ORIGINAL ARTICLE

Plant-pollinator interactions in a biodiverse meadow are rather stable and tight for 3 consecutive years

Qiang FANG[1,2] and Shuangquan HUANG[2]

[1]College of Agriculture, Henan University of Science and Technology, Luoyang, China and [2]Institute of Evolution & Ecology, School of Life Sciences, Central China Normal University, Wuhan, China

Abstract

Plant–pollinator interactions can be highly variable across years in natural communities. Although variation in the species composition and its basic structure has been investigated to understand the dynamic nature of pollination networks, little is known about the temporal dynamic of interaction strength between the same plant and pollinator species in any natural community. Pollinator-mediated selection on the evolution of floral traits could be diminished if plant–pollinator interactions vary temporally. To quantify the temporal variation in plant–pollinator interactions and the interaction strength (observed visits), we compared weighted networks between plants and pollinators in a biodiverse alpine meadow in Shangri-La, southwest China for 3 consecutive years. Although plant–pollinator interactions were highly dynamic such that identical interactions only accounted for 10.7% of the total between pair years, the diversity of interactions was stable. These identical interactions contributed 41.2% of total visits and were similar in strength and weighted nestedness. For plant species, 72.6% of species were visited by identical pollinator species between pair years, accounting for over half of the total visits and three-quarters at the functional group level. More generalized pollinators contributed more connectiveness and were more central in networks across years. However, there was no similar or even opposite trend for plant species, which suggested that specialized plant species may also be central in pollinator networks. The variation in pollinator composition decreased as pollinator species numbers increased, suggesting that generalized plants experienced stable pollinator partition. The stable, tight interactions between generalized pollinators and specialized plants represent cornerstones of the studied community.

Key words: interaction strength, plant–pollinator interaction, quantitative network, temporal variation, turnover

INTRODUCTION

To understand the evolutionary diversification of plant–pollinator interactions, studies ranging from a single species to entire communities are required (Waser & Ollerton 2006). Investigations of plant–pollinator interactions at the community level have shown that extreme mutualism between a single plant species and a

Correspondence: Shuangquan Huang, School of Life Sciences, Central China Normal University, Wuhan 430079, China.
Email: hsq@mail.ccnu.edu.cn

single pollinator species is rare; one plant species is usually pollinated by multiple pollinator species. Features of plant–pollinator networks have been described, such as partner number, core composition and the identity of pairwise interactions, as well as some basic topology and complex organization (Jordano *et al.* 2006; Minckley & Roulston 2006; Petanidou & Potts 2006; Burkle & Alarcón 2011). Meanwhile, basic patterns of network dynamics have been investigated recently, particularly in the network structure and species turnover (Alarcón 2008; Petanidou *et al.* 2008; Dupont *et al.* 2009; Fang & Huang 2012). However, few studies have focused on interaction strength to examine the dynamic relationship between plants and pollinators in natural communities.

In mutualistic networks, the interaction strength (observed visits) can be used to qualify the degree of coevolutionary relationships (Vázquez *et al.* 2005). Interactions between pairwise species are an important, but often ignored, part of biodiversity (Hagen *et al.* 2012). The variation in interaction duration and strength at community level limits our knowledge of network stability and species diversification. The hypothesis of pollinator-mediated selection on floral evolution is questioned if pollinator species are diverse and vary temporally, in which case pollinators' selective role in floral traits could be diminished (Herrera 1988; Schemske & Horvitz 1989; Waser *et al.* 1996). The duration of interaction between pairwise plant and pollinator species measures whether flowers experience stable, pollinator-mediated selection. Investigation of plant–pollinator networks from different communities suggests that ecological generalization predominates (Dupont *et al.* 2003; Basilio *et al.* 2006; Philipp *et al.* 2006). Specialists were highly variable in temporal persistence, and, thus, did not contribute much to community stability (Memmott *et al.* 2004; Kaiser-Bunbury *et al.* 2010; Olesen *et al.* 2011). Generalized plants were generally pollinated by various pollinator functional groups and had higher variation in pollinator compositions compared to specialized plants. However, it remains unclear whether the visitation partitions, the relative visiting frequency of different functional groups, are stable across years. To understand the dynamics of the network, it is important to analyze not only variation in the structure and turnover of species composition, but also temporal variation in interaction strength.

