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The reliability of regional ecological knowledge to build local interaction networks: a test using seed-dispersal networks across land-bridge islands

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Building ecological networks is the fundamental basis of depicting how species in communities interact, but sampling complex interaction networks is extremely labour intensive. Recently, indirect ecological information has been applied to build interaction networks. Here we propose to extend the source of indirect ecological information, and applied regional ecological knowledge to build local interaction networks. Using a high-resolution dataset consisting of 22 locally observed networks with 17 572 seed-dispersal events, we test the reliability of indirectly derived local networks based on regional ecological knowledge (REK) across islands. We found that species richness strongly influenced 'local interaction rewiring' (i.e. the proportion of locally observed interactions among regionally interacting species), and all network properties were biased using REK-based networks. Notably, species richness and local interaction rewiring strongly affected estimations of REK-based network structures. However, locally observed and REK-based networks detected the same trends of how network structure correlates to island area and isolation. These results suggest that we should use REK-based networks cautiously for reflecting actual interaction patterns of local networks, but highlight that REK-based networks have great potential for comparative studies across environmental gradients. The use of indirect regional ecological information may thus advance our understanding of biogeographical patterns of species interactions.

1. Introduction

Species do not live in isolation; they are entangled into ecological networks of interactions with other species [1]. High-quality ecological networks of biotic interactions are important for ecologists to better understand local ecological processes and community structure [1–3]. However, building ecological interaction networks over time and space is challenging, mostly due to the intensive fieldwork required to sample reliable ecological networks [4–6]. Even after a long-term intensive sampling, one may only get a limited portion of local ecological interaction networks in biologically diverse ecosystems or logistically remote

sites [7]. Thus, there is an increasing need of cost-effective approaches to build reliable ecological networks that provide robust estimates of community structures and the processes structuring ecological networks [8].

Recently, indirect ecological information was used to predict and collect potential pairwise species interactions [5,9,10]. For example, Ong *et al.* built plant–frugivore interaction networks based on information on interactions accumulated through observations by many people in many local places over long periods of time [5]; hence the resulting networks may be more useful to describe broad-scale processes, or even historical interactions [11]. Another example is inferring potential interactions from trait-matching rules [12,13], which recently has been used to build novel networks involving introduced species [14]. Although these indirect methods can identify species interactions widely and include interactions that are hard to sample [15], they often underestimated interaction variations due to environmental and biogeographical drivers known to impact species interactions [16]. For example, the loss of interspecific interactions is faster and ahead of species loss [17]. Species may locally coexist but have already lost their functionality, resulting in their interactions unlikely to occur (e.g. 'empty forest syndrome') [18,19]. Thus, one should be cautious about inferring interactions from indirect ecological information even when species coexist, especially in highly heterogeneous environments such as fragmented landscapes.

Habitat loss and resulting fragmentation are indeed among the main drivers of species and interactions loss worldwide [20], leaving fewer species within remnant fragments compared with continuous habitats [21]. Indirect ecological information may underestimate the impacts of environmental filtering on interactions within local fragments, for example, by the reduction in forest area. For example, forest fragmentation leads to a drastic loss of seed-dispersal interactions and functionality [22], even if mutualistic species remain in forest fragments [23]. However, species loss may also promote interaction generalization for some remaining species [23], for example, dietary expansion of frugivores when fruit resources are less available in smaller fragments [24]. Overall, network connectance (i.e. the proportion of observed interactions relative to the total possible interactions) often decreases with increased species richness [25–28]. Taken together, we predict that a higher proportion of potential interactions will be observed in species-poor habitats than within a given region. Moreover, although indirect ecological information is useful to study broad-scale interaction networks, it remains unclear whether it can be used to reveal local-scale processes, especially for systems consisting of depauperated ecological networks with many remnant species [29].

Here we propose an approach to build local seed-dispersal networks from regional ecological knowledge (REK) in a fragmented landscape consisting of artificial land-bridge islands. A regional interaction network constructed from all observed interactions between species of a regional species pool may provide powerful evidence for understanding the structure of local networks [30]. Local interaction networks can be constructed based on the regional network and the local community composition (species pool), which may enable us to evaluate local-scale ecological processes [31]. However, it remains unknown whether keeping all observed interactions in the region between interacting species would affect our evaluation of local networks' actual structure, because interactions may be context-dependent [16,23,32]. For example, changing resource availability would influence interaction variations of consumers [33]. Thus, we need to evaluate the implications of using REK-based indirectly derived networks for the study of actual ecological networks.

To examine the reliability of using a REK-based method to construct local interaction networks, we used an unprecedented dataset on 17 572 seed-dispersal events recorded using camera trapping on 22 artificial land-bridge islands in the Thousand Island Lake region, China. Although a combined approach using various methods (e.g. DNA barcoding, visual observation and faeces samples) may optimize sampling of plant–frugivore interactions [4], it needs high labour and/or financial costs to be employed at large spatial/temporal scales. Camera trapping provides high-resolution data of seed-dispersal interactions and the possibility of sampling a comparable and high-quality interaction network for each island [24], given that it allows us to monitor plants with similar fruiting periods simultaneously over multiple islands [4,34]. Camera trap data can therefore be used as a baseline to assess the quality of local ecological networks, avoiding network property biases due to incomplete sampling [35]. Using this dataset, we evaluated the potential applications of REK to build local ecological networks for each island. We used local species lists to derive REK-based networks for each island, and estimated biases in network metrics between locally observed networks and REK-based networks. Specifically, we examined: (1) whether species richness affects the proportion of locally observed interactions relative to regionally observed interactions (i.e. local interaction rewiring) using REK-based networks, (2) whether there are significant biases in network structures between locally observed and REK-based networks, (3) whether the estimated network structures of both locally observed and REK-based networks have similar responses to habitat fragmentation (i.e. island area and isolation in our study), and (4) whether species richness and local interaction rewiring affect our estimations of network metrics built by REK-based methods. We aim to find a general guideline that can be used elsewhere to build ecological networks at the local scale using indirect ecological information, like REK in our study, to address research questions fusing network ecology with biogeography and macroecology.

