

SPATIOTEMPORAL DYNAMICS OF BUTTERFLIES AND THEIR FLORAL RESOURCES

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Adrienne Kendra Antonsen

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Adrienne Kendra Antonsen

The Supervisory Committee certifies that this *disquisition* complies with North Dakota
State University's regulations and meets the accepted standards for the degree of

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SUPERVISORY COMMITTEE:

Jason Harmon

Chair

Torre Hovick

Ryan Limb

Benjamin Geaumont

Approved:

07/02/2020

Date

Frank Casey

Department Chair

ABSTRACT

Butterflies fulfill a unique role among insect pollinators as long-distance flyers. This makes butterflies particularly valuable as vectors of genetic diversity among spatially isolated plant populations. Like many insects, though, butterfly populations have experienced significant declines in recent years. To help inform conservation efforts, and to investigate community and species level dynamics, I studied butterflies and their floral resources as part of a three year pollinator survey across the state of North Dakota. At the community level, I analyzed butterfly-flower interaction networks across space and time. I then examined the specialization of individual species within those networks and their contributions to network structure. I also evaluated spatial and temporal distribution patterns of monarch butterflies, regal fritillaries, and their plant resources. Results revealed dynamic spatiotemporal relationships between butterflies and their plant resources that have important implications for conservation efforts and the study of ecological communities.

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DEDICATION

This thesis is dedicated to my sweet fur baby, Prince, the best little data entry helper and writing buddy there ever was.

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1. PLANT-POLLINATOR INTERACTION NETWORKS: WHAT QUESTIONS, TAXA, AND REGIONS ARE WE STUDYING?

1.1. Introduction

Plant-pollinator interactions have long-fascinated ecologists (Darwin 1878). In recent years these interactions have received even more attention from both ecologists and the general public due to rising awareness of the threats that pollinators face and the ecological services they provide (Potts et al 2010). Despite the importance of these interactions, their study at the community level has long been inhibited by a lack of analytical methods capable of interpreting such interconnected webs. Network ecology has recently introduced tools that now allow the statistical analysis of these complex ecological systems, and the predictive ability of network models continues to grow (Poisot et al 2016).

Research on these pollination networks began at the single network scale, analyzing the properties of an individual interaction network that describes one group of interacting plant and pollinator species (Bascompte 2007, Ings et al 2009, Olesen et al 2006). Studies were primarily focused on characterizing network structure and attempting to find consistent patterns in network organization (Bascompte and Jordano 2007, Jordano et al 2003, Vazquez et al 2009). As the field progressed, research moved toward analyzing multiple networks against each other using explicit hypothesis testing to discern how plant-pollinator interactions vary along environmental gradients or between experimental treatments (Valdovinos 2019). Studying plant-pollinator interaction networks across such gradients can reveal important ecological community dynamics that have implications for coevolutionary processes and extinction risk (Tylianakis and Morris 2017).

Previous reviews have provided insights into the history, methodology, applications, and findings of pollination network research (Bascompte 2007, Ings et al 2009, Olesen et al 2006). Authors have also discussed the theoretical evolution of the field and suggested potential future directions (Dormann et al 2017, Knight et al 2018, Poisot et al 2016). Invaluable how-to guides, from methodological techniques (Delmas et al 2019, Dormann 2020, Pellissier et al 2018) to practical applications (Elle et al 2012, Kaiser-Bunbury and Bluethgen 2015), have also been published to aid researchers interested in pursuing network analysis research. In addition, several attempts to synthesize the findings of interaction network research have been performed, including meta-analyses of networks' ability to indicate environmental quality (Rollin et al 2016, Soares et al 2017), network response to habitat loss (Ferreira et al 2013, Fortuna et al 2013), and spatiotemporal variation among networks (Burkle and Alarcon 2011, Trojelsgaard and Olesen 2016). What has been lacking so far, though, is a systematic review of the types of hypothesis-driven questions researchers have asked by comparing two or more pollination networks that vary across a gradient or treatment.

It is my goal to illuminate the multitude of research avenues within the field of comparative plant-pollinator network ecology and identify areas in need of further study. I aim to do this by systematically assessing the available published plant-pollinator network research and synthesizing:

1. The types of questions that have been studied.
2. The pollinator taxa that have been included in these studies.
3. The regions where this research has taken place.

1.2. Methods

To compile published plant-pollinator network research articles I performed a comprehensive literature search between December of 2019 and May of 2020. I used the topic query (plant* AND pollinat* AND network*) within all databases on Web of Science. Of the roughly 2,000 results, I selected papers that included network analysis of novel empirical plant-pollinator interaction data collected across gradients or treatments. I included both visitation networks, where interaction data is collected by visually observing contact between floral visitors and the reproductive parts of a flower, and pollen networks, where interaction data is collected by identifying the pollen present on pollinator specimens. I excluded articles that focused on simulations, models, or informing methodology, that analyzed pollination efficacy by comparing visitation and pollen networks, or that conducted a meta-analysis of previously published data.

I analyzed the 204 studies that remained (Appendix A). I recorded the following methodological data from each article: whether the study was observational or experimental (or both), the plant-pollinator interaction type recorded (visitation, pollen, or both), and the independent variable(s) networks were compared across. Next, I recorded the taxonomic orders and classes of the pollinator taxa that were included in each study, referring to appendices and supplemental material when orders were not stated within the article text. If orders could not be determined through either the text or supplementary material they were recorded as “Unlisted”. Finally, I recorded the region each study was performed in at the continental, latitudinal, country, and habitat level. Latitude was categorized according to the following zones: tropical (<23.27°), subtropical (23.27°-35.00°), temperate (35.00°-66.33°), polar (>66.33°), or multiple. Habitat was

categorized as cage experiment, crop, dune, forest, marginal (including fallows, field margins, and roadsides), montane meadow, grassland, scrubland, urban, wetland, or multiple.

1.3. Results

1.3.1. Questions

The independent variables used by researchers were grouped into 15 distinct categories (Table 1.1). There was not an overwhelming bias toward any particular variable or question. Instead, studies fell along a relatively even distribution of research topics (Figure 1.1). Questions were posed at varying scales, including studies of multiple communities across expansive gradients, comparisons between sites at the regional level, differences in within-community assemblages, and species-level trait variation.

Table 1.1. Plant-pollinator network independent variables. Each variable that plant-pollinator networks were compared across was classified as belonging to one of 15 categories. Variable synonyms and sub-categories that were studied in the reviewed articles are listed.

Independent Variable	Synonyms and Sub-Categories Included
Altitude	Elevation.
Anthropogenic Disturbance	Urbanization; development; artificial light; human foot traffic.
Climate	Precipitation; temperature; wind.
Community Composition (Plants)	Relative abundance, richness, diversity, and/or identities of all or a subset of plant species.
Community Composition (Pollinators)	Relative abundance, richness, diversity, and/or identities of all or a subset of pollinator species.
Community Composition (Plants and Pollinators)	Diversity, evenness, or turnover of plant-pollinator species assemblages.
Habitat	Classification of environmental community, or biotope, at varying levels of specificity. Broadly, habitat types included cage experiment, crop, dune, forest, marginal (roadsides, ruderal), montane meadow, grassland, scrubland, rocky outcrops, urban, and wetland. Includes studies conducted along successional gradients.
Invasive Species	Presence/absence and/or densities of invasive or exotic plants and/or pollinators (specific sub-category of community composition).
Land Management	Protection status; logging interval; grazing intensity; farming system (conventional or organic) or intensity; mechanical disturbance; pesticide usage; nitrogen enhancement.
Landscape Configuration	Fragmentation; patch size; proportions of surrounding land cover types; distance to environmental feature (e.g. nearest forest edge).
Natural Disturbance	Fire; flooding; volcanic eruption; herbivory.
Restoration	Restoration status/stage.
Space	Scale (local or regional); latitude; distance between sites; geographic location.
Species Traits	Morphological, behavioral, chemical, or developmental traits of plants and/or pollinators.
Time	Time of day; day; week; month; season; year; decade; century.

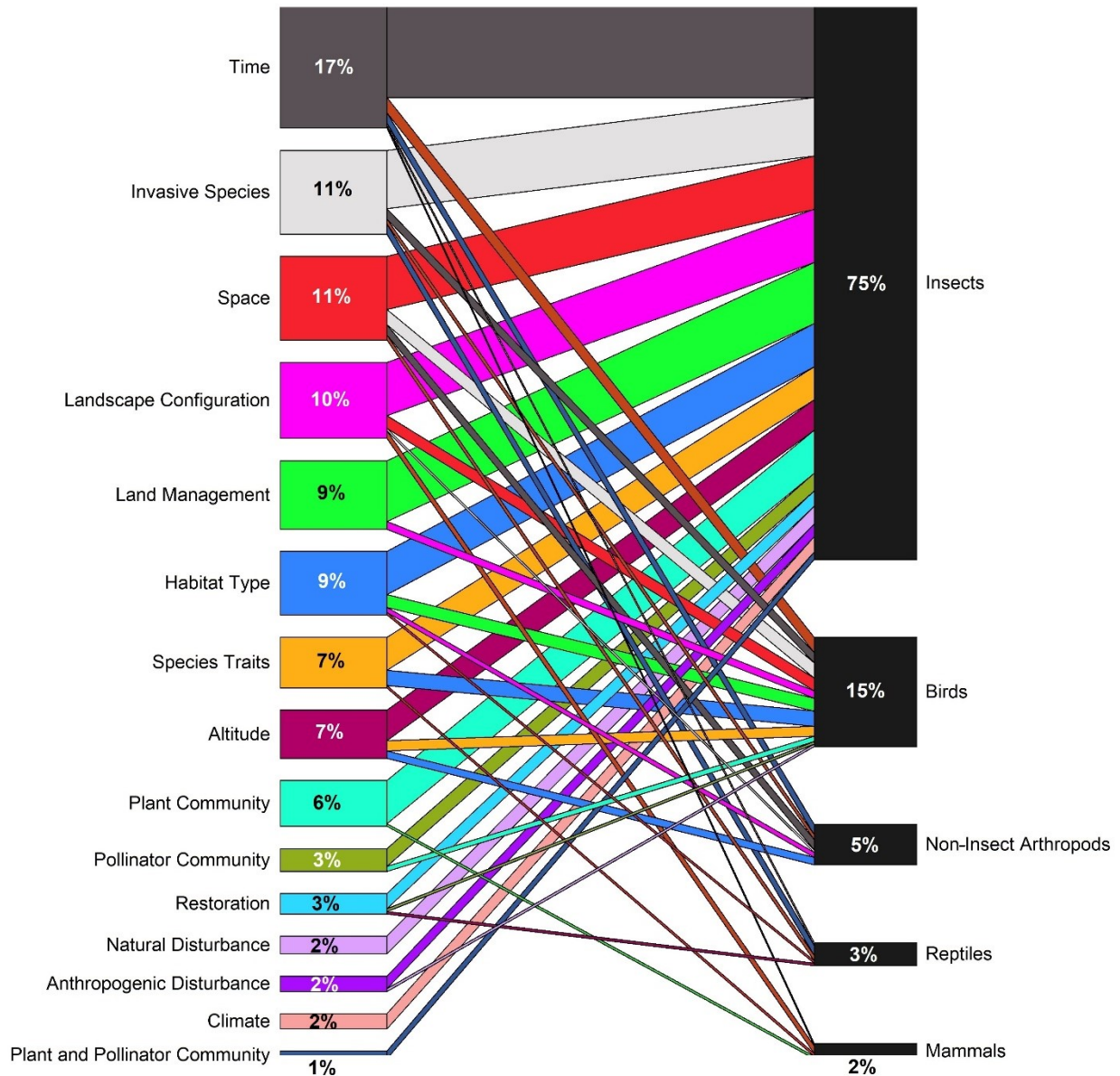


Figure 1.1. Plant-pollinator network questions and taxa. Bipartite network graphs are a commonly used visual aid in plant-pollinator networks that feature plant species on one side, pollinator species on the other, and weighted links connecting them to show interaction frequency. Here I use the visual tool to illustrate the types of variables that plant-pollinator networks have compared by (left, defined in further detail in Table 1), and the types of pollinators the questions have been asked of (right). Bars are sized relative to and labeled with the percentage at which each variable or taxa was included among all studies. Links are colored according to the independent variable studied to illustrate the diversity of questions posed to each pollinator group. Graphic created in R using the bipartite package (Dormann et al 2008).

1.3.2. Taxa

Taxa that were studied with plant-pollinator networks belonged to the following taxonomic classes: insects (*Insecta*), non-insect arthropods (*Arthropoda*), birds (*Aves*), mammals, (*Mammalia*), and reptiles (*Reptilia*). The majority of articles studied insect pollinators. All 15 independent variable categories were studied in relation to insects (Table 1.1, Figure 1.1). The “big four” insect orders (Hymenoptera, Diptera, Lepidoptera, and Coleoptera) that comprise the majority of all flower visiting insects (Krenn et al 2005) received the most research attention, with 93% of the reviewed articles including at least one of them. The remaining floral-visitors belonged to 25 other taxonomic orders (Figure 1.2). Species richness of an order (Gill et al 2020, GBIF Secretariat 2019, Uetz and Etzold 1996, Zhang 2011) was significantly related to the number of times that order was included as a pollinator in a study (Figure 1.3).

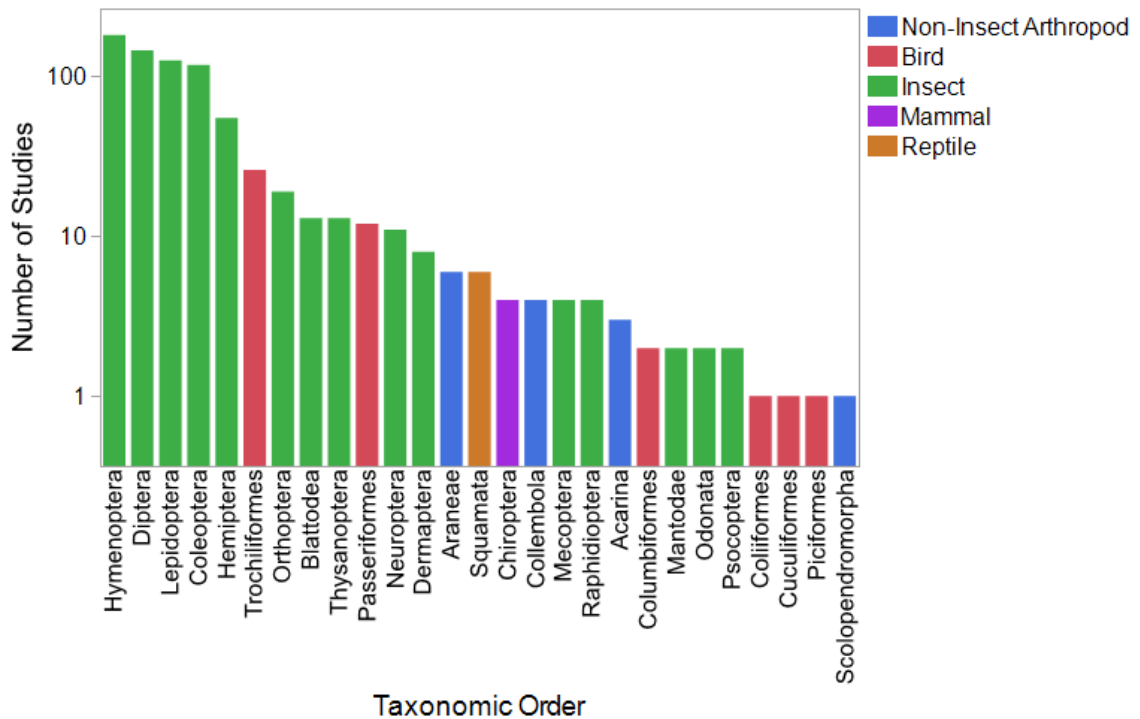


Figure 1.2. Taxonomic orders studied. Pollinator taxa in descending order from most to least often included in the reviewed studies. Y axis displayed on log scale for clarity.

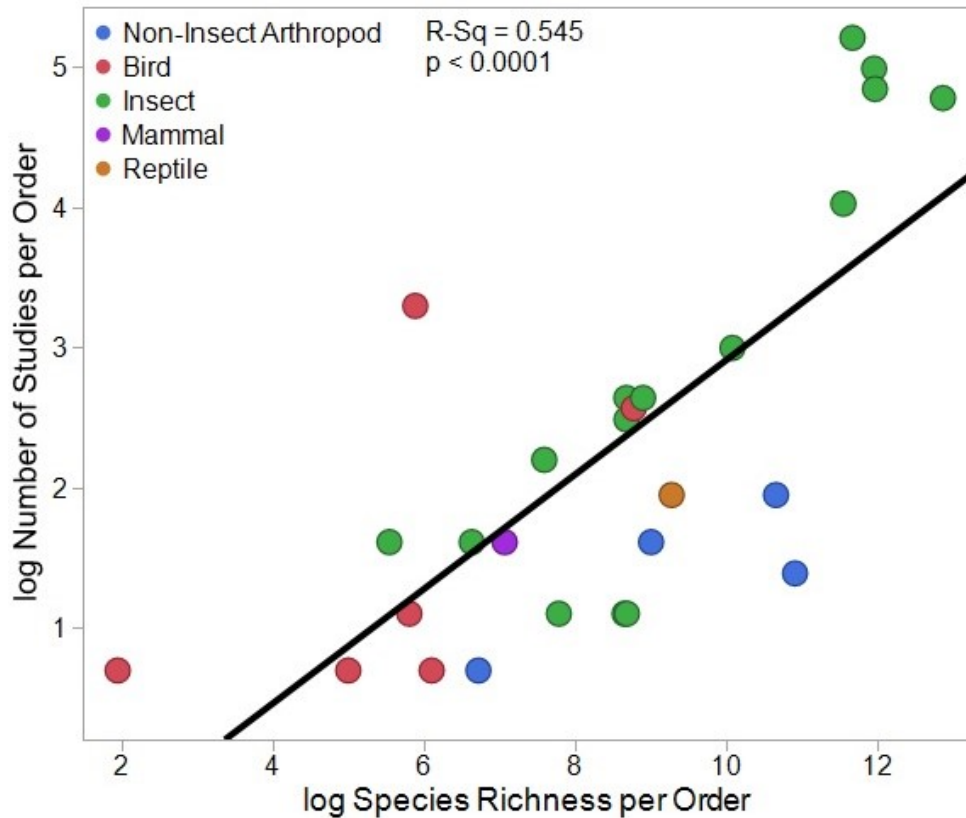


Figure 1.3. Number of studies and species richness of taxonomic orders. The number of times a pollinator order was included in a network study was significantly related to the species richness of that order.

1.3.3. Regions

The reviewed network studies utilized plant-pollinator interaction data collected worldwide from every continent except Antarctica (Figure 1.4). Most studies were conducted in Europe (34%), followed by North America (23%), South America (18%), Africa (12%), Asia (6%), and Oceania (2%). Studies including data collected from multiple continents comprised the remaining 3% of studies. By latitude, the majority of studies were conducted in temperate ecosystems (54%), followed by tropical (22%), subtropical (18%), and polar systems (2%). Studies including data from multiple latitude zones made up 4% of studies.

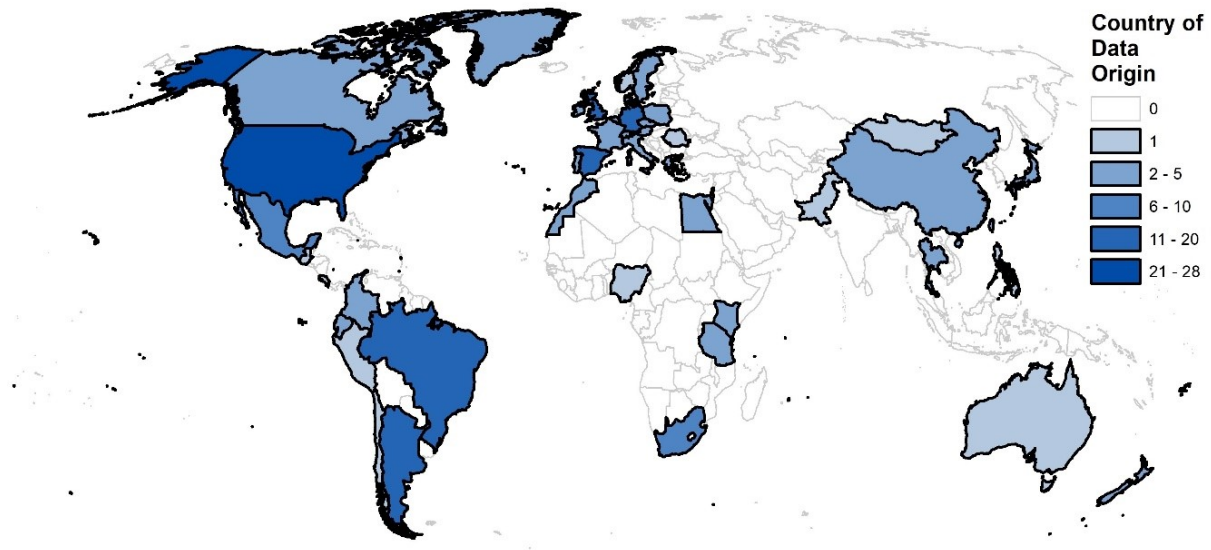


Figure 1.4. Geographic origin of plant-pollinator network data. Multi-network studies of plant-pollinator interactions have been conducted worldwide, with the highest densities of data collected in Europe and the Americas.

Studies were conducted in a variety of habitats. Most studies took place in scrublands (22%), grasslands (20%), and forests (15%). Other studies took place in montane meadows (5%), crops (4%), marginal landscapes (including fallows, field margins, and roadsides, 4%), dunes (2%), urban environments (1%), and cage experiments (1%). A single study (0.5%) was conducted in a wetland system. A large proportion of studies collected and analyzed interaction data from multiple environments (22%). Finally, 2% of studies did not list any information about the environmental characteristics where research took place.

1.4. Discussion

As the field of ecological network research has expanded, so has the diversity of study systems. In this literature review I have sought to quantify and categorize the questions, taxa, and regions that have been studied with plant-pollinator networks with the intent to summarize the state of the field and reveal areas in need of future study.

1.4.1. Questions

It is clear that many lines of inquiry have been pursued in plant-pollinator network ecology. Beyond the independent variables studied, several additional methodological nuances distinguished studies from one another. For instance, species can be studied at a taxonomic group or at the individual level. Interaction networks with nodes representing individuals of a single pollinator species, instead of multiple species in a community, can be used to analyze floral constancy behavior of pollinators (Pornon et al 2019) as well as arthropod community dynamics among individual plants (Kuppler et al 2016). Another important methodological aspect is how studies grouped their interaction data into networks. Some studies analyzed site-level networks, while others combined multiple sites of the same treatment together. Temporal aspects are particularly important given species phenologies. If networks are separated by treatment but aggregated across years, for example, then the lack of links between species that would never co-occur in time will affect how well network specialization calculations reflect the actual community and species in question (Sajjad et al 2017). Designing effective interaction network studies requires careful attention to the selection of appropriate methodology for the question being asked.

The articles I reviewed asked questions that have important implications for plant and pollinator conservation. Climatic variables, invasive species, and natural and anthropogenic disturbances are all currently causing disruptions in pollination interaction networks (Dalsgaard 2020, Jamieson et al 2017, Nicholson and Egan 2020, Scott-Brown and Koch 2020). Network research centered around those variables provides valuable insight into how pollination networks may respond to changing environmental conditions. Plants and pollinators are also experiencing spatiotemporal shifts in response to global change that are resulting in novel communities

(Rafferty 2017), making network studies across spatial, temporal, and community compositional gradients particularly important. Meanwhile, studies on restoration efforts and land management practices that best support interacting plants and pollinators help inform steps we can take to protect these communities from upcoming challenges.

1.4.2. Taxa

A diverse suite of flower-visiting taxa have been studied with plant-pollinator networks, but the vast majority of research has focused on bees, flies, butterflies, and beetles. While the overwhelming dominance of these four orders may initially appear as favoritism, it likely reflects their status as the most common and species-rich of all floral visitors (Krenn et al 2005, Zhang 2011). In fact, when all pollinator orders are viewed together, a significant relationship appears between the species richness of an order and the frequency of its appearance within the reviewed studies (Figure 3). Consequently, existing research on the network dynamics of a particular pollinator taxon is largely proportional to that taxon's abundance.

While this may accurately reflect the overall community of floral-visitors, it leaves a dearth of knowledge for less abundant taxa that also provide important pollination services (Regan et al 2015). For instance, bats are the most important vertebrate pollinator in terms of plant reproductive success (Ratto et al 2018) yet only four of the reviewed studies included bats in their network data (de Santiago-Hernandez et al 2019, Sritongchuay and Bumrungsri 2016, Sritongchuay et al 2019a, Sritongchuay et al 2019b). Similarly, moths represent the majority of nocturnal pollinators and many plant species are specialized specifically for pollination by moths (Hahn and Bruhl 2016), yet only five studies included nocturnal moths (Banza et al 2019, Devoto et al 2011, Hembry et al 2018, Knop et al 2017, Sazatornil et al 2016). Beyond the potential conservation applications of such data, important ecological processes will likely be

revealed when comparing daytime and nighttime networks due to the vastly different floral-seeking behavior of diurnal and nocturnal pollinators, namely the use of olfactory versus visual cues. Despite the difficulties of collecting interaction data under the dark of night, nocturnal taxa warrant increased attention in plant-pollinator network research.

In addition to information lacking on critical taxa, some studies did not list the identities of the taxa included in their networks at all and simply lumped them together as “plants” and “pollinators”. Other times this information was buried within supplementary data tables. Care should be taken in future studies to explicitly identify the pollinators included in analyses because different taxa can behave very differently within interaction networks (Rodriguez-Girones and Santamaria 2010). If the field of network ecology intends to continue advancing, we must be able to look deeper at within-network dynamic comparisons. To do this, knowing the species compositions of networks is vital.

1.4.3. Regions

The imbalanced spatial distribution of network data that has been analyzed thus far also stunts our understanding of pollination networks. Pollination network research is particularly lacking in much of Africa and in northern and southeastern Asia (Figure 4). Further, studies conducted in anthropogenic landscapes like crops, marginal lands, and urban centers are vastly dwarfed by networks studied in more natural systems. These regions and environments should be made a priority in network research to not only expand our understanding of plant-pollinator interactions worldwide but also reflect the impact rapid expansion of human development will continue to have on these communities.

1.5. Conclusions

Plants, pollinators, and the interactions between them offer a myriad of potential research avenues. The explosion in plant-pollinator network studies in the short time since ecological network tools were introduced is a testament to this. This review has highlighted the multitude of questions that have been asked of pollination networks thus far, yet this is likely just the beginning of a rapidly advancing field of inquiry. Plant-pollinator systems that have received significant network research attention present a body of knowledge that can be built upon by asking increasingly complex questions. Variables, taxa, and regions that have been neglected thus-far, on the other hand, offer systems ripe for exploration. By expanding the communities we are studying with interaction networks we will be able to develop a deeper understanding and appreciation of the intertwined dynamics of plants and their pollinators.

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2. SPATIOTEMPORAL DYNAMICS OF BUTTERFLY-FLOWER INTERACTION NETWORKS

2.1. Introduction

Biological communities are complex systems composed of dynamic parts and fluctuating interactions. This complexity poses challenges to the study of entire communities. Plant and insect communities, and the interactions between them, can be particularly daunting to study due to the sheer magnitude of species and individuals involved. Over half of all described species belong to plants and insects (Futuyma and Agrawal 2009). Meanwhile, insects contribute a very small percentage of the Earth's total biomass (Yang and Gratton 2014). The diminutive size and innumerable diversity of insects makes the study of their community-level dynamics especially formidable. However, increasingly useful tools have recently been developed that allow us to study plants and insects in powerful ways.

