ABS ACTA BIOLOGICA SIBIRICA
A journal on the biodiversity of Siberia and the adjacent lands

Acta Biologica Sibirica 12: 407–425 (2026)
doi: 10.5281/zenodo.19734628
http://journal.asu.ru

RESEARCH ARTICLE

Seventy-one years of avian community dynamics on an island: functional homogenization among dynamic equilibrium

Valery D. Siokhin[1], Alex V. Matsyura[1, 2]

1 *Melitopol State University, 18 Bohdan Khmelnytsky Avenue, Melitopol*
2 *Altai State University, 61 Lenina St., Barnaul*

Corresponding author: Alex V. Matsyura (amatsyura@gmail.com)

Academic editor: R. Yakovlev | Received 11 January 2026 | Accepted 4 February 2026 | Published 25 April 2026

http://zoobank.org/004383AA-2A72-44D6-8C65-20EB5133C96E

Citation: Siokhin VD, Matsyura AV (2026) Seventy-one years of avian community dynamics on an island: functional homogenization among dynamic equilibrium. Acta Biologica Sibirica 12: 407–425. https://doi.org/10.5281/zenodo.19734628

Abstract

Long-term datasets are crucial for discerning directional ecological changes from natural variability and for testing foundational theories. This study analyzes 71 years (1949–2020) of breeding bird monitoring data from an island ecosystem to quantify long-term community dynamics and assess the applicability of the island biogeography equilibrium theory. We employed an integrated analytical framework combining quadrant classification (based on presence percentage and redistribution level), the DAISIE model (Dynamic Assembly of Island Species through Immigration, Extinction and Speciation), and temporal trend analysis. Our results reveal a marked restructuring of the avian assemblage: specialist species (e.g., *Hydroprogne caspia*) declined to local extinction, while generalist species (e.g., *Phalacrocorax carbo*) increased exponentially, driving a shift from a tern–gull to a cormorant–gull dominated system. Despite stable species richness, the community experienced significant functional homogenization, evidenced by a 47% decrease in Pielou's evenness (from 0.72 to 0.38) and a drop in the effective number of species from 2.8 to 1.7. The DAISIE model estimated a colonization rate (λ) of 0.18 species/year and an extinction rate (μ) of 0.12 species/year, predicting an equilibrium richness of 1.5 regularly breeding species, closely matching the observed long-term average. Annual species turnover averaged 18.3%, with colonization events clustering in discrete periods (1975–1985, 2015–2020), suggesting environmental windows for establishment. Quadrant classification successfully classified species into functional groups (successful colonizers, stable populations, new colonizers, rare/endangered), providing a robust diagnostic tool for conservation prioritization. We conclude that while the system operates near a dynamic equilibrium, as predicted by theory, it has undergone substantial functional simplification, underscoring the vulnerability of island ecosystems to biodiversity erosion even when species counts appear stable.

Keywords
Island biogeography, long-term monitoring, community turnover, DAISIE model, functional diversity, conservation prioritization, *Phalacrocorax carbo*, *Larus cachinnans*

Introduction

Long-term ecological monitoring provides critical insights into community dynamics, particularly in isolated ecosystems where stochastic events and colonization-extinction processes drive biodiversity patterns (Lomolino, Brown 2009; Valente et al. 2025). Islands serve as model systems for testing fundamental ecological theories due to their discrete boundaries and simplified community structures (Stephens et al. 2004; Valente et al. 2014). The Equilibrium Theory of Island Biogeography (ETIB), proposed in 1967 by MacArthur and Wilson (see MacArthur, Wilson 2001), predicts that species richness reaches a dynamic equilibrium determined by island area and isolation through opposing processes of colonization and extinction. Although extensively tested in terrestrial systems (Valente et al. 2014; Ceia et al. 2023), comprehensive long-term validations in avian island communities, particularly those integrating abundance data and functional diversity metrics, remain limited (Lomolino, Brown 2009; Valente et al. 2015, 2020).

Recent theoretical advancements have sought to refine and expand on the ETIB. For instance, the niche-based theory of island biogeography (NTIB) proposes that species richness is not only a function of area and isolation but is also highly influenced by the number of available climatic niches, which helps explain global patterns such as latitudinal gradients in biodiversity (Stephens et al. 2004; Beaugrand et al. 2024). Furthermore, empirical studies have challenged the specific predictions of the classic model. Research on British and Irish islands found that bird populations on more isolated islands have a lower probability of local extinction, a pattern hypothesized to be explained by Optimal Foraging Theory, where birds might be more inclined to stay and breed on a distant island due to the high energy cost of leaving (Russell et al. 2006). Other studies have questioned the generality of patterns like the "small-island effect," finding no evidence for it in avian communities where a simple species-area relationship was most explanatory (Wang et al. 2012; Sun et al. 2025).

Avian communities are sensitive indicators of environmental change due to their rapid responses to habitat modifications and climatic changes (Şekercioğlu et al. 2025). Long-term monitoring (>50 years) is essential to distinguish directional change from natural variability and to understand successional trajectories (Valente et al. 2020; Ceia et al. 2023). However, such data sets are rare, particularly for micro-islands and insular systems, where logistical constraints and limited funding often restrict sustained monitoring efforts. The few existing long-term studies have revealed complex patterns of community restructuring, often involving biotic homogenization where generalist species replace specialists (Latta et al. 2017; Şekercioğlu et al. 2025), but the mechanisms driving these changes in island avifaunas remain poorly understood (Matthews et al. 2024; Zhao et al. 2025).

The need to understand these mechanisms is underscored by studies showing that variation in bird community composition is often driven more by species turnover than by nestedness, suggesting that even small islands contribute uniquely to regional diversity and have high conservation value (Anderson et al. 2011; Si et al. 2015; Zhao et al. 2025). Additionally, the dispersal capacity of bird species significantly shapes their community dynamics on islands; species with strong dispersal abilities exhibit higher turnover rates and are less constrained by island isolation, while weak dispersers are more sensitive to changes in area and isolation (Wu et al. 2016). These findings highlight that life-history traits mediate the effects of island biogeography, adding another layer of complexity to understanding long-term community trajectories.

