

## Research



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# Habitat fragmentation increases specialization of multi-trophic interactions by high species turnover

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Habitat fragmentation is altering species interactions worldwide. However, the mechanisms underlying the response of network specialization to habitat fragmentation remain unknown, especially for multi-trophic interactions. We here collected a large dataset consisting of 2670 observations of tri-trophic interactions among plants, sap-sucking aphids and honeydew-collecting ants on 18 forested islands in the Thousand Island Lake, China. For each island, we constructed an antagonistic plant–aphid and a mutualistic aphid–ant network, and tested how network specialization varied with island area and isolation. We found that both networks exhibited higher specialization on smaller islands, while only aphid–ant networks had increased specialization on more isolated islands. Variations in network specialization among islands was primarily driven by species turnover, which was interlinked across trophic levels as fragmentation increased the specialization of both antagonistic and mutualistic networks through bottom-up effects via plant and aphid communities. These findings reveal that species on small and isolated islands display higher specialization mainly due to effects of fragmentation on species turnover, with behavioural changes causing interaction rewiring playing only a minor role. Our study highlights the significance of adopting a multi-trophic perspective when exploring patterns and processes in structuring ecological networks in fragmented landscapes.

## 1. Introduction

Human-induced habitat fragmentation influences the patterns of community structure and species interactions [1–3], and these effects are often evident in variations of network properties [4–7]. As a central property of interaction networks, network specialization is closely linked to the stability of ecological communities [8–11], and has been frequently reported to be affected by habitat fragmentation [8,12,13]. However, the mechanisms that drive the response of network specialization to habitat fragmentation remain poorly understood. Moreover, research on ecological networks in fragmented habitats has

predominantly focused on interactions between two trophic levels, neglecting that species are commonly engaged in a myriad of interactions across multiple trophic levels [14–16]. As a basic conceptual framework for understanding habitat fragmentation, island biogeography theory (IBT) has been used widely to test the effects of area and isolation in fragmented landscapes on the maintenance of species diversity [17]. By adopting the framework of IBT to explore the stability of ecological communities along fragmentation gradients (i.e. the effect of area and isolation on multiple trophic interactions), we can gain deep insights into how fragmentation shapes ecological communities [6].

Interactions between plants, sap-sucking aphids and honeydew-collecting ants are common tri-trophic relationships in forest ecosystems [18–20]. These so-called trophobioses consist of two distinct interaction types: antagonistic plant–aphid and mutualistic aphid–ant interactions. Aphids are herbivores that extract plant sap, while ants are normally mutualistic with aphids by providing protection (ants repel predators and clear the honeydew to prevent aphids from developing fungal infections caused by honeydew accumulation) in return for their honeydew supply [18]. Both interactions play an essential role in ecosystem energy fluxes [21], but have only been studied in few ecosystems [22–25]. Previous studies indicate that antagonistic networks are usually more specialized and modular than mutualistic networks, while mutualistic networks are more nested than antagonistic networks [26,27]. Studies of trophobioses also showed that plant–aphid networks are usually more specialized than the mutualistic aphid–ant networks [22,24,28]. Typically, highly specialized interactions are considered less stable under changing or unpredictable conditions, as species within these networks are susceptible to local co-extinction [8,29]. In turn, communities with more generalized species are in general predicted to be more stable due to redundant interactions among species in the interaction network [30,31]. However, when generalized species with many interactions are lost, the cascading effects produced by multiple indirect paths can also result in network collapse [32]. In the context of habitat fragmentation, exploring the mechanisms causing variations in specialization of trophobioses is therefore crucial for predicting how fragmentation influences biodiversity more broadly [8,33,34].

To understand the mechanisms that structure interaction networks, network dissimilarity (interaction  $\beta$ -diversity) can be partitioned into two components: species turnover ( $\beta_{ST}$ ; i.e. changes in community composition) and interaction rewiring ( $\beta_{OS}$ ; i.e. flexibility of interactions among shared species) [35,36]. Previous studies have found that turnover of specialized species among fragments and the behavioural changes of generalists (interaction rewiring) can cause significant changes in network specialization [37]. Habitat fragmentation is often accompanied by species loss and species turnover [38]. The constraints on interaction partner selection in antagonistic networks (e.g. plant–aphid) may therefore translate into higher species turnover under anthropogenic habitat fragmentation, causing variations in plant–aphid network structure across fragments [8,27]. For example, when a given plant species is lost, its aphid herbivores may not be able to interact with other plant species in the community. They will thus disappear together from the network [24]. However, besides species turnover, interaction flexibility allows generalized species to rewire their interactions to new partners within the

community after fragmentation [39]. Moreover, different trophic levels could be interlinked within an ecosystem [40], and species turnover of a single trophic level may exert a bottom-up or top-down effect across other trophic levels [41–43], leading to a more general impact of habitat fragmentation on patterns of species composition and interaction [44–46]. Despite recent advancements in our understanding of network dynamics [27,47,48], it remains poorly understood how species turnover and interaction rewiring shape specialization in trophobioses systems across fragmented landscapes.

Here, we explore three questions to pinpoint the mechanism causing habitat fragmentation to affect network specialization of trophobioses: (1) Does the degree of network specialization in trophobioses vary with habitat area and isolation? (2) Does the spatial variation in network specialization among fragments primarily result from species turnover or interaction rewiring? (3) Specifically, does the variation in community composition (species turnover) of a single trophic level exert a bottom-up or top-down effect on network specialization through the interactions among trophic levels? For our study system, we hypothesize that the degree of network specialization in trophobioses will vary with habitat area due to high species turnover caused by habitat fragmentation. On the other hand, we predict that the different interacting groups (plant–aphid and aphid–ant) have different responses to the degree of isolation. Furthermore, we expect that both bottom-up and top-down effects in trophobioses influence network specialization.

