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Spatial and Temporal Variation in Wild Pollination Service in the Mongolian Steppe

Abstract

Despite the importance of wild pollination as an ecosystem service, little is known about the spatial and temporal variation of pollination services. Variation in insect pollinator emergence or forb flowers can lead to inconsistent delivery of pollination service to the forb community. A variety of factors, such as air temperature, flower abundance, pollinator abundance, and forb species richness influence the stability of pollination service. All of these factors exhibit spatial and temporal variability. Furthermore, anthropogenic disturbances endanger the persistence of pollination service. To assess the variability of pollination we compared the number of insect flower visits at different locations throughout the summer for two consecutive years in Dalbay Valley, Mongolia. Within this spatio-temporal framework, we investigated the stability of plant-pollinator networks and the effect of ungulate grazing cessation on pollinator visits.

Flower visits, forb flower abundance, and measures of plant-pollinator network stability varied greatly over space and time. Hymenoptera visits were positively correlated with only network specialization and Diptera visits were positively correlated with only network nestedness. The exclusion of ungulate grazing altered the composition and abundance of both the forb species and flower visitor communities, but there was no difference in total flower visits between grazed and ungrazed plots. Our results suggest the forb and pollinator community may persist despite the removal of the consistent ungulate grazing pressure. Furthermore, the contribution towards network stability may not be synergistic. Hymenoptera visits were associated with increased network specialization, which tends to lower plant-pollinator network resilience against perturbations, while Diptera visits were associated with increased nestedness, which tends to increase network resilience.

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SPATIAL AND TEMPORAL VARIATION IN WILD POLLINATION SERVICE IN
THE MONGOLIAN STEPPE

Daniel Sung Song

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SPATIAL AND TEMPORAL VARIATION IN WILD POLLINATION SERVICE IN
THE MONGOLIAN STEPPE

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For Mom, Dad, Hannah, and Sylvia, without whom I would be lost.

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ABSTRACT

SPATIAL AND TEMPORAL VARIATION IN WILD POLLINATION SERVICE IN THE MONGOLIAN STEPPE

Daniel S. Song

Brenda B. Casper

Despite the importance of wild pollination as an ecosystem service, little is known about the spatial and temporal variation of pollination services. Variation in insect pollinator emergence or forb flowers can lead to inconsistent delivery of pollination service to the forb community. A variety of factors, such as air temperature, flower abundance, pollinator abundance, and forb species richness influence the stability of pollination service. All of these factors exhibit spatial and temporal variability. Furthermore, anthropogenic disturbances endanger the persistence of pollination service. To assess the variability of pollination we compared the number of insect flower visits at different locations throughout the summer for two consecutive years in Dalbay Valley, Mongolia. Within this spatio-temporal framework, we investigated the stability of plant-pollinator networks and the effect of ungulate grazing cessation on pollinator visits.

Flower visits, forb flower abundance, and measures of plant-pollinator network stability varied greatly over space and time. Hymenoptera visits were positively correlated with only network specialization and Diptera visits were positively correlated with only network nestedness. The exclusion of ungulate grazing altered the composition

and abundance of both the forb species and flower visitor communities, but there was no difference in total flower visits between grazed and ungrazed plots. Our results suggest the forb and pollinator community may persist despite the removal of the consistent ungulate grazing pressure. Furthermore, the contribution towards network stability may not be synergistic. Hymenoptera visits were associated with increased network specialization, which tends to lower plant-pollinator network resilience against perturbations, while Diptera visits were associated with increased nestedness, which tends to increase network resilience.

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INTRODUCTION

Humans rely on a multitude of ecosystem goods and services for our well-being and one such example is pollination: angiosperms pollinated by insects. For many people, the morphology and phenotypic characters of angiosperm flowers appear to have an obvious connection to some type of pollinator. In some cases, flowers have such uniquely modified flower structures, such as elongated spurs, the flowers may be visited by an exclusive set of pollinators. The importance of insects for pollination was not lost on Darwin as he remarked “if such great moths were to become extinct in Madagascar, assuredly the *Angraecum* would become extinct” (Darwin 1862, g. 202). The mutualistic interactions between angiosperms and insect pollinators have facilitated the radiation of both groups (Pellmyr 1992). Habitat degradation and land-use change have adversely affected pollination services, threatening the annual \$210 billion value of industries associated with pollination (Gallai et al. 2009). In light of pollination’s central role in co-evolutionary processes and its importance to humans, a better understanding of where and when plant-pollinator interactions take place is vitally important.

Pollination is a model system for studying mutualisms. The system allows researchers to examine two trophic levels and how they interact with each other, rather than focusing on only one trophic level in isolation. Pollination also allows for the examination of ecological function and evolution of both plant and insect traits (review: Bronstein et al. 2006). Currently, the world is witnessing a global decline in pollination (Potts et al. 2010). Additionally, 63-73% of all flowering plants are found to be pollen limited (Ashman et al. 2004). The intricate causes of decline are not likely to be

understood by studying populations or a few selected species of plants. Due to complex interactions between plant and pollinator communities, there is a need for an integrative approach to investigate the causes of variation in visitation. Specifically, there needs to be an emphasis on plant and pollinator communities, rather than populations, and an emphasis on mechanisms, rather than description, to fully understand how pollination functions.

Spatial and temporal variation

There is considerably spatial variation in the pollination service delivered to plant communities. Population-level studies show the number of visits can vary by greater than one order of magnitude, even for populations separated by a mere 100 meters (Price et al. 2005). The heterogeneity of plant community composition has a strong influence on the diversity and number of pollinator visits (Steffan-Dewenter et al. 2001). Moreover, the diversity of pollinators varies greatly over large areas of land (Burkle and Alarcón 2011). Despite this, often a few insect visitors serve as the primary pollinators in any given point in space (Moeller 2004).

An insect's visit to a flower is not only dependent upon both partners presence in space but also in time. Our concern for pollination services stems from the fact that insect mediated pollination is almost exclusively a seasonal process, which is particularly vulnerable to phenological mismatch due to changes in climate (Rafferty et al. 2015). There is evidence that forb flowering phenology differs in duration and peak production among species. Recent research shows significant non-uniform shifts in flowering phenology over a 39 year window, where some species flowered earlier while others later

(CaraDonna et al. 2014). Due to this variation in resource availability, we expect the community composition and abundance of flower visitors to also vary. Pollinators are also susceptible to phenological shifts. Over a 130 year period, North American generalist bee populations have progressively emerged earlier in the season (Bartomeus et al. 2011). Furthermore, insect pollinators vary in the rewards they seek from flowers. Many specialist pollinators, such as bumblebees, require nectar rewards, while others, such as generalist flies, tend to forage on pollen. Thus, the standing forb community composition and flower abundance influences which pollinators will visit.

One major hurdle in addressing temporal and spatial variation at the community level is the intensive sampling required. Most studies aggregate observations conducted in different weeks, or even months. Aggregation of daily observations throughout a season obscures any detectable variation in visitation and limits answering questions about daily, seasonal, and yearly structuring of plant-pollinator interactions. Currently, only a handful of empirical community level studies have been conducted at the hourly time-scale (Baldock et al. 2010) or daily time-scale (Basilio et al. 2006, Olesen et al. 2008, Dupont et al. 2009). Additionally, the aggregation of data presents a challenge to address questions about spatial and temporal visitation variation. Many studies employ walking random transects, which does not allow for quantifying floral abundance of different plant species.

Plant-pollinator networks

The resurgence of pollination studies can be primarily attributed to new applications of a statistical tool: network analysis. When applied to plant and pollinator

communities, network analysis characterizes (1) all of the plant species each pollinator species visits and all of the pollinator species visiting each plant species as well as (2) the frequencies of these interactions (Fig. I.1). Network analysis allows researchers to visualize and quantify interactions between plants and pollinators in novel ways (Jordano et al. 2003). The number of pollinator visits, coupled with forb flower abundance, can be used to create indices to characterize the entire interaction network. Thus far, researchers have used network methods to describe convergent topologies of plant-animal networks (Bascompte et al. 2003), colonization and extinction processes of plants and pollinators (Campbell et al. 2011), effects of invasive species on existing plant-pollinator interactions (Russo et al. 2014), and the relationship between network structure and number of coexisting species (Bastolla et al. 2009).

Researchers have described the general features of plant-pollination community patterns. As the total number of species in plant and pollinator communities increase, the proportion of total possible plant-pollinator pairings decreases (Olesen and Jordano 2002). Plant-pollinator communities tend to be asymmetric in their interactions: if a plant species relies heavily on a pollinator, the pollinator tends not to rely heavily on the plant, and vice versa (Vazquez and Aizen 2004). Consequently, co-evolutionary pairing between plants and pollinations may be weaker than previously thought. Lastly, plant-pollinator communities cope with extinctions of specialized species and tolerate the loss of the most highly visited plant/pollinating insect (Memmott et al. 2004). Although plant-pollinator interactions have been described generally, the field has yet to sufficiently address the sources of variation in pollinator visitation.

Many plant-pollinator network studies have focused on network metrics rather than focus on explanatory variables that could inform the metrics (but see Stang et al. 2006, Gong and Huang 2011). One such factor is the temporal dynamics of plant-pollinator interactions, which is often ignored by aggregating all observed interactions over time into one large plant-pollinator network. This approach assumes that interactions are not influenced by any other factors such as neighboring plant species, plant or pollinator species composition, flowering progression during the season, or functional trait composition.

Plant-pollinator networks provide the framework to investigate the relationship between network topology and network stability. Simulations show removing the most well-connected pollinators caused linear declines in forb species diversity rather than a sharp decline resembling exponential decay (Memmott et al. 2004). The tolerance in networks to extinctions is attributed to the redundancy of flower visitors for each forb species, or the nested topology of the networks. Also, well-connected pollinators are better able to persist in networks experiencing land-use changes (Winfree et al. 2014). Furthermore, the likelihood that species are lost from plant-pollinator networks is negatively related to both the number of interacting partners and visit frequency (Aizen et al. 2012).

Grazing and pollination

Pollination is sensitive to disturbances. Habitat loss and agricultural intensification have been shown to negatively affect the richness of bee species within a community and their abundance (Winfree et al. 2009). Human induced land

transformations negatively impact habitat species diversity and ecosystem functioning (Hooper et al. 2005). Land-use change, such as changing animal grazing intensities, affects the composition of flower communities. This change in species composition and abundance also alters the flower resource available to pollinators.

Grazing has an indirect effect on pollination, mediated through the forb community. Grazing increased some forb species population densities as well as reduced others (Vázquez and Simberloff 2004). Also, flowers damaged through florivory receive fewer visits than those that are undamaged (Cardel and Koptur 2010). The indirect effect of grazing on flower visitors is also equally ambiguous. Bee flower visitors have been not only shown to increase with grazing intensity (Vulliamy et al. 2006) but also shown to not be affected by grazing (Sjödin et al. 2008). Furthermore, the effect of grazing on bees species richness has been demonstrated to be positive (Carvell 2002) as well as neutral (Sjödin et al. 2008). With such great consequences accompanying the introduction of ungulate grazing, how do pollination services respond to the cessation of grazing?

We can form expectations about how the flower visitor community will respond to changes in forb communities when grazing is excluded. Flower abundance and forb species diversity are positively related to flower visitor species richness (Potts et al. 2003, Stang et al. 2006). Additionally, some flower visitors, such as bumblebees, tend to forage for nectar and pollen as well as have a capacity to learn complex morphologies, such as those of leguminous flowers (Raine and Chittka 2007). Other flower visitors, such as short-tongued flies, require open flowers to access pollen or nectar resources. Thus, if grazing alters the abundance and diversity of flowers through changes in forb species

composition, we expect insect flower visitors to also change their visitation to forb communities.

Mongolia

Grasslands support important ecological services but face degradation through change in land-use and agricultural practices. The Mongolia grasslands are part of the Eurasian steppe, the world's largest contiguous herbaceous system (Fig. I.2). In Mongolia, an astounding 75% of the land is used for grazing livestock and pastoralism (Batima et al. 2008). To complicate matters, many of these lands that have been subject to pastoralism since 800 BC (Barfield 1992) are experiencing release from grazing pressure. This is primarily attributed to the human rural-to-city migration associated with the liberalization of the economy (Morris and Bruun 2005). The current transformation in society and land-use practices provides the opportunity to study how alterations to grazing patterns will affect the composition and abundance of forb species and the flower visitor communities that service them.

Dissertation chapters

In Chapter 1 we characterize the spatial and temporal variability in pollination. I examine the forb and pollinator community composition, number of pollinator visits, and flower abundance. I structured the data collection at two time scales: throughout the day and over the summer season. I also set up plots at two different locations on a south-facing slope. In Chapter 2 I tested the relationship between stability measures of plant-pollinator network and ecological factors. I tested a causal path model relating two

network metrics and several ecological factors, such as number of pollinator visits and plant species richness. Finally, in Chapter 3 I examine the effect of excluding livestock grazing on plant and pollinator communities as well as the number of pollinator visits.

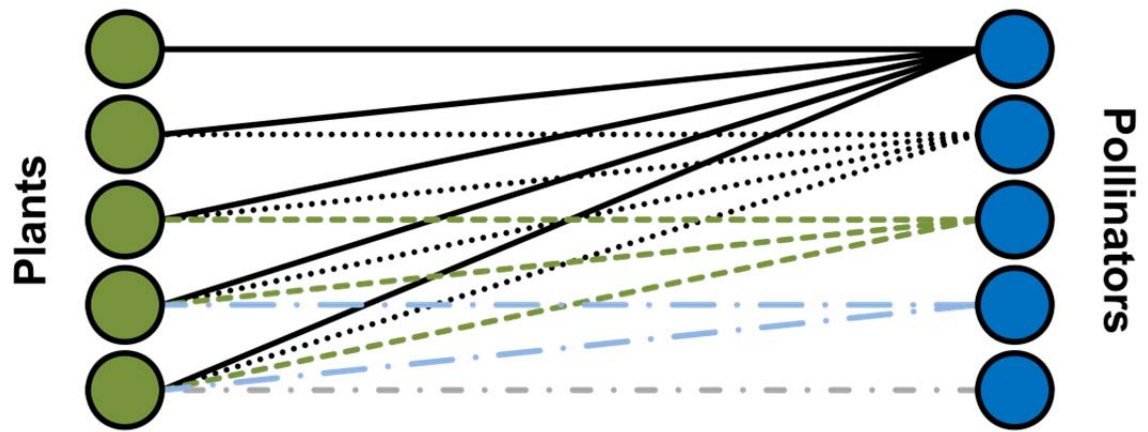


Figure I.1: Visual representation of a plant-pollinator network. Green filled circles represent a species of plants (i.e. angiosperms), and blue filled circles represent pollinators (i.e. insects). The different lines connecting the two communities indicate an observed pairwise interaction between a particular pollinator and angiosperm species.

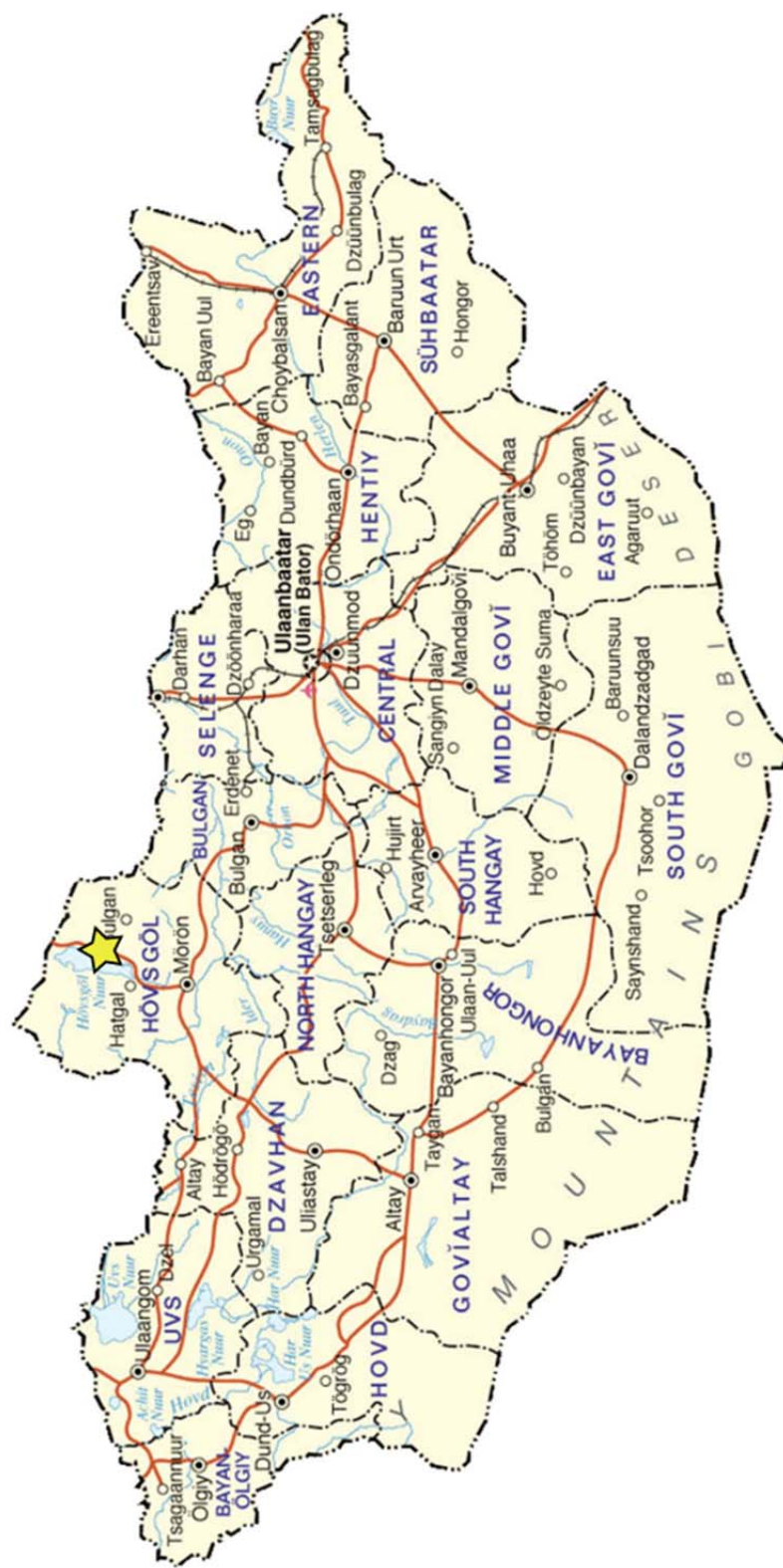


Figure I.2: Map of Mongolia. Our field-site, denoted by the yellow star, was located on the western side of Lake Hövsgöl (51°01.405'N, 100°45.600'E).

CHAPTER ONE: THE SPATIAL VARIATION IN THE INFLUENCE OF AIR TEMPERATURE AND FLOWER ABUNDANCE ON POLLINATOR VISITS

1.1 Abstract

Predicted global change, such as land-use change, is likely to affect important ecological services, such as pollination. These changes are likely to alter the variability of pollinator visits over time and space. Recently, plant-pollinator interactions at the community level have been well documented using network analysis. However, few community level studies have examined the relative importance of ecological factors to pollination over different temporal and spatial scales, particularly relevant factors such as air temperature and flower abundance. To better understand the sources contributing to the variation in pollination service, we monitored and collected pollinator visitors from permanent plots in the mountain steppe of northern Mongolia at two locations on a south-facing slope. The experiment was structured at two different temporal scales and at two different sites. The relative importance of temperature and flower abundance as well as the pollinator visits varied significantly over time and space. The significance and explanatory power of air temperature and flower abundance depended upon the position on the landscape. Air temperature, alone, was positively related to the total number of pollinator visits on the lower part of the slope whereas both air temperature and flower abundance were important on the upper part of the slope. Considering the underlying factors to explain the variation in pollination reveals that plant-pollinator communities may be differentially vulnerable to changes in air temperature or flower abundance. This

spatial and temporal variation will be particularly important when considering what the impact future disturbances may have on this important ecological service.

1.2 Introduction

Insect pollinators provide a critical ecosystem service, facilitating sexual reproduction in entomophilous plants and influencing diversity in plant communities. Pollination is largely a generalized mutualism, in which many species of the pollinator community tend to visit multiple plant species (Johnson and Steiner 2000). However, the community of flower visitors may depend on the composition of the plant community (Flanagan et al. 2011). Thus, it is necessary to consider entire pollinator and plant communities when investigating the ecological factors impacting pollinator activity.

Variation in air temperature, both within a day and through the season, influences pollinator activity. A classic study demonstrated optimal temperatures for insect flight (Taylor 1963). However, optimal flight temperatures vary among insect pollinator species (Hodkinson 2005), thus making it difficult to predict how temperature influences pollinator visits to plant communities as a whole. Temperature also indirectly influences pollination by affecting nectar production (Wyatt et al. 1992), flowering phenology (Miller-Rushing and Inouye 2009), and flower abundance (Inouye 2008). Potential disruptions of pollinator service, caused by habitat modification or climate change, provide a clear reason to investigate more fully the link between air temperature and community level pollinator visits (Memmot et al. 2007).