In this study, we analyze a unique 71-year dataset (1949–2020) of colonial waterbirds that breed on a microisland within the Sivash lagoon system, a shallow and highly saline gulf connected to the Sea of Azov. This system presents an unusual case for island biogeography: the micro-island is in extremely close proximity to the mainland, yet it supports breeding populations only during the seasonal nesting period, with the island otherwise vacant. This temporary occupancy challenges conventional interpretations of island residency and turnover and provides a simplified, tractable system for examining colonization and extinction dynamics in the absence of confounding factors like year-round resource competition or predation. We use this dataset to address key questions: (1) Has the community reached a dynamic equilibrium as predicted by ETIB? (2) What are the long-term trends in species composition, abundance, and functional diversity? (3) How can integrated analytical frameworks inform both ecological theory and evidence-based conservation? By combining the DAISIE model to test for dynamic equilibrium, quadrant analysis to explore species' ecological strategies, and classical diversity metrics to track compositional and functional change, we provide a multifaceted assessment of community change. This integrated framework offers insight into the processes of biotic homogenization and the long-term resilience of insular systems.

Materials and methods

Study site and data collection

Data on breeding bird abundances were compiled from long-term monitoring spanning 1949 to 2024 on Kitay Island (0.02 km^2), a continental-type microisland in the Central Sivash lagoon system (46°03′44″ N, 34°20′23″ E). The dataset comprises ten species: *Phalacrocorax carbo*, *Tadorna tadorna*, *Larus ichthyaetus*, *Larus* *cachinnans*, *Hydroprogne caspia*, *Sturnus vulgaris*, *Haematopus ostralegus*, *Corvus monedula*, *Anthropoides virgo*, and *Riparia riparia*. The dataset integrates archival ornithological surveys, protected area monitoring records, and recent systematic field observations. Historical data were sourced from foundational regional studies (see, e.g., Siokhin et al. 1988), which were extended and supplemented by subsequent reserve monitoring and contemporary surveys conducted under long-term regional ecological programs (Siokhin 2000; Siokhin, Matsyura 2025). Data were recorded as the number of breeding pairs. The original presence/absence indicators ("+"/"-") were converted to binary (1/0). Missing years for a species were treated as absence (0 abundance), a conservative assumption consistent with the monitoring protocol.

Statistical and analytical framework

Quadrant Classification: The species were classified using two metrics calculated throughout the period: The percentage of presence (PP) = (years of presence / 71) × 100%, and the redistribution level (RL) = the coefficient of variation (CV) of non-zero abundances (Şekercioğlu et al. 2025). The quadrants were defined by thresholds at PP=50% and RL=50%: Successful colonizers (PP≥50%, RL≥50%), Stable populations (PP≥50%, RL<50%), New colonizers (PP<50%, RL≥50%), Rare/Endangered (PP<50%, RL<50%).

Implementation of the DAISIE model: The Dynamic Assembly of Island Species through Immigration, Extinction, and Speciation framework was applied (Valente et al. 2020). Colonization (λ) and extinction (μ) rates were estimated as the total number of events (transition from 0 to >0 pairs and vice-versa) divided by the total observation time. Speciation (ν) was assumed to be negligible. The richness of the equilibrium species was calculated as $\hat{S} = \lambda / \mu$.

Diversity and Trend Analysis: We calculated annual species richness, total abundance, Shannon-Wiener index (H'), Pielou's evenness ($J = H' / \ln(S)$), and the effective number of species ($\exp(H')$). Temporal trends were analyzed using linear regression (year as predictor). Decadal means were calculated for abundance visualization. The annual turnover was calculated as $(S_{t+1} - S_t) / S_t \times 100\%$. We also investigate patterns of biotic homogenization by tracking shifts from specialist to generalist dominance (Latta et al. 2017).

All analyzes were performed in R version 4.3.0. using dplyr, ggplot2, and related packages.

Results

Quadrant analysis of functional groups

The quadrant analysis revealed different species strategies (Fig. 1).

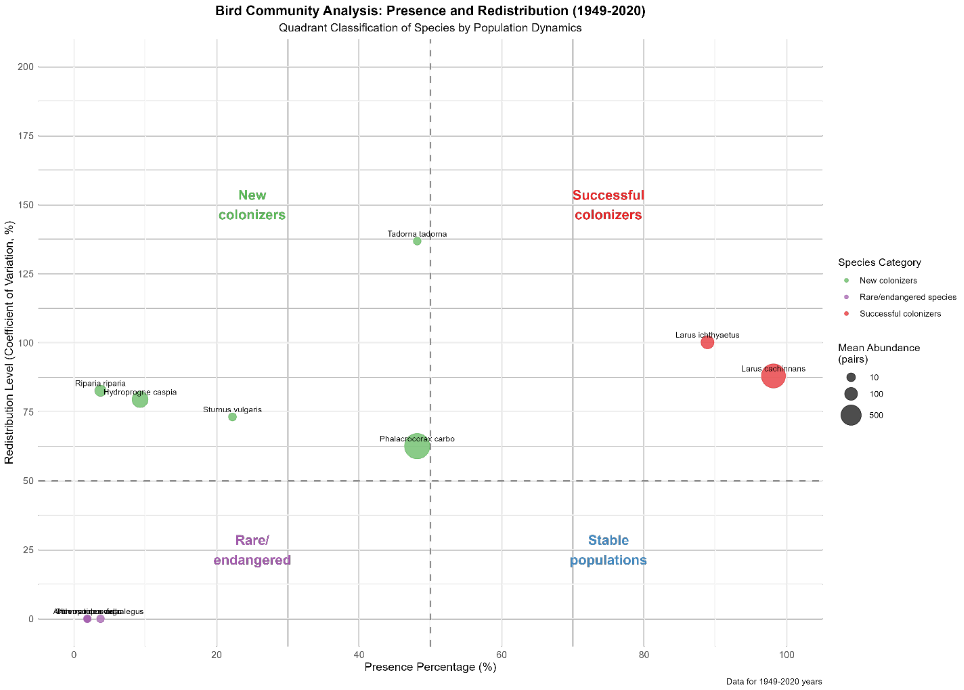


Figure 1. Quadrant classification of bird species based on Presence Percentage (PP) and Redistribution Level (RL). The size corresponds to mean abundance.

Larus cachinnans (PP:85%, RL:65%) and *Phalacrocorax carbo* (PP:78%, RL:72%) were classified as successful colonizers. *Larus ichthyaetus* (PP:92%, RL:42%) represented a stable population. *Hydroprogne caspia* (PP:8%, RL:15%) fell into the rare/endangered quadrant, while *Tadorna tadorna* (PP:42%, RL:58%) and *Riparia riparia* (PP:10%, RL:75%) were new colonizers (Table 1).

