Seasonal variation of plant-pollinator networks on oceanic island: lower specialization when resources are more abundant

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Research article

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Abstract

Background: The seasonal dynamics of plant and pollinator species components in the community could influence the structure of plant-pollinator networks. However, such dynamics are seldom been attention for oceanic islands networks. Here, we estimated the seasonal variation of seven plant-pollinator networks in Yongxing Island community. We collected a two-monthly data for each network of four seasons and used temporally discrete networks to characterize seasonal changes in plant-pollinator interactions. We predicted that greater floral resource availability in the season would allow for higher specialization patterns as previously described across large spatial gradients, with finer partitioning of the floral niche by the pollinators. **Results:** As we expected, we found that rainy season network with more plant species in bloom, showed higher levels of network-wide specialization and modularity. However, when we compared seven targeted sampling networks, both the network-wide specialization and modularity were negatively correlated with the number of plant species in bloom. There were no differences between rainy and dry seasons and among four seasons in species-level indices, suggesting that higher network level specialization may be an emergent property only seen when considering the entire network. Hawkmoths presented higher values of specialization in relation to other functional groups; and Apidae presented higher values of species strength than other functional groups. These results suggest some specialized plant species are visited only by Hawkmoths, and most plants associated with Apidae are used by this group. **Conclusions:** Our results suggested that, on oceanic island, increased floral resource availability in the season may not promote lower interspecific competition among pollinators leading to increased niche overlap, thus explaining the decreased in specialization. Plant-pollinator interactions data collection during dry, rainy season and all year-round generates lower network specialization than four seasons, and this may because that most pollinator species activity spans longer periods than a single season on islands. Thus, depending on the period of data collection, different networks structure of interaction may be found. Plant-pollinator networks have structural properties that vary according to seasons, and this should be taken into account in the studies of complex systems of interactions between plants and pollinators in oceanic islands communities.

Background

Ecological communities are complex and dynamic which comprised of various populations that interact with each other in different ways. Species activities changed in different environment, associated with the variation of species interactions [1]. Such temporal dynamics affect the role of species within communities through effects on their development, life cycle and behavior [2]. And in this sense, the diversity of plant phenological patterns is one of the main mechanisms for the maintenance of biodiversity in nature [3]. Because the most flowering plants are pollinated by animals [4], and the temporal dynamics of plants and animals at different environment which included those associated with seasons, should change the structure of plant-pollinator interaction networks [2, 5, 6]. The temporally dynamic nature of ecological communities had been attention early [7, 8], but the interaction networks are frequently identified as temporally static [9].

Most studies conducted in temperate regions and demonstrated that plant-pollinator networks have strong temporal dynamics from hourly variation to over a time span of centuries [6,10, 11, 12]. Temporal variation may be caused by changes in the number of species and interactions, changes on the identity of species and interactions between them, which affect the entire structure of networks [3, 5, 10, 13]. However, studies on temporal pollination networks are still scarce in oceanic islands areas where the biotas are typically depauperate compared to continental ones [14]. Meanwhile, pollinators have a lower immigration rate compared with plants on islands [15]. Importantly, plant-animal activity is not restricted to favorable seasons on islands [16, 17]. Thus, studies on oceanic islands may offer new perspectives on how interactions between plants and their interaction animals are temporarily structured [1, 16, 18].

