

Geographic variation in the robustness of pollination networks is mediated by modularity

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Abstract

Aim: Extinctions and coextinctions seriously threaten global plant–pollinator assemblies, and thus a better understanding of the geographic variability in their robustness is urgently required. Although the geographic patterns of species extinction rates are frequently explored, it remains largely unknown how the subsequent coextinction risk of species varies across environments. We hypothesize that the geographic variation of network robustness to extinctions is mediated by modularity – the tendency of a network to be organized in modules of strongly interacting species – because modularity buffers perturbations and varies across environments.

Location: Global.

Time period: Current.

Major taxa studied: Flowering plants and their animal pollinators.

Methods: Using 79 pollination networks, we first explored the variation of network robustness across geographic and climatic gradients and, second, analysed the role of modularity in explaining the association between robustness and those environmental gradients. We quantified the robustness of taxonomic, functional and phylogenetic diversity of pollinators under simulated coextinctions triggered by specialist-first, generalist-first, and random plant removals.

Results: Only the robustness of phylogenetic diversity under specialist-first removals showed a global latitudinal trend by which robustness increased towards the tropics on mainlands but increased towards the poles on islands. Generally, robustness was strongly promoted by modularity, and also directly dampened by insularity and precipitation seasonality (PS). Through the mediation of modularity, robustness was indirectly increased by actual evapotranspiration and PS, and decreased by the interaction between PS and insularity. Besides, network size and sampling area affected robustness but did not influence modularity.

Main conclusions: The indirect environmental effect on robustness via modularity was prevalent, which supports our hypothesis and reveals the importance of network structure in mediating the geographic variation of network robustness. The global pattern of robustness indicates the phylogenetic diversity of pollinators is relatively vulnerable to the loss of specialist plants in tropical islands and high-latitude mainland compared to other regions.

KEYWORDS

ecological networks, functional groups, island, latitudinal gradients, macroecology, phylogenetic diversity

1 | INTRODUCTION

Pollination of flowering plants by animals provides essential ecosystem services such as maintaining biodiversity and agricultural productivity (Aguilar et al., 2006; Klein et al., 2007). However, pollinators are seriously threatened by global change (Potts et al., 2010; Watanabe, 1994). Extensive research effort concerning this problem has revealed that the rates of species extinctions in many taxa including plants and pollinators change across latitudes with varying environments (Cardillo, 1999; Mittelbach et al., 2007; Vamosi & Vamosi, 2008; Weir & Schluter, 2007). But the risk of extinction-induced coextinctions, which may lead to many more species being lost than originally expected (Dunne et al., 2002; Koh et al., 2004; Memmott et al., 2004; Rezende et al., 2007; Solé & Montoya, 2001), has rarely been explored across environmental gradients. It is also little known how the impact of coextinctions on trait and phylogenetic diversity may change in communities across different environments, which is key to understanding the functional consequences of coextinctions (Vieira et al., 2013).

A small number of studies have found that species coextinction risk may vary along geographic and environmental gradients (Bascompte et al., 2019; Dalsgaard et al., 2018). For example, Bascompte et al. (2019) showed that Mediterranean pollination networks tend to suffer more coextinctions than Eurosiberian counterparts because networks at low latitudes contain species with narrower geographic ranges and suffer more from climate change, and this higher extinction rate may push the networks closer to a threshold of collapse. Even when facing the same level of primary extinctions, the coextinction risk of species in networks – also termed as *network robustness* – may vary across networks as a result of topological differences (Burgos et al., 2007; Dunne et al., 2002; Memmott et al., 2004; Thébault & Fontaine, 2010). Therefore, the environment can not only affect species coextinction risk by altering the extent of primary extinctions, but can also affect the robustness of interaction networks through their effects on the network structure (Colwell et al., 2012).

Among the topological structures that could potentially affect network robustness, a prominent one is modularity, defined as the extent to which a network can be divided into modules where species interact much more frequently among themselves than with species from other modules (Bascompte & Olesen, 2015; Newman, 2004; Olesen et al., 2007). Modularity closely bridges network robustness and environmental conditions for two reasons. First, modularity has been suggested to promote community stability by buffering the spread of a perturbation across the entire network (Gilarranz et al., 2017; May, 1972; Stouffer & Bascompte, 2011). This can reduce the loss of taxonomic diversity and, therefore, may provide

more protection to functional and phylogenetic diversity given that species within modules are functionally and phylogenetically conserved (Carstensen et al., 2016; Donatti et al., 2011; Hutchinson et al., 2017; Rezende et al., 2009).

Second, the modular structure is shaped by several types of environmental factors (Martín González et al., 2015; Schleuning, Ingmann, et al., 2014; Trøjelsgaard & Olesen, 2016). Current climatic factors linked to productivity and seasonality have been shown to promote modularity because they encourage niche partitioning among species by increasing resource abundance and phenophase difference, respectively (Bascompte & Olesen, 2015; Martín González et al., 2012; Maruyama et al., 2018; Trøjelsgaard & Olesen, 2013). Past climate instability has been found to hinder biotic specialization and modularity by interrupting coevolution between species over long periods of time (Dalsgaard et al., 2013; Martín González et al., 2015). These climatic factors may drive modularity and thus robustness to vary across geographic gradients such as latitude and altitude (Dalsgaard et al., 2017; Lara-Romero et al., 2019; Ramos-Jiliberto et al., 2010; Schleuning, Ingmann, et al., 2014; Trøjelsgaard & Olesen, 2013).

In addition to climatic factors, insularity is expected to shape network modularity because interacting species face unique biotic and abiotic environments on islands (Maruyama et al., 2018; Traveset et al., 2015), such as a wetter, warmer and less seasonal climate compared to mainlands (Weigelt et al., 2013), depauperate pollinator faunas and lower pollinator/plant ratios (Traveset et al., 2016; Trøjelsgaard & Olesen, 2013), higher number and density of alien species (D'Antonio & Dudley, 1995; Sax et al., 2002; Simberloff, 1995), and a high level of disturbance (e.g. hurricanes; Rivera-Marchand & Ackerman, 2006). Hence, the relationship between modularity and climates may differ between island and mainland communities, which still remains to be tested. More importantly, it is largely unknown whether all these environmental effects on modularity could shape the latitudinal and altitudinal patterns of network robustness, and how important modularity is in explaining geographic gradients of robustness.

