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RESEARCH ARTICLE

Island Biogeography and Life-History Traits Stabilize Island Bird Communities

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ABSTRACT

Islands are model systems for testing and developing ecological theories. Despite extensive research on island biodiversity, the importance of the biogeographic context for biodiversity–stability relationships is poorly understood. We addressed this knowledge gap by integrating the Equilibrium Theory of Island Biogeography (ETIB) with a functional perspective to explore island biodiversity–stability relationships. We conducted annual breeding bird surveys across 36 land-bridge islands in eastern China over 13 years. Using this long-term dataset, we quantified avian temporal community stability (and its components of population stability and population asynchrony) and tested how island biogeographic factors (i.e., island area, isolation, colonization rates, and extinction rates) and biodiversity facets (i.e., species richness, average population size, and life-history traits) interact to influence stability. We found larger islands supported higher species richness due to colonization–extinction dynamics and habitat heterogeneity, which in turn promote both population stability and asynchrony. In addition, larger islands harbored larger and individually more stable populations over time. In contrast, island isolation had a weak net effect on stability, as its positive and negative influences through different pathways balanced each other out. Furthermore, species with 'fast' life-history traits, characterized by shorter generation times, contributed more to community stability. These findings clarify multiple pathways through which biogeographic factors shape avian community dynamics on islands. Our study thus illustrates how island biotas maintain community stability and provides insights for preserving biodiversity and ecosystem functioning in fragmented or island-like landscapes facing rapid biodiversity loss in an era of global change.

Yuhao Zhao and Di Zeng should be considered joint first authors.

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1 | Introduction

Islands are model systems for developing and testing fundamental theories in ecology and evolution (Whittaker et al. 2023). A seminal example is the Equilibrium Theory of Island Biogeography (ETIB), which elegantly predicts species richness from the dynamic balance of colonization and extinction rates while assuming ecological equivalence of species (i.e., species neutrality) (MacArthur and Wilson 1963, 1967). Recent extensions of ETIB have incorporated functional ecology (Jacquet et al. 2017), illustrating how ecological strategies determined by functional traits shape the assembly of island biotas (Whittaker et al. 2014; Si et al. 2022; Barajas Barbosa et al. 2023). While ETIB and functional ecology have significantly advanced our comprehension of island biodiversity patterns, the contribution of these patterns to maintaining ecosystem functioning over time (i.e., ecosystem stability) has yet to be examined thoroughly (Gonzalez et al. 2020). As island ecosystem functions may be destabilized by biodiversity loss and environmental perturbations, clarifying the processes and mechanisms of biodiversity–stability relationships is imperative for the sustainability of island ecosystem management (Wardle and Zackrisson 2005; Hautier et al. 2015; Fanin et al. 2018).

Temporal community stability, defined as the ratio of the temporal mean to the standard deviation of community productivity (e.g., abundance or biomass) (Thibaut and Connolly 2013), is a critical facet of ecosystem stability. Stable communities are better protected against species loss and biological invasions, thereby ensuring the provisioning of ecosystem services (Pimm 1984). Although ETIB's spatial (e.g., accounting for differences in island area and isolation) and temporal (e.g., the processes of colonization and extinction) perspectives (Gonzalez and Chaneton 2002; Greig et al. 2022), as well as trait-based perspectives (Tolmos et al. 2024), may underlie community stability, they have yet to be tested empirically in island contexts (but see Teittinen et al. 2022 for a relevant study of an aquatic microcosm). To fill this gap, we propose a framework that incorporates ETIB and functional ecology, aiming to advance our understanding of the mechanisms underlying island biodiversity–stability relationships (Figure 1; Table 1).

According to the ETIB and its extensions, larger and less isolated islands can support relatively larger population sizes, which will lead to lower extinction rates by reducing the chance of inbreeding (Brown and Kodric-Brown 1977) and/or demographic stochasticity (Pimm et al. 1988). Meanwhile, larger and less isolated islands possess higher colonization rates through target and distance effects (MacArthur and Wilson 1963, 1967; Lomolino 1990). Both lower extinction rates and higher colonization rates are theorized to result in higher species richness. A community with more species is expected to contain species with differential responses to abiotic drivers (Tredennick et al. 2017), consequently promoting asynchronous population fluctuations among species over time (Yachi and Loreau 1999; McCann 2000). This population

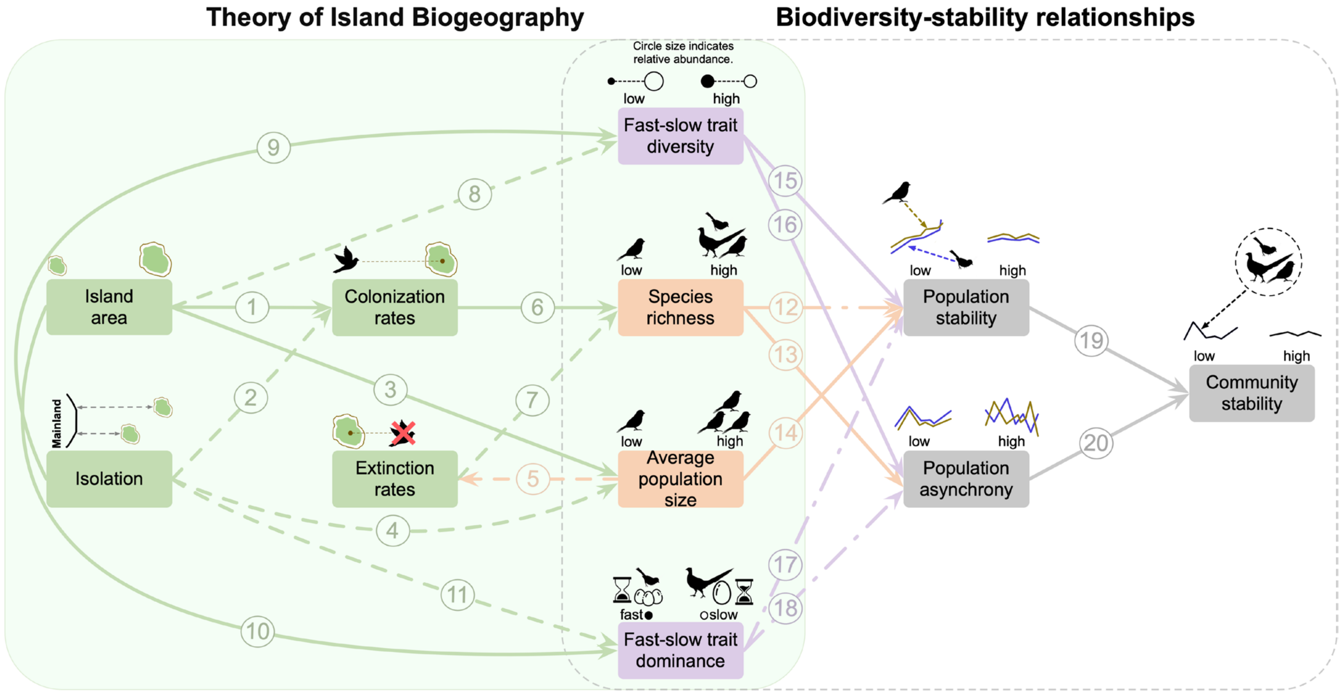

FIGURE 1 | The hypothesized pathways through which island biogeographic factors, average population size, species richness, and 'fast-slow' life-history traits (left, green background) may influence island biodiversity–stability relationships (right, dashed frame). Colored rectangles represent measured metrics and arrows represent hypothesized pathways between metrics. Solid and dashed lines indicate positive or negative relationships, respectively. Dot-dashed lines indicate the possibility for either positive or negative relationships. Sketches illustrating the meaning of each metric are partly modified from https://www.freepik.com/. Black and white circles above fast-slow trait dominance and diversity represent 'fast' and 'slow' species, respectively. Green rectangles: Island biogeographic factors; Grapefruit rectangle: Species richness and average population size; Purple rectangles: 'fast-slow' trait metrics; Grey rectangles: Stability metrics. See Table 1 in the main text for the rationale behind each pathway.

TABLE 1 | Hypothesized pathways and associated processes and mechanisms related to island bird community stability (see also Figure 1).

