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Larger habitat islands maintain more persistent mutualistic assemblages

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Habitat loss and fragmentation threaten biodiversity by reducing species richness and disrupting ecological interactions. But it is poorly understood how reduced habitat area and increased isolation impact community persistence, as measured by its capacity to maintain multispecies coexistence. We draw on an intensive, multi-year field study of mutualistic interactions in plant-frugivore and plant-pollinator networks across 41 islands in an insular fragmented landscape formed by dam construction in 1959. We show that the loss of island area after inundation is the primary driver that reduces the persistence of mutualistic assemblages, beyond merely reducing species richness. We further identify structural mechanisms of persistence: on larger islands, decreasing network modularity enhances persistence in both plant-frugivore and plant-pollinator communities, whereas increasing nestedness contributes to persistence only in plant-pollinator communities. These findings represent a conceptual advance in understanding the impact of habitat loss on biodiversity by showing that species loss in small habitat fragments may result from the reduced capacity of their mutualistic communities to support species coexistence, mediated by changes in network structure. We urge to include evaluations of community persistence into the design of conservation and habitat restoration strategies to more effectively mitigate the long-term impacts of habitat loss and fragmentation on biodiversity.

Understanding species persistence in fragmented landscapes has long been a central focus in ecology[1,2]. Across the world, increasing habitat loss and isolating habitat fragments have created 'habitat islands' of varying sizes and degrees of isolation, resulting in local and global extinctions of some species[2], while other species continually face challenges to persist[3]. The Theory of Island Biogeography (TIB)[4] has provided a foundational framework for evaluating the processes underlying species richness patterns across islands and island-like habitats[5,6]. Originally developed for oceanic islands, TIB posits that species richness is shaped by a dynamic balance between colonization

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and extinction[4], which in turn is influenced by island area and isolation. However, TIB assumes all species being functionally equivalent[7], which overlooks species' ecological differences and their interactions in shaping species coexistence. Given the central role of species assemblages and their interspecific interactions in regulating species coexistence[8] and biodiversity[9], incorporating species interactions into the framework of TIB could enhance our understanding of the ecological mechanisms driving species richness in remnant habitats resulting from habitat loss and fragmentation[10].

Mutualistic interactions between plants and animals are key to maintain biodiversity[9] and ecosystem functioning[11]. However, habitat loss threatens these interactions[1,12], which may disrupt mutualisms and triggers cascading effects that accelerate species loss[13]. The persistence of mutualistic assemblages can therefore modulate species coexistence and shape species richness patterns in communities[14,15]. Structural stability[14,16] provides a complementary perspective by quantifying a mutualistic community's capacity to maintain persistence of all species (i.e., at positive abundances) across a range of environmental conditions[17], thereby capturing its resilience to additional perturbations[18]. Within this framework, we can use structural stability as a proxy of community persistence to estimate the potential of a mutualistic community to sustain multispecies coexistence under environmental change[19,20]. This approach offers a valuable tool for exploring biodiversity dynamics in mutualistic systems[16]. From a coexistence perspective, more persistent mutualistic assemblages (i.e., those with greater structural stability) are likewise expected to harbour higher species richness[18,21]. Therefore, higher species richness on larger habitats may be attributed to their greater community persistence, with more persistent assemblages experiencing lower extinction rates of resident species and higher establishment success of newly arriving ones. Yet, despite its theoretical significance, empirical studies on how environmental change affects the persistence of mutualistic assemblages remain scarce (but see Ref.[22]). This gap is particularly evident in small and isolated habitats, limiting our understanding of the mechanisms linking species interactions and community persistence in such contexts.

Beyond the non-random species loss and community assembly, habitat loss and fragmentation can also re-organize species interactions[23,24], thereby influencing overall community persistence. Mutualistic networks integrate species compositions with their interactions[25], revealing structural properties such as nestedness and modularity[26] that may mediate how habitat loss and fragmentation affect community persistence. For example, mutualistic networks with nested structures would be more robust and persistent within remnant habitats[27]. Nestedness, the tendency for specialist species interacting with subsets of the partners of generalist species, may contribute to maintaining structural stability[16,21]. On the other hand, modularity, the tendency for species to form densely connected subsets (i.e., modules)[28], has been associated with conflicting views regarding its influence on network stability[29,30]. This is because habitat loss and fragmentation may generate contrasting drivers of modularity, such as prevalent generalist interactions leading to lower modularity[31], or increased resource competition promoting higher modularity[32]. These contrasting mechanisms introduce uncertainty into how modularity mediates the effects of habitat loss and fragmentation on community persistence. While previous studies have highlighted the negative effects of reduced habitat area on mutualistic interactions through changes in network structures[24,26,33], the direct link between these structural shifts and community persistence remains poorly understood. A more integrated assessment of community persistence, grounded in both structural stability and network analyses, may therefore offer deeper insights into how habitat loss and fragmentation affect biodiversity maintenance. Importantly, this understanding can inform more effective conservation and habitat management strategies in degraded ecosystems characterized by small-sized and isolated habitats.

In this study, we assessed the impacts of reduced habitat area and increased isolation on the persistence of mutualistic assemblages across reservoir land-bridge islands in the Thousand Island Lake system, China (Fig. 1a). This subtropical archipelago offers a unique natural laboratory to examine how variation in island area and isolation affect ecological dynamics within a framework rooted in TIB[34]. Following the uniform clear-felling of all forests and the subsequent dam-induced inundation that created the reservoir islands in 1959, the region has experienced nearly seven decades of natural secondary succession without human disturbance[35]. Additionally, the adjacent continuous mainland forest provides a large, low-isolation reference for examining how network architecture and community dynamic respond to the gradients of island area and isolation. The lack of similar studies is partly attributable to the challenges of documenting mutualistic interactions over large spatial scales in the field[36,37]. Nevertheless, across a total of 41 islands and multiple nearby mainland sites (Fig. 1b), we have successfully obtained high-quality data across spatiotemporal resolutions on both plant-frugivore[38,39] and pollinator[27] communities, along with their interactions (Fig. 1c). Our dataset achieved high levels of interaction-sampling completeness across islands (frugivory: mean ± s.d. = 0.98 ± 0.01; pollination: 0.68 ± 0.03) and on the mainland (frugivory: 0.98; pollination: 0.85) over three years. These two interaction types capture the mutualistic processes of seed production (pollination) and seed dispersal (frugivory), which provide complementary insights by covering the full reproductive life cycle of angiosperm plants. Relative to the nearby mainland, these data have revealed pronounced species loss and network simplification on reservoir islands created by dam-induced inundation[24,27] (Fig. 2a), primarily as a consequence of habitat loss.