Here, we hypothesized that environmental factors affect network robustness (including taxonomic, functional and phylogenetic diversity) by influencing the modularity of pollination networks (Figure 1). Specifically, we expect higher robustness in more productive and seasonal environments with a stable past climate, which favours modularity. Due to these environmental effects, robustness may present latitudinal and altitudinal gradients (Figure 1). But the direction of these gradients is hard to predict because insularity may influence some of the relationships between climates and modularity (Figure 1). We also considered sampling effort since it potentially confounds the environmental gradients of modularity and robustness by

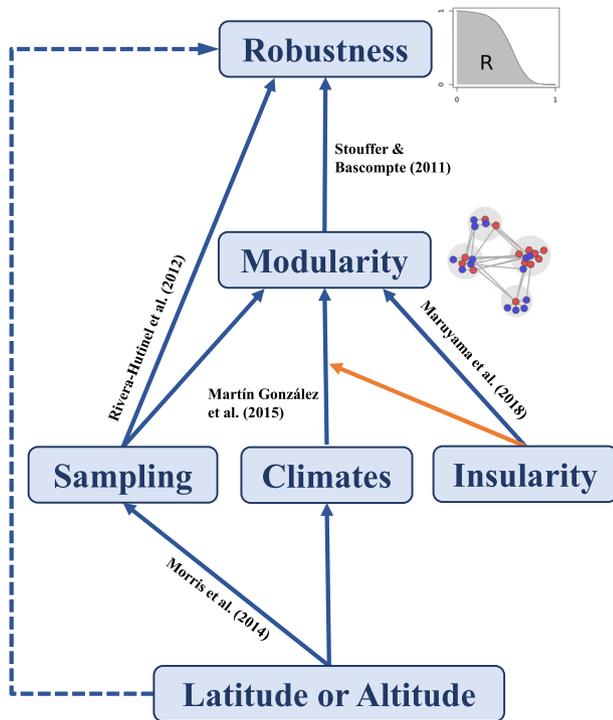


FIGURE 1 Conceptual diagram of the hypothesis in this paper, showing the relationships among geographic and climatic factors, sampling effect, modularity and robustness. The insert plot beside robustness shows that robustness is measured by the area below the curve of proportional loss of pollinator diversity versus plant removals. The plot aside modularity depicts a modular network with red and blue nodes indicating pollinators and plants, respectively. The solid blue arrows indicate direct effects along with their main references, while the dashed blue and solid orange arrows indicate untested indirect effects and interaction effects, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

altering network size and causing taxonomic bias (Doré et al., 2020; Morris et al., 2014; Rivera-Hutinel et al., 2012). To test this, we compiled a global dataset of 79 plant-pollinator networks with data on geography, climate, sampling effort, species diversity, pollinator phylogeny, and functional groups. We aimed to (a) evaluate the associations between geographic, sampling and environmental factors and robustness for taxonomic, functional and phylogenetic diversity, and (b) quantify to what degree the relationships between environments and robustness are mediated by modularity.

2 | MATERIAL AND METHODS

2.1 | Dataset

2.1.1 | Pollination network data

Data for this study were compiled from open-source databases (Interaction Web DataBase, <http://www.ecologia.ib.usp.br/iwdb>; Web of Life, <http://www.web-of-life.es>), and the literature (searching Google Scholar from 1990 to 2019 with the following keywords: 'pollination network' or 'plant-pollinator interaction' or 'mutualistic network'). We only included community-wide pollination networks with their main taxa identified to species level. A global set of 79 plant-pollinator interaction networks was eventually collected (Figure 2; Supporting Information Table S1). Each network is presented as a matrix of plant and pollinator species, and each matrix cell has a value of either 1 or 0, indicating the presence or absence of a link. Although some networks include quantitative data, most have only qualitative data. We, therefore, restricted our analysis to the use of binary information (i.e. presence-absence of links).

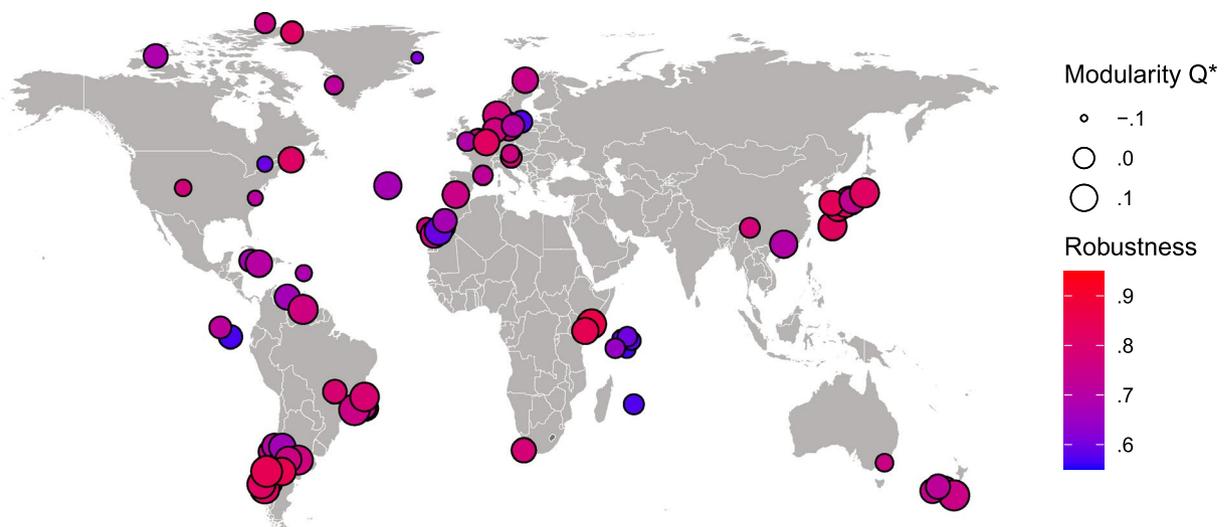


FIGURE 2 Global map of modularity and robustness of phylogenetic diversity to specialist-first removal in 79 pollination networks used in the study. The size and colour of the circles illustrate the level of modularity and robustness, respectively. For clarity, circles for some study locations were slightly moved to minimize overlap [Colour figure can be viewed at wileyonlinelibrary.com]

2.1.2 | Environmental variables

We recorded longitude and latitude for each network location and obtained four current climatic variables from WorldClim 1.4 at a resolution of 30 arc-seconds (Hijmans et al., 2005; <http://www.worldclim.org>): mean annual temperature, mean annual precipitation, temperature seasonality (standard deviation) and precipitation seasonality (coefficient of variation). We also obtained actual evapotranspiration (AET) and potential evapotranspiration (PET) data from Ahn and Tateishi (1994), which measure water flux and thermal input, respectively. To obtain the altitude data, we used the description from original sources where altitude is available and for those networks with no description we extracted altitude from the elevation data at a resolution of 30 arc-seconds from WorldClim 1.4 (Hijmans et al., 2005; <http://www.worldclim.org>). We described palaeoclimate instability by calculating the velocity of change in mean annual temperature and mean annual precipitation between the Last Glacial Maximum (LGM) and the present. Annual climate data in the LGM were obtained from WorldClim 1.4 at a resolution of 2.5 arc-minutes (Hijmans et al., 2005; <http://www.worldclim.org>), which were estimated by the Community Climate System Model Version 4 (CCSM4; Gent et al., 2011). Furthermore, each network site was categorized as island or mainland according to biogeographic standards from previous studies (Trøjelsgaard & Olesen, 2013), where continental island was grouped with the mainland category since pollination networks from continental islands are more similar to their mainland counterparts than to those from oceanic islands (Traveset et al., 2016).