## 2. Material and methods

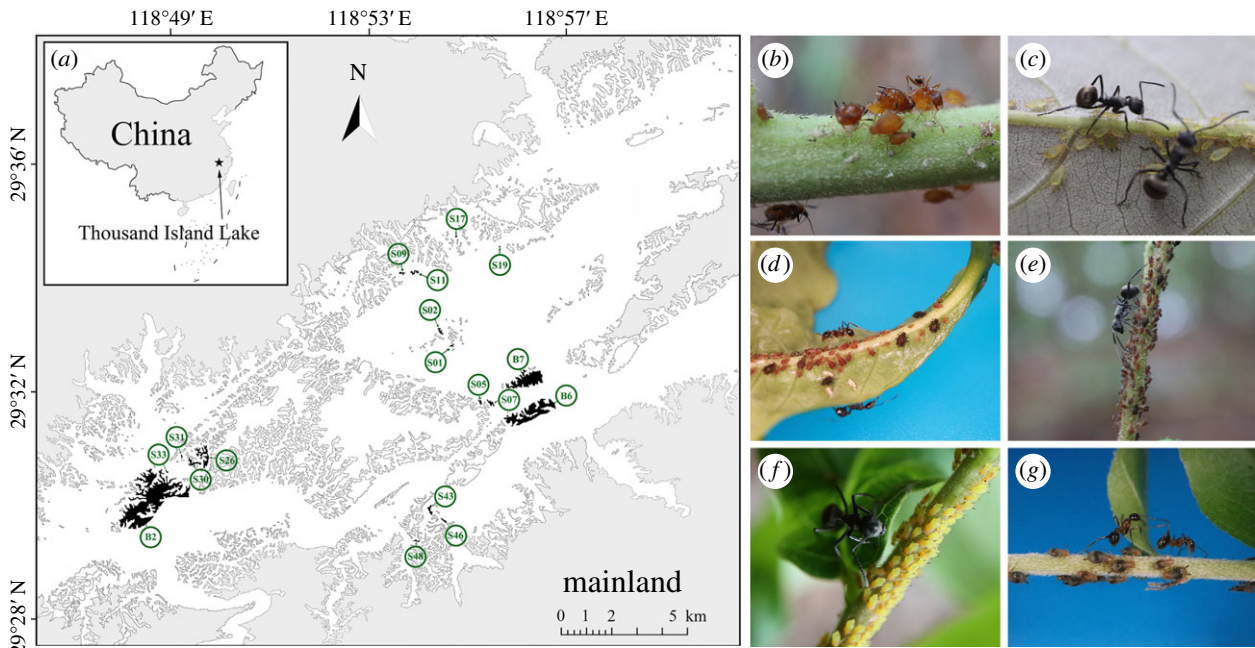
### (a) Study site

This study was conducted in the Thousand Island Lake (Zhejiang Province, eastern China, 29°22′–29°50′ N; 118°34′–119°15′ E), a large artificial land-bridge island system formed in 1959 by the construction of the Xin’anjiang Dam for hydroelectric production [16,17]. The lake has a flooding area of approximately 580 km<sup>2</sup> and 1078 islands (previously hilltops of continuous forest) larger than 0.25 ha at the highwater level (108 m). The lake region is characterized by a typical seasonal subtropical monsoon climate (hot and humid summers, cool and relatively dry winters). The mean annual temperature is 17.0 °C and the daily temperature ranges from –7.6 °C in January to 41.8 °C in July. Mean annual precipitation is 1430 mm, mainly concentrated in the rainy season between April and June [49]. The main vegetation type is a diverse mix of subtropical deciduous and coniferous forests (mean coverage per island ~ 82.6%), mainly consisting of *Pinus massoniana* Lamb, with many broad-leaved trees and shrubs [14].

### (b) Data collection

We conducted field surveys for plant–aphid–ant interactions on 18 forest islands representing the habitat fragmentation gradients in island area (minimum 0.08 ha—maximum 128.04 ha) and isolation (i.e. distance to the mainland: minimum 356 m—maximum 3725 m; figure 1; table 1). Island area and isolation are uncorrelated (Pearson’s coefficient  $r = -0.17$ ,  $p = 0.49$ ).

We surveyed plant–aphid–ant interactions in 2020 and 2021 (from mid-May to mid-August in each year) using line transects. Each transect had a width of 10 m and length of 400 m. To standardize the sampling effort relative to island area, the number of transects on each island is roughly proportional to the logarithm of island area [50]. As a result, we set five transects on the largest study island (area > 100 ha), four transects on the island of 52 ha,



**Figure 1.** (a) The 18 study islands (in black) in the Thousand Island Lake, Zhejiang, China. (b–g) Exemplary trophobioses illustrating the diversity of participating plants, aphids and ants in this study. (b) *Pheidole* sp1 ant tending the aphid *Aulacophoroides hoffmanni* on the plant *Wisteria sinensis*. (c) *Polyrhachis dives* tending *Eutrichosiphum pasaniae* on *Castanopsis sclerophylla*. (d) *Pheidole nodus* tending *Aphis* sp1 on *Gardenia jasminoides*. (e) *P. dives* tending *Aphis* sp1 on *Eurya muricata*. (f) *Polyrhachis dives* tending *Aphis eugeniae* on *Glochidion puberum*. (g) *Pheidole nodus* tending *Greenidea kuwanai* on *Quercus acutissima*. Photos (b–g) taken by Xue Zhang.

