



## AN ABSTRACT OF THE THESIS OF

Vera W. Pfeiffer for the degree of Master of Science  
in Geography presented on June 1, 2012

Title: Influence of Spatial and Temporal Factors on Plants, Pollinators and Plant-pollinator Interactions in Montane Meadows of the Western Cascades Range

Abstract Approved: \_\_\_\_\_

Julia A. Jones

### Abstract

Montane meadows comprise less than 5% of the landscape of the western Cascades of Oregon, but they provide habitat for diverse species of plants and pollinators. Little is known about plant-pollinator network structure at these sites. This study quantified plant-pollinator interactions over the summer of 2011, based on six observations of 10 permanent subplots in 15 meadows, stratified by size and isolation. The study examined (1) relationships between richness and abundance of flowers, pollinators, and interactions; (2) distribution of abundance and richness of flowers, pollinators, and interactions with regards to surrounding meadow habitat; (3) change in flower and pollinator abundance over the season; (4) factors associated with the presence of various guilds of pollinators; and (5) the structure of plant-pollinator networks. The study showed that (1) richness of pollinators increased 2x faster than

richness of flowers with increased abundance; (2) density of flowers and interactions was positively correlated with meadow size and diversity of pollinators and interactions were both correlated with surrounding habitat at two spatial scales; (3) peak flower abundance coincided with or preceded peaks in pollinator populations; (4) abundance of three guilds of bees exhibited different patterns of association to surrounding habitat and meadow soil moisture corresponding to various dispersal potential and phenology of guild species; and (5) the number of network pairings for plants and pollinators increased with increasing species richness of potential interaction partners and all networks were found to be significantly nested. Results of this study indicate that plant-pollinator networks are complex assemblages of species, in which spatial and temporal patterns of habitat affect species composition and network structure. In particular, flower and pollinator abundance and richness are depressed in small and isolated meadows. Significant nestedness emerged as a pattern of network level organization across the study meadows.

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Influence of Spatial and Temporal Factors on Plants, Pollinators and Plant-pollinator  
Interactions in Montane Meadows of the Western Cascades Range

by  
Vera W. Pfeiffer

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Vera W. Pfeiffer, Author

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## CONTRIBUTION OF AUTHORS

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**TITLE:** Influence of Spatial and Temporal Factors on Plants, Pollinators and Plant-pollinator Interactions in Montane Meadows of the Western Cascades Range

## **CHAPTER 1 INTRODUCTION**

Building on concepts of island biogeography and landscape ecology, ecological research has increasingly emphasized the effects of habitat composition and spatial configuration on ecological processes. However, relatively few studies have focused on plant-pollinator interactions, despite their enormous importance to native and managed ecosystems. Animal-mediated pollination supports flowering plants in almost every ecosystem on earth (Ghazoul 2005). While self-compatibility is widespread, many wild plants rely upon insect pollinators to produce fruit and seed. Most wild plant populations (62-73% of those investigated), showed evidence of pollination limitation or the circumstance under which more pollinators results in more seeds produced. For pollinator visitation not only facilitates transfer of outcrossed conspecific pollen, but also increase the total quantity of pollen deposited upon floral stigmas, both of which increase fruit and seed production in plant populations (NRC 2007). In ecosystems undergoing human-development, research has revealed parallel declines in associated plant-pollinator systems; and greater declines for plant species reliant upon out-crossing from animal pollination relative to other plants. This finding suggests that habitat loss and fragmentation adversely affect pollination (Biesmeijer et al. 2006).

Widespread declines in pollinators have been observed beyond the most widely publicized declines in *Apis mellifera*, European honey bee associated with colony collapse disorder. While some bee species have not shown any potentially threatening trends, other native bees have also exhibited alarming patterns, bringing national attention to issues of pollination conservation. Four *Bombus* spp. have exhibited dramatic declines of up to 96% and geographic range contractions of 23-87%. High pathogen levels and low genetic diversity have been recorded within these declining populations. Assessment of potential causal factors is lacking, partially due to the difficulty of locating wild *Bombus* colonies (Cameron et al. 2011).

Not only abundance of pollinators are important to alleviate pollination limitation, but evidence exists for improvement of pollination quality from pollinator diversity for certain floral morphologies (Hoehn 2008). The quality of strawberries (*Fragaria* sp.) is affected by the composition of the pollinator community, requiring large and medium sized apoids for pollination of the top pistols, and small apoids for the bottom and sides, though the pollen quantity delivered by single visits by each bee did not differ (Chagnon et al. 1993).

Three principal themes pervade the existing, sparse literature regarding plant-pollinator interaction biogeography: (1) effects of habitat size and isolation on richness and abundance; (2) the structure and dynamics of plant-pollinator interaction networks; and (3) the diverse roles of “guilds,” subsets of pollinator species with similar life histories. This research undertaking compares plants, pollinators, and plant-pollinator interactions surveyed across fifteen montane meadows in the western

Cascades to better understand the following research questions (1) Do species richness, evenness, and diversity increase corresponding to increased meadow size and meadow proximity for plants, pollinators, and plant-pollinator interactions, and at which spatial scales? (2) How do flower and pollinator density, timing, and the presence of particular pollinator guilds respond to soil moisture in the study meadows and surrounding landscape? (3) How does the structure of plant-pollinator networks compare across montane meadows representing a gradient of size, meadow proximity, and soil moisture?

## **CHAPTER 2 THE EFFECTS OF SURROUNDING HABITAT ON PLANT, POLLINATOR AND INTERACTION ABUNDANCE AND RICHNESS**

Vera Pfeiffer, Julia Jones, Andy Moldenke, Matt Betts

In preparation for journal submission

## ABSTRACT

Montane meadows comprise less than 5% of the landscape of the Western Cascades of Oregon, but they provide habitat for diverse species of plants and pollinators. This study quantified plant-pollinator interactions over the summer of 2011, based on six observations of ten permanent subplots in fifteen meadows, stratified by size and isolation. The study examined: (1) relationships between richness and abundance of flowers, pollinators, and interactions; (2) abundance and diversity of flowers, pollinators, and interactions and their relationship to meadow size and the amount of meadow area within 3 km; and (3) abundance of several bee guilds based on meadow size and surrounding meadow area. The study showed that: (1) richness of pollinators increased two times faster than richness of flowers with increased abundance; (2) density of flowers and interactions was positively correlated with meadow size, and diversity of pollinators and interactions was correlated with the amount of surrounding meadow at multiple spatial scales; and (3) *Apis mellifera* abundance was positively associated with high amounts of meadow within 1500 m, whereas *Bombus* spp. were limited in the most extensive meadow complex. The amount of surrounding meadow area, rather than the amount of meadow available nearby, was related to plant-pollinator community richness at multiple spatial scales, emphasizing the variability of pollinator dispersal capacity and landscape scale habitat requirements of pollinator species.

## INTRODUCTION

Island biogeography theory posits that larger islands of habitat will support more abundant populations and greater species richness. Local population extinction rates decrease with the greater population sizes generally supported by larger habitat islands, and the arrival of new species increases when surrounding habitat is in closer proximity. Species richness is predicted to increase with increased habitat within the spatial scales related to the phenomena described above (MacArthur and Wilson 1967). In hills occupied by native shrub and herb species that are “islands” in a sea of intensive cultivation in the Argentine Pampas, plants, pollinators, and plant-pollinator interaction richness increased with increasing hill area and to a lesser extent, increased habitat in the surrounding matrix based on a distance weighted patch model (Sabatino et al. 2010).

Different species utilize habitat at different spatial scales based on species- and landscape-specific foraging behavior. Re-colonization events also take place across variable isolation distances based on species-specific dispersal potential. Pollinator communities are composed of highly diverse species known to possess highly variable dispersal potential (Ricketts et al. 2008, Zurbuchen et al. 2010, Carvell et al. 2012). Landscape-specific characteristics such as the proximity of floral resources have been shown to affect flower-visitors, as foraging range and efficiency of pollinator species decreases with increased foraging distance (Zurbuchen et al. 2010, Carvell et al. 2012).

Ricketts et al. (2008) conducted a meta-analysis to assess the response of native pollinators dominated by bees to habitat based upon 23 studies of 16 crops over 5 continents. They found a significant decrease in visitation rate to 50% of maximum visitation at 0.6 km from defined habitat, and a 50% decrease in pollinator richness 1.5 km from defined habitat. Richness declines at more distant scales than visitation frequency, because richness only requires the presence of one individual, while visitation rates are a quantitative measure of abundance.

Pollinator “guilds” have been shown to respond to the amount of surrounding habitat at different spatial scales. Visitation by *Bombus* spp. and *Apis mellifera* to an experimentally positioned array of six flower species was found to be unrelated to the amount of local habitat in previous literature, but solitary bee abundance was positively correlated to the amount of habitat within 750 m radius in the surrounding matrix; this study was conducted in intensively managed farmland with patchily distributed natural habitat in Germany (Steffan-Dewenter 2002). In a colony-specific foraging distance study, Carvell et al. (2012) estimated average foraging distances of 750 m - 775 m for two *Bombus* species.

This study quantified plant-pollinator interactions over the summer 2011, based on six observations of 10 permanent subplots in 15 meadows, stratified by size and isolation. The study tested the following hypotheses (1) abundance of flowers and interactions increase with increasing surrounding habitat at near spatial scales (2) richness, evenness and diversity of surveyed flowers, flower and pollinator presence in the network, and plant-pollinator interactions increase with increased surrounding

meadow habitat. The abundance, richness, evenness and diversity of communities were compared with meadow size, weighted proximity, and amount of surrounding habitat at eight spatial scales (250 m to 3000 m) to identify the scales of greatest relevance to populations in this study system.

## METHODS

### *Study site description*

Non-forest habitat in the western Cascades is composed of conifer sapling fields, broad-leaved shrub fields, and mesic and xeric herb-dominated meadows (Swanson and James 1975). Fluvial, glacial, and mass movement processes have created a steeply sloped, deeply dissected landscape within the past four million years. Fire is an important disturbance processes responsible for creating some ephemeral non-forest habitat. The past century of fire suppression has resulted in widespread loss of non-forested habitat. It is likely that non-forested habitat comprises a smaller proportion of the landscape than ever before in this region under this climatic regime. Non-forest patches shrunk from 5.5% to 2.5% of the landscape between 1946 and 2000 (Takaoka and Swanson 2008). Highland (2011) found that the highest proportion of montane meadow was lost at Carpenter Mountain Complex among the HJA meadow complexes (Carpenter, Frissell/M2 and Lookout). A sizable amount of habitat was lost at Lookout Mountain as well, while the M2/Frissell complex maintained more stable habitat abundance. Rice (2009) found that Bunchgrass

meadows, the smallest complex included in the study with virtually no surrounding meadow area experienced a similar rate of meadow loss to Lookout Mountain. The largest meadow complex, Cone Peak, likely exhibits the least proportional meadow loss, though this complex lies outside the extent of past meadow analyses.

Sampling was conducted in five central western Cascades montane meadow complexes between Cone Peak ( $44^{\circ}24'32''$  N,  $122^{\circ}08'02''$  W) and Lookout Mountain ( $44^{\circ}12'15''$  N,  $122^{\circ}07'50''$  W). All study meadows were located west of the High Cascades Crest at elevations above 1000m. The study region experiences a maritime climate defined by warm dry summers, and mild, wet winters. Approximately 70% of precipitation falls from November to March (Takaoka et al. 2008). A seasonal snowpack develops above 1000m and melts on south-facing slopes before north-facing slopes. The study meadows are bordered by forests of the Pacific silver fir zone (Franklin and Dyrness 1988). Mesic and xeric meadows occur throughout this matrix (Franklin and Halpern 1999).

### *Meadow Selection*

Fifteen study meadows were chosen from the five meadow complexes in a stratified-random design. Sampled meadows were stratified by size (large, small) and meadow complexes were stratified by isolation; one large meadow and two small meadows were randomly chosen from each complex, except in the case of Lookout Mountain and Carpenter Mountain meadows. Only one small meadow was chosen on

Lookout Mountain because of sampling limitations. The extra meadow was replaced with another randomly selected meadow on Carpenter Mountain. All meadows were located within a 1 hour hike to the sampling site. Four meadow complexes were located along the crest of the western (older, lower Cascades) from Cone Peak to Lookout Mountain. The fifth meadow complex was located on the western slope of the eastern (younger, high) Cascades.

#### *Field sampling*

Plant and pollinator interactions were surveyed within these 15 study meadows throughout the 2011 growing season. Meadows were visited 5-6 times during the summer between 13 July – 13 September. In each meadow, two parallel 60m transects were located along the long axis of the meadow. The two transects were spaced 20m apart and centered at the midpoint of the meadow length, then width. Five permanent 3 x 3m plots were placed at 15-m intervals along each of these transects (ten plots total). Thus, the sampled area was 90 m<sup>2</sup> in each meadow within a 1,200 m<sup>2</sup> central rectangular zone irrespective of meadow size. This standardized area method was chosen so that the same area would be sampled in all meadows. If plots were placed randomly around the meadows, the greater spatial extent surveyed in larger meadows would likely contain more diverse species due to spatial-autocorrelation alone. This sampling effect could obscure the measurement of

community diversity. A map of the study area and plot structure is shown in Appendix A (Figure A6).

#### *Plant-Pollinator Survey design*

##### Flower sampling

All flowering plants were identified and counted within each 3m x 3m plot. The number of stalks was counted, and the number of flowers was counted on each stalk (up to ten stalks per plant species). Flower abundance was estimated by multiplying the number of stalks by the number of flowers per stalk. Compact inflorescences (Asteraceae) were counted as one flower. If plant species could not be identified at least one individual plant was collected for identification in the lab. This method is similar to past protocols in published literature (Sabatino 2010).

