ECOGRAPHY

Research

Stable species and interactions in plant–pollinator networks deviate from core position in fragmented habitats

EDITOR'S CHOICE

Peng Ren, Xingfeng Si and Ping Ding

P. Ren (https://orcid.org/0000-0001-6033-6188) and P. Ding (https://orcid.org/0000-0001-5825-0932) ✉ (dingping@zju.edu.cn), MOE Key Laboratory of Biosystems Homeostasis & Protection, College of Life Sciences, Zhejiang Univ., Hangzhou, Zhejiang, P. R. China. – X. Si (https://orcid.org/0000-0003-4465-2759), Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal Univ., Shanghai, P. R. China.

Ecography
2022: e06102
doi: 10.1111/ecog.06102

Subject Editor: Daniel Stouffer
Editor-in-Chief: Miguel Araújo
Accepted 13 April 2022

Species and their interactions are more dynamic over time and space in fragmented habitats than in continuous habitats. In fragmented habitats, the low nestedness of mutualistic networks may be related to the position change of stable (high persistence over time/space) species and interactions in the networks. Previous studies have shown that stable species and interactions tend to be in the core position of mutualistic networks. However, in fragmented habitats, it remains unknown whether stable species or interactions still tend to be in the core position. To address this gap, here we evaluated the correlation between the position of proximity to the network core and the temporal/spatial stability of species and interactions, using the observation of 42 plant–pollinator networks conducted in a fragmented island landscape over 3 years. We showed that temporally/spatially stable species and interactions deviated from the network core to varying degrees. Temporally stable plants were most likely to deviate from the network core, followed by pollinators and interactions, while only spatially stable pollinators tend to deviate from the network core. When unstable species (present in few time/space points, typically specialists) and interactions occupy the network core, they cannot interact with most species in the network as generalists do, resulting in the decrease of network nestedness. Therefore, from the perspective of position and stability, stable species and interactions deviate from the network core in fragmented habitats, which is an important reason for the decrease of nestedness in mutualistic networks. Our study suggests that protecting plants which occupy the core in large plant–pollinator networks is essential for maintaining the network persistence in fragmented habitats.

Keywords: habitat fragmentation, mutualistic networks, nestedness, network core, spatio-temporal persistence, stability

NORDIC SOCIETY OIKOS

www.ecography.org

Introduction

Ecological networks are sensitive to variable environments, which can cause dramatic changes of species and their interactions in the network (Tylianakis et al. 2008, Garibaldi et al. 2011, Schleuning et al. 2016, Fortin et al. 2021). The stability (i.e. the persistence over time/space) of species and interactions is closely related to their position within the network (Alarcón et al. 2008, Aizen et al. 2012, Emer et al. 2016, Chacoff et al. 2018, Zografou et al. 2020). Previous studies have found that stable species (i.e. species with high persistence over time/space, usually generalists) (Delmas et al. 2019, Zografou et al. 2020) and stable interactions (Fang and Huang 2016, Chacoff et al. 2018, Resasco et al. 2021) tend to be in the core position of plant–pollinator networks. Stable species tend to interact cohesively and form the network core (the most densely connected region of the network), which is essential for maintaining the high nestedness of plant–pollinator networks (Chacoff et al. 2018, Zografou et al. 2020, Resasco et al. 2021). However, when unstable species and interactions occupy the network core, the loose connection of them is hard to form the network core, which will result in decrease of network nestedness (Chacoff et al. 2018, Zografou et al. 2020).

Previous studies have shown that habitat fragmentation typically has a negative impact on plant–pollinator networks (Bascompte and Stouffer 2009, Spiesman and Inouye 2013, Grass et al. 2018). That is, habitat fragmentation destabilizes species and interactions over time or space, and even leads to the non-random loss of them in fragmented patches (Aizen et al. 2012), the reorganization of them in plant–pollinator networks (Aizen et al. 2012, 2016, Spiesman and Inouye 2013) and the decrease of network nestedness (Thébault and Fontaine 2010, Evans et al. 2013, Trøjelsgaard and Olesen 2016, McWilliams et al. 2019). Species in fragmented habitats cannot get so many partners as in a comparable continuous habitat (Aizen et al. 2012, Spiesman and Inouye 2013, Grass et al. 2018). Species (including stable species) will lose some partners in fragmented habitats, so stable species losing partners may not remain in the densely connected region of the network, i.e. deviating from the network core. Besides, the loss of the peripheral species in the network, which is most vulnerable to be lost by loss of interactions or partners (Miele et al. 2020), can also lead to the change (shrinkage or collapse) of the network core and the decrease of network nestedness (Nielsen and Totland 2014). Based on the above analysis, however, no studies have explored the reason for the decrease of network nestedness from the perspective of whether stable species and interactions deviate from the network core. There exists a knowledge gap whether stable species and interactions deviate from the network core in fragmented habitats, leading to the decrease of network nestedness. Therefore, we propose a hypothesis that stable species and interactions deviate from the network core in fragmented habitats (Fig. 1).

In addition, we further assess which one of the three (stable plants, stable pollinators or stable interactions) most easily deviates from the network core. In fragmented habitats, plants in the network are expected to more easily deviate from the network core than pollinators, since the reduction of the patch area will directly lead to the reduction of plant resources (Spiesman and Inouye 2013, Grass et al. 2018). Compared with pollinators, plants are more likely to be constrained by isolation because they cannot disperse actively in a short time (Greenleaf et al. 2007). However, in our study, the highly isolated islands are less affected by human activities, so it is difficult to predict that the effect of isolation on plants or pollinators is negative (making them deviate from the core position with the increase of isolation), neutral or positive. Indeed, pollinators tend to have high mobility and be less affected by isolation (Winfree et al. 2011), and meanwhile, pollinators have a high potential for adaptively switching interaction partners (Kaiser-Bunbury et al. 2010, Evans et al. 2013, Ponisio et al. 2017, Grass et al. 2018). The implementation of interactions depends primarily on the activities of pollinators in fragmented habitats (Aguilar et al. 2006), so pollinators and interactions should be similar in how easily they deviate from the network core.

In fragmented systems, patch area and isolation are the predominant elements of habitat fragmentation (Fahrig 2017). In this study, our goal is to evaluate how stable species and interactions respond to island area and isolation, i.e. whether stable species and interactions deviate from the network core in fragmented habitats. To achieve our goal, we conducted a three-year survey of plant–pollinator networks on 41 islands and mainland in the Thousand Island Lake (TIL) of China. For these plant–pollinator networks, we use linear regression to explore whether temporally/spatially stable species and interactions deviate from the network core in fragmented habitats. To further ensure whether the deviation from the network core is caused by the effects of habitat fragmentation, we created null model networks to imitate the process that species and interactions occupy different network positions.

Material and methods

Study site and data collection

Thousand Island Lake is located in Zhejiang Province, eastern China (29°22″–29°50″N, 118°34″–119°15″E; Fig. 2). The large artificial reservoir was created in 1959 by the construction of the Xin'anjiang Dam for hydroelectricity production, resulting in the flooding of an area of approximately 580 km^2 at the high-water mark of 108 m. It contains 1078 islands (0.25–1320 ha) that were former hilltops (Si et al. 2017). The main habitat type is unmanaged secondary forest (mean coverage per island = 82.6%), where the dominant plant species is *Pinus massoniana* (Liu et al. 2018). The average annual temperature is 17.0°C, ranging from −7.6°C to 41.8°C (Wang et al. 2010).