Here, we predict species richness on islands would be strongly correlated with the persistence of mutualistic assemblages, measured as structural stability. Similar to species loss, we expect mutualistic assemblages on islands, particularly on small and isolated islands, to be less persistent than those on the mainland. Furthermore, we test whether variation in community persistence across islands was driven by differences in network modularity and nestedness (Fig. 2b). Given differences in trophic specialization and mutualistic strategies between frugivores and pollinators, we expect that these two types of mutualistic assemblages would differ in the key network-structural drivers of their community persistence. Our results show that, in line with their higher species richness, larger habitat islands maintain greater persistence of mutualistic assemblages. On larger islands, decreasing network modularity for both plant-frugivore and plant-pollinator communities, and increasing nestedness for plant-pollinator communities, mitigated the decline in community persistence associated with habitat loss. Taken together, these findings demonstrate the negative impacts of habitat loss and fragmentation on mutualistic community persistence and highlight the critical role of network structure in modulating ecological stability in fragmented landscapes.

Results

Over the three-year sampling, we documented a total of 21,409 events of bird frugivory and 19,486 individual pollination interactions in this lake region. For plant-frugivore communities, we have recorded 319 pairwise interactions between 31species of fleshy-fruited plants and 39 species of frugivorous birds across 22 islands (mean ± s.d. per island: 9.23 ± 4.14 plant species, 16.36 ± 6.28 bird species and 52.59 ± 35.89 interactions), along with 219 interactions between 28 plant and 31 bird species on the nearby mainland. For plant-pollinator communities, we recorded 2824 pairwise interactions between 67 species of flowering plants and 310 species of insect pollinators across 41 islands (mean ± s.d. per island: 17.05 ± 9.27 plant species, 82.37 ± 51.90 insect species and 162.27 ± 192.56 interactions), along with 1158 interactions between

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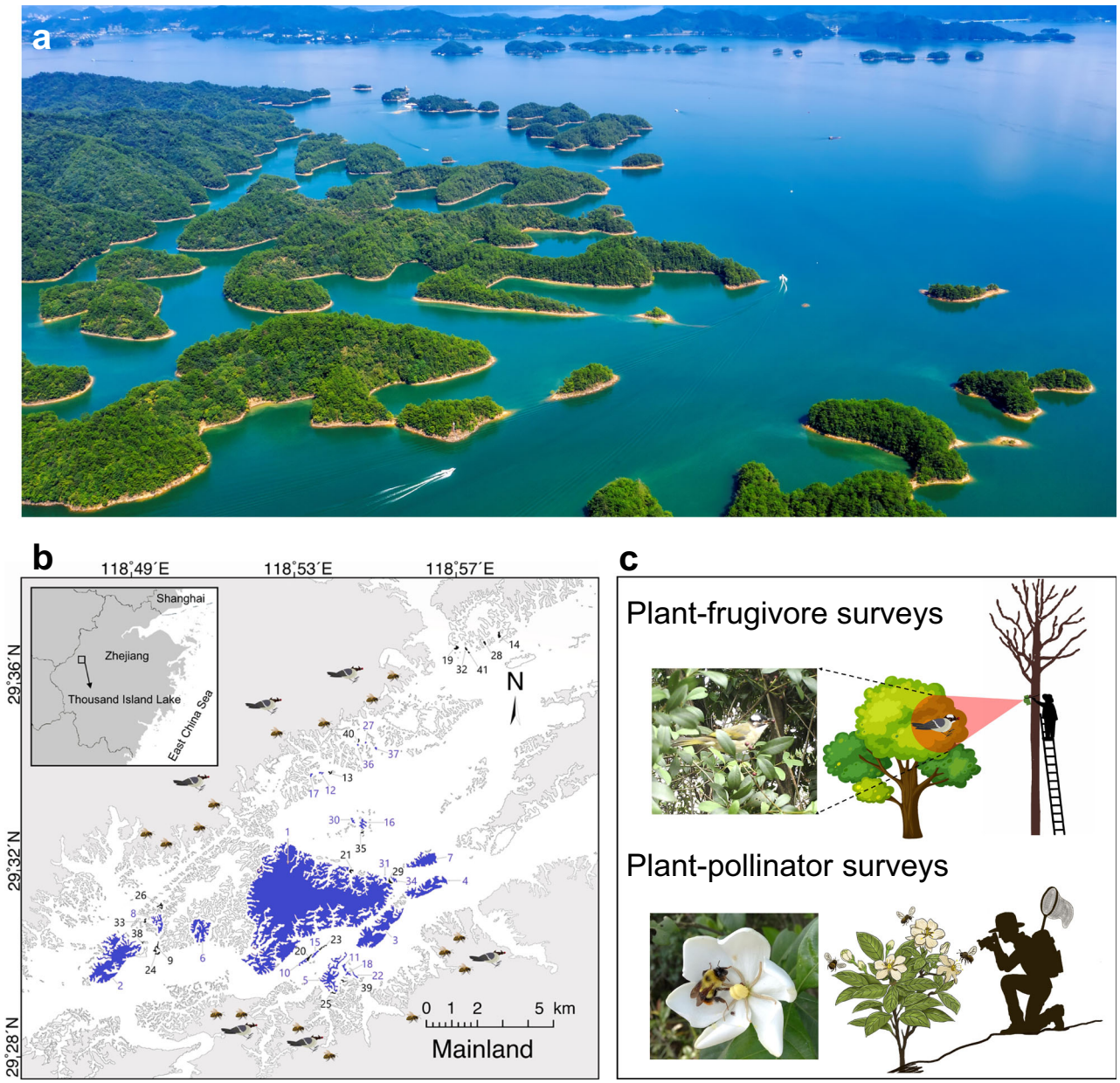

Fig. 1 | Study system and sampling design. a Aerial view of the insular fragmented landscape at the Thousand Island Lake, eastern China. **b** Map of the 41 study islands: 22 islands (blue) were surveyed for both plant-frugivore and plant-pollinator interactions, while other 19 islands (black) were surveyed only for plant-pollinator interactions. Sampling also included six mainland sites for plant-frugivore surveys and 16 mainland sites for plant-pollinator surveys (see illustrations). The island and mainland boundaries were digitized at a scale of 1:50,000 from SPOT-6 imagery, and the resulting digitized maps were rasterized and processed using FRAGSTATS 4.2 and ArcGIS 10.4. **c** Illustration of survey methods: plant-frugivore surveys involved the usage of arboreal camera trapping, while plant-pollinator surveys employed direct field observation. The aerial photograph in **a** was taken by Jingcao Pan. Bird, pollinator and survey-method illustrations were created by Xue Zhang. The map in **b** was modified from Zhu et al. "Interconnecting fragmented forests: Small and mobile birds are cornerstones in the plant–frugivore meta-network", *Proc. Natl. Acad. Sci. U.S.A.* 122 (7) e2415846122, https://doi.org/10.1073/pnas.2415846122 (2025). The plant-frugivore photograph in **c** was taken by Chen Zhu, and the plant-pollinator photograph in **c** was taken by Peng Ren.

