



Year-to-year variation in the topology of a plant–pollinator interaction network

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Vigorous discussion of the degree of specialization in pollination interactions, combined with advances in the analysis of complex networks, has revitalized the study of entire plant–pollinator communities. Noticeably rare, however, are attempts to quantify temporal variation in the structure of plant–pollinator networks, and to determine whether the status of species as specialists or generalists is stable. Here we show that network structure varied through time in a montane meadow community from southern California, USA, in that pollinator species did not form the same links with plant species across years. Furthermore, composition of the generalized core group of species in the network varied among summers, as did the identity of those species involved in relationships that appeared to be reciprocally specialized within any one summer. These differences appear to be related to severe drought conditions experienced in the second summer of the 3 year study. In contrast to this variation, the pollinator community remained similarly highly nested in all three summers, even though species were packed into the nested matrix differently from year to year. These results suggest that plant–pollinator networks vary in detail through time, while retaining some basic topological properties. This dynamic aspect of community-scale interactions has implications for both ecological and evolutionary inferences about pollination mutualisms.

Plant–pollinator interactions have a long history of study at the level of entire ecological communities (Robertson 1929, Moldenke 1975). The past decade has witnessed a renewed focus on pollinator communities (Waser and Ollerton 2006), fueled in large part by the realization that they can be viewed profitably as complex networks (Proulx et al. 2005). For example, recent studies of communities of flowering plants and their animal pollinators have sought to characterize network properties, such as species–link distributions, i.e. the distribution of specialists to generalists, using null models that incorporate species abundances (Vázquez and Aizen 2003), and by fitting them with power-law relationships (Jordano et al. 2003). Numerous studies suggest that pollination networks are both highly asymmetric, such that specialists with few links usually interact with generalists that have many links; and nested, such that more specialized taxa interact with a subset of the partners that associate with more generalized taxa (Petanidou and Ellis 1996, Bascompte et al. 2003, Ollerton et al. 2003, Vázquez and Aizen 2004, 2006, Minckley and Roulston 2006, Jordano et al. 2006). However, small subgroups of interacting species, i.e. compartments, may also occur in such networks (Dicks et al. 2002, Olesen et al. 2007).

Noticeably rare among published studies are explorations of temporal variation in network topology, i.e. in the actual species-level pattern of plant–pollinator interactions

observed over time. Most analyses are single season ‘snapshots’ or combine data across years, and thus do not consider temporal variability (but see Basilio et al. 2006, Medan et al. 2006, Petanidou and Potts 2006, Burkle 2008, Olesen et al. 2008, Petanidou et al. 2008). Documenting whether the topology of plant–pollinator interaction networks varies is a desirable goal, because it tests an implicit prevailing hypothesis of constant topology. For example, Bascompte et al. (2006) argue that the properties of pollination networks can illuminate past coevolutionary history, which assumes relative fixity of interactions.

In fact there is good reason to erect an alternative hypothesis of variable topology. Insect pollinator populations often fluctuate between years (Williams et al. 2001), so that their role as generalists and specialists might fluctuate inter-annually as their populations rise and fall. Plant communities may be expected to vary less over short time scales if the species are predominantly long-lived perennials; however, flower production of whole populations can vary substantially as the same individuals are affected by local climate (Tepedino and Stanton 1980, Ollerton and Lack 1998), which suggest that plants may be at least as sensitive as the pollinators to annual variations in temperature and rainfall. We also now know that plant populations can experience qualitatively or quantitatively

different pollinator environments through time (Herrera 1988, Cane et al. 2005, Price et al. 2005, Ollerton et al. 2007). Such variation could potentially alter network structure and result in shifts in the species that occupy specific ecological roles, e.g. the generalized core group of species with which most specialists interact. For example, abundant plant or pollinator species in any year are likely to interact with a large number of partner species and function as generalists, whereas relatively rare species are likely to interact with only a few partners and function as specialists (Dupont et al. 2003, Ollerton et al. 2003, Vázquez and Aizen 2004, Stang et al. 2006).

Too few data yet exist to make strong arguments for either of these alternatives, but a strong argument exists at this point for simply characterizing variation in network properties through time. Here we present results from a montane plant–pollinator community in southern California, USA, surveyed over three consecutive summers. We asked three questions about the structure of the resulting pollination network: 1) does topology vary across years, assessed as the number of plant–pollinator links and flower visits?; 2) does topology vary when assessed as the degree of nestedness of interactions, nestedness being a common topological feature that is currently discussed in the literature? and 3) does the identity of the core group of generalist plants and pollinators, and conversely of species that appear to be reciprocally specialized, vary between years? Finding affirmative answers to the first and third questions, but not the second, we discuss implications for the ecology and evolution of the mutualistic partners, and of the mutualism itself.

Methods

Study system and pollinator surveys

In 2001 we chose a montane meadow system in the San Bernardino Mountains of southern California, USA (34°13'N, 116°57'W; ~2300 m elevation), located within openings in a yellow pine forest (Jeffrey pine, *Pinus jeffreyi* and ponderosa pine, *P. ponderosa*). At each of three sites, separated by ≤ 0.5 km, we established four 50 × 1 m belt transects. During the summers of 2001, 2002 and 2003, we surveyed each of the 12 transects for pollinator visits to flowers 1–3 times per week, for six weeks beginning in mid-June and ending in early August. Surveys usually took place between 08:00–18:00 h under favorable weather conditions. A survey involved a pair of observers slowly walking the belt transect, taking 20–40 min in the process, and recording only those visits in which an animal arrived at a flower and contacted the plant's reproductive structures while actively searching for pollen and/or nectar (Memmott 1999). We limited our search to hummingbirds and insects belonging to the insect orders most commonly associated with pollination (Coleoptera, Diptera, Hymenoptera and Lepidoptera). Hummingbird and hawkmoth foraging bouts were recorded whenever observed within ~10 m of the transect belts, because these larger pollinators are less likely to approach in the presence of observers. Easily identifiable insects, such as butterflies, were usually captured, identified, and released, whereas other insects were placed in indivi-

dually labeled vials. Insect specimens were sorted into operational taxonomic units and identified to family, and higher level of resolution if possible. Voucher specimens are in R. Alarcón's possession and will be deposited at an entomological museum.

At weekly intervals we also estimated floral abundance by counting the number of open floral units, either individual flowers or compact inflorescences (e.g. in the Asteraceae), in 10 1-m² plots spaced at 5 m intervals along each transect. Because some plots did not contain flowers in a given census, we pooled the total number of open floral units across all 120 plots to calculate a weekly estimate of flower abundances for each plant species. We limited analyses to those plant species that were recorded in all three summers, and tested for weekly and annual variation in flower abundances.

