



Simulated high-intensity phorophyte removal mitigates the robustness of epiphyte community and destroys commensal network structure

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ABSTRACT

Interspecies interactions deserve more attention in biodiversity conservation since the elimination of only one species can indirectly impede the dependent species through ecological networks. Phorophytes, which provide physical support, constitute the basis for the occurrence of epiphytes. Epiphytes and their host phorophytes thus form a typical commensal interaction network. However, the impacts of phorophyte removals on the diversity and stability of epiphyte communities are poorly understood. Such understanding may illuminate guidance on forest protection and management. In this study, two species-based networks (raw species-based network and standardized species-based network) and one raw individual-based network between vascular epiphytes and phorophytes were analyzed in a tropical rainforest in Southwest China. Based on the construction of second extinction models, the robustness of epiphyte community and the dynamic of network structure were calculated for raw species-based network and individual-based network under different phorophyte removal scenarios. As a result, all three epiphyte-phorophyte networks exhibited low connectivity and moderate modularity; the nestedness of the standardized species-based network was lower than that of the raw species-based network, but remained higher than that of the raw individual-based network. The removal of the strongest interactor could lead to the rapid collapse of epiphytic communities, while the reverse order increased community robustness. Most importantly, for raw species-based and individual-based networks, we found the curves of modularity and nestedness started changing drastically and fluctuated frequently when the phorophytes' removal rate approaches 80%. Our results suggest that the keystone phorophytes (such as generalists, large individuals and abundant species) should receive special attention in conservation efforts to sustain tropical epiphytic systems; and when subject to removal, the intensity of phorophyte removal should be kept below certain threshold to achieve long-term stability of epiphytic communities.

1. Introduction

Among the principal drivers of anthropogenic disturbance, deforestation involving logging, burning and damaging of forests, have posed major threats to biodiversity in the tropical rainforest (Gibson et al., 2011). Forest loss is more profound than simple removal of tree species when the ecosystems are regarded as complex networks through inter-specific interactions (Colwell et al., 2012). Moreover, there is an emerging insight into ecology of exploring the effects of species loss on

interspecies interactions and community stability using ecological networks. Network approach offers the computation of several metrics, such as connectance, nestedness, modularity, and specialization, to describe topological structure and to quantitatively analyze community stability (Almeida-Neto et al., 2008; Dormann et al., 2009; Ceballos et al., 2016). Mutualistic networks often exhibit a highly nested architecture in which the most specialist species interact with a subset of those interacting with highly connected species (Bascompte et al., 2003; Spiesman and Inouye, 2013). Antagonistic networks, however, are

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consistently more modular, i.e., a pattern of subgroups of weakly interconnected species internally composed of strongly interconnected species (Olesen et al., 2007). Highly nested networks are tolerant to species loss because a core of generalist species maintain links to other species (Herrera et al., 2021), whereas high modularity improves community stability as the propagation of disturbances is limited by weak interactions between modules (Grilli et al., 2016; Dejean et al., 2018).

Epiphytes are non-parasitic plants that germinate and grow on phorophytes (the host of epiphytes) at all stages of life (Zotz, 2013). The relationship between epiphytes and their phorophytes is a typical commensal interaction because epiphytes take phorophytes as physical habitats and the phorophyte is commonly unaffected (Ceballos et al., 2016; Francisco et al., 2018). This means that removing phorophytes is highly destructive to the epiphytic communities they support (Francisco et al., 2018). For the epiphyte community on phorophytes, commensal networks are formed by vascular epiphytes, phorophyte individuals or species, and their interactions. Compared with mutualistic and antagonistic interactions, epiphyte-phorophyte network structure shows nested structure with low specialization and modularity (Piazzon et al., 2011; Ceballos et al., 2016; Francisco et al., 2018; Francisco et al., 2019; Naranjo et al., 2019; Hu et al., 2021). In fact, the low modularity in the common pattern is probably due to low level of specialization and lack of co-evolutionary processes between the interacting partners (Naranjo et al., 2019). The origin of nested patterns, however, is attributed to neutral processes, where interactions are mainly determined by the relative abundance of species in the community (Krishna et al., 2008).

Under the commensal interaction, the removal of phorophyte species (primary extinction) could trigger a cascade of the loss of dependent epiphyte (secondary extinction), thus affecting the stability of epiphyte community. Model of secondary extinction has received particular attention for its ease of quantifiable parameters among the stability indicators in ecological studies (Xi et al., 2021). In models, robustness of ecological community is calculated by assuming random or targeted sequential removal of species in an interaction network, and considering extinctions whenever a species is left without interactions (Memmott et al., 2004; Kaiser-Bunbury et al., 2010). As a result, the order of species primary extinction may affect robustness throughout secondary extinctions (Dunne and Williams, 2009; Bastazini et al., 2019). Losses of highly connected interactors can also drive a cascade of secondary extinctions compared to random losses of less connected species (Memmott et al., 2004; Kaiser-Bunbury et al., 2010). Studies on food webs showed that the risk of second extinctions is higher under the removal of an autotroph than removal of a top predator (Borrvall et al., 2000). Nevertheless, for the epiphyte-phorophyte commensal network, the number and intensity of interactions are directly related to phorophyte species, size, and abundance (Sáyago et al., 2013; Francisco et al., 2018; Zotarelli et al., 2019). Hence, removal scenarios based on those indices (the identity, abundance and size) of the phorophyte should be considered to explore the robustness of epiphyte community under phorophyte loss.