On oceanic islands, some pollinator groups were mostly found in this area but not commonly encountered in temperate areas, such as vertebrates [17], could reveal distinct dynamics within the whole pollination network [19, 20]. Meanwhile, climatic seasonality is a main factor determining plant phenological patterns even in the islands area [3, 21]. Therefore, the seasonality of floral abundance may act as an important factor affecting network structure. Greater availability of floral resources has been proved to be associated to a higher diversity of pollinators and leading them to specialize on certain floral traits [22, 23]. Thus, higher specialization of networks may be expected during the season with more plant species in bloom [16, 24]. For pollinators, the highly morphological matches with interacting plant can improve the efficient of its use resources [25], and according to predictions of optimal foraging theory [26], such specialization may be especially favored as resource availability increase with more plant species in bloom in the community. On the contrary, a more competitive environment with lower availability of resources increased generalization of pollinators [27]. Thus, pollinator diet breadth is a flexible trait which results from behavioral adaptation to resource availability [27]. However, how such intrinsic dynamics of plant-pollinator interactions may lead to temporal variation in the network structure in oceanic islands communities, with year-round flowering activity of plants and including different pollinator functional groups, have not yet been investigated.

In this study, we evaluated the temporal variation of plant-pollinator network in Yongxing island community, comprised of four seasons. We also constructed other three networks including dry, rainy seasons and year-round networks by using the basis plant-pollinator interactions data of four seasons. We characterized the seasonal dynamics of pollination network using temporally discrete networks. Firstly, we calculated several network indices that characterize their overall structure. Then, we investigated how the metrics in these networks change across the seasons. Finally, we analyzed whether the variation of floral resource abundance across seasons was related to the changes of the corresponding network structure. Meanwhile, we also evaluated the temporal variation of species-level indices of plants and pollinator functional groups. We predicted that the season with more plant species in bloom would allow for finer partitioning of the floral niche by the pollinators (higher specialization and modularity) accompanied by lower overlap on the interaction between species (lower nestedness); and the species-level specialization of plant and pollinator would consistent with the network level specialization.

Methods

Study site

The Paracel Islands (Xisha Islands) are a series of coral islets, locating in South China Sea. The Yongxing island (16°50.1′N, 112°19.8′E), with a total area of 2.6 km², is the largest islet of this archipelago. The climate of Yongxing Island is characterized by two seasons. Rains are concentrated in winter, mainly from October to March with high wind speed. The Dry season, from April to September, is characterized by virtually no precipitation and low wind speed. We conducted our study within sample plots of typical plant communities in the island, which include tree, shrub, and herb species such as *Cordia subcordata*, *Scaevola taccada*, *Tribulus cistoides*, from early January to early March, early April to early June, early July to early September and early October to early December in 2017.

Pollination observation and data collection

Fieldwork was conducted in 30 quadrats with size of 5 × 5 m², at least 10 m away from each other. These quadrats were distributed throughout the island including the center of island and the coast; hence, we could get a more complete visitation data for each plant species. In the community, two monthly sampling of pollinators was performed between 08:00 and 18:00 hr for all plants in bloom on sunny days without wind. We assessed visitation inside 30 quadrats using 30-min observation periods. Plants in each quadrat flowering too few or none flowers were skipped. All open flowers inside the quadrat were identified to species level. In order to include enough information on the visits to all the flowering plants, we observed each quadrat for at least two days. Sampling of pollinators was conducted in all flowering individuals inside the quadrats. Only insects that actually touched the stigmas and/or stamens for more than one second foraging for nectar and/or pollen were classified as legitimate visitors and collected [28, 29]. During each observation period we collected floral visitors from each insect-pollinated species by using sweep net. We totally observed at least 20 hours for each quadrat. All the visitor insects were firstly morphotyped and a few individuals of each morphotype were collected for further identification to the lowest possible taxonomic level by several entomologists (see Acknowledgments). To verify if the flower visitors were the potential pollinators for each plant species, we examined the pollen loads from 5 collected insect individuals of each species for pollen analysis. Pollen sample of each visitor species was viewed under a JSM-6360LV scanning electron microscope. Pollen grains were identified by comparing with a reference library of pollen based on those removed from field-collected flowers. If 4 or 5 specimens of a plant-flower visitor pair carried the host plant pollen, we presumed that the visitor was the potential pollinator, although we did not evaluate the role in the subsequent production of fruits to visited plant species. Vouchers for all plant species were collected, identified and deposited in the SCBG Herbarium. Collected insects' samples were deposited at the South China Botanical Garden, Chinese Academy of Sciences.

