

Deliberately increased network connectance in a plant-pollinator community experiment

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Networks are a popular way to visually represent and analyse interactions between species in ecological communities, and there have been several recent calls for interaction network measures to be targets of conservation and management efforts. However, it is challenging to deliberately manipulate empirical network properties. Our objective was to determine whether the network property of connectance could be manipulated in a planned and deliberate fashion, without altering the size of the community. Connectance (proportion of realized interactions out of total number of possible interactions) is often used as a proxy for community complexity, and theory also suggests it is related to community robustness and stability. We designed a field experiment to increase the connectance of a mutualistic community by manipulating the attractiveness of plant species in a bee-plant interaction network. Specifically, we applied a chemical fertilizer to enhance the floral display and resource quality provided by experimental plants, and assessed the effect on bee community structure. We found the connectance was significantly higher in fertilized plots relative to controls. This manipulation was associated with a significant increase in both the species richness (+41%) and abundance (+77%) of pollinators; there were more pollinator species in treatment plots, and these pollinators visited more plant species with a higher frequency. This study shows that a network property can indeed be altered experimentally; here we were able to deliberately increase the connectance of a bee-plant network while keeping constant both the number of plant species and the background community of potential floral visitors. Deliberate manipulation of experimental community structure therefore could be a valuable avenue for future research. Integration of network theory with empirical research also has the potential to inform the design of network control approaches.

Keywords: community level; connectance; diversity; management; network; plant-pollinator.

1. Introduction

It has become increasingly common to represent ecological communities as complex interaction networks [1] and such networks are easily modified to specifically represent mutualistic interactions between species [2]. There is a large body of observational work detailing the structural properties of mutualistic networks [3], and much theory addressing the potential ecological importance of the architecture of these communities [4, 5]. Network properties have frequently been recommended as management targets [6–9] and there are many studies that evaluate network structure as an emergent property of manipulated communities

(e.g. [10]). In general, experimental manipulations of ecological networks aim to determine whether any property has been affected; these include, for example, removing a species [10, 11], fertilization [12] and shifting flowering phenology [13]. However, such studies are not directed at changing a specific property in a deliberate fashion. Thus, it has not been demonstrated that managers can take direct action deliberately to manipulate particular structural properties [9]. Indeed, it is difficult to conceptualize how many of these properties, which are emergent attributes of complex webs of dynamic and labile interactions, might be manipulated.

One particular challenge to directly manipulating network-level properties is to do so without changing the size of the network. Many network properties strongly depend on the number of species in the community (or nodes in the network) [14] and the interaction structure of species within the community can be sensitive to the presence or absence of a single species [11]. Eradicating a species from a community can be challenging and potentially detrimental [11, 15, 16], while there are many risks to introducing new species (e.g. biocontrol agents [17, 18]). Connectance (also known as ‘density’ [7]); however, is a relatively simple network-level property and can be expressed as the number of realized links (i.e. species–species interactions) divided by the number of possible links. It summarizes the complexity of the interactions in a community and has been tied theoretically to community stability [5] and robustness to species loss [19]. As such, it has been suggested as a possible valuable management target [7, 9]. Furthermore, it can hypothetically be manipulated without adding or removing species from the community by changing the number of realized links relative to the number of potential links.

One area where networks have the potential to provide useful recommendations for management and conservation is the mutualistic interactions between plants and their pollinators [7]. This area is of particular interest in contemporary work because of the valuable service floral visitors, and especially bees [20–24], provide by pollinating crops in agricultural systems [25]. The number of pollinator-dependent crop species has increased over time [26], but the domesticated crop pollinators, honey bees, on which we would traditionally rely are threatened by a suite of hazards [27, 28]. For this reason, many land managers are turning to communities of native bees to supplement or replace the honey bee as primary crop pollinators [24, 29] and strategies to ensure such communities thrive are being developed. For example, land managers might plant habitat along crop field margins to provide floral resources the bees are lacking [30], especially when crops are not in flower [31]. The effectiveness of the pollination services provided by wild pollinators has been strongly tied to the species richness and abundance of the bee community [21, 24, 32, 33]. Management of pollination services; however, focuses not only the number of bee species in the community [22, 24, 34], but also on increasing the stability and efficacy of the community [35]; in essence, the objectives are to improve and manage community structure, with the intent to enhance community function [21, 22, 24, 33, 34].