The elimination of ecological interactions and the alteration of network structural characteristics are the potential consequence of phorophyte removal, as species richness and abundance are the primary drivers of variation in network architecture (Spiesman and Inouye, 2013; Neff et al., 2021). Previous studies on ecological network revealed that anthropogenic disturbance led to significant changes in structure and stability of networks (Spiesman and Inouye, 2013; Messeder et al., 2020). Epiphyte-phorophyte networks properties from old-growth and disturbed forest fragments have showed considerable differences based on both qualitative and quantitative matrices (Piazzon et al., 2011). Yet, the dynamic trend of network structure and its relationship with community stability has been controversial due to unclear and even conflicting results. For instance, the emerging structure of plant-pollinator networks is more nested under agricultural intensification, and the plant-herbivore network is more modular (Morrison and Dirzo, 2020). But the topological structure of the individual-based palm-pollinator network is not affected by fragmentation in a tropical forest (Dáttilo

et al., 2015). Connectors and network hubs are important contributors to the modular structure, and the modularity after their removal will promote cascading effects; such that the removal of generalists causes a rapid collapse of the community (Gaiarsa and Guimaraes, 2019). Therefore, simulating network dynamics to predict possible changes of network structure can help guide in management efforts towards biological conservation.

This study mainly focuses on the structures of species-based and individual-based epiphyte-phorophyte networks, the impacts of phorophyte removal on robustness of epiphyte community and network structure, given the significance of the latter in identifying the response of communities to human disturbance. Firstly, we calculated the network structural metrics before removing phorophytes and analyzed phorophyte traits that influenced the distribution of epiphytes. Then, we estimated the robustness of epiphytic communities, and assessed the effect of coextinction on three network metrics by setting up phorophyte removal scenarios to simulate the secondary extinctions of epiphytes. Finally, we applied these current theoretical predictions of network structure to highlight implications for management and conservation policies.

2. Material and methods

2.1. Study site and data

The analyses in the present study relied upon inventories of tree census data and epiphyte distribution data collected from the canopy crane plot (1.44 ha, divided into 36 20 m × 20 m quadrats) within the Xishuangbanna National Nature Reserve (101°35', 21°37'N) in south Yunnan, China (Fig. A.1). The landscape of the study site is a pristine tropical seasonal rainforest dominated by *Parashorea chinensis* (Dipterocarpaceae). According to the census data from the National Forest Ecosystem Research Station at Xishuangbanna (XTRES), 7835 and 9345 individual trees with a trunk circumference (TC) greater than 1.5 cm were recorded in 2014 and 2019, respectively. Five parameters of phorophytes characteristic including species name, trunk circumference (TC), tree height, crown size and crown illumination index (CII, detailed description in Table A.1) were available from XTRES. The analysis of five parameters was based on census data recorded in 2019 and supplementary data in 2014. The diameter at breast height (DBH) used in the analysis was converted by trunk circumference (TC, measured at the height of 1.3 m above ground) ($DBH = TC/\pi$). To avoid sampling bias, all individual trees in the plot were investigated in 2017, 267 of them hosted vascular epiphytes, which we identified as phorophytes. Each individual of vascular epiphyte and its position on phorophyte was recorded using canopy crane and identified in Restoration Ecology Group, Xishuangbanna Tropical Botanical Garden. Unidentified trees and epiphytes were denoted by family name, and distinguished using codes (Table A.2-A.3).

2.2. Factor analysis

The accumulation curve of epiphyte species was plotted against the number of phorophyte individuals to estimate network sampling completeness within the study area (Colwell, et al. 2012). To estimate the extrapolated species richness in species pool, the number of unobserved species of epiphytes was estimated by adaptive coherence estimator (Colwell, et al. 2012). Wilcoxon rank sum test was performed to assess the difference of the tree traits (DBH, tree height, crown area and CII) between phorophytes (with epiphyte) and non-phorophytes (without epiphyte) after removal of individual trees with incomplete trait data. Generalized linear mixed model (GLMM) (family: binomial; link function: 'logit') was used to test the effects of phorophyte traits (as fixed effects) on the presence of epiphytes (presence as '1', absence as '0'). Similarly, GLMM (family: Poisson; link function: 'log') was used to test the effects of phorophyte traits (as fixed effects) on epiphyte richness

(species number). The quadrat was regarded as a random factor in both GLMMs.

2.3. Network analysis

The analysis focused on the interaction datasets as quantitative and qualitative matrices based on species- and individual-level of phorophytes. In the quantitative matrix, the interaction strength is distinguished by cell value; the qualitative matrix, also known as binary matrix, only shows the presence or absence of interaction without strength distinction. In total, three matrices describing the interaction between epiphyte and their phorophyte were analyzed: (1) In the raw species-based matrix, the rows present the phorophyte species, the columns present the epiphyte species and the specific values in cells correspond to the number of phorophyte individuals with epiphytes attach to the phorophyte species. Since different sampling intensities among different phorophyte species has been suggested as a key factor that influence the distribution of epiphytes (Cortes-Anzures et al., 2020), we used the standardized species-based matrix to correct the effect of the phorophyte species abundance in the forest (Vergara-Torres et al., 2010). (2) In the standardized species-based matrix, the cell values were calculated as standardized residual, i.e., the ratio of the difference between observed connection (in raw species-based matrix) and expected connection (taking into account the number of individuals of the phorophytes), and the squared root of the expected connection (Cortes-Anzures et al., 2020). (3) In the individual-based matrix, the rows present the phorophyte individuals, and the cell values in 0 and 1 represent the absence and presence of epiphyte, respectively. We visualized matrices as three networks, including raw species-based network, standardized species-based network and raw individual-based network, to characterize the interaction structures in the community.