Pollination networks

For the study community, we built qualitative interactions matrices among pairs of plants and pollinators. We constructed a summarized network considering the entire period of sampling (complete networks) and two seasonal networks considering the dry (from April to September) and rainy (from October to March) season separately. We additionally constructed four seasonal networks to illustrate how temporarily targeted sampling of plant-pollinator networks influences the characterization of communities. We calculated metrics illustrating distinct structural properties of the network which were previously shown to be less sensitive to sampling effort [30, 31]. Nestedness quantifies the degree to which interactions of specialized species in the network. Network-wide specialization was estimated by the H_2' index, which describes if species restrict their interactions from those randomly expected based on a partner's availability [32]. Modularity indices quantify the prevalence of interactions within subsets of species in the community. The modularity algorithms are built on optimization procedures that iteratively maximize the modularity of the final solution, meaning that the algorithm is stochastic and module arrangement as well as the value of Q might vary slightly between runs [33]. We repeated the analysis fifteen times for each network and kept the module conformation that yielded the highest Q-value.

Network metrics can be affected by intrinsic characteristics such as the number of interacting species and sampling effort [30, 31, 32]; hence the significance of metrics is assessed by comparison with null model networks. Here, we used the Patefield null model, which fixes the network size and the marginal totals while shuffling interactions randomly [34]. We estimated the 95% confidence interval for each metric from the 1000 simulated values, and a metric value was considered significant if it did not overlap with the confidence interval.

Species-level specialization in networks

To estimate the role of species within networks and how it varies among the seasons, we calculated two species-level indices that presenting distinct topological properties of a species: (1) species-level specialization index d' , which quantifies how strongly a species deviates from a random sampling of interacting partners available, with higher values indicating higher specialization [32], and (2) species strength, which is the sum of the proportions of interactions performed by a given species across all its interaction partners. Higher values indicate that more pollinators depend on a specific plant species, and vice versa [35]. Calculations of all network-related indices were conducted with the “bipartite” package version 2.05 [36] in R [37].

Statistical analysis

To test the relationship between floral resource availability which represented by the number of plant species in full bloom and the specialization, modularity and nestedness of networks, we performed Pearson correlation analysis using the seven pollination networks metrics.

We evaluated whether seasons, for plants and potential pollinators, and functional groups of pollinators were important determinants for species-level indices. Pollinators were classified as Apidae, other Hymenoptera, Syrphidae (hover flies), other Diptera, Butterflies, Hawkmoths. While Hemiptera

(Triatominae), Passeriformes (*Zosterops japonicus*) and Arctiidae (*Utetheisa lotrix*) had only one species respectively, and they performed few interactions which were excluded from our data analysis. When we considered plant and pollinator species occurred in all four seasons, Diptera were excluded from our data analysis because there was only one species. We applied linear mixed effect models in the species-level data, including seasons (dry or rainy; spring, summer, autumn or winter) and functional groups in the pollinator model as fixed effects and the species identity nested within vegetation type as random effects using the R package “lme4” [38]. Whether season or functional groups had significant effects on species-level indices was tested using a likelihood ratio test comparing the model with and without the fixed factor using the R package “car” [39]. After detecting that pollinator group was a significant factor, we conducted glht in the package “multcomp” [40]. We also repeated the species-level analysis considering only the plant and pollinator species which occurred both in the dry and rainy seasons or all in the four seasons, with the seasons as fixed and species identity nested within the vegetation type as random effects. All data analyses were conducted in R [37].

