

USE OF BOTANICAL GARDENS AS ARKS FOR CONSERVING POLLINATORS AND PLANT-POLLINATOR INTERACTIONS: A CASE STUDY FROM THE UNITED STATES NORTHERN GREAT PLAINS

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Abstract—Botanical gardens have contributed to plant conservation through the maintenance of both living and preserved plant specimens for decades. However, there is still a large gap in the literature about the potential conservation value that botanical gardens could provide to local pollinators. We investigated how plant-pollinator interaction network structure and diversity may differ between botanical gardens and native habitats by sampling and comparing two environments: a restored native grassland patch within a local botanical garden and fifteen native, remnant temperate grassland sites in the Northern Great Plains. We found pollinator diversity within the botanical garden’s restored native grassland patch to be at the high end of the distribution of the remnant temperate grassland sites throughout the entire flowering season. However, plant diversity and network community metrics between the two environments remained similar throughout, except that remnant temperate grasslands have more links (higher connectance) with pollinators than the garden patch. Overall, our findings demonstrate the promising role restored native grassland patches in botanical gardens could play as reservoirs for local pollinator communities by supporting plant-pollinator interactions comparable to those found in native habitat remnants in the same region.

Keywords—Functional diversity, generalized pollination, network analysis, natural areas, pollinator diversity, specialized pollination

INTRODUCTION

Biodiversity loss is a global crisis that many countries have attempted to address through numerous methods of preservation and conservation management strategies (Benedict & McMahon 2006; Mutia 2009; Hostetler et al. 2011; Bortree et al. 2013). Seed banking is one strategy that has been implemented for the conservation of plant species in botanical gardens (Hurka 1994; Primack & Miller-Rushing 2008; Powledge 2011; Miller et al. 2016; Chen & Sun 2018). Botanical gardens and urban green spaces may also serve as potential reservoirs for pollinators (Pinheiro et al. 2006; Tonietto et al. 2011; Levé et al. 2019; Buchholz et al. 2020). However, there is still a gap in the understanding of how botanical gardens support

pollinators and preserve plant-pollinator interactions. For example, a literature search (Web of Science, April 7th, 2022) using the terms “botanical gardens and pollinator diversity” and “botanical gardens and plant diversity” resulted in 20 and 372 citations, respectively, and demonstrated much greater focus on the contribution of botanical gardens to the conservation and diversity of plants than pollinators. Clearly, the potential conservation value botanical gardens hold could extend beyond plant conservation. These gardens could provide space for several resources that pollinators utilize (i.e., foraging and nesting resources), even in areas that would typically be considered resource-poor (e.g., cities) (Lewis et al. 2019; Tew et al. 2021).

With approximately 1,775 botanical gardens worldwide (Botanic Gardens Conservation International, 2020), these sites could provide space for increasingly important conservation resources that can be utilized to alleviate the accumulating threats towards pollinators (i.e., habitat loss and fragmentation, pesticide use, pathogens, and invasive species introductions) (Kearns et al. 1998; Kremen et al. 2002; Steffan-Dewenter et al. 2005). Habitat loss and fragmentation are two primary causes for pollinator decline due to their negative impacts on nesting and refuge sites, and the availability of flower resources in both quantity and quality (Potts et al. 2010; Vanbergen et al. 2013; Habel et al. 2019). Negative impacts from habitat loss and fragmentation are expected to continue with increased urbanization and agricultural intensification (Foley et al. 2005; Lundgren & Fausti 2015; United Nations Department of Economic and Social Affairs (UN DESA) 2018). Pollinator decline is particularly concerning considering animal-driven pollination is essential to the reproduction of over 70% of flowering plant species (Potts et al. 2010) and 35% of crops globally (Klein et al. 2007; Vanbergen et al. 2013).

With the space and habitat that is left, can we look to botanical gardens as a proxy for native habitat to provide refugia for pollinators? Urban green spaces and botanical gardens can positively influence pollinator abundance and/or diversity depending on total area, floral abundance, and degree of urbanization (Tommasi et al. 2004; Gotlieb et al. 2011; Fortel et al. 2014; Micholap et al. 2017). In the United States, there are even cities that support a greater diversity of native bees than neighbouring rural areas (US Fish and Wildlife Service, 2015; Hall et al. 2017). For instance, the addition of green roofs in Chicago serves as an example of how urban interfaces can utilize space to support bee communities (Tonietto et al. 2011). Furthermore, there is a rise in initiatives to promote expanding urban private and public garden space with the hopes of promoting and sustaining stable pollinator communities (e.g., The Million Pollinator Garden Challenge sponsored in part by the United States Botanic Garden Conservatory). With the increased interest in carving out urban spaces for pollinators, there is a need to assess the resiliency of plant-pollinator interaction network structures to species loss in the

context of botanical gardens (Spiesman & Inouye 2013). The stability of pollination services is dependent upon maintaining diverse and resilient plant-pollinator communities (Klein et al. 2007). Network theory has been utilized to examine the structure of plant-pollinator communities through mutualistic interactions, which can promote the maintenance of biodiversity and community stability when the negative effects of interspecific competition are alleviated through the sharing of mutualistic partners. (Memmott et al. 2004; Bascompte et al. 2006; Blüthgen et al. 2008; Dupont et al. 2009; Hadley & Betts 2012; Spiesman & Inouye 2013; Soares et al. 2017; Redhead et al. 2018). Using a network-based approach, we can assess how plant-pollinator communities are structured in botanical gardens to determine if they may serve as supplementary resources for preserving plant-pollinator interactions. However, we lack information on how plant-pollinator interactions in botanical gardens compare to nearby natural habitats.

We focus our study in McCrory Gardens, a botanical garden located in Brookings, (eastern) South Dakota, with approximately 1,850 herbaceous plant species. The garden is located within the Prairie Coteau, a region in the Northern Great Plains which supports some of the largest remaining tracts of tallgrass habitat within an actively transforming and working landscape (Bauman et al. 2016). In the centre of McCrory Gardens, we focused our sampling within a 1,600 m² area designated as a restored native grassland patch that was established in 2018. This planted native grassland garden, embedded within a larger landscape of varying patches of natural and modified habitat, provides a study system with which to compare plant-pollinator communities within botanical gardens to those found in natural remnant habitats. Habitat loss and fragmentation is still a substantial threat to the temperate grasslands of the Northern Great Plains with documented rates of conversion from grassland to agricultural crops reaching ~1.0 - 5.4% annually from 2006 to 2011 (Wright & Wimberly 2013). From 2006 - 2016, Lu et al. 2018 found that within the western Corn Belt (i.e., North Dakota, South Dakota, Nebraska, Iowa and Minnesota), croplands increased by approximately 1.1 million hectares and 82% of the new croplands were converted from grasslands. The state of South

Dakota alone contributed to 31% of the 1.1-million-hectare cropland expansion (Lu et al. 2018). A better understanding of plant-pollinator interaction network structure in botanical gardens and their role in pollinator conservation will become increasingly important for future management decisions seeking to bolster pollination services.

