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TIL20: A review of island biogeography and habitat fragmentation studies on subtropical reservoir islands of Thousand Island Lake, China

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ABSTRACT

Reservoir islands formed by dam construction have the same history, clear boundaries, and large numbers that provide a natural platform for testing theories in ecology and biogeography. In this paper, we review studies of multiple zoological taxa on reservoir islands of a large lake in eastern China (Thousand Island Lake). This lake, created in 1959, has 1 078 artificial land-bridge islands of varying areas and isolation. Our review summarizes the decades-long studies in island biogeography and habitat fragmentation from this island system, grouped into three topics: species richness ("how many species are there"), community structure ("who are they"), and species interaction ("how they interact with each other"). Our findings support the predictions of the Equilibrium Theory of Island Biogeography and extend this theory to predict community structure of island faunas by moving beyond assumptions of species equivalency. In addition, the extensive studies on ecological networks, including mutualistic, antagonistic, and parasitic interactions, reveal the negative impacts of habitat loss on the maintenance of such networks, even as increasing forest edge enhances the robustness of pollination networks. At the end of this review, we proposed several future research directions based on current studies that are simultaneously at the frontier of ecology and biogeography.

Keywords: Biodiversity conservation; Community assembly; Species extinction; Island; Species interaction

INTRODUCTION

The Equilibrium Theory of Island Biogeography (ETIB) proposed by MacArthur and Wilson explicitly examined the species richness on an island through the dynamic processes of species colonization and extinction (MacArthur & Wilson, 1967). ETIB was originally proposed based on oceanic islands, especially on volcanic islands with empty starting environments (Whittaker et al., 2023). In this case, community dynamics at the initial stage are dominated by colonization over extinction until a state of equilibrium is reached (Figure 1A). Beyond predicting species richness on oceanic islands, ETIB has been extended to the studies of habitat fragmentation on "habitat islands" that are not surrounded by the homogeneous matrix of water (Diamond et al., 1976; Matthews et al., 2023). However, the spatiotemporal consequences of habitat fragmentation studies are generally more minor at the ecological scale (i.e., <100 years) than island biogeographical studies on oceanic islands at the evolutionary scale that spans millions of years (and which have had time to equilibrate). ETIB can thus be directly used for habitat fragmentation studies in systems that are formed simultaneously, such that no fragments are ecologically older than others (Watling & Donnelly, 2006; Whittaker et al., 2000).

Habitat fragmentation is the phenomenon of continuous habitats turning into isolated patches, and is considered one of the major threats to biodiversity maintenance in the Anthropocene (Fahrig, 2003; Taubert et al., 2018); but see Fahrig (2017). Given the rapidly increasing trend of habitat fragmentation worldwide, there is a pressing need for scientists to understand the effects of habitat fragmentation on biodiversity maintenance and community assembly (Haddad

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et al., 2015; Wilson et al., 2016). At the local scale, biodiversity usually experiences a quick loss and steadily declines after continuous forests are fragmented, a process termed “species relaxation” (Ferraz et al., 2003; Jones et al., 2016; Si et al., 2014b). In this case, the community dynamic is dominated by local extinction (or species emigration) over colonization (or species immigration) until a new equilibrium is reached and the biological community approaches saturation based on the capacity of the new environment (Figure 1A).

Reservoir islands, formed by dam construction, serve as a powerful model system to directly connect the research fields of island biogeography and habitat fragmentation (Diamond, 2001; Wu et al., 2004). First, the rising water level creates reservoir islands simultaneously, starting at the moment of dam completion (Si et al., 2014b). This identical time-of-origin excludes many confounding factors that plague habitat fragmentation studies in oceanic island systems, such as differences in stages of forest succession, and alternative geological origins (Ewers & Didham, 2006). Second, one doesn’t need to involve evolutionary processes in contemporary systems given the relatively short history (hundreds of years or <100 years), especially for vertebrates that have relatively long lifespans (Si et al., 2017a, 2018). This advantage enables researchers to tease apart the ecological effect from the evolutionary effect and specifically examine which ecological processes determine biodiversity patterns and community assembly (e.g., Ricklefs, 1987). Finally, unlike in metaphorical islands of alternative terrestrial habitat types, water provides a homogenous matrix surrounding the distinct habitat patches. Compared to patches in exclusively terrestrial systems that are easier to reach, human activities are much lower on reservoir islands. As a result, reservoir island systems provide a unique natural experiment for studying island biogeography and habitat fragmentation (Figure 1B).

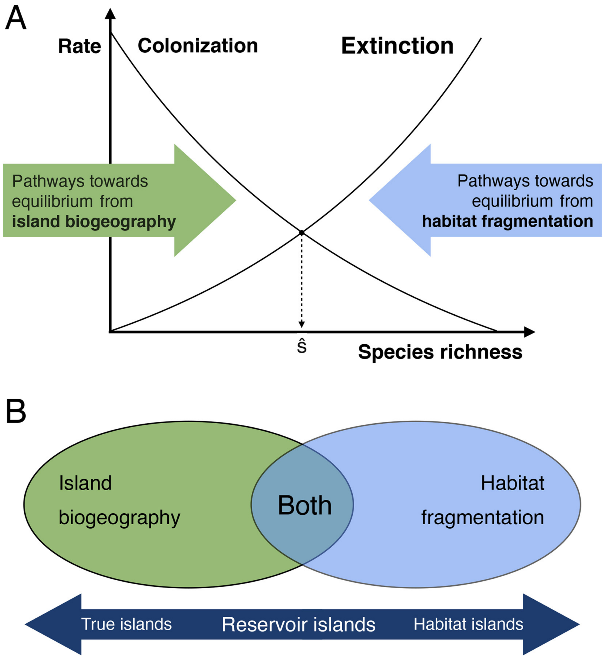


Figure 1 Alternative pathways towards equilibrium of the Theory of Island Biogeography, from island biogeography (community dynamic starting from empty communities) and habitat fragmentation (community dynamic starting from saturated communities) (A). Reservoir islands serve to connect island biogeography and habitat fragmentation (B)

True islands are surrounded by water, and habitat islands are surrounded by inhospitable habitats for a given taxa. Note that Ŝ is the predicted species richness on an island when it reaches a state of equilibrium with equal colonization and extinction rates.

THOUSAND ISLAND LAKE AS AN EXAMPLE OF RESERVOIR ISLAND SYSTEMS

There are 57 985 large dams all over the world, and the pace of dam construction continues to proliferate (Mulligan et al., 2020). Dam construction inundates hilltops in river basins and forms reservoir islands within a newly fragmented landscape (Wu et al., 2004). Pioneering studies in reservoir systems include Lago Guri in Venezuela (Terborgh et al., 2001), Gatun Lake in Panama (Wright, 1985), Chiew Larn Reservoir in Thailand (Gibson et al., 2013), and Balbina Reservoir in Brazil (Palmeirim et al., 2024). Thousand Island Lake (TIL) is one such reservoir island system in China. It has hosted research in island biogeography and habitat fragmentation since 2003 (Wilson et al., 2016), and research outputs from TIL continue to grow rapidly.

Background information about Thousand Island Lake

Thousand Island Lake (Qiandao Lake, or “千岛湖” in Chinese) is located in western Zhejiang Province of eastern China (N29°22′–29°50′, E118°34′–119°15′). The lake was formed in 1959 for hydroelectricity generation by constructing Xin’an Dam (Figure 2). The previous hilltops in this region were quickly inundated by the rising water that became the current land-bridge islands. The area of the lake region is 580 km^2, and there are 1 078 islands with an area >0.25 ha when the lake is at its highest water level (108 m). The region’s forests were clear-cut during the 1950s, and current vegetation on reservoir islands was secondarily regenerated (Liu et al., 2019). After the 1960s, the lake and surrounding habitats were strictly protected as a national forest park and an important water resource for drinking in eastern China. Except for a few islands used for tourism in the north region of the lake, human activities on the islands are minimal. The vegetation on the islands is consistent with natural secondary forest for the region: mainly dominated by *Pinus massoniana*, along with many broad-leaved tree and shrub species (Wang et al., 2011; Wilson et al., 2016). The lake region has a typical subtropical monsoon climate with marked seasonality. The annual precipitation of the region is 1 430 mm, mainly concentrated in rainy season between April and June. The average annual temperature is 17.0°C, and the daily temperature ranges from –7.6°C in January to 41.8°C in July (Si et al., 2017a, 2018).