One tool increasingly used to study the relationships between plants and insects in a community is the interaction network. At its simplest, the interaction network shows what species are interacting and at what frequency. A principal goal of studying such interaction networks is to reveal the processes that bind biological communities together (Leger et al 2015). With origins in food web theory, interaction networks quantify the identity and magnitude of the links formed between two groups of interacting organisms. Networks can represent all types of interactions along the antagonism-mutualism spectrum, and can include any number of interacting trophic levels.

Bipartite networks are comprised of links between, and not within, two discrete and non-overlapping groups of individual nodes (Beckett 2016, Guimera et al 2007, Larremore et al 2014). Among insects and plants, bipartite networks can represent plant-herbivore or plant-

pollinator interactions. In these bipartite networks, the nodes belonging to both the upper and lower categorical levels typically represent species (Kaiser-Bunbury and Bluethgen 2015, Pellissier et al 2018). Insect-plant networks can also be composed of interactions between individuals (Pornon et al 2019).

Once created, networks can be analyzed using a variety of different metrics. Each metric provides information about the interacting ecological system at different levels including the whole system, groups, species, interactions, and individuals (Delmas 2018). For example, network-level metrics quantify the structure of the entire interacting community. One important network-level metric, network specialization (H_2'), uses interaction frequencies to calculate how selective species are in their interactions across an entire network (Bluethgen et al 2006). H_2' can then be compared between networks to assess similarities and differences in community specialization. Another prominent metric, modularity (Q), measures the level of compartmentalization within a network of subsets, or modules, of species that interact more closely with each other than with species outside of their module (Olesen et al 2007). The species composition and structure of modules can give insight into community assembly, co-existence, and stability (Leger et al 2015, Thebault and Fontaine 2010).

Species-level metrics can be compared both within and between interaction networks. Metrics at this level focus on the position and role of a species within an interaction network, and they can illuminate unique facets of a species' ecological functioning (Delmas et al 2018). Among-module connectivity (c) and within-module degree (z) characterize a species in relation to the modular structure of the overarching network (Olesen et al 2007). Node strength, also known as species strength, represents how influential a species is on the opposite group of species (Bascompte et al 2006). For instance, the node strength of a pollinator species indicates

how dependent the overall floral community is on that pollinator's services. Specialization (d') is the species-level equivalent of network specialization ($H2'$), and quantifies the selectivity of individual species (Blüthgen 2006).

Studying how these species-level measures vary within communities of similar compositions along environmental gradients can reveal potential mechanisms behind variation in species interactions (Delmas et al 2018). Floral visitation networks are often studied along temporal gradients. The temporal scale at which networks are analyzed can have a large impact on results and interpretations. For instance, combining all plant-insect interactions from a multi-year study can mask within-year patterns, leading to potential misinterpretations of network structural properties and species roles. Although plant-pollinator networks typically maintain similar network-level characteristics between years, there is often significant annual variation in the composition of species, their interactions, and the resulting values of species-level metrics (Alarcon et al 2008, Chacoff et al 2018, Dupont et al 2009, Olesen et al 2011, Petanidou et al 2008). Further, floral-visitation networks also often demonstrate within-year variation. As a season progresses and species turnover occurs based on phenology, the identity and frequency of interacting species pairs change and impact both network- and species-level characteristics (Arroyo-Correa et al 2019, Basilio et al 2006, Bendel et al 2019, CaraDonna et al 2017, Miele et al 2020, Olesen et al 2008, Rasmussen et al 2013, Souza et al 2018, Traveset et al 2015). Thus, seasonal networks reveal more ecologically relevant processes than aggregated data (Sajjad et al 2017).

Spatial gradients also provide ample opportunities to study floral-visitation networks. As with time, interaction data aggregated across large spatial scales can mask important within-network processes. Species turnover and environmental conditions influence both potential and

realized interactions at local (Junker et al 2019), regional (Trojelsgaard et al 2015), and global scales (Trojelsgaard et al 2013). These influences can then have cascading effects upon network structure (Trojelsgaard et al 2013), and species-level characteristics such as network role and specialization (Watts et al 2016). Similar to findings with time, network-level characteristics are often conserved across space while species and interaction characteristics change (Carstensen et al 2016). Altogether, this leaves the study of spatiotemporal floral visitation networks ripe with research opportunities.

Floral-visitation networks are most often conducted from the plant-perspective by observing flowers and recording the organisms that visit and feed upon them (Jordano et al 2006). This leads to the majority of these networks being interpreted in terms of what floral visitors are more important for plant reproductive success, assuming effective pollination. It also results in the most common floral visitors, namely Hymenoptera and Diptera, receiving the bulk of attention and study (see Chapter 1). Less frequently are interaction networks studied from the animal-perspective, especially for relatively infrequent floral visitors. One reason for this is the increased complexity of observing floral visits by small and mobile animals as compared to monitoring stationary flowering plants. This has led to a lack of information available on the dynamics of the interactions between plants and their less common floral-visitors, and the interpretation from the point of view of visitors and the food resources they depend on.

I aim to contribute to this knowledge gap using a butterfly-flower interaction data set unique in its extensive spatiotemporal coverage and animal-based perspective. The richness of this data set will allow us to delve beyond network-level statistics and investigate dynamics at the species level. My goal is to determine if and how these butterfly-flower interaction networks exhibit spatiotemporal variation with the following research questions:

1. Do butterfly-flower interaction network specialization and modularity vary across time and/or space?
2. Are the most influential species in a network, as defined by modular roles, consistent across time and/or space?
3. Are the network roles and specialization of individual species maintained across time and/or space?

2.2. Methods

2.2.1. Study Area

This study took place across the spatial extent of the state of North Dakota in the United States of America. North Dakota is a grassland-dominated region in the North American Great Plains that spans from the dry hills and buttes of the badlands in the west to the wet flat glaciated plains of the east. Diverse climate, soil, and hydrology exist along this gradient, forming landscapes with distinct ecological characteristics across the expanse of the state (Sanderson 2016).

Anthropogenic change is prevalent across North Dakota. Row crop cultivation dominates the eastern half of the state in the wetter Red River Valley and prairie pothole region. Ranching, grazing, and oil development proliferate in the western half of the state where conditions are drier and topography more variable. Historically, tallgrass prairie blanketed the eastern half of the state and mixed cool season grasses covered the west, but invasive cool season grasses like Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) have taken hold across the entirety of the state (Murphy and Grant 2005). It is within this mosaic of intensive land-use, restored grasslands, and native prairie remnants that we conducted our surveys. All of our

surveys were conducted in grasslands, both public and privately owned, and included both native and restored prairie.

Under the United States Environmental Protection Agency Level III Ecoregion classification scheme, North Dakota encompasses four ecoregions (Figure 2.1): the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48) (Omernik 1987). Unlike political boundaries, ecoregions are intended to reflect distinct biotic communities (Smith et al 2018), although the extent to which ecoregions delineate distinct species assemblages varies by geographic location, climate, topography, taxa, and species traits (Gonzalez-Reyes 2017, Smith et al 2020). Plant and pollinator communities have been found to vary significantly in their species compositions across ecoregions (Kelly and Elle 2020), which should thus affect what plant-pollinator interactions occur in an ecoregion.

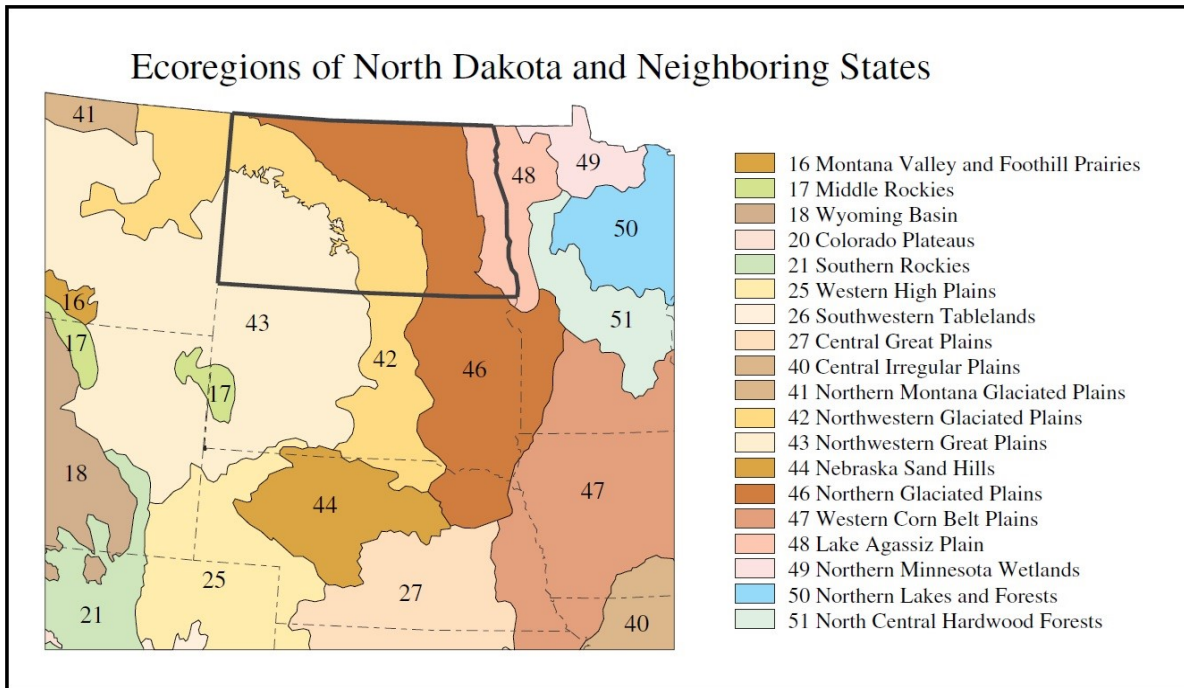


Figure 2.1. North Dakota ecoregions. North Dakota encompasses four Level III Ecoregions as defined by the EPA that are spread across a roughly west-east gradient (United States Environmental Protection Agency 2019).

2.2.2. Butterfly Survey Methods

Over the course of 2017 through 2019, we surveyed three grassland sites in each of North Dakota's 53 counties (Figure 2.2). We visited each site two times per summer for a total of 954 site visits. One site per county, the site with the highest floral diversity recorded during the first study season, was surveyed in all years. The other two sites per county changed annually. To maximize both spatial and temporal coverage, five teams of two surveyed the state simultaneously, each team responsible for a different section of the state.

We surveyed butterflies between late May and mid-September. We surveyed during optimal conditions for butterflies to ensure the highest probability of detection and minimize bias: between 0900 and 1800 hours, air temperature 21-35 °C, wind speed under 25 km/hr, and cloud cover less than 50% (Royer et al 1998).

Two observers simultaneously conducted butterfly surveys at each site. Each observer performed 40 minutes of butterfly surveys per site visit. In 2017 and 2018 this time was split between a 100 m fixed transect survey for 10 minutes, and a 30 minute roaming visual encounter survey across 4 ha to increase the detection probability of rare species (Kral et al 2018). All butterflies observed were recorded regardless of distance from observer. After finding higher species detection rates from our 2017 and 2018 transect surveys when compared to the roaming surveys, we performed all 40 minutes of butterfly surveys along a total of 400 m of fixed transects in 2019.

Every observed butterfly's species and behavior at detection (flying, courting, fighting, resting, nectaring, mating, ovipositing, mudpuddling, or dead) was recorded. Butterflies were recorded as nectaring only when butterflies were seen actively probing a flower with their

proboscis, and the associated flower species from each nectaring observation was also recorded. I used these nectaring observations to construct floral visitation networks.

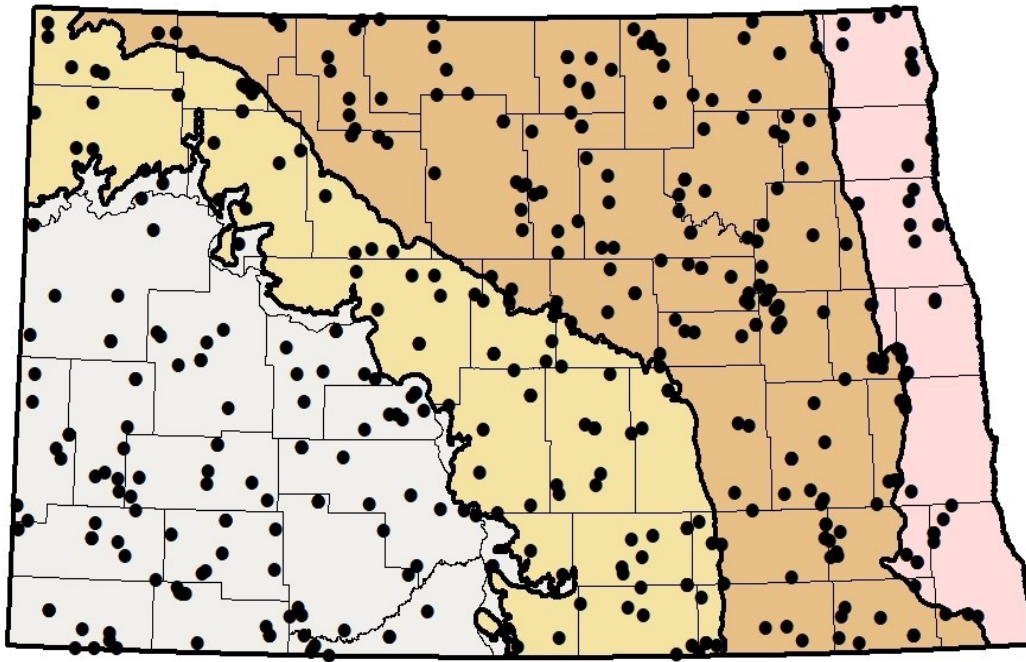


Figure 2.2. Survey site locations. Points show site locations for butterfly surveys conducted in North Dakota from 2017 to 2019. County borders are included and ecoregions are outlined and colored as follows from west to east: ecoregion 43 (beige), 42 (yellow), 46 (orange), and 48 (pink).

2.2.3. Floral Survey Methods

We also measured the abundance of plant species in flower during every site visit to determine the nectar resources available to butterflies at the time of survey. Each observer performed 400 meters of floral belt transects within their butterfly survey area. Observers recorded the number of flowering ramets (stems) per plant species that fell within 2.5 m on either side of these transects.

2.2.4. Network Analysis

To achieve my overall objective of analyzing spatiotemporal patterns of butterfly-flower interactions, I partitioned all butterfly nectaring observations by time of season and ecoregion. I

combined data from all years in order to have enough interactions per network to allow analysis, with the caveat of masking potential yearly differences. I defined time period as early (before July), mid (July), or late (after July) summer, similar to how other studies have partitioned networks by season (Bendel et al 2019, Miele et al 2020, Tucker and Rehan 2016). I defined ecoregions by the EPA Level III delineation (Figure 2.1). This led to a total of 12 separate interaction networks: each of the four ecoregions (referred to hereafter as 43, 42, 46, or 48) during either early, mid, or late summer (referred to hereafter as E, M, or L). One network was excluded from analyses due to a low number of total interactions. The remaining 11 ecoregion-season networks were then analyzed in addition to the full three year statewide network.

Interaction networks can be described at both the network level and species level. Network-level metrics quantify characteristics of entire networks, while species-level metrics quantify characteristics of individual species within metrics. I calculated the network-level metrics specialization H_2' and modularity Q to characterize interactions at the system level. I also calculated the species-level metrics specialization d' , node strength, within-module degree z , and among-module connectivity c for each species in each network. Together, these metrics quantify multiple aspects of a species' network functional role (Junker et al 2019, Nielsen and Totland 2014, Schleuning et al 2014). All network analyses were calculated in R (R Core Team 2020) using bipartite package version 2.15 (Dormann et al 2008, Dormann et al 2009, Dormann 2011).

2.2.5. Network-Level Characteristics

H_2' quantifies the deviation of the observed interactions in a network from what would be expected by chance given the network's size (Bluethgen et al 2006). In other words, a species exhibits no specialization if the identities of its interaction partners could be completely

explained by partner availability rather than any active selection. $H2'$ ranges from 0 (no specialization) to 1 (total specialization). Q measures the degree to which a network is organized into modules, also known as compartments, which are subgroups comprised of species that closely interact with one another (Delmas et al 2019, Dormann et al 2017, Newman 2006). Q ranges from 0 (modular structure no different than expected by chance) to 1 (data fully supports modular division of network) (Dormann and Strauss 2014). I calculated Q using the `metaComputeModules` function in Program R (Beckett 2016). I standardized $H2'$ and Q to z-scores using 1000 randomized networks calculated with method “vaznull” (Vazquez et al 2007), which randomizes species interactions while maintaining network connectance, to allow comparisons between networks of different sizes and configurations (Morrison and Mendenhall 2020, Nielsen and Totland 2014, Saunders and Rader 2019). Metric z-scores are hereafter referred to with Δ .

2.2.6. Modular Roles

One way to define how important a species is within a network is to determine its modular role. Modules, also known as compartments, are groups of species that interact more closely with one another than with other species in the network (Dormann and Strauss 2014). Species are assigned modular roles based on how many links they form both within their own module and between other modules (Olesen et al 2007). Important modular species, thought to contribute to network stability, are defined as module hubs, connectors, or network hubs (Olesen et al 2007, Figure 2.3). Module hubs form high numbers of links within their own module, connectors form links between many different modules, and network hubs fulfill both of those criteria. Species that fulfill neither of those criteria are classified as peripheral.

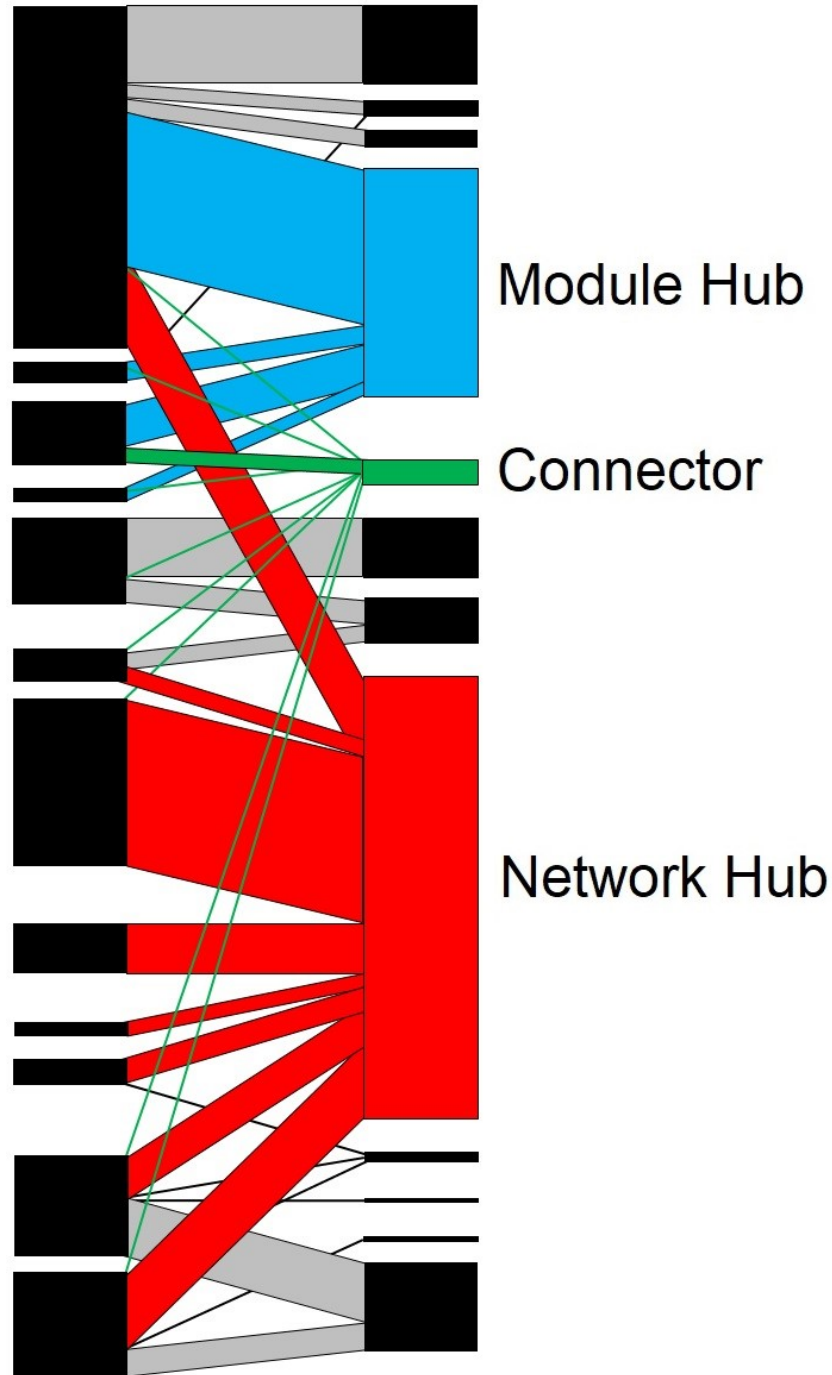


Figure 2.3. Modular role illustration. The importance of a species can be defined based on the distribution of its interactions relative to network compartments, or modules, of closely interacting species. Species that form high numbers of within-module interactions are called module hubs (blue), and species that form links that connect many different modules together are called connectors (green). Species that do both are defined as network hubs (red), and are considered the most important contributors to network stability.

I first calculated the within-module degree z and among-module connectivity c of each species in all the networks. Within-module degree z measures the standardized number of interactions a species has within its own module. Among-module connectivity c measures the extent to which a species' interactions link multiple modules together. A species' modular role is defined based on the relationship of its c and z values to discrete critical threshold values calculated from null models (Olesen et al 2007).

I determined critical threshold values of c and z for each network by calculating the 97.5% quantile of the randomized networks' c and z values. These critical thresholds are single values that c and z can be compared against to define a species' modular role (Saunders and Rader 2019). Species roles were then categorized as follows: network hub ($c > \text{critical } c, z > \text{critical } z$), module hub ($c < \text{critical } c, z > \text{critical } z$), connector ($c > \text{critical } c, z < \text{critical } z$), or peripheral ($c < \text{critical } c, z < \text{critical } z$) (Olesen et al 2007). Module hubs and connectors are considered generalists, while peripheral species are considered specialists. Species that are classified as network hubs, also known as super generalists, are considered to be particularly important to maintaining network stability due to their high number of interactions both within their own module and between other modules (Olesen et al 2007).

2.2.7. Species-Level Characteristics

I selected two species-level metrics, node strength and specialization d' , that help define a species' network role in addition to its modular role. Node strength, also known as species strength, quantifies the influence a species has upon the opposite group on the species. It represents the magnitude to which a floral-visitor acts upon the floral community and vice versa. Specialization d' measures the extent to which an individual species' interactions deviate relative to the abundance of potential partners (Bluethgen et al 2006). Typically, a species' interaction

frequency is considered equivalent to its relative abundance. This may pose problems in interpreting results if species' interaction numbers do not correspond to their true abundance (i.e. if a wide-ranging invasive plant is rarely nectared upon it would appear rare in a network if equating its abundance to interaction frequency alone) (Dormann et al 2008). To avoid this pitfall I calculated d' using the independent abundance data from our visual butterfly observations and floral belt transects (Dormann 2020). If a flower that was nectared upon was never observed during our floral belt transects it was assigned an abundance of one.

As with the network-level metrics $H2'$ and Q , I standardized our species-level metrics c , z , d' , and node strength to z-scores to allow comparisons between networks of different sizes. Only four butterfly and two flower species were observed in all 11 ecoregion-season networks. To analyze the spatial and temporal variation of a greater number of species I pooled the data from all three seasons to analyze species-level changes across ecoregions, and then from all four ecoregions to analyze changes across seasons. For species that were observed in the same ecoregion or season multiple times (i.e. multiple seasons in one ecoregion, or multiple ecoregions within one season) I averaged the species-level metrics from the corresponding ecoregion-season networks (Krasnov et al 2012, Schleuning et al 2014).

I analyzed butterflies and flowers separately to determine whether their network roles responded similarly across space and time. I performed pairwise correlation tests between every ecoregion-pair to compare Δc , Δz , $\Delta d'$, and Δ node strength of the 19 butterfly and 21 flower species that were observed in all four ecoregions, and then between every season-pair for the 23 butterfly and 21 flower species that were observed in all three seasons. Significant correlations would indicate that species acted consistently between networks, while non-significant correlations would indicate no consistency between networks (Nielsen and Totland 2014).

2.3. Results

2.3.1. Summary Data

Over our three years of data collection, we observed 136,745 individual butterflies belonging to 64 different species, and 3,848,402 individual flowering stems belonging to 409 different species. Of these observations, we recorded 16,183 individual nectaring observations of 48 different butterfly species (Appendix B) utilizing 152 different floral species (Appendix C). The number of observations during a single plot or transect survey of any unique species-species interaction ranged from 1 to 770 (median=1). This excludes an extreme outlier of a swarm of 2,981 painted ladies (*Vanessa cardui*) nectaring on a colony of white sweet clover (*Melilotus alba*) during a single plot survey in 2017.

2.3.2. Network-Level Characteristics

Once the outlier was removed the whole network (W) was comprised of 13,202 total interactions and 3,510 unique interactions (number of interacting butterfly-flower species pairs). The whole network was both significantly specialized ($H_2' = 0.33$, $p < .001$), meaning interactions could not be explained by species abundances alone, and significantly modular ($Q = 0.36$, $p < .001$), indicating a structure composed of closely interacting species subgroups that interact at low rates with other subgroups.

The individual ecoregion-season networks each contained between 14 and 28 butterfly species (21.33 (mean) ± 4.40 (SD)) and between 16 and 53 flower species (36.42 ± 10.94) species. Flower species outnumbered butterfly species in all networks. Number of total interactions varied between 27 and 4,004 (999.83 ± 1046.08), and unique interactions between 21 and 237 (107.67 ± 52.24). All network graphs are included in Appendix D.

Network 48E was not significantly specialized ($H2' = 0.46$, $p = .07$) or modular ($Q = 0.73$, $p = .40$) and had too few interactions ($n=27$, 18 of which were single unique observations) to allow meaningful statistical analysis so it was excluded from further analysis. In the remaining networks, specialization $\Delta H2'$ ranged between 2.63 and 36.98 and modularity ΔQ ranged between 3.43 and 40.86. Networks exhibited contrasting spatiotemporal patterns of specialization and modularity, with seasonal variation occurring within each ecoregion and an especially large difference across space between ecoregion 48 and the three western networks (Figure 2.4).

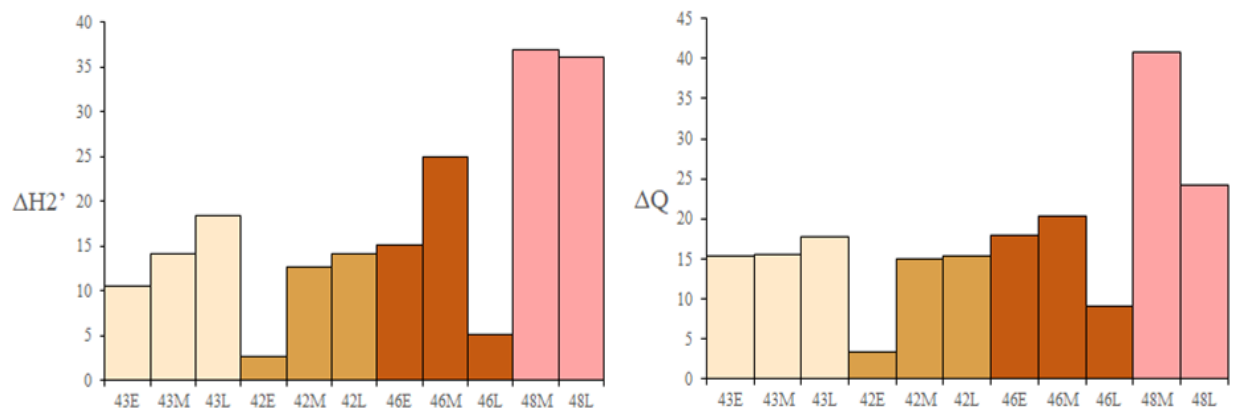


Figure 2.4. Network-level specialization and modularity. Standardized network-level specialization ($\Delta H2'$, top) and modularity (ΔQ , bottom) of each ecoregion-season network. Networks are coded by their ecoregion and season, and bars are colored by ecoregion. Ecoregions are arranged west to east along the x-axis, with three columns each corresponding to early (before July), mid (July), and late (after July) summer. Network 48E is not included due to its small size which prevented network analysis.