We measured the diversity of plant-pollinator communities within natural temperate grassland areas and a restored grassland patch in a botanical garden, then quantified plant-pollinator interactions using a network-based approach to answer the following questions: 1) How does the pollinator diversity found within a restored grassland patch located in a botanical garden compare to the diversity found within native temperate grassland sites? 2) Likewise, how does the diversity of the insect-pollinated plant community within a restored grassland patch compare to that of native temperate grassland sites? And 3) What is the overall structure of plant-pollinator community interactions within a restored grassland patch located in a botanical garden and how do they compare on average to plant-pollinator networks in native temperate grassland sites? These questions become increasingly relevant with the progressive loss of biodiversity as urbanization and agricultural intensification continues to encroach upon natural landscapes (Ramankutty et al. 1999; Hoekstra et al. 2005).

MATERIALS AND METHODS

STUDY AREA

McCrary Gardens (longitude: -96.791080, latitude: 44.309100) is a botanical garden located in Brookings, South Dakota, that is operated and maintained by South Dakota State University (SDSU). The garden is located 300 m from an 18 ha SDSU agricultural plot to the north and about 2 km from private farmland to the east. Otherwise, it is surrounded by the SDSU campus, residential housing and apartments, shopping malls, large box stores, and major thoroughfares. Founded in the early 1960s, McCrary Gardens contains roughly 10 ha of display gardens that showcases approximately 1,200 herbaceous cultivars, 510 non-native herbaceous species and 90 native herbaceous species. The garden's origin began

with a mission to maintain a research garden that displays and educates the public on plant species that were or are a part of the South Dakota landscape. In continuation with this original mission statement, the Prairie Centennial Garden was established in 2018 in the centre of McCrary Gardens where it currently supports approximately 50 native herbaceous species. This 1,600 m² plot is a restoration native grassland garden with 85% of the plants grown from seed by the McCrary Gardens staff (seeds provided by Prairie Moon Nursery in Winona, Minnesota & Jelitto Perennial Seeds) and the remaining 15% of plants were relocated or reused from other areas within McCrary Gardens. Seed from Jelitto was not locally sourced but came from locations as close as Minnesota and as far as Colorado. No insecticides are used within McCrary Gardens. Chemical treatments such as glyphosate and 2-4D are used sparingly for spot treatment of colony-forming noxious weeds (i.e., Canada thistle) and for the control of broadleaf weeds in turf every other fall, respectively.

To compare the diversity of insect pollinators and plants, and plant-pollinator interaction network structure between the botanical garden and native temperate grassland remnants, we selected fifteen remnant temperate grassland sites within the Prairie Coteau region in eastern South Dakota. Within South Dakota, this region covers approximately 17 counties and harbours some of the largest remaining patches of native tallgrass habitat in the Northern Great Plains (Bauman et al. 2016). In eastern South Dakota, approximately 17% of the undisturbed grasslands within the Prairie Coteau region remain intact making this a valuable resource for tallgrass habitat in the Northern Great Plains. Remnant temperate grassland sites ranged in size from 8 to > 400 hectares and were selected based on quality of the site as advised by local experts and managers (see *Acknowledgements*), as well as manifesting a range of site characteristics, including size, local landscape use, and proximity to other semi-disturbed grasslands. Full description of site names, location coordinates, county, size, and ownership are provided in Table S1.

DATA COLLECTION

Pollinator observations

We conducted pollinator observations in the restored native grassland patch (Prairie Centennial Garden) inside McCrory Gardens and fifteen remnant temperate grassland sites within eastern South Dakota between May and October 2019. We sampled a total of 10 transects within the restored native grassland patch in McCrory Gardens and 114 transects across all remnants of temperate grassland sites throughout the entire growing season for one year. All 124 transects mentioned above were used to compare diversity and interaction network structure between remnant temperate grassland sites and the restored native grassland patch in McCrory Gardens.

Pollinator observations were conducted for 30 minutes along 30 x 1 m transects on days warm enough to allow insect flight and in time periods when pollinators are expected to be active (15 - 35°C, between 08:00 - 17:00 hours). We divided the sampling into three seasons: early (May - June), mid (July - August) and late (September - October). We surveyed one transect per sampling day per site, typically sampling each site at least one time every two weeks if weather and site conditions allowed (i.e., bloom status or flooding conditions). We sampled 11 days in the early season (approximately 1 - 4 samples per site), 30 days in the mid-season (approximately 4 - 7 samples per site), and 7 days in the late season (1 sample per site) for a total of 48 sampling days in 2019. Average temperatures and precipitation for each season is as follows: early season temperatures typically range 6 - 32°C with approximately 8.6 cm of average rainfall, mid-season temperatures typically range from 11 - 33°C with approximately 7 cm of average rainfall, and late season temperatures typically range from -4 - 28°C with approximately 4.5 cm of average rainfall (WeatherSpark, 2021). Season intervals were primarily selected based on consistent flowering phenology shifts found in the plant communities of the Prairie Coteau. For example, species belonging to the genera *Anemone* (Ranunculaceae), *Viola* (Violaceae), and *Sisyrinchium* (Iridaceae) bloomed predominately in the early season, while the mid and late seasons were dominated by species in the Fabaceae and Asteraceae (legume and sunflower families, respectively). Though

these two families were found predominately in both seasons, the mid season is distinct as this period marked a peak in the number of families in bloom with approximately six times more families present in our surveys in comparison to other seasons. Late season was characterized by a distinct shift in floral composition in which Asteraceae became the most prominent family in all sites with nearly all other families no longer flowering for the year.