Four metrics of three networks including connectance, nestedness, specialization and modularity were calculated to analyze the interaction structure between vascular epiphytes and phorophytes (see metrics description in Box 1). Moreover, the nested rank was calculated to represent phorophytes' contribution to the nested structure (Alarcón et al., 2008); that is, to identify the importance of phorophyte in the network. Significance of nestedness and modularity was assessed using empirical values from the null distribution, in which 1,000 random matrices were generated using a null model.

2.4. Phorophyte removal scenario settings

We simulated second extinction using sequential removal of phorophytes, and recorded the number of surviving epiphyte species

assuming an extinction only after losing all phorophytes in specific network (Kaiser-Bunbury et al., 2010). Sequential removal of all phorophytes therefore leads to the eventual extinction of all the nodes (Mariani et al., 2019). For raw species-based network, we followed five primary phorophyte species extinction sequences: extinctions based on random choice of species (scenario Random); extinctions based on species abundance either with first removal of the most abundant (scenario Abun1 → 0) or the least abundant (scenario Abun0 → 1) species; extinctions based on species nested rank either with first removal of the lowest order (scenario NR0 → 1) or the highest order (scenario NR1 → 0) species. For standardized species-based network, we followed two primary phorophyte species extinction sequences based on standardized link density: either with first removal of the most link density (scenario Link1 → 0) or the least link density (scenario Link0 → 1) species. For raw individual-based network, we followed five primary phorophyte individual extinction sequences: extinctions based on random choice of individuals (scenario Random); extinctions based on individual DBH either with first removal of the largest (scenario DBH1 → 0) or the smallest (scenario DBH0 → 1) individual; extinctions based on individual nested rank either with first removal of the lowest order (scenario NR0 → 1) or the highest order (scenario NR1 → 0) individual (Table 1).

Scenario DBH0 → 1 and scenario Abun0 → 1 simulated a probable sequential extinction under natural condition, because small individual and rare species, which also tend to be the specialist in nested structure, appear at high risk of real-world extinction (Kaiser-Bunbury et al., 2010). On the contrary, scenario DBH1 → 0 and scenario Abun1 → 0 explored the robustness of networks to lose the highly connected nodes which represented the worst scenario. However, these scenarios could simulate forest management practices such as timber harvesting and selective logging. Additionally, four other scenarios based on nested rank and link density (scenario NR0 → 1, NR1 → 0, Link0 → 1 and Link1 → 0) considered the role of phorophyte in commensal interaction networks. These can be used to explore keystone phorophytes that requires protection in the overall network in forest management, although the phorophyte removal scenarios rarely occur in reality. Considering that DBH measurements, that are directly related to basal area, were more accurate and complete than the other three traits; Per Sanger and Kirkpatrick (2015) and Sáyago et al. (2013), DBH was used in the present study to characterize the phorophyte size.

2.5. Robustness and structure dynamic

Robustness was quantified by the area below the second extinction curves that plotted the proportion of the epiphyte survival against the proportion of the phorophyte removal under different removal scenarios

Box 1

Description of the four metrics of network structure analyzed in this study.

- (1) **Connectance (C)** is calculated by the proportion of possible links actually observed in a network (Dunne and Williams, 2009). $C = L / (I \times J)$ for bipartite networks, L describes the number of realized links; I and J are the number of species of epiphyte and phorophyte, respectively. The index uses only binary information and ignores interaction strength.
- (2) **Nestedness** is the pattern that specialists (species with fewer interactions) interact with a subset of patterners with which generalists (species with more interactions) also interact (Bascompte et al., 2003), was quantified by NODF (Nestedness metric based on Overlap and Decreasing Fill) for qualitative data and WNODF (Weight NODF) for quantitative data (Almeida-Neto et al., 2008; Almeida-Neto and Ulrich, 2011).
- (3) **Specialistion** is measured by frequency-based index H_2' (standardized two-dimensional Shannon entropy) to describe the degree of specialization of an entire interaction network, representing an assemblage of species and their interaction partners based on the quantitative network (Bluthgen et al., 2006).
- (4) **Modularity** is quantified with QuanBiMoalgorith (Q) to describe the extent to which species aggregate into subsets under interaction in weighted bipartite networks (Olesen et al., 2007; Dormann and Strauss, 2014).

Table 1
Removal scenarios and the results of robustness under removal scenario.

Network	Removal scenario	Removal sequence	Robustness
Raw species-based network	Scenario NR0 → 1	from low nested contribution to high nested contribution	0.959
	Scenario Abun0 → 1	from low species abundance to high species abundance	0.904
	Scenario Random	Randomly	0.661
	Scenario Abun1 → 0	from high species abundance to low species abundance	0.414
	Scenario NR1 → 0	from high nested contribution to low nested contribution	0.132
Standardized species-based network	Scenario Link1 → 0	from most links to least links after standardization	0.124
	Scenario Link0 → 1	from least links to most links after standardization	0.961
Raw individual-based network	Scenario NR0 → 1	from low nested contribution to high nested contribution	0.899
	Scenario DBH0 → 1	from small individual DBH to large individual DBH	0.881
	Scenario Random	Randomly	0.692
	Scenario DBH1 → 0	from large individual DBH to small individual DBH	0.301
	Scenario NR1 → 0	from high nested contribution to low nested contribution	0.215

(Burgos et al., 2007; Pocock et al., 2012). R close to 0 corresponds to a rapid reduction in the slope of the curve, reflecting a disturbed system after the first species removal; whereas R close to 1 represents a robust system, where the decrease in the curve is slow, i.e., a system in which most epiphytes remain after the removal of most phorophytes (Morrison et al., 2020). The Wilcoxon signed-rank test was performed to explore differences in dynamic of second extinction among different simulated scenarios.

