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Research article

Spatiotemporal dynamics of migratory birds reshape seed dispersal and conservation implications on fragmented islands[☆]

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ABSTRACT

Seed dispersal by frugivorous birds underpins forest regeneration and biodiversity conservation in fragmented landscapes. Migratory frugivores, through their seasonal movements, connect distant plant populations, but their roles in plant–bird interaction networks remain poorly quantified amid global declines in migratory bird populations. How these birds mediate plant–animal interactions across space and time, and how they functionally differ from residents, remains unclear. Using arboreal camera trapping over three fruiting seasons (2019–2022), we recorded 10,992 interactions (343 unique links) between 31 fleshy-fruited plants and 48 bird species (15 migratory, 33 resident) across 13 reservoir islands in the Thousand Island Lake of China. Migratory birds accounted for 14 % of all interactions, with 99.3 % occurring during the autumn/winter fruiting peaks (October–January), and interacted with 67.7 % of the plant species. Despite their lower overall richness, smaller islands (<10 ha) hosted 43 % of migratory interactions, highlighting their importance as stopover sites. In contrast, larger islands (>30 ha) supported more frugivore richness but lower migratory proportions, acting as refugia for residents. Network analyses showed no significant differences in species roles (degree, species strength, specialization *d'*) between migratory and resident birds though migrants expanded the spatial and temporal scope of seed dispersal. These findings challenge area-centric conservation priorities by revealing the complementary roles of small and large islands. We advocate conserving island networks through seasonal management aligned with fruiting phenology, restoring native fruiting plants with staggered phenologies to buffer climate-driven mismatches, and enhancing habitat connectivity to sustain seed dispersal and ecosystem resilience in fragmented landscapes.

1. Introduction

Seed dispersal is a fundamental ecological function that sustains plant population dynamics, facilitates genetic exchange, and underpins community assembly and ecosystem resilience as a key regulating service (Howe and Smallwood, 1982). This process is critical for forest regeneration, particularly in fragmented landscapes where isolated habitat patches hinder natural plant recruitment and connectivity (McConkey et al., 2012). Effective seed dispersal is a vital ecosystem service and connects isolated habitat patches, thereby ensuring the conservation of biodiversity persistence and contributing to ecosystem stability (Cordeiro and Howe, 2003). Indeed, over half of the world's plant species depend on animal-mediated dispersal (Fricke et al., 2022), underscoring the important role of frugivorous (i.e., fruit-eating)

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animals in maintaining global biodiversity and ecosystem integrity (Rogers et al., 2021; Schleuning et al., 2015; Vizentin-Bugoni et al., 2021).

Frugivorous birds are key agents in seed dispersal, actively transporting seeds and thus enhancing plant regeneration across fragmented landscapes (Wandrag et al., 2017). Migratory frugivorous birds, in particular, play a unique role in mediating long-distance seed dispersal over broad spatial scales (González-Varo et al., 2019; Howe and De Steven, 1979; Jordano, 1982; Tellería et al., 2005), thereby improving connectivity among isolated habitats in both human-modified and natural landscapes (Viana et al., 2016a,b). Moreover, by dispersing seeds to cooler areas (e.g., higher altitudes or latitudes), these birds can help plant populations escaping from changing climatic conditions, mitigating some impacts of climate change (González-Varo et al., 2021; Lovas-Kiss et al., 2023; Viana et al., 2016a). However, migratory frugivorous birds are increasingly threatened by environmental changes that may undermine their ecological role. Habitat fragmentation, for instance, may disrupt their migratory routes and stopover sites, reduce access to key fruiting resources, and lead to changes in movement behavior and survival (Robinson et al., 1995; Whytock et al., 2018). In addition, climate-driven phenological mismatches between fruit availability may further constrain their effectiveness as seed dispersers (González-Varo et al., 2021; Saino et al., 2011). These pressures have contributed to declines in many migratory bird populations (Rosenberg et al., 2019; Runge et al., 2015), potentially compromising their role in forest regeneration and biodiversity maintenance (Mendes et al., 2024; Ramos-Robles et al., 2016). Despite their vital ecological functions, our understanding of the spatiotemporal dynamics of migratory frugivorous bird communities in fragmented landscapes remains limited. Moreover, we lack comprehensive insights into their relative contribution to seed dispersal of fleshy-fruited plants and their specific roles in plant–bird interaction networks (Bauer and Hoye, 2014; Costa et al., 2020; Naoe et al., 2011).

Global habitat fragmentation, primarily driven by human activities such as dam construction (Wu et al., 2003) and climate change, continues to threaten bird populations (Haddad et al., 2015). Core concepts to measure habitat fragmentation are patch area and isolation. The Equilibrium Theory of Island Biogeography is based on these core concepts and was originally developed to explain species richness in relatively stable resident communities (MacArthur and Wilson, 1967). However, migratory birds, with their transient and highly mobile nature, may respond differently to these landscape features (Baldwin and Myers, 2024; Haest et al., 2020; Viana et al., 2016a). For instance, islands can serve as critical stopover sites for migratory species (Guo et al., 2023), influencing resource availability and seed dispersal opportunities. Previous studies have shown that island characteristics shape bird community composition (Stracey and Pimm, 2009) and that migratory species often exhibit distinct responses to habitat alterations compared to residents (Levey et al., 2025). By comparing the responses of migratory and resident frugivorous birds using the principles of Island Biogeography, we can gain clearer insights into their distinct spatiotemporal dynamics (La Sorte et al., 2022; Tarifa et al., 2024). Notably, most studies in fragmented landscapes have focused on resident birds (Marjakangas et al., 2020; Si et al., 2014), while migratory species remain underexplored (Kubelka et al., 2022; Tarifa et al., 2024; Tellería et al., 2005). Understanding when and where migratory birds interact with fleshy-fruited plants, how they contribute to seed dispersal, is critical for developing effective conservation strategies in fragmented landscapes.