From our roster of sites, which included the restored native grassland patch in McCrory Gardens and the fifteen temperate grassland sites, we randomly sampled each site until flowering ceased at each location. Location and direction of transects were randomized at each visit using a list of randomly generated numbers to determine distance and cardinal direction from the starting point before placing transects down. Transects were geospatially referenced using a Trimble Geo 7x Global Positioning System (GPS) unit with 1 - 100 cm accuracy. We walked the entire length of the transect and recorded all plant-pollinator interactions within one meter of the transect line on both sides. We defined pollinators as insect floral visitors that contacted both the male and female reproductive parts of the flower, a commonly used criterion (Fenster et al. 2004). We documented each pollinator and the associated insect-pollinated plant species when an interaction occurred. Additionally, we documented pollinator return visits to plants. Return visits were only documented when the observer could see the same insect within their line of sight fly off the flower and then land back on it again. Otherwise, all other visits were documented as new interactions. The pollinator observations in our study only focus on diurnal pollinators, however, this does not present a significant bias in our sampling. Our data set portrays a robust, representative sample of the plant-pollinator networks in this region considering only one species (*Silene vulgaris*) detected in our floral surveys (described in the next section) relies on nocturnal pollination, and this one species was only present in 1 transect of the 124 sampled.

Pollinators were identified in situ to family and genus, then to morphospecies to quantify insect diversity. Insect voucher specimens were collected in the field with an aspirator and net, later

identified to the lowest taxonomic level and then categorized into functional groups (functional groups defined in Fenster et al. 2004). Specimens were identified using resources available through discoverlife.org, bugguide.net, and Key to the Genera of Nearctic Syrphidae (Miranda et al. 2013). Voucher insect specimens were verified for sampling completeness using the help of experts and the Severin-McDaniel Insect Research Collection available at South Dakota State University (Tables S2 and S3). Although we recorded morphospecies in the field, we found genus to be the lowest, most robust taxonomic level in the data set for insect pollinators that could be identified with accuracy. Approximately 99.5% of total insect pollinator samples collected and observed within McCrory Gardens were identified to genus. Samples from McCrory Gardens that we were unable to identify to genus were sorted based on morphology and given a dummy genus name so they could still be included for analysis.

Floral surveys

Floral surveys were conducted directly after insect pollinator observation surveys along the same transect with a 1 m² quadrat. The quadrat was placed at each meter mark from 0 to 30 m. At each meter, we documented the presence of each insect-pollinated plant species, number of individuals per species, percent cover of each species within a quadrat, number of flowering units per individual -defined as a unit of one flower (e.g., Ranunculaceae) or capitula (e.g., Asteraceae) requiring flight of a small pollinator to reach another flowering unit. We also quantified the symmetry of flowers (radial vs. bilateral), since symmetry is often related to the degree of pollinator specialization (Fenster et al. 2004, Fenster & Marten-Rodriguez 2007). For instance, bilateral symmetry is associated with specialization. Hence, a greater proportion of either radial or bilateral symmetry may affect the parameters of network analyses at the remnant temperate grassland communities and the restored native grassland patch in McCrory Gardens. Chi-square tests were implemented in Microsoft Excel to examine differences in floral morphology (radial vs. bilateral symmetry) between the restored native grassland patch in McCrory Gardens and remnant temperate grassland communities.

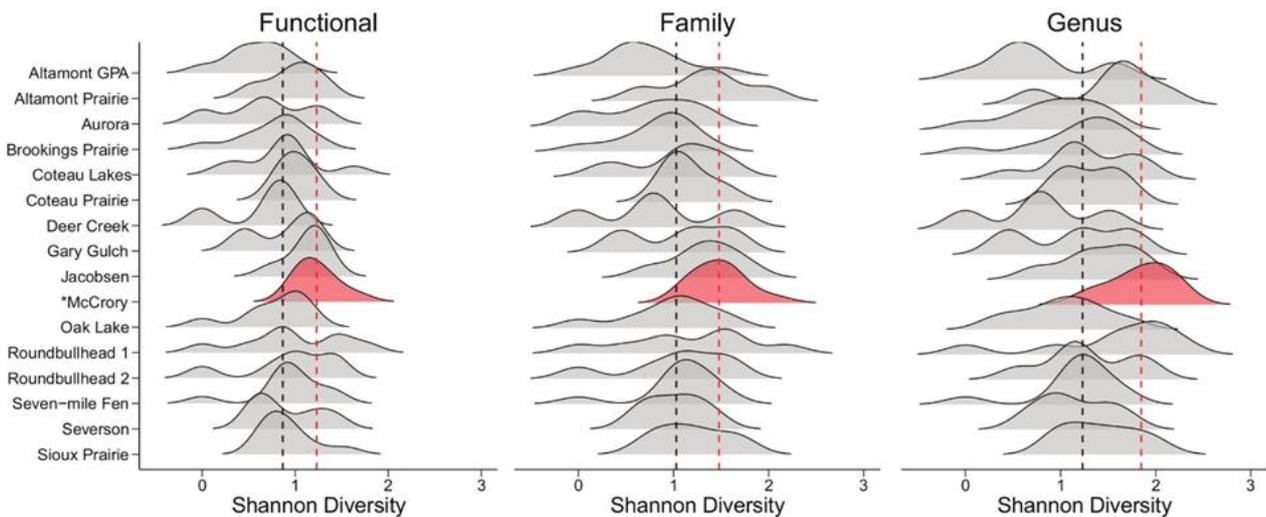
Plant voucher specimens were not collected in McCrory Gardens, but photographs were taken and then verified by head gardener, Chris Schlenker. In the remnant temperate grassland sites, plant voucher specimens were collected and identified using Van Bruggen (1985), verified with the help of experts (see *Acknowledgements*) and are curated at the C. A. Taylor Herbarium at South Dakota State University (Tables S4 and S5). Digitized plant collections for this study may be accessed on the Consortium of Northern Great Plains Herbaria (<https://ngptherbaria.org/portal/>).

POLLINATOR AND PLANT DIVERSITY

Pollinator and plant diversities were measured with Shannon and Jaccard indices using the 'vegan' package, version 3.6.3, in R (R Core Team 2013; Oksanen et al. 2019). The Shannon index takes richness and evenness into account to measure the diversity within a community, while the Jaccard similarity index measures the similarity between two sites by dividing the total number of observations from the two sites by the number of observations for one of the sites. We used both alpha and beta diversity indices to compare community diversity and composition between remnant temperate grassland sites and the restored native grassland patch in McCrory Gardens. Shannon and Jaccard indices were calculated at the functional, family, and genus level for each site within and across seasons to collectively compare pollinator community diversity and composition. Values used to calculate both diversity indices did not include return visits recorded during observation surveys. We generated correlation plots with Bonferroni-corrected *p* values for all the pollinator diversity metrics, i.e., genus, family and functional diversity, and found they were not correlated in the restored native grassland patch in McCrory Gardens (Table S6). However, we found all pollinator diversity metrics were correlated at the site level for the remnant temperate grassland sites (Vilella-Arnizaut 2021). We provide distribution data by site for all three categories of pollinator diversity (Fig. 1A).