To quantify interaction strength in a pollination network, here we investigated plant–pollinator interactions in a biodiverse alpine meadow over 3 years. Does topology of the network vary across years? Do plant–pollinator interactions vary in strength and nestedness contribution across years? We used the weighted-interaction nestedness estimator (WINE) to calculate the contribution of identical interaction to total network nestedness and compare interaction strength between years to explore the dynamic nature of the mutualistic network (Galeano *et al.* 2009). Specialized species are peripheral in the qualitative network but may become central in the quantitative network if we consider the interaction strength. We examined whether generalized plants are highly dynamic in pollinator composition and whether the generalized plants maintain stable relationships with various pollinators.

MATERIALS AND METHODS

Study community

To document interaction frequency between plants and pollinators, we investigated pollinator visits in an alpine meadow, a field station at Shangri-La Alpine Botanical Garden (27°54′5″N, 99°38′17″E, 3300 to 3350 m a.s.l.), Shangri-La, Yunnan Province, China from 2008 to 2010. The site is located southeast of the Hengduan Mountains, one of the richest biodiversity hotspots in the world (Myers *et al.* 2000). Pollinators were recorded within an 800 × 250 m plot, where alpine flowers flourished in the sloping meadow. Species composition and visit numbers of each year are listed in Table S1.

Sample procedure

Pollinator visitations were recorded in the daytime from 0900 to 1800 hrs from 13 July 2008 to 24 August 2008, 15 June 2009 to 27 August 2009 and 25 June 2010 to 29 August 2010, encompassing the period of peak flowering of most species in the Hengduan Mountains. The peak period of insect activity was from 1100 to 1600 hrs. Outside of this time period, low temperature limited pollinator activity, except by moths. We monitored all flowers from all species observable from a fixed observation plot for a period of 30 min. Because inadequate sample procedure would make rare species inevitably "specialized" (Vázquez *et al.* 2006), we chose some observation sites specifically to include rare species in order to assure that they were adequately sampled. We recorded a pollination visit if an insect contacted the plant's reproductive structures while actively searching for pollen and/or nectar, without regard to variation in pollination effectiveness (Memmott 1999). The visitation to a capitulum of *Aster* and Dipsacaceae or an umble of Umbelliferae species was identified

as one visitation, regardless of how many small flowers that pollinator contacted. Using this observation procedure, each plant species was observed for a minimum of 2 h. In total, we observed for 135, 174 and 184 h on clear days in 2008, 2009 and 2010, respectively. Common and easily identified pollinator species were identified and released in the field and unknown visitors were collected for further identification to species or higher level groups.

Network parameters

The plant–pollinator interactions were used to create pollinator by plant matrices (A × P). In quantitative matrices, each cell represents the observed visits. Summary statistics for each matrix were then calculated (Table 1). We used rarefaction analysis to compare the interaction diversity to delegate our sample effort for each year. Rarefaction analysis allows comparison of species richness among samples of different sizes (Gotelli & Colwell 2001), or in our case, a rarefaction curve is used to assess the relationship between observed visits and total number of unique interactions. Using EcoSim 7.0 (Gotelli & Entsminger 2001), we generated rarefaction curves and their 95% confidence intervals for all 3 years. For each year, the expected number of plant–pollinator interactions was estimated from 10 000 random subsamples of flower visits. To evaluate whether a species is ecologically specialized, we followed the approach of Fenster et al. (2004). If one pollinator species contributes over 75% of total visits or all pollinators belong to one functional group, the plant species would be considered as ecologically specialized. Pollinators were separated into 9 functional groups based on similar behavior (bumblebee, muscoid fly, hoverfly, solitary bee, ant, wasp, butterfly, beetle and beefly) following a previ-

ous study at the field station (Fenster et al. 2004; Gong & Huang 2009). Network level generalization was calculated by the index H_2' (Blüthgen et al. 2006), which represented a scale-independent index to characterize specialization of the entire network. H_2' was calculated on webpage http://nils.mib.man.ac.uk/~nils/stat/.