Pathways	Processes and mechanisms
① Island area → colonization rates (+)	Larger islands will have a higher probability of being colonized by individuals (target effect) (Lomolino 1990).
② Isolation → colonization rates (−)	More isolated islands possess lower colonization rates as they receive fewer immigrant species (distance effect) (MacArthur and Wilson 1963, 1967).
③ Island area → average population size (+) ④ Isolation → average population size (−)	Larger islands will possess higher average population sizes of individual species (area effect) (MacArthur and Wilson 1963, 1967). Islands close to potential sources receive more immigrating individuals of already present species (rescue effect) (Brown and Kodric-Brown 1977).
⑤ Average population size → extinction rates (−)	Larger populations will have lower extinction risk by reducing the chances of inbreeding (Brown and Kodric-Brown 1977) and/or demographic stochasticity (Pimm et al. 1988).
⑥ Colonization rates → species richness (+) ⑦ Extinction rates → species richness (−)	Higher colonization rates and lower extinction rates will result in higher species richness according to the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur and Wilson 1963, 1967).
⑧ Island area → fast-slow trait diversity (+) ⑨ Isolation → fast-slow trait diversity (−)	Fast-slow trait diversity (i.e., functional dispersion of the first axis of a PCA relating to the 'fast-slow' continuum; see Methods for more details) indicates the diversity and complementarity of 'fast-slow' traits. Larger islands contain a broader range of habitats (Wardle et al. 2003; Barajas-Barbosa et al. 2020) whereas less isolated islands are relatively easier for birds to colonize. In both cases, we expect a wider range of species with a diversity of 'fast-slow' life-history strategies will co-exist (i.e., niche complementarity) (Si et al. 2017; Zhao et al. 2020).
⑩ Island area → fast-slow trait dominance (−) ⑪ Isolation → fast-slow trait dominance (+)	In our study system, a higher value of fast-slow trait dominance (i.e., community-weighted mean of the first axis of a PCA relating to the 'fast-slow' continuum; see Methods for more details) indicates a higher proportion of 'slow' species in a community. According to the 'island syndrome' model (Adler and Levins 1994; Terborgh et al. 2001), island communities will be dominated by 'slow' species because they may experience less interspecific competition and predation risk due to fewer predator and competitor species compared to the mainland, especially on small and more isolated islands (Novosolov and Meiri 2013).
⑫ Species richness → population stability (±)	Higher species richness will reduce population stability if there are strong competitive interactions among different species in the community (Ives et al. 1999; Lehman and Tilman 2000). Alternatively, population stability will be enhanced if the number of weak (or mutualistic and facilitative) interactions increases with species richness (Jiang and Pu 2009).
⑬ Species richness → population asynchrony (+)	Species will respond differently to temporal fluctuations, so year-to-year abundance changes in some species will be offset by fluctuations of other species (McNaughton 1978; Gonzalez and Loreau 2009). Thus, higher species richness will increase the chance that an island community contains species that will respond differently to abiotic drivers, promoting population asynchrony (McCann 2000; de Mazancourt et al. 2013).
⑭ Average population size → population stability (+)	Communities with larger average population size may remain stable under environmental fluctuations through the buffer effect (Brown 1969).

(Continues)

TABLE 1 | (Continued)

Pathways	Processes and mechanisms
⑮ Fast-slow trait diversity → population stability (+) ⑯ Fast-slow trait diversity → population asynchrony (+)	Communities with a diversity of 'fast-slow' traits will have higher stability through the joint role of 'fast' (higher resilience) and 'slow' (greater resistance) species (Craven et al. 2018; Li et al. 2021) (see also below).
⑰ Fast-slow trait dominance → population stability (±) ⑱ Fast-slow trait dominance → population asynchrony (±)	'Fast' species have high reproductive output and can be more resilient after disturbance (O'Connor 1981). In contrast, 'slow' species are more resistant to disturbance (Hua et al. 2013). Thus, communities dominated either by 'fast' or 'slow' species may increase or decrease population stability and asynchrony depending on environmental variability (Li et al. 2021).
⑲ Population stability → community stability (+) ⑳ Population asynchrony → community stability (+)	Theoretical and empirical studies have shown that community stability is a product of abundance-weighted average species-level invariability (i.e., population stability) and the synchrony of population fluctuations (i.e., population asynchrony) (Thibaut and Connolly 2013; Wang et al. 2019; Olivier et al. 2020; Schnabel et al. 2021).

asynchrony is a key factor that can enhance community stability (Thibaut and Connolly 2013; Xu et al. 2021). Population stability, another factor that influences community stability, is defined as the weighted average stability of all co-occurring species (Thibaut and Connolly 2013; Xu et al. 2021). Unlike population asynchrony, population stability may either increase or decrease with species richness depending on the interaction types among co-occurring species (May 1973; Jiang and Pu 2009). For example, in the context of birds, an insular community with more species may have reduced population stability if antagonistic interactions (e.g., competition) dominate, while population stability may be enhanced if mutualistic and facilitative interactions (e.g., mixed-species bird flocks) are more prevalent (Table 1). In addition, population stability could be strengthened by a higher average population size of all species within an island because larger populations may remain more stable under environmental fluctuation through the buffer effect (Brown 1969). Collectively, island area and isolation could affect community stability via the integration of species richness–population stability, population size–population stability, and species richness–population asynchrony relationships (Figure 1; Table 1).

From a trait-based perspective, the impacts of island area and isolation on community stability could be mediated through the functional traits of co-occurring species (de Bello et al. 2021). The 'fast-slow' continuum, representative of life-history strategies, offers a nuanced understanding of such effects (Reich 2014; Neyret et al. 2024). Specifically, species with higher rates of resource uptake and growth (e.g., small body sizes, short life spans, and high fecundity) are characterized as 'fast' species, which are able to recover rapidly after disturbances (i.e., higher resilience) (Bird et al. 2020). Conversely, 'slow' species are those with conservative traits of slower rates of growth and resource uptake (Albaladejo-Robles et al. 2023) and exhibit greater resistance to environmental stress and instability (Cooke et al. 2019). Larger and less isolated islands harbor not only higher species richness (through colonization-extinction dynamics) but also a broader spectrum of 'fast-slow' traits as they provide either abundant resources or improved accessibility to potential colonizers (i.e., if more species can colonize, a broader spectrum of fast–slow traits is likely to be represented) (Schrader et al. 2021; Zhao et al. 2024). Accordingly, islands with a greater diversity of 'fast-slow' strategies may have higher stability, as they likely include 'fast' species with higher resilience as well as 'slow' species with higher resistance (Craven et al. 2018). Studies have shown that islands tend to favor 'slow' species (Novosolov and Meiri 2013), likely because island populations experience reduced predation and interspecific competition pressures (Adler and Levins 1994; Terborgh et al. 2001). However, the relative contributions of these pathways to community stability on islands remain to be empirically evaluated (Table 1).

In this study, we used annual breeding bird surveying data collected on 36 islands from 2009 to 2021 (a total of 13 years) in a land-bridge island system, the Thousand Island Lake, China, to examine the community stability of island birds under our proposed framework (Figure 1; Table 1). We focused on birds as they provide key ecosystem services in island forests, such as seed dispersal and pollination among isolated islands (Anderson et al. 2011; Li et al. 2022). For each island, we calculated bird community stability and partitioned community stability into population stability and population asynchrony based on species' abundances (i.e., relative abundance after accounting for species' imperfect detection and temporal autocorrelation). We then applied piecewise structural equation modelling (SEM) to quantify how components of community stability are affected by species richness, average population size, and traits related to 'fast-slow' life-history strategies, and the extent to which biodiversity–stability relationships are determined by island biogeographic factors (island area, isolation, colonization rates, or extinction rates). We find that species richness and average population size are the main drivers of avian community stability via the direct and indirect (i.e., colonization-extinction dynamics) effects of island area, revealing the important role of ETIB in predicting bird community stability on islands.

2 | Materials and Methods

2.1 | Study Area

This study was carried out in an artificial land-bridge island system, namely Thousand Island Lake (TIL), which was formed due to dam construction in 1959 in eastern China (29°22′–29°50′ N, 118°34′–119°15′ E). The flooding converted hilltops into islands, with a total number of 1078 islands at the highest water level (108 m). The lake area is approximately 580 km^2 (total island area is 41 km^2). The forests around TIL were nearly clear-cut by local people during the late 1950s, and thus all islands have experienced the same successional history (Wilson et al. 2016). Since the 1960s, the local government has established a strict protection policy such that the islands in TIL have been rarely disturbed. Currently, the main vegetation on these islands is secondary successional forest dominated by Masson pine (*Pinus massoniana*) with a mixture of broad-leaved tree species (e.g., *Loropetalum chinense*, *Vaccinium carlesii*, and *Rhododendron simsii*) (Ren et al. 2023). The region has a typical monsoon climate with a hot summer (June to August) and a cold winter (November to January). The average annual temperature is 17.0°C, with the daily temperature ranging from −7.6°C in January to 41.8°C in July (Si et al. 2014). The annual precipitation of the region is 1430 mm, mainly concentrated in the rainy season from April to June (Si et al. 2014).