We expect the role of temperature in affecting pollinator activity to vary spatially. First, plant and pollinator community composition varies across the landscape (Price et

al. 2005). Furthermore, this spatial heterogeneity is not constant, as plant and pollinator communities, thus their interactions, change over time. Second, spatial variation in the composition of plant communities affects pollinators differentially, such as solitary bees, which exhibit habitat preferences (Gathmann and Tschardt 2002), while bumblebees visit habitat types indiscriminately (< 750 m radius; Steffan-Dewenter et al. 2002).

To investigate the relative importance of air temperature and flower abundance in driving community level pollinator visitation, we conducted a temporally and spatially structured study in a mountain steppe community of northern Mongolia. This structuring allowed us to examine the temporal and spatial variation of pollinator visits as it relates to air temperature and flower abundance. We quantified total flower abundance and total pollinator visits throughout the flowering season in permanent observation plots and replicated the design at two locations on a south-facing slope. We examined flowering times of the different species and how pollinator community composition changed throughout the season. We then used path analysis to evaluate whether and to what extent temperature explained pollinator visits directly and indirectly, through flower abundance, at each of the two locations.

1.3 Materials and methods

Ethics Statement

All appropriate permits were obtained for our fieldwork and collection. The Ministry of Environment and Green Development of Mongolia authorized the work in the long-term ecological research site in the Lake Hövsgöl National Park and permitted export of insect specimens. No permits are required by the United States by U.S. Fish and

Wildlife Service for the import of dead insect specimens, which are not endangered or threatened, for scientific use to the United States (USFWS Form 3-177). None of the species within the scope of this study are endangered or threatened.

This study was conducted in 2011, between June and August in the Dalbay River Valley in northern Mongolia (51°01.405' N, 100°45.600' E, elevation 1670 to 1800 m), where the average annual air temperature is -4.5 °C (Nandintsetseg et al. 2007), with average monthly temperatures ranging from -21 °C (Jan.) to 12 °C (July). Regionally, average annual precipitation over the last 40 years was 265 mm (Namkhajantsan 2006). In 2011, an on-site meteorological station recorded 137 mm of rainfall (Jun. to Aug.). Permafrost is not present on the south-facing slope, where this study was conducted, but is found in a nearby riparian zone and on north-facing slopes under the taiga forest of mostly *Larix sibirica*. We worked at two elevations on a south-facing slope, the Lower slope at 1670 m.a.s.l and the Upper slope at 1800 m.a.s.l.

The mixture of sedges (e.g. *Carex* sp.), grasses (e.g. *Festuca lenensis*, *Poa attenuata*) and forbs (e.g. *Aster alpinus*, *Potentilla* spp., *Artemisia commutata*, *Thymus gobicus*) in the steppe vegetation varies with elevation. Total vegetative cover is greater on the Lower slope, where sedges and grasses dominate; the Upper slope has less dense vegetative cover and a greater abundance of certain forb species, such as the legumes *Astragalus mongholicus*, *Oxytropis strobilacea*, *Oxytropis viridiflava*, and *Vicia multifida*. Measured in total flower production, *Artemisia frigida* is the most abundant forb on the Upper slope, and *Thymus gobicus* on the Lower slope (See Liancourt et al. 2012 for more detailed information regarding the vegetation).

Our experimental design makes use of permanent plots, which provides greater consistency in tracking plant community composition, floral abundance of different species, and insect visitation than when using temporary transects. Twelve 2 x 2 m plots were established at the two elevations on the south-facing slope in early June 2011, six at the base of the south-facing slope (i.e. “Lower slope”) and six on the upper part of the slope (i.e. “Upper slope,” where the incline was $\sim 20^\circ$). Plots were spaced approximately 30 m apart at each location and the approximate distance between the two sets of plots was 300 m and no more than 500 m.

Observations were made over a total 211.5 hours during 47 observation days between 13 June and 11 August (for exact dates see Appendix A.1). Observations consisted of 30-min sessions and were grouped into three daily time periods: 830-1200, 1200-1530, and 1530-1900. Three random plots, chosen without replacement, were observed in each time period, for a total of nine plots observed each day. Four consecutive days of observation constituted an observation round. Each plot was observed three times per observation round, once in each daily time period. We completed a total of 11 four-day observation rounds over the season. Observations were made by standing within 0.5 m of the plot but changing positions frequently to observe the plot from all four sides. A plot was not observed if it contained no flowers in anthesis.

Insects were considered pollinators if they met three criteria: (1) landed on a flower for at least three seconds, (2) touched anthers or stigmas, and (3) appeared to collect nectar or pollen. We interpreted an insect to be collecting nectar or pollen if the insect moved into the flower head or down to the base of an open flower. Insects meeting these criteria were collected using a butterfly net or aspirator and killed in a diethyl ether.

While collecting insects with butterfly nets flowers were unavoidably damaged. The butterfly net was placed over flowers rather than used in a sweeping motion, if at all possible. Easily identifiable, conspicuous, and common insect visitors (e.g. four butterfly species, two ant species) were captured and released outside the observation plot. All other pollinators were killed in diethyl ether and pinned for later identification. In the rare cases when an insect's behavior met the three criteria of a pollinator but was not captured, its visitation was not recorded. Fewer than 10 individual insects meeting the criteria as pollinators were not captured, thus not recorded. For each 30-minute observation session, the total number of flowers in anthesis was recorded for all entomophilous flowering species in the plot. Compact inflorescences, such as the capitulum of *Aster alpinus* and *Scabiosa comosa*, were counted as an individual flower.

Air temperature at the two slope elevations was recorded throughout the season using HOBO dataloggers (Pro v2; Onset Computers, MA, USA). Dataloggers were located in nearby experimental plots that were a part of a climate manipulation study (Liancourt et al. 2013) and were located in other experimental plots within 5 m of a pollinator observation plot. Air temperature was measured continuously in 10-minute intervals at 15 cm above the soil.

To answer how pollinator visits vary temporally, we used ANOVA to compare the number of visits at two temporal scales: within-day and within-season. We fit three main fixed effects: slope location, time period within-day, observation round within-season, and plot as a fourth random factor; the model was factorial with the four-way interaction removed. Floral abundance was included as a covariate. We used nonmetric multidimensional scaling (Euclidean distance) to examine pollinator community

composition over all 11 sampling rounds and composition at each Round was calculated as the sum of visits per insect order. To determine the degree to which biotic and abiotic factors contribute to pollinator visits, we used path analysis to evaluate the contribution of floral abundance and temperature to pollinator visitors within each slope location. The number of pollinator visits, flower abundance, and air temperature were pooled across plots. This was due to negligible variation in air temperature between plots and because two temperature dataloggers were sporadically tampered with, rendering two plots without temperature data for some observations.

ANOVA was performed using JMP 7.0 (SAS Institute, Cary, NC). Path models were analyzed in R-3.0.0 (R Development Core Team 2013) using package “lavaan” (function: sem; Rosseel 2012); NMDS was performed using package “vegan” (function: metaMDS; Oksanen et al. 2013). For all analyses, the number of visits and floral abundance data were \log_{10} transformed; a value of 1 was added to before transformation due to the presence of zeroes. Air temperatures for each plot were averaged within each four-day observation rounds.

1.4 Results

There were a total of 26 flowering entomophilous species on the Lower slope and 21 on the Upper slope, with a subset of 13 species common to both. A total of 55,166 flowers were counted throughout the entire season, 28,399 on the Lower slope and 26,767 on the Upper (Appendix A.2). Peak flowering on the Lower slope occurred between 14 July and 17 July 2011 (Round 6; Fig. 1.1; Appendix A.3) and on the Upper slope between 20 July and 23 July 2011(Round-7). During this time there was a total of

946 recorded pollinator visits, with 573 the Lower slope and 373 on the Upper. Over the entire flowering season, the pollinator community on the pollinators that visited the Lower slope was composed of a wider range of insect orders compared to the Upper (Fig. 1.2). The Lower and Upper slope had the same number of plant families although two plant families were exclusive to each of the slope locations.

Pollinator visits varied significantly as a function of slope location and both time scales (Table 1.1; Fig. 1.3). On the Lower slope, the visitation within-season peaked between 20 July and 23 July 2011 (Round-7) whereas on the Upper slope visitation peaked between 14 July and 17 July 2011 (Round 6). On the Lower slope, within-day visitation peaked during mid-day while visits during morning and afternoon periods were not significantly different from each other; on the Upper slope, mid-day visitation peak was sustained for the third period (Fig. 1.3). Within-day \times within-season \times slope interaction was not significant.

Path analysis showed the relationship between temperature and floral abundance to pollinator visits differed between the two slope locations. On the Upper slope, visits were significantly related to temperature and flower abundance but temperature was not significantly related to flower abundance (Fig. 1.4a). On the Lower slope, pollinator visits were significantly related to temperature but not flower abundance; temperature was not significantly related to flower abundance (Fig 1.4b). The range of mean daily air temperature was between 14.5°C and 24.7°C (Appendix A.4). Air temperature for both locations peaked between 6 July and 9 July 2011 (Round-6). Over the entire season, air temperatures between locations were significantly different, with the Lower slope slightly warmer than the Upper, 18.6 C and 17.7 C, respectively.

1.5 Discussion

Air temperature explained significant temporal variation in pollinator visits in the Mongolia mountain steppe but its explanatory power and the explanatory significance of flower abundance varied within the landscape. This spatial variability in the relationship between air temperature, available flowers, and pollinator visits is likely due to the differences in species composition of plant and pollinator communities, even over the relatively short distance of less than 500 m. Among the plant species that flowered, 13 of 26 on the Lower slope and 8 of 21 on the Upper slope, were exclusive to that location. Similarly, Hymenopteran pollinators, mainly nectar-foraging *Bombus* spp., made up a much larger proportion of the Upper slope pollinator community. We believe these differences in the pollinator community may be a consequence of two different factors. First, flower abundance and species composition differs between the two slope locations and may be driving the difference in pollinator visits. Second, the proximity of nesting sites to the Upper slope may result in higher visits. While over large distances, the nesting site may influence foraging patterns, it is unlikely that the distance between plots, less than 500 m, and the elevation difference, less than 200 m, act as a significant barrier for pollinators, particularly for bumblebees (Walther-Hellwig and Frankl 2000).

The greater explanatory significance of flower abundance on the Upper slope may be due the larger proportion of leguminous species. Bumblebees tend to prefer bilaterally symmetrical flowers (Rodriguez et al. 2004), like those of the legumes, on which their foraging times are 45% faster (West and Lavery 1997). Additionally, the clustering of morphologically similar flowers on the Upper slope may explain the concentration of

bumblebee visits, which tend to prefer foraging from morphologically similar flowers (Raine and Chittka 2007). Effectively, the pollinator community on the Upper slope is more specialized, where a large proportion of the community displays preferences for certain leguminous plant species.

The significant variation in visits throughout the daily time periods may be best explained by the lack of flower closures during the day and thermal budgeting by pollinators. Unlike in some systems where flower closures can occur within three hours, almost all flowers remained open throughout the day in our study. Also, while optimal temperatures differ between insect species (Vicens and Bosch 2000), size is strongly correlated with the rate at which heat is gained and lost (Pereboom and Biesmeijer 2003). Smaller bodied bees and flies may reduce activity during the cooler temperatures of the morning and late afternoons, when bigger bodied bumblebees may still be active. This may explain the daily pollinator visits peaking during the warm mid-day. Thermal budgeting may also explain the peak number of visits during the two middle rounds of the season, the warmest time of the year.

There are two other considerations for the pollination services in northern Mongolia: low visitation and the response of pollination to global change. First, we observed fewer visitors than other studies conducted in the Mediterranean or tropics. The low numbers of flower visitors throughout the vegetative growing season begs the question of the importance of outcross pollination. On one hand, all but one plant species I observed was perennial. Additionally, all of the plant species included in this study were able to set seed to some degree (D. Song, unpublished data). The long-lived life strategy and the ability to self-pollinate is ideal for such low numbers of flower visitors. Whether

the plant-community exists to service to flower visitors or vice versa needs to be explored further.

Second, how predicted increases in global temperatures affect pollination services depends on the temperature responses of both pollinator and plant species. Higher temperatures can decrease flower longevity (Arroyo et al. 2013). On the other hand, our study and the work of others in high latitude or altitude systems suggests increased temperature may result in increased insect activity due adaptations that maximize heat absorption (Heinrich 1996, Hodkinson 2005). Thus, increased temperatures may not necessarily reduce plant reproduction. As for plants, climate change induces shifts in flowering phenology and whether pollination is affected will also depend on whether temporal synchrony is disrupted (Burkle et al. 2013). There is known resilience in plant-pollinator communities against phenological change with different pollinators species filling in for those that drop out (Bartomeus et al. 2013a) or by the plant and pollinator communities changing phenology concurrently (Bartomeus et al. 2013b). Lastly, other climatic factors may affect pollination service, such as wind speed, solar radiation, and precipitation.

Conclusion

We showed the importance of air temperature and flower abundance for community level pollination by studying well resolved spatial and temporal community pollination data. Aggregating such data over space and time, as is necessary in constructing some plant-pollinator networks, obscures the reasons why some pollinator species never visit some plant species, also known as “forbidden links” (Olesen et al. 2011). Aggregating data hinders distinguishing interactions that do not occur due to the

lack of overlap in time or space (Schweiger et al. 2008) from other explanations, such as trait mismatch (Campbell et al. 2011) or evolutionary history (Rezende et al. 2007). Understanding the causes for missing plant-pollinator interactions is the key to understanding how pollination service will respond to future disturbances.

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Table 1.1: Temporal and spatial effects on pollinator visits. Analysis of variance of the number of pollinator visits at two locations over two time periods and showing main effects and interaction terms.

Source of Variation	df	F	<i>p</i>	%VC
WD	2, 221	8.04	0.001	
WS	10, 103	2.76	0.005	
WD \times WS	20, 221	1.07	0.384	
Slope	1, 10	5.26	0.045	
Slope \times WD	2, 220	1.34	0.264	
Slope \times WS	10, 100	2.80	0.004	
Slope \times WD \times WS	20, 221	0.69	0.837	
Flower abundance	1, 170	5.26	0.023	
<i>Plot</i>				0.565
<i>Plot \times WD</i>				0.000
<i>Plot \times WS</i>				3.292
<i>Plot \times Slope</i>				1.089
<i>Plot \times WD \times Slope</i>				0.000
<i>Plot \times WS \times Slope</i>				6.027
<i>Residual</i>				89.03
Total				100.00

Within-day (WD), within-season (WS), and slope. Italicized source of variation denotes random model term.

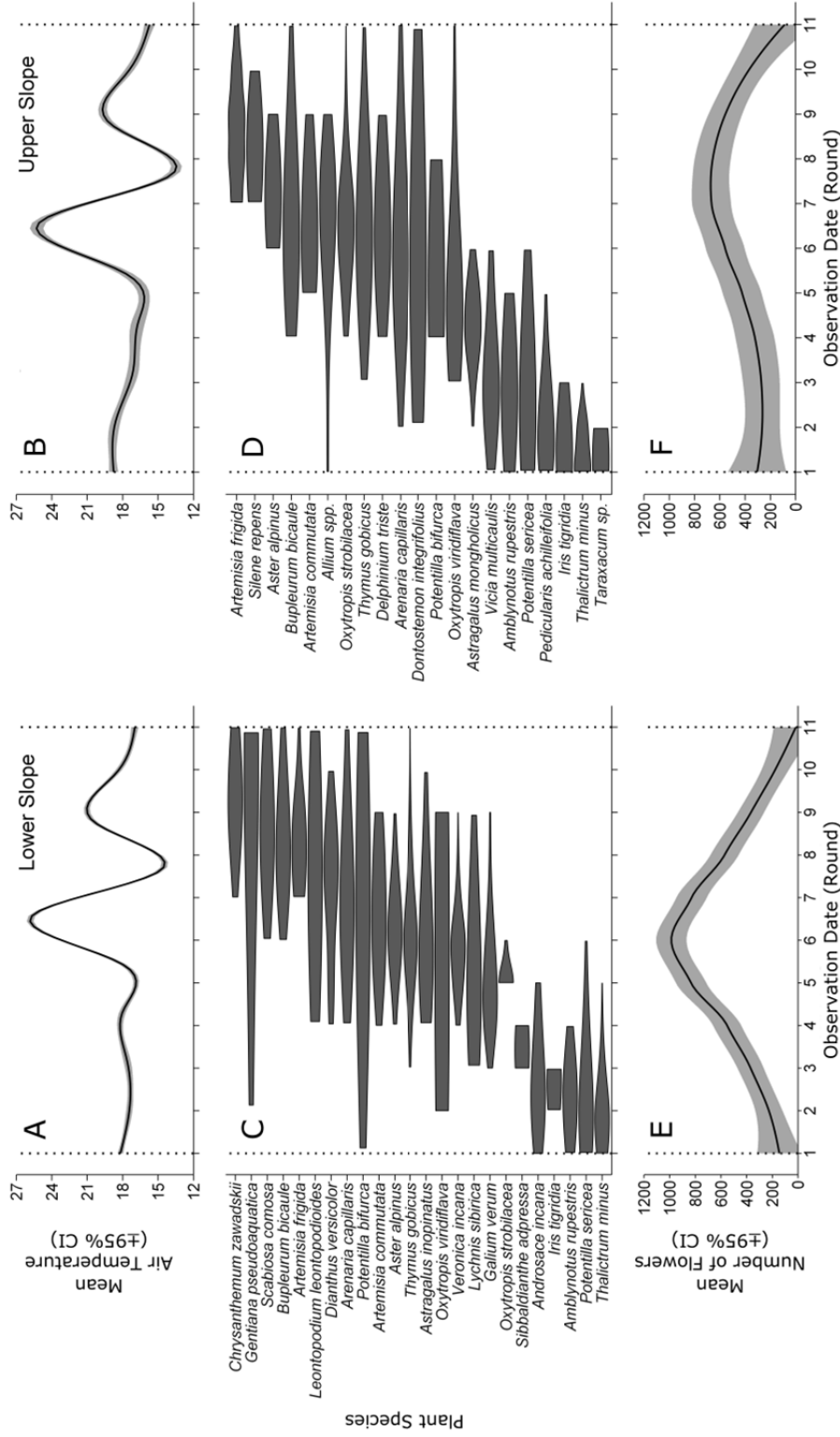


Figure 1.1: Temporal and spatial variation in air temperature, forb phenology, and flower abundance for two slope locations. (A, B) Mean air temperature with 95% CI, (C, D) flowering phenology across sampling rounds, and (E, F) mean flower abundance with 95% CI for the entire season (Rounds) for the Lower and Upper slope. Bar densities for the flowering phenology (C,D) are scaled relative to the total floral abundance for each species on a given slope.

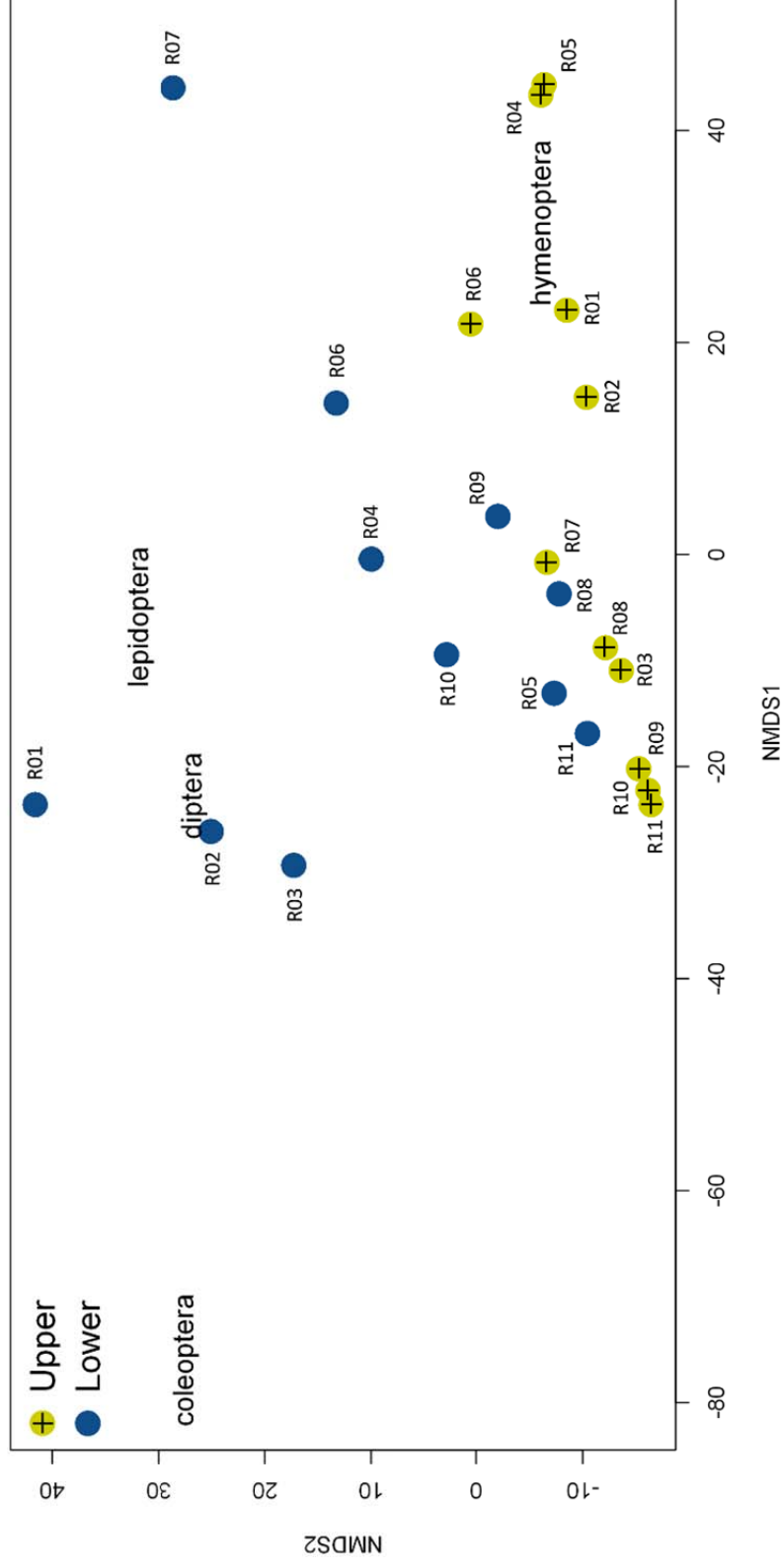


Figure 1.2: Analysis of the composition of the pollinator community. NMDS ordination of the visiting pollinator community at each sampling Round (1-11) over the entire season for both slope locations. Each colored point represents a particular point within the season of vegetative growth (Round 1-11). The colored points represent the community of visits made by four insect orders: Coleoptera, Diptera, Hymenoptera, and Lepidoptera. Color differentiates slope location and round number is adjacent to the respective point. For specific dates, see A.4. The proximity of a colored point to the label of an insect order indicates the dominant insect visitor for that particular community of pollinator visits.