Introduction of focal zoological taxa on reservoir islands of Thousand Island Lake

Our research team in TIL conducted the earliest bird surveys in 2003 on nine islands and increased to 20 islands two years later. Since 2007, the number of survey islands has increased to 42, encompassing gradients of island area and isolation in the TIL system. Although the total number of islands for bird surveys varied, 36 of these 42 studied islands have consistent bird data up to the present (Si et al., 2017a). Plants have also been surveyed on 41 islands since 2007 (Yu et al., 2012), and 29 islands have vegetation plots that have been surveyed every five years since 2009 (Liu et al., 2019).

In the following subsections, we will introduce the field sampling methods of various zoological taxa (Figure 3) to help

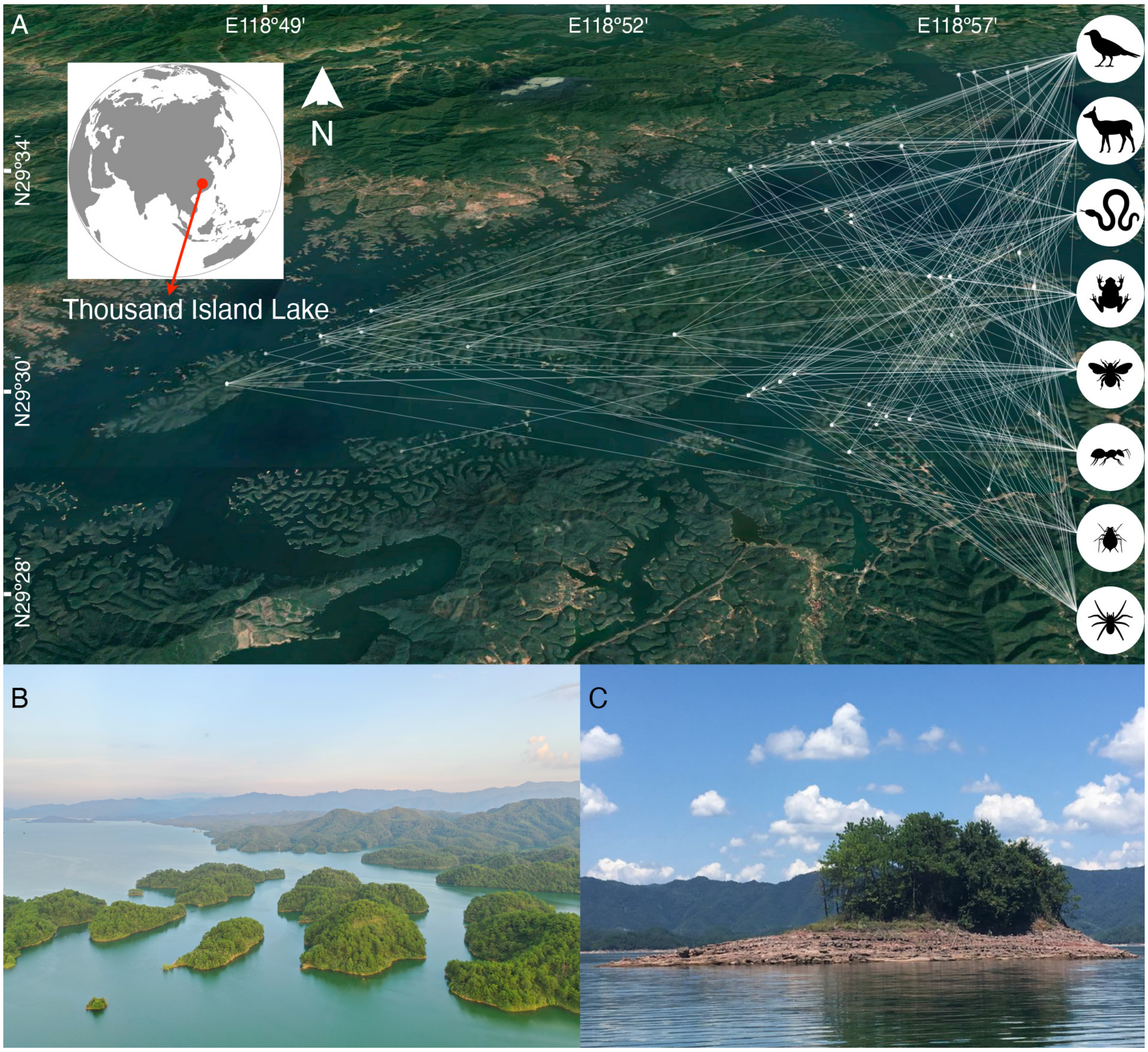


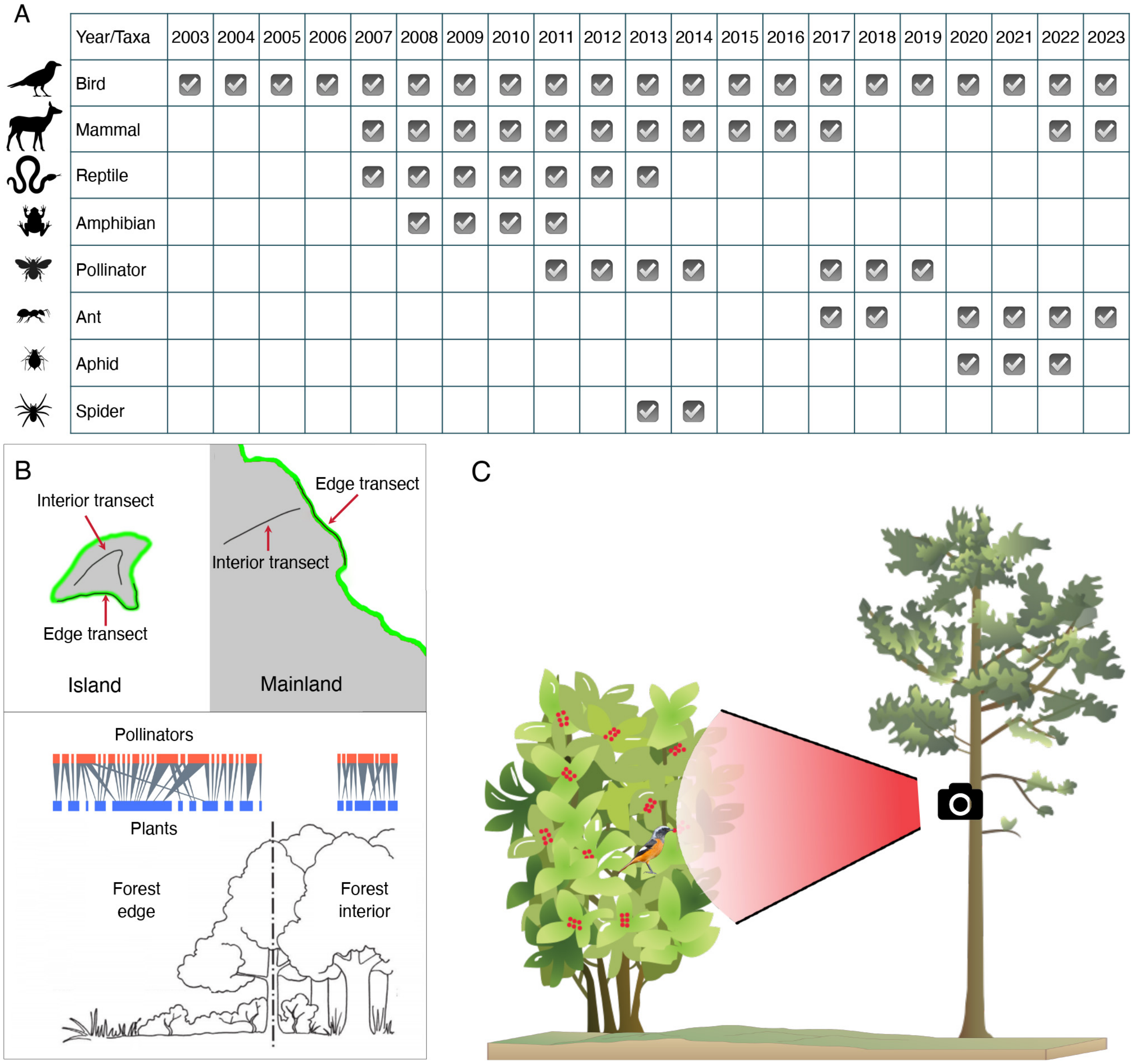
Figure 2 The map of Thousand Island Lake, China

A: Study islands for various zoological taxa (including, from top to bottom, birds, mammals, reptiles, amphibians, pollinators, ants, aphids, and spiders). B: The landscape of the lake. Photo by Wande Li. C: A small island. Photo by Xingfeng Si.

the readers understand the process of biodiversity data collection. However, one can go to Section 3 directly for research results and discussion for our project.