2.2 | Target Taxon

Birds are a fundamental component of many ecosystems and their stability is vital for maintaining multiple ecosystem functions and services including seed dispersal, pollination, and pest control (Sekercioglu et al. 2016; Gaston 2022). They have served as an ideal group for investigating island biogeography (Valente et al. 2020) and biodiversity–stability dynamics (Hong et al. 2023; White et al. 2023). As a highly mobile taxon, birds regularly colonize (immigration) and go extinct (emigration, or local extinction) on islands, allowing the straightforward quantification of colonization-extinction dynamics (Valente et al. 2020; Martínez et al. 2023). In addition, extensive data on avian life-history strategies facilitate categorization into ‘fast-slow’ spectra reflecting ecological resilience and resistance (Tobias et al. 2022; Hong et al. 2023). Therefore, using birds as a model system to test how species richness and functional traits mediate the effects of island biogeographic factors on stability components (see Figure 1 and Table 1) will provide novel perspectives on the processes shaping island community assembly and ecosystem functioning.

2.3 | Bird Surveys

A subset of 36 islands that encompass as much variation in area and isolation as possible (Figure 2; Table S1; see also the island attributes section below) was selected to conduct long-term bird surveys. We placed transects on each island, with the number of transects (and total transect length) proportional to the logarithm of island area, resulting in one to eight transects on each study island (Table S1). We then surveyed the bird communities on each island during the breeding season (April to June) annually from 2009 to 2021, a total of 13 years. During each survey, skilled observers walked each transect at a constant speed (2 km/h) and recorded the identity and the

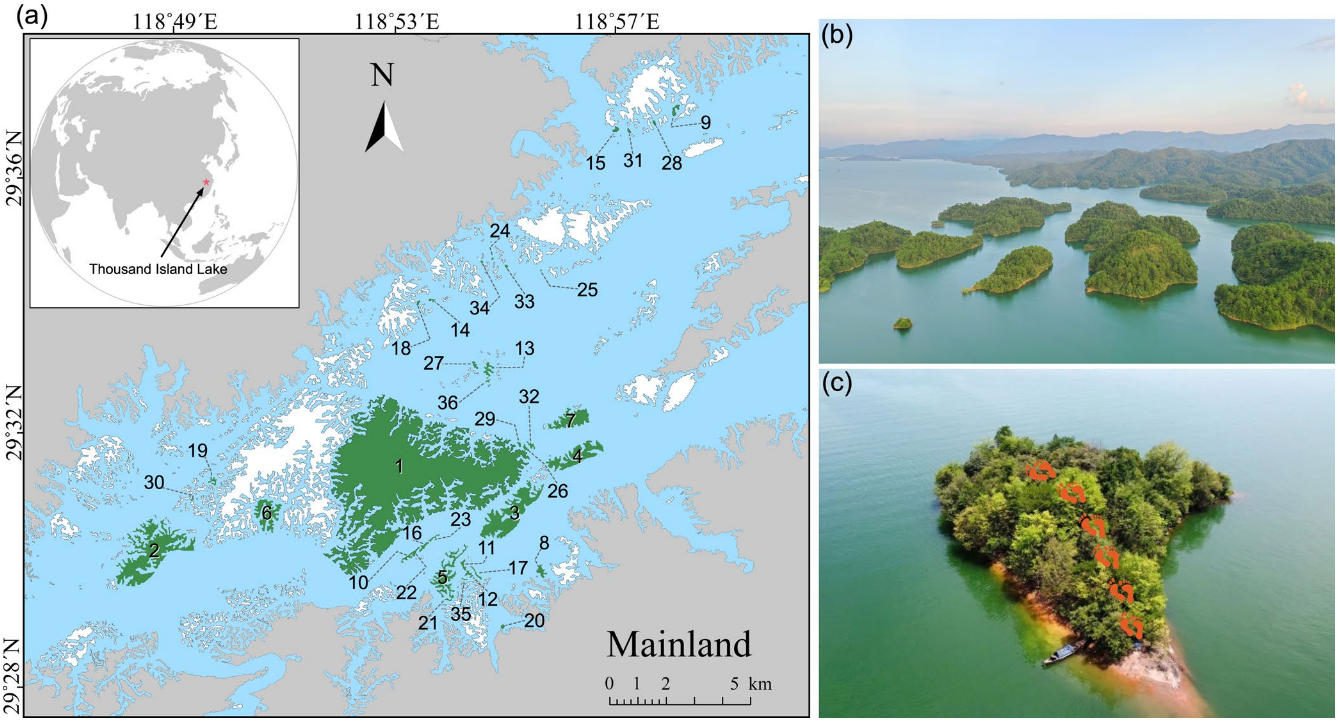

FIGURE 2 | The 36 study islands (in green) in Thousand Island Lake, eastern China (a). Islands are labelled by decreasing area (i.e., #1 is the largest island). The remaining unsurveyed islands and the mainland are, respectively, in white and in light grey, whereas the water matrix is in blue. Part of the Lake showing a selection of islands that were forested hilltops before the inundation in 1959 (b). The smallest island (i.e., #36 in a) in the study region (c). The footprints represent the bird survey transect on this island. Photo credits: Wande Li (b) and Di Zeng (c).

number of each bird species seen or heard. In each month, the surveys were conducted three times except for surveys in 2009 and 2010 where surveys were conducted five times. Thus, we undertook a total of 15 or 9 surveys for each breeding season, depending on the year. Surveys usually began from 0.5 h after dawn to 11:00 AM, and continued from 3:00 PM to 0.5 h before sunset (Si et al. 2017, 2018). Here we focused on terrestrial resident and summer migratory birds and excluded species primarily associated with aquatic habitats (e.g., ducks, gulls, and diving birds). As a result, we retained 89 species for the following analyses (Table S2).

In a previous study, we found that many birds are frequently undetected (i.e., imperfect detection) on the study islands (Si et al. 2018). Thus, before calculating biodiversity and stability metrics, we used zero-inflated Poisson (ZIP) binomial N-mixture models to estimate the expected bird abundance on each transect across the survey islands during our 13-year bird survey after accounting for species' imperfect detection and temporal autocorrelation (MacKenzie et al. 2002). Please see Supporting Text S1 for more information.

2.4 | Island Attributes

We initially selected island area (c. 0.57 to 1300 ha) and distance to the mainland (c. 20 to 3700 m) because these two variables are recognized as the key determinants of the colonization and extinction rates in the framework of Equilibrium Theory of Island Biogeography (ETIB) (MacArthur and Wilson 1967; Losos and Ricklefs 2010). However, isolation can be quantified using various metrics, the use of all of which is based on the principal assumption that increased island isolation (i.e., the increased distance of an island from potential sources) reduces the probability of dispersal and colonization events (Weigelt and Kreft 2013). Given the relatively close proximity of islands within our study system (Si et al. 2024), we additionally considered two alternative isolation metrics, which are the distance to the nearest larger landmass (c. 17 to 1650 m) and the distance to the nearest landmass of any size (c. 9 to 103 m) (Si et al. 2014). All island attributes were calculated in ArcGIS for a water level of 100 m a.s.l. (Table S1).

2.5 | Stability at Community and Population Levels

Temporal community stability was calculated as the inverse of the coefficient of variation (CV) of the total abundance (i.e., island-level relative abundance; Supporting Text S1) of the bird community on each island across sampling years (Tilman et al. 2006; Liang et al. 2021):

$$\text{community stability} = \frac{1}{\text{CV}} = \frac{\mu_j}{\sigma_j}$$

where μ_j and σ_j represent the temporal mean and standard deviation of the abundance of the bird community on island j. The temporal stability of community abundance decreases when the CV of the community abundance increases. Population stability was measured as the weighted average of species-level stability (Thibaut and Connolly 2013):

$$\text{population stability} = \frac{\mu_j}{\sum_i \sigma_{i,j}}$$

where $\sigma_{i,j}$ is the temporal standard deviation of the abundance of bird i on island j. Note that we did not find directional changes in species abundance to affect community and population stability (see Supporting Text S2). Population asynchrony is calculated following Loreau and de Mazancourt (2008):

$$\text{population asynchrony} = 1 - \frac{\sigma_j^2}{\left(\sum_i \sigma_{i,j}\right)^2}$$

Population asynchrony ranges from 0 (maximum synchrony) to 1 (maximum asynchrony) and increases if the variance in individual species abundance increases relative to the variance in community abundance. The stability metrics were calculated using the *codyn* R package (Hallett et al. 2016).

