abundance) and assemblage composition across a range of island sizes, degrees of isolation and habitat quality, and what factors contribute to these patterns? We anticipate higher sonotype richness in larger and more evenly shaped islands. Those characteristics contribute to the persistence of larger populations (MacArthur & Wilson, 1967) and are likely to harbour a greater diversity of microhabitats, higher structural and compositional complexity of forest habitat and lower intensity of edge effects (Pfeifer et al., 2017).

ii) Do species' responses to fragmentation depend on their habitat affinity? Recorded bats were divided according to their sonotype call shape into constant frequency (CF), frequency-modulated (FM) and quasi-constant frequency (QCF) (see López-Bosch et al., 2021 for classification details). CF and FM echolocating bats (hereinafter 'forest bats') are mostly associated with highly cluttered environments, whereas QCF (hereinafter 'open-space bats') have a higher affinity towards open habitats (Jones & Rayner, 1989). Thus, whereas we anticipate forest bats to be particularly sensitive to island area, with higher sonotype richness and activity in larger islands, we predict open-space bats to exhibit higher sonotype richness and activity in smaller island due to their tendency to forage above the water surface and near forest edges.

## Materials and Methods

### Study area

This study was conducted at Thousand Island Lake (TIL) in western Zhejiang Province, China (Fig. 1). This artificial reservoir was created in 1959 by the construction of a hydropower dam in the Xin'anjiang River. Damming flooded over 573 km<sup>2</sup>, creating 1078 land-bridge islands ranging in size from 0.25 to 1289 ha. TIL has a typical sub-tropical monsoon climate and is strongly seasonal, with hot and humid summers and cold to mild winters (average annual temperature is 17°C, ranging from –



**Figure 1.** (A) Map of Thousand Island Lake (TIL) in Zhejiang Province, China. Surveyed islands are numbered according to Table S1 and red-coloured; remaining islands and the mainland are, respectively, orange and light orange-coloured, whereas the water matrix is represented in blue. (B) Photo of the landscape at TIL. (C) Water-proof box containing an AudioMoth detector. (D) Distribution of island sizes at TIL; grey bars account for all islands in the system, whereas red dots account for the surveyed islands (not to scale).

7.6°C in January to 41.8°C in July; annual precipitation is 1430 mm; Wang et al., 2010). Most of the islands are covered with mixed sub-tropical deciduous/coniferous secondary forests dominated by Masson's pine *Pinus massoniana*, alongside broad-leaved trees and shrub vegetation (Si et al., 2014). The mean forest coverage per island is 83% (Ding et al., 2013). The lake is located within the Qiandaohu National Forest Park and borders the Qianjiangyuan National Forest Park. The islands sampled in this study are the same islands where other taxa were previously surveyed (e.g. Wang et al., 2010; Wilson et al., 2016).

### Acoustic surveys

Fieldwork was conducted in May 2019. Weather conditions in terms of temperature, precipitation and wind speed were fairly constant within this time period and no fieldwork was conducted on days with heavy rain or wind. Bats were surveyed in 36 islands of variable sizes (0.57–1289.23; mean ( $\pm$ SD): 48.74  $\pm$  214.91 ha) and degrees of isolation (21.85–3712.21; 1477.8  $\pm$  865.44 m from the mainland; Fig. 1). To account for differences in microhabitat diversity within islands, our sampling effort was scaled according to island size, so that from one to eight sampling sites were established per island (53 sampling sites in total): eight in the largest island

(1289.23 ha), four in the two islands with areas 143.19 and 109.03 ha, two in the four islands with the area between 32.29 and 55.08 ha and onesite in the 29 islands <10 ha (Table S1). In islands, where more than one detector was deployed, we primarily chose their locations by maximizing the distance between them and thus enlarging the spatial sampling cover within that island. In each sampling site, bats were surveyed during three consecutive nights using one AudioMoth<sup>®</sup> v1.0.0 detector (López-Baucells et al., 2021). This is an open-source, programmable device capable of recording animal calls up to 384 kHz (Hill et al., 2018). Each AudioMoth was placed within an appropriate waterproof box (Fig. 1C) and attached to a tree trunk at a height of ~2 m, facing forest trails. To minimise confounding effects such as those driven by edge habitat, AudioMoths were placed at the island's interior, 141.76  $\pm$  221.23 m from the edge at mid-large islands (32.29–1289.23 ha) and at least 15 m from the edge in small islands (<1 ha). Each detector was configured to record at a sample rate of 384 kHz and to continuously record from half an hour before sunset to half an hour after sunrise, generating 5-min wav files.

### Bioacoustic analysis

Our unit of measure for bat activity was a 'bat pass', defined as two or more pulses of a single species/sonotype

detected in a 5-s recording (see Torrent et al., 2018). Feeding buzzes and social calls were not included in the analysis. AudioMoth wav files were split into 5-s long recordings using Kaleidoscope v.1.1.1. software (Wildlife Acoustics, USA). We then used the same software to select only files containing bat calls. To do so, we used a pulse detection algorithm that selects recordings containing pulses with a frequency of maximum energy between 10 and 250 kHz, with a minimum pulse length of 2 ms and a maximum of 500 ms. When two or more sonotypes were identified in one 5-s file, a single bat pass for each sonotype was counted. Following Tuneu-Corral et al. (2020), we clustered all 5-s files according to their similarity on different acoustic parameters (i.e. for each pulse, frequency of maximum energy, start frequency, end frequency, maximum frequency, minimum frequency and duration), and file tagging was conducted manually using Avisoft SasLab Pro 5.2.12 software (Avisoft Bioacoustics, Germany).

