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Plant-Pollinator Network Dynamics of the Little Fork Shale Barren

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FACULTY COMMITTEE:

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Acknowledgments

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Abstract

Shale barrens are steep sloping mountainside ecosystems characterized by rocky Upper Devonian age shale substrate, high light, and low water availability. They form an array of biogeographical “islands” throughout Mid-Appalachia whose niche dynamics, response to disturbance, and pollination ecology remain to be investigated. Using network analysis, this project addresses three objectives to fill gaps in shale barren pollination ecology. (i) Compare vegetative species composition, richness, diversity, and evenness to a descriptive vegetation study completed at the same site 27 years prior. ii) Outline the topology of plant-pollinator networks including identifying phenologically accurate networks, the architecture of such networks, and identifying plant species network hubs and key pollinators groups. (iii) Examine the scale of within-season interaction variation, whether that variation is reflective of fluctuations in pollinator activity, and that variation’s relationship to changes in weather conditions. Plant and pollinator data were collected via pollinator observation and flowering inventory surveys conducted on within 10-day monitoring periods through the full growing season of Little Fork Shale Barren (Pendleton Co.,West Virginia). General vegetation surveys occurred in the late summer to late fall at the same site. Comparisons between the current vegetation community and results from a 1994 survey of the site show a significant increase in community species richness and diversity. Analysis of large scale interaction data revealed the presence of diverse interaction networks with degree distributions, connectances, and levels of nestedness comparable to networks in other ecosystems. Fine scale interaction data showed the system experiences high within-season interaction turnover dictated by interaction rewiring. Simulation models confirmed that species abundance and phenology constrain interaction turnover and interaction rewiring. Linear regression analysis of weather conditions and pollinator activity found median temperature to have the strongest relationship with higher pollinator activity at greater median temperatures.

Our findings expose the depth and dynamics of biodiversity and ecological function present in a superficially understood “barren” ecosystem.

Introduction

Of the approximately 352,000 species of flowering plants described, an estimated 87.5% use animal facilitated pollination as their primary means of reproduction (Ollerton et al, 2011). The ecological mechanisms of pollination are among the more complex and foundational mutualistic networks present in nature and comprise a multitude of interactions that occur between plant and pollinator species (Mitchell et al., 2009; Ballantyna et al., 2017). In the face of ecological change, the assemblage and complexity of these plant-pollinator networks can either ensure functional resilience or result in a disrupting cascade that threatens network collapse (Nieslen and Bascompte, 2007; Dupont and Olesen, 2012; Soares et al., 2017; Robinson et al., 2018). Discerning whether resilience or disruption of network functionality will occur requires quantification of community interactions and dynamics. Applying a network analysis approach to a plant community and pollinator community has strong potential in quantifying ecosystem integrity and contextualizing assembly and disassembly dynamics between the two interdependent communities (Elle et al., 2012; Soares et al., 2017). Also, using a network analysis approach to describe intercommunity dynamics has the potential to help predict impacts of ecological change and inform conservation efforts for vulnerable ecosystems, communities, and species (Hegland et al., 2009; Biella et al., 2017; Soares et al., 2017). Shale barrens, which are frequently the focus of conservation efforts, are particularly vulnerable ecosystems that have not been subjected to such a study of the within season dynamics of their plant and pollinator communities. (Keener, 1983; Norris and Sullivan, 2002).

Plant - Pollinator Networks

A plant-pollinator network provides a broad view of many distinct relationships between species in plant and pollinator communities of a given area. Unlike food webs, which are an example of an antagonistic network where species benefit at the expense of their partner, plant-pollinator networks are mutualistic networks where partners benefit from their interaction. Plant-pollinator networks are systems of goods and services exchanges between various plant and pollinator species in which both parties benefit at some cost to themselves (Bronstein, 1994). The pollinator typically collects pollen or nectar as an energy source, and reproduction in the plant is facilitated by pollinator visitation. Both parties expend energy to maintain this relationship. This is a simplified description of a ubiquitous natural relationship and a vital ecosystem service (Kearns et al., 1998; Potts et al., 2003). However, the complexity of interactions extends beyond this basic mutualistic paradigm with the degree of dependence between partners being typically unequal. Species have varying interaction plasticity and are categorized across a gradient between two interaction extremes: specialist and generalist (Vazquez and Aizen, 2003; Landry, 2010). Specialist species participate in an obligate interaction in which they rely solely on a single species or narrow group of species for resources. In contrast, generalist species act less selectively and interact with multiple species that meet the same need. In a network, both generalist and specialist often interact with one another or with other species in the same category creating a nested array of interactions (Bascompte and Jordano, 2007; Landry, 2010). The accumulation of these independent exchange interactions between a plant species and a pollinator species is what forms intricate networks in ecosystems. Mutualistic networks require no spatial minimum or maximum, but can encompass any spatial range from small sections of mature forests (Nielsen and Bascompte, 2007) to entire portions of the arctic tundra (Schmidt et al., 2017). Also, an ecosystem is not limited to a single network but can support multiple nested networks at differing times or seasons. These networks are free flowing and depend on the activity of participating species, thus a comprehensive understanding of these relationships requires a comprehensive analysis.

Network Analysis Approach

The various interactions between groups or species in an ecosystem are intangible. However, they become tangible through the application of a network analysis approach that uses

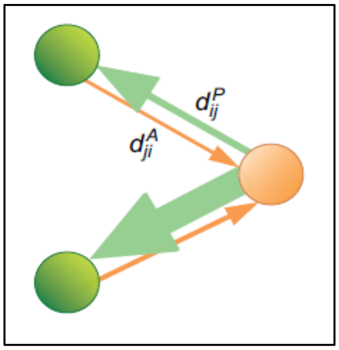


Figure 1 A small bipartite network representing interactions between nodes (circles). The degree of dependence between the plant (d_{ji}^{A}) and animal (d_{ij}^{P}) is represented by the thickness of arrows with thicker arrows indicating a stronger dependence. Bascompte and Jordano, 2007

statistics and math to produce discrete figures and graphs delineating relationships (Bascompte and Jordano, 2007; Ramos-Jiliberto et al., 2012). Plant-pollinator networks are two-grouped or bipartite networks with a set of plant species and a set of pollinator species. Group size can vary based on scope of interest or sampling effort. In a network graph, species present in a surveyed ecosystem are defined as ‘nodes’ and are represented by a shape (Figure 1). Nodes are connected by ‘links’ that represent a recorded interaction or relationship between species, plants linking to pollinators and vice versa (Bluthgen, 2009; Bascompte, 2007). The width of a link describes the occurrence frequency of an interaction with wider links indicating a higher occurrence frequency. The higher the occurrence frequency of an interaction between two species, the stronger the interaction. The number of links and nodes, the density of links, and the distribution of links between nodes are used to interpret trends and characteristics that contribute to a network’s architecture (Bascompte and Jordano, 2007; Gomez et al., 2011). Network structure can be viewed broadly at network level, revealing the pattern of all linkages between node sets, or narrowly at node-specific level, revealing the linkage between individual nodes. When analyzing at a network level, there are three assumptions of ecological network structure (Figure 2). First, ecological network are typically asymmetrical in the number of species participating, i.e. more pollinator species than plant species or vice versa, and in the level of dependency between species or communities (Gomez et al., 2011; Soares et al., 2017). Second, ecological networks are heterogeneous structures with the distribution of links skewed to a set of highly connected nodes acting as hubs holding the network together and the bulk of nodes in either community supporting a few interactions (Bascompte and Jordano, 2007). Third, the pattern of interactions between nodes may create nested compartments where subsets connect

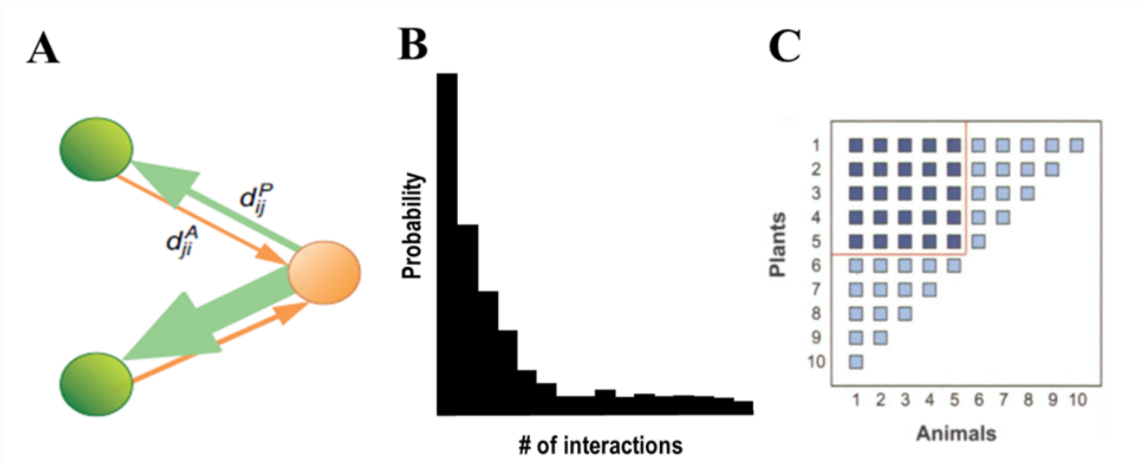


Figure 2. The three assumptions of mutualistic networks. Networks are asymmetrical (A), heterogeneous (B), and nested (C). A) The degree of dependence between the plant (d_{ji}^{A}) and animal (d_{ij}^{P}) is represented by the thickness of arrows with thicker arrows indicating a stronger dependence. Bascompte and Jordano, 2007. B) Frequency distribution of interactions per species showing that most species support very few interactions and a few species support very many. C) A plant-animal interaction matrix showing complete nestedness. With a core of highly connected species (dark blue) and peripheral species (light blue) interacting with species present in that core. Filled squares represent an observed interaction. Bascompte and Jordano, 2007.

cohesively to individual nodes and one can detect networks within networks (Nielsen and Bascompte, 2007; Landry, 2010; Elle et al., 2012; Soares et al., 2017). An example of a nested array would be a specialist plant species interacting with a subset of pollinator species that visit a generalist plant. At a node-specific level, two metrics relate to the pairwise patterns of links between individual nodes and define a species' role in a network. One metric is species degree, the number of links spanning from a node. The second metric is species strength, the proportion of all links for an individual node stemming from another single node (Bascompte and Jordano, 2007; Okuyama and Holland, 2008). A species' role in a network can either be described as a specialized interaction contributing to functional redundancy or a network hub supporting most network interactions or in between.

Network Robustness

The metrics defined and described prior are used to construct a network, and that architecture describes a network's functional robustness (Bascompte and Jordano, 2007; Ramos-Jiliberto et al., 2012). Network robustness is described as the fraction of species that must be removed for a network to fragment. Like other ecological concepts such as system sensitivity and elasticity, robustness describes is a network's resilience to disturbance and capability to avoid network collapse (Tylianakis et al., 2010). Recent research has provided little consistency when connecting structural properties to functional ecosystem dynamics. For example, does high network nestedness translate into a more reproductively successful plant community (Gomez et al., 2011)? However, structurally derived network robustness does have the power to predict impacts from ecological change. In some ecosystems, changes in network structure stemming from community composition changes are localized, and the effects of change are minimal to overall network function (Thébault and Fontaine, 2010). In others, changes create a ripple effect that cascade, ultimately decreasing or disrupting network function. The current literature has found that highly robust networks are those that are highly complex, heterogeneous, and well nested (Bascompte and Jordano, 2007; Tylianakis et al., 2010). However, the impacts of species loss on network function does depend on the role of the species lost, namely, is the species a specialist or a generalist. Specialist, species that support a narrow range of partners, have a very low connection into the network while generalists, species that support a broad range of partners, are highly connected. This difference in connections leads to differences in network impacts with their removal (Figure 3). At the loss of a specialist, network structure that suggests robustness should absorb the absence of that species and network function is left relatively unchanged. In contrast, networks are quite fragile to the loss of their most generalized species with rippling effects, such as secondary extinctions, likely to occur following

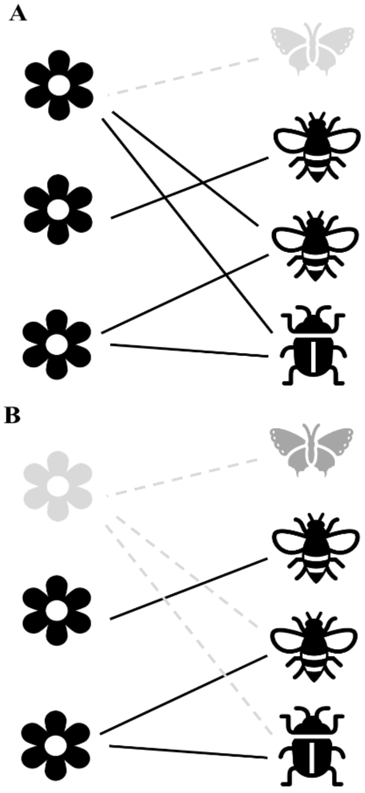


Figure 3. The effects of species role on species loss in a robust network. A) Removal of a specialist species (gray) results in little distribution to other interactions and species in the network. B) Removal of a generalist species (light gray) results in rippling effects to other species as well as secondary extinctions (dark gray).

their removal (Bascompte and Stouffer, 2009). Recent research has supported that the likelihood of cascading impacts is associated with the combinations of strong interactions and that ecological networks are robust to random losses of species (Gomez et al., 2011; Ramos-Jiliberto et al., 2012). However, comparing analyses is challenging depending on the study, ecosystem and communities in question, and ecosystem threats (Blüthgen, 2010).