The dynamics of the network structure were described by simulating continuous change of network metrics under different removal scenarios. On the basis of the observed network, a new network was formed once a phorophyte was removed, and we calculated structural metrics of the restructured network. As the species were removed until only one remaining, a series of values for these metrics were calculated and continuous curves were drawn representing the trend of the three metrics change as the proportion of phorophyte removal increases.

All analyses were performed in R statistical software v 4.1.2 (R Core Team, 2021). To analyze the adequacy of the sample and estimate true richness, respectively, the 'specaccum' and 'estimateR' functions in 'vegan' package (Gotelli and Colwell, 2001) were performed. The 'ggplot2' (Ginestet, 2011) and 'ggpubr' (Kassambara, 2019) packages were used for visualizing Wilcoxon rank sum test. The 'lme4' (Bates et al., 2015) was used to build the GLMMs. The 'bipartite' package (Dormann, 2019) was used to perform the analysis of interaction network. The extinction curves were generated by 'second.extinct' function; the robustness was calculated using 'robustness' function; networks were visualized by 'plotweb' function. Except for the nested rank from the 'species level' function, other network metrics were carried out using the 'network level' function. To simplify the complex process of repeatedly calculating network structure after phorophyte removal, we combined 'second.extinct' and 'network level' functions (R script was available in [supplementary materials Text A.1](#)).

3. Results

3.1. Distribution of epiphyte species

267 phorophytes were colonized by vascular epiphytes in 1.44 ha canopy crane site. A total of 531 interactions occurred between 77 phorophyte species (Table A.2) and 67 vascular epiphyte species (Table A.3). The adaptive coherence estimator indicates that 138 epiphyte species were in the study area. The smoothed curve of epiphyte species accumulation was available in the [supplementary materials \(Fig. A.2\)](#). As the phorophytes, four traits including DBH, height, crown area and CII were significantly higher compared to the non-phorophytes based on the results of nonparametric rank sum test (Fig. 1). DBH and CII significantly affected the epiphyte occurrence ($P < 0.01$; see GLMM

analysis in Table A.4). DBH, crown area and CII significantly influenced the richness of epiphytes ($P < 0.01$), while phorophyte height had no significant effect (Table A.4).

3.2. Structures of epiphyte-phorophyte networks

Structure analyses of raw species-based and individual-based networks showed low level of connectance ($C = 0.05$ and $C = 0.03$, respectively) and significant moderate modularity ($Q = 0.44$, $P < 0.001$; and $Q = 0.54$, $P < 0.001$, respectively) (Table A.5). However, the raw species-based network exhibited a moderate nested structure (NODF = 44.30), while the raw individual-based network displayed a weak nested structure (NODF = 15.40) (Fig. 2). The weighted NODF of the species-based network after standardization (weight NODF = 10.30) was 55 % lower compared to the raw species-based network (weight NODF = 22.83). In contrast, the specialization of the standardized species-based network ($H_2' = 0.68$) was higher than the raw species-based network ($H_2' = 0.10$). The observed values of all indices are significantly different from the simulated results of the null model ($P < 0.001$). *Parashorea chinensis* (Dipterocarpaceae) mostly contributed to the nested structures, followed by *Drypetes hoensis* (Euphorbiaceae) and *Semecarpus reticulate* (Anacardiaceae), while *Parashorea chinensis* (Dipterocarpaceae), *Canarium album* (Burseraceae) and *Nephelium chryseum* (Sapindaceae) were the top three species of links strength in standardized species-based network.

3.3. The robustness of epiphyte community

The secondary extinction curves under sequential phorophyte removal were significantly distant from those under random removal for raw species-based and individual-based networks (Fig. 3). The result of Wilcoxon signed-rank test confirmed the significant differences among scenarios. On the one hand, both raw species-based and individual-based networks had high robustness ($R = 0.959$ for raw species-based network and $R = 0.899$ for raw individual-based network) under phorophytes removal from low to high nested contributions (scenario NR0 → 1), and low robustness ($R = 0.132$ for raw species-based network and $R = 0.215$ for raw individual-based network) under phorophytes removal from large to small nested contributions (scenario NR1 → 0). The sequential removal of the most abundant species (scenario Abun1 → 0, $R = 0.414$) and the largest individual (scenario DBH1 → 0, $R = 0.301$) resulted in lower robustness than the random phorophyte removals (scenario Random, $R = 0.661$ for species-based network and $R = 0.692$ for raw individual-based network). On the other hand, the secondary extinction curves based on nested rank and species abundance were significantly distant for species-based network, in particular, under scenario NR1 → 0 and Abun1 → 0. Nonetheless, only a slight difference