2.3.3. Modular Roles

Modular roles, which categorize species contribution to network stability based on the distribution of their interactions within and between network modules (Olesen et al 2007), were inconsistent across networks. In the whole network, only flower species filled important modular roles. Three were connectors and three were module hubs. All other species were classified as peripheral; no network hubs were identified in the whole network. Important modular species

identified within the ecoregion-season networks differed from those in the whole network, and varied from one another (Table 2.1).

Table 2.1. Important modular species. Species identified as filling important modular roles varied across both season and ecoregion. Roles were defined relative to critical threshold values of among-module connectivity (*c*) and within-module degree (*z*). Only species categorized as a network hub (high *c*, high *z*), connector (high *c*, low *z*), or module hub (low *c*, high *z*) are listed. The majority of species were classified as peripheral (low *c*, low *z*) and are not listed. Asterisks denote butterflies, all other species are flowers. Species codes are defined in Appendix A.

	Network Hubs	Connectors	Module Hubs
Whole Network		CIRARV, MEDSAT, SOLCAN	ASTAGR, CIRFLO, ECHANG
43E	ACHMIL	PHYLUD	
43M	MEDSAT	COLPHI*	
43L		MEDSAT	GRISQU
42E			
42M		CIRARV, MONFIS	MEDSAT
42L			MEDSAT
46E		COETUL*, ELACOM, EUPESU	
46M		POLMYS*	VANCAR*
46L			GRISQU, MEDSAT, VANCAR*
48M		VANCAR*	VERSTR
48L		DANPLE*	SOLCAN

2.3.4. Temporal Correlations of Species Characteristics

Temporally, only butterflies exhibited any significant correlations in species level metrics (Figure 2.5). Butterfly Δz values were significantly correlated between early and mid-summer ($r = .60, p = .003$). Butterfly $\Delta \text{Node Strength}$ values were significantly correlated between early and mid-summer ($r = .66, p < .0001$) and early and late summer ($r = .44, p = .04$). Butterfly $\Delta d'$ values were significantly correlated between mid and late summer ($r = .75, p < .001$). Non-significant correlation graphs are included in Appendix E.

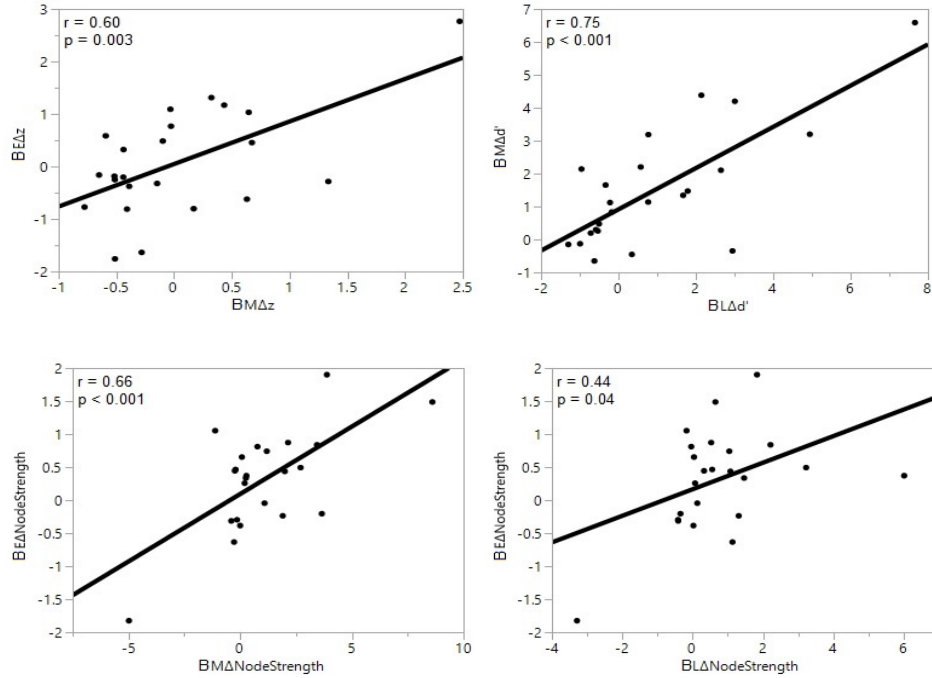


Figure 2.5. Significant temporal correlations between species-level metrics. Among the three possible season pairings (early-mid, mid-late, and early-late) all significant correlations between species-level metrics belonged to butterflies. Within-module degree z was consistent between early and mid-summer, specialization d' was consistent between mid and late summer, and node strength was conserved between both early and mid, and early and late summer.

2.3.5. Spatial Correlations of Species Characteristics

Spatially, both butterflies and flowers had at least one instance of a conserved species level metric (Figure 2.6). Flowers exhibited significant correlation in $\Delta d'$ values in the non-adjacent ecoregions 43 and 46 ($r = .79$, $p < .001$). Butterfly Δ Node Strength values were significantly correlated between two pairs of adjacent ecoregions: 43 and 42 ($r = .56$, $p = .01$), and 46 and 48 ($r = .60$, $p = .01$). Butterfly $\Delta d'$ values were significantly correlated between the adjacent ecoregions 42 and 46 ($r = .76$, $p < .001$). Non-significant correlation graphs are included in Appendix E.

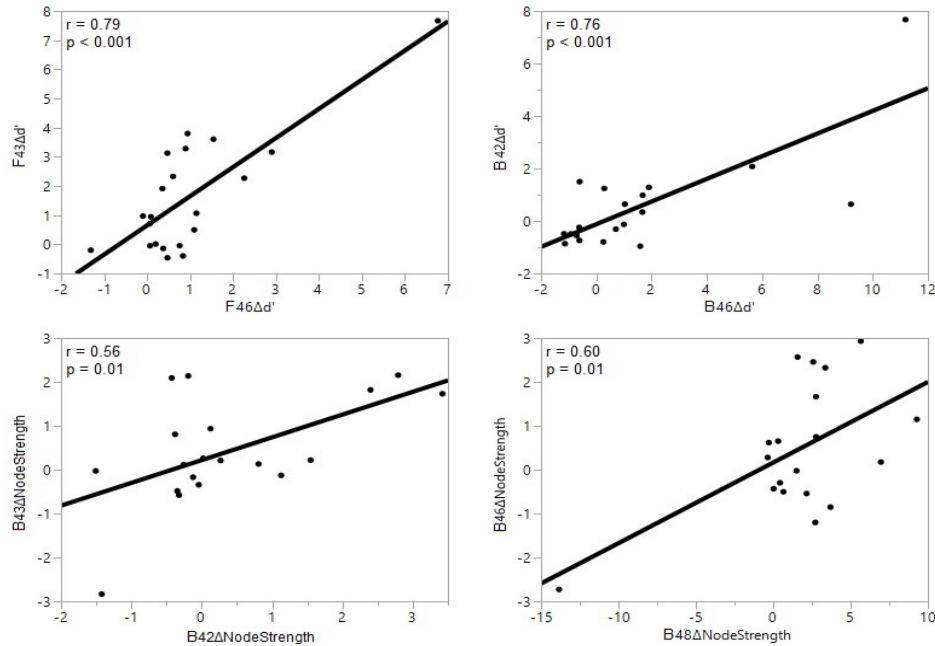


Figure 2.6. Significant spatial correlations between species-level metrics. Among the six possible ecoregion pairings (43-42, 43-46, 43-48, 42-46, 42-48, and 46-48) there was one instance of consistency in a species-level network metric for flowers (F; specialization d' between ecoregions 43 and 46) and three for butterflies (B; specialization d' between ecoregions 42 and 46, and node strength between ecoregions 43 and 42, and 46 and 48).

2.4. Discussion

My study goal was to assess if and how network-level characteristics, species modular roles, and species-level characteristics vary across space and time in a statewide butterfly-flower interaction data set. Previous studies of floral visitation networks along spatiotemporal gradients have found distinct interaction patterns along these gradients which otherwise would have been obscured in a single cumulative network (Cuartas-Hernandez and Medel 2015, Dupont et al 2009, Edwards et al 2019, Traveset et al 2015). I have built upon this body of work with a spatiotemporal data set unique in its large spatial coverage of interaction data collected at a fine scale. Similar to previous work, my results indicate a spatiotemporally dynamic system, with both network characteristics and species roles within networks exhibiting significant variation by both season and ecoregion.

2.4.1. Network-Level Characteristics

Network-level metrics reflect characteristics of all interactions considered together. I analyzed network specialization to determine whether interaction frequencies indicated active selection between partnering species, and modularity to determine if subgroups of closely interacting species existed within the network. Combined, all of the interactions within our three-year statewide study formed a significantly specialized network. Network specialization, where interaction frequency is not predicted by relative species abundance, is a common characteristic of floral visitation networks irrespective of network size (Blüthgen et al 2007). The network-level specialization of our data set thus matches network predictions, despite butterflies often being considered opportunistic feeders, and indicates that the butterflies in our study system exhibit preferential foraging which may reflect variation in floral resource quality (Lebeau et al 2017). However, spatiotemporal aggregation is likely resulting in an overestimation of species' foraging specialization. Temporal and spatial aggregation result in species being included in the network that would never co-occur in space or time. The lack of interactions between these species is then mistakenly interpreted as the specialization of an insect selecting against a floral species rather than reflecting the impossibility of the interaction (Sajjad et al 2017).

The whole network was also significantly modular. Floral visitation networks often become progressively more modular as the number of species increases, and modular structure is expected when over 150 species are involved (Olesen et al 2007). The whole network was comprised of 200 species, 48 butterflies and 152 flowers, so its modularity was in line with these expectations. The modular nature of the network suggests the existence of subgroups of closely interacting species that may reflect co-evolutionary units, ecological niche partitioning, functional similarity, or phylogenetic relatedness (Danieli-Silva et al 2012, Olesen et al 2007).

Separating the full interaction data set into ecoregion-season subnetworks revealed variation underlying the properties calculated from the whole network (Figure 2.4). We found distinct spatial patterns of interactions across ecoregions, which is somewhat surprising given research that found no variation in floral visitation network metrics across ecoregional boundaries (Kelly and Elle 2020). While specialization and modularity values were relatively consistent across the three westernmost ecoregions, easternmost ecoregion 48 showed a stark contrast with much higher values comparatively. Furthermore, individual ecoregions differed amongst each other when the seasonal component was considered. The two western ecoregions displayed different temporal network-level trends than the two eastern ecoregions. In the west, both network specialization and modularity moderately increased in a stepwise fashion as the summer season progressed from early to mid to late summer. Conversely, in the eastern networks, specialization and modularity declined from mid to late summer. These trends were possibly driven by a population explosion of painted lady butterflies that took place during the 2017 field season. Painted lady butterflies display highly variable inter-annual abundance in North America (Williams 1970), with massive influxes occurring approximately every five to ten years (Vandenbosch 2003). In 2017, they migrated across North America in exceptionally high numbers, exerting significant effects upon floral-visitation networks (Edwards et al 2019).

Across North Dakota, the painted lady population boom was far less pronounced in the west than in the east. Despite having the lowest number of sites, ecoregion 48 had the second greatest number of total butterfly-flower interactions, largely due to painted ladies. Temporally, painted ladies made up the largest proportion of nectaring observations in mid-summer. The variable dominance of painted ladies in the ecoregion-season networks is striking, with painted ladies accounting for more and more of the interactions in progressively easternly networks until

comprising nearly all of the interactions in networks 48M and 48L (Figure 2.7, Appendix D).

Altogether, the influence of painted lady butterflies undoubtedly played a significant role in the contrasting spatiotemporal network-level trends in our data set.

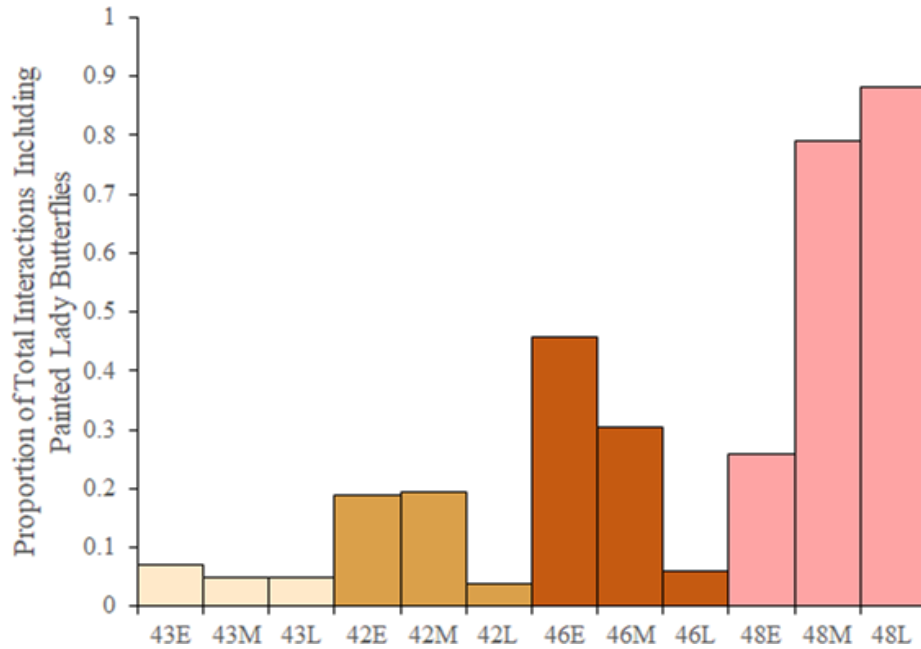


Figure 2.7. Proportion of nectaring observations by painted lady butterflies. The proportion of butterfly-flower interactions per ecoregion-season network involving painted ladies progressively increased from west to east. Networks are coded by their ecoregion and season. Ecoregions are arranged west to east along the x-axis, with three columns each corresponding to early (before July), mid (July), and late (after July) summer.

2.4.2. Modular Roles

I first analyzed species roles within networks by analyzing their within- and between-module interactions. If a species has a high number of links within its module it is considered a module hub. If a species has a high number of links between multiple modules it is considered a connector. High numbers of links both within- and between-modules classify a species as a network hub. Species assigned to any of these three modular roles represent important species in a network, with network hubs being the most influential.

Six species were identified with important modular roles in the full network, and all were flowers. Of the six, three were connectors and three were module hubs. No network hubs were identified, and all remaining species were considered peripheral. This breakdown matches expectations that only a small subset of species have important modular roles, but in our case the number of important species is particularly low. On average in pollination networks, approximately 85% of species are classified as peripheral, 11% as connectors, 3% as module hubs, and 1% as network hubs (Olesen 2007). Our network, on the other hand, was 96.5% peripheral species, 0.015% each of connectors and module hubs, and no network hubs. This result suggests that within- and among-module interactions are distributed more homogeneously among the species in our butterfly-flower interaction network than in typical plant-pollinator networks, and as such, individual species may exert similar levels of influence on overall network architecture.

This low ratio of important modular species was also found across the ecoregion-season networks, but the identity of the species classified as important varied spatiotemporally. Unlike in the whole network, several ecoregion-season networks identified butterfly species as filling important modular roles. Unsurprisingly, painted lady butterflies were the most frequent of the butterfly module influencers. They were classified as either connectors or module hubs in both eastern ecoregions, and in both mid and late summer. This corresponds to the same spatiotemporal pattern of painted lady influences we found at the network level. The other butterflies identified as important belonged to four different species, were all connectors, and varied by season and ecoregion.

Flowers were identified as playing important modular roles more often than butterflies, a common finding in plant-pollinator networks (Hackett et al 2019, Nielsen and Totland 2014).

Alfalfa (*Medicago sativa*) was far and away the most prominent, being classified once as a network hub, twice as a connector, and three times as a module hub. As with painted ladies, this is unsurprising given the incredible abundance of alfalfa, which accounted for over 20% of all flowering stems counted in our floral resource surveys. It was classified as modularly important in both mid and late summer, and in all ecoregions except easternmost ecoregion 48. The other important floral species were classified only one or two times within networks corresponding to their respective spatial range and flowering phenology.

Previous studies have had similar results, finding consistency in the relative proportion of core and peripheral species but shifts in their species identities across space (Watts et al 2016) and time (Larson et al 2016, Miele et al 2020). These patterns suggest a dynamic cycling within interaction networks in the identity of the most integral species at any given time or location. As such, no single species can be identified as the most influential within our butterfly-flower study system, and species identified as important at the whole network level do not necessarily reflect the species most important at different points in space and time.

The identities of the modularly important species can also be used to inform management decisions. Hubs and connectors that keep rare species linked to the overarching network, potentially bolstering the stability of threatened populations, may warrant their own attention during targeted conservation efforts (Larson et al 2014). Invasive species, on the other hand, can be ranked by the threat they pose to a rare species based on the overlap in their interaction partners (Larson et al 2014). At the community level, modularity analysis can serve as a risk assessment tool for invasive species removal by identifying native species that may rely on the invader (Larson et al 2016).

In our networks, two noxious weeds were identified as connectors: leafy spurge (*Euphorbia esula*) in early summer in eastern central North Dakota, and Canada thistle (*Cirsium arvense*) in mid-summer in the western central region of the state. The implications are two-fold. On one hand, these undesirable species may be providing important floral resources for butterflies in otherwise inhospitable landscapes. However, by binding many modules in the butterfly-flower network together, these weeds are likely having pervasive effects across the entire community. Knowing the seasons and regions where these plants are most important may help land managers anticipate where and when potential negative side effects of their removal could occur.

A diverse suite of plant species occupied important modular roles at different points in space and time in our networks. Region-specific hubs and connectors may be useful targets for local conservation butterfly-flower community conservation efforts. One native species was identified as important more than once: curlycup gumweed (*Grindelia squarrosa*) was a module hub in late summer in both the far west and eastern central parts of the state. This species may be a particularly important floral resource for late-season butterflies across the state. Further, all but one of the important flower species were either purple or yellow, indicating these colors are likely significant attractors of butterflies in our region and may be well suited for conservation seed mixes.

Ultimately, modular roles identify keystone species that exert significant influence on ecological communities (Saunders and Rader 2019). Our results have potential conservation implications for the northern Great Plains. Moreover, the modularity analysis methodology utilized here can be applied elsewhere to reveal critical species in other regions that may otherwise be overlooked.

2.4.3. Species-Level Characteristics

Correlation analyses of species-level metrics were performed by season and by ecoregion to assess whether a species maintained its role across time and/or space. When comparing the values of those metrics across seasons and ecoregions the majority of analyses showed no significant correlation, indicating that species roles were not maintained. Out of 72 total correlation analyses, only eight were significant. Seven of those eight significant correlations belonged to butterflies, suggesting butterflies exhibited slightly less variation in their network roles than flowers did. This matches previous findings where floral-visitors exhibited higher levels of consistency in their roles than flowers did within interaction networks along a gradient of landscape degradation (Nielsen and Totland 2014).

The few occasions of correlated species roles deserve consideration. Between seasons, only butterflies exhibited any consistency in their species-level network characteristics. In most of these cases consistencies occurred across consecutive seasons (i.e. early to mid, or mid to late). These suggest that butterfly interactions have consistent characteristics across some time intervals. On the other hand, the correlation that occurred between non-consecutive seasons is more difficult to interpret. Perhaps peak floral abundance in mid-summer causes butterfly foraging behavior to shift from that in early summer, but then reverts back in late summer after resources diminish. Other factors that may influence the patterns in species-level metrics over time include changes in community composition, relative species abundances, or climatic events that act at local or regional spatial scales.

Across space, flower species exhibited one significant correlation in their specialization that occurred between two non-adjacent ecoregions. All of the butterflies' role consistencies, on the other hand, occurred across adjacent ecoregions. Again, it's easier to conceptualize a species

exhibiting consistent network behavior across adjacent ecoregions, as regions that border each other likely share more characteristics than non-adjacent regions. The consistency of floral specialization between ecoregions that do not share a border is more puzzling. There may be a shared characteristic in the non-adjacent ecoregions that is temporarily disrupted in the middle ecoregion. For instance, the entirety of the ecoregion separating the floral consistency in specialization straddles the Missouri River, a massive geological feature that could potentially alter interactions in its vicinity. Alternatively, these spatial patterns could also be influenced by community dynamics unrelated to space, or temporal processes occurring at any time throughout the summer season.

Our findings suggest that butterflies and flowers demonstrate minimal spatiotemporal consistency in their network roles. Given the spatial diversity in landscape and weather characteristics, and the temporal variation in butterfly flight periods and floral bloom times, this lack of correlation is understandable. Other studies have also found considerable variation in species-level metrics across both space (Watts et al 2016) and time (Souza et al 2018). This highlights the importance of spatiotemporal considerations when interpreting species-level metrics within ecological networks, especially in networks of aggregated interaction data (Sajjad et al 2017).

2.4.4. Conclusions

Our study has revealed that butterfly-flower communities can exhibit substantial spatiotemporal variation in the properties of their system- and species-level interactions, and adds to the growing body of evidence that dynamic processes are taking place within interaction networks across environmental gradients (Tylianakis and Morris 2017). These results have important implications. First, it is critical to scale network studies according to the questions

being asked, as aggregating interaction data into single networks can potentially mask important spatiotemporal processes. Further, conservation decisions should take the variability of species interactions into account when planning for species of concern, because the most important resources a species depends upon can significantly differ across space and time. Continued interaction network research at complementary micro and macro scales will help further illuminate the mechanisms underlying species interaction dynamics.

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3. DISTRIBUTIONS OF THE MONARCH BUTTERFLY (*DANAUS PLEXIPPUS*), REGAL FRITILLARY (*SPEYERIA IDALIA*), AND THEIR FOOD RESOURCES THROUGH SPACE AND TIME

3.1. Introduction

Animals are dynamic through space and time, and so are many of the resources they depend on (Brough et al 2020, Costa et al 2019, Donaire et al 2019, Dou et al 2019, Nishikawa et al 2019, Rayl et al 2018, Wang et al 2020). This can present a considerable challenge when trying to determine why we observe animals in one place and time and not others. To understand how species are interacting with their environments, we must determine their distributions and then seek out the processes driving those patterns. Doing so in a spatially and temporally explicit manner can help answer ecological questions, provide baselines to monitor population trends, and inform targeted conservation efforts (Powney and Isaac 2015). For specific organisms like butterflies, this requires determining their species-specific distributions as well as those of their host and nectar plants, something we currently lack for many species, particularly those of conservation concern.

Butterfly food resources, whether in the form of a larval host plant or adult nectar source, are significant predictors of butterfly abundance, especially for diet and habitat specialists (Curtis et al 2015, Fourcade and Öckinger 2017). While host plants have been extensively studied for butterflies, nectar resources have received far less attention (Curtis et al 2015, Wallisdevries et al 2012) despite playing a vital role in sustaining adults throughout their dispersal and breeding seasons. However, the variability of both butterflies and their resources across environmental gradients can make it difficult to directly assess correlations between the two. Spatiotemporal influences also complicate the interpretation of correlations between butterfly and resource

abundance because it can be difficult to identify whether resources are attracting butterflies or they just happen to have overlapping distributions (Thomas and Taylor 2006).

While many studies exist studying distributions of butterflies, they are often limited in either space or time. The largest scale butterfly studies come from the UK where long-term monitoring efforts through the UK Butterfly Monitoring Scheme (UKBMS) provide nationwide methodically collected data dating back to 1976 (Dennis et al 2017). These data provide critical information on butterflies across both space and time, but such a rich butterfly data set exists nowhere else in the world. Further, many of these long-term data sets have comprehensive butterfly information but lack accompanying data on their plant resources, so comparisons between butterfly and resource require the gathering of additional resource-specific data (Curtis et al 2015).

To address large-scale distribution questions in places where butterflies have not systematically been studied through time, large-scale studies are critical. Further, systematic coverage with equal effort across space and time is crucial to accurately assess true spatial and temporal distributions of both the butterflies and their resources. If a tradeoff is necessary, higher site number trumps higher site-level survey effort when the goal is to determine distributions across expansive survey areas, although higher survey effort is increasingly important for rarer species (Loos et al 2015). Ideally, studies will cover expansive spatial and temporal scales while maintaining a high level of effort per survey, and this is often only possible when using records collected by an extensive network of volunteers (Powney and Isaac 2015, Dennis et al 2017). However, these data sets can have an intrinsic distributional bias toward areas and dates studied at higher rates (Powney and Isaac 2015).

In an effort to determine abundance distributions for butterflies in the Northern Great Plains, we have conducted a systematic statewide survey across North Dakota covering a large spatial extent with high temporal frequency. Monarchs (*Danaus plexippus*) and regal fritillaries (*Speyeria idalia*) are ideal organisms to study distribution questions because they have highly specialized resources that can be simultaneously studied along with the butterflies. They are also of conservation concern, both being currently considered for listing under the Endangered Species Act, yet in North Dakota they still exist in high enough numbers to find robust patterns and analyze with sufficient statistical power. The objective of this chapter is to identify to what extent monarchs and regal fritillary distributions across North Dakota are related to the distributions of their associated host and nectar plants while accounting for spatiotemporal distribution patterns. To do this I have the following objectives for both monarch butterflies and regal fritillaries:

1. Determine the spatial and temporal distributions of each butterfly species and monarch larval host plants across North Dakota.
2. Identify the most important floral resources of each butterfly species using observations of nectaring events.
3. Analyze the relationship between butterfly and plant resource abundance by performing detrended regressions that reduce spatiotemporal influences.

3.2. Methods

3.2.1. North Dakota Grasslands

North Dakota is a grassland-dominated region in the North American Great Plains with an area of 183,273 km². North Dakota has a landscape gradient that goes from the drier hills and buttes of the badlands in the west to the wetter flat glaciated plains of the east. Diverse climate,

soil, and hydrology exist along this gradient, forming landscapes with distinct ecological characteristics across the expanse of the state.

North Dakota can be considered as containing four different life zones (Royer 2003): the western deserts southwest of the Missouri River, the temperate forests, wetlands, and prairies both northwest and southeast of the Missouri River, and the oak and aspen woodland dominated area northeast of Devils Lake and the Turtle Mountains. In our project we surveyed exclusively in grasslands, either restored or native, but did so across all life zones.

Anthropogenic change is prevalent across North Dakota. Row crop cultivation dominates the eastern half of the state in the wetter Red River Valley and prairie pothole region. Ranching, grazing, and oil development proliferate in the western half of the state where conditions are drier and topography more variable. Historically, warm season tallgrass prairie blanketed the eastern half of the state and mixed cool season grasses covered the west, but invasive cool season grasses like Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) have taken hold across the entirety of the state (Murphy and Grant 2005). It is within this mosaic of intensive land-use, restored grasslands, and native prairie remnants that we conducted our surveys. All of our surveys were conducted in grasslands, both public and privately owned, and included both native and restored prairie.

3.2.2. Monarch Butterfly Natural History

3.2.2.1. Spatial and Temporal Distribution

In North America, two primary monarch butterfly populations exist on either side of the Rocky Mountains (Malcolm 2018). In our study we focus on the eastern population, which is renowned for its annual migration between overwintering grounds in Oyamel fir tree forests of central Mexico and breeding grounds in the eastern United States and Canada (Reppert and de

Roode 2018). During their summer breeding season, monarchs travel progressively northward from their overwintering grounds as they breed (Batalden et al 2007). As they travel, monarchs rely on milkweed plants (*Asclepias* sp.) to lay eggs on and produce offspring that continue the multi-generational migration process (Lemoine 2015). This reliance on milkweed as a larval host largely restricts monarchs to regions and habitats where the plant grows (Lemoine 2015).