Interactions across time

Like other ecological networks, plant-pollinator networks have long been studied as static entities. As technologies and techniques to study these interaction networks have improved, they reveal the inherent error that accompanies viewing interaction networks in such a fixed view. Plant-pollinator networks are dynamic in nature with variation in their structure and node composition occurring across time and space. This recent acknowledgement of the potential daily, seasonal, and annual temporal patterns of plant-pollinator interaction networks has opened the door for exploring not only network topology but also the mechanisms behind network formation and dissolution. Efforts to explore intra- and inter-annual patterns of network structure have included analyzing network components at shorter, more biologically relevant periods as opposed to aggregating observations into networks representing arbitrary seasons or complete flowering periods. Analyzing plant-pollinator networks along more biologically appropriate periods can reveal the scale of variation among interactions as well as the ecological consequences of such variation. An approach to analyzing the dynamics of plant-pollinator networks is to quantify their temporal interaction turnover, the changes in the composition of interactions. Interaction turnover consists of two additive components: species turnover and interaction rewiring. Species turnover is the change in species present when comparing two networks. Change in species composition of each community can occur when species change activity level (i.e. move from active to inactive) or change occurrence status (i.e. go extinct or are introduced to a new location). Interaction rewiring is the change in who is interacting with whom among the same pool of co-occurring species. These two components play a role in how and why plant-pollinator interaction networks assemble and disassemble overtime, however there is relatively very little understood of each's relative importance in temporal interaction turnover. Quantifying temporal interaction turnover and identifying the role species turnover and interaction rewiring play in the construction of plant-pollinator networks can provide important contributions to understanding not only the dynamic nature of such networks but also their resilience to ecological changes.

Threats to Network Function

Threats to network function include climate change and habitat loss or degradation with changes in community composition being the most pervasive threat (Inouye, 2008; Elle et al., 2012; Biella et al., 2017). Changes in community composition include loss of species, loss of functionally similar groups, and invasive species introduction (Gomez et al., 2011). Changes in the species composition of either community, through species loss or introduction, can have a profound, lasting effect on network architecture and overall productivity. Extinction of a species represents the loss of a node and all links to that node. The cascading impacts of a species' removal depends on its degree and strength, sum of dependencies, in the network (Brosi and Briggs, 2013). Loss of a generalist species, one supporting a high number of interactions and therefore having a high degree, would create a cascading effect, while loss of a specialist species results in a loss of interaction redundancy and reduces network resilience (Tylianakis et al., 2010; Elle et al., 2012). Shifts in community compositions also stem from invasion of exotic species, though there is ambiguity surrounding the effects of invasion on network structure (Bascompte and Jordano, 2007; Aizen et al., 2008). Many invasive species are pollination generalists and have the potential to shift interaction trends to fit their phenology or compete with native species for pollinators (Bartomeus et al., 2008; Mckinney and Gooddell, 2011). In this context, invasive species can potentially disrupt network function and harm plant and pollinator communities. Conversely, invasive species may become so well integrated into a network structure, acting as a generalist or network hub, that they end up playing a role in preserving network function (Parra-Tabla et al., 2019). Invasive species management and native species population protection are the leading motivators for ecological conservation, but uncertainty surrounding invasive species' impact on pollination systems could result in unexpected consequences following conservation efforts (Pejchar and Mooney, 2009).

Network Analysis in Conservation

Historically, conservation efforts have applied a two-dimensional approach to three-dimensional systems and have not considered dynamic interactions between service providers at the ecosystem level (Elle et al., 2012). Ecological metrics such as species richness, diversity, and abundance are long standing justifications for conservation action but provide little insight into ecosystem or interspecies dynamics. A network analysis approach provides that needed three-dimensional view to plant and pollinator communities of conservation concern while also collecting traditional ecological data such as those used to build functional community composition lists (Elle et al., 2012; Soares et al., 2017). This approach identifies generalist species that act as network hubs whose extinction would lead to dramatic losses in network function. It also identifies specialization in ecosystems by identifying redundant interactions that, if lost, would reduce network resilience to disturbance (Gomez et al., 2011; Elle et al., 2012; Brosi and Briggs, 2013). A network analysis approach can describe interaction dynamics between species and the evolutionary processes generating the interactions (Bascompte, 2007). Also, network analysis can be used to map ecosystem phenology and species richness trends which could inform planning and scheduling of conservation efforts and management plans (Fantinato et al., 2016; Biella et al., 2017). Lastly, application of a network analysis approach has the potential to inform implications of ecological disturbances stemming from climate change, disease or pest outbreaks, habitat loss or alteration as well as restoration efforts (Inouye, 2008; Hegland et al., 2009; Elle et al., 2012; Goulson et al., 2015) Therefore, predicting the impacts of change in a network without the context of associated species dynamics would result in ill-informed predictions of ecosystem structure and potentially unsuccessful conservation efforts.

Neglected Ecosystem: Mid-Appalachian Shale Barrens

Conservation efforts prioritize the biologically significant and/or rare, and shale barrens are a globally rare ecosystem in the central Appalachian Mountains that is of conservation concern. Shale barrens are described as steep sloping mountainsides defined by rocky Upper Devonian age shale substrate, high light, and low water availability (Braunschweig et al., 1999; Norris and Sullivan, 2002). The aggregation of these conditions creates dry, substrate specific ecosystems pocketed among the Appalachian temperate forests that support a unique vegetative community often characterized by rare, threatened, and endemic species (Keener, 1983; Kalhorn et al., 2003). These ecosystems support a sparse canopy and open barren understory. Woody species, such bear oak (*Quercus ilicifolia*) and Virginia pine (*Pinus virginiana*), that occur on shale barrens are scrubby and sparse due to soil and water conditions. Open spaces in the understory are occupied by a xeric, high light herbaceous plant community that comprises three groups: distinctly western species, shale favoring species, and true endemics (Brooks, 1965). Distinctly western species, such as tall grama grass (*Bouteloua curtipendula*), are a small group of plants found on shale barrens and nowhere else east of the Ozarks. These plants are adapted for dry conditions more typical of the western United States but can persist in the east due to shale barrens. Shale favoring species are plants that have a wide distribution in eastern North American, but their most productive and characteristic development occurs in shale-based substrate. These shale-favoring species, including creeping phlox (*Phlox subulata*) and Pennsylvania sedge (*Carex pensylvanica*), comprise a large portion of shale barren vegetation. The third group, true endemics, comprises 18 species including Kate’s Mountain clover (*Trifolium virginicum*) and shale barren rockcress (*Boechera serotina*) whose distributions are restricted to shale barrens. These species occur at varying abundances among Mid-Appalachia and nowhere else in the world.

Due to their rarity, there are few details to the life history of shale barren endemics including dispersal, evolutionary history, ecological roles, and pollination (Keener, 1983; Norris and Sullivan, 2003). Even less information is available on invertebrate species found in shale barrens. Work by Wheeler (1997; 1999; 2000; and Bartlett, 2006) provides some of the only comprehensive information on insect diversity of shale barrens with work by Kalhorn (et al., 2003) providing the only bee inventory. Other information regarding shale barren pollinators is restricted to that of two species of butterfly, *Euchloe olympia* (Olympia marble) and *Pyrugus wyandot* (Appalachian grizzled skipper), which are recorded as using shale endemic species for resources and as host plants (Norris and Sullivan, 2003). Ultimately, shale barrens form an array of biogeographical “islands” in Mid-Appalachia, whose evolutionary history, niche dynamics, species distribution, response to disturbance, and pollination biology remain to be investigated.

In this study, I applied a network analysis approach to explore the interactions between the plant and pollinator communities of a shale barren ecosystem located in eastern West Virginia. This site is recorded as supporting up to seven endemic plant species, including the endangered shale barren rockcress (*Boechera serotina*). Using this method, I addressed several broad objectives. (i) Compare vegetative species composition, richness, diversity, and evenness to a descriptive vegetation study completed at the same site 27 years prior. Based on prior casual observations of the site and the passage of time, I expected to find significant increases in all community parameters. (ii) Outline the topology of plant-pollinator networks including identifying phenologically accurate networks, the architecture of such networks, and identifying plant species network hubs and key pollinators groups. (iii) Examine the scale of within-season interaction variation, whether that variation is reflective of fluctuations in pollinator activity, and that variation’s relationship to changes in weather conditions. Recent research studying interaction turnover of plant-pollinator networks have found that within-season interaction turnover is consistently high (Simanonok and Burkle, 2014; CaraDonna et. al., 2017), thus I predict this to be also true for the LFSB. One of the ecological requirements for an interaction to occur is for interacting species to be found at abundance levels that promote their interaction (Vasquez et al, 2009). Changes in species abundance has been found to predict the level of interaction turnover between two networks (CaraDonna et. al., 2017), but pollinator abundance, namely their foraging activity, is known to fluctuate frequently. Thus, if species abundance also predicts interaction turnover values in the LFSB, I am predicting that variations in pollinator abundance will be reflected in interaction turnover values through the season. Those variations in pollinator abundance, then, will be well predicted by the temperature and relative humidity on the day of surveying.

Methods

Site Description

Surveys of vegetation and pollinators were conducted from April 21st to October 10th, 2020 at the Little Fork Shale Barren (LFSB), Naval Security Group Activity and Sugar Grove Research Station, Sugar Grove, West Virginia (38.514167 N, 79.276389 W). LFSB (1.6 ha) is located in Pendleton County close to the border with Virginia and is one of seven shale barrens in the valley of the South Fork of the South Branch of the Potomac River (Bartgis, 1987). The site has a south-southeast aspect with the top of the ridge lying at 2100m. Jarret (1997) described the site's vascular plant community as sparsely vegetated with Pennsylvania sedge (*Carex pensylvanica*) accounting for 75% of herbaceous cover in the understory and chestnut oak (*Quercus montana*) dominating the overstory. Six endemic species have been detected at this site in the past (Jarret, 1997): shale barren rock cress (*Boechera serotina*), mountain nailwort (*Paronychia montana*), shale barren bindweed (*Calystegia spithamaea* ssp. *purshiana*), shale barren pussytoes (*Antennaria virginica*), heart-leaf skullcap (*Scutellaria ovata* ssp. *rugosa*), and

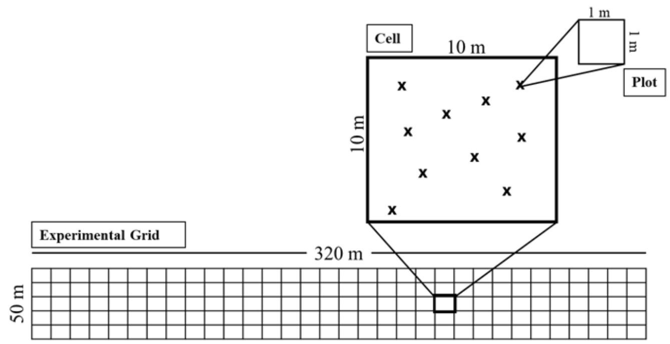


Figure 4. Diagram of 50 m x 320 m experimental grid dividing the LFSB site into 160 individual 10 m X 10 m cells. A cell is isolated to display locations of 1 m^2 plots used for pollinator surveys, which are areas of high flowering activity. An example of flower-visitor survey locations within a cell are denoted with an "x" in the isolated cell.

shale barren nodding onion (*Allium oxyphilum*). The study conducted by Jarret (1997) utilized a grid layout established by the West Virginia Department of Natural Resources (WVDNR) for long term monitoring of *B. serotina* at LFSB (Figure 4). The grid had an area of 50 m X 320 m (16,000 m^2) and was divided into 160 individual 10 m X 10 m cells. Cells were identified by their row and column position within the grid, which corresponded to the location of the grid marker in the lower left corner of the cell. Therefore, the bottom left most cell was designated as being column one, row one (1-1) and the top, left most cell was designated as being column 1, row 5 (1-5). Sampling of the vegetation community and for active flowering and plant-animal interactions was conducted in these cells.

