



The importance of interannual variation and bottom–up nitrogen enrichment for plant–pollinator networks

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Striking changes in food web structure occur with alterations in resource supply. Like predator–prey interactions, many mutualisms are also consumer–resource interactions. However, no studies have explored how the structure of plant–pollinator networks may be affected by nutrient enrichment. For three years, we enriched plots of subalpine plant communities with nitrogen and observed subsequent effects on plant–pollinator network structure. Although nitrogen enrichment affects floral abundance and rates of pollinator visitation, we found no effects of nitrogen enrichment on the core group of generalist plants and pollinators or on plant–pollinator network structure parameters, such as network topology (the identity and frequency of interactions) and the degree of nestedness. However, individual plant and pollinator taxa were packed into the nested networks differently among nitrogen treatments. In particular, pollinators visited different numbers and types of plants in the nested networks, suggesting weak, widespread effects of nitrogen addition on individual taxa. Independent of nitrogen enrichment, there were large interannual differences in network structure and interactions, due to species turnover among years and flexibility in interacting with new partners. These data suggest that the community structure of small-scale mutualistic networks may be relatively robust to short-term bottom–up changes in the resource supply, but sensitive to variation in the opportunistic behavior and turnover of plant and pollinator species among years.

Trophic interactions are fundamentally important in communities, providing pathways for the flow of energy and nutrients and contributing to the distribution and abundance of species (Hunter and Price 1992). Bottom–up forces play a central role in structuring trophic interactions, and dramatic changes in food webs can occur with alterations in the resource supply (Bukovinszky et al. 2008). High resource availability can increase plant quality and the abundance of consumers in terrestrial and aquatic systems, altering interactions at higher trophic levels (Forkner and Hunter 2000). In food webs, positive, negative, and nonlinear relationships between productivity and the number of feeding links per species (i.e. diet breadth) have been found for individual consumers, but no relationship has been detected across predators within the food web (Arim and Jaksic 2005). Thus, despite dynamic changes in individual links, network structure may be robust to changes in the resource base (Arim and Jaksic 2005).

Mutualisms can be considered consumer–resource interactions (Holland et al. 2005), and many mutualistic interactions are web-like in structure (Jordano et al. 2003). The bottom–up effects of resource addition on plant–pollinator networks are unknown, but predictions can be made based on flowering plant responses to resource

additions, food web theory and optimal foraging theory. The addition of nutrients to flowering plants can affect the quantity and quality of the floral resource supply. For example, the addition of low to moderate nitrogen or fertilizer to individual plants can increase nectar and flower production as well as flower size (Munoz et al. 2005, Burkle 2008), while high or chronic fertilization of plant assemblages can increase the competitive dominance of some species, such as grasses, and reduce species richness, especially of flowering forbs (Bowman et al. 1993).

Food web theory predicts that web structure should be affected by traits of the component species at the resource base that affect, for example, the behavior of consumers (Bukovinszky et al. 2008). Indeed, pollinators behaviorally respond to variation in floral resources, being attracted to plants with large flowers and floral displays and copious nectar (Mitchell 1994). An increase in nectar resources at the community level could allow insects to expand their diet breadth and increase diet overlap if nectar accumulation permits insects with short proboscises to gain access to typically inaccessible nectar. Or, increased floral resources may simply attract more total pollinator species (Potts et al. 2003). Alternatively, increased floral resources might decrease diet breadth and overlap of pollinators and the

structural complexity of plant–pollinator webs if pollinators forage only from highly rewarding species or only from their preferred hosts, assuming that these plants respond positively to resource addition (Tepedino 1980). Many predictions about how flowering plants and pollinators will respond to resource addition derive from manipulations of individual plants and observations of their pollinators (Munoz et al. 2005). However, plant–pollinator networks, like food webs, are emergent properties of systems, and the degree to which nutrient supply affects their structure remains unexplored, representing a critical gap in the study of mutualistic networks.

In addition to the potential for either immediate or delayed bottom–up effects of nutrient enrichment (Theodose and Bowman 1997, Munoz et al. 2005), the structure of plant–pollinator networks may also be subject to interannual variation in species interactions (Basilio et al. 2006, Medan et al. 2006, Petanidou and Potts 2006, Alarcón et al. 2008, Olesen et al. 2008, Petanidou et al. 2008). Although the causes of interannual variation in plant–pollinator interactions are not well understood, Olesen et al. (2008) have shown that both the abundance and phenophase of plants and pollinators are important for the number of interactions maintained by each species. Thus, a variety of factors, including climatic fluctuations (Alarcón et al. 2008), that influence the timing and production of flowers and pollinator abundance and behavior, may be likely drivers of observed variation in pollination networks.

We investigated the bottom–up effects of nitrogen (N) enrichment on the structure of plant–pollinator networks and the generalization of species interactions across multiple years. For three years, we added different levels of N to plots in subalpine meadows and observed plant–pollinator interactions. We focused on the subalpine because flower production in these ecosystems is often N-limited (de Valpine and Harte 2001, Burkle 2008), and pollinators are often energy (nectar) limited (Montgomerie and Gass 1981). Additionally, other research in this system has shown that low levels of N enrichment increase flower production, while high levels of N enrichment have the opposite effect. These alterations in flower abundance occur without affecting plant species richness but nevertheless change pollinator visitation rates (Burkle 2008). Flower abundance is an important determinant of plant–pollinator network structure (Stang et al. 2006); thus, different levels of N enrichment may have strong and divergent effects on floral resource supply as well as the structure of plant–pollinator networks. We studied the effects of N-enrichment over multiple years because temporal dynamics can have powerful effects on network structure (Petanidou et al. 2008); however, the relative importance of bottom–up N-enrichment versus interannual variation on small-scale network structure is unknown and was investigated here. Specifically, we studied how N addition and interannual variation influenced (1) the diversity of plant–pollinator interactions, (2) the generalist core of interactors, (3) the frequency and identity of interactions (network topology), and (4) network nestedness. Finally, we investigated flower abundance and phenophase as potential mechanisms influencing plant–pollinator interactions and networks.