Reservoir islands resulting from dam construction can serve as important stopover sites for migratory birds (La Sorte et al., 2022; López-Iborra et al., 2022). These islands, varying in area and isolation, provide natural laboratories for studying plant-frugivore interactions, making them ideal for elucidating the ecological roles of migratory birds in fragmented landscapes (Howe and De Steven, 1979; Li et al., 2022). Migratory birds, which travel annually between breeding and wintering grounds, may enhance seed dispersal services for some plants, particularly when their fruiting periods overlap with the passage of migratory birds (Jordano, 1982; Pizo and Camargo, 2018). However, the inherent challenges associated with long-term field sampling have led many studies to focus on a limited number of plant species or confined spatial areas (Costa et al., 2020; Howe and De Steven, 1979; Jordano, 1982; Pizo and Camargo, 2018). Consequently, there is a pressing need for comprehensive studies that encompass a broader range of plant species and extend across multiple spatial scales to fully elucidate the complex ecological dynamics within these fragmented landscapes.

In this study, we used the Thousand Island Lake (TIL) in eastern China as our research system, which is characterized by a dam-induced fragmented landscape. TIL lies on an important East Asian migratory bird flyway (Yong et al., 2018) and has been established as a model system for habitat fragmentation studies (Si et al., 2024). To comprehensively capture the roles of migratory frugivorous birds, we used arboreal camera trapping—an emerging technique that enables continuous and non-invasive monitoring over a three-year period across 13 forested islands (Zhu et al., 2022). This approach allowed us to document interactions of frugivorous migratory and resident bird species and fruity-fleshed plants. Our study aimed to address three questions: 1) How do island area and isolation affect the richness and proportion of migratory frugivorous birds? 2) What are the temporal dynamics between migratory birds and fleshy-fruited plants? 3) How do the structural roles of migratory frugivorous birds in plant–bird interaction networks differ from those of resident birds?

According to the Theory of Island Biogeography, larger islands typically support more species due to lower extinction rates, while more isolated islands tend to host fewer species because of reduced immigration rates (MacArthur and Wilson, 1967). We anticipated that resident frugivorous birds would follow these predictions, exhibiting positive species–area and negative species–isolation relationships. In contrast, migratory frugivorous birds, owing to their high mobility, might be less constrained by island size and isolation, leading to weaker or non-significant relationships (Fig. 1a, b). Specifically, we predicted that smaller and more isolated islands would harbor a higher proportion of migratory frugivorous birds relative to the overall frugivorous bird community (Fig. 1c, d). Given that the peak fruiting period for many plant species in the TIL system typically occurs during the autumn and winter months (Zhu et al., 2024), and that migratory frugivorous birds are capable of tracking fruit availability (Tellería et al., 2005), we expected that the bird–plant interactions involving migratory species would reach their highest frequency during this seasonal window. Finally, we hypothesized that some plant species would exhibit seasonal shifting in the proportion of their seed dispersal interactions mediated by migratory birds (Ramos-Robles et al., 2016).

2. Methods

2.1. Study region

This study was conducted in the Thousand Island Lake (TIL; 29°22′–29°50′N, 118°34′–119°15′E), located in Zhejiang Province of eastern China (Fig. 2a). TIL was formed in 1959 following the construction of the Xin'an River Dam. The reservoir covers approximately 58,000 ha, with 1078 islands exceeding 0.25 ha at a water level of 108 m. After nearly 60 years of forest conservation effort, these islands have developed extensive forest vegetation, achieving a coverage rate of 88.5 % (Hu et al., 2011). The island's vegetation is predominantly composed of natural secondary Masson pine (*Pinus massoniana*) forests, with an understory rich in broad-leaved trees and shrubs, including a relatively diverse array of fleshy-fruited plants (Fig. 2b-d), approximately 34 species (Li et al., 2022). TIL is located in a humid subtropical monsoon climate zone, characterized by hot, humid summers and cold, dry winters with low precipitation. The rainy season occurs mainly from April to June, with an annual average precipitation of approximately 1430 mm.