three transects on the island of 29 ha, two transects on islands with an area between 1 and 10 ha, and one on each of the remaining islands with an area < 1 ha. Along each transect, we visually screened all woody and herbaceous plants for trophobioses. For each individual woody plant, we carefully inspected roots in shallow soil and three branches (including their leaves and bark) for aphids and interacting ants [24]. For taller woody plants (above 2 m), we only sampled branches under 2 m, i.e. excluding the interactions occurring in the canopy. Herbaceous plants were completely surveyed. Each interaction was recorded and photographed. We consider as an interaction each observed event of one ant species interacting with one aphid species or one aphid species on an individual plant, regardless of the number of individuals involved (see also [24,25]). We collected voucher specimens of all interacting aphid and ant species with a soft brush soaked in alcohol and preserved them in 95% ethanol at  $-20^{\circ}\text{C}$  for identification. Aphids were identified based on the exterior morphology of slide-mounted specimens using the online key ‘Aphids on the world’s plants’ (Blackman & Eastop. See <http://aphid.speciesfile.org>) and DNA barcoding (electronic supplementary material, appendix S1); sequences were deposited in GenBank (electronic supplementary material, table S1). Ants were identified as species or morphospecies using the reference collection sampled previously in the same region [51]. To estimate the diversity of plants on the study islands, we surveyed a  $10 \times 10$  m plot every 20 m along the transect and divided the plots into four  $5 \times 5$  m subplots to record the species richness and abundance of all plants (including trees, shrubs, herbs and lianas).

Ant-attended aphids can often be detected by searching for ants moving up tree trunks, making them easier to find than unattended aphids. To avoid such bias in the investigation, before fieldwork commenced we used the online key ‘Aphids on the world’s plants’ (Blackman & Eastop; see <http://aphid.speciesfile.org>) to make a ‘host plant–aphid’ list of the potential host plants in the study area, summarizing the specific parts of each plant species that were likely to have aphids and the morphology of the aphids. In addition, all transects were investigated by the same three individual investigators. In this way we minimized

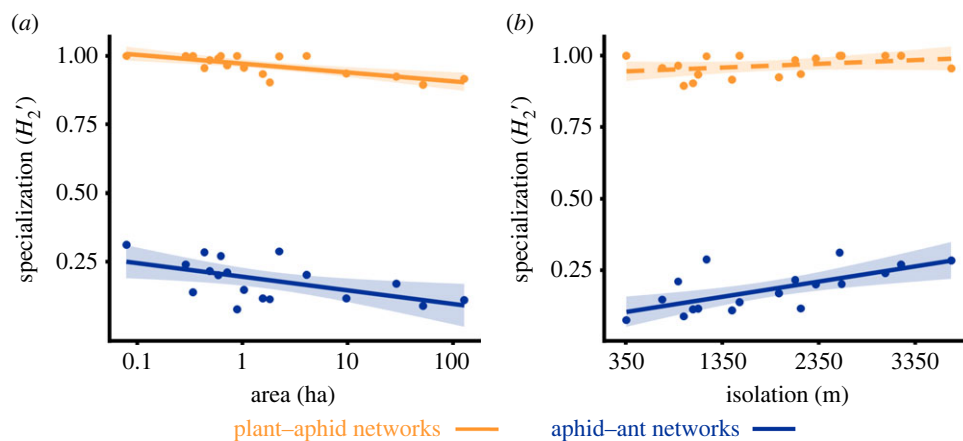
the possibility that plant–aphid interactions were overlooked. We thus believe that the plant–aphid and aphid–ant networks have similar quality.

To estimate the sampling completeness of plant–aphid and aphid–ant interactions on each island, we used ‘sample coverage’ measured as the proportion of the total number of individuals (i.e. interaction frequency) in a community belonging to the interactions represented in the sample [52]. We calculated the sample coverage for each island using the *iNEXT* function in the R package ‘iNEXT’, ver. 2.0.20 [53]. We also used a generalized linear model (GLM) with the Poisson family to assess the effects of island area and isolation on species richness of plants, aphids and ants, respectively.

### (c) Network specialization along island area and isolation

For each island, we constructed an antagonistic plant–aphid network and a mutualistic aphid–ant network based on a weighted pairwise interaction matrix. To assess the degree of specialization in both types of networks, we used three metrics: specialization  $H_2'$  (weighted complementary specialization) [54], weighted generality  $G_{\text{qw}}$  (weighted mean effective number of species in the lower trophic level per species in the higher level) [55] and weighted vulnerability  $V_{\text{qw}}$  (weighted mean effective number of species in the higher trophic level per species in the lower level) [55,56].  $H_2'$  characterizes the specialization of the entire network by quantifying the extent that interaction frequencies deviate from expected frequencies given the species’ total frequencies [54].  $H_2'$  is independent of species’ abundances and network size, enabling the comparison of interaction patterns across networks of different dimensions [54].  $G_{\text{qw}}$  and  $V_{\text{qw}}$  describe the functional redundancy of species at higher and lower trophic levels, respectively [55]. At the network level, large values of  $H_2'$  indicate high specialization (range: 0–1), while low values of  $G_{\text{qw}}$  and  $V_{\text{qw}}$  indicate high specialization.