Ultimately, the northward monarch migration lasts into the fall and extends into Canada before the monarchs journey back southward to their overwintering grounds (Lemoine 2015). Declines in monarch numbers have been indicated over the past several decades by the reduction in hectares occupied by monarchs at their overwintering grounds (Agrawal and Inamine 2018).

In North Dakota previous work indicates that monarchs can occur statewide, with numbers particularly high in late summer when the southern migration begins (Royer 2003). Although they occur widely they tend to be more concentrated east of the Missouri River, and they are on the wing in the state from early spring in mid-May until mid-October (Marrone 2002).

3.2.2.2. *Host Plants*

The monarch butterfly's dependence on milkweed as a host plant is well known. Larvae feed and adults oviposit exclusively on milkweed (Lemoine 2015). Monarchs are flexible in what type of milkweed they utilize, with adults ovipositing and larvae feeding upon at least nine different species of milkweed (Baker and Potter 2018, Pocius et al 2017, Pocius et al 2018a, Pocius et al 2018b). High correlation exists between milkweed density at a site and immature monarch presence, but the relationship between milkweed density and adult monarchs is less clear (Lukens et al 2020).

Milkweeds occur statewide in North Dakota, with nine milkweed species documented (USDA 2020). Each species exhibits a unique spatial distribution, with most concentrated either on the eastern border or along the Missouri Coteau region spanning from the southeast to northwest corners of the state (Kartesz 2014).

3.2.2.3. Nectar Plants

Milkweeds also provide an important nectar source for adult monarchs, but the entire suite of floral species the butterfly will nectar on is less known. Historically, the monarch's relationship with milkweed as a host plant has been much more heavily studied than their nectar sources. Of those that have been documented, floral species of high use by monarchs include milkweeds, blazing stars (*Liatris* sp.), thistles (family Asteraceae), bergamot (*Monarda* sp.), and goldenrods (*Solidago* sp.) (Lukens et al 2020, Marrone 2002). Different floral species are utilized throughout the growing season, with early, mid, and late flowering species providing season-long resources and monarchs adaptively foraging as floral species turnover occurs.

3.2.3. Regal Fritillary Natural History

3.2.3.1. Spatial and Temporal Distribution

Historically, regal fritillaries were distributed across a great expanse of central and eastern North America (Selby 2007). However, likely due to habitat loss, fragmentation, and forest encroachment, regal fritillary populations have plummeted in the eastern United States, with only two isolated populations remaining in Pennsylvania and Virginia (Selby 2007). Travelling westward, regal fritillary populations grow progressively more abundant, with scattered populations in the Midwest and larger, more connected populations in the Great Plains (Selby 2007, Williams et al 2003). Larger, more contiguous grasslands in the Great Plains compared to eastern North America likely contribute to the maintenance of these higher regal

fritillary numbers since the butterflies are generally restricted to large tracts of grasslands with high floral density (Marrone 2002).

First instar regal fritillary larvae overwinter in leaf litter (Kopper et al 2000). Adult males emerge before females around mid-June in the Dakotas, and females emerge later around early July (Marrone 2002). The greatest number of regal fritillaries on the wing occurs in July when both sexes are present (Royer 2003). After mating occurs male numbers dwindle and females delay oviposition until late August (Royer 2003). Females tend to disperse greater distances during their late summer oviposition, with many northern dispersers observed (Royer 2003). Female numbers then decrease, with regal fritillary flight season ending in mid-September in the Dakotas (Marrone 2002). Regal fritillaries have a dispersive tendency so can occur statewide in North Dakota, but are concentrated in the southern half of the state, with a shifting concentration reported from the southwest to the southeast in recent years (Royer 2003). Population sizes fluctuate year to year (Marrone 2002).

3.2.3.2. *Host Plants*

Regal fritillaries use violets (*Viola* sp.) as their host plant. Violets are spring ephemerals that bloom in spring and senesce during summer and fall. Regal fritillaries, however, don't oviposit eggs until the fall. Unlike many other butterflies, regal fritillaries don't oviposit directly on their host plants. Instead, they lay eggs in a fashion dubbed a "sweepstakes" strategy, laying high numbers of eggs across the landscape seemingly irrespective of proximity to violets (Kopper et al 2000). It seems that, rather than targeting violets, regal fritillaries oviposit in locations that provide adequate shelter for overwintering larvae (Kopper et al 2000). Perhaps because of this, most data indicate no correlation between violet densities and regal fritillary presence (Kopper et al 2000, Mason 2001, Swartz et al 2015).

In the Dakotas, prairie violet (*Viola pedatifida*) and Nuttall's violet (*Viola nuttallii*) appear to be the primary host species used by regal fritillaries (Marrone 2002, Royer 2003). Both of these species are located statewide in North Dakota but are concentrated along the Missouri Coteau region that stretches from the southeast to northwest corners of the state (Kartesz 2014).

Violets are small and patchy across the landscape (Kopper et al 2000). Due to this patchiness and their springtime ephemeral nature, surveys for the plant must be tailored specifically for violets, taking place in the spring and being fine scale enough to detect the easily overlooked plant (Kopper et al 2000, Mason 2001). Our statewide protocol (see Vegetation Survey Methods) dictated vegetation sampling in the summer, thus we were unable to capture adequate data on violet distributions. This prevented us from analyzing their correlations with regal fritillaries.

3.2.3.3. Nectar Plants

Previous research indicates that popular nectar sources for regal fritillaries include milkweeds, thistles, blazing stars, bergamot, coneflowers (*Echinacea* sp.), vervain (*Verbena* sp.), and alfalfa (*Medicago sativa*) (Marrone 2002, Mason 2001, Royer 2003, Swartz et al 2015). Milkweeds provide an early-flowering nectar source that is important for emerging males (Swartz et al 2015). However, results from studies on the relationship between nectar plant density and regal fritillary presence have been ambiguous (Swartz et al 2015, Mason 2001).

3.2.4. Butterfly Survey Methods

Over the course of 2017 through 2019 we surveyed three grassland sites in each of North Dakota's 53 counties, visiting each site two times per summer for a total of 954 site visits. To maximize both spatial and temporal coverage, five teams of two surveyed the state simultaneously, each team responsible for a different section of the state.

Our butterfly surveys took place between late May and mid-September. We only surveyed during optimal conditions for butterflies to ensure the highest probability of detection and minimize biased sampling: between 0900 and 1800 hours, air temperature 21-35 °C, wind speed under 25 km/hr, and cloud cover less than 50% (Royer et al. 1998).

Two observers simultaneously conducted butterfly surveys at each site. Each observer performed 40 minutes of butterfly surveys per site visit. In 2017 and 2018 this time was split between a 100 m fixed transect survey for 10 minutes, and a 30 minute roaming visual encounter survey across 4 ha to increase the detection probability of rare species (Kral et al 2018). All butterflies observed were recorded regardless of distance from observer. After finding higher species detection rates from our 2017 and 2018 transect surveys when compared to the roaming surveys, we performed all 40 minutes of butterfly surveys along a total of 400 m of fixed transects in 2019.

For any butterflies not immediately identifiable survey time was paused to capture and identify or photograph the specimen. Butterflies seen actively probing a flower with their proboscis were recorded as nectaring and the floral species being used was also recorded.

3.2.5. Plant Survey Methods

We used floral belt transects to quantify floral resources available to butterflies during each survey. Each observer performed 400 meters of floral belt transects within their butterfly survey area. Observers recorded the number of flowering ramets (stems) per plant species that fell within 2.5 m on either side of these transects. In 2017 and 2018 we also measured the percent cover of both flowering and non-flowering milkweed once per site between late June and the end of the season using 37 one square meter quadrats distributed evenly throughout the butterfly survey area.

3.2.6. Statistical Analysis

To analyze the correlation between monarch and regal fritillary butterfly abundance per survey, abundance of nectar plants in flower per survey, and host plant average percent cover per site, we detrended our butterfly observation data to reduce the influence of spatial and temporal distributions between the taxa. Detrending spatiotemporal data is necessary when outside variables influence data in a systematic way (Gasch et al 2015). In our data monarch abundance followed an east-west gradient, allowing us to detrend abundance data by longitude. The north-south gradient of regal fritillary observations similarly allowed us to detrend abundance data by latitude. Further, due to both butterfly species' parabolic temporal distribution through the summer season, we detrended all butterfly observation data by day of year.

To detrend our data, we first calculated the residuals of the log of the number of observations of each butterfly species per survey by day of year using a quadratic fit due to the butterfly species' parabolic temporal abundance distributions. Then, we calculated the residuals of those values by either longitude for monarchs or latitude for regal fritillaries using a linear fit to account for each species' linear spatial abundance distributions. We then used those values to perform linear regressions of butterfly abundance per survey with that of their plant resources to assess butterfly-plant relationships with reduced influence of their distinct spatiotemporal distributions.

3.3. Results

3.3.1. Monarch Butterfly Distribution

We observed 519 individual monarchs in 2017, 1,237 in 2018, and 714 in 2019 for a total of 2,470 observations. The higher observations in 2018 compared to the other years was not a

phenomenon unique to monarchs, but rather was observed across all butterfly species seen during our statewide survey, and was possibly an effect of higher precipitation in 2018.

Monarchs were observed across much of North Dakota, with the highest concentration in the eastern half of the state (Figure 3.1).

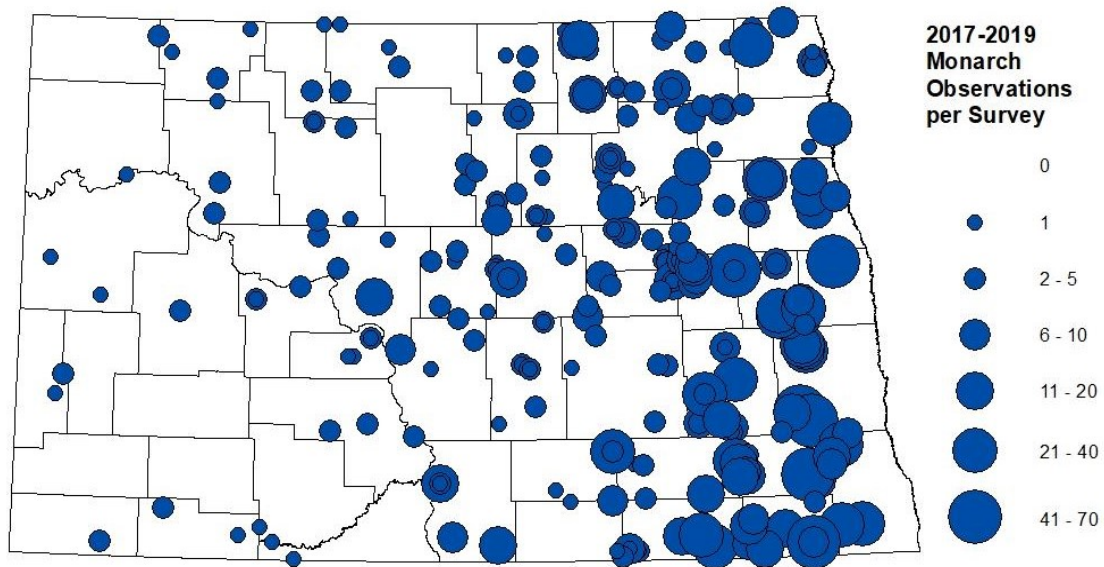


Figure 3.1. Monarch butterfly spatial distribution. Spatial distribution of monarch observations across North Dakota in 2017-2019. Larger circles correspond to higher numbers of observations.

Monarchs were observed throughout our entire field season in all three years. The observed flight periods were June 3-August 30 in 2017, June 4-August 29 in 2018, and June 3-September 17 in 2019. Monarch observations peaked in late July every year (Figure 3.2).

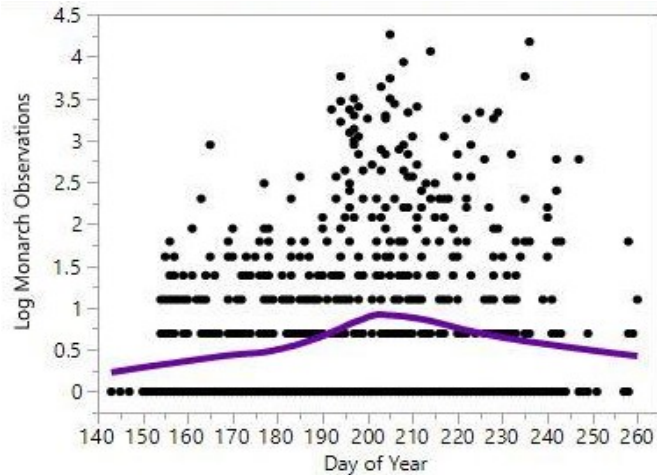


Figure 3.2. Monarch butterfly temporal distribution. Temporal distribution of monarch observations across North Dakota from 2017-2019. Each data point represents the total number of monarch observations per day, log transformed for clarity. The kernel-weighted smoothed line illustrates the general data trend, with monarchs on the wing season-long and peaking in numbers in late July.

3.3.2. Milkweed Cover

During our 2017 and 2018 vegetation cover quadrat surveys, we detected a total of 9 different milkweed species. Our three most frequently observed species were common milkweed (*A. syriaca*), showy milkweed (*A. speciosa*), and oval leaf milkweed (*A. ovalifolia*). The other species (whorled (*A. verticillata*), plains (*A. pumila*), woolly (*A. lanuginosa*), green (*A. viridis*), swamp (*A. incarnata*), and slimleaf (*A. stenophylla*)) were all detected sporadically at low numbers.

Similar to the spatial distribution we observed with monarchs, milkweeds were detected across most of North Dakota with the highest concentration in the eastern half of the state (Figure 3.3). I found a positive relationship between milkweed cover and monarch observations (Figure 3.4), even after taking these overlapping distributions into account with the spatiotemporal residuals.

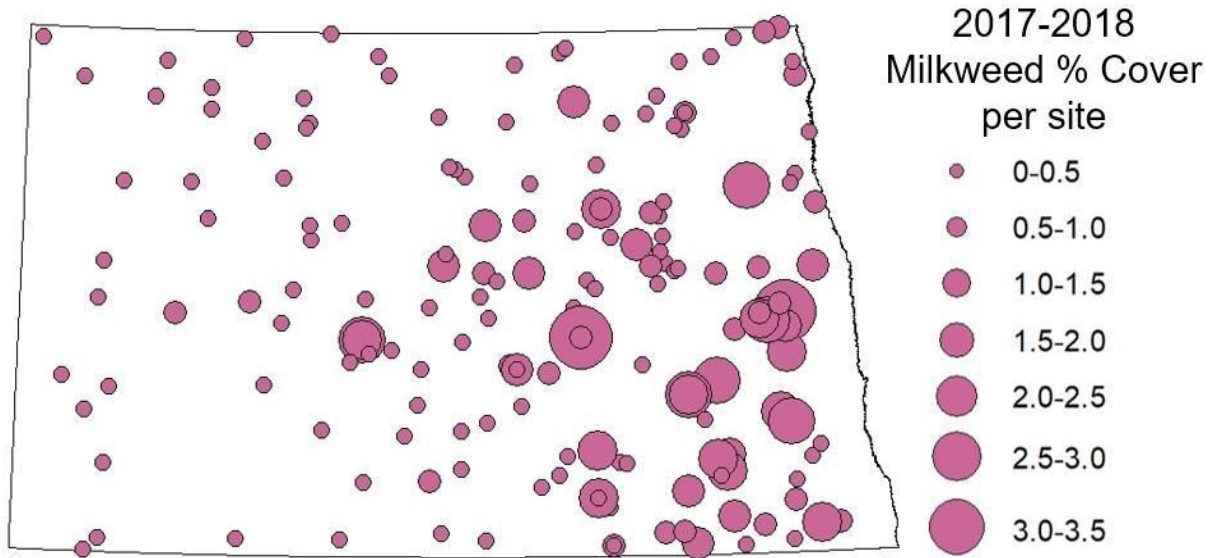


Figure 3.3. Milkweed cover spatial distribution. Spatial distribution of milkweed cover observed across North Dakota during our 2017 and 2018 vegetation surveys. Larger circles correspond to higher percent cover of milkweed at a site.

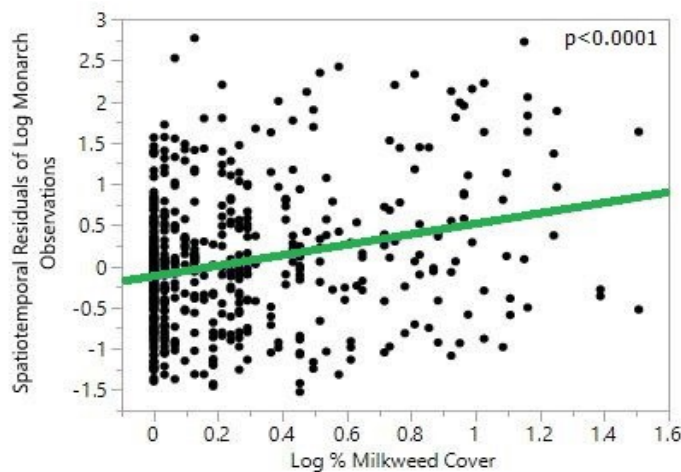


Figure 3.4. Monarch butterfly observations relative to milkweed cover. Spatiotemporal residuals of monarch observations had a significantly positive relationship with milkweed cover, indicating a positive relationship between the abundance of monarchs observed at a site and the density of their host plants at that site ($p < 0.0001$).

3.3.3. Monarch Butterfly Nectaring Observations

During our three seasons of butterfly surveys we observed 230 instances of monarch butterflies nectaring. A total of 36 different floral species were used, and they exhibited high

variability of abundance in relation to use (Figure 3.5). The top three floral groups that were utilized by monarchs were milkweeds, thistles, and blazing stars.

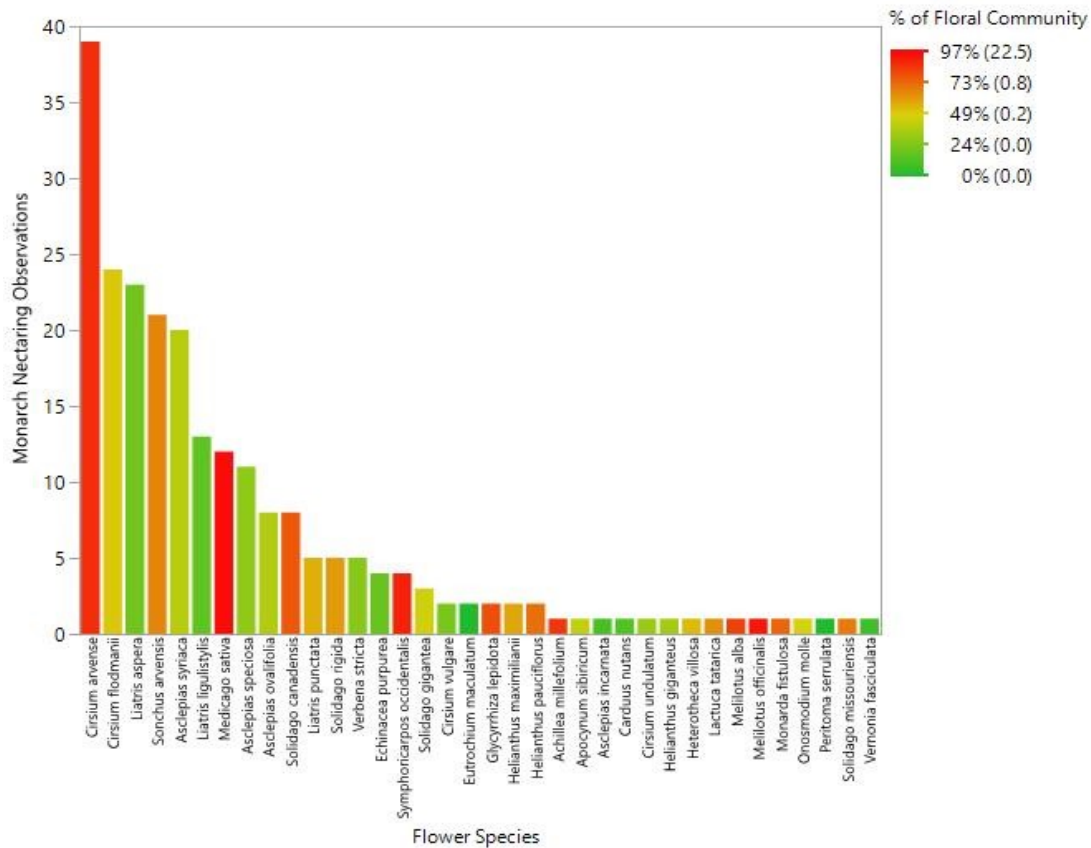


Figure 3.5. Monarch butterfly nectaring observations. We recorded 230 observations of monarchs nectaring on 36 different plant species from 2017-2019 across North Dakota. Bars are colored by quantiles of percentage of the total floral community, with more common species in red and rarer species in green, to illustrate nectar use compared to the flower’s abundance.

The data from our floral belt surveys revealed that each of these three groups had unique spatial and temporal distributions. Flowering milkweed were concentrated in the east (Figure 3.6); thistles were observed statewide (Figure 3.7) with exotic species concentrated in the east (Figure 3.8) and native species evenly distributed except largely absent from easternmost edge of the state (Figure 3.9); and blazing stars were concentrated in the west (Figure 3.10). Milkweeds bloomed earliest (Figure 3.11), exotic and native thistle flowers peaked in mid-summer (Figure 3.12), and blazing stars bloomed in late summer (Figure 3.13).

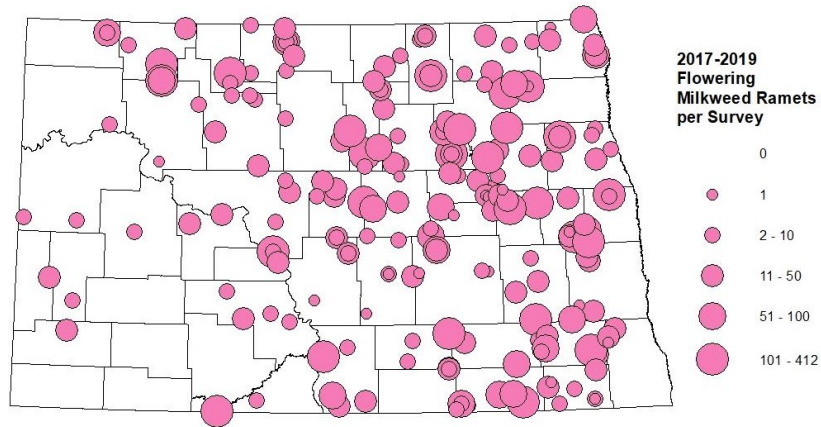


Figure 3.6. Flowering milkweed spatial distribution. Larger circles represent higher numbers of flowering stems counted during our floral belt transects from 2017 to 2019.

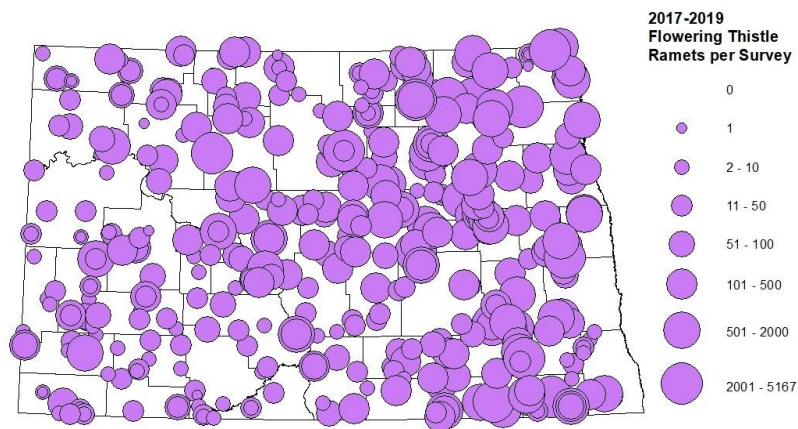


Figure 3.7. Flowering thistle spatial distribution. Larger circles represent higher numbers of flowering stems counted during our floral belt transects from 2017 to 2019.

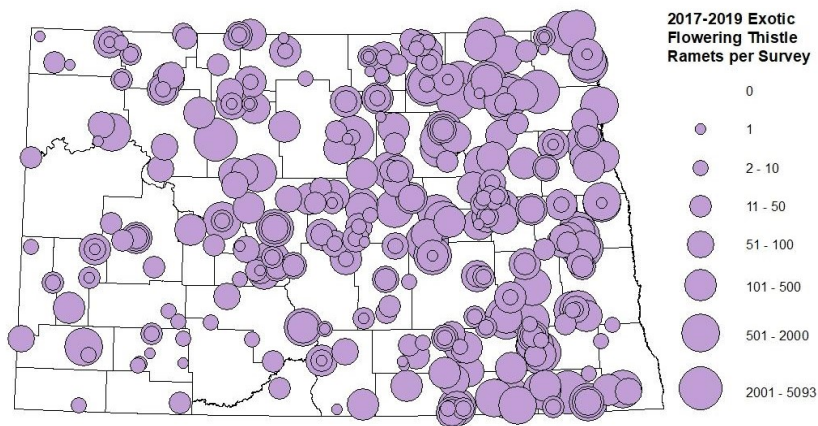


Figure 3.8. Flowering exotic thistle spatial distribution. Larger circles represent higher numbers of flowering stems counted during our floral belt transects from 2017 to 2019.

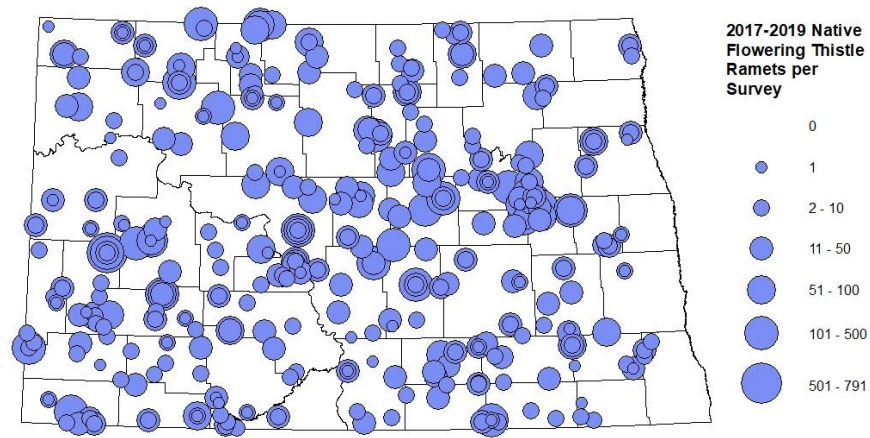


Figure 3.9. Flowering native thistle spatial distribution. Larger circles represent higher numbers of flowering stems counted during our floral belt transects from 2017 to 2019.

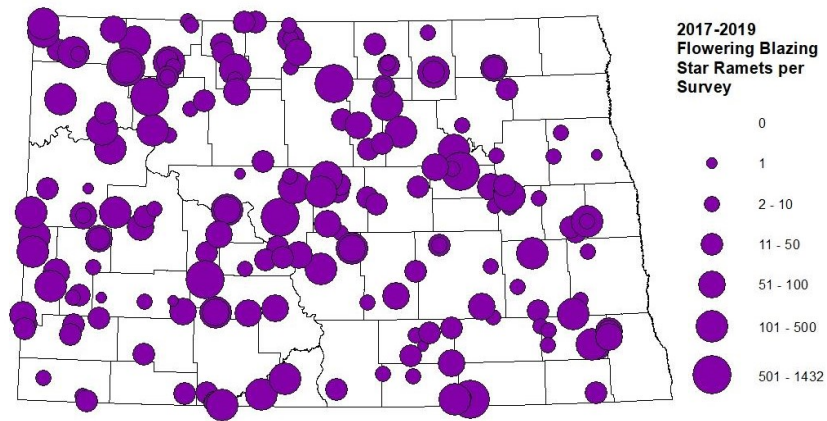


Figure 3.10. Flowering blazing star spatial distribution. Larger circles represent higher numbers of flowering stems counted during our floral belt transects from 2017 to 2019.

