Habitat and adaptive foraging impacts on the topology and conservation of plant-pollinator interaction networks

by

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Abstract

Plant-pollinator mutualistic interactions are crucial for maintaining global biodiversity. Therefore, it is important to identify the behaviors that confer stability to these communities by evaluating emergent patterns of community organization using network analysis for effective biodiversity conservation. In the U.S. Great Plains, habitat loss resulting from agricultural intensification has contributed to steep declines in pollinator populations. Private land conservation programs such as the Conservation Reserve Program (CRP) offer a potential solution to declining pollinator populations. However, most work has focused on bees with less effort to assess overall pollinator community structure in these conservation plantings. In addition to studying simple metrics of diversity, plant-pollinator network topology can provide insight into the behavior and ecological dynamics that structure these communities, such as adaptive foraging. Although theory has often implicitly assumed that plant-pollinator interactions are static, there is mounting evidence that pollinator species continually switch the plant species with which they interact to maximize energy gain per cost and enhance the efficiency of resource utilization. Pollinators may adapt their foraging choices to maximize mutualistic benefits or minimize competitive costs, but it is difficult to separate these influences on community structure and stability empirically. To address these issues, I performed empirical observations of plant-pollinator interactions on different CRP planting types as well as non-CRP grasslands and simulated plant-pollinator community dynamics with different adaptive foraging strategies. The objectives of this work were to: a) evaluate how local- and landscape-scale habitat characteristics influence the effectiveness of CRP planting types in supporting pollinator communities and b) examine how different adaptive foraging strategies and pollinator dependence on plants impact community stability and the resulting network topology in comparison to empirical networks.

Pollinator community composition differed across CRP planting types, whereas pollinator abundance and diversity were more influenced by site-specific habitat characteristics, such as forb species richness and grassland habitat availability. Habitat characteristics had an interactive effect on pollinators such that landscape-scale habitat availability modulated the availability and diversity of pollinators that could use floral resources within CRP plantings. Plant-pollinator networks were specialized and modular, indicating that pollinator foraging decisions are guided more by niche partitioning in response to the abundance of competitors and the diversity of floral resources. In the simulation model, adaptive foraging resulted in less stable pollinator communities but larger pollinator populations, which suggests that without interaction switching interspecific competition kept pollinator populations at lower densities, but not so low as to result in competitive exclusion. Additionally, empirical network topology was most similar to that of simulated networks when pollinators were highly dependent on plants for survival. These findings offer insights into how the habitat characteristics of conservation plantings impact pollinator communities while highlighting the ecological dynamics that confer stability to plant-pollinator networks.

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Dedication

I dedicate this thesis to the critters and plants that I have spent years admiring and studying. Thank you for keeping me busy!

Introduction

Pollinator populations are declining in the U.S. Great Plains due to habitat loss resulting from the conversion of native grasslands to row-crop agriculture and the invasion of woody plants and exotic grasses (Samson et al. 2004, Potts et al. 2010). Private land conservation programs, such as the Conservation Reserve Program (CRP), offer a potential solution to declining pollinator populations in the Great Plains where much of the land is privately owned. The CRP is a voluntary cost-share assistance and rental payment program administered by the United States Department of Agriculture's (USDA) Farm Service Agency (FSA) in which agricultural producers and landowners cease production on environmentally sensitive cropland and instead establish conservation cover for 10- to 15-year periods. Created by the Food Security Act of 1985, the CRP is the largest voluntary, private land conservation program in the U.S. with a large proportion of enrollment in the Great Plains, where conservation cover is often established in the form of grasslands (Otto et al. 2018, Augustine et al. 2021, FSA 2021). As of November 2024, over 10.5 million ha (26 million acres) were enrolled in the CRP, with over 800,000 ha (2 million acres) of land enrolled in Kansas (FSA 2024).

The CRP was created with the initial goal of reducing soil erosion (Stubbs 2014). Over time the program's goals have expanded to include improving water quality and establishing wildlife habitat (Otto et al. 2018). The CRP includes over 40 conservation practices (CPs) that focus on restoring specific environmental functions or ecosystem services. Popular CPs in Kansas include the Establishment of Permanent Native Grasses (CP-2), Rare and Declining Habitat (CP-25), and Pollinator Habitat (CP-42), which differ primarily in the composition of the plant community, particularly with regards to the overall proportion of grasses and forbs in the seed mix. Previous research on the impact of CRP plantings on pollinator communities lacks

information on floral resource utilization by non-bee pollinators (Otto et al. 2018, Arathi et al. 2019, Quinlan et al. 2021, Wen et al. 2022, Kraus et al. 2023), and thus there is little evidence that the CRP is contributing to the conservation of resilient pollinator communities. Moreover, few studies compare the effectiveness of different CRP planting types with regards to their impact on pollinator communities and the influence of local and landscape habitat features, such as local floral resource availability, soil properties, and landscape composition.

Network analysis allows us to understand how CRP plantings impact community structure and identify the ecological processes that drive the patterns of community organization. Using a network approach, we can visualize plant-pollinator interactions as a network of interconnected nodes joined by edges, in which the nodes are plant or pollinator species, and the edges are their interactions. We can quantify network topology, or the pattern of interactions, using metrics such as nestedness, network specialization, and modularity, which also inform us about the ecological dynamics that structure these communities (Bascompte et al. 2003, Bascompte and Jordano 2007, Blüthgen et al. 2008, Vázquez et al. 2009a). Nestedness refers to the degree to which specialists interact with a subset of species with which generalists interact. Highly nested networks consist of generalists that interact with many other species and specialists that interact with a subset of the species with which generalists interact. High nestedness indicates that species are targeting locally abundant resources, which results in high niche overlap between species and thereby introduces functional redundancy and confers structural stability by ensuring the stable persistence of species over time (Bascompte and Jordano 2007, Bascompte and Scheffer 2023). Network specialization (H_2') refers to the overall specialization of all species in the network (Blüthgen et al. 2006). A highly specialized network is characterized by reciprocal specialization of all species in the network and is an indicator of

niche partitioning in response to strong interspecific competition for resources. Lastly, modularity describes the degree to which species form clusters or modules, with interactions being frequent within modules and rare between modules. Similar to network specialization, high modularity indicates strong resource partitioning. High network specialization and modularity may result in lower stability due to a lack of redundancy (Blüthgen et al. 2008). However, high network specialization and modularity may confer stability to networks by preventing disturbances from permeating through an entire network (Stouffer and Bascompte 2011).

Network analysis can also identify the behaviors that confer community stability by allowing species to persist over time, such as adaptive foraging (Bastolla et al. 2009, Kaiser-Bunbury et al. 2010). Recent research has indicated that plant-pollinator communities are dynamic in nature wherein pollinators continually switch the plant species with which they interact (Zhang et al. 2011, Valdovinos et al. 2013, Spiesman and Gratton 2016). Pollinators may adapt their behaviors to maximize the mutualistic benefit (i.e., floral rewards) or reduce the cost (i.e., interspecific competition) of foraging, thereby concentrating their foraging effort on a few plant species rather than visiting every plant in the community. However, it is difficult to separate the influences of adaptive foraging based on mutualism and competition on community structure and stability empirically, and thus a simulation approach can be implemented to understand the drivers of adaptive foraging and the resulting impact on community stability.

In this work, I combined empirical and simulated approaches to determine how habitat and adaptive foraging impact the behavior of plant-pollinator communities by evaluating network topology. For my first objective, I evaluated the effectiveness of different CRP planting types in supporting pollinator communities and investigated how local- and landscape-scale habitat characteristics influence the effectiveness of CRP plantings. To accomplish these

objectives, I examined the effects of different CRP planting types on pollinator abundance, pollinator richness, and plant-pollinator network topology. Additionally, I explored how the abundance and richness of floral resources, land cover in the surrounding landscape, and soil texture impact pollinator abundance, pollinator richness, and plant-pollinator network topology across these different CRP planting types.

For my second objective, I used a plant-pollinator network simulation model to examine how different adaptive foraging strategies based on maximizing mutualistic benefits and/or minimizing competitive costs impacts community stability and the resulting network topology. Additionally, I explored how the mutualistic dependence of pollinators on plants modulates the effects of adaptive foraging on community stability. Lastly, I compared the topology of simulated networks to empirical networks to evaluate which adaptive foraging strategies and level of mutualistic dependence results in the most realistic network topologies.

Chapter 1 - Local and landscape habitat impacts on plant-pollinator interactions on Conservation Reserve Program land

Introduction

Habitat loss has contributed to steep declines in pollinator populations around the world (Potts et al. 2010). In the U.S. Great Plains, where prairies once dominated, this habitat loss is largely attributed to the conversion of native grasslands to row-crop agriculture and the invasion of woody plants and exotic grasses (Samson et al. 2004). Agroecosystems primarily comprised of corn, soybean, and wheat have replaced much of the region's native prairie (Lark et al. 2015). These simplified landscapes lack the native flowering plants that are used as foraging and nesting habitat by pollinators. Consequently, effective conservation programs are necessary to protect beneficial species and the ecosystem services they provide in the face of agricultural expansion and intensification (Lin and Huang 2019).

Most of the land in Great Plains is privately owned, and thus private land conservation programs offer a potential solution to declining pollinator populations in this region. The Conservation Reserve Program (CRP) is a voluntary cost-share assistance and rental payment program administered by the Farm Service Agency in which agricultural producers and landowners cease production on environmentally sensitive cropland and instead establish conservation cover for 10- to 15-year periods. The CRP includes over 40 conservation practices (CPs) that focus on restoring specific environmental functions or ecosystem services. Popular CPs in Kansas include the Establishment of Permanent Native Grasses (CP-2), Rare and Declining Habitat (CP-25), and Pollinator Habitat (CP-42), which differ primarily in the composition of the plant community, particularly with regards to the overall proportion of grasses and forbs in the seed mix. Although some studies have evaluated the impact of CRP

plantings on pollinator communities (Otto et al. 2018, Arathi et al. 2019, McMinn-Sauder et al. 2020, Quinlan et al. 2021, Wen et al. 2022, Kraus et al. 2023), floral resource utilization by non-bee pollinators is often absent from these assessments and thus there is little evidence that the CRP is contributing to the conservation of resilient pollinator communities. Moreover, there are few studies comparing the effectiveness of different CPs, particularly with regards to their impact on pollinator communities.

The impacts of CRP plantings on pollinators may be determined by local habitat features and the quality of the surrounding landscape. Pollinator communities have generally been found to respond positively to greater local floral resource availability or diversity (Scheper et al. 2015, Gómez-Martínez et al. 2022, Maurer et al. 2022, Lichtenberg et al. 2025). Additionally, because 70% of bee species nest underground, soil characteristics, such as soil texture, can influence the nesting, sheltering, or overwintering habitat of pollinators (Cane 1991, Antoine and Forrest 2021). The composition of habitat in the landscape surrounding a conservation planting has also been found to impact local ecological processes (Öckinger et al. 2012, Tscharntke et al. 2012, Kennedy et al. 2013, Adedoja and Mallinger 2025). For example, the amount of natural habitat cover in the landscape can impact the dispersal of pollinators between habitat patches and thus influence the availability of pollinators that can (re)colonize a given habitat patch (M'Gonigle et al. 2015, Griffin and Haddad 2021, Warzecha et al. 2021). Local and landscape habitat characteristics may have an interactive effect on pollinator communities in conservation plantings such that the colonization of plantings with a diverse set of floral resources depends on the quality of the habitat in the surrounding landscape, for instance (Kennedy et al. 2013, Warzecha et al. 2021).

Furthermore, it is unknown if different taxonomic groups respond differently to local and landscape habitat features on CRP land, which is important if land managers are interested in conserving specific taxa or safeguarding certain ecosystem services. Pollinator taxa may respond differently to the amount or configuration of natural habitat cover in the landscape (Sjödin et al. 2008, Jauker et al. 2009, Öckinger et al. 2012, Orford et al. 2015, Bergholz et al. 2022). Non-syrphid flies, for instance, have not been reported to be threatened by agricultural practices and thus may provide valuable pollination services in agroecosystems with little natural habitat cover (Orford et al. 2015), whereas lepidopterans are likely to be more dependent on natural habitat cover due to their host plant specificity (Öckinger et al. 2012). Although there is evidence that bees may prefer sandier soil as nesting habitat (Cane 1991, Antoine and Forrest 2021), there is limited information in the literature on how non-bee pollinators respond to soil properties (Sjödin et al. 2008, Lichtenberg et al. 2025). Nevertheless, different pollinator taxa may play important roles in maintaining pollination services. Lepidopterans and flies, for example, may be important for promoting genetic dispersal between distant plant populations by providing pollination services across longer distances than bees, which are central-place foragers (Ssymank et al. 2008, Travers et al. 2011). Additionally, different pollinator taxa may visit distinct subsets of the plant community (Borchardt et al. 2024) or differ in their sensitivity to disturbances (García et al. 2018, Lazarina et al. 2019), thereby impacting the maintenance of pollination services in the face of disturbances. Consequently, it is important to investigate the responses of different pollinator taxa to local and landscape habitat features on CRP land when evaluating the effectiveness of these plantings.

Much of the research on CRP plantings quantifies their effectiveness using simple metrics of diversity (Arathi et al. 2019, Quinlan et al. 2021, Kraus et al. 2023). However, these diversity

metrics fail to provide insight into the ecological processes that structure pollinator communities, such as pollinator foraging behavior. One way to understand how CRP plantings impact pollinator communities and their floral resource utilization is to make detailed observations of the pollinators visiting plants and quantify these plant-pollinator interactions using network analysis. We can quantify network topology using metrics such as nestedness, network specialization, and modularity to understand associations between species in a community and identify the ecological processes that drive the patterns of community organization.

Nestedness refers to the degree to which specialists interact with a subset of species with which generalists interact. Highly nested networks consist of generalists that interact with many other species and specialists that interact with a subset of the species with which generalists interact (Figure 1.1A). High nestedness indicates that species are targeting locally abundant resources, resulting in high niche overlap between species (Bascompte and Jordano 2007, Bascompte and Scheffer 2023). Network specialization (H_2') refers to the overall specialization of all species in the network (Blüthgen et al. 2006). A highly specialized network is characterized by reciprocal specialization of all species in the network (Figure 1.1B) and is an indicator of niche partitioning in response to strong interspecific competition for resources. Lastly, modularity describes the degree to which species form clusters or modules, with interactions being frequent within modules and rare between modules (Figure 1.1C). Similar to network specialization, high modularity indicates strong resource partitioning. Network analysis allows us to understand how conservation plantings, such as the CRP, impact community structure and functioning. Employing a systems approach to pollinator conservation allows conservation practitioners to support overall structure and maintain ecosystem functionality rather than just conserve a few species (Borchardt et al. 2021). Furthermore, this network approach can provide insight into how pollinator foraging

behavior responds to habitat features, such as the availability and diversity of resources, which can then inform the design of conservation plantings.

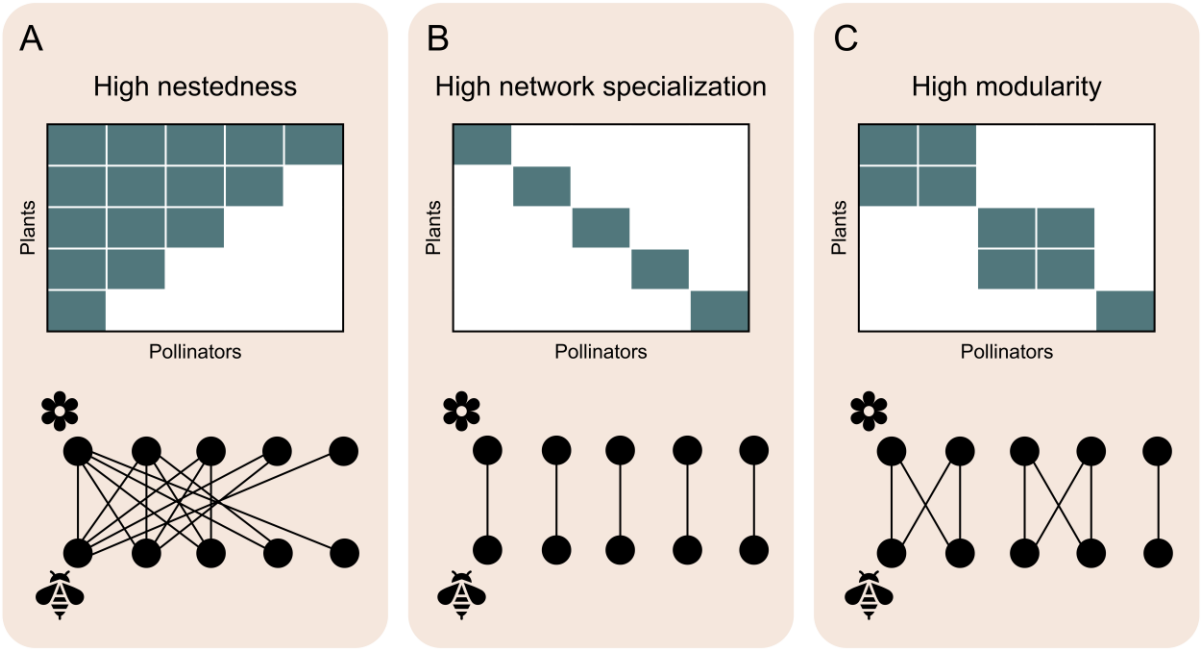

Figure 1.1. The topology of plant-pollinator interaction networks as quantified by nestedness (A), network specialization (B), and modularity (C).