We calculated network metrics ( $H_2'$ ,  $G_{\text{qw}}$  and  $V_{\text{qw}}$ ) using the *networklevel* and *grouplevel* functions in the R package ‘bipartite’,



**Figure 2.** Changes in network specialization ( $H_2'$ ) of plant–aphid (orange) and aphid–ant (blue) networks along area (a) and isolation (b) gradients on 18 islands of the Thousand Island Lake, China. The linear fitted lines are based on multiple linear regression models (see §2, Material and methods). Island area (ha) was log-transformed to normalize model residuals. Solid lines indicate significant relationships ( $p < 0.05$ ), whereas dotted lines represent non-significant relationships ( $p > 0.05$ ). Shaded polygons specify the 95% confidence interval.

v. 2.18 [57]. We then used multiple linear regression models to examine how island area and isolation relate to the specialization degree of the interaction networks ( $H_2'$ ,  $G_{qw}$  and  $V_{qw}$ ).

#### (d) Beta diversity of trophobioses networks

For both types of networks, we measured the variation in network structure between islands using the binary Sørensen dissimilarity index [58], in which interaction dissimilarity is calculated between two networks  $M$  and  $N$  as  $\beta_{WN} = (b + c) / (2a + b + c)$ , wherein  $a$  is the number of interactions occurring in both networks,  $b$  is the number of interactions occurring only in the network  $M$ , and  $c$  is the number of interactions occurring only in the network  $N$ . Furthermore, we partitioned  $\beta_{WN}$  into interaction dissimilarity due to species turnover ( $\beta_{ST}$ ) and interaction rewiring ( $\beta_{OS}$ ; i.e. flexibility of interactions among shared species) [35], following the partitioning approach of Novotny [59]. Partitioning total beta diversity allows us to evaluate whether the variations in network structure among islands are either mostly affected by differences in species turnover ( $\beta_{ST}$ ) or by interaction rewiring ( $\beta_{OS}$ ) [47].

We calculated interaction dissimilarity among networks with the *betalinkr\_multi* function by setting the parameter 'index' as 'sorensen' and 'partitioning' as 'commondenom' in the R package 'bipartite', v. 2.18 [35,60]. We compared interaction dissimilarity of species turnover ( $\beta_{ST}$ ) and interaction rewiring ( $\beta_{OS}$ ) in this study using the two-tailed *t*-test.

#### (e) Effects of species dissimilarity and interaction rewiring on network specialization

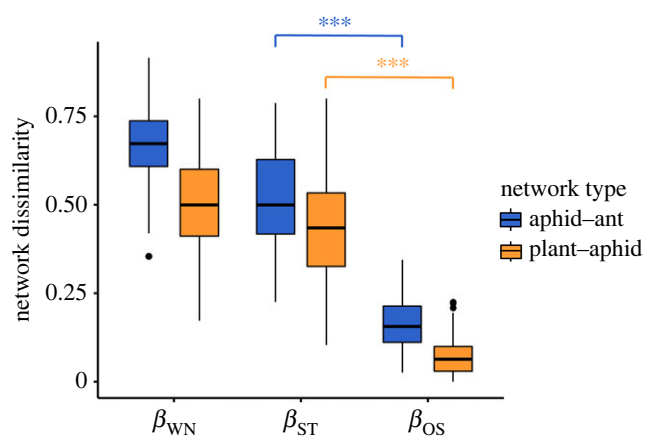
We used path analyses and multiple regression on distance matrices (MRMs) to assess the role of species dissimilarity in driving specialization of both antagonistic and mutualistic networks by applying the *MRM* function in the R package 'ecodist', v. 2.0.7 [61,62]. The conceptual path models (electronic supplementary material, figure S4) hypothesized direct and indirect relationships among island characteristics (i.e. area and isolation), species dissimilarity and variation in network specializations of both types of interactions. Considering that both bottom-up and top-down effects may occur between plant–aphid–ant communities [63–65], we constructed two conceptual path models (electronic supplementary material, figure S4). We calculated pairwise species dissimilarity among islands with the *beta.pair* function in the R package 'betapart', v. 1.5.4 [66]. We used a d-separation test to assess model fit (i.e. Fisher's C statistic and  $\chi^2$ -based *p*-value) [67]. A non-significant *p*-value

( $p > 0.05$ ) indicates a good model fit to data for the respective model structure [68]. We refined the original model by dropping non-significant links, beginning with the least significant, and continuing stepwise until the minimum Akaike information criterion (AIC) value was obtained. MRMs were performed to obtain *p*-values that were used to calculate the C statistic in the best-fit model. We calculated range-standardized coefficients for each predictor variable [61,69].

To estimate the variation of network specialization due to interaction rewiring, we used relative specialization ( $rH_2'$ ) to assess the difference in specialization between the observed network and an expected network based on a regional network (i.e. a network that consists of data from all 18 island networks) for plant–aphid and aphid–ant interactions, respectively [70]. The regional network represents observed interactions among all interacting species in our study region [71]. For each network on an island, we assembled an expected network that included the same species as in the observed network, but with their interaction frequencies derived from the regional network. We used this expected network to calculate the expected  $H_2'$ . The deviation of the level of specialization between the observed and expected networks can estimate the change of local structures due to interaction rewiring, i.e. changes in the behaviour of the species themselves [70]. In this way, the relative specialization ( $rH_2'$ ) estimates specialization changes in island networks due to interaction rewiring (electronic supplementary material, figure S5). All statistical analyses were conducted in R v. 4.1.1 (www.r-project.org).