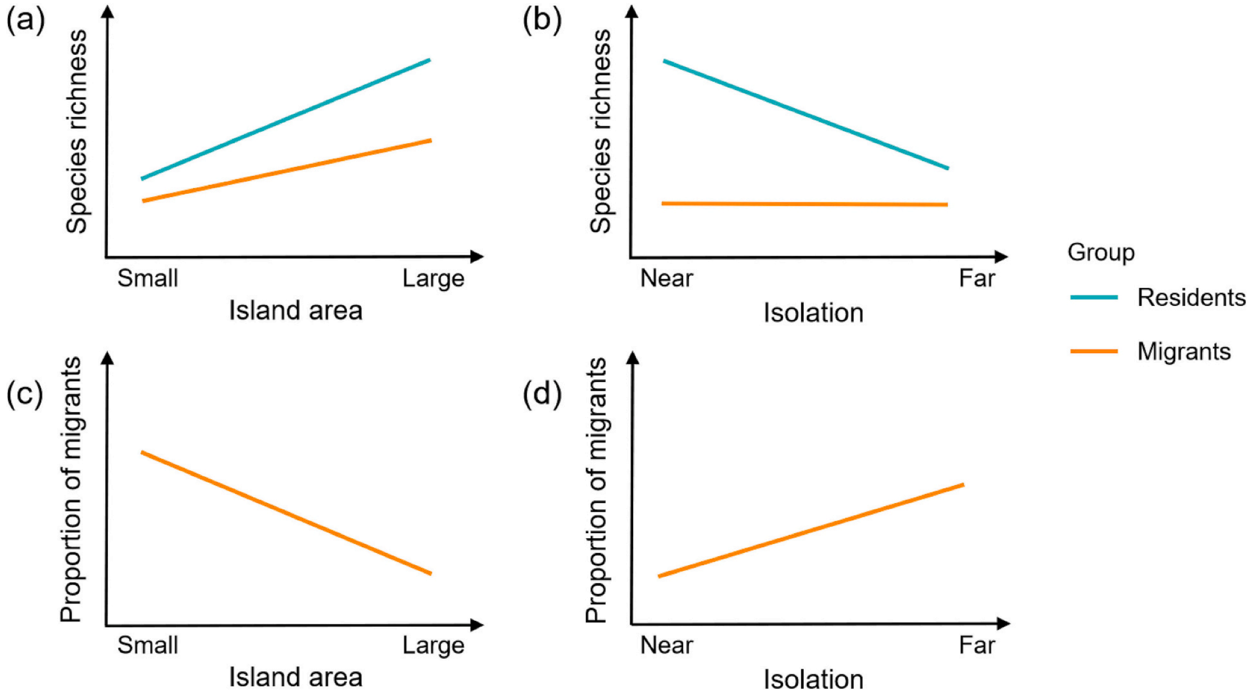

Fig. 1. Hypothetical impacts of habitat fragmentation on the species richness of resident and migratory frugivorous birds, as well as the proportional richness of migratory frugivorous birds on forest islands. Stronger species-area and isolation effects are expected for resident species compared to migratory species (a + b), which may result in a greater proportion of migrants on smaller islands (c) and more isolated ones (d).

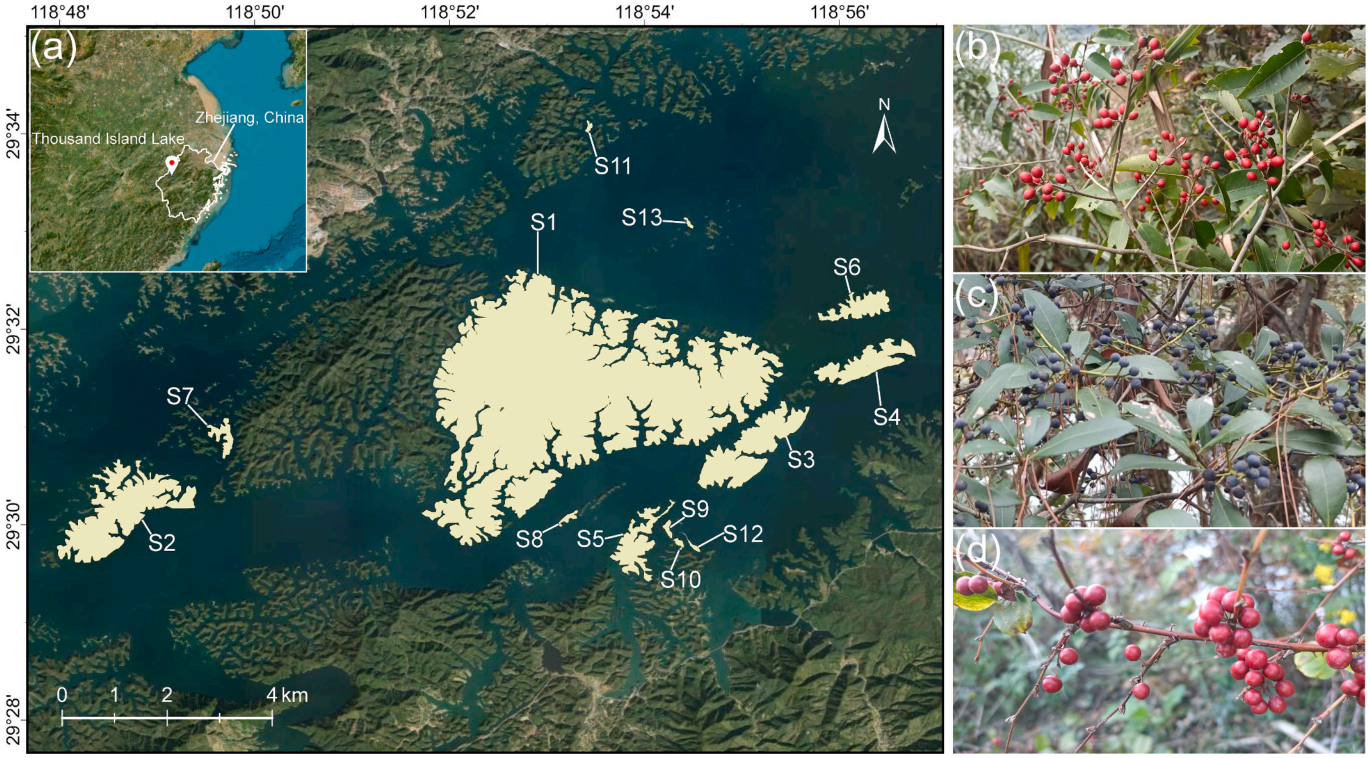

Fig. 2. Study region and some common fleshy-fruited plant species in the Thousand Island Lake, Zhejiang, China. (a) Spatial distribution of surveyed islands labeled in decreasing order of area from S1 (largest) to S13 (smallest). The cyan colour around the surveyed islands indicates the lake water. The right panel illustrates three representative fleshy-fruited plant species: *Ilex chinensis* (b), *Rhaphiolepis indica* (c), and *Smilax china* (d). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The average annual temperature is 17 °C, with daily temperatures ranging from a low of −7.6 °C in January to a high of 41.8 °C in July (Si et al., 2014).

2.2. Sampling design

In this study, we surveyed 13 islands within the TIL system from July

2019 to January 2022, covering three major fruiting seasons (T1, T2, and T3; each spanning from July to the following January). This sampling period was chosen to align with the primary fruiting seasons of our target plant species (Liu et al., 2019; Zhu et al., 2025), thereby optimizing sampling efficiency and data quality. While 22 islands were initially surveyed across all three fruiting seasons, nine were excluded from analysis due to insufficient fleshy-fruited plant data, which limited the ability to reliably assess plant-frugivore interaction dynamics. These excluded islands (area range: 0.59–35.64 ha; isolation range: 640–3262 m; Table S1) either lacked fleshy-fruited plants during one or more sampling periods (T1/T3) or supported only one to two fruiting species—below the threshold necessary for meaningful network inference. Notably, observations from these excluded islands indicate that both migratory and resident frugivores were present, sometimes in substantial numbers (Table S1). For example, on the smallest excluded island (0.59 ha), up to ten migratory and 19 resident species were recorded across the sampling periods. This suggests that small islands can support diverse frugivore communities. However, the absence or scarcity of fleshy-fruited plants constrained interaction sampling, and their exclusion was based on ecological data limitations rather than avian presence per se.