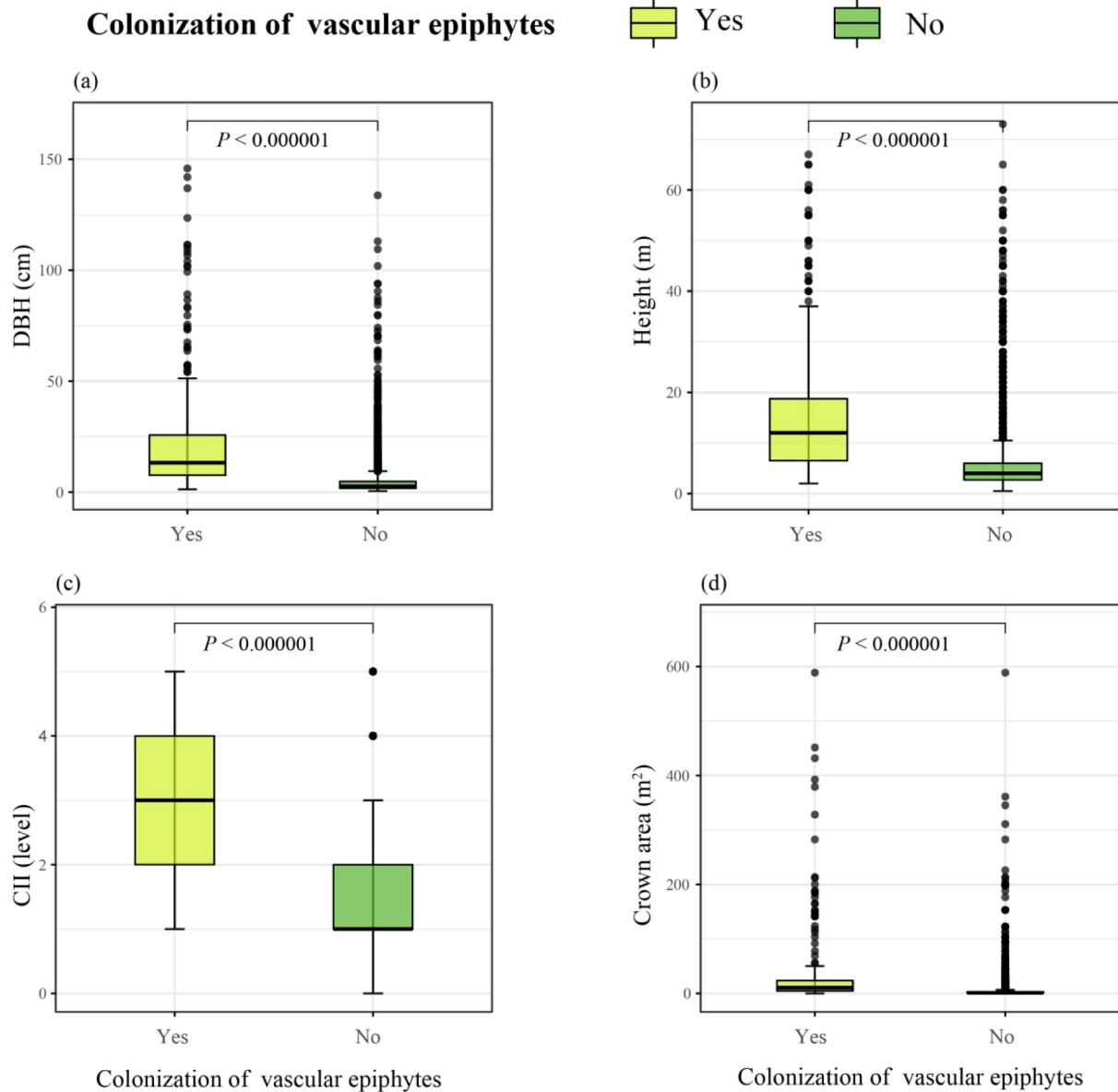


Fig. 1. Difference of four traits between phorophyte (Yes) and non-phorophyte (No) individuals.

occurred between the scenario NR1 \rightarrow 0 and scenario DBH1 \rightarrow 0 for raw individual-based network. For the standardized species-based network, the simulated curves of phorophyte removal by link strength (scenario Link1 \rightarrow 0 and scenario Link0 \rightarrow 1) almost overlapped with those of phorophyte removal by nested rank of raw species-based network (Fig. 3).

3.4. The dynamic of epiphyte-phorophyte network structure

The phorophytes removal under different scenarios showed the dynamic trends of connectance and modularity were relatively consistent, that is, connectance increased and modularity decreased in raw species-based and individual-based networks (Fig. 4). Connectance and modularity changed slightly until 80 % of phorophytes removal, although the dynamic curve of connectance in scenario NR1 \rightarrow 0 and scenario Link1 \rightarrow 0 showed a significant deviation in the species-based network. Oppositely, the nestedness fluctuated greatly among different removal scenarios (Fig. 4). In scenarios NR1 \rightarrow 0, Link1 \rightarrow 0, and Abun1 \rightarrow 0, the NODF initially changed rapidly, despite the small phorophytes removal. Under scenario NR1 \rightarrow 0, the nestedness approximated zero when the

removal ratio had reached about 40 % in the raw species-based network, and about 20 % in the raw individual-based network. However, some patterns occurred between the nestedness dynamics of the two networks (particularly noticeable for the individual-based). For the same proportion of phorophyte removal, the nestedness were lower in scenarios NR1 \rightarrow 0, DBH1 \rightarrow 0, Abun1 \rightarrow 0, and Link1 \rightarrow 0 compared to the random removal scenario. Then, the dynamic curves were intertwined and the structure of the two networks exhibited desultorily fluctuation in almost all simulation scenarios after 80 % of phorophyte removal.

4. Discussion

To explore the effects of phorophyte removal on robustness of epiphyte community, we investigated the structure of epiphyte-phorophyte networks in the tropical rainforest of Xishuangbanna and conducted a first attempt to predict extinction cascades in epiphyte-phorophyte networks. Our results suggest that the species-based and individual-based network exhibited different topology structure. Simulations predict that high-intensity phorophyte removal (the removal of large, abundant and highly-connected phorophytes, and the proportion