## 3. Results

We recorded a total of 1438 independent antagonistic plant–aphid and 1232 mutualistic aphid–ant interactions on 18 islands. These interactions involved 77 unique plant–aphid interactions and 146 unique aphid–ant interactions that consisted of 41 plant species, 24 aphid species and 35 ant species (figure 1 and electronic supplementary material, tables S2 and S3). The mean sample coverages (sampling completeness on each island) for plant–aphid and aphid–ant interactions were  $0.91 \pm 0.06$  (mean  $\pm$  s.d.) and  $0.76 \pm 0.10$  (mean  $\pm$  s.d.), respectively (electronic supplementary material, figure S1). The number of plant species, aphid species and ant species increased significantly with island area ( $p < 0.001$ ), while isolation had no relationship with species richness in any of the three groups (electronic supplementary material, figure S2).



**Figure 3.** Comparison of components of plant-aphid and aphid-ant network dissimilarities among islands: total network dissimilarity ( $\beta_{WN}$ ), turnover in species composition ( $\beta_{ST}$ ) and interaction rewiring ( $\beta_{OS}$ ) among 18 islands of the Thousand Island Lake, China. Boxes indicate the first and third quartiles (Q1 and Q3), horizontal lines inside boxes are medians, vertical lines indicate Q1/Q3 + 1.5  $\times$  interquartile ranges (IQR) and points are outliers. Asterisks indicate significant differences ( $p < 0.001$ ) between  $\beta_{ST}$  and  $\beta_{OS}$  via a two-tailed  $t$ -test for both plant-aphid and aphid-ant networks.

Irrespective of the network metric used ( $H_2'$ ,  $G_{qw}$  and  $V_{qw}$ ), antagonistic plant-aphid networks exhibited a higher degree of specialization than mutualistic aphid-ant networks (figure 2 and electronic supplementary material, figure S3). Overall, specialization degree correlated with both island area and isolation. Specifically, specialization ( $H_2'$ ) decreased while vulnerability ( $V_{qw}$ ) increased with increasing island area for both plant-aphid ( $\beta = -0.013$ ,  $p < 0.01$  for  $H_2'$ ;  $\beta = 0.04$ ,  $p < 0.001$  for  $V_{qw}$ ) and aphid-ant ( $\beta = -0.015$ ,  $p < 0.05$  for  $H_2'$ ;  $\beta = 0.312$ ,  $p < 0.05$  for  $V_{qw}$ ) networks. Network generality ( $G_{qw}$ ) of aphid-ant networks ( $\beta = 0.184$ ,  $p < 0.05$ ) also increased with island area, but area was not significantly correlated with network generality for plant-aphid networks. Network specialization ( $H_2'$ ) of aphid-ant networks ( $\beta = 4.367 \times 10^{-5}$ ,  $p < 0.01$ ) significantly increased with island isolation (figure 2, electronic supplementary material, figure S3 and table S4).

Network dissimilarity ( $\beta_{WN}$ ) of aphid-ant networks (mean  $0.67 \pm 0.11$  s.d.) was higher than that of plant-aphid networks (mean  $0.51 \pm 0.13$  s.d.) and both were primarily driven by species turnover ( $\beta_{ST}$ ) (figure 3 and electronic supplementary material, table S5;  $t = -29.09$ ,  $p < 0.001$  for plant-aphid networks;  $t = -28.42$ ,  $p < 0.001$  for aphid-ant networks). Network rewiring ( $\beta_{OS}$ ) and species turnover ( $\beta_{ST}$ ) were higher in aphid-ant networks than that in plant-aphid networks (figure 3 and electronic supplementary material, table S5).

Differences in species composition (i.e. species dissimilarity) were affected by difference in island area and isolation, and had an overall positive effect on the variation of specialization ( $H_2'$ ) in both antagonistic and mutualistic networks (figure 4 and electronic supplementary material, table S6). Although the AIC values of the bottom-up and top-down models were similar (Fisher's C [24] = 20.56,  $p = 0.66$ , AIC = 56.56 for bottom-up model; Fisher's C [20] = 16.07,  $p = 0.71$ , AIC = 56.07 for top-down model), habitat fragmentation affected specialization of both antagonistic and mutualistic networks through a bottom-up effect from plant to aphid, and directly through aphid dissimilarity as shown by path

models (figure 4 and electronic supplementary material, table S6). Path models indicated that 29% of the variance in plant-aphid specialization ( $H_2'$ ) was explained directly by island area, and indirectly through the mediation of species composition by habitat fragmentation (i.e. bottom-up effect between plant dissimilarity and aphid dissimilarity). In aphid-ant networks, 16% of the variance in the degree of specialization ( $H_2'$ ) was explained directly by isolation, and indirectly through habitat fragmentation-mediated differences in species composition (i.e. bottom-up effect between plant dissimilarity and aphid dissimilarity; figure 4 and electronic supplementary material, table S6). In the bottom-up model, plant dissimilarity was directly affected by island area and isolation, and changes in aphid dissimilarity and ant dissimilarity were indirectly mediated by plant dissimilarity and aphid dissimilarity, respectively (figure 4a and electronic supplementary material, table S6.1).