Motivated by a theoretical interest in testing whether deliberate manipulation of a network measure is logistically feasible, and if so, whether such a manipulation could be used in a real field system, we designed an experiment to increase the connectance of a simple bee-plant network. We address two questions: (1) can connectance be experimentally increased and (2) does an increase in connectance relate to some measurable response in pollinator community composition over short time scales? Our experimental treatment was the application of a chemical fertilizer to increase the floral resources provided by four plant species, a management action that does not change the number of species or individuals of plants. To the best of our knowledge, this is the first experiment to deliberately attempt to manipulate a specific network-level property. Our results show that we can indeed alter the complexity of mutualistic networks, and that network level properties might thus be suitable for directing management objectives in the field.

2. Materials and methods

In the spring of 2012, individuals of each of four native perennial plant species were planted in 10 2×2 m plots established 100 m apart along a transect in the Arboretum at the Pennsylvania State University. The plots were surrounded by a matrix consisting largely of grasses, but with weedy components such as thistles (*Carduus acanthoides* and *Cirsium arvense*), horsenettle (*Solanum carolinense*), teasel (*Dipsacus* spp.), knapweed (*Centaurea maculosa*), crown vetch (*Securigara varia*), bird's foot trefoil (*Lotus corniculatus*) and clovers (*Trifolium repens* and *T. pretense*). The four plant species used in this study were *Veronicastrum virginicum* (L.) Farw. (culver's root), *Eupatorium perfoliatum* L. (common bonese), *Pycnanthemum tenuifolium* Schrad. (mountain mint) and *Monarda fistulosa* L. (bergamot). These species were chosen based on prior research addressing their potential for floral resource provisioning in agroecosystems [31, 36]; among the 25 species evaluated, *V. virginicum*, *E. perfoliatum* and *M. fistulosa* were the three most highly visited species, while *P. tenuifolium* was a less well-visited species and thus had the greatest potential for an increase in linkage [36].

The plots were paired spatially, and one plot of each pair was randomly selected to receive a fertilization treatment consisting of 14.3 g NPK 11-35-15 dissolved in 7.6 l of water applied every 3–4 days as recommended by the manufacturer, depending on rain, while control plots received 7.6 l of water at the same time. This level of fertilization is relatively low compared to most agricultural applications (especially in terms of nitrogen), but is typical for cultivated ornamental plants. In all, there were five fertilized and five control plots along the transect. All plots received 7.6 l of water every non-treatment day unless there was substantial rainfall. Fertilization treatment began in early May and continued through the duration of the experiment, which was terminated in the first week of August. The individual experimental plants were grown in pots, and the surrounding vegetation did not receive water or fertilizer. The number of florets (*P. tenuifolium*), racemes (*V. virginicum*) or flower heads (*M. fistulosa* and *E. perfoliatum*) for each plant species were counted for every sampling period (see below). For species with flower heads or racemes comprising many florets (i.e. *V. virginicum*, *M. fistulosa* and *E. perfoliatum*), a subset of the heads or racemes was selected, on which the florets were counted, yielding an estimate of the average number of florets per head or raceme for each individual of each species. This estimate of number of florets per individual over the entire summer was used as a proxy for total floral display. At the end of the experiment, we collected and measured all above ground plant biomass.

Bee visitors that landed on the reproductive parts of flowers of each species in each plot were collected with a Bioquip Insect Vacuum (a modified hand-held vacuum) [37] for 2 min 9 times throughout the summer, for a total of 3 h of sampling time for each species. Such information about insects collected directly on flowers is commonly used to build interaction networks [10, 23, 31, 38, 39]. In addition to the vacuum sampling, insects were also collected in bee bowls to give a more complete picture of the background community of bee species present in the area and able to visit the flowers in the plots; these bowls allowed us to increase the amount of sampling and also detected species we did not detect with the vacuum method [40]. Three bowls (one each of yellow, white and blue) were situated adjacent to the plots during a sampling period, and filled with soapy water. They were collected after 24 h. There were four bee bowl collections during the summer. The vacuum and pan sampling began after first anthesis of the plant species with the earliest phenology (*M. fistulosa*) in mid-June and continued until the termination of the experiment in early August. The majority of our sampling occurred during the overlap of the flowering seasons of the four species in the month of July. Bee specimens (superfamily Apoidea) collected from the bee bowls were washed, pinned and identified to the species level. Species level identifications were confirmed by L. R. Donovall at the Pennsylvania Department of Agriculture in Harrisburg, PA and

voucher specimens are available at the Pennsylvania State University. The bee bowls collect a substantially different community of bees than active sampling of bees on flowers, and the two methods are often considered complementary to each other [41]. Here, by using both an active and a passive trap, we were able to better characterize both the species present in the wider bee community and the subset that actually visit flowers.