2.1.3 | Taxonomic, functional group and phylogenetic diversity

Local plant and pollinator taxonomic diversities were obtained from the number of plant and animal species in each network, respectively.

Before classifying the pollinator functional group and constructing the pollinator phylogeny, we first verified animal species names with the 'gnr_resolve' function in the R package 'taxize', which accessed a range of taxonomic databases (Chamberlain & Szocs, 2013; Chamberlain et al., 2020). Then we used the corrected species name to obtain the taxonomy by the function 'taxize::classification' in R, with preferential acceptance of classifications returned by the National Center for Biotechnology Information (NCBI) database (Chamberlain & Szocs, 2013; Chamberlain et al., 2020). Unidentified species without any returned taxonomic information were excluded. According to the taxonomy, we categorized pollinators into 27 functional groups (Supporting Information Appendix S1), including 11 widely accepted pollinator groups such as bees, butterflies and beetles according to the literature of pollination syndromes (Fægri & van der Pijl, 1979), and 16 groups that are less common but at least have been observed as pollinators in some cases, such as hemipteran and thysanopteran insects (Fægri & van der Pijl, 1979; Ishida et al., 2009; Ollerton, 2017; Varatharajan et al., 2016). Relatively rare pollinator

groups may be less specialized for pollination, but they show distinct traits and behaviours between each other. Therefore, we treated them as separate functional groups based on taxonomy. We excluded species that were not identified to a sufficient taxonomic level allowing functional group classification. To calculate functional group diversity in each network, we used the Hill's number of the Shannon diversity index, that is, $\exp(H)$ with H as the original Shannon index (Hill, 1973), because the Hill's number more accurately reflects the proportional change in diversity than the original index does (Jost, 2007).

To obtain sufficiently well-resolved phylogenies for pollinators, we used the aforementioned pollinator taxonomy to construct a taxonomic tree, and incorporated the estimated divergence times of pollinators based on the published mega-phylogeny of animals (Hedges & Kumar, 2009; Hutchinson et al., 2017; Misof et al., 2014). The divergence dates of the remaining nodes in the tree were dated using the 'bladj' function from PHYLACOM 4.2 where the branch length from a resolved node to the tip is split between those intervening nodes (Webb et al., 2008). To include the maximum number of species possible without compromising the quality of the phylogeny, the unresolved nodes with taxa not identified to species level were left as soft polytomies (see methods in Rezende et al., 2007). With the obtained pollinator phylogenies, we used the mean pairwise phylogenetic distance to indicate phylogenetic diversity of pollinators in each network.

2.1.4 | Sampling efforts

Since we combined data from different studies, sampling efforts may correlate with network properties and thereby confound macroecological trends (Schleuning, Ingmann, et al., 2014; Trøjelsgaard & Olesen, 2013). Thus, we also collected sampling time for 32 networks and sampling area for 29 networks from the original reference where sampling data were available, and used sampling time, area and network size (sum of plant and animal species) to test whether sampling effort influenced network robustness and modularity. Network size was log-transformed in subsequent analyses. Besides, we also investigated the taxonomy distribution of pollinator communities across geographic regions in order to check potential taxonomic bias due to different sampling.

2.2 | Modularity algorithm and null model

We applied Newman and Girvan's Q to measure the level of modularity of each network (Newman & Girvan, 2004), because it is widely used to quantify modularity in bipartite ecological networks (Carstensen et al., 2016; Olesen et al., 2007; Thébault & Fontaine, 2010; Trøjelsgaard & Olesen, 2013). The results are robust to the choice of modularity index (Supporting Information Appendix S2). We used simulated annealing as the optimization algorithm to search for the partition of the network into modules

that maximizes modularity (Guimerà & Amaral, 2005a, 2005b). The modularity calculation was implemented in the software MODULAR (Marquitti et al., 2013).

As the variation in sampling intensity among empirical networks could unduly influence modularity, we used a null model 'Degreeprobable' (Bascompte et al., 2003; Beckett et al., 2014) to calculate corrected modularity values. In this null model, the probability of drawing an interaction between a plant–pollinator pair is proportional to the average normalized degree of the animal species and the plant species: $l_{ij} = \frac{1}{2} \left(\frac{d_j}{r} + \frac{k_i}{c} \right)$, where l_{ij} is the probability of assigning an interaction to the i th row and j th column of the null matrix, d_j is the degree of the j th column, k_i is the degree of the i th row, and r and c are the respective number of rows and columns of the matrix. We corrected modularity values Q for each network in the following way: $Q^* = \frac{Q_{observed} - \bar{Q}_{random}}{Q_{random}}$, where Q^* is the relative modularity, $Q_{observed}$ is the observed modularity value and \bar{Q}_{random} is the mean modularity of 100 randomizations from the null model (Bascompte et al., 2003). To confirm these corrections were effective, we tested the influence of sampling time and area on relative modularity.

2.3 | Measuring robustness and the buffering effect of modularity

To measure the robustness of pollination networks, we used the stochastic coextinction model (SCM) to simulate species coextinction in the networks (Vieira & Almeida-Neto, 2015). In the SCM, the probability of species i going extinct due to the extinction of a mutualistic partner species j is calculated as $P_{ij} = M_i d_{ij}$, with M_i being species i 's intrinsic dependence on the mutualism and d_{ij} being the dependence on each of its mutualistic partners. d_{ij} is estimated as the number of visits recorded between species i and j divided by the total number of visits involving species i . In our study d_{ij} is equal to $1/\text{numbers of focal species } i\text{'s partners}$ since our networks are binary. For simplicity, we assumed species without interactions would go extinct from networks, thus we set M of all species equal to 1. In general, the SCM describes both the deterministic and stochastic nature of coextinctions, and is able to simulate secondary and higher level coextinctions (Vieira & Almeida-Neto, 2015). We used the SCM to simulate a complete extinction process: removing plant species of each network until the whole network goes extinct. This extinction process was performed under each of the following three scenarios of primary removal: random, specialist-first (from least to most connected species) and generalist-first (from most to least connected species). During each complete extinction process, we tracked the remaining taxonomic, functional and phylogenetic diversity of pollinators, and obtained extinction curves of the remaining proportion of pollinator diversity (current diversity weighted by original diversity) versus the proportion of removed plant species. Since the SCM is a random process, we repeated the complete extinction process 10,000 times for each network under each removal scenario. Then we obtained an

averaged extinction curve from all replicates, and calculated robustness as the area below the averaged extinction curve for each type of diversity under each removal scenario (Burgos et al., 2007).