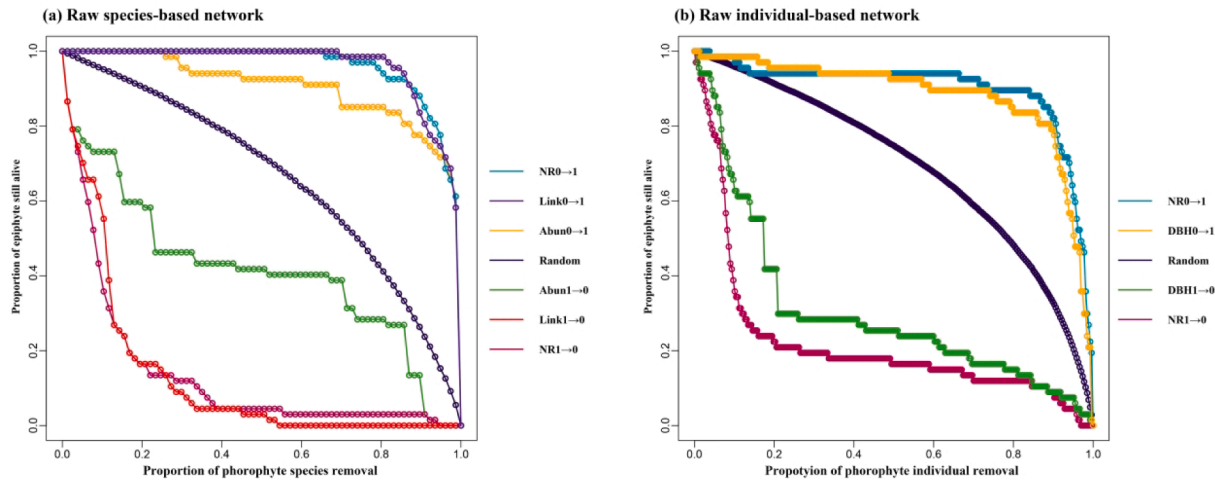


Fig. 3. Secondary extinction curves of vascular epiphytes under different scenarios of phorophyte removal. As the proportion of phorophyte species removal increases from 0 to 1, proportion of living epiphyte decreased from 1 to 0. Continuous solid lines in different colors represent different simulated scenarios. Only one line was displayed when curves overlapped. The NR, Link, Abun, DBH and Random indicate removal scenarios based on nested rank, link density, species abundance, individual DBH and random choice of species; 0 → 1 indicates phorophytes are removed in ascending order and 1 → 0 indicates phorophytes are removed in descending order. See Table 1 for abbreviations.

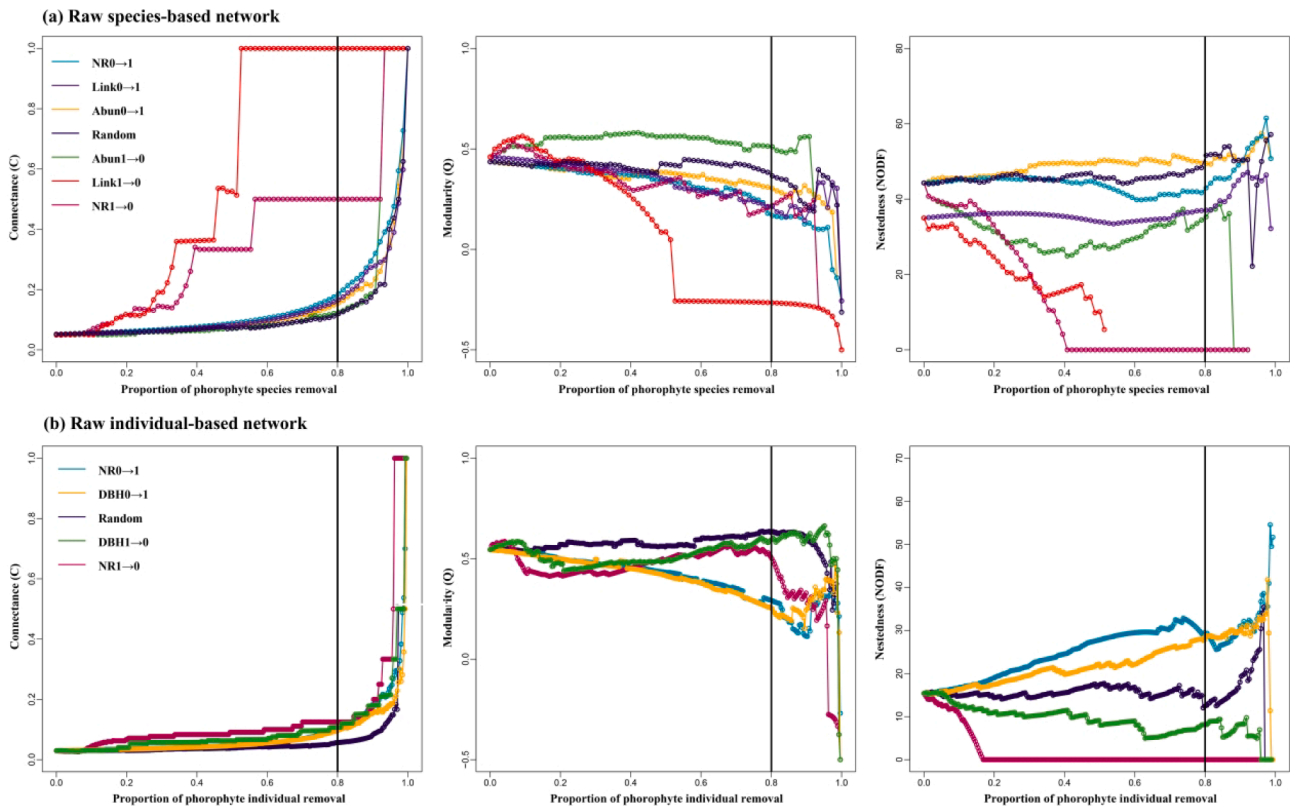


Fig. 4. Structure dynamic of three metrics in (a) raw species-based network and (b) raw individual-based network under different scenarios. The black line is the 80 % removal threshold. The NR, Link, Abun, DBH and Random represent removal scenarios based on nested rank, link density, species abundance, individual DBH and random choice of species; 0 → 1 indicates from small to large and 1 → 0 indicates from large to small. The detailed meanings are described in Table 1. All the indicators in scenarios Link1 → 0 and Link0 → 1 were calculated for standardized species-based network. NR, Link, Abun, DBH and Random.

of phorophytes removal reached about 80 %) reduced the robustness of the epiphytic community and drastically changed the network structure. The results suggest that selective logging can be acceptable in forest management, but keystone phorophytes should be protected and large-scale logging should be avoided to protect epiphyte diversity.