For the purpose of building interaction networks, our collections were focused on the bee community because bees are often considered to be the primary pollinators in agricultural systems and much of the work on pollination services has focused on this group of species (e.g. [20–24]). However, observational data were also collected on the wider insect community that visited the flowers in our experimental plots, including wasps, ants, moths, butterflies, beetles and flies. Because these data are of a lower (and more variable) taxonomic resolution, they are presented only in the supplemental materials, reserving the network analyses for the species level resolution obtained by the vacuum trap data (Supporting Information and Supplementary Table S3).

Generalized Linear Mixed-Effects Models (specifically in the package `lme4` in R [42]) were used to test for differences in the number of florets and destructive biomass of each plant species, as well as the abundance of bee specimens and bee species richness in vacuum and pan traps (separately), with fertilizer as the fixed effect and sampling date and plot as random effects. We used Gaussian errors for the number of florets and biomass and Poisson errors for bee species richness. However, we used an inverse Gaussian distribution in the abundance data because of overdispersion in the errors. A paired t-test was used to determine whether the proportion of realized links increased for any of the plant or bee species individually. A two sample chi-square comparison was also performed to test the association of all bee species with fertilized versus unfertilized plots and a one way chi-square analysis to test whether individual species were more likely to be found in fertilized plots than one would expect given random (50%) chance. In the one way chi-square analysis, a Yates correction was used for 1 degree of freedom [43]. The Yates correction subtracts 0.5 from the difference between observed and expected frequencies to account for the upward bias of Pearson's chi-square tests on contingency tables [43].

To determine whether there was a significant change in network connectance, interaction matrices were generated for each plot, comprising the sum of all interactions between bee species and plant species over the summer. For each interaction matrix, the number of unique interactions, the interaction frequency (abundance of a particular species on a particular plant), and connectance were calculated. Connectance is measured as the number of realized links divided by the number of possible links which, in a bipartite network such as this one, constitutes the number of possible interacting pairs of species [44]. The number of possible links (i.e. possible interactions) was defined as the total number of bee species collected in *any plot* multiplied by the number of plant species in flower at any plot at any time during the summer. These represent the bees present in the spatial area of the plots and able to visit the flowers. The number of realized links was obtained from the vacuum trap data of actual visitation by bee individuals to flower species in each plot. We also conducted this same analysis while restricting the number of possible bee species in the system to just those that were found in unfertilized plots to determine whether differences in bee species richness were driving changes in network structure. We compared the results from the real system to a null model where we constructed networks of a range of sizes reflecting the full scope of observed sizes and filled each one with interactions randomly selected from the distribution of real interactions. We repeated this random selection 1,000 times at each network size and averaged across the iterations to obtain average frequency of visitation and connectance values.

3. Results

A total of 24 bee species were collected on the plants using the vacuum trap, and 21 species in the bee bowls. Overall, 388 bee specimens were collected, comprising 34 species (Table 1). Among the bee species, there were significantly more individuals of *Augochlorella aurata*, *Halictus ligatus*, *Lasioglossum viridatum* and *Bombus impatiens* ($p < 0.01$, Table 1) as well as *Hylaeus mesillae* ($p < 0.05$, Table 1) caught in fertilized plots than unfertilized plots and no species were negatively associated with the fertilized plots ($p > 0.05$, Table 1). There were a few species that were either absent in fertilized plots (*Bombus ternarius*, *Lasioglossum coriaceum* and *Megachile rotundata*), or reduced in abundance (*Apis mellifera*, *Bombus bimaculatus* and *Xylocopa virginica*). The species that were absent were in low abundance in unfertilized plots, and most of the declines in abundance were very small. The largest decline in visitation was in *A. mellifera*; six fewer individuals were found in fertilized plots than unfertilized plots. None of the declines or absences were significant in fertilized relative to unfertilized plots (Table 1).