The objectives of this study are to: a) evaluate the effectiveness of different CRP planting types in supporting pollinator communities and b) investigate how local- and landscape-scale habitat characteristics influence the effectiveness of CRP plantings. To accomplish these objectives, I will examine the effects of CP-2, CP-25, and CP-42 plantings as well as non-CRP grasslands on pollinator abundance, pollinator richness, and plant-pollinator network topology. Additionally, I am interested in how the abundance and richness of floral resources, land cover in the surrounding landscape, and soil texture impact pollinator abundance, pollinator richness, and plant-pollinator network topology across these different CRP planting types. Understanding the effectiveness of CRP plantings and the impact of habitat at different spatial scales on plant-

pollinator communities can be used to make recommendations for improving pollinator conservation plantings in the Great Plains.

Methods

Study area

Observations of plant-pollinator interactions were conducted at 22 study sites located in northeastern Kansas where the natural landscape is tallgrass prairie characterized by tall, warm-season grasses and a diverse mix of forbs (Lauenroth 1999). Nineteen sites were located on privately-owned land enrolled in the Conservation Reserve Program, and three sites were located on public grasslands (Figure 1.2). The CRP sites were enrolled in one of three conservation practices—CP-2 (Permanent Native Grasses), CP-25 (Rare and Declining Habitat), and CP-42 (Pollinator Habitat). Of the CRP sites, six were enrolled in CP-2, eight were enrolled in CP-25, and five were enrolled in CP-42. These conservation practices differ in the proportion of grasses and forbs in their seed mixes, with CP-2 containing the smallest proportion of forbs followed by CP-25 and CP-42, respectively.

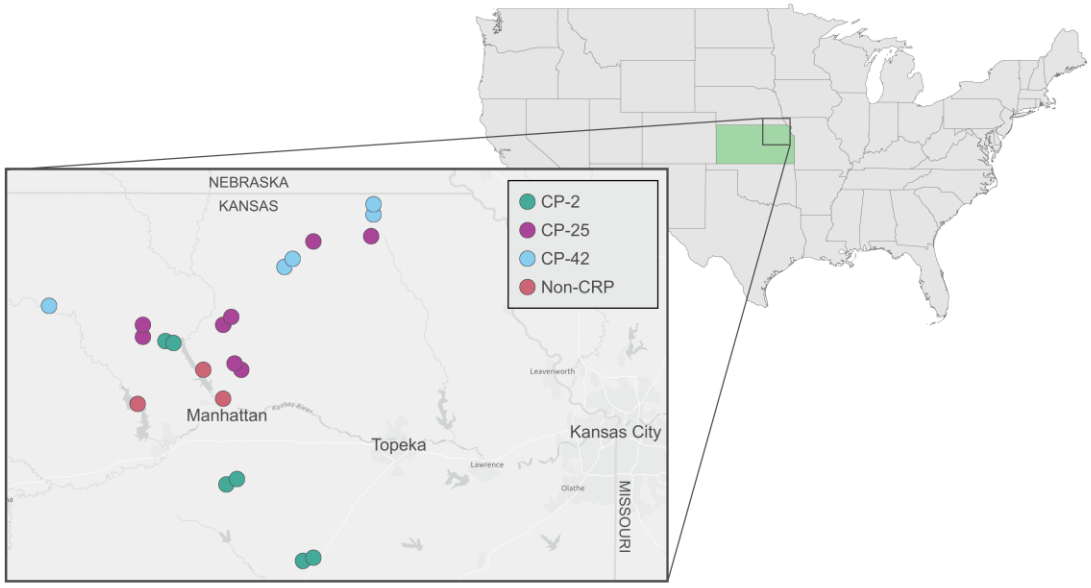

Figure 1.2. Location of CRP plantings and non-CRP grasslands in northeastern Kansas. Circle color reflects the planting type.

Pollinator and forb community sampling

Each site was sampled once or twice between June and August 2024. Site sampling by CRP planting type was randomized to prevent confounding CRP planting type with sampling month. During each sampling bout, I quantified plant-pollinator interactions within the same 20 × 20 m plot using timed focal floral observation surveys. Each forb species in flower was observed for 20 minutes total, with observations divided between two individuals of a given species whenever possible. During this observation period, any flower visitor that was seen touching the reproductive parts of the flower (hereafter referred to as a pollinator) was collected using an aerial net or a handheld insect vacuum. Once collected, pollinators were transferred to a plastic cup and stored on ice to be identified later. Due to conservation concern about bumble bees in the region (i.e., *Bombus pensylvanicus* and *B. fraternus*) (USFWS 2021, USFWS 2024),

these taxa were recorded on video before being released, and identifications were made from these videos. Pollinator observations were made between the hours of 07:00 and 17:00 local time on warm days (> 21°C and < 32°C) with relatively low wind (< 15 mph). These observations were usually completed in one day, but occasionally poor weather required observation to be finished on another day. Bee specimen identification was performed by Dr. Zach Portman at the University of Minnesota. Non-bee specimens were identified to the lowest possible taxonomic level by the author. Most of these individuals were identified to species, including syrphid flies (Diptera: Syrphidae), bee flies (Diptera: Bombyliidae), and tangle-veined flies (Diptera: Nemestrinidae). The keys used to identify these fly taxa include *The Manual of Nearctic Diptera* (McAlpine 1981), *The bee flies (Diptera: Bombyliidae) of Ontario, with a key to the species of eastern Canada* (Kits et al. 2008), *Key to the genera of Nearctic Syrphidae* (Miranda et al. 2013), and *Field/Photo ID for Flies* (Dankowicz and Dankowicz 2024). Skippers (Lepidoptera: Hesperiidae), pierid butterflies (Lepidoptera: Pieridae), gossamer-winged butterflies (Lepidoptera: Lycaenidae), and brush-footed butterflies (Lepidoptera: Nymphalidae) were identified to species using specific Discover Life keys (https://www.discoverlife.org/) and the Nebraska Butterflies website (Dankert et al. 2024). Beetles were identified using *American Beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea* (Arnett et al. 2002). The few individuals that were not identified to the species level were assigned a unique morphospecies ID.

During each sampling bout, forb species richness and community composition were measured by conducting a complete census of the forb community in flower at each site. Forb abundance was measured as the number of forb stems with flowering heads along two parallel 2 × 20 m belt transects.

Soil sampling

Soil texture analysis was performed to evaluate nesting habitat for ground-nesting pollinators. Soil samples were collected during June 2025, for soil composition is unlikely to change substantially from one year to the next (Varallyay 1990). Three composite soil samples consisting of three individual soil cores were collected at each site. Litter was cleared from the soil surface and soil cores were collected to a depth of 10–30 cm. All soil samples were oven-dried at 60°C for one week and ground to pass through a 2 mm sieve. Soil texture was measured in the lab using the hydrometer method (Bouyoucos 1962). The ground samples were suspended in a solution of water and soap and left to settle for 48 hours. The thickness of the sand, silt, and clay layers was measured to the nearest mm, and the proportion of sand, silt, and clay in each composite soil sample was calculated.

Landcover variables

To determine the composition of the landscape surrounding the study sites, buffer zones with radii of 0.5 km, 1.0 km, 1.5 km, and 2.0 km centered around each study site were established in R v4.4.2 (R Core Team 2024). Using land cover data from the 2024 USDA Cropland Data Layer (USDA NASS 2024), the area covered by different land cover classes was calculated. Several crop classes, including corn, wheat, soybean, and sorghum, were aggregated into ‘agriculture’. The dominant land cover classes were agriculture, grassland/pasture, forest, and developed land. The proportion of land within each buffer zone covered by these dominant land cover classes was calculated.

Statistical analysis

Cumulative observation time at each site varied greatly due to differences in forb richness, and thus differences in pollinator abundance may be attributed to differences in

sampling time. Consequently, relative pollinator abundance was calculated by dividing pollinator abundance by total time spent sampling each site. To account for the effect of sampling effort on pollinator richness, I estimated species richness using the Chao 1 estimator (Chao 1984). Chao 1 is a non-parametric abundance-based estimator of species richness that adjusts for the number of species present but not detected based on information on the rare species in the assemblage, namely the singletons and doubletons (Gotelli and Colwell 2011). This approach to estimating species richness was used because of its usefulness when sample sizes are low (Chao 1984). Chao 1 was calculated using the iNEXT package v3.1.0 (Hsieh et al. 2024). I did not observe any pollinators at one site and thus was unable to calculate Chao 1 due to the lack of singletons or doubletons upon which to base the calculation, so that site was excluded from analyses using Chao 1.

I used linear models to evaluate the impact of local- and landscape-scale habitat characteristics on relative pollinator abundance and estimated pollinator richness. I used Akaike's Information Criterion corrected for small sample sizes (AICc) to determine which component soil texture (i.e., the percentage of sand, silt, or clay), and which land cover class (i.e., agriculture, grassland/pasture, forest, or developed land) and buffer size to use as predictor variables in statistical analyses. The percentage of sand in the soil and the proportion of grassland cover within a 1 km radius were the variables that resulted in the most parsimonious models (lowest AICc values), and therefore these variables were used in statistical analyses.

I used a model selection approach with AICc to select the best-fit model for relative pollinator abundance and estimated pollinator richness. For each response variable, I generated a global model that included the abundance and richness of forbs in flower, the proportion of grassland cover, the percentage of sand in the soil, and CRP planting type as predictor variables.

I also included interactions between forb abundance and grassland cover and between forb richness and grassland cover as predictor variables in these global models. I compared models of all possible subsets of this global model and selected the most parsimonious model (lowest AICc) for each response variable using the MuMIn package v1.48.11 (Burnham and Anderson 2002, Bartoń 2025). This package generates a set of submodels that contain all possible combinations of predictor variables from the global model and ranks the submodels according to AICc. Model fit was evaluated by visually checking the residuals diagnostics. The global model for estimated pollinator richness showed signs of heterogeneity of variance, so I log-transformed the Chao 1 estimator before proceeding with model selection. I repeated these analyses for common pollinator taxa, namely beetles, flies, and bees, to examine how these taxa respond to local- and landscape-scale habitat characteristics.

To determine the impact of local- and landscape-scale habitat variables on pollinator community composition, I performed a distance-based redundancy analysis (dbRDA) using Bray-Curtis dissimilarities (Legendre and Anderson 1999). dbRDA was performed using only species with two or more individuals across all study sites so the results were not biased by rare species. The abundance and richness of forbs in flower, the proportion of grassland cover, the percentage of sand in the soil, and CRP planting type were included as predictor variables. The significance of each predictor variable was assessed using 1,000 permutations. This analysis was performed using the vegan package v2.6.10 (Oksanen et al. 2025). Statistically significant species and taxonomic group scores *(*$P \leq 0.05$) were vectorized onto the resulting ordination using the *envfit* function in the vegan package to visually evaluate species/taxonomic group associations with sites. Indicator species analysis was performed using the indicspecies package v1.8.0 (Cáceres and Legendre 2009) to explore the relationship between species occurrence or

abundance and CRP planting types. Community composition analyses were performed at the species level and the taxonomic group level. dbRDA was performed using forb species data as well to determine if forb community composition was significantly different between CRP planting types.

Network analysis

I combined visitation data from each sampling bout to form quantitative plant-pollinator interaction networks for each site, in which interaction strength between each plant-pollinator pair is weighted by the visitation rate. Two sites generated networks with too few species and thus these networks were removed from the analysis. I calculated three network metrics—nestedness (Bascompte et al. 2003), network specialization (Blüthgen et al. 2006), and modularity (Olesen et al. 2007)—using the bipartite package v2.20 (Dormann et al. 2009). I calculated nestedness as "Weighted Nestedness metric based on Overlap and Decreasing Fill" (WNODF; Almeida-Neto and Ulrich 2011) and network specialization (H_2') using the *networklevel* function (Almeida-Neto et al. 2008). I calculated modularity using the *computeModules* function (Beckett 2016). To determine if the observed network topology was different than what would be expected due to random chance, I generated 1,000 null models using the *nullmodel* function. I used the "r2dtable" method when generating null models, which randomizes each empirical network while keeping constant the number of species in the network and the number of interactions per species (Dormann et al. 2009). I calculated z-scores to standardize network metrics and compare relative network topology among sites as $z = (x - \mu)/\sigma$, where x is the empirical network metric, μ is the average network metric score of 1,000 null models, and σ is the standard deviation of 1,000 null models. I then performed a two-tailed permutation test to test whether the difference in network topology between observed networks

and null models was statistically significant at $P < 0.05$. I examined the drivers of network topology using linear models that included relative pollinator abundance, estimated pollinator richness, the abundance and richness of forbs in flower, the proportion of grassland cover, the percentage of sand in the soil, and CRP planting type as predictor variables. I also included interactions between forb abundance and grassland cover and between forb richness and grassland cover as predictor variables in these global models. For each network metric, I generated a global model that included all these predictor variables and performed model selection to select the most parsimonious model (lowest AICc) out of all possible subsets of the global model.

Results

I recorded a total of 476 interactions between 142 pollinator species and 57 flowering plant species. Hymenoptera comprised the majority of the interactions recorded with 185 interactions (38.9%) divided among 13 families. Of these 13 families, five were families of bees, seven were families of wasps, and one consisted of ants. Coleoptera comprised the second-most interactions with 176 interactions (37.0%) divided among 11 families. I recorded 66 interactions (13.9%) across 14 families of Diptera, 25 interactions (5.3%) across 10 families of Hemiptera, and 21 interactions (4.4%) across 5 families of Lepidoptera. I also observed two interactions (0.4%) across two families of Orthoptera and one interaction (0.2%) from Neuroptera.

The best model of relative pollinator abundance included forb richness, grassland cover in the surrounding landscape, and their interaction as predictor variables ($P = 0.002$, $R^2_{adjusted} = 0.472$, Table 1.1A). There was a significant positive relationship between pollinator abundance and the interaction between forb richness and grassland cover, suggesting that these habitat variables have an interactive effect on pollinator abundance ($F = 10.149$, $P = 0.005$, Figure

1.3A). The response of pollinator abundance to habitat characteristics varied when analyzing common pollinator taxa separately. Beetle abundance increased significantly with increases in the percentage of sand in the soil (F = 5.632, P = 0.030, Table 1.1B) and was greater on CP-25 sites compared to the other CRP planting types (F = 7.478, P = 0.002, Table 1.1B). Additionally, both fly and bee abundance increased with increases in forb richness (F = 3.563, P = 0.074, Table 1.1C; F = 3.842, P = 0.064, Table 1.1D). Belowground-nesting bee abundance was also found to increase with increases in forb richness (F = 5.923, P = 0.024, Table 1.1E) when analyzed separately from aboveground-nesting bees.

Table 1.1. Results of the best models of relative pollinator abundance (A), beetle abundance (B), fly abundance (C), bee abundance (D), and belowground-nesting bee abundance (E). Significant P values are shown in boldface type.

Predictor	Estimate	SE	F	df	P
Model					
(A) Relative pollinator abundance					
Intercept	0.293	0.076	14.915	1	**0.001**
Forb richness	-0.016	0.006	7.272	1	**0.015**
Grassland cover	-0.333	0.095	12.323	1	**0.003**
Forb richness × Grassland cover	0.025	0.008	10.149	1	**0.005**
(B) Relative beetle abundance					
Intercept	-0.013	0.023	0.382	1	0.545
Percent sand	0.062	0.026	5.632	1	**0.030**
CRP planting type			7.478	3	**0.002**
CP-2	0.003	0.012			
CP-25	0.035	0.013			
CP-42	-0.000	0.012			
(C) Relative fly abundance					
Intercept	3.517×10^{-4}	0.005	0.004	1	0.948
Forb richness	0.001	4.031×10^{-4}	3.563	1	0.074
(D) Relative bee abundance					
Intercept	0.004	0.004	0.184	1	0.672
Forb richness	0.002	0.002	3.842	1	0.064
(E) Relative belowground-nesting bee abundance					

Intercept	0.001	0.008	0.010	1	0.922
Forb richness	0.001	0.001	5.923	1	**0.025**

The best model of estimated pollinator richness included forb richness, grassland cover, the interaction between forb richness and grassland cover, and the percentage of sand in the soil as predictor variables ($P < 0.001$, $R^2_{adjusted} = 0.748$, Table 1.2A). There was an interactive effect of forb richness and grassland cover on estimated pollinator richness ($F = 10.248$, $P = 0.006$, Figure 1.3B). Moreover, estimated pollinator richness increased significantly with increases in the percentage of sand in the soil ($F = 16.291$, $P = 0.001$, Figure A.1). Estimated beetle richness was found to decrease with increases in the percentage of sand in the soil ($F = 2.888$, $P = 0.106$, Table 1.2B), whereas estimated fly richness was found to increase with increases in forb richness ($F = 3.609$, $P = 0.080$, Table 1.2C). Estimated bee richness increased significantly with increases in forb abundance ($F = 8.344$, $P = 0.011$, Table 1.2D). This positive relationship with forb abundance was maintained when belowground-nesting bee richness was analyzed separately ($F = 12.987$, $P = 0.003$, Table 1.2E).

Table 1.2. Results of the best models of estimated pollinator richness (A), beetle richness (B), fly richness (C), bee richness (D), and belowground-nesting bee richness (E). Significant *P* values are shown in boldface type.