54 plant and 269 pollinator species on the nearby mainland. More sampling information about mutualistic communities can be found in Supplementary Table 1. Island structural stability, defined as the average probability that a species can tolerate random environmental perturbations (see Methods for calculation), strongly correlates with species richness, both for plant-frugivore communities (plant: Kendall's $\tau = 0.68$, $z = 4.18$, $P < 0.001$; frugivore: $\tau = 0.67$, $z = 4.28$, $P < 0.001$) and pollinator communities (plant: Kendall's $\tau = 0.53$, $z = 4.78$, $P < 0.001$; pollinator: $\tau = 0.81$, $z = 7.47$, $P < 0.001$).

Island area had significantly positive effects on the structural stability of both mutualistic assemblages (plant-frugivore: regression slope $\beta = 0.008$, $t_{(18)} = 7.58$, $P < 0.001$, 95% CI [0.006, 0.011]; plant-pollinator: $\beta = 0.004$, $t_{(37)} = 10.85$, $P < 0.001$, 95% CI [0.003, 0.005]) (Fig. 3). Island isolation, quantified by two metrics (the distance to the mainland and the distance to the nearest island), did not affect structural stability (Supplementary Table 2), suggesting that habitat loss is the primary driver of reduced community persistence. Structural stability on the islands was significantly lower than that on the mainland (plant-frugivore: one-sample t-test, $t_{(21)} = -26.40$, $P < 0.001$; plant-

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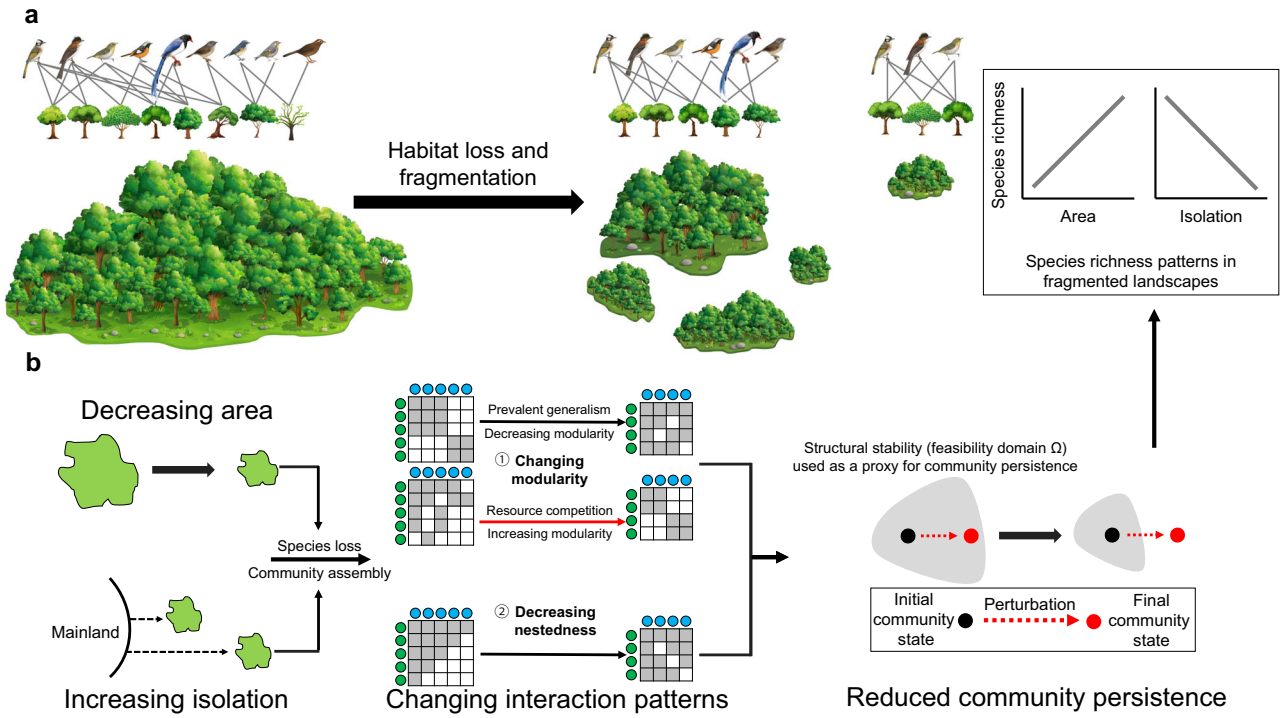

Fig. 2 | Hypothesized impacts of habitat loss and fragmentation on mutualistic communities. a The combined process of habitat loss and fragmentation is expected to decrease species richness and simplify interaction networks of mutualistic communities, with more pronounced effects on smaller and more isolated fragments (islands in our case). **b** Hypothesized pathways through which island area and isolation may influence community persistence, measured as the structural stability of mutualistic networks: decreasing area and increasing isolation are expected to change interaction patterns between species (i.e., nested[14,21] and modular[29,30] structures; see hypotheses in main text) and reduce the persistence of mutualistic assemblages. In the interaction matrices, grey cells indicate realized interactions between plant (green) and animal (blue) species. A reduced community persistence means that a perturbation shifting the community from an initial state (black circle) to a final state (red circle) can result in extinctions if the new community state moves outside the feasibility domain (grey area), measured as the parameter space leading to a dynamically stable equilibrium of the mutualistic system[16], with all species persisting at positive abundances. Consequently, variation in community persistence is expected to shape species richness patterns in landscapes characterised by habitat loss and fragmentation. Bird drawings in **a** were produced by Bai Xiao, Liang Su, and Jing Qian. Plant and island illustrations in **a** were produced by Xue Zhang. Conceptual illustrations in **b** were created by Chen Zhu.

pollinator: $t_{(40)} = -103.21$, $P < 0.001$) (Fig. 3). On average, island structural stability declined by 17% (from 21% to 10%) for plant-frugivore communities and by 22% (from 23% to 15%) for plant-pollinator communities when compared to mainland, highlighting the negative effects of habitat loss and fragmentation on community persistence.