2. Material and methods

(a) Study area

Our study was conducted in the Thousand Island Lake (electronic supplementary material, figure S1), a fragmented landscape formed by damming in western Zhejiang Province, eastern China (29°22′–29°50′ N, 118°34′–119°15′ E). The lake was created in 1959 and contains more than 1000 islands covered with secondary forest. Trees on islands were clear-cut before dam construction, and thus all islands initiated their succession from a similar condition. Currently, most of these forested areas (approx. 90%) are dominated by Masson pine (*Pinus massoniana*) in the canopy, with many native fleshy-fruited plants in the sub-canopy and understory, including abundant shrubs such as *Vaccinium carlesii*, *Eurya muricate* and *Lindera glauca* [34]. This region has a typical subtropical monsoon climate with marked seasonality (hot and humid summers, and cool to mild winters) [36]. We monitored plant–frugivore interactions in this artificial island archipelago since 2019 [37]. Because the distributions of plants and seed-dispersers have been investigated [38], our study system provides
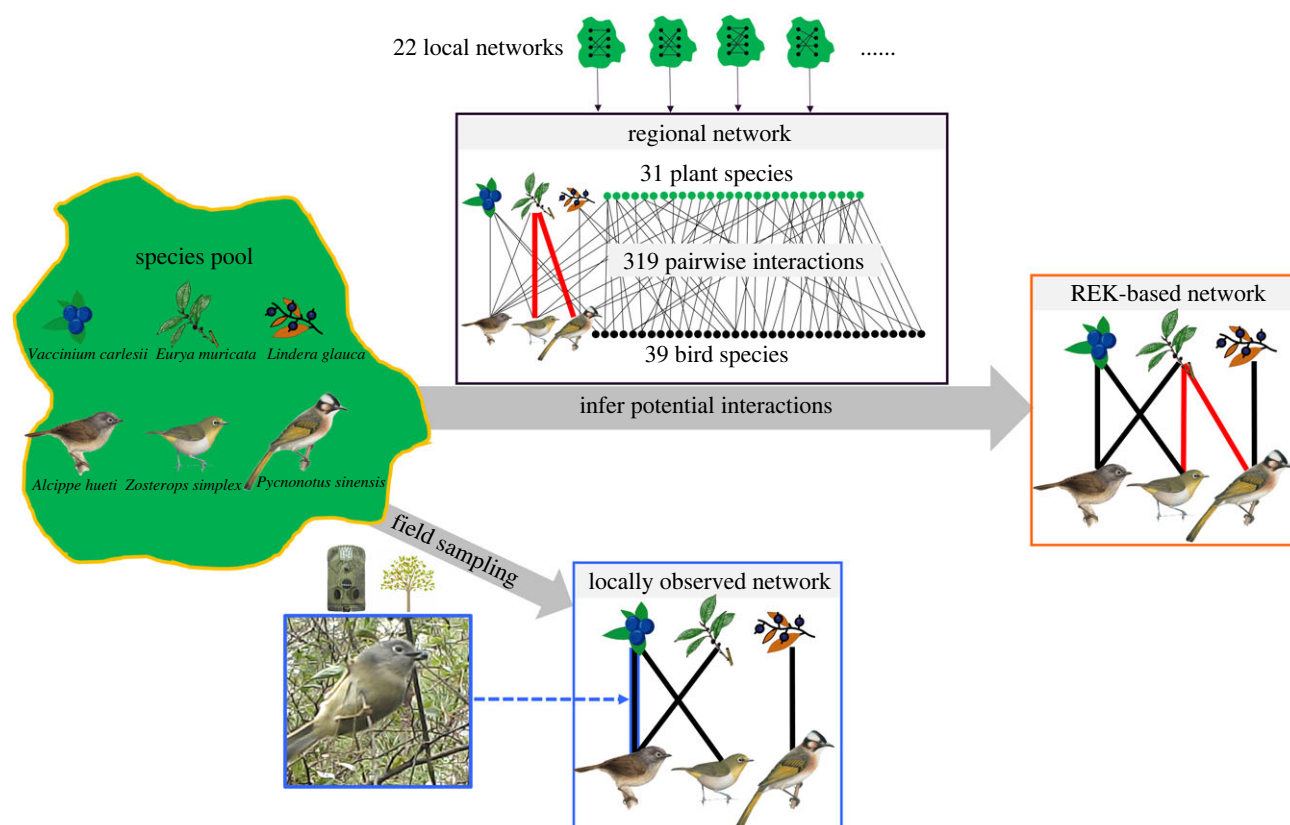
Figure 1. Illustration of two types of local networks (i.e. island-wide networks in our study) and the regional network across all islands (i.e. landscape-level network). By carrying out field sampling (i.e. using arboreal cameras in our study), we collected locally observed interactions to build a locally observed network (lower, blue box) for each study island. Based on all interactions across all islands, we derived a species pool of interacting species (in the left island) and build a regional network (upper, black box) based on all seed-dispersal interactions collected across all our study islands (319 unique interactions among 39 bird species and 31 plant species). By matching interactions of locally occurring species with those in the regional network, we build a REK-based network (right, orange box) for each study island. Black thick lines indicate locally observed interactions; red lines indicate regionally observed interactions inferred based on the regional network (i.e. using regional ecological knowledge). We show three representative species of birds and plants of the regional species pool (see electronic supplementary material, tables S3 and S4). Bird drawings were produced by Liang Su, Bai Xiao and Jing Qian. Plant drawings were produced by Xue Zhang. The photo of bird frugivory was taken by camera traps.

an ideal platform for the studies of building local plant–bird networks from a regional perspective, given the rich information of bird and plant distributions in this system.