##### Pollinator sampling

A fixed-area plant-pollinator interaction watch was conducted on each plot for a period of 15 minutes on each sampling date, with a maximum of 75 minutes of watch per plot over the sampling period (15 minutes per date \* 6 dates). Each meadow was sampled for a maximum of 150 minutes per visit (15 minutes per plot \* 10 plots) and 750 minutes (12.5 hrs) equaling six observation rounds over the sampling period, for a maximum grand total of 11,250 minutes (187.5 hr).. This method is similar to

protocols in the literature (Sabatino 2010). For each minute, the observer systematically scanned the 3m x 3m area for small and large pollinators and recorded (a) the weather: sunny or cloudy, and windy or not windy (b) all visits by a particular pollinator species to a particular flower species including both the pollinator species and plant species on the datasheet. A ‘visit’ was defined as contact between the potential pollinator and the reproductive part of the flower. If no interactions occurred a 0 was recorded for that watch minute. If multiple interactions occurred each pollinator to flower species pair was recorded once, an individual may be entered twice during a minute if it visited multiple species of flower. If more than one individual of a given pollinator species was observed in the plot during a watch minute, each individual was recorded separately. When possible, the number of interactions between each plant species-pollinator individual pair during the minute was recorded, but this was not possible during all peak visitation times so these individual frequency per minute data were not used in this study. Unidentified pollinators were captured in order to assure proper identification, then released if possible, or euthanized and transported back to the HJ Andrews headquarters for identification with the assistance of a reference collection, available regional keys, and expert advise (A. Moldenke). When no flowers were present in a permanent sample plot, that plot was skipped during the monitoring visits. This variability in floral blooms causes variation in total observed minutes, especially during the early and late sampling weeks, weather condition data and interaction rates are located in Appendix A (Tables A2, A3, A4, and A5).

## Omitted Data

Fifty-one observations were removed from the analyzed dataset; in these cases an interaction was recorded, but the pollinator was not identified and could not be sampled. The maximum minute omission count was four potential/unseen interactions per meadow per watch date. Total minutes watched in each meadow are shown in Appendix A (Table A4).

Additionally, 181 observed interactions (of 10,278 total observed interactions) were not captured and pollinators could only be identified by pollinator order. The interactions identified by order were not used in the richness, evenness, and diversity analyses, because it was unclear whether novel species were included in these groups.

## *Lab analysis*

### Plant Identification

Sampled insects and flowers were identified by Andy Moldenke (Faculty Botany and Plant Pathology, Oregon State University) and the pollinator network team (Alina Kanaski, Samantha Monier, Tiffany Harper, and Tim Luttermoser) with the help of species lists from the HJ Andrews Forest and Hitchcock and Cronquist (1969). When plants could not be identified by the data collection team in the field, the plants were sampled and pressed in order to identify them in the laboratory.

## Pollinator Identification

We attempted to capture all pollinators that contacted the reproductive structures of the plants located within the plot unless the pollinator was extremely common. Once we had samples of pollinator species on record, replicate pollinators of the same species were not sampled if they could be identified in the field. Pollinators were pinned in the lab, cataloged with capture location date and species identification and subsequently stored in the Oregon State University Arthropod museum. Species were identified by Dr. Andy Moldenke and pollination REU team using available insect keys.

### *Spatial data sources*

#### Aerial Photos

Meadow habitat estimates were obtained from a digital layer of meadow polygons created by Highland (2011) and expanded by Vera Pfeiffer to include the wider landscape surrounding HJA complexes, as well as the Bunchgrass and Cone Peak complexes from 0.5m resolution digital aerial imagery obtained in 2005 and available from Oregon Explorer ([www.oregonexplorer.net](http://www.oregonexplorer.net)). Natural montane meadows were distinguished from clear cuts and other non-forest patch types visually by their irregular border, light green/brown shade, and homogenous texture.

## Digital Elevation Model (DEM)

A 10m Digital Elevation Model (DEM) available from USGS was used to interpolate a three-dimensional surface to estimate meadow surface area. The area of steep meadows could be vastly underestimated using 2-dimensional area alone.

### *Spatial data analysis*

#### Meadow surface area

The Digital Elevation Model (DEM) was processed to estimate a three dimensional surface. First the DEM was processed by filling all sinks. The DEM was then converted to a Triangulated Irregular Network (TIN). The TIN was clipped using the meadow polygon file attained by digitizing the aerial photos. This meadow TIN was clipped at each desired buffer radius (250 m– 3000 m) around each study meadow using Model Builder, and multipatch files were built in ESRI ArcGIS v. 9.3 to determine meadow surface area (i.e. the sum of the area of all triangles in the TIN).

#### Meadow proximity index

Meadow habitat surrounding each sampled meadow was measured using a distance weighted patch technique. The proximity index weights the surrounding meadows or “habitat islands” based on their distance away from the study meadow.

Proximity index techniques use exponential decay estimated by a field measured dispersal factor specific to the species under consideration. In the Sabatino (2010) pollinator network study, a weighted distance measure was used based on dispersal measurements obtained from a meta-analysis of many diverse pollinator studies collected with a wide geographical distribution. In this case the dispersal information available predicts rather long dispersal rates, potentially irrelevant to many of our pollinators in the dense conifer forest matrix.

The meadow proximity index for pollinators is based upon a generalized dispersal kernel developed from observational studies, and unverified, because there are so many different species, and evidence of actual dispersal distances is scarce. The index used is:

$$\sum_{i \neq j} A^{(-\beta d_{i,j})}$$

(Sabatino et al. 2010)

Sabatino et al. (2010) uses the index to estimate surrounding habitat for pollinators in the Argentine Pampas, wild hills are their habitat islands in a matrix of cropland. Significant relationships with surrounding habitat are not observed, but plant, pollinator and interaction richness are positively related to the immediate hill size. The decay term is based on a rather high dispersal rate, so the meadow area does not decay rapidly. Sabatino et al. (2010) applied it to all meadow/hill area within the surrounding 10km radius. In our study sites the index correlates most closely with habitat within the surrounding 2000m radius.

Sabatino et al. (2010) chose this simple weighted distance model from a prominent proximity index review. In the base equation:

$$H_x = \sum_{i \neq x} A_i e^{-d_i/D}$$

( Winfree et al. 2005)

the term 1/D or  $\beta$  (Sabatino et al. 2010) is a mobility constant scaled to the study organism. Sabatino et al. (2010) used 0.46 from the Ricketts et al. (2008) meta-analysis of edge effects on bee abundance and diversity described above. It is based on 16 different agricultural crops in nine different countries (half tropical, half temperate), where the matrix is likely to be more penetrable than coniferous forest. At least one study didn't include natural habitat at all, which strongly supports overestimation of mobility from (real) habitat. The studies used in the metaanalysis did include quite a variety of insect pollinators, dominated by bees, but also considering flies, beetles etc. The model predicts a 50% decay in species richness with a distance of 1.5km.

Ricketts et al. (2008) discusses the mixed results concerning this estimate for pollinator dispersal and the response of pollinators to surrounding habitat in the introduction of the metaanalysis noting that while some studies have found affects, others have found no effect of surrounding habitat on pollinator populations. This is not unexpected given the diversity of pollinators and landscapes in question. There may be much different behavioral responses at play considering the focus of these studies on agricultural landscapes, rather than natural pollinator communities.

### *Statistical analysis*

#### Richness, evenness, and diversity

Species richness was calculated as the total number of species observed.

Rarified richness and Chao estimates of sample plot or site richness were also compared to better understand richness sampling and actual site species richness at each location. Rarified richness and Chao estimates were calculated in EstimateS and R statistical software (Colwell 2005, R Development Core Team 2006). These values are shown in Appendix C (Tables C1, C2, C3, and C4).

The diversity and evenness of flowers, pollinators and plant-pollinator interactions were described in each meadow using PIE evenness (Simpson diversity) and Shannon diversity statistics. Appendix C (Tables C1, C2, C3, and C4) exhibits these quantified indices for full season and peak season meadow data.

The evenness of the communities was estimated using the probability of an interspecific encounter or PIE index, also known as Simpson Diversity. This value ranges from 0 to 1 where high values indicate increased evenness or lack of dominance (Simpson 1949). The formula was named PIE by Hurlbert (1971) for use as an evenness metric (Baev and Penev 1995). Probability of an Interspecific Encounter (PIE or Simpson diversity) is calculated as follows:

$$PIE' = 1 - \sum_i p_i^2$$

where p is equal to proportion ith species at site.

Shannon diversity is probably the most commonly used diversity statistic (Shannon and Weaver 1949). Shannon diversity is more sensitive to species richness compared with the Simpson's diversity or PIE index.

$$H' = - \sum (p_i \ln p_i)$$

where s is the number of species at a site, n is the total number of individuals,  $p_i$  is the percentage of  $i^{\text{th}}$  species at a site, and  $n_i$  is the number of  $i^{\text{th}}$  species at a site.

### Statistical Assumptions and Transformations

The central limit theorem states that the variance around the mean is distributed normally for a sufficiently large sample size. When the sample size is small or moderate, the approximation provided by the central limit theorem may produce a confidence interval that does not cover the appropriate coverage probability. The sample size equaled 15 meadows in almost all cases. This moderate sample size obscures estimation of the true underlying distributions to assess whether the data may be skewed. Univariate normality is not required for the least squares estimates of regression parameters to be meaningful, however some transformations may help improve the statistical properties. Some of the independent and dependent variables used in this study cross multiple orders of magnitude. Log transformations were used to improve the symmetry of variance distribution for meadow area, meadow area in the surrounding matrix, species richness, species richness estimates, and interaction abundance. Log transformations also emphasize the effect of increased abundance at

low values more than high values, which represents an ecological hypothesis that increased habitat amount or increased accumulation of species richness and abundance are more important when the values are low. Evenness and diversity index values do not require any transformations.

## RESULTS

### *Plants, pollinators, and plant-pollinator interactions*

Flowers and plant-pollinator interactions were surveyed throughout the entire growing season in 15 meadows, each containing ten permanent survey plots. From the exhaustive flower survey data zero or eight to 40 flowering plant species were observed in the study meadows. Zero to 18 species of flower were blooming in the plots on any given watch day. On several occasions no flowers were blooming in the permanent plots and therefore no plots were observed to quantify pollination interactions. From the interaction data, full-season meadow networks ranged in size from 6 to 31 plant species, and 21 to 87 pollinator species per meadow. Across the season, 28 to 222 interactions were observed in the full season study meadow networks. Overall, 10,278 interactions were observed and recorded between 248 species of pollinators and 78 species of plants from 23 plant families (10,097 were identified to species or genus. 7,644 interactions occurred during the peak season during weeks 2-4. The most rich and abundant families were Asteraceae (14% of species and 31% of visits), Scrophulariaceae (12% and 10%), Rosaceae (10% and

4%), and Polemoniaceae, including *Gilia capitata* (8% and 19%). The five most visited flower species accounted for 51% of all interactions and the 15 most-visited flower species accounted for 81% of all interactions. All visitors were insects except for two species of hummingbirds *Calypte anna* and *Selasphorus rufus*. Assemblages of flower visitors were dominated by Hymenoptera (33% of species and 51% of visits) and Diptera (32% and 30%) of visitors; followed by Lepidoptera (13% and 5%), Hemiptera (11% and 3%), Coleoptera (9% and 10%), and Trochiliformes, Orthoptera, Thysanoptera, Araneae with (<1% and <1% each). The 10 most common flower visitors accounted for 68% of all visits. Only eleven pollinator species accounted for more than 1% of the total of all visits observed, while the remaining 245 flower visiting species accounted for less than 1% of the visits (1% = 103 visits). Across the networks, 1170 unique interactions were observed between identified plant and pollinator species. Network diagrams constructed for each meadow based on full season network interactions are presented in Appendix I.

**Table 1 Ten most common flower, pollinators, and interactions.** This table displays the ten most common flower, pollinators, and interaction based on the plant-pollinator network interaction dataset. Each included species or interaction is accompanied by the percentage of the total number of interactions in which they participated.

<b>10 Most Common Plants</b>	<b>Pollinators</b>	<b>Interactions</b>
<i>Gilia capitata</i> (18%)	<i>Bombus mixtus</i> (20%)	<i>A. mellifera &amp; G. capitata</i> (7%)
<i>Eriophyllum lanatum</i> (14%)	<i>Apis mellifera</i> (14%)	<i>E. hirtus &amp; E. lanatum</i> (5%)
<i>Erigeron foliosus</i> (7%)	<i>Eristalis hirtus</i> (9%)	<i>B. mixtus &amp; D. nuttallianum</i> (2%)
<i>Sedum spathulifolium</i> (5%)	<i>Bombus bifarius</i> (7%)	<i>B. major &amp; G. capitata</i> (2%)
<i>Ligusticum grayii</i> (5%)	<i>Epicauta puncticollis</i> (5%)	<i>B. mixtus &amp; S. spathulifolium</i> (2%)
<i>Achillea millefolium</i> (4%)	<i>Bombylius major</i> (4%)	<i>B. mixtus &amp; L. laxiflorus</i> (2%)
<i>Lupinus laxiflorus</i> (4%)	<i>Chrysotoxum fasciatum</i> (3%)	<i>A. mellifera &amp; E. lanatum</i> (2%)
<i>Delphinium nuttallianum</i> (4%)	<i>Bombus vosnesenskii</i> (2%)	<i>B. mixtus &amp; C. callilepis</i> (2%)
<i>Penstemon procerus</i> (3%)	<i>Coccinella trifasciata</i> (2%)	<i>E. puncticollis &amp; E. lanatum</i> (2%)
<i>Erigonium umbellatum</i> (3%)	<i>Eschatocerepis constrictus</i> (2%)	<i>C. fasciatum &amp; G. capitata</i> (2%)

Across the whole dataset of all recorded interactions, just over 20% (21 of 100 flower species) of surveyed flowers were not included in the interaction network; these flower species composed 5% of the watched flowers on the basis of flower abundance.

#### *Species and interaction richness*

Individual-based rarefaction was used to evaluate the richness per individual (versus richness per plot) of floral survey, network plant, pollinator, and interaction richness. Rarefaction curves were generated for each plot and for each meadow.