Network modularity was a key mediator linking island area to the structural stability of mutualistic communities (Fig. 4a). Structural equation models revealed strong negative effects of modularity on structural stability across both plant-frugivore (standardized path coefficient, hereafter $\beta_{std} = -0.43$, $P < 0.001$, $t_{(19)} = -4.67$, 95% CI [−0.63, −0.24]) and plant-pollinator networks ($\beta_{std} = -0.49$, $P < 0.001$, $t_{(38)} = -4.38$, 95% CI [−0.72, −0.26]), with island area exerting significant negative effects on modularity (plant-frugivore: $\beta_{std} = -0.64$, $P = 0.002$, $t_{(20)} = -3.68$, 95% CI [−1.00, −0.28]; plant-pollinator: $\beta_{std} = -0.82$, $P < 0.001$, $t_{(39)} = -8.94$, 95% CI [−1.01, −0.63]). By contrast, nestedness (quantified by the NODF metric) mediated the effects of island area only in plant-pollinator communities, showing a positive path to structural stability ($\beta_{std} = 0.31$, $P < 0.001$, $t_{(38)} = 3.87$, 95% CI [0.15, 0.48]; Fig. 4b), while nestedness played no detectable role in plant-frugivore communities (Supplementary Table 3). When using the updated NODF metric that incorporates ties between equal-degree rows and columns (see Methods), we found qualitatively similar relationships between network nestedness and structural stability in the SEM models (Supplementary Fig. 1). Sensitivity analyses confirmed that results for plant-pollinator communities remained consistent when restricting the analysis to the 22 islands with both pollination and frugivory data (Supplementary Fig. 2). In all cases, the direct effect of island area on structural stability was stronger than the indirect effects mediated though network structures (Supplementary Table 4).

Using residualized metrics (controlling for species richness and the other network metric), structural stability remained negatively associated with modularity, not with nestedness, in plant-frugivore communities (Supplementary Fig. 3a, b). In plant-pollinator communities, structural stability was significantly associated only with nestedness and was no longer associated with modularity (Supplementary Fig. 3c, d), implying that the apparent effect of modularity may be mediated by variation in network size (i.e., species richness).

When species richness was controlled for and island assemblages were resampled (see the null model in Methods), the positive relationships between island area and structural stability remained (Supplementary Fig. 4; Supplementary Table 5), whereas island isolation still showed no significant effect. This highlights the role of community reassembly in shaping community persistence following habitat loss and fragmentation through changes in species composition and the structure of their interactions.

Discussion

We present the empirical evidence that habitat loss and fragmentation diminish the persistence of mutualistic assemblages, extending beyond its effect on simply lowering species richness. Community persistence, quantified as network structural stability, was strongly and positively related to both island area and species richness. This result suggests that larger habitat islands not only support more species but also foster more stable and resilient ecological communities,

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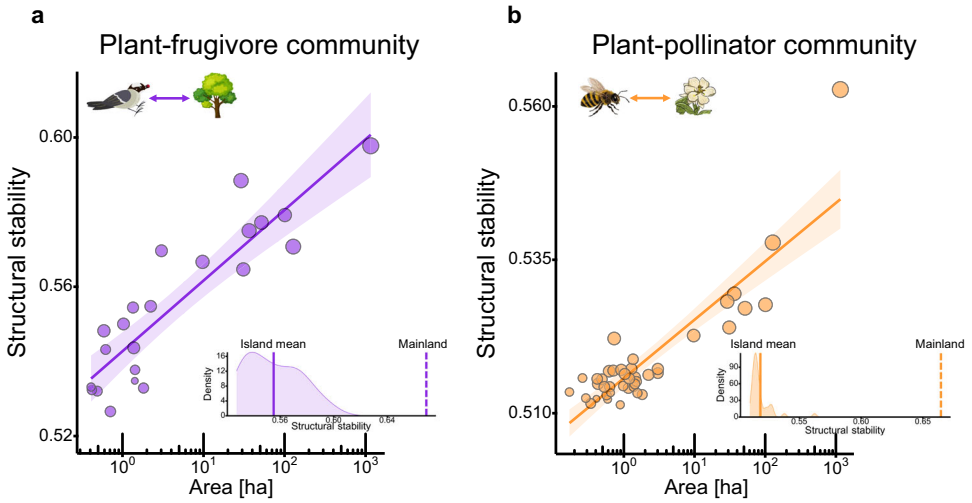

Fig. 3 | Modelled effects of island area on the structural stability of mutualistic communities on study islands and their comparison with those on the mainland in the Thousand Island Lake, China. a Plant-frugivore community. **b** Plant-pollinator community. Purple indicates the plant-frugivore community, and orange indicates the plant-pollinator community. Plots show partial effects of island area (log-transformed; ha) after controlling for both island isolation metrics (by setting to mean values). The size of each point is proportional to the total species richness of plants and animal mutualists on each island. Solid lines show fitted relationships from two-sided multiple linear regression models (plant-frugivore: regression slope $\beta = 0.008$, $t_{(18)} = 7.58$, $P < 0.001$, 95% CI [0.006, 0.011]; plant-pollinator: $\beta = 0.004$, $t_{(37)} = 10.85$, $P < 0.001$, 95% CI [0.003, 0.005]; Supplementary Table 2), and shaded areas indicate 95% confidence intervals. No adjustment for multiple comparisons was applied. The inserted density plots show the distribution of structural stability values for the plant-frugivore community ($n = 22$) and plant-pollinator community ($n = 41$) on study islands, with vertical lines representing the mean structural stability for the islands. Dotted lines indicate the corresponding structural stability on the mainland. Bird, pollinator and plant illustrations were created by Xue Zhang. Source data are provided as a Source Data file.

potentially enhancing their ability to withstand environmental fluctuations and perturbations. Thus, the presence of large patches could promote species' long-term coexistence in fragmented landscapes. As species have different responses to the reduction of their habitat area (e.g., habitat loss often disproportionately affects habitat specialists[40]), future research should incorporate species-specific characteristics into assessments of community persistence to further unravel the formation of the species-area relationship[41].

Building on insights from TIB and its extended hypotheses, larger islands are more easily discovered and colonized (target effect)[42] while also sustaining larger populations that reduce extinction rates (area effect)[4]. Our findings extend this framework: the enhanced species richness on larger islands may also reflect the greater capacity of their mutualistic communities to support species coexistence. Specifically, these communities facilitate the successful establishment of new immigrant species while maintaining the populations of resident species. Notably, our analyses controlling for species richness showed that this pattern of community persistence is not simply a by-product of species number (Supplementary Fig. 4). Rather, we interpret this pattern as reflecting the underlying structure of community reassembly[43], whereby changes in species composition and interaction characteristics can influence the potential of species coexistence. Species assemblages on larger islands are more likely to have compositions associated with greater persistence[44,45], unlike those on smaller islands. Thus, the ecological processes driving community reassembly, such as trait-mediated species sorting and interaction filtering[39], may therefore play a central role in shaping community stability.