In addition to a significant increase in the average abundance of bees in both pan and vacuum traps ($p < 0.05$, Fig. 1 and Table 2), there was also a significant difference in the bee species composition associated with fertilized versus unfertilized plots (two sample chi-square 51.98, df 33, $p < 0.01$). While the vacuum traps detected significantly more bee species on average in fertilized plots ($p = 0.001$, Table 2), the pan traps did not ($p = 0.19$, Table 1). Because many of the pollinator species collected in our study (Table 1) can forage more than 100 m, it is likely that the fertilized plants are only locally increasing pollinator abundance and richness compared to unfertilized ones by attracting opportunistic pollinators in the environment.

Connectance was measured as the total number of realized links divided by the total number of possible links; here, the possible links are defined by the bee species collected in any plot over the summer (i.e. bees present in the community and available to visit plants). The number of possible links was therefore the same for both fertilized and unfertilized plots. In contrast, the number of realized links, defined as the documented interactions between bee visitors and plant species (vacuum collected specimens), increased significantly with fertilization (Fig. 2, Table 2). In our experiment, we carefully controlled for community size (i.e. number of possible links) by constraining the number of plant species and measuring the background community of possible bee species. The proportion of bee species captured visiting flowers relative to the total number of available bee species was greater in fertilized plots than in unfertilized plots. Analyses of connectance for our observational data (with their inherently lower taxonomic resolution) show no significant effect of the experimental treatments (Supplementary Table S3).

We also found a significant relationship between the summed interaction frequency (bee abundance) and connectance ($p = 0.0005$, Fig. 2(a)) and between connectance and the plot-level species richness of pollinators ($p = 0.0121$, Fig. 2(b)). Given the fixed background community size, higher species richness was positively correlated with connectance; plots that had a higher diversity of bee visitors also had a higher connectance (Fig. 2(b)). Connectance is still higher in fertilized plots when we control for network size by restricting the number of available species to those in the unfertilized plots, but the increase is no longer significant ($p = 0.1$). In other words, more bee species were found to visit more plant species in fertilized plots, and in greater numbers, and the increase in connectance is likely mostly due to the increase in both bee abundance and richness. The results from our null model are consistent with the results of the experiment. When we randomly select the interactions in networks of varying sizes, there is a strong association between connectance and network size, though the slope is slightly steeper in the real system than in the null model (Supplementary Fig. S1).

Fertilization resulted in a significant increase in the biomass of three of the four plant species ($p < 0.05$, Table 3). The number of florets was higher on average for all fertilized plants, except *P. tenuifolium*, but

TABLE 1 *Bee species collected and their abundance in fertilized and unfertilized plots, combining both vacuum and pan traps across the season. The one-way chi-square values test whether each species associates with a fertilized or unfertilized plot more than would be expected, given a random (i.e. 50%) chance; there is a Yates correction for 1 degree of freedom. Significance of $p < 0.05$ is indicated by one asterisk (*), while significance of $p < 0.01$ is indicated by two asterisks (**)*

Species	Fertilized	Unfertilized	Sum	χ^2	Significance
<i>Agapostemon virescens</i>	2	1	3	0.00	
<i>Anthidellum notatum</i>	3	2	5	0.00	
<i>Apis mellifera</i>	27	33	60	0.42	
<i>Augochlora pura</i>	11	6	17	0.94	
<i>Augochlarella aurata</i>	15	3	18	6.72	**
<i>Bombus bimaculatus</i>	8	9	17	0.00	
<i>Bombus impatiens</i>	48	24	72	7.35	**
<i>Bombus ternarius</i>	0	3	3	1.33	
<i>Calliopsis andreniformis</i>	7	2	9	1.78	
<i>Ceratina calcarata</i>	1	0	1	0.00	
<i>Ceratina dupla</i>	1	1	2	0.50	
<i>Halictus confusus</i>	1	1	2	0.50	
<i>Halictus ligatus</i>	38	13	51	11.29	**
<i>Halictus rubicundus</i>	7	4	11	0.36	
<i>Holcopasites calliopsidis</i>	2	0	2	0.50	
<i>Hoplitis pilosifrons</i>	1	0	1	0.00	
<i>Hylaeus affinis</i>	22	20	42	0.02	
<i>Hylaeus mesillae</i>	6	0	6	4.17	*
<i>Hylaeus modestus</i>	3	1	4	0.25	
<i>Lasioglossum admirandum</i>	10	3	13	2.77	
<i>Lasioglossum coriaceum</i>	0	1	1	0.00	
<i>Lasioglossum imitatum</i>	7	5	12	0.08	
<i>Lasioglossum males</i>	1	2	3	0.00	
<i>Lasioglossum pectorale</i>	1	0	1	0.00	
<i>Lasioglossum pilosum</i>	1	0	1	0.00	
<i>Lasioglossum tegulare</i>	4	0	4	2.25	
<i>Lasioglossum versatum</i>	1	0	1	0.00	
<i>Lasioglossum viridatum</i>	12	1	13	7.69	**
<i>Lasioglossum zonulum</i>	1	0	1	0.00	
<i>Megachile pugnata</i>	1	0	1	0.00	
<i>Megachile rotundata</i>	0	1	1	0.00	
<i>Melissodes bimaculata</i>	3	0	3	1.33	
<i>Sphecodes illinoensis</i>	1	0	1	0.00	
<i>Xylocopa virginica</i>	2	4	6	0.17	