Chao richness estimates were also calculated based on the abundance of singleton and doubleton observations in the dataset. These estimates are included in Appendix C. These richness estimates were all highly correlated.

Individual-based rarefaction richness was highly correlated with richness per plot or richness density. Rarified richness equaled 95% of the value of plot floral richness. This shows the almost 1:1 increase in plot level floral richness and rarified species richness. Network flower rarified richness increased with increased network flower richness at both the plot level and the meadow level where correlation coefficients equaled 0.58 and 0.88. While richness estimates for pollinators were also correlated, Chao estimates for pollinators showed several very high pollinator richness estimates. These high estimates were often at plots with rather low abundance in meadows with high richness. This effect was diminished when data were assessed at the meadow level.

#### *Abundance and species richness*

Species richness accumulated with abundance at different rates for flowers, pollinators and interactions (Appendix D). Flower species richness in the plots increases by 1.7 times the natural log of total flower abundance in the plots or 3.1 times the floral abundance value based on the meadow level data. The relationships are best described using the logarithmic functions:  $y = 1.7 \ln(\text{abund})$ , ( $R^2 = 0.38$ ) and  $y = 3.1 \ln(\text{abund})$ , ( $R^2 = 0.13$ ) respectively. The quadratic equation had a worse fit for

this relationship, though it better describes pollinator and interaction richness as a function of abundance matching the steeper initial increase. The total flower richness values within the plots were much lower than the total meadow floral richness observations underscoring the importance of using meadow totals of all plots for estimation of sampled richness in the meadow community. Comparisons between abundance and richness in the network can be explored in Appendix D.

The relationship between network floral richness rises at 1.8 times the natural log value of network flower abundance based on the plot data and 3.4 times the natural log value of network flower abundance based on the meadow data. The logarithmic formula better fits this point distribution compared to the quadratic equation. On average four species of flowers per plot weren't observed to be visited, decreasing the network floral richness from the total floral richness dramatically at the plot level. Fifty percent of plots had four sp of flower not visited, and 99% had 10 or less not visited. In the full dataset only 20% of flower species were not visited composing 5% of the total watched flowers by abundance.

Pollinator richness increases rapidly at 4.1 times the natural log of pollinator abundance for the plot level ( $R^2 = 0.51$ ) and 9.8 times the natural log of pollinator abundance for the meadow level ( $R^2 = 0.44$ ), exhibiting a positive relationship. This is twice the rate observed for surveyed or network flowers.

The relationship between interaction richness and interaction abundance also increases very rapidly at 6 times the natural log of interaction abundance for the plot

level data and 20.8 times the natural log of interaction abundance for meadow level data.

#### *Abundance, richness, and diversity across the network*

Floral abundance and interaction abundance were positively correlated. Total interaction abundance equaled 67% the total surveyed floral abundance on average. Total floral abundance explains a significant amount of variation in interaction abundance ( $R^2 = 0.73$ ). Total plant richness explains a significant amount of variation in network plant richness ( $R^2 = 0.88$ ), and network plant richness increases almost 1:1 (90%) with total plot flower richness. Log pollinator richness increases by 1.2 times of log surveyed flower richness ( $R^2$  value = 0.15), overall network pollinator richness is higher than plant richness (Appendix D).

Interaction richness also increased with plant and pollinator richness. Pollinator richness values were higher than plant richness values and pollinator richness explained a larger proportion of the variation in interaction richness ( $R^2 = 0.97$  versus  $R^2 = 0.20$  or 0.05 for plants) at the meadow level. At the plot level the tight relationship between pollinator richness and interaction richness is even more visible. Interaction richness increases significantly with plant richness as well, but a great deal more variability exists at plots with intermediate plant richness values. Plant and pollinator Shannon diversity are also correlated with interaction richness. These plots show a high degree of variability across these positive relationships. Again

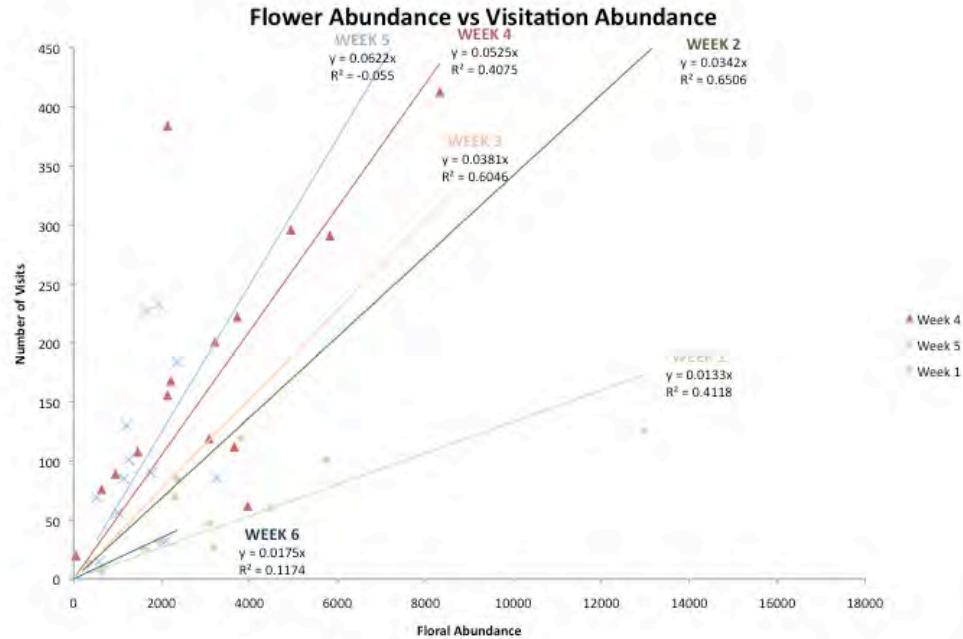
pollinator Shannon diversity is more significantly correlated to interaction richness than plant Shannon diversity.

*Richness, evenness, and Shannon diversity*

Richness, evenness, and diversity estimates were positively correlated for plants, pollinators, and interactions. None of the variables showed a tight 1:1 correlation so all three are used in subsequent analyses to describe varying community characteristics. Richness and evenness both explained more variance in Shannon diversity than richness vs evenness or vice versa because the Shannon diversity index is influenced by both richness and evenness. The highest variability in Shannon diversity exists at middle richness values.

*Flower abundance vs. interaction abundance across the growing season*

Flower abundance was significantly correlated to pollinator abundance throughout most of the season, however, this trend was most significant during the peak season (weeks 3 - 4).



**Figure 1 Flower abundance vs. visitation abundance through the season.** This figure shows the average visitation per floral abundance during each watch period based on the fifteen study meadows observed. Increased utilization of floral resources by pollinators is observed from week 1 to week 5. Both floral and pollinator abundance dramatically decline during the sixth observation period. Points marking the total floral abundance and interaction abundance for each meadow are shown for weeks 1, 4, and 5.

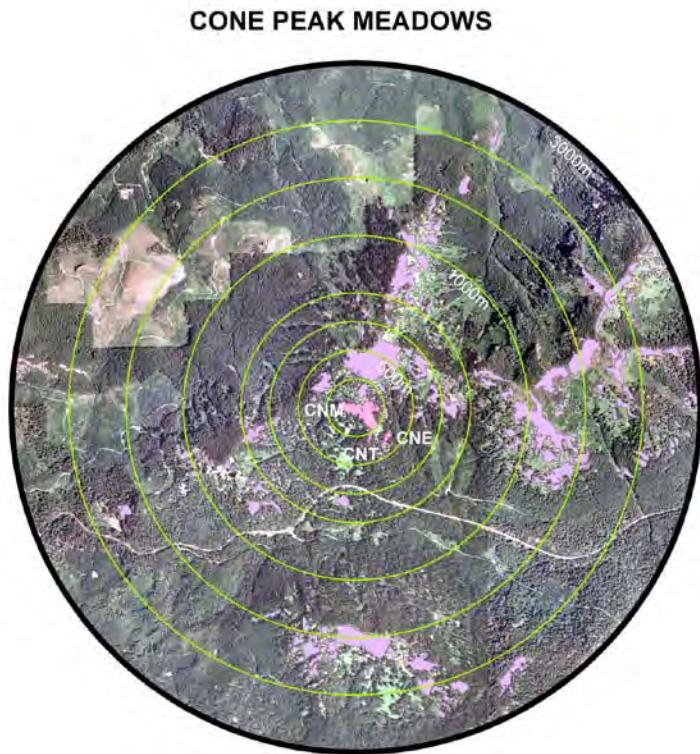
At the start of the study period during week 1, flower abundance increased more rapidly than pollinator abundance. The number of visits equaled 1% of the floral abundance. Pollinator abundance increased in week 2, at which time visitation frequency equaled 3% of the floral abundance. During week 3, visitation increased to 4% of floral abundance; by week 4, 5% of floral abundance, and by week 5, 6% of floral abundance on average although the average rate of increase did not significantly describe the data points. During week 6 there was a huge amount of variability also not described by the average trendline. The meadows which retained the highest

moisture during week 6 also had the highest visitation. During week 3 and 4, flower abundance explained pollinator visitation abundance with highly significant figures ( $R^2 = 0.67$ ,  $p = 0.0002$  and  $R^2 = .50$  and  $p = .003$ , respectively). This trend shows that pollinator abundance increased through the peak season to exploit the available floral resources at a greater rate. As floral resources declined at the end of the season, pollinators likewise could not be supported and died in all but the most moist meadows.

*Abundance, richness, evenness, and diversity as functions of meadow in the surrounding landscape*

Meadow flower, pollinator, and interaction abundance, richness, evenness, and diversity was compared to meadow size, meadow proximity index, and the amount of meadow area within each landscape sector to gauge the most relevant spatial scales of surrounding habitat for various groups within the network. These comparisons were made twice (1) using data from all site visits obtained across the season and (2) using data from the peak season weeks during which all meadows were visited. 7,644 of the 10,097 total interactions from which pollinators were identified to species or genus were observed during these peak weeks. All meadow peaks in plant-pollinator interactions occurred during this period except for Carpenter Basin, which peaked in week 5. Results from full season data and peak season data were very similar and can be observed in Appendix D3. The following tables show the correlation coefficients for comparisons between plant, pollinator and interaction abundance richness,

evenness, and diversity and meadow area in the surrounding landscape for meadow level data during the peak season. Accompanying figures display the  $R^2$  values for the landscape sectors only. Significant response to meadow size is noted beside the figure. The orange outline around an  $R^2$  data point in the charts following each table describe a significant relationship between amount of surrounding meadow within a landscape sector and the column variable ( $p < 0.05$ ), while the orange center indicates an almost significant response.

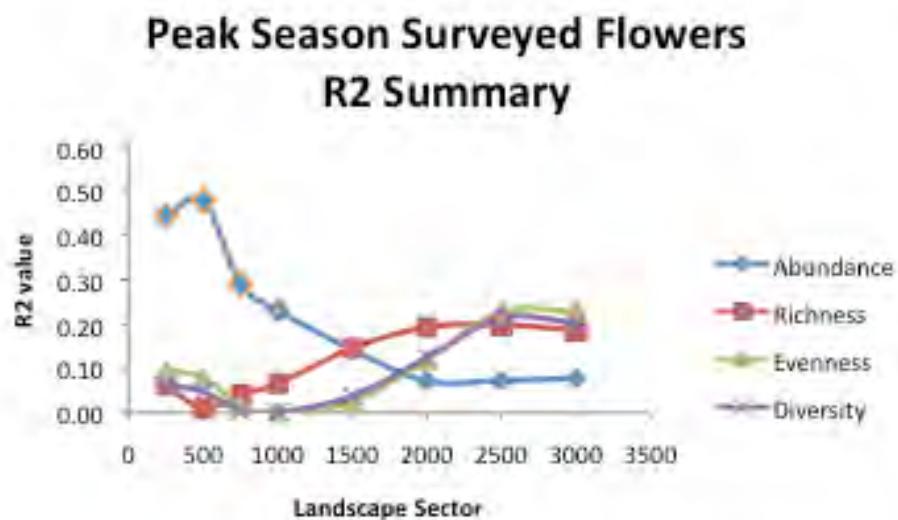


**Figure 2 Cone Peak Main 250 m – 3000 m landscape sectors.** The above figure shows terrain within the 3000m landscape sector surrounding Cone Main meadow. In the following analysis richness, evenness, and diversity are compared to the area within each landscape sector surrounding all the study meadows.

*Summary  $R^2$  values for amount of meadow area within each landscape sector vs. peak season data (weeks 2-4)*

**Table 2 Landscape sectors vs. surveyed flower peak season data.**  $R^2$  values and p values for linear models comparing the log value of the amount of meadow with the given landscape sector to the log abundance, log richness, evenness, or diversity values for the peak season data.