We also establish a mechanistic link between changes in network structures and community persistence under habitat loss, underscoring the importance of mutualistic networks in promoting species coexistence[9]. Structural features such as low modularity in plant-frugivore networks and high nestedness in plant-pollinator networks were most associated with community persistence, despite overall variation in network size across islands (Supplementary Fig. 3). While network modularity can enhance stability in some contexts[29], our results suggest that high modularity may reduce community persistence. However, this pattern may partly reflect that small, species-poor networks tend to be more modular, so the apparent negative effect of modularity on community persistence may be driven by its relationship to species richness (Supplementary Fig. 3c). One plausible explanation is that effective competition may become stronger when mutualistic partners are restricted within modules[14]. In the context of binary networks, potential resource competitions may promote modular structures[32], as evidenced by a higher proportion of within-module interactions in smaller-sized networks (Supplementary Fig. 5). In contrast, nested structures minimize effective interspecific competition to support multispecies coexistence[14,21]. Compared with small islands, nested structures are more easily established than on larger islands because they harbour a broader spectrum of generalist and specialist species[46], thus fostering community persistence even in the presence of high species turnover[47].

Importantly, we observed contrasting dynamics between plant-frugivore and plant-pollinator systems. In plant-frugivore systems, high dispersal ability of birds may weaken the association between network nestedness and community persistence, as birds have a better capacity to move across nearby islands in search of fruit resources[39]. Such high connectivity can blur the expected local assembly patterns and decouple the association between nestedness and persistence. By contrast, the pollinators in our study were primarily insects with limited dispersal capacity, often confined to a single island unless passively dispersed by wind. Simulations further supported these distinctions. For small-sized island communities, higher nestedness in plant-frugivore networks and lower modularity in plant-pollinator networks were both associated with increased community persistence (Supplementary Fig. 6). These findings highlight the importance of distinguishing community characteristics and local processes in shaping landscape-level patterns, such as the role of ecological drift in small-size island communities[48].

The mechanisms driving community persistence in different mutualistic assemblages reflect their distinct ecological strategies. From the plant's perspective, seed dispersal by a diverse range of frugivores reduces seed aggregation and enhances germination

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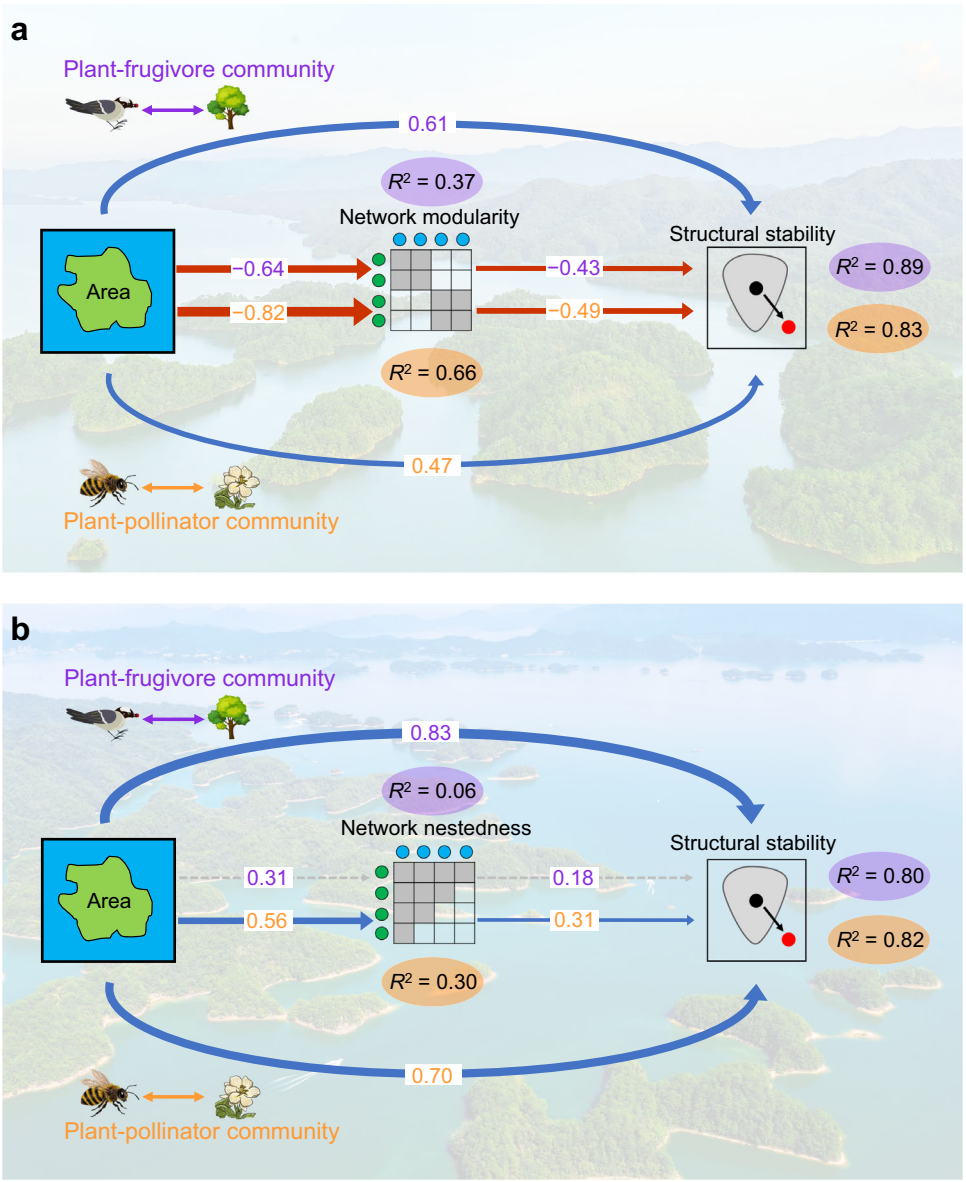

Fig. 4 | Path diagrams for the piecewise structural equation models (SEMs) showing how island area influences structural stability through network structures. a Network modularity as a mediator. **b** Network nestedness as a mediator. Arrows represent the direction of hypothesized causal relationships among variables, with arrow size proportional to the standardized regression coefficient of each pairwise relationship (i.e., effect size shown along each path). Path coefficients were estimated using piecewise structural equation models composed of two-sided linear models. No adjustment for multiple comparisons was applied. Blue arrows indicate positive regression coefficients, while red arrows indicate negative coefficients. The solid lines indicate significant paths (Supplementary Table 3), while grey dotted lines represent non-significant paths. The variance explained (adjusted R^2 values) are shown alongside the response variables. Path coefficients and variance explained are shown in purple frames for plant-frugivore communities (top panels of each SEM) and in orange frames for plant-pollinator communities (bottom panels). Bird, pollinator and plant illustrations were created by Xue Zhang. Schematic elements in the SEM diagrams were created by Chen Zhu. Background photographs in **a** and **b** were taken by Wande Li and Jingcao Pan, respectively. Source data are provided as a Source Data file.

success[49], while generalized feeding strategies support frugivore survival on resource-limited islands. Because trophic specialization tends to generate modularity[28], generalized and less modular plant-frugivore networks are therefore expected to promote species coexistence within island communities, even at the meta-community scale. In contrast, in plant-pollinator systems, plants often benefit disproportionately more from specialist pollinators to ensure conspecific pollen transfer[50]. At the same time, generalization in pollination networks can contribute to community stability[51], which is important for pollinator persistence on islands. Given this balance of benefits, nested structures in plant-pollinator networks are particularly important for promoting species coexistence accordingly, consistent with previous findings on network robustness to species loss[27]. Therefore, associated biological features are key to shaping species coexistence through their influence on the structural organization of communities.

