

RESEARCH ARTICLE

Diversity and Distribution of Floral Resources Influence the Restoration of Plant–Pollinator Networks on a Reclaimed Strip Mine

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Abstract

Plant–pollinator mutualisms are one of the several functional relationships that must be reinstated to ensure the long-term success of habitat restoration projects. These mutualisms are unlikely to reinstate themselves until all of the resource requirements of pollinators have been met. By meeting these requirements, projects can improve their long-term success. We hypothesized that pollinator assemblage and structure and stability of plant–pollinator networks depend both on aspects of the surrounding landscape and of the restoration effort itself. We predicted that pollinator species diversity and network stability would be negatively associated with distance from remnant habitat, but that local floral diversity might rescue pollinator diversity and network stability in locations distant from the remnant. We created plots of native prairie on a reclaimed strip mine in central Ohio, U.S.A. that ranged in floral diversity

and isolation from the remnant habitat. We found that the pollinator diversity declined with distance from the remnant habitat. Furthermore, reduced pollinator diversity in low floral diversity plots far from the remnant habitat was associated with loss of network stability. High floral diversity, however, compensated for losses in pollinator diversity in plots far from the remnant habitat through the attraction of generalist pollinators. Generalist pollinators increased network connectance and plant-niche overlap. As a result, network robustness of high floral diversity plots was independent of isolation. We conclude that the aspects of the restoration effort itself, such as floral community composition, can be successfully tailored to incorporate the restoration of pollinators and improve success given a particular landscape context.

Key words: diversity, ecosystem function, network analysis, pollinator assemblage, pollinator restoration, prairies.

Introduction

The primary goal of restoration is to return degraded ecosystems to pre-disturbance composition, structure, and function (Jordan et al. 1999). In principle, the composition and structure of a plant community can be restored with the addition of native plants and the removal or control of invasive ones (Hobbs & Norton 1996). However, how to restore functional relationships between plants and the organisms they interact with is less well established. Pollination is one of the several functional relationships that must be reinstated for ecological restoration to be successful (Dixon 2009). Animal pollinators play a fundamental role in the maintenance of plant communities and contribute to the reproduction of >70%

of flowering plant species (Kearns et al. 1998). Pollination mutualisms are not likely to reinstate themselves in degraded plant communities until the floral, nesting, and over-wintering resource requirements of pollinators have been met (Exeler et al. 2009; Roulston & Goodell 2011). By giving special attention to these habitat requirements, pollination services are more likely to be reinstated, which in turn will have positive effects on the reproductive success of the restored plant community (Menz et al. 2010).

When considering the restoration of pollination function, special care should be directed toward promoting pollinator richness. Pollinator richness has been shown to promote the reproductive output (Gomez et al. 2007), genetic resilience (Wilcock & Neiland 2002), and community stability (Steffan-Dewenter et al. 2005) of a variety of ecosystems. Closely linked to the richness of insects is the distribution and diversity of the floral resources on which they depend (Potts et al. 2003; Steffan-Dewenter 2003; Hegland & Boeke 2006). As a result, ecologists must carefully consider the floral community when restoring pollination mutualisms.

Because pollinator assemblages are taxonomically and ecologically diverse, floral resources are likely to affect subsets of these assemblages differently. Bees are central-place foragers

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and require suitable floral resources within the flight range of their nesting habitat (Michener 2000). Bee flight range tends to decline with body size, which varies greatly between species (Greenleaf et al. 2007). Some of the smallest bees typically forage within a few hundred meters of the nesting habitat (Zurbuchen et al. 2011). Even distances as short as 100 m can serve as a filter, eliminating potential pollinators from area isolated from nesting habitat or other essential resources (Carvalho et al. 2010). Lepidopteran and Dipteran pollinator species, on the other hand, are not central-place foragers, but require specific ovipositing and larval substrates to be distributed throughout the habitat (Scott 1986; Schweiger et al. 2007). Thus, butterfly and hoverfly assemblages are likely to respond to floral distribution differently than bee assemblages (Bergman et al. 2004; Jauker et al. 2009).

Restoration ecologists are increasingly challenged by how to conserve and restore functional plant–pollinator interactions in a community context (Memmott 1999). Considering the extent that plants and pollinators are interconnected, small changes in either community are likely to have cascading effects across multiple species. By using network analysis ecologists can transcend the narrow habitat and taxonomic boundaries of species-specific approaches, and develop overarching descriptions of diverse and interconnected plant–pollinator assemblages. In restoration, network statistics can provide the “meter stick” to which the progress of projects can be accessed. Using network analysis, ecologists can compare networks from restored sites to those of intact sites to form conclusions about the relative success of projects (Forup et al. 2008; Williams 2011).