To quantify modularity's contribution to network robustness, we measured the ability of network modules to buffer coextinctions according to Gilarranz et al. (2017). Specifically, we compared the number of coextinctions between inside and outside the module where primary removal occurred, and the comparison was made for coextinctions occurring at two topological distances (1 or 3 nodes away) from the primarily removed species. For each complete extinction process of the SCM, we recorded whether coextinctions at a certain distance occurred inside or outside the module. After all repetitions of a complete extinction process were done, we calculated the ratio of coextinct species outside focal modules to coextinct species inside the modules (spread ratio = S_{out}/S_{in}). A ratio smaller than 1 means the modular structure in the network can buffer the coextinctions spreading to a certain distance outside the module. Thus the spread ratio decreases with more distinct module partition and higher modularity (Gilarranz et al., 2017).

2.4 | Statistical analyses

To test the geographic pattern of robustness, we used a linear mixed model to evaluate the general associations of robustness with network size and geographic variables (altitude, absolute latitude, insularity and two interaction terms: insularity with altitude and with latitude) across different types of diversity, and removal scenarios. Both network identity and the interaction term between types of diversity and removal scenarios are considered random effects because the types of removal scenarios are nested within the types of diversity. To quantify the role of modularity in driving the geographic gradient of robustness, we first used ordinary least square (OLS) regression models to fit relationships of robustness versus modularity, and robustness versus spread ratio at distance 1 and 3, respectively. Second, we fitted an OLS model to test the relationship of modularity and geographic variables (absolute latitude, altitude, insularity and their interaction term). Third, we fitted structural equation models (SEMs) to identify the environmental driver of geographic variability in robustness and quantify the strength of modularity's mediation between environments and robustness.

Specifically, we constructed the SEM for each type of robustness based on the assumption that environments may indirectly affect robustness through modularity. To select the most important predictors of modularity and robustness, we fitted a linear mixed model for robustness and simple linear model for modularity, with all the environmental variables (except temperature seasonality since it is highly correlated to other variables; Supporting Information Figure S1) and network size as predictors. After the step-wise selection based on Akaike information criterion (AIC), the final linear models contain modularity and insularity as predictors of robustness, and AET and precipitation seasonality (PS) as predictors of modularity. Despite being excluded by selection, network size was manually retained to

account for sampling effects. Thus the primary SEM included network size, AET, PS, insularity and their interaction terms as predictors of both modularity and robustness. To select the final SEM, we eliminated non-significant paths and variables one by one based on the p -value of the path and AIC of the model. The model fit of the SEMs was evaluated by a chi-square test, a comparative fit index (CFI) and the root mean square error of approximation (RMSEA). Models were accepted for a satisfactory fit if $p > .05$ in the chi-square test, CFI $> .9$ and RMSEA $< .07$ (Shipley, 2016). All SEM analyses were conducted using the R package 'lavaan' (Rosseel, 2012).

Lastly, we analysed possible factors that may have confounding effects on our results. We tested the effect of sampling time and area on robustness and modularity by OLS models. We also investigated the taxonomic composition of pollinators across geographic regions. Furthermore, the spatial autocorrelation in residuals of all regression models was assessed by computing Moran's I correlograms using the 'ncf' package in R (Bjørnstad, 2020), with distance classes of 1,000 km and a truncation distance of 10,000 km. The OLS models with robustness versus modularity and spread ratio showed significant positive spatial autocorrelation. Thus we re-ran these models using a simultaneous autoregressive (SAR) model, which specifies the autoregressive processes within the error term (Kissling & Carl, 2007). The SAR modelling was conducted using the 'spdep' package in R (Bivand & Wong, 2018). All the above statistical analyses were done in R 3.6.2 (R Core Team, 2019).

3 | RESULTS

3.1 | Geographic pattern of network robustness and modularity

First, robustness across different types of diversity and removal scenarios was not significantly affected by altitude, but was lower in island networks compared to mainland networks (Table 1; Supporting Information Figure S2). Second, the latitudinal gradient of robustness differs between island and mainland sites, that is, robustness tended to increase with latitude in island networks but decrease

with latitude in mainland networks (Table 1; Figure 3). Despite the general consistency across different types of diversity and removal scenarios, the island and mainland latitudinal robustness patterns are both significant only in the case of phylogenetic diversity under specialist-first removal (Figure 3). Besides, only island latitudinal patterns were found to be significant in the other three types of robustness (functional diversity under specialist-first and random removal, phylogenetic diversity under random removal), and only the mainland latitudinal pattern was significant in robustness of phylogenetic diversity under generalist-first removal (Figure 3). There was no significant latitudinal pattern for robustness of taxonomic diversity. Thus, the latitudinal gradient in robustness was clearest for phylogenetic diversity, intermediate for functional diversity, and least clear for taxonomic diversity (Figure 3). The effect of insularity on latitudinal trends of robustness was less prominent under the scenario of generalist-first removal compared to other removal scenarios (Figure 3).

The opposite latitudinal trend of robustness between island and mainland networks can be explained by the changes of modularity across latitudes and the effect of modularity on robustness. The robustness of functional, phylogenetic and taxonomic diversity generally increased with modularity and decreased with spread ratio at distance 1 (Figure 4a). The effect of modularity on robustness was relatively larger in the case of phylogenetic diversity compared to other types of diversity, but did not show clear differences among removal types (Figure 4a). Most types of robustness increased with spread ratio at distance 3, but the effect size of spread ratio at distance 3 on robustness is much smaller than that at distance 1 (Figure 4a; Supporting Information Figure S4). Thus, modularity had a positive effect on robustness mainly by buffering coextinction spread from a removed plant to its pollinators in other modules. Meanwhile, modularity was lower in island networks than in mainland networks, with no significant effect of altitude (Supporting Information Table S3), and modularity also presented opposite relationships with absolute latitude between island and mainland networks, with a positive relationship in island sites but a negative one in mainland sites (Figure 4b; Supporting Information Table S3).