We surveyed plant–pollinator interactions on 41 islands and at 16 mainland sites (Fig. 2). We selected islands that encompassed as much variation in island area and isolation (measured as the distance from the focal island to the mainland)

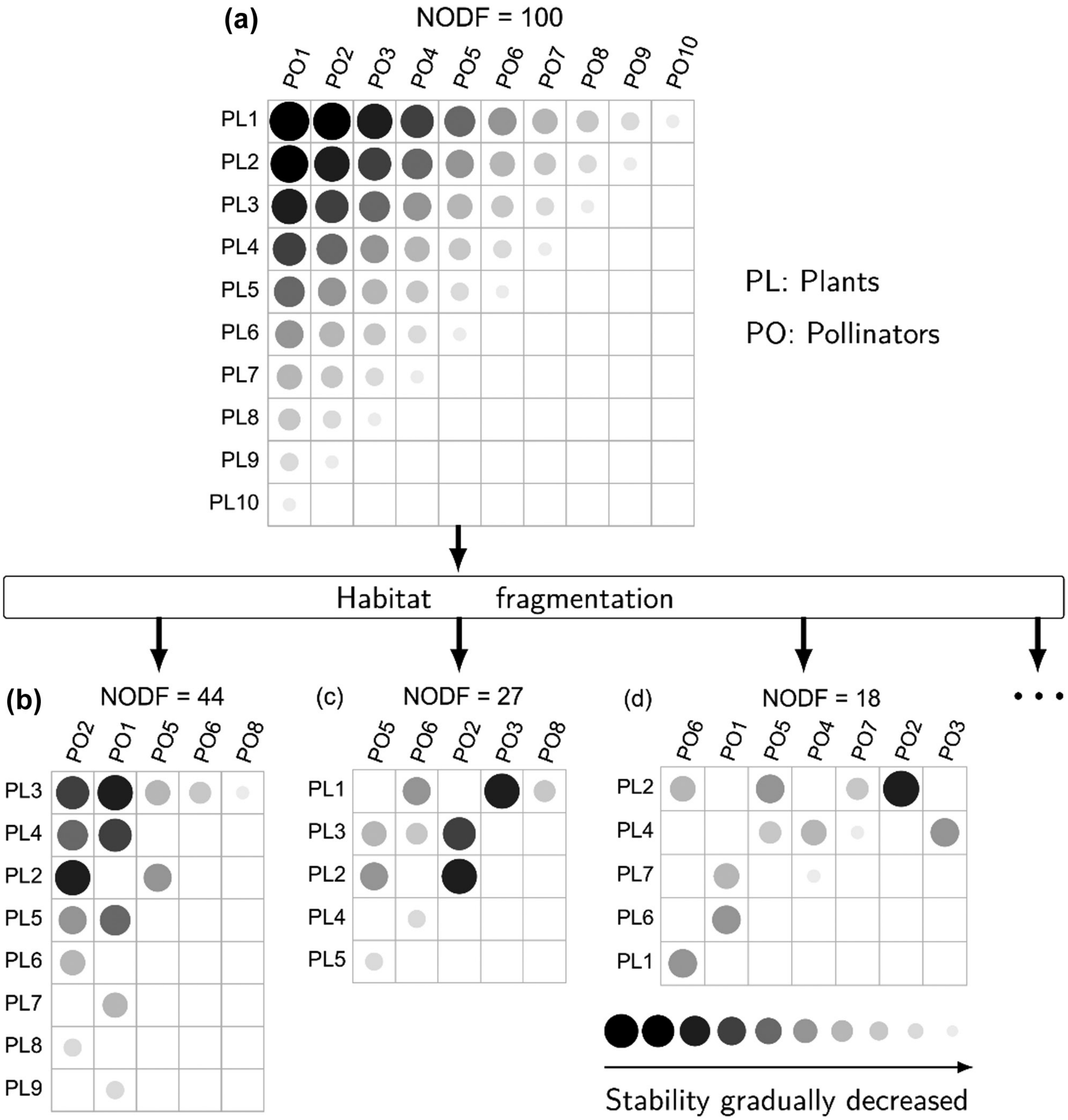

Figure 1. The hypothesis is that the effect of habitat fragmentation changes the positions of stable species and interactions, and makes them deviate from the network core. (a) The perfectly nested plant–pollinator networks in continuous habitat, where stable species and interactions tend to be in the core position within the network; (b–d) Networks in fragmented habitats (sub-networks that randomly draw from the perfectly nested network *a*, where the more stable the species or interactions are, the more likely they are to persist in sub-networks) with low nestedness, where stable species and interactions deviate from the network core.

as possible. We selected mainland sites that contained similar types of vegetation as found on islands. We established paired transect lines (100 × 4 m), with one along the edge and one extending perpendicular from the edge to the interior of the island. The number of pairs of transects on each island varied from one to sixteen, and was roughly proportional to *ln*-transformed island size (Schoereder et al. 2004) (Supporting information). On islands with more than two pairs of transects, each pair was separated by ≥ 0.5 km. Along each transect, we observed individual flowering branches of shrubs and trees, or the whole plant of herbs under 3.5 m of height. Due to the larger number of flowering plants at edges, we conducted 15-minute surveys for edge transects and 10-minute surveys for interior transects. We carried out observations only in calm and sunny weather, from 8:30 to 12:00 h and from 13:00 to 17:00 h. Because flowering phenology differed among species, we sampled once every two weeks, on average, with six surveys conducted at each site from 20 April to 20 July in 2017, with seven surveys at each site from 23 March to 14 July in 2018, and with seven surveys at each site from 13 March to 20 July