Predictor	Estimate	SE	*F*	df	*P*
Model					
(A) Estimated pollinator richness					
Intercept	9.391	1.844	25.924	1	**< 0.001**
Forb richness	-0.298	0.143	4.365	1	0.053
Grassland cover	-9.197	2.399	14.687	1	**0.002**
Percent sand	-3.208	0.795	16.291	1	**0.001**
Forb richness × Grassland cover	0.644	0.201	10.248	1	**0.006**
(B) Estimated beetle richness					
Intercept	8.842	2.155	16.835	1	**0.001**

	Percent sand	0.062	4.526	2.888	1	0.106
(C)	Estimated fly richness					
	Intercept	-6.882	6.705	1.053	1	0.324
	Forb richness	0.887	0.467	3.609	1	0.080
(D)	Estimated bee richness					
	Intercept	5.448	1.683	10.484	1	**0.005**
	Forb abundance	0.027	0.009	8.344	1	**0.011**
(E)	Estimated belowground-nesting bee richness					
	Intercept	3.910	1.336	8.567	1	**0.011**
	Forb abundance	0.025	0.007	12.987	1	**0.003**

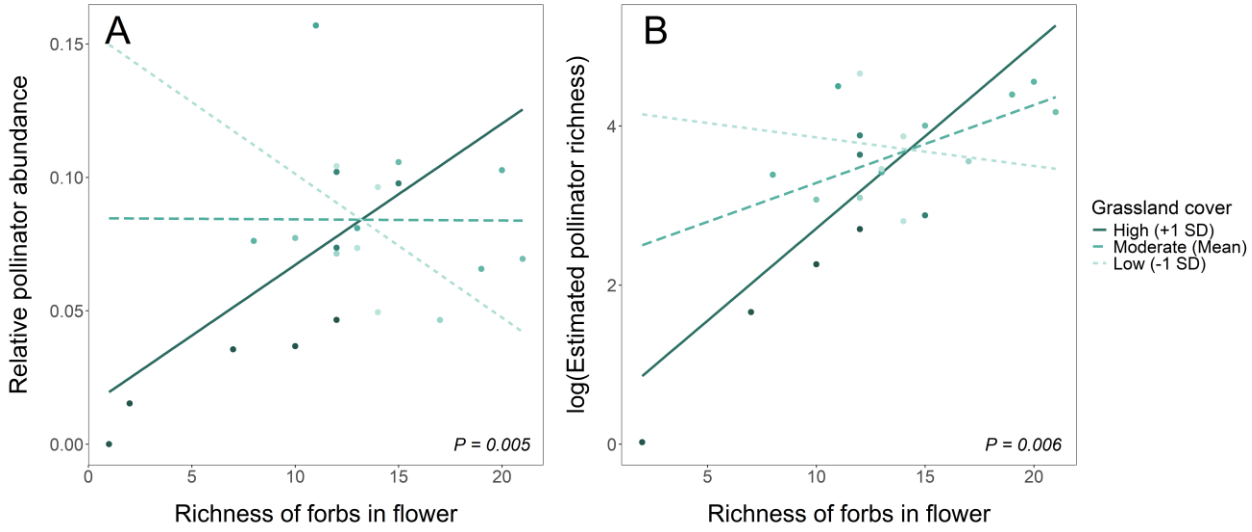

Figure 1.3. Interaction between forb richness and grassland cover in the surrounding landscape and its effect on relative pollinator abundance (A) and estimated pollinator richness (B). The amount of grassland cover in the surrounding landscape is a continuous variable, and thus grassland cover was broken down by standard deviation to visualize in a 2D plot. Solid, dark lines indicate grassland cover one standard deviation above the mean. Dashed green lines indicate the mean grassland cover. Dashed light green lines indicate grassland cover one standard deviation below the mean.

dbRDA results showed that pollinator community composition was significantly different between CRP planting types when analyzed at the species level ($F = 1.749$, $P = 0.002$, Figure 1.4A, Table A.1). There was a marginal effect of forb richness on pollinator community composition ($F = 1.565$, $P = 0.080$, Table A.1), but no other predictor variable significantly affected composition. There was little overlap in the pollinator communities in non-CRP grasslands, CP-2 plantings, and CP-25/CP-42 plantings (Figure 1.4A). Based on the taxonomic group vectors, beetles ($P = 0.004$), syrphid flies ($P = 0.032$), belowground-nesting bees ($P = 0.005$), and true bugs ($P = 0.008$) were significant drivers of differences in pollinator community composition between sites and were all associated with CP-25 and CP-24 plantings (Figure 1.4A). The environmental vectors indicated that syrphid flies were positively associated with forb abundance whereas belowground-nesting bees and beetles were positively associated with forb richness. Results from fitting species vectors onto the ordination plot indicated that *Typocerus* sp. 1 ($P = 0.013$), Chrysomelidae sp. 1 ($P = 0.006$), Formicidae sp. 2 ($P = 0.028$), *Halictus ligatus* ($P = 0.036$), Alydidae sp. 1 ($P = 0.045$), *Epicauta* sp. 2 ($P = 0.034$), Curculionidae sp. 1 ($P = 0.016$), Curculionidae sp. 2 ($P = 0.011$), and *Erynnis* sp.1 ($P = 0.030$) were significant drivers of differences in pollinator community composition between sites (Figure A.2). *Typocerus* sp. 1, *Halictus ligatus*, Alydidae sp. 1, and Formicidae sp. 2 were associated with CP-25 and CP-42 sites while Chrysomelidae sp. 1 was associated with CP-25 sites. Curculionidae sp. 1 and *Epicauta* sp. 2 were associated with CP-2 sites whereas *Erynnis* sp. 1 and Curculionidae sp. 2 were associated with non-CRP sites. Indicator species analysis identified three species that contributed to the dissimilarities between CRP planting types; *Erynnis* sp. 1 and Curculionidae sp. 2 were significantly associated with non-CRP grasslands (*P*

= 0.02, $P = 0.04$), whereas *Lasioglossum disparile* was significantly associated with CP-42 plantings ($P = 0.05$).

When analyzed at the taxonomic group level, dbRDA results indicated that pollinator community composition was significantly affected by CRP planting type ($F = 1.621$, $P = 0.049$, Table A.2) and forb richness ($F = 4.698$, $P = 0.001$, Table A.2) and marginally affected by percent sand ($F = 1.954$, $P = 0.073$, Table A.2). Based on the taxonomic group vectors, beetles ($P = 0.004$), syrphid flies ($P = 0.001$), ants ($P = 0.040$), belowground-nesting bees ($P = 0.001$), non-syrphid flies ($P = 0.011$), and true bugs ($P = 0.010$) were significant drivers of differences in pollinator community composition between sites at the taxonomic group level (Figure 1.4B). Beetles, true bugs, belowground-nesting bees, and non-syrphid flies were associated with both CP-25 and CP-42 plantings whereas ants and syrphid flies were associated with just CP-25 sites. Moreover, indicator species analysis indicated a significant association between true bugs and CP-25 and CP-42 plantings ($P = 0.01$). dbRDA results indicated that forb community composition did not differ significantly between CRP planting types ($F = 1.749$, $P = 0.723$, Table A.3). There was considerable overlap in the forb communities at CP-2, CP-25, and CP-42 sites, whereas non-CRP grasslands had unique forb communities (Figure A.3).

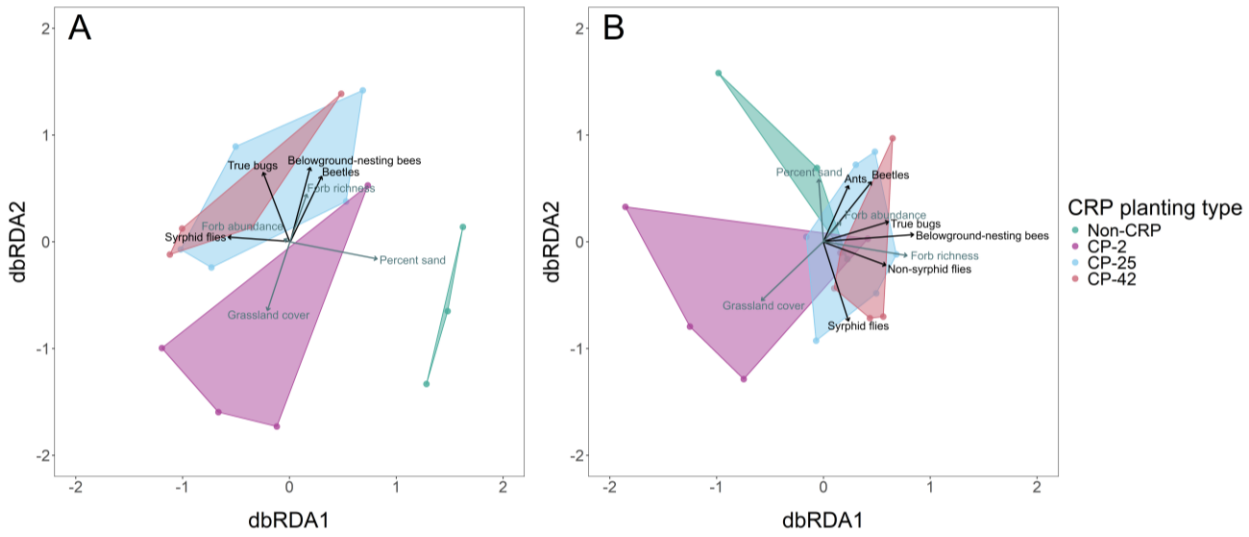

Figure 1.4. Distance-based redundancy analysis biplot for species-level pollinator community data (A) and data grouped by taxonomic group (B). Hull color represents CRP planting type. Black vectors represent significant taxonomic group scores ($P \leq 0.05$). Green vectors represent habitat variables.

The two-tailed permutation test revealed that most of the networks were significantly more specialized (14 of 20 networks), more modular (14 of 20 networks), and less nested (7 of 20 networks) than expected by chance based on the null model (Figure 1.5). Plant-pollinator networks at non-CRP sites were not significantly specialized or nested. Relative nestedness decreased with increases in pollinator abundance ($F = 3.060$, $P = 0.101$, Figure 1.6A). Relative network specialization increased with increases in pollinator abundance ($F = 5.428$, $P = 0.033$, Figure 1.6B) and forb richness ($F = 3.151$, $P = 0.094$, Figure 1.6C). Similarly, relative modularity increased with increases in pollinator abundance ($F = 7.814$, $P = 0.012$, Figure 1.6D).

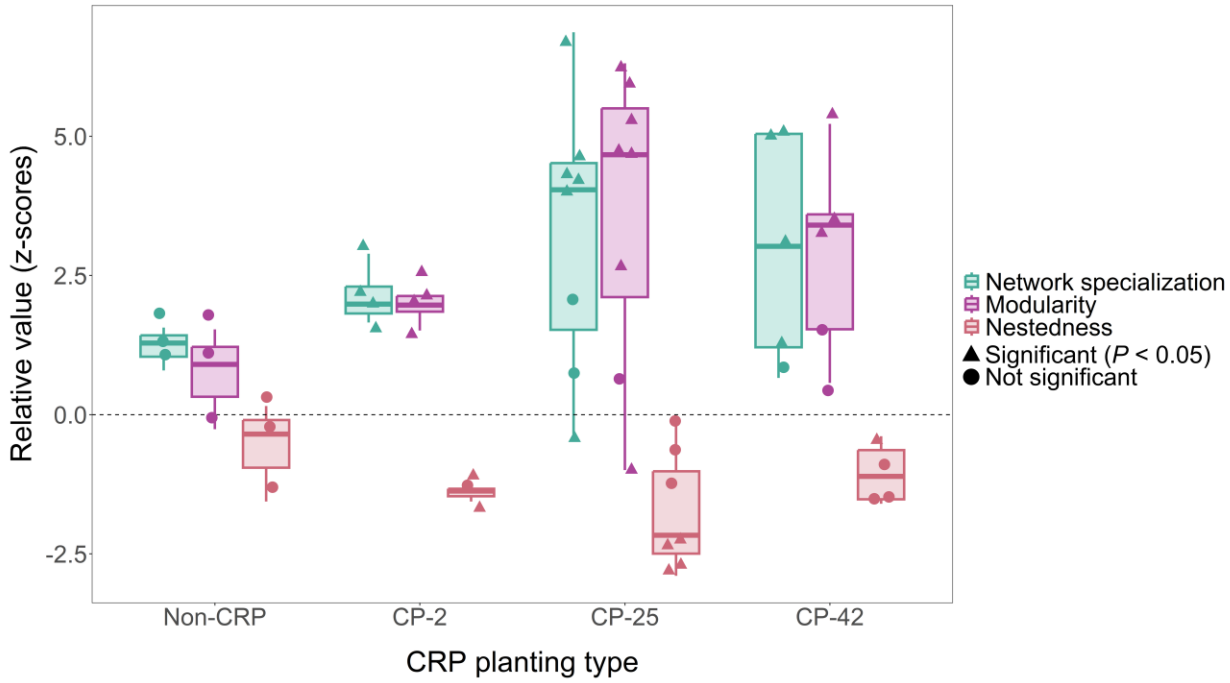

Figure 1.5. Relative network specialization, modularity, and nestedness values (z-scores) for each CRP planting type. Triangles indicate significant values ($P < 0.05$).

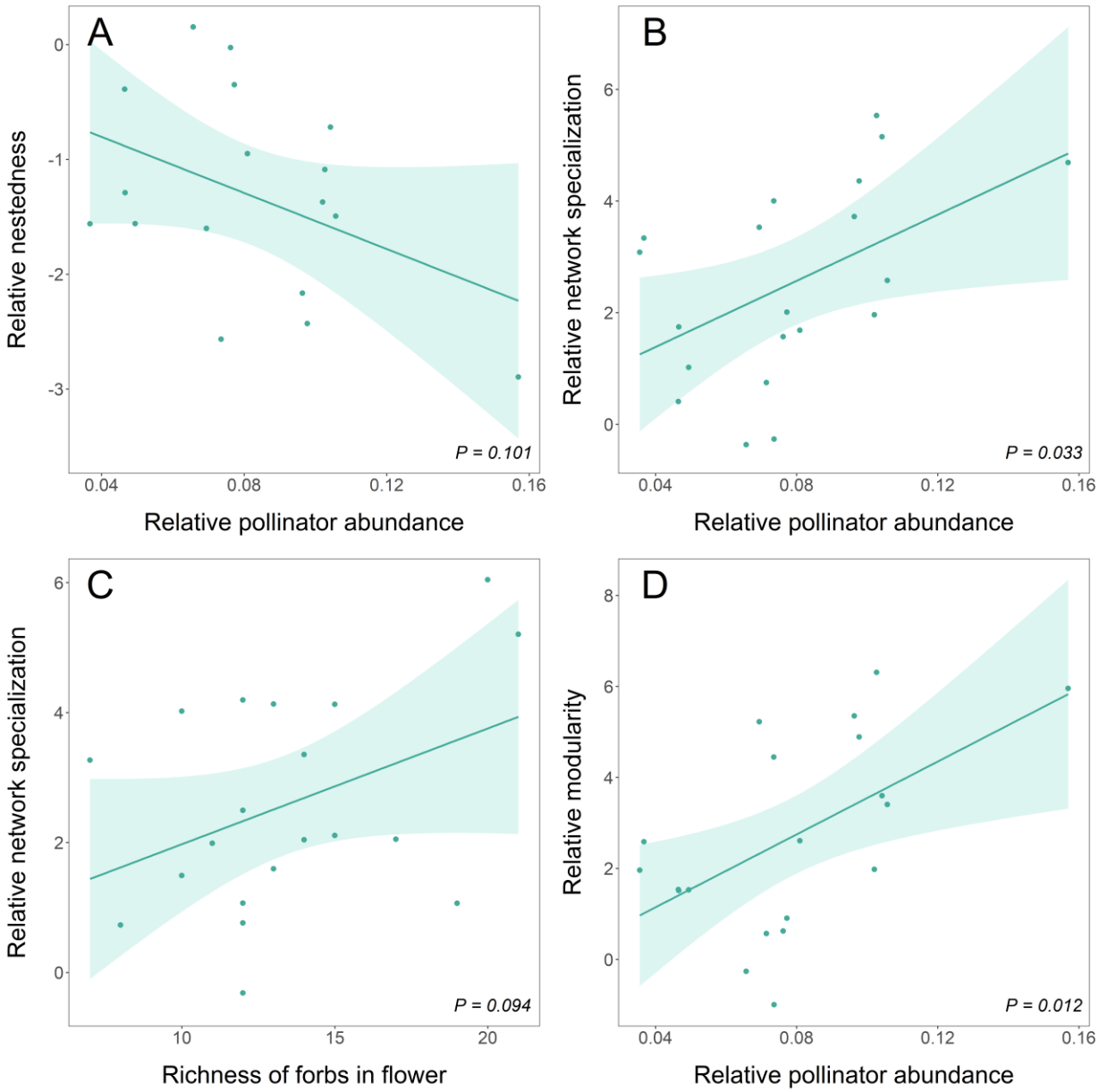

Figure 1.6. Partial residuals plots showing the effects of pollinator abundance on relative nestedness (A), pollinator abundance (B) and forb richness (C) on relative network specialization, and pollinator abundance on relative modularity (D).

Discussion

Pollinator abundance and richness were more influenced by site-specific habitat characteristics than CRP planting type per se. Both pollinator abundance and richness were

associated with the interaction between forb richness and grassland cover. When grassland cover in the surrounding landscape was high, both pollinator abundance and richness increased with increasing forb richness. However, pollinator abundance and richness decreased with increases in forb richness when grassland cover was low. These findings suggest that landscape context may determine the success of local land management practices in conserving pollinators (Tscharntke et al. 2012, Scheper et al. 2015, Warzecha et al. 2021, Adedoja and Mallinger 2025).

In this study, habitat characteristics had an interactive effect on pollinators such that habitat availability in the surrounding landscape may be modulating the availability and diversity of pollinators that can use floral resources within local habitat patches (Kennedy et al. 2013, Warzecha et al. 2021). In areas with high grassland cover, the landscape acts as a source of pollinators that are attracted to a patch by high floral resource diversity, thus promoting the colonization of conservation plantings. On the other hand, areas of low grassland cover may support smaller, less diverse pollinator communities, and therefore there may be too few pollinators available in the landscape to see a positive response to high floral resource diversity. Alternatively, pollinator communities may be deterred from conservation plantings in areas with low grassland cover due to the prevalence of agricultural weeds (Boinot and Alignier 2022), which may be unattractive to pollinators (Stein et al. 2020, Wen et al. 2022). However, there is mixed evidence regarding the relationship between the abundance/diversity of weedy species and natural habitat cover, with some studies finding more weedy species in areas with high natural habitat cover (Gabriel et al. 2005, Medeiros et al. 2016, Boinot et al. 2023). Although these findings indicate that high grassland cover and floral resource diversity lead to greater pollinator abundance and diversity in CRP plantings, future research should monitor pollinator communities over time to determine whether these conservation plantings promote pollinator

persistence rather than simply leading to transient increases in abundance/diversity (M'Gonigle et al. 2015).