(b) Sampling seed-dispersal interactions

We used a recently popularized technique, arboreal camera trapping, to sample seed-dispersal interactions at the region scale, because this method has been proven to effectively document species interactions in arboreal habitats over large spatial and temporal scales [24,34]. Specifically for our system, frugivores of different body sizes (e.g. small-bodied passerines and larger mammals) from multiple vertical strata (e.g. canopy and understory) and their foraging behaviours have been documented to be effectively recorded when the sensitivity of the camera was set to high [34]. Combined with the line-transect method and camera trapping, we collected plant–frugivore interaction data on 22 islands from June 2019 to January 2022 (three fruiting seasons, each from June to next January), covering the gradients of island area and isolation in this lake system (electronic supplementary material, table S1 and figure S2). Here we used mutualistic seed-dispersal networks as our study object. For frugivores, we only used birds as our targeted animals and excluded mammals (no fruit bats in this system) because (1) we cannot confirm the identities of most mammal individuals, (2) cannot confirm whether they participated in seed dispersal due to the relatively low quality of black-and-white images taken at night, and (3) the

isolation of water among islands sufficiently precludes the movements of frugivorous mammals. We selected fleshy-fruited species that are bird-dispersed as our targeted plants. We used independent interaction events of a particular frugivore as interaction frequency with focal plants [39].

Our goal was to build seed-dispersal networks between fleshy-fruited plant species and the frugivorous birds that disperse their seeds (note that more than half of the birds recorded in this lake system were potential frugivores) [37]. Thus, we only focused on plant–bird interactions that may lead to seed dispersal. Here we used a conservative rule to select seed-dispersal interactions, i.e. those in which the bird was clearly observed swallowing entire fruits. More sampling details are given in electronic supplementary material, appendix S1.

We used 'sample coverage' to measure the sampling completeness of pairwise interactions, which is defined as the proportion of the total number of interaction events (i.e. interaction individuals) in a community belonging to the interactions represented in the sample [40]. We estimated sample coverage of interactions using method 'abundance' with *iNEXT* function in the R package 'iNEXT', ver. 2.0.20 [41].

(c) Building locally observed and REK-based networks

We classified seed-dispersal interactions between pairs of bird and plant species co-occurring on each focal island into two categories (figure 1):

(1) Locally observed interaction: we collected accurately recorded interactions, and identified highly probable interactions between interacting partners within a specific camera (i.e. indirect evidence; see electronic supplementary material, appendix S1, and Zhu *et al.* [34]). Thus, the locally observed interactions were from direct field sampling.

(2) Regionally observed interaction: based on field sampling on each island, we collected local species information of birds and plants (species pool in figure 1). We matched interactions between pairs of birds and plants based on the regional network. Besides locally observed interactions (i.e. confirmed on the focal island), there were interactions between co-occurring pairs of plant and bird species that had been observed somewhere else in the study area (i.e. potentially observable) but not on the focal island, which were defined as 'regionally observed interactions' (red links in figure 1). As a result, the regionally observed interactions were identified from regional ecological knowledge (i.e. REK-based interactions) in our region.

We built both types of local seed-dispersal networks on each of the 22 islands (figure 1). First, for each island, we used only locally observed interactions to build a *locally observed network* (blue box in figure 1). Locally observed networks were built with sampling data collected on the focal island, and thus they were considered as empirical local networks. Second, we built a *REK-based network* that included locally observed and regionally observed interactions (orange box in figure 1). Pairwise interaction frequency in each REK-based network was derived from the regional network and scaled by the total number of interactions (interaction abundance) observed on that island, which is therefore the number of interactions in the corresponding locally observed network. Especially, we calculated relative interaction frequency between pairwise bird and plant species of a REK-based network (i.e. pairwise interaction frequency divided by the total frequency of the REK-based network), then multiplied relative interaction frequency by original total frequency from its corresponding locally observed network to estimate pairwise interaction frequency of the REK-based network. Thus, a REK-based network is an extended version compared with the locally observed network.

(d) Data analysis

For each island, we assessed the proportion of locally observed interactions relative to the total number of regionally observed interactions using β'_{OS} (local interaction rewiring), which was used to quantify observed interactions at the local-island level considering the overall potential interactions at the regional-landscape level (electronic supplementary material, figure S3) [42,43]. Here we used the partitioning approach following Novotny [44] with Sørensen dissimilarity [45], which removes the dissimilarity generated by the difference in interaction richness between networks [46,47]. In this framework, we can calculate β_{OS} (interaction rewiring) between network M and N using equation (2.1):

$$\beta_{OS} = \frac{b_0 + c_0}{2a + b + c},\qquad(2.1)$$

where b_0 and c_0 are the number of interactions only in the M_{shared} and N_{shared}, respectively (M_{shared} and N_{shared} are the subsets of M and N that contain the same species); a is the number of interactions that exist in both M and N; and b and c are the number of interactions only in M and N, respectively. When we set M to a local network and N to the regional network, there would be no unique species and interactions in M (as M is a subnetwork of N), that is, $b_0 = 0$ and $b = 0$. Thus, we can calculate β'_{OS} using equation (2.2):

$$\beta'_{OS} = \frac{c_0}{2a + c},\qquad(2.2)$$

where a and c_0 are the number of observed and unobserved interactions in a local network, respectively; c is the number of interactions in the regional network other than the given local network. To fit with our study, we modified the calculation of β'_{OS} using equation (2.3):