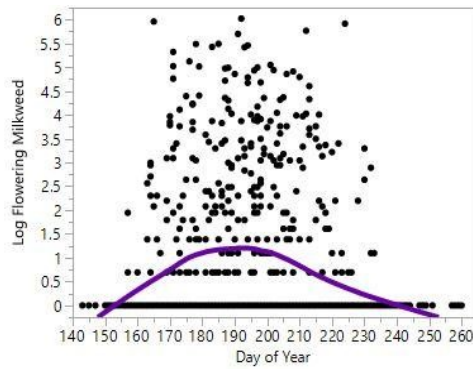


Figure 3.11. Flowering milkweed temporal distribution. Each data point represents the total number of flowering stems recorded per day across our 2017-2019 field seasons, log transformed for clarity. The kernel-weighted smoothed line illustrates the general data trend, with milkweeds flowering in early summer and senescing before season end.

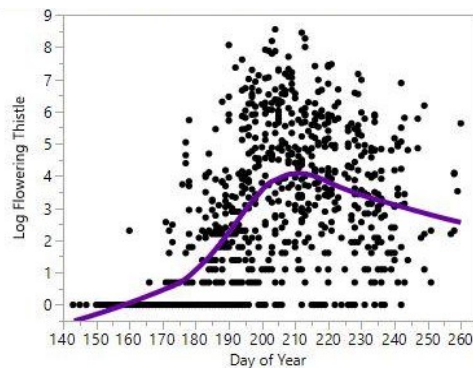


Figure 3.12. Flowering thistle temporal distribution. Each data point represents the total number of flowering stems of exotic and native thistles recorded per day across our 2017-2019 field seasons, log transformed for clarity. The kernel-weighted smoothed line illustrates the general data trend, with thistle flowers peaking in mid-summer.

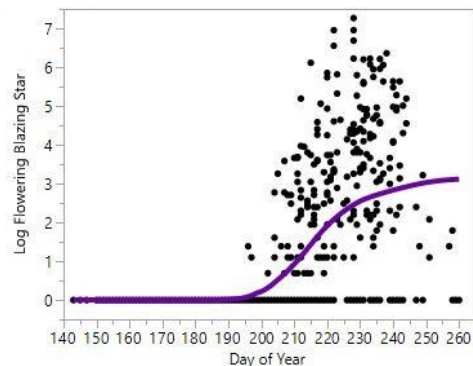


Figure 3.13. Flowering blazing star temporal distribution. Each data point represents the total number of flowering stems recorded per day across our 2017-2019 field seasons, log transformed for clarity. The kernel-weighted smoothed line illustrates the general data trend, with blazing star flowers appearing only in late summer.

To analyze the correlation between monarchs and their top nectar sources I used the longitudinal, day of year, and milkweed cover residuals of monarch observations to limit the influence of those three factors on the floral relationships. Monarch abundance had variable relationships with the abundance of their top nectar sources. Monarchs exhibited a significantly positive relationship with flowering milkweed and exotic thistles, but no significant relationship with native thistles or blazing stars (Figure 3.14).

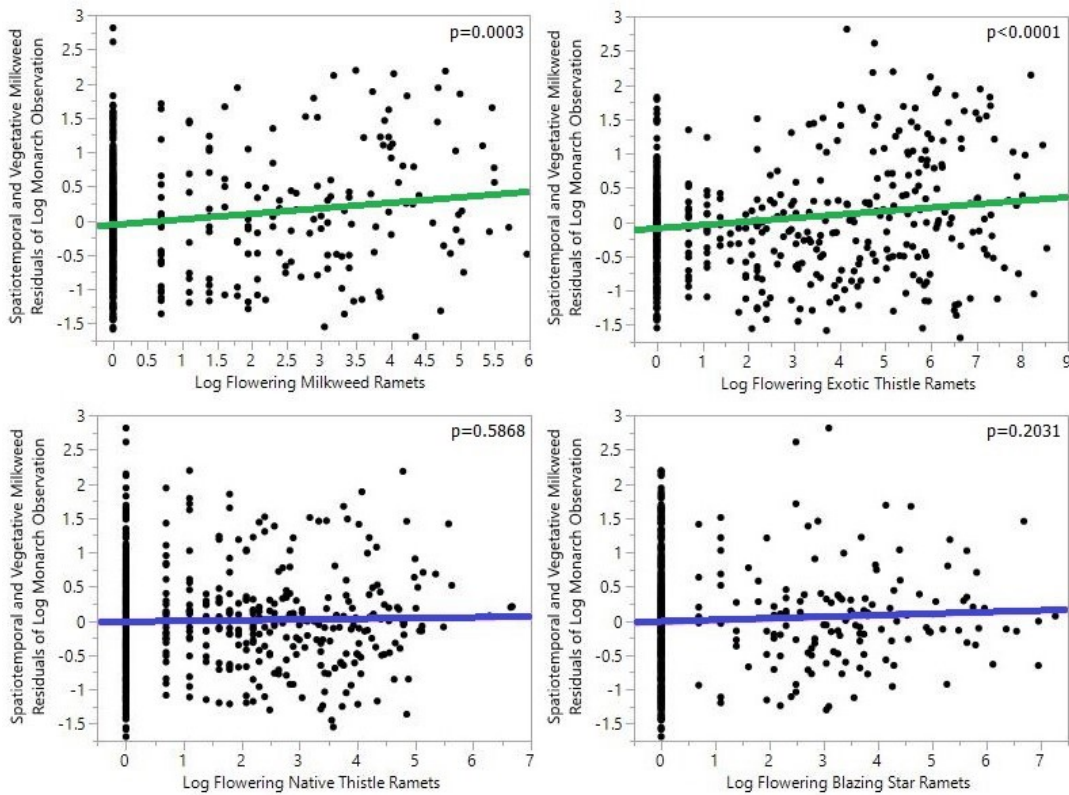


Figure 3.14. Monarch butterfly observations relative to nectar source abundance. Detrended monarch observations exhibited variable relationships with their most used nectar sources, having a positive relationship with flowering milkweed and exotic thistles (top), but no relationship with native thistles or blazing stars (bottom).

3.3.4. Regal Fritillary Distribution

We observed 472 individual regal fritillaries in 2017, 823 in 2018, and 590 in 2019 for a total of 1,885 observations. Like monarchs, the higher observations in 2018 compared to the other years was not a phenomenon unique to regal fritillaries, but rather was observed across all

butterfly species seen during our statewide survey, and was possibly an effect of higher precipitation in 2018.

Regal fritillaries were observed across much of North Dakota, with the highest concentration in the southern half of the state particularly in the southwest (Figure 3.15). Regal fritillaries were first observed in late June or early July and were detected through late August all three years. The flight periods observed were June 22-August 29 in 2017, June 27-August 25 in 2018, and July 7-August 28 in 2019. Regal fritillary observations peaked in late July (Figure 3.16). To avoid including surveys conducted prior to when regal fritillaries were on the wing and able to be observed, data points before June 22nd were excluded for all analyses of regal fritillary correlations with plants.

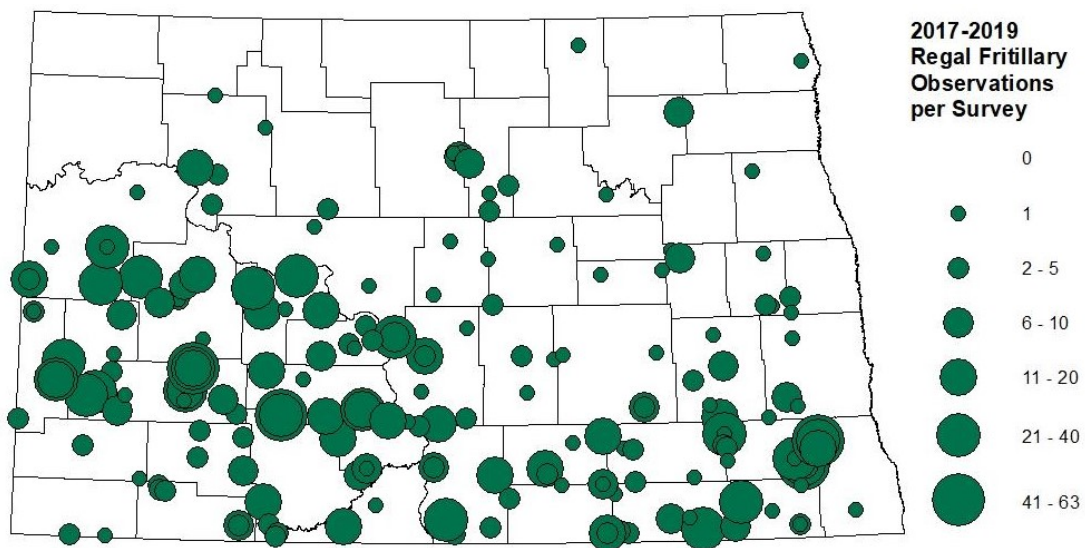


Figure 3.15. Regal fritillary spatial distribution. Spatial distribution of regal fritillary observations across North Dakota in 2017-2019. Larger circles correspond to higher numbers of observations.

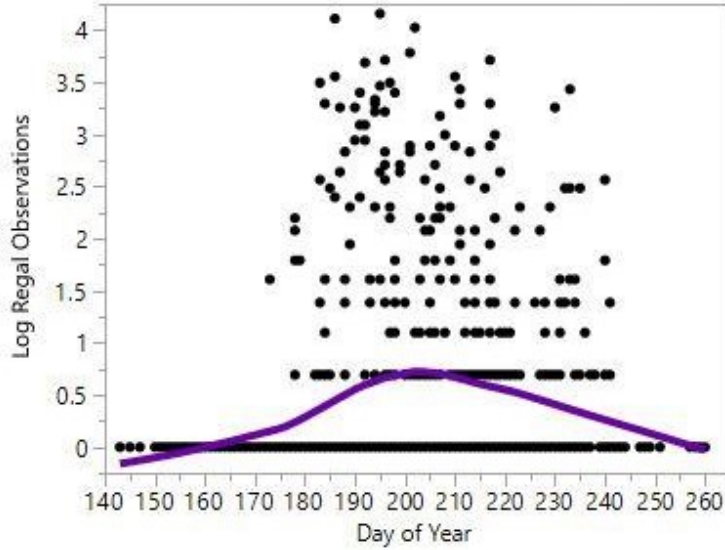


Figure 3.16. Regal fritillary temporal distribution. Temporal distribution of regal fritillary observations across North Dakota from 2017-2019. Each data point represents the total number of regal fritillary observations per day, log transformed for clarity. The kernel-weighted smoothed line illustrates the general data trend, with regal fritillaries on the wing beginning in late June and peaking in numbers in late July.

3.3.5. Regal Fritillary Nectaring Observations

During our 2017-2019 butterfly surveys we observed 83 instances of regal fritillaries nectaring from a total of 10 different floral species of varying abundances (Figure 3.17). Thistle species made up over 60% of the nectaring observations, with the native Flodman’s thistle (*Cirsium flodmanii*) alone accounting for over 45% of the total observations. Thistles have dense statewide distribution in North Dakota (Figure 3.7) and their flowering peaks in mid-summer (Figure 3.12).

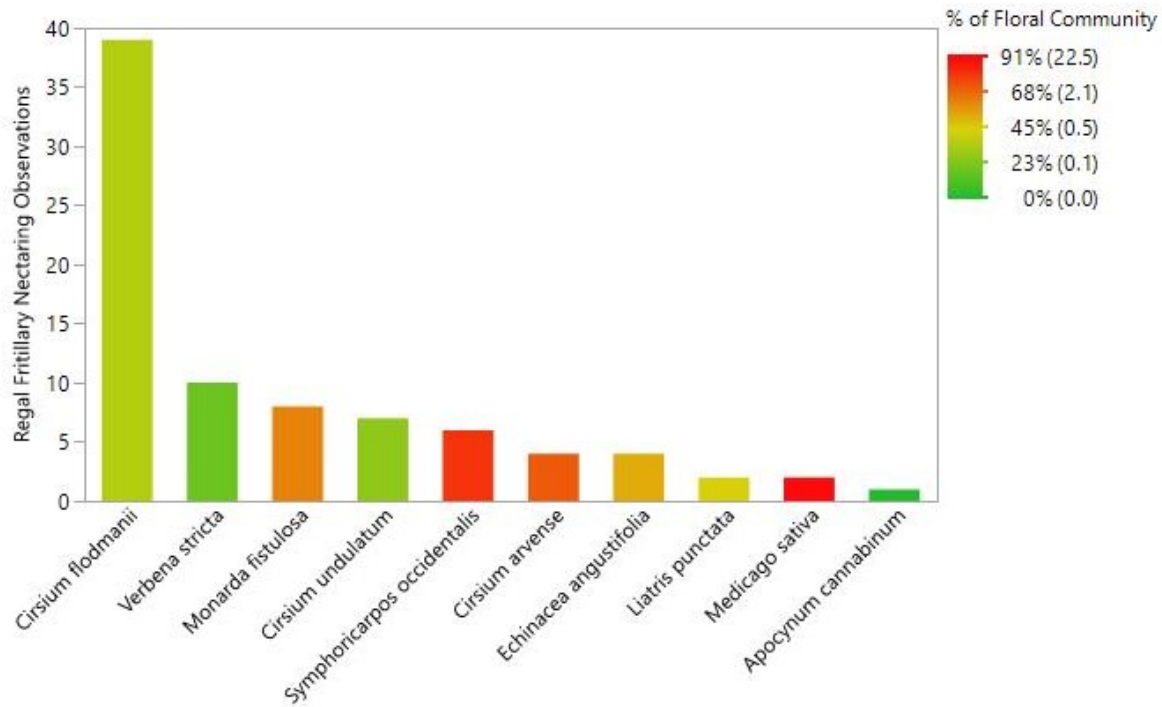


Figure 3.17. Regal fritillary nectaring observations. We observed 83 instances of regal fritillaries nectaring on 10 different plant species from 2017-2019 across North Dakota. Bars are colored by quantiles of percentage of the total floral community, with more common species in red and rarer species in green, to illustrate nectar use compared to the flower’s abundance.

Regal fritillaries responded differentially to flowering thistles depending on their origin. The butterflies showed a positive relationship with native species, and a negative relationship with exotic species (Figure 3.18). This trend remained constant when individually considering the three thistle species that regal fritillaries were seen nectaring on (Figure 3.19).

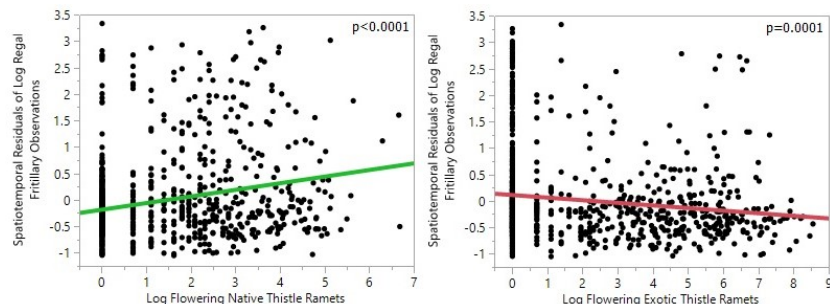


Figure 3.18. Regal fritillary observations relative to native and exotic thistle abundance. With spatial and temporal influences mitigated, regal fritillary observations were significantly positively related to native flowering thistles (left) and significantly negatively related to exotic flowering thistles (right).

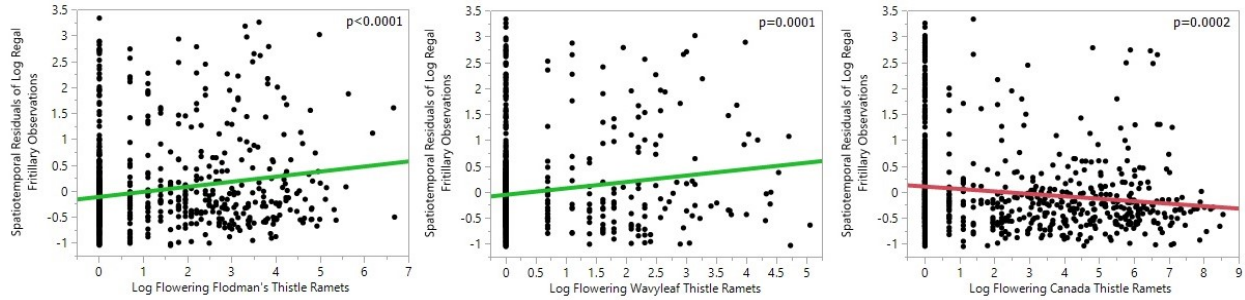


Figure 3.19. Regal fritillary observations relative to Flodman’s, wavyleaf, and Canada thistle. Regal fritillary observations were positively related to both native thistle species it was observed nectaring on (Flodman’s thistle, left, and wavyleaf thistle, center), but negatively related to the exotic thistle species it was seen nectaring on (Canada thistle, right).

Despite being cited as important nectar sources for regal fritillaries (Marrone 2002, Mason 2001, Royer 2003, Swartz et al 2015), I found no significant correlation between regal fritillaries and either flowering milkweed or blazing stars (Figure 3.20).

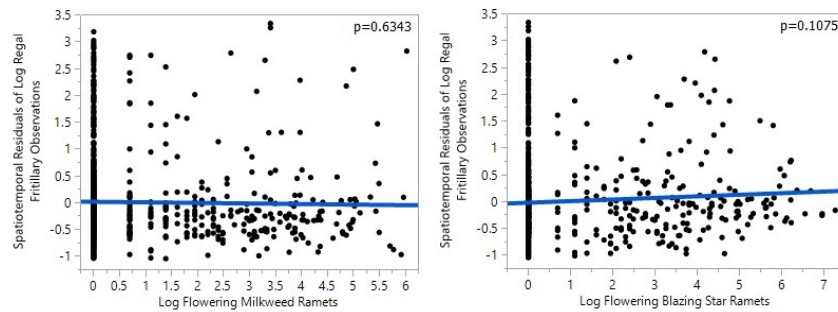


Figure 3.20. Regal fritillary observations relative to flowering milkweed and blazing star. Regal fritillary observations were not significantly related to the abundance of either flowering milkweed (left) or flowering blazing star (right).

3.4. Discussion

In this study I aimed to determine the spatial and temporal distributions in North Dakota of monarch butterflies, regal fritillaries, and their plant resources. I then sought to determine the relationship between the butterfly species and their resources given their overlapping and/or contrasting spatiotemporal distributions.

3.4.1. Monarch Butterfly Distribution

The concentration of monarch observations in the eastern half of North Dakota matches expectations, as maps of the eastern migrating monarch population distribution in North America often show a drop off in abundance at central North Dakota moving west (Flockhart et al 2013, Howard and Davis 2009). However, we also saw many monarchs, albeit at lower concentrations, in the western half of the state. Our observations of monarchs adjacent to the North Dakota-Montana border indicate that, at times, the eastern migrating monarch population likely extends into eastern Montana. This should be considered as monarch conservation efforts move forward so that these western strays are not ignored.

Monarchs are known to fly from spring into fall in the Midwest of North America, and our summer-long observations matched expectations. The peak abundance in late July also matches expectations as this corresponds to their reproduction period when numbers are actively increasing, while earlier and later time periods mainly involve northward and southward migrating monarchs respectively.

Monarch spatial distribution mirrored that of both milkweed cover measured during vegetation surveys and flowering milkweed measured during floral transect surveys, all exhibiting an eastern concentration. This matches expectations, as monarchs require milkweed for oviposition to produce future generations, and so are expected to co-occur with the host plant. This result gives further evidence to the correlation of adult presence, and not just larval presence, with milkweeds (Lukens et al 2020). The correlation between monarchs and floral milkweed was independent of milkweed cover, providing support that monarchs depend upon milkweed floral resources in addition to its role as a host.

3.4.2. Monarch Butterfly Nectaring Observations

The three floral groups that monarchs most often were observed nectaring upon were milkweeds, thistles, and blazing stars. These three groups have all been cited as important monarch nectar sources (Lukens et al 2020, Marrone 2002). However, monarch observations only had a significantly positive relationship with the abundance of milkweeds and exotic thistles. This implies that variables beyond the abundance of preferred floral species are likely influencing monarch presence. Climatic conditions and community compositions associated with blazing stars and native thistles may not suit monarchs as well as that of milkweeds and exotic thistles. Overall these results indicate that monarchs will use blazing stars and native thistles when they happen to co-occur, but their abundance may be more strongly influenced by flowering milkweeds, exotic thistles, and other factors.

These floral groups were distributed differentially across North Dakota in both space and time such that, when grouped together, these highly used food sources were available evenly across the entirety of the state and during the entirety of the monarch flight season. Rather than focusing on any single high use nectar source when planning seed mixes targeted toward monarchs, suites of species should be considered to ensure high quality food resources are available to support monarchs across their entire spatial and temporal distributions (Myers et al 2012, Pywell et al 2011). Our results suggest that milkweeds and thistles serve as especially important food sources for adult monarchs, and the complementary early flowering of milkweed and summer-long flowering of thistles maintain nectar supply through the monarch flight period.

Despite the majority of monarch conservation research focusing on planting milkweed (Luna and Dumroese 2013, Pitman et al 2018, Pleasants 2017, Pleasants and Oberhauser 2013), our findings suggest that both host and nectar plants should be considered. There were

significant positive relationships between monarchs and flowering thistles and milkweeds independent of the butterfly's relationship with milkweed cover. This indicates that, in addition to serving as a host plant, milkweed also serves as an important early blooming nectar source. Mid and late season flowers like native thistles and blazing stars should also be planted to help ensure monarchs have adequate food sources throughout their flight season in the Great Plains.

3.4.3. Regal Fritillary Distribution

Our data revealed a southern concentration of our regal fritillaries in North Dakota. This trend matched expectations, but the higher concentration in the southwest compared to the southeast was somewhat surprising given recent observations of an eastward shift in their abundance distribution in the state (Royer 2003).

Regal fritillaries weren't detected until mid-June in all of our field seasons, and continued flying through the end August. This matched expectations, as males are recorded as emerging in mid-June and flying into August, and females emerging in early July and flying to mid-September (Marrone 2002). Although we did not observe any regal fritillaries in September this is likely due to our minimal surveys during that month, only occurring at low numbers in our third field season due to weather delays.

3.4.4. Regal Fritillary Nectaring Observations

In previous research, relationships between regal fritillaries and the density of documented nectar sources have been inconsistent (Swartz et al 2015, Mason 2001). Similarly, we found mixed responses of regal fritillaries to commonly cited preferred floral species. We found no relationship between regal fritillary butterfly abundance with either milkweeds or blazing stars, which are considered important for the species (Marrone 2002, Mason 2001, Royer 2003, Swartz et al 2015). However, we only observed two instances of regal fritillaries nectaring

on blazing star, and had no observations of the butterfly using milkweed. The most highly utilized nectar sources by regal fritillaries were thistles, primarily native species, which are also cited as an important nectar source for the species (Marrone 2002, Mason 2001, Royer 2003, Swartz et al 2015). Regal fritillaries had a significant positive relationship with native flowering thistles after accounting for spatiotemporal trends. So, despite previous ambiguous findings on regal fritillary response to nectar sources, our results align with the observations we made of actual foraging events.

The expansive distribution across the spatial extent of North Dakota and long blooming time of thistles may play a role in why they are an oft-utilized nectar source for adult regal fritillary butterflies. Although some of our regal fritillary nectaring observations were on exotic thistles, the butterflies had a significant negative relationship with flowering exotic thistles. Together, these results indicate that regal fritillaries may be sensitive to habitat quality, occasionally utilizing exotic thistles due to their high abundance and prevalent distribution while actively seeking out native thistles and the higher quality habitat they are usually associated with (Powell et al 2011).

3.4.5. Management Implications

The floral resources identified as the most used nectar sources for monarch butterflies and regal fritillaries have important implications for land management strategies aimed at bolstering populations of these two species. The idea of the lepidopteran pollination syndrome, known as psychophily, has included a preferred floral color spectrum of red, orange, yellow, and purple, blue, and white flowers (Margaoan et al 2019, Reddi and Bai 1984), but the validity of this historical concept is debatable (Gomez and Zamora 2006, Medan et al 2006, Ollerton et al 2009, Waser 2006). This wide spectrum also gives little in the way of highlighting specific floral

colors that best suit butterflies. Reality suggests a finer delineation of color preference at the species level (Briggs et al 2018, Neumayer and Spaethe 2007, Pohl et al 2011).

Our findings suggest that both monarchs and regal fritillaries most often use pink, and especially purple, flowers. The three floral groups most utilized by monarchs, that is, milkweeds, thistles, and blazing stars, all fall within the pink to purple color spectrum. All of the flower species utilized by regal fritillaries also fell within this spectrum. Based on these results, in addition to the specific species of high use that we have identified, management efforts aimed at supplying nectar sources for these two species may choose to select flowers in the pink to purple color range.

3.5. Conclusions

When considering monarch butterflies and regal fritillaries together as two species of conservation concern, we see that complementary conservation efforts can be implemented where both species occur. In North Dakota the southeastern portion of the state has the highest concentration of both monarchs, which are densest in the east, and regal fritillaries, which are densest in the south. Certain flowers, namely thistles, are highly utilized as nectar sources by both butterfly species. Fostering populations of native thistles in the southeast of North Dakota and other regions where these species co-occur, in addition to ensuring availability of both butterfly species' host plants, will likely provide high benefits to both of these at risk butterflies.

Butterflies use diverse resources, including both host and nectar plants, that must be considered together when attempting to determine what environmental variables best support their populations. Time and space further complicate the matter, as correlations between a butterfly and plant species may just be due to overlapping distributions, and not necessarily due to butterfly use of those plants. Important relationships can be revealed when these

considerations are in place, giving stronger support to conservation efforts focusing on increasing specific resources to support butterfly populations.