Likewise, plant diversity was calculated at the family, genus, and species level by site and season with the Shannon and Jaccard indices, then compared within and across seasons. We also generated correlation plots with Bonferroni-

A) Pollinator



B) Plant

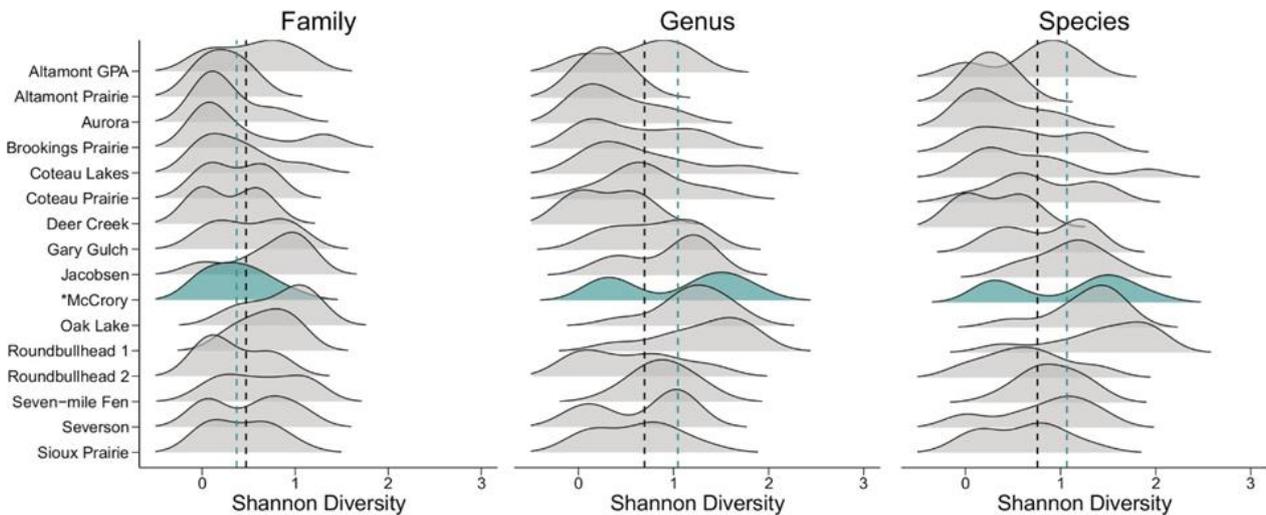


Figure 1. Density distribution of Shannon diversity of a) pollinators at the functional, family, and genus level and b) plants at the family, genus and species level for remnant temperate grassland sites and McCrory Gardens in the Prairie Coteau near and in Brookings, South Dakota averaged across the three sampling seasons (May - October 2019). Distributions represent sampling from transects at respective sites. Gray distributions represent remnant temperate grassland sites, while red (pollinators) and green (plants) represent McCrory Gardens. Black dashed lines are means across all remnant sites, while red (pollinators) and green (plants) are means for McCrory Gardens.

corrected p values for all plant diversity levels in the restored native grassland patch in McCrory Gardens and found that plant species diversity was correlated with family diversity and genus diversity (Table S7). Thus, we focus on plant species diversity in our results and comparisons, but as above, we provide distribution data for the three categories of plant diversity for completeness (Fig. 1B).

STATISTICAL ANALYSES

Null modelling of plant and pollinator diversity

To examine plant and pollinator diversity for the entirety of the study, we averaged diversity values across all sampling periods for each transect. Because we wanted to compare how pollinator and plant diversity of our single botanical garden compared to 15 restored native

grassland sites, we created a null distribution of expected diversity based on all 114 transects across all native temperate grassland sites. We used bootstrap analysis to create null distributions for expected diversity data by drawing and averaging 10 random transect values (equal to the number of transects sampled at the botanical garden) and repeating this process 1000 times. We calculated two standard deviations around the mean for each null distribution. Thus, the two standard deviations define the area in which 95% of the means of the resampled 10 transects were found. The average diversity value for the botanical garden was then plotted onto these distributions to compare where our botanical garden site fell in relation to what we might expect given the diversity in surrounding native temperate grasslands. We used this process to compare pollinator (functional group, family, genus) and plant (family, genus, species) diversity. All calculations were carried out in R (R Core Team 2013; Oksanen et al. 2019).

Non-metric multidimensional scaling

We implemented non-metric multidimensional scaling (NMDS) to visualize similarities in community composition for all plant (family, genus, species) and pollinator (functional group, family, genus) communities from May through October. Plots were created with the function 'metaMDS' in the 'vegan' package, version 3.6.3, in R (R Core Team 2013; Oksanen et al. 2019). Distances in NMDS plots were calculated using the option 'jaccard' in the 'metaMDS' function. Stress values for all NMDS plots were below the acceptable cut-off level of 0.2, with a single exception (pollinator genus diversity, stress = 0.209).

Network analysis

We built quantitative visitation networks for each site using transects as our replicates to quantify plant-pollinator interaction network structure. We calculated network metrics for each transect in the restored native grassland patch in McCrory Gardens and all remnant temperate grassland communities. We used transects as our replicates to compare network metrics between the two environments. We present our network metric comparisons based on the entire flowering season (May - October) because of limited sampling in the early and late seasons in both remnant temperate

grassland sites and the restored native grassland patch in McCrory Gardens. The Deer Creek site was excluded from all network analyses as there were too few interactions to generate network-level metrics. Networks were constructed using a matrix of interactions between plants and pollinators including unique and return visits recorded during pollinator observation surveys. Documenting return visits allows us to quantify plant-pollinator communities using weighted network values that also account for visitation frequency. For each network, we calculated network specialization ($H2'$), connectance, and nestedness. We also provide the means of each network metric within a given season using transects as our replicates for the restored native grassland patch within McCrory Gardens and all remnant temperate grassland sites. All network metrics were calculated using the 'bipartite' package in R (Dormann et al. 2009).

