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Author for correspondence:
*Dianxiang Zhang, Email: dx-zhang@scbg.ac.cn

A half-day flowering pattern helps plants sharing pollinators in an oceanic island community

Xiangping Wang, Tong Zeng, Mingsong Wu and Dianxiang Zhang*

Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, Guangdong, China

Abstract

The temporal pattern of flower opening and closure is a feature of the biology of many plant species, particularly those inhabiting oceanic islands where flowering generally lasts for only a few hours per day. Additionally, flower visitors often seek different floral sources on a timely basis, thus the relative timing of interactions is central to their status in pollination competition, or in the facilitation of pollination among co-flowering plants sharing pollinators. However, few studies have examined the impacts of daily temporal variation in flowering patterns on the pollinator network and competition on a community scale. In order to examine whether the daily pattern of flower opening and closure can impose temporal dynamics on interspecific interactions within a single day, plant–pollinator interaction networks (AM subweb and PM subweb) were quantified, and the relevant interactions between the two subwebs were compared using the Bray–Curtis dissimilarity of visitation frequencies in an oceanic island community (Paracel Islands, South China Sea). The role of species within networks and its variation between two subwebs were assessed by calculating the species-level specialization and species strength of each plant and pollinator species. The quantitative plant–pollinator interaction dissimilarity between morning and afternoon subsets was 0.69, and this value dropped to 0.58 when considering plant species flowering throughout the day. In our study, this dissimilarity between the two subwebs might be explained by the morning peak activity rather than a preference for morning flowers. No significant differences were detected in the species-level specialization and species strength of plants flowering all day from morning to afternoon at the community level. The flower visitation rates of native honeybee *Apis cerana* were not significantly different between morning and afternoon for most of the whole-day flowering plants. However, plant species only flowering either in the morning or the afternoon differed in the rate of visitation by *A. cerana*. The analyses of variation in the visitation rates of pollinators shared by plants within a single day in the studied community suggest that daily structuring at a community level and half-day staggered flowering during the morning or afternoon might reduce competitive interactions in oceanic insular habitats.

Introduction

Network analysis tools are important and have become widely used in pollination studies (Vázquez *et al.* 2009). It is widely known that the generation of plant–pollinator interaction networks involves the summation of flower visitation data collected over periods of days, weeks, months, or even years. Studies on plant–pollinator interaction networks have addressed temporal structure over both the seasonal and annual timescale (Burkle *et al.* 2013, Dupont *et al.* 2009, Fang & Huang 2012, 2016; Funamoto 2019, Kaiser-Bunbury *et al.* 2010, Medan *et al.* 2006, Petanidou *et al.* 2008, Sajjad *et al.* 2017, Souza *et al.* 2018). However, not all of the detectable links between plants and pollinators occur at the same time. The impact of certain plant–pollinator interactions depends critically on their relative timing (Baldock *et al.* 2011). For example, plant–pollinator interactions over field seasons or years generate many temporal 'forbidden links' (Carvalheiro *et al.* 2014, Jordano *et al.* 2003), in which specific plant–pollinator interactions cannot be discovered due to differences in plant and pollinator seasonal phenology. Nonetheless, the finer-scale temporal dynamics of plant–pollinator networks, such as variations in the network structure within a single day, have received limited attention so far (Baldock *et al.* 2011, Fründ *et al.* 2011, Olesen *et al.* 2008). Changes in the flower opening patterns of plant species within a single day may affect the whole pollination network through the dynamics of competition for pollinators. Although optimal flower opening times could be predicted by models (Miyake & Yahara 1999), studies focused on the effect of flower opening and closure on network dynamics are lacking.

Flowers of many plant species open for a limited time period during the day, and the resulting flowering pattern is influenced by the endogenous rhythms of plants induced by changes in light, temperature and humidity (van Doorn & van Meeteren 2003, von Hase *et al.* 2006). Therefore, flowers of such species often close in the morning, around midday, or early afternoon (van Doorn & Kamdee 2014). The daily pattern of flower opening and closure, however, has rarely been connected to plant–pollinator interactions (Fründ *et al.* 2011), which can provide information on pollination network structure, and can help predict community dynamics (Kaiser-Bunbury & Blüthgen 2015, Vázquez *et al.* 2009).

Oceanic islands are particularly well-suited for studying the effects of flower opening and closure on plant–pollinator interactions and community structure over the one-day timescale. On the one hand, global ecosystems markedly differ in floral longevity, with plants on islands tending to have the shortest-lived flowers due to lower elevation, higher temperature and lower water availability than those inhabiting mainlands (Jorgensen & Arathi 2013, Vesprini & Pacini 2005). On Yongxing Island (Paracel Islands, South China Sea), a high proportion of plant species opens their flowers in the morning and closes them around noon, while other species only open them during the afternoon (flower opening and closure times for 37 species are presented in Table S1). Oceanic islands harbour plants flowering for several hours a day, thus providing an ideal community to study the daily temporal characteristics of pollination networks. On the other hand, pollinators are a limiting resource on such islands due to their isolation and the relatively poor dispersal ability of insects (Bernardello *et al.* 2001, Gillespie & Roderick 2002, Traveset *et al.* 2016, Whittaker & Fernández-Palacios 2007). The reproductive success of co-flowering plant species influence each other through the sharing of pollinators, as well as competition for pollination services (Mitchell *et al.* 2009, van der Kooi *et al.* 2016). Highly generalized species easily settle in island communities (Kaiser-Bunbury *et al.* 2009), although most islands are inhabited by a limited number of insect species, thus plants may be subject to strong interspecific competition for pollinators (Traveset *et al.* 2013). Competition for pollinator visits can result in the structuring of communities by competitive exclusion, thus leading to minimized competition between plant species for pollinators in communities structured in this manner (Pauw 2013). One adaptation to minimize this competition may be a shift in flowering time (Devaux & Lande 2010). The opening and closure of flowers may be regulated by light and temperature signals from the environment (Maguvu *et al.* 2018), although they may also be influenced by biotic factors, such as pollinators. One of the most challenging questions is how plant species coexist when they share a limited pool of pollinators, as pollinator sharing may result in the deleterious effect of interspecific pollination that hinders plant reproductive success for both interacting plant species (Flanagan *et al.* 2009). Competition for pollination services may also cause the ecological sorting of flowering phenology (Aizen & Vázquez 2006). The temporal separation of blooming time of co-flowering species may reduce competition for pollination and permit coexistence. However, the question of whether flower opening and closure time could affect plant–pollinator interactions, and the mechanism of sharing a limited pollinator pool among co-flowering plants remain largely unexplored.

In the current study, the effects of early flower closure and late flower opening on plant–pollinator interaction networks are analysed. The following questions are addressed: (1) Is there temporal variation between morning and afternoon in plant–pollinator interaction networks and species-level specialization? (2) Do the pollinator species of early-closing plants only visit them during the morning and switch to other plants flowering in the afternoon? Is there a difference between morning and afternoon in the visitation rate of shared pollinators of whole-day flowering plants?