3.6. References

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**APPENDIX A. BIBLIOGRAPHY OF PLANT-POLLINATOR NETWORK STUDIES
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APPENDIX B. BUTTERFLY SPECIES INCLUDED IN NETWORK ANALYSIS

Butterfly Species Code	Scientific Name	Common Name
ANALOG	<i>Anatrytone logan</i>	Delaware Skipper
ANCNUM	<i>Ancyloxypha numitor</i>	Least Skipper
ATRHIA	<i>Atrytonopsis hianna</i>	Dusted Skipper
BOLBEL	<i>Boloria bellona</i>	Meadow Fritillary
BOLSEL	<i>Boloria selene</i>	Silver Bordered Fritillary
CERPEG	<i>Cercyonis pegala</i>	Common Wood Nymph
CHLGOR	<i>Chlosyne gorgone</i>	Gorgone Checkerspot
COETUL	<i>Coenonympha tullia</i>	Common Ringlet
COLEUR	<i>Colias eurytheme</i>	Orange Sulphur
COLPHI	<i>Colias philodice</i>	Clouded Sulphur
DANPLE	<i>Danaus plexippus</i>	Monarch
EPACLA	<i>Epargyreus clarus</i>	Silver Spotted Skipper
EUPCLA	<i>Euptoieta claudia</i>	Variiegated Fritillary
EVECOM	<i>Everes comyntas</i>	Eastern Tailed Blue
GLALYG	<i>Glaucopsyche lygdamus</i>	Silvery Blue
HESCOM	<i>Hesperia comma</i>	Common Branded Skipper
HESDAK	<i>Hesperia dacotae</i>	Dakota Skipper
HESLEO	<i>Hesperia leonardus</i>	Leonard's/Pawnee Skipper
HESUNC	<i>Hesperia uncas</i>	Uncas Skipper
LIMARC	<i>Limenitis archippus</i>	Viceroy
LYCDIO	<i>Lycaena dione</i>	Gray Copper
LYCHYL	<i>Lycaena hyllus</i>	Bronze Copper
LYCMEL	<i>Lycaeides melissa</i>	Melissa Blue
NYMANT	<i>Nymphalis antiopa</i>	Mourning Cloak
OARGAR	<i>Oarisma garita</i>	Garita Skipperling
PAPGLA	<i>Papilio glaucus</i>	Eastern Tiger Swallowtail
PAPPOL	<i>Papilio polyxenes</i>	Black Swallowtail
PHYBAT	<i>Phyciodes batesii</i>	Tawny Crescent
PHYCOC	<i>Phyciodes cocyta</i>	Northern Crescent
PHYTHA	<i>Phyciodes tharos</i>	Pearl Crescent
PIERAP	<i>Pieris rapae</i>	Cabbage White
PLEICA	<i>Plebejus icarioides</i>	Boisduval's Blue
PLESAE	<i>Plebejus saepiolus</i>	Greenish Blue
POAHOB	<i>Poanes hobomok</i>	Hobomok Skipper
POLMYS	<i>Polites mystic</i>	Long Dash Skipper
POLORI	<i>Polites origenes</i>	Crossline Skipper
POLPEC	<i>Polites peckius</i>	Peck's Skipper
POLTHE	<i>Polites themistocles</i>	Tawny-edged Skipper
PONPRO	<i>Pontia protodice</i>	Checkered White
PYRCOM	<i>Pyrgus communis</i>	Common Checkered Skipper
SATTIT	<i>Satyrium titus</i>	Coral Hairstreak
SPEAPH	<i>Speyeria aphrodite</i>	Aphrodite Fritillary
SPECAL	<i>Speyeria callippe</i>	Callippe Fritillary
SPECYB	<i>Speyeria cybele</i>	Great Spangled Fritillary
SPEIDA	<i>Speyeria idalia</i>	Regal Fritillary
VANATA	<i>Vanessa atalanta</i>	Red Admiral
VANCAR	<i>Vanessa cardui</i>	Painted Lady
VANVIR	<i>Vanessa virginiensis</i>	American Lady

APPENDIX C. FLOWER SPECIES INCLUDED IN NETWORK ANALYSIS

Flower Species Code	Scientific Name	Common Name	Origin
ACHMIL	<i>Achillea millefolium</i>	Yarrow	Native
AGAFOE	<i>Agastache foeniculum</i>	Blue giant hyssop	Native
AGOGLA	<i>Agoseris glauca</i>	False dandelion	Native
ALLSTE	<i>Allium stellatum</i>	Pink prairie onion	Native
ALLTEX	<i>Allium textile</i>	White textile onion	Native
AMOCAN	<i>Amorpha canescens</i>	Lead plant	Native
ANECAN	<i>Anemone canadensis</i>	Canada anemone	Native
ANTNEG	<i>Antennaria neglecta</i>	Field pussytoes	Native
ANTPAR	<i>Antennaria parlinii</i>	Parlin's pussytoes	Native
APOCAN	<i>Apocynum cannabinum</i>	Hemp dogbane	Native
APOSIB	<i>Apocynum sibiricum</i>	Clasping dogbane	Native
ARTFRI	<i>Artemisia frigida</i>	Fringed sagewort	Native
ARTLUD	<i>Artemisia ludoviciana</i>	White sage	Native
ASCINC	<i>Asclepias incarnata</i>	Swamp milkweed	Native
ASCOVA	<i>Asclepias ovalifolia</i>	Oval-leaf milkweed	Native
ASCPUM	<i>Asclepias pumila</i>	Low milkweed	Native
ASCSPE	<i>Asclepias speciosa</i>	Showy milkweed	Native
ASCSYR	<i>Asclepias syriaca</i>	Common milkweed	Native
ASCVER	<i>Asclepias verticillata</i>	Whorled milkweed	Native
ASTADS	<i>Astragalus adsurgens</i>	Prairie milkvetch	Native
ASTAGR	<i>Astragalus agrestis</i>	Field milkvetch	Native
ASTCAN	<i>Astragalus canadensis</i>	Canada milkvetch	Native
ASTCIC	<i>Astragalus cicer</i>	Cicer Milkvetch	Exotic
ASTFLE	<i>Astragalus flexuosus</i>	Slender milkvetch	Native
ASTMIS	<i>Astragalus missouriensis</i>	Missouri milkvetch	Native
ASTPEC	<i>Astragalus pectinatus</i>	Narrow-leaved milkvetch	Native
CALSEP	<i>Calystegia sepium</i>	Hedge bindweed	Native
CALSER	<i>Calylophus serrulatus</i>	Yellow sundrops	Native
CAMROT	<i>Campanula rotundifolia</i>	Harebell	Native
CARACA	<i>Carduus acanthoides</i>	Plumeless thistle	Exotic
CARARB	<i>Caragana arborescens</i>	Siberian peashrub	Exotic
CARNUT	<i>Carduus nutans</i>	Nodding thistle	Exotic
CERARV	<i>Cerastium arvense</i>	Field chickweed	Native
CIRARV	<i>Cirsium arvense</i>	Canada thistle	Exotic
CIRFLO	<i>Cirsium flodmanii</i>	Flodman's thistle	Native
CIRUND	<i>Cirsium undulatum</i>	Wavyleaf thistle	Native
CIRVUL	<i>Cirsium vulgare</i>	Bull thistle	Exotic
CONARV	<i>Convolvulus arvensis</i>	Field bindweed	Exotic
CORVAR	<i>Coronilla varia</i>	Crown vetch	Exotic
DALPUR	<i>Dalea purpurea</i>	Purple prairie clover	Native
DALVIL	<i>Dalea villosa</i>	Silky prairie clover	Native
DESPIN	<i>Descurainia pinnata</i>	Tansy mustard	Native
DRYARG	<i>Drymocallis arguta</i>	Tall cinquefoil	Native
ECHANG	<i>Echinacea angustifolia</i>	Narrow-leaved purple coneflower	Native
ECHPUR	<i>Echinacea purpurea</i>	Purple Coneflower	Native
ELACOM	<i>Elaeagnus commutata</i>	Silverberry	Native
ERIFLA	<i>Eriogonum flavum</i>	Golden buckwheat	Native
ERIPAU	<i>Eriogonum pauciflorum</i>	Fewflower buckwheat	Native
ERIPUM	<i>Erigeron pumilus</i>	Shaggy fleabane	Native
ERISTR	<i>Erigeron strigosus</i>	Daisy fleabane	Native
ERYASP	<i>Erysimum asperum</i>	Western wallflower	Native
ERYINC	<i>Erysimum inconspicuum</i>	Small-flowered wallflower	Native

Flower Species Code	Scientific Name	Common Name	Origin
EUPESU	<i>Euphorbia esula</i>	Leafy spurge	Exotic
EUTGRA	<i>Euthamia graminifolia</i>	Grass-leaved goldenrod	Native
EUTMAC	<i>Eutrochium maculatum</i>	Spotted Joe-pye weed	Native
GAIARI	<i>Gaillardia aristata</i>	Blanketflower	Native
GALBOR	<i>Galium boreale</i>	Northern bedstraw	Native
GAUCOC	<i>Gaura coccinea</i>	Scarlet gaura	Native
GLYLEP	<i>Glycyrrhiza lepidota</i>	Wild licorice	Native
GRISQU	<i>Grindelia squarrosa</i>	Curlycup gumweed	Native
GUTSAR	<i>Gutierrezia sarothrae</i>	Broom snakeweed	Native
HELGIG	<i>Helianthus giganteus</i>	Giant sunflower	Native
HELGRO	<i>Helianthus grosseserratus</i>	Sawtooth sunflower	Native
HELHEL	<i>Heliopsis helianthoides</i>	Smooth oxeye	Native
HELMAX	<i>Helianthus maximilianii</i>	Maximilian sunflower	Native
HELPAU	<i>Helianthus pauciflorus</i>	Stiff sunflower	Native
HESMAT	<i>Hesperis matronalis</i>	Dame's rocket	Exotic
HETVIL	<i>Heterotheca villosa</i>	Hairy false goldenaster	Native
HYMRIC	<i>Hymenoxys richardsonii</i>	Pingue rubberweed	Native
LACLUUD	<i>Lactuca ludoviciana</i>	Western wild lettuce	Native
LACSER	<i>Lactuca serriola</i>	Prickly lettuce	Exotic
LACTAT	<i>Lactuca tatarica</i>	Showy blue lettuce	Native
LIAASP	<i>Liatris aspera</i>	Rough blazing star	Native
LIALIG	<i>Liatris ligulistylis</i>	Northern plains blazing star	Native
LIAPUN	<i>Liatris punctata</i>	Dotted blazing star	Native
LIAPYC	<i>Liatris pycnostachya</i>	Prairie blazing star	Native
LILPHI	<i>Lilium philadelphicum</i>	Wood lily	Native
LINLEW	<i>Linum lewisii</i>	Blue flax	Native
LINSUL	<i>Linum sulcatum</i>	Grooved (small-flowered) yellow flax	Native
LINVUL	<i>Linaria vulgaris</i>	Butter and eggs	Exotic
LITCAN	<i>Lithospermum canescens</i>	Hoary puccoon	Native
LOBSPI	<i>Lobelia spicata</i>	Pale-spike lobelia	Native
LONBEL	<i>Lonicera bella</i>	Showy honeysuckle	Exotic
LONMAA	<i>Lonicera maackii</i>	Amur honeysuckle	Exotic
LOTPUR	<i>Lotus purshianus</i>	American birds-food trefoil	Native
LUPARG	<i>Lupinus argenteus</i>	Silvery lupine	Native
LYGJUN	<i>Lygodesmia juncea</i>	Skeletonweed	Native
LYSQUA	<i>Lysimachia quadriflora</i>	Prairie loosestrife	Native
LYTALA	<i>Lythrum alatum</i>	Winged loosestrife	Native
MEDFAL	<i>Medicago falcata</i>	Yellow alfalfa	Exotic
MEDLUP	<i>Medicago lupulina</i>	Black medic	Exotic
MEDSAT	<i>Medicago sativa</i>	Alfalfa (purple/blue/white)	Exotic
MELALB	<i>Melilotus alba</i>	White sweet clover	Exotic
MELOFF	<i>Melilotus officinalis</i>	Yellow sweet clover	Exotic
MONFIS	<i>Monarda fistulosa</i>	Wild bergamot; Bee balm	Native
ONOMOL	<i>Onosmodium molle</i>	False gromwell	Native
OXYCAM	<i>Oxytropis campestris</i>	Field locoweed	Native
OXYLAM	<i>Oxytropis lambertii</i>	Lambert's locoweed	Native
PACCAN	<i>Packera cana</i>	Woolly groundsel	Native
PACPAU	<i>Packera paupercula</i>	Balsam ragwort	Native
PACPLA	<i>Packera plattensis</i>	Prairie ragwort	Native
PACPSE	<i>Packera pseudoaurea</i>	Western heart-leaved groundsel	Native
PEDARG	<i>Pedimelum argophyllum</i>	Silverleaf scurfpea	Native
PEDESC	<i>Pedimelum esculentum</i>	Prairie turnip	Native
PENGRAC	<i>Penstemon gracilis</i>	Slender beardtongue	Native
PERAMP	<i>Persicaria amphibia</i>	Swamp smartweed	Native
PERSER	<i>Peritoma serrulata</i>	Rocky mountain bee plant	Native

Flower Species Code	Scientific Name	Common Name	Origin
PHYLUD	<i>Physaria ludoviciana</i>	Bladderpod	Native
POLALB	<i>Polygala alba</i>	White milkwort	Native
POTANS	<i>Potentilla anserina</i>	Silverweed cinquefoil	Native
POTPEN	<i>Potentilla pensylvanica</i>	Pennsylvania cinquefoil	Native
RATCOL	<i>Ratibida columnifera</i>	Prairie coneflower	Native
ROSARK	<i>Rosa arkansana</i>	Prairie rose	Native
RUDHIR	<i>Rudbeckia hirta</i>	Black-eyed Susan	Native
SENINT	<i>Senecio integerrimus</i>	Lambstongue ragwort	Native
SISLOE	<i>Sisymbrium loeselii</i>	Tall hedge mustard	Exotic
SISMON	<i>Sisyrinchium montanum</i>	Mountain blue eyed grass	Native
SOLCAN	<i>Solidago canadensis</i>	Canada goldenrod	Native
SOLGIG	<i>Solidago gigantea</i>	Giant goldenrod	Native
SOLMIS	<i>Solidago missouriensis</i>	Missouri goldenrod	Native
SOLMOL	<i>Solidago mollis</i>	Velvety goldenrod	Native
SOLNEM	<i>Solidago nemoralis</i>	Gray goldenrod	Native
SOLPTA	<i>Solidago ptarmicoides</i>	Upland white goldenrod	Native
SOLRIG	<i>Solidago rigida</i>	Stiff goldenrod	Native
SONARV	<i>Sonchus arvensis</i>	Sowthistle	Exotic
SPHCOC	<i>Sphaeralcea coccinea</i>	Scarlet globemallow	Native
SPIALB	<i>Spiraea alba</i>	White meadowsweet	Native
STAPAL	<i>Stachys palustris</i>	Marsh hedge nettle	Native
SYMBOR	<i>Symphyotrichum boreale</i>	Northern bog aster	Native
SYMERI	<i>Symphyotrichum ericoides</i>	White heath aster	Native
SYMFAL	<i>Symphyotrichum falcatum</i>	White prairie aster	Native
SYMLAE	<i>Symphyotrichum laeve</i>	Smooth blue aster	Native
SYMLAN	<i>Symphyotrichum lanceolatum</i>	Panicked aster	Native
SYMOBL	<i>Symphyotrichum oblongifolium</i>	Aromatic aster	Native
SYMOCC	<i>Symphoricarpos occidentalis</i>	Western snowberry	Native
SYMSE	<i>Symphyotrichum sericeum</i>	Silky aster	Native
TANVUL	<i>Tanacetum vulgare</i>	Common tansy	Exotic
TARERY	<i>Taraxacum erythrospermum</i>	Red-seeded dandelion	Exotic
TAROFF	<i>Taraxacum officinale</i>	Common dandelion	Exotic
TEPPAL	<i>Tephrosia palustris</i>	Marsh Ragwort	Native
TEUCAN	<i>Teucrium canadense</i>	Germander	Native
TRADUB	<i>Tragopogon dubius</i>	Yellow goat's beard	Exotic
TRIINO	<i>Tripleurospermum inodorum</i>	Scentless false mayweed	Exotic
TRIPRA	<i>Trifolium pratense</i>	Red clover	Exotic
TRIREP	<i>Trifolium repens</i>	White clover	Exotic
VERFAS	<i>Vernonia fasciculata</i>	Prairie ironweed	Native
VERHAS	<i>Verbena hastata</i>	Blue vervain	Native
VERSTR	<i>Verbena stricta</i>	Hoary vervain	Native
VICAME	<i>Vicia americana</i>	American vetch	Native
ZIZAPT	<i>Zizia aptera</i>	Heart-leaved Alexanders	Native
ZIZAUR	<i>Zizia aurea</i>	Golden Alexanders	Native

APPENDIX D. INTERACTION NETWORK GRAPHS

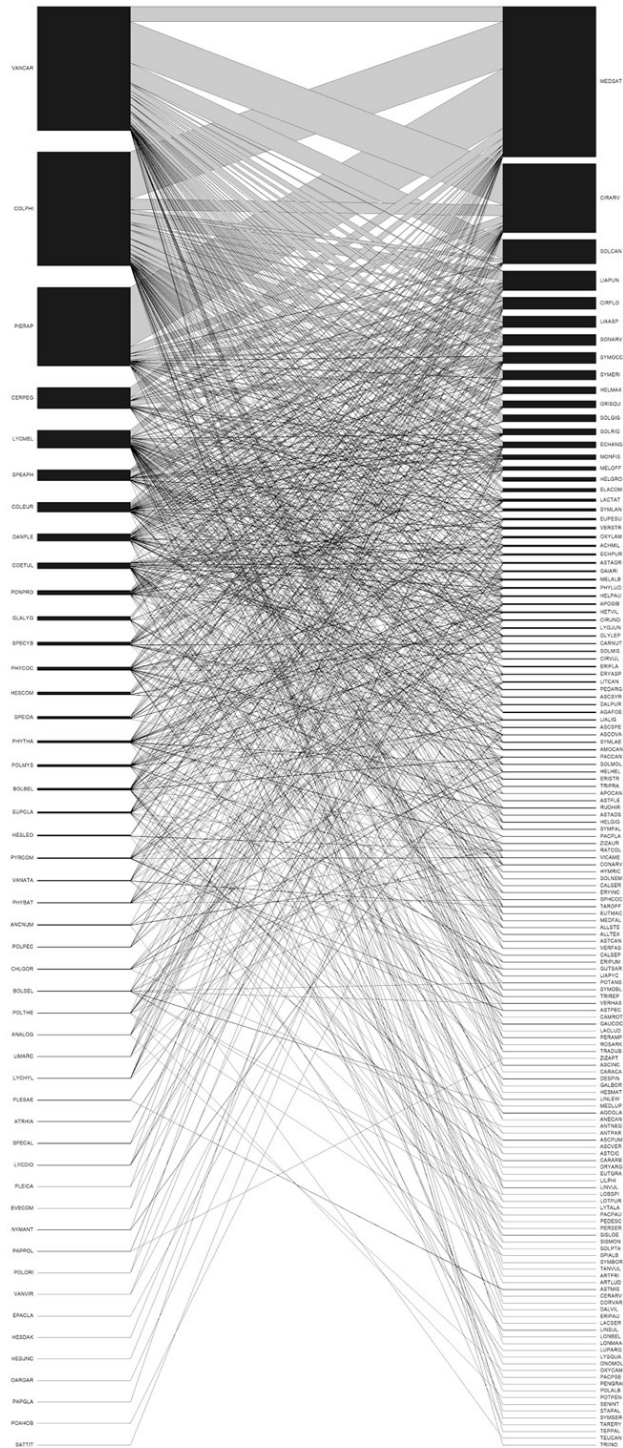


Figure D1. Whole interaction network. Full network featuring all butterfly-flower interaction data from the three-year statewide data set from North Dakota during 2017 to 2019. Boxes and links are sized proportionally to the total number of interactions between the two linked species. Boxes on the left represent butterfly species, and boxes on the right represent plant species. Species code definitions are listed in Appendices B and C.

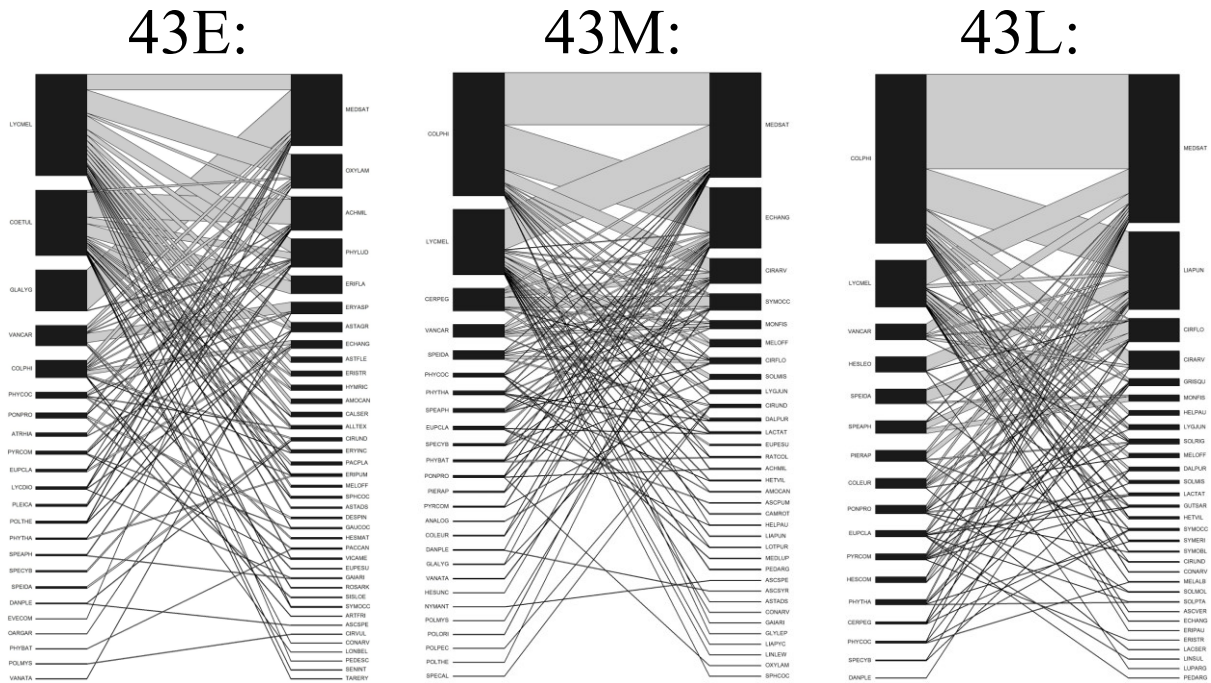
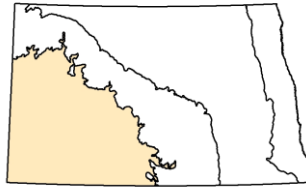


Figure D2. Ecoregion 43 interaction networks. Butterfly-flower interaction networks during early (before July), mid (July), and late (after July) summer in Ecoregion 43, the Northwestern Great Plains, from 2017-2019 in North Dakota. Boxes and links are sized proportionally to the total number of interactions between the two linked species. Boxes on the left represent butterfly species, and boxes on the right represent plant species. Species code definitions are listed in Appendices B and C.

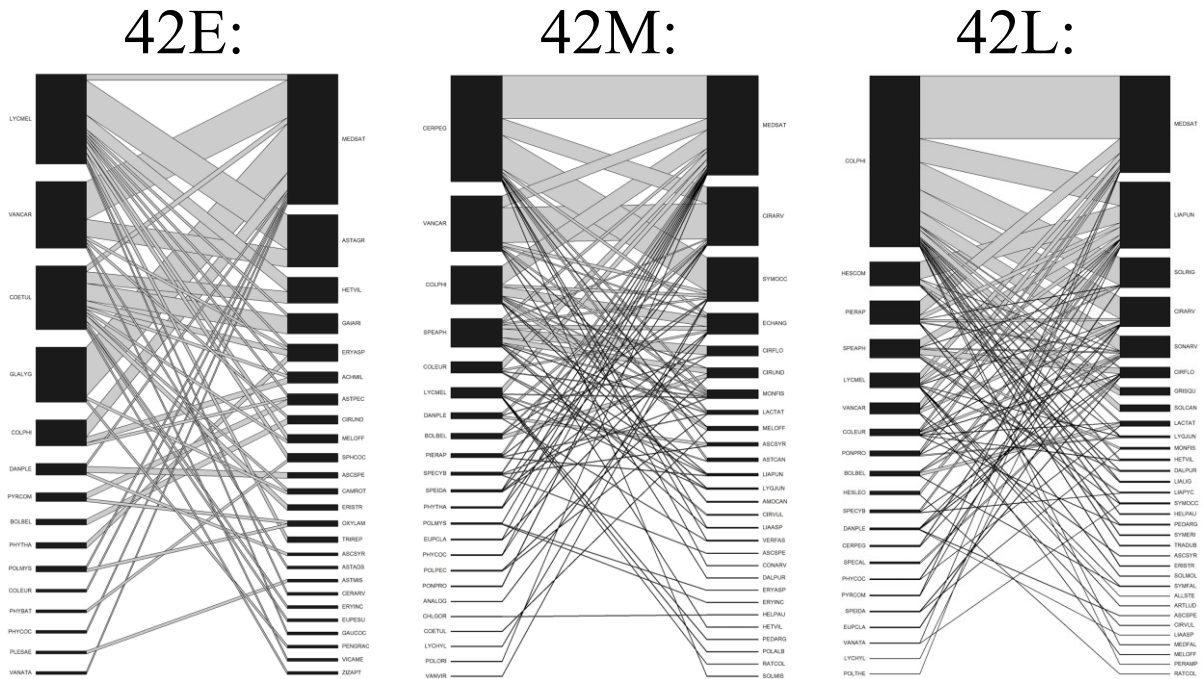
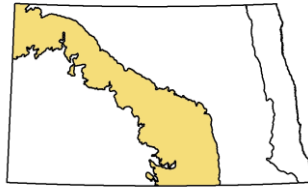


Figure D3. Ecoregion 42 interaction networks. Butterfly-flower interaction networks during early (E, before July), mid (M, July), and late (L, after July) summer in Ecoregion 42, the Northwestern Glaciated Plains, from 2017-2019 in North Dakota. Boxes and links are sized proportionally to the total number of interactions. Boxes on the left represent butterfly species, and boxes on the right represent plant species. Species code definitions are listed in Appendices B and C.

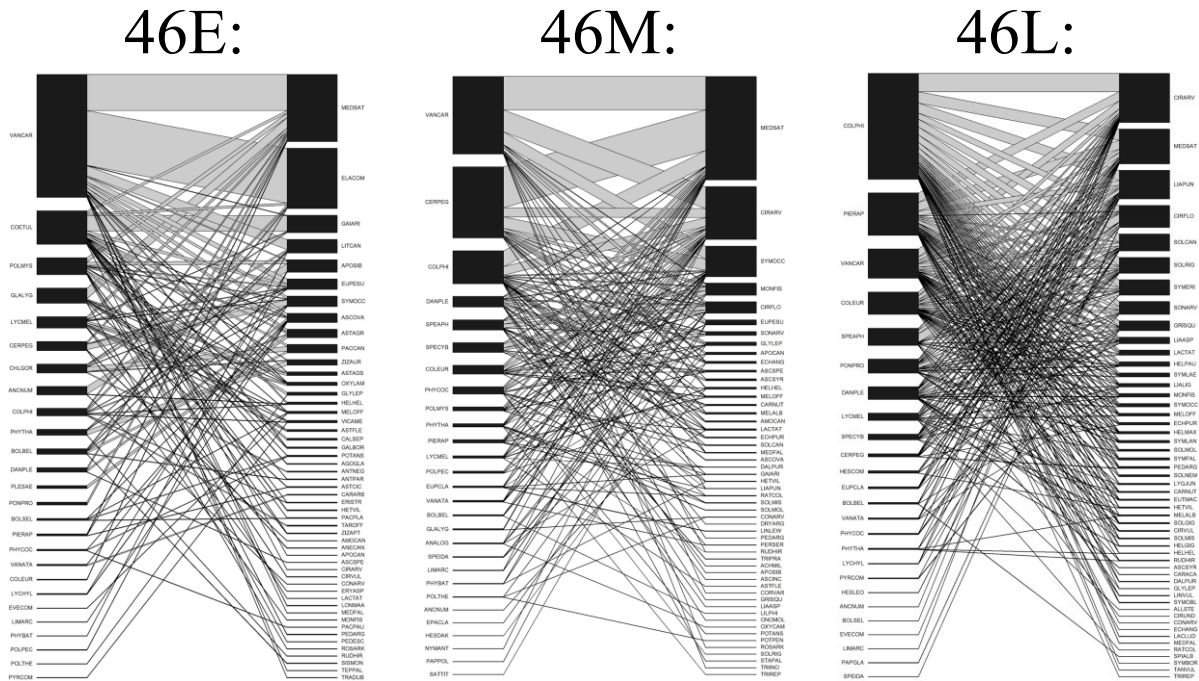
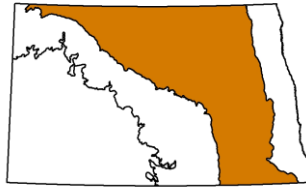


Figure D4. Ecoregion 46 interaction networks. Butterfly-flower interaction networks during early (before July), mid (July), and late (after July) summer in Ecoregion 46, the Northern Glaciated Plains, from 2017-2019 in North Dakota. Boxes and links are sized proportionally to the total number of interactions. Boxes on the left represent butterfly species, and boxes on the right represent plant species. Species code definitions are listed in Appendices B and C.