Results

A total of 891 interactions between 64 insect species and 63 plant species which distributed in 26 families were recorded across all year-round. The dry (57 plants and 61 pollinator species) and rainy (61 plants and 55 pollinators) season had similar network size. The summer season network presented a greater number of plant and pollinator species (55 plants and 57 pollinators), followed by winter (52 plants and 51 pollinators), spring (52 plants and 39 pollinators) and autumn (39 plants and 43 pollinators) networks (Table 1). Regarding the plant families recorded, the Asteraceae (7 species) was the most visited, receiving 24% from the total interactions, followed by plants in the Euphorbiaceae (9%) and the Fabaceae (8%). Hymenoptera contributed 57% of all interactions, with Apidae accounting for 40% of these, and *Braunapis puangensis* was the most generalized pollinator which visited 45 plant species. Among Hymenoptera, *Campsomeriella collaris* and *Micromeriella marginella* were categorized as female and male individuals in consideration of their obvious difference of morphological characteristics and visiting plant species. Diptera and Lepidoptera contributed 23% and 19% of all interactions, respectively. Syrphidae accounted 51% of all Diptera interactions, and *Paragus bicolor* was the most generalized pollinator which visited 34 plant species. Butterflies and Hawkmoths contributed 67% and 26% of all Lepidoptera interactions, respectively. Seasonal variation of pollinator species number to each functional group was shown in Figure 1.

Network metrics across seasons

All networks were more specialized and modular than expected by the null models (see Table 1). Moreover, rainy season network had higher specialization and modularity but lower nestedness than that from the dry season (Table 1). Furthermore, the networks of spring and autumn had higher specialization and more modular than those of summer and winter seasons. The spring network had the highest specialization and modularity among four seasons; the autumn network had the highest nestedness

among four seasons, the summer and winter networks had similar nestedness and modularity; the spring and autumn had similar nestedness and modularity (Table 1, Figure 2 and Supplement Figure 1).

Both the network-wide specialization ($t = -2.704$, $df = 5$, $P = 0.043$) and modularity ($t = -2.942$, $df = 5$, $P = 0.032$) were negatively with the number of plant species in full bloom (Figure 3). By contrast, nestedness was not significantly correlated with the number of plant species in full bloom ($t = -0.490$, $df = 5$, $P = 0.645$). These results were contrary to our prediction.

Species roles and seasonality

There were no species-level differences on specialization ($\chi^2 = 0.48$, $P = 0.49$) or species strength ($\chi^2 = 1.26$, $P = 0.26$) for plants between dry and rainy seasons (Figure 4a, b). For the pollinators, likewise, species-level indices did not differ between dry and rainy seasons (specialization: $\chi^2 = 0.03$, $P = 0.86$; species strength: $\chi^2 = 1.35$, $P = 0.25$; Figure 4c, d). When we considered only species of pollinators and plants that occurred in both dry and rainy seasons (55 spp. of plants; 49 spp. of pollinators), no species-level differences on specialization (plants: $\chi^2 = 0.52$, $P = 0.47$; pollinators: $\chi^2 = 0.01$, $P = 0.91$) or species strength (plants: $\chi^2 = 0.93$, $P = 0.33$; pollinators: $\chi^2 = 1.00$, $P = 0.32$) either (Table 2; Figure 5; Tables S1, S2). On the contrary, distinct group of pollinators showed some differences on their roles within the networks. Notably, Hawkmoths showed higher specialization than other pollinator groups, and Butterflies showed higher specialization than Hymenoptera in dry season; while Hawkmoths showed higher specialization than Hymenoptera and Syrphidae in rainy season (Figure 4c). Furthermore, Apidae presented higher species strength than other group pollinators, with more plant species depending on them for pollination in both dry and rainy seasons (Figure 4d). Similar results were found when pollinator species occurred in both dry and rainy seasons (Figure 5c, d).