2.6 | Colonization and Extinction Rates

In this study, the annual colonization (*Pc*) and extinction (*Pe*) rates for a focal species on a particular island were defined as the probability of this species being present (absent for extinction rates) on this island when it was absent (present for extinction rates) in the previous year based on the metapopulation models developed by Gotelli and Taylor (1999). Thus, four possible statuses can be observed (A|P, A|A, P|A, and P|P where A represents absence and P represents presence, and A|P represents absence in the first time point but presence in the second time point) for a focal species during two consecutive surveying years. Following the above, the species-specific colonization and extinction rates were calculated as:

$$Pc_{i,j} = N_{i,j}(\text{A}|\text{P}) / \left[N_{i,j}(\text{A}|\text{P}) + N_{i,j}(\text{A}|\text{A})\right]$$

$$Pe_{i,j} = N_{i,j}(\text{P}|\text{A}) / \left[N_{i,j}(\text{P}|\text{A}) + N_{i,j}(\text{P}|\text{P})\right]$$

where $N_{i,j}$(A|P), $N_{i,j}$(A|A), $N_{i,j}$(P|A), and $N_{i,j}$(P|P) are the number of observed statuses (A|P, A|A, P|A, and P|P) for species i on island j. We then averaged *Pc* and *Pe* across all species present on an island to obtain the colonization and extinction rates for each island (Martínez et al. 2023). Note that we converted the posterior expected community matrix into a presence and absence matrix to calculate the colonization and extinction rates.

2.7 | Fast-Slow Traits

To capture the 'fast-slow' continuum of the 89 bird species recorded in this study, we selected body mass (g), clutch size (i.e., number of eggs per year), egg size (mm^3), maximum longevity (number of years), incubation time (number of days), and fledging time (number of days). Incubation time and fledging time were then summed to calculate the duration of nesting time (number of days). The detailed descriptions of each trait and their theoretical connections to the ETIB are summarized in Table S3. Body mass, clutch size, and egg size were obtained from a dataset specific to Chinese birds (Wang et al. 2021). Maximum longevity was compiled from Bird et al. (2020). Incubation time and fledging time were firstly sourced from a life-history database of birds (Myhrvold et al. 2015) and then supplemented by manually searching through books, websites, and other literature. Data were lacking for incubation time for 22 species and for fledging time for 24 species (Table S2). We then used a random forest model that incorporates phylogenetic information to impute missing traits (Penone et al. 2014). Please see Supporting Text S3 for more information.

We conducted a principal components analysis (PCA) on the above five traits (body mass, clutch size, egg size, maximum longevity, nesting time duration) using the *PCA* function in the 'FactoMineR' R package (Lê et al. 2008). Before conducting the PCA, we log-transformed all traits to meet the assumption of a normal distribution. The first axis of the PCA explains 60.7% of the total variation and can be interpreted as the 'fast-slow' continuum in life-history strategies considering the loadings of the five traits (Figure S1; Table S4). Specifically, a larger, positive value of the first axis indicates 'slow' species, characterized by larger body mass and egg size, longer duration of nesting time and longevity, and smaller clutch size. In contrast, a smaller, negative value of the first axis represents 'fast' species, characterized by smaller body mass and egg size, shorter duration of nesting time and longevity, and larger clutch size. We thus used the first axis of the PCA as the 'fast-slow' trait for further analyses.

2.8 | Biodiversity Components

We calculated the (i) average population size of all species, (ii) species richness, and the (iii) community-weighted mean and (iv) functional dispersion of the first axis of a PCA relating to the 'fast-slow' continuum (i.e., fast-slow trait dominance and fast-slow trait diversity, respectively) on each island per year and averaged the values across 13 years to get one value per metric per island. In addition to species richness, we also calculated Shannon diversity (Shannon 1948) and Simpson diversity (Simpson 1949) as they both integrate species' richness and relative abundance to varying extents (Roswell et al. 2021). However, species richness had a very strong, positive correlation with the other two species diversity indices (Shannon diversity: Pearson's $r = 0.950$; Simpson diversity: Pearson's $r = 0.961$). Since the predictions of ETIB mainly focus on the number of species on islands, we used species richness in the following analyses. Fast-slow trait dominance represents the relatively dominant role of 'fast' or 'slow' species within an island, whereas fast-slow trait diversity reflects the potential complementarity in fast-slow strategies of co-occurring species within each island (Craven et al. 2018). The community-weighted mean and functional dispersion of the fast-slow trait (i.e., the first axis of the PCA of five life-history traits; Figure S1; Table S4; see also above) were calculated using the *dbFD* function in the 'FD' package (Laliberté et al. 2014).

2.9 | Statistical Analyses

We used piecewise structural equation models (SEM) to test how island biogeographic factors affect community stability through different biodiversity metrics. The piecewise SEM employs separate linear models with local rather than global parameter estimation. These models are then integrated into a single directed acyclic graph (Shipley 2009). Here, we built the initial SEM based on our hypothesized causal paths (Figure 1 and Table 1) using the 'piecewiseSEM' R package (Lefcheck 2016). We tested the overall model fit using Shipley's *d*-separation test via Fisher's C statistic (Shipley 2009) and found that the initial SEM lacked several statistically significant paths and some of the hypothesized paths were non-significant (Supporting Text S4). We thus refitted the SEM by adding all missing paths and removing non-significant paths (see Supporting Text S4). We calculated direct, indirect, and total effects in the final SEM by adjusting for multicollinearity among variables using the *bootEff* function (with 1000 bootstrap resamples) in the 'semEff' R package (Murphy 2022). Although local estimation provides robustness for fitting smaller datasets (Lefcheck 2016) and we used more than five samples per estimated variable in all models as recommended by Grace et al. (2015), we note that the sample size of our study is relatively small (i.e., 36 islands). Thus, to further test the robustness of our results, we conducted two additional analyses: (1) we broke apart the full SEM into sub-models (i.e., multiple regression models) and applied model selection on each sub-model (Supporting Text S5); and (2) we used Bayesian SEM (Supporting Text S6), which is argued to be an appropriate approach for handling small sample sizes and estimating the uncertainty of parameter estimates (Smid et al. 2020). The additional analyses yielded qualitatively similar results (Supporting Texts S4–S7), and we thus only report the results based on the piecewise SEM because this method can identify missing paths. Note that we first built the SEMs using distance to the mainland as the isolation metric (Supporting Text S4), before fitting two additional SEMs using alternative isolation metrics, namely distance to the nearest larger landmass and distance to the nearest landmass (Supporting Text S7). In all models, island area, average population size, species richness, community stability, and population stability were log-transformed to improve the normality of the model residuals. All variables were standardized to have a mean of zero and a standard deviation of one using the *scale* function before analysis. Model assumptions of normality and heterogeneity were inspected visually. All analyses were performed in R version 4.2.3 (R Core Team 2023).

3 | Results

Our final piecewise structural equation model (SEM), which considered distance to the mainland as the isolation metric, demonstrated a good fit with the empirical data (Fisher's $C = 63.70$, $\mathrm{df} = 66$, $p = 0.557$; Figure 3). Consistent with our prediction, island area increased average population size ($\beta_{\text{direct}} = 0.850$). Island area also increased species richness ($\beta_{\text{indirect}} = 0.262$) by enhancing colonization rates and reducing extinction rates through higher average population size (Figure 3 and Figures S2, S3, and S4a). Moreover, island area directly increased species richness ($\beta_{\text{direct}} = 0.266$; Figure 3), which was missed from our hypothesized paths (see Supporting Texts S5 and S6). Contrary to our hypothesis, distance to the mainland was positively associated with average population size ($\beta_{\text{direct}} = 0.332$), indicating that islands far away from the mainland support larger average bird populations (Figure 3