Statistical analyses

Previous work suggests that solitary bees can effectively forage over distances of up to 600 m (Gathmann and Tscharntke 2002), whereas honeybees and bumblebees have foraging ranges of 1–6 km (Goulson 2003), and migratory hummingbirds and hawkmoths much further. Since our sites were ≤ 500 m from one another and we frequently observed pollinators flying between them (e.g. bumblebees, butterflies, honeybees, hawkmoths, hummingbirds and large syrphid flies), we concluded that most pollinators used floral resources on a spatial scale that encompassed all three sites. We therefore pooled observations to create a single pollinator by plant interaction matrix ($A \times P$) for each of the three years of study, in which cell values indicate the number of times pollinator species 'a' was observed visiting flowers of plant species 'p' in that year. Although some insects might not freely move between sites, this would not alter our main results, since we surveyed the same sites across all three years. Summary statistics for each matrix were then calculated, including the total number of flower visits recorded (V), number of unique plant–pollinator associations, or links, observed (K), and median and maximum number of links per plant and pollinator species. These matrices will be deposited at the Interaction Web Database (<http://www.nceas.ucsb.edu/interactionweb/index.html>) hosted by the National Center for Ecological Analysis and Synthesis, at the Univ. of California, Santa Barbara, USA.

Question 1. Is there annual variation in the topology of the plant–pollinator network?

Rarefaction analysis is ideal for comparing richness (i.e. observed numbers of unique plant–pollinator associations, or links) across samples in which the sampling effort (i.e. number of individual flower visits tallied) differs (Gotelli and Colwell 2001). To characterize annual variation in the number of links observed (K) as a function of the total number of flower visits tallied (V) we used EcoSim 7.71 (Gotelli and Entsminger 2001) to generate rarefaction curves and their 95% confidence intervals for each year. The rarefaction algorithm generated the expected number of plant–pollinator links for each year based on 10 000 random sub-samples of flower visits along a series of

sampling levels necessary to construct the curve. In addition, we generated the cumulative rarefaction curve across all three years to determine if the number of links observed across years differed from those recorded in a single year.

To investigate concordance between the $A \times P$ interaction matrices from different years we performed an orthogonal, least-squares Procrustes analysis using the FATHOM toolbox (Jones 2002) implemented in MatLab 7.1. Procrustes analysis is frequently used in morphometric studies but also is suitable for community-scale ecological comparisons (Jackson 1995, Peres-Neto and Jackson 2001). The approach is analogous to mapping the positions of pollinator 'landmarks' between two superimposed floral 'landscapes'. This algorithm minimizes the sum-of-squares distances between corresponding observations (pollinator species) in two $A \times P$ matrices by translating, reflecting, rotating and scaling one matrix to fit the other (Jackson 1995, Jones 2002). The resulting m^2 statistic is a symmetric measure of goodness-of-fit and varies from 0 to 1, with 0 indicating that the matrices are identical (Jackson 1995, Jones 2002). Significance of the statistic was determined by a permutation test (10 000 permutations; Jackson 1995, Peres-Neto and Jackson 2001).

Previous work suggests that Procrustes analysis can outperform the Mantel test in determining the concordance between matrices, and may be easier to interpret since the output also produces vector residuals for each observation, which measure the deviation in positions between the two superimposed matrices (Jackson 1995, Peres-Neto and Jackson 2001). We used the vector residuals to identify those pollinator species that exhibited the greatest change between two years. We analyzed visitation data for the full $A \times P$ matrices, as well as for reduced $A \times P$ matrices in which only those species that were observed in all three years were included. To construct the full $A \times P$ matrices we included a row (A) or column (P) for each species observed in any year. When a species was not observed in a given year the corresponding row or column was filled with zeros. Since both analyses produced similar results (with critical α corrected for three comparisons = 0.0167), we limit our presentation to the full $A \times P$ matrices.

Any differences in network properties between years might be due sample size, i.e. recording a finite number of pollinator-flower visits, rather than to true inter-annual variation. To gauge the likelihood of such a sampling effect we partitioned the data from each summer into two subsets, derived respectively from observations made on alternating days (i.e. observations from the first, third ... observation days versus those from the second, fourth ... days). We compared each of the six resulting $A \times P$ sub-matrices to one another using Procrustes analyses and corrected for the multiple pair-wise comparisons ($n=15$; setting $\alpha=0.0033$). Thus if we detect similar patterns of inter-annual concurrence using the smaller sub-matrices as we did with the full matrices, this would suggest that our sampling regime was sufficient to detect structural changes in topology.

Sub-sampling from a sample is standard practice in statistics, being the basis for inference about actual para-

eters (means, variances and higher moments) of populations. This is especially apparent in modern resampling methods (Wu 1986). Pseudo-replication, on the other hand, refers to the error of believing one has more replicates than is actually true, because one misses the fact that supposed replicates are not independent. We have not used sub-samples as replicates; we only examined their similarity to make sure of our interpretation of year-to-year variation.

Question 2. Does the degree of nestedness and the packing of species in the network vary between years?

We analyzed binary versions of the $A \times P$ matrices with the ANINHADO program (<<http://www.guimaraes.bio.br/softwares.html>>; Guimarães and Guimarães 2006), to arrive at a measure of nestedness. The program calculates the temperature (T) statistic, a measure of disorder of the network, which ranges from 0° for a perfectly nested matrix to 100° for a randomly organized matrix. In a perfectly-nested network the most generalized plant and pollinator species have links with all the partner species in the community, and each successively more specialized species interacts with a subset of the partners with which the previous species interacts, such that species with a single link will only interact with the most generalized partner species. The statistical significance of T is calculated by a Monte Carlo randomization procedure which generates 10 000 random matrices and their temperatures to compare with the actual matrix temperature. We used the CE null model, which limits the probability of observing an interaction between plants and pollinators as a function of their degree of specialization (Bascompte et al. 2003, Guimarães and Guimarães 2006). We also followed Bascompte et al. (2003) in converting T to the nestedness index N ($N=(100-T)/100$), which ranges from 0, when the network is randomly organized, to 1, when it is perfectly nested.

Finally, we calculated the 'ranked position' and the idiosyncratic temperature (IT) for plant and pollinator species observed in all three summers. A species rank (ranges = 1 to A, for pollinators and 1 to P for plants) is its position within the $A \times P$ matrix when the network is arranged to exhibit its maximum nestedness (Guimarães and Guimarães 2006), such that the most generalized plant and pollinator species receive the rank of 1, the next most generalized a rank of 2, and so on. To correct for differences in the number of pollinator and plant species observed in a given summer, we standardized the rank values by dividing them by the total number of pollinators (A) and plants (P) observed that summer, respectively. The IT, on the other hand, is a measure of how a species' pattern of interactions deviates from the expected pattern given its position in a perfectly nested matrix (Atmar and Patterson 1993), such that larger IT values suggests a species has more links established to unexpected partners species compared to the expectation of perfect nestedness. We then calculated the Spearman's rank correlation between these values to determine if species were 'packed' into the community matrix similarly in each of the three years.

Question 3. Does the identity of the core group of generalist species, and conversely of groups of plants and pollinators that appear to be reciprocally specialized, vary between years?