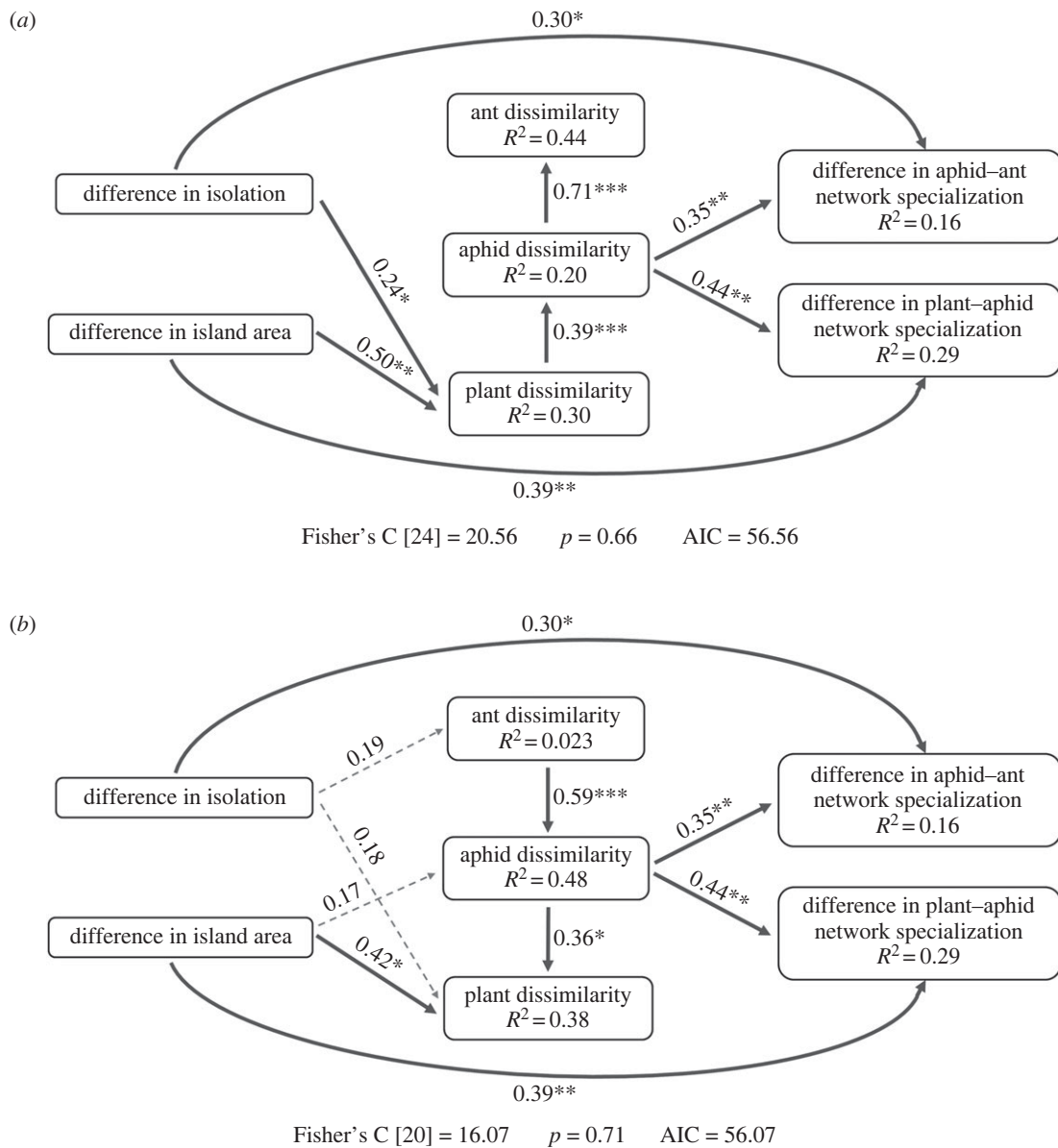
Relative specialization ( $rH_2'$ ) of plant-aphid and aphid-ant networks both decreased with island area (figure 5 and electronic supplementary material, table S7;  $\beta = -0.009$ ,  $p < 0.05$  for plant-aphid networks;  $\beta = -0.019$ ,  $p < 0.01$  for aphid-ant networks). The  $rH_2'$  of aphid-ant networks increased with isolation (figure 5 and electronic supplementary material, table S7;  $\beta = 3.715 \times 10^{-5}$ ,  $p < 0.01$ ), but  $rH_2'$  of plant-aphid networks was not significantly correlated with isolation. Aphid-ant networks consistently had a higher  $rH_2'$  than plant-aphid networks.

## 4. Discussion

Based on a comprehensive dataset of plant-aphid-ant interactions collected on 18 forest islands in a large reservoir, our study examined the effects of habitat fragmentation (i.e. island area and isolation) on network specialization. We found that habitat fragmentation increases network specialization of plant-aphid-ant interactions primarily by increasing species turnover, as turnover within a single trophic level exerts both bottom-up and top-down effects across trophic levels. In addition, habitat fragmentation increases the specialization degree of both antagonistic and mutualistic networks by bottom-up effects from plant communities to aphid communities. These findings reveal that cascading trophic interactions that may interlink trophic levels and species in small and isolated fragments could be more specialized mainly due to high species turnover among forest islands.