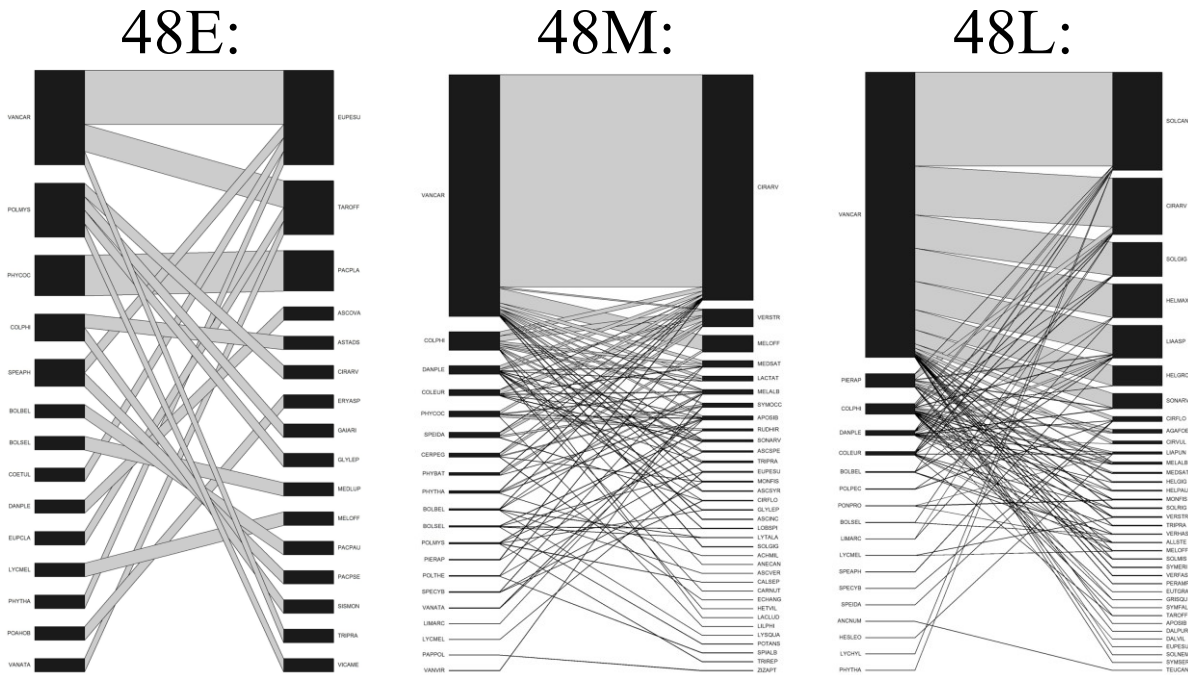
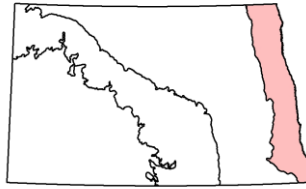


Figure D5. Ecoregion 48 interaction networks. Butterfly-flower interaction networks during early (before July), mid (July), and late (after July) summer in Ecoregion 48, the Lake Agassiz Plain, from 2017-2019 in North Dakota. Boxes and links are sized proportionally to the total number of interactions. Boxes on the left represent butterfly species, and boxes on the right represent plant species. Species code definitions are listed in Appendices B and C.

APPENDIX E. SPECIES-LEVEL METRIC CORRELATIONS

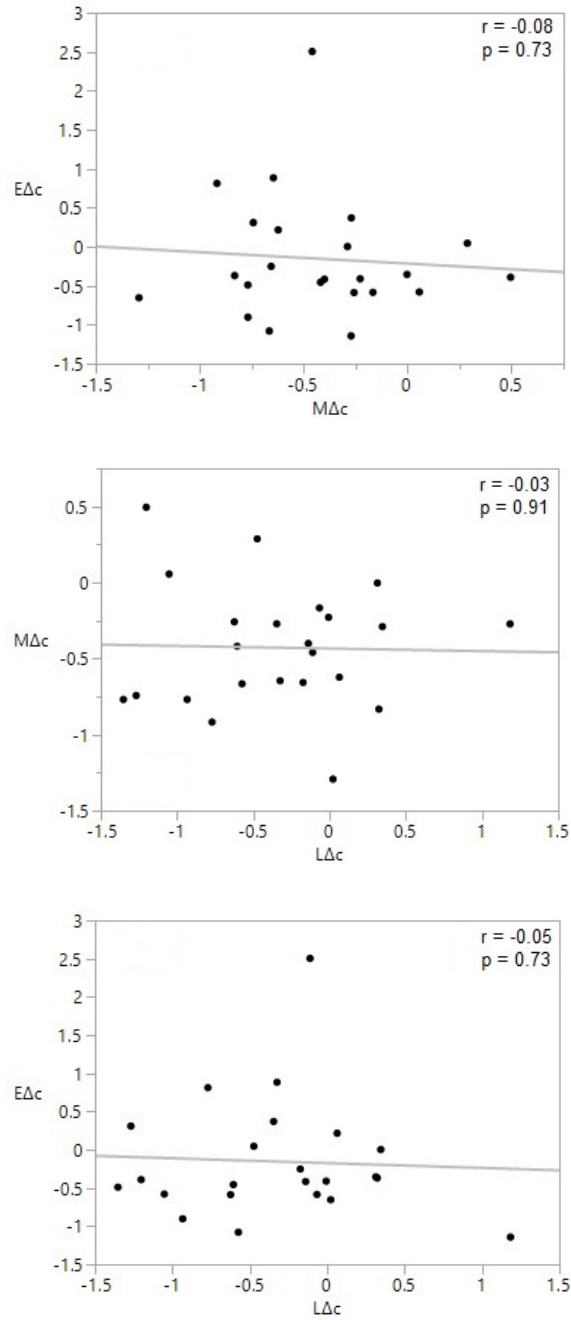


Figure E1. Butterfly among-module connectivity correlations by season. Butterfly species' Δc values were not significantly correlated across seasons. Seasons are defined as early summer (E, before July), mid-summer (M, July), and late summer (L, after July).

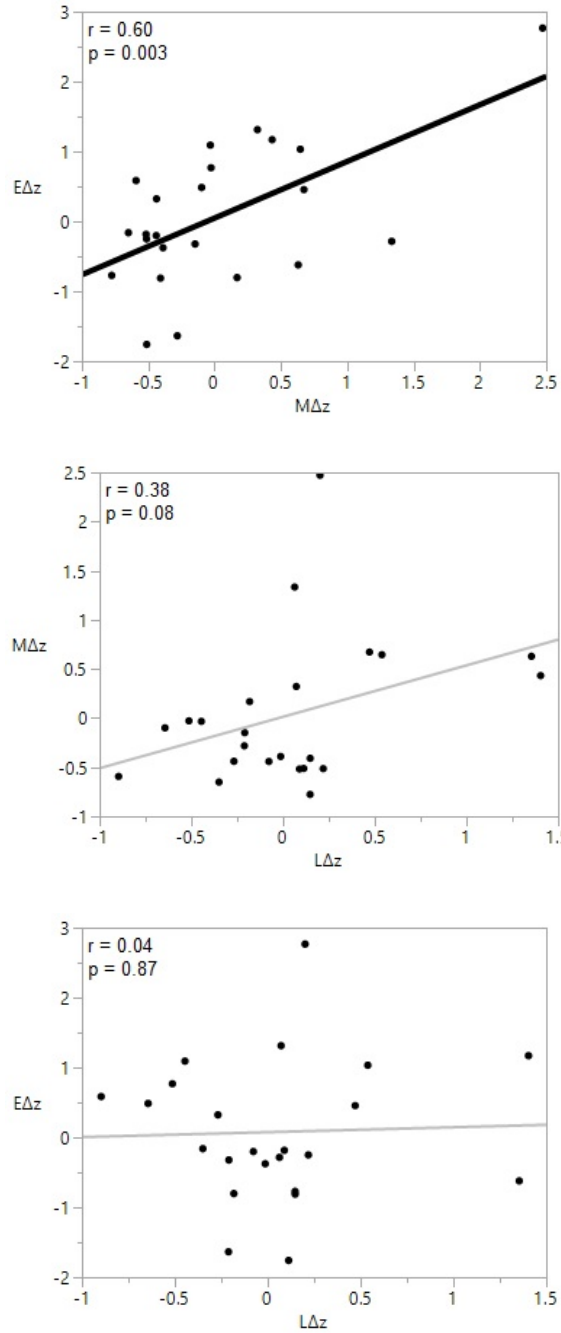


Figure E2. Butterfly within-module degree correlations by season. Butterfly species' Δz values were significantly correlated across early and mid-summer, and were uncorrelated across early and late, and mid and late summer. Seasons are defined as early summer (E, before July), mid-summer (M, July), and late summer (L, after July).

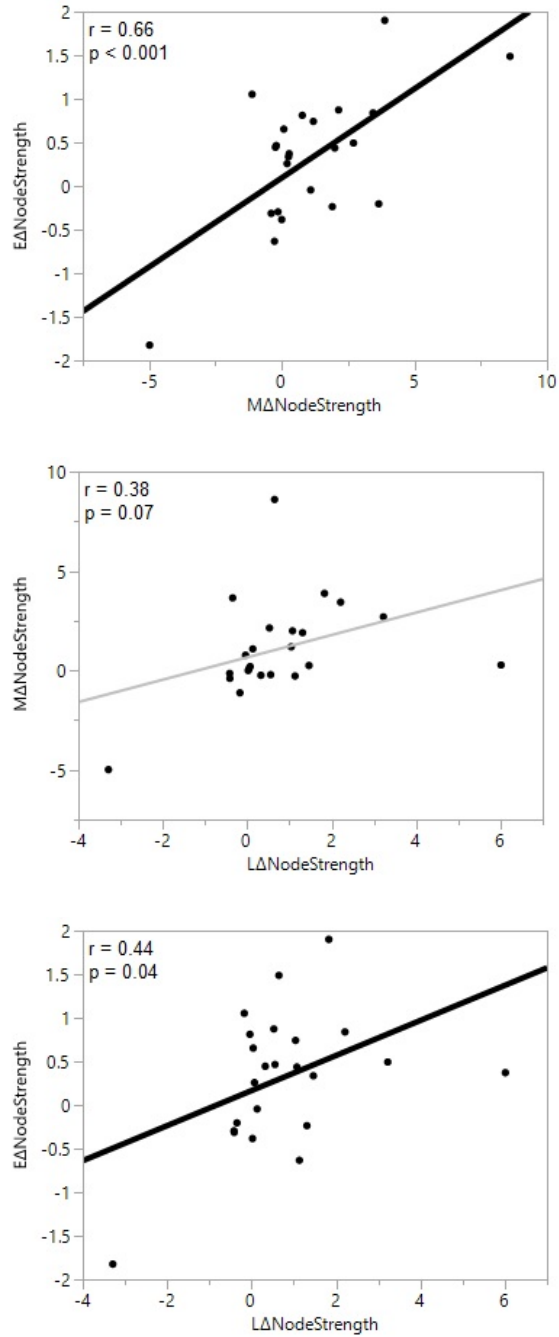


Figure E3. Butterfly node strength correlations by season. Butterfly species' Δ Node Strength values were significantly correlated across early and mid, and early and late summer, and were uncorrelated across mid and late summer. Seasons are defined as early summer (E, before July), mid-summer (M, July), and late summer (L, after July).

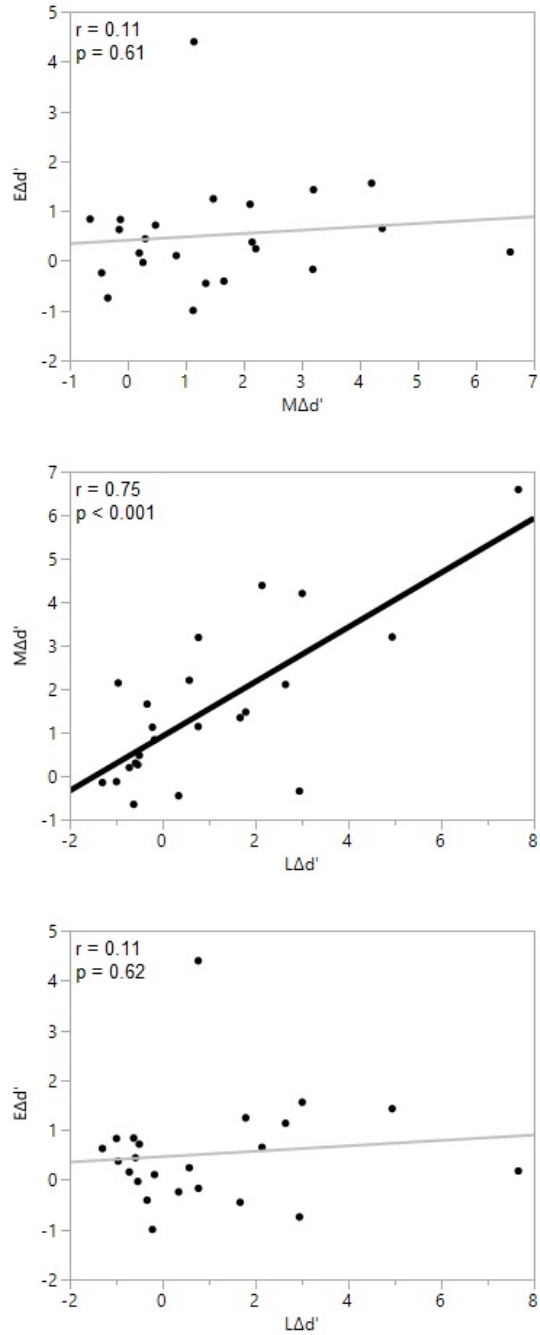


Figure E4. Butterfly specialization correlations by season. Butterfly species' $\Delta d'$ values were significantly correlated across mid and late summer, and were uncorrelated across early and mid, and early and late summer. Seasons are defined as early summer (E, before July), mid-summer (M, July), and late summer (L, after July).

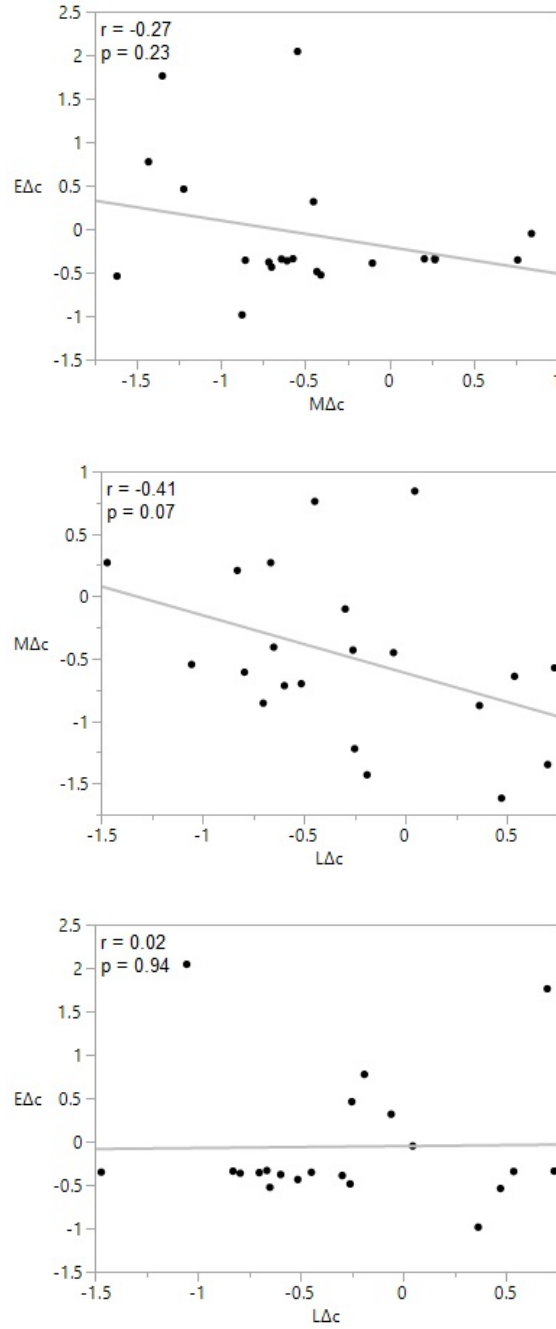


Figure E5. Floral among-module connectivity correlations by season. Flower species' Δc values were not significantly correlated across seasons. Seasons are defined as early summer (E, before July), mid-summer (M, July), and late summer (L, after July).

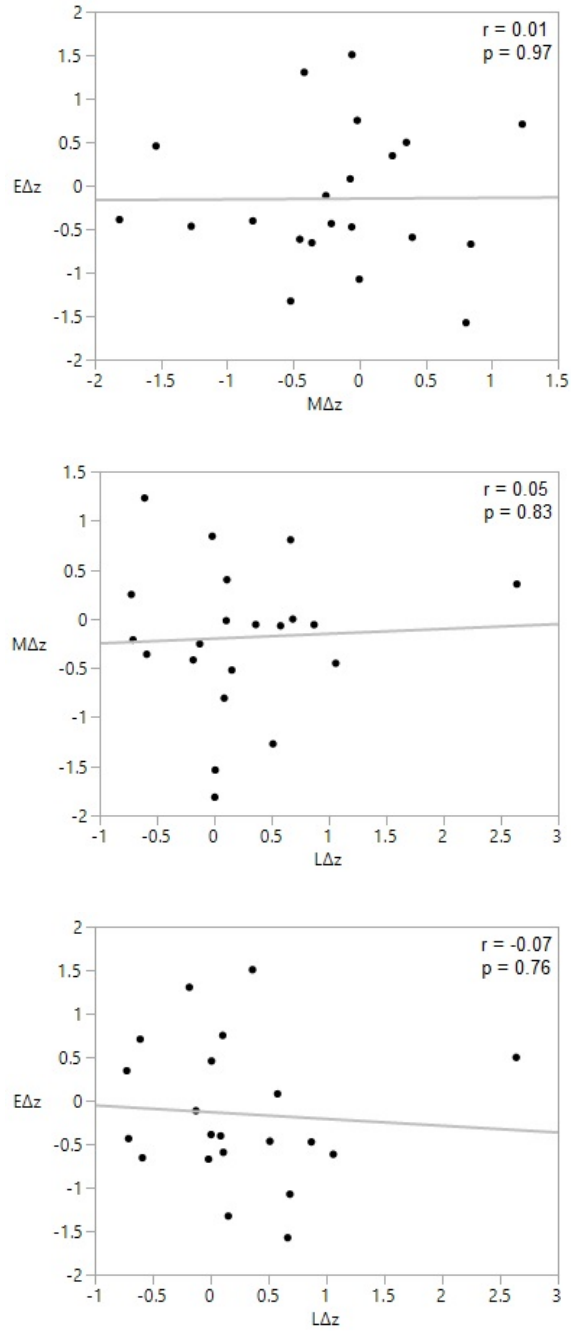


Figure E6. Floral within-module degree correlations by season. Flower species' Δz values were not significantly correlated across seasons. Seasons are defined as early summer (E, before July), mid-summer (M, July), and late summer (L, after July).

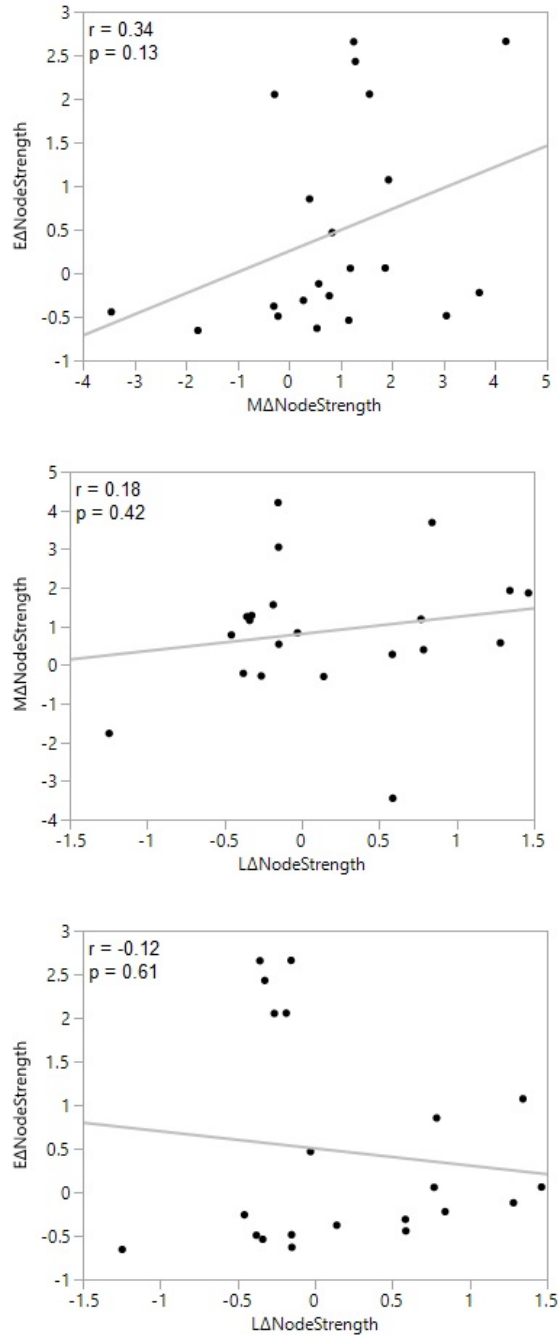


Figure E7. Floral node strength correlations by season. Flower species' $\Delta\text{Node Strength}$ values were not significantly correlated across seasons. Seasons are defined as early summer (E, before July), mid-summer (M, July), and late summer (L, after July).

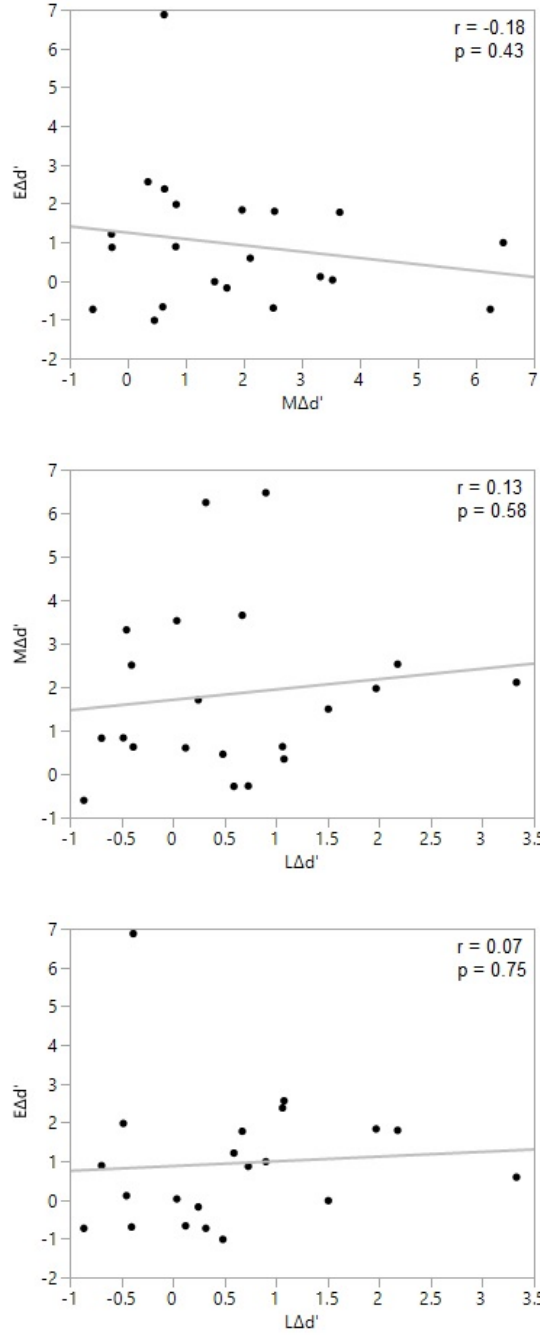


Figure E8. Floral specialization correlations by season. Flower species' $\Delta d'$ values were not significantly correlated across seasons. Seasons are defined as early summer (E, before July), mid-summer (M, July), and late summer (L, after July).

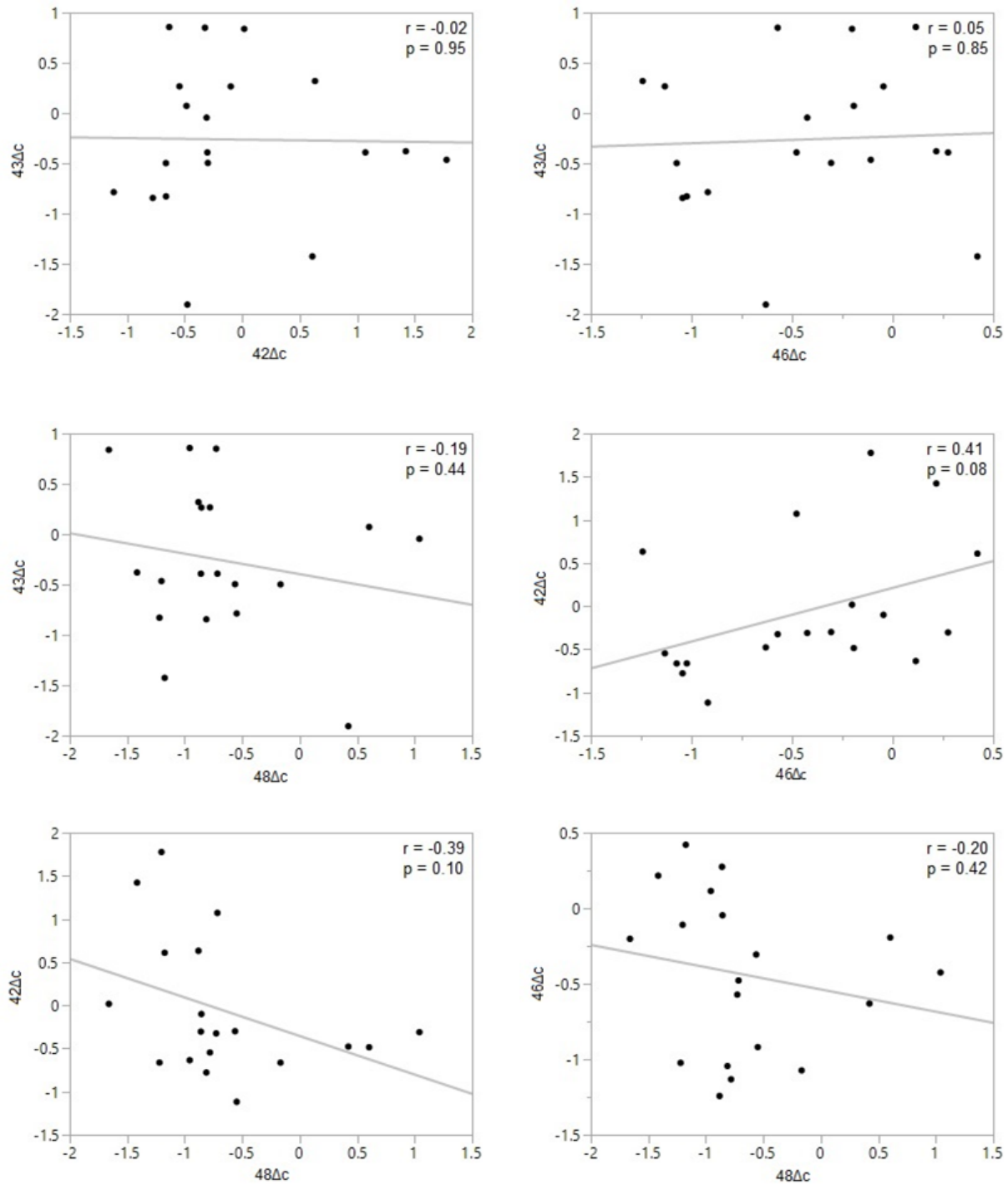


Figure E9. Butterfly among-module connectivity correlations by ecoregion. Butterfly species' Δc values were not significantly correlated across any ecoregions. Ecoregions in North Dakota are, in order from west to east, the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48).