	Estimate	SE	df	t value	Pr(> t)
(Intercept)	0.410	0.072	12.938	5.725	.000***
Size	-0.008	0.007	72.000	-1.212	.229
Lat	0.002	0.001	72.000	2.724	.008**
Mainland	0.125	0.026	72.000	4.737	.000***
Alt	0.000	0.000	72.000	-0.983	.329
Lat:Mainland	-0.003	0.001	72.000	-3.463	.001**
Alt:Mainland	0.000	0.000	72.000	0.392	.696

** $p < .01$.; *** $p < .001$.

TABLE 1 Results of linear mixed models of robustness versus network size (Size); absolute latitude (Lat); insularity – mainland and island (Intercept); and altitude (Alt). Types of diversity and removal scenarios were set as random effects. The coefficients of determination of the model are reported: conditional $R^2 = .918$, marginal $R^2 = .019$. Conditional R^2 describes the proportion of variance explained by both the fixed and random factors, while marginal R^2 describes the proportion of variance explained by the fixed factors alone

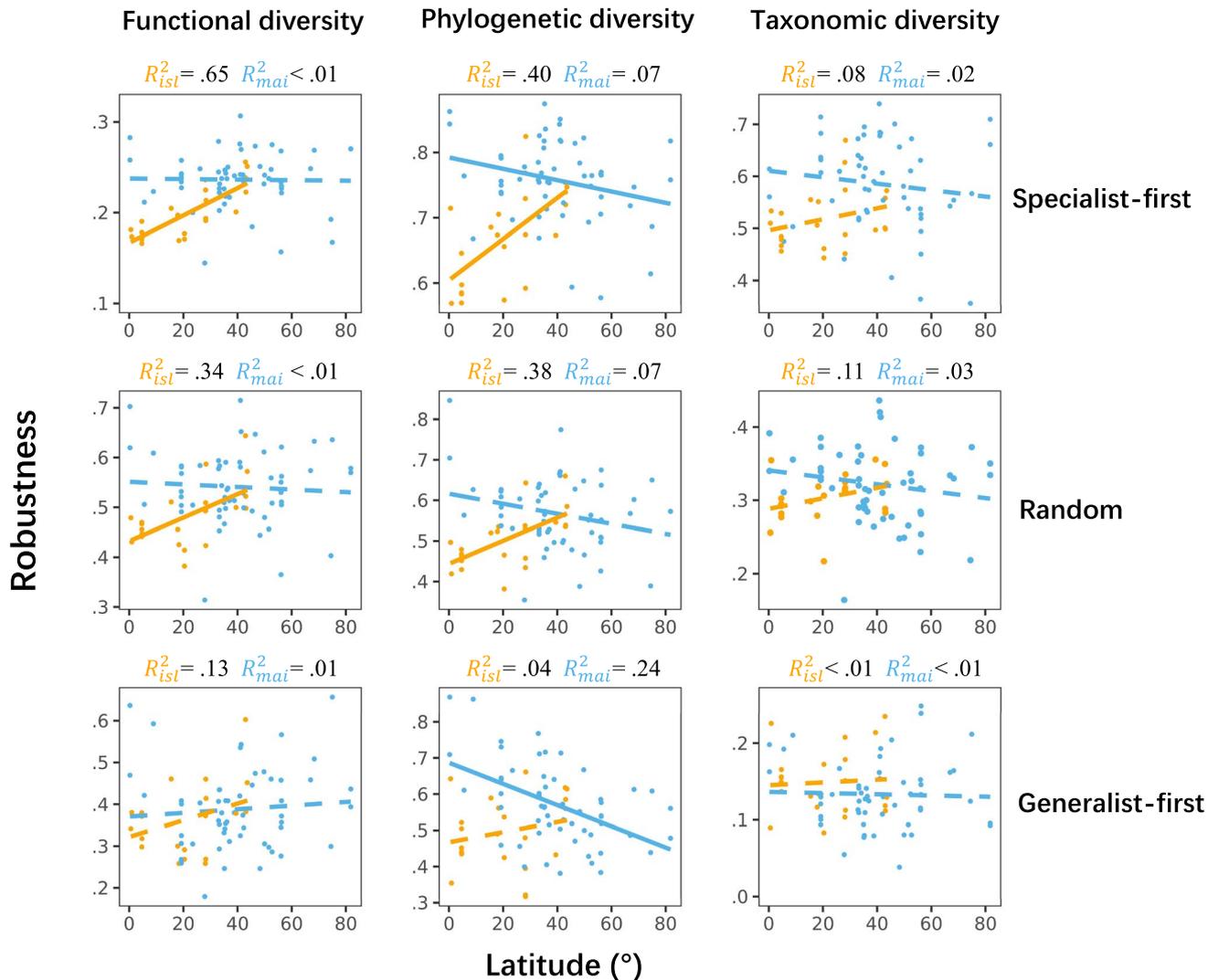


FIGURE 3 Relationships between absolute latitude and robustness across different types of diversity (columns) and removal scenarios (rows) in mainland (blue; $n = 57$) and island (orange; $n = 22$) networks. Solid, dashed and long-dashed lines indicate significant ($p < .05$), non-significant ($p > .05$), and marginal trends ($p = .051$), respectively. R^2 of the fitted lines are reported for island networks (R^2_{ist}) and mainland networks (R^2_{mai}) [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | The mediation of modularity between environments and robustness

All the final SEMs of robustness were acceptable and most of them supported the indirect path of environment \rightarrow modularity \rightarrow robustness (eight out of nine), except robustness of phylogenetic diversity under the generalist-first removal, which was weakly affected by modularity (Figure 5; Supporting Information Figure S6; Table S4). The indirect environmental effects were caused by modularity's predictors including AET, PS, and the interaction term of island and PS. The SEMs revealed that AET increased modularity, and PS promoted modularity in the mainland but dampened it in islands (Figure 5; Supporting Information Figure S6). These effects of climates and the fact that AET and PS generally decrease with latitude (Supporting Information Figure S7) explain the opposite latitudinal patterns of modularity and robustness of phylogenetic diversity in response to specialist-first removal between islands and the mainland.