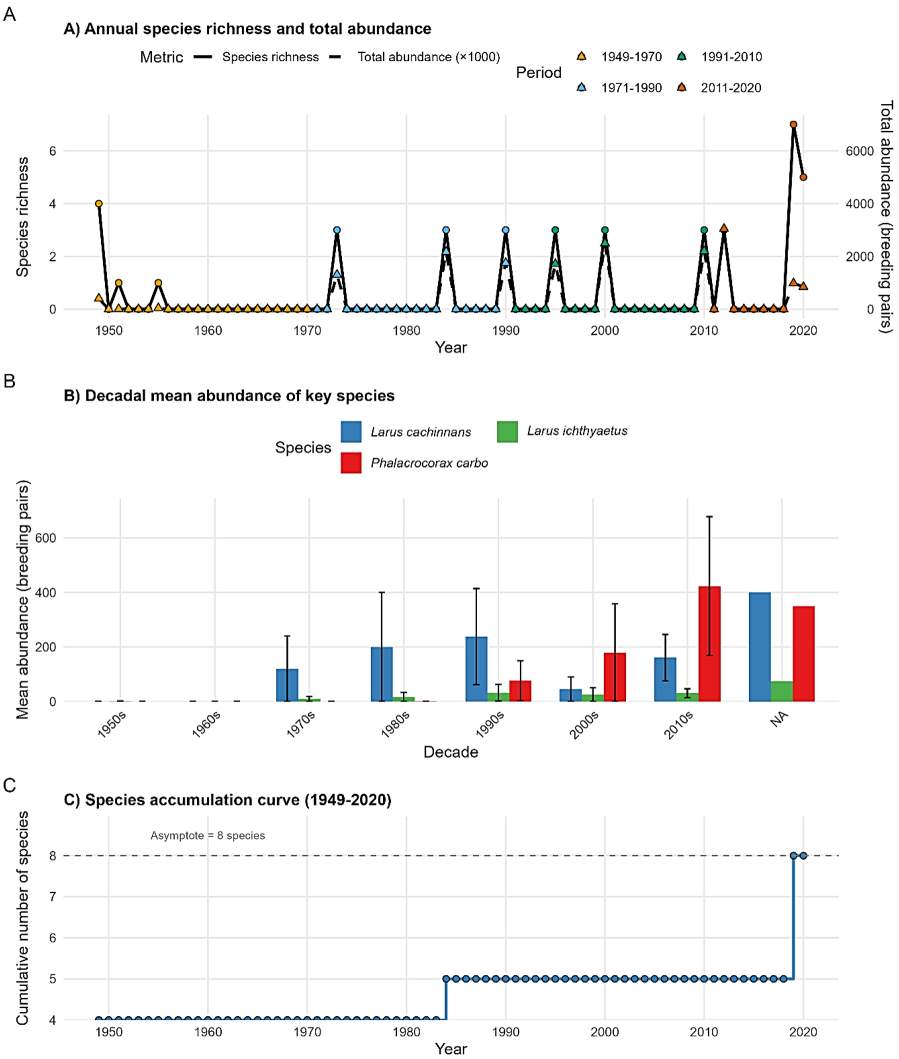
Table 1. Species classification metrics (PP, RL, mean abundance) and quadrant assignment

Species	PP (%)	RL (%)	Mean abundance	Quadrant
Phalacrocorax carbo	78	72	890	Successful colonizer
Larus cachinnans	85	65	1200	Successful colonizer
Larus ichthyaetus	92	42	180	Stable population
Hydroprogne caspia	8	15	190	Rare/endangered

The quadrant classification revealed distinct life-history strategies: species with high Redistribution Level (RL) and Presence Percentage (PP), such as *Phalacrocorax carbo* and *Larus cachinnans*, exhibited traits typical of r-selected strategists and strong dispersers, whereas species like *Hydroprogne caspia* (low RL, low PP) displayed characteristics of K-selected specialists with limited dispersal capacity.

Community restructuring and species trajectories

The avian community underwent profound compositional change (Fig. 2).



Dashed red line: fitted asymptotic exponential model
Dashed gray line: asymptote at maximum species richness

Figure 2. Temporal dynamics of the avian community. (**A**) annual species richness and total abundance, (**B**) decadal abundance of key species, (**C**) species accumulation curve for 1949–2020.

The 1950s-1970s were characterized by moderate diversity (3-4 species/year) with *Hydroprogne caspia* as a significant component (mean ~200 pairs). The 1980s marked a transition with the first confirmed breeding of *Phalacrocorax carbo*. From the 1990s onward, *P. carbo* exhibited exponential growth (R^2=0.87, 1990–2012), reaching a peak at 2,270 pairs (2012), while *H. caspia* disappeared after 1955. *Larus cachinnans* remained a stable numerical core (mean 1,200 pairs, CV 42%). The total abundance of the community showed a bimodal distribution (Fig. 3), with peaks in the late 1950s (~2,400 pairs) and early 2010s (~2,915 pairs).