Our findings emphasize that larger habitat patches enhance the persistence of mutualistic communities by supporting structurally organized interactions that emerge during community reassembly. Hydropower dam construction inundates large areas of continuous terrestrial habitats and leaves highly fragmented archipelagos of reservoir islands, resulting in long-term species loss and extinction debt in remnant communities[52]. Our results further reveal a deeper impact: as habitat area declines, dam-induced insularization undermines the resilience of remaining communities, potentially increasing

the risk of cascading biodiversity loss via coextinctions among interacted species. This insight moves beyond the traditional focus on species numbers, demonstrating that habitat loss also erodes the structural foundations of multispecies coexistence. Although the effects of habitat loss on mutualistic network structures have been well documented[33,53,54], we show that structural changes in modularity and nestedness can have alarming consequences by reducing community persistence. Given that our insular system, created by dam-induced inundation, shares key features with many habitat-fragmentation systems worldwide in terms of habitat area and isolation[34,35], our findings are particularly relevant to fragmented landscapes with largely inhospitable matrices, such as remnant forest fragments embedded in agricultural or urban landscapes. Looking ahead, an important direction for future research is to assess whether these patterns hold on oceanic islands, where distinct environments and evolutionary history may shape unique assembly dynamics[55–57]. Taken together, our work bridges a critical gap between island biogeography theory and community dynamics, highlighting that conservation strategies should address not only species richness but also community resilience across fragmented landscapes.

As forest regeneration and connectivity are increasingly recognized as key global conservation priorities[3,58], our findings underscore the urgency of maintaining sufficient habitat area to sustain and restore mutualistic interactions[59], which is therefore essential for maintaining long-term community stability. Moreover, restoration efforts should prioritize rebuilding mutualistic interactions, especially in small patches, for example by reintroducing species that enhance nestedness and among-module connectivity. Importantly, ecological restoration must be tailored to the specific interaction patterns of mutualistic communities, given their distinct ecological roles and differential sensitivities to fragmentation-driven shifts. The persistence metrics applied in this study provide valuable and quantitative tools for evaluating restoration outcomes beyond species richness, enabling the design of functionally informed conservation strategies. This approach is especially crucial in highly fragmented regions with hostile surrounding matrices, where accelerating global change imposes additional stress on already vulnerable ecosystems[60]. Ultimately, preventing further habitat loss and restoring interaction networks are as crucial as protecting species themselves for maintaining ecosystem resilience in the face of ongoing global change.

Methods

Study area

This study was carried out in the Thousand Island Lake, Zhejiang Province, eastern China (29°22′–29°50′ N, 118°34′–119°15′ E). The fragmented landscape was formed by the construction of the Xin'an River Dam for hydroelectricity in 1959, creating an insular area of approximately 573 km^2 at the high-water level (108 m). As a result, this artificial island archipelago includes 1078 land-bridge islands (area >0.25 ha) out of former hilltops (Fig. 1a). The surrounding mainland is covered with dense and unfragmented forests, which can be considered an ideal reference for community structures prior to habitat loss and fragmentation caused by dam-induced inundation[27]. Compared with the continuous forests on the mainland, all forests on the islands were clear-cut prior to lake formation, resetting mutualistic assemblages from a similar starting condition. Over the past six decades, forests on islands are undergoing natural secondary succession without human disturbance[35]. At present, the natural vegetation type on islands is a mix of subtropical deciduous and coniferous forest, dominated by *Pinus massoniana* in the canopy and broad-leaved plants in the subcanopy and understory[61]. Biotic pollination is mainly mediated by insects, whereas seed dispersal is mainly mediated by birds. The climate of this system is typical of the subtropical monsoon zone, with strong seasonal differences (hot and humid summers, and cool and mild winters).

Field sampling

All fieldwork complied with relevant institutional, national and local regulations. Field surveys were conducted with permission from Xin'an River Ecological Development Group Corporation and Thousand Island Lake National Forest Park.

We conducted a three-year sampling of mutualistic interactions for both plant-pollinator and plant-frugivore communities on a total of 41 islands (41 for pollination interactions and 22 for frugivory interactions) and multiple mainland sites (16 for pollination interactions and six for frugivory interactions) (Fig. 1b; Supplementary Table 1). The study islands were selected to achieve as much variation as possible in island area, with a focus on forest area, and in isolation, measured as the distance to the mainland. Mainland sites were selected to achieve high spatial coverage of continuous inland mountains around the lake margin and include similar vegetation types to those on the islands. For pollination interaction surveys, paired transect lines (100 × 4 m) were established on the study islands, with one along the edge and one extending perpendicular from the edge to the interior of the island[27]. The number of transect pairs on each study island varied from one to 16, depending on island area. The same strategy of transect lines was conducted for the 16 mainland sites, with a similar sampling effort to that of the largest island (i.e., 16 transect pairs); For frugivory interaction surveys, continuous transect lines (20 m wide) were established on the study islands (eight lines for the largest islands), running along the mountain ridge from the edge to the interior to cover as many habitat types as possible[61]. The total length of transect lines on each island was roughly proportional to the logarithm of the island area[62]. On the six mainland sites, 11 transect lines were established to keep the sampling area approximately equal to the largest island (i.e., a similar total length of transect lines)[24].

We used field observation to sampling pollination interactions on each transect line (Fig. 1c). We conducted surveys in calm and sunny weather, from 8:30 to 12:00 h and from 13:00 to 17:00 h, once every two weeks, on average. Overall, 20 surveys were conducted from March to July in 2017, 2018, and 2019, respectively. These surveying months represent the peak flowering period with frequent pollinator activities, ensuring that our sampling covered all dominant plant species in this region. During the field sampling, we considered an insect to be a potential pollinator only if it contacted anthers and/or stigmas of the flowers. For pollinator or plant species that could not be identified in the field, we collected voucher specimens and identified their taxonomy by specialists in the laboratory. More sampling details and sampling completeness of pollination interactions can be found in Ren et al.[27].