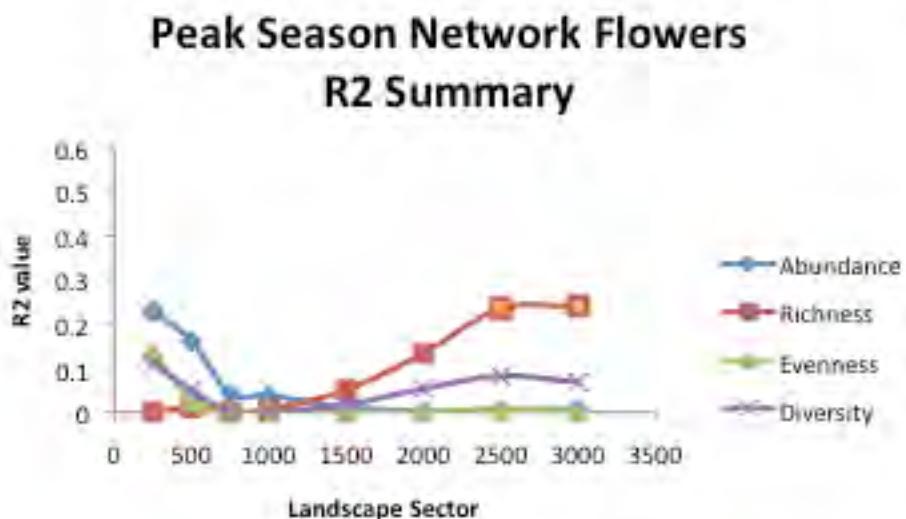
Landscape Sector (m)	Flower Abundance	Flower Richness	Flower Evenness	Flower Diversity
Meadow Size Meadow	0.49	0.01 **	0.08	0.31
Proximity 250	0.12	0.23	0.17	0.14
500	0.44	0.01 **	0.06	0.39
750	0.48	0.01 **	0.01	0.75
1000	0.29	0.04 *	0.04	0.49
1500	0.23	0.08 .	0.07	0.38
2000	0.14	0.19	0.15	0.18
2500	0.07	0.36	0.19	0.12
3000	0.07	0.35	0.20	0.11
	0.08	0.34	0.19	0.12
			0.23	0.08 .
				0.20
				0.11



**Figure 3 Landscape sectors vs. surveyed flower peak season data correlation coefficients.**  $R^2$  values for landscape sector vs surveyed floral abundance, richness, evenness, and diversity at peak season

**Table 3 Landscape sectors vs. network flower peak season data.**  $R^2$  values and p values for linear models comparing the log value of the amount of meadow with the given landscape sector to the log abundance, log richness, evenness, or diversity values for the peak season data.

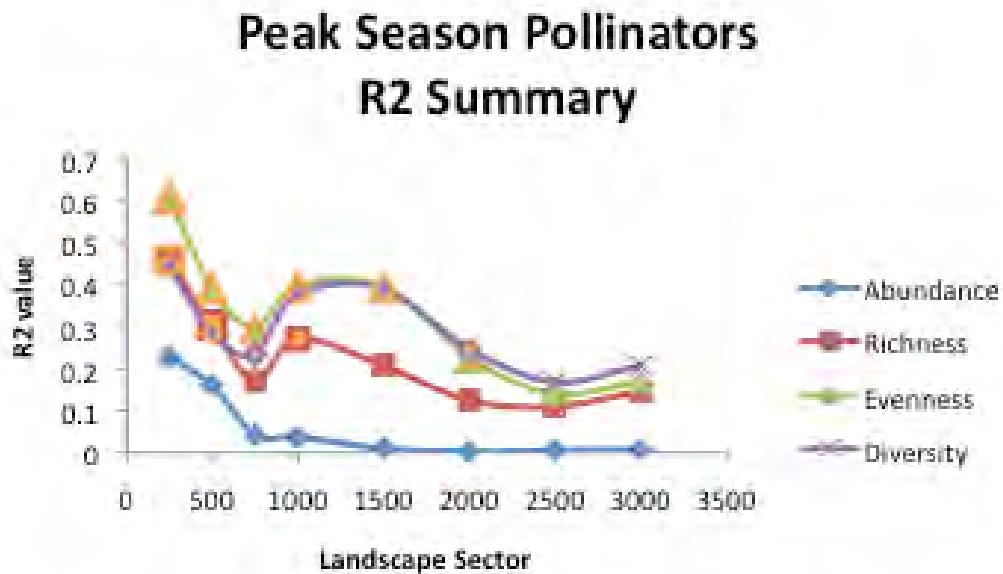
Landscape Sector (m)	Interaction	Flower Richness		Flower Evenness		Flower Diversity	
	Abundance						
Meadow Size	0.43	0.01 *	0.03	0.52	0.01	0.81	0.02
Meadow Proximity	0.01	0.70	0.15	0.17	0.00	0.95	0.04
250	0.23	0.08 .	0.00	0.95	0.14	0.19	0.11
500	0.16	0.16	0.01	0.72	0.03	0.58	0.05
750	0.04	0.48	0.00	0.92	0.00	0.94	0.00
1000	0.04	0.51	0.01	0.79	0.00	0.88	0.00
1500	0.01	0.72	0.05	0.44	0.00	0.95	0.02
2000	0.00	0.85	0.13	0.20	0.00	0.91	0.05
2500	0.01	0.80	0.23	0.08 .	0.01	0.81	0.08
3000	0.01	0.76	0.24	0.08 .	0.00	0.89	0.07
							0.37



**Figure 4 Landscape sectors vs. network flower peak season data correlation coefficients.**  $R^2$  values for landscape sector vs network floral abundance, richness, evenness, and diversity at peak season.

**Table 4 Landscape sectors vs. pollinator peak season data.**  $R^2$  values and p values for linear models comparing the log value of the amount of meadow with the given landscape sector to the log abundance, log richness, evenness, or diversity values for the peak season data.

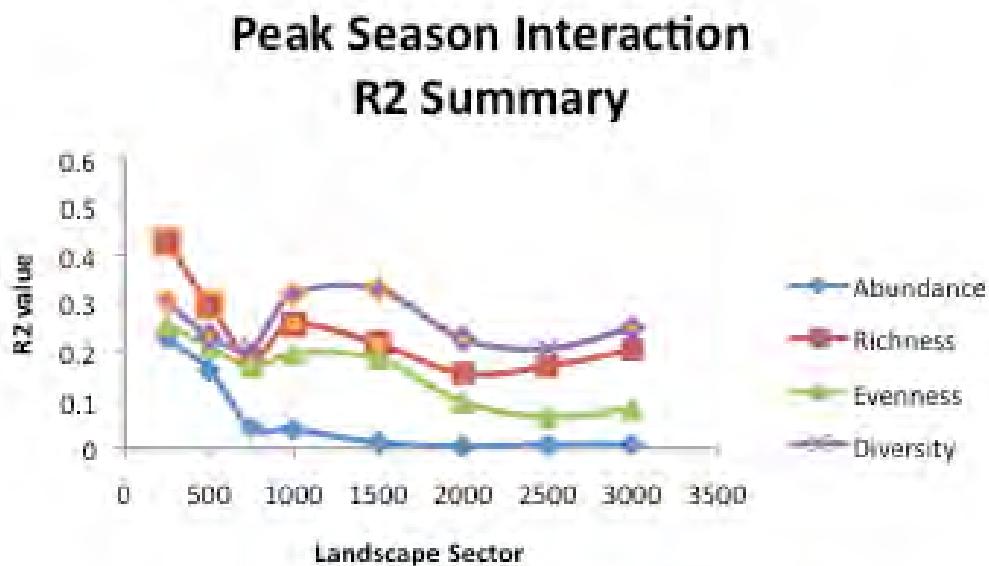
Landscape Sector (m)	Interaction	Pollinator Richness	Pollinator Evenness	Pollinator Diversity
	Abundance			
Meadow Size	0.43	0.01 *	0.17	0.14
Meadow			0.04	0.51
Proximity	0.01	0.70	0.24	0.07 .
250	0.23	0.08 .	0.61	0.00 **
500	0.16	0.16	0.39	0.02 *
750	0.04	0.48	0.30	0.04 *
1000	0.04	0.51	0.40	0.02 *
1500	0.01	0.72	0.40	0.02 *
2000	0.00	0.85	0.23	0.09 .
2500	0.01	0.80	0.14	0.17
3000	0.01	0.76	0.17	0.21



**Figure 5 Landscape sectors vs. pollinator peak season data correlation coefficients.**  $R^2$  values for landscape sector vs network pollinator abundance, richness, evenness, and diversity at peak season.

**Table 5 Landscape sectors vs. interaction peak season data.**  $R^2$  values and p values for linear models comparing the log value of the amount of meadow within the given landscape sector to the log abundance, log richness, evenness, or diversity values for the peak season data.

Landscape Sector (m)	Interaction Abundance	Interaction Richness	Interaction Evenness	Interaction Diversity
Meadow Size	0.43	0.01 *	0.27	0.06 .
Meadow Proximity	0.01	0.70	0.21	0.10 .
250	0.23	0.08 .	0.43	0.01 *
500	0.16	0.16	0.30	0.04 *
750	0.04	0.48	0.19	0.12
1000	0.04	0.51	0.26	0.06 .
1500	0.01	0.72	0.22	0.09 .
2000	0.00	0.85	0.15	0.17
2500	0.01	0.80	0.17	0.15
3000	0.01	0.76	0.20	0.11



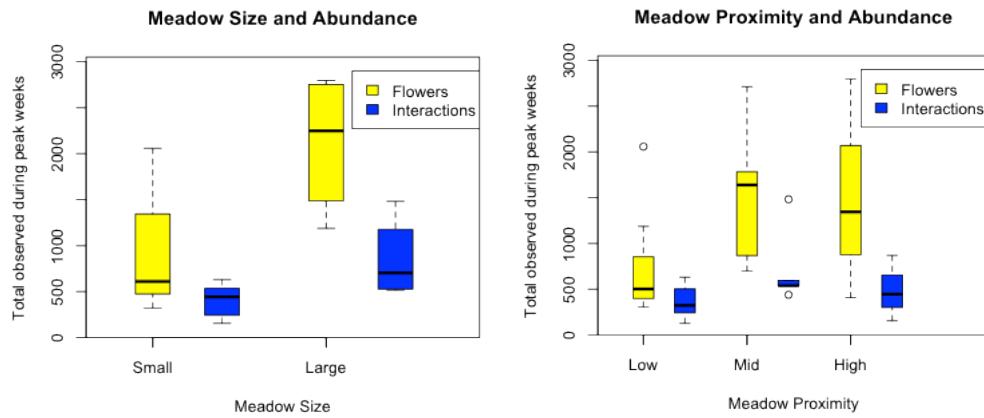
**Figure 6 Landscape sectors vs. interaction peak season data correlation coefficients.**  $R^2$  values for landscape sector vs network interaction abundance, richness, evenness, and diversity at peak season

*Flower and interaction abundance as a function of meadow size and surrounding meadow area*

Flower and interaction density (“abundance” within the permanent plots) was compared with meadow size, weighted meadow proximity index, and log-transformed habitat within each landscape sector. Flower abundance was calculated as the sum of flowers blooming in the study meadow permanent plots over all meadow watch dates through the summer. Interaction abundance was the sum of all interactions observed in the study meadow permanent plots over all meadow watch dates though the summer. Floral and interaction density produced highly significantly positive correlations with meadow size based on the full season data ( $R^2 = 0.54$   $p = 0.003$ ,  $R^2 = 0.46$   $p = 0.008$  respectively), and the peak season data ( $R^2 = 0.49$   $p = 0.01$ ,  $R^2 = 0.43$   $p = 0.01$  respectively). Bunchgrass Summit was omitted from all linear models. The floral abundance was also highly significantly correlated to meadow in the surrounding 250m ( $R^2 = 0.54$ ,  $p = 0.003$ ), 500m ( $R^2 = 0.51$ ,  $p = 0.005$ ), and significantly related to 750m ( $R^2 = 0.30$ ,  $p = 0.04$ ) landscape sectors based on full season data. Similarly, the floral abundance was highly significantly correlated to meadow in the surrounding 250m ( $R^2 = 0.44$ ,  $p = 0.01$ ), 500m ( $R^2 = 0.48$ ,  $p = 0.01$ ), and significantly related to 750m ( $R^2 = 0.29$ ,  $p = 0.04$ ) landscape sectors based on peak season data. Peak season flower abundance increased by 44% ( $R^2 = 0.49$ ) with increasing meadow size over the range of the meadows surveyed, while pollinator abundance increased by 32% ( $R^2 = 0.43$ ) with increasing meadow size across the wide extent of meadow sizes included in the study. Other known environmental variables

(meadow moisture, soil type) do not correlate with the meadow size gradient. Bunchgrass Summit was excluded from comparisons between community descriptors and meadow size due to the incredibly low abundance and richness and huge meadow size.

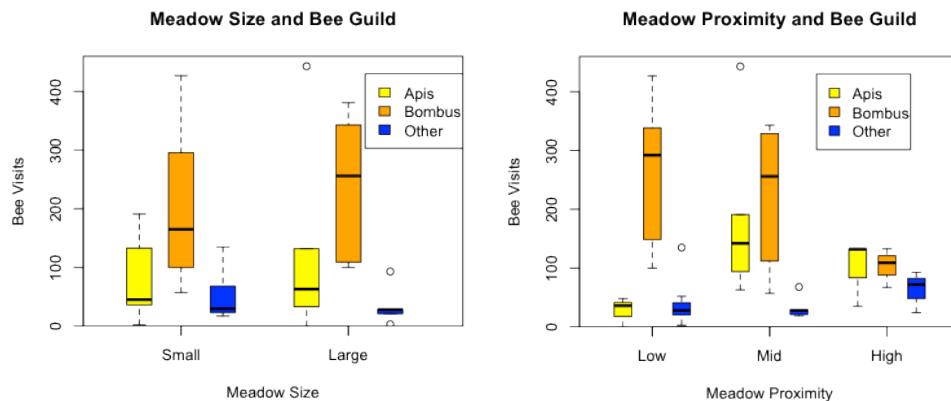
The following boxplots show the distribution of floral and interaction abundance by meadow size: small ( $n = 10$ ) and large meadows ( $n = 4$ ) without BS and by meadow proximity: low ( $n = 7$ ), mid ( $n = 5$ ), and high ( $n = 3$ ). Bunchgrass Summit is removed from the meadow size comparisons due to its exceptionally low abundance and great size, similar to the previous analysis. While abundance did not correlate strongly to surrounding meadow area in landscape sectors beyond the most local (250m, 500m, 750m). Abundance exhibited a log-curve shaped response to habitat proximity in larger surrounding landscape sectors. This trend is shown in by the low abundance values in the meadows with low meadow proximity values.



**Figure 7 Meadow size and proximity vs. flower and interaction abundance.** The above boxplots show flower abundance in small vs. large meadows, and meadows with low, moderate and high amounts of surrounding habitat.