Methods

Nitrogen manipulations

We worked in meadow study sites near the Rocky Mountain Biological Laboratory (RMBL) in Colorado, USA (2900 m). Mountain ecosystems often have low nutrient supply, and productivity in these systems can be limited by soil N (Bowman et al. 1993). In the summer 2005, we identified 24 plots (16 m² each) with similar abundance and species richness of perennial angiosperms with a diversity of floral forms (Appendix 1). Each plot received one of three N treatments over three summers (2005–2007): control, low-N addition (1 g N m⁻² year⁻¹), or high-N addition (20 g N m⁻² year⁻¹) in 10 aqueous doses of ammonium-nitrate applied throughout the growing season. To the control treatment, we also added an equal amount of water as in the low-N and high-N treatments to control for water addition. The low-N treatment was similar to atmospheric N deposition in the Front Range of the Rocky Mountains (Sievering et al. 1996). In the high-N treatment, N should have been abundant to plants even after chemical and microbial immobilization (Eviner et al. 2000). The plots were located in four separate meadow sites. Although pollinators could fly and choose among plots (0.012–0.096 km apart) within a meadow site, it is unlikely that they flew among sites. Sites were 0.8–2.7 km apart, separated by forests and topographical changes. We chose our plot size and arrangement for three reasons: (1) to maximize observation of insect visitors and reflect the scale at which many pollinators make foraging decisions inside a meadow (Klinkhamer et al. 2001), (2) to encompass a scale at which both nested structure and pollinator choice may be present (Summerville et al. 2002), and (3) soil N availability varies naturally at this scale in this system (Dunne 2000).

Pollinator observations

Each plot was observed for one hour per week during peak insect activity (~09:00–16:00) in good weather across the flowering season (June–August). For all flower–visitor interactions observed, we recorded the identity of the plant and pollinator and the frequency of the interaction. We only recorded interactions in which visitors were actively contacting floral reproductive parts. For analyses, we identified the plants to species and the pollinators to family (the lowest common taxonomic unit collected for all pollinators; Appendix 1). Because we did not want to disturb the pollinators during their foraging, we did not collect insects for identification to genus or species. Our goal here was to investigate the effects of nitrogen addition on the structure of plant–pollinator interactions, and elsewhere, we performed detailed analyses of visitation by the small subset of pollinators that could be identified to species or morphospecies while foraging (Burkle 2008).

One caveat is that plants and pollinators were identified to different taxonomic resolution (species vs family, respectively), and taxonomic lumping can affect interpretation of food web properties (Solow and Beet 1998). We have retained the species-level classification of plants to take advantage of this level of detail and avoid problems

associated with lumping plants. Moreover, if we classified plants by family, we would lose half of the resolution because many plants were in the Asteraceae, a dominant family in this system (Appendix 1). To determine if this difference in classification level between plants and pollinators influenced the outcome of our analyses, we repeated all analyses with both plants and pollinators classified to family (analyses not shown). The results were qualitatively similar, and we report only the analyses with plants identified to species and pollinators identified to family. By classifying pollinators by family, we are investigating functional groups of species with similar body sizes (Dalsgaard et al. 2008), as the variation in body size among families averages 5.7 times as great as the variation in body size within families ($F_{19,165} = 5.69$, $p < 0.0001$; Burkle and Irwin unpubl.). Furthermore, pollinator body size and tongue length are highly positively correlated (bees: Waddington and Herbst 1987, West-Eberhard 2003, Borrell 2007, M. Stang unpubl.; moths: Agosta and Janzen 2005), and pollinator tongue length may be an important predictor of observed patterns of species interactions in pollination webs (Stang et al. 2007).

We observed the plots for a total of 126 h in 2005, 178 h in 2006, and 168 h in 2007. The number of observation hours per N treatment did not vary significantly within summers ($F_{2,21} < 0.64$, $p > 0.39$). Rarefaction curves created from visitation data from each year (1000 sub-samples; EcoSim 7.72; Gotelli and Entsminger 2004) did not overlap for the majority of the visitation range (Fig. 1), suggesting that although we observed plots for similar numbers of hours in each year, the number of realized plant–pollinator links increased across years. However, we do not consider this increase to be an artifact of increased proficiency at observing because the number of rarefied pollinator families observed reached an asymptote in each year, indicating that there were simply more pollinator families (and their interactions with plants) in 2007. Thus, results from the analyses should not be the result of sampling artifacts.

Data analyses

How does the diversity of interactions and the composition and abundance of flowers and visiting pollinators vary among N treatments and years?

For each plot in each year, we calculated the rarefied richness and evenness of all pollinators visiting all plants and compared among N treatments, years, and their interaction using MANOVA. We also calculated the richness and evenness of all pollinators visiting each plant species and of all plants visited by each pollinator family and compared N treatments, years, and their interaction using MANOVAs. We included plant species or pollinator family, respectively, as a factor in the MANOVA to control for taxon-specific differences in responses.

For each plot in each year, we calculated the total number of flowers of each plant species and the total number of visits by each pollinator family and compared the composition and abundance of flowers and pollinators of each pairwise plot combination using Bray–Curtis dissimilarity (Sørensen index). We compared among N treatments and years using multivariate analysis of variances (500 permutations) based on our calculated Bray–Curtis

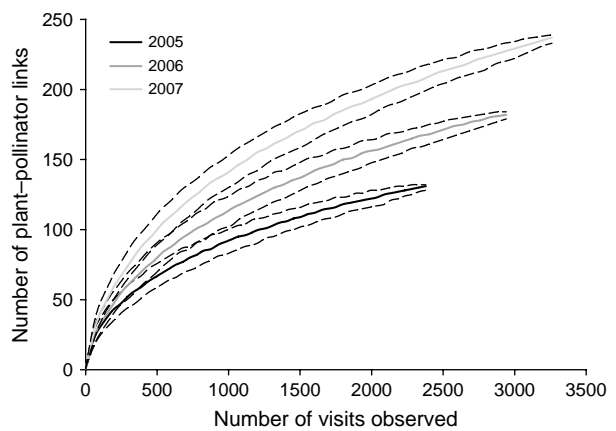


Figure 1. Rarefaction curves (solid lines) and their 95% confidence intervals (dashed lines) of the number of plant–pollinator links as a function of the number of visits from each of the three years of observations.

dissimilarities. We also included site as a factor in these analyses to determine whether dissimilarity in flower and pollinator composition and abundance varied across space. These analyses were performed with the vegan package 1.16–17 in R 2.8.1.

Do the members of the generalist core of interactors vary among N treatments and years?