RESULTS

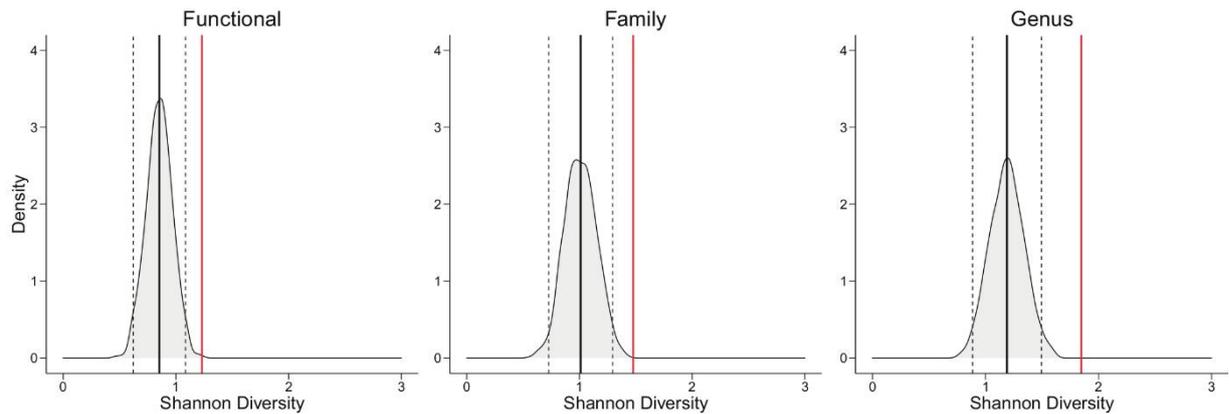
POLLINATOR COMMUNITY

Within the restored native grassland patch in McCrory Gardens, we observed 10 functional groups, 25 families, and 48 genera of pollinating insects. Among all 15 remnant temperate grassland communities, we observed 10 functional groups, 45 families, and 79 genera of pollinating insects (Tables S2 and S3).

COMPARISON OF POLLINATOR DIVERSITY

Shannon diversity of pollinator genera within the restored native grassland patch at McCrory Gardens for the entire sampling season (May through October) ranged from 1.28 - 2.28 (10 transects sampled, mean = 1.848 ± 0.103 (1 SE)), while the Shannon diversity of pollinator genera across all remnant temperate grassland sites ranged from 0 - 2.31 (114 transects sampled, Mean = 1.194 ± 0.048 (1SE); Fig. 1A). Pollinator diversity of our single restored grassland site at McCrory Gardens was relatively high when plotted against the null distribution for functional, family, and genus-level diversity values generated from remnant grassland sites. For every measure of diversity, the McCrory Gardens mean fell outside two standard deviations of the means of the resampled distribution of the remnant grassland sites (Fig. 2A). The same pattern held when examined by season (Fig. S1A). Early season

A) Pollinator



B) Plant

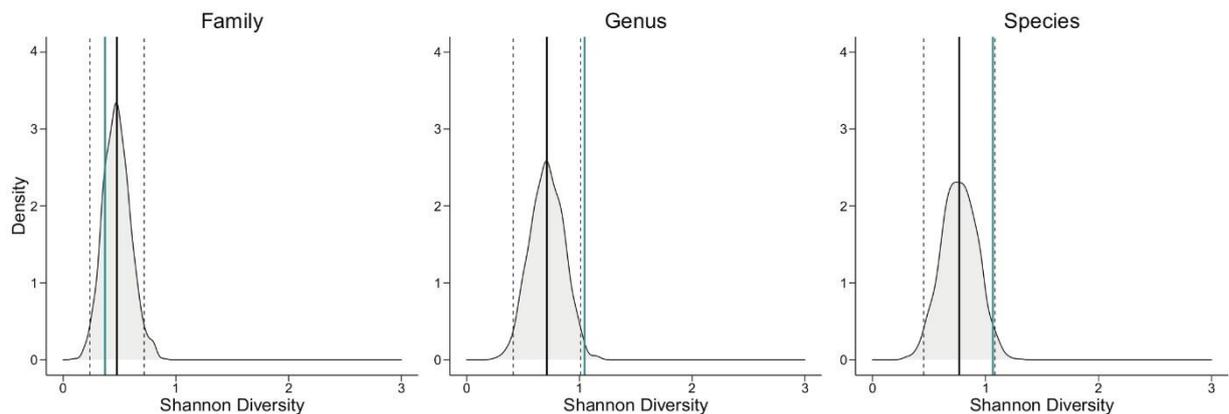


Figure 2. Kernel density distributions of **A)** diversity of pollinators and **B)** diversity of plants identified at remnant temperate grassland sites in the Prairie Coteau near Brookings, South Dakota. The dotted lines show 2 standard deviations from the mean (solid black line) of each distribution, which corresponds to roughly 95% of the area under the curve. Mean McCrory diversity values are indicated for pollinators (red lines) and plants (green lines).

pollinator genus diversity at McCrory Gardens was 1.77 with Syrphidae (54%), Muscidae (15%) and Vespidae (12%) comprising the majority of observations. Within remnant temperate grassland sites, early season pollinator genus diversity ranged from 0 - 2.03 with Syrphidae (36%), Muscidae (20%), Chloropidae (14.5%), and Halictidae (14%) observed most often. Mid-season pollinator genus diversity within the restored native grassland patch at McCrory Gardens ranged from 1.28 - 2.28 with Syrphidae (31%), Cantharidae (20%), and Tachinidae (9%) comprising the majority of observations. Mid-season pollinator genus diversity within remnant temperate grassland sites ranged from 0 - 2.31 with Apidae (27%), Syrphidae (25.7%), Cantharidae

(12.5%), and Halictidae (11%) as the most common pollinators. During the late season, pollinator genus diversity within the restored native grassland patch in McCrory Gardens was 2.10 with Apidae and Syrphidae constituting nearly all observations during this season at 68 and 25%, respectively. Within remnant temperate grassland sites, late season pollinator genus diversity ranged from 0.3 - 1.9 with Syrphidae and Halictidae constituting 58 and 28% of observations, respectively.

SIMILARITY OF POLLINATOR COMMUNITIES

When comparing sites across all seasons (May - October), functional group composition demonstrated the greatest values of Jaccard similarity (up to 0.81) between sites (Fig. 3). The

restored native grassland patch in McCrory Gardens shared the greatest similarity value in functional group composition with Seven-mile fen (0.81), a mesic remnant grassland managed through cattle-grazing, across the entire sampling season. Jaccard similarity values for all other taxonomic levels dropped below 0.5 (range of 0.01 - 0.25) when comparing across and within season, which indicates our sites were not similar in pollinator family and genus composition. This trend is also reflected in the mid-season, with functional group being the only taxonomic level with similarity values above 0.5 (Fig. S2). Indeed, McCrory fell outside of the cluster of remnant grasslands when visualized using NMDS, indicating differences in community composition (Fig. S3).

PLANT COMMUNITY

We sampled a total of 7 families, 19 genera, and 23 species of insect-pollinated plants within the restored native grassland patch in McCrory Gardens. Among all 15 remnant temperate

grassland communities, we sampled a total of 24 families, 61 genera, and 87 plant species (Tables S4 and S5).