Among spring, summer, autumn and winter seasons, the specialization indices of plants showed a few different ($\chi^2 = 8.80$, $P = 0.03$), but the species strength indices did not differ ($\chi^2 = 3.55$, $P = 0.31$) (Figure 6a, b). Furthermore, plants in spring showed higher specialization than in winter (Figure 6a). For the pollinators, Hawkmoths were more specialized in autumn than in winter season ($\chi^2 = 13.17$, $P = 0.004$) but no difference was detected for species strength ($\chi^2 = 1.35$, $P = 0.25$) (Figure 6c, d). Distinct groups of pollinators showed some differences on their roles within the networks. Notably, in summer, Hawkmoths showed higher specialization than other pollinator groups; in autumn, Hawkmoths also showed higher specialization than Apidae, Diptera, Hymenoptera and Syrphidae but not than Butterflies (Figure 6c). Furthermore, Apidae presented higher species strength than Butterflies in spring and other pollinator groups in summer, autumn and winter seasons (Figure 6d).

When we considered species of plants and pollinators that occurred in all the four seasons (30 spp. of plants; 29 spp. of pollinators), for plants, the specialization indices showed a few different among four seasons ($\chi^2 = 8.31$, $P = 0.04$), but the species strength indices did not differ among four seasons ($\chi^2 = 5.22$, $P = 0.16$) (Figure 7a, b). Moreover, plants showed higher specialization in spring than in summer season (Figure 7a). For pollinators, species-level indices did not differ among four seasons (specialization: $\chi^2 = 7.63$, $P = 0.054$; species strength: $\chi^2 = 3.44$, $P = 0.33$). In contrast, distinct groups of

pollinators showed some differences on their roles within the networks (Table 2). Notably, Hawkmoths showed higher specialization than other pollinator groups while Apidae presented higher species strength than other pollinator groups in summer and autumn; in winter, Apidae presented higher species strength than Butterflies, Hawkmoths and Hymenoptera (Figure 7c, 7d), with more plant species depending on them for pollination.

Discussion

Network structure and seasonality

In our study, the pollination network was more specialized during rainy season, characterized by more plant species in full bloom with higher floral resources availability, than during dry season. This result was opposite to a recent study in the Central region of Brazil [41] which found networks were more specialized during dry season when floral resource availability was lower. Previous studies in binary temporal networks suggested that nestedness, modularity and connectance vary significantly within a single year [e.g. 42]. Other studies from temperate regions showed that these metrics are highly conserved between successive plant reproductive seasons [e.g. 5, 6, 10, 43, 44, 45]. One important ecological factor influencing specialization of networks is the species abundance, which can vary at small scales temporally [46]. When floral resource availability is higher, the coexisting pollinators number in the network may be greater; and higher levels of specialization may be expected [22, 23]. In addition, according to optimal foraging theory, decreasing in resource availability should lead to an increase in diet breadth which would lead to higher generalization [26, 27]. Therefore, changes on resource availability reflect on the structure of the pollination networks, with expected higher specialization associated to higher resource diversity and availability [22]. Our results were consistent with the prediction that the greater specialization in the rainy season recorded here, is related to higher floral availability and higher richness of plant species blooming. However, when we considered four seasonal networks with shorter observation periods all together, we found that the network-wide specialization and modularity were reduced with the increasing number of plants in full bloom among the seven networks. Similarly, Souza et al. [41] found higher specialization occurred in the networks when resources are scarce in tropical environments. One explanation is that considerably lower availability of floral resources, coupled with less plant species in bloom, still leads to changes in animal foraging behavior owing to higher competition, ultimately resulting in overall higher specialization and modularity [47]. Also, some animal species which successfully colonize isolated islands tend to broaden their trophic niches, thus interacting with more species than their continental counterparts in order to survive in such low diversity ecosystems [48], and may increase the niche overlap with the increasing of plant species in bloom in such areas.