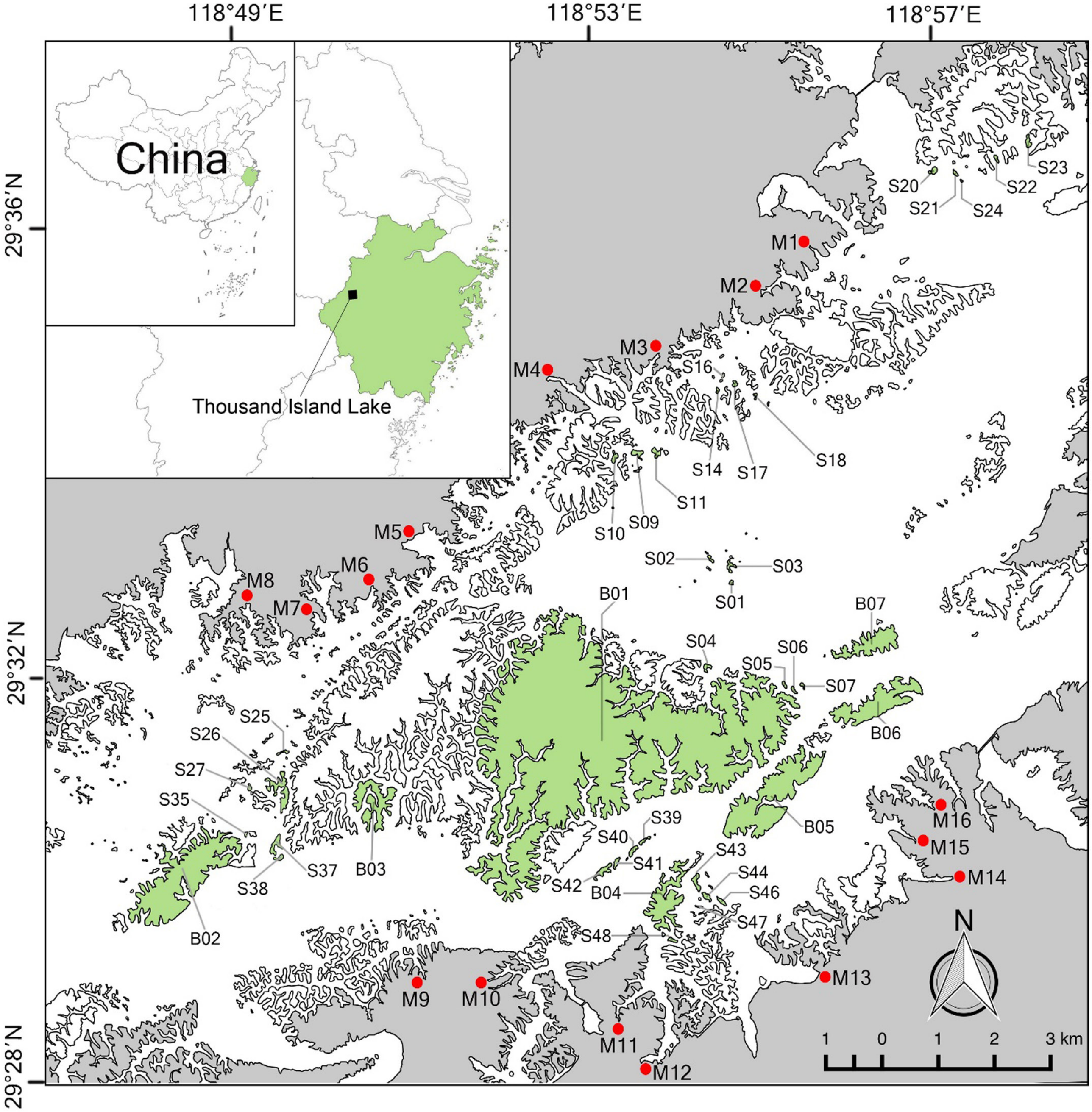

Figure 2.Map of the study region showing the 41 study islands (green shading; B01–B07, S01–S07, S09-S11, S14, S16-S18, S20-S27, S35, S37-S44, S46-S48) and the mainland sampling sites (grey shading and blue dots; M1–M16) at the Thousand Island Lake, Zhejiang Province, eastern China.

in 2019. These surveying periods represent the peak flowering time and have the highest pollinator activities, ensuring that our survey period covered the entire flowering period of all dominant plant species in the TIL.

During the sampling periods, we considered an insect to be a pollinator only if it physically touched the anthers and/or stigmas of the flowers (Vázquez et al. 2005). For pollinators and plant species that could not be identified immediately in the field, we captured voucher specimens using a sweep-net and identified the taxonomies in the laboratory (the identifications were later verified by specialists, see Acknowledgments). We recorded the number of pollinators visiting each flowering species during the sampling period and ensured the insect taxon of these pollinators. We also estimated the flower area of each plant along each transect at each sampling period, then calculated the flower area of each island. We used the same sampling strategy for the 16 mainland sites (representing the whole mainland), with a sampling effort designed to match the number of surveys on the largest island (i.e. 16 pairs of edge and interior transects) (Fig. 2; Supporting information). The list including the plants, flower area, pollinators and pollinator abundance is presented in Supporting information.

Sampling completeness

Achieving high-level sampling completeness of species and interactions (especially interactions) is a considerable challenge for studying ecological networks (Chacoff et al. 2012). We conducted analyses to ensure that our results do not stem from sampling artefacts. We used 'sample coverage' to measure the sampling completeness of plants, pollinators and interactions, which is defined as the proportion of the total number of individuals in a community belonging to the species represented in the sample (Chao and Jost 2012). We calculate the sample coverage using the R package *iNEXT*, ver. 2.0.20 (Hsieh et al. 2016).

The position of species and interactions in the network

Diverse centrality indices provide useful measures for the influential nodes according to different topological patterns (Lü et al. 2016). We used two benchmark centrality indices, i.e. betweenness centrality (*BC*) and closeness centrality (*CC*), to evaluate the position of plants and pollinators in the network. *BC* of a given species denotes the proportion of all shortest paths between all pairs of species in a network that pass through the given species (Newman 2003, Delmas et al. 2019), where high *BC* values indicate that species tend to act as module connectors in modular networks. *CC* of a given species denotes the shortest path length between the given species and all other species in the network (Freeman 1978, Delmas et al. 2019), where high *CC* values indicate that species are close to many other species and efficiently influence the overall network. We used two additional indices, i.e. proximity to core (*Proxcore*) (Chacoff et al. 2018) and core-periphery structure (*Coper*) (Miele et al. 2020), to evaluate the position of interactions in networks. *Proxcore* is calculated as the difference between 1 with standardized Euclidean distance to the upper-left cell in the nested network (Almeida-Neto et al. 2008, Chacoff et al. 2018), where high *Proxcore* values indicate that interactions are near to the network core. *Coper* is based on the stochastic block model (SBM) (Newman and Leicht 2007, González et al. 2020, Miele et al. 2020). For the plant–pollinator networks, the SBM infers groups of statistically equivalent nodes, i.e. species are connected in a similar way in the same group (González et al. 2020), then species are grouped into core species and peripheral species. Therefore, interactions in the network are divided into four groups when the core–periphery structure exists (each species ordering is represented by 1 (core) or 2 (periphery)): group C11 represents the core; groups C12 and C21 represents interactions between core and periphery; group C22 represents the periphery. That is, the interactions are divided into three groups consisting of core, between core and periphery, and periphery. Compared with the *Proxcore*, *Coper* could loosely rank the position of each interaction in core, between core and periphery, and in periphery. The *Proxcore* and *Coper* methods describe the position characteristic of interactions in the network from different perspectives. *Proxcore* is based on the standardized Euclidean distance of nestedness metrics (i.e. presence of hierarchical subsets of interactions), while *Coper* is based on the statistically equivalent nodes (González et al. 2020). Therefore, we used the *Proxcore* to precisely rank the position of each interaction relative to the core of the network, and the *Coper* to loosely rank the position of each interaction in core, between core and periphery, and in periphery. We calculated *BC* and *CC* scores using function *ND* in R package '*bipartite*', ver. 2.16 (Dormann et al. 2021), *Proxcore* scores using function *interaction.stability.r* (Chacoff et al. 2018), and *Coper* scores using function *cpness* in package '*econetwork*', ver. 0.6.0 (Vincent et al. 2021).

Measuring stability over time and space

We studied the stability of plants, pollinators and interactions over time (in different years) and over space (in different islands), respectively. We measured the stability of plants and pollinators by calculating $1/CV$ (a measure of stability), using flower area and pollinator abundance, respectively. The notation CV is defined as the coefficient of variation, called variability, which is equal to the standard deviation divided by the mean. The index $1/CV$ could perform well at species- or community-levels, in situation where the data contains no or a small proportion of cases with one observation so that there are relatively few fluctuations (Kefi et al. 2019). However, with the use of $1/CV$, two issues arise when calculating the stability of interactions (Chacoff et al. 2018), as presented below.

First, the frequency of interactions usually widely varies over time and space due to environmental factors, such as phenology, climate change and habitat fragmentation (Fortuna and Bascompte 2006, Hegland et al. 2009, Rafferty and Ives 2011, Chase et al. 2020, Peralta et al. 2020). These variations thus lead to considerable number of interactions only occurred once over time or space (Petanidou et al. 2008, Aizen et al. 2012, Chacoff et al. 2018). For these interactions, the value $1/CV$ is derived to be a constant value $(1/CV = \sqrt{1/n})$ which only relates to the total number of n years or n sites (details of this derivation in the Supporting information). Second and more importantly, the value $1/CV$ neglects the span of interactions over time and space, which makes some rarely occurred interactions more stable than widely occurred interactions. The above two aspects lead to inaccurate calculations of the stability of interactions. Consequently, here we propose a new method to calculate $1/CV$, in order to appropriately evaluate the stability of interactions. The new method considers two perspectives for the stability of interactions: the span (denoted as S, the number of years or sites in which non-zero interaction was observed; Supporting information) and the variability (CV), which avoids the case where rarely occurred interactions are more stable than widely occurred interactions. Obviously, the larger the value *S*, the broader the span of interactions over time or space. The proposed new method can be used to appropriately evaluate the stability of interactions over time and space. More specifically, within a given year or location, the span of interactions can be obtained based on the number of years (across temporal analyses) or islands (across spatial analyses) that interactions occurred. Then the stability (the value $1/CV$) of the interactions is overall higher with larger values *S* than that with smaller values *S*. The above calculations and analyses imply that *S* is the primary factor to consider when we evaluate the stability of the interactions, and further we can evaluate the stability of different interactions within the same span.