Data Collection and Analyses

General Vegetation Surveys

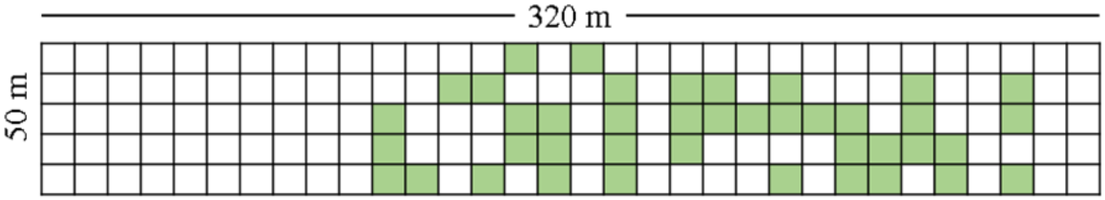


Figure 5. Diagram of 50 m X 320 m experimental grid dividing the LFSB site into 160 individual 10 m X 10 m cells. Cells selected for weekly vegetation surveys from August to October are denoted in green (Jarret, 1997).

Sampling of shale barren vegetation followed methods provided by Jarrett (1997). Sampling occurred on a bimonthly basis starting August 26 through October 10, 2020. Sampling was conducted within 40 cells located within a 50 m x 200 m section of the 16,000 m^2 grid (Figure 5). Surveys of the understory community within each cell occurred within a 1 m^2 quadrat randomly placed within the cell. All vascular plants present within each quadrat were identified and estimates of cover recorded. Estimates of bare ground, i.e. strictly shale fragments or exposed rock, and dense leaf litter cover, are void of vegetation but without direct access to the substrate, were also recorded within each quadrat. Plants were identified to species or, in some cases, genus based on their stage of growth and development using the *Flora of Virginia*, *Flora of West Virginia*, and/or *Newcomb's Wildflower Guide*. Any plants that could not be confidently identified in the field were collected for later identification.

Data collected from vegetation surveys were used to determine the extent of vegetated versus unvegetated space of the site as well as calculate the mean species richness, Shannon diversity index (H'), and equitability per cell. Species richness and species diversity were calculated using the 'vegan' package, commonly used for most community ecology calculations, in R (Oksanen et. al., 2021). Equitability is a measure of distribution or evenness of diversity ranging from 0 (no evenness of diversity) and 1 (complete evenness) and was calculated as:

$$J = H'/H'_{max}$$

where H'_{max} is the ln(s) and s is the number of species recorded in a quadrat (Jarret, 1997). Maximum H' assumes even distribution of species within a quadrat. For each species found, the mean estimated cover per quadrat and the importance value, which is calculated as the average of the mean relative frequency and mean relative cover, was calculated. Following tests for normality, comparisons between the current study's mean species richness, species diversity (H'), and equitability per cell results and results from Jarrett (1997) were completed using a Wilcoxon signed-rank test.

Flowering Inventories

To avoid allocating sampling efforts towards cells that lacked any flowering activity, inventories of species flowering within every cell occurred on a 10-day cycle starting on April

21^{st}, 2020. To minimize site disturbance, cells were surveyed from their bottom, downslope end, using 8X binoculars. A species was considered flowering if greater than 1% of all flowers were open, and reproductive parts were visible between, or present within unfolded flower parts (Dupont and Olesen, 2012). Plants that were flowerings were identified to species. A voucher specimen was collected of each species recorded during flowering inventories and are housed in the Norlyn L. Bodkin Herbarium at James Madison University. Data collected from these inventories formed the first criteria to determine locality for flower-visitor observations. Cells identified as having species in flower were further reviewed for an estimate of total flower cover, i.e. cover of flowers from all identified actively flowering species. Cells with a total flower coverage constituting at least 5% of ground cover were marked for flower-visitor observations within 10-day monitoring period.

Pollinator Observations

Individual cells that met the designated total flower coverage threshold were subsampled with flower-visitor observations using 1 m^2 plots. These quadrats were placed at sites of high flowering activity, relative to the respective cell (Figure 4). High flowering activity is described as a high density of flowers (~3 floral units/10 cm) of a single species or two or more species in flower present. Cells identified for flower-visitor observations had a minimum of one to a maximum of 10 flower-visitor surveys that could occur within the cell. Pollinator observations were also conducted for every plant marked flowering to ensure the species was not inadvertently excluded from any constructed networks due to its low abundance or concentration. At an identified site, the number of floral units present within the plot was recorded and floral units were observed for all flower visitors for a 10-minute period. A floral unit is defined from the perspective of a pollinator as opposed to inflorescence morphology. Thus, a floral unit was distinguished from another by the distance that a small pollinator would have to fly, as opposed to walk, in order to collect resources (Saville, 1993; Cusser and Goodell, 2013). For example, a single inflorescence of a woodland sunflower (*Helianthus divaricatus*) would be counted as a single floral unit. For simplicity, flower visitors are referred to as pollinators, though undoubtedly their roles as effective mutualists may vary. Pollinators that touched the reproductive parts of a flower within a floral unit were recorded as well as the plant species visited, and the number of floral units visited by a pollinator. Every independent landing was recorded as an independent visitation. Pollinator observations were conducted within one to four days following a flowering inventory between the times of 0830 and 1600. Observations were not conducted in the case of rain and/or high winds (>8-12 mph). Relative humidity and temperature (℃) were measured prior to the first observation of the day, after the final observation, and on every hour in between using a Vernier LabQuest 2. All observations were conducted by the same observer through the field season to ensure continuity of pollinator in-field identifications. Pollinators were identified to the finest taxonomic level possible, and those not identified in the field or through photography were collected using an aspirator. Sampling completeness was analyzed using the Chao estimator (Chao et al. 2009; Appendix A)

Plant-Pollinator Network Metrics

Data collected from pollinator observations were used to construct a full season and seasonal unit interaction networks, which were characterized by several metrics and parameters. To construct the complete shale barren interaction network, all data from the entire sampling season were pooled. This complete shale barren network was used to identify core generalists of the ecosystem. However, a complete network of the entire season does not accurately represent the extent of interactions since it pools together species that, in-reality, do not phenologically co-occur and would never interact. To address this artifact, phenological units networks were identified using the flowering phenology of the site using a modified method used by Fantinato et al. (2016) and Biella et al. (2017). A presence-absence matrix of flowering activity was constructed in which the rows were the 51 plant species recorded in flower through inventories and the columns were monitoring periods. A species recorded as in flower (present) during a monitoring period was marked with a 1, whereas species not recorded (absent) were marked with a 0. Pairwise Spearman correlation was then calculated comparing all monitoring periods to identify significantly correlated monitoring periods based on their species in flower. Monitoring periods found to be significantly correlated, and not with other monitoring periods, must overlap in the species in flower for that time, forming a phenological unit. From these phenological unit interaction networks, the following were calculated (Appendix B): number of plant species (P), number of pollinator species (A), mean linkage of species from each community, websize (total number of potential interactions, $S = P \text{ x } A$), number of observed pairwise interactions, degree of each species, species strength, degree distribution, web asymmetry, interaction strength asymmetry, connectance, specialization ($H2$), and nestedness temperature (T). The ‘bipartite’ package (Dormann et. al., 2008) in R was used to calculate all but the distribution of degrees, which was calculated using the ‘igraph’ package (Csardi and Nepusz, 2006) in R (version 4.0.4). Nestedness temperature (T) ranges from 0 to 100, with 100 representing low levels of nestedness (N). Level of nestedness was calculated as $N = (100 – T)/100$, with values ranging from 0 to 1 (maximum nestedness). Most network level metrics – connectance, generalization, and nestedness – range from 0 to 1 with 1 representing maximum values such as complete connectance or complete specialization. Interaction strength asymmetry is the only metric to range from -1 to 1, with values approaching -1 or 1 conferring greater interaction dependence. Positive values for interaction strength asymmetry indicate higher dependence present in the pollinator community and negative values indicate higher dependence in the plant community.

Interaction Turnover and Weather Conditions

To address questions of within season variation in plant-pollinator interactions and its patterns, the interaction turnover, interaction rewiring, and species turnover between monitoring periods were calculated using the ‘betalink’ package in R (Poisot, 2016). Interaction turnover, the change in pair-wise interactions between present members of the plant and pollinator communities, was computed as

$$\beta_{int} = \frac{\mathrm{a+b+c}}{(2a+b+c)/2} - 1$$

where β_{int} is the interaction turnover between two successive monitoring period networks, *a* is the number of pair-wise interactions shared between networks, *b* is the number of interactions unique to the first network, and *c* the number of interactions unique to the second. Interaction turnover can range from 0 to 1, with higher values representing greater changes in who is present and who is interacting with whom between monitoring periods. Interaction turnover is a presence-based dissimilarity index which can be separated as $\beta_{int} = \beta_{rw} + \beta_{st}$, where the two components are the contributions of interaction rewiring (β_{rw}) and species turnover (β_{st}). Following a check for normality, determination of whether interaction rewiring or species turnover contributes the most to interaction turnover was accomplished using a two-tailed t-test.

Exploration into the impact of pollinator activity on interaction turnover requires an assessment of the forces constraining interaction turnover in a system. Following methods developed by CaraDonna et. al. (2017), it was determined whether species activity, and/or abundance, and phenology constrain within-season interaction turnover. Confirmation of this constraint required the construction of two probability-based simulation models that considered 1) species' phenological overlap and 2) species' phenological overlap x relative abundance. In order to interact, plants need to be flowering and pollinators foraging at the same time. The simulation model considering only phenological overlap provides a null expectation of interaction turnover and interaction rewiring based on the most fundamental requirement for interactions to occur. Temporally co-occurring plant and pollinator species also need to be present in numbers that support their interaction, with plant and pollinator species occurring in greater amounts being more likely to interact.

Following Vazquez (et al., 2009), matrices describing the probability of plant and pollinator species present during a monitoring period interacting were constructed. For the null model considering only phenological overlap, plant and pollinator species present during a monitoring period had equal probability of interacting. For the second model considering phenology and abundance, the probability of a co-occurring plant and pollinator species was weighted by their respective relative abundances, or relative activity for pollinators, during the monitoring period. Plant species abundance was calculated as the total number of floral units recorded during a monitoring period divided by the number of pollinator observations completed within that monitoring period. Pollinator species activity was calculated as the total number of visitations made within a monitoring period. Due to this study's focus on understanding the plant communities' perspective in interaction networks, pollinator activity as opposed to absolute abundance, i.e. occurrence, during monitoring periods was calculated. Next, 1000 predicted interaction matrices based on the constructed probability matrices of each monitoring period were calculated using the 'mgen( )' command part of the 'betalink' package in R (Poisot et. al., 2012). For each monitoring period simulation, the number of links between species was held to the number of links observed in the field. The simulated interaction matrices included all flowering plant species recorded from flowering inventories, meaning their plant species composition differed from their observed monitoring period network counterpart, and simulations allowed for changes in interactions between all co-occurring species. The interaction turnover between simulated monitoring period interaction matrices was then calculated and mean simulated interaction turnover values to observed values was compared using a standard effect size (SES) approach:

$$\text{SES} = \frac{\beta obs - \mu(\beta sim)}{\sigma(\beta sim)}$$

The SES indicates the number of standard deviations an observed interaction turnover value is removed from the mean of the simulated model, given the standard deviation of the model output across 1000 iterations. Assuming a normal distribution, SES values falling between -1.96 and 1.96 (95% confidence interval) indicated that the observed values were predicted by the model. Values outside of the range indicated that the interaction turnover was not constrained by the included ecological constraints. Lastly, a linear regression analysis was used to examine any relationship between pollinator activity and median weather conditions of the monitoring period with Akaike information criterion (AIC) used to determine best-fit models.