In this study, we evaluated how the distribution and diversity of floral resources influence the composition of invertebrate pollinator assemblages and the structure and stability of plant–pollinator networks in recently constructed patches of native prairie. Our experimental restoration patches were located in central Ohio, U.S.A. within a grassland landscape that was formerly surface mined for coal. The patches varied in distance from a remnant hardwood forest and in the richness of plants seeded. Our objectives were to first identify how pollinator assemblages change with distance from the remnant habitat and then to determine how these changes affect the structure and stability of plant–pollinator networks. In the case of negative effects of isolation on pollinator richness, we wanted to investigate whether manipulating floral species richness of the restoration would mitigate the reduced pollinator richness and benefit network stability. To answer these questions, we described the pollinator assemblages, as well as the structure and stability of the plant–pollinator networks, for each of our constructed patches. We hypothesized that the remnant forest, because it was undisturbed by the mining, likely serves as a source habitat for some of the pollinator species found in the surrounding disturbed grassland. The forest is also likely to provide shelter, nesting sites, nest materials, and seasonal resources for some pollinator species. Therefore, we predicted that increased distance from the forest would negatively affect pollinator richness. In turn, losses of pollinator richness would negatively affect plant–pollinator

network structure and stability. We further hypothesized that high floral richness would attract a high richness of pollinators, even in distant patches. Thus, the effects of isolation on the pollinator assemblage and network stability were predicted to be less severe than in patches with low floral richness.

Methods

Study System

This study was conducted at The Wilds, a 4,000 ha reclaimed mine site in Muskingum County, OH (lat 39.824922°N, long -81.74893°W), U.S.A. The site was surface mined for coal until the mid-1980s and soon after recontoured and seeded with a low diversity of non-native grasses and forbes as mandated by the 1977 Surface Mining Control and Reclamation Act (Day et al. 1978). The property is grassland in a state of arrested succession, unable to support tree growth because of shallow, infertile soils. Along one edge of the approximately 1-km² study area remains a remnant hardwood forest (Fig. 1), left undisturbed by the mining. In 2009, 48 circular plots of 10-m radius and separated by 70–100 m were treated with herbicide to kill vegetation, tilled to break up the hard soil, and seeded. Sixteen of the plots were seeded with a low diversity of prairie plant species. The remaining 32 plots were seeded with half as much by weight of the same low

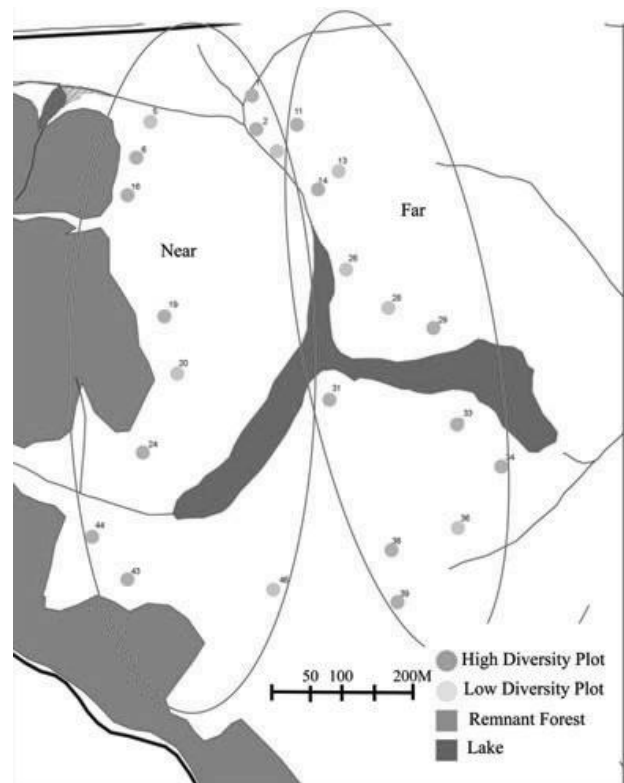


Figure 1. Map of the study site at the Wilds Conservation Park in Muskingum County, OH, U.S.A.