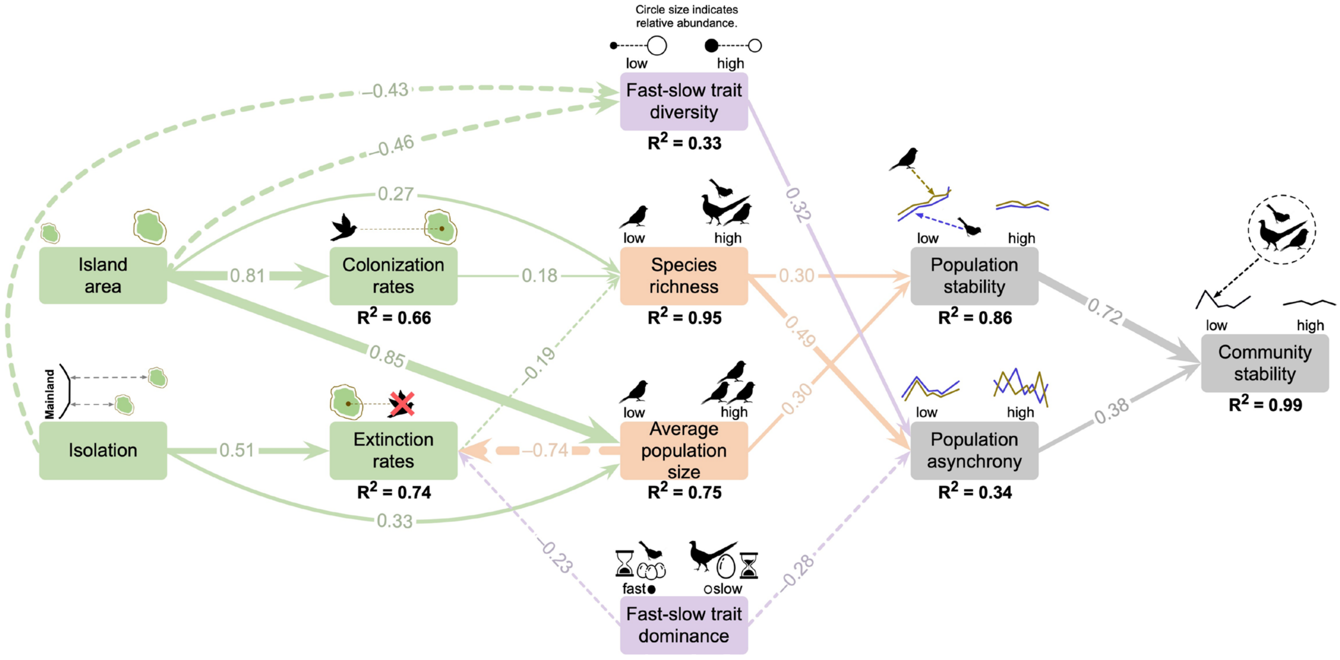

FIGURE 3 | The final structural equation model (SEM) depicting the pathways between island biogeographic factors, biodiversity facets, and the stability (and its components) of breeding bird communities across 36 islands of Thousand Island Lake, China. Piecewise SEM (Fisher's C statistic: $C=63.70$, df $=66$, $p=0.557$) exploring the effects of island area, isolation (measured as the distance to the mainland), colonization rates, extinction rates, species richness, average population size, and fast-slow trait dominance and diversity on population stability, population asynchrony, and community stability of island birds spanning 13 years. Colored rectangles represent measured metrics and single arrows represent observed relationships between metrics. Solid and dashed lines indicate significant positive and negative relationships, respectively. Standardized path coefficients are shown along each line and line width is scaled by the magnitude of the standardized path coefficient. The R^2 below each colored rectangle represents the explained proportion of variance. We do not show pairwise correlations among variables for simplification. Fast-slow trait dominance and diversity were calculated as the community-weighted mean and functional dispersion of the first axis of a PCA relating to the 'fast-slow' continuum, respectively.

and Figure S5b). In addition, distance to the mainland directly increased extinction rates ($\beta_{\text{direct}}=0.509$; Figure 3 and Figure S6a). Consequently, distance to the mainland had a weak net effect on species richness ($\beta_{\text{total}}=-0.050$), resulting from the balancing of its direct positive effect on extinction rates and an indirect negative effect through average population size (Figure 3 and Figure S3). Surprisingly, island area negatively affected fast-slow trait diversity ($\beta_{\text{direct}}=-0.461$; Figure 3 and Figure S7a). Distance to the mainland had a negative impact on fast-slow trait diversity ($\beta_{\text{direct}}=-0.432$) as predicted (Figure 3 and Figure S7b), suggesting that smaller and less isolated islands harbor greater diversity of 'fast-slow' traits.

Species richness ($\beta_{\text{direct}}=0.300$) and average population size ($\beta_{\text{direct}}=0.296$) were both positively related to population stability (Figure 3 and Figure S8). As hypothesized, the three biodiversity facets—species richness ($\beta_{\text{direct}}=0.488$), diversity of 'fast-slow' strategies ($\beta_{\text{direct}}=0.316$), and dominance of 'fast' species ($\beta_{\text{direct}}=-0.278$)—positively affected population asynchrony (Figure S9), thereby contributing to asynchronous dynamics among coexisting species. Notably, population stability ($\beta_{\text{direct}}=0.721$) had stronger direct effects on community stability than population asynchrony ($\beta_{\text{direct}}=0.379$) (Figures 3 and 4).

Our SEM further reveals indirect pathways through which island biogeographic factors shape community stability and its components. Specifically, island area strengthened community stability ($\beta_{\text{total}}=0.388$; Table S5) via its indirect effects on population stability ($\beta_{\text{indirect}}=0.410$) and, to a lesser extent, population asynchrony ($\beta_{\text{indirect}}=0.113$) (Figure 4). Distance to the mainland had an overall non-significant effect on community stability ($\beta_{\text{total}}=-0.001$; Table S5), with a positive indirect effect on population stability ($\beta_{\text{indirect}}=0.083$) and a negative indirect effect on population asynchrony ($\beta_{\text{indirect}}=-0.161$) (Figure 4). However, both colonization and extinction rates played relatively weak roles in modulating community stability via species richness ($\beta_{\text{total}}=0.071$ and -0.075, respectively; Figure 4; Table S5).

When considering alternative island isolation metrics, we found that distance to the nearest landmass also had an overall non-significant impact on community stability (Supporting Text S7; Table S6). However, unlike distance to the mainland, the net effect of distance to the nearest landmass on community stability was driven primarily by a positive, direct effect on population stability and a negative, direct effect on population asynchrony (Supporting Text S7; Table S6). In contrast, when island isolation was measured as distance to the nearest larger landmass, we found a weak direct positive effect on population stability, resulting in a limited overall contribution to community stability (see Supporting Text S7 for more details; Table S7).

Taken together, island area, species richness, and average population size were the predominant factors regulating bird population stability and community stability (Figure 4; Tables S5–S7;

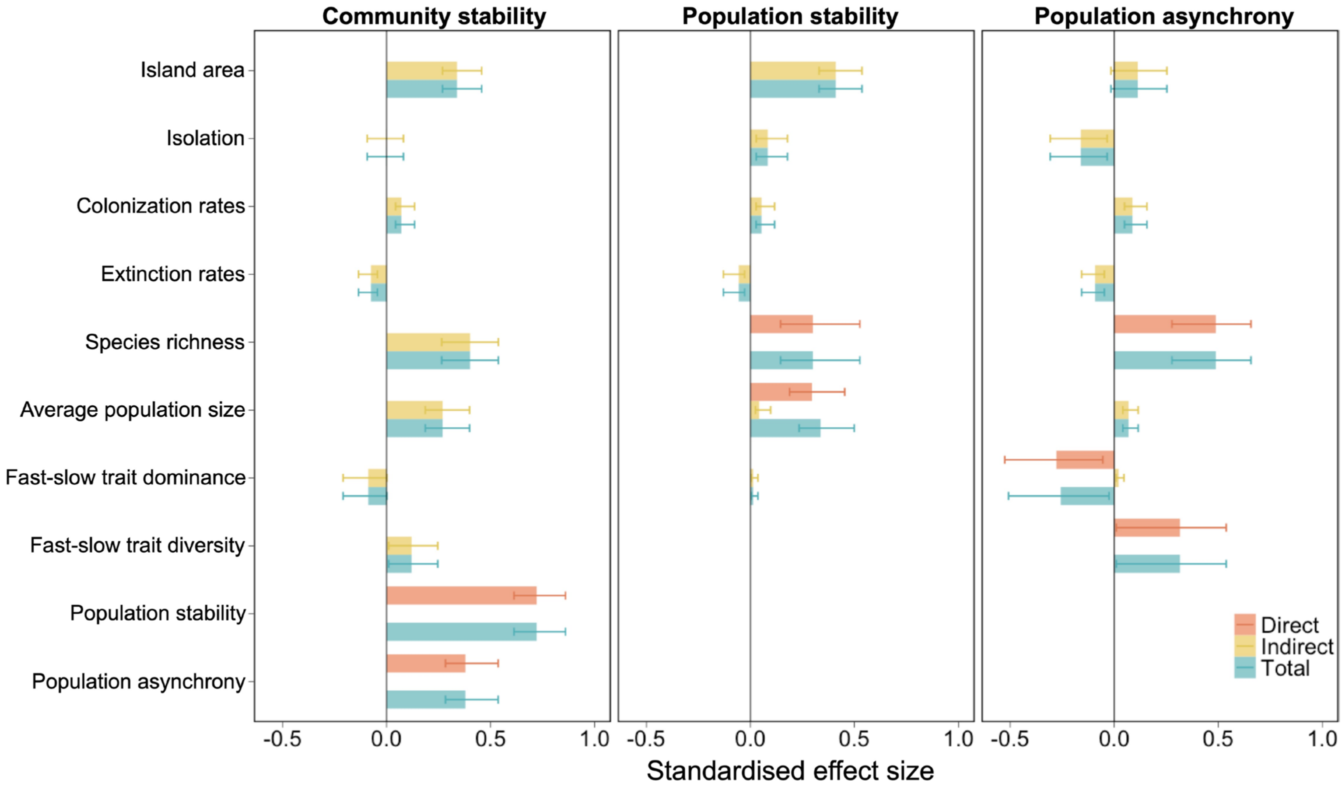

FIGURE 4 | Summary of the direct, indirect, and total effects of island biogeographic factors (isolation was measured as the distance to the mainland) and biodiversity facets on stability variables in Figure 3. Bars and error bars represent mean ± 95% CI; $n = 10{,}000$ bootstrapped estimates for each dependent variable.