Pollinator taxa responded differently to local- and landscape-scale habitat characteristics. Many studies have reported an association between belowground-nesting bees and sandier soils, which may be preferred nesting habitat due to better drainage (Cane 1991, Sjödin et al. 2008, Antoine et al. 2025). However, in this study, soil texture did not impact the abundance or diversity of bees even when separated by nesting guild, which suggests that bees respond more strongly to the availability of floral resources than soil properties (Antoine and Forrest 2021). Beetle abundance and richness, on the other hand, were found to respond to soil texture. There is a lack of information on the impact of soil texture on non-bee pollinators (Lichtenberg et al. 2025), and thus this result provides new insight into how non-bee taxa respond to conservation plantings with different soil textures. Additionally, pollinator community composition differed between CRP planting types. Belowground-nesting bees, syrphid and non-syrphid flies, beetles, ants, and true bugs were more associated with CP-25 and CP-42 plantings. Syrphid flies were negatively associated with non-CRP grasslands whereas beetles were negatively associated with CP-2 plantings. Although non-CRP grasslands had unique forb communities, forb community composition did not differ significantly between CP-2, CP-25, and CP-42 plantings, which suggests that differences in pollinator community composition cannot be explained entirely by the composition of the forb communities at these sites.

Based on these results, land management strategies may differ depending on the pollinator taxa that are of conservation interest. Bees are highly effective pollinators (Page et al. 2021), but as central place foragers they are constrained by the need to provision a nest in a fixed location. Lepidopterans and flies, on the other hand, travel longer distances than bees and thus

may be important for promoting genetic dispersal between distant plant populations (Ssymank et al. 2008, Travers et al. 2011). Additionally, non-syrphid flies may be less impacted by agricultural practices than other pollinator taxa and therefore may provide valuable pollination services in agroecosystems with little natural habitat cover as a result (Orford et al. 2015). Moreover, pollinator taxa may differ in their sensitivity to disturbances such as fire (García et al. 2018, Lazarina et al. 2019) and exposure to pesticides (Henriques Martins et al. 2024), thereby impacting the maintenance of pollination services in the face of disturbances and anthropogenic change. Consequently, it is important to consider these insights into how different pollinator taxa respond to local and landscape habitat features to manage CRP plantings in accordance with conservation needs.

Plant-pollinator networks were more specialized and modular, which may indicate that pollinator foraging decisions are guided more by the avoidance of interspecific competition than by the pursuit of locally abundant floral resources, which we would expect to result in a nested network topology (Spiesman and Gratton 2016). Greater pollinator abundance resulted in more specialized/modular and less nested plant-pollinator networks, suggesting that the number of competitors increases the need for niche partitioning. Similarly, relative network specialized increased with increases in forb richness, which may indicate that a greater availability of floral resources increases the opportunity for niche partitioning by providing more dimensions in which niches can be partitioned (MacArthur and Levins 1967). Consequently, this niche partitioning may prevent competitive exclusion by allowing pollinator species to diverge their resource use and thus promotes greater biodiversity. Specialized, modular networks may exhibit less functional redundancy, thereby reducing the stability of these communities (Blüthgen et al. 2008). Alternatively, specialized/modular networks may confer stability to these communities by

buffering the spread of perturbations, such as disease outbreaks, and preventing extinction cascades (Stouffer and Bascompte 2011).

Private land conservation programs such as the CRP may be necessary to support pollinators in the face of agricultural expansion and intensification in the Great Plains. Previous research on the effectiveness of CRP plantings has found mixed results. In some studies, CRP plantings have been found to contain more floral resources and thus support larger pollinator populations compared to non-CRP fields (Quinlan et al. 2021). Other work has found that pollinator responses to floral resource availability within CRP plantings are mixed (Kraus et al. 2023, Wen et al. 2022). Arathi et al. (2019) noticed differences in bee community composition between pollinator-friendly CRP plantings and grass-dominated CRP plantings, although bee abundance and diversity did not differ by planting type. Similarly, Kraus et al. (2023) found that pollinator-friendly CP-42 plantings only resulted in a slight increase in pollinator diversity compared to other CRP plantings. However, pollinator community composition did not differ by CRP planting type when comparing pollinator plantings to other CRP practices (Kraus et al. 2023).

Taken together, these results demonstrate that the effectiveness of CRP plantings in supporting pollinator communities depends on several factors, including the local availability of floral resources and the landscape context, and is not determined by CRP planting type alone. The cost of different CRP planting seed mixes varies and is often greater for mixes that contain a greater diversity of forbs, such as CP-25 and CP-42. However, CRP plantings do not differ significantly in the resulting abundance and diversity of floral resources such that less expensive seed mixes are necessarily ineffective at supporting pollinators. CRP landowners are limited in their ability to maintain diverse forb communities through prescribed burning and conservation

grazing, and therefore successional processes may result in similar forb communities across different CRP planting types. Consequently, my findings demonstrate that private landowners can effectively support pollinator communities without the financial burden associated with purchasing expensive seed mixes. Instead, the quality of the local and landscape-scale habitat is more important than the specific CRP plantings that are established. In landscapes with a large amount of natural habitat cover, conservation plantings with greater floral resource availability and diversity are expected to effectively support pollinator communities. However, it may be more important to establish additional conservation plantings than to invest in a single high-quality planting in landscapes with little to no natural habitat cover.

Conclusion

Local- and landscape-scale habitat characteristics influence the effectiveness of CRP plantings in supporting pollinator communities in the Great Plains. Pollinator abundance and diversity were more affected by site-specific habitat features but were not significantly associated with CRP planting type. Accordingly, the quality of the local and landscape habitat was more important for conserving pollinators than the specific CRP planting type, which may suggest that local management using prescribed fire and/or grazing is necessary to see the benefits of more diverse, expensive CRP seed mixes. The positive conditional effect of forb richness suggests that more diverse, expensive seed mixes can support pollinator communities, but their effectiveness depends on the quality of the habitat in the surrounding landscape. Consequently, it is important that conservation practitioners consider the interactive relationship between local and landscape resource availability when deciding where to establish conservation plantings. Pollinator community composition differed significantly across CRP planting types and thus land management strategies may differ depending on the pollinator taxa that are of

conservation interest. Plant-pollinator network topology indicated that pollinator foraging decisions are guided more by niche partitioning in response to the abundance of competitors and the diversity of floral resources than the pursuit of locally abundant floral resources. Therefore, it is important to provide diverse resources for pollinators to promote species coexistence.

Chapter 2 - Adaptive foraging strategies and mutualistic dependence impacts on plant-pollinator community stability

Introduction

Mutualistic interactions between plants and animals maintain global biodiversity and support ecosystem function (Bascompte and Jordano 2007, Bastolla et al. 2009). Historically community ecologists identified that large mutualistic assemblages with many interacting species are unstable such that few species are able to persist over time (May 1972). There is mounting evidence that large, complex communities are in fact dynamic in nature, thereby conferring stability to these communities by ensuring that many species survive over time (Kaiser-Bunbury et al. 2010, Zhang et al. 2011, Valdovinos et al. 2013, Spiesman and Gratton 2016, CaraDonna et al. 2017, Langendorf et al. 2025). However, theory has often implicitly assumed that interactions between species in communities are static for simplicity and thus fails to consider the impacts of this dynamism (Dunne et al. 2002, Memmott et al. 2004, Srinivasan et al. 2007). This dynamic behavior is also reflected in food webs where optimal foraging theory has predicted that species alter their foraging decisions to maximize fitness by maximizing the energy gained for a given amount of effort (Beckerman et al. 2006). Although pollinator foraging decisions are guided by mutualism and competition, optimal foraging theory has scarcely been extended to understanding the dynamic behavior of plant-pollinator interactions.

In mutualistic communities of plants and pollinators, pollinator species continually switch the plant species with which they interact to maximize energy gain per cost and enhance the efficiency of resource utilization (Zhang et al. 2011). Pollinators may adapt their behaviors to maximize the mutualistic benefit (i.e., floral rewards) or reduce the cost (i.e., interspecific competition) of foraging. For example, a pollinator may maximize benefits by visiting plant

species that offer more abundant or higher quality floral resources. Alternatively, a pollinator may reduce costs by visiting plants that are visited by few other pollinator species or weaker competitors. When applied to mutualistic assemblages of plants and pollinators, optimal foraging theory suggests that it may be more beneficial for pollinators to concentrate their foraging effort on a few plant species rather than visiting every plant in the community. Thus, the individual foraging behavior of pollinators may result in a more constrained diet breadth by maximizing mutualistic benefits, minimizing energy-demanding costs, or balancing both benefits and costs. This adaptive foraging behavior in response to mutualistic and competitive dynamics is thought to lead to greater stability and diversity in plant-pollinator communities (Kaiser-Bunbury et al. 2010, Zhang et al. 2011, Spiesman and Gratton 2016, Valdovinos et al. 2016, CaraDonna et al. 2017). However, it is difficult to separate the influences of mutualism and competition on community structure and stability empirically. Thus, a simulation approach can be used to understand the drivers of adaptive foraging and the resulting impact on community structure and stability.

One way to understand how adaptive foraging impacts plant-pollinator communities is by visualizing interactions between plants and their pollinators as mutualistic networks. Network topology, or the pattern of interactions between species, is an emergent property that can identify the behaviors that drive plant-pollinator communities and may be important for providing community stability (Bastolla et al. 2009, Kaiser-Bunbury et al. 2010, Zhang et al. 2011). For instance, network specialization (H_2') and modularity indicate that species are partitioning niches to reduce interspecific competition for resources and thus prevent competitive exclusion (Blüthgen et al. 2008). On the other hand, nestedness may be explained by a greater encounter

rate of generalist species, which tend to be more abundant than specialists, and thus indicates that species are foraging in pursuit of highly abundant resources (Vázquez et al. 2009b).

Pollinator species may differ in the degree to which they depend on floral resources for survival as mutualists of plants, which is often referred to as mutualistic dependence. Obligate mutualists have negative intrinsic growth rates in the absence of their interaction partners, and thus they rely on the mutualistic benefits provided by their partners to survive (Hale and Valdovinos 2021). Although most species are not truly obligate in that they must interact with a specific partner to have positive population growth, many facultative mutualists require mutualistic interactions with several partners to prevent mortality from exceeding reproduction (Hale and Valdovinos 2021). Mutualistic dependence can impact community stability by affecting the probability of secondary extinctions when species drop below a threshold that is required for positive population growth (Vanbergen et al. 2017, Valdovinos and Marsland 2021).

I used a plant-pollinator network simulation model to examine how different adaptive foraging strategies based on maximizing mutualistic benefits and/or minimizing competitive costs impacts community stability and the resulting network topology. I also explored how the mutualistic dependence of pollinators on plants modulates the effects of adaptive foraging on community stability. Lastly, I compared the topology of simulated networks to empirical networks to evaluate which adaptive foraging strategies and level of mutualistic dependence results in the most realistic network topologies. I hypothesized that pollinator persistence and abundance would be greatest with adaptive foraging that prioritized both maximizing benefits and minimizing costs. Furthermore, I expected adaptive foraging to result in more specialized and modular networks, and that modularity and specialization would increase with larger networks. Through this work, I hope to understand the impacts of different adaptive foraging

strategies on pollinator communities and evaluate how the results of these simulated networks compare to empirical networks to determine how pollinator communities are making foraging decisions.

Methods

Local and regional network dynamics

I began this simulation model by generating three regional meta-networks from which 15 local networks were randomly drawn. The meta-networks consisted of 75 plant species and 200 pollinator species. The meta-networks represented the independent (i.e., true) preferences of each pollinator for each plant without considering the influences of interspecific competition and/or species abundances. I assumed that these meta-networks were nested in topology with moderate connectance in accordance with the binary topology of many reported empirical networks (reviewed in Valdovinos 2019). To ensure that the meta-networks had a nested topology, I assigned binary interactions to pairs of species based on the outer product of two gamma distributions until the desired connectance of 0.2 was reached. Interaction weights for each meta-network were then generated from a uniform distribution between 0 and 0.5. From each meta-network, I generated five small, five medium, and five large local networks consisting of 10, 20, and 40 plant species, respectively. I generated these local networks by randomly selecting the specified number of plant species and including all pollinator species that interacted with the selected plants as well as the meta-network interaction weights for the selected plant-pollinator pairs. Interaction weights for the selected plant-pollinator pairs represented the starting interaction frequencies for the local network replicates. I assumed that plant-pollinator pairs that did not interact in the meta-network could be explained by biological constraints ('forbidden links') and thus were unable to interact in the local networks (Jordano et al. 2003, Jordano 2016).

Population dynamics

I assumed that both plant and pollinator species experienced intraspecific and interspecific competition, and that interacting plant-pollinator species pairs experienced mutualism. I assumed that all plant species in the local networks competed with one another for a shared resource and that most pairs of plant species exerted a weak competitive effect on one another. Therefore, the interspecific competition coefficients (α_{ij}) for each pair of plant species were sampled from a gamma distribution with a shape (α) of 0.15 and a rate (θ) of 4 (Valdovinos et al. 2013). Plant-specific competition coefficients (c_{ijk}) represented the negative competitive effect of pollinator j on pollinator i for plant species k and were established at the meta-network level, for I assumed that these values resulted from the coevolution of all plant and pollinator species within the regional community. These coefficients were sampled from a normal distribution with a mean of 0.6 and a standard deviation of 0.1 to reflect a community in which most pollinator species exert a moderate competitive effect on one another (Valdovinos et al. 2013). Interspecific competition between pollinator species only occurred if two species visited one or more of the same plant species in the local network. Consequently, interspecific competition coefficients between pollinators (α_{ij}) were calculated as the sum of the plant-specific competition coefficients (c_{ijk}) for each plant species k that was shared by pollinators i and j. If two pollinators did not visit any common plant species, then $\alpha_{ij} = 0$. The intraspecific competition coefficients (a_{ii}) for all plant and pollinator species varied between randomly 0.99 and 1.01 (Valdovinos et al. 2013). Similar to the plant-specific competition coefficients, mutualism coefficients were established at the meta-network level. I assumed that the visitation rates between plant and pollinator species at the regional level reflected the degree of mutual benefit between species, and thus the interaction weights for each meta-network were used as the

mutualism coefficients. Handling time (h) for all plant species was fixed at 0.1 (Bastolla et al. 2009, Zhang et al. 2011).

Table 2.1. Model variables and parameters.

Symbol	Meaning
Population growth models:	
N_i	Density of plant population i
M_j	Density of pollinator population j
r_i	Intrinsic growth rate of plant i
b_i	Intrinsic growth rate of pollinator i; Determines level of mutualistic dependence of pollinator i on benefits received from plants
c_{ijk}	Plant-specific competition between pollinator j on pollinator i for plant k
C_{ij}	Cost to population growth that pollinator i incurs due to competition for plant j
γ_{ik}	Benefit to population growth that plant i receives by interacting with pollinator k, or vice versa
α_{ij} / α_{ii}	Per-capita competitive effect of species i on species j / per-capita effect of species i on itself (i.e., density dependence)
h	Handling time (constant)
$\delta j_i j_k$	Indicates whether plant j is shared by pollinators i and k; Equals 1 if pollinators i and k both visit plant j (otherwise equals 0)
v_{ik}	Binary interaction matrix; Equals 1 if pollinator i visits plant k (otherwise equals 0)
Contingency model of optimal foraging:	
P_{ij}	Profitability of plant j for pollinator i; Rate of energy gain for pollinator i foraging on plant j
E_k	Rate of energy intake by pollinator i with diet breath in order of plant profitability of k
V_{ij}	Visitation rate of pollinator i to plant j

I assumed that interspecific competition between pollinators for access to a given plant species resulted in the incurrence of costs. These costs (C_{ij}) represented a negative contribution

to pollinator *i*'s population growth rate due to competition with all other pollinators for common plant *j*:

$$C_{ij} = \sum_k c_{ijk} M_k \delta_{j_i j_k} \quad [1]$$

where $\delta_{j_i j_k}$ equals 1 if pollinators *i* and *k* both visit plant *j* and 0 otherwise.

I simulated the population dynamics of each plant and pollinator species by following a model similar to those used in other studies (Bastolla et al. 2009, Zhang et al. 2011) that incorporates density dependent growth, interspecific competition, and a saturating (type II; Holling 1959) functional response. A saturating functional response assumes that consumers are limited by their capacity to consume resources and is characterized by a decreasing rate of resource consumption with increases in resource density. Moreover, this functional response assumes that there are no costs associated with switching to different resources, such as searching or learning time. Therefore, plant population growth was modeled as:

$$\frac{dN_i}{dt} = r_i N_i - \sum_j \alpha_{ij} N_i N_j + \frac{\sum_k N_i M_k \gamma_{ik} v_{ik}}{1+\sum_k h \gamma_{ik} v_{ik} M_k} \quad [2]$$

where r_i is the intrinsic growth rate of plant *i,* α_{ij} is the per-capita competitive effect of plant *i* on plant *j*, N_i and N_j are the population densities of plant *i* and plant *j*, γ_{ik} is the benefit to population growth that plant *i* receives by interacting with pollinator *k,* v_{ik} is the binary interaction matrix, *h* is the handling time, and M_k is the population density of pollinator *k*. Pollinator population growth was modeled as:

$$\frac{dM_i}{dt} = b_i M_i - \alpha_{ii} M_i + \frac{\sum_k M_i N_k \gamma_{ik} v_{ik}}{1+\sum_k (h+C_{ik}) \gamma_{ik} v_{ik} N_k} \quad [3]$$

where b_i is the intrinsic growth rate of pollinator *i,* α_{ii} is the density-dependent coefficient, M_i is the population densities of pollinator *i*, γ_{ik} is the benefit to population growth that pollinator *i* receives by interacting with plant *k,* C_{ik} is the cost to population growth that pollinator *i* incurs by

competing with other pollinators for access to plant k, v_{ik} is the binary interaction matrix, h is the handling time, and N_k is the population density of plant k.