COMPARISON OF PLANT DIVERSITY

Within the restored native grassland patch at McCrory Gardens, Shannon diversity of insect-pollinated plant species across the entire sampling season (May - October) ranged from 0.25 - 1.96 (10 transects sampled, Mean = 1.066 ± 0.206 (1 SE); Fig. 1B). These values fell within the range of Shannon diversity values calculated for insect-pollinated plant species in remnant temperate grassland sites from May - October (114 transects, Mean = 0.769 ± 0.049 (1 SE), range = 0 to 2; Fig. 1B). This result was also reflected in the season comparisons where plant diversity at the Garden site were always within the distribution of plant diversity values of the remnant grassland sites (Fig. S1B). Comparing the season-long average plant diversity of our single restored grassland site within the botanical gardens to the 15 remnant grassland sites using

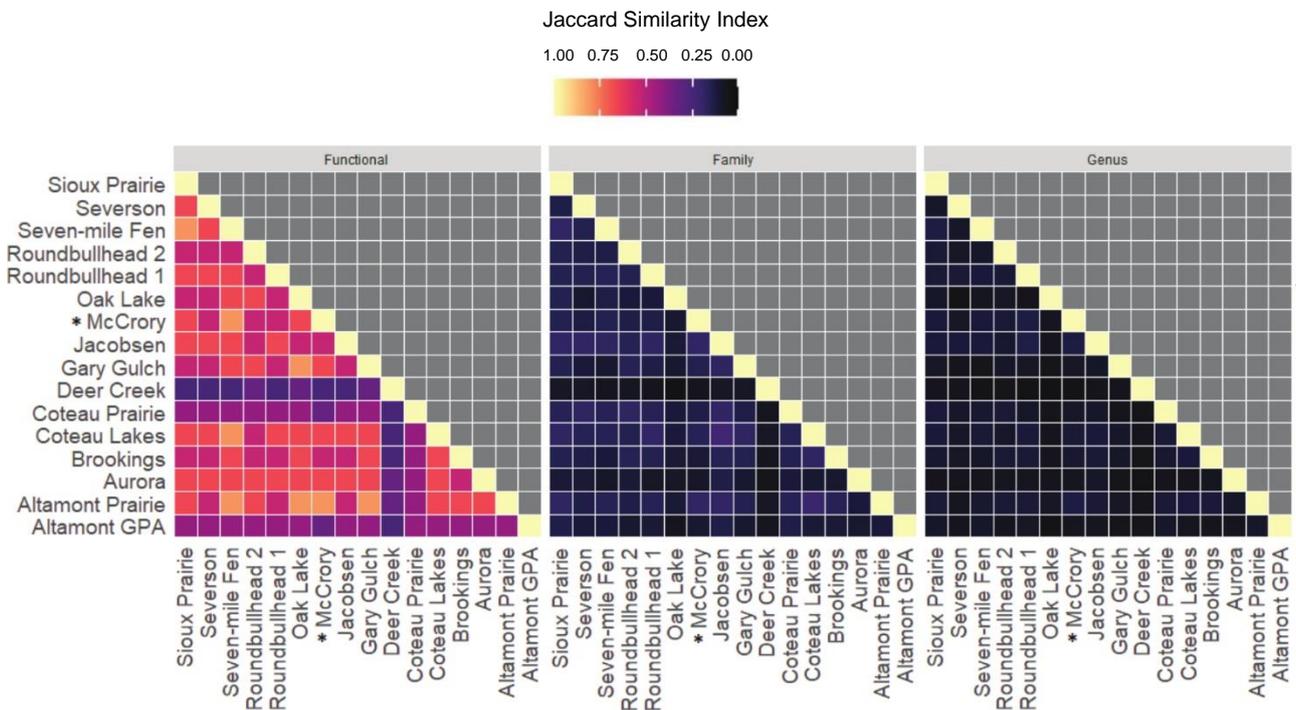


Figure 3. Distribution of Jaccard Similarity index values comparing pollinator functional group, family, and genus composition between remnant temperate grassland sites in the Prairie Coteau near Brookings, South Dakota and McCrory Gardens across the three sampling seasons (May - October 2019). All sites are represented on the x and y axis. The Jaccard Similarity index ranges from 0 to 1, with a value of 0 indicating that sites are completely dissimilar and 1 indicating sites completely overlap in composition. Warmer, lighter tones on the chart indicate values that are approaching 1. McCrory Gardens is distinguished with an asterisk.

bootstrap resampling to create a null distribution suggested no difference because for every measure of diversity; the mean of the McCrory Gardens site was within two standard deviations of the means of the resampled distribution of the remnant grassland sites (Fig. 2B). Early season plant species diversity in the restored native grassland patch was 0.25 with *Achillea millefolium* as the most common species recorded in early season sampling. Within remnant temperate grassland sites, early season plant species diversity ranged from 0 - 1.33 with *Anemone canadensis*, *Gallium boreali*, and *Fragaria virginiana* as the most common species found. Mid-season plant species diversity within the restored native grassland patch ranged from 0.27 - 1.96 with *Coreopsis tictoria* and *Achillea millefolium* as the most common species recorded. Mid-season plant species diversity within remnant temperate grassland sites ranged from 0 - 2 with *Melilotus sp.*, *Anemone canadensis*, and *Amorpha canescens* as the most common species. Late season plant species diversity within the restored native grassland patch was 1.2 with *Helianthus maximiliani* recorded most commonly, while late season plant species diversity within remnant temperate grassland sites ranged from 0.17 - 1.5 with *Symphyotrichum lanceolatum*, *Symphyotrichum ericoides* and *Heliopsis helianthoides* as the most common species.

SIMILARITY OF PLANT COMMUNITIES

When we compared insect-pollinated plant composition across and within seasons, all sites demonstrated values well below 0.5 (range of 0.01 - 0.3) for each taxonomic level, indicating our sites were not similar in family, genus or species composition. One exception to this trend is in the late season, where most sites had similarity values of 0.5 or 1. This is likely because only three families were detected when we sampled our sites in the late season (Fig. S4). This dissimilarity is demonstrated by the separation of McCrory Gardens from the remnant grassland sites in our NMDS (Fig. S5).

PLANT SYMMETRY COMPARISON

Out of 23 insect-pollinated plant species in the restored native grassland patch, we determined 4 species displayed bilateral symmetry while 19 species displayed radial symmetry. Across remnant temperate grassland communities, we determined 25 species exhibited bilateral

symmetry while 62 species exhibited radial symmetry. After conducting a chi-square test, we found no difference between environments with regard to the proportion of floral morphology, χ^2 (1 df, $N = 110$) = 1.17, $P > 0.50$.