The identification of the sonotype(s) in each of the 5-s files was undertaken following the acoustic key available in López-Bosch et al. (2021) (for sonograms, sonogram description and bat species known to China with similar echolocation characteristics of the different sonotypes recorded at the TIL, see Data S1). Following Estrada-Villegas et al. (2010), we classified bats as either open-space sonotypes (bats with CF and FM echolocation calls and typically associated with uncluttered space) or forest sonotypes (bats with QCF echolocation calls and typically associated with uncluttered space).

### Island variables

Seven island variables were used to explain bat diversity and assemblage composition in the archipelagic landscape. We considered island size (ha; AREA), shape index (SHAPE) defined as  $[\text{SHAPE} = \frac{P}{200[(\pi \text{TA})^{0.5}]}]$ , as described in Laurance and Yensen (1991), proximity index (PROX) consisting of the sum of all island areas divided by the squared sum of edge-to-edge distances from the island to all islands within a 500-m buffer (McGarigal et al., 2012), island maximum elevation (m; ELEV) and shortest Euclidian distance of the sampled island to (i) mainland (m; DIST.MAIN), (ii) the largest island (Island 1) (m; DIST.LARGE) and (iii) nearest island regardless of size (m; DIST.NEAR). To account for differences of within-island habitat diversity, we obtained the number of habitat types present in each sampled island (HAB.RICH), including coniferous forest, broad-leaved forests, coniferous-broad-leaf forests, bamboo groves, shrubs, grass and farmlands. All variables were obtained from Si et al. (2014), except habitat richness, obtained from Wang et al. (2010) and proximity index which was extracted from georeferenced shapefiles

from the study area ArcMap 10.1 (ESRI, 2012) (for a detailed description of each variable see Table S2).

### Data analysis

We summed the number of bat passes obtained for each sampling site during the three sampling nights and totalled these numbers within islands where more than one detector was deployed. To assess the adequacy of bat sampling in each island, we used a sample coverage estimator (*sensu* Chao et al., 2014), which estimates the proportion of the total number of bat passes in an assemblage that belongs to the sonotype represented in the sample. Our sample estimates were adequate, averaging  $0.998 \pm 0.002$  (Table S1). Sonotype activity (number of bat passes) was considered as a proxy of sonotype abundance (Kunz et al., 2009) and, due to differences in sampling effort between sampled islands, was further standardized by dividing the number of bat passes by the number of detectors deployed in each island. For each island, sonotype assemblage composition was examined using a non-metric multi-dimensional scaling (NMDS) ordinations based on the quantitative Bray-Curtis similarity matrix of sonotype composition using the vegan R package (Oksanen et al., 2013). The first two axes of the NMDS allowed us to preserve the original dissimilarities in the reduced number of dimensions (stress = 0.098). The scores of these two NMDS axes were then used in further analyses (e.g. Benchimol & Peres, 2015). Prior to analysis, we scrutinized the distribution of each response variable, and all variables related to bat activity (i.e., overall bat assemblage, ensemble- and sonotype-level activity) were  $\log_{10}$ -transformed. In addition, to improve model fit, the following environmental variables were also  $\log$ -transformed: AREA, DIST.LARGE, PROX, SHAPE, HABITAT.DIV and ELEVATION (e.g. Frey-Ehrenbold et al., 2013). All the analyses were conducted using R 3.6.1 (R Core Team 2019).

To examine the effects of island variables on assemblage-level bat metrics—sonotype richness, activity ( $\log_{10} x$ ) and assemblage composition (NMDS axes 1 and 2)—we applied generalized linear models (GLMs) using a Gaussian error structure. Severe collinearity between predictor variables can undermine model inference (Dormann et al., 2013). We therefore quantified collinearity through pairwise correlations between all island variables using Pearson correlations. AREA, SHAPE, HABITAT.DIV and ELEVATION were highly correlated ( $r > 0.75$ ). From those four variables, we used individual models with each one and selected the variable included in the model with the lowest Akaike Information Criteria corrected for small sample sizes (AICc) and explaining the highest data variance (sonotype richness, activity [ $\log_{10} x$ ] and composition) using a GLM with a Gaussian error structure

(Burnham & Anderson, 2002). The variable AREA consistently presented the lowest AIC and explained the higher variance (Table S3) and was retained in subsequent analysis. Given that species–area relationships in habitat islands typically follow a power law (Matthews et al., 2016), to account for any potential non-linear relationship, GLMs were additionally fitted both including and excluding the quadratic term of island size. Based on AIC (Burnham & Anderson, 2002), the quadratic term of AREA improved model fitting when considering sonotype richness and the number of forest sonotypes as response variables (Tables S3 and S4). For these two cases, the quadratic term of AREA was retained in subsequent analyses. Moreover, to further improve model fitting in the analysis examining variation in sonotype richness, we removed one clear outlier (*island 4*). In this outlier, the number of sonotypes was relatively low ( $S = 4$ ) in relation to island size (40 ha), likely due to any adverse meteorological conditions during the three nights in which the detectors were deployed. After the removal of *island 4* from the analysis, model fit increased, as given by the difference in the values of AICc (i.e.  $AICc = 9.32$ ;  $AICc = AICc_i - AICc_{\min}$  in which  $i = i$ th model), and variance explained ( $R^2$ ) increased from 0.29 to 0.35.