Bird surveys: In this long-term project (20 years from 2003 to 2023), bird surveys follow a standardized transect survey protocol (Bibby et al., 2000). In brief, we surveyed birds in the breeding season (April–June) and winter (November–January) for all 400-m transects (transects on small islands are <400 m due to logistical restrictions). The number of transects on each island was roughly proportional to the $\log_{10}$-transformed island area (Schoereder et al., 2004). Each transect was surveyed 15 times per season from 2007 to 2010 and nine times per season after 2011. During each survey, we recorded all birds seen or heard, as well as the species' typical behaviours (e.g., carrying nesting materials or territorial singing and fighting) and observed nests and juveniles. More details about bird surveys can be found in Si et al. (2018) and Wang et al. (2011). Our project also sampled bird blood for malaria parasites studies (Han et al., 2023), as well as surveyed the fruiting trees with fresh fruits that birds eat, using the emerging technology of arboreal camera trapping (Zhu et al., 2021, 2022).

Mammal surveys: We started mammal surveys in the TIL system in 2007. We set transects of live traps on 37 islands for small non-volant mammals, including most islands used for bird surveys. The small mammal surveys were conducted in spring (March–May), summer (June–August), and/or autumn (September–November) from 2007 to 2008, from 2014 to 2017, and from 2022 to 2023 (Wang et al., 2010; Zeng et al., 2019). All traps were baited with fresh peanuts and operated for four to five consecutive nights with regular checks each morning. We identified each newly captured individual, marked it with a numbered ear tag, and then recorded its sex, reproductive status, and body mass before releasing it. To monitor the medium- to large-sized mammals, we set camera traps without baits on 32 islands in 2014, and increasing to 40 islands in 2016 to match islands with bird surveys. In brief, the number of cameras was proportional to the $\log_{10}$-transformed island area. Cameras were placed over 200 m apart on sites with multiple monitoring stations. We tied the camera to the tree at a height of 50 cm above the ground. The camera faced north or south to avoid the false trigger by sunlight (Si et al., 2014a). Each camera was programmed to take three photos with a 10-second video per trigger, and the time interval



Year/Taxa	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023
Bird	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑
Mammal					☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑					☑	☑
Reptile					☑	☑	☑	☑	☑	☑	☑										
Amphibian						☑	☑	☑	☑												
Pollinator									☑	☑	☑	☑			☑	☑	☑				
Ant															☑	☑		☑	☑	☑	☑
Aphid																		☑	☑	☑	
Spider											☑	☑									

Figure 3 The survey years of each zoological taxon (A), the sampling design for pollination network surveys (B), and the illustration of sampling plant-frugivorous bird interactions using arboreal camera trapping (C) in the long-term research on islands of Thousand Island Lake, China

The sampling transects of pollinator surveys are at the forest edge and interior of the island and the mainland. The green and grey colors represent the edge and interior zones, respectively. Black lines within the green and grey are the areas of the forest edge and interior, respectively. The forest edge usually contains more plant and pollinator species with a more complex network structure than the forest interior (Ren et al., 2023). Two tree silhouettes in C are from Jane Hawkey, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/media-library/); bird image by Wande Li.

between each trigger was 15 seconds. We set all cameras to run 24 hours daily and checked the memory cards and batteries every three months. More details about the mammal survey can be found in (Zeng et al., 2019).

Plant-pollinator interaction surveys: For pollinator surveys, we recorded plant-pollinator interactions on 41 islands and at 16 mainland sites from 2017 to 2019. We established paired transect lines (100 m×4 m), with one along the forest edge and one extending perpendicular from the forest edge to the interior of the island (Figure 3B). The number of transect pairs on each island varied from 1 to 16, which was roughly proportional to the $\log_{10}$-transformed island area. On islands with more than two transect pairs, each pair was separated by ≥500 m. Along each transect, we observed individual flowering branches of shrubs and trees or the whole plant of herbs under 3.5 m height. Due to the larger number of flowering plants at forest edges, we conducted 15-minute surveys for edge transects and 10-minute surveys for interior transects. We sampled once every two weeks from March to July (a total of 20 surveys for each transect over three years). We randomized the sequence in which transects were sampled during the 2-week sampling periods to overcome potential differences in phenology within or between sites. These survey periods represent the peak periods of flowering and insect visiting flowers, ensuring that our survey periods covered almost the entire flowering phenology of all dominant plant species in the TIL region (Ren et al., 2022, 2023).

Plant-frugivore interaction surveys: Since 2019, we have been sampling plant-frugivore interactions on 22 islands and six nearby mainland sites using the recently developed technique of arboreal camera trapping (Figure 3C), which allows us to document plant-frugivore interactions over large spatial and temporal scales effectively (Zhu et al., 2022). In brief, we used line transects following bird survey protocols to search for fleshy-fruited plant individuals along transects twice a month during the primary fruiting season (from July to January). Upon encountering an individual tree with mature fruits, we installed infrared cameras on the branches of nearby trees to monitor frugivorous interactions. Regular checks ensured the continuous operation of the cameras. Retrieval occurred when the fruits were close to dropping from the target individuals. We systematically reviewed over 1 000 000 photos and videos per year taken by the cameras, containing frugivorous species and their foraging behaviors, to acquire plant-frugivore interactions. Interaction frequency between pairwise species (i.e., frugivorous bird or mammal and its plant partner, or vice versa) were estimated from independent interaction events. More details about the surveying methods can be found in Li et al. (2022) and Zhu et al. (2022).

Avian malaria parasite surveys: For avian malaria parasites, we captured birds using mist nets between March and December from 2019 to 2021 on 24 islands and six mainland sites according to the standardized protocol suggested by the National Bird Banding Center of China (http://ifeep.caf.ac.cn/info/1105/2203.htm). We deployed mist nets along the bird survey transects, with the number of mist nets was proportional to the $\log_{10}$-transformed island area. In the field, we measured the morphological traits of birds and collected blood samples from each bird's brachial vein (the blood volume never exceeded 1% of the bird's body mass). Blood was stored in 95% ethanol at –20ºC for further molecular analyses. After sampling, all birds were immediately released at the location of capture. In the lab, we used nested PCR to amplify the 479 bp fragment of the cytochrome-b gene (cyt-b) of haemosporidians (Hellgren et al., 2004). We identified parasite species by comparing them with lineages in the MalAvi database through the BLAST module (Bensch et al., 2009). We measured the relative infection intensity using qPCR (quantitative polymerase chain reaction). In our samples, most birds are sexually monomorphic species. Consequently, we leveraged molecular methods of CHD gene (Chromo Helicase DNA-binding gene) to identify the sex of each bird individual (Fridolfsson & Ellegren, 1999; Griffiths et al., 1998). Our final data consisted of individual and species-level bird traits and environmental factors to disentangle the host-parasite interactions in the TIL. See more details in Han et al. (2023).

Ant and spider surveys: Ants were sampled on 33 islands and 21 mainland sites between April and August, 2017 and 2018, using pitfall traps, Winkler litter extraction, and hand collection (Agosti et al., 2000). We set transects with a maximum length of 200 m on surveying islands and mainland sites. Twenty pitfall traps were placed along each transect, 10 m apart, while ground leaf litter samples were gathered in five random locations along each transect. Each trap had a volume of 180 mL (diameter=62 mm, depth=77 mm) and rain guards to prevent flooding. A solution of ethanol and propylene glycol (1:1, c. 40 mL) was used to preserve the ant specimens caught in the traps. During sampling periods, traps were opened for five consecutive nights and checked every two or three days to avoid overfilling. Leaf litters were sifted through a 10×10-mm wire mesh metal hoop and placed in a Winkler sack with two 4×4-mm grid size mesh bags for two days. Finally, a team of four trained collectors actively searched for ant individuals and colonies on the ground, in the leaf litter, or on low-growing vegetation along the transects. Ants were also passively collected during the study of plant-aphid-ant interaction since 2020 (Zhang et al., 2023) and thermal adaptation of different ant species since 2022 (unpublished data). See more details in (Zhao et al., 2020).