Materials and Methods

Study site and periods

The Xisha Islands (Paracel Islands) are a series of coral islets, formed about 7000 years ago through coral growth and crust uplift (Taylor & Hayes 1980), located in the South China Sea (15°46′–17°08′N, 110°11′–112°54′E). Yongxing Island (16°49′N, 112°20′E), with a total area of 2.6 km^2, is the largest islet of this archipelago. The data on flowering plants and potential pollinators were collected from 1 July to 31 August 2018 in Yongxing Island community. Sampling was conducted in 30 quadrats sized 5×5 m^2, at least 10 m away from each other. Plant species in blooming had not changed across the two-monthly period, and all pollinator species were present over the full two months. To maximize the possibility of detecting different floral visitors and reduce the effects of geographic distribution, we collected data at quadrats rather than species.

Pollination data collection

Pollinators were investigated on sunny days without wind over two consecutive months, between 8:00 h and 18:00 h (the webs have data before 12:00 h and after 13:00 h). Flowers or flower heads were counted for each plant species of 30 quadrats. In each quadrat, visitation was quantified for each plant species with at least 15 floral units. Animal visits to flowers of each plant species were recorded during 30-min observations in each sampling interval (08:00–12:00 and 13:00–18:00). Each quadrat was observed for two consecutive days. For each observation interval, each visit was recorded if a visitor contacted with the anther and/or stigma for more than 1 s of a floral unit. Return back visits of the same individual in its foraging bout to the same floral unit were counted as a second visit. Therefore, all flower visiting insects that feed on flowers were recorded, regardless of the efficacy of their visit. The sampling times in AM and PM were long enough (nearly 200 hours) for collecting the pollination data. All flower visitors were firstly morphotyped and noted to family in the field and captured for further identification to the lowest possible taxonomic level in the laboratory by entomologists (see Acknowledgements).

To verify if the flower visitors are the potential pollinators for each plant species, the pollen loads from five collected insect individuals of each species were examined for pollen analysis. Pollen grains on the body of visitors were taken off with gelatin cubes and then transferred to a clean slide (Tong & Huang 2018). The slides were warmed gently to melt the jelly, and pollen samples were viewed under electron microscope. Pollen grains were identified by comparing with a reference library of pollen based on those removed from field-collected flowers (Fang & Huang 2013). If four or five specimens of a plant-flower visitor pair carried the host plant pollen, we presumed that the visitor was a potential pollinator (hereafter, named 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 (international acronym: IBSC). Samples of collected insects were deposited at the South China Botanical Garden, Chinese Academy of Sciences.

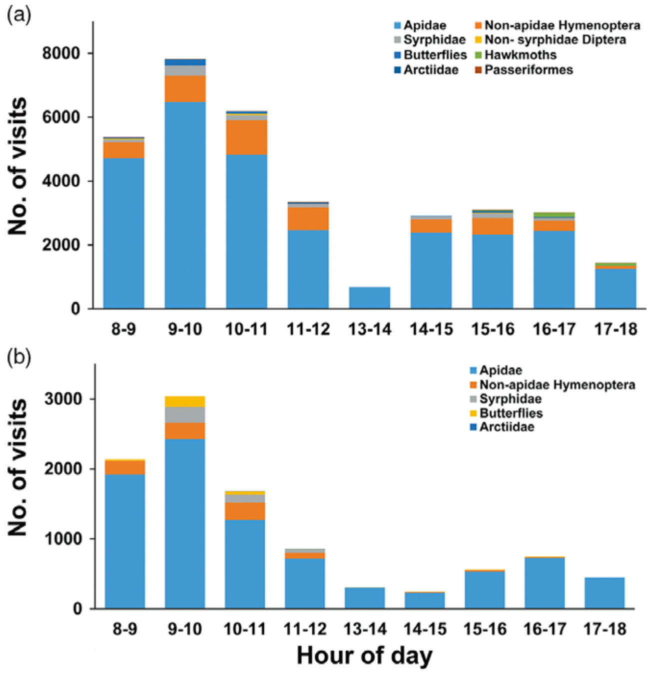

Figure 1. Circadian pattern of flower visitation to (a) all plants in the Yongxing Island community and (b) plant species blooming only in the morning or afternoon. (a) and (b) suggest that Apidae was the most active pollinators through the whole day, and plants flowering during the morning or afternoon were competition for their pollination service.

Data analysis

We conducted two quantitative bipartite plant–pollinator networks from the two-monthly data for Yongxing Island community, using visitation frequencies of pollinator species to each plant species as a surrogate of interaction strength. To analyse the temporal dynamics of plant–pollinator interactions within a single day, we separated the network into morning (AM) and afternoon (PM) subwebs. For this purpose, 'noon' was defined as the time of solar zenith (13:00 h) (Fründ *et al.* 2011). We calculated metrics illustrating distinct structural properties of the network which were previously shown to be less sensitive to sampling effort (Fründ *et al.* 2016, Vizentin-Bugoni *et al.* 2016). Connectance (and weighted connectance) which is the fraction of interactions occurring in the network, increasing with network generalization. Nestedness (and weighted nestedness) quantifies the degree of interactions of specialized species in the network. Network-wide specialization (H_2') describes if species restrict their interactions from those randomly expected based on a partner's availability (Blüthgen *et al.* 2006), ranging from 0 (low specialization) to 1 (high specialization). Network modularity (Q) quantifies the prevalence of interactions within subsets of species in the community. Q was calculated using the *QuaBiMo* algorithm based on a hierarchical random graph approach adapted for quantitative bipartite networks (Dormann & Strauss 2014). We ran the *QuaBiMo* algorithm 10 times and retained the iteration with highest Q value, as the algorithm is a stochastic process. NODF is the nestedness measure, correcting for matrix fill and matrix dimensions, ranging from 0 (non-nestedness) to 100 (perfect nesting). Network metrics can be influenced by intrinsic characteristics such as the number of interacting species and sampling effort (Blüthgen *et al.* 2006, Fründ *et al.* 2016, Vizentin-Bugoni *et al.* 2016); hence the significance of metrics is assessed by comparison with null model networks. We used the Patefield null model, which fixes the network size and the marginal totals while shuffling interactions randomly (Patefield 1981). 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. The quantitative bipartite plant–pollinator networks were compared between two subwebs using Bray–Curtis dissimilarity of visitation frequencies.