To characterize the core group of generalist plant and pollinator species that specialists primarily interact with, we used algorithms developed for social network analysis and implemented in UCINET 6.29 (<<http://www.analytictech.com/>>; Borgatti et al. 2002). The ‘weak components of valued graphs’ algorithm clusters species based on the number of flower visits recorded, such that plants and pollinators are grouped with the species that they interact with most frequently, thus forming a hierarchically nested series of maximally connected sub-networks with specified cut-off values, i.e. number of visits observed (Borgatti et al. 2002, de Nooy et al. 2005). For example, if pollinator X was observed to visit plant Y 100 times, and plant Z 80 times, X would be clustered with Y at the 100 visit cut-off, and clustered with both Y and Z at the 80 visit cut-off. Thus the core group of generalists, and the asymmetrical specialists that primarily interact with them, will typically form a large cluster separate from those species involved in reciprocally-specialized relationships. To separate the core group of generalists we identified those species that were abundant and interacted with a large fraction of potential partners. Since species abundances and degree of generalization form a continuum (Vázquez and Aizen 2003), making the designation of a ‘generalized core’ somewhat arbitrary, we established two levels for including a plant or pollinator species in the core group of generalists; a relaxed set of criteria in which species must participate in $\geq 1\%$ of the total number of visits (V) recorded during that year, as well as interacting with $\geq 10\%$ of the potential partner species in the community; and a more restrictive set of criteria in which species must participate in $\geq 2\%$ of the total number of visits observed and interact with $\geq 20\%$ of the potential partners. We then calculated ‘eigenvector centrality scores’, which are proportional to the sum of the ‘centrality’ scores of the partner species that a particular species interacts with, such that species with larger values tend to interact with more generalized species (Hanneman and Riddle 2005, Jordano et al. 2006). Finally, we compared the values between the species inside and outside the generalized core to confirm that we had identified the more central species.

We also compared the species composition between pairs of years of the core groups of generalized species identified by the two sets of criteria, by calculating Sorensen’s similarity index, ($S_i = 2a/2a + b + c$, where a = number of species in common, b and c = number of species unique to summers 1 and 2, respectively), which ranges from 0 when no species are shared to 1 when the samples are identical.

To identify reciprocally-specialized groups plants and pollinators, we again used the output from the components algorithm to locate small clusters of species, separate from the generalized core, that repeatedly interact with one another (cutoff ≥ 5 visits) but also infrequently interact with other species in the community. Thus only those groups whose partners appeared to be mutually associated with each other were regarded as comprising reciprocally-specialized groups. We used Sorensen’s index to compare the similarity of species in these groups between years.

The components algorithm is ideal for identifying reciprocally-specialized groups of species, or compartments, since there is no need to remove rare species, as is often necessary when using ordination techniques (e.g. Dicks et al. 2002) due to the ‘arching effect’ caused by their presence (technically their absence) in samples (McCune and Grace 2002). In addition, the components algorithm allows one to evaluate the ‘frequency’ of plant-pollinator interactions, thereby taking advantage of more biologically-relevant data than techniques that search for regions in the network with greater densities of links, i.e. modules (Olesen et al. 2007), which rely only on presence/absence data. In addition, to evaluate if the diversity of partners that plant and pollinator species interacted with (i.e. degree of ecological generalization) varied across years, we used Spearman’s rank correlations to compare the number of links, k_i , recorded for the subset of species that we observed in all three summers, as well as comparing Shannon–Weiner diversity index ($H' = -\sum p_i \ln p_i$) values and eigenvector centrality scores between years.

Results

In the summers of 2001, 2002 and 2003, we observed pollinator flower-visits for totals of 84, 74 and 72 h, respectively. This effort yielded 1711 flower visits (V) to 38 plant species by 127 pollinator species for a total of 338 species–species links (K) in 2001, 1232 flower visits to 39 plant species by 122 pollinator species for a total of 311 links in 2002, and 1089 flower visits to 35 plant species by 125 pollinator species for a total of 288 links in 2003. Plant species established links to medians of 3.5 pollinator species in 2001 (max = 47), 5 in 2002 (max = 51), and 4 in 2003 (max = 58). Pollinators in turn established links to medians of 2 plant species in 2001 (max = 20), 1 in 2002 (max = 13) and 1 in 2003 (max = 19). When pooled across all three summers we observed 4032 flower visits to 56 plant species by 232 pollinators for a total of 754 plant–pollinator links, with plants interacting with a median of 6 pollinators (max = 112) and pollinators interacting with a median of 2 plant species (max = 30).

Only 20 plant species (35.7% of the total) and 42 pollinator species (18.1%) were observed to interact with a particular mutualistic partner in all three summers, which accounted for 2,112 (52.3%) of the total visits observed and 230 (30.5%) of the total links recorded. Many plant species (18 species, 32.1% of the total) were observed being visited in only one year, whereas another 18 species were observed being visited in two years. For pollinators, 129 species (55.6% of the total) were observed visiting flowers in only one year, whereas far fewer (61 species, 26.3%) were observed in two years.

We analyzed weekly flower abundances for the 21 plant species we observed in the 120 1m² plots across summers using a repeated measures ANOVA model with the degrees of freedom adjusted for lack of homogeneity of covariance (Greenhouse–Geisser correction). Flower abundances varied between years ($F_{1,1, 21,4} = 6.55$, $p = 0.017$) with significantly fewer flowers produced in 2002 (mean = 74.4, SE = 24.6) compared to 2001 (mean = 138.2, SE = 31.8; Bonferroni corrected post-hoc comparisons, mean difference = 61.7,

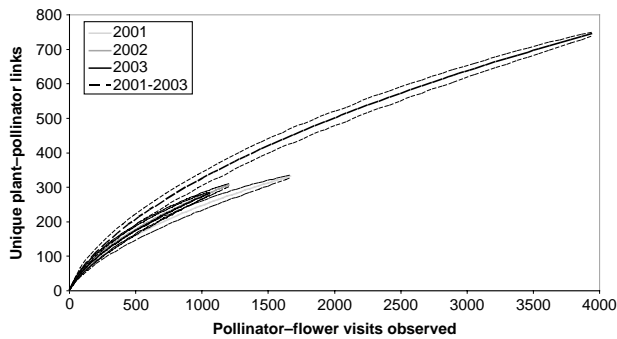


Figure 1. Rarefaction curves ($\pm 95\%$ CI) for the number of unique plant-pollinator links (K) recorded versus the number of visits observed. The accumulation of plant-pollinator links observed over the entire 3 year period is significantly greater than what is observed in a single summer, indicating significant annual variation in the identity of plant-pollinator links observed.

SE = 19.6, $p = 0.015$) and 2003 (mean = 313.3, SE = 91.6; mean difference = 236.9, SE = 86.2, $p = 0.037$); however there was no significant difference between 2001 and 2003 (mean difference = 175.1, SE = 77.5, $p = 0.106$). Also, we did not detect variation in total number of flowers available during a given census week ($F_{2,9}, 58.7 = 2.06$, $p = 0.177$), nor did we detect a census week by year interaction in the number of flowers available ($F_{2,8}, 55.2 = 1.48$, $p = 0.150$).