The final set of 13 islands retained for analysis encompassed the full natural range of island area (0.96–1289 ha) and isolation (727–3134 m) within the TIL system (Table S2). Moreover, island area and isolation were not significantly correlated (Pearson's $r = -0.23$, $p = 0.45$), allowing their respective effects on frugivore communities to be disentangled. Smaller islands (<10 ha) exhibited higher temporal variability in fleshy-fruited plant composition than larger islands (>30 ha) (Zhu et al., 2025). The selected islands thus provided a representative and ecologically informative basis for examining plant-frugivore interactions across insular gradients. Isolation was quantified as the minimum linear distance from each island to the nearest point on the mainland shoreline, a widely used metric in island biogeography that reflects dispersal limitation from source communities.

On each study island, we established 20-m-wide line transects to study plant–bird interactions using a proportional sampling method (Schoereder et al., 2004). Transects were systematically positioned along ridge-lines, following established bird survey protocols (Si et al., 2014). Placement prioritized topographic continuity from the island edges to the interiors, ensuring coverage of habitat types where fleshy-fruited plants are found (Zhu et al., 2022). The total length of transects (i.e., sampling efforts) on each island was approximately proportional to the logarithm of the island's area. As a result, eight transects were set on the largest island (area > 1000 ha), four on islands between 100 and 1000 ha, two on islands between 10 and 100 ha, and one on each of the remaining islands (mostly around 1 ha; see Table S2).

2.3. *Frugivorous bird survey and sampling plant–bird interactions*

2.3.1. *Monitoring fleshy-fruited plants*

To evaluate the diversity of migratory frugivorous birds and their role in fruit consumption, we conducted exhaustive searches for fleshy-fruited plant species along established transects at least twice monthly from early July through January. Upon identifying plants with ripening fruits, we installed infrared cameras (LTL Acorn 6210 MC) at optimal locations near high-density fruit clusters, mounting them at heights of 0.5–8.0 m (using ladders as needed) and setting sensitivity to high. To reduce redundancy, only one camera per species was deployed within a 20 m radius, prioritizing the individual with the most abundant fruits (Li et al., 2022; Zhu et al., 2022). This arboreal camera-trapping approach has been validated in the TIL system, with previous studies using the same model and settings reliably recorded frugivores from ~6 g passerines (e.g., *Aegithalos concinnus*) to ~3200 g mammals (e.g., *Paguma larvata*), as well as ground-foraging species such as *Lophura nycthemera*, across canopy, understory, and ground strata (Li et al., 2022; Zhu et al., 2022, 2023).

2.3.2. *Camera deployment and operation*

The number of cameras deployed varied annually to reflect natural fluctuations in fruit production: 136 cameras in the first sampling period (T1), 216 in the second (T2), and 195 in the third (T3). Cameras operated continuously (24 h per day) in a "3 + 1" mode, capturing three photos followed by a 10-s video when triggered by a vertebrate, with a 10-s delay between triggers to conserve memory and battery life. Routine checks every two weeks allowed us to adjust camera angles, retrieve data, and replace batteries. When fruits on a monitored plant were either fully consumed or nearly all had fallen, we retrieved the cameras and transferred the image data from the SD card to a laptop.

2.3.3. *Data processing and interaction classification*

Over the study period, we processed 2,721,115 image files (photos and videos) from 13 islands. Although the infrared cameras also captured images of other fruit-eating animals (e.g., rodents and mammals like the Masked Palm Civet), our study focused exclusively on bird–plant interactions. Notably, rodents and Masked Palm Civet are primarily nocturnal and are unlikely to contribute to across-islands seed dispersal. To ensure data accuracy and minimize oversight, each camera's recordings were cross-checked by two experienced bird observers. Plant–bird interactions were classified as legitimate seed dispersal events based on fruit-handling behaviors. Specifically, interactions were recorded if birds exhibited fruit swallowing (ingestion of entire fruits), which is strongly associated with effective seed dispersal (Simmons et al., 2018). Events characterized by fruit pecking were also included whenever pecking resulted in partial or full ingestion of fruits, particularly when seeds were small. Additionally, birds merely present in the camera's field of view without engaging in foraging activities were not considered interacting agents. This conservative approach minimizes false positives and aligns with established protocols for inferring mutualistic interactions from behavioral observations (Snow and Snow, 1988).

2.3.4. *Quantifying interaction frequencies*

To quantify interaction frequencies between migratory/resident birds and fleshy-fruited plants, we defined an independent frugivory event as consecutive photos or videos of the same plant–bird interaction captured by a single camera, separated by more than five minutes (Zhu et al., 2022). This temporal threshold minimizes overcounting repeated visits by the same individual. In instances where multiple individuals of the same bird species were observed feeding simultaneously on a single fleshy-fruited plant, the interaction frequency was weighted by the number of birds present. Interaction frequency for each plant–bird pair was then calculated as the total number of weighted, independent events recorded during the sampling period. These events served as a proxy for the mutualistic effect of birds on seed dispersal potential.

2.3.5. *Integrating with broader avian community surveys*

To contextualize the frugivorous bird and their interaction data within the broader avian community, we conducted systematic bird surveys across the study islands (see full details in supplementary methods in Appendix 1). This allowed us to compare the species–area/isolation relationships between the frugivore-specific and the overall bird community (The list of overall bird species on the islands is shown in Table S3). Bird species were classified as either migratory or resident based on their seasonal occurrence patterns (Billerman et al., 2022).