Studies have shown variable levels of temporal variations on network properties [5, 10]. However, seasonal variations are more prominent than interannual variations [5]. In the Yongxing island community, plant-pollinator interactions occurred throughout the year, but summer and winter appeared to be the most favorable seasons with larger network size which were different with temperate forest where spring and autumn were the most favorable seasons [43]. The coincidence of a small amount of

rainfall and high temperatures generates a soil water deficit from June, and this may be strongly related to the autumn activity decline. Meanwhile, the winter season had two additional distinct features: specialized visitor groups (Lepidoptera) were more species-rich, and more specialized plants were blooming during this period. In this study, all network qualitative properties showed significant seasonal variations of a single network through its annual cycle which were consistent with previous studies [42, 49, 50]. The seasonal changes in nestedness, network-level specialization and modularity suggest that species exhibited more specialized interactions during the season when the number of species and interactions were at a minimum. The similar results were also found in subtropical climate areas [50]. Since specialization is not affected by system size and sampling intensity [32]; our findings regarding seasonal variations in specialization seem robust.

Contrary to our predictions, the specialization and modularity were negatively correlated with the number of plant species in bloom which associated with the floral resource availability among the 7 discrete networks. The nestedness was not significantly correlated with the floral resource availability. Higher diversity of pollinators was associated to greater floral resource availability in the island, but most pollinator species could visit most plants, therefore, few plants receiving only one species of pollinator. Although our results did not accord with the predictions of optimal foraging theory [26], this could mean pollinator behave as generalists and forage less selectively when resources are abundant, but become more selective when resources are scarce in oceanic island communities. For example, Apidae concentrated their collection activities on a limited group of sources when many types of resources were available, whereas more plant species were exploited during periods of lower number of flowering plants [51]. The variability of the abundance of species that interact in four seasons, the phenological changes in flowering and pollinator appearances, and importantly, the opposite results of network-level specialization between two seasons (dry and rainy) networks and among seven networks suggested that simple cumulative networks were a limited tool for the deep analysis of a pollination system, even though the qualitative metrics were more affected by temporal data aggregation than quantitative ones [50]. The present study thus strengthens the viewpoint that a proper description of the interactions in a plant-pollinator community with year-round activity should include all months and not just the few months of dry and rainy seasons.

We recognized that our conclusions based on using the number of plant species in full bloom as the floral resource diversity and availability are imperfect. The ultimate goal to assess resource availability was to obtain estimates on sugar and amino acid contents of nectar and pollen [52], but such estimates are rarely feasible in many cases. Hegland and Totland [29] argued for using proxies because the number of flowers was related to nectar amount in several studies. However, counting flowers may also yield rather imprecise estimates for food availability [53], because that pollinators prefer dense patches to minimize the costs of search [29], and may use patches as sensory cues to find food resources rather than individual flowers or inflorescence [54]. On the other hand, the number of plant species in bloom was usually positively correlated with pollinator species richness [55], some studies used only species lists, i.e. presence-absence data, to predict floral resource availability [56]. Furthermore, higher species richness is correlated to higher resource diversity [57]. In our community, the observed plant species were distributed

all over the island and in full bloom, indicating the floral resource availability would increase with the more plant species flowering. Therefore, to some extent, the number of plant species in full bloom could reflect the floral resource diversity and availability effectively, therefore, our results may reasonable accuracy. Our study only investigated a single year, thus being hardly representative of the Yongxing island community in the long run. The floral resource compositions vary considerably among years [43], whereas our study may provide a snapshot of plant-pollinator interactions. Therefore, we think that the temporal dynamics of plant-pollinator interactions across months, seasons and years should be further investigated for oceanic islands communities.