We used pitfalls to collect spiders from April 2013 to September 2014 (Wu et al., 2017) and in 2018 (unpublished data) on 31 islands, respectively. In brief, we set transects with pitfall traps (plastic cups with 200 mL and 75 mm in diameter) to sample the ground-dwelling spiders on study islands. One trap contained three cups positioned 2 m apart at the vertices of an equilateral triangle. The distance between traps was 50 m along the transect. All cups were buried with the rim flushing with the ground surface and had rain covers. Each cup had a 100 mL mixture of ethanol and monoethylene glycol (3:1). The traps were set with closed lips at least one week before operating. Collected spiders were stored in 70% ethanol. See more details in Wu et al. (2017).

Aphid surveys: Aphid surveys were conducted from mid-May to mid-August in 2020 and 2021 on 18 islands using line transects. A team of three trained collectors actively searched for the presence of aphid populations, on the leaves, stems, and roots in shallow soil of all plants along each transect. We photographed each aphid population and recorded the number of individuals in it and collected voucher specimens of all aphid populations for identification based on exterior morphology and DNA barcoding. See more details in Zhang et al. (2023).

BIODIVERSITY RESEARCH ON RESERVOIR ISLANDS OF THOUSAND ISLAND LAKE

Broadly speaking, biodiversity research aims to understand three interrelated topics in a given region: species richness ("how many species are there"), community structure ("who are they"), and species interaction ("how they interact with each other") (e.g., Magurran, 1988). In this section, we review the past and ongoing zoological research on reservoir islands of Thousand Island Lake, China, including taxa of birds, mammals, amphibians, reptiles, and arthropods, following the framework of the three topics (Figure 4).

Species richness

The core model of the Equilibrium Theory of Island Biogeography (ETIB) assumes species are ecologically equivalent, and the chances of a species arriving at or leaving an island depend on the island's area and isolation (MacArthur & Wilson, 1967). Following this, large islands are predicted to have more species because of lower local extinction rates than smaller islands (i.e., area effect), and islands that are close to the mainland, or to other island groups, will have more species because of higher colonization rates in comparison to more remote islands (i.e., distance effect). Together, these processes should result in a low rate of faunal change (temporal turnover rate) on large and remote islands.

Extensive studies have been conducted in oceanic island systems to test the area and distance effects proposed by ETIB, and the patterns generally follow the predictions of ETIB (Losos & Ricklefs, 2010). However, oceanic and reservoir islands have inherent differences in original geological

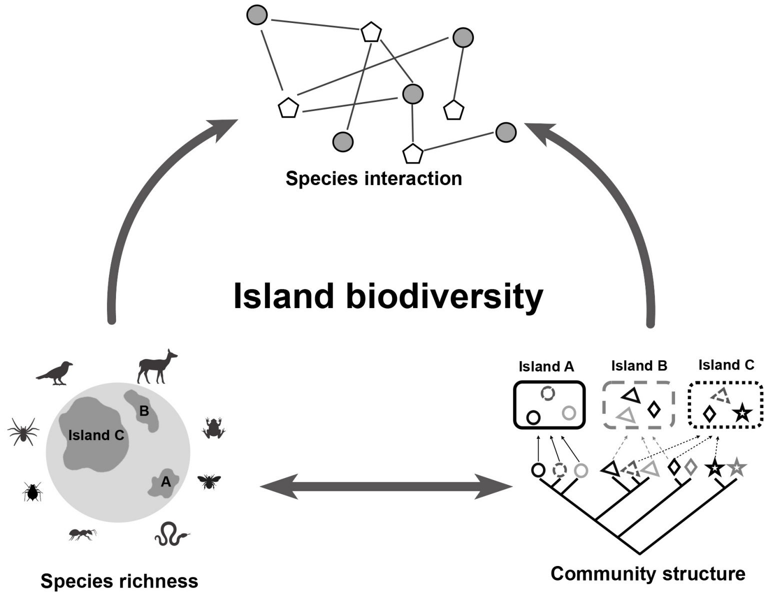


Figure 4 Biodiversity studies on reservoir islands of Thousand Island Lake, China that are grouped into three topics: species richness ("how many species are there"), community structure ("who are they"), and species interaction ("how they interact with each other")

conditions and the spatiotemporal scale (Figure 1A). For example, one may not detect the distance effect in reservoir island systems due to the relatively short distance among reservoir islands. It thus requires us to test whether the predictions of ETIB from oceanic islands are still applicable in reservoir island systems. With the replicated bird survey data across 20 years from TIL, we can examine the area and distance effects proposed by ETIB, and associated target effect (large island increases colonization rates) (Johnson, 1980; Lomolino, 1990) and rescue effect (close islands decreases extinction rates) (Brown & Kodric-Brown, 1977) on reservoir islands with contemporary age from a perspective of habitat fragmentation.

Analyzing breeding bird community data surveyed on reservoir islands in TIL indicated that birds had higher colonization rates and lower extinction rates on larger islands, resulting in more absolute numbers of colonization and observed extinction events—species come in and move out frequently across years on larger islands (i.e., higher pool turnover rates) (Si et al., 2014b). However, species' temporal turnover rates on larger islands (i.e., island turnover rates) were lower because species richness increased even more with area (Si et al., 2014b). This finding verified the area effect and target effect that large islands have more species because more species arrive, and fewer species leave the islands, consistent with the predictions of ETIB on British oceanic islands (Russell et al., 2006), or reservoir islands of Lago Guri in Venezuela (Terborgh et al., 1997). We also found bird assemblages in TIL have a high temporal turnover (30.5% per year) across species (Si et al., 2014b). The high turnover rates on these islands indicate bird species are dynamic across years, while the estimated value of turnover was much higher than for other studies (mostly 1–10% per year) in terrestrial vertebrates and plants (Schoener, 1983). The possible explanation was that bird assemblages in TIL may not reach a state of equilibrium, which would elevate extinction rates, or may be a result of stochastic processes (Boulinier et al., 2001), given the short distances among islands in TIL that birds can frequently leave and re-enter an island (Russell et al., 2006). However, turnover rates, along with colonization and extinction rates, have no clear trends with isolation, which may be due to the relatively short distances among islands. Most bird species have relatively good capacity of dispersal abilities, and the evidence from the famous fragmentation experiment in Brazil (BDPPF) verified that bird species were reasonably common for long-distance movements among fragmented patches (Van Houtan et al., 2007). Although we lack direct evidence of bird species movements among study islands, we expect these movements to weaken distance effects in TIL.

Considering the ecological differences of bird species, we used the same set of bird data collected on reservoir islands of TIL and analyzed bird functional diversity (including species' functional traits) (Tilman, 2001) and phylogenetic diversity (including species' evolutionary histories) (Faith, 1992). Our results showed that large islands still support higher functional and phylogenetic bird diversity than small islands, further supporting the area effect as the patterns found in species richness (Si et al., 2016, 2017a). The positive functional or phylogenetic diversity-area relationships were also observed in the Azores Archipelago (Whittaker et al., 2014), while the *z*-value of the fitted power regression was lower than other systems (0.1 in TIL versus 0.2–0.3 as reviewed by Rosenzweig (1995)). The relatively homogeneous vegetation on islands of TIL with low habitat diversity may prevent spatial turnover of species across habitats. In addition, birds can use nearby islands, which may also reduce the effect of habitat fragmentation, resulting in low *z*-value. In TIL, we found lower functional-phylogenetic diversity of bird communities on remoter islands, indicating a distance effect was detected when measuring biodiversity by including the ecological differences of species traits and evolutionary histories (Si et al., 2017a). This finding suggests that the distance effect may still exist in an island system with a small spatiotemporal scale (i.e., 580 km^2 and 60 years). For example, open water with short distances may reduce the frequency of movements among islands for some understory passerine species who prefer to stay in inner forest habitats of an island due to the fear of predators out of forests (Han et al., 2024; Si et al., 2017a). However, the decrement in detecting distance effects in understory species appears to be compensated for by increasing numbers of non-understory species with relatively high dispersal abilities. Including species' ecological differences in biodiversity studies can thus help us better detect biodiversity patterns and community dynamics at a fine spatiotemporal scale.