To check the role of species within networks and how it varies between morning and afternoon, we calculated two species-level indices that present distinct topological properties of a species: (1) species-level specialization index d′, which quantifies the level of specialization of each species based on its discrimination from random selection of interacting partners, with higher values indicating higher specialization (Blüthgen *et al.* 2006), ranging from 0 (no specialization) to 1 (perfect specialists); and (2) species strength, which is the sum of the proportions of interactions performed by a given species across all its interaction partners, with higher values indicating that more pollinators depend on a specific plant species, and vice versa (Bascompte *et al.* 2006). Web plots and all network-related indices calculation were created with the 'bipartite' package version 2.05 (Dormann *et al.* 2008) in R3.4.4 (R Development Core Team 2016). We compared species-level specialization and species strength of whole-day flowering plant species and different functional pollinator groups between morning and afternoon subwebs by one-way analysis (ANOVA) of variance using Tukey HSD's method in IBM SPSS 19.0, and data were presented as mean ± SE.

To assess the effect of half-day blooming flowers on the competition of pollinators among pollinator-sharing plants in the community, we calculated separately for morning and afternoon visitation rate to five whole-day flowering plant species (*Morinda citrifolia*, *Sesuvium portulacastrum*, *Scaevola taccada*, *Tridax procumbens* and *Wedelia trilobata*) which were mainly specialized visited by the most common pollinator *Apis cerana* in the community. Since *A. cerana* was the main pollinator species of the six half-day flowering plant species, we compared the difference of visitation rate by *A. cerana* among four morning flowering plant species and two afternoon flowering plant species. We also calculated separately for morning and afternoon visitation rate of six whole-day flowering plant species by another two Apidae visitor species in the community, because these two visitor species were also shared by half-day flowering plants and whole-day flowering plants: *Ceratina lieftincki* visiting *Phyla nodiflora*, *Tridax procumbens* and *Wedelia trilobata*, and *Braunapis puangensis* visiting *Messerschmidia argentea*, *Scaevola taccada* and *Tridax procumbens*. Finally, we calculated separately for morning and afternoon visitation rate of *Canavalia maritima* and *Cordia subcordata* which were high specialized species and attracted different pollinator spectrum. Visitation rate was calculated as the number of visits from each pollinator species per hour per flower for each plant species. We used generalized linear mixed-effects models (negative binomial) for the visitation rate data. Morning or afternoon was included in the model as fixed effect, and species identity was included as a random effect using the 'lme4' R package. Visitation rate of the plant species by the same pollinator species were compared between morning and afternoon by one-way analysis (ANOVA) of variance using Tukey HSD's method in IBM SPSS 19.0 and data were presented as mean ± SE.

Table 1. Network metrics for the quantitative plant–pollinator networks from Yongxing Island community, showing the values for morning, afternoon and whole-day networks. * represents network metrics which are significant (do not overlap null model expectations) (95% confidence interval).

Network metrics	Morning	Afternoon	Whole day
Connectance	0.201*	0.166*	0.193*
Weighted connectance	0.048*	0.051*	0.048*
Nestedness	16.237*	12.095*	16.483*
Weighted nestedness	0.357*	0.349*	0.387*
NODF	42.704*	41.389*	43.002*
Weighted NODF	19.257*	18.826*	19.081*
Interaction evenness	0.416*	0.357*	0.418*
Specialization H2	0.649	0.730*	0.677*
Modularity Q	0.551*	0.458*	0.552*
Number of pollinators	28	29	32
Number of plants	34	25	37

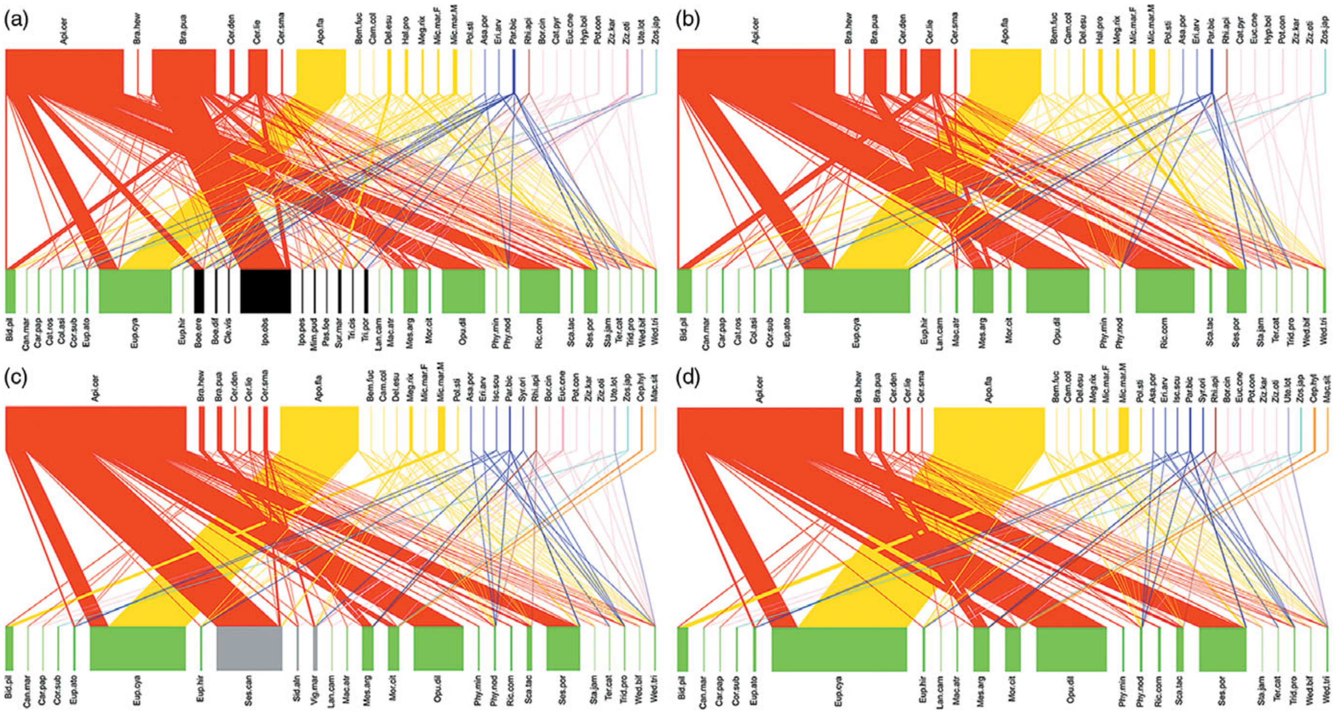

Figure 2. Quantitative plant–pollinator interaction networks change between morning and afternoon in Yongxing Island community. (a) and (c) Morning subweb (all interactions observed before 12:00 h), (b) and (d) Afternoon subweb (after 13:00 h). The rectangles represent pollinator species (top row) and plant species (bottom row), and the connecting lines represent links between plant and pollinator species. The width of rectangles and connecting lines are proportional to the visitation frequency per nodes. Pollinator group are colour-coded as follows: red, Apidae; yellow, non-Apidae hymenoptera; blue, Syrphidae; brown, non-Syrphidae diptera; pink, butterflies; purple, Arctiidae; cyan, Passeriformes; orange, hawkmoths. Plant species are colour-coded as follows: green, whole-day flowering plants; black, morning flowering plants; grey, afternoon flowering plants. All networks are drawn to the same scale. Full species names of plants, and flowering open and closure times are available in Table S1. Full species names of pollinators and the original links between plants and pollinators in the whole day are available in Table S2.