richness mixture in addition to one of two higher diversity seed mixtures (applied to 16 plots each) (Appendix S1, Supporting Information). Since seeding, native adventives and non-native plant species common to the Midwest have also established in the plots (Appendix S1). We focused our sampling effort on a subset of the 48 plots: 8 low floral richness and 16 high floral richness plots, and 8 of each seeding mixture (Fig. 1). The two high floral diversity seed mixtures were grouped for analysis because they shared similar floral richness and pollinator assemblages. Plots were mapped using a Trimble Geo-XT GPS with post-processing and the distance to the nearest remnant forest edge measured in ArcGIS v. 9.2 (ESRI 2009).

Floral Sampling

To quantify the floral community, a total of four floral surveys were carried out between June and August 2010. Surveys were timed seasonally to encompass main pollinator flight activity. During each survey, we counted the number of floral units in 12 randomly placed 1-m² quadrats in each plot. Floral units were defined from the pollinator's perspective rather than by flower or inflorescence morphology (Appendix S1). Thus, one floral unit was separated from another by the distance that a small pollinator would have to fly rather than walk (Saville 1993).

Pollinator Sampling

To quantify the pollinator assemblage, surveys were performed on warm, dry days (22–38°C) with moderate wind speed (0.1–3.4 m/second), between 08:00 and 16:00 hours. We collected all visitors to flowers within our 12 1-m² quadrats for 10 minutes. Insects were identified as pollinators if they were observed probing floral reproductive parts. Pollinators were collected with nets and put into individual clean waxed paper envelopes and placed into a kill jar charged with ethyl acetate. Clean envelopes were used for each insect to avoid pollen contamination between specimens. To ensure that we collected insect specimens foraging on less abundant floral species, we performed a 40-minute sample of the entire plot in addition to the 12 randomly placed quadrats. In the 40-minute sample, we collected all insects seen foraging anywhere within the 10-m radius plot.

Processing Specimens

To extend the record of pollinator visitation to include flowers visited in the recent past, we analyzed the pollen load of insect specimens. We rubbed a small cube of fuchsin-stained gelatin (approximately 2 cubic mm) over each specimen, specifically targeting pollen held in specialized pollen-carrying structures such as scopa (Bosch et al. 2009). The gelatin was then mounted onto glass slides and examined under 400× magnification using differential interference contrast microscopy. To avoid contamination, laboratory utensils and work surfaces were cleaned after each specimen. In most cases, pollen grains were identified to species with the aid of a reference

collection. However, in the cases of *Trifolium* and *Melilotus*, we recorded pollen to genus level because those species could not be clearly distinguished by pollen morphology. We only recorded the presence of pollen with more than 15 grains per slide. Pollens with fewer than 15 grains per slide were likely the result of contamination and were removed from analysis. Contamination was minimal and 97.8% of slides with pollen contained more than 15 grains for each species. Pollinators were then identified to the lowest possible taxonomic level. Of the 2,086 specimens collected, 1,982 were identified to species. The remaining 104 specimens, primarily Diptera of the families Sarcophagidae and Tachinidae, were identified to morphospecies; these specimens accounted for less than 5% of the total collected specimens.

Pollinator Community Analysis

To determine how pollinator assemblages varied with distance from the remnant habitat, we analyzed changes in pollinator abundance, evenness, and species richness using linear regression. We tested evenness using H/H_{\max} , where H is the Shannon richness index and H_{\max} is its maximum value [$\log(\text{species richness})$]. Non-metric multidimensional scaling (NMDS) was used to determine if pollinator assemblage differed with distance (Anderson 2001). Using the R statistical program (Oksanen et al. 2009), we determined Bray–Curtis distances from differences in the relative abundance of pollinators for the 11 most abundant genera. These 11 genera accounted for 87% of the total specimens. The remaining specimens were grouped into four categories based on order: uncommon Hymenoptera, uncommon Diptera, uncommon Lepidoptera, and uncommon Coleoptera. The term “uncommon” is used without reference to the real-world abundance of those species, but rather to the frequency at which they were collected at our study site. Ordination values were determined using 50 runs of 200 iterations with random starting positions, accepted stress less than 10 and instability less than 0.0003. We arbitrarily grouped plots by distance from the forest (near and far) for both floral richness treatments (high and low). Plots within 250 m of the remnant habitat were classified as “near” ($n = 12$), and plots farther than 300 m were classified as “far” ($n = 12$) (Fig. 1). Adonis tests were used to determine if differences between the groups were statistically significant (Anderson 2001). As plots were close enough for pollinators to fly between them, we checked for spatial autocorrelation using a Mantel test (999 permutations). Chao–Sørensen similarity values were calculated for pollinator assemblages in all site pairs, and the geographical distances between all site pairs were measured using ArcGIS v. 9.2 (ESRI 2009). We found no significant autocorrelation (Mantel statistic $r = 0.01154$, $p = 0.45$).