We used UCINET (ver. 6) to identify the core generalist group of plants and pollinators (Alarcón et al. 2008). For plants and pollinators together in each treatment per year and in each year, we calculated eigenvector centrality scores; taxa with larger values tend to interact with more generalized taxa (Jordano et al. 2006). The core generalists were delineated by separating the plants and pollinators with the highest eigenvector centrality scores that also participated in $> 5\%$ of the visits and interacted with $> 25\%$ of the taxa in that N treatment or year (Alarcón et al. 2008). We compared the core groups to determine if generalists differed among N treatments and years.

Does the topology of plant–pollinator networks vary among N treatments and years?

Here, we asked whether the same plants and pollinators interact with each other and with the same frequency among N treatments and do they maintain these interaction patterns through time. First, we created plant \times pollinator matrices for each plot in each year, indicating the frequency of the interaction. We examined the similarity between pollinator \times plant interaction matrices (i.e. whether pollinator families used plant species in similar ways among N treatments and years) using Procrustes analyses (R 2.8.1). Procrustes analysis can be used for community-level ecological comparisons (Jackson 1995) by mapping the positions of pollinators between two superimposed floral backgrounds (e.g. comparing pollinator \times plant matrices between two plots) and minimizing the sums-of-squares distances between the two matrices (Alarcón et al. 2008). We determined the significance of the resulting goodness-of-fit statistic (m^2) with a permutation test set to 1000. When m^2 approaches 0, there is a good fit between the two

matrices and indicates similar network topology (similarity in the identity and frequency of interactions), but when m^2 approaches 1, there is a poor fit and indicates different network topology. We did not apply the Bonferroni correction to significance levels (here and below) because it inflates the type II error rate; instead, we reported unadjusted significance values (Moran 2003). We used the m^2 values of each plot-plot comparison to test the effects of N treatment and year on plant-pollinator network topology using multivariate analysis of variances (500 permutations, vegan package 1.16–17 in R 2.8.1). We included site as a factor in this analysis to determine whether network topologies were similar across space. We also tested for interactions between N treatment and year or site to determine whether time or space influenced the effects of N, but we found no interactions and removed them from the final model. We predicted that patterns of pollinator visitation, and thus network topology, would vary both among N treatments (due to changes in pollinator visitation rates and richness of visitors to plant species) and years (due to interannual variation in pollinator composition and population sizes; Herrera 1988).

We then used vector residuals to identify pollinator families that exhibited the greatest changes in interactions (Alarcón et al. 2008, MatLab ver. 7.4). Network topology was only affected by year (and not N treatment or site), so all observation data were pooled across N treatments and sites within a year to create pollinator \times plant matrices for each year, indicating the frequency of each interaction. Large vector residuals indicate large changes in position in pollinators between two matrices, highlighting pollinator families that had altered patterns of visitation among years.

Do the patterns of network nestedness vary among N treatments and years?

Nested networks are common in ecological systems (Bascompte et al. 2003), containing specialists interacting with subsets of generalists. Understanding alterations in nestedness is important because the degree of nestedness may indicate how robust species and interactions will be to perturbations (Bascompte et al. 2003), such as the bottom-up effects of N addition. We used ANINHADO to calculate the nestedness of each pollinator \times plant matrix for each N treatment per year and for each year (Guimaraes and Guimaraes 2006). We measured nestedness in units of temperature (T), with 0° representing a perfectly nested network and 100° representing a random network. To determine the significance of temperature, we used a Monte Carlo randomization procedure with a null model in which the probability of an interaction occurring was proportional to the number of interactions in which the plant and pollinator participated. We also calculated the idiosyncratic temperature, a measure of how a species' pattern of links deviated from the pattern expected in a perfectly nested matrix, of all taxa seen within a year and in all years. Finally, we calculated Spearman rank correlations to determine if taxa were packed into the community matrices similarly in N treatments within years and in each year (Alarcón et al. 2008). Here we assessed whether community members were ranked similarly in the number and identity of the other

taxa with which they interacted across N treatments and years. Because N addition to plant assemblages can influence the abundance, phenology and morphology of flowers (Munoz et al. 2005, Burkle 2008), which are important determinants of network structure (Stang et al. 2006), we predicted that N addition would alter the nestedness of plant-pollinator networks. In the absence of variation in resource supply, floral resources produced by many plant species can be relatively predictable (Price and Waser 1998), so we hypothesized that plant-pollinator interactions in control plots would remain highly nested, while N-addition would disrupt the predictable presentation of floral rewards, rendering plant-pollinator interactions more random and decreasing network nestedness. Such a finding could indicate that pollinators may be opportunistic in their foraging decisions.

Investigating mechanism behind network structure: are flower abundance and phenophase associated with the number of interactions observed among N treatments and years?

Investigating the mechanism(s) driving patterns of network structure is important. The same patterns or structure can have different causes (Paine 1994); identifying associated mechanisms may facilitate the generalization of results across webs (Leibold and Tessier 1998). Flower abundance and phenophase (length of the flowering season per species) can positively influence the number of interactions between plants and pollinators (Stang et al. 2006, Olesen et al. 2008). Thus, for each flowering species, we recorded the total number of flowers produced and the number of days in bloom. For each N treatment per year and for each year, we used multiple regression to investigate the relationship between the total number of flowers and mean phenophase (log-transformed) on the observed number of pollinator families (log-transformed) visiting each plant species. It is important to note that flower abundance and phenophase were positively correlated in all cases ($0.37 < r < 0.65$, $p < 0.08$, $n > 20$). To screen for collinearity between flower number and phenophase, we calculated variance inflation factors for treatments and years (VIFs). All VIFs were < 1.73 , suggesting that collinearity did not strongly affect the results.

Results

Overall, we observed 35 pollinator families and 41 plant species participating in 8796 individual interactions. We found that 54% of pollinator families and 59% of plant species participated in at least one interaction in all three years. In 2005, 2006 and 2007, we observed 23, 25 and 32 pollinator families visiting 33, 31 and 31 plant species for a total of 133, 183 and 239 unique interactions, respectively.

How does the diversity of interactions and the composition and abundance of flowers and visiting pollinators vary among N treatments and years?