Question 1. Is there annual variation in the topology of the plant-pollinator network?

Although we recorded more plant-pollinator links (K) and visits (V) in 2001 than in 2002 or 2003, the 2001 rarefaction curve and its 95% CI fell below the 2002 and 2003 rarefaction curves (Fig. 1). This suggests that when one takes the number of observed flower visits into account, the diversity of plant-pollinator links observed in 2001 was lower than in the subsequent two years. The 2002 and 2003 curves, on the other hand, overlapped along their lengths, suggesting that similar numbers of plant-pollinator links were realized during those years. However the accumulation

of plant-pollinator links observed over the entire three year period is significantly greater than what was observed in a single summer, indicating significant annual variation in the identity of plant-pollinator links (Fig. 1). Given that the cumulative rarefaction curve did not show clear signs of an asymptote, it is likely that further sampling would reveal additional links (compare Polis 1991).

Procrustes analysis on the full (232×56) $A \times P$ matrices revealed that network topology was not constant across years. The 2001 and 2003 matrices were highly concordant, ($m^2 = 0.2471$, $p = 0.0001$), meaning that the pollinator species present in those years usually visited the plant species present in a similar manner. In contrast, correspondence was weak (m^2 approaching 1) and non-significant (using a critical $\alpha = 0.0167$) between the 2002 matrix and those of 2001 ($m^2 = 0.9268$, $p = 0.0214$) or 2003 ($m^2 = 0.9638$, $p = 0.0502$).

Residual vectors from the procrustes analysis are listed in Table 1 for the five pollinator species with the greatest between-year variation in species interactions. In many instances not only did the number of links and frequency of visits change, but also the identity of the species that these pollinators interacted with, as estimated by the quantitative version of the Sorensen's index (Table 1). For example, the hawkmoth *Hyles lineata* (Sphingidae) was observed at 203 flowers of two plant species in 2001, but was not observed at all in 2002 (SI = 0.0). Likewise, the honey bee *Apis mellifera* (Apidae) was observed at 373 flowers of 20 plant species in 2001, but at only 11 flowers of four species in 2002 (SI = 0.06). Both of these pollinators reappeared in 2003, with *H. lineata* observed at 141 flowers of one species and *A. mellifera* at 226 flowers of 14 plant species. However, in terms of the composition of the plant species involved, the similarity was less than 40% (*Hyles lineata* SI = 0.10, *Apis mellifera* SI = 0.34). It is unlikely that the low numbers of visits recorded in 2002 and the differences in their patterns of interactions were sampling artifacts, since these are large insects, easily detected from a distance of many meters.

Table 1. Residual vectors from procrustes analyses for the top five pollinator species with the greatest between-year variations in interactions, along with changes observed in the numbers of flower visits, links to plant species, and the quantitative Sorensen's similarity index (range = 0–1, with 1 representing identical samples).

Species	Order/Family	Residuals	\Delta links	\Delta visits	SI
2001 vs 2002					
<i>Hyles lineata</i>	Lepidoptera	0.643	2	203	0.00
<i>Apis mellifera</i>	Hymenoptera	0.482	16	333	0.06
<i>Hylaeus</i> sp. 2	Hymenoptera	0.465	3	91	0.00
<i>Plebejus saepiolus</i>	Lepidoptera	0.430	9	118	0.00
<i>Hylaeus</i> sp. 1	Hymenoptera	0.342	2	62	0.36
2001 vs 2003					
<i>Selasphorus rufus</i>	Trochilidae	0.308	2	110	0.00
Anthomyiidae sp. 3	Diptera	0.189	11	76	0.00
<i>Bombus vosnesenskii</i>	Hymenoptera	0.142	1	13	0.43
Melyridae sp. 5	Coleoptera	0.117	3	66	0.10
Anthomyiidae sp. 2	Diptera	0.115	4	48	0.04
2002 vs 2003					
<i>Hyles lineata</i>	Lepidoptera	0.724	1	141	0.00
<i>Hylaeus</i> sp. 2	Hymenoptera	0.459	5	92	0.08
<i>Apis mellifera</i>	Hymenoptera	0.447	10	215	0.05
<i>Plebejus saepiolus</i>	Hymenoptera	0.427	9	118	0.03
<i>Hylaeus</i> sp. 1	Hymenoptera	0.350	0	83	0.25

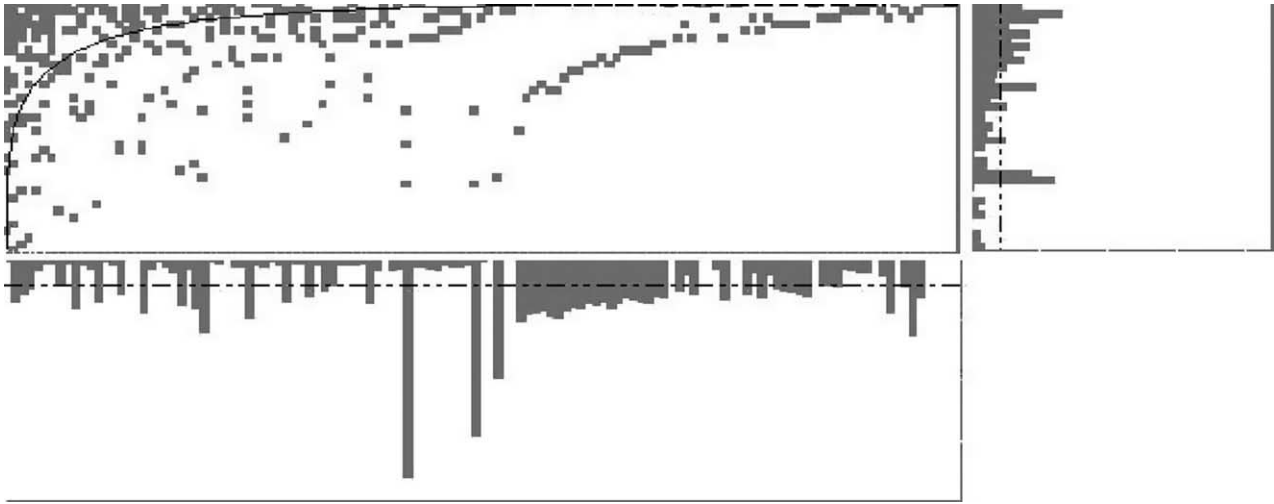


Figure 2. An example of a nestedness diagram (2001 season; 2002 and 2003 not shown). The most ecologically generalized species occur in the upper left corner. The solid line indicates the isocline of perfect nestedness. The panels to the right and below depict the idiosyncratic temperatures for plant and pollinator species, respectively, with the dashed line depicting the matrix temperature ($T = 4.28$). Length of the bars is proportional to how much a species' pattern of links deviated from what is expected in a perfectly nested matrix.