$$\beta'_{OS} = \frac{R_{obs}}{L_{obs} + R_{region}},\qquad(2.3)$$

where L_{obs} and R_{obs} are the number of locally observed and regionally observed (but locally unobserved) interactions in a given local network, respectively; R_{region} is the number of interactions in the regional network. Thus, β'_{OS} evaluated the relative proportion of locally observed interactions for local communities, that is, local interaction rewiring, considering all observable interactions in the region; values close to 0 indicate the presence of most observable interactions in a local network (low level of local interaction rewiring), while values close to 1 suggest the loss of most observable interactions even though all, or almost all, species from the regional network are locally co-occurring (high level of local interaction rewiring) [42]. When fewer species co-occur, values will be lower than 1, due to the lack of interactions as a direct result of species' absence. We tested the relationship between local interaction rewiring and network size (plant richness × bird richness). We also used the partitioning approach following Poisot *et al.* [43] (electronic supplementary material, appendix S2) to examine the sensitivity of methodological choices. Moreover, given that regionally rare interactions that we may miss in the locally observed networks can affect our estimation of local interaction rewiring, we repeated the above analysis by artificially removing rare interactions from our dataset [48].

To test whether the network structures of locally observed and REK-based networks differed from each other, we used weighted connectance, weighted nestedness (weighted NODF), weighted modularity and specialization (H_2') as metrics for quantitative network analyses, and used connectance, nestedness (NODF) and modularity as metrics for binary network analysis. These metrics are commonly used to describe network structures [49,50]. We computed modularity using the algorithm provided by Beckett [51], which computes modularity 100 times to obtain the highest value of modularity for each quantitative or binary network per island. Then, we used one-tailed Wilcoxon matched pairs signed rank tests to determine whether network metrics differed significantly between locally observed and REK-based networks. We also tested whether the differences in network metrics between locally observed and REK-based networks (i.e. Δ values) were systematically biased. Finally, we used multiple linear regression models to examine whether network metrics of locally observed and REK-based networks related significantly to island area and isolation (the distance to the mainland). Island area was not correlated to isolation (Pearson's correlation coefficient $r = -0.15$, $p = 0.51$). We used both quantitative and binary networks for comparative analyses and a null model approach to correct network metrics by fixing specific properties (e.g. size) of the network [52]. All metrics were standardized using equation (2.4):

$$Z = \frac{(m_{obs} - \overline{m}_{null})}{SD(m_{null})},\qquad(2.4)$$

where m_{obs} is the observed value of a metric, $\overline{m}_{null}$ is the mean of null networks' values, and $SD(m_{null})$ is the standard deviation of null networks' values. All standardized network metrics described the extent an input network departs from a random network generated by null models [53,54]. Here, we used the Patefield null model, which fixes the network size as well as the marginal sums of each row and column for quantitative networks (i.e. constrains both the species richness and the total number of interactions per species) [55]. For binary networks, we used the equiprobable null model, which constructs the simulated matrices
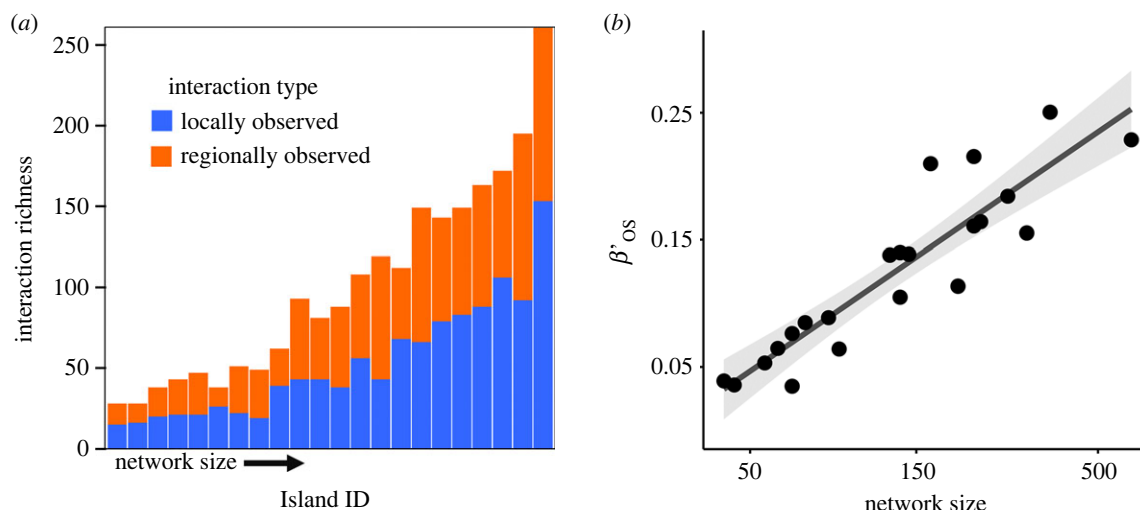
Figure 2. (a) Seed-dispersal interaction richness of two interaction types (locally observed and regionally observed interactions) for each of the 22 islands included in this study and (b) the relationship between network size (i.e. plant richness × bird richness) and local interaction rewiring (β'_{OS}), that is, the proportion of locally observed interactions relative to regionally observed interactions for each local community, considering all observable interactions across the region. Network size was log-transformed to normalize model residuals. The solid line shows significant relationship ($p < 0.001$, $R^2 = 0.82$).

using a probability matrix based on the degree of species [56]. All networks were randomized 1000 times. All network metrics were calculated using the 'bipartite' package, ver. 2.18 [57].

(e) Simulations of REK-based networks

To test whether species richness and local interaction rewiring affect our estimations of network metrics built by REK-based methods, we simulated REK-based networks based on species and their interactions within the regional network. For each gradient of species richness, we randomly selected n plant species and $n + 2$ bird species, and then matched their interactions from the regional network. Note that selected species had at least one observable interaction with each other, otherwise, we would reselect species assembly. We took n to be 5–24 for setting 20 gradients of species richness (i.e. 12–50 species), according to observed plant richness (5–24) on study islands and the highest species richness on the largest island (50; electronic supplementary material, table S2). For each gradient of species richness, we set six levels of local interaction rewiring, i.e. keeping between 50 and 100% of the observable interactions (interaction richness) of the simulated networks. We used the above-mentioned seven metrics to estimate network structures of 100 simulated networks for each gradient of species richness and local interaction rewiring. Throughout the study, all statistical analyses were conducted in R v. 4.1.1 (www.r-project.org).