At the plot level, the rarefied richness and evenness of pollinator families visiting all plants per plot were not

affected by N treatment ($\lambda = 0.96$, $F_{4,106} = 0.62$, $p = 0.65$) but differed among years ($\lambda = 0.25$, $F_{4,106} = 26.41$, $p < 0.0001$). There was no interaction between N treatment and year ($\lambda = 0.91$, $F_{8,106} = 0.64$, $p = 0.74$). Rarefied richness was 79% and 30% greater in 2007 than in 2005 or 2006, respectively (Fig. 2a, $F_{2,60} = 84.7$, $p < 0.0001$), and evenness was 31% and 16% greater in 2007 than in 2005 or 2006, respectively (Fig. 2b, $F_{2,60} = 22.5$, $p < 0.0001$). These changes in richness and evenness over time were driven by a decline in the dominance of Apidae and a rise in other pollinator families, including small bees and flies in the Halictidae, Syrphidae and Anthomyiidae.

At the individual taxon level, we observed a similar pattern as at the plot level. N treatment did not affect the rarefied richness and evenness of pollinators visiting a plant species ($\lambda = 0.99$, $F_{4,638} = 0.12$, $p = 0.98$) or of plants used by a pollinator ($\lambda = 0.99$, $F_{4,924} = 1.75$, $p = 0.14$), but year did (respectively, $\lambda = 0.62$, $F_{4,638} = 43.12$, $p < 0.0001$; $\lambda = 0.95$, $F_{4,924} = 6.19$, $p < 0.0001$). Again, there were no interactions between N treatment and year ($p > 0.78$ in both cases). Richness and evenness of both visiting pollinators and plants used were greater in 2007 than in 2005 or 2006 ($F_{2,320} > 11.3$, $p < 0.0001$). These differ-

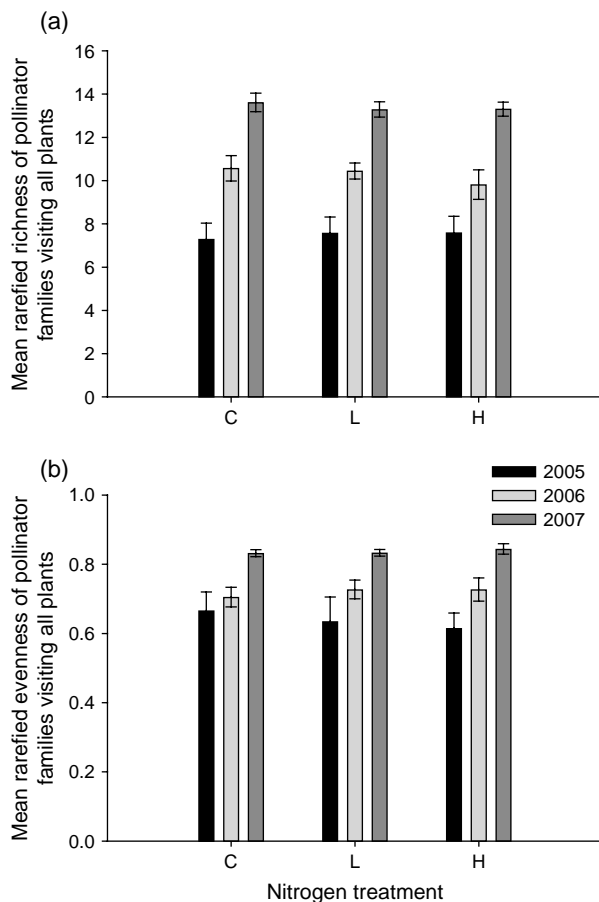


Figure 2. The mean rarefied richness (a) and rarefied evenness (b) of pollinator families visiting all plants did not differ among nitrogen treatments (C = control, L = low-N addition, H = high-N addition) but varied across the three years of treatment (2005 = black, 2006 = light gray, 2007 = dark gray). Error bars are \pm SE.

ences among years were driven primarily by changes in the dominant floral visitors to a species and, to a lesser degree, by changes in the diet breadth (i.e. feeding links) of pollinators, suggesting some degree of flexibility and opportunism in foraging.

The degree of dissimilarity between plots in their composition and abundance of flowers was influenced by N treatments ($F_{2,65} = 3.27$, $p < 0.002$), years ($F_{1,65} = 6.15$, $p < 0.002$), and sites ($F_{3,65} = 15.93$, $p < 0.002$). Plots in comparable conditions (i.e. the same N treatment and close in time and space) had greater similarity in their floral assemblages than plots in different conditions. The degree of dissimilarity between plots in their composition and abundance of pollinator visits differed among years ($F_{1,65} = 39.60$, $p < 0.002$) and sites ($F_{3,65} = 11.30$, $p < 0.002$) but not among N treatments ($F_{2,65} = 0.62$, $p = 0.80$), suggesting that the pollinator assemblage visiting plots was similar across N treatments but was dissimilar to plots separated in time and space.

Do the members of the generalist core of interactors vary among N treatments and years?

The identities of the core plants and pollinators were similar across N treatments within a year (Fig. 3). Thus, we did not find more total plant and pollinator taxa categorized as generalists in low-N addition treatments due to novel visitation by pollinators. However, the identity and rank order of the core plants and pollinators differed substantially among years (Fig. 3). For plants, *Heliomeris*, *Helianthella*, *Potentilla* and *Erigeron* were members of the generalist core in 2005, while *Potentilla* dominated as the primary core plant species in 2006 and 2007. For pollinators, Apidae dominated the core group of pollinator generalists in 2005, Halictidae in 2006 and Anthomyiidae in 2007.

Does the topology of plant-pollinator networks vary among N treatments and years?

Network topology was not affected by N treatment ($F_{2,65} = 1.43$, $p = 0.14$) or site ($F_{3,65} = 1.53$, $p = 0.11$) but was affected by year ($F_{1,65} = 11.97$, $p = 0.002$), indicating that the pollinators present in one year visited the plant species in different N treatments and sites similarly. However, large differences in visitation occurred among years (Table 1). The changes in interactions among years were due to large fluctuations in abundances of certain pollinator families, especially pollinators in the Apidae and Anthomyiidae. Between 2005 and 2007, the total number of visits by Apidae dropped from 1430 to 322 visits with a loss of 12 links to plant species, while the total number of visits by Anthomyiidae increased from 7 to 705 visits, with a gain of 19 links to plant species (Fig. 4). Interestingly, despite the differences in network structure among years, levels of connectance (percentage of realized links) were similar: 18% (2005), 24% (2006) and 24% (2007).

Do the patterns of network nestedness vary among N treatments and years?