Most SEMs also include direct environmental effects on robustness (Figure 5; Supporting Information Figure S6). Insularity directly dampened robustness and was the most common direct environmental factor of robustness across models (seven out of nine). PS also directly decreased robustness in five cases, while AET showed a positive direct effect on robustness in only one case. Network size was also a common direct predictor of different types of robustness (seven out of nine). Its effect was strongest on robustness of taxonomic diversity under random and generalist-first removal, but the effect direction of network size varied across types of robustness. Although there were direct environmental effects on robustness, the strongest direct effect on robustness came from modularity in most cases (six out of nine), which means that environmental effects (except insularity) were mainly mediated by modularity, especially in the case of robustness of phylogenetic diversity under specialist-first removal, which showed a clear geographic pattern (Figure 5). When modularity had a weak effect on robustness, such as robustness of

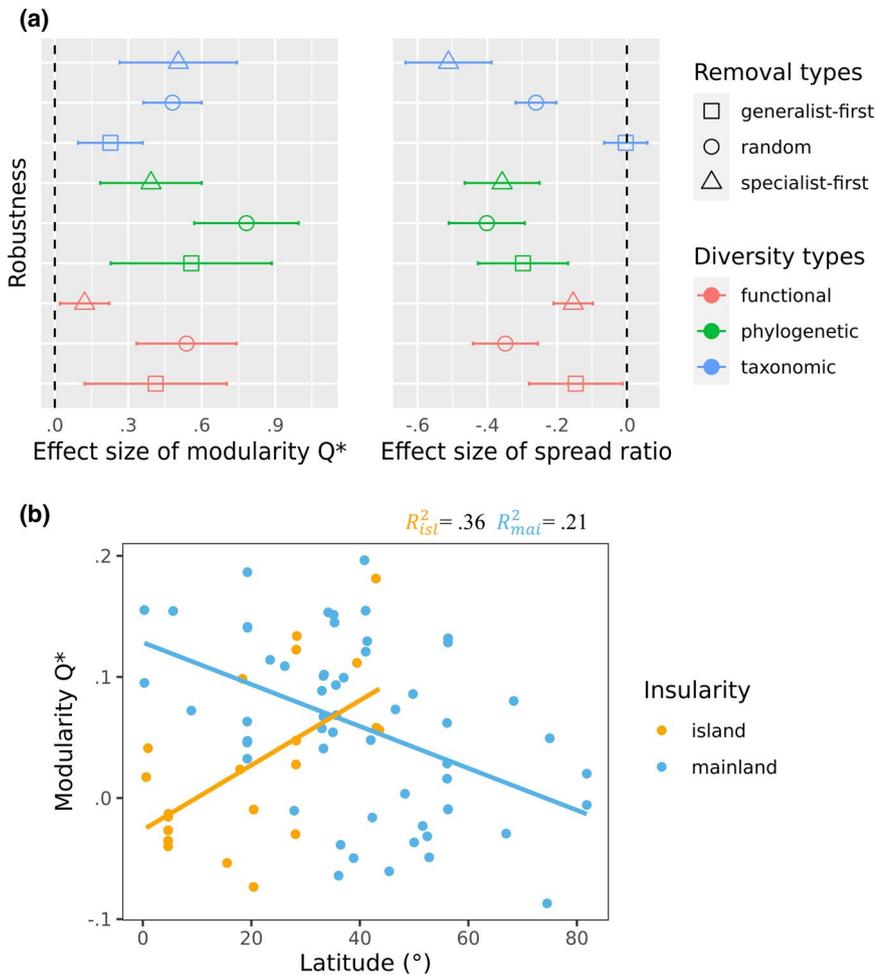


FIGURE 4 (a) Effect of relative modularity and spread ratio at distance 1 on robustness across different types of diversity and removal scenarios obtained from the slopes of simultaneous autoregressive (SAR) models. Lower spread ratios indicate higher buffering effects of the modular structure, which results from high modularity. R^2 for each SAR model is shown in Supporting Information Table S2. (b) Relationships between relative modularity and absolute latitude in island (orange, $n = 22$) and mainland networks (blue, $n = 57$). Both of the relationships are significant ($p < .05$). R^2 of the fitted lines are given for island networks (R^2_{isl}) and mainland networks (R^2_{mai}) [Colour figure can be viewed at wileyonlinelibrary.com]

phylogenetic diversity under generalist-first removal, environments tended to have strong direct effects on robustness (Figure 5).

3.3 | Sampling effects

As we showed in the SEMs, network size affected all types of robustness except robustness of functional and taxonomic diversity under specialist-first removals. Besides, robustness based on phylogenetic diversity was neither affected by sampling time, nor area (Supporting Information Figure S9). Robustness of taxonomic and functional diversity was not associated with sampling time, but decreased with sampling area (except for robustness of taxonomic diversity under generalist-first removals; Supporting Information Figures S10, S11). Nevertheless, relative modularity was not significantly associated with either sampling time or area, or network size (Supporting Information Figure S12). Despite their effect on some types of robustness, sampling time, area and network size were not significantly influenced by latitude, insularity or their interaction term (Supporting Information Figure S13). The composition of pollinator taxonomic order varied across latitudinal regions and insularity, with higher proportions of hymenopteran, lepidopteran and vertebrate pollinators in the tropics than non-tropics, a higher proportion of dipterans towards the cold regions, lower proportion of hymenopterans in islands compared to

mainlands, and existence of squamata and passeriforme only in tropical islands (Supporting Information Figure S14). The 'other' pollinators (except the denoted orders) were present in higher proportions in islands and in the temperate region (Supporting Information Figure S14).

4 | DISCUSSION

Among types of robustness, only robustness of phylogenetic diversity under specialist-first removal showed a significant opposite latitudinal trend between islands and mainlands. The direct drivers of robustness included modularity, insularity, network size, AET and PS, with modularity being the strongest one in most cases. Through the mediation of modularity, the effects of AET, PS and interaction between PS and insularity led to the latitudinal pattern of robustness. These results support our hypothesis that environments influence robustness via modularity, and imply that the phylogenetic diversity of pollinators is relatively vulnerable to the loss of specialized plants in tropical islands and high-latitude mainlands compared to other regions. Similar findings regarding the role of modularity in mediating the persistence of ecological networks in the face of anthropogenic influences have been found for marine food webs (Gilarranz, Mora, & Bascompte, 2016), thus highlighting the potential generality of this mechanism.