Supporting Text S7). While species richness, fast-slow trait diversity, and dominance were the most important factors affecting population asynchrony (Figure 4; Tables S5–S7; Supporting Text S7). These insights illustrate the nuanced and complex roles island biogeographic factors and biodiversity facets play in shaping the temporal dynamics of avian community stability across the study islands.

4 | Discussion

Biodiversity–stability theory and island biogeography theory represent two foundational theories in ecology, but they are typically studied independently (Gonzalez et al. 2020). Here, we integrate the Equilibrium Theory of Island Biogeography (ETIB) and functional ecology within the framework of biodiversity–stability theory (Figure 1) to assess the underlying ecological mechanisms of avian community stability on land-bridge islands (Figure 3). Our results reveal that (1) ETIB serves as a robust approach for predicting biodiversity–stability relationships, with larger islands supporting more stable avian communities; (2) conversely, through the lens of ‘fast-slow’ life-history strategies, smaller and less isolated islands exhibit a positive, albeit weak, link with avian stability; and (3) isolation had an overall non-significant effect on avian stability, as the effects from multiple pathways balanced each other out. These findings provide empirical support linking island biogeography with the theory of biodiversity–stability, demonstrating the multiple pathways through which island area and isolation influence temporal community dynamics.

4.1 | ETIB and the Biodiversity–Stability Relationship

Our SEM reveals that island area is the most important biogeographic factor, increasing community stability through positive species richness–population stability, population size–population stability, and species richness–population asynchrony relationships, which are partly driven by colonization–extinction dynamics. Island area was the main driver determining colonization and extinction rates of bird communities (Figure S2), which is consistent with the findings of previous research in our study system (Si et al. 2014; Martínez et al. 2023). However, we note that the effect of island area on extinction rates was mediated by average population size (Figure 3). In years when resources are limited, or environmental conditions are less favorable, large populations can accommodate a temporary decline without nearing extinction thresholds (Pimm et al. 1988).

Although the ETIB and its extensions predict a positive effect of colonization rates and a negative effect of extinction rates on species richness, our findings extend beyond this by showing that island area also can have a direct, positive effect on species richness (Figure 3). This suggests that larger islands may have retained more species following flooding and island formation (Jones et al. 2016) due to their higher habitat quality and the presence of more diverse habitat types (Liu et al. 2019). While passive sampling effects—higher sampling intensity on larger islands—could affect the true species richness–area relationship (Chase et al. 2019), our transect-level analyses confirm that such biases did not influence our results (see Supporting Text S8). As a result, larger islands support more species not only through colonization–extinction dynamics, but also possibly via high habitat heterogeneity and quality (Gooriah et al. 2021; Matthews et al. 2023), indicating that multiple co-occurring mechanisms associated with island biogeography stabilize island bird communities.

During the breeding season, breeding bird pairs have distinct territories. Thus, the competition for resources among birds can be intense, especially on fragmented habitat islands with limited resources (Si et al. 2017), which could result in a negative effect of bird richness on population stability (Ives et al. 1999). Contrary to this expectation, our findings reveal a robust, positive relationship between species richness and population stability (Figure 3; Supporting Text S7), an uncommon pattern in natural ecosystems and observational studies (Houlahan et al. 2018; Xu et al. 2021). This unexpected pattern may be explained by the divergence in microhabitat utilization among bird species. On larger islands, where habitats are more diverse and resources more abundant, birds may exploit different layers of forests through vertical stratification (Thiel et al. 2021) and/or specialize in habitats to reduce interspecific competition. For instance, ground-foraging species (e.g., common pheasant *Phasianus colchicus* and silver pheasant *Lophura nycthemera*) may coexist with aerial-foraging species (e.g., black kite *Milvus migrans* and common kestrel *Falco tinnunculus*) that utilize distinct forest strata. Thus, the positive species richness–population stability relationship could capture the effects of habitat heterogeneity on larger islands (Connor and McCoy 1979). In other words, although there are more species on larger islands, the competition may be weakened through divergence in resource use.

In addition to higher species richness, larger islands support higher average population size because they contain a greater amount of habitable area and resources (MacArthur and Wilson 1967; Whittaker et al. 2023). Higher average population size, in turn, increases population stability in our study system (Figure 3; Supporting Text S7). For birds with a larger population size, the relative impact of demographic fluctuations will be reduced (Pimm et al. 1988; Matthies et al. 2004). In small populations, a few individual losses can dramatically change population dynamics, while in larger populations, these impacts are spread out, leading to greater stability (Brown 1969). We note that average population size is an important driver of population stability, but has often been overlooked in many previous stability studies (Xu et al. 2021).

Theoretical frameworks suggest that community stability is determined by both population stability and population asynchrony (Xu et al. 2021). Numerous empirical studies have demonstrated that species richness enhances asynchronous fluctuations among species, which underpin positive relationships between diversity and community stability (Egli et al. 2020; Hautier et al. 2020; Olivier et al. 2020; Schnabel et al. 2021). Our findings align with this body of work, confirming the positive species richness–population asynchrony relationship (Figure 3). The mechanisms underlying the species richness–population asynchrony relationship may be either niche-driven (i.e., compensatory effects) or neutral (i.e., statistical-averaging effects) or both (Zhao et al. 2022). We found that the positive relationship between species richness and population asynchrony observed in our study was primarily attributable to the statistical-averaging effect (Supporting Text S9; Figure S10). The statistical-averaging effect implies that the increased species richness associated with colonization-extinction dynamics inherently leads to greater asynchrony across the community (Diamond 1969; Doak et al. 1998). As more species, each with unique demographic rates, gradually occupy an island, their individual variations tend to balance out, resulting in a more stable community response to environmental variability (Zhao et al. 2022). Our findings are in line with long-term grassland experiments that identified demographic stochasticity as the primary process driving biodiversity–stability relationships (de Mazancourt et al. 2013).

To our surprise, we found that islands far from the mainland contain higher average population sizes. Further analysis indicated that abundant species on these isolated islands may indicate a relatively greater dispersal capacity, as reflected by the high community-weighted mean of the hand-wing index (see Supporting Text S10). Notably, the majority of species with a high hand-wing index are predominantly summer migrants (Table S2), which may selectively occupy islands far from the mainland to reduce niche overlap with resident species. Additionally, the remote islands within our study system are devoid of predators, such as the leopard cat (*Prionailurus bengalensis*) (Zeng et al. 2019), due to their limited ability to disperse across water (based on field observations). On the one hand, with reduced predation pressure and niche overlap, populations on remote islands experience fewer random disturbances, which leads to increased stability. On the other hand, islands far from the mainland generally have lower species richness (Figure S3), primarily due to relatively higher extinction rates (Figure 3). As illustrated above, the higher proportion of summer migrants on these isolated islands may also introduce greater instability through annual migration cycles (Hong et al. 2023).

When considering alternative isolation metrics, we found that populations on islands located farther from the nearest larger island or the mainland are more stable (Supporting Text S7). This pattern could be explained by the negative target effect, whereby nearby larger islands act as sinks, attracting individuals from the focal island (see Wang et al. 2023 for more details) and thereby increasing the frequency of extinction events through emigration and destabilizing local population dynamics through demographic fluctuations (Holt 1992). In contrast, we observed that islands close to one another tended to support more stable populations but exhibited lower levels of population asynchrony (Supporting Text S7). This may be attributed to the rescue effect (Abbott 2011; Wang et al. 2015), in which neighbouring small islands serve as stepping stones that buffer population declines by facilitating colonization (Gilpin 1980), thus enhancing population stability while reducing population asynchrony. Despite these contrasting pathways linking different isolation measures to stability components, the overall effects of isolation on community stability remained weak (Tables S5–S7), particularly after accounting for the effects of fast-slow life-history traits (see below).