Numerical solutions to these population growth models were obtained using the Euler method with a time step size (s) of 0.01. The model was run for 15,000 iterations or 150 time steps (i.e., generations). Population densities for all plant and pollinator species started at 1.0. At the end of the model run, a species was considered extinct if its population density was less than 1×10^{-7}. Plant species were assigned a positive intrinsic growth rate (r_i) of 1.0, which assumed that the mutualism was facultative for plants. Pollinator species were assigned a negative intrinsic growth rate (b_i), which assumed that the mutualism was obligate for pollinators. I evaluated different levels of mutualistic dependence of pollinators on plants by varying the intrinsic growth rate of pollinators. The intrinsic growth rate of pollinators was set as either –0.2, –0.4, or –0.8 wherein the lower (i.e., more negative) the intrinsic growth rate of pollinators, the higher the level of pollinator dependence on plants. Therefore, a lower intrinsic growth rate resulted in pollinators being more dependent on floral resources to maintain a positive population growth rate.

Adaptive foraging strategies

I implemented a contingency model of optimal foraging adapted from Beckerman et al. (2006) to determine the dynamic diet breadth of individual pollinator species (i.e., how many plant species each pollinator will visit). On each time step (i.e., every 100 iterations), each pollinator species evaluated the available plant species and switched its interaction partners based on profitability, assuming the most profitable plant species is always visited. Profitability was calculated as the rate of energy gain for pollinator i foraging on plant j based on the cost and the benefit to population growth contributed by each plant species:

$$P_{ij} = \frac{\gamma_{ij}}{h + C_{ij}} \quad [4]$$

For each pollinator, plant species were ranked in order of decreasing profitability. The model sets diet breadth for pollinator *i* as the number of plant species, taken in order of profitability (*k*), that maximizes the rate of energy intake (E_k):

$$E_k = \frac{\sum_{i=1}^{k} \gamma_{ij} N_i}{1 + \sum_{i=1}^{k} (h + C_{ij}) N_i} \quad [5]$$

After interaction switching occurred, the binary interaction matrix was updated, and competition values (C_{ij}) were recalculated to reflect the new interaction pairings. The visitation rate of each pollinator species to each plant species was calculated based on the population densities of extant pollinator species, the benefit that pollinator *i* receives from plant *j*, and the cost that pollinator *i* incurs by visiting plant *j*:

$$V_{ij} = v_{ij} M_i e^{(\gamma_{ij} - C_{ij})} \quad [6]$$

I used $e^{(\gamma_{ij} - C_{ij})}$ to ensure that the visitation rate is never less than 0 and prevent extremely small interaction frequencies when the cost outweighs the benefit.

I simulated pollinator foraging with and without interaction switching to evaluate how different adaptive foraging strategies impacts community stability and network topology. When interaction switching occurred, pollinators decided which plants to visit and how frequently to visit them according to three treatments. In the first switching treatment, pollinators decided which plants to visit using the contingency model of optimal foraging as previously described and therefore they evaluated both the cost and benefit associated with visiting each plant species when deciding which plants to switch to and how frequently to visit them. In the second treatment, pollinators focused solely on minimizing the cost associated with interspecific competition for each plant species while ignoring the mutualistic benefit when making foraging

decisions. Consequently, profitability was calculated as $P_{ij} = \frac{1}{h+C_{ij}}$ and the visitation rate was calculated as $V_{ij} = v_{ij}M_i e^{(-C_{ij})}$. The third treatment involved the pollinators focusing solely on maximizing the mutualistic benefit associated with visiting each plant species while ignoring the competitive cost, and thus profitability was calculated as $P_{ij} = \frac{\gamma_{ij}}{h}$ and the visitation rate was calculated as $V_{ij} = v_{ij}M_i e^{(\gamma_{ij})}$. As a control, no interaction switching occurred and therefore the binary interaction network remained the same throughout the model run. However, interaction frequencies were continually updated according to Eq. 6. As mentioned previously, I varied the intrinsic growth rate of pollinators (b_i) to evaluate different levels of pollinator dependence on plants. These growth rate treatments were nested within the switching treatments. Consequently, each local network replicate was run through the simulation 12 times, cycling through the four switching treatments and then through the three intrinsic growth rates for each of the switching treatments. At the end of each model run, pollinator community stability was quantified as species persistence, which was calculated as the fraction of initial species that survived to the end of a model run. Additionally, total pollinator abundance across all surviving species were calculated at the end of each model run.

Network analysis

I calculated four network metrics for the resulting quantitative networks—nestedness (Bascompte et al. 2003), network specialization (Blüthgen et al. 2006), modularity (Olesen et al. 2007), and connectance—at the start and the end of the simulation. I calculated nestedness as "Weighted Nestedness metric based on Overlap and Decreasing Fill" (WNODF) using the bipartite package v2.20 (Almeida-Neto and Ulrich 2011, Dormann et al. 2009) in R v4.4.2 (R Core Team 2024). Specialization (H_2') and connectance were also calculated using the bipartite

package. I calculated modularity based on Clauset et al.'s (2004) formulation using the igraph package v2.1.4 (Csardi and Nepusz 2006). This formulation implements the fast greedy module detection algorithm to find the network conformation that maximizes the value of modularity. Ending network metrics were calculated as the average of the metric values for the last four time steps. To determine if observed network topology was different than what would be expected due to random chance, I generated 1,000 null models using the "swsh_samp" method from the vegan package v2.6.10 (Oksanen et al. 2025). The "swsh_samp" method shuffles the original non-zero values over the entire matrix while preserving column and row frequencies. I calculated relative nestedness, specialization, and modularity by generating z-scores: $z = (x - \mu) / \sigma$, where x is the observed network metric, μ is the average network metric value of 1,000 null models, and σ is the standard deviation of 1,000 null models. I calculated z-scores using the quantitative networks from the last four time steps. These four z-scores were then averaged to compute an equilibria z-score.

Comparison to empirical networks

I compared the topology of simulated networks to empirical plant-pollinator networks to determine which switching treatment and level of mutualistic dependence resulted in the most realistic network topologies. I gathered visitation data from four empirical studies (Spiesman and Inouye 2013, Spiesman and Gratton 2016, Carstensen et al. 2017, Ch. 1) to compare network topology across different habitat types and species assemblages and thus assess the generality of the results. In all four studies, the authors quantified plant-pollinator interactions using a timed focal floral observation sampling protocol in which they observed forb species in flower for a period of time and collected and/or recorded any pollinators that visited each forb during the observation period. The authors performed these observations at several sites and then generated

one local interaction network per site. Visitation data from the local networks were then pooled to form a regional meta-network. Spiesman and Inouye (2013) performed monthly observations of plant-pollinator interactions at fifteen sites in the sandhills of northern Florida between June and September 2010. Spiesman and Gratton (2016) performed monthly observations of plant-pollinator interactions at ten sites in the grasslands of southern Wisconsin between June and August 2013. Carstensen et al. (2017) conducted observations at seven sites in the rupestrian grasslands in southeastern Brazil between October and December 2012. They sampled one site per day and rotated sites throughout the week (Carstensen et al. 2017). Lastly, I included observations of plant-pollinator interactions that I performed at 22 sites in the tallgrass prairie in northeastern Kansas between June and August 2024. I used visitation data from these studies to generate local quantitative plant-pollinator networks, in which interaction strength between each plant-pollinator pair was weighted by the visitation rate. I performed a null model analysis using the "swsh_samp" null model and calculated z-scores to compare relative network topology between empirical and simulated networks.

Results

Model runs typically equilibrated after 40 time steps (i.e., generations) and either reached dynamic equilibria characterized by bounded limit cycles with interaction switching (Figure 2.1A), or stable equilibria without interaction switching (Figure 2.1B). Pollinator persistence was typically greatest when pollinators did not switch interaction partners, suggesting that pollinator communities are more stable without adaptive foraging (Figure 2.2). However, pollinator abundance was typically lowest when pollinators did not switch partners (Figure 2.3). When interaction switching occurred, maximizing benefits typically resulted in greater pollinator persistence, particularly when pollinator dependence on plants was low or high and when

networks were small (Figure 2.2). Pollinator abundance was typically greatest when pollinators switched partners to maximize benefits (Figure 2.3). Switching partners to both minimize costs and maximize benefits resulted in the greatest pollinator persistence only at a moderate level of pollinator dependence on plants and medium network size (Figure 2.2). Switching partners to minimize costs often resulted in the most pollinator species going extinct (Figure 2.2).

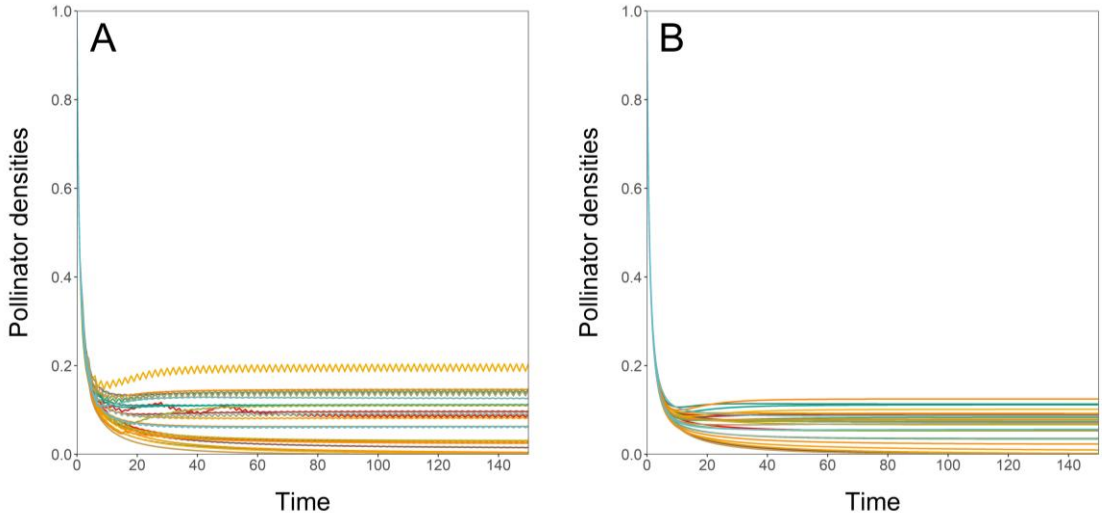

Figure 2.1. Example model runs showing pollinator community dynamics with (A) and without (B) interaction switching. Different colors represent different species population dynamics over 150 time steps.

Plant and pollinator persistence responded differently to network size, with greater plant persistence in small networks and greater pollinator persistence in large networks. Similarly, more pollinator species persisted when the level of mutualistic dependence of pollinators on plants was low whereas more plant species persisted when mutualistic dependence was high. Plant and pollinator abundance both increased with network size and with a lower dependence of pollinators on plants. Differences in pollinator abundance between switching treatments were

most pronounced at a low level of mutualistic dependence and when networks were larger (Figure 2.3).

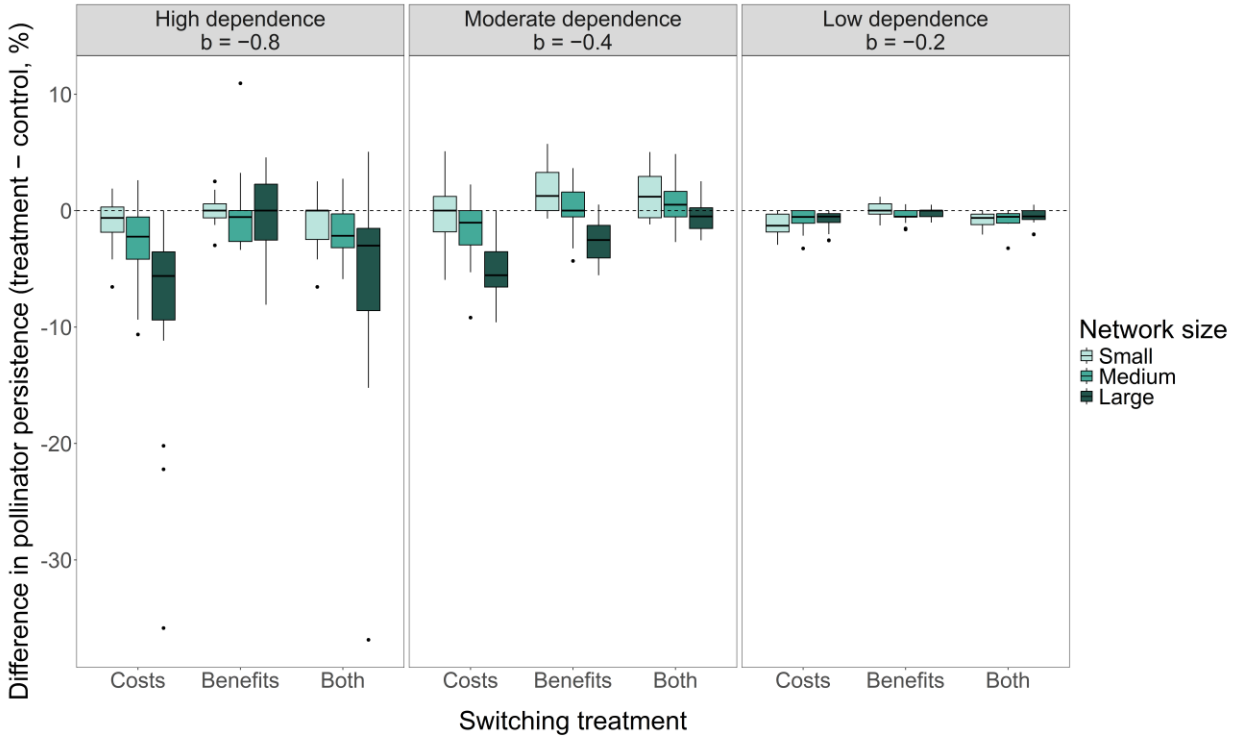

Figure 2.2. Difference in pollinator persistence (%) between the three switching treatments (minimizing costs, maximizing benefits, and both) and the no switching control across three levels of pollinator dependence on plants. Horizontal lines indicate the medians, boxes indicate the first and third quartiles, and error bars indicate the range. Box colors indicate network size (small, medium, or large).

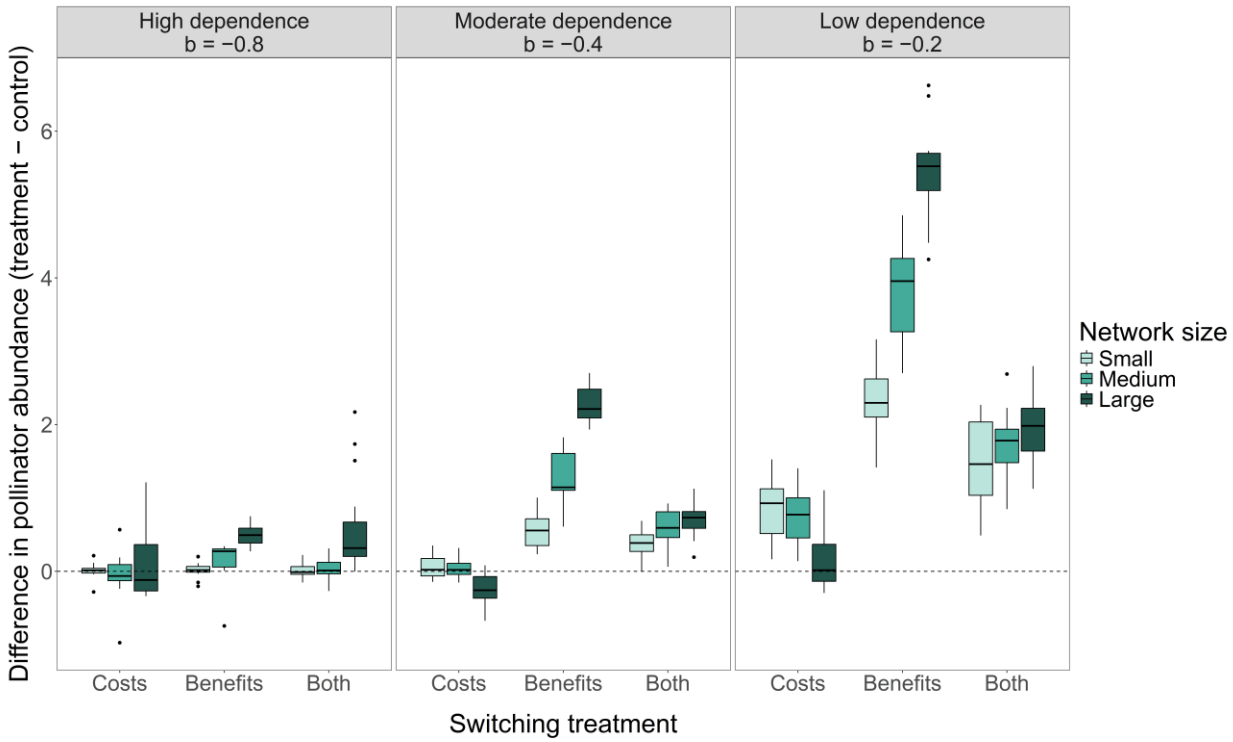

Figure 2.3. Difference in pollinator abundance between the three switching treatments (minimizing costs, maximizing benefits, and both) and the no switching control across three levels of pollinator dependence on plants. Horizontal lines indicate the medians, boxes indicate the first and third quartiles, and error bars indicate the range. Box colors indicate network size (small, medium, or large).