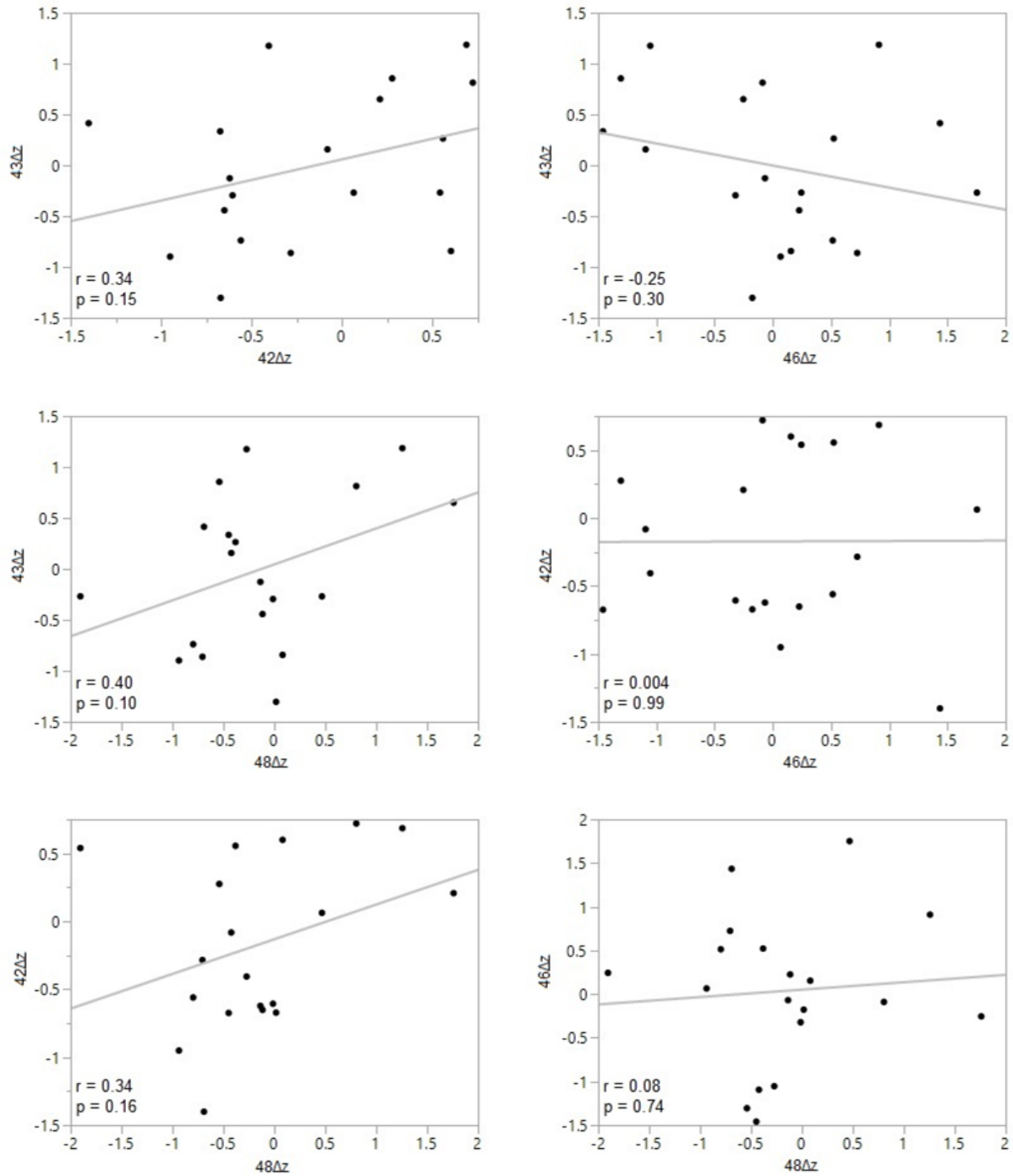


Figure E10. Butterfly within-module degree correlations by ecoregion. Butterfly species' Δz values were not significantly correlated across any ecoregions. Ecoregions in North Dakota are, in order from west to east, the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48).

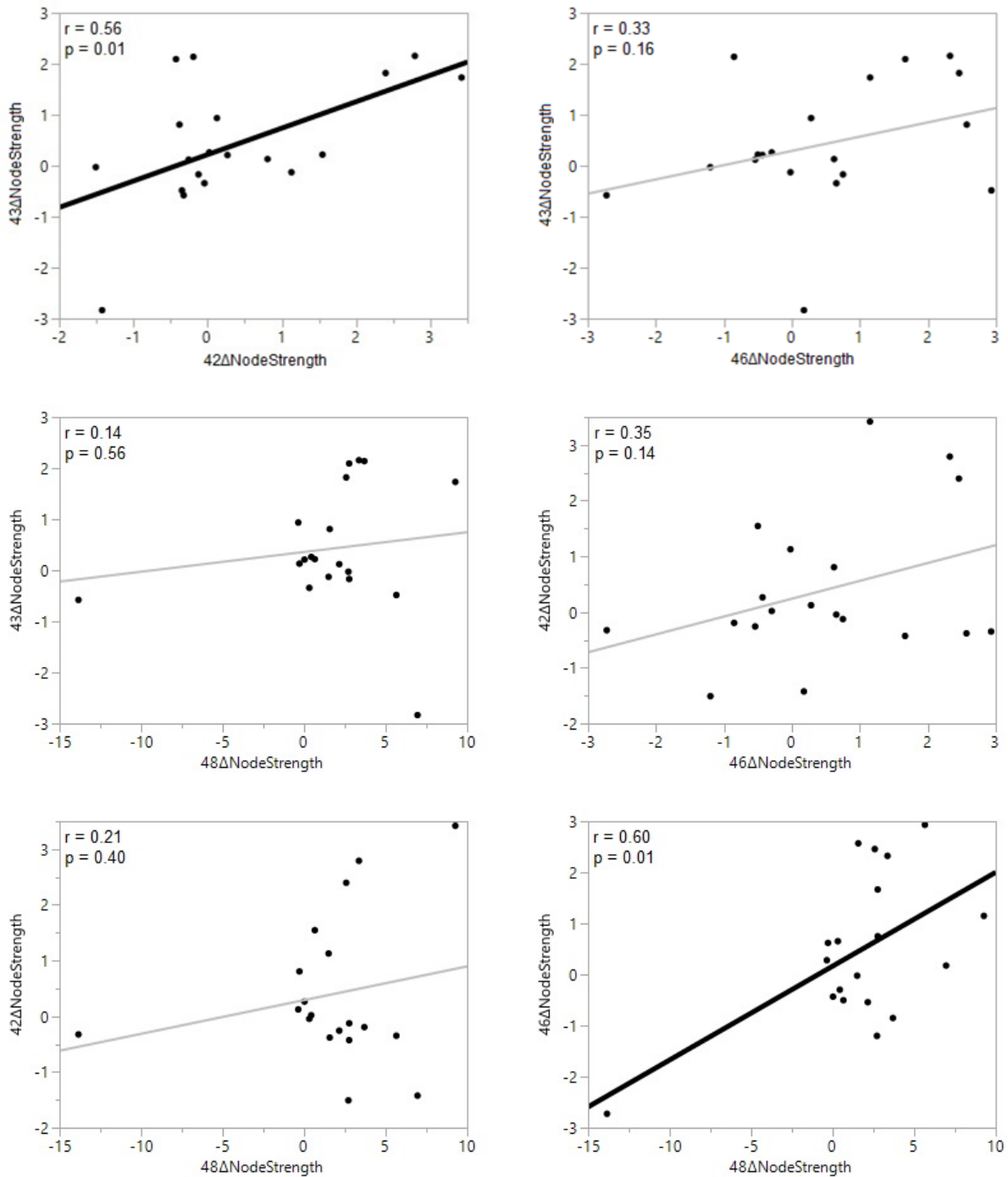


Figure E11. Butterfly node strength correlations by ecoregion. Butterfly species' Δ Node Strength values were significantly correlated across adjacent ecoregions 43 and 42, and adjacent ecoregions 46 and 48, and were uncorrelated across the other ecoregions. Ecoregions in North Dakota are, in order from west to east, the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48).

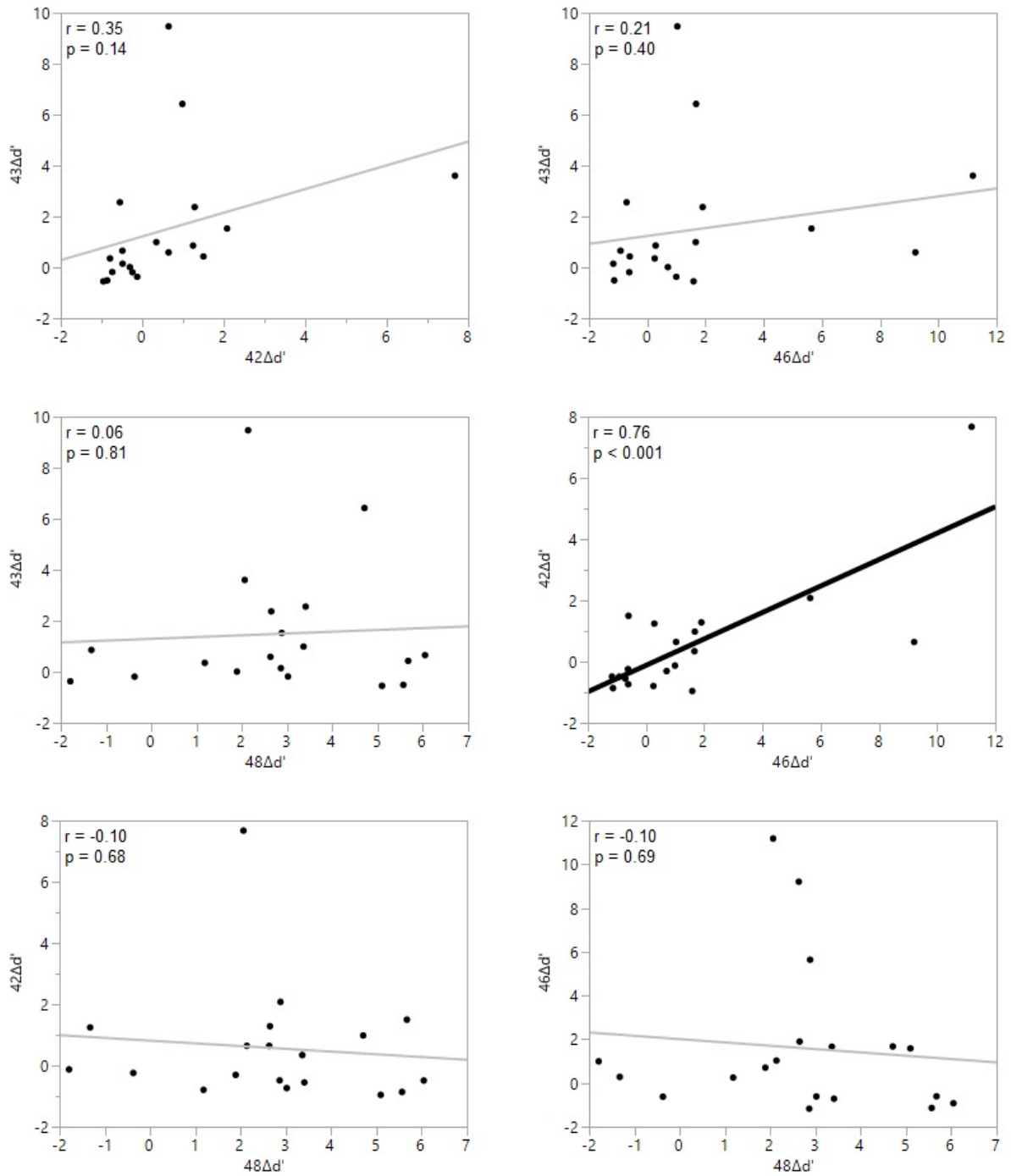


Figure E12. Butterfly specialization correlations by ecoregion. Butterfly species' $\Delta d'$ values were significantly correlated across adjacent ecoregions 42 and 46, and were uncorrelated across the other ecoregions. Ecoregions in North Dakota are, in order from west to east, the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48).

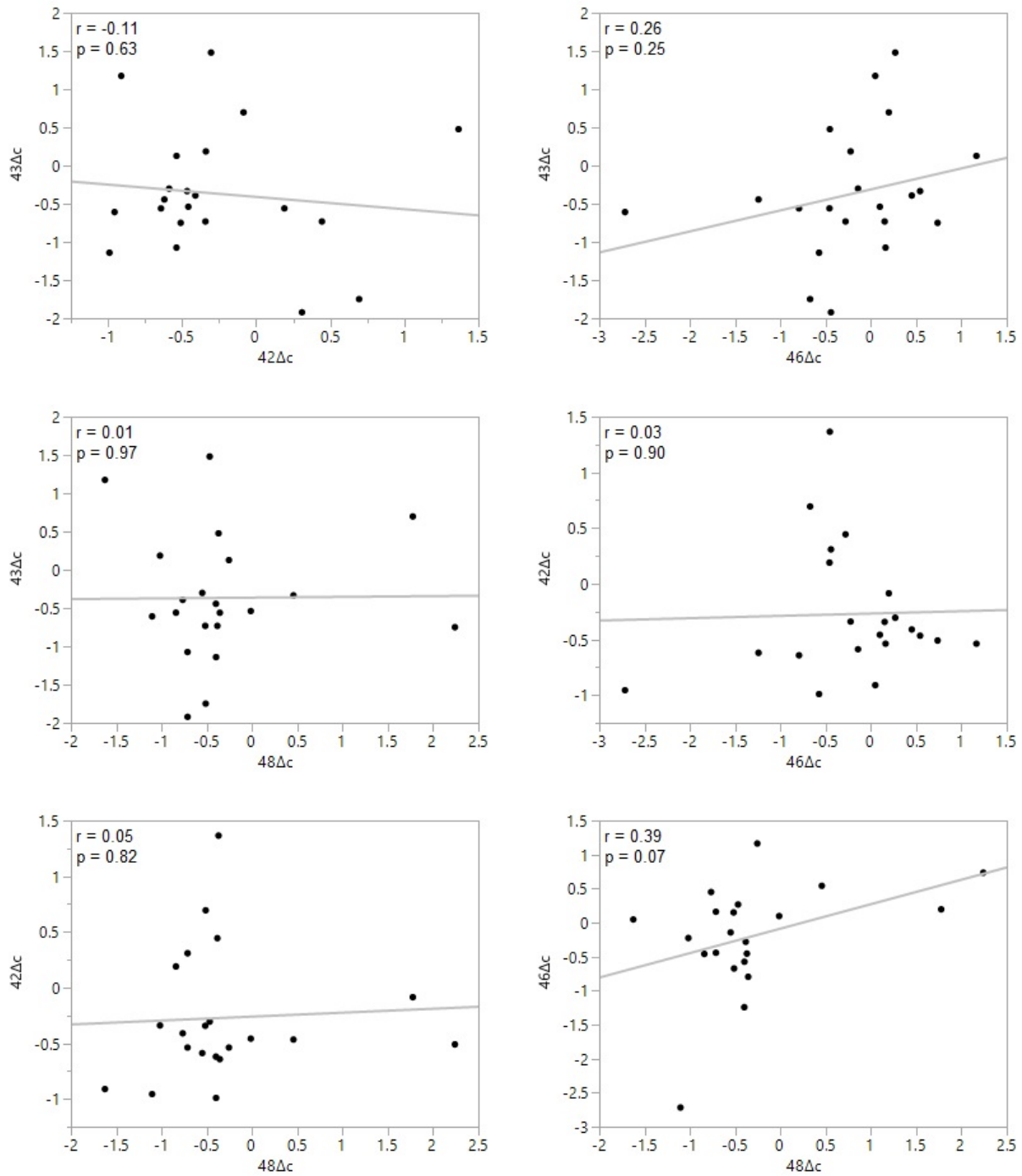


Figure E13. Floral among-module connectivity correlations by ecoregion. Flower species' Δc values were not significantly correlated across any ecoregions. Ecoregions in North Dakota are, in order from west to east, the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48).

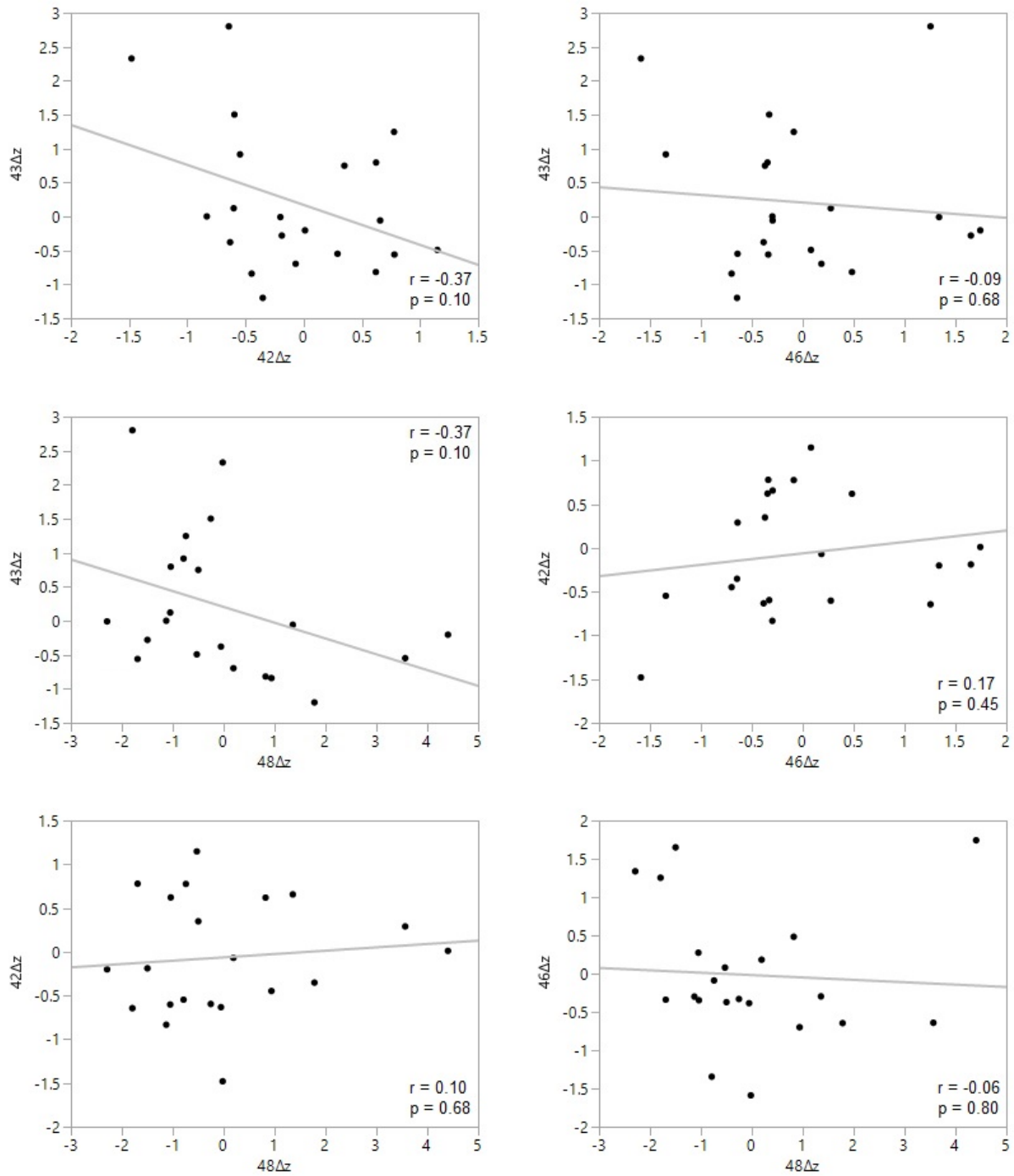


Figure E14. Floral within-module degree correlations by ecoregion. Flower species' Δz values were not significantly correlated across any ecoregions. Ecoregions in North Dakota are, in order from west to east, the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48).

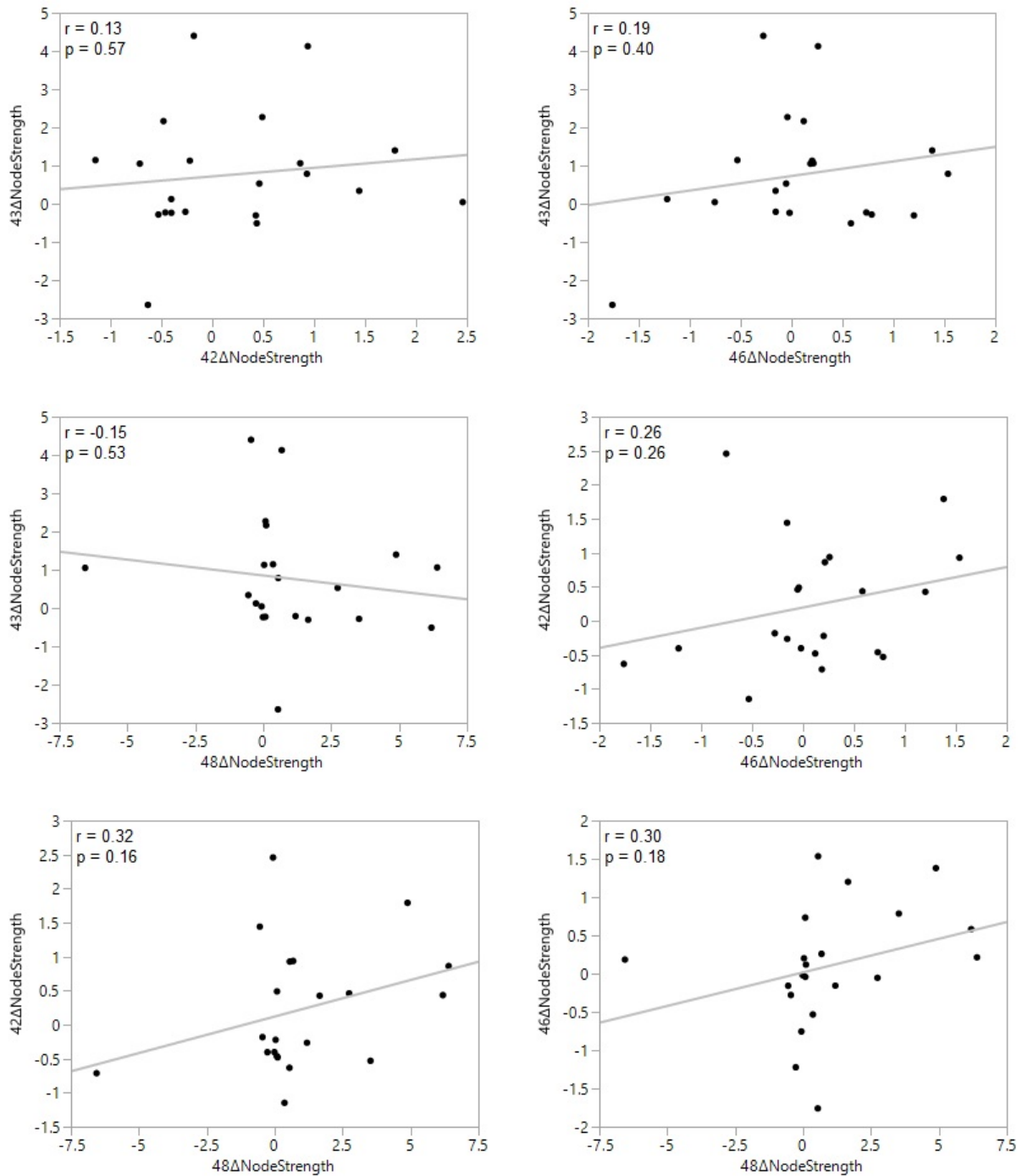


Figure E15. Floral node strength correlations by ecoregion. Flower species' Δ Node Strength values were not significantly correlated across any ecoregions. Ecoregions in North Dakota are, in order from west to east, the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48).

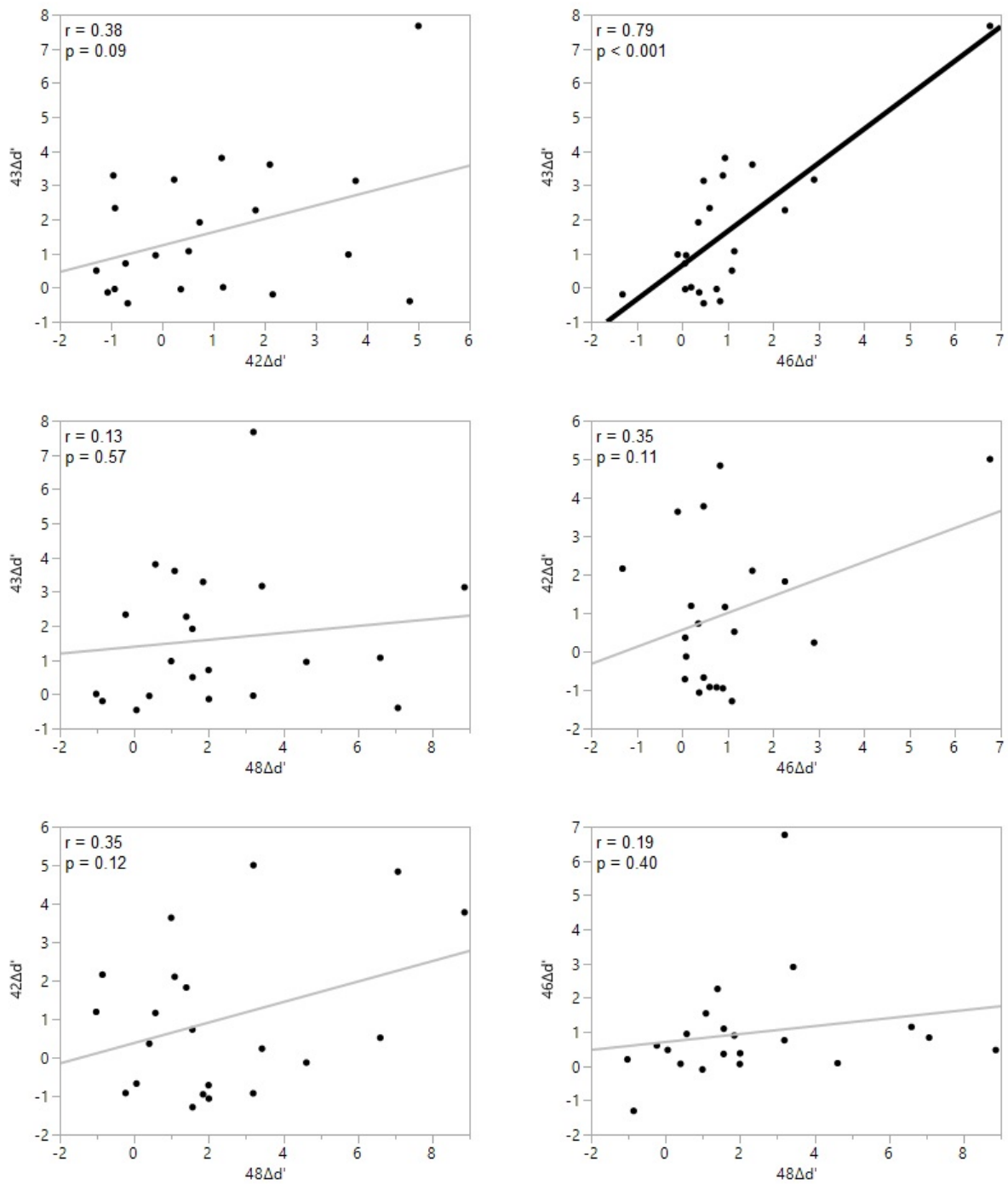


Figure E16. Floral specialization correlations by ecoregion. Flower species' $\Delta d'$ values were significantly correlated between non-adjacent ecoregions 43 and 46, and were uncorrelated across the other ecoregions. Ecoregions in North Dakota are, in order from west to east, the Northwestern Great Plains (43), Northwestern Glaciated Plains (42), Northern Glaciated Plains (46), and Lake Agassiz Plain (48).