We used arboreal camera trapping to sample frugivory interactions of birds on each transect line (Fig. 1c). Arboreal camera trapping has been proven to be an effective method for recording frugivory interactions in arboreal habitats on a large spatiotemporal scale[61]. We monitored transect lines twice a month and searched for fleshy-fruited plants from July to next January in 2019, 2020, and 2021, respectively. These surveying months represent the fruit maturation period for most of fleshy-fruited plant species in this region. We placed cameras facing areas with plentiful fruits and checked all cameras every two weeks to keep them running. Fleshy-fruited individuals were monitored from the onset of ripening until the fruits dropped. All photos and videos were checked by at least two people to acquire frugivory interactions. Here we used frugivory interactions that may lead to seed dispersal[39], identifying a species as a potential seed disperser based on its seed handling behaviour of swallowing entire fruits from photos or videos. More sampling details and sampling completeness of frugivory interactions can be found in Zhu et al.[61] and Zhu et al.[38], respectively.

For both pollination and frugivory interactions, we combined data from multiple interaction surveys and built bipartite species-based networks for each study island and the mainland. In this study, we

consistently used the forest-covered area at the 105 m water level to estimate island area and isolation for all study islands[27].

Calculating structural stability

We used structural stability to assess community persistence. The concept of structural stability quantifies the range of environmental conditions under which a community can persist—also known as feasibility[18,63]. Considering the parsimonious model of community dynamics and the structural theoretical background developed for binary networks[64], our following analyses were exclusively conducted using binary networks, a common approach in structural stability researches[17,18,21,63]. Each binary network represents the presence (1) or absence (0) of an observed interaction between two species. We used a generalized Lotka-Volterra model to describe the population dynamics of species in a given mutualistic network as:

$$\begin{cases} \frac{dN_i^{(P)}}{dt} = N_i^{(P)}\left(r_i^{(P)} - \sum_j \alpha_{ij}^{(P)} N_j^{(P)} + \sum_j \gamma_{ij}^{(P)} N_j^{(A)}\right) \\ \frac{dN_i^{(A)}}{dt} = N_i^{(A)}\left(r_i^{(A)} - \sum_j \alpha_{ij}^{(A)} N_j^{(A)} + \sum_j \gamma_{ij}^{(A)} N_j^{(P)}\right) \end{cases} \quad (1)$$

where N_i corresponds to the population size (or abundance) of plant (P) and animal (A) species i, respectively; r_i is the intrinsic growth rate of species i; α_{ij} is the intraguild competition; and γ_{ij} is the benefit received via mutualistic interactions (i.e., interaction strength between species i and j). Then the interaction matrix $\boldsymbol{\alpha}$ could be represented as:

$$\boldsymbol{\alpha} = \begin{bmatrix} \alpha^P & -\gamma^P \\ -\gamma^A & \alpha^A \end{bmatrix} \quad (2)$$

For the competition parameters, we used a mean field approximation where we set $\alpha_{ii}^{(P)} = \alpha_{ii}^{(A)} = 1$ and $\alpha_{ij}^{(P)} = \alpha_{ij}^{(A)} = \boldsymbol{\rho}$ $(i \neq j)$. Note that in our study, we mainly focus on mutualistic effects and thus neglect intra-trophic competition ($\boldsymbol{\rho}$ = 0)[17,21]. The mutualistic benefit is parameterized[17,21,65] as:

$$\gamma_{ij} = \frac{\gamma_0 \cdot m_{ij}}{k_i^{\delta}} \quad (3)$$

where γ_0 represents the overall level of mutualistic strength (or average mutualistic strength), m_{ij} = 1 if species i and j interact and 0 otherwise, k_i is the number of species interacting (mutualistic partners) with species i. δ is the mutualistic trade-off, controlling the interaction strength difference between specialist and generalist species[62]. δ was set to 0.5 (values between 0 and 1 lead to the same conclusions)[16,17,21]. The γ_0 was set as half the average mutualistic strength that could maintain the stability of the system[63,66]. For mutualistic communities in the fragmented landscape, γ_0 was set as half the average mutualistic strength of the regional network (i.e., the network across all fragments) at the stability threshold. The stability conditions derived from the linear model remain valid for a broader class of nonlinear mutualistic systems when γ_0 is set below the critical threshold, as this parameterization confines the dynamics to a conservatively stable regime[16]. In fact, the nonlinear system is known to tolerate even higher levels of mutualism, making the linear model's conditions a sufficient guarantee of global stability in our case.

Then, we analytically estimated the parameter space of intrinsic growth rates leading to positive species abundances[67]. For the interaction matrix $\boldsymbol{\alpha}$, the range of intrinsic growth rates that could lead to an equilibrium state of the system is called the feasibility domain $D_F(\boldsymbol{\alpha})$. Given a_{ij} is the element of matrix $\boldsymbol{\alpha}$, this feasibility domain can be written as:

$$D_F(\boldsymbol{\alpha}) = \left\{ r_i = \sum_{j=1}^{S} a_{ij} N_j^*, with\, N_i^* > 0 | i = 1, 2, \ldots, S \right\} \quad (4)$$

which construct an algebraic cone (the normalized parameter space of intrinsic growth rates) in the Euclidean space R^S (S is the total number of plant and animal species). We could measure the feasibility domain $D_F(\boldsymbol{\alpha})$ by calculating the normalized solid angle $\Omega(\boldsymbol{\alpha})$ as:

$$\Omega(\boldsymbol{\alpha}) = \frac{vol\left(D_F(\boldsymbol{\alpha}) \cap \mathbb{B}^S\right)}{vol\left(\mathbb{B}^S\right)} \quad (5)$$

which is the proportion of a unit S-dimension ball $\mathbb{B}^S$ in R^S that is shared with feasibility domain[21]. Analytically, the size $\Omega(\boldsymbol{\alpha})$ of the feasibility domain can be efficiently computed via a quasi-Monte Carlo method[17,21,68]. The size of the feasibility domain is biased by the dimension of the community[69], that is, it decreases by increasing community size. To compare communities containing different species number S between islands, the feasibility domain is normalized[17,63] as:

$$\omega(\boldsymbol{\alpha}) = \Omega(\boldsymbol{\alpha})^{1/S} \quad (6)$$

As a result, the scaled value of the feasibility domain ranges between zero and one[18]. Overall, this measure of structural stability (i.e., feasibility domain) estimated the probability that all species in a given mutualistic community can tolerate random environmental perturbations (i.e., maintain positive equilibrium abundances and avoid extinction).

Network structures

Nestedness, a pattern of the more specialist species interacting with proper subsets of those species that interact with the more generalist species, has been widely documented in mutualistic plant-animal systems[46]. Previous studies have demonstrated that nested structures in mutualistic networks promote community stability[21,30]. Modularity, a patten of species forming densely connected subsets (i.e., modules or compartments), has also been shown to influence network stability[29] and persistence[30]. Thus, we selected nestedness and modularity as two key network-level metrics to represent the structural features of mutualistic networks in this study. We calculated the nestedness value of each network as the NODF metric based on overlap and decreasing fill[70]. We computed modularity using the DIRTLPAwb+ algorithm, which is designed to maximize the modularity value[71]. For each island network, we ran the algorithm 100 times and retained the highest value of modularity. Both NODF and modularity values were calculated using the bipartite package[72] in R. Additionally, we computed nestedness using the updated NODF metric proposed by Fortuna et al.[73], in which overlap between equal-degree rows/columns ("ties") contributes to nestedness—unlike in the raw NODF, which assigns such pairs zero. The raw and updated NODF were highly correlated in both plant-frugivore (Pearson's r = 0.97, P < 0.001) and plant-pollinator (r = 0.70, P < 0.001) networks.