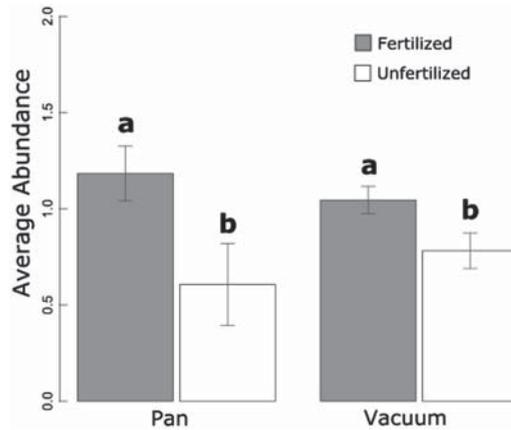


FIG. 1. The relationship between the abundance of all bees collected in plots (averaged over sampling period and plot) for pan and vacuum traps. Fertilized plots (dark grey) had a significantly higher average abundance of bees than unfertilized (white) within a trap type ($p < 0.05$).

TABLE 2 The average pollinator species richness, abundance and connectance in fertilized and unfertilized plots, separated by trap type. Because species–species interactions were not recorded in pan collections, there is no measure of connectance for the pan trap. Standard errors are included for each measure

Bees in trap type	Fertilized	Unfertilized
Pan		
Pollinator species richness	6.2 ± 1.59	3.4 ± 1.29
Abundance	9.8 ± 2.87	4.4 ± 1.75
Vacuum		
Pollinator species richness	11.6 ± 0.81	8.4 ± 0.93
Abundance	39.8 ± 5.31	23.6 ± 4.88
Connectance	0.127 ± 0.011	0.089 ± 0.007

this increase was not significant ($p > 0.05$, Table 3). Even though they did not have significantly larger floral displays, the plant species showed a significant increase in biomass that may indicate that the plants were healthier in general. It is possible that this increase in biomass was driving the change in pollinator visitation. Plants fertilized with vermicompost have also been shown to have higher quality nectar, which is attractive to bumblebees in greenhouse experiments [45]; a similar change in nectar quality may be responsible for the increased attractiveness of our experimental plants. It is also possible that the fertilization resulted in a higher pollen quality.

Pycnanthemum tenuifolium was selected for our study because it was previously found to be poorly visited relative to the other three plant species [31]; thus, we expected it to experience the largest increase in visitation. Instead, there was a significant increase in the frequency of visitation