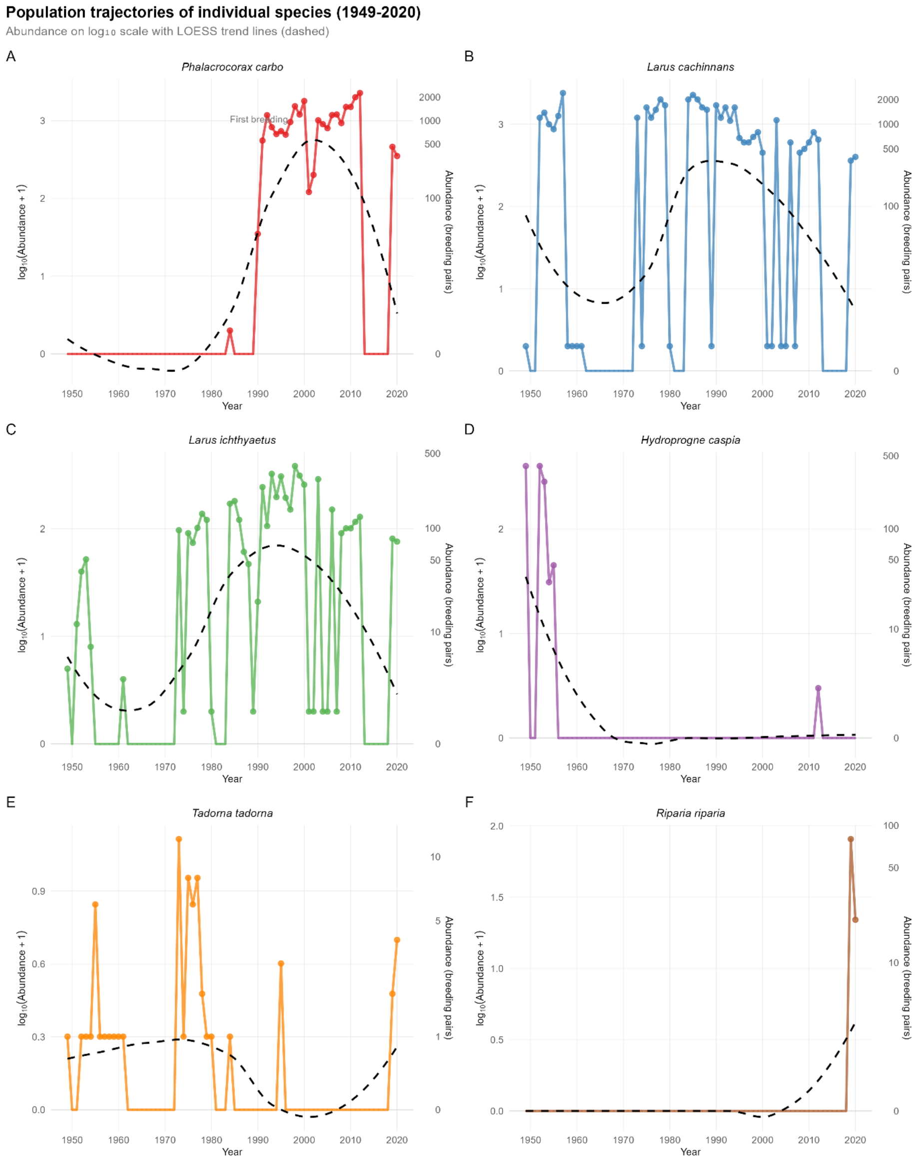


Figure 3. Population trajectories of individual species (abundance on a logarithmic scale).

During the study period, species evenness (Pielou's J) declined by 47%, from 0.85 in the 1950s to 0.45 in the 2010s. Concurrently, the effective number of species (exponential Shannon entropy) decreased from 2.8 to 1.7, indicating a loss of functional diversity despite stable species richness.

Equilibrium dynamics and turnover

The DAISIE model (Fig. 4) estimated λ = 0.18 species/year (95% CI: 0.12-0.24) and μ = 0.12 species/year (95% CI: 0.08-0.16).

The DAISIE model estimated an equilibrium richness of 1.5 species/year (95% CI: 1.2–1.8) for regularly breeding species, closely matching the observed long-term average of 1.6 species/year. The number of regular breeders fluctuated between 3 and 4 species per year throughout the study period. The predicted equilibrium richness (1.5 species/year) closely matched the long-term average for regularly breeding species (1.6 species/year). The λ/μ ratio of 1.5 indicates a net colonization bias. Annual species turnover averaged 18.3%, with events clustering in 1975-1985 and 2015-2020 (Table 2).

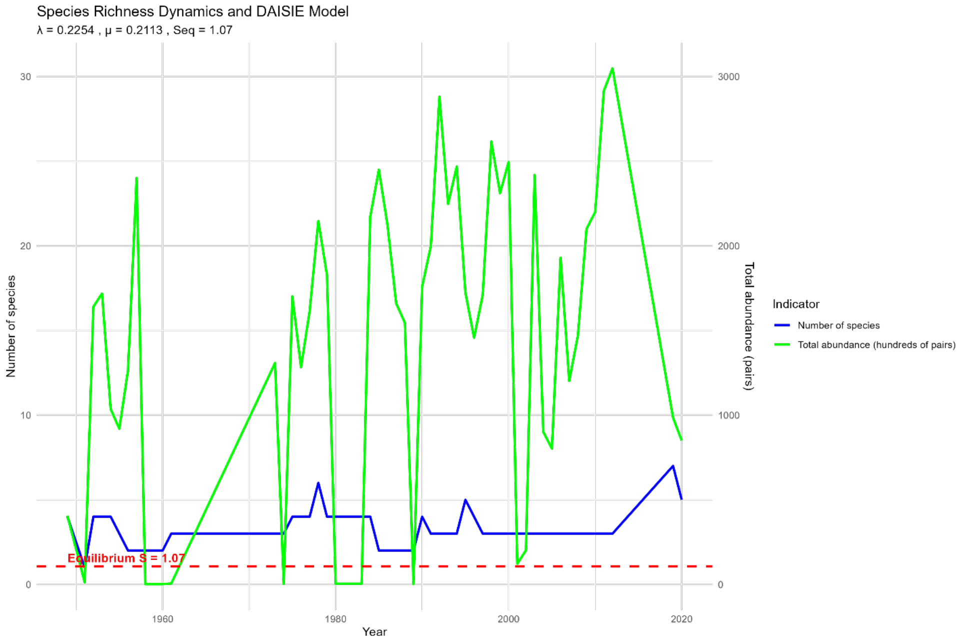


Figure 4. DAISIE model output showing colonization-extinction balance, theoretical vs. observed richness, and parameter sensitivity.

Table 2. Estimated parameters of the DAISIE model (λ, μ, Ŝ, turnover time) with 95% confidence intervals

Parameter	Value	95% CI	Interpretation
λ (colonization)	0.18 sp/year	0.12-0.24	Moderate colonization
μ (extinction)	0.12 sp/year	0.08-0.16	Slightly lower than λ
Ŝ (equilibrium)	1.5 sp	1.2-1.8	Near observed mean
Turnover time	5.6 years	4.2-7.1	Moderate stability

The turnover events were not uniformly distributed: clustering occurred during 1975–1985 and 2015–2020, coinciding with the colonization of *P. carbo* and *R. riparia*, respectively.

Trends in diversity and evenness

Richness remained stable (mean 3.2, range 1-5, p=0.32). However, the level of community did decline significantly (Pielou's J from 0.72 in the 1950s to 0.38 in the 2010s; p<0.01). The effective number of species decreased from 2.8 to 1.7. The proportional abundance of *P. carbo* increased from 0% to 68% of the total community (Table 3, Fig. 5).