### Bee guild abundance and surrounding meadow area

Hymenopterans (bees), the most prevalent order and the order most associated with pollination, were assessed separately for response to meadow size and surrounding habitat. Bees were separated into three guilds: (1) *Apis mellifera*- the European honey bee (2) *Bombus* spp.- the eight species of bumble bee observed (3) All other (native, solitary) bees. Unlike the visitation abundance of all pollinators, none of the three bee guilds responded to meadow size. *Apis mellifera* visitation was low in the smallest meadow complexes (Bunchgrass and Carpenter) and high in large meadow complexes (Lookout, Frissell, and Cone). *Bombus* spp. visitation was very low in the most extensive meadow complex (Cone Peak) and high, though highly variable, in the small and moderately sized complexes. Solitary bee visitation was slightly higher in the most extensive meadow complex.



**Figure 8 Meadow size and proximity vs. bee guild abundance.** The above boxplots show the abundance of three bee guilds: (1) *Apis mellifera* (2) *Bombus* spp. and (3) Solitary bees in small vs. large meadows, and meadows with low, moderate, and high amounts of surrounding habitat.

*Peak season plot flower, network flower, pollinator, and interaction richness as a function of meadow size and surrounding meadow area*

While floral richness was not significantly correlated to surrounding meadow area, an almost significant relationship was observed between network floral richness and surrounding meadow area at the largest (2500m and 3000m) landscape sectors. Surveyed flower evenness and diversity exhibited almost significant relationships to the 2500m landscape sector and the 3000m landscape sector, respectively. Pollinator and interaction richness and diversity were significantly correlated to surrounding meadow area at multiple scales. In the full season dataset, pollinator richness and interaction richness were positively associated with meadow size.

Surrounding meadow area explains a significant portion of pollinator and interaction richness through a linear model at multiple scales. During the peak season weeks, pollinator richness rose by 17% ( $R^2 = 0.45$ ) with habitat within 250m, 25% ( $R^2 = 0.29$ ) with habitat within 500m, and 27% ( $R^2 = 0.26$ ) with meadow area within 1000m across the size range of meadows included in the study. In the full season dataset, interaction richness rises by a rate similar to pollinators, only a few percentage points higher at each scale: 22% ( $R^2 = 0.49$ ) with meadow area within 250m, 31% ( $R^2 = 0.28$ ) with habitat within 500m, 24% ( $R^2 = 0.18$ ) with meadow area within 750m. In the peak season dataset, interaction richness showed a significant response to the 250m and 500m landscape sectors ( $R^2 = 0.43$ ,  $p=0.01$  and  $R^2 = 0.30$   $p=0.04$ , respectively). Also an almost significant correlation was exhibited between

interaction richness and habitat within the 1500m landscape sector ( $R^2 = 0.26$ ,  $p=0.06$ ) and the 1500m landscape sector ( $R^2 = 0.22$ ,  $p=0.09$ ).

A significant quadratic model better described the increase in pollinator and interaction richness response to increasing habitat in the 1000m landscape sector and above. This model fits the steep increase in slope in meadows with low to middle surrounding habitat area at the “meadow complex” scale. Floral richness in the network increased by 24% with increasing meadow habitat within 2500m and 3000m when BS was excluded based on a linear model that did not explain 95% of the variation in the data ( $R^2=0.2$ ). Pollinator and Interaction richness rose by 20 and 27% respectively with  $R^2$  values of 0.23 each with habitat within the 3000m sector.

Rarified richness echoed similar findings for network and pollinator richness at the meadow complex scale (3000m). However significant positive relationships were not found at the meadow scale. It seems likely the positive relationship between richness at the meadow scale is due to the increased abundance with increased meadow size, shown previously which may indicate pollination limitation (discussion section). In both plot flower and network flower rarified richness, a decrease in rarified richness was significantly explained by increasing meadow habitat at 250m (decrease of 20%,  $R^2 = 0.24$ ) and 500m (decrease of 35%,  $R^2 = 0.23$ ). Chao estimates indicated a significant increase in pollinator richness with meadow size without BS, where pollinator richness increased by 9%. Quadratic formulas fit the network plant richness at 2500m and 3000m scales.

*Plot flower, network flower, pollinator, and interaction evenness as a function of meadow size and surrounding meadow area*

Evenness did not significantly increase with meadow size for plants, pollinators and interactions, however pollinator and interaction evenness exhibited strong positive responses to near meadow area and moderate spatial scales. Meadow proximity explained pollinator evenness best with a quadratic formula ( $R^2 = 0.5$ ); the linear model showed a 24% average increase in evenness with increasing meadow proximity. This positive change in evenness across meadow proximity and greater landscape sectors described by the quadratic formula, occurred almost entirely in meadows with very low surrounding meadow area. Pollinator and interaction evenness increased significantly with meadow area within local landscape sectors and again at the complex scale after meadow reshuffling. Pollinator evenness rose by 14 % with an increase in meadow habitat within 250m ( $R^2 = 0.39$ ), 23% rise with habitat within 500m ( $R^2 = 0.37$ ), 21% ( $R^2 = 0.26$ ) rise with meadow area within 750m, 28% rise with habitat within 1000m in the full season dataset. In the peak season dataset pollinator evenness and was highly significantly correlated to meadow area within 250m ( $R^2 = 0.61$ ,  $p = 0.00^{**}$ ), and significantly correlated to surrounding meadow area within 500m ( $R^2 = 0.39$ ,  $p = 0.02$ ), 750m ( $R^2 = 0.30$ ,  $p = 0.04$ ), 1000m ( $R^2 = 0.40$ ,  $p = 0.02$ ), and 1500m ( $R^2 = 0.4$ ,  $p = 0.02$ ). In the peak season dataset, interaction evenness and was almost significantly correlated to habitat within 250m ( $R^2 = 0.26$ ,  $p = 0.07$ ) and 500m ( $R^2 = 0.21$ ,  $p = 0.10$ ). In the full season dataset the second peak in

evenness significance at 1000m, 1500m was stronger than the local scale peak at 250m, 500m for pollinators.

*Peak season plot flower, network flower, pollinator, and interaction diversity as a function of meadow size and surrounding meadow area*

Diversity was not significantly correlated with meadow size for plants, pollinators or interactions, however it showed the same pervasive fit to a quadratic function with meadow proximity for pollinators ( $R^2 = 0.59$ ) and interactions ( $R^2 = 0.49$ ) and two peaks of significance for pollinators and interactions at 250m/500m and 1000m/1500m. Pollinator diversity and interaction diversity are significantly related to surrounding meadow area most strongly where evenness or both evenness and richness are high.

## DISCUSSION

### *Species Richness Estimates*

The rarified flower richness or average richness recorded from 25 individuals selected randomly without replacement over 50 iterations showed very little difference in richness measures of network flowers which accrued a much higher abundance compared to species richness. Pollinator and interaction rarefaction estimates often did not approach a strong asymptote. This shows that rarified richness measured at 25 individuals responds differently to observed plot richness. In arthropod communities

with exceptionally high diversity, and highly unequal populations, it may not be conceptually valid to use an interpolation limited to such a small number of individuals. The Chao abundance-based species richness is based upon the proportion of singletons and doubletons in the dataset, hence this estimate is unnecessary for floral richness. Chao richness estimates cannot fall below the observed richness, but may extrapolate far beyond the observed richness. Several plots show Chao estimates several times the measured species richness of network flowers reaching beyond the exhaustively sampled flower data at the plot level. For pollinators, it appears likely that Chao estimates respond with dramatically increased values in interaction poor permanent plots located in meadows with high diversity, due to their tendency to accumulate singleton observations. These results introduce several differences between rarified richness, Chao richness and observed richness. Variability between these values is exaggerated in the plots compared to meadow level network data underscoring the importance of conducting network analyses and richness, diversity, and evenness analyses at the meadow level.

#### *Species Richness, Evenness, and Diversity*

For the 150 plots, richness of flowers, pollinators, and interactions increased with abundance. Richness of pollinators increased 2x faster than richness of flowers and in turn, interaction richness increased 2x times faster than richness of pollinators. These observations reflect the large number of pollinator species ( $n = 270$ ) relative to

plant species ( $n = 76$ ) and the many resulting pollinator-plant interactions. Richness variability was examined to test the effects of surrounding meadow area on plant and pollinator richness.

*Abundance, Richness, Evenness, Diversity and surrounding meadow area*

Richness, abundance, and diversity of flowers, pollinators, and interactions were positively correlated with surrounding meadow area however they responded to habitat at different scales.

The abundance of flowers and plant-pollinator interactions were positively related to meadow size. Floral density was also positively related to the amount of surrounding meadow area within 250m and 500m, but not beyond. These findings suggest that meadow edges may serve as barriers to dispersal of pollinators, or meadow size may limit plant population size and density of flowers. Several non-mutually exclusive hypotheses may explain the dependence of floral density upon immediate and local meadow space. Pollination limitation (limited abundance or richness of pollinators) may depress seed production in plants. Most of the floral species in the study system are generally considered self-compatible perennials, which may or may not prevent pollination limitation as an explanatory factor. Alternatively, climatic variables such as moisture and temperature may limit floral populations. Drought has been observed to limit seed production in floral populations at the end of the season at these study sites when flowers dry before setting seed (Mojica et al.

2010). Frost damage has been observed to cause high rate of floral population decline in years of low snowpack when wintery conditions affect early flower communities. A second hypothesis to explain the positive relationship between floral abundance and meadow habitat at small scales is that greater climatic heterogeneity and moisture heterogeneity with increased area of meadow may help formation of seed banks and seed establishment, promoting higher flower abundance. Small meadows were more homogeneous than large meadows, and most were rocky dry outcrops or moist “basin” meadows. Small meadows of these types may be more likely than large meadows to experience early snowmelt and late summer moisture shortage (rocky outcrops) or late winter conditions causing frost damage to new blooms (Inouye 2008).

The reasons for high plant and pollinator diversity in the western Cascades compared to Bunchgrass meadows were not clear. Bunchgrass meadows were the smallest meadow complex included in the study, with greater isolation from other meadows compared to the Western Cascades Ridge. Meadow complexes in the western Cascades experienced Native American burning for much of the Holocene (Highland 2011 and other sources). All montane meadow complexes have experienced extensive tree invasion, especially in mesic areas, in the past 60 years (Halpern et al. in press, Rice 2009, Rice et al. 2012). Despite this, floral communities may not have responded very much to meadow contraction; some meadow perennials can live for very long temporal scales, and seed banks maintained in the top soil may allow the populations to persist after years of disturbance. Halpern et al. (in press)

found a very high rate of return of meadow herbs 3 years and more after manipulative fire treatments in the Bunchgrass meadow system.

While floral richness was not significantly correlated to meadow surroundings, however, floral richness was almost significantly related to meadow habitat within 3000 m. Floral richness was low in the Bunchgrass meadows, and remained relatively high across all the complexes along the Western Cascades ridge. Patchily distributed montane meadows of xeric to mesic conditions have persisted along this older mountain range for an immeasurable amount of time, and lie in closer proximity to other meadows than the Bunchgrass Complex. While meadow complexes have experienced extensive tree invasion especially in mesic meadow area in the past 60 years, floral communities are not likely to experience rapid turnover. Many meadow perennials can live for very long temporal scales, and seed banks maintained in the top soil may allow the populations to persist after years of disturbance.

Spatial patterns of montane meadow complexes may provide floral resources for short and long-distance dispersing pollinators, and thereby contribute to increased richness of plant-pollinator interactions. Richness of pollinators and plant-pollinator interactions was related to meadow habitat at two spatial scales: 250 to 500 m, and 1000 to 1500 m, but not to meadow habitat at the 750 m scale. Amounts of meadow habitat within the 250 to 500m scale were not correlated to amounts of habitat at the 1000 to 1500m scale. This multi-scale response to meadow habitat amounts exhibited by both pollinator and interaction richness may be the result of dispersal potential of various groups of pollinator species. Past research suggests that smaller solitary bees

may forage close to their nests, whereas *Apis mellifera* and *Bombus* spp. may forage over distances up to several km. As a result, richness of pollinators and of plant-pollinator interactions would be expected to respond to meadow habitat availability at both short and long distances, as demonstrated in this study. These findings imply that meadow size is not a simple concept, but instead depends on surrounding meadow habitat availability as a function of distance and species dispersal potential (Steffan-Dewenter et al. 2002)

Pollinators and interaction richness was dramatically affected by current surrounding habitat as expected likely due to high rates of extinction and colonization of local populations based on a strong dependence on floral resources through the season. Local colonization and extinctions are likely in pollinator populations due to their precarious dependence upon phenological timing with dynamic montane meadow floral blooms. Therefore, it is expected that greater and more heterogeneous local and regional pools would maintain species richness at higher levels.

#### *Bee guild abundance compared with meadow size and surrounding meadow area*

*Apis mellifera* visitation exhibits a strong threshold response when compared with meadow proximity, where *Apis mellifera* visitation was very low in smaller complexes compared to more extensive meadow complexes (Bunchgrass and Carpenter vs. Lookout, Frissell, and Cone). *Apis mellifera* visitation appeared positively associated with meadow size in study meadows where there was a large

amount of habitat within the surrounding complex. The Lookout Mountain meadow complex is composed of smaller patches than the other two complexes and experienced lower *Apis mellifera* visitation. Due to the greater dispersal ability of *Apis mellifera* and social-colony life history characteristic, the 15 meadows are not independent because the presence of a single colony in a complex could produce high visitation rates to all meadows. In this study, the three large complexes experience high visitation while the two small complexes experienced low visitation. M2 exhibited incredibly high *Apis mellifera* visitation and the Cone Peak meadows are lower than might be expected with so much surrounding habitat. However, the Cone Peak meadows dried rapidly at the end of the season. These observations support the hypothesis that *Apis mellifera* requires a significant amount of dry and moist (representing early and late season habitat in the surrounding landscape).

