



# Plant breeding systems influence the seasonal dynamics of plant-pollinator networks in a subtropical forest

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Received: 19 February 2020 / Accepted: 19 January 2021  
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## Abstract

Temporal dynamics of plant-pollinator interactions inform the mechanisms of community assembly and stability. However, most studies on the dynamics of pollination networks do not consider plant reproductive traits thus offering poor understanding of the mechanism of how networks maintain stable structure under seasonal changes in flower community. We studied seasonal dynamics of pollination networks in a subtropical monsoon forest in China with a clear rainy season (April–September) and dry season (October–March) over 2 consecutive years. We constructed dioecy-ignored networks (combining visitations to dioecious male and female plants by ignoring the difference between dioecious and hermaphroditic plants) and dioecy-considered networks (excluding those visitations that only occurred either on dioecious male or female plants) for eight sampling sessions for each season. Although flower richness and flower abundance were higher in the rainy season than in the dry season, no pronounced seasonal difference was found in network specialization, nestedness and modularity for both networks. There were only significant differences in plant community robustness and pollinator specialization between seasons for dioecy-considered networks but not for dioecy-ignored networks. Furthermore, we found the flower abundance of dioecious and hermaphrodite plants mostly showed trade-off variation between rainy and dry seasons. Our results suggest various plant reproductive traits affect the temporal dynamics of pollination networks, which should be considered for conservation of plant-pollinator interactions in forest communities.

**Keyword** Plant-pollinator network · Seasonality · Stability · Plant breeding systems · Subtropical forest

## Introduction

Theoretical and empirical studies suggest the importance of the temporal variation of species interaction networks in predicting the assembly and stability of complex communities under environmental change (Poisot et al. 2015; Ponisio et al. 2017; Valdovinos 2019). Thus, understanding the temporal dynamics of species interaction networks would benefit biodiversity conservation and ecosystem

restoration (Kaiser-Bunbury et al. 2010, 2017). In recent years, the spatial–temporal dynamics of ecological networks have been increasingly explored (Baldock et al. 2011; Burkle and Alarcón 2011; Kaartinen and Roslin, 2012; Trøjelsgaard and Olesen 2016; Chacoff et al. 2018). It has been shown that the constituent species and their interactions in networks change across different spatial and temporal scales, although most of the network structure properties seem to have low variability (Alarcón et al. 2008; Petanidou et al. 2008; Plein et al. 2013; Kemp et al. 2017). However, why these temporal changes in species composition and interaction do not seem to cascade their effect on network properties has not been well understood especially in pollination networks in seasonal habitats. To understand how the variation in species interactions transcends their effect on network structure across seasons, it is necessary to incorporate life history traits of species and analyze the change in temporal resource compartments (McMeans et al. 2015; Saavedra et al. 2016; Humphries et al. 2017).

Communicated by Katherine L. Gross.

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Life history traits such as plant reproductive traits could affect the temporal dynamics of network structure in plant-pollinator networks. Plant with different breeding systems show different dependence on the pollinators, and thus the network structure and dynamics of plant-pollinator could also be influenced by incorporating plant breeding systems (Petry et al. 2013; Devaux et al. 2014; Zhang and He 2017). Furthermore, plants with different breeding systems could also form temporal resource compartments and mediate seasonal dynamics of pollination network. For example, hermaphroditic and dioecious plants can have different flowering peaking times across season (Kang and Bawa 2003; Ohya et al. 2017), and thus affect the compositions and specialization of pollinator partners. As a result, the temporal resource compartments formed from hermaphrodites and from dioecious plants, respectively, could respond asynchronously as a trade-off variation and contribute to the stability of the overall pollinator community at the seasonal scale (McMeans et al. 2015). Plant breeding systems thus could be an important factor mediating the dynamics of plant-pollinator networks. However, no study has by far considered the effects of breeding systems of host plants on the seasonal dynamics of the plant-pollinator networks.