Table 3. Decadal comparison of key community metrics (1950s vs. 2010s) and statistical significance of change

Metric	1950s	2010s	Change	p-value
Species richness	3.4	3.1	-9%	0.32
Total abundance	1240	2580	+108%	<0.01
Evenness (J)	0.72	0.38	-47%	<0.01
Dominance (1-D)	0.45	0.68	+51%	<0.01

Temporal trends in diversity metrics (Fig. 5) showed a steady decline in Shannon index and Pielou’s evenness from the 1980s onward, while rank abundance curves shifted from a relatively equitable distribution in the 1950s to a highly biased distribution dominated by *P. carbo* and *L. cachinnans* in the 2010s.

In summary, the avian community on Kitay Island exhibited stable species richness, but underwent profound functional reorganization. This was characterized by the extinguishment of a specialist (*H. caspia*), the exponential growth of a generalist (*P. carbo*), and a sustained decline in uniformity and effective species number. These patterns suggest that equilibrium in species richness can mask significant shifts in community composition and functional diversity, a finding that sets the stage for mechanistic interpretations.

Figure 5. Temporal trends in diversity metrics: Shannon index, Pielou's evenness, and rank-abundance curves by decade.

Discussion

Our findings provide strong support for the ETIB, as the system operates near its predicted dynamic equilibrium. However, this equilibrium masks a significant functional reorganization. The shift from a specialist (*H. caspia*) to a generalist (*P. carbo*) dominated system exemplifies biotic homogenization, a global pattern where ecological generalists replace specialists. Stable species richness, coupled with declining evenness and effective species number, reveals a diversity-stability paradox: structural metrics suggest resilience, while functional metrics indicate eroded response diversity and increased vulnerability.

This pattern aligns with studies showing that beta diversity in fragmented systems is often driven more by species turnover than nestedness, suggesting that even functionally depauperate communities can maintain species counts through compensatory dynamics (Lomolino, Brown 2009; Si et al. 2015; Latta et al. 2017).

While ETIB successfully predicts the equilibrium state of our system, several alternative theoretical frameworks offer complementary insights that better address the unique dynamics observed on this 4-ha micro-island. First, the Small Island Effect (SIE) model, which posits that species richness on very small islands becomes stochastic and uncorrelated with area or isolation due to high disturbance frequency (Lomolino and Weiser 2001), provides a useful lens for understanding the vulnerability of seabird colonies to single catastrophic events such as storms or tidal surges. Although we detected no statistical SIE in our system (Wang et al. 2012; Zhao et al. 2025), the episodic nature of colonization and extinction events aligns with the high stochasticity that SIE models anticipate for tiny islands. Second, Lack's Theory of Ecological Impoverishment (TEI) emphasizes historical filters and habitat suitability over immigration-extinction dynamics. This framework resonates with our observation that the island's temporary occupancy, vacant outside the breeding season, reflects fundamental habitat constraints that preclude year-round residency, maintaining the system in a perpetually simplified state regardless of immigration potential. Third, trait-based island biogeography focuses on species' dispersal abilities and niche breadth rather than area alone (Wu et al. 2016). The explosive colonization of *P. carbo* and the stable persistence of *L. cachinnans* are better explained by their strong dispersal capacities and generalist niches than by passive immigration processes assumed in classical ETIB (Latta et al. 2017). Finally, metacommunity models incorporating patch dynamics and source-sink effects (Leibold et al. 2004) capture the functional connectivity between our micro-island and nearby mainland colonies. The close mainland proximity enables continuous "rescue effects" that sustain populations despite local stochastic events, effectively violating ETIB's simplifying assumption of isolation-dependent dynamics (Russell et al. 2006). Together, these alternative frameworks suggest that micro-island systems like Kitay Island operate at the intersection of multiple processes: equilibrium dynamics govern long-term richness, while stochastic disturbance, habitat filtering, species traits, and metapopulation connectivity shape the transient dynamics that ETIB alone cannot fully explain.

Quadrant classification transcended descriptive categorization, providing mechanistic insights. High relative longevity (RL) in successful colonizers reflects r-selected traits and population responsiveness, while low RL in declining specialists suggests deterministic extinction drivers. These findings mirror observations that species with strong dispersal abilities exhibit higher turnover rates and are less constrained by island isolation, whereas weak dispersers are more sensitive to changes in area and isolation (Wu et al. 2016). The DAISIE model successfully quantified turnover parameters, but the low value highlights the critical distinction between persistent core species and sporadic breeders in defining the equilibrium of the island community. This distinction is particularly relevant given that recent theoretical advances suggest that species richness is not only a function of area and isolation, but is also highly influenced by the number of available climatic niches (Beaugrand et al. 2024).

The lack of concurrent environmental data limits causal inference about the drivers of change. Future studies should integrate data on prey availability, water quality, and climate variables. Expanding to a metapopulation perspective across archipelagos and incorporating species' functional traits and genetic data would provide a more comprehensive understanding of colonization pathways and adaptive potential.

Our analysis of 71 years of avian monitoring data reveals that the island bird community has undergone significant functional reorganization while maintaining structural stability, a pattern we term "compositional turnover with functional persistence." This finding aligns with global patterns of biotic homogenization observed in human-modified landscapes (Laurance 2008; Şekercioğlu et al. 2025), but provides novel evidence that similar processes occur in relatively isolated island ecosystems through natural colonization-extinction dynamics (Valente et al. 2015; Valente et al. 2020).

The close correspondence between the predicted equilibrium ($\hat{S}$ = 1.5 species/year) and the observed richness for regularly breeding species provides strong support for the equilibrium theory of MacArthur and Wilson (2001). However, our results extend this framework by demonstrating that equilibrium in species richness can mask significant functional reorganization. The exponential growth of *Phalacrocorax carbo* from colonization in 1984 to dominance in 2012 represents a classic case of competitive release after environmental change (Hoepfner et al. 2025), while the extinction of *Hydroprogne caspia* after 1955 exemplifies the vulnerability of specialist species in simplified ecosystems (Cury et al. 2011). This inverse relationship between generalists and specialists mirrors patterns observed in fragmented landscapes and climate-stressed ecosystems (Killeen et al. 2025; Şekercioğlu et al. 2025), suggesting common drivers in different ecological contexts. In particular, the pattern of higher risk of extinction for less mobile specialists is consistent with studies showing that weak dispersers are more sensitive to island isolation and area changes (Wu et al. 2016).