A candidate model set was further constructed using all additive combinations of the four explanatory variables retained, and models were ranked based on AICc, using the MuMIn R package (Bartoń, 2020). To account for model uncertainty in multi-model inference, model averaging was used to obtain parameter estimates from the most plausible models (i.e.  $0 < \Delta AICc < 2$ ) (Burnham & Anderson, 2002). Prior to analysis, explanatory variables were centred and scaled ( $x = 0$ ,  $\sigma = 1$ ).

We further examined the relationship between bat metrics at the ensemble- and sonotype-level and island variables, using the above-mentioned modelling procedures. At the ensemble level, response variables were the richness and activity of forest and open-space sonotypes, whereas at the sonotype-level the response variable was the activity of the nine sonotypes recorded in at least 20 islands (Table 2).

## Results

We obtained 22 875 five-min recordings from 108 detector-sampling nights. From this, we identified 15 distinct sonotypes, corresponding to eight single-species sonotypes and seven sonotypes with two or more species (Table S5). Eight sonotypes were classified as forest sonotypes and seven as open-space sonotypes (Table 1).

### Overall assemblage responses

Sonotype richness was affected by the quadratic term of island size ( $\beta_{\text{AREA}}^2 = 1.09$ ,  $P = 0.001$ ; Figs. 2A and 3B,

Tables S6 and S7, Fig. S1). Thus, while no area effect was observed for relatively small islands, island area increased sonotype richness at islands larger than  $33.8 \pm 2.1$  ha (Fig. 2A and Table S8). Sonotype activity was higher at islands more isolated from the mainland ( $\beta_{\text{DIST.MAIN}} = 0.18$ ,  $P = 0.014$ , Fig. 3E). Regardless of island size, some islands overlapped in terms of bat assemblage composition (Fig. 2C). In fact, as also noted for sonotype activity, when considering the first axis of the NMDS, assemblage composition was affected by the degree of isolation from the mainland ( $\beta_{\text{DIST.MAIN}} = -0.10$ ,  $P = 0.011$ , Fig. 3A). The second axis of the NMDS, however, was not predicted by any of the variables considered (Tables S6 and S7).

### Ensemble-specific responses

Open-space sonotypes accounted for 96% of the bat activity recorded, whereas forest sonotypes only accounted for the remaining 4%. Overall, islands harbouring a higher number of sonotypes also supported a higher number of forest sonotypes (Fig. 3). Across the whole range of island areas, richness of forest sonotypes increased with island area ( $\beta_{\text{AREA}} = 0.19$ ,  $P = 0.016$ ;  $\beta_{\text{AREA}}^2 = 0.21$ ,  $P = 0.033$ ; Fig. 3C), but richness of open-space sonotypes did not (Fig. 3D). On the other hand, the activity of forest sonotypes was not affected by any of the variables considered (Fig. 3F), whereas the activity of open-space sonotypes increased in more isolated islands ( $\beta_{\text{DIST.MAIN}} = 0.19$ ,  $P = 0.016$ ; Fig. 3G, Tables S9 and S10).

### Sonotype-specific responses

The most widespread and abundant sonotype was *Nyct.avi*, detected in all islands and accounting for 52% of the total bat passes (28 587 bat passes). Other highly abundant sonotypes were the open-space *Mini.Vesp.* (13 676 bat passes; 25%) and *Vesp.II35* sonotypes (7118 bat passes; 13%), recorded at 35 and 28 islands, respectively. The least detected sonotype was the open-space *Emb.Mol*, with only six bat-passes (0.01%) recorded across three islands. Of the nine sonotypes recorded at more than 20 islands (seven open-space and two forest sonotypes), the most important predictors were distance to the mainland (for *Nyct.avi* and *Vesp.II40*) or distance to largest island (for *Mini.Vesp.*), which both increased sonotype activity (Table 2). Other than for the open-space sonotype *Vesp.I*, island area did not affect bat activity at the sonotype level (Fig. 4).

## Discussion

The rapid expansion of hydropower development across tropical and sub-tropical regions is increasingly creating

**Table 1.** List of potential species and associated sonotypes expected to occur within the biogeographical area that includes the region of Thousand Island Lake.

Sonotype name	Abbreviation	Potential species	Call type—FMaxE (kHz) <sup>3</sup>	Ensemble	No. of bat passes	No. of occupied islands
Murinae/Vespertilionidae	Muri.Vesp.	<i>Murina leucogaster</i> <sup>1</sup> , <i>Harpiocephalus harpia</i>	FM (>50)	Forest	1131 (2.07%)	35
Hipposideridae I	Hippo.I	<i>Hipposideros armiger</i>	CF-FM (60–70)	Forest	444 (0.81%)	22
Rhinolophus I	Rhino.I	<i>Rhinolophus pearsonii</i> , <i>R. macrotis</i>	CF-FM-CF (60–70)	Forest	347 (0.64%)	4
Rhinolophus luctus	Rhino.luc	<i>Rhinolophus luctus</i>	CF-FM-CF (30–40)	Forest	340 (0.62%)	9
Myotis	Myotis	<i>Myotis altarium</i> <sup>1</sup> , <i>M. chinensis</i> , <i>M. fimbriatus</i> , <i>M. laniger</i> , <i>M. pilosus</i>	FM (40–60)	Forest	23 (0.04%)	7
la io	la.io	<i>la io</i> <sup>2</sup>	FM (20–30)	Forest	16 (0.03%)	11
Rhinolophus II	Rhino.II	<i>Rhinolophus affinis</i> , <i>R. ferrumequinum</i> , <i>R. sinicus</i>	CF-FM-CF (82)	Forest	14 (0.03%)	3
Scotomanes ornatus	Scoto.orn	<i>Scotomanes ornatus</i>	FM (30–40)	Forest	14 (0.03%)	7
Nyctalus aviator	Nyct.avi	<i>Nyctalus aviator</i> <sup>2</sup>	QCF (20–25)	Open	28 587 (52.35%)	36
Miniopteridae/ Vespertilionidae	Mini.Vesp.	<i>Miniopterus fuliginosus</i> , <i>Pipistrellus abramus</i>	FM-QCF (45–55)	Open	13 676 (25.04%)	35
Vespertilionidae II 35	Vesp.II35	<i>Hypsugo alaschanicus</i> <sup>1</sup>	FM-QCF (30–40)	Open	7118 (13.04%)	28
Vespertilionidae II 40	Vesp.II40	<i>Hypsugo pulveratus</i>	FM-QCF (40–45)	Open	2189 (4.01%)	31
Vespertilionidae I	Vesp.I	<i>Nyctalus plancyi</i> , <i>Eptesicus pachyomus</i> , <i>Vespertilio sinensis</i> <sup>1</sup>	QCF (25–30)	Open	511 (0.84%)	21
Tadarida	Tadarida	<i>Tadarida latouchei</i> <sup>1</sup>	QCF (10–15)	Open	190 (0.35%)	30
Embalonuridae/Molossidae	Emb.Mol	<i>Chaerephon plicatus</i> <sup>1</sup> , <i>Taphozous melanopogon</i> <sup>1</sup>	QCF (30–35)	Open	6 (0.01%)	3