Plant–Pollinator Network Analysis

To determine how plant–pollinator network structure and stability changed with distance from the remnant habitat, we built quantitative plant–pollinator interaction networks for

each plot. Networks were constructed in which the cell values indicate the number of times that the individual pollinators of species “a” were collected foraging on flowers of plant species “p” plus the number of times that the pollen of plant species “p” was found on pollinator species “a.” By combining visitation and pollen load data in the same network, we avoided the dangers of undersampling interactions and can be confident in our estimation of network parameters (Bluthgen & Menzel 2006). For each network, we calculated connectance, plant-niche overlap, and robustness. Both connectance and plant-niche overlap describe network architecture. Connectance is the proportion of realized links and provides a measure of network generalization adjusted for network size, with higher values indicating greater generalization (Lundgren & Olesen 2005). Thus, in a maximally connected network, where nearly all pollinators interact with nearly all plants, connectance approaches one. Plant-niche overlap quantifies the extent to which pollinators are shared by plant species. We determined plant-niche overlap using Horn’s index where a value of 0 indicates no common pollinators between plants, and a value near 1 indicates many shared pollinators (Mueller & Altenberg 1985). To determine how network architecture affects network stability, we calculated the robustness of each network. Rather than describing network architecture itself, robustness quantifies a network’s ability to retain its structure following the removal, or extinction, of species (Dunne et al. 2002). We simulated extinction by removing plant species and observing which pollinators were left without forage resources. Pollinator species were considered to go “extinct” when all of their plant hosts had been removed from the network. We used the bipartite package in R to execute a removal algorithm in which plant species were removed at random without replacement. Although either plants or pollinators could have been removed in the simulation, we chose to remove plant species because in a restoration context, the presence and absence of plants is usually manipulated rather than the pollinators. Simulations were repeated 999 times for each network. We used the technique developed by Borgo et al. (2007) to quantify the robustness with a single parameter r , which ranges from 0 to 1. A network in which r approaches 0 is considered fragile, such that even if a very few plants are eliminated, most pollinators would go extinct. Likewise networks with r approaching 1 are considered robust. In a robust network, most pollinators survive even if a large fraction of the plant species is eliminated. Our simulation assumed that all plant species were equally effective as forage resources so that a pollinator must lose all of its plant hosts before going extinct. We also assumed that the pollinators remaining after plant removal did not expand their local floral diet, a shift that could rescue some insect species from going extinct even when their preferred plants are eliminated. We feel that this assumption is justified because the combination of visitation and pollen records and intensive, season-long sampling likely captured most of the resources used by each species. To quantify how generalized pollinator species were within networks, we used the metric d' , which gives the specialization of each pollinator based on its discrimination

from random selection of plants (Bluthgen & Menzel 2006). The metric d' accounts for the frequency of interactions by giving more weight to frequent interactions. Data were first tested for, and met, assumptions of normality and equality of variances; then the trends were analyzed using linear regression.

Results

Floral Communities

Floral richness was significantly higher in plots seeded with high richness seed mixtures (one-sided t test, $df = 22$, $t = 2.93$, $p = 0.004$). Low richness plots averaged 14 plant species per plot (SE = 0.67), whereas high richness plots averaged 19 species per plot (SE = 0.625). There was no significant effect of the seeding treatment on floral abundance (two-sided t test, $df = 22$, $t = 0.611$, $p = 0.555$). Low richness plots averaged 998 floral units per plot (SE = 42.75) and high richness plots averaged 936 floral units per plot (SE = 61.5). We found no relationship between distance from the remnant forest and floral abundance (linear regression, f -statistic = 1.21 on 1 and 22 df , $r^2 = 0.05212$, $p = 0.283$) or floral richness (linear regression, f -statistic = 0.2726 on 1 and 22 df , $r^2 = 0.01224$, $p = 0.607$).