2.4. *Sampling completeness of plant–bird interactions*

Prior to the statistical analyses, we evaluated the sampling completeness for plant–bird interactions on each island following Grass et al. (2018) to exclude any potential bias resulting from incomplete sampling. For each fruiting period (T1, T2, and T3), we constructed an interaction matrix for each island, with matrix values representing the frequency of observed interactions. Sampling completeness was estimated using the Chao1 asymptotic richness estimator (Chao, 1984), which is calculated by dividing the observed interaction richness by the estimated interaction richness. At the same time, we further evaluated by plotting accumulation curves of unique pairwise interactions against month of sampling (Fig. S1). The average sampling completeness was 75 % ± 12 % (mean ± SD) for T1, 82 % ± 10 % for T2, and 89 % ± 8 % for T3 (Table S4), indicating adequate sampling. Furthermore, the sampling completeness of each fruiting period was found to be independent of island area (T1: Pearson's $r = 0.026$, $p = 0.93$; T2: $r = -0.15$, $p = 0.62$; T3: $r = -0.16$, $p = 0.61$).

2.5. *Statistical analysis*

2.5.1. *Effects of island area and isolation on migratory bird communities*

To assess the influence of island area and isolation (both treated as continuous variables) on migratory bird communities (species richness and proportion) in the TIL system, we used generalized linear mixed models (GLMMs). Analyses were conducted for both frugivorous and the overall bird communities. Species richness was modeled as count data using a Poisson error distribution, while the proportion of migratory species (number of migratory species divided by the total number of migratory and resident species) was modeled using a binomial error distribution. Island area and/or isolation were included as fixed effects, and island identity was incorporated as a random effect to account for repeated measurements across the three sampling periods and unobserved heterogeneity among islands. Island area was $\log_{10}$-transformed to improve model interpretability and meet underlying assumptions. GLMMs were performed using the *glmer()* function from the *lme4* package (Bates et al., 2015). Model diagnostics, including assessments of residual patterns and overdispersion, were conducted using the *performance* (Lüdecke et al., 2021) and *DHARMa* packages (Hartig, 2016). Model predictions were generated using the *ggeffects* package (Lüdecke, 2018).

2.5.2. *Temporal dynamics of migratory bird–plant interactions*

To characterize temporal dynamics in the proportion of plant–bird interactions mediated by migratory birds, we analyzed monthly interaction frequencies aggregated across all 13 study islands over three sampling periods. We calculated the monthly proportion of interactions involving migratory birds relative to those involving resident birds, ranging from 0 % (no migratory interactions) to 100 % (all interactions by migratory birds). At the plant species level, we assessed interaction dynamics by calculating the monthly percentage of frugivory events involving migratory birds. We also pooled data across the three sampling periods to quantify overall interaction proportions for each plant species. Additionally, we examined how temporal shifts in fleshy-fruited plant richness influenced the proportion of interactions mediated by migratory birds.

2.5.3. *Structural roles of migratory vs. resident birds in interaction networks*

To assess whether migratory frugivorous birds play different structural roles compared to resident species within plant–bird interaction networks, we conducted species-level analyses across three sampling periods. For each period, we constructed a weighted interaction matrix, with cell values indicating the frequency of interactions between each bird and plant species. Using the *specieslevel()* function from the *bipartite* package (Dormann, 2011), we calculated three commonly used metrics for each bird species: (1) Degree, that is, the number of unique plant species a bird interacted with, reflecting its partner breadth. (2) Species strength, representing the weighted sum of a bird species' relative dependency across all its interacting plant species, reflecting its overall importance or influence within the network (Bascompte et al., 2006). (3) Specialization *d'*, quantifying the extent to which a bird species interacts preferentially with specific plant partners, relative to their overall availability. It reflects whether a species tends to behave as a selective specialist or a generalist opportunist (Blüthgen et al., 2006). To account for variation in network size and sampling effort across the three fruiting periods, we normalized both degree and species strength within each network, enabling meaningful cross-network comparisons. Differences between migratory and resident bird species were assessed using Wilcoxon rank-sum tests for degree and species strength, and the Student's *t*-test for specialization *d'*. All statistical analyses were performed in R version 4.4.3 (R Core Team, 2025).

3. Results

Across 13 islands over the three main fruiting periods, we recorded a total of 10,992 interactions (343 unique pairwise links) between 31 fleshy-fruited plant species (547 individual plants; Table S5) and 48 bird species (Table S6). These interactions involved 33 resident and 15 migratory frugivorous bird species (Table S6). Notably, interactions between fleshy-fruited plant and migratory birds totaled 1543 (82 unique pairwise links), accounting for 14.04 % of all interactions. Specifically, the proportion of interactions involving migratory birds was 7.28 % during the first sampling period (T1), 25.31 % in the second (T2), and 9.68 % in the third (T3).

3.1. *Effects of island area and isolation on migratory and resident frugivorous birds*

Both migratory and resident frugivorous bird richness increased with island area (migrants: $\beta = 0.186$, SE = 0.085, $p = 0.028$; residents: $\beta = 0.412$, SE = 0.076, $p < 0.001$; see Fig. 3, Table S7). However, within the frugivorous guild, the proportion of migratory species decreased with increasing island area ($\beta = -0.265$, SE = 0.126, $p = 0.035$; Fig. 3, Table S7). This trend persisted even when both island area and isolation were considered in the model, with the proportion of migratory frugivores still decreasing as island area increased ($\beta = -0.245$, SE = 0.131, $p = 0.061$; Table S7). Island isolation had no significant effect on frugivorous species composition (all $p > 0.1$). Notably, this area-dependent decline in the proportion of migratory species was not observed in the broader avian community, where no significant relationship was found ($\beta = -0.011$, SE = 0.06, $p = 0.855$; Fig. S2, Table S8).

3.2. *Temporal dynamics and species roles of plant–migratory bird interactions*

During the three primary fruiting periods, temporal variation in plant–bird interactions was observed across the 13 study islands. From July to September, interactions were predominantly mediated by resident birds. Due to winter visitors, interactions involving migratory birds increased notably in October and reached a peak between October and the following January. Notably, the monthly contribution of migratory birds varied across years, with the highest recorded value reaching 50.15 % in December of the second year (Fig. 4).