Most networks were significantly less nested (Figure 2.4A) and more specialized/modular (Figure 2.4B–C) than expected by chance. Networks were the most modular when pollinators switched partners to minimize costs, especially at larger network sizes (Figure 2.4C). Across all switching treatments, networks generally became less nested (Figure 2.5A), more specialized (Figure 2.5B), and more modular (Figure 2.5C) over the course of the model runs. Connectance was greater without interaction switching (Figure B.1). Switching based on minimizing competitive costs typically resulted in more modular networks than expected by chance (Figure 2.4C). Relative network specialization increased with network size (Figure 2.4B).

High levels of mutualistic dependence of pollinators on plants resulted in more connected networks (Figure B.1). These networks also became more connected over the course of the model runs (Figure B.2).

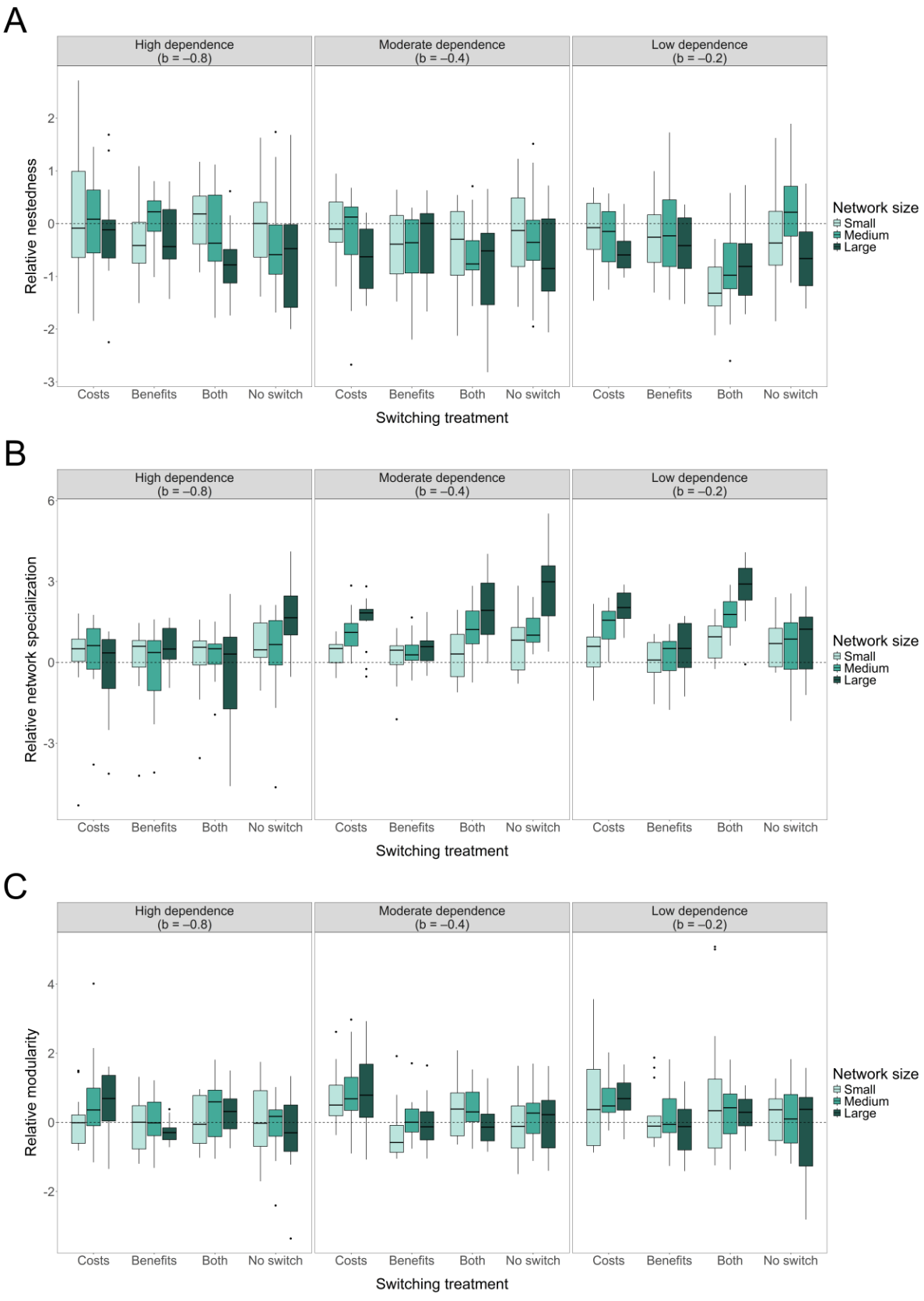
A
High dependence (b = –0.8)
Moderate dependence (b = –0.4)
Low dependence (b = –0.2)
Relative nestedness
2
1
0
-1
-2
-3
Costs
Benefits
Both
No switch
Switching treatment
Network size
Small
Medium
Large
B
Relative network specialization
6
3
0
-3
C
Relative modularity
4
2
0
-2

Figure 2.4. Relative nestedness (A), network specialization (B), and modularity (C) across the three switching treatments (minimizing costs, maximizing benefits, and both) and the no switching control and the three levels of pollinator dependence on plants. Horizontal lines indicate the medians, boxes indicate the first and third quartiles, and error bars indicate the range. Box colors indicate network size (small, medium, or large).

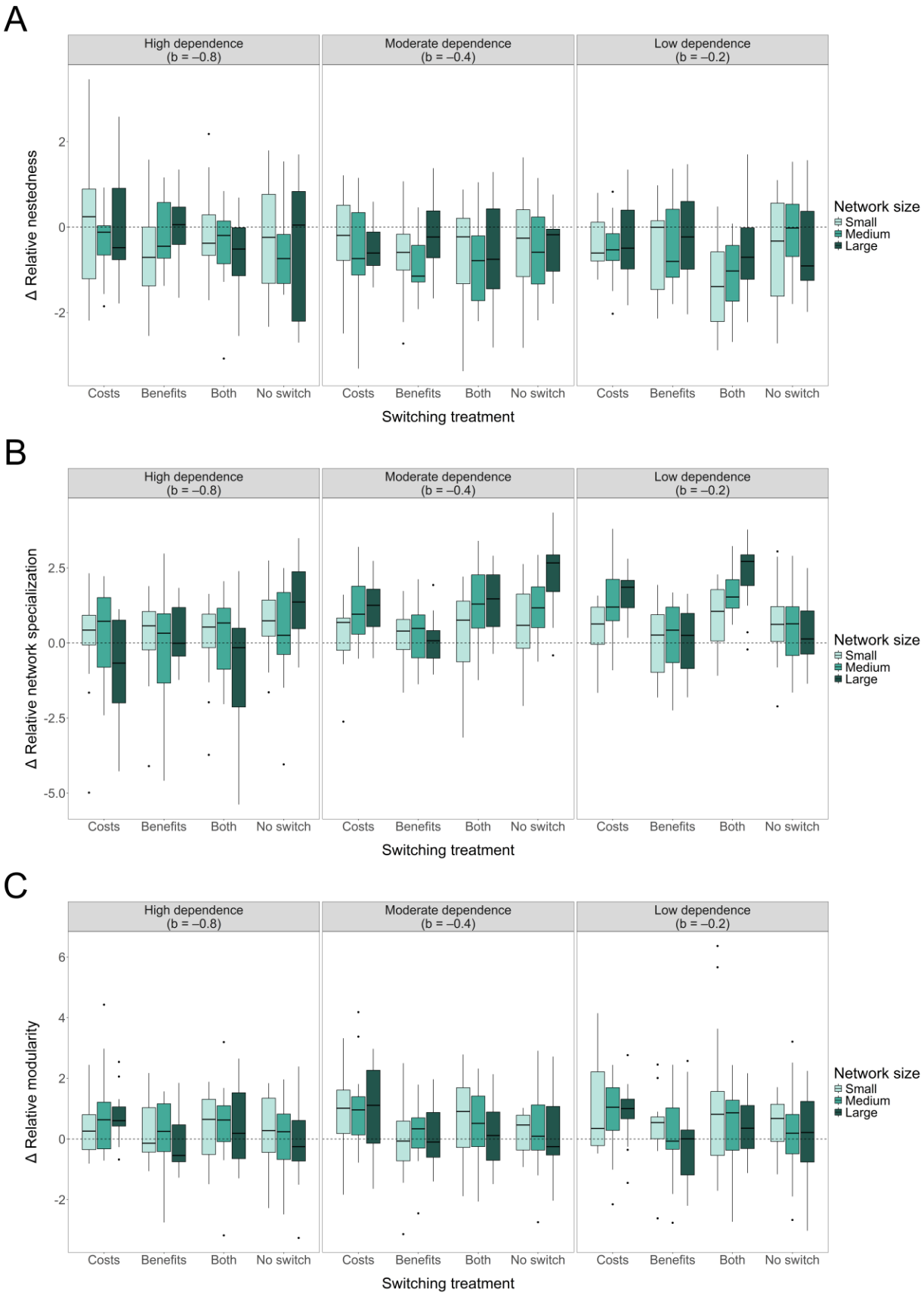
A
High dependence (b = –0.8)
Moderate dependence (b = –0.4)
Low dependence (b = –0.2)
Δ Relative nestedness
2
0
-2
Costs
Benefits
Both
No switch
Switching treatment
Network size
Small
Medium
Large
B
Δ Relative network specialization
2.5
0.0
-2.5
-5.0
C
Δ Relative modularity
6
4
2

Figure 2.5. Change in relative nestedness (A), network specialization (B), and modularity (C) from the start to the end of the model runs across the three switching treatments (minimizing costs, maximizing benefits, and both) and the no switching control and the three levels of pollinator dependence on plants. Horizontal lines indicate the medians, boxes indicate the first and third quartiles, and error bars indicate the range. Box colors indicate network size (small, medium, or large).

Empirical networks and simulated networks were similar in their relative modularity relative to pollinator richness (Figure 2.6B) whereas empirical networks were generally more nested (Figure 2.6A) and less specialized (Figure 2.6C) than simulated networks across a range of pollinator richness values. Generally, simulated networks aligned most with the empirical networks from Kansas (Ch. 1) and Florida (Spiesman and Gratton 2016) across all three network metrics. Simulated networks were less nested (Figure 2.6A), less modular (Figure 2.6B), and more specialized (Figure 2.6C) than empirical networks from Brazil (Carstensen et al. 2017) and Wisconsin (Spiesman and Gratton 2016). Empirical networks aligned better with simulated networks in which pollinator dependence on plants was high and this result occurred regardless of starting network size (Figure B.3). Among the empirical networks, there was a negative relationship between pollinator richness and relative network specialization (Figure 2.6C). However, there was a positive relationship between pollinator richness and relative nestedness (Figure 2.6A), and between richness and relative modularity (Figure 2.6B).

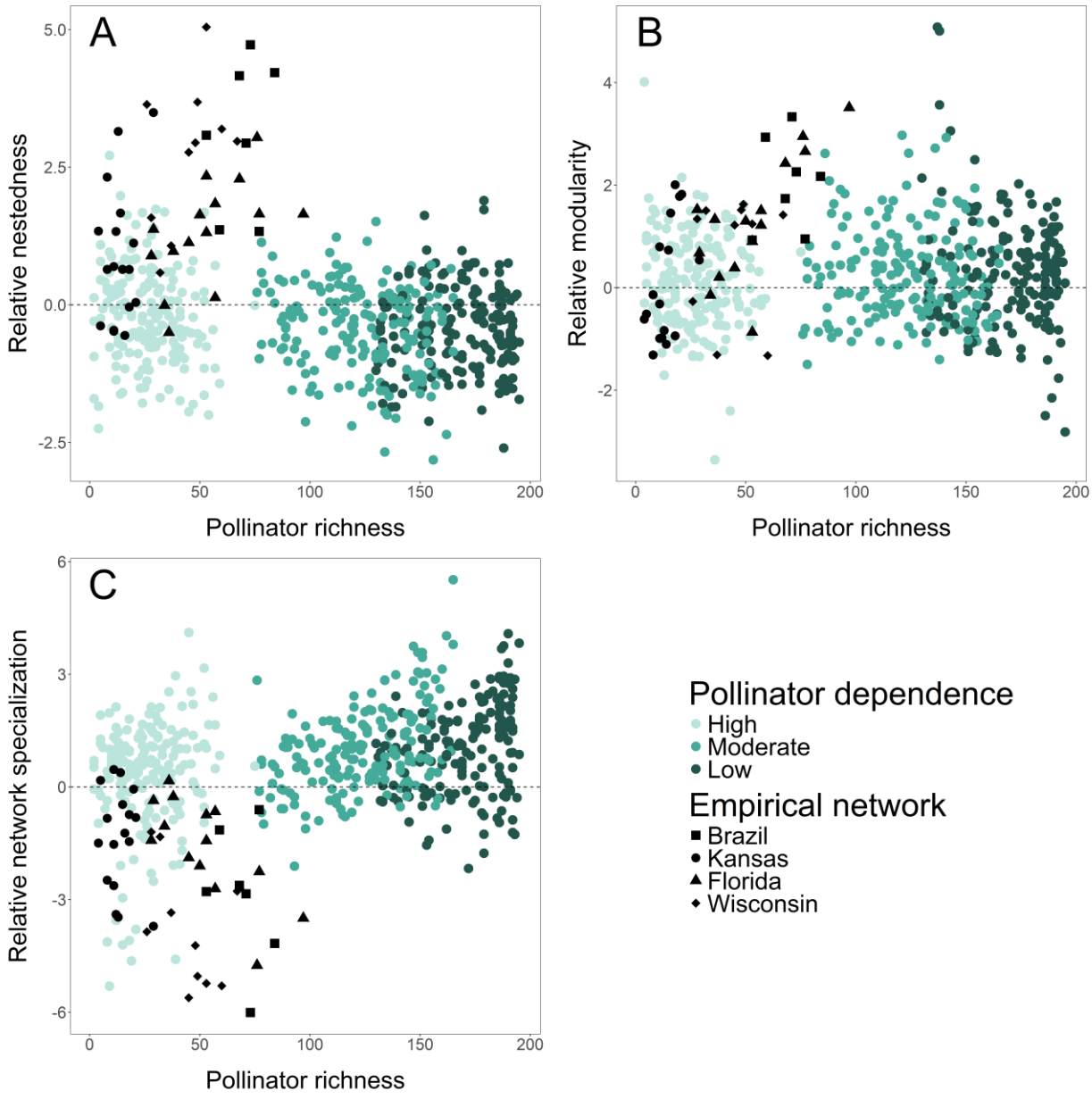

Figure 2.6. Relationship between pollinator richness and relative nestedness (A), modularity (B), and network specialization (C) of empirical networks (black) compared to simulated networks (green). The shape of the empirical network points represents the study from which the data were acquired. The color of simulated network points represents the level of pollinator dependence on plants. Empirical networks have the most overlap with simulated networks in which pollinators are highly dependent on plants for survival.

Discussion

In replicate model runs, pollinator communities typically exhibited the greatest species persistence at low population densities when pollinators did not switch interaction partners whereas interaction switching resulted in higher pollinator population densities. In this model, pollinators were at risk of extinction if they had too few interaction partners and thus could not receive sufficient mutualistic benefits to maintain a positive population growth rate, or if they incurred high costs from competing with other species for floral resources that outweighed the benefits gained from those resources. For competitive exclusion to occur, competitors must have sufficiently large populations that they are able to exert a meaningful competitive effect on other species. Without adaptive foraging, interspecific competition kept pollinator populations at lower densities, but not so low as to result in competitive exclusion. Consequently, fewer pollinator species went extinct when they did not switch interaction partners and thus these communities were more stable due to the maintenance of a greater diversity of coexisting species over time (Valdovinos et al. 2019). However, when pollinators were allowed to switch partners, their populations grew large enough that weak competitors were competitively excluded and thus were driven to extinction. Furthermore, this suggests that adaptive foraging may be beneficial for maximizing total pollinator biomass.

These results differ from the conclusions of many studies that have found interaction switching and rewiring to confer community stability (Beckerman et al. 2006, Kaiser-Bunbury et al. 2010, Zhang et al. 2011, Ramos-Jiliberto et al. 2012, Valdovinos et al. 2013, Valdovinos et al. 2016). Interaction switching has been found to result in a nested network architecture (Zhang et al. 2011), which may enhance the number of coexisting species (Bastolla et al. 2009). Additionally, there is evidence that interaction rewiring can enhance network robustness after

species go extinct (Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012). Adaptive foraging has also been found to increase the persistence and diversity of species by promoting niche partitioning among species within guilds and reversing the destabilizing effects of nested network topology (Valdovinos et al. 2013, Valdovinos et al. 2016). In this model, more pollinator species were able to persist despite their inability to partition niches through adaptive foraging because the costs incurred by competition with other species were not often large enough to negatively impact species' population growth rates.

Foraging decisions that balanced benefits and costs resulted in more stable communities in medium-sized networks with a moderate level of pollinator dependence on plants. This could highlight a scenario in which adapting to both mutualism and competition is beneficial. As network size increases, pollinators have access to more plant species from which they could obtain floral resources, but they also encounter more competitors with which to compete for those resources. Therefore, it may be advantageous for pollinators to balance benefits and costs when there is a moderate number of floral resources and competitors. This adaptive foraging strategy may be particularly advantageous when pollinators are moderately dependent on plants. At low dependence levels, pollinators may be less concerned with balancing benefits and costs because they can maintain positive population growth rates more easily. Similarly, at high dependence levels, pollinators may need to focus on gaining mutualistic benefits to offset the low intrinsic growth rate and maintain a positive population growth rate.