3. Results

(a) Species and interaction richness

After sampling plant–frugivore interactions on 22 islands over three years, we have recorded 17 572 seed-dispersal events with a high sample coverage of pairwise species–species interactions for each island (mean 0.98 ± 0.01 s.d.; electronic supplementary material, table S2). From these events, we created a seed-dispersal interactions database for the study region, including 39 bird species and 31 fleshy-fruited plant species with 712 fruiting individuals (electronic supplementary material, tables S3 and S4). The regional network involved 319 unique seed-dispersal interactions from direct sampling data. At the local-island level, more than half of interactions could be clearly identified as seed-dispersal interactions (i.e. locally

observed interactions) (mean 51.7 ± 8.2 s.d. %; figure 2a). We identified regionally observed interactions using REK, which accounted for nearly half of the total potential interactions (mean $48.3\% \pm 8.2\%$ s.d.). The REK-based networks included a range of 12 to 108 interactions (regionally observed interactions) per island than the locally observed interactions (electronic supplementary material, table S2). Compared with locally observed networks, the number of unique interactions in REK-based networks increased by 46% to 177%. Local interaction rewiring (β'_{OS}) showed a significantly positive relationship with network size (figure 2b), which can be also found when we used the partitioning approach of network dissimilarity following Poisot *et al.* [43] (electronic supplementary material, figure S4). The sensitivity analysis on rare interactions implies that the result of local interaction rewiring was robust to potential sampling bias and network sizes (electronic supplementary material, figure S5)

(b) Biases in network metrics between networks

All network metrics were clearly biased after expanding locally observed networks into REK-based networks (figure 3). REK-based networks' connectance and nestedness were significantly overestimated, while modularity and specialization were significantly underestimated when compared to locally observed networks. The density distributions of Δ values show there were significant deviations from zero (figure 3). Except connectance and binary modularity, most Δ values of locally observed and REK-based networks had non-significant trends with island area and isolation (electronic supplementary material, figure S6 and table S5), indicating that the degrees of overestimation or underestimation were not systematically biased.

(c) Local network structures along island area and isolation

All the standardized quantitative and binary metrics of both locally observed and REK-based networks had significant relationships with island area (figure 4; electronic supplementary material, table S6), while none of them had significant relationships with island isolation. In all cases, the metrics of
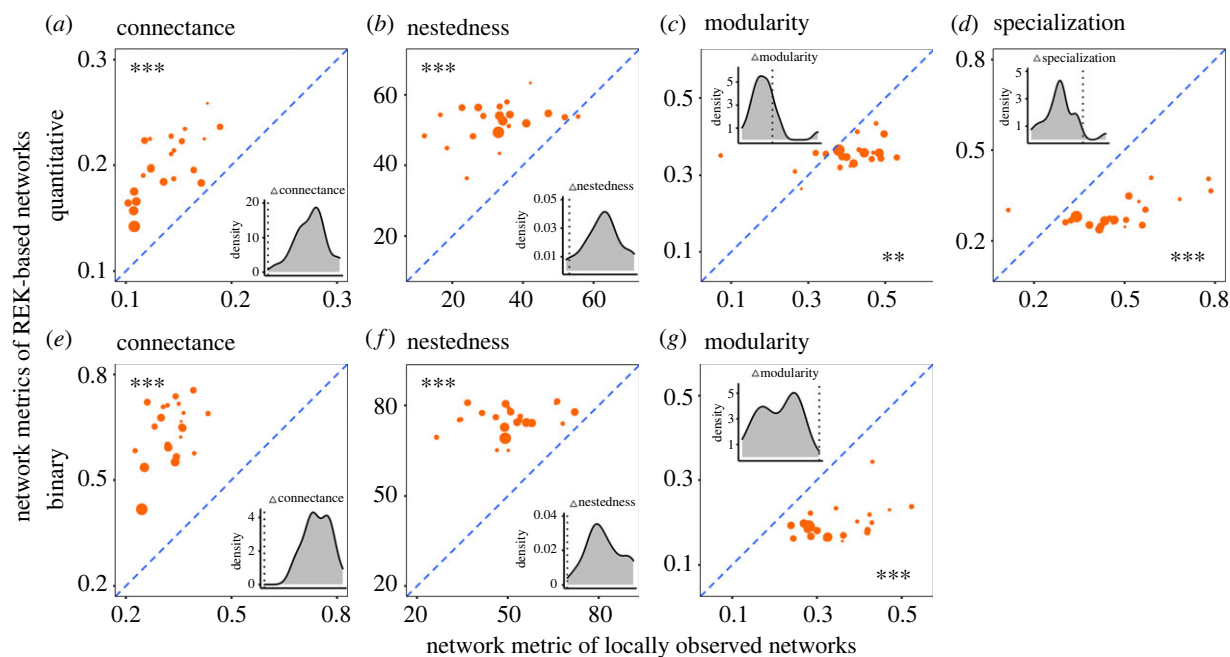
Figure 3. Relationships between network metrics calculated for the REK-based (*y*-axes) and locally observed (*x*-axes) networks. The dashed line shows the 1 : 1 relationship, indicating no change in metric values. Point size is related to network size. The significance of Wilcoxon matched pairs signed rank tests is shown in the top-left corner or bottom-right corner (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). Each inset is the density distribution of Δ values of both networks' metric, with the vertical dashed line showing the zero value. See Material and methods for details regarding calculation of network metrics and statistical analysis.

both locally observed and REK-based networks showed consistent and similar trends along gradients of island area and isolation. For quantitative networks, weighted connectance and nestedness decreased, while modularity and specialization increased with increasing island area; but binary networks' metrics showed opposite patterns to those of quantitative networks.