For interactions with the same value *S* in terms of the new method, we can further evaluate the stability of each interaction. To do this, we calculate the stability using the equation $1/CV$ = mean/standard deviation. But in this case, the zero observed interaction abundance is excluded when we calculate the value 'mean' (the mean of non-zero observations), since we have considered their *S* values. Indeed, the span is divided in terms of observed values that are non-zero, i.e. the value *S* will decrease by one as soon as one zero observation occurs. Now we calculate $1/CV$ of interactions, i.e. (Eq. 1):

$$1/CV = \begin{cases} \dfrac{\text{mean}\left(\sum_{i=1}^{n} f_i\right)}{\left(f_i\right)}, & \sigma\left(f_i\right) \neq 0 \\ \text{mean}\left(\sum_{i=1}^{n} f_i\right), & \sigma\left(f_i\right) = 0 \end{cases} \tag{1}$$

where the f_i is the interaction frequency at the *i*th year or island, and $\sigma(f_i)$ is the standard deviation of the interaction frequency at the total years or islands. For interactions that only occurred once, i.e. the case where $\sigma(f_i) = 0$, $1/CV$ is equal to their frequency. As a result, after obtaining $1/CV$ based on the two perspectives of the span *S* and the variability, we can avoid biases inherent in previous calculation method of stability and evaluate the stability of interactions more appropriately.

Statistical analyses

Previous studies have shown that temporal stability and spatial stability, stability and frequency, as well as stability and generalization, are highly correlated respectively (Chacoff et al. 2018, Zografou et al. 2020, Resasco et al. 2021). In our study, we also explore and further justify the above three correlations. Specifically, we calculate Spearman's rank correlation coefficients between temporal stability and spatial stability (for plants, pollinators and interactions), between temporal/spatial stability and frequency (for plants, pollinators and interactions) and between temporal/spatial stability and generalization (for plants and pollinators). To calculate the generalization value of species, we used functions *species-level* in R package '*bipartite*', ver. 2.16 (Dormann et al. 2021).

To explore whether temporally/spatially stable species and interactions deviate from the network core, we calculate Spearman's coefficients of the correlation between the position of proximity to the network core and the temporal/spatial stability (here called position-stability correlation) of plants, pollinators and interactions. For the position-stability correlation of plants and pollinators, we calculate the correlations between betweenness centrality and stability ($BC - 1/CV$), and between closeness centrality and stability ($CC - 1/CV$). For the position-stability correlation of interactions, we calculate the correlations between core-periphery and stability ($Coper - 1/CV$), and between position of proximity to the network core and stability ($Proxcore - 1/CV$). We use ANOVA analysis to show whether the position-stability correlations among plants, pollinators and interactions are significantly different from each other between temporal and spatial scales. For the networks in 41 islands, we use linear regression to explore how island attributes affect Spearman's coefficients. As the two major attributes, area and isolation have no correlation with each other (Pearson's $r = -0.14$, $p = 0.38$). The results of linear regressions could show whether island area and isolation change the positions of temporally/spatially stable species and interactions, making them deviate from the network core. The linear regression coefficients could show the likelihood of temporally/spatially stable plants, pollinators and interactions deviate from the network core. Using linear regression to Spearman's coefficients is credible proved by the linear mixed models (Supporting information). We run linear regressions using the *lm* function in R, then the obtained predictor effect plots showed marginal effects of each predictor on the response variables in the linear regression models, by using R package '*effects*', ver. 4.2-0 (Fox and Weisberg 2018).

To further ensure whether the deviation from the network core is caused by the effects of habitat fragmentation, we created null model networks under the background of excluding the effects of habitat fragmentation, to imitate the process that they occupy different positions in the network in different patches (islands in our study). In order to exclude the effects of habitat fragmentation on null model networks, interactions in the created null model networks were required to be neutral. The neutrality implied random (stochastic) encounters of individuals, so in plant–pollinator networks, species abundances are expected to play an important role in predicting interactions (Vázquez et al. 2009). Indeed, the neutrality of interactions denotes that only species abundance drives the interactions (Chacoff et al. 2018), which excludes some ecological processes likely influencing interactions, such as morphological barriers and spatial/temporal non-overlap in species distribution. That is, the neutrality would simplify the ecological process of constructing plant–pollinator networks and exclude the effects of habitat fragmentation.

Specifically, we combined them to build one pool network, using the observed three-year plant–pollinator networks