In TIL, the area effect was also found in other zoological taxa. By analyzing ant communities with detailed species-level traits and phylogenetic trees, we found large islands support higher ant taxonomic, functional and phylogenetic diversity (Zhao et al., 2020). Beyond the traditional measurement of species richness by counting the number of species on an island, recent studies of animal soundscapes revealed that large islands have higher soundscape diversity (the diversity of sounds emanating from a landscape) than small islands, indicating large islands support more diverse vocal bird species (Han et al., 2024), and more sonotypes of bats (López-Bosch et al., 2022), again consensus with the area effect of ETIB. Area effects are widely reported in fragmented landscapes or island systems (Matthews et al., 2021; Palmeirim et al., 2024; Rosenzweig, 1995), and our results in TIL are no exception. However, area effects may not be detected when the area decreases beyond a threshold, yielding species richness that varies independently with island area. This pattern was defined as "small island effect". In TIL, we didn't detect small island effects in birds (Wang et al., 2012), though it does for snakes (Wang et al., 2015) and mammals (Chen et al., 2019), suggesting the necessity of considering species' dispersal capacity, population density, and/or habitat diversity in examining small island effects. Using the long-term bird dataset of TIL, we further examined the spatiotemporal patterns of area effect, which is the species-time-area relationship (STAR) and tested its generality in island systems using TIL as an example. We found that STAR models at island and transect levels have a negative space-time interaction, suggesting smaller slopes for the species-area relationship over longer time intervals. This finding implies that the STAR patterns can be generalized to island systems (Song et al., 2018).

Among various fragmented systems, the matrix of water in reservoir island systems makes it unique. A fragment can be defined as a habitat suitable for certain taxa surrounded by an inhospitable matrix, or the "habitat-matrix" structure of fragmented landscapes. In TIL and other "true island systems" (Matthews et al., 2016), the water between habitat patches is literally an inhospitable matrix for terrestrial focal taxa, and cannot support their survival. However, water is habitat for fish that live in a pond, and land is the matrix of pond ecosystems. Similarly, the surrounding matrix is the impervious surface of roads or buildings in urban ecosystems (Liu et al., 2023) or disturbed landcovers of farmland in grassland ecosystems (Yan et al., 2022), although species can still use the matrix in these systems, which are not true matrices as the water in island systems (Mendenhall et al., 2014). These fragmented systems follow similar habitat-matrix structures, and our findings and analytical protocols can be applied to other fragmented systems. It should be noted that the various kinds of matrices for different taxa can affect species' movement efficiency and habitat use among fragmented patches that may hinder our capacity to detect the distance effect and its strength (Crooks & Sanjayan, 2006). For example, a rodent species may fail to cross a 100-m length of water between two forested patches, but could cross it if the matrix is road or farmland that can be used. Although these fragmented systems have similar habitat-matrix structures, one should carefully consider the effect of matrix types among patches when explaining biodiversity patterns in different fragmented landscapes because matrix types are closely related to species' movement and dispersal (Ricketts, 2001) and many species can use these inhabitable matrices following a gradient of habitat use that may alter the strength of both area and distance effects versus true island systems (Frishkoff et al., 2019).

Community structure

In addition to addressing how many species are on an island, another aspect of biodiversity studies focuses on species identity, i.e., "what is the structure of a community?" (e.g., Si et al., 2017a). Suppose two islands have the same species richness but are all different species. Due to their distinct identities (in terms of traits and evolutionary histories), these two groups of species may offer unique (or complementary) ecosystem functions. Compositional differences cannot be detected by merely focusing on species richness on islands. Instead, examining how species vary among islands (i.e., beta diversity), which has been less explored in island biogeographical studies compared to the studies of alpha diversity, could advance our knowledge of the mechanisms underlying community assembly (Patiño et al., 2017). In TIL, we studied beta diversity patterns (or the variations in species composition) of birds, ants, and spiders and their community structures (species similarity in traits and evolutionary histories) across island area and isolation.

Beta diversity measures the variation of species composition among sites (Anderson et al., 2011; Si et al., 2017b). In this project, we measured bird beta diversity among islands using the Sørensen index. We found bird beta diversity increased with the difference in island area, indicating that islands with contrasting area differences have more different bird communities (Si et al., 2015), with similar findings in spiders (Wu et al., 2017) but not in ants (Zhao et al., 2021). Since beta diversity is comprised of two components—species turnover (or species replacement) and nestedness (species loss or gain) (Baselga, 2010)—it is critical to partition beta diversity, as merging these two components can prevent the understanding of ecological processes behind observed patterns (Si et al., 2015, 2017b). Irrespective of biological taxa, species turnover is the dominant component of overall beta diversity in birds, ants, and spiders. This finding is in contrast to the patterns found in insectivorous bats, rodents, and lizards in the Balbina reservoir in Brazil, where they used the Jaccard index to calculate beta diversity and found nestedness dominated the overall beta diversity (Di Ponzio et al., 2023; Palmeirim et al., 2021). The discrepancy may be partially due to the inclusion of the mainland forest sites into the calculation of beta diversity, which will lead to higher nestedness components as most species on islands were a subset of the mainland sites.

Despite the dominance of the turnover component at the taxonomic and phylogenetic dimensions, nestedness becomes more important in explaining the overall beta diversity when considering species traits and migratory status (Chen et al., 2018; Si et al., 2015; Wu et al., 2017; Zhao et al., 2021). These findings suggest that among islands, animal species, at least for winter residential and migratory birds, ants, and spiders, have frequent turnover and are replaced by each other, resulting in species turnover being the dominant component. However, these species with frequent turnover events have similar ecological functions. In other words, the roles of traits are almost unaltered for these taxonomically different species (i.e., the evidence of functional and phylogenetic redundancy) (Si et al., 2016). Thus, we can observe functional nestedness contributed half of the total beta diversity compared with the dominance of turnover (90%) in the taxonomic beta diversity. These studies suggest that different species in fragmented habitats share similar functional roles, indicating that habitat fragmentation may homogenize species functions for birds, ants, and spiders that act in forest ecosystems.

In island biogeography studies, extensive research have examined species richness patterns on islands (Losos & Ricklefs, 2010). However, we are still unclear whether the ETIB can predict community structure on islands by considering species identity (not just predicting how many species on an island, but to predict who are they). By analyzing community structure, one typically integrates null models with traits and phylogenies (i.e., functional and phylogenetic diversity) to test if the observed communities were more functionally (and phylogenetically) similar (i.e., clustered) or dissimilar (i.e., overdispersed) than communities generated randomly from species pools (Cadotte et al., 2019; Triantis et al., 2022; Webb et al., 2002; Zhao et al., 2024). In this project, we extended the ETIB to community measures by moving beyond assumptions of species equivalency by considering species' traits and phylogenies (Si et al., 2017a). By inferring from the standardized effect size (SES) of a composite functional-phylogenetic distance (FPD) indices (Cadotte et al., 2013), we found that island avifauna were more clustered than null communities, with smaller islands tend to possess more clustered communities (Si et al., 2017a). A similar tendency was also found for ants, i.e., communities switched from phylogenetic and functional clustering on smaller islands to overdispersion on larger islands (Zhao et al., 2020). These results indicate the dominant role of environmental filtering in structuring island faunas, especially for small islands with high environmental stress and limited habitat types that favor species with broad diets to survival. In addition, we found a mismatch between the phylogenetic and functional structures of ant communities in that the overall phylogenetic structure tended to be clustered while the functional structure tended to be overdispersed. It provides evidence that the selected traits and phylogenetic information could infer different assembly mechanisms, at least for ants in our study region (Zhao et al., 2020). Although the patterns of community structure on reservoir islands vary with taxa, we proposed a framework of island biological community structure relying on the findings from TIL after considering ecological and evolutionary processes that can be applied to island systems with broader spatiotemporal scales (Si et al., 2022).

Species interaction

Species are not isolated in nature, and instead engage in complex interactions as part of "an entangled bank" (Darwin, 1859). The earlier biodiversity studies from TIL focused more on single taxa and did not consider species interactions across trophic levels or biological groups due to the lack of fundamental distribution information across taxa. Recently, we have explored multiple ecological networks on reservoir islands of TIL, including plant-frugivorous bird networks, plant-invertebrate pollination networks, rodent-oak seed-dispersal networks, bird-malaria parasitic interactions, as well as ant-aphid-plant multi-trophic interactions and mixed-species bird flocks.