The plant-pollinator networks exhibited highly nested structure in all N treatments and years ($p < 0.0001$ in all cases). However, correlations of idiosyncratic temperatures

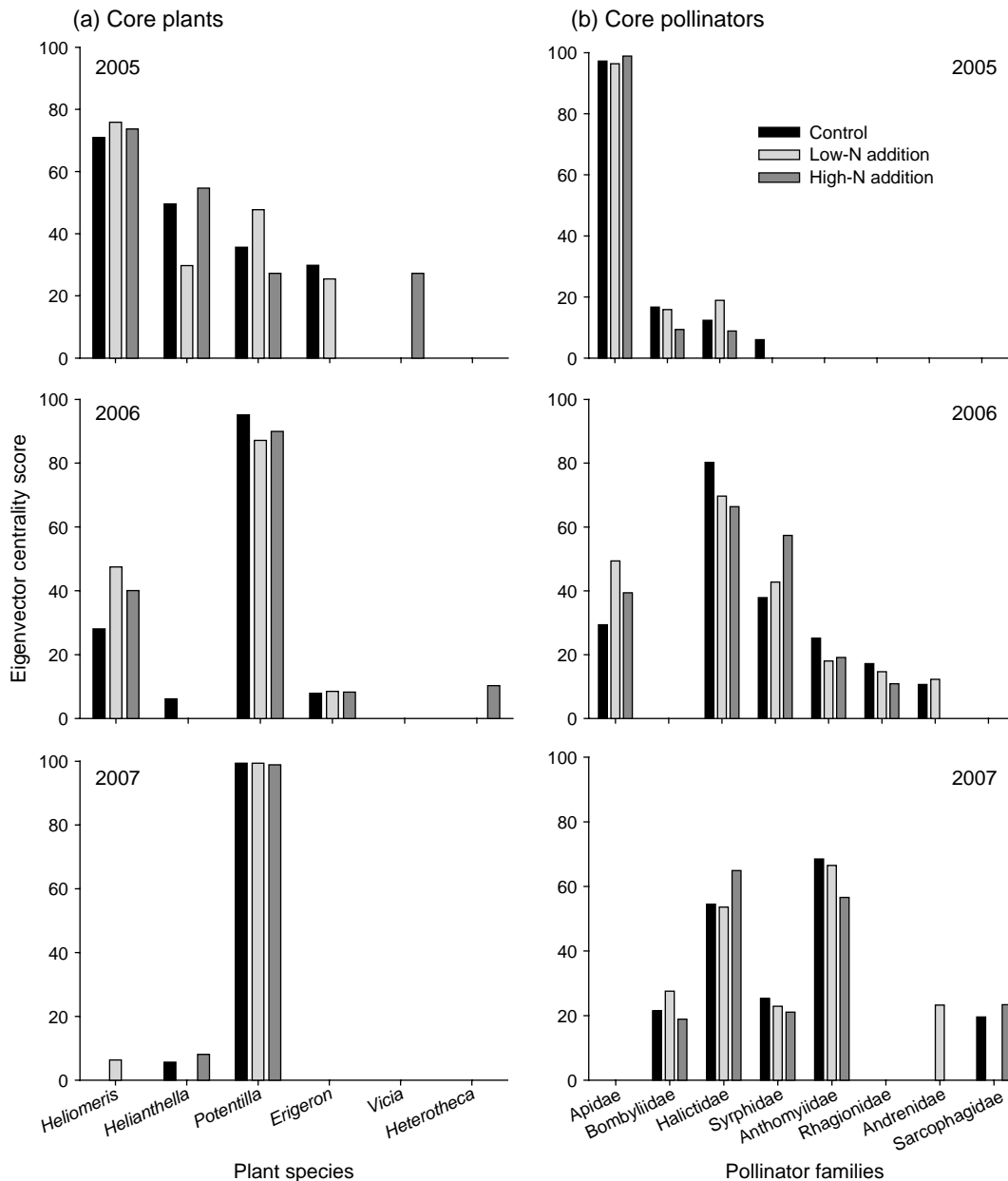


Figure 3. The identity and rank order (ranked by eigenvector centrality score) of plants and pollinators comprising the core group of generalists was similar across N treatments (control, low nitrogen addition, or high nitrogen addition), but different among years. Larger eigenvector centrality scores indicate that the family (pollinator) or species (plant) was more generalized. Plants are referred to by their genus (full species names are given in Appendix 1).

indicated that plants and pollinators were not packed into N treatments or years similarly ($0.96 < p < 0.082$ in all cases except one), suggesting differences in the rank order and degree of nestedness of individual taxa among N treatments and years. Thus, although the overall nested network structure remained the same, plants and pollinators were not in the same location in the nested matrices across years and N treatments. The only instance in this study where plants and pollinators held similar positions in the nested matrix between N treatments was in 2007, where we found a significant positive relationship of idiosyncratic temperatures between control and low-N treatments ($p = 0.027$, $\rho = 0.36$, $n = 38$), indicating that, in this comparison, plant visitation patterns by pollinators were similar.

Investigating mechanism behind network structure: are flower abundance and phenophase associated with the number of interactions observed among N treatments and years?

Both flower abundance and phenophase were important in predicting the number of visiting pollinator families, but their relative importance as predictors varied among N treatments and years. In 2005, only flower abundance had a significant positive effect on the number of interacting pollinator families ($F_{1,30} = 11.96$, $p = 0.0016$), while only phenophase had a significant positive effect in 2006 ($F_{1,28} = 27.64$, $p < 0.0001$). In 2007, both flower abundance ($F_{1,27} = 3.96$, $p = 0.057$) and phenophase ($F_{1,27} = 3.44$, $p = 0.075$) had positive effects (albeit not highly significant)