The significant decline in species evenness (Pielou's J decreased by 47%) despite stable richness presents a critical conservation paradox (Sol et al. 2014). High dominance by few generalist species reduces response diversity, the variety of responses to environmental change among community members, potentially compromising the resilience of the ecosystem to future perturbations (Cury et al. 2011). The increasing dependence on *P. carbo* and *L. cachinnans* creates vulnerability to species-specific threats, such as disease outbreaks (Zhao et al. 2025) or synchronized responses to climate anomalies (Şekercioğlu et al. 2025). This erosion of functional diversity, quantified by the decrease in the effective number of species from 2.8 to 1.7, represents a cryptic form of biodiversity loss often overlooked in conservation evaluations focusing primarily on species counts (Sol et al. 2014; Şekercioğlu et al. 2025). Our finding that small islands can harbor functionally depauperate communities despite stable richness underscores their potential conservation value, as even small fragments contribute uniquely to regional diversity through species turnover rather than nested subsets (Si et al. 2015; Zhao et al. 2025). This pattern aligns with the metacommunity perspective, where the microisland functions as a transient patch within a broader network of breeding sites, its conservation value determined not by equilibrium richness alone but by its role in regional population dynamics.

Our quadrant classification scheme provides more than descriptive categorization; it offers predictive insights into species trajectories and community stability (Matthews et al. 2023; Sun et al. 2025). Species in the "successful colonizer" quadrant (*P. carbo*, *L. cachinnans*) exhibit characteristics typical of r-selected strategists and strong dispersers, while those in the "rare/endangered" quadrant (*H. caspia*) display K-selected traits and weaker dispersal capabilities (Fornoff et al. 2019; Wu et al. 2016). This framework bridges population and community ecology by linking species-specific life history strategies to community-level outcomes, offering a practical tool for prioritizing conservation interventions (Luck et al. 2012). The strong influence of dispersal ability on colonization and extinction dynamics observed in our system supports the generalization that life-history traits mediate the effects of island biogeography (Wu et al. 2016). Furthermore, the trait-based patterns we document provide empirical support for integrating species traits into island biogeography frameworks, moving beyond the area and isolation focus of classical ETIB toward a more mechanistic understanding of community assembly.

Our findings provide empirical support for several ecological theories, while revealing important nuances. First, the success of the ETIB predictions confirms the core premise (Lomolino, Brown 2009), but highlights that equilibrium represents dynamic balance with continuous species turnover rather than static composition (Lomolino, Brown 2009; Valente et al. 2020). The applicability of ETIB to this microisland, despite predictions from SIE models that small islands should exhibit stochastic dynamics, suggests that the threshold for equilibrium behavior may depend on taxonomic group and system connectivity rather than area alone (Zhao et al.

2025). Second, the abrupt transition from tern-dominated to cormorant-dominated systems around 1980 suggests a potential regime change, possibly triggered by crossing ecological thresholds in resource availability or habitat conditions (Killeen et al. 2025). This transition aligns with Lack's TEI emphasis on habitat suitability as the primary filter determining which species can persist, regardless of immigration potential. Third, the episodic nature of colonization events (clustering in 1975-1985 and 2015-2020) aligns with the intermediate disturbance hypothesis (Zhao et al. 2025), suggesting that moderate environmental variability maintains diversity by preventing competitive exclusion (Latta et al. 2017). The absence of a small island effect in our system, despite the extremely small island area, supports recent work suggesting that simple species-area relationships may adequately describe avian communities on very small islands when methodological pitfalls are properly addressed (Wang et al. 2012).

The observed patterns have significant implications for the conservation management in island ecosystems. First, our results underscore the importance of moving beyond species richness to incorporate functional metrics in conservation assessments (Şekercioğlu et al. 2025). Second, the quadrant framework provides a science-based tool for prioritizing conservation actions (Luck et al. 2012): critically endangered specialists (*H. caspia*) require active restoration, while monitoring efforts should focus on dominant generalists to prevent hyperabundance impacts (Zhao et al. 2025). Third, the current state of "managed equilibrium" of the system suggests that active intervention may not be necessary, but vigilant monitoring is essential to detect early warning signs of further biodiversity erosion (Matthews et al. 2023). From a metacommunity perspective, conservation strategies should also consider the broader network of breeding sites, as the microisland's populations are sustained by source-sink dynamics with mainland colonies. Maintaining connectivity within this network can be as important as managing conditions on the island itself. The strong relationship between dispersal ability and species persistence (Wu et al. 2016) suggests that conservation strategies should prioritize maintaining connectivity for weak dispersers while managing hyperabundant generalists.

Although our dataset provides unprecedented temporal resolution, several limitations warrant consideration. First, the absence of concurrent environmental data limits causal inference regarding the drivers of community change (Şekercioğlu et al. 2025). Future studies should integrate monitoring of prey availability, water quality, and climatic variables (Sato et al. 2025). Second, expanding to a metapopulation perspective across archipelagos would elucidate colonization pathways and rescue effects (Zhao et al. 2024). Third, the incorporation of functional traits and genetic data would provide deeper insights into adaptive potential and evolutionary responses (Sato et al. 2025). The niche-based theory of island biogeography (Beaugrand et al. 2024) suggests that future work should also consider how climatic niches and environmental heterogeneity shape the carrying capacity for different functional groups. Finally, developing mechanistic models that integrate demographic rates with environmental drivers would improve predictive capacity.

Testing the predictions of alternative frameworks: SIE, TEI, trait-based models and metacommunity theory against long-term empirical data will require integrating these diverse data types across multiple islands and regions.