Results

The present study yielded a total of 33,864 interactions between 32 pollinator species and 37 plant species distributed across 21 families for all of the evaluated periods. In the AM subweb, 22,735 visits between 34 plant species and 28 pollinator species were recorded, compared with 11,129 visits between 25 plant species and 29 pollinator species in the PM subweb. More than a third (34.0%) of all observed interactions in the AM subweb were associated with 10 morning flowering plant species, while the PM subweb was characterized by three afternoon flowering plant species accounting for 20.7% of all observed interactions (Figure 1). The flower opening and closure times in a single day for 37 plant species are shown in Table S1. Plant–pollinator interactions involving plants blooming in the morning or in the afternoon occurred

Table 2. Comparison of species-level species strength and specialization (d′) (means ± SE) of each functional pollinator group between morning and afternoon networks in the Yongxing Island community.

	Specialization (d′)				Species strength			
Pollinator functional group	df	Mean square	F	P	df	Mean square	F	P
Apidae	1	0.009	0.259	0.62	1	3.308	0.227	0.64
Non-apidae Hymenoptera	1	0.104	1.283	0.28	1	0.265	0.426	0.53
Syrphidae	1	0.070	0.883	0.40	1	0.007	0.049	0.84
Butterflies	1	0.002	0.024	0.88	1	0.006	0.021	0.89

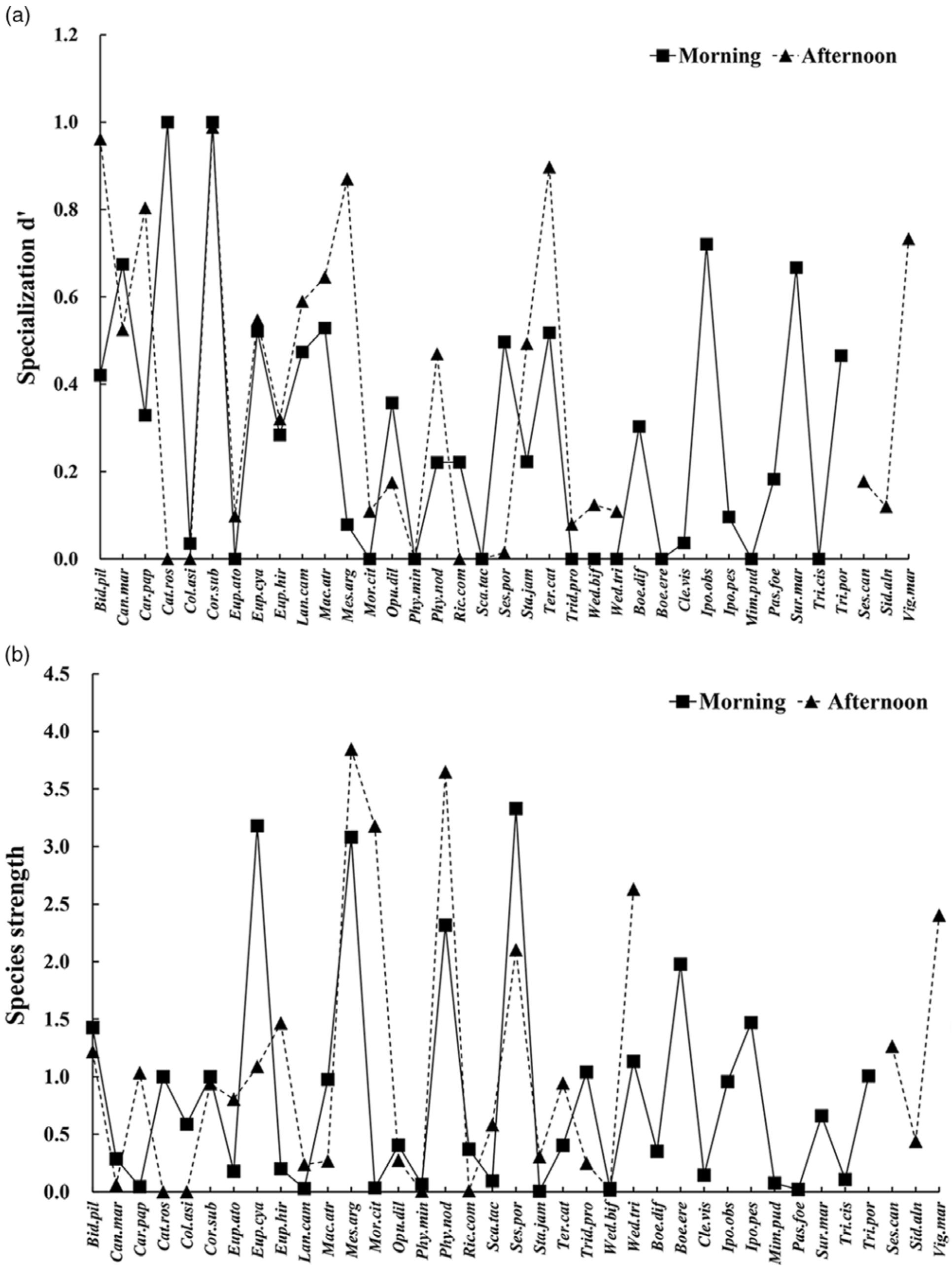

Figure 3. Changes of species-level specialization (a) and species strength (b) of each plant species between morning and afternoon in the Yongxing Island community.

mainly between 9 am and 10 am, or 4 pm and 5 pm, respectively (Figure 1). Pollinator specimens observed were representatives of Apidae, non-Apidae Hymenoptera, Syrphidae, non-Syrphidae Diptera, butterflies, hawkmoths, Arctiidae and Passeriformes. The dominant pollinator taxon was Apidae representing 81.3% and 81.6% of all recorded visits in the morning and afternoon