(d) Simulated REK-based networks along species richness and local interaction rewiring

For simulated REK-based networks, the influences of species richness and local interaction rewiring differed depending on the specific network metrics (figure 5; electronic supplementary material, figures S7 and S8). Connectance and nestedness were higher when a higher proportion of interactions were 'observed' in the simulations (higher interaction richness), but modularity and specialization showed the opposite patterns. Except for nestedness, other network metrics varied along the species richness gradients, but they gradually reached an asymptotic value as species richness increased. Notably, quantitative and binary modularity showed an opposite relationship with species richness. Connectance and specialization decreased with increasing level of species richness.

4. Discussion

We tested the reliability of using REK to build local ecological networks. We found that species richness largely predicted the proportion of locally observed interactions when REK-based networks were constructed. However, although most network metrics were significantly biased when using REK-based networks relative to locally observed networks, both had similar responses to island area and isolation. The simulations show that species richness and local interaction rewiring would

influence our estimations of network structures when using a REK-based network for a given local community. Taken together, our study suggests that we should use REK-based networks cautiously for reflecting actual interaction patterns of local networks, but we also show that networks built by relatively coarse interaction data (i.e. indirect ecological information; REK in our case) are acceptable to evaluate ecological network trends along environmental gradients.

(a) Building networks using regional ecological knowledge

A high-quality regional network can establish a strong basis for building local interaction networks using REK and may thus provide key information for understanding and evaluating local interaction patterns. Due to the labour-intensive collection of species interactions, building ecological networks across spatial or temporal scales is challenging, particularly where fieldwork is costly and time-consuming [5]. To overcome these challenges of sampling interactions directly, we used a regional interaction network [58] to infer potential interactions indirectly from known species pools, which provides a strong tool to reflect local patterns and processes [59,60]. With a high-quality inventory of species interactions in a region, the regional network largely avoids 'forbidden interactions' [15], facilitating the compilation of potential interactions at the local scale. Prior work has also indicated that network structures characterizing local assembly processes could be inherited from a regional network [61].

In our study, we recorded a large number of interaction events through uninterrupted monitoring during fruiting seasons for over three years, and achieved a high sampling coverage (approx. 98% in average) for each island that enabled us to construct a high-quality regional network. We found that only an average of 51.7% of all potential interactions were locally observed on each island (similar to the result of 55%
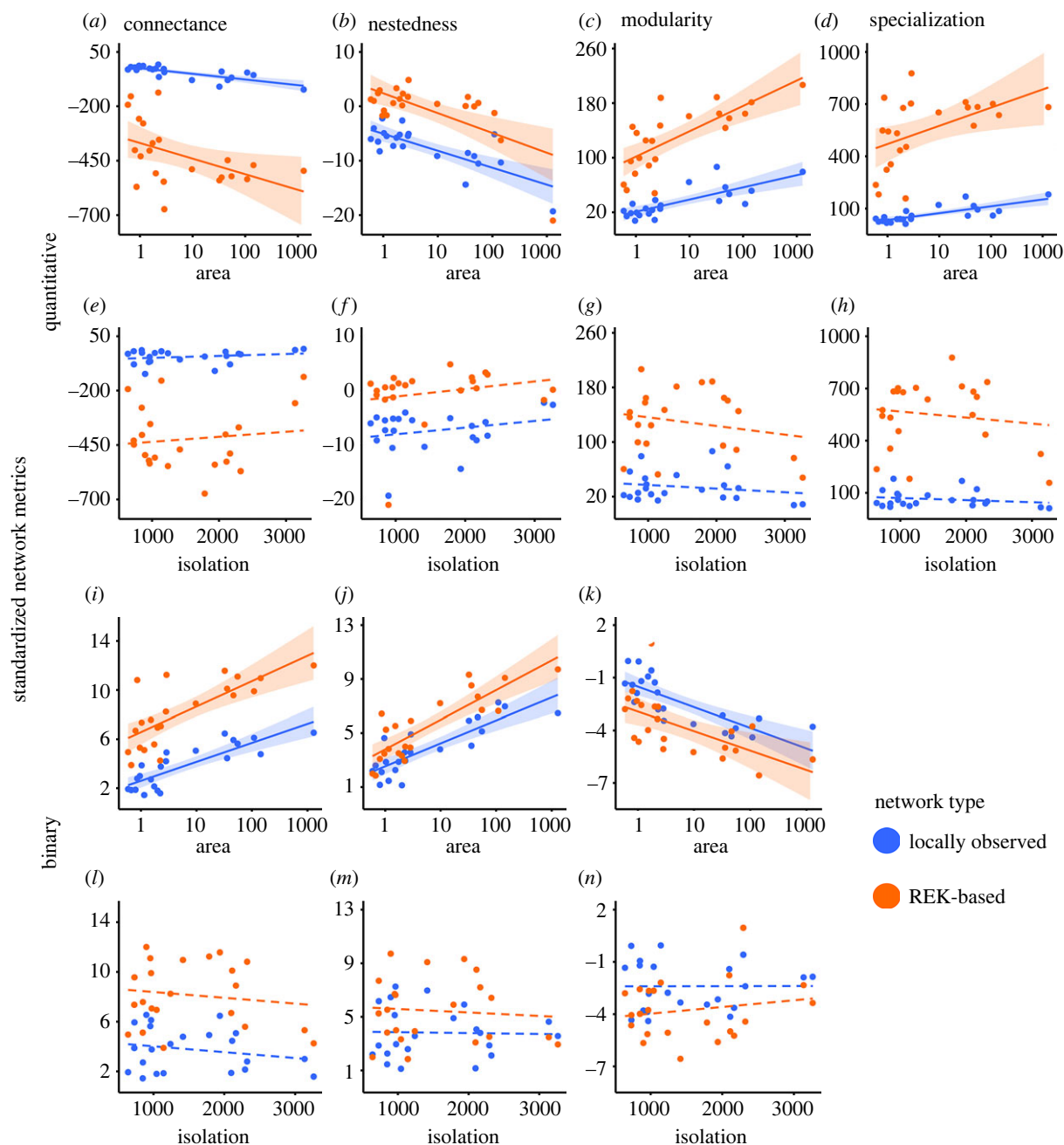
Figure 4. Relationships between standardized network metrics (quantitative, upper panels; and binary, lower panels) and island geography (area and isolation). The coloured lines represent best-fit linear regressions of locally observed and REK-based standardized network metrics: connectance (a,e,i,l), nestedness (b,f,j,m), modularity (c,g,k,n) and specialization (d,h). Island area (ha) was log-transformed to normalize model residuals. The value of each network metric was standardized by null model networks with the same size (see equation (2.4)). All solid lines show significant relationships ($p < 0.05$; electronic supplementary material, table S6).