4.2 | 'Fast-Slow' Life-History Traits and the Biodiversity–Stability Relationship

We found an overall weak negative effect of island area ($\beta_{\text{total}} = -0.055$) and distance to the mainland ($\beta_{\text{total}} = -0.052$) on community stability that was mediated by fast-slow trait diversity (Table S5). Although larger islands and islands close to the mainland possess more species, our results are consistent with the idea that these biogeographic factors constrain trait space, suggesting that the avian communities on these islands may be more resilient due to higher functional similarity (Dick 2023). Moreover, communities with higher fast-slow trait diversity are stabilized by increased population asynchrony (Figure 3; Supporting Text S7), which is largely driven by niche differentiation and compensatory mechanisms (Figure S10). This supports the hypothesis that a diverse array of life-history strategies enhances the capacity to cope with disturbances and the ability to recover, thereby promoting greater compensatory interactions among species (Craven et al. 2018; Li et al. 2021; Zheng et al. 2024).

We also observed that the dominance of ‘fast’ species enhances community stability through population asynchrony, which was determined exclusively by the distance to the nearest landmass (Supporting Text S7). Similar to the effect of fast-slow trait diversity, the impact of fast-slow trait dominance on population asynchrony is also attributable to the compensatory effect (Figure S10), highlighting that ‘fast’ species may respond distinctively to environmental changes. In other words, ‘slow’ species are more resistant (Májeková et al. 2014; Conti et al. 2023) and persist once established, evidenced by our finding that communities dominated by ‘slow’ species have lower extinction rates (Figure S4). The variability of ‘fast’ species suggests that if one species declines or disappears following environmental disturbances, another can increase its abundance due to reduced competition and newly available niche space (Blondel et al. 1988), thereby enhancing compensatory dynamics within the community. Notably, if the species going extinct exhibit functional redundancy in ecological roles (such as seed dispersal or insect control) with the remaining and/or colonizing species, the temporal dynamics of island bird communities and the continuity of ecosystem services will remain stable as the remaining and/or colonizing species can continue to fulfill these critical ecosystem functions.

5 | Conclusion

Our study introduces a novel integrative framework that synthesizes two complementary theories—island biogeography and biodiversity–stability—to decompose the temporal dynamics of island bird communities. Our findings affirm the ETIB as a pivotal model for understanding these dynamics, with island area, colonization–extinction processes, species richness, and average population size collectively stabilizing island bird communities. Additionally, we find that community stability is influenced by traits associated with life history strategies, emphasizing the importance of incorporating multiple trait dimensions in the study of stability (de Bello et al. 2021).

Our research highlights the role of large patches in enhancing community stability, offering implications for maintaining long-term ecological stability in fragmented habitats (Greig et al. 2022). By integrating island biogeography and biodiversity–stability frameworks, our approach not only sheds light on the mechanisms underpinning community dynamics but also enhances our understanding of ecosystem functioning within increasingly fragmented or island-like landscapes (see also Liang et al. 2025).