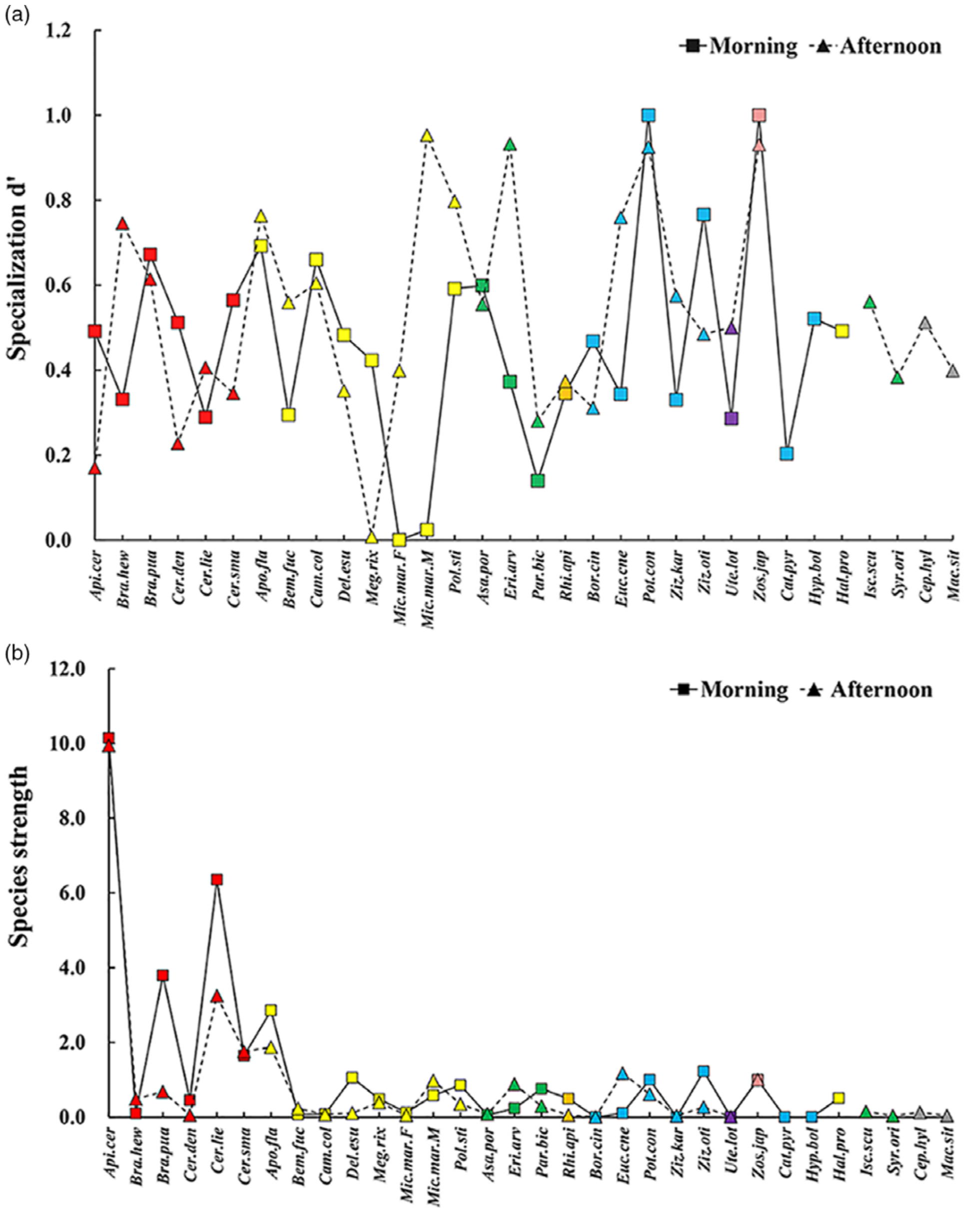

Figure 4. Changes of species-level specialization (a) and species strength (b) of each pollinator species between morning and afternoon in the Yongxing Island community. Functional pollinator groups are colour-coded as follow: red, Apidae; yellow, non-Apidae hymenoptera; green, Syrphidae; orange, non-Syrphidae diptera; blue, butterflies; purple, Arctiidae; pink, Passeriformes; grey, hawkmoths.

networks, respectively, accounting for more visits in total than the other functional groups combined (Figure 1). In addition, visits by *A. cerana* made up 61.8% and 88.9% of all Apidae visits in the morning and afternoon networks, respectively.

Clear temporal variation in the plant–pollinator interactions was observed upon visual comparisons of morning and afternoon networks (Figure 2). The Bray-Curtis dissimilarities of plant–pollinator interaction between morning and afternoon subsets was quantified as 0.69, and this value dropped to 0.58 when only whole-day flowering plants were considered. Meanwhile, most network-level indices presented higher values for the morning when compared with the afternoon network (Table 1).

Neither species-level differences in specialization ($F = 0.394$, $P = 0.53$) or species strength ($F = 0.222$, $P = 0.64$) were detected for whole-day flowering plant species, nor did species-level indices differ between morning and afternoon networks for the different functional groups (Table 2). Furthermore, certain plant and pollinator species presented higher specialization and species strength in morning networks compared with afternoon ones, while others showed the opposite trend (Figures 3 and 4).

For whole-day flowering plants, the rates of flower visitation by *A. cerana* were not significantly different between the morning and the afternoon ($z = 1.580$, $P = 0.11$): *Morinda citrifolia* ($F = 1.887$, $P = 0.18$), *Sesuvium portulacastrum* ($F = 0.328$, $P = 0.58$), *Scaevola taccada* ($F = 0.614$, $P = 0.44$) and *Tridax procumbens* ($F = 0.376$, $P = 0.54$); however, *Wedelia trilobata* flowers were visited less frequently during the afternoon than the morning ($F = 8.065$, $P = 0.007$) (Figure 5). Nonetheless, plant species blooming only in the morning (four species) or the afternoon (two species) showed some differences in the rates of visitation by *A. cerana* ($df = 5$, $F = 7.547$, $P < 0.001$). Notably, the visitation rate of *Sesbania cannabina*, which flowers in the afternoon, was significantly higher than that of plants flowering during the morning (Figure 5). The rates of visitation by *Ceratina lieftincki* of whole-day flowering plant species, specifically of *Phyla nodiflora* ($F = 1.592$, $P = 0.22$), *T. procumbens* ($F = 0.550$, $P = 0.46$) and *W. trilobata* ($F = 3.540$, $P = 0.07$) did not