Frugivory: Seed dispersal mediated by frugivores, especially by birds, plays a critical role in plant community dynamics and forest regenerations within fragmented landscapes (Cordeiro & Howe, 2003; Fricke & Svenning, 2020). However, it is challenging to record plant-frugivorous bird interactions across a large spatial scale, given the intensive labor costs in the field (Quintero et al., 2022). To address this, we applied the emerging technology of arboreal camera trapping to monitor plant-frugivore interactions on 22 islands and six nearby mainland sites in TIL (Zhu et al., 2022). Our data with high temporal resolutions on frugivorous bird interactions collected by arboreal camera traps revealed that the Silver Pheasant (*Lophura nycthemera*), the largest fruit-eating bird in the TIL system, exhibits arboreal foraging behavior (Zhu et al., 2021). Despite being traditionally considered a ground-dwelling species, our study found their frequent feeding behaviors in trees that were not reported in the literature, with interaction frequency to be highest on islands with intermediate size in TIL (i.e., 10–100 ha) (Li et al., 2023). Meanwhile, we constructed plant-frugivore trophic networks and the spatial metanetwork among frugivore networks, involving three scales of topological analyses: macro-scale (network structure), meso-scale (motif), and micro-scale (individuals' role) as well as network dissimilarity across islands. We analyzed network structures and interaction patterns on reservoir islands and the mainland in TIL. Results showed that the mainland and large islands hold more species and consequently, more unique interactions. In contrast, small islands consisted mainly of interacting generalists. Intriguingly, our research also detected evidence of interaction release, showing the dietary expansion of frugivores, particularly on small islands (Li et al., 2022). Using the high-resolution data, we compared the structure of local networks of an island built by direct records from the camera trapped interactions of the focal island, with that built by integrating indirect records from the camera trapped interactions of the regional network and local species pools. Our results suggest we should cautiously use indirectly derived networks from regional ecological information when examining local network indices (e.g., connectance, nestedness, or modularity). However, indirectly derived networks can be used in comparative studies when analyzing the trends of network indices across environmental gradients (Zhu et al., 2023).

Since frugivores like birds can serve as mobile links and potentially transfer seeds between islands, it is necessary to understand ecological processes associated with plant-frugivore interactions from the metacommunity perspective (Emer et al., 2018). In this project, we found the context-dependency related to habitat fragmentation of plant-frugivore interactions with an invasive plant (*Phytolacca americana*) and suggested that generalist avian frugivores with high seed-dispersal potentials are promoting landscape-level plant invasion (Zhu et al., 2024), emphasizing the need for targeted conservation strategies to mitigate the impacts of invasive species spreads. To better understand the contributions of frugivores on landscape connectivity, further studies can investigate species movement trajectories, such as the radio-tracking surveys for frugivores on land-bridge islands in French Guiana (Henry et al., 2007). Taken together, studying plant-frugivore interactions can help us reveal species persistence and maintain functionality in fragmented habitats.

Future studies integrating network approaches with functional traits across various temporal resolutions can enhance our understanding of the frugivory impact on, for example, the dynamics of seed rain and seedings (González-Varo et al., 2019), as well as other ecosystem functioning (Harvey et al., 2017).

Seed dispersal and predation: Scatter-hoarding rodents play a key role in plant regeneration in various forest ecosystems (Vander Wall, 1990, 2010; Vander Wall & Beck, 2012; Zeng et al., 2019). Such rodents act both as seed dispersers and seed predators of plants, which leads to a dual effect on plant regenerations and, thus, non-monotonic rodent-plant interactions (Zeng et al., 2021). However, it remains challenging to quantify the outcomes of rodent-plant interactions (Bogdziewicz et al., 2020). Several theoretical studies have shown that the non-monotonic interactions depend on the population density of rodents (Wang & DeAngelis, 2012; Yan & Zhang, 2014; Zhang, 2003; Zhang et al., 2015), such that density-dependent non-monotonic models indicated a mutualism at low population density but antagonism at high population density. To test this prediction, we traced seed fates of *Quercus serrata* dispersed by rodents using tagged seeds (Xiao et al., 2006) on 21 islands with different rodent abundance in the TIL (Zeng et al., 2021). We found that the proportion of germinated seeds showed a dome-shaped relationship with rodent abundance. This result indicated that rodent abundance triggered a switch between relative mutualism and predation in a rodent-plant system. Our study highlights the importance of the association between rodent abundance and seedling establishment in predicting the non-monotonicity in rodent-plant interactions.

Seed size is an important functional trait to determine the outcome of rodent-plant interactions (Cao et al., 2016; Dylewski et al., 2020; Fricke et al., 2019; Vander Wall, 2010). Sized-related seed selection by rodents may ultimately affect seed germination and seedling survival (Howe et al., 2006; Maron et al., 2018). As an important mortality factor, the effects of rodent predation may vary across life stages, potentially leading to conflicting outcomes between seed germination and early seedling survival (Pérez-Ramos et al., 2012; Schupp, 1995). We conducted seed-sowing experiments in plots with and without rodent exclosures to assess the impacts of sized-related seed selection by rodents on plant regeneration in TIL (Zeng et al., 2022). Our experiments showed that rodent predation mainly affected successful seed germination, reducing the survival of large-sized seeds but not for the early seedling stage. During the early seedling stage, seedlings developing from large seeds had a higher survival rate. Our study implies that large-size seed predation by rodents in seed germination may be the main factor limiting the regeneration of oak species in TIL. However, the dynamics of rodent-plant interactions are also influenced by physiological traits of the seeds (Li et al., 2024) and the behavioral traits of the rodents (Brehm & Mortelliti, 2022; Brehm et al., 2019). Thus, one should consider the physiological seed traits and the behavioral variations among rodent individuals to better understand the interactions between rodents and plants.

Habitat fragmentation, such as in the TIL system, can affect rodent abundance and seed availability and thus alter the net outcomes of rodent-plant interactions (Morán-López et al., 2015; Zeng et al., 2019). Defaunation is the elimination of animals, particularly large vertebrates from natural communities, mainly resulting from habitat fragmentation (Dirzo et al., 2014; Young et al., 2016). Previous studies indicated that defaunation could also indirectly trigger vital consequences on plant-animal interactions (Galetti et al., 2006, 2015). The loss of large vertebrates would release rodents from top-down controls or resource competition (Terborgh et al., 2001), causing higher seed mortality and lower seed dispersal. However, the indirect effects of habitat fragmentation mediated by defaunation on plant-animal interactions are always overlooked (Kurten, 2013; Zeng et al., 2019). To bridge this gap, we conducted seed dispersal and seed-sowing experiments on 21 islands and used a seed dispersal effectiveness framework to assess the outcomes of rodent seed dispersal (Zeng et al., 2019). We also used camera traps and a defaunation index (Giacomini & Galetti, 2013) to assess the loss of large-bodied mammals on experimental islands. Our study found that island area had positive effects on seed dispersal effectiveness because the degrees of defaunation and rodent competition for acorns were lower on larger islands. Isolation had net negative effects on seed dispersal effectiveness, but these were not routed through defaunation and rodent competition for acorns. Our results highlight that defaunation plays a critical role in mediating the cascading effects of habitat fragmentation on rodent-plant interactions. However, the extent of these cascading effects on rodent-plant interactions may vary with the severity and historical context of the fragmentation. Specifically, rodent-plant interactions in our contemporary reservoir island system (60 years) were mainly shaped by life-history traits that determine the use of resources after habitat fragmentation (Zeng et al., 2019). By contrast, rodent-plant interactions on oceanic islands or in insular systems with highly impervious matrices were more directly affected by fragmentation (Swihart et al., 2003). Consequently, it is necessary to conduct comparable studies across similar systems with varying fragmentation histories and severity to elucidate the impact of fragmentation on conditional mutualisms between plants and rodents.

Pollination: Ecosystem decay due to habitat fragmentation and edge effects can exacerbate insect pollinator decline due to habitat loss (Fortuna & Bascompte, 2006; Grass et al., 2018; Millard et al., 2021; Spiesman & Inouye, 2013). However, in forested ecosystems, open light-filled forest edges support more flowers and pollinators than the dark interior within closed-canopy forests, such that forest edges might be beneficial for pollinators (Ewers & Didham, 2006; Hadley & Betts, 2012; Ibáñez et al., 2014; Morreale et al., 2021). The mismatch in observations is almost certainly because most studies on the effects of habitat fragmentation on plant-pollinator communities have focused on open-habitat systems such as grasslands or croplands where edge effects are probably negative or neutral (Aizen et al., 2012, 2016; Grass et al., 2018).