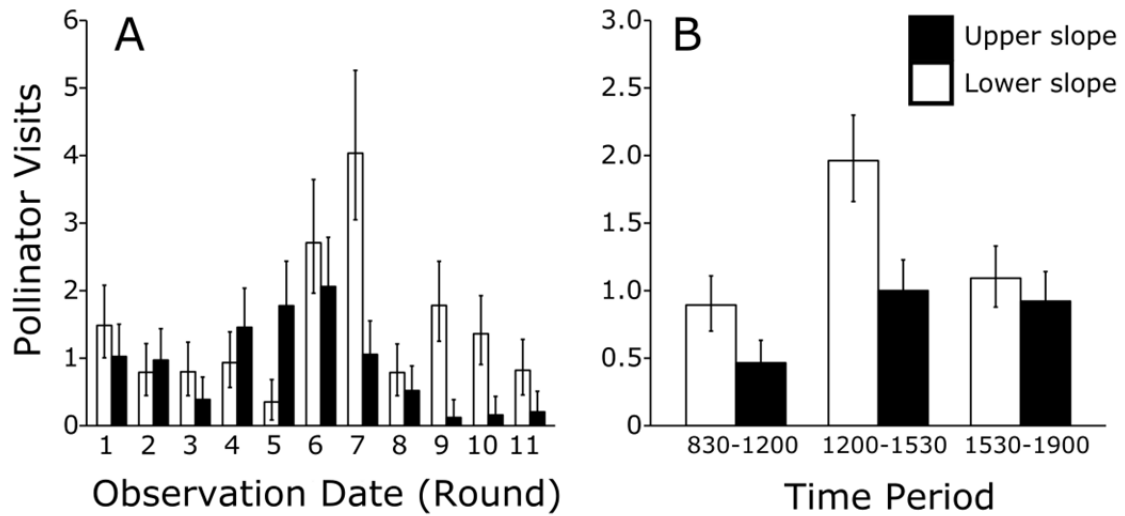


Figure 1.3: Daily and hourly variation in pollinator visits at two slope locations. Mean number of pollinator visits (\pm 95% CI) observed within plots at both slope locations (A) across the entire season and (B) over three time periods. Number of visits and confidence intervals were calculated from back-transformed least squares means.

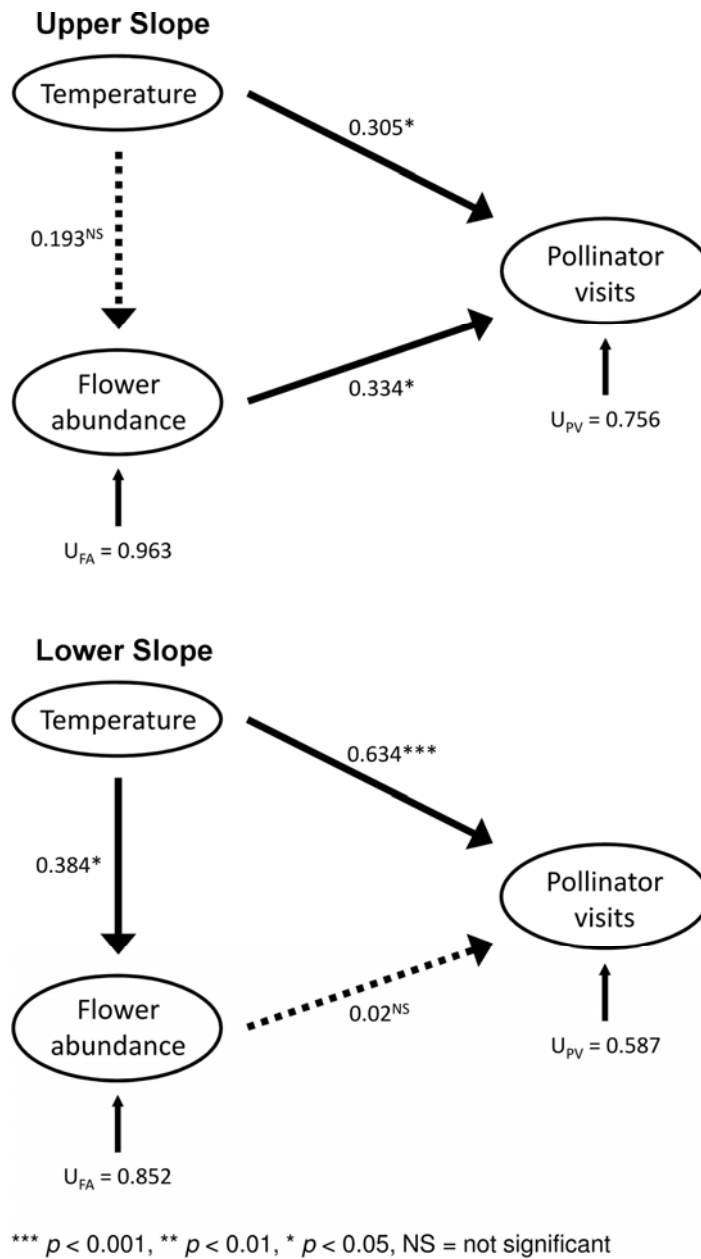


Figure 1.4: Relative importance of air temperature and flower abundance on pollinator visits. Hypothesized path analysis showing the relative contribution of air temperature and floral abundance to pollinator visitation for the (A) Lower and (B) Upper slope. Arrow indicates hypothetical causal direction. Standardized β -coefficients are shown with significance and unexplained variance, U. Dashed bars denote statistically non-significant relationships. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS: $p > 0.05$.

CHAPTER TWO: SPATIAL AND TEMPORAL VARIATION IN THE STABILITY OF PLANT-POLLINATOR NETWORKS

2.1 Abstract

Ecological services are influenced by the stability of interspecific interactions. This is especially true for insect pollination services, which vary over space and through time. Understanding how plant-pollinator networks respond to changes in species abundance and composition can provide insights into the stability of the services they provide. We studied multiple communities of insect visitors on two south-facing locations in northern Mongolia throughout the vegetative growing season and constructed plant-pollinator networks from the interactions we observed. We quantified two measures, specialization and nestedness, both of which are related to network resistance and resilience. We used Akaike information criterion to examine plants and insects in the network and ecological factors to select the best-supported model explaining specialization and nestedness. Among the 8 factors we analyzed, we found the best explanatory factors were: forb species richness and visits made by Hymenoptera and Diptera. We constructed a path model to test the relationship between these variables and the network metrics. Hymenoptera visits were correlated with network specialization and not nestedness; Diptera visits were positively related to nestedness and not specialization. Network specialization varied over time and between the two locations on the south-facing slope. Nestedness was greater at the Lower slope location but did not differ temporally. Our results indicate that plant-pollinator networks stability varies considerably and that not all interacting partners contribute equally to network stability.

The variation in network metrics indicates that plant-pollinator networks may be vulnerable at different positions within a landscape or a particular time during the season. Relating complex network topological metrics to specific ecological factors allows for better understanding of network structure and its response to potential changes in pollinator or plant species abundances.

2.2 Introduction

The stark realization that global environmental change negatively impacts ecosystem services has spurred studies to enable a better understanding of how these services can be stabilized and consistently delivered. Pollination is one such ecosystem service. In particular, insect flower visits (pollination, hereafter) to entomophilous angiosperm (forbs, hereafter) communities are sensitive to habitat fragmentation (Aguilar et al. 2006), agricultural intensification (González-Varo et al. 2013), climate change (Memmott et al. 2007), and species invasions (Moroñ et al. 2009). Unstable delivery of wild pollination services is of special concern due to the role of wild pollinators in the maintenance of wild plant diversity (Ollerton et al. 2011) and contribution to productivity of agricultural crops (Garibaldi et al. 2013). Despite the importance of maintaining stability in pollination services, few studies have examined how stability is related to ecological factors, such as species abundance and overall community composition.

One way to measure stability of pollination services is to analyze pollination as interaction networks. Flower visits in plant-pollinator networks are represented as two sets of interacting partners: forbs and flower visitors. The number of visits from different insects to particular plant species is used to compute indices that describe the network

topology (Bascompte et al. 2003, Olesen et al. 2008, Bascompte and Jordano 2007, Blüthgen and Klein 2011). Within the plant-pollinator network framework, the stability of pollination services can be examined in two ways, by: (1) the degree that particular pollinators specialize on particular forbs or visit generally across multiple species and vice versa, and (2) the degree to which species interactions are nested.

The level of generalization or specialization is important to understanding the persistence of pollination services (Waser et al. 1997, Fenster et al. 2004, Pauw and Stanway 2015). Network stability depends on generalist pollinators visiting a variety of flowering species and any one flowering species being visited by a wide array of flower visitors. Generalist pollinators can be associated with high niche overlap, providing redundancy of pollination service to plants (Blüthgen and Klein 2011). Networks with higher levels of generalization are able to persist even after the significant loss of species within the network (Memmott et al. 2004). Additionally, pollinators with higher levels of specialization tend to be more vulnerable to extinction than less specialized pollinators (Aizen et al. 2012, Weiner et al. 2014).

The structural organization of interactions between forbs and pollinators also influences network stability. Within a nested network, specialist species tend to interact with a subset of the species with whom generalists interact (Bascompte et al. 2003). In highly nested networks, a core of generalists interact with partners with whom other generalists interact. As a consequence of this high-level of inter-connectedness, in the case of species loss, a core set of generalists and their interactions are able to persist. Another facet of highly nested networks is decreased interspecific competition, which allows greater number of coexisting species (Bastolla et al. 2009) and species abundance

(Suweis et al. 2013). Lastly, highly nested networks also confer flexibility in response to perturbations (Okuyama and Holland 2008).

Plant-pollinator interactions depend on the availability of flower resources and active insects, which is influenced by considerable spatial and temporal variation in species abundance and community composition. Typically, as the number of flowering forb species available to pollinators increases within a season, pollinator specialization also increases (Ebeling et al. 2011). Furthermore, new species entering a network tend to interact with generalist species (Olesen et al. 2008). The spatial ubiquity of specific plant-pollinator interactions is positively related to patch proximity (Dupont et al. 2014) and interaction frequency (Carstensen et al. 2014). Different pollinators employ different foraging strategies and forb flower resource availability is periodic. Thus, we expect network stability to vary throughout the season and over space coinciding with changes in forb flower and pollinator abundance and community composition.

Examining spatial and temporal network variation allows meaningful comparisons and the ability to assess how network topology responds to changes in species abundance and composition. Network indices gauge the stability of pollination services. Yet, conducting a highly resolved temporal and spatial pollination study is tedious. As such, the majority of studies focus on indices calculated from networks constructed by combining observations made in the same plant community over time and space. This approach cannot reveal the influences driving the spatial and temporal variation in stability. In light of global environmental change, understanding where and when pollination services exhibit vulnerabilities is critical to understanding how these services respond to perturbations.

We undertook a study in the montane steppe in northern Mongolia to determine how network stability might vary across the landscape, throughout the season, and with the community composition for species and flower visitors. We repeatedly observed insect visitation to entomophilous forb species in permanent plots at two different locations on a south-facing slope. To characterize network stability, we calculated two commonly used indices: specialization (H_2' ; Blüthgen et al. 2006) and nestedness (NODF; Almeida-Neto et al. 2008). Specifically, we ask (1) does network stability vary over time and space and (2) what ecological factors, such as forb species richness or the identity of visiting pollinators, best explain network stability.

2.3 Material and methods

Field Site

Plant observation and pollinator sampling was conducted in 2011 in Dalbay river valley, Mongolia (51° 01.405' N 100° 45.600' E; elevation 1800 m a.s.l). The study took place at two locations: one located on the valley floor, referred to as the “Lower” slope (elevation 1,670 m a.s.l), and on the Upper part of a steep south-facing slope, “Upper” slope, (elevation 1,800 m a.s.l. with an incline of ~20°). The two sites were separated by approximately 500 m. An on-site meteorological station (HOBO U30 Station; Onset Computers, Bourne, MA, USA) recorded a total of 137 mm of precipitation between June and August with a total of 207 mm between August 2010 and August 2011 (see Liancourt et al. 2013 for more specific site characteristics).

Although the plants present at both slope locations are typical of mountain steppe, including sedges, grasses, and short forbs, their abundance and composition differ

significantly among the Slope locations. The Lower slope is dominated by *Carex pediformis* while the most common species on the Upper slope is *Potentilla acaulis*. The vegetation on the Upper slope is patchier than the Lower, with some large statured-herbaceous forbs (*e.g.* *Astragalus mongholicus*). Almost all forb species at both locations are perennial except two annuals: *Dontostemon integrifolius* and *Draba nemorasa*, neither of which we observed being visited by an insect.

Observations

Observations of flower visitors and pollinator sampling took place over a total of 211.5 hours during 47 observation days between 13 June and 11 August 2011 (for exact dates, see Table 2.1). We established permanent plots that were observed throughout the season, which provide greater consistency in tracking temporal changes compared to temporary transects. Six 2×2 m plots were established at each of the two slope locations for a total of 12 plots. Each plot was located within a 9×9 m fenced areas for protection from livestock grazing (see Spence et al. 2014); the plots were spaced at least 30 m apart at each slope location.

Within a consecutive four-day period, we observed each of the 12 plots once during each of three diurnal periods: 830–1200, 1200–1530, and 1530–1800. For each day of observation we randomly chose nine plots to observe from among the 36 possible plot \times diurnal period \times slope location combinations. These plots and times were selected without replacement, resulting in one observation of a plot during each diurnal time period for each four-day period. We completed 11 four-day periods between June and August. Observations were made for 30-minutes by standing within 0.5 m of the plot but changing positions to observe the plot from all sides. A plot was only observed if it

contained at least one flower in anthesis. All flowers in anthesis were counted for each plot observation regardless of their presence in previous plot observations.

An insect visiting a flower was considered a pollinator if it landed on a flower for at least three seconds and either (1) touched anthers or stigmas or (2) apparently collected nectar or pollen. We interpreted an insect to be collecting nectar or pollen if the insect moved into the flower head or down to the base of an open flower. Insects were then collected using a butterfly net or aspirator, killed in diethyl ether, and pinned. In the case where a pollinator eluded capture, the visitation was not recorded; this was true of only 10 individuals. For each 30-minute observation session, the total number of flowers in anthesis for every forb species was recorded. Composite inflorescences, such as the capitula of *Aster alpinus* and *Scabiosa comosa*, were counted as one individual flower. Insects were identified to genus and grouped into morpho-species with the help of curators at the Academy of Natural Sciences of Drexel University.

Plant-Pollinator Networks

Separate plant-pollinator networks were created from observations of each of the six plots at each Slope location for each four-day period. Each plot observation was transformed into a matrix consisting of rows denoted by each forb species and columns denoted by the genera of flower visitors (Fig. 2.1). Each cell value corresponds to the number of visits a forb species received from that particular genus of the flower visitor. Due to low visitation frequency (i.e. high proportion of zeros populating interaction matrices; see Appendix B.1), we pooled our four-day observation data into three seasonal periods (Early, Peak, and Late). This resulted in 36 plant-pollinator networks: three seasonal periods for each of 12 plots. Of the 36 networks, four networks did not contain a

flower visit and an additional seven networks were extremely small in size (e.g. 1 or 2 visitors) and we were not able to compute both network indices from these networks.

Thus, we conducted all of our statistical analyses on the remaining 25 networks.

Network Metrics

For each of our plant-pollinator networks we computed two metrics related to network stability: specialization and nestedness. Both measures are quantified at the community level. We used the H_2' specialization index (Blüthgen et al. 2006) derived from Shannon entropy and measures the degree of interaction partitioning among two interacting groups within a bipartite network. This measure of specialization describes the exclusiveness of interactions (Blüthgen 2010). For example, within a network, if all of the pollinator species visits only one unique forb species (e.g. high exclusivity), H_2' is high. As the proportion of shared partners increases (e.g. low niche differentiation), H_2' decreases. Values of H_2' range from 0 (extreme generalization) to 1 (extreme specialization). This measures the plant and pollinator community-wide specializations. Importantly, H_2' is not affected by network size or sampling effort (Blüthgen et al. 2006).

The nestedness index we computed, NODF, is the weighted Nestedness metric based on Overlap and Decreasing Fill (Almeida-Neto et al. 2008, Almeida-Neto and Ulrich 2011). Nestedness, as applied to bipartite networks, attempts to measure the degree to which specialist interactions are a subset of more generalist interactions (Bascompte and Jordano 2007). The NODF index examines pairwise cell values among rows and among column. The resultant statistic of each pairwise comparison among rows and columns is a proportion of cells with Lower values than the reference column or row. The output NODF value is the mean paired value for all pairwise comparisons of rows

and columns. NODF ranges from 0 (minimally filled) to 100 (perfect nestedness). This nestedness index is robust against type 1 statistical errors (Almeida-Neto et al. 2008).

Statistical Analyses

We used mixed-model ANOVA using restricted maximum likelihood estimation to test spatial (Lower and Upper slope) and temporal variation (Early, Peak, and Late) of our network metrics. Slope location and seasonal time point were fixed effects; plot was treated as a random factor as was any interaction term including plot. The three-way interaction was included in the error term. The ANOVA was conducted using JMP v10.0 (SAS Institute, Cary, NC).

We used a model selection procedure with corrected Akaike information criterion (AIC_c) values to identify the best factors that explain both H_2' and NODF. We assessed the level of support for the following explanatory factors: (1) forb species richness, (2) total flower abundance, (3) number of visiting insect genera, (4) total number of species within the network (i.e. network size), (5) total number of visits, and the number of visits by insects of (6) Diptera, (7) Hymenoptera, and (8) Lepidoptera. The AIC_c values were calculated in R-3.1.2 (R Development Core Team 2014) using package “MuMIn” (function: dredge; Bartoń 2014). We used a structural equation framework to investigate the relationship between factors and network metrics, H_2' and NODF. For simple linear regressions between network metrics and explanatory factors see Appendices B.2 and B.3. We evaluated the model using R-3.1.2 using package “lavaan” (function: sem; Rosseel 2012).

2.4 Results

Overall, we recorded 513 visits to flowers on the Lower slope and 359 visits on the Upper. The community of flower visitors was comprised of insects from Diptera, Hymenoptera, and Lepidoptera. Bumblebees (Hymenoptera: *Bombus*) were the most abundant flower visitor overall (Table 2.2) and on both the Lower and Upper slope, 143 (28% of all visits on the Lower slope) and 217 (60%), respectively (Fig. 2.2). *Bombus* flower visitors made up 71% of the total visits made to leguminous species and 44% of all the visits *Bombus* made were to leguminous species (Table 2.3). We recorded 27,017 flowers in anthesis on the Lower slope and 19,970 on the Upper (Fig. 2.3). Of the 34 flowering forb species insects visited 28 of them. Our overall visitation rate was 0.02 visits per flower. Of the 34 species, 26 were found Lower slope and 21 on the Upper, with a subset of 13 common to both. On the Lower slope, *Thymus gobicus* produced the most flowers, (7,318, 27% of all flowers on the Lower slope); *Artemisia frigida* produced the most on the Upper (4,441, 22%).