Data analysis

To measure the nestedness of a weighted matrix, we analyzed the weighted matrix using WINE in R (bipartite package). WINE calculates the nestedness of a network taking into account the weight of interactions (Galeano et al. 2009). WINE calculates a z-score of actual weighted-interaction nestedness and the z-score is compared to those of 100 random generated matrices. Weighted nestedness will be 0 for random distribution and 1 for perfect nestedness. A P-value that is lower than 0.05 indicates that the observed network is significantly nested. In addition, WINE provides a measure ($d_{ij}.w$) of the contribution of each interaction to total nestedness, measuring the interference to network structure if the interaction was removed.

To test the species composition dynamic in quantitative networks, we also calculated "nominal eigenvector centrality," which is an effort to find the central species in terms of the overall structure of the interactions (Jordano et al. 2006; Alarcón et al. 2008). Eigenvector centrality measures how close a species is to other highly central species within a matrix. Species with larger values tend to interact with more generalized species and be more central (Hanneman & Riddle 2005; Jordano et al. 2006; Alarcón et al. 2008). Nominal eigenvector centrality for each plant or pollinator species was calculated as the proportion total eigenvector centrality that was accounted for by each species. We used Spearman rank correlations to investigate how a species' generalization level affects its nominal eigenvector centrality to network for each plant and pollinator species.

To test the stability of interactions, we first compared the weighted nestedness contribution of identical interactions across observed pair years. Then we tested whether identical interactions were in constant frequency between years. To do so, we first separated interactions into 6 categories, according to observed visit frequencies (1–10, 11–20 etc., up to 50 visits; or any visit number greater than 50) for 3 years. We calculated the proportion of interaction turnover in each category that observed 2 years. Then we compared observed identical interactions to test whether strengths are stable. We also calculated Bray–Curtis distance of visit partition

Table 1 Main properties of quantitative pollination network in Shangri-La alpine meadow for three years

	2008	2009	2010
Plant species (n)	88	108	121
Pollinator species (n)	128	165	165
Interaction number	790	987	911
Total visits	7216	10 309	8469
Specialization (H_2')	0.86	0.81	0.85
Weighted nestedness	0.62**	0.61**	0.55**

**$P < 0.01$.

for each plant species between all pairs of years to represent pollinator variation (Bray & Curtis 1957). Visitation in each functional group was standardized by divided total visits for each plant of each year. Therefore, the Bray–Curtis distance ranges from "0," which signifies that the plant species have same visit partition; "1" means that the plant experiences an entirely different pollinator preference.

We used SPSS 13.0 to conduct standard statistical tests. The bipartite package in R 2.8.1 was used for matrix calculations. All means are presented as ± SD.

RESULTS

The rarefaction curves of 3 years were all represented as asymptotic, suggesting that our sample efforts were sufficient and comparable between years. The rarefaction curve of 2009 was higher than those of the other 2 years (Fig. 1), indicating that interaction diversity was highest in 2009. Although we observed more plants and pollinators in 2010, the interaction diversity was not higher. The network-level specialization (H_2') was 0.84 ± 0.03, indicating that our networks were relatively specialized. Quantitative networks were all significantly nested by weighted method for 3 years (Table

1). The nestedness contribution of identical interactions across pair years were positively related in all 3 pairs, 2008 versus 2009 (Spearman correlation: $\rho = 0.24$, $P < 0.01$, $n = 169$); 2008 versus 2010 ($\rho = 0.26$, $P < 0.01$, $n = 164$); 2009 versus 2010 ($\rho = 0.26$, $P < 0.01$, $n = 187$), indicating that identical interactions contributed relatively stable nestedness to network structure.