Analysis of Pollinator Assemblages

We captured a total of 2,086 pollinator specimens of 103 species. The specimens were of four orders: Hymenoptera (56 species), Diptera (34 species), Lepidoptera (10 species), and Coleoptera (3 species). Six species comprised 65% of the specimens: *Bombus impatiens*, *Apis mellifera*, *Toxomerus marginatus*, *Eristalis transversa*, *Halictus ligatus*, and *Lasioglossum mitchelli*. Of the remaining species, 33 were singletons representing the only specimen caught of that species and 26 were doubletons.

We found no association between pollinator abundance or evenness and distance from remnant forest for either floral treatment (Table 1). Pollinator richness was negatively associated with increased distance from the forest for both low and high floral diversity plots (Table 1; Fig. 2a & 2b). Although the composition pollinator assemblages in low floral richness plots did not vary with distance from the remnant habitat (Adonis, $df = 7$, f -statistic = 1.32, $p = 0.2786$, Fig. 3), high floral richness plots far from the remnant habitat harbored significantly different pollinator assemblages than those close to the forest edge (Adonis, $df = 15$, f -statistic = 3.11, $p = 0.024$, Fig. 4). Distant plots lacked a significant proportion of uncommon Hymenoptera species, including species of *Megachile*, *Augochlora*, *Augochloropsis*, *Andrena*, *Heriades*, and *Hoplitis* (two-sided t test, $df = 14$, $t = 2.78$, $p = 0.014$), and uncommon Diptera species including species of *Allograpta*, *Syritta*, *Tropida*, and *Hedriodiscus* (two-sided t test, $df = 14$, $t = 2.31$, $p = 0.03$). Distant plots also lacked a significant proportion of the abundant dipteran genus *Toxomerus* (two-sided t test, $df = 14$, $t = 3.73$, $p = 0.002$). As a result,

Table 1. The fit of linear models comparing pollinator abundance, evenness, richness, network connectance, plant-niche overlap, and robustness with distance from the remnant forest for both high and low diversity plots.

		Estimate	df	Residual SE	Multiple r^2	f statistic	p Value
Low floral diversity	Pollinator abundance	84.649	6	12.560	0.095	0.628	0.458
	Pollinator evenness	0.817	6	0.091	0.155	1.104	0.334
	Pollinator richness	-0.025	6	2.171	0.829	29.120	0.002*
	Connectance	1.645e-04	6	0.037	0.413	4.216	0.086
	Plant-niche overlap	1.543e-04	6	0.039	0.357	3.331	0.118
	Robustness	-2.291e-04	6	0.036	0.597	8.890	0.025*
High floral diversity	Pollinator abundance	82.457	14	28.020	0.032	0.460	0.508
	Pollinator evenness	8.297e-01	14	0.052	0.075	1.128	0.306
	Pollinator richness	-0.013646	14	5.428	0.213	3.980	0.049*
	Connectance	8.760e-05	14	0.031	0.253	4.737	0.047*
	Plant-niche overlap	1.459e-04	14	0.051	0.260	4.929	0.043*
	Robustness	7.169e-06	14	0.012	0.016	0.222	0.645

*Indicates a significant relationship at the $\alpha = 0.05$ level.

common Hymenoptera species comprised proportionally more of the pollinator assemblage of distant, high floral richness plots (two-sided t test, $df = 14$, $t = 3.55$, $p = 0.003$), including species of the genera *Bombus*, *Halictus*, *Apis*, *Ceratina*, and *Xylocopa*. Floral visitor specialization (d') in our networks ranged from very generalized ($d' = 0.005$) to relatively specialized ($d' = 0.791$). Those species that increased in relative abundance in distant, high richness plots were among the most generalized floral visitors (Table 2).

Plant-Pollinator Network Analysis

We observed pollinators foraging on 47 flower species and found 45 species of pollen on collected specimens. Visitation and pollen load networks were similar in composition, and in the 24 networks we observed 728 unique plant-pollinator interactions.

In high richness plots, connectance and plant-niche overlap both increased with distance from the forest (Table 1; Fig. 2d & 2f), yet network robustness did not vary significantly across the site (Table 1; Fig. 2h). In low richness plots, connectance and plant-niche overlap did not vary significantly across the site (Table 1; Fig. 2c & 2e), but network robustness declined with distance from the remnant forest (Table 1; Fig. 2g).