Statistical analyses

We employed Kendall's correlation tests to assess the relationships between species richness and structural stability on study islands, accounting for cases where species richness was equal among certain islands. We used multiple linear regression models to assess the effects of island area (log-transformed) and isolation (the distance to the mainland and the distance to the nearest island) on structural stability. For both frugivory and pollination models, variance inflation factors (VIFs) for all predictors were less than 2, indicating no problematic

collinearity. To test the robustness of our findings, we recalculated structural stability using different parameter settings for mutualistic trade-off (δ) and mutualistic strength (γ_0). The results, presented in Supplementary Fig. 7 and Supplementary Fig. 8, respectively, confirmed that the positive relationship between island area and structural stability remained unchanged (Fig. 3). We conducted a one-sample t-test to determine whether the mean structural stability of island mutualistic assemblages differed significantly from that on the mainland.

Based on the multiple linear regression results, we found that island area was the only significant predictor of structural stability. Therefore, we further assessed the direct/indirect effects of island area on structural stability through network structures using structural equation models (SEMs). We specifically assumed that (1) habitat loss and fragmentation (island area in our case) affect modularity and nestedness of mutualistic networks[24,33]; (2) the effects of habitat loss and fragmentation on structural stability are mainly through network modularity and nestedness (Fig. 2b). The piecewise SEM incorporates several linear models with local estimation of parameters into a directed acyclic graph[74], allowing for fitting more data distributions. Moreover, piecewise SEM can allow greater robustness in fitting smaller sizes[75], which is more proper for our study cases. Given the commonly observed correlation patterns between network modularity and nestedness[76] and the limited sample sizes (22 islands for plant-frugivore communities and 41 for plant-pollinator communities), we constructed separate SEMs incorporating either modularity or nestedness to avoid multicollinearity and overparameterization. Given the variability in sample sizes and model complexities between the two SEM models, we opted to report the adjusted individual R-squared, providing a more reliable indication of the true explanatory power of the models. SEMs and model testing were performed using the piecewiseSEM package[75]. Because these SEMs are saturated (d.f. = 0), Shipley's d-separation test yields Fisher's $C = 0$ ($P = 1$) by construction[74]; therefore overall goodness-of-fit cannot be assessed, and we focus on standardized path coefficients and adjusted R^2. Using the updated NODF, the piecewise SEM results were qualitatively unchanged for plant-frugivore communities (no mediated effect; Supplementary Fig. 1). In plant-pollinator communities, network nestedness remained positively linked to structural stability, but was unrelated to island area (Supplementary Fig. 1), likely because the updated NODF counts the overlap between pairs of species with equal degree, which are more common on small islands, thereby inflating nestedness relative to the raw metric (see the updated NODF above).

To further examine the independent effects of network structures on structural stability, we conducted partial regression analyses accounting for the potential confounding effect of network size (i.e., the product of plant and animal species richness), as network size may affect both of network structures[32]. Specifically, we controlled for network size and the non-focal network metric (i.e., nestedness when testing modularity, and modularity when testing nestedness) in each analysis.

Additionally, we analysed whether the influence of habitat loss and fragmentation on structural stability was independent of species richness—specifically, whether variations in structural stability among islands were driven by the specific mutualistic assemblages per se (i.e., species combinations and their interactions). To control for species richness effects, we used the minimum number of species observed across study islands (five plant species and seven animal species for plant-frugivore communities; seven plant species and 26 animal species for plant-pollinator communities; Supplementary Table 1) to construct null networks across islands. For each island, we built null networks by randomly selecting the target number of plant and animal species (see above) from the observed network on that island. All realized interactions among the selected species in the local network were retained (Supplementary Fig. 9). To ensure valid null networks, we required that each selected plant had at least one interaction with the selected animals and each selected animal had at least one interaction with the selected plants. If the selection resulted in isolated species (i.e., without any realized interactions), the draw was discarded and repeated until all species had at least one partner (details in Code availability). Overall, for each random selection of a null network, species were sampled with equal probability, and the degree of each selected species was determined by its realized interactions with the co-selected species in the local observed network (Supplementary Fig. 9). We generated 1,000 valid null networks with constant network size to calculate the mean structural stability for each island, and then used multiple linear regression models to evaluate the effects of island area and isolation on structural stability (see above) when maintaining consistent species richness across study islands. Note that Island #25 was excluded from the null analysis of plant-pollinator communities because it was not possible to generate a null network with seven plant species and 26 pollinator species, ensuring that each species had at least one interaction.

We simulated mutualistic networks to examine the relationships between network structures and structural stability in the context of consistent species richness and interaction richness (i.e., controlling for variation in network connectance), based on observed communities on study islands and the regional interaction pool. We selected four islands spanning a gradient of island area (101.02, 51.89, 2.23, and 0.41 ha; Supplementary Table 1), with corresponding gradients in species and interaction richness (plant-frugivore interactions: 79, 83, 43, and 16; plant-pollination interactions: 360, 367, 106, and 33). For each island, we simulated 1,000 mutualistic networks following these steps: (1) we randomly selected the same number of plant and animal species as observed on each island, drawing from the complete regional species pool (including both islands and mainland). If the total number of potential interactions among the selected species was lower than the observed interaction richness on the island, this step was repeated; (2) we then randomly selected interactions among the chosen species to match the observed interaction richness, ensuring that every species maintained at least one interaction (details in Code availability). For each simulated network, we calculated structural stability, nestedness (NODF), and modularity, and used Pearson's correlation tests to assess the relationships among these metrics. All statistical analyses were conducted using R version 4.2.1 (www.r-project.org)[77].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data supporting the findings of this study are available in Figshare (https://doi.org/10.6084/m9.figshare.30174802)[78]. Source data are provided with this paper.

Code availability

All scripts that are needed to reproduce the analyses are available in Figshare (https://doi.org/10.6084/m9.figshare.30174802)[78].

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Author contributions

C.Z., X.S., and P.D. conceived the idea and designed the study, with support from P.R.; C.Z., P.R., and W.L. conducted the fieldwork; C.Z. analysed data with assistance from P.R. and L.C.; C.S. and L.C. contributed to statistical modelling; C.Z. led the writing, with substantial contributions from J.B., X.S., B.D., F.G., Y.Z., D.Z., and P.D.

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Competing interests

The authors declare no competing interests.

Additional information

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