Temporal-spatial variation (ANOVA)

H₂' varied with the seasonal periods, being greater at peak season ($F_{2,19} = 3.62$, $p < 0.05$; Table 2.4) but then declining precipitously during the Late season on the Lower slope only (Slope \times within-season interaction; $F_{2,19} = 4.55$, $p = 0.02$; Fig. 2.4). NODF also differed by slope location but not across the season. NODF values for networks on the Lower slope were greater, 22.14 ± 4.09 (mean \pm SE), than those on the Upper, 8.10 ± 4.51 ($F_{1,10} = 5.21$, $p < 0.05$). NODF did not vary significantly between the three within-season periods.

Model selection

Based on AIC_c , the best supported explanatory model for the response variable H_2' included only the number of visits by Hymenoptera, AIC_c weight = 0.18. The best supported explanatory model for NODF included the number of visits by Diptera and forb species richness, AIC_c weight = 0.14.

Path model

Overall, the contribution to H_2' and NODF by Diptera and Hymenoptera differed significantly. H_2' was positively correlated to the number of flower visits by hymenopteran insects (Fig. 2.5). The number of flower visits made by Diptera was positively correlated with NODF. Interestingly, NODF was not significantly related to visits from hymenopteran insects nor was H_2' related to the number of visits from Diptera. There was also no significant relationship between H_2' and NODF nor was there a significant relationship between the number of visits made by Hymenoptera and Diptera (Table 2.5). Forb species richness was positively correlated with the number of visits made by Hymenoptera.

2.5 Discussion

Uncovering the factors that best explain the stability of ecosystem services is vital. While previous studies have demonstrated the variation in pollination services across space (Brosi et al. 2009) and time (Olesen et al. 2008), our work uncovers variation in two key measures of network stability, including factors that contribute to that stability. Our results show that not only does the presence of certain pollinators explain a significant proportion of variation in network nestedness and specialization but also that groups of pollinators influence these two measures in different ways.

We believe there are three primary reasons why the number Hymenoptera visits are strongly associated with network specialization. First, bumblebees, which constitute a large proportion of the total Hymenoptera visits, have a strong affinity towards leguminous forb species (Goulson et al. 2005). In our system, leguminous forbs are among the few species producing high levels of nectar (D. Song, unpublished data). Yet, there are only six leguminous species of the total 32 forb species found at both sites. These leguminous species, by flower abundance and species presence, are predominantly on the Upper slope. Second, our results are consistent with data that demonstrate that at high elevation, bumblebees tend to emerge later and closer to the peak of the vegetative growing season (Pyke et al. 2011). One important consequence of their emergence closer to the peak flowering period is the phenological matching with leguminous species, which results in visits to only a smaller subset of the entire flowering community. Third, bumblebees are known to their fidelity to flowers of particular forb species (i.e. constancy; Raine and Chittka 2007) and our results suggest that bumblebees were primarily attracted to legumes. This constancy acts to further limit their foraging choices. Thus, bumblebee foraging behavior and their distribution over time act as constraints by reducing the potential pool of forbs they are able to visit. As a result, when Hymenoptera enter the network in large numbers, they are also more specialized relative to other pollinators.

The positive relationship between Diptera visits and nestedness can be explained by their generalist foraging behavior. The plant community on the Lower slope consists of small and open flowers with little or no nectar reward. Thus, unlike the foraging resources available for Hymenoptera visitors, Diptera visitors to flowers are able to

forage from a large subset of the community. Diptera, such as Syrphidae (i.e. hover-flies), have been shown to be effective pollinators (Szymank et al. 2008) and constitute a high proportion of flower visitors at higher latitudes (Kanstrup and Olesen 2000, Elberling and Olesen 1999). Fly pollinators have long been known to visit forb species that possess easily accessible pollen (Holloway 1976). Diptera visitors to flowers likewise tend to forage primarily for pollen (Goulsen and Wright 1998).

In addition to the variation in the composition and abundance of plants and pollinators over space and time, network specialization may also be explained by the functional traits of the plants and pollinators in the system. The level of specialization observed within networks depends on the distribution of interactions among plants and pollinators. This distribution of interactions is influenced by the ability of pollinators to use different plant species as foraging sources. Within spatial and temporal constraints, the ability to use different plant species or switch between them depends strongly on morphological matching (Stang et al. 2006, Stang et al. 2009, Santamaría and Rodríguez-Gironés 2007). Furthermore, morphological traits for both plants and pollinators vary and may be grouped according to phylogenetic relatedness (Rezende et al. 2007). Future work on interaction networks could focus on the functional traits and phylogenetic relatedness to identify the core group of pollinators most closely associated with network stability. This information will further our understanding of the influence trait matching and evolutionary history has in shaping plant-pollinator networks.

The specific interactions between a plant and pollinator may not be as important for network stability as the consistent presence of a core group of pollinators. Our work corroborates previous work demonstrating the positive relationship between generalist

pollinators and nestedness (Aizen et al. 2008, Bascompte et al. 2003). Moreover, previous studies have shown that despite a high degree of temporal turnover in specific plant-pollinator lineages, network metrics tend to remain relatively consistent (Dupont et al. 2009, Petanidou et al. 2008). Together, if a core group of generalist species is a consistent component of the plant-pollinator network through time, irrespective of their specific identity, that group should be positively related to nestedness. In our study, Diptera formed the core group of flower visitors throughout the season.

Broadly, our work suggests that the overall stability of pollination services may hinge upon the balance among disparate groups of pollinators stabilizing or destabilizing the network. Recent work has shown that nested networks have high stability and allows coexistence over a larger portion of a species range (Rohr et al. 2014). Additionally, increased specialization is generally thought to decrease stability in face of perturbations (see review Clavel et al. 2010; but see Benadi et al. 2013). In our system, the specialist Hymenoptera visitors do not integrate into the network in a way that makes it more stable. Rather, they enter the network and are more likely to interact among a disparate group of plants, such as the leguminous species, as opposed to the entire community plants (i.e. module). If we focus solely on the benefits gained, a specialist plant benefits by the visits of specialist pollinators through increased pollination efficiency: specialized pollinators tend to reduce pollen loss and reduce deposition of heterospecific pollen (Johnson and Steiner 2000). Specialist pollinators also receive the benefit of specific types of rewards, whether protein or carbohydrate (Schiestl and Schlüter 2009). But typically, highly specialized interactions come at the cost of reduced niche overlap, redundancy, and network stability. To hedge against this vulnerability, generalist

pollinators need also to be present to act as stabilizing forces in the network. The resulting network has specialist pollinators that are able to interact in an isolated module within the larger network. Thus, the network may contain “cheaters” that leverage the existing stability for their own risk-tolerant behavior while not contributing to the overall stability of the network.

Our approach captured the dynamic nature of pollination and allowed us to study the variation in network stability. We structured our study based on the daily changes in pollinator visits throughout the entire vegetative growing season and at two different locations. This allowed us to relate the intra-seasonal change in flower abundance, for species composition, and activity of pollinators to network specialization and nestedness. Otherwise, the aggregation of observations into one indiscriminant network would obfuscate the significant spatial and temporal variation in network stability.

Studies have documented both network specialization and nestedness in systems all over the world. Overall our visitation rate was 0.02 visits per flower. For reference, scientists studying a perennial plant population in Norway observed an average of 0.09 visits per flower (Lázaro et al. 2015). In the temperate rain forests on an island off the coast of Chile, the plant community received, on average, 1.2 visits per flower (Smith-Ramírez et al. 2005). Despite the large variation in visitation frequency and overall number of visits observed in our study compared to others, our network metrics are well within globally observed values for specialization (Bluthgen et al. 2007, Schleuning et al. 2012) and nestedness (Dalsgaard et al. 2013). The relatively consistent network metrics, despite differences in the plant communities and geographic location, is consistent with previously published results (Petanidou et al. 2008). Stability of pollination services for

plant communities that receive both low visitation rates and total number of visits may be even more important than areas where pollinators are more abundant.

Stability of ecosystem services is particularly important for systems subject to perturbations, such as land-use change and agricultural intensification (Clough et al. 2014, Weiner et al. 2014). In Mongolia, socio-economic changes are resulting in the change in land-use practices. The Mongolian steppe has been subject to pastoralism since 800 B.C. (Barfield 1992) but due to the rural-to-city migration of people in Mongolia, many lands are likely to be abandoned and grazing practices are changed (Batima et al. 2008, Morris and Bruun 2005). Furthermore, Mongolia has experienced rapid warming over the past 50 years ($+\Delta 1.7^{\circ}\text{C}$; Namkhajantsan 2006). Predicted climate and land-use change in the region has been shown to impact the flower production of all plants (Liancourt et al. 2012, Spence et al. 2014,). Thus, for a system experiencing significant and abrupt perturbations, understanding the drivers that stabilize pollination services is critical for mitigation efforts.

Conclusion

We find that variation in measures typically associated with network stability can be explained by the particular pollinator groups. These metrics vary with the changes in the pollinator community. The variation in plant community, particularly species richness, is also important but only for one group of pollinators. For conservation efforts, the impact of perturbations, such as species invasions or land-use change, on wild pollination services may depend on the impact felt by a core group of pollinators. More broadly, our work suggests that the overall stability of pollination services may hinge

upon multiple groups of pollinators contributing to different components of network stability.

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Table 2.1: Start and end dates for observation time periods. Three observation periods and sampling were conducted in Dalbay Valley, Mongolia between June and August 2011.

Time Periods	Start Date	End Date
Early	13-Jun-2011	26-Jun-2011
Peak	01-Jul-2011	28-Jul-2011
Late	30-Jul-2011	11-Aug-2011

Table 2.2: Total number of flower visits observed. Each value represents the number of flower visits observed by each insect genus for three observation periods in Dalbay Valley, Mongolia between June and August 2011. For exact dates, see Table 2.1.

Order	Genus	Early	Peak	Late
Diptera	<i>Anthrax</i>	0	4	0
Diptera	<i>Chrysotoxum</i>	0	13	3
Diptera	<i>Cynomya</i>	111	14	0
Diptera	<i>Deopalpus</i>	7	51	8
Diptera	<i>Dolichopodidae</i>	0	1	0
Diptera	<i>Epistrophe</i>	0	2	0
Diptera	<i>Eristalis</i>	0	4	1
Diptera	<i>Eumerus</i>	0	0	0
Diptera	<i>Eupeodes</i>	0	4	0
Diptera	<i>Paragus</i>	0	5	5
Diptera	<i>Spallanzania</i>	0	1	1
Diptera	<i>Sphaerophoria</i>	3	7	0
Diptera	<i>Syrphus</i>	0	2	1
Diptera	<i>Systoechus</i>	0	6	1
Hymenoptera	<i>Anthophora</i>	2	74	7
Hymenoptera	<i>Bombus</i>	71	254	35
Hymenoptera	<i>Colletes</i>	30	37	0
Hymenoptera	<i>Formica</i>	3	26	4
Lepidoptera	<i>Argynnis</i>	0	18	15
Lepidoptera	<i>Boeberia</i>	0	2	0
Lepidoptera	Microlepidoptera	15	3	0
Lepidoptera	<i>Polyommatus</i>	1	18	2

Table 2.3: Flower visits for each plant species and insect genus. Each cell represents the number of interactions observed between plant species (rows) and pollinators (columns) in northern Mongolia between June and August 2011.

Plant species	Insect order																				
	Diptera										Hymenoptera									Lepidoptera	
	Insect genus																				
<i>Anthrax</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Allium</i> sp.	4	0	1	16	1	0	0	0	0	2	0	3	0	0	4	0	0	11	4	0	0
<i>Arenaria capillaris</i>	0	0	6	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Artemisia commutata</i>	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Artemisia frigida</i>	0	3	0	16	0	0	0	1	0	0	0	0	0	0	1	4	9	2	0	0	1
<i>Aster alpinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11	0	0	0	0
<i>Astragalus inopinatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	37	93	0	0	0
<i>Astragalus mongholicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
<i>Bupleurum bicaule</i>	0	0	0	9	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Chrysanthemum zawadskii</i>	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	1	1	0	0	0
<i>Delphinium triste</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0
<i>Dianthus versicolor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Table 2.3: Flower visits for each plant species and insect genus. (Continued) Each cell represents the number of interactions observed between plant species (rows) and pollinators (columns) in northern Mongolia between June and August 2011

	Insect order																				
	Diptera								Hymenoptera								Lepidoptera				
	Insect genus																				
Plant species	Anthrax	Chrysotoxum	Cynomya	Deopalpus	Dolichopodidae	Epistrophe	Eristalis	Eupeodes	Paragus	Spallanzania	Sphaerophoria	Syrphus	Systoechus	Anthophora	Bombus	Colletes	Formica	Argynnis	Boeberia	Microlepidoptera	Polymnatus
Galium verum	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0
Gentiana pseudoaquatica	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Iris tigridia	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Leontopodium leontopodioides	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lychnis sibirica	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Oxytropis strobilacea	0	0	0	0	0	0	0	0	0	0	0	0	0	14	25	1	0	0	0	1	3
Oxytropis viridiflava	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0
Pedicularis achilleifolia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	50	0	0	0	0	0	0
Potentilla acaulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
Potentilla bifurca	0	0	0	3	0	0	0	0	2	0	2	0	0	0	0	0	3	0	0	1	0

Table 2.3: Flower visits for each plant species and insect genus. (Continued) Each cell represents the number of interactions observed between plant species (rows) and pollinators (columns) in northern Mongolia between June and August 2011

Plant species	Insect order																			
	Diptera								Hymenoptera								Lepidoptera			
	Insect genus																			
<i>Anthrax</i>	0	0	82	7	0	0	0	0	0	1	0	2	0	0	0	0	0	0	10	0
<i>Potentilla sericea</i>	0	2	0	0	0	0	3	0	0	0	1	0	0	0	11	85	0	32	1	0
<i>Scabiosa comosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
<i>Taraxacum</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thalictrum minus</i>	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thymus gobicus</i>	0	1	0	0	0	0	0	0	0	0	0	1	0	1	2	6	1	0	1	0
<i>Veronica incana</i>	0	8	0	2	0	2	1	4	1	1	0	1	2	0	11	25	8	0	0	0
<i>Vicia multicaulis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	0	0	0	0

Table 2.4: Temporal and spatial variation of network specialization and nestedness.

Results of the linear mixed model analysis testing the main effects and their interaction on two plant-pollinator network metrics, specialization (H_2') and nestedness (NODF). Both network metrics were computed for each of 25 plant-pollinator networks. Plant-pollinator networks were comprised of observation data collected in Dalbay Valley, Mongolia, between June and August 2011. Bold values indicate $p < 0.05$. Plot was considered a random factor.

Effect	H_2'			NODF		
	df	F	p	df	F	p
Within-Season	2, 19	3.62	0.0464	2, 14	0.72	0.5021
Slope	1, 19	0.30	0.5927	1, 10	5.21	0.0459
Slope \times Within-Season	2, 19	4.54	0.0244	2, 14	1.27	0.3115

Table 2.5: Correlative and causal relationships between network indices, total visits, and species richness. Hypothesized relationship between forb species richness, the number of flower visits made by Hymenoptera ($Visits_{Hym}$) and Diptera ($Visits_{Dip}$), and two plant-pollinator network metrics: specialization (H_2') and nestedness (NODF). Results shown are from the path model analysis between these hypothesized relationships. Standardized β -coefficients are shown with significance level ($\chi^2 = 6.838$, $df = 2$, $p = 0.033$, $RMSEA = 0.311$, $CFI = 0.849$). Bold values indicate $p < 0.05$.

Regressions	Standardized Estimate	Standard Error	Z-value	p-value
$H_2' \sim Visits_{Hym}$	0.591	0.166	3.567	> 0.001
$H_2' \sim Visits_{Dip}$	0.044	0.166	0.267	0.789
$NODF \sim Visits_{Hym}$	0.100	0.153	0.653	0.514
$NODF \sim Visits_{Dip}$	0.675	0.153	4.425	> 0.001
$Visits_{Hym} \sim Forb$ species richness	0.545	0.168	3.249	0.001
$Visits_{Dip} \sim Forb$ species richness	-0.151	0.198	-0.762	0.446
Covariances				
$H_2' \sim NODF$	0.140	0.196	0.712	0.476
$Visits_{Hym} \sim Visits_{Dip}$	-0.134	0.196	-0.683	0.495

Single tilde (\sim) represents regression analysis (i.e. *a priori* assumption of causality) and double tilde ($\sim\sim$) represents correlations



Figure 2.1: Photographs of insects that visit *Aster alpinus* flowers in Dalbay Valley. (Clockwise) *Bombus* (Hymenoptera: Apidae), *Polyommatus* (Lepidoptera: Lycaenidae), and unidentified Diptera.

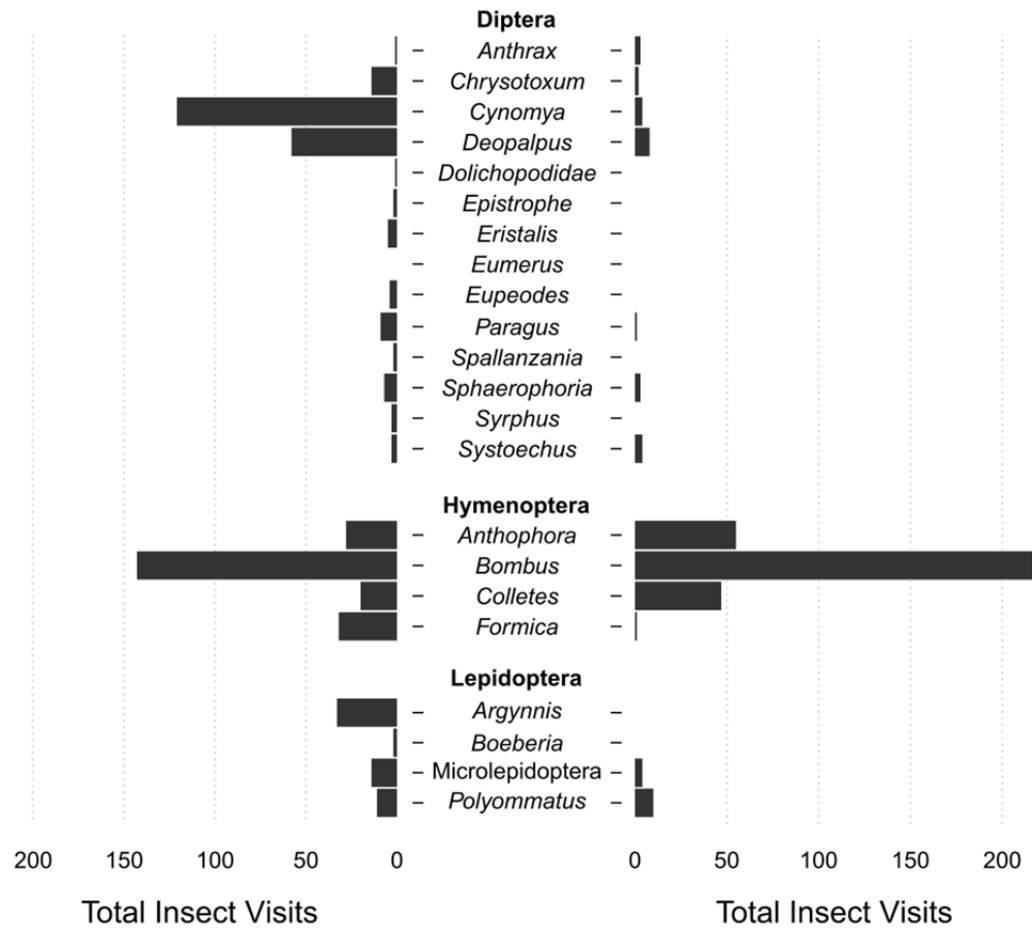


Figure 2.2: Total number of flower visits made by insects. Total number of visits observed within plots located on the Lower and Upper slopes the Dalbay Valley in northern Mongolia. The observations span June to August 2011, for exact dates see Table 2.1.