Our analyses of the 6 sub-matrices suggest that the correspondence between 2001 and 2003, and lack of fit with 2002, is not simply a consequence of sample size. The m^2 -values calculated between sub-matrices indicate that the level of correspondence between 2001 and 2003 (mean = 0.3332, SE = 0.0227) was similar to that between the two sub-matrices in any given year (mean = 0.3671, SE = 0.1122, $t = 0.348$, DF = 5, $p = 0.7419$). In contrast, the level of correspondence between the 2002 sub-matrices and those of 2001 and 2003 was low (mean = 0.9539, SE = 0.0091) and non-significant in all cases ($p > 0.0033$), and differed from the m^2 -values calculated between the sub-matrices in any given year as well as the 2001 vs 2003 comparisons ($t = 14.2077$, DF = 13, $p < 0.0001$).

Question 2. Does the pattern of nestedness in the network vary between years?

The plant-pollinator network exhibited a highly nested structure (Fig. 2) in each of the three summers surveyed (2001, $N = 0.957$; 2002, $N = 0.950$; 2003, $N = 0.954$), as well as when the data were pooled across summers (2001–2003, $N = 0.968$). Overall there was little between-year variation in nestedness values, with mean nestedness of 0.954 (SE = 0.002). The correlations of the standardized rankings were also conserved among the 42 pollinator species observed across the three summers (Spearman rank correlation, critical $\alpha = 0.0167$: 2001 vs 2002, $\rho = 0.5897$, $p < 0.0001$; 2001 vs 2003, $\rho = 0.4581$, $p = 0.0023$; 2002 vs 2003, $\rho = 0.4981$, $p = 0.0008$), whereas among the 20 plant species the rankings were positively correlated only between 2001 and 2002 (2001 vs 2002, $\rho = 0.8391$, $p < 0.0001$; 2001 vs 2003, $\rho = 0.1444$, $p = 0.5437$; 2002 vs 2003, $\rho = 0.2872$, $p = 0.2195$). However correlations of idiosyncratic temperature values for plants (Spearman rank correlation, $\alpha = 0.0167$: 2001 vs 2002, $\rho = 0.318$, $p = 0.172$; 2001 vs 2003, $\rho = 0.202$, $p = 0.394$; 2002 vs 2003, $\rho = 0.277$, $p = 0.237$) and pollinator species (2001 vs 2002, $\rho = 0.277$, $p = 0.077$; 2001 vs 2003, $\rho = 0.137$, $p = 0.386$; 2002 vs 2003,

$\rho = 0.314$, $p = 0.043$) suggest that they were not interacting similarly with partner species in the nested matrix in all three years. This finding reinforces the result in relation to question 1 (above) that the pattern of species interactions varied between years.

Question 3. Does the identity of the core group of generalist species, and conversely of plants and pollinators that appear to be reciprocally specialized, vary between years?

The components algorithm identified a large hierarchical cluster of species that was primarily composed of abundant generalists and their asymmetrical specialists (Fig. 3). The eigenvector centrality scores for species within the generalized core group were significantly greater than those outside the core, for both the relaxed criteria ($V \geq 1\%$, $K \geq 10\%$; Mann-Whitney U tests: 2001, $Z = -6.963$, $p < 0.001$; 2002, $Z = -7.202$, $p < 0.001$; 2003, $Z = -6.549$, $p < 0.001$) and the more restrictive criteria ($V \geq 2\%$, $K \geq 20\%$; 2001, $Z = -4.679$, $p < 0.001$; 2002, $Z = -4.000$, $p < 0.001$; 2003, $Z = -4.784$, $p < 0.001$) indicating that we correctly identified the more interconnected species in the network (Table 2). However, the identity of species comprising the core group varied across years. Only two plant species, *Achillea millefolium* (yarrow, Asteraceae) and *Sphenosciadium capitellatum* (button parsley, Apiaceae), and five pollinator species, *Bombus vosnesenskii* (bumble bee, Apidae), *Anthaxia* sp. 1 (metallic beetle, Buprestidae), *Hylaeus* sp. 1 (yellow-masked solitary bee, Colletidae), *Melyridae* sp. 5 (soft-winged flower beetle, Melyridae), and *Scraptiidae* sp. 1 (false flower beetle, Scraptiidae) were consistently identified as members of the generalized core group in all three summers under the relaxed criteria, whereas only three species, *Achillea millefolium*, *Bombus vosnesenskii* and *Anthaxia* sp. 1, were members under the more restrictive criteria (Table 2). Overall, the identity of species that comprised the generalized core varied from year to year, with the resemblance being $\leq 50\%$ between any two summers for both the relaxed (2001 vs 2002,

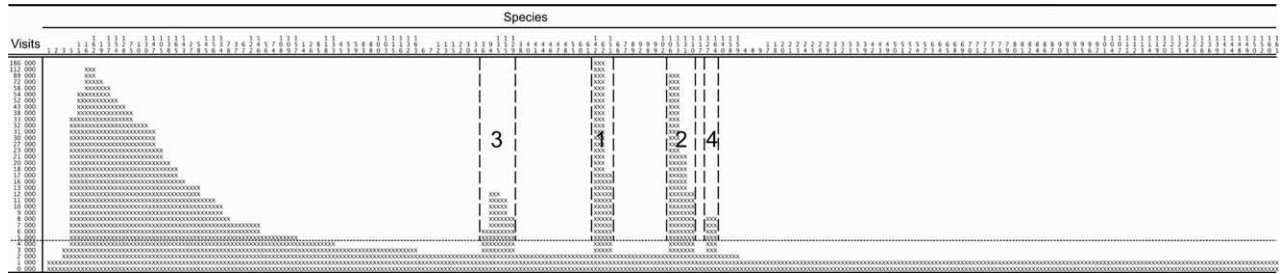


Figure 3. An example of a weak components clustering diagram (2001 season; tail end of the distribution not shown). Species (represented by numbers across the top, Supplementary material Appendix 1) are ordered such that plants and pollinators are grouped with the species that they interact with most frequently, thus forming a series of maximally connected sub-networks at specified cut-off values (listed on the left). The large cluster is composed of generalist species that interacted frequently with one another, and of some of their asymmetrical specialists. The numbered clusters represent plant and pollinator species that appear to be reciprocally specialized at the ≥ 5 visits cut-off value (dotted line; Table 3). For example, in cluster 1, *Hyles lineata* (no. 62) and *Lilium parryi* (no. 142) are connected at the 189 visits cut-off value, with *Penstemon caesius* (no. 151) joining the cluster at the 17 visits cut-off value.

Table 2. Core groups of generalist plant and pollinator species as identified by the components algorithm and relaxed criteria ($V \geq 1\%$, $K \geq 10\%$; Methods). V is the number of visits observed, and K is the number of links established in a given year. The species are ranked according to their normalized eigenvector ('Norm. eig.') values, which summarize the extent to which a species' partners are generalists. Those species that meet the more restrictive criteria for core membership ($V \geq 2\%$, $K \geq 20\%$) are listed in bold.