Author Contributions

Yuhao Zhao: conceptualization, formal analysis, methodology, visualization, writing – original draft, writing – review and editing. **Di Zeng:** conceptualization, data curation, methodology, visualization, writing – review and editing. **Thomas J. Matthews:** validation, writing – review and editing. **Dylan Craven:** validation, writing – review and editing. **Morgan W. Tingley:** methodology, writing – review and editing. **Shaopeng Wang:** methodology, validation, writing – review and editing. **Shao-peng Li:** validation, writing – review and editing. **Ping Ding:** conceptualization, data curation, funding acquisition, supervision, writing – review and editing. **Xingfeng Si:** conceptualization, data curation, funding acquisition, supervision, validation, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data needed to evaluate the conclusions in the paper are present in the Dryad (Zhao et al. 2025; DOI: 10.5061/dryad.tmpg4f56x) and the Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S7:1** Summary of direct, indirect, and total effects of island biogeographic factors, biodiversity facets on stability variables in Model 4.1 (see above). Bars and error bars represent mean ± 95% CI; $n = 10{,}000$ bootstrapped estimates for each dependent variable. Isolation is measured as distance to the nearest larger landmass. **Figure S7:2** Summary of direct, indirect, and total effects of island biogeographic factors, biodiversity facets on stability variables in Model 4.2 (see above). Bars and error bars represent mean ± 95% CI; $n = 10{,}000$ bootstrapped estimates for each dependent variable. Isolation is measured as distance to the nearest landmass. **Figure S1:** The principal component analysis (PCA) graph of the five ‘fast-slow’ traits of 89 avian species in the Thousand Island Lake, China. The brown arrow indicates the species switched from ‘fast’ (species with smaller body mass and egg size, shorter duration of nesting time and longevity, and lager clutch size) to ‘slow’ (species with larger body mass and egg size, longer duration of nesting time and longevity, and smaller clutch size) species along the first Axis (see Method for more details). **Figure S2:** Summary of direct, indirect, and total effects of variables on colonization and extinction rates in Figure 3 in the main text. Bars and error bars represent mean ± 95% CI; $n = 10{,}000$ bootstrapped estimates for each dependent variable. Isolation was measured as the distance to the mainland. **Figure S3:** Summary of direct, indirect, and total effects of variables on species richness, average population size, and fast-slow trait diversity in Figure 3 in the main text. Bars and error bars represent mean ± 95% CI; $n = 10{,}000$ bootstrapped estimates for each dependent variable. Isolation was measured as the distance to the mainland. **Figure S4:** Relationships between island biogeographical factors and species richness of breeding bird communities on 36 islands in the Thousand Island Lake, China. Plots showing the effect of island area (a), colonization rates (b), and extinction rates (c) on species richness, derived from the final piecewise SEM (see Figure 3 and Table S15). **Figure S5:** Relationships between island biogeographical factors (isolation was measured as the distance to the mainland) and average populations size of breeding bird communities on 36 islands in the Thousand Island Lake, China. Plots showing the effect of island area (a) and isolation (b) on average population size, derived from the final piecewise SEM (see Figure 3 and Table S15). **Figure S6:** Relationships between island biogeographical factors (isolation was measured as the distance to the mainland) and biodiversity facets and extinction rates of breeding bird communities on 36 islands in the Thousand Island Lake, China. Plots showing the effect of isolation (a), average population size (b), and fast-slow trait dominance (c) on extinction rates, derived from the final piecewise SEM (see Figure 3 and Table S14). **Figure S7:** Relationships between island biogeographical factors (isolation was measured as the distance to the mainland) and fast-slow trait diversity of breeding bird communities on 36 islands in the Thousand Island Lake, China. Plots showing the effect of island area (a) and isolation (b) on fast-slow trait diversity (calculated as the functional dispersion of the first axis of PCA relating to the 'fast-slow' continuum, see Method for more details), derived from the final piecewise SEM (see Figure 3 and Table S16). **Figure S8:** Relationships between island biodiversity facets and population stability of breeding bird communities on 36 islands in the Thousand Island Lake, China. Plots showing the effect of species richness (a) and average population size (b) on population stability, derived from the final piecewise SEM (see Figure 3 and Table S17). **Figure S9:** Relationships between island biodiversity facets and population asynchrony of breeding bird communities on 36 islands in the Thousand Island Lake, China. Plots showing the effect of species richness (a), fast-slow trait dominance (b, calculated as the community-weighted mean of the first axis of PCA relating to the 'fast-slow' continuum, see Method for more details), and fast-slow trait diversity (c, calculated as the functional dispersion of the first axis of PCA relating to the 'fast-slow' continuum, see Method for more details) on population asynchrony, derived from the final piecewise SEM (see Figure 3 and Table S18). **Figure S10:** The structural equation model (SEM) depicting the pathways between island biogeographical factors, biodiversity facets, and stability and its components (with population asynchrony being partitioned into compensatory effect and statistical-averaging effect) of breeding bird communities across 36 islands of Thousand Island Lake, China. Piecewise SEM (Fisher's C statistic: $C = 90.419$, df = 86, $p = 0.351$) exploring the effects of island area, isolation (measured as the distance to the mainland), colonization rates, extinction rates, species richness, average population size, fast-slow trait dominance (calculated as the community-weighted mean of the first axis of PCA relating to the 'fast-slow' continuum, see Method for more details), and fast-slow trait diversity (calculated as the functional dispersion of the first axis of PCA relating to the 'fast-slow' continuum, see Method for more details) on population stability, compensatory effect, statistical-averaging effect (see Supporting Text S9 for more details), and community stability of island birds spanning 13 years. Colored rectangles represent measured metrics and single arrows represent observed relationships between metrics. Solid and dashed lines indicate significant positive and negative relationships, respectively. Standardized path coefficients are shown along each line and line width is scaled by the magnitude of the standardized path coefficient. The R^2 below each colored rectangle represents the explained proportion of variances in the independent variables. We do not show pairwise correlations among variables for simplification. **Figure S11:** Phylogenetic tree of 89 terrestrial breeding birds on 36 study islands in the Thousand Island Lake, China. The phylogenetic tree was constructed from a Maximum Clade Credibility tree of Bayesian analyses. The unit of branch length is million years. See more details in the Supporting Text S3. **Figure S12:** Summary of direct, indirect, and total effects of island biogeographical factors, biodiversity facets on stability variables in Model 6 (derived from transect-level analysis, see Supporting Text S8 for more details). Bars and error bars represent mean ± 95% CI; $n = 10{,}000$ bootstrapped estimates for each dependent variable. **Table S1:** Characteristics of 36 study islands in the Thousand Island Lake, China. Each island is numbered as in Figure 2 in the main text. **Table S2:** The migratory status and selected traits of 89 avian species in the Thousand Island Lake, China. R = Resident. S = Summer migrants. **Table S3:** Description and the theoretical connections to the Equilibrium Theory of Island Biogeography (ETIB) of five life-history traits. **Table S4:** Loadings of the principal components obtained from PCA analysis of five bird life-history traits. **Table S5:** Total effect of each path from island biogeographical factors (isolation measured as the distance to the mainland), biodiversity facets, and stability variables directing to the community stability of breeding bird communities across 36 islands of Thousand Island Lake, China. Path that involving more than two variables were multiplied by the standardized parameter estimates. Note that isolation is measured as the distance to the mainland. See Figure 3 in the main text and model 4 in the Supporting Text S4 for figure illustration. **Table S6:** Total effect of each path from island biogeographical factors (isolation measured as the distance to the nearest landmass), biodiversity facets, and stability variables directing to the community stability of breeding bird communities across 36 islands of Thousand Island Lake, China. Path that involving more than two variables were multiplied by the standardized parameter estimates. See Figure S7.2 and model 4.2 in the Supporting Text S7 for figure illustration. **Table S7:** Total effect of each path from island biogeographical factors (isolation measured as the distance to the nearest larger landmass), biodiversity facets, and stability variables directing to the community stability of breeding bird communities across 36 islands of Thousand Island Lake, China. Path that involving more than two variables were multiplied by the standardized parameter estimates. See Figure S7.1 and model 4.1 in the Supporting Text S7 for figure illustration. **Table S8:** The description of hyper-prior distribution parameters used in our JAGS model. See Supporting Text S1 for more details. **Table S9:** The results of the first-time model running with a total of 80,000 iterations, 40,000 warmups and thinned by 50. Rhat < 1.1 indicates convergence of parameters. **Table S10:** The results of the second-time model running with a total of 100,000 iterations, 50,000 warmups and thinned by 50. Rhat < 1.1 indicates convergence of parameters. **Table S11:** The results of the third-time model running with a total of 120,000 iterations, 60,000 warmups and thinned by 50. Rhat < 1.1 indicates convergence of parameters. **Table S12:** The results of the fourth-time model running with a total of 120,000 iterations, 50,000 warmups, thinned by 50 and an informative prior for ω (beta distribution with alpha = 14.212, beta = 3.078) based on the result from the third model running. Rhat < 1.1 indicates convergence of parameters. **Table S13:** Correlation among independent variables. Fast-slow trait dominance and diversity were calculated as community-weighted mean and functional dispersion of the first axis of PCA relating to the 'fast-slow' continuum, respectively. See methods for more details. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. **Table S14:** Results of information-theoretic-based model selection for the effects of island area and isolation on colonization rates and the effect of island area, isolation (measured as the distance to the mainland), average population size, and fast-slow trait dominance on extinction rates. Fast-slow trait dominance was calculated as community-weighted mean of the first axis of PCA relating to the 'fast-slow' continuum. We present all selected models. AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). **Table S15:** Results of information-theoretic-based model selection for the effects of island area, isolation, colonization rates, and extinction rates on species richness and the effects of island area and isolation (measured as the distance to the mainland) on average population size. We present all selected models. AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). Shaded background indicates the models' ΔAICc < 2. **Table S16:** Results of information-theoretic-based model selection for the effects of island area and isolation (measured as the distance to the mainland) on fast-slow trait dominance and diversity. Fast-slow trait dominance and diversity were calculated as community-weighted mean and functional dispersion of the first axis of PCA relating to the 'fast-slow' continuum, respectively. See methods for more details. We present all selected models. AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). **Table S17:** Results of information-theoretic-based model selection for the effects of species richness, average population size, colonization rates, and fast-slow trait dominance and fast-slow trait diversity on population stability. Fast-slow trait dominance and diversity were calculated as community-weighted mean and functional dispersion of the first axis of PCA relating to the 'fast-slow' continuum, respectively. See methods for more details. We present all selected models. AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). Shaded background indicates the models' ΔAICc <2. **Table S18:** Results of information-theoretic-based model selection for the effects of species richness, fast-slow trait dominance and fast-slow trait diversity on population asynchrony. Fast-slow trait dominance and diversity were calculated as community-weighted mean and functional dispersion of the first axis of PCA relating to the 'fast-slow' continuum, respectively. See methods for more details. We present all selected models. AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). Shaded background indicates the models' ΔAICc <2. **Table S19:** The initial and final Bayesian SEM outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the mainland), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All variables were standardized to mean = 0 and SD = 1. The Posterior samples (22500) were summarized to show the Bayesian point estimate (median), standard error (median absolute deviation), and 95% highest density intervals (HDIs). HDIs that do not include zero are marked in bold font. BESS is the bulk effective sample size and TESS is the tail effective samples size. Rhat is the diagnostic value of Gelman-Rubin statistic and Rhat less than 1.01 indicates the convergence of parameters. **Table S20:** The five customized prior setting used in the prior sensitivity analysis for Bayesian SEMs. "N" represents the normal distribution, "IG" represents the invert gamma distribution, and "Student" represents the student distribution. **Table S21:** The sensitivity analysis for priors of the initial Bayesian SEM for outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the mainland), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All absolute relative deviations (in red) were less than 0.1 (see Supporting Text S6). Prior types can be found in Table S20. **Table S22:** The sensitivity analysis for priors of the final Bayesian SEM for outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the mainland), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All absolute relative deviations (in red) were less than 0.1 (see Supporting Text S6). Prior types can be found in Table S18. **Table S23:** The initial and final Bayesian SEM outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the nearest large island), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All variables were standardized to mean = 0 and SD = 1. The Posterior samples (22500) were summarized to show the Bayesian point estimate (median), standard error (median absolute deviation), and 95% highest density intervals (HDIs). HDIs that do not include zero are marked in bold font. BESS is the bulk effective sample size and TESS is the tail effective samples size. Rhat is the diagnostic value of Gelman-Rubin statistic and Rhat less than 1.01 indicates the convergence of parameters. **Table S24:** The initial and final Bayesian SEM outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the nearest landmass), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All variables were standardized to mean = 0 and SD = 1. The Posterior samples (22500) were summarized to show the Bayesian point estimate (median), standard error (median absolute deviation), and 95% highest density intervals (HDIs). HDIs that do not include zero are marked in bold font. BESS is the bulk effective sample size and TESS is the tail effective samples size. Rhat is the diagnostic value of Gelman-Rubin statistic and Rhat less than 1.01 indicates the convergence of parameters. **Table S25:** The sensitivity analysis for priors of the initial Bayesian SEM for outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the nearest large island), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All absolute relative deviations (in red) were less than 0.1 (see Supporting Text S6). Prior types can be found in Table S18. **Table S26:** The sensitivity analysis for priors of the initial Bayesian SEM for outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the nearest landmass), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All absolute relative deviations (in red) were less than 0.1 (see Supporting Text S6). Prior types can be found in Table S18. **Table S27:** The sensitivity analysis for priors of the final Bayesian SEM for outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the nearest large island), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All absolute relative deviations (in red) were less than 0.1 (see Supporting Text S6). Prior types can be found in Table S18. **Table S28:** The sensitivity analysis for priors of the final Bayesian SEM for outputs for pathways between island biogeographical factors (Isolation is measured as the distance to the nearest landmass), biodiversity facets, and stability and its components of breeding bird communities across 36 islands of Thousand Island Lake, China. All absolute relative deviations (in red) were less than 0.1 (see Supporting Text S6). Prior types can be found in Table S18.