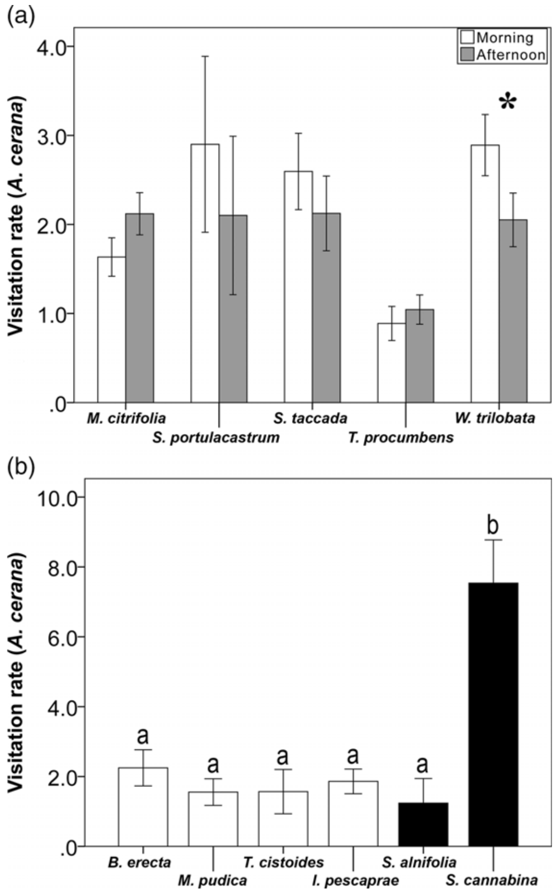

Figure 5. (a) Comparison of visitation rate (means ± SE) of *Apis cerana* to whole-day flowering plant species between morning and afternoon. These plant species have a pollinator spectrum overlapping with morning flowering plant species; (b) Comparison of visitation rate (means ± SE) of *Apis cerana* among morning flowering plant species (white) and afternoon flowering plant species (black). * and different letters represent that significant difference are detected using one-way ANOVA, P < 0.05. For (b), significant differences according to the post hoc Tukey tests are indicated by different letters (Tukey test: P < 0.05).

significantly differ between morning and afternoon (z = 0.836, P = 0.40). Meanwhile, the rates of visitation by *Braunapis puangensis* of whole-day flowering plant species showed certain differences between morning and afternoon (z = 3.163, P = 0.002): *S. taccada* (F = 2.219, P = 0.15) and *T. procumbens* (F = 1.628, P = 0.12), however, the visitation rate of *Messerschmidia argentea* (F = 13.211, P = 0.001) was reduced in the afternoon (Figure 6). No difference was detected between the visitation rates of two plant species attracting a different pollinator spectrum before and after noon: *C. smaragdula* visiting *Canavalia maritima* (F = 0.711, P = 0.41); *Zosterops japonicus* visiting *Cordia subcordata* (F = 2.801, P = 0.12).

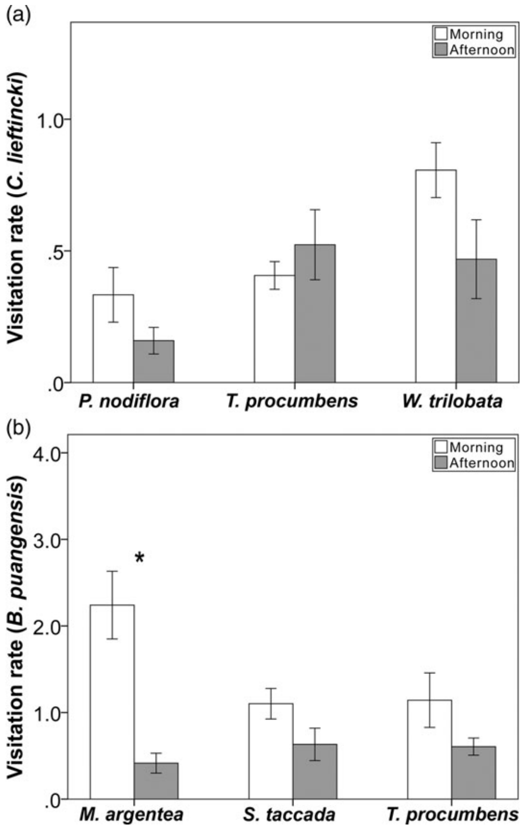

Figure 6. Comparison of visitation rate (means ± SE) of (a) *Ceratina lieftincki* and (b) *Braunapis puangensis* to whole-day flowering plant species between morning and afternoon. These plant species have a pollinator spectrum overlapping with morning flowering plant species. * represents significant difference detected using one-way ANOVA, P < 0.05.

Discussion

The data obtained demonstrate that most plant–pollinator interactions occurred during the morning, which is likely the result of the domination of morning flowering plant species in the Yongxing Island community. The observed interactions in the morning and afternoon might be explained by the sampling design, where observation time was not relatively homogeneously distributed across the main period of pollinator activity (Schwarz *et al.* 2020). Early flowering plant species had high visitation rates by pollinators, thus early flower closure and late flower opening may have a significant impact on plant–pollinator networks. In our model, the quantitative dissimilarity of plant–pollinator interaction between morning and afternoon networks was lower when only whole-day flowering plants were considered. Moreover, the morning subweb presented higher values for most network indices when compared with the afternoon subweb, thereby the temporal variation of network structure within a single day might be influenced by the presence of half-day flowering plants closing their flowers around noon or opening their flowers during the afternoon.

In the plant–pollinator community of our study, pollinators did not present a clear pattern of daily activity; their foraging activity declined in the afternoon but did not completely diminish. This contrasts with the results of Fründ *et al.* (2011) for a community in Southern Germany, where a number of pollinator species specialized on Cichorioideae were absent during the afternoon, while their flowers closed around noon. According to other studies, the within-day variation in insect activity patterns was considered likely due to abiotic or biotic factors (Lienhard *et al.* 2010, Stone *et al.* 1999). In the community of the present study, the lower afternoon foraging activity might be due to the morning peak of insect activity rather than a preference for morning half-day flowering plants. Although the differences in species-level specialization and species strength of whole-day flowering plant species and various functional pollinator groups were insignificant between morning and afternoon networks, these two indices of plant and pollinator species still showed a certain level of temporal variation within a single day. Thus, no stable role of these plant and pollinator species could be established over a one-day timescale, suggesting that plant species share a pool of generalist pollinators, which provide a certain level of pollination and plant population maintenance on oceanic islands.