At the species level 21 of the 31 monitored fleshy-fruited plant species (67.74 %) showed variable interaction frequencies with migratory birds over the three sampling periods (Fig. 4). For example, migratory bird species accounted for only 0.7 % of interactions with *Rubus lambertianus*, but 75 % of interactions with *Callicarpa giraldii*. Individual plant species showed notable fluctuations in their interactions with migratory birds across different fruiting periods and months. Notably, five species (i.e., *Smilax china*, *Symplocos paniculata*, *Callicarpa giraldii*, *Rhaphiolepis indica*, and *Ilex rotunda*) were observed to interact exclusively with migratory birds during specific periods (e.g., in winter) (Fig. 4). A weak positive association was detected between fleshy-fruited plant species richness and the monthly contribution of migratory bird interactions (Pearson's $r = 0.368$, $p = 0.100$). Furthermore, no significant differences were detected between migratory and resident frugivorous bird species in their mean normalized values for the three network metrics—degree, species strength, and specialization *d'*—across the

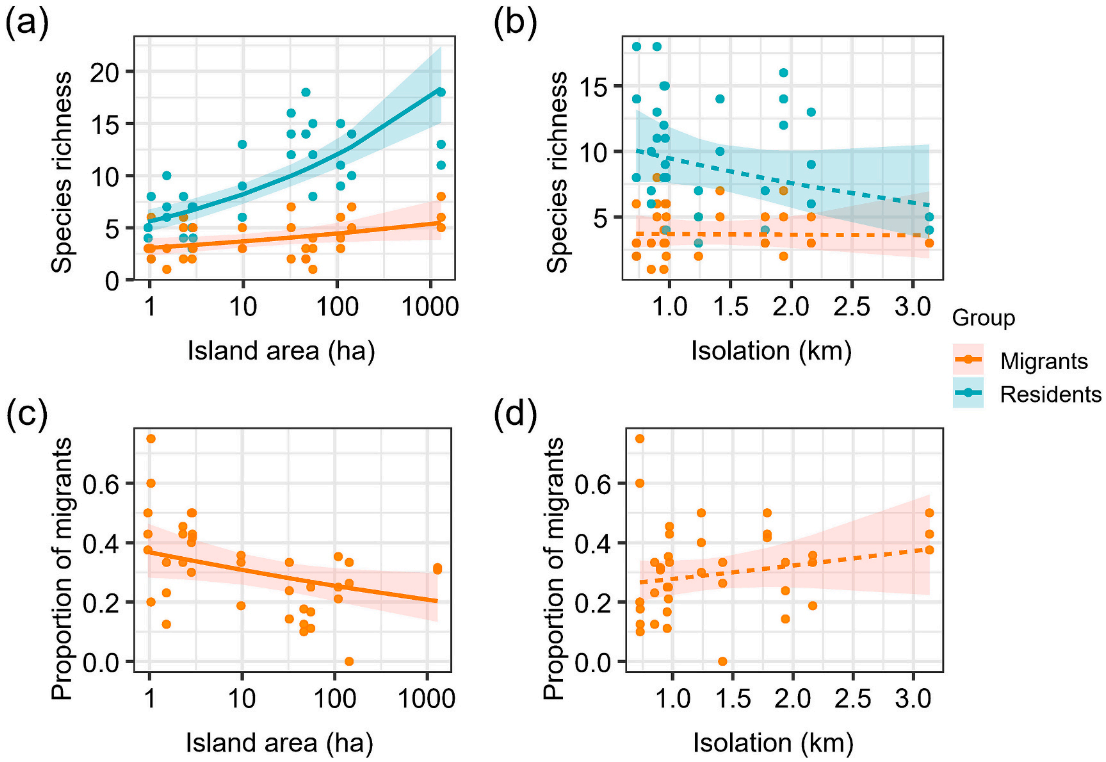

Fig. 3. Effect of island attributes on migratory and resident frugivorous birds in the Thousand Island Lake, Zhejiang, China. Relationships between species richness of migrants (orange) and residents (green) against island area or isolation (a + b). Relationships between the proportion of migratory species richness and island area or isolation (c + d). Curves show predicted means derived from generalized linear mixed models, with solid lines indicating significant relationships ($p < 0.05$) and dashed lines representing non-significant trends. Shaded bands denote 95 % confidence intervals, and dots reflect raw data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

three sampling periods (Fig. 5).

4. Discussion

In this study, we used arboreal camera trapping on 13 forested reservoir islands in eastern China to collect detailed, multi-year data on plant-frugivore interactions. By distinguishing between resident and migratory birds, we examined how island area, isolation, and temporal dynamics influence these interactions in a fragmented landscape. Our findings support and extend foundational ecological theory. First, consistent with the Theory of Island Biogeography, species richness of both migratory and resident frugivores increased with island area, with a stronger effect for residents. This suggests that larger islands provide more stable habitats for residents, while migratory birds, due to their mobility, can exploit a broader range of island sizes. Smaller islands, in particular, hosted a higher proportion of migratory frugivores, highlighting their role as stepping stones in fragmented habitats. Second, migratory bird–plant interactions showed strong temporal structuring, peaking in autumn and winter, which aligns with local fruiting phenology. This emphasizes the role of migratory birds in tracking ephemeral food resources and their contribution to seed dispersal during key phenological windows. Third, despite differences in spatial and temporal dynamics, migratory and resident birds played comparable structural roles in interaction networks, indicating functional redundancy that may enhance network resilience. Together, these findings underscore the importance of migratory frugivores in maintaining connectivity and promoting plant regeneration in fragmented landscapes, while also extending classical ecological theory to account for the dynamics of mobile species.