in Gravel *et al.* [59]). This indicates that local filtrations of species interactions occur between islands in the fragmented landscape of the Thousand Island Lake system. Notably, potential missing interactions in the locally observed networks would lead to an overestimation of local interaction rewiring. We should thus require locally observed interactions to be more completely sampled when we study the variations of local-scale interaction in a region. By estimating local interaction rewiring from a regional perspective [42], we found that local interaction rewiring correlated positively with species richness (figure 2), which implies that the influence of environmental contexts on interaction variations could be driven by species diversity in local communities. This finding reveals non-stochastic organization of local ecological networks, and supports that we could thus predict local

interaction rewiring by community assembly to better reflect local-scale interaction patterns and processes from a regional perspective. Given that more reliable and accessible empirical data on species interactions are accumulating worldwide [62], unbiased regional networks will expand our ability to predict the variability of interactions between local species under environmental change.

(b) The reliability of REK-based networks

We found that REK-based networks had clear biases in all network properties (figure 3), but they performed similar to locally observed networks obtained through considerable sampling efforts when evaluating how network structures change along fragmentation gradients (figure 4). Compared
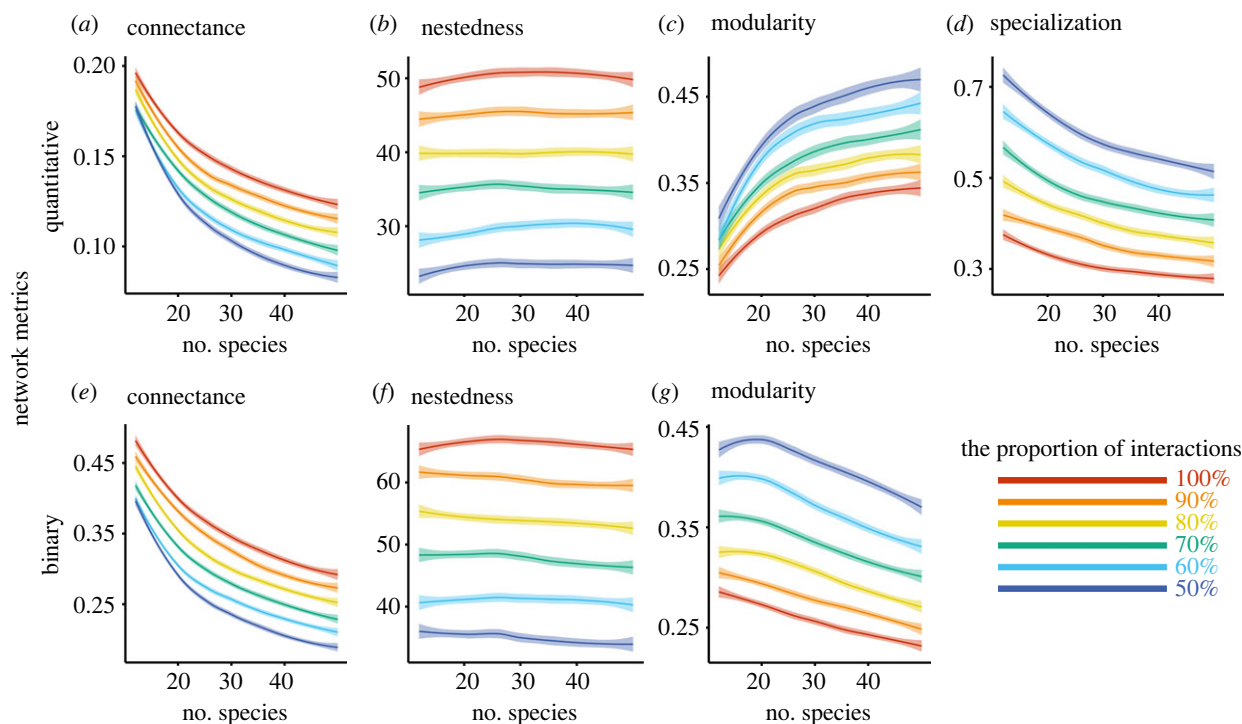
Figure 5. The simulations of REK-based networks' metrics (quantitative, upper panels; and binary, lower panels) along the gradients of species richness (*x*-axis) and local interaction rewiring (coloured lines). Species richness was measured as the number of plant and bird species we selected (12–50 species in 20 gradients). Local interaction rewiring was evaluated through the proportion of 'observed' interactions we kept in each simulation (i.e. the proportion of randomly observed/all observable interactions; 100% to 50% in six gradients). For each network metric and gradient of species richness and local interaction rewiring, we calculated 100 simulated values of each network metric. Each coloured bar presents the 95% confidence interval.

with REK-based networks, locally observed network structures were less nested and connected, but more modular and specialized. REK-based networks include more interactions of interacting species, making them more connected and generalized than locally observed networks. We also found that REK-based networks were more nested, as mutualistic networks often show stronger nestedness with higher interaction complexity [63,64]. Ecological factors such as flexible foraging driven by environmental contexts could explain the loss (or realization) of interactions among regionally interacting species within the local island-level networks, leading to the observed variations in network structures [65]. This indicates that we should be cautious when using indirect ecological information to describe local network structures, especially if we intend to understand actual processes at the local scale. Therefore, for the purpose of understanding local interaction patterns, we recommend building local networks with high-resolution datasets of locally observed species interactions, rather than using indirect networks such as those built with REK or other kinds of local ecological knowledge over broad temporal and spatial scales (e.g. [5]).