A positive relation was observed between nominal eigenvector centrality and generalization level for pollinators (Table 2), indicating that more generalized pollinators contributed more network connectiveness and were more centrally positioned in the network. In contrast, nominal eigenvector centrality and generalization level were not related for plants in 2008 and 2010, and were even negatively related in 2009 (Table 2). This

Table 2 Correlation between generalization level and nominal eigenvector centrality for plants and pollinators

|	2008	2009	2010
Plants	0.03	−0.23*	0.02
Pollinators	0.83**	0.71**	0.73**

*$P < 0.05$; **$P < 0.01$.
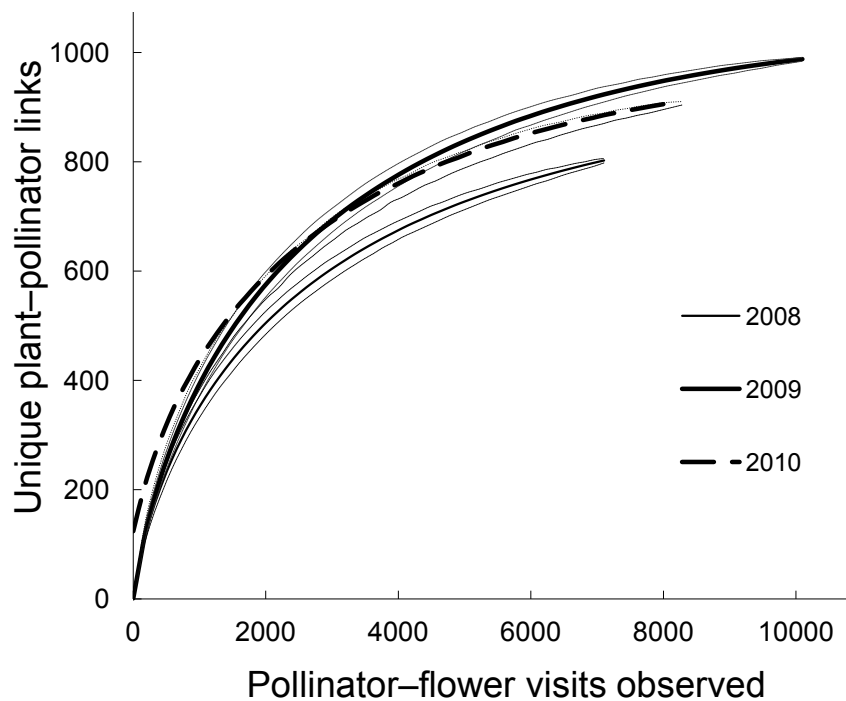
Figure 1 Rarefaction curves (± 95% confidence interval) for the number of plant–pollinator interactions recorded versus the number of visits observed.

Table 3 Comparison of each pair years for identical plant and interactions according to the strength of total visit for each plant species (Mean ± SE)

	2008 vs. 2009	2008 vs. 2010	2009 vs. 2010
Identical plant species	75	78	105
Plants had identical interactions	70	68	90
Identical interactions of total visits for each plant	0.49 ± 0.34	0.57 ± 0.31	0.50 ± 0.33
Identical functional group of total visit for each plant	0.72 ± 0.30	0.78 ± 0.24	0.75 ± 0.27

suggested that plant species with low generalization level were more central (core position) in the network and contributed more to network connectiveness in 2009. In our community, (specialized) pollinators with low generalization level tended to visit generalized plants in relatively low frequency, whereas plants with low generalization level (i.e. specialized plants), such as *Pedicularis* species, tended to be visited by generalized pollinators in high frequency. The asymmetry in interaction strength resulted in a relatively highly specialized quantitative network, although the binary network was quite generalized. The most generalized pollinator, *Bombus friseanus* Skorikov behaved as a super-generalist, whose nominal eigenvector centrality (99.1 in 2008, 99.5 in 2009 and 97.2 in 2010, respectively) was several times the second pollinator species (*Bombus festivus* Smith, 10.7 in 2008, 7.1 in 2009 and 19.7 in 2010, respectively).