Changes at seasonal scales underlie vast variations observed in nature, and their effects on the dynamics of plant-pollinator interactions have also been noticed (Santos et al. 2014; CaraDonna et al. 2017; Weinstein and Graham 2017; Souza et al. 2018; Banza et al. 2019). Temporal changes in flower resource availability could affect the overall network structure. However, the literature is not unequivocal on how seasonal dynamics in flower resources could affect network structure patterns related to specialization. Santos et al. (2014) found higher niche overlap and lower network specialization in lower resource season, while Souza et al. (2018) suggested higher network specialization with higher modularity in lower resource season. These contradictory results suggest the high flexibility in pollinator specialization could affect structure patterns in plant-pollinator networks (Fründ et al. 2010; Zhang et al. 2011; Tinoco et al. 2017; Weinstein and Graham 2017). However, little is known about why network structure may maintain against or change along the variation in floral resources across seasons.

In this paper, we studied seasonal changes in plant-pollinator networks incorporating plant breeding systems in a subtropical monsoon forest, China, with an attempt to address the following three questions: (1) Do dioecy-considered networks (incorporating plant breeding systems) show significant different seasonal dynamics in structure properties from dioecy-ignored networks (ignoring plant breeding systems)? (2) Does flower abundance of plant groups of different breeding systems (hermaphrodites versus dioecious) and the corresponding visits of pollinator groups (bees versus non-bee pollinators) show trade-off across seasons? (3)

Do flower and pollinator communities change across seasons in both dioecy-considered and dioecy-ignored networks?

## Materials and methods

### Study site

The study was carried out in Heishiding Nature Reserve (111°53'E, 23°27'N; 150–927 m in altitude range) in southern China, with a subtropical moist monsoon climate. The annual temperature is  $19.6 \pm 5.6$  °C and the mean monthly temperature ranges from 13.2 °C in January to 24.7 °C in July. Annual precipitation is about  $1743 \pm 1013$  mm, occurring mainly between April and September (rainy season with 79% of annual rainfall) and a pronounced dry season lasts from October to March. A 50 ha stem-mapping plot was established in the reserve in 2011. Two 4 ha (200 × 200 m) sites were set up within the 50 ha plot, with one located in the valley and one on the ridge (more detail in Zhang and He 2017). In each of the rainy and dry seasons, each site was sampled four times (called four sessions) and each sampling session lasted for a week or two (Table S1). As these two sites separated only by 100 m distance and many pollinators can easily fly between them, we, therefore, pooled observations to create a single interaction matrix for each session and each year.

Free-standing tree/shrub species with the diameter at breast height (DBH)  $\geq 1$  cm in the plot were tagged, mapped, measured and identified to species. We checked the names and classified the sexual systems of these species, mostly with reference to *Flora of China* (<http://www.efloras.org/>). Three dominant types of sexual systems were included: 18 hermaphroditic species, 9 dioecious species and one monoecious species. Their sexual systems were further identified by floral morphologies in the field by observing the presence of male and female organs (two species described as hermaphroditic in *Flora of China*—*Pittosporum grabratum* and *Microtropis gracilipes*—were dioecious in our study).

### Flower visitor survey

We randomly sampled individuals of each flowering species and counted the number of flowers in about 1 m<sup>3</sup> space of the sampled individuals. We then observed pollinators on the flowering individuals (Zhang and He 2017). Each individual was observed for 30 min during four 2 h-intervals between 9:00 and 17:00 on a warm day with no rain and low wind. In total, 306 h of observation were conducted in 2 years and the mean observation time for each species was 10.9 h. For dioecious plants, we sampled both male and female individuals with the nearest location and adjacent time interval (Zhang and He 2017). Visitors that contacted reproductive organs

of a flower were noted as potential pollinators and their frequencies were recorded. Although we recognized that not all such visitors are pollinators, we followed the common practices of assuming visitors are a proxy of pollination (Vázquez et al. 2005). Samples of visitors were captured and identified in the field or sent to specialists for identification if we were uncertain about their species identity. Voucher samples of these visitors were deposited in ECNU-Alberta joint lab for Biodiversity studies.