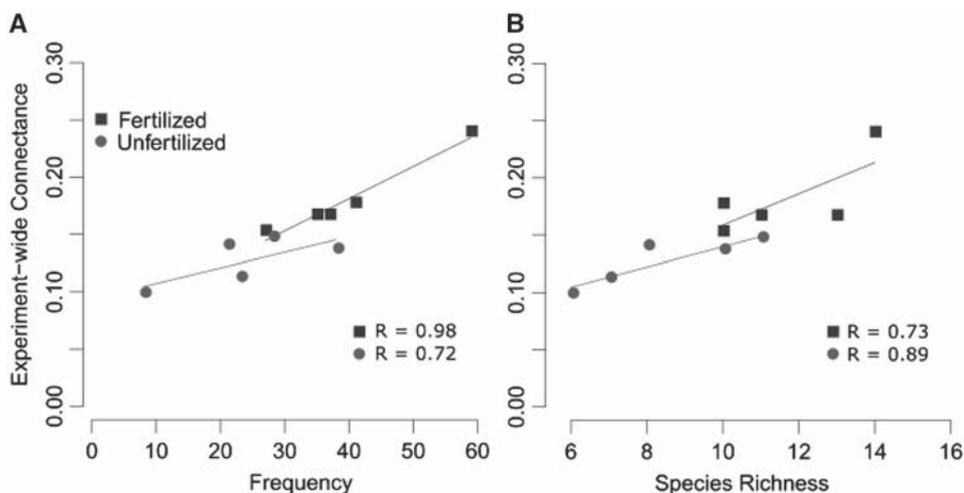


FIG. 2. The relationship between connectance and the frequency of visitation (A) and species richness of pollinators (B) in fertilized (black square) and unfertilized (gray circle) plots. This relationship is significant for some R^2 values (frequency: $p = 0.003$ for fertilized and $p = 0.171$ for unfertilized and species richness: $p = 0.162$ for fertilized and $p = 0.045$ for unfertilized). When fertilized and unfertilized plots are analyzed together, the relationships between connectance and frequency of visitation and species richness are significant ($p = 0.0005$, $R^2 = 0.799$ and $p = 0.012$, $R^2 = 0.566$, respectively).

TABLE 3 The number of florets averaged across the season (rounded to the nearest integer) and the final biomass (in grams) for each of the four plant species in the study, with standard errors. There was no significant effect on the number of florets for any species ($p > 0.05$), but there was a significant increase in the biomass of *E. perfoliatum*, *P. tenuifolium* and *V. virginicum* ($p < 0.05$). Bold p values indicate significance at the $p < 0.05$ level.

Species	Florets			Biomass (g)		
	Fertilized	Unfertilized	p value	Fertilized	Unfertilized	p value
<i>Eupatorium perfoliatum</i>	52 ± 36	40 ± 13	0.38	193.6 ± 29.4	83.4 ± 20.1	0.02
<i>Monarda fistulosa</i>	960 ± 230	662 ± 194	0.21	98.5 ± 3.5	90 ± 14.6	0.41
<i>Pycnanthemum tenuifolium</i>	253 ± 99	269 ± 65	0.46	133.2 ± 10.9	48.3 ± 15.2	0.002
<i>Veronicastrum virginicum</i>	712 ± 253	418 ± 197	0.22	174.8 ± 26.3	102.8 ± 7.1	0.04

to *V. virginicum* ($p < 0.05$), the species that had the highest diversity of bee visitors in previous research as well as the highest abundance of bee visitors in this study. The realized degree (i.e. individual species connectance) was consistently higher in fertilized plots for all plant species, but this increase was only significant for *V. virginicum* ($p < 0.05$, Supplementary Table S1 [31]). Of the 13 bee species found in both treatment types, only one had a significantly higher realized degree in fertilized plots (Supplementary Table S2). However, the realized degree was consistently, though not significantly, higher in fertilized plots for all bee species that were found in both plot types (Supplementary Table S2).

4. Discussion

While there has been much theoretical and empirical work addressing the importance of the structure of ecological networks, we are not aware of any experiments that deliberately attempt to manipulate specific network properties in real ecological systems. There have been many calls for empirical tests of properties of ecological networks (e.g. [46]); however, experiments involving deliberate manipulations of such structural properties are both conceptually and logistically challenging. At the same time, structural properties of networks representing ecological interactions are thought to be critical indicators of the health and function of the community [3–5, 7]. We specifically designed our study to determine whether we could in fact intentionally manipulate a network-level property and, if so, whether it would have the desired (and hypothesized) impact on the community. Our work suggests that network-level properties can indeed be manipulated.

We focused on one structural property, connectance, thought to be an important indicator of the stability and robustness of ecological communities [5, 19]. We were able to experimentally increase the connectance of a bee-plant community (via a greater proportion of realized interactions). Mechanistically, the observed increase in connectance in treatment plots was the result of two contributing factors. First, they had higher visitor species richness; in other words, connectance increased because additional species visited fertilized plants. Second, the bee species in fertilized plots also had a consistently higher proportion of realized links (Supplementary Table S2). Pollinators visited more plant species in fertilized plots with a higher frequency. The few species lower in abundance (or absent) from fertilized plots were not significantly so, and represented primarily generalist species able to visit a broad variety of plant species. The less common and parasitic species (e.g. *Calliopsis andreniformis*, *Holcopasites calliopsidis* and *Sphecodes illinoensis*) are better represented in fertilized plots. The species significantly more abundant in fertilized plots are all generalists.