Between pair years, interactions with tighter strength tended to have fewer turnovers ($\rho = -0.57$, $P < 0.01$, $n = 36$, Fig. 2), suggesting a steady tight relationship in the community. By contrast, weak interactions (less than 10 visits) were highly dynamic (up to 90% turnover in comparison). Although identical interactions were only $10.7 \pm 0.2\%$ of total interactions for each year, they accounted for $41.2 \pm 7.8\%$ of total visits. Strength of identical interactions across pair years were all positively related (2008 *vs* 2009, $\rho = 0.30$, $P < 0.01$, $n = 169$; 2008 *vs* 2010, $\rho = 0.49$, $P < 0.01$, $n = 164$; 2009 *vs* 2010, $\rho = 0.39$, $P < 0.01$, $n = 187$). Moreover, the interactions that were observed all 3 years were also positively related (2008 *vs* 2009, $\rho = 0.25$, $P = 0.03$; 2008 versus 2010, $\rho = 0.53$, $P < 0.01$; 2009 versus 2010, $\rho = 0.27$, $P = 0.02$, all $n = 78$). Although highly dynamic in interaction turnover and strength, there were $72.6\% \pm 10.2\%$ plant species with identical interactions between all pair years, which accounted for over half of total visits (Table 3). At the pollinator functional group level, nearly three-quarters
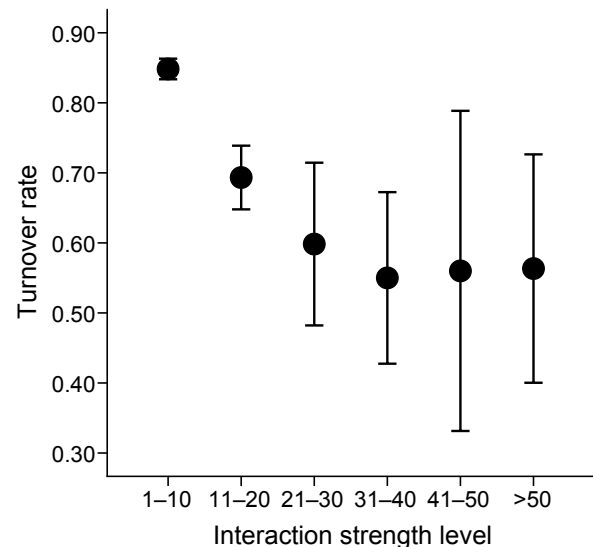
Figure 2 Turnover rates between visit time ranks in each pair of years (mean ± SD). Interactions were separated into 6 categories according to frequency of visits: 1–10, 11–20, 21–30, 31–40, 41–50, and 50+ visits.

of visits were contributed by identical functional groups (Table 3). These results indicated that most plant species experienced stable visitations by similar pollinators. For generalized plant species (average at least 5 pollinators), Bray–Curtis distances, which represent pollinator variation at functional pollinator level, were even negatively related to numbers of pollinator species (Pearson correlation: $\alpha = -0.27$, $P = 0.03$). It suggested that not only specialized plants established stable relationships with pollinators, but also generalized plants experienced stable pollinator partitions. Among the 78 interactions that were observed all 3 years, 38 (48.7%) were contributed by bumblebees, indicating the predominant position of bumblebees in our community in all years. Across 3 years, bumblebees visited specialized plant genera, in-

cluding *Aconitum*, *Astragalus*, *Delphinium*, *Lotus*, *Pedicularis* and *Primula*, in high frequency.

DISCUSSION

Our investigation indicated that interaction strength between plants and pollinators was steady across 3 years in a biodiverse hotspot. The plant–pollinator networks were highly nested when visit frequency was considered. Tight and high connectivity interactions between relatively specialized plants and generalized pollinators transformed the pollination network into a steady weighted asymmetrical structure, highlighting the importance of specialized plants. The generalized plant species were of low variation in visitor partition, suggesting that the generalized plant species were also in stable relationships with pollinators at the community level.