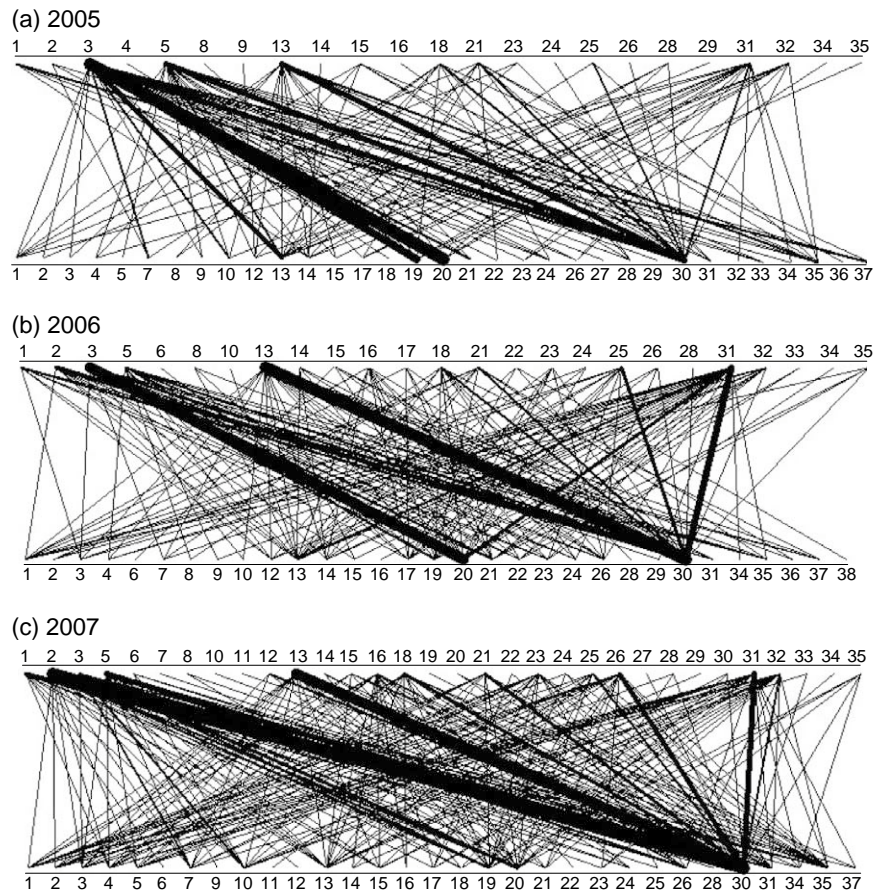


Figure 4. Graphic representation of the plant–pollinator community in (a) 2005, (b) 2006 and (c) 2007. Plants are along the bottom and pollinators are along the top of each web. The identities of plants and pollinators are indicated by numbers and are the same across years (see Appendix 2 for names). The width of the links is proportional to the frequency of the interaction within a year.

forces may also contribute to the structuring of plant–pollinator networks, although the mechanisms remain unexplored.

One possible explanation for a lack of effect of N enrichment on plant–pollinator networks is that, due to morphological and phenological constraints, pollinators have limited opportunities to alter their patterns of visitation (Stang et al. 2007) and diet breadth. However, this explanation seems unlikely for most bees, flies and butterflies in this system given that the majority of plant species had an open morphology (Appendix 2) with rewards accessible to many pollinator types (Appendix 1). Alternatively, plant–animal mutualisms consistently display nested properties (Bascompte et al. 2003), and irrespective of network size, plant–pollinator interactions typically center around a core of generalist species (Jordano et al. 2006). Thus, changes in floral abundance or the composition of non-core species due to N addition may not affect the presence of a generalist core and associated network structure. Additional experiments manipulating basal resources in plant–pollinator networks, plant or pollinator morphology, and the abundance of members of the generalist core will provide further insight into the importance of bottom–up effects, or lack thereof, on plant–pollinator network structure.

Three caveats are important in the interpretation of our results. First, the spatial scale of observation can affect

estimates of network nestedness (Wright et al. 1998). The plots in this study were 16 m² each and may have been too embedded in the same overarching plant–pollinator community to detect changes in nestedness and other network parameters as a result of N addition. Larger shifts in interactions may occur if N availability was altered at the scale of the watershed, which may remove the ability of pollinators to choose among areas of different resource supply if they are limited in flight range or if chronic N addition leads to wide-scale changes in plant species composition. Large spatial changes in plant composition associated with extinctions and invasions have altered pollination webs, resulting in co-extinctions and altered patterns of pollinator visitation and pollination (Memmott et al. 2004). Such large-scale studies of nutrient enrichment on plant–pollinator networks remain unexplored. Second, it is unknown if resolving pollinators to family instead of species masked any effects of N treatments. There are tradeoffs in collecting pollinators for identification versus allowing them to visit flowers naturally. We chose not to collect pollinators because of our interest in detailed and continuous behavioral observation (Burkle 2008). We cannot rule out the possibility that species-level pollinator responses to changes in floral composition and abundance were cancelled out when lumped at the family-level. Additional observations focused on pollinator collection and identification and comparison of species- and

family-level plant–pollinator networks will provide additional ecological insight. Third, our results suggest that given more time for observations, additional plant–pollinator links would be recorded (Fig. 1). Thus, even with substantial observation effort, many of the rare plant–pollinator links will be missed, and less extensive observations may give a misleading representation of interactions (Petanidou and Potts 2006). Because we used the same methods and sampling effort throughout our study, our comparisons among N treatments and years are valid, but caution should be used when making quantitative comparisons of the networks reported here with other networks from published studies.

The majority of plant–pollinator interactions in our networks were generalized and the networks exhibited nested structure, in agreement with recent work documenting the organization of many mutualistic interactions (Jordano et al. 2003, but see Olesen et al. 2007). The nested structure of mutualistic interactions is different from the compartmentalized structure of antagonistic interactions (e.g. predator–prey, herbivore–plant), where there are strong interactions within compartments (subgroups of species) but little interaction among compartments (Prado and Lewinsohn 2004). Thus, despite the consumer–resource nature of some mutualisms, there appear to be fundamental and predictable differences in the structure of mutualistic versus antagonistic interactions, suggesting that the form of an interaction may mediate its effects on community dynamics. The generalization of plant–pollinator interactions and the nested structure of networks have important implications for the degree to which species and interactions will be affected by perturbations (Bascompte et al. 2003). For example, plant species diversity is expected to decline in conjunction with the loss of pollinator species (Biesmeijer et al. 2006). However, Memmott et al. (2004) demonstrated the relative tolerance of pollination networks to plant extinction with the removal of pollinator species, due to the nested structure of these networks compared to the rapid losses of species from compartmentalized food webs. Similarly, Fortuna and Bascompte (2006) found that plant–animal mutualist networks begin to lose species more quickly after simulated habitat loss than random communities, but the mutualist networks persist under conditions of more severe habitat loss, presumably due to their nested structure. Further research comparing mutualistic and antagonistic networks and their response to resource addition and environmental change is necessary to understand the causes and consequences of their structure.