4.1. *Effects of island area and isolation on migratory birds*

Our study demonstrates that migratory and resident frugivores exhibit distinct species–area relationships (SARs) across islands. Both groups show positive SARs, but residents have a steeper slope compared to migrants, resulting in a decrease in the proportion of migratory species as island area increases. This pattern is specific to frugivores, because similar SAR slopes for migratory and resident species in the broader bird community, with no area-dependent shifts in migratory proportion. This divergence likely arises because migratory frugivores' high mobility enables them to exploit ephemeral fruit resources across various island sizes, whereas resident frugivores rely on stable resource bases that scale with habitat area (Li et al., 2023; Tellería et al., 2005). While larger islands inherently sustain more resident species due to resource stability, small islands also play a crucial role. For instance, in our study, 43.23 % of all interactions involving migratory frugivorous birds occurred on small islands (<10 ha; Table S4), highlighting their importance as stopover habitats. These findings suggest that even small islands offer essential foraging opportunities for migrant birds, potentially contributing to landscape-scale functional connectivity if dispersed seeds establish in suitable habitats (Gounand et al., 2018; Jordano et al., 2007). Therefore, our study emphasizes the importance of protecting both large and small islands.

We found that neither migratory nor resident frugivorous bird richness was influenced by island isolation, nor did the proportion of migratory frugivores show a significant relationship with isolation. This is likely due to the high mobility of migratory birds, which can easily traverse short distances between islands. For resident frugivores, the lack of isolation effects can be attributed to the small distances between study islands and the presence of forest patches that serve as stepping stones. The most isolated islands are still < 4 km from the mainland, and despite testing various isolation metrics (Li et al., 2022; Si et al., 2014),

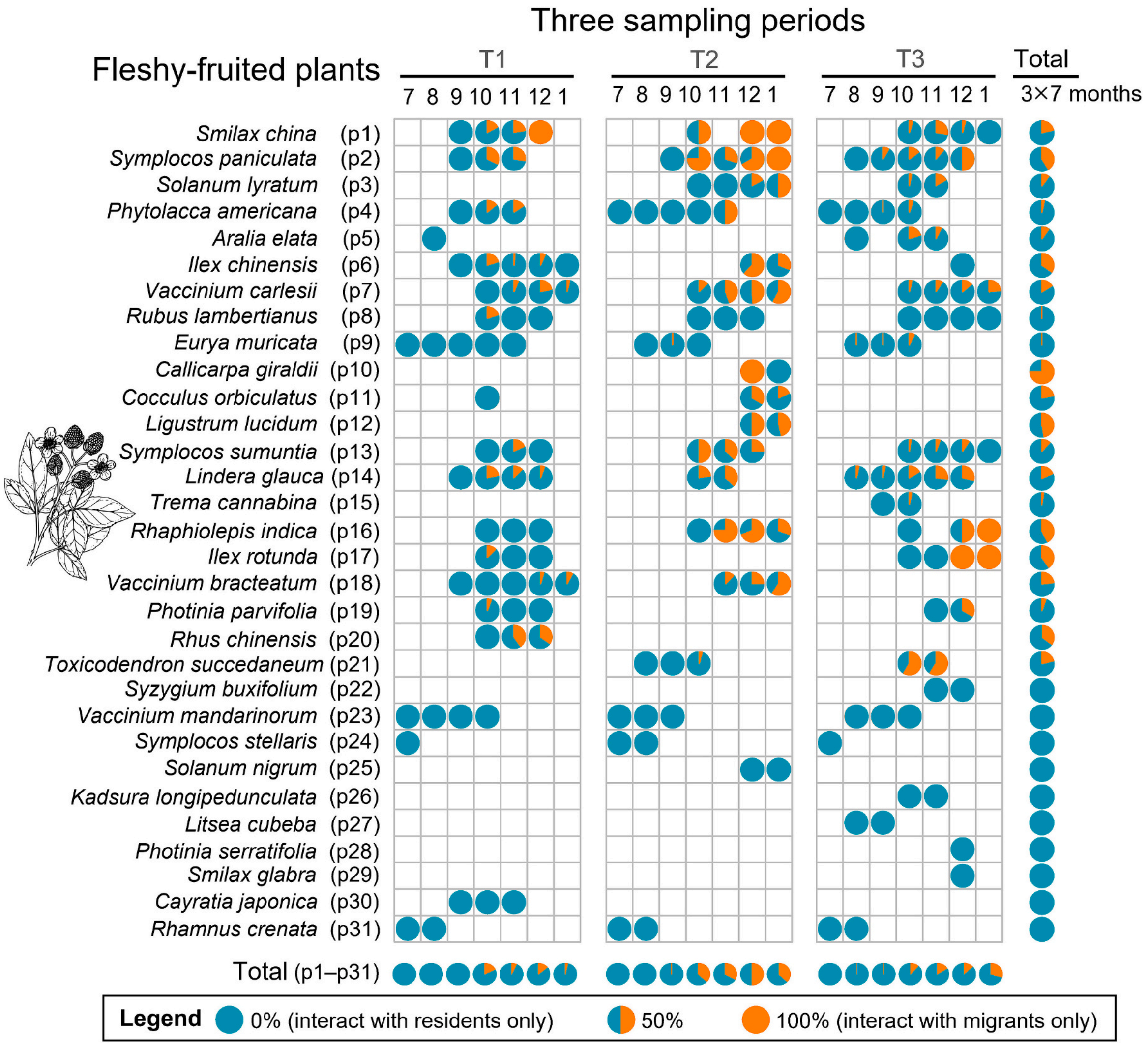

Fig. 4. The proportion of interactions between fleshy-fruited plants and migratory birds across each sampling period on 13 islands in the Thousand Island Lake, Zhejiang, China. The matrix is formed by fleshy-fruited plants (rows) and each sampling month (columns) across the study period. Cells within this matrix contain pie charts illustrating frugivorous bird interactions with fleshy-fruited plants recorded during specific months and in total. If interactions are exclusively with resident birds, the cell displays a green circle; if exclusively with migratory birds, an orange circle is shown; if both resident and migratory birds are involved, the pie chart within the cell depicts the proportion of each interaction, with a higher orange segment indicating a greater involvement of migratory birds. Empty cells without any filled circles denote months where no plant–frugivorous bird interactions were observed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the results consistently show minimal isolation effects on bird communities. Overall, the limited isolation in our study system appears too small to significantly affect bird species composition.