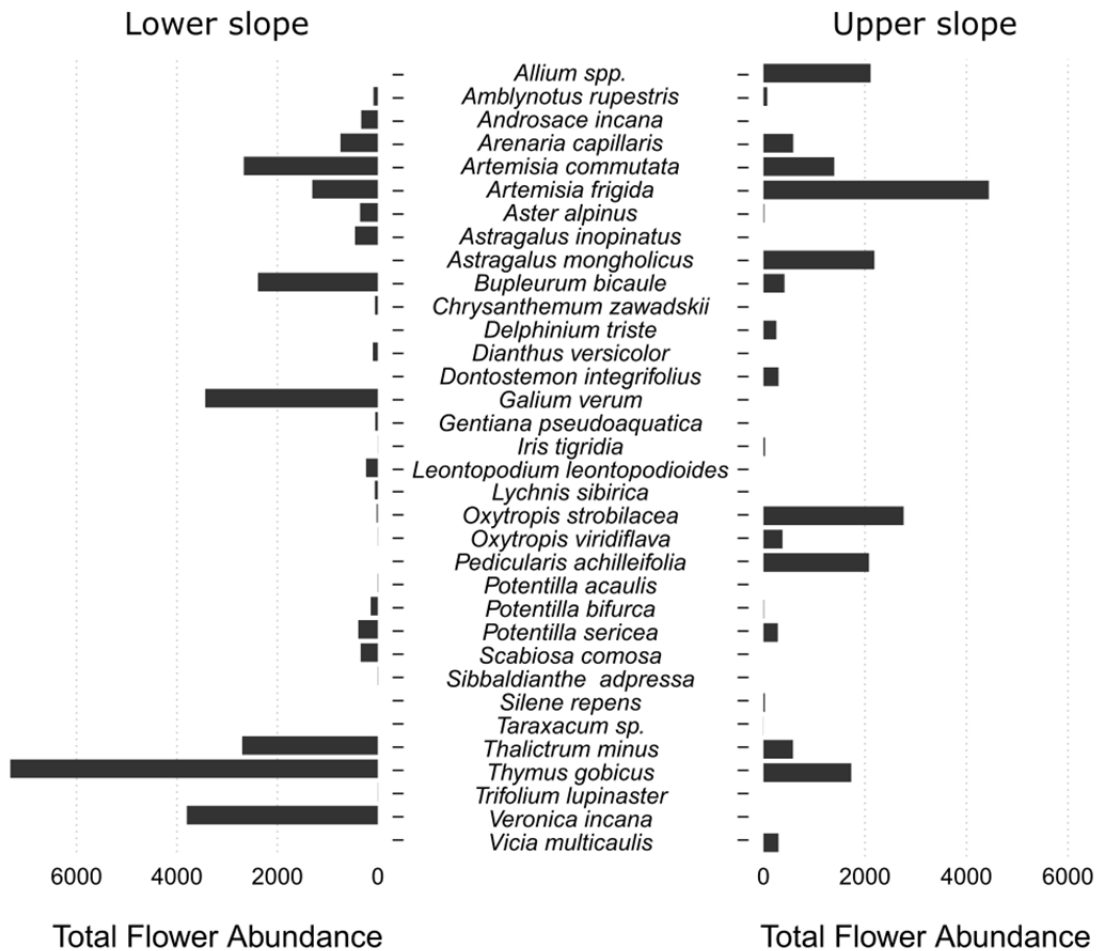


Figure 2.3: Total number of flowers produced by entomophilous plant species. Figure shows the total number of flowers recorded within plots on the Lower and Upper slope. Observations dates and plot locations were the same as in Figure 2.2.

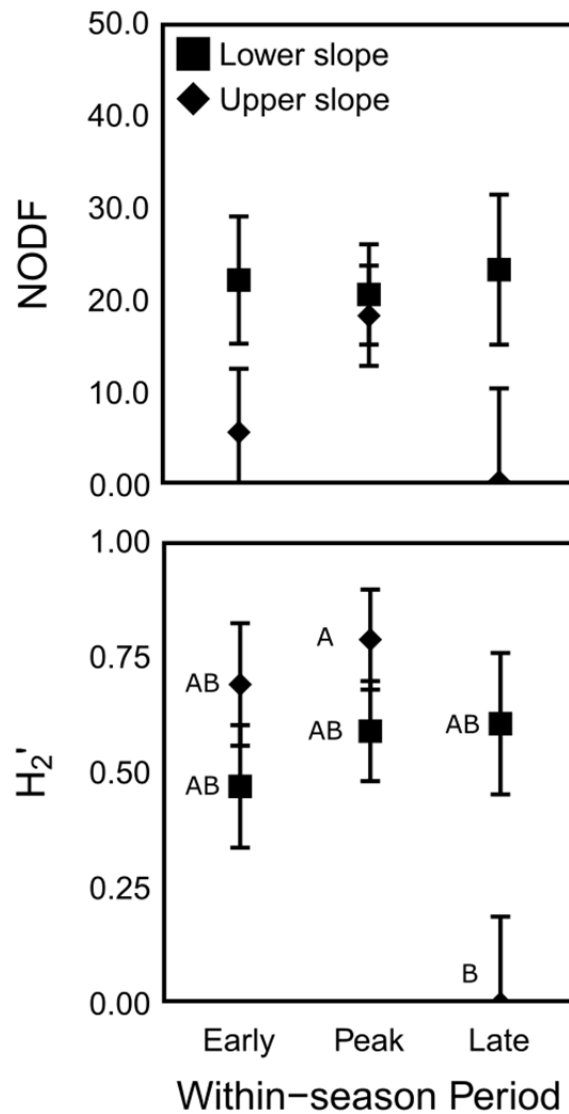


Figure 2.4: Spatial and temporal variation in network specialization and nestedness. Variation (mean ± 1 SE) in plant-pollinator network (top) nestedness, NODF, and (bottom) specialization, H_2' , over Slope location (Lower, Upper slope) and within-season period (Early, Peak, Late) span June to August 2011 in the Dalbay Valley, in northern Mongolia. Squares indicate networks on the Lower slope and diamond symbols indicate plots on the Upper slope. Different letters indicate significantly different means (Tukey's HSD, $p < 0.05$). Slope had a significant effect on nestedness (see Table 2.4).

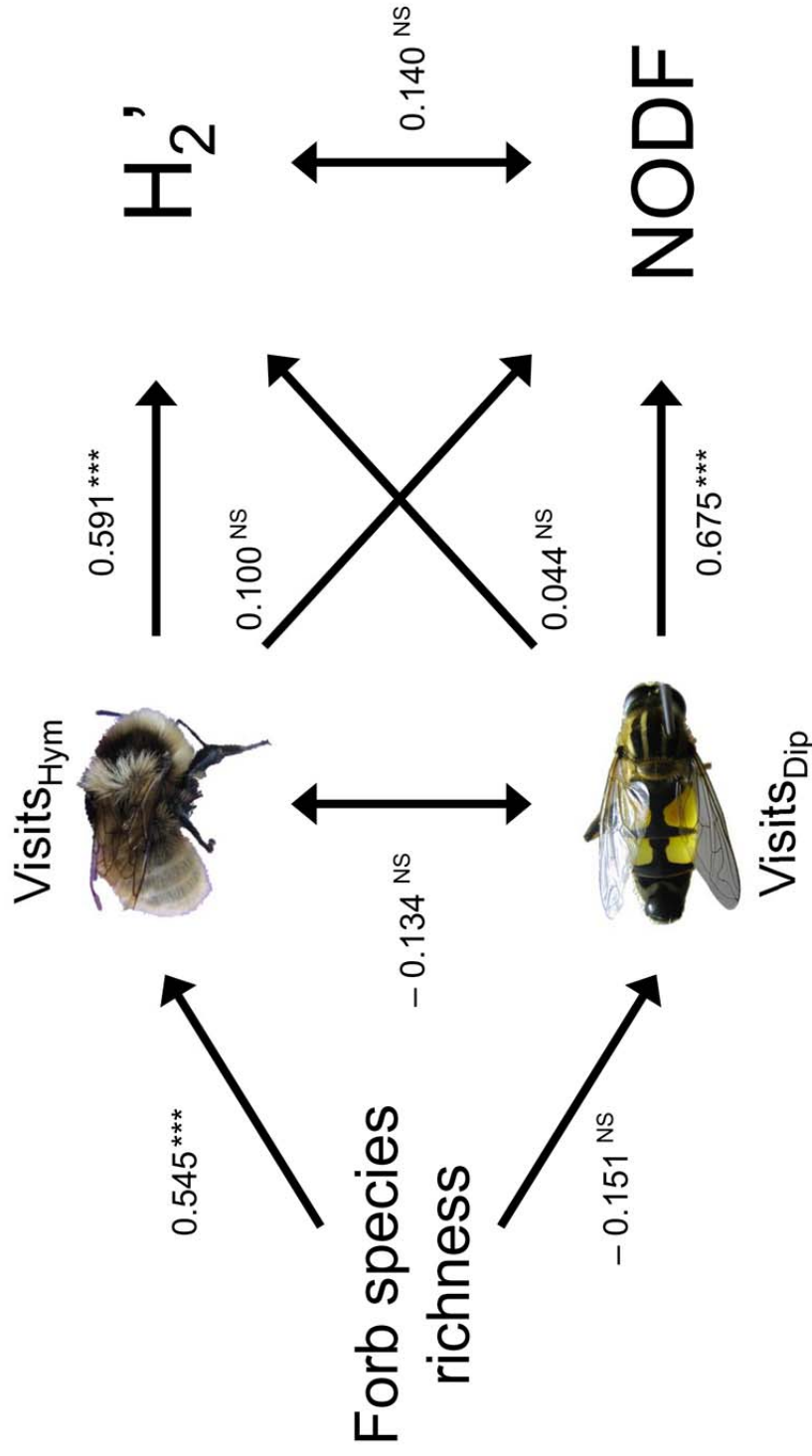


Figure 2.5: Results from a hypothesized path model. Analysis is between forb species richness, the number of flower visits made by Hymenoptera (Visits_{Hym}) and Diptera (Visits_{Dip}), and two plant-pollinator network metrics: H₂' (specialization) and NODF (nestedness). Standardized β -coefficients are shown with significance level. Single arrows indicate hypothetical causal direction while double headed arrows indicate co-varying relationship. $^{***} p < 0.001$, $^{**} p < 0.01$, $^{*} p < 0.05$, $^{NS} p > 0.05$.

CHAPTER THREE: THE EFFECTS OF GRAZING CESSATION ON POLLINATION SERVICES IN THE MONGOLIAN STEPPE

3.1 Abstract

Land use change, such as habitat loss and fragmentation can have large impacts on ecosystems. Specifically, biotic interactions can be disrupted and ecological services reduced. In particular, changes in historical grazing practices directly and indirectly impact wild pollination. While many lands have long been used as grazing pastures, changes in socio-economic conditions and lifestyles are resulting in land abandonment. We investigated how the removal of grazing pressure from the mountain steppe would alter forb and flower visitor communities.

Canonical analysis of principle coordinates showed that plant and flower visitor communities differed significantly between plots where grazing was allowed and where grazing was excluded. Surprisingly, the exclusion of grazing did not affect overall forb or flower visitor taxonomic richness. Overall total flower abundance did not differ between treatments, but during the peak of the season, there was greater flower abundance in plots where grazing was excluded. Among the flower visitor insect orders observed, only Hymenopteran insect composition differed between treatments. There was no overall visitation difference among key individual insects.

The forb and flower communities within historically grazed lands showed an immediate response to grazing cessation. Although forb community structure and flower abundance at the peak differed between treatments, total flower visitation remained

unaffected. The flower visitor community can buffer changes to the forb community and deliver consistent pollination service in the face of land use change.

3.2 Introduction

Land use change resulting in habitat loss, fragmentation, or over-exploitation, has large impacts on ecosystem services and is linked to declines in water availability, soil quality (Schroter et al. 2005), and species biodiversity (Kleijn et al. 2009). Furthermore, changes in land use practices alter plant communities, which directly and indirectly affect pollination. Pollination is an essential ecological service (Kremen et al. 2007) and reduced pollinator availability can threaten local plant diversity in natural systems (Potts et al. 2010) as well as cause a decline in yields in insect-pollinated crops (Garibaldi et al. 2013). Thus, it is important to understand how land use change affects the number and diversity of pollinators and the services they provide (Winfrey et al. 2011).

Light to moderate grazing by domestic herds is a land use practiced in many systems, for millennia in some. In these systems, the cessation of grazing is better viewed as a disturbance and likely to bring about changes in plant-pollinator interactions. This is the case for the steppe in Mongolia, where we conducted this study. The Mongolian steppe has been subject to pastoralism since 800 B.C. (Barfield 1992). An astounding 75% of the land in Mongolia is used for livestock grazing (Batima et al. 2008) but the Mongolian steppe grasslands are experiencing a drastic change in land use practices. The rural-to-city migration of people in Mongolia is resulting in the release of lands from grazing pressure (Morris and Bruum 2005). Such important changes can feed back to

affect plant communities but how grazing cessation affects wild pollination services is poorly understood.

Cessation of grazing could alter pollination services through several mechanisms. First, it could alter plant community structure. Release from grazing pressure tends to reduce overall plant species diversity (Darwin 1859, Hansson and Hakan 2000, Pykala 2003, Dullinger et al. 2003), largely by altering competitive interactions among plants, resulting in a switch of the dominant species (Marton et al. 2008). Without grazers to remove standing biomass, grazing cessation leads to taller and more erect plants (McNaughton 1984, Peco et al. 2005), which could obscure flowers and lead to a reduction in visitation (Dickson and Petit 2006). Lastly, there is no uniform effect on the abundance of forb species as species have been shown to increase as well as decrease due to grazing cessation (Peco et al. 2005).

If grazing cessation alters the abundance and diversity of insect-pollinated flowers, we expect the abundance or composition of insect flower visitors to also change. Flower visitor species richness is positively related to flower abundance and species richness (Potts et al. 2003) and flower morphology diversity (Stang et al. 2006). Thus, changes in the forb community could also differentially affect insect-flower visitors. Some insects, such as bumblebees, have a capacity to learn complex morphologies, such as those of leguminous flowers (Raine and Chittka 2007) and, as such, could respond to changes in abundance of those flowers. Other flower visitors, such as short-tongued flies, should respond more to changes in the abundance of open flowers with more access pollen or nectar resources.

In this study we examine how the elimination of grazing in the Mongolian steppe alters forb flower production and insect flower visitation throughout the growing season. Our objective was to experimentally evaluate how grazing cessation altered (1) forb flower community composition, including flower abundance, and (2) insect flower visitor community composition and number of visits. A better understanding of how grazing cessation alters wild pollination service will provide valuable insight for how future land use changes will affect ecosystem functioning.

3.3 Materials and methods

Study site

This study was conducted 12 June to 12 August 2012 on the south-facing slope in the Dalbay River Valley in northern Mongolia (51°01.405' N, 100°45.600' E, altitude 1670m). The average annual temperature is -4.5 °C (Nandintsetseg et al. 2007), with average monthly temperatures ranging from -21 °C (Jan.) to 12°C (July). Regionally, the average annual precipitation over the last 40 years is 265 mm (Namkhajantsan 2006). An onsite meteorological station recorded 228 mm of rain fall June to August (pers. comm. B. Boldgiv). Permafrost occurs in the region but is not present on the south-facing slope, where this study was conducted.

The most abundant species by plant cover are sedges (e.g. *Carex* spp.) and grasses (e.g. *Festuca lenensis*, *Koeleria macrantha*; see Spence et al. 2014 for more detailed information regarding the plant community). The forb community consists of primarily of perennial species (e.g. *Thymus gobicus*, *Aster alpinius*, *Galium verum*) and few annual species (e.g. *Dontostemon itegrifolius*). There is also a variety of flower morphologies:

zygomorphic and closed (e.g. *Astragalus mongholicus*), actinomorphic (e.g. *Potentilla sericea*), and open composite capitula (e.g. *Aster alpinus*). The forb community is also diverse in their stature ranging from prostrate species (e.g. *Thymus gobicus*) to erect and tall (e.g. *Thalictrum minus*, > 20 cm). The site is used as grazing pastures by nomadic herders in the region. Grazing at the site typically occurs during autumn through spring. The primary grazers are yaks, cows, and horses but also include goats and sheep.

Design

Our design makes use of permanent observation plots rather than temporary transects, providing greater consistency for tracking forb community composition, flower abundance of different species, and insect visitation. We established twelve 2×2 m observation “plots” on the south facing slope (1670 m A.S.L.) in early August 2011. Experimental “treatments” consisted of grazed and ungrazed plots that were paired into six blocks. To simulate the complete cessation of grazing, each ungrazed plot was located within a 9×9 m fenced area that excluded livestock grazing throughout the year. Each grazed plot was located within a 3×9 m area, where fences excluded grazers between June and August but were removed to allow grazers access to the area for the remainder of the year. Each block was spaced approximately 30 m apart.

Observations

Flower visits made within plots were observed at three different time “periods” throughout the day: 830-1200, 1200-1530, and 1530-1900 for a total of 216 hours over the season. A single observation was made for 30 minutes and all 12 plots were observed once in each daily time period over four consecutive days. Four-day observation sets were separated by one or two days when no observations were made. Two consecutive

four-day observation sets were combined to create an observation “round” for the purpose of statistical analysis. We completed a total of six eight-day rounds for this study.

At the beginning of each 30-minute observation session, the total number of flowers in anthesis within the plot was counted for each species. Inflorescences, such as the capitulum of *Aster alpinus* and *Scabiosa comosa*, were counted as individual flower units. If a plot did not contain any flowers in anthesis, the plot was not included. Observations were made by standing within 0.5 m of the plot but changing positions to observe the plot from all four sides. For relative abundance of flowers and flower visitors see Appendices C.1 and C.2.

Sampling

Each flower insect visitor was observed and a successful flower visit was recorded if it met three criteria: (1) landed on a flower or inflorescence for at least three seconds, (2) touched anthers or stigmas, and (3) probed for collected nectar or pollen. We considered an insect as probing for nectar or pollen if it moved into the flower head or down to the base of an open flower. To minimize disturbance to flowers and other visiting insects within the plot, visitors were caught after they left the center of the plot area. Fewer than 20 individual insects meeting the three criteria were not captured and thus, the visits from these insects were not recorded. Two conspicuous and easily identifiable butterfly species and two ant species were captured, positively identified, and released outside of the plot area after observations of that plot were finished. All other pollinators were killed in diethyl ether and pinned (vouchered specimen deposited at the Department of Entomology of the Academy of Natural Sciences, Philadelphia).

Statistical analyses

For the community level analysis, we analyzed a community matrix for forbs containing 33 species and separately analyzed a community matrix for flower visitors containing 32 insect families using canonical analysis of principal coordinates (CAP; modified implementation of CAP described by Anderson and Willis 2003) using R-3.0.3 (R Core Team 2014) with the “vegan” package (Oksanen et al. 2013). Both forb and flower visitor community data matrices consisted of 205 rows, with each row corresponding to a unique observation of a plot for each grazing status, period, and round. Observations of plots with no flowers in anthesis were omitted from both the forb and flower visitor community matrices. Dissimilarity distances were calculated using Bray-Curtis dissimilarity index (Faith et al. 1987). To examine if any of the insect orders had differential responses to the grazing treatments, the flower visitor community was also analyzed by insect order, after omitting the single visitor representing Hemiptera.

Each CAP analysis was followed by a permutation ANOVA with 999 permutations to examine the effects of several factors: grazing, round, plot, and their interactions. The permutation ANOVA for the flower visitor community included the scores of the first two axes from a NMDS ordination of the forb community data as covariates. For both the forb and flower visitor matrices, we included all observations where there was at least one flower in anthesis. There were plots that contained flowers in anthesis but did not receive any visits. This meant that there were zeroes included in the flower visitor community matrix. To calculate dissimilarity distances using Bray-Curtis we added 1×10^{-5} to any cell with a zero. The data for the forb community and insect flower visitor community were raw counts and were square-root transformed.

Further analyses were conducted to determine whether flower abundance of individual forb species' and total number of visits from insect families was affected by the grazing treatments. We selected six forb species and six insect families with the highest average correlation with the first two CAP axes of their respective community level CAP analyses. Separate split-block ANOVAs were performed on the flower abundance for each forb species and number of visits for each insect family. The data were unbalanced, thus the model only included the main effects of grazing treatment, round, and time period, with plot as a random factor. The fit of the mixed ANOVA models were evaluated using the R package "lme4" (using restricted maximum likelihood, Bates et al. 2014) and *p* values were calculated using Satterthwaite's approximation with the package "lmerTest" (Kuznetsova et al. 2014). *p*-values were adjusted for multiple comparisons (*n* = 6) using Bonferroni correction.

To determine the effect of grazing cessation on the total flower abundance throughout the season, we used ANOVA using restricted maximum likelihood to examine the main effects of grazing treatment, round, time period, with plot as a random factor. The model was fully factorial with the four-way interaction removed as it is included in the error term. We then further examined the round \times grazing treatment using orthogonal contrasts. These analyses were done using JMP 10.0 (SAS Institute, Cary, NC) on count data that were square-root transformed to meet assumptions of normality.

3.4 Results

Forb community

The grazing treatments significantly altered the forb flowering community composition (Table 3.1). The ungrazed plots had greater flower production than the grazed plots (Fig. 3.1). Individual forb species flower abundance change varied in response to the grazing treatment (Fig. 3.2). Certain forb species only occurred in one or the other grazing treatment: three forb species were exclusive to grazed plots while another three were only found in ungrazed plots. Surprisingly, exclusion of grazing did not significantly affect forb species richness. Finally, the effect of the grazing treatment on forb community composition varied over the progression of the growing season (grazing \times treatment, Table 3.1).