*Bombus* spp. visitation did not respond to meadow size, but experienced very low values in the more extensive meadow complexes. These low values for *Bombus* spp. in Cone Peak meadows differentiate it's habitat preferences from both *Apis mellifera* and the solitary bees included in the study. *Bombus* spp. visitation was highly stratified within the smaller to mid-size complexes. The meadows that showed high soil moisture in week 5 also showed high *Bombus* spp. visitation.

Solitary bee visitation did not respond to meadow size. The driest meadows stand out above the rest for high solitary bee visitation. As the vast majority of native solitary bees nest in the soil, higher availability of exposed soil would be a likely explanatory factor for this observation. These meadows each included a great amount

of sandy, rocky immature exposed soil. Of these meadows, Carpenter Saddle stood above the rest with the highest visitation abundance. Carpenter Saddle also maintained the highest amount of soil moisture until the end of the season from these dry meadows.

Solitary bees abundance did not respond to TCI defined dry habitat in the surrounding landscape. Carpenter Saddle stood out from these regressions with a very high value of visits despite low surrounding dry habitat. It's position in the saddle by Carpenter Mountain may have inflated its TCI values from actual moisture regime. There was very little total habitat in the landscape around the meadow.

## CONCLUSIONS

In this study of fifteen 0.12 to 8.12 ha meadows in the Cascade Range of Oregon, floral richness was very high in both small and large meadows along the Western Cascades crest, but much lower in the Bunchgrass meadow complex. These patterns suggest that flowering species richness is the result of meta-population dynamics over very long temporal scales, as small and large meadows in the western cascades complexes were likely connected before the encroachment of conifer forest under fire suppression. This “memory” or retained high species richness is commonly referred to as extinction debt. Pollinator populations responded to closer scales of habitat, which have changed significantly in the past century, indicating a faster response to vegetation changes in the surrounding landscape.

The density of flowers and of flower-pollinator interactions were significantly positively correlated to meadow size (measured as the open area bounded by forest). Hence, flower and pollinator populations will likely decline not only due to increased meadow loss, but also due to increased meadow fragmentation. While floral species richness was almost significantly related to complex size (surrounding habitat within 3000m), the richness, evenness and diversity of pollinators and plant-pollinator interactions were best explained by the amount of meadow habitat at two different spatial scales: within 250/500m and 1000m/1500m of the sampled meadow. This is thought to be caused by different mobility limitations of pollinator species. As expected, richness of pollinators and of flower species increased with abundance of pollinators and flower species, but pollinator richness increased at twice the rate of floral richness.

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**CHAPTER 3 FLORAL ABUNDANCE, BEE GUILD PHENOLOGY, AND  
BEE GUILD PRESENCE IN DRY AND MOIST MEADOWS**

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In preparation for journal submission

## ABSTRACT

Montane meadows of the western Cascades system are characterized by heterogeneity in moisture regime, phenology, and floral resources. This study utilized surveys of plants and plant-pollinator interactions to investigate relationships between soil moisture, phenology, and the abundance of three bee guilds. The study examined: (1) the effect of soil moisture on flower and pollinator abundance; (2) patterns of flower and pollinator abundance over the season; and (3) the relationship between soil moisture and the abundance of various guilds of bees. The study showed that (1) flowers and pollinators were slightly more abundant in sites with relatively low soil moisture during the early season and relatively high soil moisture during the late season; (2) peak flower abundance coincided with or preceded peaks in pollinator populations; and (3) *Apis mellifera* abundance appeared to be synchronized with the shifting timing of floral abundance among meadows within a complex, possibly indicating pollinator movement among meadows in search of sites with high floral density. In contrast, the abundance of solitary bees was related to the timing of local floral abundance. The abundance of *Bombus* spp. peaked late in the season, consistent with colony growth over the season, and interaction observations were slightly higher at moist compared to dry meadows. Results of this study indicate that plant pollinator networks are complex assemblages of species, which respond to uniquely defined habitat requirements and exhibit specific temporal patterns of habitat use. The results

imply that environmental heterogeneity, not just area, is important to sustain diverse species.

## INTRODUCTION

Physical environmental variables influence plant and pollinator phenology, eliciting unique responses for both plant and pollinator phenophase. The likelihood of temporal mismatch between floral bloom and pollinator provisioning activity may lead to general trends in habitat specific pollinator species. The temporal distribution of plants and pollinators underlie the structure of plant-pollinator networks; non-overlapping phenology explained 22 to 28% of unobserved links, and extensive temporal overlap of plants and pollinator interactions resulted in a high probability of interaction in a Mediterranean scrub community (Olesen 2011).

Mutual dependence between plants and pollinators has resulted in associated declines and change in species range. Biesmeier et al. (2006) described parallel declines in plant and pollinator populations in fragmented landscapes. The presence of a generalist pollinator has been shown to influence the geographical range of a California plant species *Clarkia xantiana* (Moeller et al. 2012). Phenological matching between pollinators and their accessible floral resources is an essential requirement to sustain the presence of a particular pollinator species as well as floral resources and pollinators. Climatic variables have been shown to influence both plant and pollinator phenology in several systems.

Climatic variables have long been associated with floral and recently, several associations have been made between climatic variables and pollinator populations. In montane meadows, snowmelt date triggers the beginning of the growing season. Earlier snowmelt dates have been associated with earlier dates of first flowering in many places around the world, however the effect of first flowering date on population size has been shown to vary between locations (Miller-Rushing et al. 2008). In the Rocky Mountain, frost damage associated with years of low snowpack was correlated with lower floral abundance of three perennial wildflowers in sub-alpine meadows. Microhabitat variability, such as cold air drains, dramatically affected floral response: two plots spaced 12 m apart experienced a difference of 2°C and 37% frost damage (Inouye 2008). In the same system, Boggs et al. (2012) detected multiple effects of snowmelt timing on the abundance of a butterfly pollinator species, *Speyeria morania*. Snowmelt timing at the start of the growing season as well as at the start of the preceding year explained 84% of the variance in population growth through a model inclusive of some density-dependent effects.

Also at the Rocky Mountain Biological Research Station, Aldridge et al. (2011) communicated evidence of a longer interval between early and late season floral abundance occurring between xeric and mesic meadow sites. This observation was documented over a 35 year period based on floral surveys of 30 2m x 2m permanent plots every two or three days (Aldridge et al. 2011).

Plants and pollinators respond to the surrounding environmental conditions with different temporal sensitivity based upon species specific characteristics as well

as differences defined by their reciprocal dependence in the mutualistic relationship. While plants benefit reproductively from animal-facilitated movement of pollen or mechanical re-distribution of self-pollen, pollinators depend upon a constant source of pollen and nectar as a food supply required for survival.

Most wild herbs in the study system described here are perennial. The few annual species, also exhibit biannual life-history patterns. Multi-annual seed banks are recognized as a pervasive feature of meadow sediment reserves; supporting return of wildflower communities several years after wildfire disturbance. As a result of life-history parameters and dependency, plants may respond at longer temporal scales with less immediate dynamics. Pollinators, gifted with increased dispersal abilities respond immediately to annual phenomenon; be it floral resource abundance or timing, climatic variability, or other environmental phenomenon. If floral resources are not available at the time of pollinator emergence, the pollinators will not be able to persist.

Montane meadows of the Cascades support diverse plant and pollinator communities rivaling species richness observed in highly diverse plant-pollinator networks on other continents. One reason for this may be the rich heterogeneity in meadow habitat based on diverse microclimates and underlying topographic and soil characteristics. While the growing season of high elevation montane meadows is highly condensed to a few months, limited by late snowpack, then progressively stronger drought conditions caused by the lack of precipitation. Rugged topography supports montane meadows with very different moisture retention and phenology.

The Cascades and surrounding valley zones supported vast historical prairie and patchy montane meadows. Non-forested wild area has declined rapidly in the past century, due to development in the valleys and widespread Douglas-fir invasion. The spatial distribution of habitat is known to affect pollinator efficiency in harvesting resources (Carvell 2012, Zurbuchen et al. 2010). The richness, evenness, and diversity of pollinators and interactions are expected to respond to the amount of surrounding habitat at relevant scales based on island biogeography theory (Pfeiffer thesis, chapter 2). To date, little field research has assessed the consequences of different spatial and temporal scale dependencies and vegetation characteristics on pollinator networks in wild landscapes. The distribution and abundance of particular plant and pollinator guilds is expected to vary based on moisture regime which directly affect the availability of floral resources at the beginning and end of the growing season.

This study examined (1) the temporal distribution of floral and pollinator abundance, and specifically the temporal distribution of *Apis mellifera*, *Bombus* spp. and native solitary bee abundance; as well as (2) the relationship of flower, pollinator, and pollinator guild abundance to meadow moisture. This study tested the hypotheses that the abundance of different pollinator guilds exhibit different patterns of abundance throughout the season based on meadow moisture and meadow moisture in the surrounding landscape, and that floral abundance is influenced temporally by meadow moisture.

## METHODS

*Study site description*

The western Cascades landscape is comprised largely by a dense matrix of coniferous forest interspersed by conspicuous montane meadows and other non-forested patches. Fire is an important disturbance processes responsible for creating some ephemeral non-forest habitat. Some meadow habitat has been stably maintained for long periods of time due to topo-edaphic conditions. In a previous study, Takaoka et al. described montane meadow change between 1946 and 2000 and found that 5.5% non-forest patches in the Cascades landscape in 1946 declined to 2.5% of the landscape in 2000. Mesic and xeric meadows with adjacent forest established after wildfire contracted significantly more than those without burns in the 150 years before 1946. 17% of xeric meadows contracted between 1946 and 2000, and 47% of mesic meadow habitat (Takaoka et al. 2008).

This study surveyed plants and plant-pollinator interactions in fifteen western Cascades montane meadows. Study meadows varied in size and topographic conditions. While some portion of each meadow could be characterized as xeric, or grass-dominated, about half of the meadows also supported some mesic vegetation or moist seeps as well. Mesic vegetation is characterized as domination by thick ferns. Full descriptions of each meadow may be reviewed in Appendix A.

*Plant-pollinator Surveys*

Plant and plant-pollinator interactions were surveyed in fifteen montane meadows six times between 13 July – 13 September over summer 2011. During each visit, five 3 x 3 m permanent plots were visited at 15 m intervals along two transects of 60 m each, for a total of ten plots per meadow. Plant-pollinator interactions were observed and recorded for 15 minutes following an exhaustive plot flower survey. Field methods are fully described in the methods section of part 2.

#### *Soil Sampling*

Soil samples were obtained from each study meadow during visit round 3 and visit round 5 of the 9-week sampling period. Cylindrical soil cores of 200cm<sup>2</sup> were obtained to a depth of 10 cm except in several cases where the soil depth limited the core sampling depth. Samples were composites of five sub-samples; four from each corner of the study meadow plots and one from the center of the plot area. Cores were taken where plant cover was minimal in order to limit interference with plants. The five subsamples were composited in the field and transported to the lab in sealed plastic bags for further analysis.

#### *Soil Moisture Calculations*

Plant-available and capillary soil moisture was calculated using gravimetric soil moisture analysis of soil cores. At the lab, plant material were removed by hand from the soil sample and a subsample of 200g was obtained and weighted to the

nearest thousandth of a gram for soil moisture determination. Each 200 g sub-sample was weighed in an airtight plastic bag, the open bag was placed in a protected location to air dry for several weeks and then re-weighted to obtain the air-dried soil weight. This air-dried sub-sample was sieved through a 2mm sieve to remove gravel (>2-mm fraction). The weight of the gravel was subtracted from the wet weight and air-dry weight to determine the <2 mm sample weight. A 10 to 20 g subsample of air-dried soil (grain size <2mm) was weighed, then dried at 120°F for 12 hours, and weighed again in order to determine the oven-dried soil weight.

Plant-available moisture and capillary moisture were determined for the <2mm fraction only as follows:

Plant-available water = (field weight - airdry weight)/(oven-dry weight)

Capillary water = (airdry weight - ovendry weight)/(oven-dry weight)

#### *Spatial data sources*

##### Aerial photos

Meadow habitat estimates were obtained from a digital layer of meadows created by Highland (2011) and doubled in size by Vera Pfeiffer from 0.5m resolution digital aerial imagery obtained in 2005 and available from Oregon Explorer ([www.oregonexplorer.net](http://www.oregonexplorer.net)).

Montane meadows were distinguished visually by their irregular boarder, light green/brown shade, and homogenous texture.

## DEM

A 10m Digital Elevation Model (DEM) available from USGS was used to interpolate a 3-dimensional surface to estimate meadow surface area. The area of steep meadows could be vastly underestimated using 2-dimensional area. The raster DEM was also used to calculate a Topographic Convergence Index (TCI) to estimate accumulated moisture in the landscape. This process is detailed in the Spatial Data Analysis section below.

## Topographic Convergence Index

The meadow moisture index used in this study to estimate the “wetness value” of meadow within the surrounding landscape is the topographic convergence index, a mathematical model based on elevation data. The TCI index was estimated from a 10 meter DEM for the study sites. All sinks were filled in the raw DEM before flow direction, accumulation, and slope layers were calculated. The TCI wetness value is based on the slope (slope) and the upslope contributing area (A) or area from which flow is accumulated:

$$TCI = \ln \left[ \frac{A}{\tan(slope)} \right]$$

(Beven and Kirkby 1979)

Low TCI values correspond to “dry” areas with high slope, and/or small amounts of upslope contributing area. High TCI values indicate “wet” areas with high upslope contributing area and less slope. These values were significantly correlated to plant available moisture except in the case of bunchgrass meadows, where very level terrain promotes TCI index up to very high values despite low plant available soil moisture. The deep sandy loam and very dense park like grass with thick grass root structures likely uptake a great quantity of water through the summer decreasing available moisture.

The TCI index was calculated as a raster file in which all pixels covering the landscape represented one value. The meadow shape files, (i.e. the meadow polygons clipped by each buffer distance: 25m, 50m, 100m, 250m, 500m, 750m, 1000m, 1500m, 2000m, 2500m, and 3000m) for each study meadow were used to clip the TCI raster. The pixel values of all cells within the meadow habitat at each scale were exported as ASCII files and the number of each pixels from defined TCI value groups (i.e. TCI <2 or TCI between 4 and 9) were divided by the total number of meadow pixels within each meadow TCI raster to obtain the proportion of meadow habitat at each scale for each meadow from each TCI value group. This proportion was then multiplied by the surface area of that meadow habitat to estimate the amount of “dry” or “wet” at a particular scale defined by the TCI value group.