4.2. *Temporal dynamics of migratory bird–plant interactions*

Our study revealed a pronounced seasonal concentration of migratory bird–plant interactions, with 99.28 % of interactions concentrated between October to January. This period coincides with the system's peak fruiting phenology, where mature fruiting species richness more than doubles from September to October. Two reasons may explain this temporal overlap. Firstly, migrants may prioritize high-resource stopovers to maximize energy efficiency, consistent with optimal migration theory (Alerstam and Lindström, 1990; Chernetsov, 2012). These resources might include fruits, but also availability of other food sources (e.g., invertebrates) (Hlaváček et al., 2025). Additionally, climatic thresholds or other unmeasured variables might be the underlying reason (Bairlein, 2003). Secondly, the higher frequency of interactions may be driven by greater migratory bird density during this period.

These findings advocate for temporally stratified conservation strategies that address both migratory resource peaks and potential resident dependencies (Hanya, 2005; Ramos-Robles et al., 2016), while acknowledging phenological plasticity in frugivore diets. We recommend designating large islands (>30 ha) as core protected areas for resident-dependent plants, but also conserving small island clusters (<10 ha) as migratory stepping stones. Management strategies should restrict human activities during the October–January peak to reduce disturbances to migratory birds. Moreover, monitoring the timing of fruiting and bird migration (phenological tracking) should be incorporated into conservation efforts to detect potential climate-driven mismatches. For example, if fruiting periods shift earlier due to warming temperatures while migratory birds arrive later, there may be a gap in available food resources, which could negatively affect bird survival and dispersal. To mitigate potential phenological mismatches between fruiting periods and migratory bird arrivals, conservation efforts should focus on preserving and restoring a diverse assemblage of native fleshy-fruited plants with staggered phenologies. This strategy can help ensure a continuous availability of food resources for migratory birds

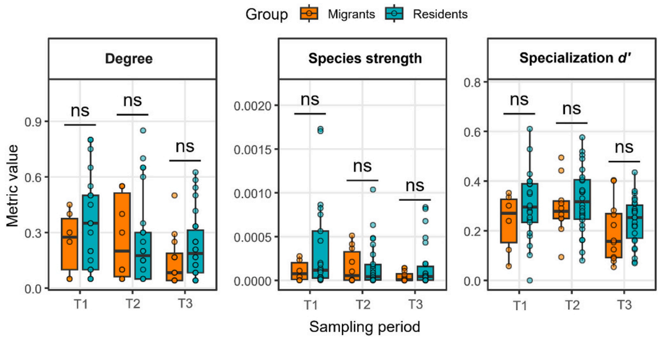

Fig. 5. Species roles of migratory and resident species on plant–frugivorous bird networks during three sampling periods. In the boxplots, T1, T2, and T3 represent the three sampling periods. The 'ns' annotation indicates no significant difference between migratory (orange) and resident (green) frugivorous birds. Each point in the boxplots corresponds to a frugivorous bird species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

throughout their stopover periods, thereby supporting their survival and migration success.

4.3. Network roles and structural redundancy

Network metrics like species degree, strength, and specialization index (*d'*) can offer valuable insights into the structural properties of ecological networks (Costa et al., 2020; Dormann, 2011). Our analysis showed that migratory and resident birds play equally important roles in the plant–bird network, highlighting their complementary contributions. This suggests that neither group is more or less important than the other, but both share similar roles in maintaining network structure. However, while these metrics capture the frequency and strength of interactions, they do not account for the broader ecological services provided by different bird species. Migratory birds, for example, are crucial for long-distance seed dispersal, enhancing gene flow and meta-population connectivity—services that resident species cannot replicate (Viana et al., 2016b).

Although both groups show structural redundancy, this redundancy helps maintain network stability through compensatory dynamics (Thébault and Fontaine, 2010). Yet, this apparent overlap in roles masks important spatial and ecological differences. Migratory birds help alleviate localized resource scarcity and facilitate cross-latitudinal nutrient fluxes, contributing to ecosystem-scale processes that are essential for ecological balance (Alerstam and Lindström, 1990). To better understand the ecological significance of migratory birds, future research would benefit from an integrative approach that combines network analysis with movement ecology, trait-based data, and empirical assessments of ecosystem services. This would allow for a more comprehensive understanding of the contributions of both migratory and resident species to ecosystem functioning.

5. Conclusions

Our study underscores the critical roles of both small (<10 ha) and large islands in supporting migratory and resident frugivores, respectively. Small islands serve as essential stopover habitats, accounting for 43.23 % of migratory bird–plant interactions, while large islands provide stable resources that sustain resident frugivore communities. The peak period for migratory bird–plant interactions occurred between October and January, aligning with the fruiting window of 67.7 % of plant species, highlighting the importance of temporal synchronization for effective seed dispersal. Despite apparent structural overlap in network metrics, migratory birds remain crucial for long-distance seed dispersal and meta-population connectivity. Given the ongoing global decline in migratory bird populations (Rosenberg et al., 2019; Runge et al., 2015), our study advocates for climate-adaptive management and targeted conservation strategies that protect both large and small islands, thereby contributing to long-term landscape connectivity.

CRediT authorship contribution statement

Wande Li: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Writing– review & editing. **Ingo Grass:** Writing – review & editing, Supervision, Conceptualization. **Chen Zhu:** Validation, Methodology, Investigation, Data curation. **Thomas Hiller:** Writing – review & editing. **Marit Kinga Kasten:** Writing – review & editing. **David Becker:** Writing – review & editing. **Sara Tassoni:** Writing – review & editing. **Ping Ding:** Resources, Project administration, Funding acquisition. **Xingfeng Si:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111283.

Data availability

Data used in the development of this study are available in figshare: https://doi.org/10.6084/m9.figshare.27909543.

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