In our research, we recorded 19486 individual pollinator interactions with plants in ca. 960 hours of flower observations from 2017–2019, constructing networks of associations between 68 flowering plants and 313 pollinators. Specifically, we found that forest edges have beneficial effects on pollinator networks, buffering plant-pollinator interaction networks from cascading secondary extinctions in the face of declining forest areas (Ren et al., 2023). Meanwhile, network nestedness is the key factor to mitigating the secondary extinctions. The plant-pollinator networks showing a low degree of nestedness in fragmented habitats may be related to the change in the position of stable species and interactions in the network (species or interactions with high persistence over space or time) that stable species and interactions deviated from the network core (Evans et al., 2013; McWilliams et al., 2019; Thébault & Fontaine, 2010; Trøjelsgaard & Olesen, 2016). We evaluated the correlation between the position of proximity to the network core and the stability of species and interactions and found that temporally/spatially stable species and interactions deviate from the network core in fragmented habitats, which is an important reason for the decrease in nestedness in plant-pollinator networks (Ren et al., 2022).

Accurate identifications of pollinators have always been a challenge due to the diverse pollinators (Giangrande, 2003) because it is challenging to identify all pollinator specimens to the species level (Mayer et al., 2011). Plant-pollinator networks constructed by mixed species levels and taxonomic categories above the species level (e.g., genus, family, or superfamily) are common, and only a few studies focusing on a single pollinator taxon have identified all species to the species level. The effects of these mixed taxonomic units in analyzing pollination networks have yet to be considered and may be a possible avenue for subsequent analyses of ecological networks.

Parasitism: Though parasitism is a prevalent phenomenon in nature, it was not until recently that host-parasite interactions drew ecologists' attention widely. Parasites comprise approximately 40% of animal species, and almost all animals have been infected by at least one species of parasite (Dobson et al., 2008; Poulin & Morand, 2000). Understanding the diversity and distribution of parasites as well as their interface with hosts and the environment can help clarify the ecological role of parasitism and advance our prediction and management of disease occurrence and public health (Stephens et al., 2016). Since Earth's ecosystems have become increasingly fragmented during the Anthropocene (Haddad et al., 2015), we explored interactions between birds and haemosporidian parasites on land-bridge islands in TIL. By screening more than 1 100 bird individuals spanning 86 species over three years, we identified 156 lineages of parasites, of which 60% are new records (Han et al., 2023). We found that bird individual- and species-level traits jointly shaped the infection probability of parasites, and host susceptibility to parasites showed moderate to low phylogenetic signals depending on the specific genus of the parasite (unpublished data). Though evidence suggested that only overall infection probability differed between fragmented and continuous habitats, the taxonomic and phylogenetic turnover of parasite assemblages were remarkably affected by geographic and environmental factors like distance, temperature, and island area. Our findings emphasized the importance of investigating the host-parasite interactions from multidimensional perspectives and calling up further disease research to integrate community ecology for mechanistic understandings of ecological interactions under infections.

Multitrophic interactions: Species are commonly entangled within myriad interactions across multiple trophic levels; research on multi-tropic interactions spanning diverse interaction types is currently at the forefront of ecological network science (Morrison et al., 2020; Timóteo et al., 2023). Interactions between plants, sap-sucking aphids, and honeydew-collecting ants are common tri-trophic relationships in forest ecosystems, which are essential in ecosystem energy fluxes (Ivens et al., 2016; Way, 1963). From the study of ant-aphid-plant interactions, we have explored the impacts of fragmentation on the network specialization of both antagonistic plant-aphid networks and mutualistic aphid-ant networks. Our findings reveal that cascading trophic interactions may interlink trophic levels, and species in small and isolated fragments could be more specialized and vulnerable to local co-extinction, mainly due to high species turnover among islands (Zhang et al., 2023). From the perspective of multiple trophic interactions, quantifying the underlying mechanisms driving the variation in network structure responding to habitat fragmentation is crucial to exploring the dynamics of ecological community structures under global fragmentation.

Mixed-species flocks: Mixed-species groups are a kind of intraguild mutualism, defined as animal groups of two or more species that move and forage together (Morse, 1970); mixed-species flocks of birds (MSFs) are particularly widespread across different habitats and regions of the world's birds (Goodale et al., 2017). Like all groups, MSFs are thought to enhance foraging efficiency and reduce predation risks (Beauchamp, 2013; Goodale et al., 2015, 2017). However, compared to monospecific groups, there may be particular benefits to MSFs because interspecific competition is generally less intense than intraspecific competition (Martínez et al., 2024). Therefore, species' flocking propensities can increase colonization rates through enhanced foraging efficiency and decrease extinction rates through reduced predation risk and interspecific competition in island systems. To test this prediction, we used a ten-year bird survey dataset collected on islands of TIL and classified bird species based on their propensities to join in monospecific flocks and MSFs (Martínez et al., 2023). Our result showed that species that participate in MSFs have greater colonization and less extinction across a gradient of island area than species that do not participate in MSFs. This result could be due to the fitness benefits of MSFs that the birds accrue on the islands, or could be a result of group movement between islands being less risky (Sieving et al., 2004; Tubelis et al., 2006). The finding indicates that the sociality of animals —their tendencies to group with other individuals, and even with individuals of other species—can be an important functional trait influencing island biogeography patterns.

MSFs can also be an important phenomenon to consider in conservation management and the response to fragmentation (Zou et al., 2018). Several studies have shown that anthropogenic fragmentation can lead to a reduction in mixed-species flocking (Mokross et al., 2014; Rutt et al., 2020). In particular, flocking may collapse in very small fragments if a "nuclear" species —a species critical to the formation or cohesion of MSFs (Goodale & Beauchamp, 2010; Moynihan, 1962) —disappears. To assess the impacts of nuclear species on MSFs at TIL, we conducted a bird survey on 31 study islands with varying areas in the winter of 2017 and the autumn of 2021 (Martínez et al., 2024). In particular, we focused on MSFs led by a highly gregarious nuclear species, Huet's Fulvetta (*Alcippe hueti*), which averages more than 20 individuals per flock. Our results showed that fulvetta-led MSFs only occurred on islands larger than 30 ha, perhaps because smaller islands cannot sustain so many individuals. This result connects the vulnerability of nuclear species in small fragments to the fact that they are often gregarious species (Goodale & Beauchamp, 2010). Therefore, understanding the ecological requirements and habitat preferences of nuclear species can be critical conserving the whole system.

Overall, our studies of MSFs at TIL highlight the importance of including intra- and inter-specific interactions, especially the positive interactions between species (e.g., facilitation), in biodiversity studies to better understand the consequence of habitat fragmentation and the community assembly of island faunas. We advocate exploring the relationships between MSF species richness and the overall bird species diversity across environmental and latitudinal gradients (Schemske et al., 2009), which will provide insights into the role of species in MSFs, as well as the importance of species interactions and the maintenance of species diversity.

FUTURE DIRECTIONS AND CAVEATS

In this review, we summarized the past and current studies in the TIL system grouped into three topics: species richness, community structure, and species interaction. Although we have covered multiple zoological taxa with decades-long research, many questions are still left to be understood in habitat fragmentation and island biogeography we raised several years ago (Wilson et al., 2016). Meanwhile, we also highlighted the caveats we learned from this long-term project that may help the researchers avoid the obstacles we experienced.

Benefiting from the systematic field surveys of many single taxa, the topics of current studies in TIL have largely switch to species interaction and ecological networks. However, with the accumulation of long-term datasets, especially for birds, we can better understand bird community dynamics in this fragmented landscape. We here list several future research directions and caveats based on our project that should be also applied to island biogeography and habitat fragmentation:

(1) Species' movement trajectories among islands. Dispersal (or "movement" in a broader sense) is a key process affecting species persistence in fragmented landscapes and altering meta-population and meta-community dynamics. In our earlier studies, we cannot obtain species' movement trajectories among islands, so we predicted species dispersal abilities from traits (e.g., hand-wing index) or their distributions on islands (e.g., the distance for a remote island we never recorded a bird species may be this species' dispersal threshold in our system). Thus, the indirect information on dispersal abilities hindered our tests of observational patterns. During our long-term field surveys, we accidentally recorded an individual swimming over water or being drowned in the water. These records provided rare direct evidence of species dispersal abilities. However, these records are too limited and insufficient to infer ecological mechanisms for maintaining biodiversity.