4.1. Commensal interaction between vascular epiphytes and their phorophytes

The topological structure of ecological networks is important for maintaining species diversity at community level (Baumgartner, 2020). Efforts to quantify the structures of epiphytic commensal networks have reported non-random patterns with nested and modular structures at a

low connectance and specialization (Ceballos et al., 2016; Mazziotto et al., 2017; Francisco et al., 2018). Furthermore, epiphyte-phorophyte networks present greater nestedness, significantly lower modularity and specialization than mutualistic networks (Piazzone et al., 2011; Naranjo et al., 2019). Our findings on the nestedness (44.30 measured by NODF) in the raw species-based network are consistent with previous pattern in epiphyte-phorophyte system, and fall within the scope of nestedness (32.17–76.88 as measured by NODF) in temperate forests of Chile and New Zealand (Taylor et al., 2016). This nested structure can be explained by the neutral theory, in which a few highly abundant species form the majority of connections in community. Supporting this explanation, species-based networks standardized by species abundance showed lower NODF and weighted NODF than the raw species-based network.

It is worth mentioning that an extremely low nestedness occurred in the raw individual-based network. The previous study on commensal network between 103 epiphytic species and 77 phorophyte individuals in Xishuangbanna showed similar low nestedness (NODF = 16.4) (Zhao et al., 2015). Indeed, excessive number of units in individual-based network dispersed the aggregation of interactions on generalists compared with species-based networks, resulting in a weakened nested structure. Though the larger phorophyte provided more diverse habitat and larger colonizing area, the proportion of connections among large phorophytes in individual-based networks was lower than the proportion of connections among highly abundant species in species-based networks. To clarify, the individual-based network standardized species abundance, but the topology showed difference between the raw and the standardized species-based network.

Individual-based analysis is necessary for epiphytic networks, although current research rarely analyzes interactions in units of phorophyte individuals (except Zhao et al. (2015)). In epiphyte community, species abundance and tree size largely predict pairwise interactions and structured interaction networks between epiphytes and phorophytes (Silva et al., 2010; Sáyo et al., 2013; Ceballos et al., 2016; Francisco et al., 2018). Here, more abundant species and larger-diameter individuals hosted more vascular epiphyte species. The increase in richness and abundance of epiphytes were correlated with phorophyte size, probably due to the increase habitat area and the time available for colonization (Francisco et al., 2018). Moreover, the habitat heterogeneity increased with tree growing, which may contribute to higher epiphyte diversity in larger trees (Woods et al., 2015). As a result, more attentions should be paid to individual-based networks rather than only species-based networks, to understand the structure of epiphytic commensal networks and its driving factors comprehensively. In individual-based networks, the epiphytic community could be regarded as a meta-community composed of epiphytes on phorophyte individual. The epiphytes growing on some individual trees, as a large pool of species, could spread to potential phorophyte individuals under suitable conditions. Analysis of individual-based networks can help to identify keystone phorophyte individuals, which could be considered as potential key targets in forest conservation and management to maintain epiphytic community stability.

4.2. Robustness of epiphyte community and dynamic of network structure under phorophyte removals

The simulations results showed that the community interactions were more robust for the random species removal than the selective species removal with many connections (Dunne et al., 2002a). Recent studies on epiphyte-phorophyte commensal network concluded that the number of secondary extinctions is higher at the beginning of elimination of phorophytes with more interactions, based on the robustness metrics (Francisco et al., 2018; Zotarelli et al., 2019). Here, the simulations of scenario DBH0 → 1 and Abun0 → 1, as the probable extinction sequence under natural condition, indicating that epiphytic communities could remain stable under minor disturbances. However, scenario

DBH1 → 0 suggested that the removal of a few large trees in the rain-forest could lead to severe impacts or even collapse of epiphyte communities. The habitat fragmentation resulting from the removal of large trees can change the local microclimate, which ultimately lead to significant reduction in epiphytes (Osie et al., 2022).

The impact of epiphytic communities on the robustness, under nested contribution rank phorophyte removal (scenario RN0 → 1 and RN1 → 0), was greater than those in order of species abundance and individual size, suggesting the network structure might be critical to the robustness of the epiphyte community. For instance, the individual TD43-114 (*Nephelium chryseum*, coded as SZ) was not a large phorophyte, but highly contributed to the nested structure; and once removed, the diversity of epiphytic community decreased rapidly. Additionally, some preferred phorophyte species (such as *Nephelium chryseum* (Sapindaceae), *Spondias lakonensis* (Anacardiaceae) and *Ficus drupacea* (Moraceae)) were disproportionately linked to several epiphyte species, as shown by standardized link strength results (Link0 → 1 and Link1 → 0). That is, only one phorophyte individual, but in fact many vascular epiphytes colonize them. Focusing on these preferred phorophyte species will improve the conservation efficiency of vascular epiphyte.