Compared to a binary matrix, a quantitative network allows us to compare interaction quantity between years, and not just variation in species composition (Vázquez *et al.* 2009; Fang & Huang 2012). The weighted nested structure emphasizes the network stability when the interaction strength is considered. Identical species across observed pair years suggested relatively stable positions (Alarcón *et al.* 2008). The identical interactions were also similar in strength and contribution to weighted nestedness. Generalized plant species established a stable relationship to various pollinators or functional groups across years despite variation in pollination effectiveness, suggesting that pollinator-mediated selection would not be diminished given that temporal variation in interaction strength was low (Herrera 1988; Schemske & Horvitz 1989). As the most generalized pollinators, the genus *Bombus* was adaptive to plants with various flower structures. Indeed, a generalized pollination system could sustain local diverse plant species and favor various flower shapes and structures (Lázaro *et al.* 2008). For most generalized plants, a negative relation between generalization levels and variation in visitor partitions also confirmed temporally stabilized preferences of diverse pollinators to specialized or generalized floral traits (Gong & Huang 2011).

In the binary matrix, specialists contributed less to the whole network because of infrequent participation. Most studied ecological networks exhibited nested assemblage patterns (Vázquez *et al.* 2009), which suggested a highly interconnected complex through shared interactions with generalist plant and pollinator species while specialists were not deeply embedded in modules

(Bascompte *et al.* 2003; Ollerton *et al.* 2003). Models of extinction simulations indicated that the extinction of remainder species will not be severe when the specialists are first removed (Memmott *et al.* 2006; Kaiser-Bunbury *et al.* 2010). In our community, however, specialists in pollination network were quite important for network connectivity in the quantitative network, especially the specialized plants. Specialized plants such as *Astragalus tongolensis*, 7 species in *Pedicularis*, *Primula poissonii*, *Primula secundiflora* and *Salvia przewalskii* were specialized to be pollinated by *Bombus* in high frequency. The stable, tight interactions between bumblebees and specialized plants may also emphasize asymmetric specialization, representing cornerstones of the interacting community (Jordano *et al.* 2006). Furthermore, the tight interactions between generalized pollinators and specialized plants implied that heterospecific pollen transfer among these specialized plants would be common (Fang & Huang 2013).

A theoretical model predicts that the relatively specialized pollination system may occur in species-rich area (Vázquez & Aizen 2006). However, our binary pollination network showed that over 90% of plants and 60% of pollinators interacted with more than one partner in any year, suggesting a rather generalized pollination system (Fang & Huang 2012). In the quantitative network, however, plants linked to similar partners with relatively stable strength, which implied a robust pattern of the pollination network from another perspective. In our community, networks were relatively specialized based on interaction strength, which was around 0.84. Network level specialization has been suggested to reduce across community maturation as species richness increases (Albretch *et al.* 2010). However, high species richness did not result in a reduced specialization level.

CONCLUSION

Our findings indicated a temporally stable relationship between plants and pollinators from the perspective of interaction strength. The highly asymmetrical structure of plant–pollinator interactions with regards to interaction strength suggested that bumblebees were positioned most centrally in the network and dominated the pollination service in the biodiverse community. Negative relations between generalization levels and variations in pollinator partitioning indicated that both specialized and generalized plant species were stably preferred by diverse pollinators. Pollination effective-

ness may vary considerably among pollinators, however, actual measurement of pollen transfer, which is a better indicator of pollination success, was not measured here. Although a large part of the interactions that constituted plant–pollinator networks seem to be opportunistically rewired, the pattern of interaction turnover, especially between specialized plants and generalized pollinators, represented a cornerstone of the interacting community.

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SUPPLEMENTARY MATERIALS

Table S1 Quantitative pollination networks in SABG for three years

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