It is still challenging to pinpoint the locations of individuals in fine spatial resolutions (meters) for small-sized animals. Emerging technologies of GPS and VHF tags allow us to track the trajectory of an individual, especially for vertebrates. In TIL, we recorded a few rodent individuals that could cross open water over 1 000 m through the same passive integrated transponder (PIT) tag of an individual captured on two islands (unpublished data). In 2021, we tracked six individuals of Eurasian jay (*Garrulus glandarius*) using our integrated equipment consisting of GPS tags, a drone, and a signal receiver with Bluetooth transmission (Jin et al., 2023). Although the field test of our equipment was limited to the lifespan of the GPS tags, our local-scale tracking system can effectively collect precise locations among islands. Given the high equipment costs and the large number of individuals required, large-scale bio-logging studies are still impossible to provide reasonable ecological data in analyzing community dynamics. At least from our project, we can conclude that bird species (e.g., Eurasian jay) tend to fly over the water to neighboring islands rather than to distant islands, while it is also possible that some poor-flying understory species (e.g., Huet's fulvetta) may stay in their habitat rather than fly over the water surface to avoid the risk of predation (Martínez et al., 2024). With the development of wildlife monitoring techniques, we can expect tracking wildlife on a large scale to be more promising.

(2) Long-term ecological monitoring. Monitoring multiple animal assemblages and species interactions continuously can offer a deeper understanding of population, community, and network dynamics (CaraDonna et al., 2021). Short-term studies may not reflect a reliable pattern of, for example, network dynamics, because a network may be constantly shifting, such that no species consistently occupies a core position within it (Miele et al., 2020). At the start of designing field surveys, one should have a rapid biodiversity assessment for the target taxa on the same sites for following comparable analyses if the field labors and logistics are allowed. Through a long-term perspective, we can thus better understand the species' roles in community assembly and the status of species within the network. In this case, we highlight the importance and necessity of having long-term ecological monitoring that can deepen our understanding of the impact of habitat fragmentation on the dynamic patterns of ecological communities and networks (Magurran et al., 2010).

Meanwhile, we advocate for manipulative experiments to accompany observational surveys, so as to tease apart the mechanisms structuring ecological communities. For example, we can manually relocate individual predator species (e.g., snakes) from large islands or the mainland to small islands to test whether forest regeneration is accelerated through trophic cascade effects of food webs (Pires et al., 2023; Terborgh et al., 2001). In TIL, these manipulative experiments are rarely done, and we should use both observational studies and manipulative experiments to explore long-term biodiversity changes and community dynamics.

(3) Disease ecology in fragmented landscapes. Deepening our understanding of host-parasite interactions is paramount for disease management and prevention. However, most disease and epidemiological research fail to consider the fragmented "world" in which hosts and parasites interact, yet instead treating environmental heterogeneity as "noise". Integrating advances in community ecology and biodiversity research may help to reconcile this obstacle. For example, Jousimo et al. (2014) used meta-population theory to demonstrate that habitat fragmentation can affect disease occurrence by regulating pathogen colonization and extinction, which may further influence the host's resistance to diseases. Therefore, studying host-parasite interactions in fragmented habitats can help to test how spatial structure influences disease dynamics and successively reveal the mechanisms that enable long-term disease persistence in wild communities.

However, our study is centered around host-parasite interactions and hasn't encompassed the non-host species (e.g., predators and other symbionts) that can also affect parasite transmission in myriad ways (Johnson et al., 2015). For example, predators may mediate the availability of susceptible hosts and successively affect disease dynamics (Young et al., 2016). Since predators are usually the most vulnerable animal taxa to habitat fragmentation, the loss of predators and other non-host species should also be considered in disease research. Like avian malaria, a certain proportion of parasites are transmitted by vectors (e.g., mosquitoes). This further complicates the tracing of disease transmission in fragmented landscapes. Nonetheless, studies on identification, distribution, and dispersal of vectors are rarely reported for vector-transmitted parasites. We thus encourage more studies to build an integrative "parasite-vector-host" framework to increase the ability to predict disease spreads or outbreaks in the Anthropocene.

(4) Multilayer networks in fragmented habitats. Most studies of ecological networks focus solely on a single type of network, including two trophic levels or functional groups (i.e., two monolayers), such as pollination, seed dispersal, phytophagy, and parasite networks (Bascompte & Jordano, 2013). In the field, recording species interactions is much more complicated than recording the species. For example, observing birds' frugivorous behaviors at multiple sites simultaneously are challenging until we applied the technique of arboreal camera trapping to monitor birds' foraging moments at a large scale across years (Zhu et al., 2023).

With the development of the field techniques and analytical methods to quantify species interactions, examining multiple layers of networks becomes possible. It is essential for revealing ecological relationships because ecological networks with a single type of species interactions fail to reflect the positions of multiple interactions within the ecosystem and their relationships with other taxa (Timóteo et al., 2023). Multilayer networks can reveal more complex ecological relationships, thereby facilitating a deeper comprehension of the positions and roles of diverse taxa within the ecosystem (Pilosof et al., 2017). For example, in the case of plant-aphid-ant interactions from TIL (Zhang et al., 2023), ants promote the continuation of the aphid community and thus have negative feedback on the plant community. However, it is still unclear whether this negative feedback differs between islands or the intensity of ants visiting aphids varies between islands. Future studies in the TIL system will encompass multiple types of species interactions to explore the structure and function of multilayer networks at the same transects of islands.

CONCLUSION

Here, we conclude our findings following the three topics of species richness, community structure, and species interaction. Studies of species richness on islands of TIL generally support the predictions of the ETIB proposed by MacArthur and Wilson. ETIB can be extended to predict the community structure of island faunas through the lens of community assembly after incorporating species' traits and evolutionary histories. We also concluded that habitat loss decreased biodiversity and network size, while forest edges increased network robustness in fragmented landscapes. Based on the traditional ETIB, the findings from our project move a further step to analyze biodiversity patterns and underlying mechanisms by considering species' ecological roles in traits and phylogenies and their interactions with other taxa and environments.

Our exploration of the community structure of island faunas has underscored the significance of species composition (beta diversity) and ecological roles (functional traits and evolutionary histories) in understanding the biodiversity patterns in TIL. Species turnover emerged as the prevalent process over nestedness in shaping overall beta diversity across taxa. In contrast, nestedness gained prominence when species ecological roles were considered, suggesting functional redundancy of taxonomically different species among reservoir islands. By integrating species' traits and evolutionary histories, we revealed that most islands, especially smaller ones, host more clustered communities, suggesting environmental filtering as a key influence in structuring insular communities across zoological taxa. While reinforcing the principles of island biogeography, our research has also refined them by integrating the nuanced ecological roles of species traits and evolutionary relationships, offering a richer, better understanding of community assembly in fragmented landscapes.

Analyzing multiple types of mutualistic and antagonistic interactions in the same island system, we found the effects of habitat fragmentation (habitat area, isolation, and edge) on species interaction are context dependent. The loss of habitat area generally resulted in fewer species and lower network size on smaller islands in frugivory, pollination, seed dispersal (rodent-plant) networks, as well as mixed-species flocks. However, habitat loss showed little effect on avian haemosporidian infections. Instead, the turnover of parasite assemblage was greatly shaped by geographical isolation and environmental factors of fragmented patches, while the evidence of isolation effects was not evident in plant-frugivore networks. Edge pollination networks maintained high network robustness to extinction following area loss, and network nestedness was the key factor, whereas networks in the interior of forests collapsed in small forest patches. When examining the biotic and abiotic factors of rodent-plant interactions, we found rodent abundance, size-dependent seed predation by rodents, and the synergistic effects of habitat fragmentation and defaunation are key determinants of plant regeneration after habitat fragmentation. Despite the inter-specific interactions among species, our research highlights the essential role of sociality, defined as the propensity of species to aggregate, as a functional trait that significantly influences island biogeography patterns. Furthermore, it is important to integrate both intra- and inter-specific positive interactions into biodiversity research to illuminate the consequences of habitat fragmentation on the assembly of island communities.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

X.S. and P.D. conceived the ideas. All authors contributed to the original writing, review and editing, and read and approved the final version of the manuscript. All authors are listed alphabetically except the first and last authors.

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