## Data analysis

We compiled community matrices of flower abundance and pollinator visiting frequencies for each sampling session in 2 years; in total there are 16 matrices ( $n=4$  sessions  $\times$  2 seasons  $\times$  2 years). To consider plant breeding systems explicitly, dioecy-ignored network (including all visitations to male and female for each dioecious species, thus ignoring the difference between dioecious plants and hermaphroditic plants, i.e., not distinguishing dioecious male and female plants) and dioecy-considered network (including interactions where two individuals of the same pollinator species separately recorded visiting both male and female flowers for each dioecious species, i.e., ignoring those pollinators that only visited either male or female plants) were built based on visitation frequencies. We used the total number of flowers in the sampling area over each session as a measure of the flower abundance for each plant species.

To test the effects of seasonality on network structure and pollinator specialization, we calculated the following network metrics for the 16 community matrices for both dioecy-ignored networks and dioecy-considered networks: connectance, modularity, nestedness, network specialization, and species specialization. All these metrics were widely used and thought to be related to community stability. Connectance measures the complexity of networks by calculating the proportion of all possible realized links ( $C=I/(A \times P)$ ). Modularity indices quantify the prevalence of interactions within subsets of species in a community. We used the LPAwb+ algorithm to calculate modularity ( $Q_w$ , Beckett 2016). Nestedness estimates the tendency for specialists to interact with generalists (Almeida-Neto et al. 2008). We used weighted *NODF* ( $wNODF$ ; Weighted Nestedness based on Overlap and Decreasing Fill) to measure the degree of nestedness of networks (Almeida-Neto and Ulrich 2011), which ranges from 0 for non-nested matrices to 100 for perfectly nested matrices. Network and species specializations ( $H_2'$  and  $d'$  range 0–1), respectively measure the degree of community level complementary specialization between plants and pollinators in the interaction networks and species level specialization based on resource availability (Blüthgen et al. 2006). As most network indices are influenced by network size, we transformed the metrics  $Q_w$ ,  $wNODF$  and  $H_2'$ ,

to  $\Delta Q_w$ ,  $\Delta H_2'$ ,  $\Delta wNODF$  by subtracting the mean value of each index generated by 1000 randomizations from the interaction matrix base on Patfield null model (Schleuning et al. 2012). The null model fixed row and column totals equal to the corresponding row and column sums of the interaction matrix (Dormann 2009). Robustness of the plant community was assessed by the topological coextinction model by simulating random extinctions of their pollinators, as the coextinction model could indicate the relationship between the network structure and community stability (Memmott et al. 2004; Burgos et al. 2007; Biella et al. 2020). We calculated all network metrics using package 'bipartite' (Dormann et al. 2009) in R3.6.1. To compare the seasonal difference of network structure patterns, flower community (abundance and richness), and pollinator community (visits and richness), we used repeated measures ANOVA.

To test whether the plant and pollinator groups vary asynchronously as a trade-off across seasons, we first divided plants into two groups (hermaphroditic and dioecious plants) and pollinators into eight functional groups (birds, bees, wasps, flies, hoverflies, butterflies, beetles, and others; see Table S2, S3) according to higher-level taxonomic classes, morphological differences in their mouthparts and behaviors important to pollination. We then used the Fisher test to assess whether the ratio of flower abundance between dioecious plants and hermaphroditic plants significantly differed across the two seasons. As bees were the most important pollinator groups and most closely associated with hermaphrodites in this forest (Zhang and He 2017), we also tested whether the ratio of visits between bee and non-bee pollinators significantly differed across seasons.

All statistical analyses were conducted using R3.6.1 (<https://www.r-project.org/>).