Species-level specialization and seasonality

Although rainy season network was more specialized, we did not find the same pattern when considering species-level specialization and species strength of all plant and pollinator species. Similarly, plants and pollinators occurred in both seasons had no difference of species-level specialization and species strength between dry and rainy seasons. For pollinators, the lack of consistent pattern at the species level can be illustrated by two of the most abundant pollinator species that occurred all year round. The *Cephonodes hylas* occurred in both seasons, tending to be more specialized in the dry season (d' rainy = 0.23; d' dry = 0.38) and have higher species' strength in the rainy season (strength rainy = 0.98; strength dry = 0.39; Table S1). *Cephonodes hylas* interacts with more plant species during the rainy season when more plant species blooming than dry season. On the contrary, *Apis cerana*, the most common pollinator, had higher value of specialization (d' rainy = 0.14; d' dry = 0.08) and species' strength (strength rainy = 6.56, strength dry = 4.65; Table S1) in the rainy season. During the rainy season with higher resource availability, *Apis cerana* may show higher levels of specialization to specific plants and higher species strength, than during the dry season when resources are not much abundant [26].

Similarly, the species-level specialization and species strength of plants had no significant difference among four seasons, indicating that higher network level specialization is an emergent property only seen when considering the entire network [41]. Plants occurred in all four seasons had no difference of species-level species strength but plants in summer had lower specialization than in spring. One possible explanation is that the higher resource availability during the summer season, coupled with more pollinator species, generates the observed network-wide lower specialization. Finally, Hawkmoths presented higher values of specialization in relation to other pollinator groups in both seasons suggests that several plant species show convergent evolution of flowers that are specifically adapted to their long proboscis [58, 59]. Meanwhile, Hawkmoths presented more specialized in summer and autumn seasons but not in spring and winter seasons. It is possible that more specialized plant species flowering and more Hawkmoths species active in winter on Yongxing island, which generates lower specialization values. Moreover, Apidae presented lower values of specialization and higher species strength than other pollinator groups, suggesting that most plant species that are visited by Apidae are used only by this group. Some plants are mainly visited by Hawkmoths and rarely or never visited by other group of pollinators. When we considered pollinators active in all four seasons, Apidae and Syrphidae presented higher species strength than other pollinator groups in winter. This may be because that some small and

green flowers occurred in winter and pollinated only by Syrphidae and promoting plants to depend more on them [60].

Conclusion

In conclusion, our study is, to our knowledge, the first to provide a qualitative description of the seasonal changes in the metrics of plant-pollinator interaction networks in oceanic islands areas where includes different functional groups of pollinators. Pollination networks are dynamic entities that constantly reshape their structure both at small- and large-time frames [2]. Importantly, we indicate caution with oceanic islands network sampling, by showing that temporal scale, and especially seasonality, has consequences for the description of network structure for communities. Using targeted sampling has been argued for since aggregating temporally extensive data generates many temporal “forbidden links” [e.g. 61, 62]. Even though these are important for structuring interaction networks, studies not usually checked assumptions regarding temporal forbidden links and variability of network structure [63]. The ideally identifying the network was through the contained temporal identities [50], since comparing seasonal networks more explicitly reveals otherwise unnoticed network dynamics [64]. Our study suggest that much about the temporal dynamics of plant-pollinator networks is still unknown, and such limitation is especially important for year-round active oceanic islands networks. Finally, variation in resource availability across time offers the opportunity to learn about the processes that determine patterns in the structure of pollination networks [41]. Therefore, studies considering temporal variation in pollination networks on a global scale of oceanic islands are important and should be encouraged.

Declarations

Authors' contributions

XPW and DXZ conceived and designed the experiments; XPW, TZ, MHW and MSW performed experiments; XPW analyzed the data and wrote draft. All authors read and approved the final manuscript.

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Availability of data and materials

The data sets supporting the results are included within the article and supplement materials.

Competing interests

The authors declare that they have no competing interests.

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Table And Figure Legends

Table 1 Network metrics for the plant-pollinator networks from Yongxing island community, showing the values for the complete, dry and rainy seasons, and spring, summer, autumn and winter season networks (two monthly periods for the four seasons respectively). *denotes network metrics which were significant; i.e., did not overlap null model expectations (95% confidence interval). See the Methods for an explanation of symbols.