While the exclusion of grazing had a strong community level effect, among the forb species we examined individually, only two of the forb species responded to the grazing exclusion (Table 3.2; Fig. 3.3; Appendix C.2 and C.3). Flower abundance for *Thalictrum minus* (Ranunculaceae) was lower in grazed plots (ANOVA $F_{3,46} = 16.3$, $p < 0.001$) while *Thymus gobicus* (Lamiaceae) was greater (ANOVA $F_{4,74} = 31.9$, $p < 0.001$). Overall, we observed a total of 33 forb species and recorded a total of 54,434 flowers. While individual flower production differed between grazing treatments, the total flower abundance across all forb species did not differ across treatments ($F_{1,10} = 3.3$, $p = 0.10$) but there was a significant treatment \times round interaction ($F_{5,23} = 3.0$, $p = 0.03$). There was greater number of flowers produced in plots where grazing was excluded but only during the peak of the season (Fig. 3.4).

Community of flower visitors

Like the forb community, the community composition of insect flower visitors was significantly affected by the grazing treatment (Table 3.1). Grazed plots received a

greater number of visits compared to ungrazed plots (Fig. 3.5), despite the greater number of flowers produced in ungrazed plots. Further analysis by insect order revealed that while the overall flower visitor community composition was altered by the grazing treatments, only the composition of the order Hymenoptera was significantly altered by the grazing treatment. The majority of families within Hymenoptera visited the grazed plots more than the ungrazed plots. The absolute number of visits made by the different insect groups was not different between grazing treatments as the majority of the flower visitors only showed a difference of 10 visits or fewer between treatments (Appendix C.4 and C.5). Of the six insect families exclusively observed in grazed plots, half were Dipteran. Whereas of the five families exclusively observed in ungrazed plots, three of them were Lepidopteran.

While grazing treatments altered insect visitor community composition and grazed plots received slightly more visits, none of the six flower visitor families we examined made significantly different number of visits to either treatment. There was a trend of Muscid flies visiting the grazed plots more than the ungrazed ones (Table 3.3; Fig. 3.6). Additionally, the total number of visits to the treatment plots did not differ ($F_{1,10} = 0.23, p = 0.64$) but there was a significant period \times treatment interaction ($F_{2,69} = 0.23, p = 0.02$), with the middle period receiving the most visits only in plots where grazing was excluded. Overall, we observed a total of 983 flower visits made by 32 insect taxa.

3.5 Discussion

Our results demonstrate that removal of consistent livestock grazing from a historically grazed system alters forb community composition and flower abundance without eliciting major changes in overall insect flower visitor abundance. While previous studies have examined the impact of introducing livestock grazing, in our study site, the cessation of grazing, rather than introduction, is the disturbance. This is an important as many rural and nomadic pastoral practices are transitioning towards a more sedentary and urban lifestyle in Mongolia.

Forb Community

The pressure that grazing exerts on plant communities is significant. Grazing is known to promote prostrate plants (McNaughton 1984, Peco et al. 2005) and lead to greater flower abundance (Vulliamy et al. 2006). Yet surprisingly, flower abundance during the peak of flower production was greater in plots where grazing was removed. The greater flower abundance in the ungrazed plots was mainly attributed to *Thymus gobicus* (Lamiaceae), which was particularly abundant during the middle of the summer growing season. We expected a prostrate species such as *Thymus gobicus* to flourish in grazed plots while other more erect and taller species to have an advantage in ungrazed plots.

There are two likely explanations for *T. gobicus* producing more flowers in ungrazed plots. One possible explanation may be related to grazing intensity. First, plots that experience light grazing intensity produced the greatest number of flowers, compared to intermediate and heavy levels of grazing (Yoshihara et al. 2008). Despite, the presence

of other more erect and taller species in our system (e.g. *Gallium verum*) that appear to be likely candidates to increase flower production without grazing, perhaps the immediate release from grazing at our field site emulates favorable levels of disturbance for *T. gobicus*. Second, *T. gobicus*' woody tissue is exposed during the non-summer seasons, thus our year-round grazing exclusion protects *T. gobicus* from non-summer grazing, which may have resulting in greater vegetative growth.

Since grazing exerts a strong force on plant communities, taller, more erect plants should do well with grazing removed. Yet again, we observed *Thalictrum minus* (Ranunculaceae) to be contrary to our expectations. *T. minus* is an erect forb species with flowers at a height between 20 cm and 50 cm above the ground (pers. obs.). Despite this, *T. minus* responded to the removal of grazing by producing fewer flowers. This may be attributable to light availability and, consequently, the lack of resources to produce flowers. In plots where grazing was excluded, litter accumulated and may act to shade plants, which may lead to decreased flower number (Kim et al. 2011). While the flowers of *T. minus* rise above almost all other species in our system, the vegetative component is short and low to the ground. Furthermore, the leaves of *T. minus* are small and compact, which may leave the plant particularly susceptible to shading. Additionally, shading and albedo reflectance by litter leads to lower soil temperatures, which have been found to reduce flower abundance (Spence et al. 2014).

While our results demonstrate a direct effect on forb community structure in terms for flower abundance, we did not detect a response in the species richness of the flowering species. Herbivory has long been thought to increase species richness in grasslands (Olf and Ritchie 1998). Communities released from grazing pressure tended

to decrease plant species diversity (Hansson and Hakan 2000, Pykala 2003, Stefan et al. 2003), but these studies took into account all plant species, not just forb species. Our study site may be different than most since the plots are high altitude and dominated by perennial forbs, with only a one annual species, *Dontostemon integrifolius*. Results from a lowland study show that there may be greater native perennial forbs species in ungrazed sites (Hayes and Holl 2003). At high elevations this may not be the case. As elevation increases, perennial forbs tend to shift towards a more conservative life history strategy and allocate resources for reproduction later than their low elevation counterparts (von Arx et al. 2006). Built into a strategy for longevity of high altitude herbaceous species may mean that they are more tolerant of disturbances, particularly one that the community has been subjected to for centuries. Another explanation for the lack of change in species richness could be that grazing, although consistent through time, is low in intensity and does not illicit a strong response when grazing was removed from the system.

Community of flower visitors

Overall, the flower visiting community appears to buffer changes to the forb community composition and flower abundance. Given the change in forb community structure, as expected, the flower visitor community structure differed between grazing treatments but there was no change in the overall number of flower visitation. This may have been due to redundancy of functional groups in the community, such as the presence of multiple taxa that forage on pollen and/or nectar. When one flower visitor drops out, another may take its place (Brittain et al. 2013).

Additionally, different insect taxa are known to respond to grazing differently (Sjodin et al. 2008). Many of the nectar foraging insects are Hymenopteran. While overall insect visitation to the ungrazed plots was not significantly different, Hymenopteran insects visited grazed plots slightly more than ungrazed plots. A consequence of grazing cessation is the accumulation of litter that would otherwise be removed by grazers (Spence et al. 2014). The litter may have obscured many of the small prostrate forb species. Thus, even with the greater number of flowers in the grazed plots, the height of the litter may have obscured many of the flowers from potential visitors (Dickson and Petit 2006).

Lastly, although there were a greater number of flowers produced in the ungrazed plots during the peak of the season, there was no commensurate increase in insect flower visitation to these plots. Thus the forb community where grazing was excluded received fewer visits per flower, even with the additional investment of resources towards reproduction. As a result, *T. gobicus*, which is not self-compatible (unpublished data), received little to no marginal gain for the resource investment towards flower production triggered by the removal of grazing.

Other Considerations

The scope of our study was to assess the immediate impact of grazing cessation from a system that has been historically grazed through nomadic pastoral practices. Although there may be further considerations for length of time since abandonment, studies examining formerly grazed lands abandoned for at least 10 years found they were not different from actively managed grasslands in terms of plant species richness and insect abundance (Sjodin et al. 2008). Even within a shorter timeframe, we detected

significant differences in community composition between treatments. Another consideration is that the primary grazers at our study site are horses, cows, and yaks. Grazing behavior from livestock can alter light availability (Bullock and Marriott 2000). Certain livestock, such as cows and horses, mainly forage on grasses, while goats and sheep tend to selectively forage on forbs (Yoshihara et al. 2008b). Had there been greater grazer diversity, diet breadth may have been increased, resulting in a more severe direct effect on the forb community after cessation (Rook et al. 2004).

In our system, grazing occurs in the fall and winter. The season in which grazing predominantly occurs can affect plant species richness and community composition (Bullock et al. 2001). This may be because summer and spring grazing has stronger direct effects on plant and flower visitor communities. Traditionally, herders divide parcels of land for grazing at the different seasons (Sneath 2001). Thus, there is the possibility of an interaction between livestock type, plant and pollinator communities, and seasonality. Furthermore, our site is unusual in that sheep and goats typically dominate livestock abundance (J. Gelhaus, pers. comm.). Consumption of flowers by grazers is more likely during the spring and summer, which may lead to reduced floral resource availability for pollinators in the season (Sugden 1985). Additionally, nesting sites for active flower visitors may be trampled, thus leading to greater insect mortality and reducing ability of insects to visit flowers (Sugden 1985).

Conclusion

The results from this study suggest that there is an immediate and direct impact on the forb community by removing grazing from a historically grazed system. Despite this, overall flower visitation to plots was unaffected, even though flower visitor community

composition differed between grazing treatments. Land abandonment is a serious problem and cessation of grazing pressure is a likely land-use change scenario the Mongolian landscape faces if current trends continue (Morris and Bruum 2005). These results emphasize the need to study how long-term grazing exclusion impacts plant and pollinator communities. Moreover, the change in grazing practices may interact with future climate change to further alter forb community composition, such as reduce species richness (Spence et al. 2014). These results may offer hope in the face of global land use change, that although the taxonomic composition was altered by grazing cessation, insect visitation to the forb community was not. Our results highlight the need for further examination of land use change in countries that similar to Mongolia to better understand how important ecosystem services, such as pollination, interacts with socio-economic changes.

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Table 3.1: Effects of grazing exclusion on the number of pollinator visits. Results of permutation test from the community level CAP analysis of total flower abundance and flower visitors examining the main effects of grazing exclusion (Treatment), within-season temporal effects (Round), Plot, and the Treatment \times Round interaction. Flower visitors were further analyzed by insect order. Percentage indicates the amount of total variation explained by the first two CAP axes. NMDS1 and NMDS2 are scores from the first two axes of an NMDS analysis of the forb community. These scores were added as covariates to account for forb community composition in the analyses of flower visitors.

Terms	Flower abundance	Flower visitors	Flower Visitors (insect order)			
			Coleoptera	Diptera	Hymenoptera	Lepidoptera
	36%	18%	56%	26%	35%	34%
Treatment (T)	0.001	0.014	0.566	0.733	0.001	0.766
Round (R)	0.001	0.001	0.001	0.001	0.001	0.327
Plot (P)	0.001	0.001	0.001	0.001	0.039	0.096
T \times R	0.001	0.169	0.633	0.84	0.436	0.856
T \times P	0.001	0.031	0.046	0.228	0.212	0.769
R \times P	0.001	0.001	0.343	0.228	0.001	0.123
T \times R \times P	0.001	0.001	0.198	0.051	0.118	0.221
NMDS1		0.229	0.291	0.016	0.199	0.602
NMDS2		0.307	0.395	0.009	0.147	0.715

Table 3.2: Comparison of flower abundance between grazed and ungrazed plots. ANOVA results (p values) comparing total flower abundance in grazed and ungrazed plots for six forb species. Table shows p values adjusted by Bonferroni correction.

Plant species	p-value
<i>Arenaria capillaris</i>	0.99
<i>Aster alpinus</i>	0.99
<i>Bupleurum bicaule</i>	0.32
<i>Galium verum</i>	0.19
<i>Thalictrum minus</i>	< 0.001
<i>Thymus gobicus</i>	< 0.001

Table 3.3: Comparison of pollinator visits between grazed and ungrazed plots.

ANOVA results (p values) comparing total flower visitors to grazed and ungrazed plots for six insect families. Table shows p values adjusted by Bonferroni correction. NS: $p > 0.10$

Insect family	<i>p-value</i>
Apidae	0.99
Formicidae	0.99
Halictidae	0.99
Muscidae	0.08
Syrphidae	0.37
Tachinidae	0.99

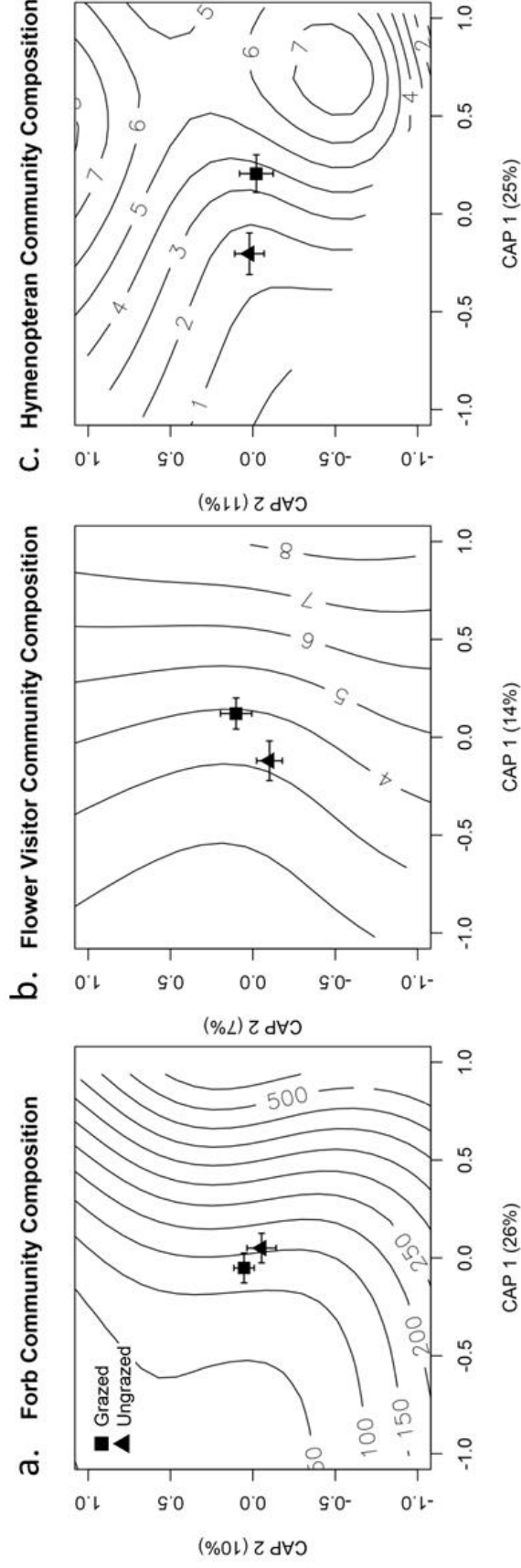


Figure 3.1: The community composition of grazed and ungrazed plots. CAP ordination plot showing the difference in community composition between grazing treatments for (a) forbs, (b) all flower visitors, and (c) only Hymenopteran visitors. Contour lines for each plot represents the mean number of (a) forbs for all forb species, (b) visits by flower species, and (c) visits from Hymenopteran flower visitors. Centroids of each forb community are indicated by symbols: square symbols represent grazed plots and triangles represent ungrazed plots. Where the symbol lies on the contour indicates mean value of (a) flowers or (b, c) visits. Percentage indicates the amount of total variation attributable to each CAP axes. Error bars extended from the centroid of each symbol represents 1 SE.

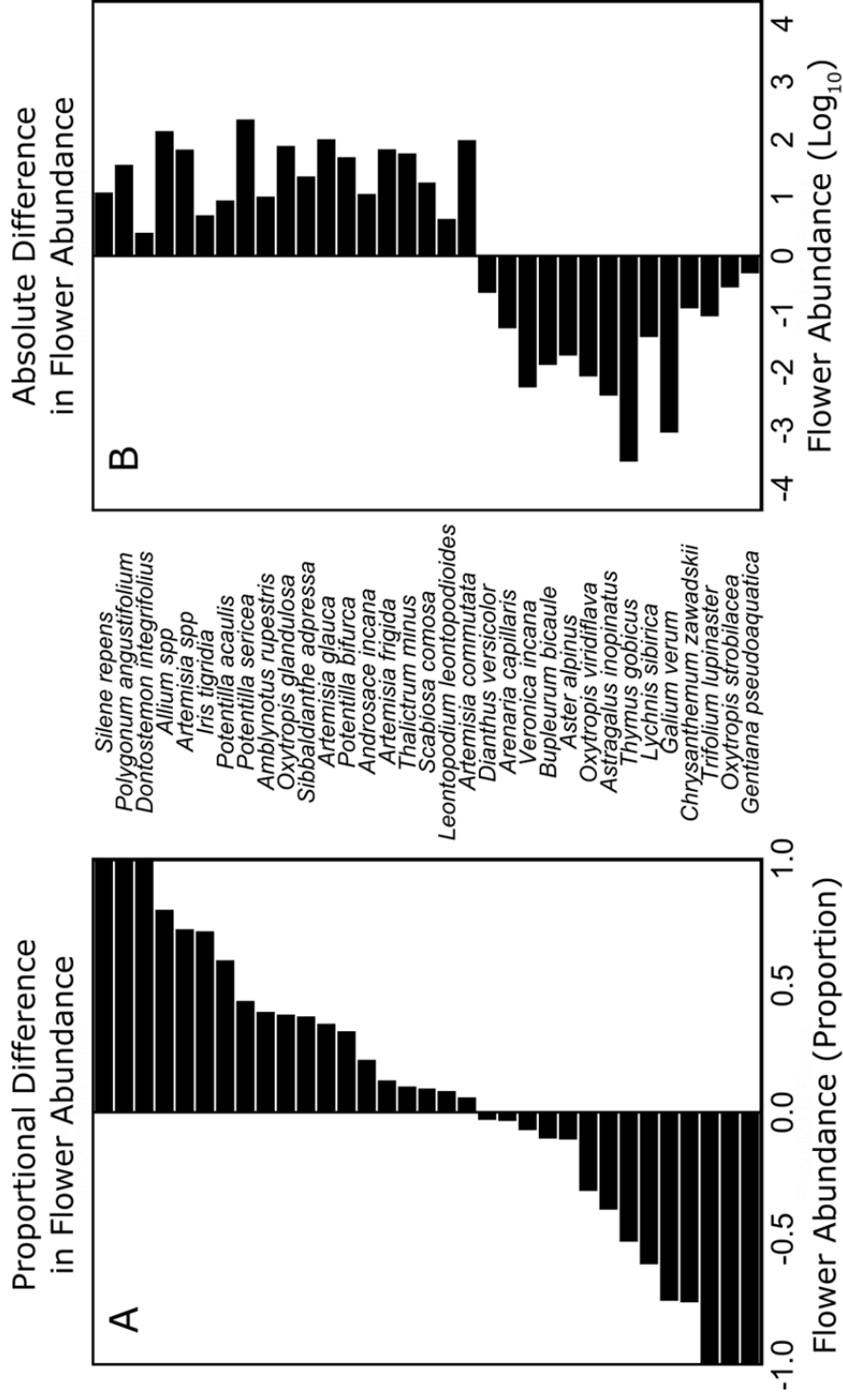


Figure 3.2: The difference in flower abundance between grazed and ungrazed plots. Flower abundance data for each forb species represented as (A) a proportion of the total number of flowers that forb produced and (B) as the absolute difference (Log_{10}). Positive values indicate greater flower abundance in grazed plots, negative values indicate greater flower abundance in ungrazed plots, and zero indicates no difference in flower abundance between grazed and ungrazed plots