Results

Vegetation Community Analysis

From the end of August to the start of October, four replicate surveys were completed within 40 cells at the Little Fork Shale Barren, which detected 69 vascular plant species and morphospecies. Species detected included members of shale barren endemics, near endemics, and characteristic shale barren species. Additionally, 51 species were found that were only found in the 2020 surveys, 13 species were found through both surveys, and 5 species were only found in the 1994 surveys (Appendix C). Surveys found that the site is sparsely vegetated with total relative coverage of detected species less than the relative cover of both bare ground and dense leaf cover (Appendix C*)*. Among species detected, Pennsylvania sedge (*Carex pensylvanica*) was found to have the highest mean estimated cover per plot (14.17) and importance value for the site at 0.215. Plantain pussytoes (*Antennaria plantagifolia*) was found to be the second most abundant species with a site importance value of 0.111 and mean estimated cover per plot of 7.74. Together, these species constituted approximately 45% of the vegetative cover of the site with the other 55% provided by the remaining 67 species and morphospecies, majority being general woodland species (Appendix C).

Comparisons using Wilcoxon signed-rank tests between this study's median species richness, species diversity, and equitability and those from Jarret et al. (1997) revealed significant changes in the site's mean species richness and species diversity (Figure 6). Results show that species richness per cell has significantly increased from 3.94 (1994) to 6.49 (2020) (V = 28.5, p = < 0.0001). Along with an increase in species richness, species diversity per cell also increased, from 0.86 (1994) to 1.27 (2020) (V = 50, p = < 0.001). The equability of cells was the only parameter where no significant difference was found, with mean equability per cell remaining around 0.6 (V = 222, p = 0.4429).

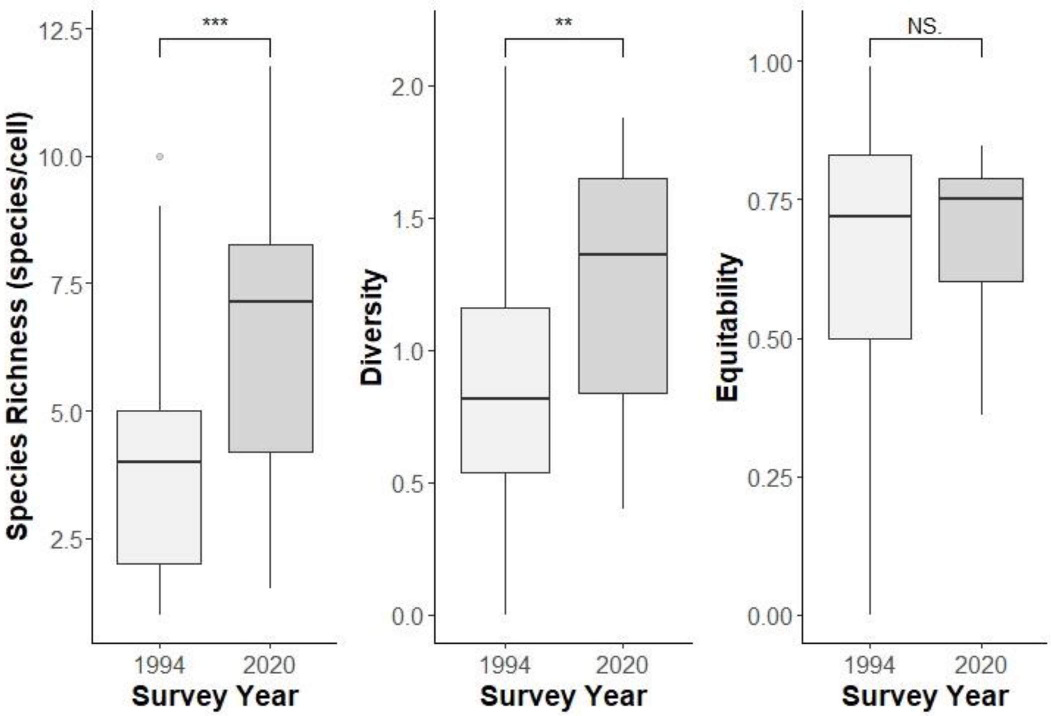


Figure 6. Comparisons of site parameters – species richness, Shannon Diversity, and equitability – between vegetation surveys conducted in 1994 and 2020 using a Wilcoxon signed-rank test. *** - p value = < 0.0001; ** - 0.001; NS. - no significance.

Plant-Pollinator Network Metrics

Over 16 monitoring periods (88.33 hrs), consisting of 530 pollinator surveys, 325 pairwise interactions between 42 flowering plants and 85 pollinator morphospecies were observed, representing 3406 individual pollinator visitations. Flowering inventories detected 51 plant species in flower through the season. Nine species had no pollinator visitations, likely due to their consistently low abundances. The full season interaction network of the shale barren system shows several core plant species present with elm-leaved goldenrod (*Solidago ulmifolia*), narrow-leafed bluet (*Houstonia longifolia*), early low-bush blueberry (*Vaccinium pallidum*), and woodland sunflower (*Helianthus divaricatus*) representing the most connected species. Though these plant species were found to serve as core generalists within the full system, their importance varied across the season depending on their phenology (Table D.1). Among pollinators, bees (Anthophila) were the core group within the system with morphospecies from this group comprising 37.6% of all pollinators observed (Table D.2). Species of small bees (body lengths 4 mm – 8 mm) were the most prevalent among all bee species, and consistently had greater interaction strengths in the system (Table D.3).

Pair-wise Spearman Correlation revealed no break in correlation between sequential monitoring periods, thus there was no objectively obvious distinct seasonal segments. However, monitoring periods observed at the beginning (MP01) and the end (MP16) of the sampling season did not overlap in flowering plant species composition. Also, there was strong pooling among monitoring periods at the extreme ends of the sampling season, with the largest cluster of significantly correlated monitoring periods found in the summer weeks. Lastly, monitoring periods closer to the middle of the sampling season (MP05 through MP08) seem to serve transitionally between the clusters formed at the start and end of the season (Appendix E). Therefore, it was concluded that three phenological units were present: the early weeks of the sampling season in spring (MP01-MP05), transitional weeks in the middle of the season approaching summer (MP05-MP08), and the summer weeks of the season (MP08-MP16) (Figure 7).

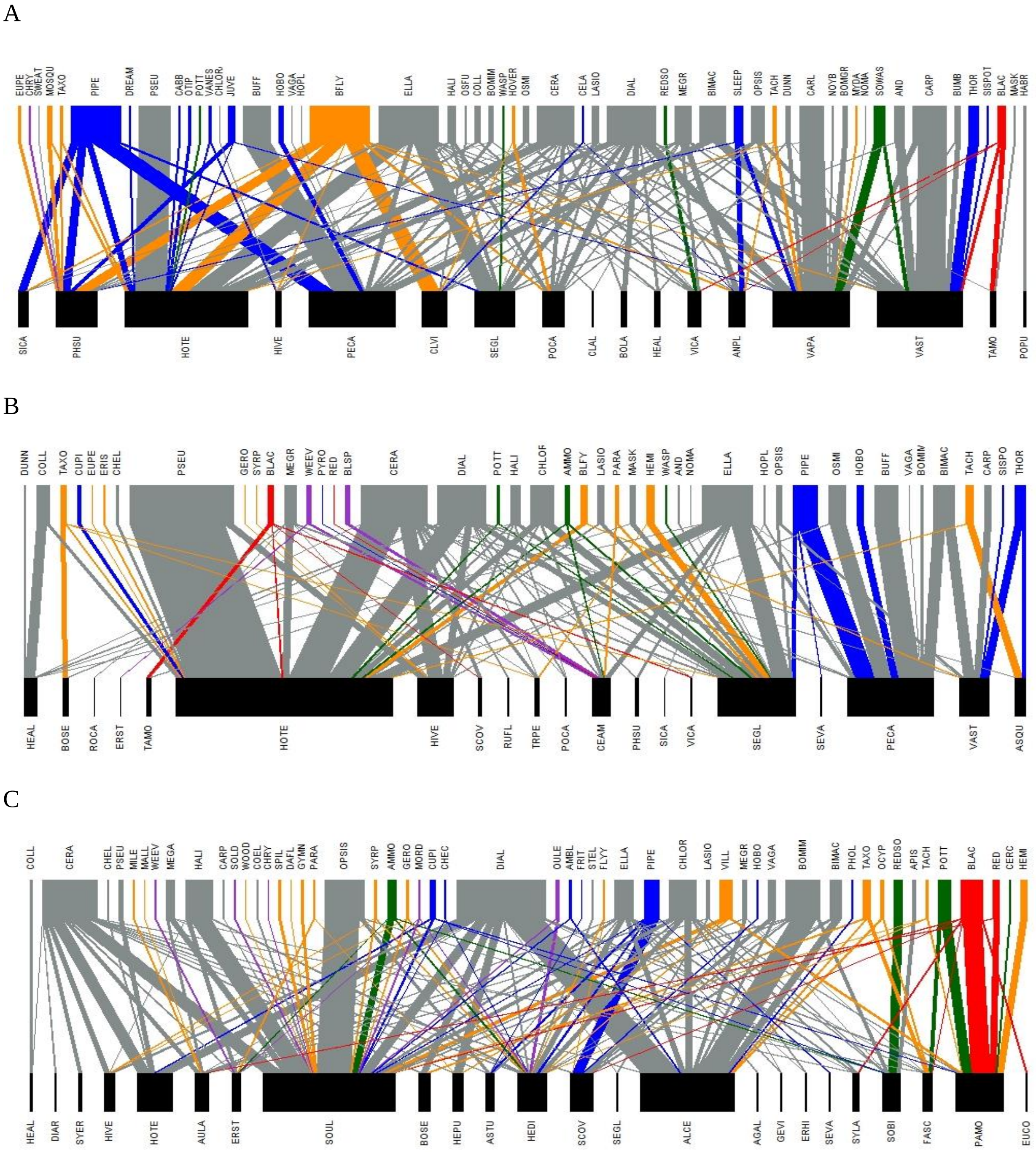


Figure 7. Quantitative interaction networks – spring (A), transitional unit (B), and summer (C) – of plant and pollinator community present at Little Fork Shale Barren (LFSB). Pollinator morphospecies are shown as rectangles at the top of each network and plant species are shown at the bottom (black). The width of the rectangles reflects the degree of a species (the number of links a species supports). Links are represented as lines between species with the width of the lines indicating the relative quantitative visitation rate between an interacting pair. Networks are labeled with species codes (Plants: Appendix F, Pollinators: Appendix G). Pollinators are colorized by their pollinator group: gray (Anthophila), blue (Lepidoptera), orange (Diptera), green (Hymenoptera), red (Formicoidea), and purple (Coleoptera).

All three networks present in the system were found to have low connectance, which was reflected in comparisons between their websize, the product of the number of plants and pollinators present in the network, and total number of observed pairwise interactions. All networks observed fewer total number of pairwise interactions than what was predicted by their respective number of plant and pollinator species. Network specialization of each unit was moderate with an average value of 0.6. Pollinator species present in each network outnumbered plant species for all three networks, which was reflected in each network's web asymmetry. However, the first phenological unit had a higher web asymmetry compared to the later transitional and summer units. Asymmetry between plants and pollinators revealed that plants present in each network supported more links per species than pollinators and typically had greater interaction degrees and interaction strength. Calculation of interaction strength asymmetry of each network resulted in positive values close to 0 (Table 1). The degree distribution of each network followed a truncated power law, i.e. greater probability species interacting with one or two species. Lastly, all networks were highly nested (Table 1).

Network Metric	Full	Spring	Transition	Summer
# of plant species (P)	42	17	20	24
# of pollinator morphospecies (A)	85	52	44	52
Websize (PxA)	3570	884	880	1248
Total # of pairwise interactions	325	139	109	154
Links per plant	17.108	13.356	14.715	15.119
Links per pollinator	11.718	5.557	4.888	7.432
Total visitations	3406	1184	1323	1631
Web Asymmetry	0.339	0.507	0.375	0.368
Interaction Strength Asymmetry	0.099	0.190	0.198	0.151
Nestedness	0.746	0.828	0.902	0.923
Connectance	0.091	0.157	0.124	0.123
Specialization (H2)	0.49	0.534	0.583	0.487

Table 1. Qualitative measures of the full network and phenological units – spring (MP01-MP05), transitional unit (MP05-MP08), and summer (MP08-MP16) – constructed for Little Fork Shale Barren. See Appendix B for metric definitions.