### (a) Specialization and island area

In this study, we observed that antagonistic plant-aphid networks exhibited higher specialization than mutualistic aphid-ant networks. Most aphid species are limited to feeding on a single plant genus or family, except for a few polyphagous species [72]. Aphids need to overcome plant defenses to survive either physically and/or chemically, and they require specific behavioural and morphological adaptations. Meanwhile, plants are defended against aphid attack by producing physical barriers and/or chemical toxic compounds. This coevolutionary 'arms race' between interacting aphids and plants can result in greater specialization between them [73]. However, mutualistic aphid-ant interactions are more generalized, since ants are not constrained to specific aphid taxa and the honeydew produced by most

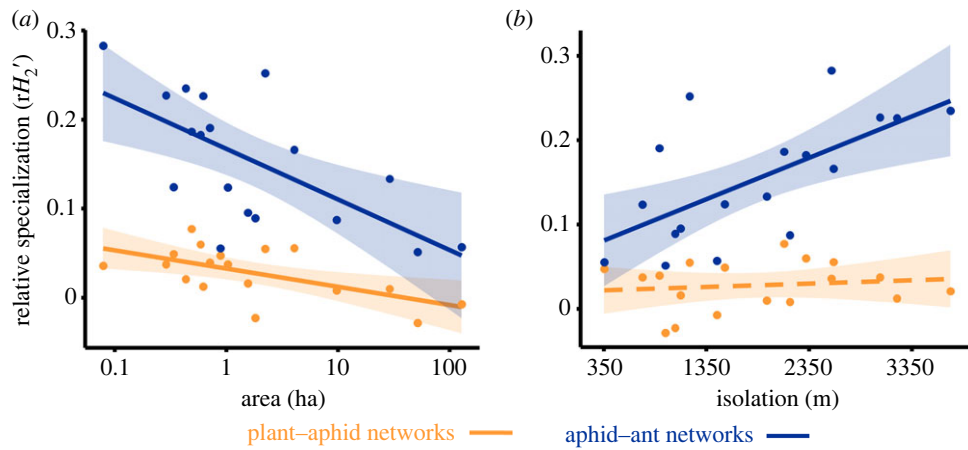


**Figure 4.** Direct and indirect links of habitat fragmentation (island area, isolation), species pairwise abundance-weighted  $\beta$  diversity (plant dissimilarity, aphid dissimilarity, ant dissimilarity) and difference in network specialization for plant–aphid and aphid–ant networks on 18 islands of the Thousand Island Lake, China. (a) ‘Bottom-up’ model, i.e. when plant dissimilarity is hypothesized to predict aphid dissimilarity, and aphid dissimilarity is hypothesized to predict ant dissimilarity. (b) The paths for the possible opposite scenario, i.e. a ‘top-down’ effect where ant dissimilarity is hypothesized to predict aphid dissimilarity and aphid dissimilarity is hypothesized to predict plant dissimilarity. All arrows in the figure represent positive relationships. Numbers under each response variable indicate the  $R^2$  for each individual MRM (multiple regression for matrix). Numbers alongside arrows indicate the range-standardized effect size of each predictor variable. Asterisks denote significance levels: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ . AICs of the two path models are: AIC = 56.56 for bottom-up model; AIC = 56.07 for top-down model.

aphids can also be collected by a broad range of ant species [28,74]. As a result, antagonistic networks were more specialized than mutualistic networks on forest islands, which is consistent with the findings from other studies [24,25].

Despite the overall higher-level specialization of antagonistic networks than mutualistic networks on forest islands, both antagonistic and mutualistic networks on small islands were more specialized. Small islands provide less available resources [75], which should increase species’ dietary breadth, resulting in a reduction in the degree of specialization [12,76]. However, the more specialized networks on smaller islands in our study may be explained by the variation in networks’ generality and vulnerability. Plant–aphid networks remained at low generality and vulnerability, and the effective number of plant species attacked by each aphid species (i.e. the generality of plant–aphid networks) did not vary with island area. Due to the high host specificity of aphids, the reduction of resource

availability on small islands may not lead to an increase in aphids’ diet breadth [73]. However, the effective number of aphid species on each plant species (i.e. the vulnerability of plant–aphid networks) decreased with decreasing island area, which may explain why plant–aphid specialization increased on small islands. Aphid–ant networks have lower generality and vulnerability on small islands. For the generalized aphid–ant interactions, the selection of interacting partners depends more on the encounter probability [74]. The decrease in island area was accompanied with a decrease in species richness of aphids and ants, which reduced the chance of selecting partners between aphids and ants and consequently lead to more specialized aphid–ant networks on small islands. Furthermore, abundance-driven mechanisms have been observed in other mutualistic systems, such as between pollinators and their flowering plants, where individuals tend to interact randomly and abundant species interact more frequently and with more



**Figure 5.** Changes in relative specialization ( $rH_2'$ ) along island area (a) and isolation (b) gradients of plant–aphid and aphid–ant networks on 18 islands of the Thousand Island Lake, China. The linear fits are based on multiple linear regression models. For each island, we derived an expected interaction network with the same species from the regional network (i.e. a landscape-level network that consists of information gathered across 18 island networks). Interaction frequency of each pairwise interaction was inherited from the regional network. Relative specialization for each island was calculated based on specialization in the observed network minus the specialization in the expected network. Thus, relative specialization was used to estimate the difference in specialization due to interaction rewiring. Plant–aphid networks are represented by orange and aphid–ant networks are represented by blue. Island area (ha) was log-transformed to normalize model residuals. Solid lines indicate significant relationships ( $p < 0.05$ ), whereas dotted lines represent non-significant relationships ( $p > 0.05$ ). Shaded polygons specify the 95% confidence interval.

species. Thus, a decrease in abundance may also result in more specialized networks [77,78].