	Order	Norm. eig.	K	V	Plants	Family	Norm. eig.	K	V
2001 Pollinators									
<i>Apis mellifera</i>	Hymenoptera	29.65	20	344	<i>Achillea millefolium</i>	Asteraceae	49.35	47	248
<i>Bombus vosnesenskii</i>	Hymenoptera	28.92	18	180	<i>Geranium richardsonii</i>	Geraniaceae	46.60	44	196
Scraptiidae sp. 1	Coleoptera	25.46	11	51	<i>Sphenosciadium capitellatum</i>	Apiaceae	38.86	35	350
Melyridae sp. 5	Coleoptera	22.66	10	103	<i>Potentilla glandulosa</i>	Rosaceae	31.51	24	74
<i>Anthaxia</i> sp. 1	Coleoptera	20.74	10	80	<i>Lupinus polyphyllus</i>	Fabaceae	27.15	25	80
Anthomyiidae sp. 2	Diptera	20.47	6	50	<i>Heracleum lanatum</i>	Apiaceae	26.41	22	55
Anthomyiidae sp. 3	Diptera	20.13	11	76	<i>Eriophyllum lanatum</i>	Asteraceae	15.98	15	36
<i>Hylaeus</i> sp. 1	Hymenoptera	16.81	5	43	<i>Lotus nevadensis</i>	Fabaceae	11.66	13	39
Conopidae sp. 1	Diptera	15.09	6	24					
Mordellidae sp. 1	Coleoptera	15.01	4	19					
<i>Cheilosia</i> sp. 2	Diptera	13.60	4	27					
2002 Pollinators									
<i>Anthaxia</i> sp. 1	Coleoptera	29.96	13	115	<i>Achillea millefolium</i>	Asteraceae	66.16	51	245
<i>Megachile</i> sp. 1	Hymenoptera	25.10	11	38	<i>Sphenosciadium capitellatum</i>	Apiaceae	28.99	22	201
<i>Ammophila</i> sp. 1	Hymenoptera	22.02	8	24	<i>Eriophyllum lanatum</i>	Asteraceae	27.99	19	81
<i>Hylaeus</i> sp. 1	Hymenoptera	21.97	7	105	<i>Lotus nevadensis</i>	Fabaceae	25.48	25	91
<i>Plebejus saepiolus</i>	Lepidoptera	21.90	12	123	<i>Geranium richardsonii</i>	Geraniaceae	25.32	19	41
<i>Bombus vosnesenskii</i>	Hymenoptera	21.50	12	90	<i>Potentilla glandulosa</i>	Rosaceae	23.54	18	29
<i>Hemipenthes</i> sp. 1	Diptera	21.05	9	19	<i>Lupinus latifolius</i>	Fabaceae	20.87	14	107
<i>Hylaeus</i> sp. 2	Hymenoptera	20.46	7	99					
Conopidae sp. 1	Diptera	19.04	6	15					
Melyridae sp. 5	Coleoptera	18.38	8	14					
Nyssonidae sp. 1	Hymenoptera	17.80	8	22					
<i>Heriades</i> sp. 1	Hymenoptera	16.42	6	29					
<i>Systoechus</i> sp. 1	Diptera	15.05	7	13					
Scraptiidae sp. 1	Coleoptera	10.44	7	36					
<i>Chelostoma</i> sp. 2	Hymenoptera	9.85	5	15					
Milichiidae sp. 1	Diptera	8.27	6	65					
<i>Osmia</i> sp. 14	Hymenoptera	6.98	5	24					
<i>Osmia</i> sp. 13	Hymenoptera	5.77	5	27					
2003 Pollinators									
<i>Bombus vosnesenskii</i>	Hymenoptera	33.52	19	167	<i>Achillea millefolium</i>	Asteraceae	69.18	58	190
<i>Apis mellifera</i>	Hymenoptera	27.95	14	226	<i>Potentilla gracilis</i>	Rosaceae	34.87	26	104
<i>Lasioglossum</i> sp. 2	Hymenoptera	26.88	12	23	<i>Perideridia parishii</i>	Apiaceae	31.20	24	77
<i>Eristalis</i> sp. 2	Diptera	18.37	5	34	<i>Madia elegans</i>	Asteraceae	23.42	16	47
Melyridae sp. 5	Coleoptera	17.82	7	37	<i>Sphenosciadium capitellatum</i>	Apiaceae	20.87	19	99
Bombylius sp. 1	Diptera	17.68	8	15	<i>Calyptridium umbellatum</i>	Portulacaceae	19.36	16	27
<i>Hylaeus</i> sp. 1	Hymenoptera	17.23	7	22	<i>Aster occidentalis</i>	Asteraceae	18.06	16	53
<i>Anthaxia</i> sp. 1	Coleoptera	17.12	7	28					
Scraptiidae sp. 1	Coleoptera	15.12	5	16					
Nyssonidae sp. 1	Hymenoptera	15.10	7	26					
Mordellidae sp. 1	Coleoptera	10.77	4	22					

Table 3. Clusters of plants and pollinators that appear reciprocally specialized within at least one summer. Visits are the total number of pollinator flower-visits observed during the particular summer, with dependence ('Dep.') values illustrating the relative importance of the interaction from the perspectives of both the animals and the plants.

	Pollinator species	Order/Family	Plant species	Family	Visits	Pollinator dep.	Plant dep.
2001							
1	<i>Hyles lineata</i>	Lepidoptera	<i>Lilium parryi</i>	Liliaceae	186	0.92	0.95
	<i>Hyles lineata</i>	Lepidoptera	<i>Penstemon caesius</i>	Scrophulariaceae	17	0.08	0.81
2	<i>Selasphorus rufus</i>	Trochilidae	<i>Penstemon labrosus</i>	Scrophulariaceae	89	0.79	0.92
	<i>Selasphorus rufus</i>	Trochilidae	<i>Castilleja miniata</i>	Scrophulariaceae	21	0.19	0.58
	<i>Stellula calliope</i>	Trochilidae	<i>Castilleja miniata</i>	Scrophulariaceae	12	0.60	0.33
3	<i>Papilio rutulus</i>	Lepidoptera	<i>Erysimum capitatum</i>	Brassicaceae	12	0.36	0.63
	<i>Papilio rutulus</i>	Lepidoptera	<i>Aquilegia formosa</i>	Ranunculaceae	8	0.24	0.73
	<i>Papilio rutulus</i>	Lepidoptera	<i>Platanthera leucostachys</i>	Orchidaceae	11	0.33	0.61
	<i>Colias eurydice</i>	Lepidoptera	<i>Platanthera leucostachys</i>	Orchidaceae	6	0.60	0.33
4	<i>Volucella mexicana</i>	Diptera	<i>Symphoricarpos rotundifolius</i>	Caprifoliaceae	8	0.73	0.89
2002							
1	<i>Selasphorus rufus</i>	Trochilidae	<i>Castilleja miniata</i>	Scrophulariaceae	49	1.00	0.77
2	Braconidae sp. 1	Hymenoptera	<i>Lepidium virginicum</i>	Brassicaceae	31	0.82	0.70
2003							
1	<i>Hyles lineata</i>	Lepidoptera	<i>Penstemon caesius</i>	Scrophulariaceae	141	1.00	0.98
2	<i>Stellula calliope</i>	Trochilidae	<i>Penstemon labrosus</i>	Scrophulariaceae	23	0.61	0.74
	<i>Stellula calliope</i>	Trochilidae	<i>Castilleja miniata</i>	Scrophulariaceae	15	0.39	1.00
3	<i>Pieris rapae</i>	Lepidoptera	<i>Sidalcea pedata</i>	Malvaceae	9	0.75	0.50
4	<i>Bomblylius</i> sp.1	Diptera	<i>Collomia linearis</i>	Polemoniaceae	7	0.47	0.70