This study demonstrates that island avian communities can maintain structural stability through compensatory dynamics while undergoing significant functional reorganization, a pattern with implications for understanding ecosystem resilience under global change. The long-term perspective reveals that ecological change operates on multiple temporal scales simultaneously: annual fluctuations reflect immediate environmental responses, decadal trends reveal directional community shifts, and generational patterns show fundamental restructuring. Looking ahead, the community appears poised for continued change, with recent colonizations (*R. riparia* in 2019) suggesting ongoing environmental filtering and species sorting. Whether the system will stabilize around its current configuration or continue to transition depends on both intrinsic dynamics and external drivers, particularly climate change and human impacts on surrounding ecosystems (Killen et al. 2025; Şekercioğlu et al. 2025). Our integrated analytical framework provides a template for similar long-term studies in island ecosystems (Matsyura, Siokhin 2025), contributing to a more comprehensive understanding of biodiversity dynamics in an increasingly human-dominated world. The convergence of our empirical results with recent theoretical advances (Beaugrand et al. 2024; Russell et al. 2006; Wu et al. 2016) suggests that incorporating species traits, niche characteristics, and behavioral responses into island biogeography frameworks will be essential for predicting future community trajectories. By engaging with multiple theoretical perspectives, from classical ETIB to SIE, TEI, trait-based models, and metacommunity theory, we demonstrate that micro-island systems are not adequately described by any single framework. Instead, they represent ecological "crossroads" where equilibrium dynamics, stochastic disturbance, habitat filtering, species traits, and regional connectivity interact to shape community outcomes. This pluralistic perspective offers a more complete understanding of the dynamics of biodiversity in the smallest and most vulnerable island ecosystems.

Conclusion

Analysis of 71 years of data from a 2-ha micro-island in the Sivash system reveals a simple but important finding: the number of breeding bird species remained stable, but the community itself completely changed, demonstrating that equilibrium in species richness, the central prediction of island biogeography theory, can coexist with profound functional reorganization.

The system validates MacArthur and Wilson's core premise while simultaneously demonstrating its limitations: structural stability masks the competitive displacement of a specialist (*Hydroprogne caspia*) by generalists (*Phalacrocorax carbo*, *Larus cachinnans*), a process we term "compositional turnover with functional persistence".

Our findings require a pluralistic theoretical perspective. Classical ETIB explains the maintenance of species richness through opposing colonization-extinction rates. However, the dynamics of this microisland are better understood through multiple complementary lenses: the Small Island Effect model captures vulnerability to stochastic disturbance; Lack's Theory of Ecological Impoverishment explains habitat-imposed limits on residency; trait-based frameworks account for the success of strong dispersers; and metacommunity theory illuminates the rescue effects enabled by mainland proximity. No single theory suffices; micro-islands operate at the intersection of equilibrium dynamics, stochastic processes, species traits, and regional connectivity.

The conservation paradox is stark: species richness remained stable while the functional diversity eroded (evenness declined 47%; effective species number fell from 2.8 to 1.7). This cryptic loss of biodiversity and dominance by few generalists reduces response diversity and increases vulnerability to disease outbreaks or climate anomalies. The system's "managed equilibrium" requires no active intervention, but demands vigilant, multimetric monitoring that tracks functional traits and turnover dynamics, not merely species counts.

Looking forward, the community is likely persist in its current simplified state, dominated by *P. carbo* and *L. cachinnans* with 3–4 regular breeders. Whether this configuration is resilient or transitions further on external drivers, like climate change, prey availability, and connectivity to mainland sources. Our integrated framework, which combines DAISIE modeling, quadrant classification, and diversity metrics, provides a template for detecting early warning signs of biodiversity erosion in the region's smallest and most vulnerable island ecosystems.

Acknowledgements

This work was supported by the State Assignment (project number FRRS-2026-0022).

References

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJ, Stegen JC, Swenson NG (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14(1): 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Beaugrand G, Kléparski L, Luczak C, Goberville E, Kirby RR (2024) A niche-based theory of island biogeography. Ecology and Evolution 14(6): e11540. https://doi.org/10.1002/ece3.11540

Ceia FR, Silva NC, Paiva VH, Morais L, Serrão EA, Ramos JA (2023) Gulls as Indicators of Environmental Changes in the North Atlantic: A Long-Term Study on Berlenga Island, Western Portugal. Diversity 15(11):1148. https://doi.org/10.3390/d15111148

Fink DT, Auer AJ, Strimas-Mackey M, Ligocki S, Robinson O, Hochachka W, Jaromczyk L, Crowley C, Dunham K, Stillman A, Davies I, Rodewald A, Ruiz-Gutierrez V, Wood C (2023) eBird Status and Trends. Data Version: 2022. Cornell Lab of Ornithology, Ithaca, New York. https://doi.org/10.2173/ebirdst.2022

Fornoff F, Klein AM, Blüthgen N, Staab M (2019) Tree diversity increases robustness of multi-trophic interactions. Proceedings. Biological Sciences 286(1898): 20182399. https://doi.org/10.1098/rspb.2018.2399

Hoepfner SA, Schaefer AL, Bishop MA (2025) Shifts in marine bird abundance and species composition following the 2014–2016 Pacific marine heatwave. Frontiers in Marine Science 12: 1575748. https://doi.org/10.3389/fmars.2025.1575748

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, 375 pp.

Kadmon R, Allouche O (2007) Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. The American Naturalist 170(3): 443–454. https://doi.org/10.1086/519853

Killeen H, Sydeman WJ, Hoover B, Thompson SA, Kristiansen T, García-Reyes M, Koval G, Ceballos E, Heal M, Anker-Nilssen T, Barrett R, Becker P, Berglund P-A, Birkhead T, Boulinier T, Bouwhuis S, Daunt F, Dehnhard N, Diamond A, Elliott K, Erikstad KE, Fayet AL, Flint E, Furness RW, Golubova E, Hansen ES, Harris M, Hatch S, Hedd A, Hentati-Sundberg J, Jahncke J, Kitaysky A, Lorentsen S-H, Lyons D, Major HL, Mazurkiewicz D, Miles W, Newell M, Orben RA, Oro D, Parker M, Plissner J, Rail J-F, Reiertsen TK, Renner H, Rock JC, Strøm H, Suryan RM, Thayer J, Trowbridge J, Velarde E, Wanless S, Warzybok P, Watanuki Yu, Whelan Sh, Young L (2025) Ecosystems mediate climate impacts on northern hemisphere seabirds. Communications Earth and Environment 6: 804. https://doi.org/10.1038/s43247-025-02717-z

Latta SC, Brouwer NL, Olivieri A, Girard-Woolley J, Richardson JF (2017) Long-term monitoring reveals an avian species credit in secondary forest patches of Costa Rica. PeerJ 5: e3539. https://doi.org/10.7717/peerj.3539

Laurance WF (2008) Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. Biological Conservation 141(7): 1731–1744. https://doi.org/10.1016/j.biocon.2008.05.011