## Results

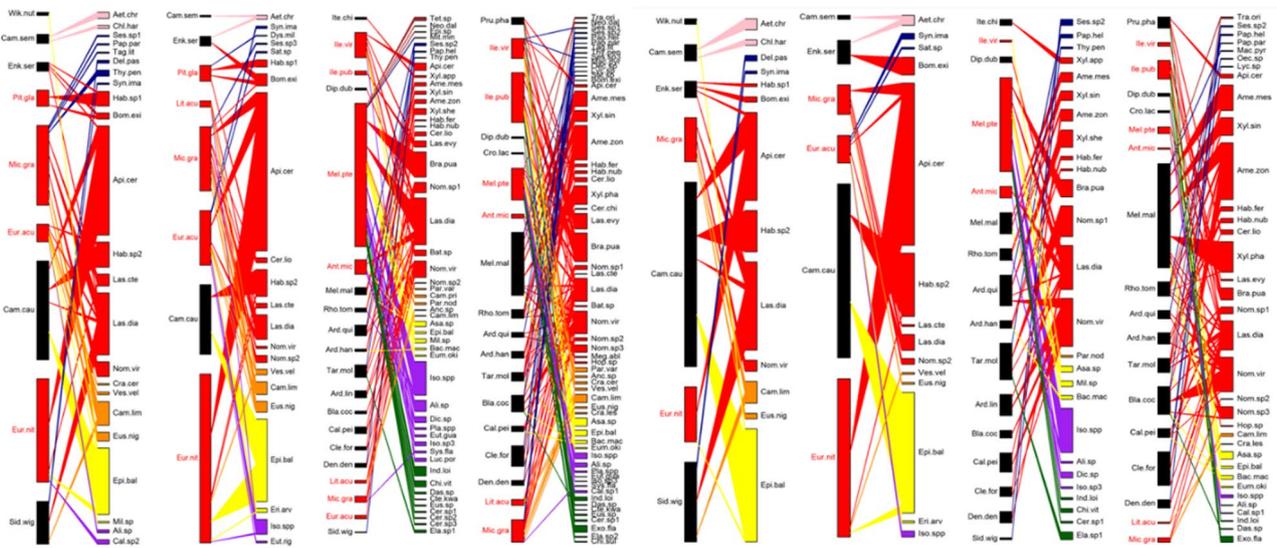
### Seasonal variation in network properties

The number of flowering plant species in the dry season ranged from 1 to 3, and pollinator richness ranged from 3 to 16 (Fig. 1; Table S1). Flowering plant richness ranged from 2 to 9 and pollinator species richness ranged from 3 to 29 in the rainy season. Network connectance was higher in the dry season than in the rainy season for both networks (Repeated measures ANOVA, for dioecy-ignored networks,  $F_{1,13} = 14.43$ ,  $P = 0.0022$ ; for dioecy-considered networks,  $F_{1,13} = 26.21$ ,  $P = 1.97e-4$ , Table 1; Table S1). However, no significant difference in network specialization ( $\Delta H_2'$ , for dioecy-ignored networks,  $F_{1,13} = 0.018$ ,  $P = 0.89$ ; for dioecy-considered networks,  $F_{1,13} = 0.093$ ,  $P = 0.77$ ) and modularity ( $\Delta Q_w$ , for dioecy-ignored networks,  $F_{1,13} = 1.12$ ,  $P = 0.31$ ; for

**(a) Dioecy-ignored networks**

**(b) Dioecy-considered networks**

Dry season 2013 Dry season 2014 Rainy season 2013 Rainy season 2014 Dry season 2013 Dry season 2014 Rainy season 2013 Rainy season 2014



**Fig. 1** Plant-pollinator networks in two seasons across 2 years in a subtropical forest in China for **a** dioecy-ignored network, combining all visitations to male and female flowers of dioecious plants and **b** dioecy-considered networks, excluding visits that only included one sex phenotype. For each network, plant species are shown on the left and colors indicate different plant groups: hermaphrodite in black, dioecy in red. Pollinators are listed on the right with colors indicate different pollinator groups. Red: bees (Hymenoptera-Apoidea), pink:

birds (Passeriformes), brown: others (Orthoptera, Hemiptera and Blattaria), blue: butterflies (including moths, Lepidoptera), orange: wasps (Hymenoptera-nonApoidae), yellow: hoverflies (Diptera-Syrphidae), purple: flies (Diptera-nonSyrphidae), and dark green: beetles (Coleoptera). Links denote interactions and link width indicates the interacting frequencies between a pair of species. See Table S2 and Table S3 for species codes