For sonograms, sonogram description and bat species known to China with similar echolocation characteristics of the different sonotypes recorded at the TIL (see Data S1).

<sup>1</sup>This species was not previously recorded in Zhejiang Province but recorded in China. The occurrence of this species therefore needs to be validated with capture data.

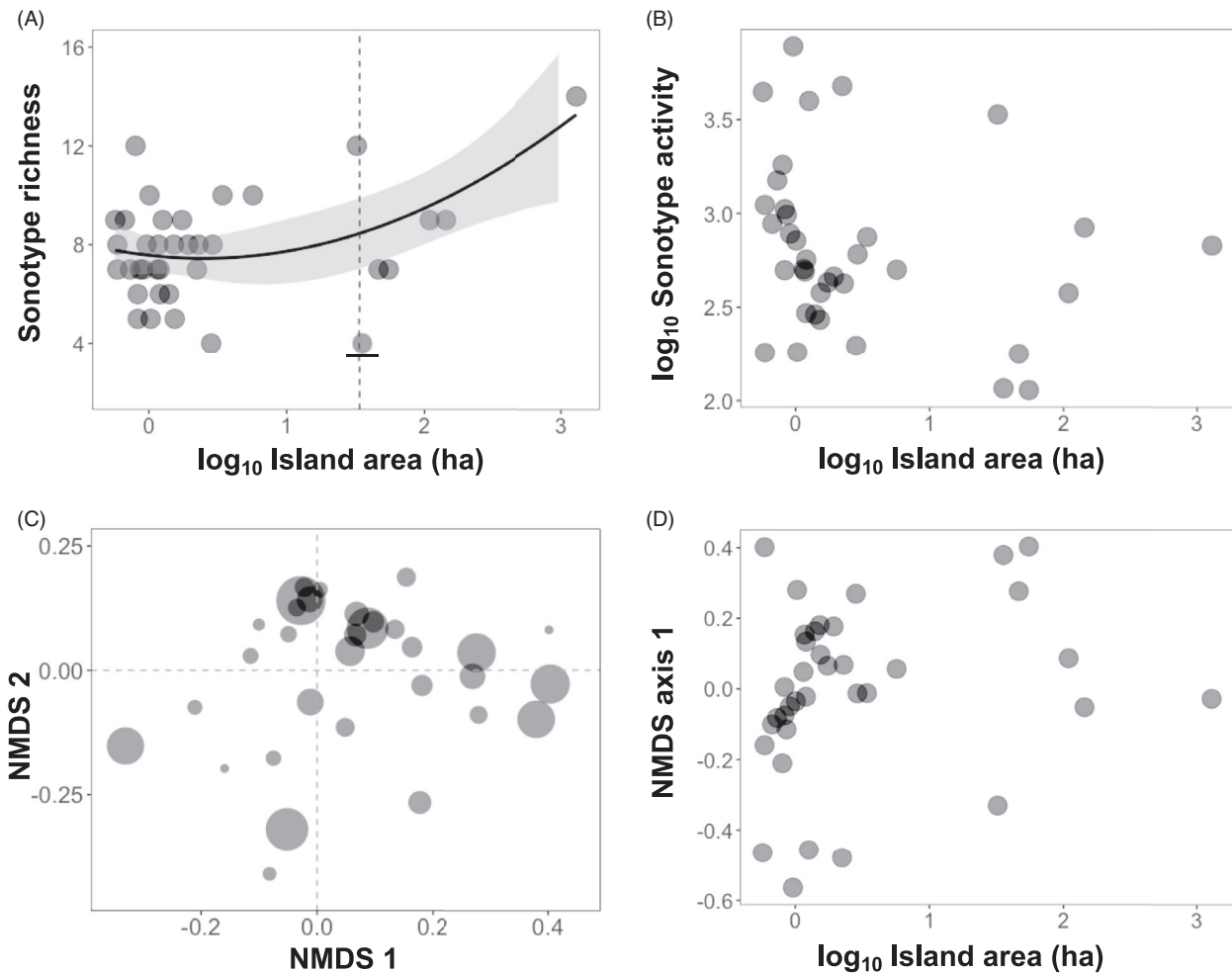
<sup>2</sup>This species was not previously recorded at Chun'an County but recorded in Zhejiang Province. The occurrence of this species therefore needs to be validated with capture data.