The topographic convergence index (TCI) index described above indicates the expected moisture level of the each grid cell based on the topography depicted using the digital elevation model (DEM). TCI depicts meadows that retain moisture at the end of the season with very high index values, and meadows with very low values dried out very quickly. The relationship between actual meadow moisture and TCI moisture is described below. It is clear that the Bunchgrass meadows do not respond in a similar way to the other meadow complexes, and TCI cannot be used as a factor for those meadows relative to the rest of the study meadows.

The meadows that retained moisture until the end of the season have the highest TCI values. The Bunchgrass meadows do not fit the curve because their high TCI values are not matched with high meadow moisture values. Because the TCI index values represent the bunchgrass meadows differently, they are eliminated from the analyses which utilized TCI as a factor. The different meadow characteristics result in dissimilar measurement of relative meadow moisture.

Average TCI from meadow within 50m is used for the following linear regressions, because that spatial area corresponds better to the area composite sampled for soil moisture in the field. The values appeared similarly distributed with the average meadow TCI.

Below, two linear regressions were performed to test for significant correlation between Soil Moisture in Week 5 and average meadow TCI value when Bunchgrass Meadows are excluded. By sight, the response of the average meadow TCI appears very exaggerated at high moisture values, so the average meadow TCI values were log

transformed. Evidence of the exaggerated high TCI values still remained after the log transformation, but the correlation is still evident. A linear regression fit all the data points, as well as the subset of data points with soil moisture above 0.05 g plant-available H<sub>2</sub>O/g oven-dried soil evaluated independently.

Small meadows exhibited low and high average TCI values. None of the large meadows exhibited very low TCI values. A likely reason for this is the increased chance of drainage pathways passing through the large meadows, which incur very high TCI values. High values have a much more pronounced effect on meadow averages because the values are so much further from the mean. In the results section, averages were not used, instead the amount of habitat with a TCI Index value less than 2, and the amount of habitat with a TCI value between 4 and 9.

### *Community Analysis*

Community analysis techniques were used to compare meadow floral and pollinator communities. The goal of this comparison was to check for strong grouping between communities, and understand if a significant amount of variation within communities was explained by one of a few potential explanatory factors (meadow size, surrounding habitat, or moisture). Flower dendograms were assessed visually and ordination plots were assessed visually and quantitatively.

### Cluster Analysis- Dendograms

Hierarchical clustering is a simple method of ecological structure analysis based upon optimization of a grouping method. Cluster analysis was used to describe the structure of wildflower communities in surveyed plots and within the networks. Ward's method was used to avoid distortion because it is one of the few space-conserving methods. Euclidean distance was used because it is compatible with the underlying principles of minimizing the within-group error sum of squares, while Sorensen distance is generally considered incompatible. This hierarchical grouping technique is a minimum variance method. Plots are clustered into groups by minimizing the error sum of squares of distances from each individual to the centroid of its groups. Groups are subsequently joined in the manner that produces the least error in the sum of squares. Once an optimal solution was determined, the strongest hypothesized explanatory factors for flower community structure were visually investigated in comparison to community structure assessed using this technique. These categorical variables, complex association, meadow, and meadow moisture groups were compared visually to reveal unforeseen dissimilarity between communities (McCune 2011).

#### Non-metric multidimensional scaling ordination

Non-metric multidimensional scaling or NMS ordination is a similar, but more complex, common ecological tool also used to describe similar ecological clustering and patterns and extract axis or gradients of variation which can be compared

quantitatively to physical variables or potential explanatory variables. NMS ordination is a very effective method to analyze non-normal ecological datasets and it was used to understand the differences between pollinator communities. This method was chosen because it avoids the assumption of linear relationships among variables. This method uses ranked distances which linearize the relationship between distances measured in the species space and environmental space. As a result the method relieves the “zero-truncation problem” and remains compatible with any distance measurement. The Sorenson distance method was chosen. NMS conducts an iterative search for the optimal position of each entity in a multi-dimensional space. While each column of data, species in this case, could represent an additional dimension, the procedure minimizes the dimensions required to describe the distance between entities, while “stress” is limited to a specified level. The stress defined as the departure from monotonicity in the relationship between the dissimilarity or distance in the original space defined by a dimension for each column/attribute, and the ordinal space with a minimized “ $k^{\text{th}}$ ” dimensionality. First the dissimilarity of the original matrix is calculated. Then the entities are placed in space randomly and their placement is adjusted and dimensionality minimized until a sufficiently low level of instability is reached and stress is acceptably small (McCune 2011).

## RESULTS

### *Cluster Analysis of Flower Communities*

Cluster analysis was used to understand the structure of wildflower communities based on (1) the full season observed flowers present in each of the permanent plots, (2) the full season network flowers observed in the plant-pollinator network based on interaction frequency within each permanent plot, (3) the sum of observed flowers present in each meadow on each watch date, and (4) the sum of network flower interaction in each meadow on each watch date. However, successful ordination results were not achieved.

In the full season plot based analyses, each permanent plot was included in this analysis described by the quantified abundance of each flower species observed in the plot summed across all watch dates. Pervasive similarity was observed between plots from different complexes and soil moisture groups in both plant dendograms. Meadow floral communities did not group distinctly by soil moisture class, meadow, or meadow complex. Dendrogram results are located in Appendix G.

Neither complex nor moisture class explained the most outstanding differences between full season flower surveys or flower abundance within the pollinator networks. The most significant overall pattern occurs between two general categories divided by amount of surrounding habitat in the largest measured landscape sectors: large complex meadows (Cone Peak, Frissell Ridge, and Lookout Mountain) and small complex meadow (Carpenter and Bunchgrass). Some plots from each group are mixed in with the opposing group, more large complex plot communities were incorporated into the small complex group. The most significant differences occur

between the plots from the large complex meadow group. These two complex size distinctions each include a significant selection of plots from different complexes within the category. The biggest differences occurred between plots from the large complex category. The greatest distance occurred between a subset of four M2 and two LO plots, a CNT and a CNM plot, and the remainder of the dataset. Other plots from these meadows were incorporated into more inclusive clades. Another small group included several BH and CPS plots. Other plots from each of these meadows also appeared in the larger, more inclusive grouping (Appendix G).

Cluster analysis of flower communities was also conducted based on the sum of flowers blooming in each meadow on each watch date as well. In this analysis, floral community dendrograms were created based on community data representing the total floral abundance in each meadow at each watch date ( $n= 15*6$ ). Some grouping of peak season watch dates and early and late season blooms was present. A second dendrogram was created based on network floral data representing the total abundance of flower species involved in network interactions at each watch date. In this dendrogram, early and late season watch dates segregated more sharply from the peak season dates. In both dendrograms, the most distance occurred between peak season groups from large complexes (i.e. watch 2 and 3 communities from Cone meadows, Lookout outcrop and Frissell ridge meadows). Overall, there was a great deal of mixing between large and small complexes due to the temporal segregation.

#### *Ordination of Pollinator Communities*

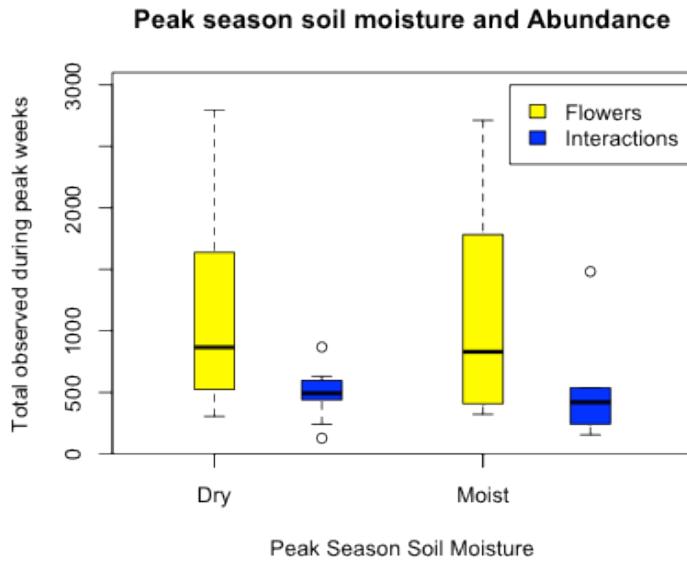
Ordination results for full season pollinator plots symbolized by complex, moisture class, and meadow are located in Appendix G. 148 full season plot records were included, only two plots in Bunchgrass Summit meadow were never visited during the season. Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space are described as follows for axes 1, 2, and 3: Increment and cumulative  $R^2$  values for Axis 1 are 0.203 and 0.203, for Axis 2 are 0.248, 0.451, and for Axis 3 are 0.310, 0.761. Increment and cumulative R-squared values were adjusted for any lack of orthogonality of axes.

Similar to floral communities, permanent plot pollinator frequency within the network summed across the season did not show significant structure by complex or moisture class. Some sorting was visible when the full season plot points were symbolized by complex, however each complex mixes in the center of the ordinal space. Meadow complexes appeared slightly clumped, but no complex stood out from the others completely. Similarly moisture classes did not segregate indicating communities from different moisture classes shared similar species composition. No physical variables were highly correlated with the explanatory axes above an  $R^2$  value of 0.25, however several surrounding habitat measures (habitat within 500m, 1500m, 2000m, 2500m, and 3000m) were loosely correlated to full season pollinator plot data with  $R^2$  values between 0.20 and 0.25. The largest landscape sectors exhibited the highest  $R^2$  values (0.24).

Non-metric multidimensional scaling ordination of pollinator communities was also preformed based on meadow sums of pollinator species visitation at each watch date. This analysis includes 81 meadow watch date datasets ( $n=81$ ), nine meadow visits, eight of which occurred at the end of the season, resulted in zero observations, two of these zero observation visits result from missed observation dates.

Pollinator communities described as the abundance of pollinators at each meadow during each watch week were contrasted using non-metric multidimensional scaling ordination. Coefficients of determination (Increment and cumulative R-squared values) for the correlations between ordination distances and distances in the original n-dimensional space were 0.237 and 0.237 for Axis 1, 0.285 and 0.522 for axis 2, 0.210 and 0.732 for axis 3. Increment and cumulative R-squared values were adjusted for any lack in orthogonality of axes. In a three-dimensional visualization in Appendix G, vector paths were used to trace the six watch periods in each meadow when communities were symbolized by watch date. Pollinator communities showed more significant structure by phenology when meadow watch communities were symbolized by watch week than by complex or moisture group. Two-dimensional plots symbolized by visitation round also depict the curved path of clumped observation dates describing the phonological turnover. More mixing took place between complex and moisture class groups, as plot watch periods segregated. Again the largest landscape sector explained some variation in the point distribution, exhibiting an R-squared value just over 0.20.

*Meadow moisture vs. species abundance*



**Figure 9 Peak season soil moisture vs. flower and interaction abundance.** The above boxplots show flower and interaction abundance in dry meadows and relatively moist meadows during the peak season.

Flower and pollinator abundance was not significantly different between the dry and moist meadow communities surveyed. Previous research show a significant linear increase in flower and interaction abundance (density) with increased meadow size.

*Meadow moisture vs. floral abundance through the season*

Floral abundance from each meadow during each watch period was plotted against measured soil moisture during week 3 and week 5 (Appendix H). At the beginning and end of the growing season moisture regimes appear to limit the floral

populations. During week 1, floral abundance was very high in the single driest meadow, and average abundance was higher in the drier meadows than the more moist meadows. Average floral abundance was higher in moist meadows than dry meadows during the final weeks. Soil moisture did not explain floral abundance during the middle of the season, and only appeared to act as a limiting factor at the beginning and end of the season.

#### Meadow moisture vs. pollinator abundance through the season

Pollinator abundance from each meadow during watch period was plotted against measured soil moisture during week 3 and week 5. Meadows that dried quickly through the sampling period showed high week 1 pollinator abundance. Meadows with very low soil moisture in week 3 and 5 not only melted earlier, but also retained the least moisture, likely due to increased soil grain size. In the earliest watches, pollinator abundance responded very strongly to dry meadow habitat. At the end of the season, a great amount of variability occurred, but low moisture in week 3 was associated with community decline at the end of the season. These charts are shown in Appendix H. Soil moisture did not explain pollinator abundance during the middle sampling weeks.

#### *Flower and interaction abundance by sampling date*

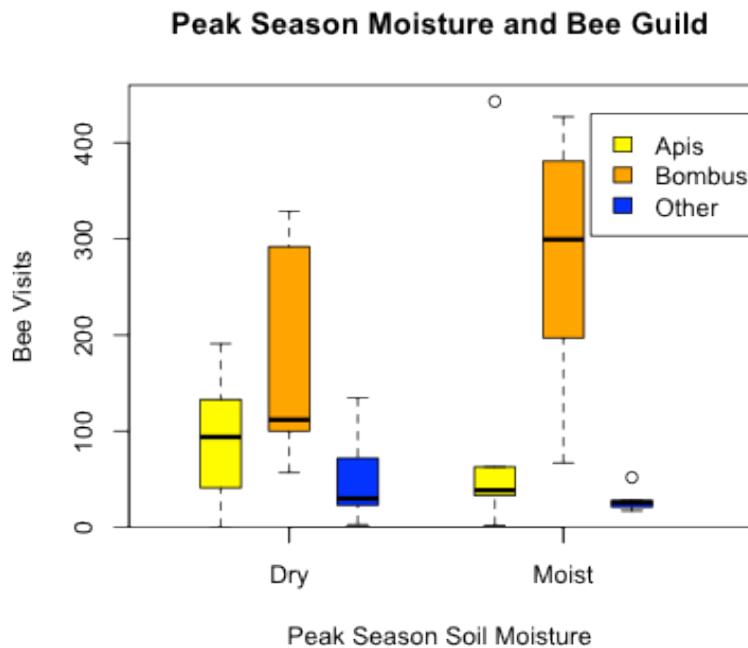
Floral abundance peak at the same time or before pollinator abundance in all sampled meadows. Descriptive charts are shown in Appendix H. Floral abundance peaked in week 1 for the Cone Peak meadows and CPS, week 2 for the Lookout meadows, M2, RP1, and BH, week 3 for RP2 and week 4 or later for the remaining Carpenter meadows and BD. RP2 exhibited a peak in floral abundance during week 3, when RP1 exhibited low floral abundance.