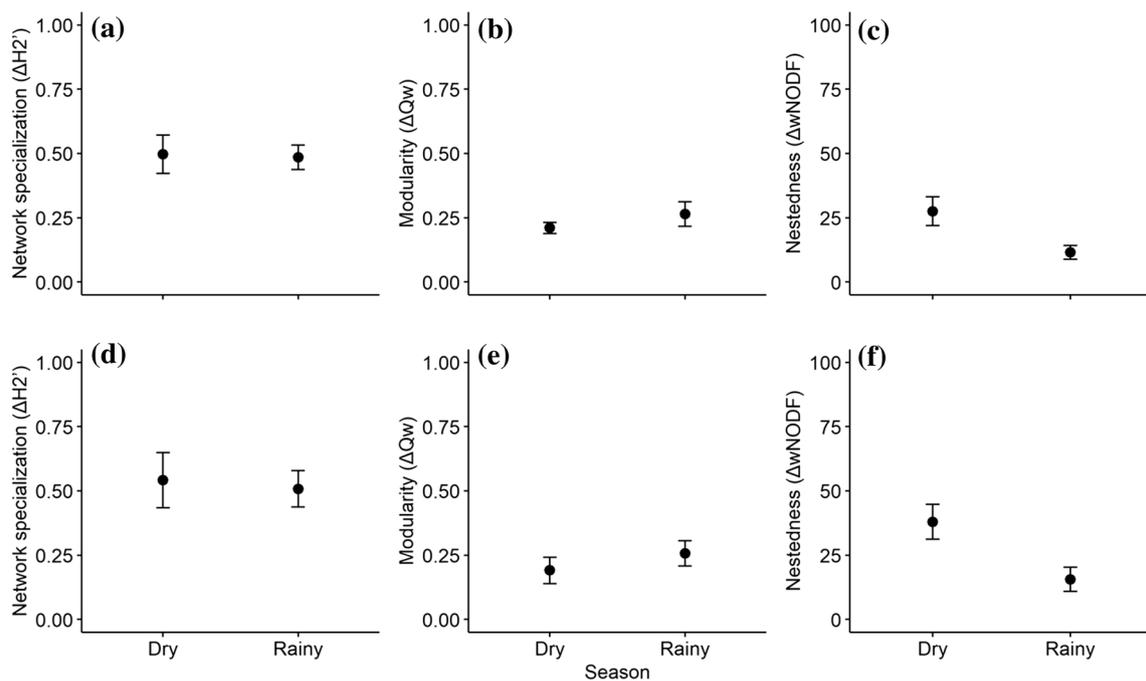
**Table 1** Results of repeated measures ANOVA ( $df = 1$ ) for seasonal variation in flower availability and network properties

Response variable	Dioecy-ignored				Dioecy-considered			
	Dry season	Rainy season	<i>F</i>	<i>P</i> value	Dry season	Rainy season	<i>F</i>	<i>P</i> value
Connectance	0.55 ± 0.10	0.31 ± 0.13	14.43	0.0022	0.75 ± 0.17	0.35 ± 0.13	26.21	1.97e-4
Robustness	0.59 ± 0.08	0.58 ± 0.05	0.30	0.59	0.76 ± 0.17	0.58 ± 0.05	7.34	0.018
$\Delta H_2'$	0.50 ± 0.21	0.48 ± 0.13	0.018	0.89	0.54 ± 0.26	0.51 ± 0.20	0.093	0.77
$\Delta Q_w$	0.21 ± 0.06	0.26 ± 0.13	1.12	0.31	0.19 ± 0.12	0.26 ± 0.14	0.85	0.38
$\Delta wNODF$	20.60 ± 17.20	11.48 ± 7.54	1.90	0.19	31.63 ± 20.60	13.66 ± 12.78	3.81	0.077
Flower richness	2.50 ± 0.53	5.25 ± 2.38	9.48	0.0088	1.75 ± 0.46	4.63 ± 2.26	11.57	0.0047
Floral abundance	218.13 ± 136.71	442.63 ± 254.88	4.49	0.054	175.25 ± 129.65	403.50 ± 223.72	5.85	0.031
Pollinator richness	7.38 ± 5.18	18.75 ± 7.89	11.39	0.0050	4.13 ± 2.47	10.25 ± 4.83	9.85	0.0078
Pollinator visits	93.75 ± 103.13	128.25 ± 80.34	0.62	0.44	44.63 ± 57.27	66.75 ± 56.66	0.72	0.41