<sup>3</sup>Call type abbreviations: FMaxE = frequency of maximum energy; FM = frequency modulated; CF = constant frequency; QCF = quasi-constant Frequency.

highly fragmented archipelagos of land-bridge forest islands, leading to local extinctions and drastic changes in species assemblages (Benchimol & Peres, 2015; Gibson et al., 2013; Jones et al., 2016). In this context, our study is the first to demonstrate how aerial insectivorous bats in East Asia are affected by dam-induced forest fragmentation. We found that bat persistence increased with island area, except for relatively small islands (<34 ha), which was perhaps due to the effect of habitat stochasticity (Barrett et al., 2003; Wang et al., 2015). In addition, as only forest sonotype richness was area sensitive, our results demonstrate that local bat sonotype extinction in TIL is a non-random process. Conversely, open-space sonotype activity increased with island isolation from the mainland.

## Island area effects

As expected according to the Theory of Island Biogeography (MacArthur & Wilson, 1967), bat sonotype richness increased with island size. Our findings are consistent with the overall negative response of terrestrial species to forest fragmentation in man-made reservoirs (Jones et al., 2016), including bats in Neotropical land-bridge islands (Cosson et al., 1999; Estrada-Villegas et al., 2010; Farneda et al., 2020; Meyer & Kalko, 2008a). Moreover, as suggested by the non-linear relationship between island area and sonotype richness, island area effects were only perceived for islands >34 ha in the area (Fig. 2A). This could be due to the 'small island effect' (SIE) (Barrett et al., 2003; Wang et al., 2015), according to which, below the

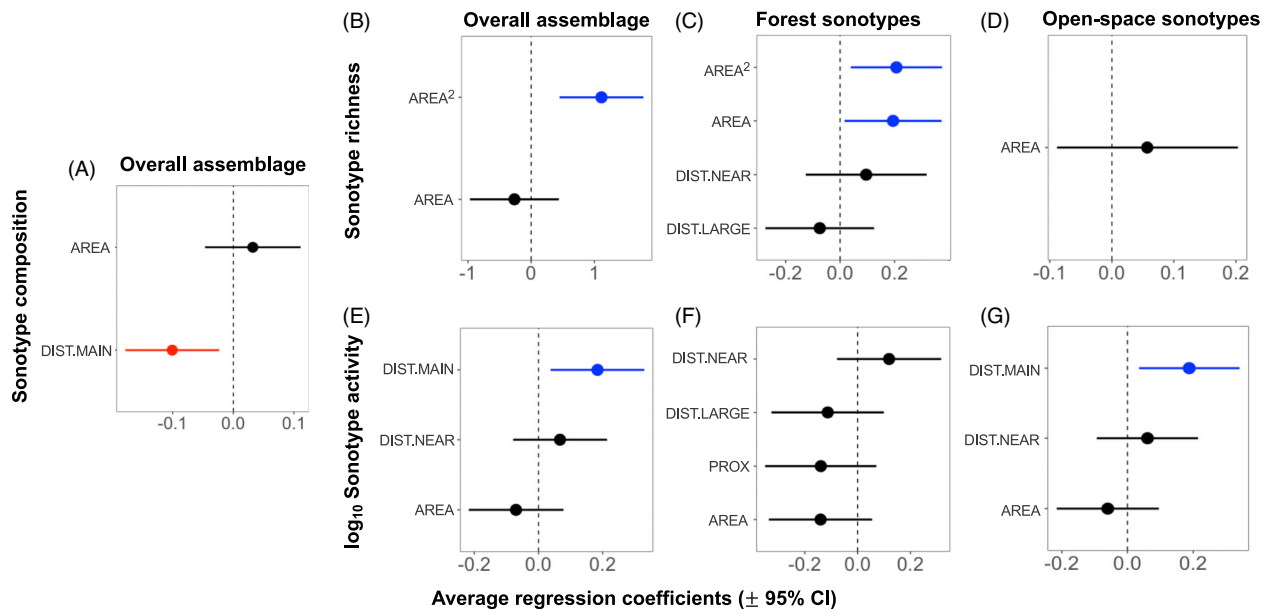


**Figure 2.** Relationships between sonotype (A) richness and (B) activity ( $\log_{10} x$ ) and island area ( $\log_{10} x$ ); (C) non-metric multi-dimensional scaling (NMDS) ordination plot; (D) relationship between sonotype composition (NMDS axis 1) and island area ( $\log_{10} x$ ). In (A), the solid black line is the model adjusted, and the shaded area represents the 95% confidence interval. Also in (A), sonotype richness was fitted including the quadratic term of island area, the underlined dot represents an outlier (island B4) not included in the model, and the vertical dashed line indicates the island size threshold (33.8 ha) above which island area has a significant positive effect on sonotype richness. In (C), circles are sized proportionally to island size ( $\log_{10} x$ ).

34 ha threshold, sonotype richness would be associated with a range of intrinsic and extrinsic factors, such as higher exposure to environmental damage from weather or more pronounced habitat stochasticity. Although we did not test for the SIE in this study, this phenomenon would help to explain why sonotype richness was unaffected by area in islands smaller than 34 ha in size. Indeed, the SIE has been suggested for Neotropical insectivorous bats inhabiting land-bridge islands (Estrada-Villegas et al., 2010) and, within TIL, observed for mid-large mammals (Chen et al., 2019), amphibians (Wang et al., 2018) and snakes (Wang et al., 2015), but not for birds (Wang et al., 2012).