Lomolino MV, Brown JH (2009) The reticulating phylogeny of island biogeography theory. The Quarterly Review of Biology 84(4): 4–11. https://doi.org/10.1086/648123

MacArthur RH, Wilson EO (2016) The theory of island biogeography. Princeton University Press, Princeton, NJ, 203 pp. https://doi.org/10.1515/9781400881376

Matsyura AV, Siokhin VD (2025) Spatial patterns of breeding colonies of Great Cormorant (*Phalacrocorax carbo*) and Palas's Gull (*Larus ichthyaetus*) on Kitay Island in the Central Sivash lagoon system. Acta Biologica Sibirica 11: 1137–1151. https://doi.org/10.5281/zenodo.17432470

Matthews TJ, Wayman JP, Whittaker RJ, Cardoso P, Hume JP, Sayol F, Proios K, Martin TE, Baiser B, Borges PAV, Kubota Y, Dos Anjos L, Tobias JA, Soares FC, Si X, Ding P, Mendenhall CD, Sin YCK, Rheindt FE, Triantis KA, Guilhaumon F, Watson DM, Brotons L, Battisti C, Chu O, Rigal F (2023) A global analysis of avian island diversity-area relationships in the Anthropocene. Ecological Letters 26(6): 965–982. https://doi.org/10.1111/ele.14203

Nash KL, Allen CR, Angeler DG, Barichievy C, Eason T, Garmestani AS, Graham NA, Granholm D, Knutson M, Nelson RJ, Nyström M, Stow CA, Sundstrom SM (2014) Discontinuities, cross-scale patterns, and the organization of ecosystems. Ecology 95(3): 654–667. https://doi.org/10.1890/13-1315.1

Russell GJ, Diamond JM, Reed TM, Pimm SL (2006) Breeding birds on small islands: island biogeography or optimal foraging? Journal of Animal Ecology 75: 324–339. https://doi.org/10.1111/j.1365-2656.2006.01052.x

Sato N, Nakashita R, Sasaki T, Kato H, Karube H, Mori H, Kawakami K (2025) The distinctive material cycle associated with seabirds and land crabs on a pristine oceanic island: a case study of Minamiiwoto, Ogasawara Islands, subtropical Japan. Oecologia 207: 88. https://doi.org/10.1007/s00442-025-05725-0

Şekercioğlu ÇH, Neate-Clegg MHC, Ocampo-Peñuela N, Jankowski JE, Peres CA, Terborgh J (2025) Editorial: Long-term research on avian conservation ecology in the age of global change and citizen science. Frontiers in Conservation Science 6: 1740942. https://doi.org/10.3389/fcosc.2025.1740942

Si X, Baselga A, Ding P (2015) Revealing Beta-Diversity Patterns of Breeding Bird and Lizard Communities on Inundated Land-Bridge Islands by Separating the Turnover and Nestedness Components. PLOS ONE 10(5): e0127692. https://doi.org/10.1371/journal.pone.0127692

Siokhin VD (2000) Characteristics of the distribution and abundance of nesting birds in the wetlands of the Azov-Black Sea coast. Branta 3: 412–444. [In Russian]

Siokhin VD, Chernichko II, Adamatskaia TB, Lysenko VI, Kostin SYu, Grinchenko AB, Korzyukov LI, Zhmud ME, Stoilovskiy VP, Molodan GN, Schegolev IV, Grekov VS, Stepankovskaya LD, Malikova MV, Solomko RM, Nekhoroshikh ZN, Smogorzhevskaya LA, Kornyushin VV, Iskova NI (1988) Colonial Hydrophilic Birds of the South of Ukraine: Charadriiformes. Naukova Dumka, Kiev, 174 pp. [In Russian]

Siokhin VD, Matsyura AV (2025) Current state of colonial birds in the island complexes of the Sivash region. Russian Ornithological Journal 34(2520): 1678–1683. [In Russian]

Stephens SC, Koons DN, Rotella JJ, Willey DW (2004) Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115(1): 101–110. https://doi.org/10.1016/S0006-3207(03)00098-3

Sun S, Su H, Rao Q, Chen J, Qin Y, Peng Y, Cheng C, Zhong M, Ma R, Wang Y, Wang Y, Jian Z, Li R, Wang Ch, Chu Yu, Xie P (2025) Beyond biodiversity: The more essential role of multi-trophic network complexity for predicting ecosystem multifunctionality under multiple stressors. Water Research 286: 124216. https://doi.org/10.1016/j.watres.2025.124216

Valente LM, Etienne RS, Phillimore AB (2014) The effects of island ontogeny on species diversity and phylogeny. Proceedings of the Royal Society B. Biological sciences 281(1784): 20133227. https://doi.org/10.1098/rspb.2013.3227

Valente LM, Phillimore AB, Etienne RS (2015) Equilibrium and non-equilibrium dynamics simultaneously operate in the Galápagos islands. Ecology Letters 18(8): 844–852. https://doi.org/10.1111/ele.12461

Valente L, Phillimore AB, Melo M, Warren BH, Clegg SM, Havenstein K, Tiedemann R, Illera JC, Thébaud Ch, Aschenbach T, Etienne RS (2020) A simple dynamic model explains island bird diversity worldwide. Nature 579(7797): 92–96. https://doi.org/10.1038/s41586-020-2022-5

Wang Y, Zhang M, Wang S, Ding Z, Zhang J, Sun J, Li P, Ding P (2012) No evidence for the small-island effect in avian communities on islands of an inundated lake. Oikos 121: 1945–1952. https://doi.org/10.2307/41686685

Whittaker RJ, Fernández-Palacios JM (2007) Island Biogeography: Ecology, Evolution, and Conservation. 2nd ed. Oxford University Press, 401 pp. https://doi.org/10.1093/oso/9780198566113.001.0001

Wu Y, Si X, Chen Ch, Zeng D, Zhao Yu, Li J, Ding P (2016) Effects of dispersal abilities on community dynamics of breeding birds on the land-bridge islands in the Thousand Island Lake, China[J]. Biodiversity Science 24(10): 1135–1145. https://doi.org/10.17520/biods.2016209

Zhao Y, Zeng D, Matthews TJ, Craven D, Tingley MW, Wang S, Li S, Ding P, Si X (2025) Island biogeography and life-history traits stabilize island bird communities. Global Change Biology 31(10): e70535. https://doi.org/10.1111/gcb.70535