The connectance of ecological networks, though sensitive to community size and ecosystem context, is believed to be relatively robust within a given ecosystem between years [38]. Indeed, it remains unperturbed even in the face of experimental warming in food webs [47] and species invasions in plant-pollinator interactions [39, 48, 49]. Thus, it is interesting that we were able to increase connectance experimentally by improving soil quality with a fertilization treatment. This suggests that it may also be possible to manipulate other network properties with management actions. For example, we might be able to alter the average degree of networks simply by trading out one species of the plant species mix with a supergeneralist; the presence of supergeneralists has the potential to dramatically alter plant-pollinator interactions in a way that affects complex network properties such as compartmentalization and nestedness [50, 51]. Interestingly, at the lower and more variable taxonomic resolution possible with observational data, the strong signal of altered connectance was lost, for bees as well as for other pollinator species (Supplementary Table S3). It is possible that observational studies have inherently lower power to detect important changes in network structure, which may hamper both inference and management efforts.

The preponderance of evidence suggests diversity is important for maximizing the stability and efficacy of ecosystem services, particularly in the case of pollinator mutualisms, where wild bees provide critical pollination services [21, 23, 24, 33, 34]. Indeed, pollinator species richness and abundance have been tied to higher fruit set [24, 34] and crop yield [21] in agricultural systems. Properties of mutualistic network structure have been theoretically tied to stability (e.g. [4, 5, 19, 52, 53]), but the relationship between these network properties and community function remains unclear [6, 8]. The relationships we show here, between interaction frequency, bee species richness and connectance, suggest, at least on this small scale, connectance might relate to the ecosystem service of pollination. More generally, our

results also agree with studies that propose a relationship between structure and community function in ecological networks [5, 19, 23]. Whether longer term or larger scale effects are obtainable is an open question, but even short-term increases in pollinator visitation may be of benefit to managers who provide floral resources on crop field margins [30]. Although this is just one case study, there is the potential for it to be replicated using a similar approach in other plant-pollinator networks and even in other putatively mutualistic systems [54].

Prior empirical [44] and theoretical [55] research shows that connectance decreases with increasing species richness because the number of possible links increases more rapidly than the number of realized links. When comparing two communities of different sizes and a similar probability of interaction, the connectance will perform be lower in a community with more species. Because we controlled for the plant community size and every plot had the same potential floral visitors, an increase in pollinator richness in a given plot resulted in a higher connectance.

In addition to species richness, the frequency of interactions (or abundance of bee individuals collected) was also significantly related to connectance. The association between frequency and connectance has been suggested by prior research, which showed a predictive relationship between the relative abundance of plants and insect visitors and the connectance of the community [1]. On the other hand, it may also be related to sampling error. Interactions that occur with higher frequency are more likely to be observed [56]; thus, increasing the frequency of rare interactions would make them more observable. Regardless, the increased attractiveness and potentially higher nectar quality of fertilized plants may have implications for the stability of bee populations. For example, bumblebees visiting plants with a higher nectar quality have been shown to have increased fitness, suggesting possible population-level effects may accrue [45].

One of the fundamental problems hampering conservation of ecological systems arises from a poor understanding of how to manage the complex interactions that lead to emergent ecosystem services. Here, we demonstrate the effects of an experimental manipulation designed to change a community-level property and assert that similar manipulations will be essential to future studies applying network theory to ecological communities. We successfully increased the proportion of realized links in a simple bee-plant community with a relatively modest perturbation. We demonstrate that this increased connectance was significantly associated with higher bee species richness and abundance. Unfortunately, this suggests that other perturbations, such as the elimination of plants on field margins or application of herbicides [57] could potentially have dramatic impacts on community function, even without reducing the species richness of the plants, by changing the quality of the floral resources available to pollinators. Managing communities of interacting species remains a significant challenge, but our results suggest that network theoretical predictions can be experimentally tested in the field, and relatively subtle manipulations, grounded in network control theory, could have significant conservation benefits. Such experiments have the potential to provide insight into the complexity of ecological systems, as well as the fundamental dynamics and control of species interaction networks.

Supplementary data

Supplementary data are available at *COMNET* online.

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