Sorensen's index [SI] = 0.500; 2001 vs 2003, SI = 0.500; 2002 vs 2003, SI = 0.381) and restrictive core membership criteria (2001 vs 2002, SI = 0.429; 2001 vs 2003, SI = 0.471; 2002 vs 2003, SI = 0.400).

In each of the three summers we identified 2 to 4 clusters of plant and pollinator species that appeared to be reciprocally specialized in that summer (Fig. 3), with the number of species in each cluster varying from 2 to 5 (Table 3). However, there was relatively little overlap across years in the identity of plants and pollinators that comprised these groups (2001 vs 2003, SI = 0.455; 2001 vs 2002, SI = 0.222; 2002 vs 2003, SI = 0.167), except as discussed below. Only one species, *Castilleja miniata* (Indian paintbrush, Scrophulariaceae; Table 3), participated in specialized relationships in all three summers. Although at a higher taxonomic/functional group level *C. miniata* was constantly visited by hummingbirds, the identity of its hummingbird pollinators varied across years. In 2001 *C. miniata* was frequently visited by both *Selasphorus rufus* and *Stellula calliope* (broad-tailed and calliope hummingbirds, both Trochilidae), whereas in 2002 we only observed the former hummingbird, and in 2003 only the latter. This 'hummingbird' cluster also included *Penstemon labrosus* (scarlet beardtongue, Scrophulariaceae) in 2001 and 2003.

For those species observed across all three summers we also estimated the inter-annual stability in their degree of generalization in partner use. We detected positive correlations between the numbers of links (K) established to partner species among all three summers, ($n = 62$, Spearman rank correlation, critical $\alpha = 0.0167$: 2001 vs 2002, $\rho = 0.693$, $p < 0.0001$; 2001 vs 2003, $\rho = 0.394$, $p = 0.0015$; 2002 vs 2003, $\rho = 0.520$, $p < 0.0001$). Thus those species that tended to interact with several partners during a given summer were observed to interact with several partners during subsequent summers and conversely, those species observed to interact with few partners during one summer were repeated observed to interact with a limited number of species. Similarly, Shannon-Weiner H'

diversity values were positively correlated for the species observed across summers (2001 vs 2002, $\rho = 0.654$, $p < 0.0001$; 2001 vs 2003, $\rho = 0.304$, $p = 0.0163$; 2002 vs 2003, $\rho = 0.550$, $p < 0.0001$), as were eigenvector centrality scores (2001 vs 2002, $\rho = 0.592$, $p < 0.0001$; 2001 vs 2003, $\rho = 0.443$, $p = 0.0003$; 2002 vs 2003, $\rho = 0.583$, $p < 0.0001$), suggesting that the degree of ecological specialization (niche breadth in use of partners) is relatively constant between years, even though the exact identities of the plants a pollinator visited, or the pollinators used by a plant, usually varied considerably.

Discussion

Our analysis of plant-pollinator interactions over a three year period supports the hypothesis that network topology and the role of pollinators and plants as specialists or generalists within a community can fluctuate dramatically through time. These results might apply more generally, insofar as the networks we studied are typical. There is evidence that this is so. For example, the numbers of pollinator species exceeded the numbers of plant species, in keeping with many other networks (Petanidou and Ellis 1993, Stang et al. 2006). The level of nestedness (0.95–0.96) also resembled that in other plant-pollinator networks (0.72–0.98, Bascompte et al. 2003). Also typical is the presence of a core of generalized plants and animals (Jordan et al. 2006) with which most specialists interact (Petanidou and Ellis 1996, Bascompte et al. 2003, Dupont et al. 2003, Ollerton et al. 2003, Vázquez and Aizen 2004, 2006, Minckley and Roulston 2006, Petanidou and Potts 2006). Finally, other workers have concluded, as we have, that compartments of reciprocally-interacting species are not a common feature of pollination networks (Bascompte et al. 2003, Dupont et al. 2003, Minckley and Roulston 2006, but see Olesen et al. 2007).

If it is accepted that our networks are typical, some general conclusions follow. For example, the topology of

the 2002 network differed from those of the other two summers, not in overall numbers of links between species, but in details of which pollinators visited which plants and in what frequencies. This suggests that ‘snapshot’ studies of plant–pollinator communities are unlikely to detect the range of actual interactions and their strengths. Furthermore, similarity in the composition of the generalized core across the three summers was less than 50%, implying that asymmetrical specialists will often interact with qualitatively different groups of generalist species in different years, because even generalists are subject to temporal fluctuations in population size. Although we detected several small groups of reciprocally specialized plant and pollinator species in each summer, the identities of the few species comprising these groups also varied across years. Only a compartment that appears to fit the ‘hummingbird syndrome’ was repeatedly observed, but the species in this compartment also varied. This suggests that some interactions might be relatively stable at a functional level, in agreement with recent discussion of ecological vs functional specialization (Fenster et al. 2004, Ollerton et al. 2007), but that compartments or modules detected in short-term studies cannot necessarily be taken as evidence of some special relationship among their component species (e.g. a coevolutionary relationship; Olesen et al. 2007) without further evidence of reciprocal selection, and evolutionary response, through time.

Our results also support the view that plant–pollinator networks are nested (Bascompte et al. 2003). Species abundance is thought to be a major factor influencing nestedness and asymmetry of interactions, with more abundant species having a greater opportunity to encounter partners and thus to appear as generalists (Dupont et al. 2003, Ollerton et al. 2003, Vázquez and Aizen 2004, Stang et al. 2007). It is intriguing that despite variation in network topology, the identity of the generalized core, and the composition of reciprocally-specialized groups, nestedness remained relatively constant. Nielsen and Bascompte (2007) suggested that nestedness is not sensitive to sampling biases, which could explain its constancy. The ranked position of species within the nested matrix also remained relatively unchanged, since these values are highly correlated with our niche breadth parameters (not shown). However, when we examined idiosyncratic temperatures, which measures how a species’ pattern of interactions deviates from the nested model, we found that patterns of interaction were not constant across summers. Stang et al. (2007) suggest that abundance relationships can produce the asymmetry observed in nested networks, but that only species-specific traits, such as flower tube depth, are needed to predict which species interact with specialists or generalists. Thus, even though individual populations fluctuate across years, the plant and pollinator species present in a community will still likely follow the ‘several rare’ to ‘few abundant’ species distribution, which could produce the relatively constant degree of nestedness we observed. This suggests that nestedness analysis may be useful for quantifying overall community structure, but that ‘details’ such as morphological constraints (Jordano et al. 2003, 2006) should not be overlooked if one truly wishes to understand how species interactions can vary.