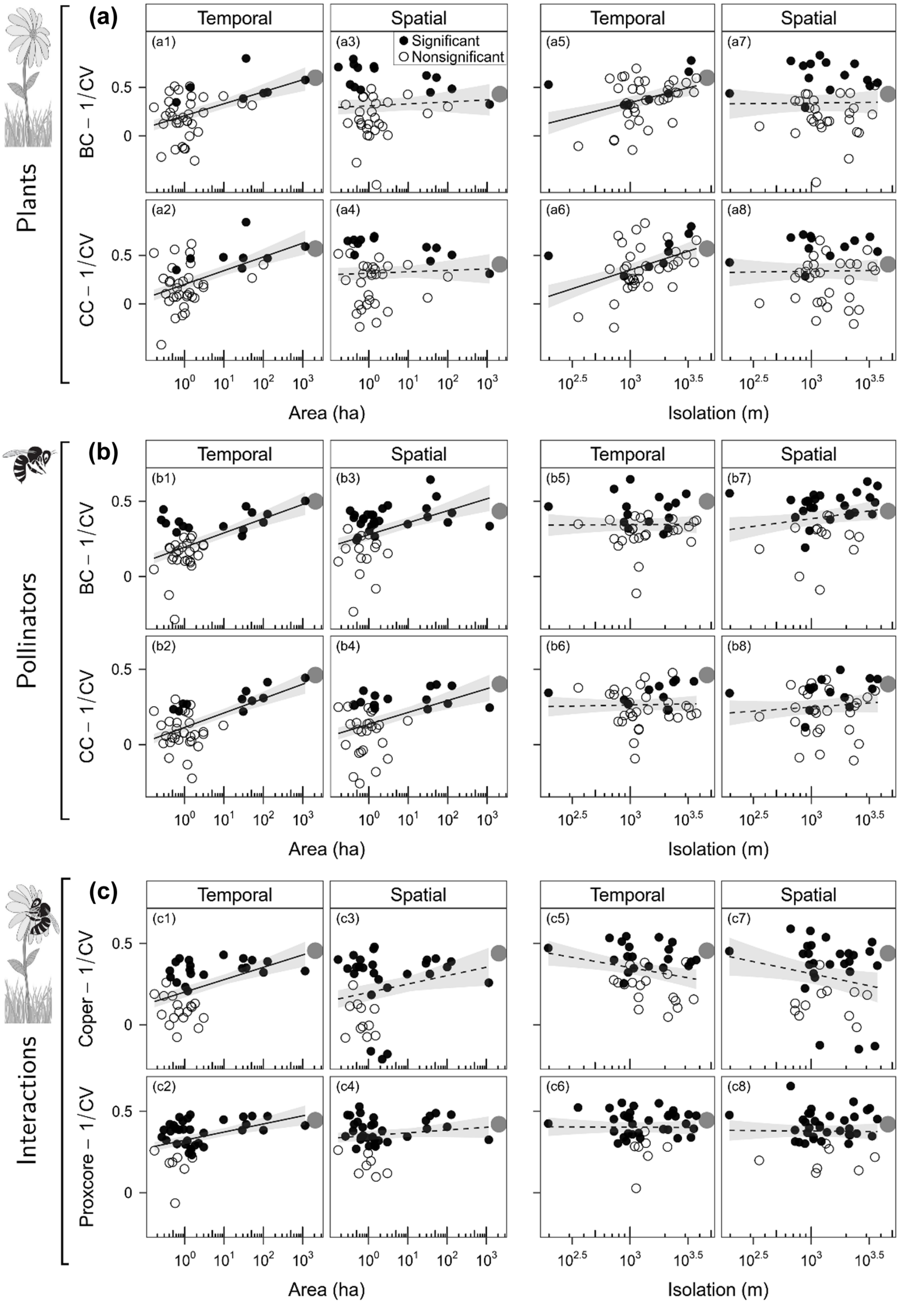

Figure 3. The predicted effects of island area and isolation on the position-stability correlation of plants (a), pollinators (b) and interactions (c) over time and space. The small black and the large grey circles show the value of position-stability correlation for 41 islands and the mainland, respectively. The position-stability correlation values of the mainland are not in the regression analysis and are only used to show the difference relative to the islands. Solid circles denote significant Spearman's coefficients and open circles denote non-significant Spearman's coefficients. Solid lines indicate significant relationships ($p < 0.05$) and dotted lines indicate non-significant relationships ($p \geq 0.05$). *BC* – 1/*CV*: the correlation between betweenness centrality and stability; *CC* – 1/*CV*: the correlation between closeness centrality and stability; *Proxcore* – 1/*CV*: the correlation between position of proximity to the network core and stability; *Coper* – 1/*CV*: the correlation between core-periphery and stability.

on 41 islands and mainland. Then we created null model networks, i.e. randomly drawing the interactions from the pool as the observed network on each island. For each randomly drawn network, by referring to the originally proposed method by Vázquez et al. (2007), we constrained the total numbers of plant species and pollinator species respectively, the abundance of interactions and the connectance, to be the same with that in the observed network, and also constrained each species to have at least one link. In the randomly drawing process, the probability of interaction among a pair of species was determined by the abundances of individuals, so those constructed null model networks represented the neutrality of interactions. Finally, the random sampling process generated 1000 null model networks for each observed network (details in Data availability statement), where Spearman's coefficients were also obtained. Then we compared the position-stability correlation (using Spearman's coefficients) of plants, pollinators and interactions between the observed network and the above generated 1000 random networks.

Based on the obtained Spearman's coefficients for each observed network and the above generated 1000 random networks, respectively, denoted as α_{obs} and α_{null}, we then calculated the standardized effect size (SES) using Eq. 2:

$$\mathrm{SES} = \left(\alpha_{obs} - \bar{\alpha}_{null}\right) / \mathrm{SD}\left(\alpha_{null}\right)$$

where $\bar{\alpha}_{null}$ is the mean of α_{null}, and $\mathrm{SD}(\alpha_{null})$ is the standard deviation of α_{null}. The SES quantifies the magnitude and direction of the difference between value α_{obs} and expected values (i.e. 95% confidence interval of values α_{null}) (Gotelli and McCabe 2002). A SES value greater than 1.96 represents that value α_{obs} is significantly higher than expected, while a SES value less than −1.96 represents that value α_{obs} is significantly lower than expected. The above cases (i.e. significantly higher/lower than expected) both indicate that stable species and interactions significantly deviate from the network core.

Our null model simulated the process that species and interactions occupied different islands. Under the background of neutrality of interactions, temporally/spatially stable species and interactions are more likely to be drawn and those drawn ones tend to occupy the core position in the network, i.e. the null model networks should have high values α_{null}. By comparing value α_{obs} with values α_{null}, we could know whether

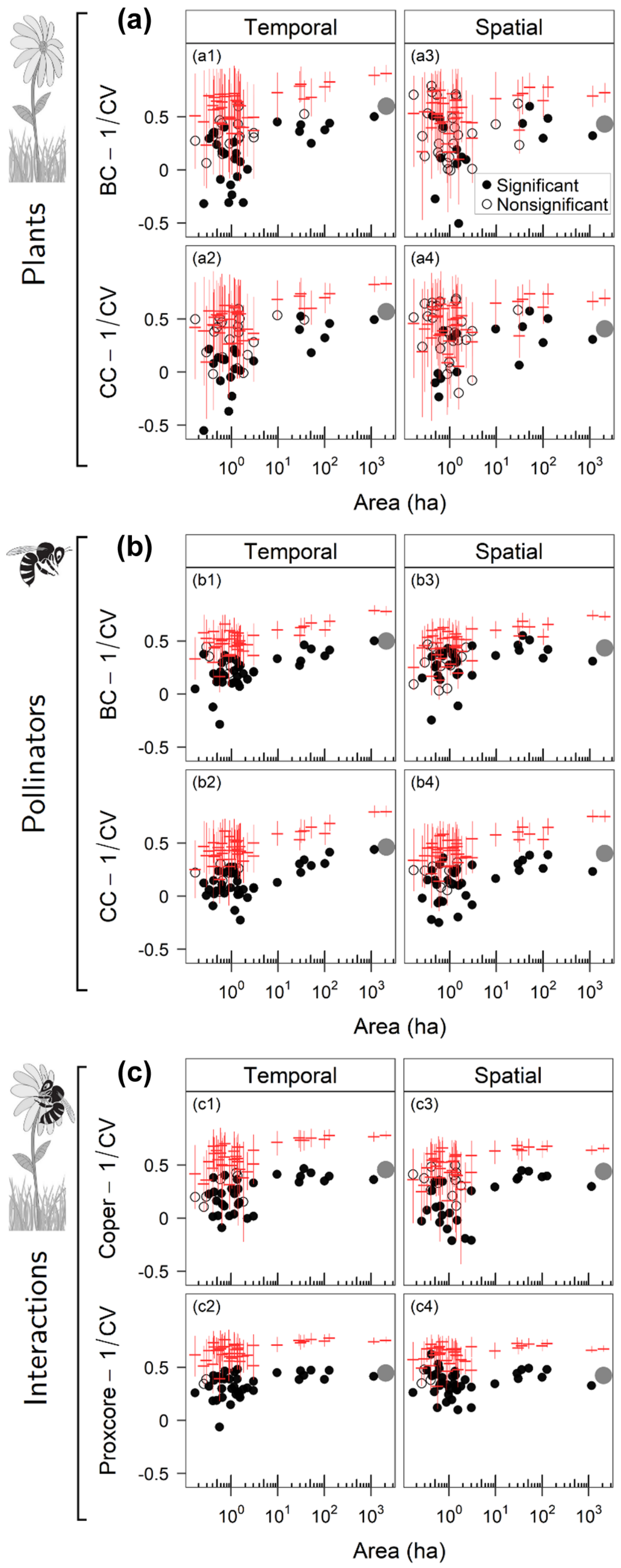

Figure 4. The results of null model. The null model was used to evaluate the ecological significance of the position-stability correlation of plants (a1–a4), pollinators (b1–b4) and interactions (c1–c4) over time and space. The small black and the large grey circles show the value of position-stability correlation for 41 islands and the mainland, respectively. Open circles indicate values α_{obs} not significantly different from expected and solid circles indicate values α_{obs} significantly lower than expected. The red short horizontal lines show the mean null model values of the position-stability correlation and the red vertical lines represent the confidence interval (95% quantiles of the null distributions) of the null model results. *BC* − 1/*CV*: the correlation between betweenness centrality and stability; *CC* − 1/*CV*: the correlation between closeness centrality and stability; *Proxcore* − 1/*CV*: the correlation between position of proximity to the network core and stability; *Coper* − 1/*CV*: the correlation between core-periphery and stability.

habitat fragmentation has significant effects on stable species and interactions, making them significantly deviate from the network core in fragmented habitats. If habitat fragmentation has significant effects on stable species and interactions, value α_{obs} should be significantly lower than expected. If habitat fragmentation has no significant effects, value α_{obs} should be not significantly different from expected, i.e. observed network was not significantly different from the null networks with neutrality (formed by random encounters of individuals), so there is expected to be some randomness in how species and interactions occupy different positions in the observed network.