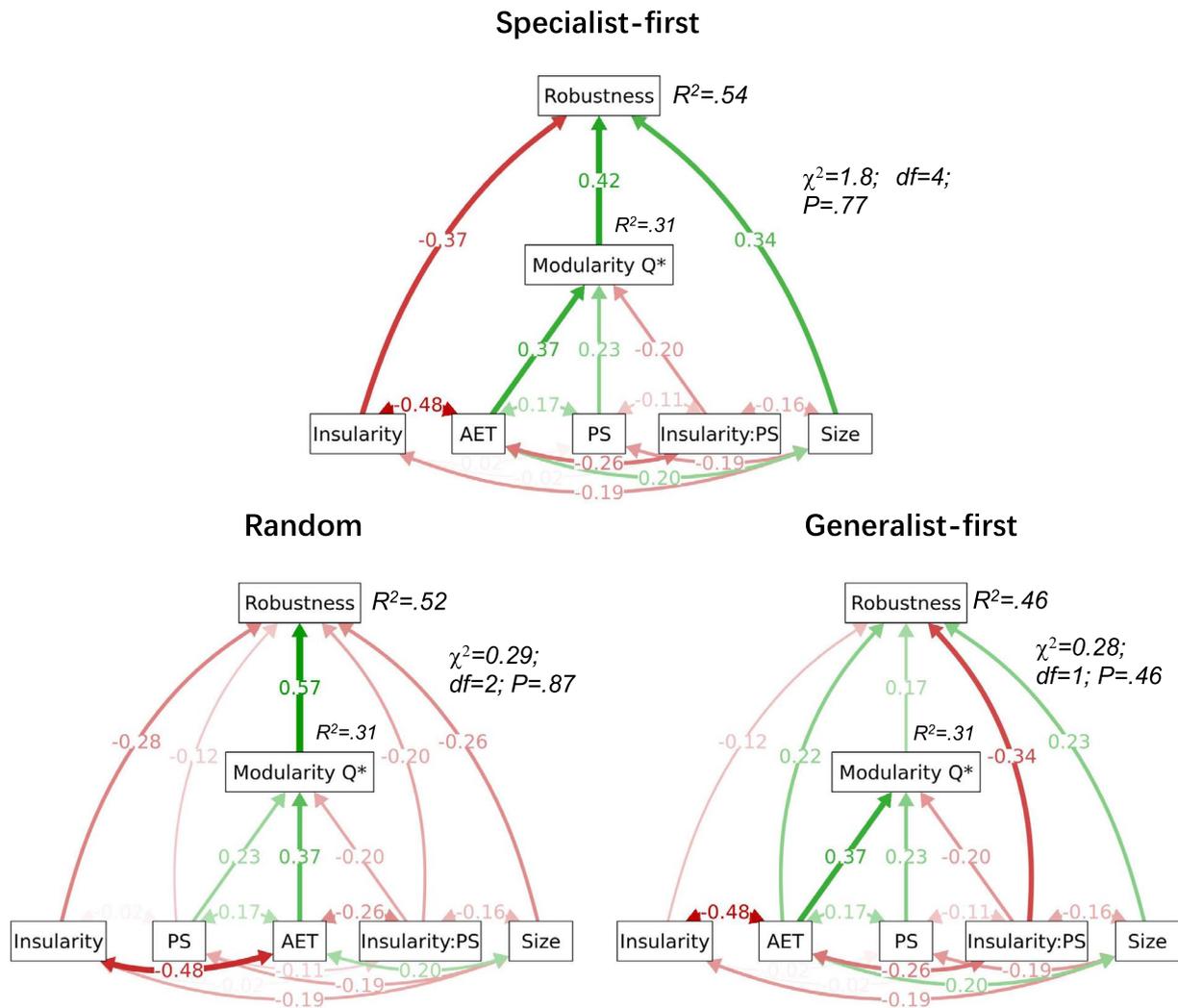


FIGURE 5 Results of the structural equation model (SEM) showing the paths from environmental factors and network size (Size; log-transformed) to robustness of phylogenetic diversity under the different removal scenarios. The environmental variables include: actual evapotranspiration (AET), precipitation seasonality (PS), insularity and the interaction term of insularity and PS. Green and red arrows indicate positive and negative relationships, respectively, with the thickness of each arrow reflecting their standardized path coefficients. Single-headed and double-headed arrows indicate directional and covariance links, respectively. SEMs for other types of robustness are shown in Supporting Information Table S4 and Figure S6 [Colour figure can be viewed at wileyonlinelibrary.com]

4.1 | Geographic pattern of robustness across types of diversity and removals

Network robustness and modularity varied weakly with altitude, which is consistent with some previous studies (Miller-Struttman & Galen, 2014; Ramos-Jiliberto et al., 2010; Trøjsgaard & Olesen, 2013). For example, Ramos-Jiliberto et al. (2010) showed that the number and size of modules change with altitude, but modularity remains significant and conserved across altitudes. The invariable modularity and robustness indicate a consistent community resistance to the spreading of harmful perturbations across altitudes, which is vital in the harsh environments associated with high elevations. The opposite latitudinal pattern of robustness between islands and mainlands in our results agrees with recent studies that revealed an inconsistency in the latitudinal gradient of ecological networks (Dalsgaard et al., 2013, 2017; Galiana et al., 2019; Pauw

& Stanway, 2015). Besides, this latitudinal pattern was more prominent regarding the robustness of phylogenetic diversity than for taxonomic and functional diversity, which is directly driven by the stronger effect of modularity on the robustness of phylogenetic diversity than other diversity types. This result partly contradicts our expectation that modularity may provide better protection to both functional and phylogenetic diversity than to taxonomic diversity since highly modular networks tend to keep coextinctions within a module where species are usually phylogenetically and functionally similar (Donatti et al., 2011; Hutchinson et al., 2017; Krasnov et al., 2012). The unexpectedly weak connection between modularity and robustness of functional diversity may result from the fact that although functional groups may force interactions to occur inside the module, they cannot limit the spatial variation of pairwise interactions, which can still lead to different levels of robustness (Carstensen et al., 2016). Meanwhile, the difference in the latitudinal

robustness trend between islands and mainlands was smaller under the scenario of generalist-first removals than under other removal scenarios. This may result from the fact that robustness of diversity under a generalist-first removal is weakly associated with modularity, because generalist-first removals targeted well-connected plants that usually act as module hubs in the networks (Olesen et al., 2007). This may have led to a quick erosion of the original modular structure at the start of removals.

4.2 | Robustness and the buffering effect of modularity

Robustness generally increased with modularity and decreased with spread ratio at distance 1 as expected (Gilarranz et al., 2017; Ramos-Robles et al., 2018; Stouffer & Bascompte, 2011), but surprisingly increased with spread ratio at distance 3. This positive relationship between robustness and spread ratio at distance 3 may result from the following mechanism: large extinction cascades within modules likely result in the elimination of module hubs in the focal module, which may cause a sudden loss of the entire module involving multiple species, unique functional groups, and phylogenetic branches (Krasnov et al., 2012; Montoya et al., 2015). Thus, when large extinction cascades are more likely to spread outside the module, a larger proportion of diversity in the network remains because the great coextinctions would not anymore concentrate in one module. The opposite relationships of robustness versus spread ratio at distances 1 and 3 indicate that modularity brings adverse effects on robustness by buffering coextinctions, but the net effect of modularity on robustness remains positive since spread ratio at distance 1 imposed a much larger effect on robustness than spread ratio at distance 3. This is consistent with previous studies implying that secondary extinctions are the major source of species loss in pollination networks (Vieira & Almeida-Neto, 2015).