In our case study, a sizeable proportion of plant species (35%) were only flowering either in the morning or the afternoon, thus reducing competition for pollination services. It is considered that the half-day flowering pattern of some plant species allows for relying on the same pollination resource, and contributes to maintaining community stability in the long term. This study showed no changes in active pollinator species throughout the day, but the same pollinator species shifted from morning flowering plants to afternoon flowering plants maximizing the utilization of floral resources throughout the day. Morning and afternoon flowering plants both mainly relied on pollination by Apidae, which may generate fierce competition for pollination services. Correspondingly, visitation rates of whole-day flowering plants by *A. cerana*, *C. lieftincki* and *B. puangensis* showed no significant differences between the times of day. Nevertheless, the flower visitation rate of *M. argentea* by *B. puangensis* was reduced during the afternoon. One potential reason is that *M. argentea* floral resources are significantly larger in the morning (Wang *et al.*, unpublished data). In addition, the target of *A. cerana* visits changed from morning flowering plants to afternoon flowering plants, as evidenced by the significantly higher visitation rate of afternoon flowering *S. cannabina* by *A. cerana*, as compared with morning flowering plants. These results were inconsistent with those of Fründ *et al.* (2011), namely that whole-day flowering plant species were in competition for pollinators of morning flowering plants, and that shared pollinators showed lower visitation rates in the morning. In the community subject to the present work, competition for pollinators among co-flowering plants sharing pollinators could be reduced due to the temporal segregation between morning and afternoon flowering species. In a similar manner, pollinators exploit *Dalechampia heteromorpha* that opens and produces pollen during the early morning hours, and subsequently switch to *D. scandens* that flowers exclusively in the afternoon, thereby minimizing competition between the two sympatric plant species (Armbruster & Herzig 1984). Overlap in the flowering times of mass-flowering dipterocarp species is significantly reduced by their staggering flowering periods, resulting in reduced competition for pollinators (Ashton *et al.* 1988). Consequently, on oceanic islands, the temporal dynamics of mutualistic and competitive interactions may be different from the patterns suggested for larger temporal scales. Hence competition for pollinators may be reduced among co-flowering plant species, while competition of pollinators is probably more pronounced between morning and afternoon flowering plants.

Theoretical work on pollination networks has shown that generalist core species make networks stable and tolerant to extinctions (Bascompte & Jordano 2007, Emer *et al.* 2016). Our analyses, however, question the assumption of functional redundancy. For example, pollinators need different plant species for providing resources at different times of the day. Nevertheless, the presence of morning or afternoon flowering suggests a flexible link structure, enabling pollinators to establish new links within the same plant community. Changes in plant–pollinator interactions over a one-day timescale should be considered in the interpretation of network data without whole-day sampling, as important interactions may be missed if sampling is restricted to a specific part of the day, and cross-day turnover may be overestimated in studies with varied sampling times (Fründ *et al.* 2011). The within-day shift pattern featured in plant–pollinator interactions may also occur in other communities, as many plant–pollinator networks are characterized by a similar circadian variation of interactions, and a high number of plant species show intra-day flower opening and pollen availability patterns (Fründ *et al.* 2011, Hoehn *et al.* 2008). In summary, the dynamics of flower opening and closure time need to be considered when designing field surveys involving pollinators, flower availability, and plant–pollinator interactions.

On oceanic islands, temporal plant–pollinator network dynamics may enhance biodiversity maintenance through temporal niche partitioning (Abdala-Roberts *et al.* 2007), which may also manifest on a daily basis. As a result of reduced competition for pollinators, respective plant communities are expected to benefit from this pattern. Owing to the poor dispersal ability of insects, islands have a depauperate pollinator fauna and a relative low pollinator/plant ratio in turn (Bernardello *et al.* 2001, Dupont *et al.* 2003, Gillespie & Roderick 2002, Stuessy *et al.* 2017, Traveset *et al.* 2016, Trøjelsgaard & Olesen 2013). The half-day flowering pattern in oceanic island communities might thus be attributed to the comparatively small number of pollinators and subsequent high competition for pollinator services. Flowering periods limited to morning or afternoon might help to reduce the amount of resources required for open flowers, such as that of water (Ashman & Schoen 1994), and may improve the visiting accuracy of pollinators by guiding them to flower specimens in need of pollination, thus enhancing pollination efficiency and effectiveness in these biogeographic areas. Since only one oceanic island was investigated in this study, more islands need to be targeted to explore the effect of within-day flowering time limit and other factors on plant–pollinator network structure.

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References

Abdala-Roberts L, Parra-Tabla V and Navarro J (2007) Is floral longevity influenced by reproductive costs and pollination success in *Cohniella ascendens* (Orchidaceae)? *Annals of Botany* **100**, 1367–1371.

Aizen MA and Vázquez DP (2006) Flowering phenologies of hummingbird plants from the temperate forest of southern South America: is there evidence of competitive displacement? *Ecography* **29**, 357–366.

Armbruster WS and Herzig AL (1984) Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. *Annals of the Missouri Botanical Garden* **71**, 1–16.

Ashman TL and Schoen DJ (1994) How long should flowers live? *Nature* **371**, 788.

Ashton PS, Givnish TJ and Appanah S (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* **132**, 44–66.

Baldock KC, Memmott J, Ruiz-Guajardo JC, Roze D and Stone GN (2011) Daily temporal structure in African savanna flower visitation networks and consequences for network sampling. *Ecology* **92**, 687–698.

Bascompte J and Jordano P (2007) Plant–animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **38**, 567–593.

Bascompte J, Jordano P and Olesen JM (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431–433.

Bernardello G, Anderson GJ, Stuessy TF and Crawford DJ (2001) A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernández Islands (Chile). *Botanical Review* **67**, 255–308.

Blüthgen N, Menzel F and Blüthgen N (2006) Measuring specialization in species interaction networks. *Ecology* **6**, 1–12.

Burkle LA, Marlin JC and Knight TM (2013) Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* **339**, 1611–1615.

Carvalheiro LG, Biesmeijer JC, Benadi G, Fründ J, Stang M, Bartomeus I . . . and Baldock KC (2014) The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecology Letters* **17**, 1389–1399.

Devaux C and Lande R (2010) Selection on variance in flowering time within and among individuals. *Evolution: International Journal of Organic Evolution* **64**, 1311–1320.

R Development Core Team (2016) *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/.

Dormann CF, Gruber B and Fründ J (2008) Introducing the bipartite package: analysing ecological networks. *R News* **8**, 8–11.

Dormann CF and Strauss R (2014) A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution* **5**, 90–98.

Dupont YL, Hansen DM and Olesen JM (2003) Structure of a plant-flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography* **26**, 301–310.

Dupont YL, Padrón B, Olesen JM and Petanidou T (2009) Spatio-temporal variation in the structure of pollination networks. *Oikos* **118**, 1261–1269.

Emer C, Memmott J, Vaughan IP, Montoya D and Tylianakis JM (2016) Species roles in plant-pollinator communities are conserved across native and alien ranges. *Diversity and Distributions* **22**, 841–852.

Fang Q and Huang SQ (2012) Relative stability of core groups in pollination networks in a biodiversity hotspot over four years. *PLoS ONE* **7**, e32663.

Fang Q and Huang SQ (2013) A directed network analysis of heterospecific pollen transfer in a biodiverse community. *Ecology* **94**, 1176–1185.

Fang Q and Huang SQ (2016) Plant-pollinator interactions in a biodiverse meadow are rather stable and tight for 3 consecutive years. *Integrative Zoology* **11**, 199–206.

Flanagan RJ, Mitchell RJ, Knutowski D and Karron JD (2009) Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). *American Journal of Botany* **96**, 809–815.

Fründ J, Dormann CF and Tscharntke T (2011) Linné's floral clock is slow without pollinators-flower closure and plant-pollinator interaction webs. *Ecology Letters* **14**, 896–904.