The interspecies interactions networks were constantly changing through the primary and secondary extinctions. Habitat loss contributes indirectly to the reorganization of interspecific interactions of plant-pollinator networks (Spiesman and Inouye 2013); and land-use changes differently affect the structure of herbivory and pollination networks (Shinohara et al., 2019). Sheykhali et al. (2020) have considered random and targeted removal as mechanisms of species extinction and found most influence of extinction on modularity. However, a large impact on connectance and modularity occurred in this study until the high-proportion removal of phorophytes. We speculated functional redundancy acts as a buffer against disturbances, representing a stabilizing mechanism for a community. Nonetheless, the removal of non-dominant phorophytes did not affect the community greatly; and a subdominant phorophyte would replace a dominant role in the network, once the latter is gone. More, the network structure changed dramatically once the disturbance intensity reached a certain threshold (i.e., phorophyte removal reached 80 %), and the stability of the community was destroyed, making recovery difficult. Therefore, controlling the intensity of deforestation is necessary to ensure the long-term stability of epiphytic communities; and protecting the large tree individuals that are essential to epiphyte community stability could be an eclectic way to conserve epiphyte biodiversity when logging is unavoidable.

Unexpectedly, the separation of connectance and modularity was not reflected in the network structure, despite the separation of secondary extinction curves of different scenarios (Fig. 4). This result indicates that the sequence of phorophyte removal played a weak role in the change of network structure. Changes of network size may be another key factor causing dynamic of network structure during the process of phorophyte removal, since disturbance alters the size and distribution of interspecific interactions for extinction cascades (Dunne et al., 2002b; Dunne and Williams, 2009). In fact, previous research reported that pollination networks from disturbed habitat are more robust to plant extinction, but this pattern is different under standardized network size and connectance (Vanbergen et al., 2017). Here, the curves of connectance and NODF under scenario Link1 → 0 exhibited significant separation in the species-based networks after standardization with species abundance. Moreover, the nestedness displayed complex responses to different simulations in both networks. First, the nested structure declined rapidly after the removal of minority of generalists, leaving only non-intersecting linkages between specialists in the community. Second, the nested structure changed messy under different scenarios when phorophyte removal reached a high proportion. Hence, considering the stability of the network structure, it is inevitable to pay more attention to the sequence and intensity of phorophyte removal.

4.3. Inspiration for epiphyte conservation

Vascular epiphytes globally account for roughly 10 % of all vascular plant species (Zotz et al., 2021), and most vascular epiphytes provide microhabitats and food for several animal species (Böhnert et al., 2016; Osie et al., 2022). Especially in tropical forest and humid montane forest, epiphytes play an important role for the regulation of water and nutrient cycles (Díaz et al., 2010; Liu et al., 2021). Despite large contribution of epiphytes to biodiversity and ecosystem services in forest ecosystems, they are still under-appreciated in forest conservation and management. Once high-intensity deforestation occurs, epiphytes probably could be undetected and irreversibly affected through commensal interaction; hence, avoiding over-exploitation of forests is crucial to maintain vascular epiphytes diversity.

Based on our simulation results in the study area, the conservation of vascular epiphytes should pay attention to both the richness of epiphytes and the network structure between epiphytes and their phorophytes. Large individuals and abundant species are generally colonized by most epiphytes and their protection is directly related to the diversity of epiphytic communities. However, few small individuals and rare species are vital to the stability of the network, and their loss can drastically change the structure of the network. Therefore, individuals TD42-50 (*Parashorea chinensis*, coded as WTS), TD22-39 (*Semecarpus reticulata*, coded as WMRTG) and TD34-25 (*Parashorea chinensis*, coded as WTS), and species *Parashorea chinensis* (Dipterocarpaceae) and *Drypetes hoensis* (Euphorbiaceae) in the study area seem important for the conservation of epiphytic plant diversity. In addition to protecting these keystone phorophyte individuals and species, controlling the proportion of logging is another aspect of maintaining network stability. Whether at the species or individual level of the phorophyte, 80 % in the area may be a theoretical threshold for logging; but the proportion of logging in real-world forest should be much lower than this value considering the effects of post-deforestation microclimate changes.

5. Conclusions

The commensal network has been ignored in the process of epiphyte community responses to phorophyte logging prediction; despite the previous investigations on the effects of deforestation on epiphyte diversity and proposed conservation strategies. In this study, high-intensity disturbance, including the removal of important species from the network and the removal of large proportion of phorophytes, affected the robustness of epiphyte community and network structure of epiphyte-phorophyte commensal network based on simulation of second extinction. The removal simulations inevitably lacked a degree of biological reality compared to removal field experiments, but produced theoretical outcomes that improved the prediction of changes under controlled conditions. Additionally, the model from this study simplified the secondary extinction process. In natural communities, however, the ability to rewire with a potential phorophyte could prevent secondary extinctions of epiphytes and markedly increased the robustness of networks by reducing the risk of cascading extinctions (Gilljam et al., 2015). Our findings provide direction for predicting the effects of different deforestation activities on epiphytic communities; but further research is needed to revise, improve and validate the accuracy of the model.

CRedit authorship contribution statement

Hai-Xia Hu: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Visualization. **Yu-Xuan Mo:** Conceptualization, Formal analysis, Visualization, Writing – review & editing. **Ting Shen:** Conceptualization, Visualization, Writing – review & editing. **Yi Wu:** Investigation, Writing – review & editing. **Xian-Meng Shi:** Writing – review & editing. **Yan-Yu Ai:** Writing – review & editing. **Hua-Zheng Lu:** Investigation, Writing – review & editing. **Sissou**

Zakari: Writing – review & editing. **Su Li:** Methodology, Formal analysis, Data curation, Writing – review & editing. **Liang Song:** Conceptualization, Investigation, Data curation, Writing – review & editing, Funding acquisition, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120586>.

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