### (b) Specialization and island isolation

Isolation only had an influence on the specialization ( $H_2'$ ) degree of aphid–ant networks, which increased towards more isolated islands. Higher specialization of aphid–ant networks on islands with higher isolation is related to community composition, as well as interaction rewiring. Previous research has suggested that ant community similarity would increase with isolation [79]. Due to the limited dispersal ability of ants, community phylogenetic and functional structure would be more clustered on more distant islands [80], which may intensify the competition for aphid–ant interactions and result in the high degree of specialization of aphid–ant networks on remote islands. However, aphids' community structure was not affected by isolation. Most aphids are weak fliers but good passive dispersers by wind [81,82], and when combined with strong reproductive capacity (cyclical parthenogenesis) this gives them the ability to colonize remote areas [72,83]. Therefore, the degree of isolation of our lake system may not limit the dispersal of aphids, which may explain why isolation was unrelated to the specialization degree of plant–aphid networks. In this study, we focus on the effects of island area and isolation on plant–aphid–ant interaction networks on islands, and we have not examined the structure of mainland trophobioses due to the lack of survey data in the mainland. Subsequent studies can compare their differences once both mainland and island data are available.

### (c) Effects of species dissimilarity and interaction rewiring on network specialization

We found that network dissimilarity in both plant–aphid and aphid–ant networks were high and predominantly driven by species turnover. This result is in line with previous studies of plant, bird and ant assemblages in the same system, which

revealed that the community assembly in fragmented landscapes is influenced by environmental filtering and species dispersal abilities [51,84,85].

In principle, habitat fragmentation can directly or indirectly affect network structures via top-down or bottom-up effects [41–43]. Both effects are known to alternate in a trophic cascade when interactions among different levels are studied [23,43]. The very similar AIC values between the bottom-up and top-down models indicate that both models were competitive. However, from the two path models, we found that fragmentation only has a direct effect on plant dissimilarity, while the effects of fragmentation on aphid dissimilarity and ant dissimilarity were indirectly mediated by plant dissimilarity and aphid dissimilarity, respectively. Therefore, we conclude that in our study, although either the bottom-up or top-down model could be the parsimonious model in model selection, habitat fragmentation increases the degree of specialization in both types of networks through bottom-up effects between plants and aphids in the plant–aphid–ant interaction. Taken together, we demonstrated that the effects of habitat fragmentation on interaction patterns were driven by community assembly at multiple trophic levels.

In this study, path models suggest that fragmentation has no direct effect on the composition of interacting ant communities. However, previous studies of ant communities in this system have found that  $\beta$  diversity of ant communities increased with inter-island distance [86]. We speculate that the overall composition of the ant communities on the islands would affect the composition of the interacting ant communities. Therefore, fragmentation may also affect plant–aphid–ant interactions through a top-down effect if the overall ant community is considered. In addition, Marjakangas *et al.* [34] provided a trait-based method for quantifying the relative influence of bottom-up and top-down effects on networks, which presents a potential way to understand the process driving multitrophic interactions. Further studies are thus needed to incorporate those considerations to better understanding the underlying mechanisms of shaping multitrophic interaction networks.

Relative specialization ( $rH_2'$ ) decreased significantly with increasing island area for both plant–aphid and aphid–ant networks. In other words, smaller islands have higher  $rH_2'$ , indicating that in both interaction types of networks, a decrease in island area leads to a loss of interspecific relations through interaction rewiring, resulting in more specialized networks. Interaction rewiring can result from differences in prey availability [47], and decreasing island area is usually accompanied by a decrease in resource availability. Our results also suggest that species richness decreased significantly with decreasing island area, which may increase competition followed by a decrease in niche overlap, ultimately resulting in an overall higher degree of specialization [10,87]. Overall, species turnover was the main factor causing the variation of network specialization among islands. In addition, a small part of the network structure change caused by habitat fragmentation is due to interaction rewiring: as island area decreases, the loss of interspecific relations among shared species results in more specialized networks.

Quantifying the underlying mechanisms driving the variation in network structure responding to environmental changes is a crucial step to expand our understanding of the drivers behind changes in biodiversity, community stability and ecosystem functioning. Similar variations in network specialization between the two network types suggest that predictions of network specialization in response to habitat fragmentation may be generalizable across interaction types within the same ecosystem. However, it is an open question whether the results can be transferred to other similar systems, as species can vary in their susceptibility to fragmentation and the matrix type can also affect interaction networks and biodiversity patterns in fragmented landscapes [12,15,88].

## 5. Conclusion

From the perspective of multiple trophic interactions that encompass antagonistic and mutualistic interactions, we

have explored the impacts of fragmentation on network specialization. We found that species interactions on small islands were more specialized and vulnerable to local co-extinction due to high species turnover caused by habitat fragmentation, regardless of interaction types. Our results showed that species turnover was interlinked across trophic levels, and habitat fragmentation increases the specialization degree of both types of networks by bottom-up effects from plants to aphids. These findings highlight the importance of taking a multi-trophic perspective of exploring the dynamics of ecological community structures in the fragmented landscapes.

**Ethics.** This work did not require ethical approval from a human subject or animal welfare committee.

**Data accessibility.** All raw data used in this manuscript are available in the electronic supplementary material [89].

**Authors' contributions.** X.Z.: conceptualization, data curation, formal analysis, methodology, visualization, writing—original draft; B.D.: formal analysis, writing—review and editing; M.S.: methodology, writing—review and editing; C.Z.: formal analysis, methodology; Y.Z.: data curation, writing—review and editing; F.G.: writing—review and editing; P.R.: formal analysis; C.C.: data curation; G.Q.: data curation; P.D.: conceptualization, funding acquisition, project administration, resources, writing—review and editing; X.S.: conceptualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

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