Network Dynamics

Sixteen fine-scale interaction networks, one for each monitoring period completed, were constructed using data collected during monitoring periods. The size of these networks varied widely with the number of pair-wise interactions per monitoring period network ranging from 11 to 55. Despite the variety in the number of pairwise interactions, all networks were found to be more specialized (mean specialization of 0.64). Calculations of interaction turnover between monitoring periods revealed that within season turnover for the system was high, ranging from 0.639 to 0.943 (Figure 8). Following a normality test, comparison between interaction rewiring and species turnover using a two-tailed t-test found that interaction turnover is primarily driven by interaction rewiring (t=4.781, df = 23.417, p < 0.001). On average, interaction rewiring accounted for almost two-thirds of interaction turnover (62.4%).

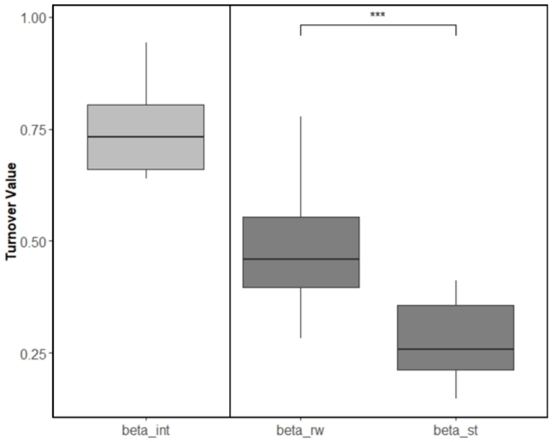


Figure 8. Within season interaction turnover (beta_int) values of Little Fork Shale Barren (LFSB). Comparisons between interaction turnover components – interaction rewiring (beta_rw) and species turnover (beta_st) – using a two-tailed t-test showed interaction rewiring having a significantly higher mean than species turnover (p value < 0.001).

Simulation models suggest that the patterns of interaction at the LFSB are non-random and that species' phenologies and relative abundance, or relative activity, were important ecological constraints of interaction turnover. Simulations considering only phenological overlap, the null model, failed to predict all turnover values, typically overestimating interaction turnover and rewiring values and underestimating species turnover (Figure 9). In contrast, probabilities of interaction considering phenological overlap and species abundance predicted interaction turnover and interaction rewiring well (Figure 10). However, this model did not predict species turnover values well, again, typically underestimating species turnover for eight of the 15 values. This result implies that species turnover is not entirely

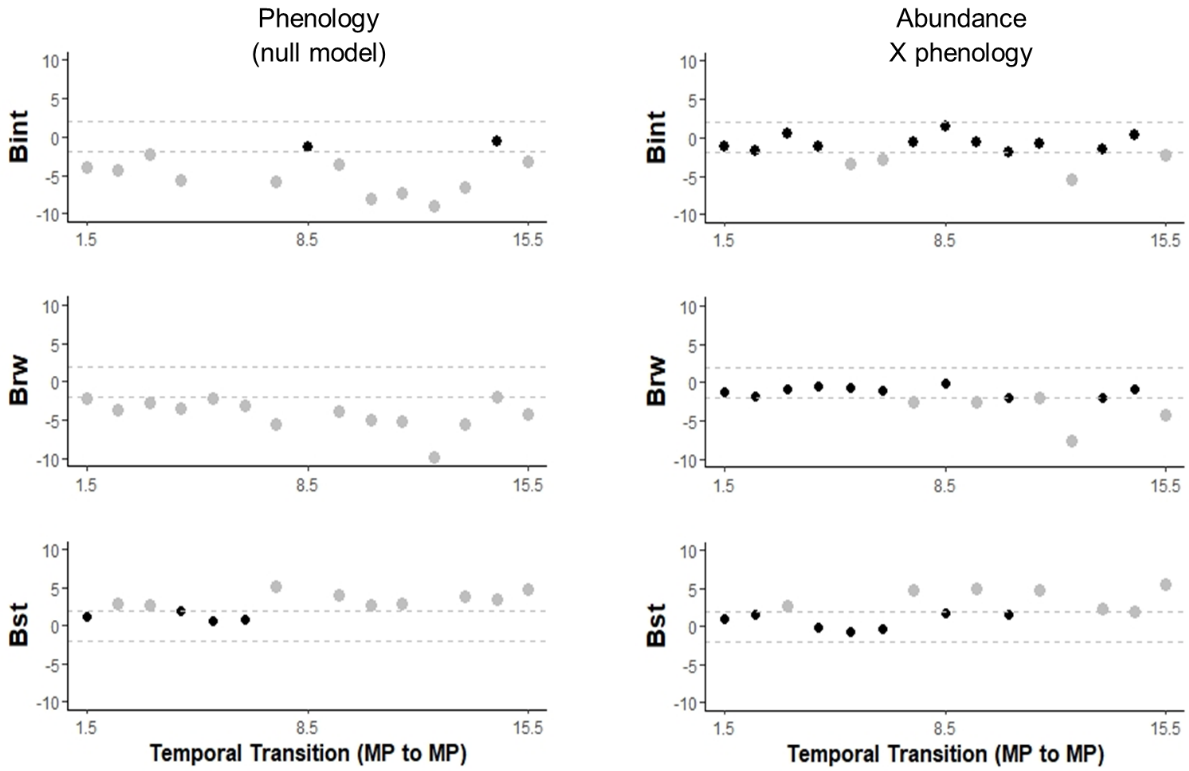


Figure 9. Standard effect size (SES) comparing observed interaction turnover values – interaction turnover (βint), interaction rewiring (βrw), species turnover (βst) – to expected values calculated from probability-based simulation model. Null model considers species probability of interacting base on phenology. Abundance x Phenology model considers species relative abundance and phenology. The dotted lines delineate the ± 1.96 standard deviation zone. Points falling within this zone (black dots) indicate that the model values and observed values are statistically indistinguishable.

constrained by species' phenologies and relative abundances and there is likely an additional ecological constraint influencing species turnover in this system. Reviews of variation in interaction turnover and fluctuations in pollinator activity through the surveying season exposed a pattern of response between the two in the latter portion of the season (Figure 10a). There were two notable declines in pollinator activity during the season, around monitoring periods 9 and 15, that coincide with two spikes of high, near complete interaction turnover. This responsive pattern is less apparent in the earlier portion of the season with a spike of high interaction turnover more in line with higher levels of pollinator activity. Lastly, linear regression analyses of weather conditions and pollinator activity found a significant relationship between pollinator activity and monitoring period median temperature, with greater pollinator activity occurring at higher median temperatures ($F_{1,13} = 5.121$, $r^2 = 0.2826$, $p = 0.0414$) (Figure 10b). AIC evaluations found the median temperature model to be the best-fit for predicting variations in pollinator activity (Appendix H).

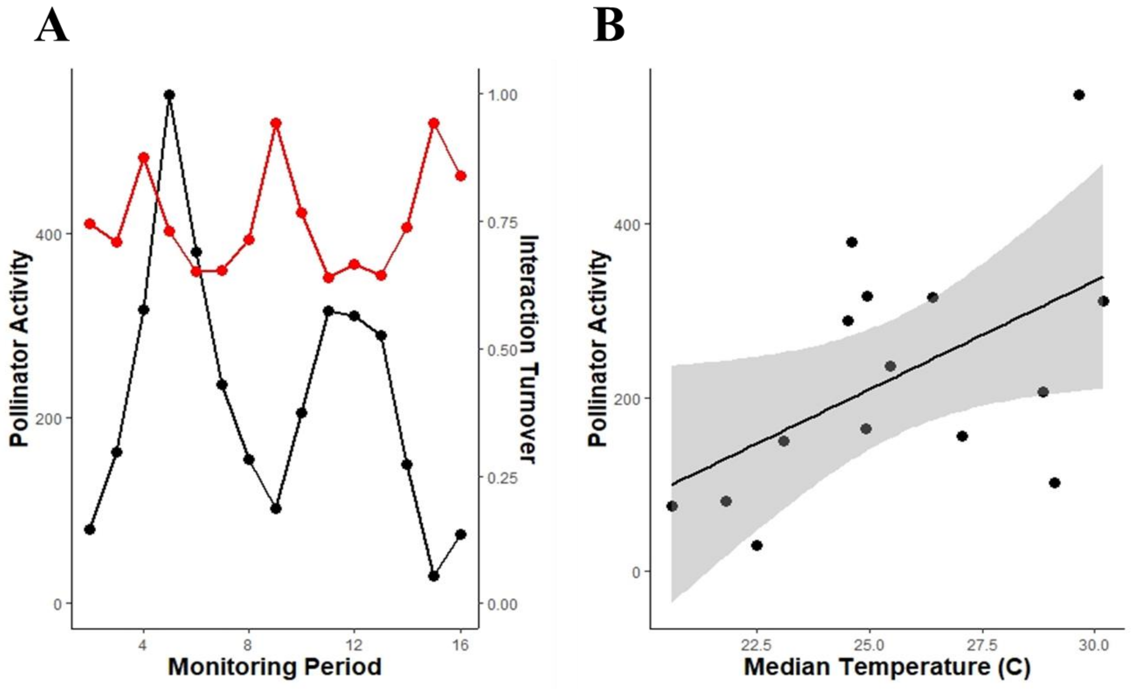


Figure 10a. Scatterplot displaying the variations in pollinator activity and interaction turnover across the monitoring periods at Littler Fork Shale Barren (LFSB). Fluctuations in pollinator activity are represented by the black line and dots. Variations in interaction turnover are represented by the red line and dots. **Figure 10b.** Linear regression relationship between median temperature (Celsius) and pollinator activity recorded at the Little Fork Shale Barren ($F_{1,13} = 5.121$, $r^2 = 0.2826$, $p = 0.0414$).

Discussion

Functional Stability of a Shale Barren Ecosystem

This study adds to the pool of information revealing the striking diversity and activity present in a shale barren ecosystem, often described as sparse and barren. Flowering inventories and surveys of vascular vegetation detected a range of species types present at Little Fork Shale Barren (LFSB) including characteristic shale barren plant species, endemics, and general woodland species not originally found through the 1994 surveys. Species characteristic of shales barrens that were found at LFSB included creeping phlox (*Phlox subulata*), Pennsylvania sedge (*Craex pensylvanica*), and narrowleaf bluet (*Houstonia longifolia*) (Braunschweig et. al., 1999).

The LFSB continues to support populations of shale barren endemics, the shale barren rockcress (*Boechera serotina*) and white-haired leather flower (*Clematis albicoma*), and near endemics, heart-leaf skullcap (*Scutellaria ovata* ssp. *rugosa*) and mountain nailwort (*Paronychia montana*) (Keener, 1983). However, LFSB supports a plant community comprising more and different species than those that were present 27 years ago. Plant populations have diversified with possible new introductions since 1994, but also it is likely that some populations have grown and shifted their distribution at the site making them more detectable through surveys. There is an increased presence of general woodland plant species, such as plantain-leaved pussytoes, which is a potential product of the contribution of deciduous trees to the soil substrate. Prominent leaf litter from the surrounding deciduous forest and resident shale barren canopy accumulating at large fallen logs and the base of standing trees at the site has possibly contributed higher amounts of organic matter to the typically shale, rocky substrate (Facelli and Pickett, 1991). Though changes have resulted in a significantly more diverse community than 27 years ago, a lingering question is what this change means for the integrity of the system as a shale barren.