PLANT-POLLINATOR NETWORK ANALYSIS

Within the restored native grassland patch in McCrory Gardens, we observed 165 unique plant-pollinator interactions and a total of 3,146 observations of pollinators visiting plants from May through October. The most common floral visitors throughout the entire sampling period in McCrory Gardens were Syrphidae (38%), Cantharidae (12%), and Apidae (11%). The plant species with the most interactions in McCrory Gardens throughout the sampling season include *Achillea millefolium* (50%), *Helianthus maximiliani* (8%), and *Solidago rigida* (7.7%). H2' mean ranged from 0.26 - 0.64 across all three seasons for the restored native grassland patch, while H2' mean ranged from 0.56 - 0.80 in the remnant temperate grassland communities (Table S8).

Within the restored native grassland patch, connectance means ranged from 0.29 - 0.67 and nestedness means ranged from 17 - 29 across all three seasons (Table S8). Likewise, within the remnant temperate grassland communities, connectance means ranged from 0.40 - 0.50 and nestedness means ranged from 25 - 34 across all three seasons (Table S8). We did not find a significant difference in H2' between environments when using transects as our replicates ($U = 423$, $N_1 = 92$, $N_2 = 10$, $P > 0.60$, Mean \pm SE: grassland remnants = 0.60 ± 0.03 , garden = 0.57 ± 0.06). Additionally, we found no significant difference in nestedness between environments ($U = 495$, $N_1 = 92$, $N_2 = 10$, $P > 0.60$, Mean \pm SE: grassland remnants = 26.4 ± 1.72 , garden = 28 ± 1.73), however, we did find the remnant temperate grassland sites to have significantly higher connectance than the restored native grassland patch ($U = 250$, $N_1 = 92$, $N_2 = 10$, $P < 0.03$, Mean \pm SE: grassland remnants = 0.44 ± 0.016 , garden = 0.34 ± 0.04).

DISCUSSION

Our study expands on the limited literature available exploring the extent to which botanical gardens can support pollinator communities and pollination services. Previous research has

examined how urbanization and impervious surfaces may impact pollinator movement (Fortel et al. 2014; Levé et al. 2019). Recent work has highlighted the potential conservation value of urban green spaces for pollinator communities, especially those found within cities (Micholap et al. 2017; Lewis et al. 2019). We further develop the role of human constructed environments by quantifying and comparing the diversity and interactions of plant-pollinator communities within a restored native grassland patch located in a botanical garden and surrounding remnant temperate grassland habitats in order to understand how these environments may differ with regards to plant-pollinator interaction network structure. We found that the restored native grassland patch in McCrory Gardens manifested a relatively high Shannon diversity for pollinator communities and an equivalent Shannon diversity for plant communities in comparison to the diversity found in remnant temperate grassland communities. Network metrics were similar across seasons between communities, except for connectance. Below, we discuss and compare the diversity and interaction network structure between remnant temperate grassland habitats and the restored native grassland patch in McCrory Gardens.

COMPARING AND CONTRASTING DIVERSITY OF THE PLANT-POLLINATOR COMMUNITIES

Summed across the flowering season, pollinator diversity within the restored native grassland patch was at the high end of all pollinator diversity indices for the remnant grassland sites (Fig. 1A). For both remnant temperate grassland communities and the restored native grassland patch, pollinator diversity was greatest in the mid and late seasons. These results indicate the restored native grassland patch in the botanical garden can maintain a relatively diverse pollinator community comparable to the diversity found within remnant temperate grassland habitats in the same region. However, results from the Jaccard similarity analyses indicate pollinator community composition between sites, even between remnant grassland sites in this study, is not similar outside of functional group composition. Maintaining pollinator diversity and composition comparable to remnant sites even at the functional group level could benefit botanical gardens and urban green spaces by promoting

community resiliency through functional redundancy (Kühnel & Blüthgen 2015). However, the low similarity of specific species composition indicates that multiple sites within a region need to be conserved to maintain pollinator diversity. These results could also indicate a difference in resources available to pollinators between McCrory Gardens versus the remnant grassland sites, which may be one cause for differences in community composition.

Floral community diversity within the restored native grassland patch overlapped with the mid to upper range of remnant temperate grassland values across all three seasons. However, the restored native grassland patch was less diverse in the early season. Similar to pollinator communities, floral community composition at all taxonomic levels was dissimilar between sites, both across and within seasons. These results reiterate the need to maintain or conserve multiple sites within a region to maintain plant diversity.

High floral diversity at the genus- and species-level within the restored native grassland patch in mid and late season was driven by Asteraceae, as approximately 96% of the individuals we documented in the garden transects belong to this family. This family also was the greatest contributor to the low floral diversity in the early season, as the majority of asters we sampled bloomed in the mid and late seasons. The difference in early season floral diversity between the restored native grassland patch and remnant temperate grassland sites highlights the challenges prairie restorations face when seeking to increase phenological diversity (Havens and Vitt 2016; White et al. 2018). High initial costs and limited commercial availability are just two of the prominent barriers conservationists face when seeking to incorporate early blooming species in restoration sites.

COMPARING AND CONTRASTING NETWORK METRICS

The greatest overlap in network metrics (i.e., nestedness, connectance, and $H2'$) between the restored native grassland patch and remnant temperate grasslands occurred during the mid-season. Indices for nestedness and $H2'$ were not different across seasons. However, values for connectance were significantly higher in the remnant temperate grassland sites than the restored native grassland patch. Connectance is

often used in ecological networks to measure community complexity and is generally positively associated with conservation value (Dunne et al. 2002; Thébault & Fontaine 2010; Tylianakis et al. 2010; Hagen et al. 2012). Communities with increased interaction complexity are expected to be more stable and robust to species loss (Dunne et al. 2002). However, Heleno (et al. 2012) noted that connectance alone should not be used to determine conservation value as it is context-specific and depends on the different conservation values of species in a network. Overall, we found that plant-pollinator community interactions in the restored native grassland patch were less complex than remnant temperate grassland sites. The higher level of complexity in plant-pollinator communities within natural habitats may be attributed to the distinct phenological shifts in the flowering community across seasons, which have evolved with the local pollinator fauna over a longer evolutionary time scale (Gomez & Zamora 2006; Minckley & Roulston 2006; Craine et al. 2012). This temporal variability could explain how natural habitats maintain more complex interactions than their garden counterparts. Successful recruitment of native plants is an ongoing challenge in restored temperate grasslands (Martin & Wilsey 2006; Gibson-Roy et al. 2007; Johnson et al. 2018) and may be an obstacle botanical gardens will have to overcome when seeking to maintain complex and stable plant-pollinator communities. Botanical gardens that wish to establish native plant restoration plots will need to consider limiting pesticide use and incorporating strategies that strike a balance between aesthetics and function to support overwintering insects and increase the complexity of plant-pollinator community interactions.