The small effects of N addition that we observed on network structure paled in comparison to the interannual variation in network structure, independent of N enrichment. Surprisingly few studies have examined interannual variation in the structure of pollination webs (Waser and Ollerton 2006). Of the limited research that has considered such interannual variation, the amount of interannual variation that we observed in dominant interactors is common (Petanidou et al. 2008). In our study, the dominant pollinator group was different in each year. These differences in plant–pollinator interactions may be consequences of pollinator abundance and population dynamics or, alternatively, influenced by large-scale climatic or other environmental factors. Alarcón et al. (2008)

suggest that a drought during one summer of their study of a plant–pollinator network in the San Bernardino Mountains, CA caused reduced flower production, thereby contributing to differences in network structure compared to two other study years with greater average precipitation. Similarly, the timing and quantity of precipitation likely influenced plant–pollinator network structure in our sub-alpine study system as well; both rain during the short summer growing season and snowfall during the winter months are important for plant growth, development, and reproduction. For instance, the summer of 2006 was unusually wet, with 40% of the total annual precipitation (56.9 cm) falling as rain between June and August (Gothic weather station, CO-10, NADP 2005–2007). Summer rainfall can influence nectar production, important for pollinator attraction, in at least one dominant plant species in this system (Campbell 1996). In contrast, 2007 was atypically dry, with total winter snowfall (883 cm) falling 20% below the 34-year average (1974–2008, b. barr) and the second earliest date of bare ground recorded (1 May; 20 days earlier than the 34-year average). Snowpack depth and the timing of snowmelt can significantly influence flower abundance in this system, with obvious implications for interactions with pollinators (Inouye 2008). Total flower production in our plots was lower in the dry year of 2007 compared to the previous two years, potentially contributing to the observed differences in network properties. Daily fluctuations in temperature during the summer months of our study were similar across all three years and likely did not contribute substantially to variation in network structure. Additional monitoring of the identity and frequency of plant–pollinator interactions in this system is necessary to determine the direction and magnitude of effects of climatic parameters on floral traits and network structure. Moreover, the presence of large interannual variation in pollinator abundances indicates the importance of temporal scale, especially when drawing conclusions about specialization and generalization in pollination partnerships and their ecological and evolutionary consequences (Petanidou et al. 2008). Contrary to our results, however, large interannual variation in other systems does not always result in large changes in network structure (Olesen et al. 2008). Our work suggests that plant–pollinator network properties may not be as invariant among years as previously thought.

In summary, by combining concepts and techniques from food web ecology and network theory, we tested the bottom–up effects of short-term nitrogen enrichment on small-scale plant–pollinator network structure. We found that bottom–up effects of nitrogen addition on plant–pollinator network structure were small relative to interannual variation in interactions, indicating the presence of other factors acting at large temporal, and possibly spatial, scales to influence network structure. Studies that consider both intrinsic and extrinsic factors at larger scales may provide additional insight into the factors controlling network structure and variation. Such an approach provides the opportunity to both understand and predict community dynamics in the face of environmental change across a range of species interactions.

Acknowledgements – We thank K. Dales, M. Hamilton and L. Senkyr for help in the field and R. Alarcón, M. Ayres, J. Bascompte, B. Bowman, S. Elliott, M. McPeck and M. Stang for comments on earlier drafts of this manuscript. R. Alarcón and J. Watling provided useful advice on the analyses. Gothic weather data were collected and supplied by b. barr. This research was funded by the Am. Philos. Soc. Lewis and Clark Fund, Botanical Soc. of America Graduate Student Research Award, Dartmouth College Cramer Fund and Graduate Alumni Research Award, Explorers' Club, Rocky Mountain Biological Laboratory Snyder Memorial Grant, Sigma-Xi Grants-in-Aid of Research, and a grant from the Natl Science Foundation DEB-0455348.

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Appendix 1. Flowering plants and pollinators observed from 2005–2007. Black dots represent the presence of a plant–pollinator interaction in at least one year.

Plant family	Plant genus and species	Andrenidae	Anthomyiidae	Apidae	Arcidae	Bombylidae	Braconidae	Buprestidae	Calliphoridae	Chrysididae	Cleridae	Coccinellidae	Colletidae	Halictidae	Hesperiidae	Ichneumonidae	Lycenidae	Mesitidae	Megachilidae	Meloidae	Miridae	Muscidae	Noctuidae	Nymphalidae	Pieridae	Rhagionidae	Sarcophagidae	Siricidae	Sphexidae	Sphingidae	Stratiomyidae	Syrphidae	Tachinidae	Tenthredinidae	Trochilidae	Vespa				
Apiaceae	<i>Ligusticum porteri</i>	•																																						
Apiaceae	<i>Pseudocymopterus montanus</i>	•	•			•								•																										
Asteraceae	<i>Achillea lanulosa</i>	•	•											•																										
Asteraceae	<i>Agoseris aurantiaca</i>													•																										
Asteraceae	<i>Agoseris glauca</i>	•	•											•																										
Asteraceae	<i>Dugaldia hoopesii</i>																																							
Asteraceae	<i>Erigeron flagellaris</i>	•	•											•																										
Asteraceae	<i>Erigeron speciosus</i>	•	•											•																										
Asteraceae	<i>Helianthella quinquenervis</i>	•	•											•																										
Asteraceae	<i>Heliomeris multiflora</i>	•	•											•																										
Asteraceae	<i>Heterotheca villosa</i>	•	•											•																										
Asteraceae	<i>Senecio canus</i>													•																										
Asteraceae	<i>Solidago multiradiata</i>																																							
Asteraceae	<i>Taraxacum officinale</i>	•	•											•																										
Boraginaceae	<i>Hackelia floribunda</i>	•	•											•																										
Boraginaceae	<i>Lithospermum ruderale</i>													•																										
Boraginaceae	<i>Mertensia fusiformis</i>													•																										
Brassicaceae	<i>Arabis hirsuta</i>													•																										
Brassicaceae	<i>Erysimum inconspicuum</i>	•	•											•																										
Campanulaceae	<i>Campanula rotundifolia</i>	•	•											•																										
Caryophyllaceae	<i>Arenaria congesta</i>													•																										
Fabaceae	<i>Lathyrus leucanthus</i>	•	•											•																										
Fabaceae	<i>Vicia americana</i>													•																										
Gentianaceae	<i>Pneumonanthe parryi</i>													•																										
Hydrophyllaceae	<i>Hydrophyllum fendleri</i>													•																										
Linaceae	<i>Linum lewisii</i>	•	•											•																										
Polemoniaceae	<i>Collomia linearis</i>													•																										
Polemoniaceae	<i>Ipomopsis aggregata</i>													•																										
Polygonaceae	<i>Eriogonum umbellatum</i>	•	•											•																										
Primulaceae	<i>Androsace septentrionalis</i>	•	•											•																										
Ranunculaceae	<i>Delphinium nuttallianum</i>	•	•											•																										
Ranunculaceae	<i>Ranunculus inamoenus</i>													•																										
Rosaceae	<i>Fragaria virginiana</i>													•																										
Rosaceae	<i>Potentilla pulcherrima</i>	•	•											•																										
Rubiaceae	<i>Galium boreale</i>													•																										
Scrophulariaceae	<i>Collinsia parviflora</i>													•																										
Valerianaceae	<i>Valeriana occidentalis</i>													•																										
Violaceae	<i>Viola praemorsa</i>													•																										