Although the organization of local networks is affected by interaction completeness [6], a robust characterization of its variation pattern along environmental gradients could be realistic [66]. The evidence of systematic biases was not obvious (electronic supplementary material, figure S6), and generally inconsequential when evaluating the relationship of network structures with gradients of island area and isolation. In this study, we standardized network metrics of locally observed and REK-based networks comparing to randomly generated networks using two null models (i.e. randomized networks based on interaction abundance of species for weighed networks and interaction richness for binary networks), leading to opposite patterns of network metrics along fragmentation

gradients for weighted and binary data. Given similar responses of network metrics to fragmentation gradients of area and isolation in both locally observed and REK-based networks, we thus conclude that it is possible to use REK-based networks to estimate how network structures vary along environmental gradients. This implies that REK-based networks can reflect the mechanisms of network organization by biological mechanisms and community complexity, supporting the validity of indirect approaches to build local networks for comparative studies in biogeography or macroecology.

Taken together, we suggest using high-quality sampling data to build local ecological networks if we aim to understand local processes operating in highly heterogeneous environments, because indirect ecological information may ignore the effects of environmental filtering on species interactions at the local scale. Nonetheless, we recommend using indirect ecological information for building ecological networks in comparative studies across environmental or geographical gradients (e.g. [60]), as indirect ecological information here seems to be at an advantage compared with more traditional methods. As it is more difficult to sample interactions than species alone [66], these networks built by indirect information may thus offer us the opportunity to describe and understand ecosystem functions along environmental gradients.

(c) The roles of species richness and local interaction rewiring in determining network structures

Species richness in a local community and its inherent interaction rewiring play important roles in determining network structures (figure 5). We simulated REK-based networks with random community assembly from our regional species pool, by controlling the effects of fragmentation on species compositions (except for species richness). Since the REK-based

network was a subset of the regional network, our results showed that connectance of REK-based networks decreased with increasing species richness, while REK-based networks had invariably similar nested structures independent of species richness. Interestingly, weighted and unweighted modularity of simulated networks had disparate patterns with increasing species richness, indicating that we should consider data types when using REK-based networks [67]. Additionally, for networks with consistent species richness and local interaction rewiring, we found nestedness and modularity were negatively correlated as observed in previous studies (e.g. [68]). A lower proportion of interactions that were 'locally observed' in simulations (high local interaction rewiring) increased modularity in REK-based networks with the consistent species richness, which may result from reduced connectance [69]. Although network specialization supposedly is independent of network size [70], our simulations showed this pattern was only observed in local networks with high species richness. Overall, these results were consistent with the commonly reported effects of species richness (or network size) and interaction variations on network metrics [28,65,71–73]. Moreover, we showed that influences of both these factors depended on specific metrics and data types (binary or quantitative).

In the Thousand Island Lake region, we can accurately estimate local interaction rewiring with species richness (network size) on local seed-dispersal systems (figure 2). This result provides empirical insights into interaction variations in the face of local community change due to environmental filtering for other regions. More importantly, we can assess local network structures by understanding the response of network metrics to species richness and local interaction rewiring. For example, following our framework, we could predict the effects of species reintroduction on communities by simulating REK-based networks [74]. To make reliable predictions about interaction patterns, we need to understand what triggers the variations of species richness and local interaction rewiring when using REK-based networks [75]. In the context of global change, our results provide evidence that one could make better estimations of network structures using indirect information to examine the effects of environmental changes across broad geographical gradients, or explore spatial scaling of interaction networks [76]. Specifically, given accelerated habitat loss and fragmentation worldwide [20], our study will contribute to describe interaction patterns across fragmented landscapes [77]. Note that although we examined the effects of species richness and local interaction rewiring on network structures, local species compositions may also determine interaction patterns (electronic supplementary material, figure S8). Future studies that integrate species compositions into the prediction of interaction patterns would provide further understanding of how local interaction rewiring affects interaction network structures. Overall, our findings suggest the importance of considering community characteristics (e.g. influencing factors of species richness and local interaction rewiring) when we attempt to explore well-sampled interaction patterns of local communities from interaction networks built by indirect information.

5. Conclusion

Building ecological networks is a fundamental process in biodiversity research. Recently, several approaches using indirect ecological information have been proposed to build local networks. We here propose to assess and understand local interaction patterns using regional ecological knowledge. Our study showed that local interaction rewiring between locally observed and REK-based networks was driven by species richness, leading to significant biases in network metrics derived from REK-based networks. However, when evaluating how habitat fragmentation influences network structures, REK-based networks performed similar to locally observed networks along the gradients of island area and isolation. Our study also suggests that assessing species richness and local interaction rewiring could help understand interaction patterns of local communities using REK-based networks. These results demonstrate that inferring species interactions from indirect ecological information has great potential, but also key limitations, as a tool for understanding the processes shaping ecological communities. In a world characterized by global change, we advocate the use of indirect ecological information for exploring ecological patterns and processes in biogeography and macroecology of species interactions.

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