Moreover, the landscape surrounding natural habitats may provide other resources (e.g., nesting resources) that some pollinators may require to thrive, particularly those whose foraging distance is shorter than other more generalized and mobile visitors (e.g., honeybees) (Beekman & Ratnieks 2000). The spatial variability of resources found within natural habitats is likely a factor contributing to the difference in connectance between environments, though landscape analysis for the garden community was beyond the scope of this paper. In general, the restored native grassland patch within McCrory Gardens

demonstrates a plant-pollinator interaction network structure similar to remnant temperate grassland sites. Nested networks displaying a higher degree of connectance are considered more resilient and stable, making them important considerations for conservation value (Memmott et al. 2004; Okuyama & Holland 2008; Thébault & Fontaine 2010). The nested pattern found in the networks in this study indicates a degree of interaction redundancy that likely contributes to community stability (Bascompte et al. 2003; Nielsen & Bascompte 2007). However, it appears that the remnant temperate grassland habitats within the Northern Great Plains support a greater degree of interaction complexity in their plant-pollinator communities. This could be concerning for maintaining stable pollination services in botanical gardens, as community complexity is associated with stable and robust communities.

CONSERVATION IMPLICATIONS

Temperate grasslands are among the least protected habitat types in the world, with conversion outpacing conservation by eight to one (Hoekstra et al. 2005). In the United States, the temperate grasslands of the Northern Great Plains are a valuable resource for approximately 40% of transported honeybee colonies from May through October by providing abundant floral resources through regional blooms (United States Department of Agriculture 2014). However, the entire Great Plains region has experienced considerable habitat loss due to landscape conversion with more than 96% of the grassland habitat of the Great Plains already converted to cropland or other less diverse vegetation (Bauman et al. 2016). Botanical gardens have the potential to provide abundant floral resources to pollinator communities within increasingly disturbed landscapes; however, the role of botanical gardens in pollinator conservation is critically understudied.

We emphasize that our sampling is highly limited as it reflects a comparison of plant-pollinator diversity and interactions at only one botanical garden versus the surrounding landscape. However, our findings demonstrate the promising role botanical gardens could play as supplemental restoration reservoirs for local pollinator communities by supporting plant-pollinator interactions comparable in many ways

to those found in natural habitat remnants in the same region. In the absence of large swaths of preserved habitat, small reservoirs have been notably valuable for wildlife conservation, though the context of the landscape is important when seeking to maximize regional insect diversity (Shafer 1995; Tscharrntke et al. 2002). Though this study does not directly examine landscape effects that may explain some differences between environments, the restored native grassland patch located in McCrory Gardens demonstrated comparable measures of plant-pollinator interaction network structure and functional group composition to natural habitats, indicating the garden's potential in serving as a beneficial patch for pollinator communities. Future work studying the influence of increased green spaces in urban areas in conjunction with conserving remaining patches of natural habitat will be invaluable in our understanding of how best to conserve pollinator communities and stable pollination services.

Our aim for this study was to further our understanding of the extent to which botanical gardens can serve as supplementary resources for pollinator communities within critically fragmented landscapes. More research focused on plant-pollinator interaction networks in botanical gardens, particularly in regions that experience distinct flowering shifts within the growing season, paired with sampling of plant-pollinator interaction networks in natural habitats could help us understand the potential role botanical gardens might play as additional sources of habitat. Because plant-pollinator interaction networks are dependent on floral resources (e.g., pollen, nectar), increasing sampling within distinct flowering seasons and environments could provide important context for conservation of pollination services on a wider scale. For example, we found that floral diversity within the restored native grassland patch in McCrory Gardens was similar to floral diversity in the remnant temperate grasslands; however, floral diversity within the restored native grassland patch was primarily driven by Asteraceae. This was also reflected in community composition dissimilarity between our restored native grassland patch and remnant temperate grassland sites. Extending the sampling period for network studies to include early season species could elucidate how early season

pollinators may be affected by this gap in resources before Asteraceae species are blooming. Consequently, gardens could adjust management once these nuances are better understood. Additionally, extending research across multiple years could provide valuable insight into how plant-pollinator communities may shift following the progression of native restoration gardens. Continued research tracking the influence of green spaces on plant-pollinator interactions over time could expand as initiatives for private and public green spaces grows. Developing and growing urban gardens may very well act similarly to habitat corridors, which have been shown to improve wildlife conservation efforts (Correa Ayram et al. 2016). By understanding the effectiveness of botanical gardens in supporting pollinator populations, we can expand our understanding of urban spaces as valuable conservation tools rather than barriers.

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APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Table of full site descriptions (i.e., site name, county, coordinates, size (ha), and ownership).

Table S2. List of the pollinators observed and identified in the Prairie Centennial Garden.

Table S3. List of pollinators observed and identified in the remnant temperate grassland sites in the Prairie Coteau region in South Dakota.

Table S4. List of the insect-pollinated plants identified in the Prairie Centennial Garden.

Table S5. List of the insect-pollinated plants identified in the remnant temperate grassland sites in the Prairie Coteau region in South Dakota.

Table S6. Table of Spearman rank correlations for pollinator diversities with Rho values and Bonferroni-corrected p values.

Table S7. Table of Spearman rank correlations for insect-pollinated plant diversities with Rho values and Bonferroni-corrected p values.

Table S8. Means of network metrics across all remnant temperate grassland sites and the Prairie Centennial Garden.

Figure S1. Distribution of Shannon diversity by site for pollinator and insect-pollinated plant communities at all taxonomic levels between remnant temperate grassland sites and the Prairie Centennial Garden for each season.

Figure S2. Distribution of Jaccard similarity values for pollinator functional group, family and genus composition separated by season.

Figure S3. NMDS plots for all pollinator communities in the remnant temperate grassland sites and Prairie Centennial Garden.

Figure S4. Distribution of Jaccard similarity values for insect-pollinated plant family, genus and species composition for the entire sampling season and for each individual season.

Figure S5. NMDS plots for all insect-pollinated plant communities in the remnant temperate grassland sites and Prairie Centennial Garden.

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