In order to further illustrate the dynamics of species and interactions in fragmented habitats (as a supplement to our results), we analyzed the turnover of species and interactions over 3 years (Poisot et al. 2012, CaraDonna et al. 2017). To calculate the turnover of species and interactions over 3 years, we used functions *betalinkr* in R package '*bipartite*', ver. 2.16 (Dormann et al. 2021). We also analyzed network nestedness (NODF) (Almeida-Neto et al. 2008) using function *nestednodf* in R package '*vegan*', ver. 2.5-7 (Oksanen et al. 2020). Throughout the study, all statistical analyses were conducted using R ver. 4.0.1 (<www.r-project.org>).

Results

Over 3 years, we recorded a total of 19 486 individual pollinator interactions with plants in 960 h of sampling, spanning 3226 interactions between 313 species of pollinators and 68 species of flowering plants. More than 88% of pollinators were identified to genus (Supporting information). By combining with 3 one-year samples in islands and mainland, we got higher sample coverage of plants (0.73–1.00) and pollinators (0.60–0.99), respectively than that of interactions (0.40–0.85). The mean sample coverages of plants, pollinators and interactions were 0.89 ± 0.02 (mean ± SD), 0.84 ± 0.03 and 0.68 ± 0.03 (Supporting information), respectively. The sample coverage of plants, pollinators and interactions in each one-year sample was slightly lower overall than in three-year sample (Supporting information). Meanwhile, the analysis on rare interactions implies that our results were robust to sampling bias (Supporting information).

Plants and pollinators that occurred in one year or one island (span $S=1$), accounted for about a quarter of the total occurrences across temporal scales (27.94% and 24.28%, respectively) and accounted for a small proportion of the total occurrences across spatial scales (4.41% and 3.51%, respectively); while more than half of interactions were in the span $S=1$ (71.61% across temporal scales and 56.14% across spatial scales; Supporting information). The results above can also be reflected by the turnover of species and interactions over 3 years, where pollinators turnover is higher than plants turnover (Supporting information) and species turnover contributed more to high interactions turnover than interactions rewiring (Supporting information). The network nestedness significantly decreased with the decrease of island area (Supporting information). Spearman's coefficients of plants, pollinators and interactions justified the significant correlation between temporal stability and spatial stability, the significant correlation between temporal/spatial stability and frequency, and the significant correlation between temporal/spatial stability and generalization (Supporting information), which shows that high-frequency species are always generalists.

According to linear regression coefficients of Spearman's coefficients of the position-stability correlation, we found that island area and isolation made temporally/spatially stable species and interactions deviate from the network core to varying degrees. Considering temporal or spatial scales, the position-stability correlation of plants was the strongest, followed by pollinators and interactions (Fig. 3). The position-stability correlation between temporal and spatial scales is also significantly different (Supporting information). More specifically, island area and isolation had a significantly positive effect on the position-stability correlations ($BC - 1/CV$ and $CC - 1/CV$) of plants across temporal scales (island area: Estimate = 0.054 and 0.061, $p < 0.01$ and $p < 0.01$, respectively; Fig. 3a1–a2; isolation: Estimate = 0.131 and 0.168, $p < 0.05$ and $p < 0.01$, respectively, Fig. 3a5–a6; Supporting information), but had no significant effect across spatial scales. Island area had a significantly positive effect on the position-stability correlations ($BC - 1/CV$ and $CC - 1/CV$) of pollinators across temporal scales (Estimate = 0.041 and 0.042, $p < 0.001$ and $p < 0.001$, respectively; Supporting information) and spatial scales (Estimate = 0.035 and 0.034, $p < 0.01$ and $p < 0.05$, respectively; Fig. 3b1–b4; Supporting information). Isolation had no significant effect on the position-stability correlation of pollinators. Island area had a significantly positive effect on the position-stability correlation ($Coper - 1/CV$ and $Proxcore - 1/CV$) of interactions across temporal scales (Estimate = 0.033 and 0.022, $p < 0.01$ and $p < 0.05$, respectively; Fig. 3a1–a2; Supporting information), but had no significant effect across spatial scales. Isolation had no significant effect on the position-stability correlation of interactions. From linear regression coefficients, we found that Spearman's coefficients of plants decreased the fastest with the decrease of island area, followed by that of pollinators and interactions. Generally, Spearman's coefficients were higher in the mainland than on islands (Fig. 3).

Considering temporal and spatial scales, the null model showed that most values α_{obs} tended to be significantly lower than expected, especially on relatively big islands (≥ 10 ha). Compared with stable plants, values α_{obs} of stable pollinators and interactions were significantly lower than expected (Fig. 4). On some relatively small islands (< 10 ha), the confidence interval of values α_{null} was broad and some values α_{obs} were not significantly different from expected, especially for plants (Fig. 4). Besides, considering temporal and spatial scales, the confidence interval of values α_{null} of $Coper - 1/CV$ were asymmetric, and broadening sharply with the decrease of island area from 10 ha (Fig. 4c1, c3). The asymmetric (the parts of red vertical line above and below the horizontal are not equal) confidence interval of values α_{null} of $Coper - 1/CV$ is because some null model networks were too small to form the core-peripheral structure and thus lost some values α_{null} of $Coper - 1/CV$.

Discussion

Previous studies showed that habitat fragmentation could simplify plant–pollinator community composition and decrease network nestedness (Aizen et al. 2012, Spiesman and Inouye 2013). The position of species and interactions in ecological networks is closely related to their functions and roles in the network (Alarcón et al. 2008, Emer et al. 2016). We found that in fragmented habitats, temporally stable plants are most likely to deviate from the network core, followed by pollinators and interactions, while only spatially stable pollinators tend to deviate from the network core. The null model results showed that temporally/spatially stable species and interactions significantly deviate from the network core in fragmented habitats, whereas in some small habitats, species and interactions occupying positions in the network have a certain degree of randomness. These findings reveal an important reason for low nestedness of plant–pollinator networks in fragmented habitats.

Sampling completeness

We attempted to overcome potential biases by increasing sampling effort (Nielsen and Bascompte 2007). In fact, the sampling completeness of interactions was generally estimated to be around 50%, lower than sampling completeness of plants and pollinators (around 70%) (Chacoff et al. 2012, 2018, Devoto et al. 2012, Grass et al. 2018, Resasco et al. 2021), including our results. In our study, the sampling completeness of interactions is lower than that of plants and pollinators. There exist some different reasons for the lower sampling completeness of interactions, such as the shorter flowering stage of some plant species (interactions are infrequently established) and the lower abundance of specialized species (species are rare), so that the established interactions are rare and difficult to detect (Dorado et al. 2011, Chacoff et al. 2012). Rare interactions are expected to be most likely to influence the results in terms of previous studies (Poisot et al. 2012, CaraDonna et al. 2017). We did test for our results by removing rare interactions, which showed no significant difference of interaction position-stability correlation between removing rare interactions and keeping all observed interactions, as well as interaction turnover (Supporting information), so our results were robust to sampling bias.