Discussion

Other studies have shown that pollinator richness increases with floral richness (Ghazoul 2006) and decreases with distance from high-quality habitat (Carvalho et al. 2010). It has also been demonstrated that plant-pollinator networks similar in structure to reference habitats can develop on restored lands (Forup et al. 2008). What has not been demonstrated until now is how these factors interact and how they affect plant-pollinator network structure and stability in a restoration context. The combined effect of distance and floral richness on pollinator assemblages was not as straightforward as we had initially predicted. Although we did find that increased

distance from the remnant habitat negatively affected pollinator richness, in turn, decreasing connectance, niche overlap, and robustness, we were surprised by the influence of floral richness. Our findings suggest that, at least during this stage of the site's development, high floral richness in areas far from remnant habitat did promote network stability. The increased stability did not result in attracting a diverse set of pollinators as we had predicted, however. Instead, high floral richness stabilized network structure in distant plots by attracting a set of highly generalized pollinators. Generalist pollinators increased network connectance and plant-niche overlap to create more redundant and robust networks far from the remnant habitat despite decreases in pollinator richness. Understanding the mechanism by which floral richness promotes network stability in plots far from remnant habitat could help in designing floral mixes that promote desirable pollinator community characteristics for future restoration projects.

Both low and high floral richness patches had lower pollinator richness far from the remnant forest. What differed between the two treatments was the greater degree of generalization in distant, high floral diversity plots. Thus, when networks in distant, high richness patches experienced our simulated species extinction, increased connectance and niche overlap created by generalized pollinators buffered them against further species loss. In contrast, networks in low floral richness patches exhibited little variation in pollinator species composition across the study site, and therefore they lacked the structural compensation to floral extinctions created by generalized pollinators. As a result, distant, low richness networks were relatively more fragile to our simulated extinctions.

Our results support the positive relationship between connectance, generalization, and robustness found in other studies (Gilbert 2009; Gonzalez et al. 2009). Generalized pollinators, by increasing network connectance, contribute to the overall structure and stability of networks, and play a more important role in the cohesiveness of communities than predicted by their relative abundance. Gonzalez et al. (2009) found that generalized pollinators helped to buffer systems from the ill effects of species loss and that networks rapidly became fragmented