A goal of this study was to outline the topology and dynamics of plant-pollinator networks present in the system; information never collected for a shale barren. Such information on the interactions between plants and pollinators lays the foundation for further understanding the changes experienced at LFSB and the consequences of such changes, particularly the system's resilience to disturbance. Surveys of the plant and pollinator communities revealed trends in the community phenology and the topology of interaction networks that suggest network robustness. One such trend is the strong overlap of flowering periods among plants that creates a consistent cascade of floral resources through the season (Fantinato et. al., 2016). Correlations of monitoring periods based on the composition of plant species in flower revealed this cascade in flowering periods with most species present for two to three monitoring periods, i.e. three to four weeks, before declining in abundance (Appendix E). The narrowleaf bluet (*H. longifolia*) was a standout species on LFSB for its consistent and persistent presence through the growing season. Though its flower production varied in abundance through the growing season, the narrowleaf bluet produced flowers for 15 of the 16 monitoring periods. The narrowleaf bluet was therefore a consistent pollinator resource, especially for more prominent pollinator groups like small bees, butterflies, and flies. Ultimately, this study determined that, in this particular growing season at LFSB, there is no obvious period absent of floral resources for the pollinator community. Though more analysis is needed to determine whether flower abundances ensure sustainment of the pollinator community and if there is fluctuation of these abundances.

This study indicates that interaction networks present in LFSB maintain a power-law degree distribution and nested structure, network characteristics typically found in other ecological networks (Bascompte and Jordano, 2007). Species degree is described as the number of the number of links a species supports and the distribution of species degree informs a network's heterogeneity (Soares et. al., 2017). The nestedness of a network is the level of cohesion between co-occurring species (Bascompte and Jordano, 2007). Highly nested networks have a core of several generalist species and many generalist-specialist interactions occurring, contributing to the preservation of specialist species and network function (Bascompte et. al., 2003; Spiesman and Inouye, 2013). Results indicate that the LFSB networks are highly cohesive and are composed of many species supporting a few interactions and a few species supporting many interactions, i.e. a heterogeneous system. These features suggest a level of diversity in interactions and participating species that is comparable to other ecological networks present in a variety of other ecotypes and infers network robustness (Bascompte et. al., 2003; Kaiser-Bunbury et. al., 2009; Nielsen and Totland, 2014; Biella et. al., 2017). An additional characteristic closely tied to conferring network complexity and, to an extent, robustness are the levels of connectance calculated for each interaction networks. A rule of thumb summarized by Bascompte and Stouffer (2009) is that the higher the connectance of a network, the higher its robustness. Though connectance ranges from 0 to 1 (full realization of linkage), most ecological interaction networks have connectances closer to 0.1 and are not significantly skewed towards specialist or generalist species (Dunne et. al., 2002). Thus, though the observed plant-pollinators networks present at LFSB are smaller than what is possible with the richness of species present, their level of complexity inferred by their connectance is similar to other ecological networks. However, to conclude that the networks of LFSB are robust would be too assumptive.

The forces maintaining the levels of network cohesion, complexity, and heterogeneity are unclear. Seeing that the site has changed and is changing, the implications of changes in those forces maintaining network structure are also unclear. Each network's interaction strength asymmetry further questions the extent of system resilience. Based on the mean linkage per species, species degrees, and interaction strength asymmetry, the plant community present at LFSB carries a higher degree of influence among interactions compared to the pollinator community. The level of asymmetry of interaction strength in a network has been found to influence the resilience of a network through the network's level of connectance. Communities with lower connectivity have a lower resilience to disturbances when there is greater asymmetry among interaction strengths (Okuyama and Holland, 2008). The lower species richness of the plant community likely contributes to the asymmetry in interactions (Nielsen and Totland, 2013), but this aspect simply highlights the importance of the plant community in maintaining network structure. The composition, diversity, and abundance of the LFSB plant community are possible characteristics that, if changed, could significantly shift network structures and function. To interpret whether the levels of connectance determined in this study protects LFSB networks from disturbance would require species-deletion experiments and simulations (Dunne et. al., 2002; Bascompt and Jordano, 2007; Okuyama and Holland, 2008).

The level of generalization of each network, the extent of niche partitioning across interacting species, was a lingering, confounding metric to confer any level of network robustness. Each phenological unit network was found to be specialized, hinting to a high level of niche partitioning and specialized interactions between species (Soares et. al., 2017). However, network specialization, as a metric, does not included or consider some ecological contexts needed to interpret the function of a system. One such oversight is the lack of recognition of the ecological identity of interacting species (Bluthgen et. al., 2006). For example, a plant species visited by multiple species of small butterflies may be identified as more generalized than another plant species visited by a small number of species representing several insect orders (Bluthgen et el., 2006). The metric also doesn't consider behavioral constraints of species and assumes that species will adjust their interactions according to partner availability. In nature, the foraging decisions of pollinators can be influenced by environmental variables as well as its own and its partner's abundance. Thus, some species have been found to perform as a specialist under certain conditions and adjust their foraging selection under other conditions (Kunin, 1996; Fort et. al., 2016; Soares et. al., 2017). The finding that interaction turnover occurring between fine-scale interaction networks is primarily driven by interaction rewiring lends some strength to the phenomenon for conditional specialization in LFSB networks. The mechanisms driving interaction flexibility of pollinators is relatively unknown, however, potential drivers identified include shifts in intra- and inter-specific competition for resources, changes in floral abundances, or changes in floral resource composition (Simanonok and Burkle, 2014). To decipher the true level of specialization present in a situation such as the LFSB networks, Bluthgen et. al. (2006) suggests a stepwise reduction of matrix size accomplished through pooling species into broad guilds or higher taxonomic units.

The present study found that the formation and change in interactions within a system is primarily constrained by species' phenological overlap and relative abundance. These results are similar to those found by CaraDonna et al. (2017) who also found that models considering species phenology and relative abundance best predicted interaction turnover between weekly interaction networks. Results from the present study, however, found that species turnover was not well predicted by our models, suggesting that an additional ecological constraint contributes to species turnover within the LFSB system. An ecological constraint that was not considered in the analysis of this study was the effect of spatial overlap in determining interactions. In order to interact, species also have to be present with in the same space. This study conducted pollinator surveys for an area approximately 18% larger than similar studies (Carstensen et. al., 2014; Carstensen et. al., 2016; CaraDonna et. al., 2017; CaraDonna and Waser, 2020). Due to the size of the area surveyed, it is possible that species observed might overlap in phenology but not spatially. How plant-pollinator interactions change across space and the underlying mechanisms behind such changes are unexplored questions in understanding the assemblage of plant-pollinator networks among ecosystems. Eventually understanding how spatial partitioning or gradients affect the assembly of plant-pollinator interaction networks has important conservation implications (Siminonok and Burkle, 2014). In shale barren systems, which range in size from 0.2 ha to 20 ha, outlining the effects of spatial overlap as an important ecological constraint on the assembly of interaction would inform the size scale of any conservation efforts. Meaning that, despite its relatively compact size, there could be spatial partitions present within a site that could require different conservation approaches.

Interaction Turnover and Pollinator Community

The importance of species relative abundance on constraining changes in interactions opens the door to exploring how fluctuations in relative abundance across time and space contributes to interaction assembly. The present study displays evidence of a relationship between the fluctuation in relative activity of the pollinator community and formation of interactions in a system broadly. Fluctuation of pollinator activity was only reflective in interaction turnover and not in interaction rewiring or species turnover. This result is likely because pollinator activity contributes to both components. Pollinator activity includes the activity of individuals within a species and unique species. Declines in pollinator activity can mean different, more limited visitation from pollinators and the potential absence of entire species under the surveying conditions. Thus, drops in pollinator activity can cause a change in both interaction rewiring and species turnover that culminates in determining the total interaction turnover. Ultimately, these results imply a sensitivity in interaction turnover to the status and daily activity of the pollinator community.

This relationship between interaction turnover and the activity levels of the pollinator community contradicts the perception that interaction formation and change in network structure is frequently driven by phenological changes in the plant community, either in its abundance or composition (Carstensen et. al., 2014; Simanonok and Burkle, 2014). However, the contradiction likely stems from the difference in time scale being examined. Changes in floral composition and abundances typically occur on a less rapid scale with most plants producing flowers for several weeks. Exceptions of rapid floral loss are possible, such as heavy herbivory or sudden, late spring frosts that can destroy flower resources overnight (CaraDonna and Waser, 2020). At LFSB, there was occasional evidence of isolated sudden flower loss from heavy deer browse, and a late spring frost did occur in mid-April 2020. However, the frost preceded the start of surveys, and an assessment of lost flower resources could not be completed. In contrast, fluctuations in pollinator activity can occur daily with peaks and crashes depending on the weather conditions, such as temperature or precipitation, at a given time. Weather conditions strongly effect the activity of pollinators. Favorable weather conditions for pollinators, sunny, warm days with very little wind. As predicted, we found a positive relationship between median temperature and visitation frequency of pollinator species. Rainfall is also an important variable in explaining the variations in interaction between plants and their pollinators, mainly for bee and fly communities (González et. al., 2009). Also, decreased temperature associated with higher elevations corresponds with higher phenotypic and ecological specialization of plant species in hummingbird driven pollination networks (Dalsgaard et. al., 2009). However, how weather conditions affect plant and pollinator communities and their interactions is relatively unclear (Burkle and Alarón, 2011). Since interactions between plants and pollinators can form at any suitable time and pollinator activity can be so heavily influenced by environmental variables, pollinator activity could become the constraining effect on link realization at particularly short time scales, i.e. day to day or week to week. In the end, the results of the present study suggest an indirect relationship between the formation of interaction networks and weather conditions via the sensitivity of the pollinator community to changes in daily weather variables. Thus, more research on understanding the impacts of dynamic environmental conditions and plant-pollinator network formation is needed.

Conclusion: Future of the Little Fork Shale Barren

This survey of Little Fork Shale Barren revealed that, like any system, it is dynamic. Change is apparent among its plant community and amongst its plant-pollinator networks. Current conditions appear to support an active and stable system of interactions between plant and pollinator species, though the resilience of that system remains unclear. Also, the plant community of LFSB is becoming more diverse and the site, while retaining some of the same populations of plant species as 27 years prior, is supporting new, less shale specific species (Appendix C). Therefore, a question arises: when does a shale barren cease to be a shale barren? This question was posed by Keener (1983**)**, and he expands the question further: can shale barrens form or re-surface? Essentially, the timeline of shale barrens is unknown. They are vulnerable to tree encroachment as biogeographical islands within a landscape of deciduous forest. The present study found signs of functional stability of plant-pollinator networks present in a shale barren in its current state as well as size. However, understanding the effect area has on the formation of interactions and the structure of its plant-pollinator networks is needed and has implications on their conservation. Habitat loss indirectly affects network nestedness via changes in species richness and abundance with decreases in both causing a reduction in network nestedness

(Speisman and Inouye, 2013). But is this true for habitat type conversion, where the surrounding habitat type absorbs the smaller, ecologically unique ecotype? Future studies should focus on determining the area needed to maintain function if spatial partitioning is occurring. Especially since shale barrens vary drastically in size (Keener, 1983). Understanding network architecture's relationship with area would inform protection of shale barren sites and the minimum or maximum area needed for conservation of network function and resilience.

Appendix A

Sampling Completeness

Using the Chao estimator to test sampling completeness for plant-pollinator interactions, we calculated the estimated pollinator richness as observations of floral species were added. We also calculated the number of additional observations needed to reach 80%, 90%, and 99% of estimated species (Chao et. al., 2009). Analyses were completed in R using the ‘vegan’ package (Oksanen et. al., 2012). Sampling completeness for pollinators was estimated to be 42% (85 observed, 100.3 estimated). We calculated that 1,398 observations would be needed to reach 80% completeness, 1,433 observations for 90% completeness, and 1,462 for 99% completeness. This level is lower than other projects studying similar questions (Chacoff et. al., 2012; Devoto et. al., 2012; Simanonok and Burkle, 2014). However, sampling for pollinator richness or interaction level is inherently problematic (Chao et. al., 2009; Chacoff et.al., 2012), and the methods were selected based on the circumstances of the site, our research questions, and the resources and persons capable of completing the study. To reach an 80% sampling completeness would have required a near three-fold increase in sampling effort.

Appendix B

Table of calculated network metric for this study and their definitions.