4.3 | The direct and indirect environmental effects on robustness

The results confirmed our hypothesis that modularity mediates the environmental effects on robustness. Among the predictors of modularity, AET promoted modularity as expected, because AET indicates the level of productivity, which encourages distinct niche partitioning among species and high levels of modularity (Kreft & Jetz, 2007; Maruyama et al., 2018; Trøjelsgaard & Olesen, 2013). In contrast, past climate stability was excluded by the model selection procedure, probably due to the correlation with PS and insularity (Supporting Information Figure S1). More importantly, we revealed the effect of insularity on the environment–network relationship for the first time: PS showed opposite effects on modularity between island and mainland networks. An explanation might be as follows: species vary in their sensitivity to seasonal change (Stemkovski et al., 2020), which means some species have a long phenophase

and they usually are generalists, such as bumblebees, while others do not (Bascompte & Olesen, 2015; Olesen et al., 2008). So the opposite effect of PS on modularity may depend on the proportion of long-phenophase generalists in the communities: in communities with few long-phenophase generalists, most species can only interact with a few co-occurring partners in a short time period and they form several phenological units, thus seasonality would promote module partitioning by minimizing the time overlap of the phenological units (Bascompte & Olesen, 2015; Martín González et al., 2012); but in communities with many long-phenophase generalists, seasonality would make the generalists become connectors among modules because the generalists co-occur with several phenological units across time (Bascompte & Olesen, 2015; Martín González et al., 2012). Meanwhile, generalists provide a more reliable source for their partners than specialists do with fluctuating populations through time (Waser et al., 1996). Thus, some species may evolve to depend on generalists, which blurs the modular structure of networks. The latter scenario may be more prominent in island communities with higher levels of generalization and longer phenophase of species compared to their mainland counterparts (Inoue, 1993; Traveset et al., 2016; Trøjelsgaard & Olesen, 2013). This could lead to the negative effect of PS on modularity of insular networks.

Our results also revealed direct environmental effects on robustness for the first time. Insular networks are naturally less robust than mainland networks independent of modularity, probably because island networks have a higher plant/pollinator ratio and these asymmetric networks are prone to collapse when some of the pollinators go extinct (Schleuning, Böhning-Gaese, et al., 2014). PS and AET were found to directly affect robustness, most likely because these climatic factors may influence the niche breadth of species besides promoting modularity. We found AET increased robustness of phylogenetic diversity under generalist-first removals, because AET as an indicator of productivity would provide a larger niche space and favor generalists with wide niche breadths (Gainsbury & Meiri, 2017; Pianka, 1966; Rohde, 1999), also because generalists have a higher chance of persisting than specialists, especially in the context of widespread coextinctions caused by generalist-first removal scenarios (Memmott et al., 2004). In contrast, PS was shown to dampen robustness of functional and phylogenetic diversity by decreasing niche breadth, probably because reduced resource availability due to seasonality may promote higher interspecific competition and lead to narrower species niches (Souza et al., 2018).

4.4 | Sampling effects

We found that sampling area decreased robustness and network size had mixed effects on robustness with a negative effect on most types. Negative sampling effects on robustness might be explained by the fact that sampling increases the chance of finding rare specialist species that are vulnerable to coextinctions (Novotný & Basset, 2000). But surprisingly, network size promoted robustness of phylogenetic diversity in specialist-first and generalist-first

removals, probably because sampling may increase the phylogenetic redundancy of the communities. Relative modularity was weakly affected by sampling factors, indicating a sufficient null-model correction of modularity.

The distribution of pollinator taxonomic orders across latitudes, islands and mainlands in this study generally fits the natural distribution revealed by previous studies, for example, dipterans dominate high latitudes while hymenopterans, especially bees, are more common towards low latitudes (Devoto et al., 2005; Elberling & Olesen, 1999), and more lizard pollinators and 'other' pollinators (can be viewed as opportunistic pollinators) occur on islands than mainlands (Fuster et al., 2020; Hervías-Parejo & Traveset, 2018; Olesen & Valido, 2003; Wang et al., 2020). The lack of mammal pollinators such as bats (Fægri & van der Pijl, 1979), and the relative rarity of bird pollinators especially in temperate regions (Zanata et al., 2017), are taxonomic biases in our dataset and in other global analyses of pollination networks (Olesen & Jordano, 2002; Traveset et al., 2016; Trøjelsgaard & Olesen, 2013). However, it has been found that most pollinators in the world are insects and so the influence of these biases might be small (Ollerton, 2017). Results also reveal that more species from 'other' taxonomic groups were found in the temperate region than in other regions, but whether it is biased compared to their actual distribution is unclear since there are few studies that have explored the distribution of these minor pollinators to our knowledge. These groups are usually opportunistic pollinators that may blur modular structure, but modularity and robustness did not appear to be lower in temperate than other regions, so even if the distribution of 'other' pollinators is confirmed to be a bias, its influence on our results was at least not apparent.

5 | CONCLUSIONS

Characterizing the extent to which climatically induced direct extinctions trigger coextinction cascades and how this changes across environments is a critical step for understanding the vulnerability of ecological communities under global climate change (Bascompte et al., 2019). Our results have revealed an opposite latitudinal gradient of network robustness of phylogenetic diversity between island and mainland pollination networks, which is mainly driven by environmental gradients of network modularity, on the one hand, and the positive effect of modularity on robustness, on the other hand. Future studies should explore whether this effect of modularity on the environmental gradient of robustness extends to other dimensions of stability, network properties, and different interaction types. Besides, more data on local networks and realistic estimates of extinction risk are still needed to undertake detailed mapping of ecosystem fragility and provide practical advice for global biodiversity conservation.

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CONFLICT OF INTEREST

All co-authors agree there are no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

HL, CC and FH conceived the study. HL and MZ collected the data. HL conducted the analysis and interpreted the results, with the help of JB, CC and ZL. HL and ZL wrote the first manuscript, and all authors contributed to the revision of the manuscript.

DATA AVAILABILITY STATEMENT

Interaction matrices, environmental variables and network indices for each pollination network, and the code to reproduce the results are available from the Figshare repository: 10.6084/m9.figshare.14035814.

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BIOSKETCH

Hanlun Liu is working on his PhD in community ecology. He is mainly interested in the structure and function of ecological networks, with a focus on the plant–pollinator and plant–plant interaction networks.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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