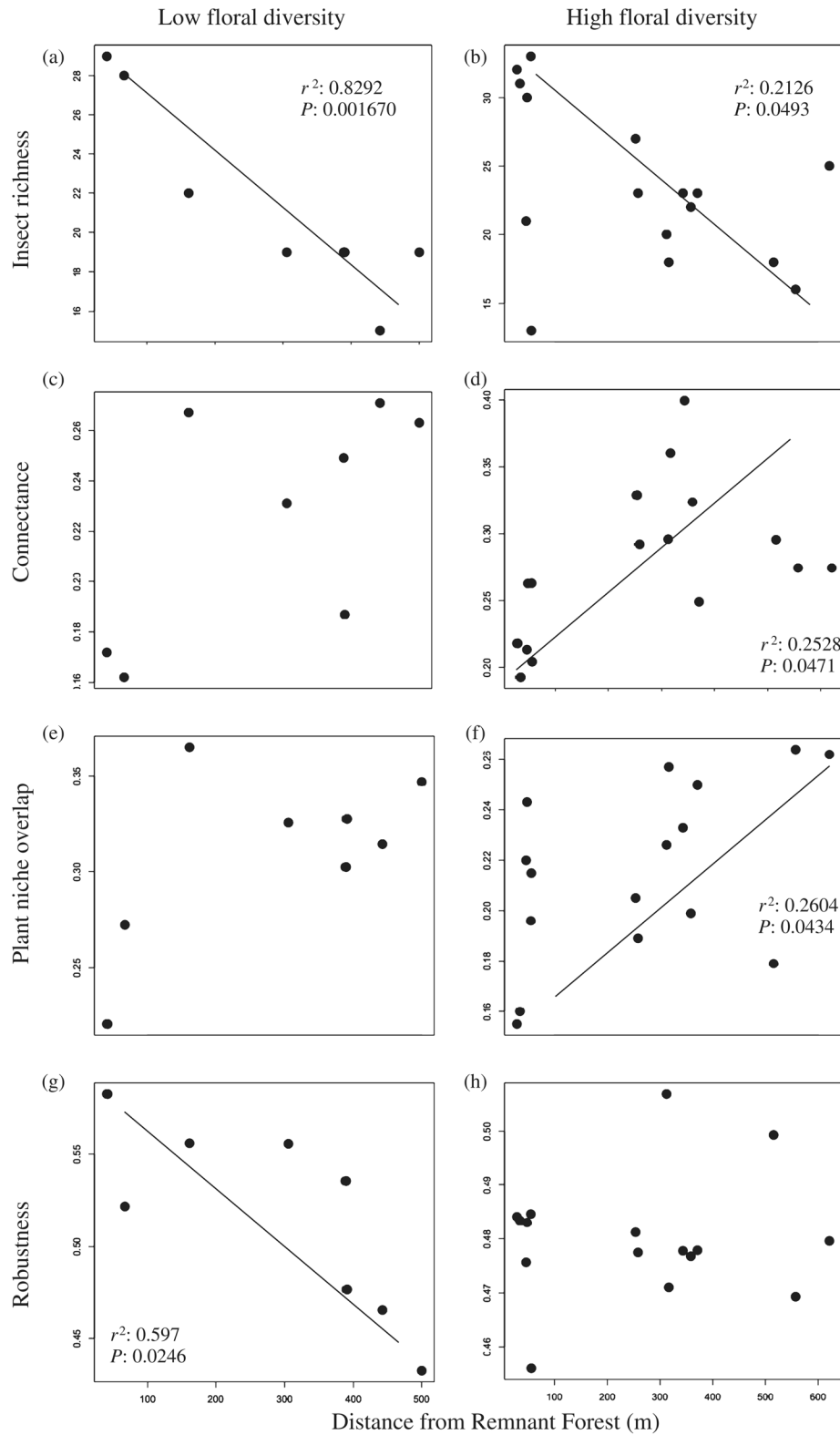


Figure 2. Changes in insect richness (a and b), network connectance (c and d), plant-niche overlap (e and f), and robustness (g and h) with distance from remnant habitat for low (a, c, e, and g) and high floral diversity plots (b, d, f, and h). Each circle represents a plot. Lines depict significant relationships.

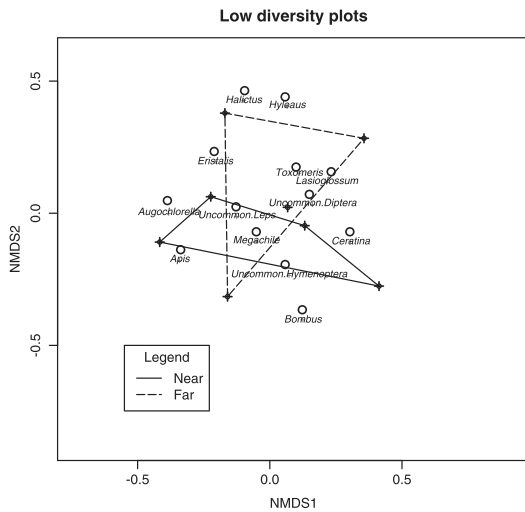


Figure 3. NMDS ordination of low diversity plots. Plots are indicated with bold crosses. Pollinator groups are indicated with species with open circle. Plots near to the remnant forest edge are <250 m ($n = 4$). Plots far from the forest edge are >300 m ($n = 4$). Adonis reveals that pollinator communities near and far from the remnant forest are not significantly different (Adonis, $df = 7$, $f = 1.32$, $p = 0.279$).

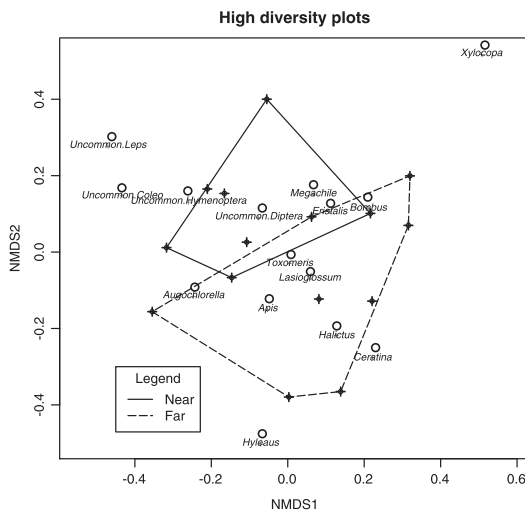


Figure 4. NMDS ordination of high diversity plots. Plots are indicated with bold crosses, and pollinator groups are indicated with small dots. Plots near to the remnant forest edge are 250 m ($<n = 8$). Plots far from the forest edge are >300 m ($n = 8$). Adonis reveals that pollinator communities near and far from the remnant forest are significantly different (Adonis, $df = 15$, $f = 3.11$, $p = 0.024$).

in simulations that removed generalized species. Here, we further demonstrate that although pollinator richness improves network stability (Potts 2009), the generalization of individual pollinators has equally positive effects on network structure. Our finding underscores the importance of attracting both a diverse set of pollinators, as well as generalized species to

Table 2. Values of d' , a measure of pollinator specialization, for some of the pollinator species.