It is unlikely that the temporal variation we describe is simply due to sampling artifacts. Although our sampling effort was lower than that in some other long-term studies (Petanidou et al. 2008), the fact that we were able to recover the same patterns using sub-samples of each summer suggests that we captured the ecologically important interactions. It is also interesting to note that the diversity of plant–pollinator links observed in 2001 was lower than in the subsequent two years, even though we recorded more flower visits that year (Fig. 1); and that network topology was most similar between 2001 and the summer with the least number of flower visits recorded, 2003. Additional sampling would undoubtedly lead to the addition of rare species and interactions, but it is unlikely that these nodes and links would significantly alter network topology. It is far more likely, in fact, that fluctuations in network properties reflect true annual variation in the abundance and phenology of the plant and pollinator populations within the community. For example, most plants produced fewer flowers in 2002 compared to the other two years. Also, feral *Apis mellifera*, which was extremely abundant in 2001 and 2003, was rarely seen in 2002, and *Hyles lineata*, which was common in 2001 and 2003, was not detected in 2002. In 2002, we also observed more pollinator species in the generalized core and fewer species in specialized relationships, suggesting that pollinators might be expanding their diet breadth when floral resources are scarce, as would be predicted by optimal diet theory (Waser 1986).

Overall, we conclude that even if most species are relatively stable in their degree of specialization, as suggested by between-season correlations of the number and diversity of partners, many will experience substantial temporal variation in the exact identity of partners. That many plant–pollinator interactions are dynamic and opportunistic is also supported by long-term studies of single populations of plant species and their pollinators, which can vary at the level of both species (Herrera 1988, Price et al. 2005) and functional groups (Ollerton et al. 2007), and by the ease with which many alien species are incorporated into plant–pollinator interaction webs (Memmott and Waser 2002). The recognition of dynamism and opportunism has many implications. Some workers have argued that asymmetrical plant–pollinator interactions and nested community structure mean that the core group of abundant generalists will dominate the evolutionary trajectory of all species within the network (Bascompte et al. 2003). But if network topology varies between seasons, and specialists experience both qualitative and quantitative variation in generalist partners, this could result in fluctuating natural selection (Waser et al. 1996). Although it is conceivable that some pollinator species will remain abundant over many plant generations (Cane et al. 2005) and thus will strongly influence selection (Vázquez et al. 2005), this seems far from certain without better long-term data. Turning to ecological implications, if plant–pollinator links are dynamic and opportunistic, this should increase the resilience of pollination networks to species loss, or shifts in phenology, perhaps rendering some conclusions (Memmott et al. 2007) overly pessimistic. The degree of competition for pollen vectors and floral resources is also likely to vary between seasons, thus potentially influencing plant and pollinator population levels in subsequent years.

Temporal fluctuation in network structure has not been examined until recently. Several previous publications described plant–pollinator communities across multiple seasons, but without explicitly analyzing network structure (Petanidou and Ellis 1993, 1996, Basilio et al. 2006, Medan et al. 2006, Petanidou and Potts 2006). For example, variability of pollinator species observed across a 4 year study of a phrygana community in Greece show that only about 20% of the insect pollinators observed were present in each year (Petanidou and Ellis 1993), a result similar to our own. Highly specialized pollinators were typically observed in a single season, whereas generalists tended to be observed in multiple years (Petanidou and Potts 2006). More recently, Petanidou et al. (2008) and Burkle (2008) have shown that overall topological features, such as degree of nestedness, remained relatively invariant, against a background of dramatic annual fluctuation in species identities. Similarly, Olesen et al.’s (2008) analysis of an arctic heathland pollination network in Greenland over two seasons found that only 20% of the pollinators and nearly two-thirds of the links detected in one season were not observed in the other. The similarity to our results is all the more striking given differences in habitat and method: the networks of Petanidou et al. (2008) and Olesen et al. (2008) are qualitative, lacking information on relative abundances of species, whereas ours and Burkle’s are quantitative; and Burkle’s study in subalpine Colorado, USA did not resolve the network to species level in all cases, whereas we, Petanidou et al. and Olesen et al. did.

Climatic fluctuations appear to be one cause of the annual variation in network structure. Data from the weather station nearest to our study site (Big Bear Lake, 34°15’N, 116°54’W) indicate that the nine-months (September–May) preceding the summer of 2002 were exceptionally dry, with total precipitation (12.01 cm) below that for the same months in any other year from 1961 through 2005 (mean = 50.37, SD = 27.26 cm). In contrast, precipitation over the same period preceding the summers of 2001 (28.3 cm) and 2003 (51.74 cm) was well within 1 SD of the 45 year average. Drought in the summer of 2002 likely caused most plants to produce significantly fewer flowers compared to 2001 and 2003.

Assuming that the overall differences in network structure stemmed mostly from fluctuations in several plant and pollinator populations, the continued changes in temperature and precipitation that are predicted for the rest of this century are likely to have dramatic effects on species abundances (Inouye et al. 2002), assemblages, patterns of interactions (Memmott et al. 2007), and the evolution of specialization by insect pollinators (Tepedino and Stanton 1980). Potentially counterbalancing these negative effects is the likelihood of opportunism, which will buffer plants and pollinators against loss of ancestral or ‘usual’ links with each other. Uncertainty about the strength of these counterbalancing effects underscores how little we still understand about the morphological, cognitive, and behavioral factors that determine which pollinators will associate with which plants. Perhaps by studying biologically important phenotypic features that functionally limit access to rewards, such as corolla depth and proboscis length

(Stang et al. 2006, 2007), we will be able to better predict which species will interact with one another if sensitive species are lost due to anthropogenic insults. There is an additional reason as well to introduce a focus on the phenotype, which has been a strength of the study of individual plants and pollinators, into community-level studies. Gómez and Zamora (2006) and Fenster et al. (2004) have suggested that different pollinators often are ‘redundant’ in terms of their effects on a given plant species, including the selection they exert on the floral phenotype (but see Ollerton et al. 2007). Future studies of plant–pollinator communities would profit from exploring the extent to which this is true, and the phenotypic correlates of substitutability. The ability of generalist plants and pollinators to interact with many mutualistic partners should have a clear phenotypic cause (Corbet 2006, Stang et al. 2006, 2007) and understanding that cause will shed light on how fluctuations in network topology influence the persistence and evolution of species within the network.

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