When bats were considered at the ensemble level, only forest sonotype richness was affected by island area across

the whole range in island size (0.6–1289 ha). Overall, bat responses to fragmentation have been associated with their echolocation call structure, vertical stratification and wing attributes such as the aspect ratio (wing length to width) and loading (body mass per wing area) (Farneda et al., 2015; Núñez et al., 2019), which further affect bat mobility (Bader et al., 2015). Forest bats, largely characterized by broad wings with a large surface that allows for greater manoeuvrability in highly cluttered environments (Audet, 1990; Jones & Rayner, 1989; Kalko et al., 1998), are thus likely to benefit from the higher habitat structural complexity associated with the larger TIL fragments. Likewise, forest-associated Neotropical insectivorous (Núñez et al., 2019; Struebig et al., 2008 but see Estrada-Villegas et al., 2010) and animalivorous bats (Cisneros



**Figure 3.** Estimates of averaged models and their 95% confidence intervals for predictors of (A) sonotype composition (denoted by the NMDS axis 1), (B) overall sonotype richness and number of (C) forest and (D) open-space sonotypes and (E) overall sonotype activity, and activity of (F) forest and (G) open-space sonotypes. Predictors include island size (AREA), distances to the mainland (DIST.MAIN), to nearest island (DIST.NEAR) and to largest island (DIST.LARGE) and the proximity index (PROX). Statistically significant positive and negative coefficients are shown in blue and red colours, respectively.

et al., 2015) were also more vulnerable to habitat fragmentation. This was also observed for other vertebrate groups including birds (Bueno et al., 2018) and small mammals (Palmeirim et al., 2018). The higher structural forest complexity found at larger islands potentially provides more roosting and foraging opportunities, allowing a higher number of forest bat sonotypes to persist. Conversely, open-space bat sonotypes tend to concentrate their activity in open habitats, such as the lake surface (Torrent et al., 2018) and forest clearings (Núñez et al., 2019), likely explaining the absence of any species–area relationship for this ensemble.

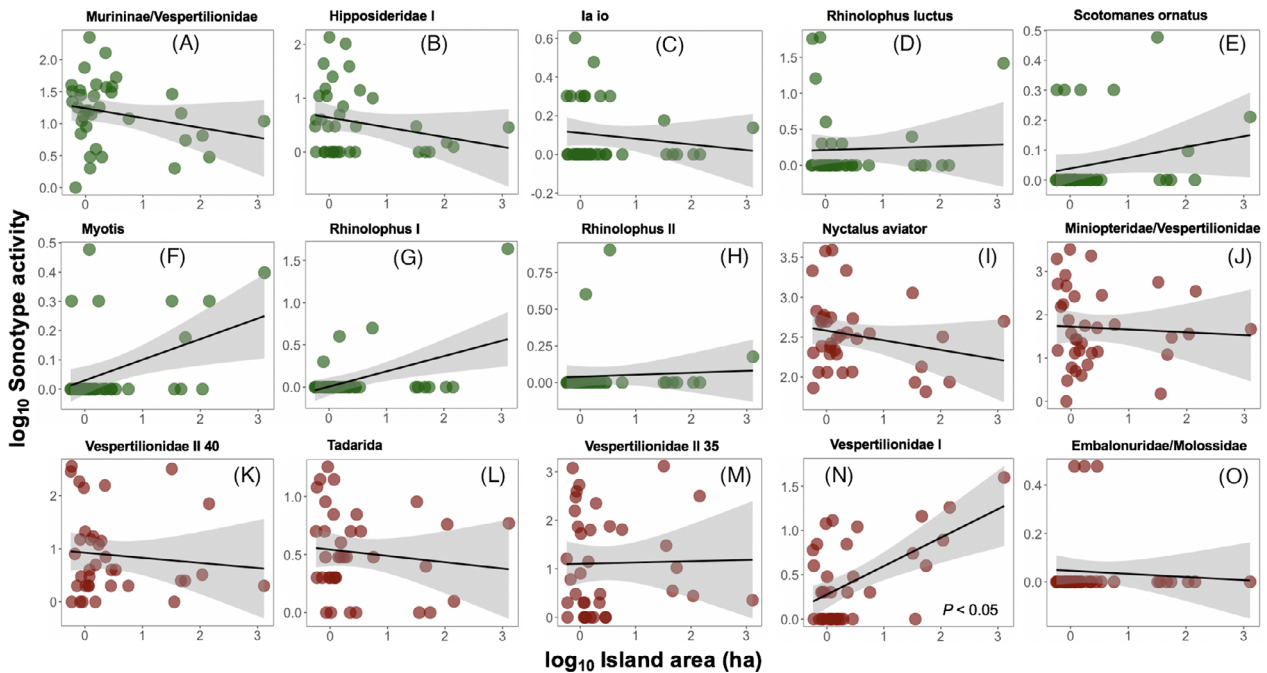
At the sonotype level, only the activity of one open-space sonotype increased with island size (Vesp.I). The higher abundance of the Vesp.I sonotype in larger islands is likely influenced by tree-roosting bat species such as *Nyctalus plancyi*, which probably benefit from the higher availability of mature trees found in larger islands (Zhu, 2008). This contrasts with other studies which found that canopy-feeding species are less sensitive to habitat fragmentation than forest specialists (Núñez et al., 2019; Rocha et al., 2018).