When adaptive foraging did occur, it was more advantageous for pollinators to prioritize pursuing more abundant or higher quality floral resources than avoiding competition with other species for those resources. We may expect pollinators to visit more plant species when maximizing benefits. In fact, there is some evidence that the number of mutualistic partners a

species has is a strong predictor of community persistence (James et al. 2012). However, this contingency model of optimal foraging limited the number of plant species a pollinator visited based on the energy required to visit each additional species. The three adaptive foraging strategies differed in how they calculate plant profitability and subsequently rank plant species. Regardless of the adaptive foraging strategy being used, pollinator diet breadth was determined by maximizing the rate of energy intake, which considers mutualistic benefits and costs associated with competition and handling. Consequently, pollinators may not have incurred large costs when they focused on maximizing benefits, meaning this strategy was less costly than expected.

In large networks there were more plant species from which pollinators could obtain floral resources, resulting in more stable pollinator communities. On the other hand, in small networks there were fewer pollinator species from which plants could obtain mutualistic benefits. With less mutualistic benefits to boost population growth, plants were more at risk of being competitively excluded by other species, resulting in less stable plant communities at smaller network sizes. When pollinators had a higher intrinsic growth rate and thus were less dependent on benefits received from plants, they were able to maintain larger populations and thus plants received greater mutualistic benefits from pollinators, resulting in larger plant populations.

Without interaction switching, networks became more connected and more specialized through time. Connectance is known to increase as species richness decreases whereas specialization is expected to increase as species richness increases for there are more niches available to allow for greater niche partitioning and more competitors present to drive niche partitioning. However, in this model the increase in connectance and specialization likely

resulted from species extinctions, which resulted in fewer potential links in the networks, rather than from lack of interaction switching itself. Minimizing costs resulted in more modular networks, likely because species were partitioning resources to reduce competition. This was particularly true at large network sizes when competition for resources was stronger. Networks may have become less nested and more specialized across all switching treatments because species were focusing their foraging efforts, whether that be to maximize benefits, minimize costs, or balance benefits and costs, regardless of the specific foraging strategy. Consequently, switching for benefits and/or costs did not result in large differences in network topology. We could expect to see greater differences in network topology when comparing directed switching to random switching and thus future efforts should include random switching to determine the impact of switching per se on community stability and network topology.

Empirical networks aligned best with simulated networks in which pollinators were highly dependent on plants for survival, which may indicate that pollinators are highly dependent on floral resources for survival in natural systems. This result occurred regardless of starting network size. It is surprising that the empirical networks showed a negative relationship between pollinator richness and relative network specialization, and a positive relationship between richness and relative nestedness. Using a different null model, Spiesman and Gratton (2016) found that the degree of complementary specialization increased with the number of competing pollinator species. However, in accordance with the findings of Spiesman and Gratton (2016) there was a positive relationship between pollinator richness and relative modularity. This may indicate that the selected null model, "swsh_samp", may be complicating the relationship between diversity and network topology.

In this model, all pollinator species within the community had the same mutualistic dependence on plants. However, pollinator species likely differ in their dependence on floral resources, particularly when considering different life stages. For example, most bees rely on floral resources for both adult and larval food, whereas syrphid flies and other flies only use floral resources as adults (Potts et al. 2003, Raguso et al. 2020). Even bee species differ in their dependence on plants for resources (Potts et al. 2003). Different levels of mutualistic dependence could impact species' extinction probabilities following the extirpation of an interaction partner (Vanbergen et al. 2017). It is likely that species have unique critical thresholds to allow population growth and may experience extinction below such thresholds (Valdovinos and Marsland 2021). As a result, we could expect to see more pronounced differences in community stability between adaptive foraging strategies if pollinator species differ not only in the competitive ability but also in their dependence on floral resources. Theory suggests asymmetric mutualistic dependence is common in mutualistic networks wherein one interaction partner is more dependent on the other (Bascompte et al. 2006). In this simulation, pollinators are obligate mutualists whereas plants are facultative mutualists. Future work could explore how obligate mutualism in plants impacts community stability and network topology.

There are several alterations that could be made to this simulation model to improve how realistically it captures the ecological dynamics between plants and pollinators. Plant and pollinator population growth rates were calculated according to the binary interaction matrix and thus did not account for the visitation rate of pollinator and plant species. Considering that interaction frequencies were calculated using pollinator population densities, which were notably lower without interaction switching, I could expect to see a different result with regards to community stability if interaction frequencies were incorporated into the calculation of

population growth rate. Additionally, evaluating relative network metrics using different null models may clear up relationship between diversity and network topology. Future work could also explore how the average degree of individual specialization (*d'*) changes over time to determine if specialists or generalists are going extinct, and if this differs according to the adaptive foraging strategy.

Conclusion

Without adaptive foraging, interspecific competition kept pollinator populations at lower densities, but not so low as to result in competitive exclusion. Consequently, more species persisted over time and thus these communities were more stable. However, when pollinators were allowed to switch partners, their populations grew large enough that weak competitors were competitively excluded and driven to extinction. When adaptive foraging did occur, it was more advantageous for pollinators to prioritize pursuing more abundant/higher quality floral resources. Comparisons between empirical and simulated networks indicated that pollinators are highly dependent on floral resources for survival in natural systems, suggesting that niche partitioning is important for species persistence. These findings demonstrate that adaptive foraging behavior has important implications for the persistence and abundance of pollinator species in plant-pollinator communities.

Conclusion

Using empirical and simulated approaches, I found that the abundance, diversity, and stability of pollinator communities are impacted by local- and landscape-habitat characteristics as well as the adaptive foraging behavior that occurs in response to resource availability and interspecific competition for resources. For my first objective, I evaluated the effectiveness of different CRP planting types in supporting pollinator communities and investigated how local- and landscape-scale habitat characteristics influence the effectiveness of CRP plantings. Although pollinator community composition differed significantly across CRP planting types, pollinator abundance and diversity were more influenced by site-specific habitat features than the specific planting type. Consequently, local management by prescribed fire and/or grazing may be needed to see the benefits of more diverse, expensive CRP seed mixes. The positive conditional effect of forb richness suggests that more diverse, expensive seed mixes can support pollinator communities, but their effectiveness depends on the quality of the landscape. Therefore, conservation practitioners should consider the interactive dynamic between local and landscape resource availability when deciding where to establish conservation plantings to maximize their effectiveness in supporting pollinator communities. Moreover, it is important to provide diverse resources for pollinators to promote species coexistence, for community structure is greatly influenced by niche partitioning in response to the abundance of competitors and the diversity of floral resources.

For my second objective, I used a plant-pollinator network simulation model to examine how different adaptive foraging strategies based on maximizing mutualistic benefits and/or minimizing competitive costs impacts community stability and the resulting network topology. Without adaptive foraging, interspecific competition kept pollinator populations at lower

densities, but not so low as to result in competitive exclusion. As a result, more species persisted over time and thus these communities were more stable. However, it was more advantageous for pollinators to prioritize pursuing more abundant/higher quality floral resources when adaptive foraging did occur. Pollinators seemed to be highly dependent on floral resources for survival in natural systems, which suggests that niche partitioning is important for species persistence.

Overall, these findings indicate that the interactive relationship between local and landscape habitat and adaptive foraging behavior in response to resource availability and interspecific competition have important consequences for community stability and biodiversity. Therefore, it is important to provide diverse resources at different spatial scales so pollinators can partition niches in response to competition, thereby promoting greater biodiversity and community stability.

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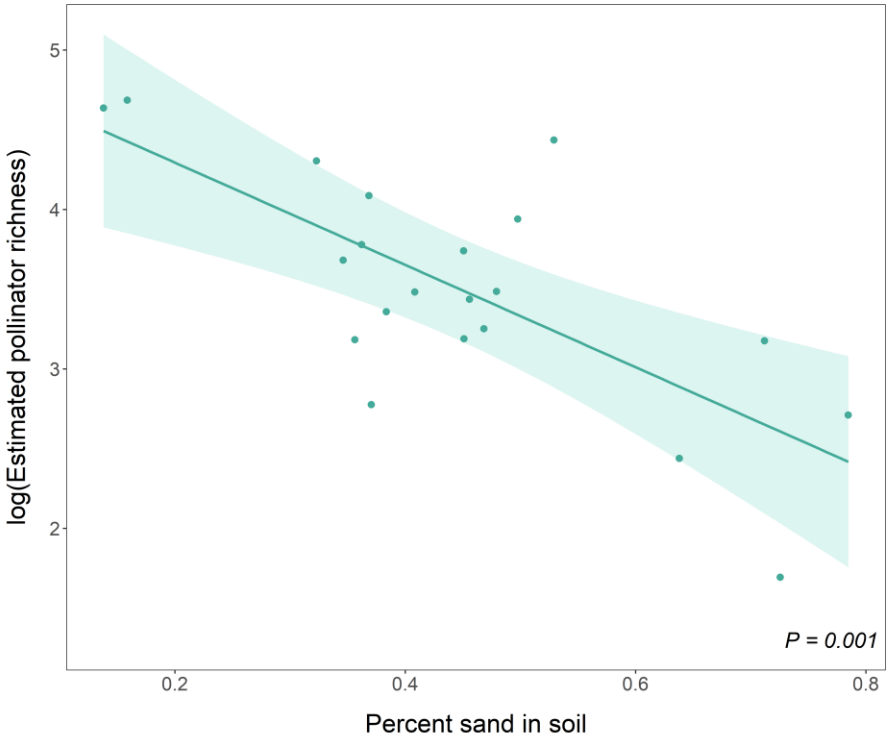
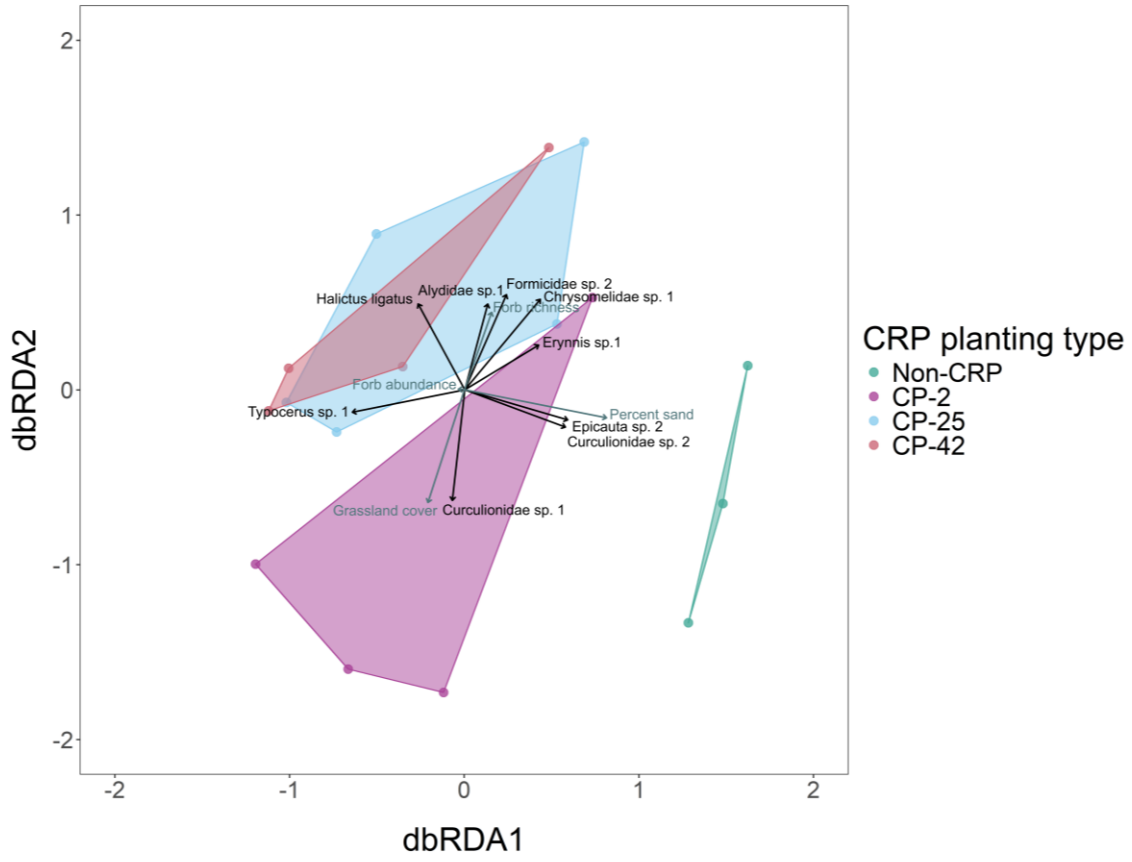
Appendix A - Chapter 1 Supplemental Material

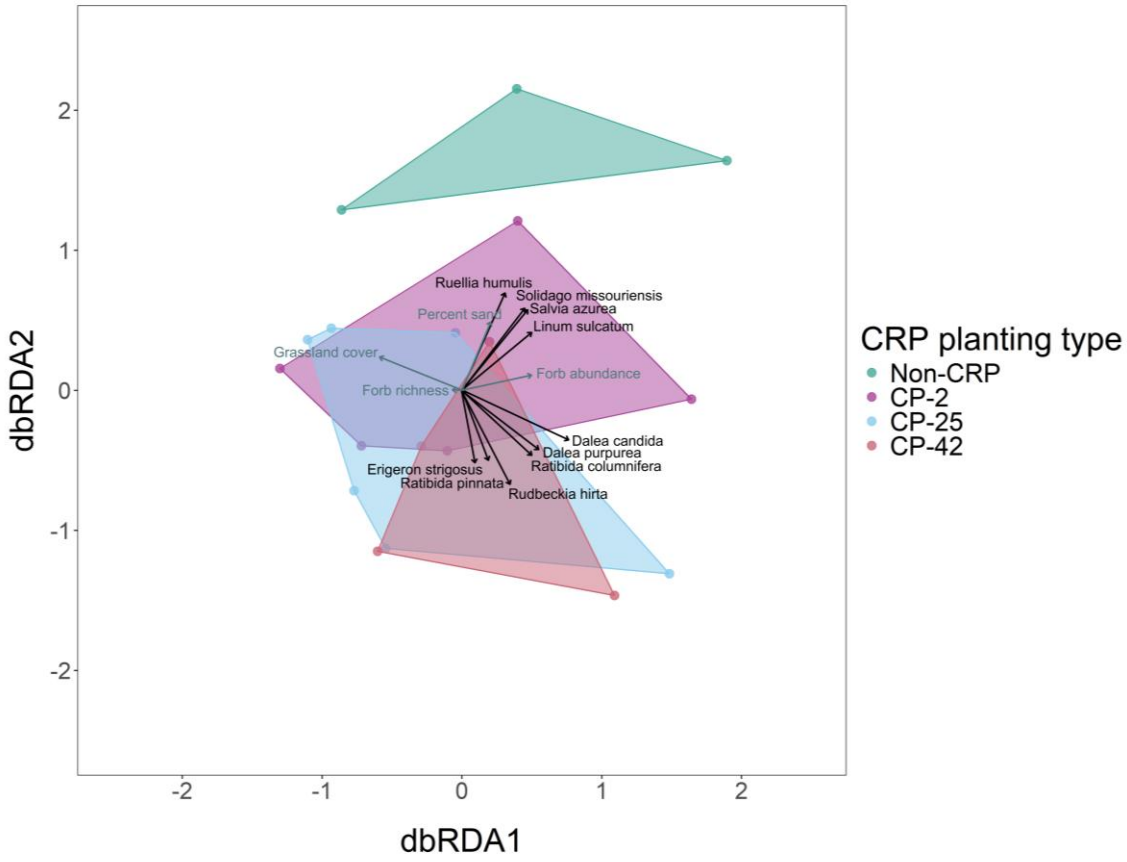
Appendix Figure A.1. Partial residuals plots showing the effects of the percentage of sand in the soil on estimated pollinator richness.



Appendix Figure A.2. Distance-based redundancy analysis biplot for species-level pollinator community data. Hull color represents CRP planting type. Black vectors represent significant species scores ($P \leq 0.05$). Green vectors represent habitat variables.



Appendix Figure A.3. Distance-based redundancy analysis for forb community data. Hull color represents CRP planting type. Black vectors represent significant species scores ($P \leq 0.05$). Green vectors represent habitat variables.



Appendix Table A.1. Results of the distance-based redundancy analysis with species-level pollinator community data. Significant *P* values are shown in boldface type.

Predictor	SS	*F*	df	*P*
Forb abundance	0.348	1.088	1	0.356
Forb richness	0.501	1.565	1	0.080
Grassland cover	0.462	1.443	1	0.117
Percent sand	0.461	1.438	1	0.118
CRP planting type	1.680	1.749	3	**0.002**

Appendix Table A.2. Results of the distance-based redundancy analysis with taxonomic group-level pollinator community data. Significant *P* values are shown in boldface type.

Predictor	SS	*F*	df	*P*
Forb abundance	0.063	0.567	1	0.815
Forb richness	0.525	4.698	1	**0.001**
Grassland cover	0.143	1.280	1	0.249
Percent sand	0.218	1.954	1	0.073
CRP planting type	0.543	1.621	3	**0.049**

Appendix Table A.3. Results of the distance-based redundancy analysis with species-level forb community data. Significant *P* values are shown in boldface type.

Predictor	SS	*F*	df	*P*
Forb abundance	0.453	1.040	1	0.414
Forb richness	0.434	0.995	1	0.496
Grassland cover	0.550	1.262	1	0.162
Percent sand	0.271	0.623	1	0.935
CRP planting type	1.680	1.749	3	0.723

Appendix Table A.4. Bee species and their nesting guild classifications.