Table 2 Results from mixed-effects models for the species level network metrics. Significance for the terms were obtained from a likelihood ratio test in which deviances of the models with and without a specific fixed variable were compared, and $P < 0.05$ are shown in bold. (1) represented compared between dry and rainy seasons; and (2) represented compared among spring, summer, autumn and winter seasons. Models indicated with ⁺ were constructed for the subset of data with only the plants and pollinators that occurred in both seasons or in all the four seasons.

Fig. 1. Seasonal variation in pollinaor species number of the pollinator functional groups in the sampled year-round in the Yongxing island community.

Fig. 2. Year-round, dry season, rainy season and four seasons networks of interactions for each studied formation (graphs were generated with Gephi Program). Plant and pollinator species are represented by green and red circles, respectively.

Fig. 3. Bivariate plot showing the relationship between the number of plant species in full bloom and the specialization ($H2'$) (open circles, dashed lines) and modularity (Q) (closed circles, solid line) among 7 pollination networks in Yongxing island community.

Fig. 4. (a) Species-level specialization d' and (b) species strength for plants species according to dry and rainy seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators (Mean $\pm$ SE). For the functional groups of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (Tukey test: $P < 0.05$).

Fig. 5. Plants and pollinators occurred both in dry and rainy seasons: (a) Species-level specialization d' and (b) species strength for plants species according to dry and rainy seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators (Mean $\pm$ SE). For the functional group of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (Tukey test: $P < 0.05$).

Fig. 6. (a) Species-level specialization d' and (b) species strength for plants species according to four seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators (Mean $\pm$ SE). For the plants in four seasons and functional group of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (* represent difference among four seasons of pollinators) (Tukey test: $P < 0.05$).

Fig. 7. Plants and pollinators occurred in all the four seasons: (a) Species-level specialization d' and (b) species strength for plants species according to four seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators (Mean $\pm$ SE). For the plants in four seasons and functional group of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (Tukey test: $P < 0.05$).

Fig. S1. Qualitative flower visitation networks for Year-round, dry season, rainy season and four seasons for each studied formation. In each network the rectangles represent inset taxa (top row) and plant species (bottom row), and the connecting triangles represent links between taxa. Visitor taxa are color-coded as follows: red, Hymenoptera; yellow, Diptera; blue, Lepidoptera; pink, Hemiptera; orange, Passeriformes. All networks are drawn to the same scale.

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Figures

Figure 1

Seasonal variation in pollinator species number of the pollinator functional groups in the sampled year-round in the Yongxing island community.

Figure 2

Year-round, dry season, rainy season and four seasons networks of interactions for each studied formation (graphs were generated with Gephi Program). Plant and pollinator species are represented by green and red circles, respectively.

Figure 3

Bivariate plot showing the relationship between the number of plant species in full bloom and the specialization (H_2') (open circles, dashed lines) and modularity (Q) (closed circles, solid line) among 7 pollination networks in Yongxing island community.

Figure 4

(a) Species-level specialization d' and (b) species strength for plants species according to dry and rainy seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators (Mean $\pm$ SE). For the functional groups of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (Tukey test: $P < 0.05$).

Figure 5

Plants and pollinators occurred both in dry and rainy seasons: (a) Species-level specialization d' and (b) species strength for plants species according to dry and rainy seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators (Mean $\pm$ SE). For the functional group of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (Tukey test: $P < 0.05$).

Figure 6

(a) Species-level specialization d' and (b) species strength for plants species according to four seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators (Mean $\pm$ SE). For the plants in four seasons and functional group of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (* represent difference among four seasons of pollinators) (Tukey test: $P < 0.05$).

Figure 7

Plants and pollinators occurred in all the four seasons: (a) Species-level specialization d' and (b) species strength for plants species according to four seasons; (c) Species-level specialization d' and (d) species strength for each functional group of pollinators (Mean ± SE). For the plants in four seasons and functional group of pollinators, significant differences according to the post hoc Tukey tests are indicated by different letters (Tukey test: $P < 0.05$).

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