Network Metric	Definitions
# of plant (P)	Number of plant species in network
# of pollinators (A)	Number of pollinator species and morphospecies
Websize (PxA)	The total possible links for the network; the product of plant species and pollinator species/morphospecies.
Total # of pairwise interactions	The total number of observed links between plant and pollinators
Links per plant	The sum of links for each plant node, average over all plant nodes
Links per pollinator	The sum of links for each pollinator node, average over all pollinator nodes
Total visitations	The total number of observed visitation events made by pollinators to plants
Degree	The number of links connected to a node
Species Strength	Sum of dependencies for a node
Degree Distribution	The frequency distribution of links among nodes
Web Asymmetry	Comparison between communities' sizes (number of nodes) in network; measure of how balanced the communities are. (0-1)
Interaction Strength Asymmetry (ISA)	Measure of dependency between plants and pollinators ((-1)-1)
Nestedness Temperature	Measure of the order of species extinction that would occur in a network: 0 = fix order, 100 = absolutely random extinction order
Nestedness	Level of subset formation in a network (interacting species form subsets) (0-1)
Connectance	The fraction of realized links in a network (0-1)
Specialization (H2)	The degree of specialization of elements within a network; identifies whether there is high or low niche partitioning. (0-1)

Appendix C

Table of average relative cover of three vegetation survey cover categories (bare ground, dense leaf cover, vegetation), mean coverage per species, and importance values (IV) (formula: (mean relative frequency + mean relative cover)/2) for the Little Fork Shale Barren. Species are listed by their importance values in descending order. The ecosystem type of each species is also provided. Ecosystem type was broadly broken down as: shale barren endemic (**endemic**), shale barren near endemic (**near endemic**), characteristic shale barren species (**characteristic**), common species found in shale barrens (but frequently found in other ecotypes) (**common**), general woodland species (**woodland**), or non-native (**exotic**). Plants not identified to species were not assigned an ecosystem type due to variations within genera. *- species detected during 1994 surveys. **-1994 surveys identified *Quercus* spp. for the site.

Coverage of Site	**Relative Cover**
Bare ground	0.251
dense leaf cover	0.303
vegetation (all)	0.445

Vegetation Cover of Site			
Species	**Type**	**Mean Coverage (cover/plot)**	**IV**
*Carex pensylvanica**	characteristic	14.17	0.21548
Antennaria plantagifolia	woodland	7.74	0.11136
Schizachyrium scoparium	characteristic	3.18	0.07143
*Asplenium platyneuron**	common	1.91	0.04776
Pinus sp.*	-	0.79	0.04772
*Scutellaria ovata ssp. rugosa**	near endemic	1.43	0.04037
*Paronychia montana**	near endemic	1.44	0.03996
*Houstonia longifolia**	characteristic	0.74	0.03899
*Vaccinium pallidum**	woodland	2.43	0.03520
Fallopia scandens	woodland	1.38	0.02918
Solidago bicolor	common	1.16	0.02595
*Phlox subulata**	characteristic	1.05	0.02389
Ambrosia artemisiifolia	woodland	1.24	0.02154
Penstemon canescens	common	0.55	0.01968
Acalypha virginica	common	0.52	0.01839
Allium cernuum	common	0.64	0.01673
Sedum glaucophyllum	common	0.81	0.01178
Vitis aestivalis	woodland	0.25	0.01127
Hieracium venosum	common	0.41	0.01102
Erechtites hieraciifolius	woodland	0.29	0.00979
Woodsia obtusa	woodland	0.40	0.00944
Pinus strobus	woodland	0.66	0.00926
Potentilla canadensis	common	0.33	0.00777
*Lespedeza repens**	woodland	0.24	0.00686
Bromus sp.	-	0.27	0.00664
*Pinus virginiana**	characteristic	0.39	0.00642

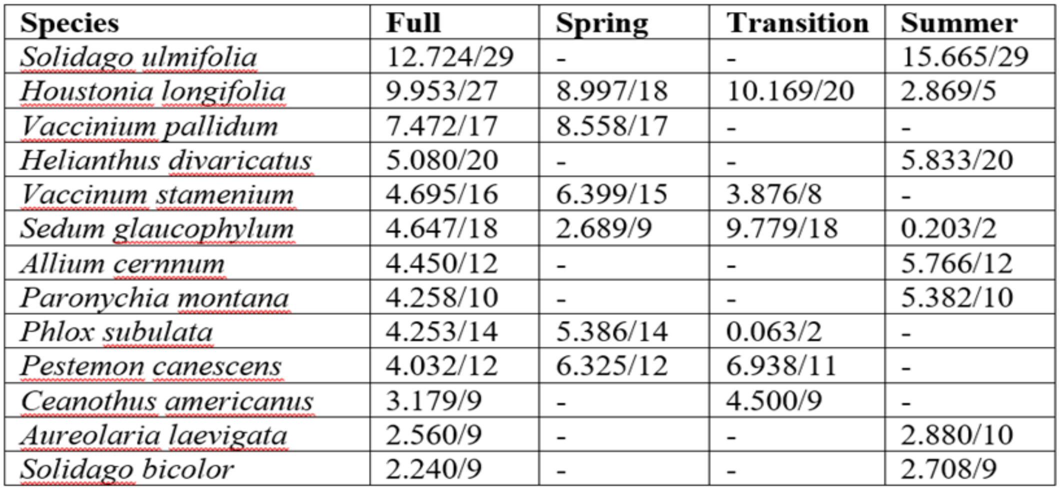
*Quercus montana***	characteristic	0.19	0.00628
*Boechera serotina**	endemic	0.14	0.00625
Dichanthelium boscii	common	0.22	0.00564
Carya sp.	-	0.17	0.00561
Amelanchier sp.	-	0.21	0.00551
Galium circaezans	woodland	0.08	0.00464
Robinia pseudoacacia	common	0.24	0.00439
Solidago ulmifolia	woodland	0.21	0.00413
Rosa carolina	common	0.21	0.00406
Vaccinium stamineum	woodland	0.34	0.00404
Rubus sp.	-	0.10	0.00393
Helianthus divaricatus	woodland	0.28	0.00387
Ceanothus americanus	woodland	0.17	0.00319
*Heuchera alba**	near endemic	0.08	0.00319
Securigera varia	exotic	0.25	0.00307
Amphicarpaea bracteata	woodland	0.08	0.00271
Hedeoma pulegioides	characteristic	0.06	0.00251
Asclepias quadrifolia	woodland	0.04	0.00238
*Quercus velutina***	woodland	0.04	0.00238
Parthenocissus quinquefolia	woodland	0.04	0.00232
Vicia caroliniana	woodland	0.08	0.00229
Crataegus chrysocarpa	common	0.13	0.00226
Symphyotrichum laeve var laeve	woodland	0.13	0.00226
Woodsia sp.	-	0.11	0.00213
Prunus sp.	-	0.04	0.00190
Fraxinus sp.	-	0.04	0.00184
Liriodendron tulipifera	woodland	0.02	0.00164
Rubus phoenicolasius	exotic	0.02	0.00164
Unknown #1_1	-	0.05	0.00148
Ageratina altissima	woodland	0.04	0.00142
Viola sp.	-	0.02	0.00116
Verbascum sp.	-	0.01	0.00109
Geum virginianum	woodland	0.03	0.00081
Oxalis sp.	-	0.03	0.00081
Smilax rotundifolia	woodland	0.03	0.00081
Carya cordiformis	woodland	0.03	0.00074
Silene caroliniana	common	0.02	0.00068
Acer rubrum	woodland	0.01	0.00055
Taraxacum sp.	-	0.01	0.00055

Appendix D

Species level metrics of plant species and pollinator morphospecies observed during monitoring periods at Little Fork Shale Barren (LFSB)

Table D.1.

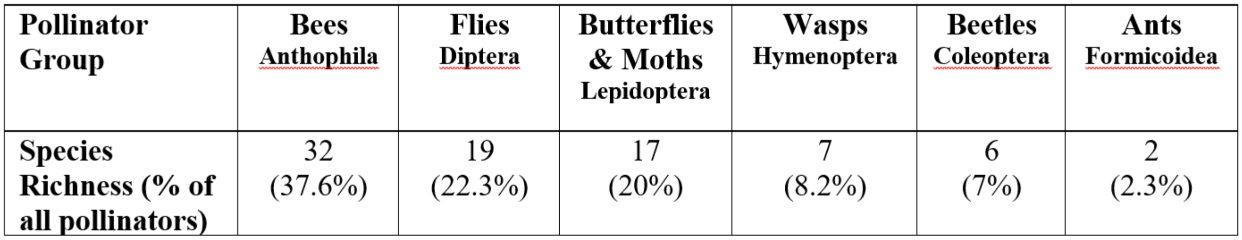
The most prevalent plant species present in the interaction networks constructed for Little Fork Shale Barren (LFSB). Values in table are the interaction strength (sum of dependencies)/degree (number of links) of each species calculated from each network: complete monitoring season of LFSB (full); monitoring periods 01-05, i.e. April 21st to start of June (Spring); monitoring periods 05-08, i.e. start of June to start of July; monitoring periods 08-16, i.e. start of July to September 22nd (Summer). (-) – plant not present in network



Species	**Full**	**Spring**	**Transition**	**Summer**
Solidago ulmifolia	12.724/29	-	-	15.665/29
Houstonia longifolia	9.953/27	8.997/18	10.169/20	2.869/5
Vaccinium pallidum	7.472/17	8.558/17	-	-
Helianthus divaricatus	5.080/20	-	-	5.833/20
Vaccinum stamenium	4.695/16	6.399/15	3.876/8	-
Sedum glaucophylum	4.647/18	2.689/9	9.779/18	0.203/2
Allium cernnum	4.450/12	-	-	5.766/12
Paronychia montana	4.258/10	-	-	5.382/10
Phlox subulata	4.253/14	5.386/14	0.063/2	-
Pestemon canescens	4.032/12	6.325/12	6.938/11	-
Ceanothus americanus	3.179/9	-	4.500/9	-
Aureolaria laevigata	2.560/9	-	-	2.880/10
Solidago bicolor	2.240/9	-	-	2.708/9

Table D.2.

A breakdown of the species richness of each pollinator group as well as their percent representation among all pollinator morphospecies recorded through pollinator observations.



Pollinator Group	**Bees** **Anthophila**	**Flies** **Diptera**	**Butterflies & Moths** **Lepidoptera**	**Wasps** **Hymenoptera**	**Beetles** **Coleoptera**	**Ants** **Formicoidea**
Species Richness (% of all pollinators)	32 (37.6%)	19 (22.3%)	17 (20%)	7 (8.2%)	6 (7%)	2 (2.3%)

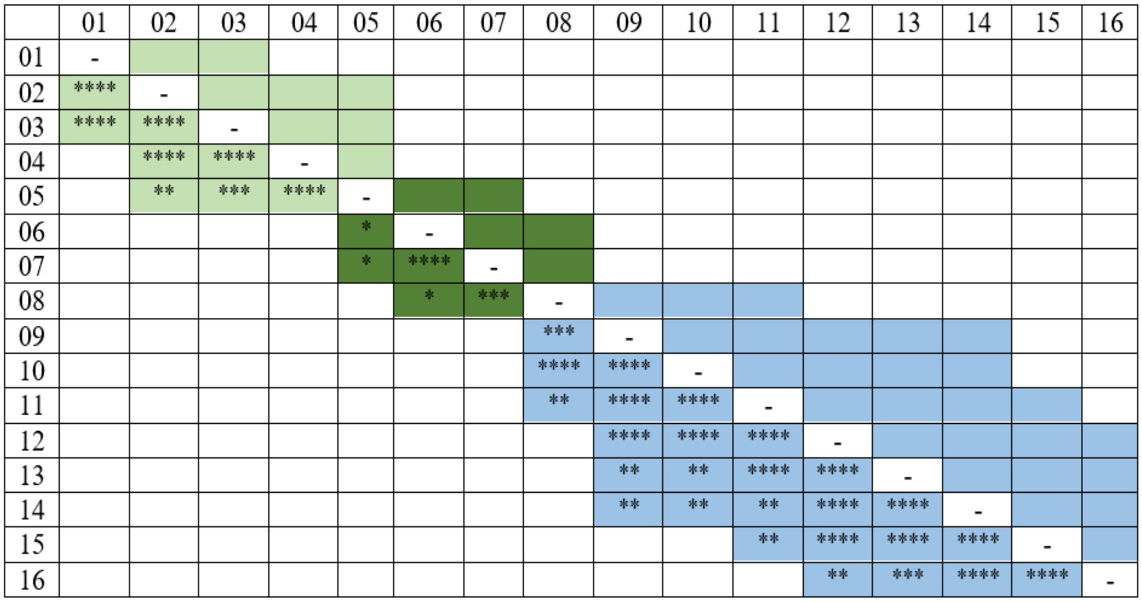
Table D.3.