Appendix 2. The numerical code for identifying plants and pollinators in Fig. 4. Floral morphology of the plants is also included. Members of insect and hummingbird families were verified as functioning as pollinators in this or other systems (one exception is footnoted) by conducting a literature search for each family.

Plants	Plant ID no.	Floral morphology	Pollinators	Pollinator ID no.
<i>Achillea lanulosa</i>	1	umbel	Andrenidae	1
<i>Agoseris aurantiaca</i>	2	open	Anthomyiidae	2
<i>Agoseris glauca</i>	3	open	Apidae	3
<i>Androsace septentrionalis</i>	4	open	Arctiidae	4
<i>Arabis hirsuta</i>	5	open	Bombyliidae	5
<i>Arenaria congesta</i>	6	open	Brachonidae	6
<i>Campanula rotundifolia</i>	7	bell	Buprestidae	7
<i>Collinsia parviflora</i>	8	zygomorphic	Calliphoridae	8
<i>Collomia linearis</i>	9	open	Chrysididae	9
<i>Delphinium nuttallianum</i>	10	zygomorphic	Cleridae	10
<i>Dugaldia hoopesii</i>	11	open	Coccinellidae	11
<i>Erigeron flagellaris</i>	12	open	Colletidae	12
<i>Erigeron speciosus</i>	13	open	Halictidae	13
<i>Eriogonum umbellatum</i>	14	umbel	Hesperidae	14
<i>Erysimum inconspicuum</i>	15	open	Ichneumonidae	15
<i>Fragaria virginiana</i>	16	open	Lycaenidae	16
<i>Galium boreale</i>	17	umbel	Masaridae	17
<i>Hackelia floribunda</i>	18	open	Megachilidae	18
<i>Helianthella quinquenervis</i>	19	open	Meloidae	19
<i>Heliomeris multiflora</i>	20	open	Miridae	20
<i>Heterotheca villosa</i>	21	open	Muscidae	21
<i>Hydrophyllum fendleri</i>	22	umbel	Noctuidae	22
<i>Ipomopsis aggregata</i>	23	tubular	Nymphalidae	23
<i>Lathyrus leucanthus</i>	24	zygomorphic	Pieridae	24
<i>Ligusticum porteri</i>	25	umbel	Rhagionidae	25
<i>Linum lewisii</i>	26	open	Sarcophagidae	26
<i>Lithospermum ruderale</i>	27	open	Siricidae ¹	27
<i>Mertensia fusiformis</i>	28	bell	Sphecidae	28
<i>Pneumonanthe parryi</i>	29	tubular	Sphingidae	29
<i>Potentilla pulcherrima</i>	30	open	Stratiomyidae	30
<i>Pseudocymopterus montanus</i>	31	umbel	Syrphidae	31
<i>Ranunculus inamoenus</i>	32	open	Tachinidae	32
<i>Senecio canus</i>	33	open	Tenthredinidae	33
<i>Solidago multiradiata</i>	34	open	Trochilidae	34
<i>Taraxacum officinale</i>	35	open	Vespidae	35
<i>Valeriana occidentalis</i>	36	umbel		
<i>Vicia americana</i>	37	zygomorphic		
<i>Viola praemorsa</i>	38	zygomorphic		

¹To our knowledge, the role of Siricid wasps as pollinators has not been previously demonstrated. As adults, they have reduced mouthparts, feeding little (or not at all), and this may limit their effectiveness as pollinators.

Appendix 3. Summary statistics for plant-pollinator interaction matrices in each of the three years of observation. Control (C), high nitrogen addition (H), and low nitrogen addition (L) are the three treatments included for each year.

Year	2005				2006				2007			
	C	H	L	Total	C	H	L	Total	C	H	L	Total
Nitrogen treatment												
Sampling hours	40.6	42.4	42.2	125.2	59.5	57.9	58.7	176.1	56.3	55.2	56.7	168.2
Total no. of taxa (plants and pollinators)	40	42	40	56	46	46	47	56	51	46	51	63
No. of pollinator families observed	16	17	15	23	22	23	22	25	29	24	25	32
No. of foraging bouts observed	785	803	850	2438	1014	884	1116	3014	1072	1017	1250	3339
No. of flower visits per foraging bout	4678	6677	7512	18867	6461	5933	8258	20652	3615	3655	5222	12492
No. of links	77	78	73	133	116	98	111	183	133	136	153	239
No. of plant species visited	24	25	25	33	24	23	25	31	22	22	26	31
Median links per plant species	2	2	2	3	3	3	3	4	4.5	4.5	5	6
Maximum links per plant species	14	11	13	15	16	15	18	20	24	20	23	28
Median visits by all poll to indiv plant	8	8	8	12	6.5	7	5	14	13.5	8.5	8.5	13
Max visits by all poll to indiv plant	259	250	311	820	530	435	595	1560	735	633	845	2213
Median links per pollinator species	2.5	3	3	3	4.5	3	3.5	5	3	6	5	4
Max links per pollinator species	15	20	18	24	16	15	19	22	12	13	16	22
Connectance	0.20	0.18	0.19	0.175	0.22	0.19	0.20	0.24	0.21	0.26	0.24	0.24
Temperature (T)	8.19	8.77	10.05	6.21	15.64	9.37	8.25	11.3	10.88	11.53	10.87	7.73
Nestedness (100-T/100)	0.92	0.91	0.90	0.94	0.84	0.91	0.92	0.89	0.89	0.88	0.89	0.92