*F* is the ratio of mean standard error between seasons to mean standard error of the replications within seasons). Network specialization, weighted modularity, and weighted nestedness were calculated by  $\Delta$ transformation of the raw metric based on Patfield null models

dioecy-considered networks,  $F_{1,13} = 0.85$ ,  $P = 0.38$ ) was found between seasons for both networks (Table 1; Fig. 2). Nestedness was not significantly different between seasons for dioecy-ignored networks and between the dry season and the rainy season for dioecy-considered networks either ( $\Delta wNODF$ , for dioecy-ignored networks,  $F_{1,13} = 1.90$ ,  $P = 0.19$ ; for dioecy-considered networks,  $F_{1,13} = 3.81$ ,

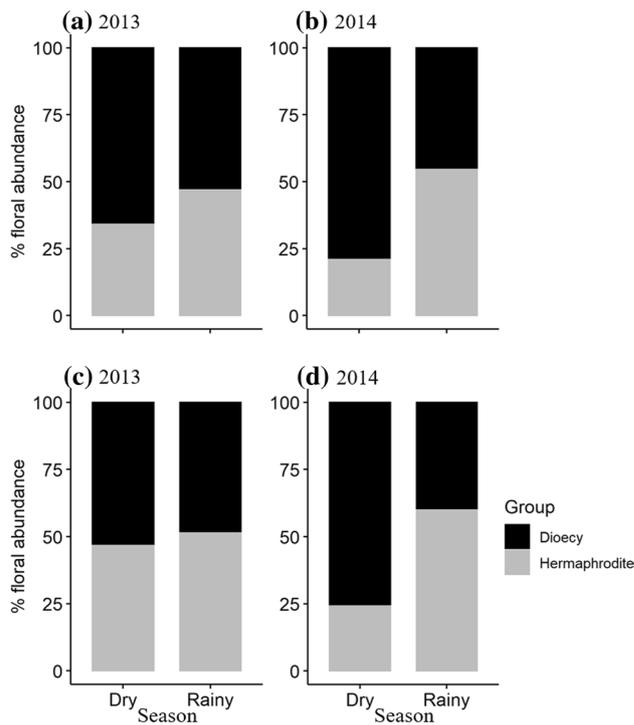
$P = 0.077$ , Table 1; Fig. 2). Plant community robustness was significantly higher in dry seasons than in rainy seasons for dioecy-considered networks but not significant for dioecy-ignored networks (for dioecy-ignored networks,  $F_{1,13} = 0.30$ ,  $P = 0.59$ ; for dioecy-considered networks,  $F_{1,13} = 7.34$ ,  $P = 0.018$ , Table 1; Table S1).



**Fig. 2** Comparisons of network level properties (using corrected values by Patefield null models) for three indices: network specialization  $H_2'$ , modularity  $Q_w$ , nestedness  $wNODF$  between seasons for **a–c** dioecy-ignored and **d–f** for dioecy-considered networks

### Seasonal variation among plant and pollinator groups

Dioecious plants had higher flower abundance in dry seasons than in rainy seasons while hermaphrodites showed relatively lower flower abundance in dry seasons than in rainy seasons for dioecy-ignored networks (Fisher’s exact test,  $P = 1.58e-9$ , D:H odds ratio = 1.71 for 2013 network,  $P < 2e-16$ , D:H odds ratio = 4.53, Fig. 3). For dioecy-considered networks, the same trade-off in flower abundance between dioecy and hermaphrodites across seasons was marginally non-significant for the network in 2013 (Fisher’s exact test,  $P = 0.057$ , D: H odds ratio = 1.21) and significant for the networks in 2014 (Fisher’s exact test,  $P = 2e-16$ , D: H odds ratio = 4.69, Fig. 3). Pollinator groups also showed different patterns of visits between dry and rainy seasons. Some pollinator groups are seasonal specialists (only occurred in one season, like birds in dry seasons, beetles and others visited dioecious plants in rainy seasons), while other groups especially bees are seasonal generalists (visited flower in both seasons, Fig. 1). We found the visits of bees (mostly visited hermaphrodite plants) and non-bee pollinators (mostly visited dioecious plants) varied differently according to the temporal resource compartments across the two seasons (Fig. S1).