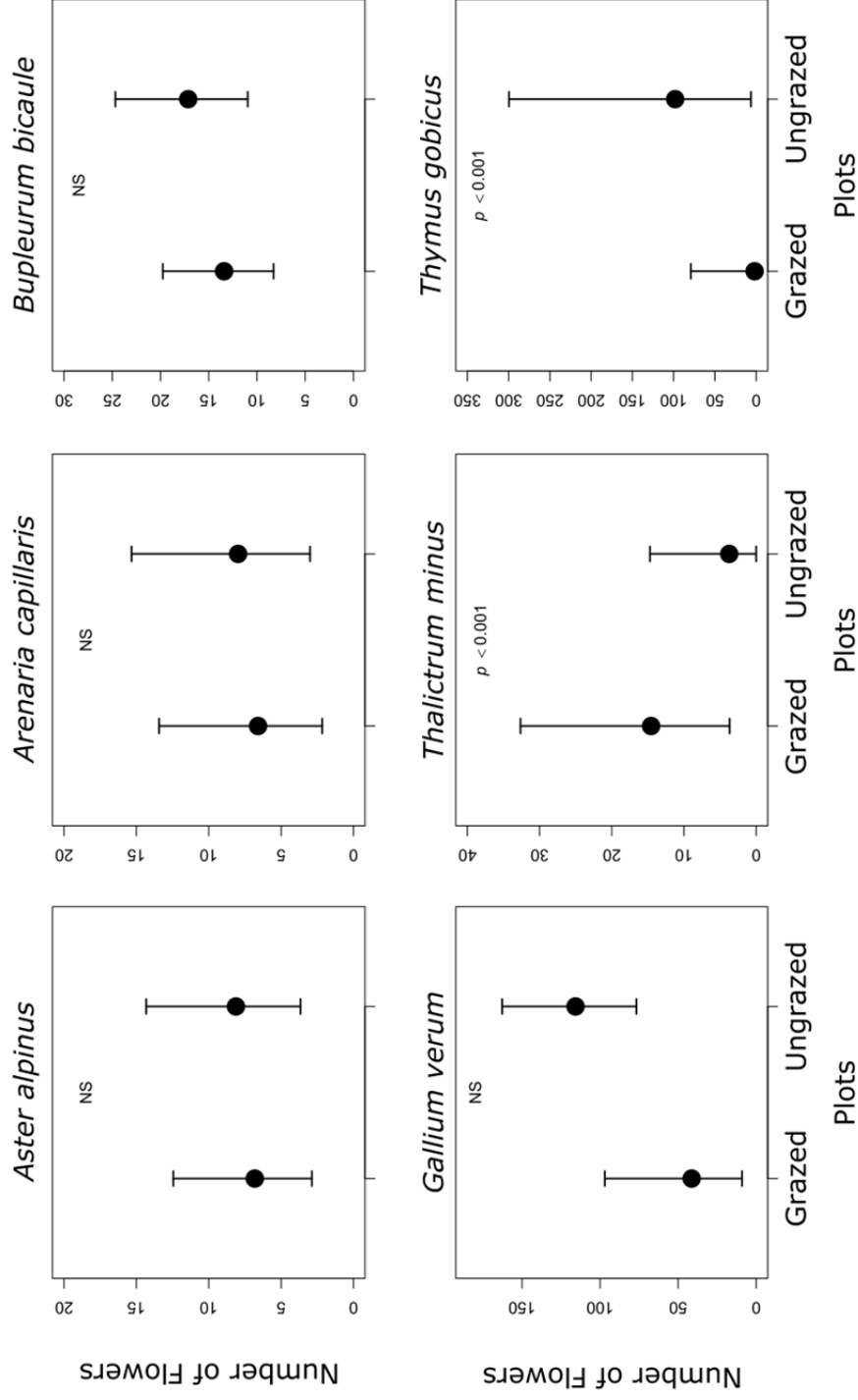


Figure 3.3: Comparison of flower abundance in grazed and ungrazed plots. Species-level ANOVA for six forb species comparing flower abundance between grazed and ungrazed plots. The six species chosen had the highest average correlation with the first two axes of the forb community CAP analysis. Means are square-root back-transformed and bars represent back-transformed 95% confidence interval. p values shown have been adjusted for multiple comparisons by Bonferroni correction ($n = 6$). NS: $p > 0.05$

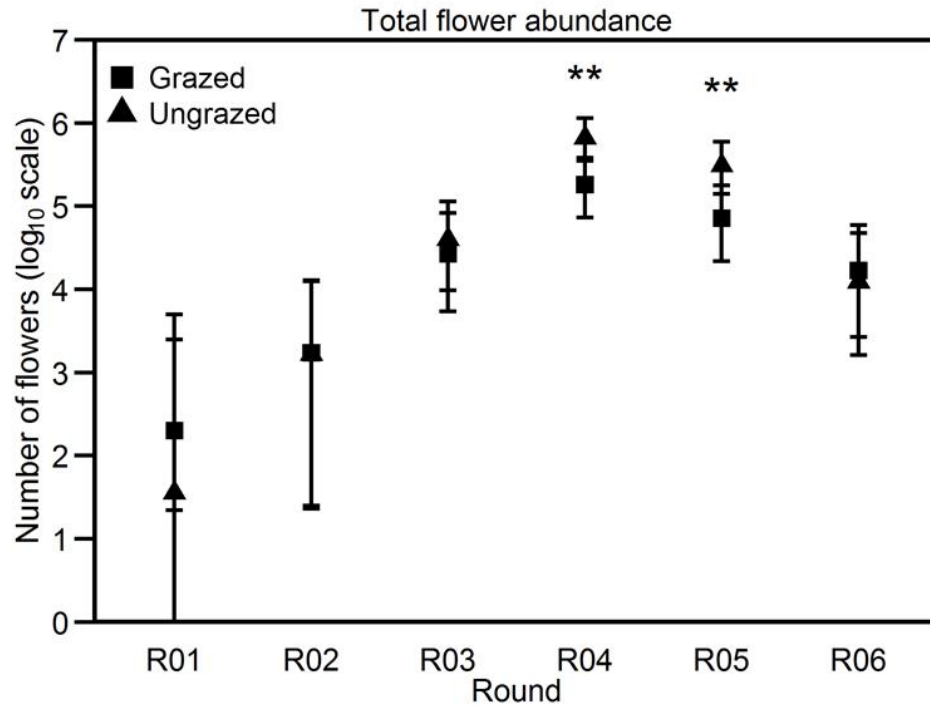


Figure 3.4: Overall flower abundance throughout the vegetative growth season.

ANOVA used to test the effect of different summer time points (Round) and grazing exclusion on flower abundance. The square symbol indicates the mean flower abundance for the grazed treatment and the triangle symbol indicates the mean flower abundance for the ungrazed treatment. Values shown are square-root back-transformed and bars represent back-transformed 95% confidence interval. ** indicates a significant difference in flower abundance between grazing treatments (orthogonal contrast, $F_{2,51} = 5.87$, $p = 0.005$).

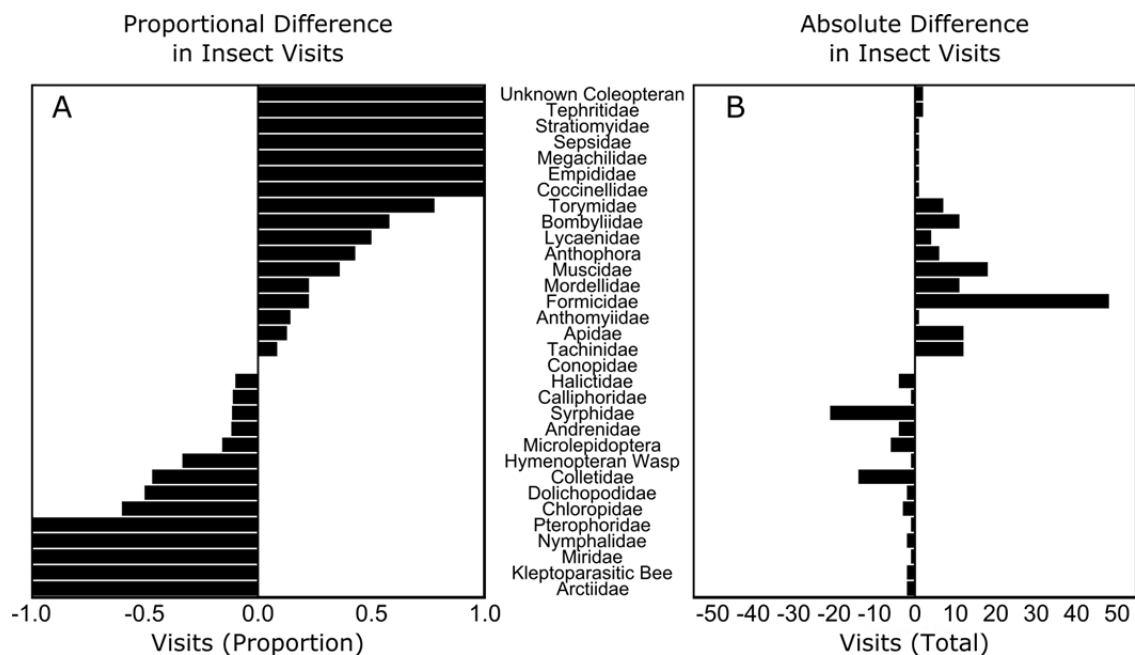


Figure 3.5: The difference in flower visits made by insects between grazed and ungrazed plots. Number of flower visits made by insect groups (insect family or morpho-species) represented as a (A) proportion of total visits and (B) as the absolute difference. Positive values indicate greater visits in grazed plots, negative values indicate greater number of visits in ungrazed plots, and zero indicates no difference in the number of visits between grazed and ungrazed plots.

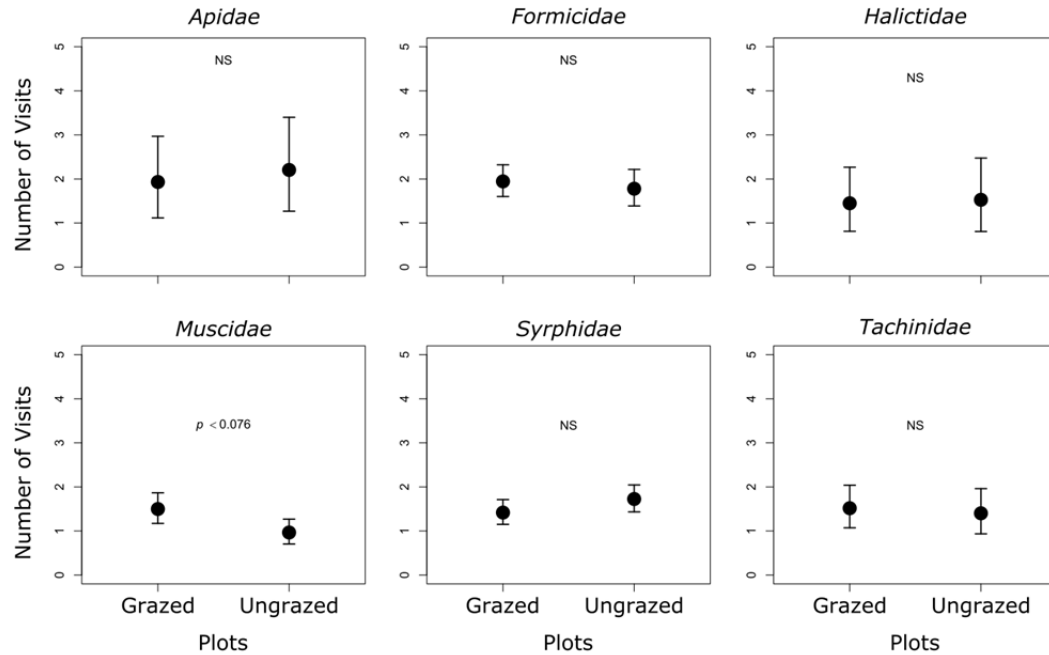


Figure 3.6: Number of insect visits between grazed and ungrazed plots. Separate ANOVAs for the number of insect visits. Analyses were conducted for six insect families observed visiting flowers. The six families chosen had the highest average correlation with the first two axes of the forb community CAP analysis. Means are square-root back-transformed and bars represent back-transformed 95% confidence interval. p values shown have been adjusted for multiple comparisons by Bonferroni correction ($n = 6$). NS: $p > 0.05$.

DISCUSSION

The consistent delivery of wild pollination services is of great concern. Wild pollination is a critical service that helps to maintain plant biodiversity (Kay and Sargent 2009) and is economically important for crops (Kremen et al. 2007, Garibaldi et al. 2013). Predicted changes in climate will introduce new variability to ecosystems, affecting temperature-dependent services, such as pollination (Memmott et al. 2007). It is critical to identify current sources of variability in wild pollination and work at the appropriate scale (Levin 1992, Chave 2013) for projecting the effects of future climate change (Rader et al. 2013, Bartomeus et al. 2013).

Our results highlight the importance of incorporating spatial and temporal variation when studying the stability of pollination services. Many studies focus on network topologies without considering the role of plant and pollinator dynamics over space and through time. Consequently, datasets are rife with instances where links between particular pollinators and particular plant species are not seemingly observed. The primary issue with aggregating data without temporal or spatial variation is the conflation of links between species that *do not* occur with those links between species that *cannot* occur. While plants and pollinators may co-occur in space and time there are factors, such as nutritional requirements and foraging behavior, which prevents interactions. But plants and pollinators may not interact because they do not co-occur in space or time. Thus, important aspects of pollination services, such as stability, may be misunderstood.

The pollination services that a plant community receives are not uniformly distributed spatially, even within local landscapes, as shown in Chapter 1 and 2. Although the plant communities at both slope locations sharing more than 50% of the species within their plant communities, there was a stark difference in visitation and networks specialization among the two slope locations. The heterogeneity of plant community composition is one important factor for determining the spatial distribution of pollination services. Within plant populations, the quantity and quality of flower rewards, such as nectar varies (Leiss and Klinkhamer 2005). In our system, the differences in pollinator communities that service plant communities is primarily due to the heterogeneous distribution of plants that produce relatively large quantities of nectar. These plants tend to be leguminous and concentrated on the Upper slope. Thus, the spatial distribution of forb species and their flower abundances strongly influence the plant-pollinator network specialization and the pollination visits servicing the plant communities.

Despite work that suggests the composition of plant and pollinator communities minimally affects network topology, our system shows certain measures of network stability are influenced by spatial differences in community composition. Previous work documented relatively stable network topologies despite large amounts of turnover in the specific plant-pollinator interactions (Petanidou et al. 2008). But our results suggest that not all network indices are equally affected by differences in community composition across space. However, we believe our results are consistent with past studies. The consistency of network topology is likely a consequence of functionally redundant species that take the place of species that are no longer present. In other words, networks tend to maintain their network architecture, despite the loss of a pollinator species, if

there is similarity in foraging behavior or spatial distribution between the species being lost and the replacement species (Weiner et al. 2013). In our system, network nestedness was significantly greater on the Lower slope than on the Upper, but specialization did not differ among the two slope locations.

The differences in network indices suggest that, effectively, the plant communities at the two slope locations differ in their strategy to attract pollinators. The community on the Lower slope is structured to maximize stability through generalist pollinators such as Diptera. A consequence of nested organization is the redundancy of functions within networks (Blüthgen and Klein 2011). As a result, the increased network nestedness confers increased network resilience by protecting against network collapse due to species loss (Aizen et al. 2012, Astegiano et al. 2015). In contrast, the plant community on the Upper slope consists mainly of leguminous forb species that primarily receive visits from specialist bumblebees. The networks on the Upper slope experience the trade-off between increased specialization, which leads to decreased ability to recover from perturbations (Clavel et al. 2010) and increased efficacy of pollination services (Johnson and Steiner 2000). Thus, the spatial variation in plant-pollinator communities leads to differences in network stability within the landscape.

This variation we observed in Chapter 1 and 2 may be influenced by a combination of plant community composition and variation in air temperature. But what mechanism can explain this variation? Throughout the season there is considerable variation in air temperature throughout the season. Optimal foraging and activity temperatures differ between insect species (Vicens and Bosch 2000). Moreover, size is positively correlated with heat loss (Pereboom and Biesmeijer 2003). Also, at higher

elevations, certain pollinators, such as bumblebees, tend delay their emergence closer to the peak flowering period (Pyke et al. 2011). This underlying mechanism driving the temporal variation in the community composition of plants and pollinators should also impact the network stability.

One important consequence of the temporal dynamics observed in plant-pollinator interactions is the variation in the network specialization. In Chapter 2 we observed bumblebees visiting nectar producing forbs, primarily leguminous species and were positively related to network specialization. The combination of increased network specialization and narrow foraging niche of the bumblebee indicates that the Hymenoptera-plant interactions may be such that the pollinators are functionally complementary (Blüthgen and Klein 2011). Therefore, our results suggest that network vulnerability varies for groups of pollinators depending on the time within the season. Diptera, which are present throughout the season, may be more resilient against perturbations compared to Hymenoptera visitors, which only occur in a limited stretch throughout the season. But this temporal variation in network vulnerability may not hold in all systems. For networks with perennial forb species, they can persist without insect-mediated pollination whereas annuals persist through pollination and their seed bank.

High species turnover within plant and pollinator communities but consistent number of visits has been previously documented over space (Carstensen et al. 2014) and time (Petanidou et al. 2008) but not in the context of disturbances. This pattern is likely related to the selection of certain types of plants and pollinators in this community. Diptera, such as Syrphidae (i.e. hover-flies), have been shown to be effective pollinators (Ssymank et al. 2008). However, the foraging behavior of Diptera flower visitors tend to

be restricted to pollen produced by flowers (Goulson and Wright 1998). While the community composition of pollinators differed between plots that were grazed and plots where grazing was excluded, the Diptera species new to either of the communities were functionally redundant. Similar to the pollinators, the forb community consists primarily of species with low-levels of nectar but open and accessible anthers for insects to forage. Thus, the specific species composition may have changed but functional redundancy resulted in consistent pollinator visits despite the cessation of grazing.

The challenge to better understanding community level interaction networks is to identify the underlying sources of variation of indices. Understanding ecological reasons why interactions do not or cannot occur is critical to mitigating loss of pollination services (i.e. forbidden links; Jordano et al. 2003). In addition to spatial and temporal barriers, the absence of an interaction between two partners may be determined by their functional or evolutionary relationship. The functional trait framework relates phenotypic traits to ecologically relevant functions (Lavorel et al. 1997). Using this framework, researchers are able to study phenotypic traits, such as corolla depth and proboscis length, to test relationships between interactions and these functional traits (Rodríguez-Gironés and Santamaría 2007, Stang et al. 2009, Junker et al. 2013).

Phylogenetic redundancy can mitigate the adverse effects that pollinator loss have on wild plant-pollinator communities (Memmott et al. 2007, Potts et al. 2010). Changes in temperature and land-use will not act on all species uniformly (González-Varo et al. 2013) and some pollinators will be differentially vulnerable. Consequently, predicting the disruption of pollination service is difficult. One way to ensure pollination success is to increase the number of pollinator species visiting a given plant (Blüthgen and Klein

2011, Brittain et al. 2013). Increasing the number of pollinator species also increases the likelihood that the suite of pollinators visiting a given plant is phylogenetically diverse, or phylogenetically complementary. Thus, due to the differential response of pollinators to disturbances, plant species with phylogenetically diverse pollinators will be less vulnerable to losses of pollinators than plant visited by less phylogenetically diverse pollinators.

Phylogeny can explain morphological characters in plants and pollinators (Johnson et al. 1998), thus, phylogenetic distance should be used when analyzing plant-pollinator interactions. For instance, among pollinators, how does phylogenetic distance correlate with the suite of plant species that the pollinators visit? We may expect co-occurring, closely related pollinators to differentiate plant visitation to minimize intra-clade competition. While we may expect closely related pollinators that occur at *different* times to share plant clades they visit. If phylogenetic relatedness among pollinators or plants is strongly related to the types of visits or visitors, phylogenetic can increase biodiversity while ensuring pollination services.

Based on previous population-level studies, evolutionary history may inform expectations of pollinator phylogenetic diversity. Some plant families receive visits from a wide number of pollinator species, such as Asteraceae, while other families, such as Orchidaceae generally have low diversity of visiting species (Johnson and Steiner 2000). Evolutionary lineage is also used to explain high correlations between certain plant species and groups of pollinators, such as orchids and bees (Pauw 2006). Furthermore, functional trait clustering within a community, such as bumblebee proboscis length, is strongly correlated with phylogenetic clustering (Harmon-Threatt and Ackerly 2013),

which suggests traits that explain pollinator visitation patterns may be conserved within lineages. Despite population-level data of phylogenetic patterns of visitation, at the community level, closely related pollinators were not more likely to visit the same plant species (Rafferty and Ives 2013). One problem with inferences made from populations is the influence of plant community composition and relative species abundance on visitation patterns. Thus far, only a handful of studies have considered phylogeny to explain plant-pollinator interactions (Rezende et al. 2007, Chamberlain et al. 2014).

All of the results presented in this dissertation serve as a reminder that the conservation of wild pollination services is still a daunting challenge. The Mongolian steppe is one of the largest areas of contiguous grassland ecosystems in the world. This work was carried out in an area that has been disproportionately impacted by climate change (Namkhajantsan 2006) while the terrestrial system is undergoing extensive land-use change (Morris and Bruun 2005, Batima et al. 2008). Since 2002, there has been an astonishing 12% reduction in grassland vegetation that coincided with the increase in animal herd sizes used for agriculture (Hilker et al. 2014). The Eurasian grasslands face grave challenges to maintain all of their ecosystem services.

Our work shows the considerable variation in pollination services across space and different temporal scales. The vulnerability of networks is not consistent through space and time, with groups of pollinators differentially influencing the network stability. Furthermore, while the cessation of grazing resulted in changes to the community composition of plants and pollinators, the absolute number of visits made to the plant community did not change. Broadly, these results suggest that perturbations may not uniformly affect pollination services. Further studies should incorporate the natural

spatial and temporal variation of plant and pollinator communities to fully account for vulnerabilities in a vital ecosystem service.

CONCLUSION

My dissertation research focuses on accounting for “hidden” sources of variation within plant-pollinator networks. To do this, I compiled spatially and temporally structured datasets of plant-pollinator interactions in northern Mongolia. I first documented the spatial and temporal variation in community composition of plants and pollinators. I also tested the relationship between biotic factors, flower abundance and total number of visits, and air temperature. I then examined the spatial and temporal variation of two network indices that represent components of stability: specialization and nestedness. Finally, I studied how the cessation of grazing altered the plant and pollinator communities. In the historically grazed lands of Mongolia, the cessation of grazing, which may occur through land abandonment, is the likely land-use change that the steppe faces. I compared the plots where grazing was excluded with the plots where grazing was allowed to continue.