The most prevalent pollinator morphospecies present in the interaction networks constructed for the Little Fork Shale Barren (LFSB). Values in table are the interaction strength (sum of dependencies)/degree (number of links) of each species calculated from each network: complete monitoring season of LFSB (full); monitoring periods 01-05, i.e. April 21st to start of June (Spring); monitoring periods 05-08, i.e. start of June to start of July; monitoring periods 08-16, i.e. start of July to September 22nd (Summer). (-) – pollinator not present in network.* - member of most represented pollinator group: small bees.

Species	**Full**	**Spring**	**Transition**	**Summer**
Ceratina sp.*	5.990/26	0.860/11	3.597/11	4.145/15
Dailictus sp.*	4.279/25	2.070/11	2.457/11	3.382/13
*Augochlorella aurata**	4.230/22	1.706/12	2.457/9	2.707/10
Battus philenor	2.972/10	1.371/5	1.274/3	1.728/5
Formicoidea	2.569/11	0.913/4	1.477/4	1.586/6
*Augochlora pura**	2.509/14	0.091/1	0.360/4	2.164/10
Bombylius major	1.640/8	1.793/8	0.038/2	-
Halictus sp.*	1.103/9	0.595/4	0.408/5	0.799/4
Augochloropsis sp.*	1.009/10	0.274/5	0.148/2	0.719/4
Bombus impatiens	0.885/9	0.223/3	0.023/1	0.662/6

Appendix E

Monitoring periods matrix (16 MP x 16 MP) representing the full monitoring season at Little Fork Shale Barren (LFSB). Colors correspond to identified phenological units present within the surveying season: spring, i.e. April 21st to start of June (light green), transition period, i.e. start of June to start of July (dark green), and summer, i.e. start of July to September 22nd (light blue). Units were identified using Spearman Correlation between monitoring periods (columns and rows). Asterisks in cells represent significance level of Spearman Correlation: * - p≤ 0.05 , ** - p≤ 0.01, *** - p≤ 0.001, **** p≤ 0.0001. Significance symbols are not reflected across the no value (-) line, but networks colors are reflected to improve identification of highly correlated monitoring periods.



	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16
01	-															
02	****	-														
03	****	****	-													
04		****	****	-												
05		**	***	****	-											
06					*	-										
07					*	****	-									
08						*	***	-								
09								***	-							
10								****	****	-						
11								**	****	****	-					
12									****	****	****	-				
13									**	**	****	****	-			
14									**	**	**	****	****	-		
15											**	****	****	****	-	
16												**	***	****	****	-

Appendix F

Scientific names and network code of plants species flowering at Little Fork Shale Barren.

Genus	**Species**	**CODE**
Ageratina	*altissima*	**AGAL**
Allium	*cernuum*	**ALCE**
Amphicarpaea	*bracteata*	**AMBR**
Antennaria	*plantaginifolia*	**ANPL**
Asclepias	*quadrifolia*	**ASQU**
Asclepias	*tuberosa*	**ASTU**
Aureolaria	*laevigata*	**AULA**
Boechera	*canadensis*	**BOCA**
Boechera	*laevigata*	**BOLA**
Boechera	*serotina*	**BOSE**
Ceanothus	*americanus*	**CEAM**
Clematis	*albicoma*	**CLAL**
Claytonia	*virginica*	**CLVI**
Conyza	*canadensis* var *pusilla*	**COCA**
Corydalis	*flava*	**COFL**
Dianthus	*armeria* ssp. *armeria*	**DIAR**
Erechtites	*hieraciifolius*	**ERHI**
Ergieron	*strigosus* var *strigosus*	**ERST**
Euphorbia	*corollata*	**EUCO**
Fallopia	*scandens*	**FASC**
Galium	*aprine*	**GAAP**
Galium	*circaezans*	**GACI**
Geum	*virginiana*	**GEVI**
Hedeoma	*pulegioides*	**HEPU**
Heuchera	*alba*	**HEAL**
Helianthus	*divaricatus*	**HEDI**
Hieracium	*venosum*	**HIVE**
Houstonia	*Lonigfolia* (*tenuifolia*)	**HOTE**
Lespedeza	*repens*	**LERE**
Paronychia	*montana*	**PAMO**
Penstemon	*canescens*	**PECA**
Persicaria	*longiseta*	**PELO**
Phlox	*subulata*	**PHSU**
Potentilla	*canadensis*	**POCA**
Polygonatum	*pubescens*	**POPU**
Rosa	*carolina*	**ROCA**
Rubus	*flagellaris*	**RUFL**
Scutellaria	*ovata*	**SCOV**
Securigera	*varia*	**SEVA**

Sedum	*glaucophyllum*	**SEGL**
Silene	*caroliniana*	**SICA**
Solidago	*bicolor*	**SOBI**
Solidago	*curtisii*	**SOCU**
Solidago	*ulmifolia*	**SOUL**
Symphyotrichium	*ericoides*	**SYER**
Symphyotrichium	*laeve*	**SYLA**
Taenidia	*montana*	**TAMO**
Triodanis	*perfoliata*	**TRPE**
Vaccinium	*pallidum*	**VAPA**
Vaccinium	*stamineum*	**VAST**
Vicia	*caroliniana*	**VICA**

Appendix G

Scientific names and network code of pollinator species and morphospecies at Little Fork Shale Barren. Bold text indicates the most specific taxonomic level identified.

Order	**Superfamily**	**Family**	**Subfamily**	**Genus**	**Subgenus**	**Species**	**CODE**
Lepidoptera		Hesperiidae		***Erynnis***		***juvenalis***	**JUVE**
Lepidoptera		Hesperiidae		***Erynnis***		***brizo***	**SLEEP**
Lepidoptera		Hesperiidae		***Erynnis***		***icelius***	**DREAM**
Lepidoptera		Hesperiidae		***Pholisora***		***catullus***	**PHOL**
Lepidoptera		Hesperiidae		***Thorybes***		***pylades***	**THOR**
Lepidoptera		Hesperiidae		***Epargyreus***		***clarus***	**SISPOT**
Lepidoptera		Hesperiidae		***Poanes***		***hobomok***	**HOBO**
Lepidoptera		Pieridae		***Anthocharis***		***midea***	**OTIP**
Lepidoptera		Pieridae		***Pieris***		***rapae***	**CABB**
Lepidoptera		Nymphalidae		***Vanessa***		***virginiensis***	**VANES**
Lepidoptera		Nymphalidae		***Speyeria***		***cybele***	**FRIT**
Lepidoptera		Lycaenidae		***Celastrina***		***ladon***	**CELA**
Lepidoptera		Nymphalidae		***Chlosyne***		***nycteis***	**CHEC**
Lepidoptera		Hesperiidae		***Amblyscirtes***		***vialis***	**AMBL**
Lepidoptera		Papilionidae		***Battus***		***philenor***	**PIPE**
Lepidoptera		Lycaenidae		***Cupido***		***comyntas***	**CUPI**
Lepidoptera		Zygaenidae		***Pyromorpha***		***dimidiata***	**PYRO**
Hymenoptera		Colletidae		***Hylaeus***			**MASK**
Hymenoptera		Colletidae		***Colletes***			**COLL**

Order	**Superfamily**	**Family**	**Subfamily**	**Genus**	**Subgenus**	**Species**	**CODE**
Hymenoptera		Halictidae		***Augochlora***			**CHLORA**
Hymenoptera		Halictidae		***Augochlorella***			**ELLA**
Hymenoptera		Halictidae		***Augochloropsis***			**OPSIS**
Hymenoptera		**Halictidae**					**SWEAT**
Hymenoptera		Halictidae		***Halictus***			**HALI**
Hymenoptera		Halictidae		***Lasioglossum***	***Lasioglossum***		**LASIO**
Hymenoptera		Halictidae		***Lasioglossum***	***Dialictus***		**DIAL**
Hymenoptera		Apidae		***Apis***		***mellifera***	**APIS**
Hymenoptera		Apidae		***Ceratina***			**CERA**
Hymenoptera		Apidae		***Nomada***		sp1	**NOMA**
Hymenoptera		Apidae		***Bombus***			**BUMB**
Hymenoptera		Apidae		***Bombus***		***griseocollis***	**BOMGRIS**
Hymenoptera		Apidae		***Bombus***		***impatiens***	**BOMIM**
Hymenoptera		Apidae		***Bombus***		***vagans***	**VAGA**
Hymenoptera		Apidae		***Bombus***		***bimaculatus***	**BIMAC**
Hymenoptera		Apidae		***Xylocopa***		***virginica***	**CARP**
Hymenoptera		Apidae		***Habropoda***			**HABR**
Hymenoptera		Andrenidae		***Andrena***		***carlini***	**CARL**
Hymenoptera		Andrenidae		***Andrena***		***dunningi***	**DUNN**

Order	**Superfamily**	**Family**	**Subfamily**	**Genus**	**Subgenus**	**Species**	**CODE**
Hymenoptera		Andrenidae		***Pseudopanurgus***			**PSEU**
Hymenoptera		Megachilidae		***Osmia***			**OSMI**
Hymenoptera		Megachilidae		***Osmia***			**OSFU**
Hymenoptera		Megachilidae		***Osmia***		***bucephala***	**BUFF**
Hymenoptera		Megachilidae		***Megachile***	***Chelostomoides***		**MEGA**
Hymenoptera		Megachilidae		***Stelis***			**STEL**
Hymenoptera		Megachilidae		***Megachile***			**CHEL**
Hymenoptera		Megachilidae		***Coelioxys***			**COEL**
Hymenoptera		Megachilidae		***Hoplitis***			**HOPL**
Diptera		Syrphidae					**DAFL**
Diptera		Syrphidae		***Syrphus***			**SYRP**
Diptera		Syrphidae		***Spilomyia***			**SPIL**
Diptera		Syrphidae		***Eupeodes***			**EUPE**
Diptera		Syrphidae		***Taxomerus***			**TAXO**
Diptera		Syrphidae		***Milesia***			**MILE**
Diptera		Syrphidae		***Mallota***			**MALL**
Diptera		Syrphidae		***Paragus***			**PARA**
Diptera		Syrphidae		***Eristlina***			**ERIS**
Diptera		Bombyliidae		***Bombylius***		***major***	**BFLY**

Order	Superfamily	Family	Subfamily	Genus	Subgenus	Species	CODE
Diptera		Bombyliidae		***Geron***			**GERO**
Diptera		Bombyliidae		***Hemipenthes***			**HEMI**
Diptera		**Mydidae**					**MYDA**
Diptera		**Tachinidae**					**TACH**
Diptera		**Rhinophoridae**					**WOOD**
Diptera		Tachinidae		***Gymnosoma***			**GYMN**
Diptera		Syrphidae		***Ocyptamus***			**OCYP**
Diptera							**FLYY**
Diptera		Bombyliidae		***Villa***			**VILL**
Hymenoptera							**WASP**
Hymenoptera		Vespidae	**Vespidae**				**SOWAS**
Hymenoptera		Vespidae	**Polistinae**				**REDSO**
Hymenoptera		Vespidae	**Eumeninae**				**POTT**
Hymenoptera		Crabronidae		***Cerceris***			**CERC**
Hymenoptera		Sphecidae		***Ammophila***			**AMMO**
Hymenoptera		**Formicoidea**					**BLAC**
Hymenoptera		**Formicoidea**					**RED**
Coleoptera		**Cantharidae**					**SOLD**
Coleoptera		Mordellidae		***Mordellistena***			**MORD**

Order	Superfamily	Family	Subfamily	Genus	Subgenus	Species	CODE
Coleoptera		**Chrysomelidae**					**BLSP**
Coleoptera		**Chrysomelidae**					**CHRY**
Coleoptera		Chrysomelidae		***Oulema***			**OULE**
Coleoptera	**Curculionoidea**						**WEEV**

Appendix H

Table of values provided following Akaike information criterion (AIC) analyses. Models are linear regressions considering: median temperature (Temp), median relative humidity (RH), both temperature and relative humidity (Temp+RH), and any interaction between the two variables (Temp*RH).

Models	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Temperature (Temp)	3	192.69	0.00	0.67	0.67	-92.26
Temp*RH	5	195.48	2.78	0.17	0.83	-89.40
Temp+RH	4	196.26	3.56	0.11	0.94	-92.13
Relative Humidity (RH)	3	197.60	4.91	0.06	1.00	-94.71

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