Family	Genus	Species	Nesting guild
Andrenidae	*Andrena*	*rudbeckiae*	Belowground
Andrenidae	*Perdita*	*ignota*	Belowground
Andrenidae	*Protoandrena*	*bancroffi*	Belowground
Andrenidae	*Protoandrena*	*cockerelli*	Belowground
Apidae	*Apis*	*mellifera*	Aboveground
Apidae	*Bombus*	*bimaculatus*	Belowground
Apidae	*Bombus*	*fraternus*	Belowground
Apidae	*Bombus*	*griseocollis*	Belowground
Apidae	*Bombus*	*impatiens*	Belowground
Apidae	*Bombus*	*pensylvanicus*	Aboveground
Apidae	*Diadasia*	*enavata*	Belowground
Apidae	*Melissodes*	*bimaculatus*	Belowground
Apidae	*Melissodes*	*communis*	Belowground
Apidae	*Melissodes*	*comptoides*	Belowground
Apidae	*Melissodes*	*denticulatus*	Belowground
Apidae	*Nomada*	*texana*	Kleptoparasite
Apidae	*Trieopeolus*	*lunatus*	Kleptoparasite
Apidae	*Xylocopa*	*virginica*	Aboveground
Colletidae	*Colletes*	*robertsonii*	Belowground
Colletidae	*Hylaeus*	*affinis*	Aboveground
Colletidae	*Hylaeus*	*mesillae* group	Aboveground
Halictidae	*Agapostemon*	*texanus*	Belowground
Halictidae	*Agapostemon*	*virescens*	Belowground
Halictidae	*Augochlorella*	*aurata*	Belowground
Halictidae	*Augochlorella*	*persimilis*	Belowground
Halictidae	*Augochloropsis*	*metallica*	Belowground
Halictidae	*Halictus*	*ligatus*	Belowground
Halictidae	*Halictus*	*parallelus*	Belowground
Halictidae	*Halictus*	*rubicundus*	Belowground
Halictidae	*Lasioglossum*	*callidum*	Belowground
Halictidae	*Lasioglossum*	*cressonii*	Belowground
Halictidae	*Lasioglossum*	*disparile*	Belowground
Halictidae	*Lasioglossum*	*ellisiae*	Belowground
Halictidae	*Lasioglossum*	*hitchensi*	Belowground
Halictidae	*Lasioglossum*	*imitatum*	Belowground
Halictidae	*Lasioglossum*	*tegulare*	Belowground
Halictidae	*Lasioglossum*	*trigeminum*	Belowground
Megachilidae	*Coelioxys*	*octodentatus*	Kleptoparasite
Megachilidae	*Heriades*	*variolosa*	Aboveground

Megachilidae	*Megachile*	*brevis*	Belowground
Megachilidae	*Megachile*	*petulans*	Belowground

Appendix Table A.5. Pollinator species and morphospecies and their total abundance across all sites.

Order	Family	Genus	Species	Abundance
Coleoptera	Buprestidae	*Acmaeodera*	sp. 1	4
Coleoptera	Cantharidae	*Belotus*	sp. 1	8
Coleoptera	Cantharidae	*Chauliognathus*	sp. 1	26
Coleoptera	Carabidae	*Agonum*	*extensicolle*	1
Coleoptera	Cerambycidae	*Dectes*	sp. 1	1
Coleoptera	Cerambycidae	*Tetraopes*	sp. 1	2
Coleoptera	Cerambycidae	*Typocerus*	sp. 1	7
Coleoptera	Chrysomelidae	*Anomoea*	sp. 1	1
Coleoptera	Chrysomelidae		sp. 1	1
Coleoptera	Chrysomelidae		sp. 2	10
Coleoptera	Chrysomelidae	*Chrysochus*	*auratus*	1
Coleoptera	Chrysomelidae		sp. 3	47
Coleoptera	Chrysomelidae	*Diabrotica*	sp. 1	5
Coleoptera	Chrysomelidae	*Diabrotica*	sp. 2	5
Coleoptera	Chrysomelidae	*Diabrotica*	sp. 3	1
Coleoptera	Chrysomelidae	*Diachus*	sp. 1	1
Coleoptera	Chrysomelidae	*Glyptina*	sp. 1	5
Coleoptera	Coccinellidae	*Cycloneda*	sp. 1	1
Coleoptera	Curculionidae		sp. 1	4
Coleoptera	Curculionidae		sp. 2	9
Coleoptera	Curculionidae		sp. 3	3
Coleoptera	Curculionidae		sp. 4	1
Coleoptera	Curculionidae		sp. 5	2
Coleoptera	Curculionidae		sp. 6	1
Coleoptera	Curculionidae		sp. 7	1
Coleoptera	Curculionidae		sp. 8	1
Coleoptera	Curculionidae		sp. 9	1
Coleoptera	Curculionidae	*Gymnetron*	sp. 1	2
Coleoptera	Dermestidae	*Cryptorhopalum*	sp. 1	11
Coleoptera	Meloidae	*Epicauta*	sp. 1	1
Coleoptera	Meloidae	*Epicauta*	sp. 2	2
Coleoptera	Scarabaeidae	*Popillia*	*japonica*	8

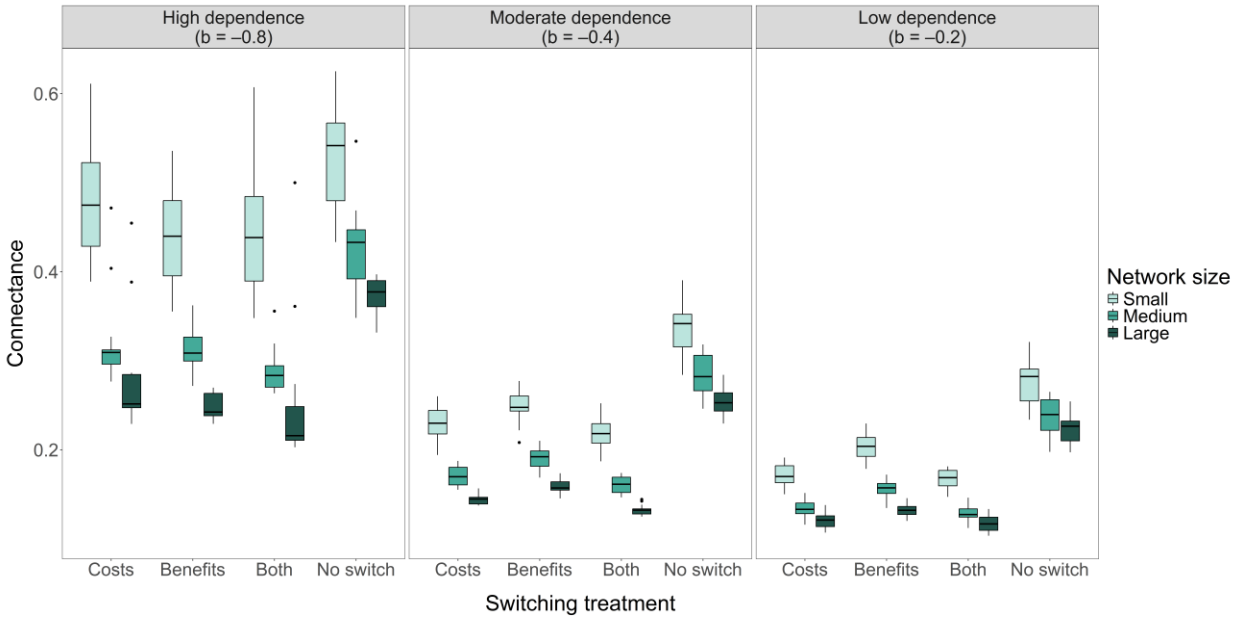
Coleoptera	Scarabaeidae	*Trichiotinus*	sp. 1	1
Coleoptera	Tenebrionidae	*Isomira*	sp. 1	1
Diptera	Asilidae		sp. 1	1
Diptera	Bombyliidae	*Exoprosopa*	*meigenii*	1
Diptera	Bombyliidae	*Hemipenthes*	*sinuosa*	2
Diptera	Conopidae		sp. 1	2
Diptera	Muscidae	*Neomyia*	*cornicina*	1
Diptera	Muscidae		sp. 1	1
Diptera	Nemestrinidae	*Neorhynchocephalus*	*volaticus*	3
Diptera	Sarcophagidae		sp. 1	1
Diptera	Scathophagidae		sp. 1	1
Diptera	Sciaridae		sp. 1	1
Diptera	Sciaridae		sp. 2	2
Diptera	Syrphidae	*Eristalis*	*stipator*	4
Diptera	Syrphidae	*Paragus*	*haemorrhous*	3
Diptera	Syrphidae	*Sphaerophoria*	sp. 1	1
Diptera	Syrphidae	*Toxomerus*	*marginatus*	29
Diptera	Tachinidae		sp. 1	2
Diptera	Tachinidae		sp. 2	2
Diptera	Tachinidae		sp. 3	1
Diptera	Tephritidae		sp. 1	1
Diptera	Tephritidae		sp. 2	1
Diptera	Tipulidae		sp. 1	1
Diptera	Ulidiidae		sp. 1	1
Hemiptera	Alydidae		sp. 1	6
Hemiptera	Cicadellidae		sp. 1	1
Hemiptera	Cixiidae		sp. 1	2
Hemiptera	Lygaeidae		sp. 1	1
Hemiptera	Lygaeidae		sp. 2	1
Hemiptera	Membracidae		sp. 1	1
Hemiptera	Miridae		sp. 1	3
Hemiptera	Miridae		sp. 2	1
Hemiptera	Nabidae		sp. 1	2
Hemiptera	Pentatomidae		sp. 1	4
Hemiptera	Reduviidae		sp. 1	1
Hemiptera	Reduviidae		sp. 2	1
Hemiptera	Thyreocordiae		sp. 1	1
Hymenoptera	Andrenidae	*Andrena*	*rudbeckiae*	1
Hymenoptera	Andrenidae	*Perdita*	*ignota*	1
Hymenoptera	Andrenidae	*Protoandrena*	*bancroffi*	1
Hymenoptera	Andrenidae	*Protoandrena*	*cockerelli*	1
Hymenoptera	Apidae	*Apis*	*mellifera*	19
Hymenoptera	Apidae	*Bombus*	*bimaculatus*	1

Hymenoptera	Apidae	*Bombus*	*fraternus*	1
Hymenoptera	Apidae	*Bombus*	*griseocollis*	1
Hymenoptera	Apidae	*Bombus*	*impatiens*	2
Hymenoptera	Apidae	*Bombus*	*pensylvanicus*	1
Hymenoptera	Apidae	*Diadasia*	*enavata*	3
Hymenoptera	Apidae	*Melissodes*	*bimaculatus*	1
Hymenoptera	Apidae	*Melissodes*	*communis*	1
Hymenoptera	Apidae	*Melissodes*	*comptoides*	3
Hymenoptera	Apidae	*Melissodes*	*denticulatus*	1
Hymenoptera	Apidae	*Nomada*	*texana*	1
Hymenoptera	Apidae	*Trieopeolus*	*lunatus*	1
Hymenoptera	Apidae	*Xylocopa*	*virginica*	4
Hymenoptera	Braconidae		sp. 1	1
Hymenoptera	Braconidae		sp. 2	1
Hymenoptera	Braconidae		sp. 3	1
Hymenoptera	Colletidae	*Colletes*	*robertsonii*	4
Hymenoptera	Colletidae	*Hylaeus*	*affinis*	1
Hymenoptera	Colletidae	*Hylaeus*	*mesillae* group	1
Hymenoptera	Crabronidae		sp. 1	1
Hymenoptera	Crabronidae		sp. 2	1
Hymenoptera	Formicidae		sp. 1	2
Hymenoptera	Formicidae		sp. 2	4
Hymenoptera	Formicidae		sp. 3	5
Hymenoptera	Formicidae		sp. 4	1
Hymenoptera	Halictidae	*Agapostemon*	*texanus*	1
Hymenoptera	Halictidae	*Agapostemon*	*virescens*	4
Hymenoptera	Halictidae	*Augochlorella*	*aurata*	40
Hymenoptera	Halictidae	*Augochlorella*	*persimilis*	18
Hymenoptera	Halictidae	*Augochloropsis*	*metallica*	2
Hymenoptera	Halictidae	*Halictus*	*ligatus*	14
Hymenoptera	Halictidae	*Halictus*	*parallelus*	1
Hymenoptera	Halictidae	*Halictus*	*rubicundus*	2
Hymenoptera	Halictidae	*Lasioglossum*	*callidum*	1
Hymenoptera	Halictidae	*Lasioglossum*	*cressonii*	1
Hymenoptera	Halictidae	*Lasioglossum*	*disparile*	4
Hymenoptera	Halictidae	*Lasioglossum*	*ellisiae*	1
Hymenoptera	Halictidae	*Lasioglossum*	*hitchensi*	3
Hymenoptera	Halictidae	*Lasioglossum*	*imitatum*	3
Hymenoptera	Halictidae	*Lasioglossum*	*tegulare*	3
Hymenoptera	Halictidae	*Lasioglossum*	*trigeminum*	2
Hymenoptera	Megachilidae	*Coelioxys*	*octodentatus*	1
Hymenoptera	Megachilidae	*Heriades*	*variolosa*	1
Hymenoptera	Megachilidae	*Megachile*	*brevis*	1

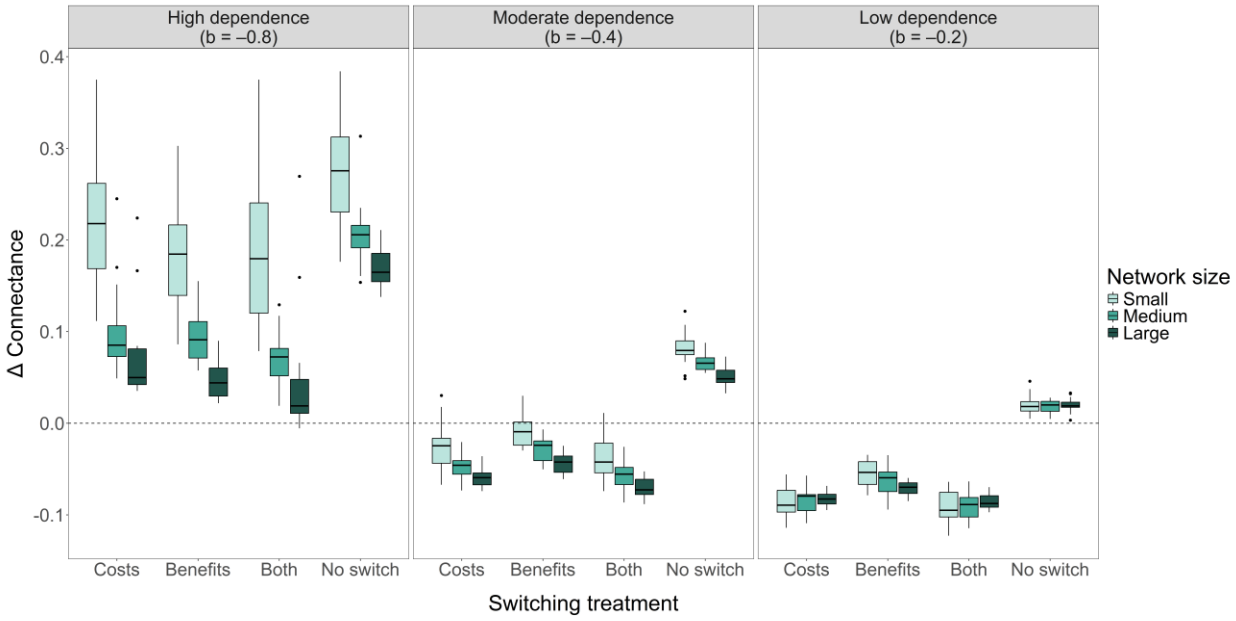
Hymenoptera	Megachilidae	*Megachile*	*petulans*	1
Hymenoptera	Pteromalidae		sp. 1	1
Hymenoptera	Rhopalosomatidae		sp. 1	1
Hymenoptera	Sphecidae		sp. 1	2
Hymenoptera	Sphecidae		sp. 2	1
Hymenoptera	Thynnidae		sp. 1	2
Hymenoptera	Vespidae		sp. 1	2
Hymenoptera	Vespidae		sp. 2	1
Hymenoptera	Vespidae		sp. 3	1
Lepidoptera			sp. 1	1
Lepidoptera	Hesperiidae	*Atalopedes*	*campestris*	3
Lepidoptera	Hesperiidae	*Epargyreus*	*clarus*	1
Lepidoptera	Hesperiidae	*Hylephila*	*phyleus*	1
Lepidoptera	Hesperiidae	*Pyrgus*	*communis*	1
Lepidoptera	Hesperiidae	*Erynnis*	sp. 1	1
Lepidoptera	Lycaenidae	*Cupido*	*comyntas*	4
Lepidoptera	Nymphalidae	*Junonia*	*coenia*	1
Lepidoptera	Nymphalidae	*Phyciodes*	*tharos*	2
Lepidoptera	Pieridae	*Nathalis*	*iole*	1
Lepidoptera	Pieridae	*Pyrisitia*	*lisa*	4
Neuroptera	Chrysopidae		sp. 1	1
Orthoptera	Oecanthidae		sp. 1	1
Orthoptera	Tettigoniidae		sp. 1	1

Appendix B - Chapter 2 Supplemental Material

Appendix Figure B.1. Connectance across the three switching treatments (minimizing costs, maximizing benefits, and both) and the no switching control and the three levels of pollinator dependence on plants. Horizontal lines indicate the medians, boxes indicate the first and third quartiles, and error bars indicate the range. Box colors indicate network size (small, medium, or large).



Appendix Figure B.2. Change in connectance from the start to the end of the model runs across the three switching treatments (minimizing costs, maximizing benefits, and both) and the no switching control and the three levels of pollinator dependence on plants. Horizontal lines indicate the medians, boxes indicate the first and third quartiles, and error bars indicate the range. Box colors indicate network size (small, medium, or large).



Appendix Figure B.3. Relationship between pollinator richness and relative nestedness (A), modularity (B), and network specialization (C) of empirical networks (black) compared to simulated networks (green). The shape of the empirical network points represents the study from which the data were acquired. The color of simulated network points represents the starting network size. Overlap between empirical networks simulated networks does not depend on starting network size.