**Island isolation effects**

According to the central tenets of the Theory of Island Biogeography, emigration rates are lower at more isolated

islands, contributing to the typically reduced number of species therein (MacArthur & Wilson, 1967). In this study, however, bat sonotype richness was unaffected by island isolation. That might be a consequence of the close proximity between islands in TIL (mean ± SD: 41.5 ± 22.2 m) and bat mobility, for those species able to cross the aquatic matrix and thus move between islands (e.g. Albrecht et al., 2007). Although our results suggest that island isolation does not pose constraints to bat persistence across TIL, the overall bat activity increased in islands farther from the mainland due to the increase in activity of open-space sonotypes. Indeed, these bats correspond to more vagile species characterized by small-surfaced, narrow wings which allow them to fly faster and cover longer distances between roosts and foraging sites (Bader et al., 2015; Norberg & Rayner, 1987). Contrary to forest bats (Pons & Cosson, 2002), open-space sonotypes appear to favour crossing the open-water matrix to reach more isolated islands (Bader et al., 2015; Meyer & Kalko, 2008b). This might allow open-space bats to take advantage of the potentially higher availability of arthropods in forest island edges (Fukui et al., 2006; Magura et al., 2001; Marques et al., 2016; Tchoumbou et al., 2020) and/or on the water surface (Torrent et al., 2018). Likewise, in Neotropical land-bridge islands, open-space bats were also less affected by isolation than their forest-associated counterparts (Estrada-Villegas et al., 2010; Meyer & Kalko,





**Figure 4.** Relationships between individual sonotype activity ( $\log_{10} x$ ) and island area ( $\log_{10} x$ ). Data are shown for each of the sonotypes recorded: (A) Murininae/Vespertilionidae, (B) Hipposideridae, (C) *Ia io*, (D) *Rhinolophus luctus*, (E) *Scotomanes ornatus*, (F) *Myotis*, (G) *Rhinolophus I*, (H) *Rhinolophus II*, (I) *Nyctalus aviator*, (J) *Miniopteridae/Vespertilionidae*, (K) *Vespertilionidae II 40*, (L) *Tadarida*, (M) *Vespertilionidae II 35*, (N) *Vespertilionidae I*, (O) *Emballonuridae/Molossidae* (see Table 1 for sonotype abbreviations). Lines are the model adjusted for all relationships, and shaded areas represent the 95% confidence interval. For the nine sonotypes recorded in more than 20 islands, the  $P$  value of any significant relationship between the sonotype activity and island area is indicated in the plot.

2008a). These results were further reinforced at the sonotype level, according to which three of the six open-space sonotypes considered, showed increased activity at islands more isolated either from the mainland (*Nyct.avi* and *Vesp.II40*) or larger islands (*Mini.Vesp.*).

In our dataset, open-space bat sonotypes accounted for 46.6% of the sonotypes and 95.6% of the bat passes recorded, therefore clearly dominating bat assemblages in TIL. Although bat responses to habitat change are related to their mobility (Bader et al., 2015), it is possible that some open-space sonotypes have occasionally been recorded even if flying at high altitudes above the detector, contributing to the particularly high activity observed for this ensemble. For instance, *Nyct.avi*, the most often recorded sonotype (52.35% of the bat passes), is an open-space forager that feeds over the forest canopy. Likewise, given the tendency of open-space insectivorous bats to forage over water (Torrent et al., 2018), bats foraging in the periphery of our sampling sites might have influenced the number of species detected in some islands—particularly the ones of smaller size—thus contributing to the eventual SIE. Moreover, bat distribution and space use can be affected by other factors like vegetation composition and roost availability (Frey-Ehrenbold et al., 2013; Rocha, López-Baucells, et al., 2017), which were not

assessed in the present study. Finally, the acoustic surveys carried out spanned a short amount of time (ca. 1 month). As bat activity may change substantially with the season and across years (Ferreira et al., 2017; Rocha, Ovaskainen, et al., 2017), our research does not capture any temporal variability of the response of bats to habitat loss and fragmentation.

### Conservation implications

Hydropower-induced fragmentation is an emergent threat to forest biodiversity across the tropics and sub-tropics (Gibson et al., 2017; Jones et al., 2016). To maintain complete bat assemblages across insular-fragmented landscapes in East Asia, including area-sensitive bat species, we recommend preserving large forest fragments (e.g. >1000 ha). In TIL, particularly given the limited suitability of the nearby mainland habitats, the largest island available (*island 1*: 1289 ha) played a major role in supporting such complete or near complete bat assemblages. Indeed, this island harboured all but one (open-space) of the 15 bat sonotypes recorded. Notwithstanding, bat sonotype richness in islands below 34 ha in size was unaffected by area, highlighting their additional conservation value as they harbour a variable (but substantial) number

**Table 2.** Averaged generalized linear models explaining individual sonotype activity ( $\log_{10} X$ ), according to island size ( $\log_{10} X$ ; AREA), distances to mainland (DIST.MAIN), to nearest island (DIST.NEAR) and to largest island ( $\log_{10} X$ ; DIST.LARGE) and the proximity index ( $\log_{10} X$ ; PROX) (see Table S2 for a detailed description of each variable).