My primary findings of my dissertation research are:

1. The influence of temperature on pollinator visits is dependent upon the position within a landscape, even locally. On the Upper slope, both air temperature and flower abundance equally explained flower visits to the forb community while on the Lower slope only air temperature was important.
2. Diptera visitors to flowers form a core functional group of pollinators that is positively associated with network nestedness. Nestedness is positively associated with resistance to the collapse of plant-pollinator networks when species are

removed from the network. Hymenoptera visitors to flowers form a core functional group of pollinators that is positively associated with network specialization. Specialization is negatively associated with network stability.

3. Due to the spatial and temporal variation in the community composition and abundance of plants and pollinators, Hymenoptera visitors of flowers may be considered network “cheaters.” This is because Hymenoptera pollinators in our system are specialists, which destabilizes the network but allows them to efficiently forage.
4. The cessation of grazing, while altering the community composition and abundance of plants and pollinators, does not alter the total number of visits a foraging community receives.

APPENDIX

Appendix A: Chapter One

Table A.1: Start and end dates for each observation round.

Round	Start Date	End Date
1	13-Jun-2011	17-Jun-2011
2	20-Jun-2011	23-Jun-2011
3	24-Jun-2011	26-Jun-2011
4	01-Jul-2011	04-Jul-2011
5	06-Jul-2011	09-Jul-2011
6	14-Jul-2011	17-Jul-2011
7	20-Jul-2011	23-Jul-2011
8	25-Jul-2011	28-Jul-2011
9	30-Jul-2011	02-Aug-2011
10	04-Aug-2011	07-Aug-2011
11	09-Aug-2011	11-Aug-2011

Table A.2: Flower abundance for each plant family and insect visits for each order on the Lower and Upper slope. Numbers reflect total flower abundance or insect visits observed across the entire season for all plots within each slope.

	Lower Slope	Upper Slope
Plant family (floral abundance)		
Apiaceae	3,014	484
Asteraceae	4,946	10,503
Boraginaceae	113	109
Brassicaceae	N/A	337
Caryophyllaceae	974	684
Dipsacaceae	348	N/A
Fabaceae	517	5,953
Gentianaceae	51	N/A
Iridaceae	3	32
Lamiaceae	7,372	1,912
Liliaceae	N/A	2,189
Orobanchaceae	N/A	3,141
Plantaginaceae	3,805	N/A
Ranunculaceae	2,825	1,047
Rosaceae	993	376
Rubiaceae	3,438	N/A
Insect order (visits)	Lower Slope	Upper Slope
Coleoptera	6	0
Diptera	250	31
Hymenoptera	233	324
Lepidoptera	84	18
Air Temperature (°C)	Lower Slope	Upper Slope
Minimum	6.382 [^]	5.668 [^]
Maximum	34.863 [#]	32.201 [#]

[^] Round 5, Period 1; [#] Round 6, Period 3. For specific dates, please see Table A.1.

Table A.3: Total flower abundance for each observation Round. Plots were observed in northern Mongolia in 2011 spanning June to August. For exact dates, please see Table A.1.

Round	Floral Abundance	
	Lower	Upper
1	1,194	1,886
2	1,642	1,601
3	7,68	1,289
4	2,298	2,155
5	5,153	2,620
6	7,282	2,892
7	4,424	4,307
8	2,606	4,285
9	1,814	3,307
10	761	1,777
11	457	648
Total	28,399	26,767

Table A.4: Mean diurnal (\pm SE) air temperature for observations plots on the Lower and Upper slope. Air temperatures were recorded by HOBO recorders (Pro v2; Onset Computers, Bourne, MA, USA). The air temperatures were averaged among all plots within each slope location for each round. For specific dates, please see Table A.1.

Round	Mean Air Temp °C \pm SE	
	Lower Slope	Upper Slope
1	18.2 \pm 0.1	18.7 \pm 0.2
2	17.6 \pm 0.1	17.9 \pm 0.2
3	16.8 \pm 0.2	16.9 \pm 0.2
4	19.1 \pm 0.1	18.1 \pm 0.3
5	15.7 \pm 0.1	14.6 \pm 0.3
6	24.5 \pm 0.1	24.7 \pm 0.3
7	20.6 \pm 0.1	19.4 \pm 0.2
8	15.8 \pm 0.1	14.5 \pm 0.2
9	20.5 \pm 0.1	19.3 \pm 0.2
10	18.5 \pm 0.2	17.5 \pm 0.2
11	16.9 \pm 0.1	15.7 \pm 0.1

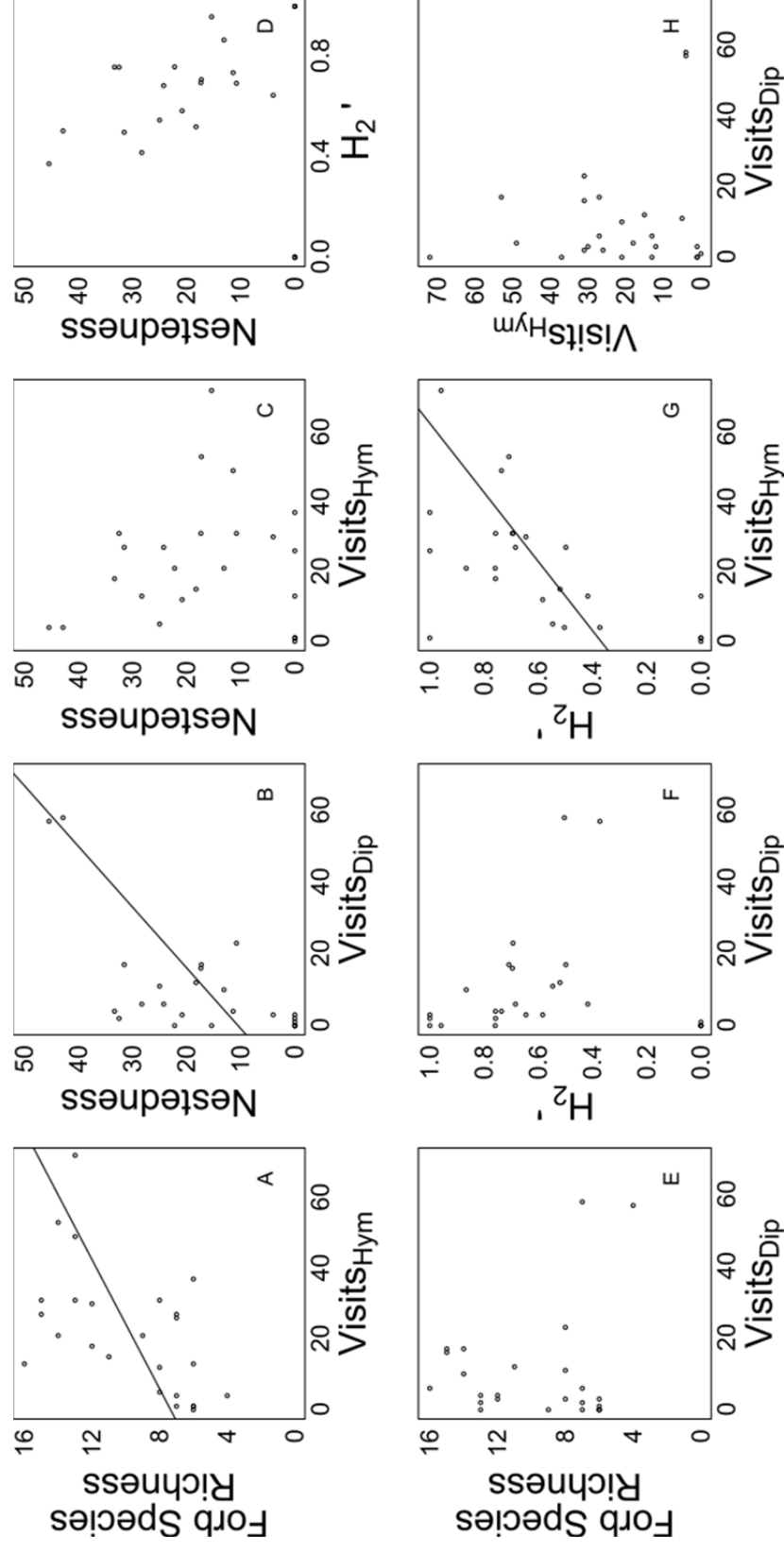
Appendix B.1: Example data compiled into matrix form for network analysis. Each cell value represents the number of interactions observed between each pollinator genera (columns) and plant species (rows).

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Appendix B.2: Simple linear regression of network indices, richness, and number of visits. Results from analysis of causal and correlative variables from the path model: forb species richness, the number of flower visits made by Hymenoptera ($\text{Visits}_{\text{Hym}}$) and Diptera ($\text{Visits}_{\text{Dip}}$), and two plant-pollinator network metrics: specialization (H_2') and nestedness (NODF).

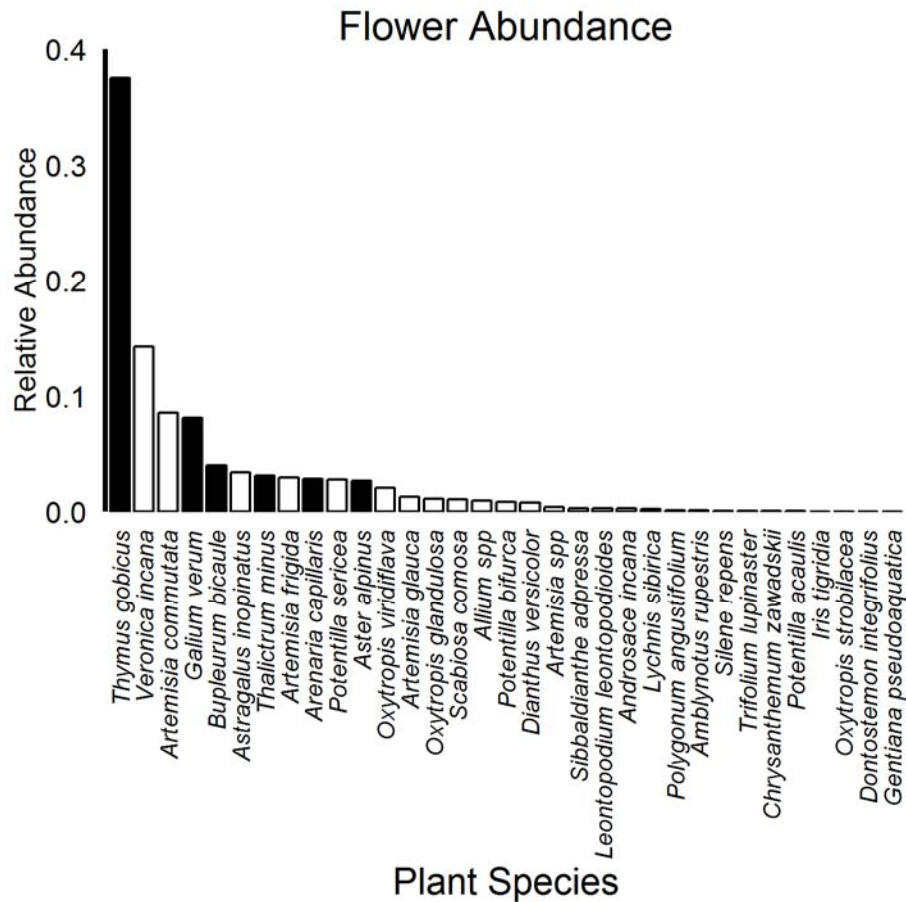
Independent variable	Response Variable	Estimate	SE	R^2	Adjusted R^2	F	df	p-value
Forb richness	$\text{Visits}_{\text{Hym}}$	0.109	0.03512	0.2969	0.2663	9.71	1,23	0.004858
Forb richness	$\text{Visits}_{\text{Dip}}$	-0.03497	0.04787	0.02268	-0.01982	0.5336	1,23	0.4725
$\text{Visits}_{\text{Dip}}$	Nestedness	0.5901	0.1416	0.4302	0.4054	17.37	1,23	< 0.001
$\text{Visits}_{\text{Hym}}$	H_2'	0.010088	0.002939	0.3387	0.3099	11.78	1,23	0.002275
Nestedness	H_2'	4.295	9.318	0.009152	-0.03393	0.2124	1,23	0.6492
$\text{Visits}_{\text{Hym}}$	$\text{Visits}_{\text{Dip}}$	-0.2234	0.2365	0.03734	-0.00451	0.9821	1,23	0.03547
$\text{Visits}_{\text{Hym}}$	Nestedness	-0.2403	0.16219	0.000954	-0.04248	0.02196	1,23	0.8835
$\text{Visits}_{\text{Dip}}$	H_2'	-0.0014	0.004169	0.004885	-0.03838	0.1129	1,23	0.7399

Appendix B.3: Relationship between network indices, pollinator visits, and species richness. Scatterplots showing the relationship between (A) Hymenoptera visits (VisitsHym) and forb species richness, (B) Diptera visits (VisitsDip) and network nestedness, (C) Hymenoptera visits and network nestedness, (D) network specialization and nestedness, (E) Diptera visits and forb species richness, (F) Diptera visits and network specialization, (G) Hymenoptera visits and network specialization, and (H) Diptera and Hymenoptera visits. Best fit lines are drawn for correlative or causal relationships that were found to be significant by path analysis (Figure 2.4). For simple regression statistic results, see Appendix B.2.

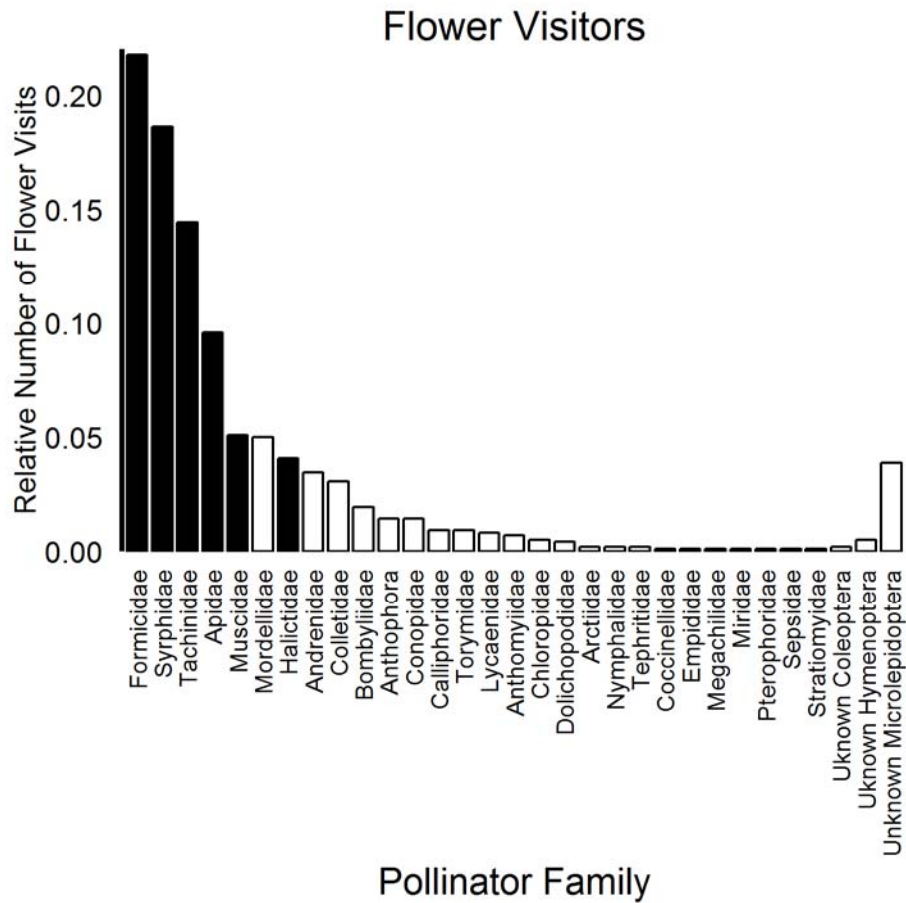


Appendix C: Chapter Three

Appendix C.1: Relative forb flower abundance of the forb species found in treatment plots. Filled in bars indicate the six species with the highest average correlation with the first two CAP axes of the forb community level analysis.



Appendix C.2: Relative number of visits, grouped by insect family and morphologically similar unidentified insect flower visitors. Filled in bars indicate the six families with the highest average correlation with the first two CAP axes of the flower visitor community level analysis.



Appendix C.3: Effects of grazing and time on flower abundance. The results are from an ANOVA of the total flower abundance for six forb species. The main effects included were Treatment (two levels: Grazed and Ungrazed), Period (three levels: morning, midday, late afternoon), and Round (six sampling points throughout the summer). Interaction terms were not included in the model due to missing data. Corrected p is the p -value after sequential Bonferroni adjustment (number of comparisons = 6), respectively.

Plant species		Round	Period	Treatment
<i>Arenaria capillaris</i>	SS	129.571	1.913	1.937
	df	3, 111.08	2, 111	1, 111.15
	F	31.0268	0.6656	1.3805
	p	<0.0001	0.516	0.2425
	Corrected p	<0.0001	1	1
<i>Aster alpinus</i>	SS	165.056	0.914	1.204
	df	3, 83.795	2, 83.195	1, 85.978
	F value	25.7247	0.1977	0.5656
	p	<0.0001	0.821	0.454
	Corrected p	<0.0001	1	1
<i>Bupleurum bicaule</i>	SS	68.231	1.493	5.608
	df	3, 90.226	2, 89.222	1, 89.949
	F	15.3038	0.4581	3.8476
	p	<0.0001	0.63396	0.05291
	Corrected p	<0.0001	1	0.31746
<i>Galium verum</i>	SS	145.57	0.69	106.91
	df	4, 24.999	2, 24.999	1, 24.999
	F	1.8038	0.0036	5.2144
	p	0.15967	0.9964	0.03117
	Corrected p	0.95802	1	0.18702
<i>Thalictrum minus</i>	SS	108.049	1.078	37.794
	df	3, 46.232	2, 45.823	1, 48.241
	F	16.2704	0.3615	18.119
	p	<0.0001	0.6986	<0.0001
	Corrected p	<0.0001	1	<0.0001
<i>Thymus gobicus</i>	SS	3691.1	9.2	1258.2
	df	4, 74.04	2, 73.746	1, 75.617
	F	31.874	0.086	39.475
	p	<0.0001	0.9179	<0.0001
	Corrected p	<0.0001	1	<0.0001

Appendix C.4: Variance for the random effects. The table lists the percent of variance component for Plot and the Residual from the ANOVA presented in Appendix C.3.

Plant species	Plot	Residual
<i>Arenaria capillaris</i>	55.22%	44.78%
<i>Aster alpinus</i>	30.89%	69.11%
<i>Bupleurum bicaule</i>	16.43%	83.57%
<i>Galium verum</i>	0%	100%
<i>Thalictrum minus</i>	66.53%	33.47%
<i>Thymus gobicus</i>	67.08%	32.92%

Appendix C.5: Effects of grazing and time on pollinator visits. The results shown are from an ANOVA of the total flower abundance for six forb species. See Appendix C.3 for further explanation of the analysis and model terms.

Insect family		Round	Period	Treatment
Apidae	SS	0.73264	0.09177	0.08567
	df	2, 34.614	2, 34.679	1, 35.328
	<i>F</i>	1.36084	0.18091	0.8353
	<i>p</i>	0.2698	0.8353	0.5598
	Corrected <i>p</i>	1	1	1
Formicidae	SS	4.0286	0.06	0.088
	df	5, 91.267	2, 89.457	1, 92.979
	<i>F</i>	3.9382	0.1729	0.4402
	<i>p</i>	0.002804	0.841503	0.508671
	Corrected <i>p</i>	0.016824	1	1
Halictidae	SS	1.09686	0.03385	0.00418
	df	4, 17.164	2, 17.639	1, 16.574
	<i>F</i>	17.164	17.639	16.574
	<i>p</i>	1.60533	0.11026	0.03138
	Corrected <i>p</i>	0.2182	0.8962	0.8616
Muscidae	SS	1	1	1
	SS	0.47478	0.19704	0.49024
	df	4, 27.989	2, 27.989	1, 27.989
	<i>F</i>	1.2311	1.5083	7.0743
	<i>p</i>	0.32027	0.23874	0.01279
Syrphidae	Corrected <i>p</i>	1	1	0.07674
	SS	0.58792	0.80428	0.36812
	df	5, 88.972	2, 88.972	1, 88.972
	<i>F</i>	1.2189	4.0882	3.5615
	<i>p</i>	0.30692	0.02002	0.0624
Tachinidae	Corrected <i>p</i>	1	0.12012	0.3744
	SS	4.1998	0.0199	0.0315
	df	5, 56.298	2, 56.481	1, 56.834
	<i>F</i>	8.0248	0.0855	0.3009
	<i>p</i>	< 0.0001	0.9182	0.5855
	Corrected <i>p</i>	< 0.0001	1	1

Appendix C6: Variance components for random effects. The table lists the percent of variance component for Plot and the Residual from the ANOVA presented in Appendix C.5.

Insect family	Plot	Residual
Apidae	22.08%	77.92%
Fomicidae	0.22%	99.78
Halictidae	18.54%	81.46%
Muscidae	0	100
Syrphidae	0	100
Tachinidae	18.12%	81.88%

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