**Fig. 3** Seasonal variations of flower abundance in dioecy and hermaphrodite in **a, b** for dioecy-ignored networks in 2013 and 2014, and **c, d** for dioecy-considered networks in 2013 and 2014

## Seasonal variation in flower and pollinator community

Flower richness was much higher in rainy seasons than in dry seasons for both networks (Repeated measures ANOVA, for dioecy-ignored networks,  $F_{1,13} = 9.74$ ,  $P = 0.0088$ ; for dioecy-considered networks,  $F_{1,13} = 11.57$ ,  $P = 0.0047$ , Table 1). Although flower abundance was significantly different between the rainy and dry season for the dioecy-considered networks ( $F_{1,13} = 5.85$ ,  $P$  value = 0.031), this was not quite significantly different for dioecy-ignored networks ( $F_{1,13} = 4.49$ ,  $P$  value = 0.054, Table 1). For pollinators, although higher pollinator richness was found in rainy seasons (for dioecy-ignored networks,  $F_{1,13} = 11.39$ ,  $P = 0.0050$ ; for dioecy-considered networks,  $F_{1,13} = 9.85$ ,  $P = 0.0078$ ), the total number of visits was not significantly different between the two seasons for both networks (for dioecy-ignored networks,  $F_{1,13} = 0.62$ ,  $P = 0.44$ ; for dioecy-considered networks,  $F_{1,13} = 0.72$ ,  $P = 0.41$ , Table 1). At the species level, pollinator specialization ( $d'$ ) was higher in rainy seasons than in dry seasons for dioecy-ignored networks (Wilcoxon test,  $W = 935.5$ ,  $P = 0.0086$ ) but not for dioecy-considered networks ( $W = 4138$ ,  $P = 0.23$ , Fig. 4).

## Discussion

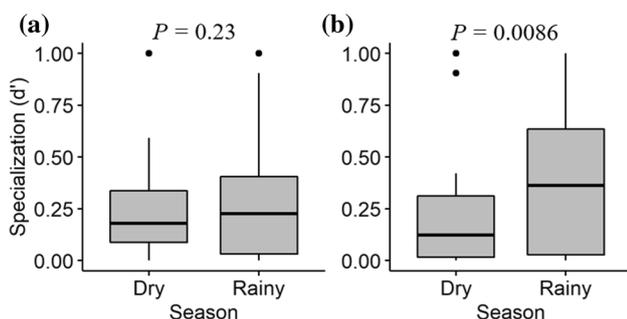
Knowledge on the temporal dynamics of ecological networks is necessary for understanding ecosystem function and stability. Although recent studies on the temporal dynamics of pollination networks have found networks can have high species turnover while also maintaining the stability of network structure, little insight has further been offered about the possible mechanisms that may mediate the stability (McMeans et al. 2015; Humphries et al. 2017; Valdovinos 2019). In this study, we found high seasonal changes in floral resources and pollinator richness, but no significant changes in network specialization, nestedness

nor modularity across seasons for both networks. In contrast, we found higher plant community robustness and lower pollinator specialization for the dioecy-considered network in the dry season than in the rainy season but not for the dioecy-ignored network. We further showed plant breeding systems could mediate community stability through the seasonal variation in tradeoff between flower resources of dioecious plants and hermaphroditic plants. These results suggest we should incorporate plant reproductive traits to understand the drivers of the dynamics of pollination networks in forest communities.