Sonotype	Model parameters	Estimate	Std. error	Adjusted SE	z value	P value
Forest sonotypes						
Murininae/Vespertilionidae	(Intercept)	1.170	0.083	0.086	13.584	<0.0001
	DIST.MAIN	0.141	0.087	0.090	1.562	0.118
	DIST.NEAR	0.151	0.087	0.090	1.685	0.092
	DIST.LARGE	0.121	0.091	0.094	1.283	0.199
	PROX	-0.125	0.091	0.094	1.327	0.185
	AREA	-0.123	0.084	0.088	1.399	0.162
Hipposideridae I	(Intercept)	0.557	0.105	0.108	5.139	<0.0001
	AREA	-0.148	0.105	0.109	1.364	0.172
	PROX	-0.085	0.107	0.111	0.770	0.441
	DIST.NEAR	0.082	0.107	0.111	0.738	0.460
	DIST.MAIN	0.065	0.107	0.111	0.586	0.558
Open-space sonotypes						
Nyctalus aviator	(Intercept)	2.526	0.070	0.073	34.695	<0.0001
	DIST.MAIN	0.177	0.072	0.075	2.370	<b>0.018</b>
	AREA	-0.063	0.073	0.076	0.827	0.408
Miniopteridae/Vespertilionidae	(Intercept)	1.695	0.141	0.146	11.583	<0.0001
	DIST.LARGE	0.306	0.153	0.159	1.928	<b>0.054</b>
	DIST.MAIN	0.169	0.151	0.157	1.072	0.284
	PROX	-0.130	0.165	0.171	0.762	0.446
Vespertilionidae II 40	(Intercept)	0.881	0.118	0.122	7.215	<0.0001
	DIST.MAIN	0.312	0.130	0.134	2.326	<b>0.020</b>
	DIST.LARGE	0.228	0.125	0.130	1.751	0.080
Tadarida	(Intercept)	0.517	0.060	0.062	8.283	<0.0001
	DIST.LARGE	-0.107	0.068	0.070	1.533	0.125
	PROX	-0.091	0.069	0.071	1.284	0.199
	DIST.MAIN	-0.048	0.062	0.064	0.753	0.451
Vespertilionidae II 35	(Intercept)	1.114	0.169	0.175	6.374	<0.0001
	DIST.NEAR	0.299	0.175	0.182	1.646	0.100
	AREA	0.154	0.184	0.191	0.805	0.421
	DIST.LARGE	0.168	0.173	0.179	0.935	0.350
	PROX	-0.166	0.173	0.180	0.924	0.355
Vespertilionidae I	(Intercept)	0.426	0.065	0.067	6.314	<0.0001
	AREA	0.266	0.067	0.069	3.850	<b>0.0001</b>
	DIST.MAIN	0.065	0.067	0.070	0.923	0.356

For each model parameter, we indicate their estimate, standard and adjusted errors and z and P values. Statistically significant P values are highlighted in bold.

of species. Our results further emphasize that species classification according to their habitat affinity could efficiently distinguish species exhibiting different patterns of persistence across the insular landscape. As such, while bat species are increasingly extinct from smaller islands, those islands tend to be mostly occupied by open-space foragers whose activity patterns increase with increasing isolation. These findings can inform guidelines aiming to minimize bat species extinction associated with hydro-power development. This includes the appropriate site selection for dam construction, avoiding the flooding of large forest areas and the creation of numerous habitat islands, from which forest bat sonotypes are primarily

extinct. Moreover, acoustic sampling methods, such as the one presented here, can aid in assessing the effects of habitat loss and insularization and thus provide key information for evidence-based policies aimed at halting the ongoing wave of dam-induced biodiversity loss across the tropics and sub-tropics.

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### Data Availability Statement

Data on bat assemblages from TIL will be made available from the Dryad Digital Repository. The R code used to run the analysis of this study will be available on request.

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## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Sampling effort allocated to surveyed aerial insectivorous bat assemblages in Thousand Island Lake, China.

**Table S2.** Description of island variables used to explain bat sonotype richness, activity and composition at Thousand Island Lake, China.

**Table S3.** Generalized Linear Models (GLMs) relating assemblage-level sonotype richness, activity ( $\log_{10} x$ ) and composition (axes 1 and 2 of the NMDS ordination analysis) to each of the correlated spatial and habitat variables: island size (AREA) including and excluding the quadratic term, shape index (SHAPE), habitat richness (HAB.RICH) and elevation (ELEV) across 36 islands in Thousand Island Lake, China.

**Table S4.** Generalized Linear Models (GLMs) relating sonotype richness and activity ( $\log_{10} x$ ) of either of the two ensembles, forest and open-space sonotypes, with island size (AREA) in Thousand Island Lake, China.

**Table S5.** Number of bat-passes recorded for each bat sonotype at each of the 36 islands surveyed in Thousand Island Lake, China.

**Table S6.** Alternative Generalized Linear Models (GLMs) explaining bat assemblage sonotype richness, activity ( $\log_{10} x$ ) and composition (axes 1 and 2 of the NMDS ordination analysis) across 36 islands in Thousand Island Lake.

**Table S7.** Average Generalized Linear Models (GLMs) explaining bat assemblage sonotype-species richness,

activity and composition across 36 islands in Thousand Island Lake.

**Table S8.** Piecewise regression analyses used to obtain the threshold from which the sonotype-species-area relationship changes the sign across 36 islands in Thousand Island Lake.

**Table S9.** Alternative Generalized Linear Models (GLMs) explaining bat sonotype richness and activity ( $\log_{10} x$ ) of foraging contrasting guilds, forest and open-space sonotypes, across 36 islands in Thousand Island Lake.

**Table S10.** Average Generalized Linear Models (GLMs) explaining sonotype and richness activity ( $\log_{10} x$ ) of two foraging guilds, forest and open-space sonotypes, across 36 islands in Thousand Island Lake.

**Figure S1.** Heatmap of Thousand Island Lake including surveyed islands colour-coded in a yellow to red gradient denoting to the number of bat sonotypes recorded.

**Data S1.** Sonograms, sonogram description and bat species known to China with similar echolocation characteristics of the different sonotypes recorded at the Thousand Island Lake (TIL).