Species	d'
<i>Bombus perplexus</i>	0.099
<i>Bombus auricomus</i>	0.141
<i>Halictus confusus</i>	0.204
<i>Toxomeris marginatus</i>	0.217
<i>Ceratina strenua</i>	0.223
<i>Apis mellifera</i>	0.244
<i>Xylocopa virginica</i>	0.249
<i>Halictus ligatus</i>	0.256
<i>Ceratina calcarata</i>	0.261
<i>Bombus bimaculatus</i>	0.279
<i>Ceratina dupla</i>	0.299
<i>Bombus impatiens</i>	0.301
<i>Augochlorella aurata</i>	0.301
<i>Augochloropsis metallica</i>	0.310
<i>Augochlorella persimilis</i>	0.310
<i>Bombus griseocollis</i>	0.315
<i>Phyciodes tharos</i>	0.359
<i>Cupido cocyta</i>	0.372
<i>Hyleaus affinis</i>	0.380
<i>Megachile mendica</i>	0.382
<i>Hyleaus mesillae</i>	0.387
<i>Hoplitis spoliata</i>	0.403
<i>Andrena brevipalpis</i>	0.433
<i>Megachile montivaga</i>	0.592
<i>Heriades leavitti</i>	0.598
<i>Melissodes bidentis</i>	0.796

A value of d' close to 0 indicates pollinator generalization, likewise $d' = 1$ indicates extreme specialization. Species in bold font are those that increase in relative abundance in distant high floral diversity plots.

encourage reproductively stable plant communities. We suggest that the promotion of generalized pollinator assemblages in temperate forest and prairie habitats, where specialized pollinators are uncommon to begin with, will encourage the reinstatement of functional mutualisms, and consequently the long-term success of restoration projects.

Beyond generalization and connectance, the manner in which participants are connected affects robustness. Estrada (2008) showed that networks with the same connectance and identical degree distributions display different degrees of resilience to species loss. Estrada concluded that the investigation of structural organization beyond connectance in networks is important in understanding why networks vary in robustness. Here, we show that both connectance and plant-niche overlap are associated with increased network robustness. With expanded plant-niche overlap, networks become structurally reinforced, increasing robustness. These results agree with the findings of Bluthgen and Klein (2011) who noted the stabilizing role of redundant species, suggesting that systems with functional redundancy may be more resilient for long periods of time following local extinctions.

Although our results support these statements, some limitations apply. Our study took place over the course of a single season. Therefore, our conclusions represent a snapshot of the community as it assembles over time. Plant-pollinator networks have been shown to be temporally

dynamic (Olesen et al. 2008), and our findings may not represent the long-term condition of the site. Temporal variation is important to consider as these communities will likely change as the restoration process proceeds. Our findings may also reflect particular features of our study system and region. Our study site, although representative of temperate prairie and grassland systems, may not translate well to other climates or seasonal regimes. In systems with a year-long pollinator activity or a high proportion of specialized plants or pollinators, such as the southwestern U.S. deserts or tropical forests, specialists and generalists may play more equal roles in stabilizing plant–pollinator networks.

Implications for Practice

- Isolation from remnant habitat can decrease pollinator richness, in turn affecting plant–pollinator network structure and stability. Projects with limited resources should focus on promoting plant diversity far from remnant habitat where it promotes network stability by attracting generalized pollinators.
- Generalized pollinators can help compensate for losses in pollinator diversity by reinforcing network structure through increased connectance and niche overlap.
- If the goal of restoration is to promote functional plant communities, then the structure and stability of plant–pollinator networks may be a better metric of community function than pollinator diversity.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Plant species, family, and floral unit of plants seeded in low and high floral diversity plots, as well as the native adventives and non-native plants that participated in plant–pollinator networks.