Evaluation on the stability of interactions

The number of interactions that only occurred once within one year or on one island was far greater than the number of plants and pollinators (Supporting information), which indicated that interactions were highly variable over time and space (Petanidou et al. 2008, Ponisio et al. 2017, Chacoff et al. 2018). This high variation of interactions can also be reflected by high turnover of interactions over 3 years (Supporting information). The results above justified for the necessity to consider the distribution span in calculating the stability of interactions. For instance, if we still used the original formula $1/CV$ to calculate the stability of interactions, then all interactions with $S = 1$ would have the same value ($1/CV = 0.577$) and no relation to their frequency (Supporting information). The position-stability correlation of interactions would be underestimated, resulting in inaccurate estimates of the effects of habitat fragmentation on interactions (Supporting information).

The effects of area and isolation on position-stability correlation

Based on the results of the position-stability correlation, the effects of habitat fragmentation are likely to alter the positions of temporally/spatially stable species and interactions, making them deviate from the network core to varying degrees. The two correlation indices ($BC - 1/CV$ and $CC - 1/CV$) show similar results of plants and pollinators, as well as the two correlation indices ($Coper - 1/CV$ and $Proxcore - 1/CV$) of interactions (Fig. 3), implying that different topological angles of the node in the network show similar trends. Specifically, on a temporal scale, plants on larger or more isolated islands showed higher correlations between position and stability (Fig. 3a1–a2, a5–a6). This result may be caused by the fact that the temporal stability of plants was the most important factor determining how many pollinators they could acquire, and further determined the position of plants in the network (Dorado and Vázquez 2014). In our study system, more remote islands will be less affected by human activities, including trampling on plants when people landed on the island and the damage to plants caused by docking of fishing boats, so plants were expected to get more pollinators on more isolated island. Across temporal and spatial scales, pollinators only on larger islands showed higher correlations between position and stability (Fig. 3b1–b4), which may be because pollinators were highly mobile and thus less affected by isolation (Winfree et al. 2011). On a temporal scale, interactions only on larger islands showed higher correlations between position and stability (Fig. 3c1–c2), which may be caused by both plants distributions and pollinators activities (Carvalheiro et al. 2014, Xiao et al. 2016). In addition, according to the regression analyses, temporally stable plants were most likely to deviate from the network core with the decrease of island area, followed by pollinators and interactions (Fig. 3; Supporting information). Indeed, the number of pollinator species was generally higher than that of plant species (Supporting information), and pollinators (especially generalists) usually exhibited high functional redundancy (Pawar 2014). Besides, the high turnover rate of interactions may mask any effects of area or isolation, ensuring that stable interactions could persist in the network.

The nestedness significantly decreased with the decrease of island area (Supporting information), which may be caused by the deviation of stable species and interactions from the network core with the decrease of island area. When stable species and interactions deviated from the network core, unstable species (typically specialists) and interactions were expected to occupy the network core. However, these unstable species cannot interact with as many species as generalists do, causing the decrease of network nestedness. Therefore, from the perspective of position and stability, deviation of stable species and interactions from the network core was an important reason for the lower nestedness of plant–pollinator networks in fragmented habitats.

The null model results indicated that temporally/spatially stable species and interactions significantly deviated from the network core in fragmented habitats, since values α_{obs} tend to be significantly lower than expected (Fig. 4), especially for pollinators and interactions. However, below-expectations are not always significant on some small islands (< 10 ha). There is expected to be some randomness in the process that species and interactions occupy different positions in networks on small islands, since there are too few species observed (indeed it is, or caused by low sampling completeness). Compared with stable pollinators and interactions, the process of stable plants occupying different positions in the network showed randomness on more small islands, which was expected because the number of plant species was generally smaller than that of pollinator species (Supporting information). A few plant species left on small islands also made these islands have a weak ability of self-regulation, which ultimately leads to very little robustness of these islands to disturbances (Hadley and Betts 2012). Meanwhile, pollinators are strongly affected by key food sources and nest sites (Ferreira et al. 2015), so the pollinators tend to pass by small islands randomly and cannot interact sufficiently with plants (Kremen et al. 2007, Carvalheiro et al. 2014), which is the main reason for randomness generated. The fact that a few species were left on small islands also explains the broader confidence interval of null model on small islands than on big islands, since the slight change of positions of stable species or interactions in the small network will lead to a remarkable change of the position-stability correlation.

Conclusions

Our study showed that temporally/spatially stable species and interactions deviated from the network core to varying degrees in fragmented habitats. Meanwhile, the null model results further indicate that the deviation from the network core is caused by the effects of habitat fragmentation. From the perspective of position and stability, our findings revealed an important reason why plant–pollinator networks have low nestedness in fragmented habitats. Additionally, we proposed a new method to appropriately evaluate the stability of interactions, which has wide applications in future research. For instance, our method can be used to address whether the change of global climate, the urbanization or the biological invasion (Hegland et al. 2009, Harrison and Winfree 2015, Valdovinos et al. 2018, Theodorou et al. 2020) will lead to the deviation of temporally/spatially stable species and interactions from the network core.

Acknowledgements – We appreciate the Xin'an River Ecological Development Group Corporation and Forestry Bureau of Chun'an County for providing the permits necessary to conduct the research in Thousand Island Lake. We are very grateful to Quangui Jiang, Miaoyuan Zhang and other members for field assistance and Maxwell C. Wilson for the map construction. We acknowledge Zhihong Xu at Zhejiang A&F Univ. for the identification of insect species. We acknowledge Shenhao Yao for the identification of plant species. We thank Xinyu Xu, Yuxiao Han and Xue Zhang for their help in data analyses. We would like to thank Elizabeth Tokarz at Yale Univ. for her assistance with English language and grammatical editing.

Funding – This study was funded by the National Natural Science Foundation of China (grant no. 32030066, 31872210, 31930073, 32071545), by the China Scholarship Council (grant no. 201906320342 to R.P.), by the Shanghai Rising-Star Program (grant no. 19QA1403300) and by the Program for Professor of Special Appointment (Eastern Scholar) (grant no. TP2020016).

Conflict of interest – We have no conflict of interest to declare.

Author contributions

Peng Ren: Data curation (equal); Formal analysis (equal); Investigation (equal); Writing – original draft (lead); Writing – review and editing (lead). **Xingfeng Si**: Funding acquisition (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Ping Ding**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06102>.

Data availability statement

Datasets are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rv15dv484. The R codes are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.5030812.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aguilar, R. et al. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. – Ecol. Lett. 9: 968–980.

Aizen, M. A. et al. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. – Science 335: 1486–1489.

Aizen, M. A. et al. 2016. The phylogenetic structure of plant–pollinator networks increases with habitat size and isolation. – Ecol. Lett. 19: 29–36.

Alarcón, R. et al. 2008. Year-to-year variation in the topology of a plant–pollinator interaction network. – Oikos 117: 1796–1807.

Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – Oikos 117: 1227–1239.

Bascompte, J. and Stouffer, D. B. 2009. The assembly and disassembly of ecological networks. – Phil. Trans. R. Soc. B 364: 1781–1787.

CaraDonna, P. J. et al. 2017. Interaction rewiring and the rapid turnover of plant–pollinator networks. – Ecol. Lett. 20: 385–394.

Carvalheiro, L. G. et al. 2014. The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. – Ecol. Lett. 17: 1389–1399.

Chacoff, N. P. et al. 2012. Evaluating sampling completeness in a desert plant–pollinator network. – J. Anim. Ecol. 81: 190–200.

Chacoff, N. P. et al. 2018. Interaction frequency, network position and the temporal persistence of interactions in a plant–pollinator network. – Ecology 99: 21–28.

Chao, A. and Jost, L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. – Ecology 93: 2533–2547.

Chase, J. M. et al. 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. – Nature 584: 238–243.

Delmas, E. et al. 2019. Analysing ecological networks of species interactions. – Biol. Rev. 94: 16–36.