Fründ J, McCann KS and Williams NM (2016) Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. *Oikos* **125**, 502–513.

Funamoto D (2019) Plant-pollinator interactions in East Asia: a review. *Journal of Pollination Ecology* **25**, 46–68.

Gillespie RG and Roderick GK (2002) Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology* **47**, 595–632.

Hoehn P, Tscharntke T, Tylianakis JM and Steffan-Dewenter I (2008) Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences* **275**, 2283–2291.

Jordano P, Bascompte J and Olesen JM (2003) Invariant properties in coevolutionary networks of plant-animal interactions. *Ecology Letters* **6**, 69–81.

Jorgensen R and Arathi HS (2013) Floral longevity and autonomous selfing are altered by pollination and water availability in *Collinsia heterophylla*. *Annals of Botany* **112**, 821–828.

Kaiser-Bunbury CN and Blüthgen N (2015) Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB Plants* **7**, plv076.

Kaiser-Bunbury CN, Memmott J and Müller CB (2009) Community structure of pollination webs of Mauritian heathland habitats. *Perspectives in Plant Ecology, Evolution and Systematics* **11**, 241–254.

Kaiser-Bunbury CN, Muff S, Memmott J and Müller CB (2010) The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecology Letters* **13**, 442–452.

Lienhard A, Mirwald L, Hötzl T, Kranner, I and Kastberger G. (2010) Trade-off between foraging activity and infestation by nest parasites in the primitively eusocial bee *Halictus scabiosae*. *Psyche: A Journal of Entomology* 2010, 707501.

Maguvu TE (2018) Effect of different photoperiods on flower opening time in *Portulaca umbraticola*. *The Horticulture Journal* **87**, 124–131.

Medan D, Basilio AM, Devoto M, Bartoloni NJ, Torretta JP and Petanidou T (2006) *Measuring generalization and connectance in temperate, year-long active systems*. In Waster NM and Ollerton J (eds), *Plant-Pollinator Interactions: From Specialization to Generalization*. Chicago, IL: University of Chicago Press, pp. 245–259.

Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM and Karron JD (2009) New frontiers in competition for pollination. *Annals of Botany* **103**, 1403–1413.

Miyake T and Yahara T (1999) Theoretical evaluation of pollen transfer by nocturnal and diurnal pollinators: when should a flower open? *Oikos* **86**, 233–240.

Olesen JM, Bascompte J, Elberling H and Jordano P (2008) Temporal dynamics in a pollination network. *Ecology* **89**, 1573–1582.

Patefield WM (1981) Algorithm AS 159: An efficient method of generating random R x C tables with given row and column totals. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* **30,** 91–97.

Pauw A (2013) Can pollination niches facilitate plant coexistence? *Trends in Ecology and Evolution* **28**, 30–37.

Petanidou T, Kallimanis AS, Tzanopoulos J, Sgardelis SP and Pantis JD (2008) Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters* **11**, 564–575.

Sajjad A, Saeed S, Ali M, Khan FZA, Kwon YJ and Devoto M (2017) Effect of temporal data aggregation on the perceived structure of a quantitative plant-floral visitor network. *Entomological Research* **47**, 380–387.

Schwarz B, Vázquez DP, CaraDonna PJ, Knight TM, Benadi G, Dormann CF, . . . and Fründ J (2020) Temporal scale-dependence of plant-pollinator networks. *Oikos* **129**, 1289–1302.

Souza CS, Maruyama PK, Aoki C, Sigrist MR, Raizer J, Gross CL and de Araujo AC (2018) Temporal variation in plant-pollinator networks from seasonal tropical environments: higher specialization when resources are scarce. *Journal of Ecology* **106**, 2409–2420.

Stone GN, Gilbert F, Willmer P, Potts S, Semida F and Zalat S (1999) Windows of opportunity and the temporal structuring of foraging activity in a desert solitary bee. *Ecological Entomology* **24**, 208–221.

Stuessy TF, Crawford DJ, López-Sepúlveda P and Ruiz EA. (eds) (2017) *Plants of Oceanic Islands: Evolution, Biogeography, and Conservation of the Flora of the Juan Fernández (Robinson Crusoe) Archipelago*. Cambridge: Cambridge University Press.

Taylor B and Hayes DE (1980) *The tectonic evolution of the South China Basin. In The Tectonic and Geologic Evolution of Southeast Asian Seas and Islands. Geophysics Monograph Series*. Washington, D.C.: AGU, vol. **23**, pp. 89–104.

Tong Y, Jian SG, Chen Q, Li YL and Xing F (2013) Vascular plant diversity of the Paracel Islands, China. *Biodiversity Science* **21**, 364–374.

Tong ZY and Huang SQ (2018) Safe sites of pollen placement: a conflict of interest between plants and bees? *Oecologia* **186**, 163–171.

Traveset A, Heleno R, Chamorro S, Vargas P, McMullen CK, Castro-Urgal R, . . . and Olesen JM (2013) Invaders of pollination networks in the Galápagos Islands: emergence of novel communities. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20123040.

Traveset A, Tur C, Trøjelsgaard K, Heleno R, Castro-Urgal R and Olesen JM (2016) Global patterns of mainland and insular pollination networks. *Global Ecology and Biogeography* **25**, 880–890.

Trøjelsgaard K and Olesen JM (2013) Macroecology of pollination networks. *Global Ecology and Biogeography* **22**, 149–162.

van Der Kooi CJ, Pen I, Staal M, Stavenga DG and Elzenga JTM (2016) Competition for pollinators and intra-communal spectral dissimilarity of flowers. *Plant Biology* **18**, 56–62.

van Doorn WG and Kamdee C (2014) Flower opening and closure: an update. *Journal of Experimental Botany* **65**, 5749–5757.

van Doorn WG and van Meeteren U (2003) Flower opening and closure: a review. *Journal of Experimental Botany* **54**, 1801–1812.

Vázquez DP, Blüthgen N, Cagnolo L and Chacoff NP (2009) Uniting pattern and process in plant-animal mutualistic networks: a review. *Annals of Botany* **103**, 1445–1457.

Vesprini JL and Pacini E (2005) Temperature-dependent floral longevity in two *Helleborus* species. *Plant Systematics and Evolution* **252**, 63–70.

Vizentin-Bugoni J, Maruyama PK, Debastiani VJ, Duarte LDS, Dalsgaard B and Sazima M (2016) Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant-hummingbird network. *Journal of Animal Ecology* **85**, 262–272.

Von Hase A, Cowling RM and Ellis AG (2006) Petal movement in cape wildflowers protects pollen from exposure to moisture. *Plant Ecology* **184**, 75–87.

Whittaker RJ and Fernández-Palacios JM (2007) *Island Biogeography: Ecology, Evolution, and Conservation.* Oxford: Oxford University Press.