## The influence of plant breeding systems on the seasonal dynamics of pollination networks

In our study, we found network connectance changed considerably between seasons for both dioecy-ignored networks and dioecy-considered networks. However, network robustness was significantly different between seasons for dioecy-ignored networks, but not for dioecy-considered networks (Table 1). This indicates incorporating plant breeding systems could affect the dynamics of plant-pollinator networks (Devaux et al. 2014; Zhang and He 2017) and suggests that differences in pollinator specialization could change robustness across seasons for dioecy-ignored networks (Memmott et al. 2004; Valdovinos 2019). We found pollinators expanded their diet and were less specialized when flower resources were low in dry seasons after considering the shared visitations between male and female plants (Fig. 4). This could result in high robustness in dry seasons for dioecy-ignored networks (Kaiser-Bunbury et al. 2010). These results answer our first question: the seasonal dynamics of pollinator networks were different with and without incorporating plant breeding systems.

Plants with different breeding systems can form different temporal compartments of flower resources and thus affect the dynamics of plant-pollinator networks (Kang and Bawa 2003; Ohya et al. 2017). Our results show dioecious plants and hermaphroditic plants in our study mostly had a tradeoff variation in flower abundance across seasons (Fig. 3). Accordingly, different pollinator groups changed their visiting frequencies which would contribute to the overall network stability across years (Fig. S1). For example, bees showed relatively high frequencies in rainy seasons, while non-bee pollinators (like hoverflies) mostly seen on dioecious plants visited relatively more in dry seasons (Fig. 1, Fig. S1). These results confirm that plant breeding systems could be important in affecting the structure and stability of pollination networks (Devaux et al. 2014; Zhang and He 2017). Our results also suggest that it is important to consider plant breeding systems in pollinator network studies.



**Fig. 4** Comparisons of pollinator specialization ( $d'$ ) between seasons. **a** Pollinator species for dioecy-ignored networks and **b** pollinator species for dioecy-considered networks

## Seasonal variations in flower resource and network specialization

In our study, we found that flower abundance and richness were generally higher in the rainy season than in the dry season (Table 1). This suggests that seasonal variation in precipitation (possibly temperature as well) may affect the flower resource in ecosystems of pronounced seasonality (Opler et al. 1976; Santos et al. 2014; Souza et al. 2018; Banza et al. 2019). Although pollinator richness was significantly higher in rainy seasons, pollinator visits did not show a difference between seasons (Table 1). This indicates that floral abundance and richness should be an important factor in regulating pollinator diversity but may not be the only factor affecting pollinator visits (Fründ et al. 2010). All together, these results answer our third question: flower and pollinator community did change significantly across seasons in the subtropical forest we studied.

Flower community could be important in mediating plant-pollinator networks across temporal scales (Fründ et al. 2010; Weinstein and Graham 2017). This process makes it possible to maintain network specialization constant even when flower resource changes significantly across seasons (Tinoco et al. 2017; Weinstein and Graham 2017). Our study is consistent with several studies that have also shown high variations in flower resources but little change in network properties (Alarcón et al. 2008; Petanidou et al. 2008). However, there are inconsistent results in the literature for the relationship between flower resource availability and network specialization when studying seasonal variation in pollination networks. For example, Santos et al. (2014) found higher niche partitioning between pollinator species and higher network specialization with greater flower diversity, while Souza et al. (2018) found opposite trends, possibly due to higher competition in lower resource seasons. Our results suggest network specialization might not change although flower resources did across seasons (Banza et al. 2019). In future studies, we should consider the difference in the characteristic of seasonality and flower-pollinator community compositions, which could account for the complex relationships between flower resources and network properties (Humphries et al. 2017).

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00442-021-04863-5>.

**Acknowledgements** We thank Zeqing Niu, Ganyan Yang, Dandan Zhang, Jinwei Li, Yun Li for identifying insect specimen. We are grateful to Buhang Li, Weinan Ye, Rui Tang and Xiaoqing Hu for their assistance in the field. FH acknowledges the support of NSERC (Canada).

**Author contribution statement** M.Z. and F.H. designed the study. M.Z. conducted fieldwork and analysed data. M.Z. and F.H. wrote the paper.

**Funding** This study was funded by the National Natural Science Foundation of China (Grant number 31901105).

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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