Devoto, M. et al. 2012. Understanding and planning ecological restoration of plant–pollinator networks. – Ecol. Lett. 15: 319–328.

Dorado, J. and Vázquez, D. P. 2014. The diversity–stability relationship in floral production. – Oikos 123: 1137–1143.

Dorado, J. et al. 2011. Rareness and specialization in plant–pollinator networks. – Ecology 92: 19–25.

Dormann, C. F. et al. 2021. Package 'bipartite'. R package ver. 2.16. – <https://CRAN.R-project.org/package=bipartite>.

Emer, C. et al. 2016. Species roles in plant–pollinator communities are conserved across native and alien ranges. – Divers. Distrib. 22: 841–852.

Evans, D. M. et al. 2013. The robustness of a network of ecological networks to habitat loss. – Ecol. Lett. 16: 844–852.

Fahrig, L. 2017. Ecological responses to habitat fragmentation per se. – Annu. Rev. Ecol. Evol. Syst. 48: 1–23.

Fang, Q. and Huang, S. 2016. Plant–pollinator interactions in a biodiverse meadow are rather stable and tight for 3 consecutive years. – Integr. Zool. 11: 199–206.

Ferreira, P. A. et al. 2015. Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic Rainforest. – Landsc. Ecol. 30: 2067–2078.

Fortin, M.-J. et al. 2021. Network ecology in dynamic landscapes. – Proc. R. Soc. B 288: 20201889.

Fortuna, M. A. and Bascompte, J. 2006. Habitat loss and the structure of plant–animal mutualistic networks. – Ecol. Lett. 9: 281–286.

Fox, J. and Weisberg, S. 2018. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. – J. Stat. Softw. 87: 1–27.

Freeman, L. C. 1978. Centrality in social networks conceptual clarification. – Soc. Netw. 1: 215–239.

Garibaldi, L. A. et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. – Ecol. Lett. 14: 1062–1072.

González, A. M. M. et al. 2020. Core-periphery structure in mutualistic networks: an epitaph for nestedness? – bioRxiv. doi: 10.1101/2020.04.02.021691.

Gotelli, N. J. and McCabe, D. J. 2002. Species co-occurrence: a meta-analysis of JM Diamond's assembly rules model. – Ecology 83: 2091–2096.

Grass, I. et al. 2018. Past and potential future effects of habitat fragmentation on structure and stability of plant–pollinator and host–parasitoid networks. – Nat. Ecol. Evol. 2: 1408–1417.

Greenleaf, S. S. et al. 2007. Bee foraging ranges and their relationship to body size. – Oecologia 153: 589–596.

Hadley, A. S. and Betts, M. G. 2012. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. – Biol. Rev. 87: 526–544.

Harrison, T. and Winfree, R. 2015. Urban drivers of plant–pollinator interactions. – Funct. Ecol. 29: 879–888.

Hegland, S. J. et al. 2009. How does climate warming affect plant–pollinator interactions? – Ecol. Lett. 12: 184–195.

Hsieh, T. et al. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). – Methods Ecol. Evol. 7: 1451–1456.

Kaiser-Bunbury, C. N. et al. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. – Ecol. Lett. 13: 442–452.

Kefi, S. et al. 2019. Advancing our understanding of ecological stability. – Ecol. Lett. 22: 1349–1356.

Kremen, C. et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. – Ecol. Lett. 10: 299–314.

Liu, J. et al. 2018. High beta diversity among small islands is due to environmental heterogeneity rather than ecological drift. – J. Biogeogr. 45: 2252–2261.

Lü, L. et al. 2016. The H-index of a network node and its relation to degree and coreness. – Nat. Commun. 7: 10168.

McWilliams, C. et al. 2019. The stability of multitrophic communities under habitat loss. – Nat. Commun. 10: 2322.

Miele, V. et al. 2020. Core-periphery dynamics in a plant–pollinator network. – J. Anim. Ecol. 89: 1670–1677.

Newman, M. E. 2003. The structure and function of complex networks. – SIAM Rev. 45: 167–256.

Newman, M. E. and Leicht, E. A. 2007. Mixture models and exploratory analysis in networks. – Proc. Natl Acad. Sci. USA 104: 9564–9569.

Nielsen, A. and Bascompte, J. 2007. Ecological networks, nestedness and sampling effort. – J. Ecol. 95: 1134–1141.

Nielsen, A. and Totland, Ø. 2014. Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. – Oikos 123: 323–333.

Oksanen, J. et al. 2020. vegan: community ecology package. R package ver. 2.5-7. – <https://CRAN.R-project.org/package=vegan>.

Pawar, S. 2014. Why are plant–pollinator networks nested? – Science 345: 383.

Peralta, G. et al. 2020. Trait matching and phenological overlap increase the spatio-temporal stability and functionality of plant–pollinator interactions. – Ecol. Lett. 23: 1107–1116.

Petanidou, T. et al. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. – Ecol. Lett. 11: 564–575.

Poisot, T. et al. 2012. The dissimilarity of species interaction networks. – Ecol. Lett. 15: 1353–1361.

Ponisio, L. C. et al. 2017. Opportunistic attachment assembles plant–pollinator networks. – Ecol. Lett. 20: 1261–1272.

Rafferty, N. E. and Ives, A. R. 2011. Effects of experimental shifts in flowering phenology on plant–pollinator interactions. – Ecol. Lett. 14: 69–74.

Resasco, J. et al. 2021. Plant–pollinator interactions between generalists persist over time and space. – Ecology 102: e03359.

Schleuning, M. et al. 2016. Ecological networks are more sensitive to plant than to animal extinction under climate change. – Nat. Commun. 7: 13965.

Schoereder, J. H., et al. 2004. Should we use proportional sampling for species–area studies? – J. Biogeorgr. 31: 1219–1226.

Si, X. et al. 2017. Functional and phylogenetic structure of island bird communities. – J. Anim. Ecol. 86: 532–542.

Spiesman, B. J. and Inouye, B. D. 2013. Habitat loss alters the architecture of plant–pollinator interaction networks. – Ecology 94: 2688–2696.

Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. – Science 329: 853–856.

Theodorou, P. et al. 2020. Urban areas as hotspots for bees and pollination but not a panacea for all insects. – Nat. Commun. 11: 576.

Trøjelsgaard, K. and Olesen, J. M. 2016. Ecological networks in motion: micro- and macroscopic variability across scales. – Funct. Ecol. 30: 1926–1935.

Tylianakis, J. M. et al. 2008. Global change and species interactions in terrestrial ecosystems. – Ecol. Lett. 11: 1351–1363.

Valdovinos, F. S. et al. 2018. Species traits and network structure predict the success and impacts of pollinator invasions. – Nat. Commun. 9: 2153.

Vázquez, D. P. et al. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. – Ecol. Lett. 8: 1088–1094.

Vázquez, D. P. et al. 2007. Species abundance and asymmetric interaction strength in ecological networks. – Oikos 116: 1120–1127.

Vázquez, D. P. et al. 2009. Evaluating multiple determinants of the structure of plant–animal mutualistic networks. – Ecology 90: 2039–2046.

Vincent, M. et al. 2021. econetwork: analyzing ecological networks. R package ver. 0.6.0. – <https://CRAN.R-project.org/package=econetwork>.

Wang, Y. et al. 2010. Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. – Divers. Distrib. 16: 862–873.

Winfree, R. et al. 2011. Native pollinators in anthropogenic habitats. – Annu. Rev. Ecol. Evol. Syst. 42: 1–22.

Xiao, Y. et al. 2016. The diverse effects of habitat fragmentation on plant–pollinator interactions. – Plant Ecol. 217: 857–868.

Zografou, K. et al. 2020. Stable generalist species anchor a dynamic pollination network. – Ecosphere 11: e03225.