Flower-visitor abundance peaked on week 2 for M2, RP1, CNT, LO, CPR, BH, BS; week 3 for RP2; week 4 for CNM, CNE, LM, CPM and CPS; and week 5 for CPB. During the peak season, RP1 exhibited a decline in pollinator abundance while it's neighboring meadow RP2 exhibited a high peak.

#### *Bee guild abundance by meadow over the season*

Bee guild abundance was shown by sampling date for each of the study meadows in Appendix H. Reciprocal behavior within complexes was observed for the *Apis mellifera*; past research indicates these bees are highly vagile foragers. *Apis mellifera* abundance showed exaggerated response to floral abundance peaks in meadows across the complex, suggesting the hypothesis that they move between local meadows to collectively target sites of high floral abundance. Native solitary bee fluctuations echoed local floral abundance, but did not show such exaggerated response, fluctuating with complexes. *Apis mellifera* visitation was high throughout

the season in the large complexes, whereas *Bombus* spp. visitation was high in the late season.



**Figure 10 Peak season soil moisture vs. bee guild abundance.** The above boxplots show bee guild abundance in dry meadows and relatively moist meadows during the peak season.

#### *Bee guild abundance and soil moisture*

When meadow were divided into dry and moist groups based on the most obvious distinction observed based on measured soil moisture (Appendix B), several trends can be observed for the three bee guilds. *Apis mellifera* and the combined solitary bee guild tended to be slightly more abundant in dry meadows. This difference in native solitary bee abundance between the moisture classes is dramatically increased when a slightly lower threshold is used. High solitary bee

abundance occurred specifically in the most dry study meadows. *Bombus* spp. displayed much higher mean abundant in moist meadows than dry meadows.

Based on visual assessment of scatter plots representing guild abundance by meadow (Appendix H), *Apis mellifera* abundance was very high in M2, where soil moisture remained high during the peak season (week 3). Meadows with low soil moisture during week 3 were drying out, and the effects of this drying on flower abundance may have limited the resources available to *Apis mellifera* colonies, which support a large number of bees throughout the season. *Bombus* spp. visitation was high in most of the meadows with high moisture during week 3 as well as several meadows with low moisture during week three. *Bombus* spp. visitation was especially low in the very dry extensive Cone Peak complex. Solitary bees favored meadows that had low soil moisture during week 3, but maintained moderate soil moisture in the late summer. The highest solitary bee abundance was recorded in CPS which exhibited relatively dry conditions during week 3, but retained more moisture to week 5 than the other early-drying meadows.

#### *Bee guild distribution based on habitat area defined by TCI values*

Bee guild abundance was compared with surrounding habitat divided into several moisture classes. None of the bee guilds responded to total habitat within all landscape sectors. Solitary bees were compared to the amount of dry habitat at all scales, based on the hypothesis that they would respond positively to the amount of

“dry” habitat in the closest vicinity. *Bombus* spp. abundance was compared to the amount of moist habitat at all scales. *Apis mellifera* was compared with the amount of dry and moist habitat at all scales. Solitary bees and bumble bees did not respond to the amount of dry or moist habitat at any scale. Though *Apis mellifera* did respond positively to the amount of dry and wet habitat at moderate scales (1000m, 1500m landscape sectors), the results are not definitive, due to a slight non-significant negative correlation between the explanatory variables.

## DISCUSSION

### *Plant and Pollinator Communities*

Meadow floral communities showed similar overall composition across the meadows with the greatest difference occurring between small and large complexes. Similar phenological patterns of flower abundance varied among meadows. Floral communities differed between early, middle (“peak”), and late parts of the study period. Flower species turnover was significantly different during week 1 and week 6 between sampling dates (early July and early September). The early and late season plots segregated into more distinct groups for the early and late season for the network floral data than the survey plot data. This may indicate that flowers offered pollen and nectar resources to pollinators for a shorter time period than indicated by the flower surveys.

Flower organization by plot watch exhibited clearer sorting than flower organization by complex. The biggest differences occurred in the peak season when flower abundance was highest. The most distant group was a selection of large complex watch dates from the early peak season (Watch 2 and 3 from Cone meadows, Lookout outcrop and Frissell ridge meadows). Overall, there was a great deal of mixing between large and small complexes. Early and late season watch data segregated more strongly in network data than observation data, possibly indicating a more limited period of anthesis for floral blooms than the temporal extent of their structural presence within the plots.

Pollinator communities also varied more by sampling date than by meadow complex or soil moisture. Full season pollinator communities were similar among all meadows with some variation explained by complex size (especially surrounding meadow in the largest landscape sectors: 2500m and 3000m). However, similar phenological patterns were exhibited between the meadows whose communities arched in a similar curve that showed some differentiation between early season, mid-season, and late season community composition.

### *Moisture Limitation*

Although soil moisture was not closely associated with floral abundance, especially during the mid-season, flower and pollinator abundance appeared limited at the beginning and end of the season based on moisture. In the early season high soil

moisture was probably associated with low temperature, which would delay spring blooms. Sites which retained snow maintained high moisture until the late season. Meadows which dried early based on the peak season week 3 moisture showed a stronger limiting effect on late season flower abundance and pollinator visitation than week 5 soil moisture. This trend is consistent with observed effects because meadows with low moisture in the early season tended to dry quickly and loose moisture by the end of the season and meadows that sustained moisture until the late season tended to preserve a cool wet climate for a longer period in the early season likely preventing desiccation of resident species. The same trend described the relationship between moisture and flower visitors even more clearly. While flowers may persist structurally for an extended period of time, their period of anthesis during which floral resources such as pollen and nectar were available to flower visitors may be more directly impacted. Without food resources, pollinators would immediately be unable to persist.

#### *Peak Flower and Pollinator Abundance*

Peak flowering and visitation happened at different times in different meadows. Floral abundance tended to peak at the same time or before pollinator abundance; earlier in the dry meadows and later in the moist meadows. Floral abundance peaked in week 1 for the Cone Peak meadows and CPS, week 2 for the Lookout meadows, M2, RP1, and BH, week 3 for RP2 and week 4 or later for the

remaining Carpenter meadows and BD. Bunchgrass Dragon was not monitored during week one, however it supported very few early season flowers during the subsequent weeks. The floral community supported by BD was dominated by late season flowers.

Pollinator abundance peaks occurred on the same date or after peaks in floral bloom. Peaks occurred on week 2 for M2, RP1, CNT, LO, CPR, BH, BS; week 3 for RP2; week 4 for CNM, CNE, LM, CPM and CPS; and week 5 for CPB. Several very dry meadows experienced late season peaks in pollinator abundance, lag times in this meadow occurred up to 2 or 3 weeks behind floral peaks (CPS, CNM, CNE). This result could be due to extinction of early season pollinators based on earlier than expected blooms in past years or the current year. This pattern has been observed at other field sites (Moldenke, unpublished data). RP2 experienced a high peak in interaction abundance while RP1 experienced very low pollinator abundance. These meadows are directly adjacent to each other, and it is important to note that highly mobile dispersers may be able to move in order to exploit this local difference in resources availability.

#### *Bee guild abundance by date*

Bee guild abundance by date is best explained by the general life history characteristics of the bee guilds described. *Apis mellifera*, the European honey bee is a social bee and a vagile disperser. *Apis mellifera* colonies over-winter, maintaining

their social organization. *Apis mellifera* visitation often appears to exhibit reciprocal tendencies within each meadow complex over the season based on floral abundance maxima. The highest visitation abundance occurred in week 2 at M2 meadow, followed by a leap in visitation at RP1. RP2 experienced high visitation in weeks 2 and 4, and a low during the leap in *Apis mellifera* presence in the neighboring meadow. In the Cone Peak complex, *Apis mellifera* visitation peaked first at CNT, then Cone Main, then at the more moist meadow with a small seep at the end of the season. In the Lookout Mountain complex, *Apis mellifera* visitation peaked initially at LO a small dry rocky meadow, then gradually inclined in the big main meadow. The gradual incline may have been caused by the potential for dispersed use of resources around a much larger meadow area. Carpenter Meadows and Bunchgrass meadows experienced very low visitation overall, but visitation was distributed according to floral abundance.

*Bombus* spp. (bumble-bees) are highly mobile bees whose queens overwinter in ground nests, to emerge in the spring and found new colonies. The queens produce new worker bees to create a colony over the summer growing season. Queens produce reproductive castes at the end of the season: males and autumn queens emerge to mate and create nests. *Bombus* spp. visitation peaked later in the season at almost all complexes. Some reciprocal tendencies may have been observed between the very near RP1 and RP2 meadows following the decline in floral resources at RP1 at peak season. *Bombus* populations were very low at Cone Peak and two of the Bunchgrass meadows where floral resources declined rapidly at the end of the season with very

low soil moisture. High *Bombus* spp. abundance occurred in the majority of the moist meadows. This trend may be caused by the guarantee of late season floral resources to support new queen emergence at the end of the summer. New queens must store pollen resources at the end of the season to sustain themselves over the winter.

Solitary bee visitation did not respond dramatically to meadow size or surrounding meadow area at any scale. Solitary bee abundance showed a slight, but non-significant increase with surrounding habitat within the largest landscape sectors. This may be explained by the increased potential for recolonization from the extensive meadow surroundings, or perhaps the immature rocky xeric soils of the most extensive meadow complex (Cone Peak) which may benefit solitary bees due to their ground nesting strategy and the availability of soil area.

## CONCLUSIONS

This study described trends in flower and pollinator abundance in western Cascades montane meadows based on meadow moisture and the temporal dynamics of communities. Results suggesting weak effects of soil moisture on plant-pollinator communities. Though stronger affects on individual species, due to unique habitat preferences. Flower and pollinator abundance were positively associated with dry meadows at the beginning of the season and moist meadows at the end of the season. Soil moisture may explain some of the scale-specific responses of pollinator abundance to surrounding meadow habitat, though further investigation is necessary to

illuminate these hypotheses. *Apis mellifera* occurred in large complexes, consistent with the longer dispersal ability, and colony life-history pattern of this guild. This species also exhibited reciprocal abundance patterns in some meadow complexes where bees appear to move between meadows based on floral abundance. Solitary bees were more abundant in dry meadow habitat with more disturbed soil which they require for nesting . *Bombus* spp. were less abundant in meadows with low soil moisture and more abundant in moist habitat where floral resources persisted until the end of the season.

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## **CHAPTER 4 DIFFERENT MAJOR GENERALISTS IN DRY AND MOIST MEADOW POLLINATOR NETWORKS**

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In preparation for journal submission

## ABSTRACT

Montane meadows of the western Cascades range support a vast diversity of plant and pollinator species. This study tested how the diversity of these plant-pollinator networks is related to nestedness and generalization, properties of networks that are theoretically conducive to resilience. This study utilized plant and plant-pollinator interaction data from fifteen meadows surveyed six times over thirteen week period to quantify the structure of plant-pollinator networks. The meadows ranged in size from 0.1 to 8.1 ha, and also varied in their isolation from other meadows. This study (1) examined the relationship between species richness and generalization (2) quantified nestedness in observed networks and (3) identified plant and pollinator generalists that occurred in all fifteen surveyed meadows. Findings confirmed (1) increasing generalization among plants was associated with increasing richness of potential pollinators, and vice-versa; (2) all fifteen study meadows had significantly nested network structure; and (3) several species of plants were the dominant generalists in xeric meadows, whereas a single genus of pollinator was the dominant generalist in relatively moist study meadows. Despite high species diversity, consistent patterns of community level organization such as significant nestedness and pervasive generalization emerged across the study meadows, which spanned a range of meadow size and isolation.

## INTRODUCTION

Plant-pollinator interactions occurring within a given spatial and temporal extent have been increasingly studied as “pollination networks” (Bascompte et al. 2006, Vazquez 2009, Sabatino et al. 2010, Aizen et al. 2012, and Pocock et al. 2012). Pollination networks are defined as a bipartite network of plants and flower-visitors and visualized often as a qualitative or quantitative matrix. Empirical evidence characterizing pollinator networks requires a great sampling effort. The need to better understand this essential and threatened ecosystem service has fueled this investment at an accelerated pace in the past two decades.

The structure of plant-pollinator networks is a novel topic of interest generating lively debate in the past decade. Many structural statistics have been devised to assess and compare network structure. A link in a plant-pollinator network is defined as an interaction between a particular plant species and a particular pollinator within the network. The connectance of the network is defined as the proportion of realized links which occur based on the number of potential links (plants\*pollinators).

Flower-visitors are predominantly arthropods which make up well over 80% of animal species, and the vast diversity of arthropod communities trumps other descriptors as a typical condition of network structure. Jordano found typically, there are four times more pollinators than plants in pollinator networks. The overall connectance of plant-pollinator networks is considered low similar to other food webs and typically decreases with network size (Jordano 1987, Olesen and Jordano 2002, Devoto et al. 2005). Generalization as a widespread characteristic of pollination

networks has been repetitively revealed along with other general structural parameters (Moldenke 1975, Waser 1996).

Trait-matching, associated with specialization, and interaction neutrality, associated with generalization, are two major mechanisms used to describe plant-pollinator linkage. Trait-matching has been highlighted persistently for centuries in pair-specific evolutionary studies illuminating the presence of tight co-evolutionary relationships between plant-pollinator mutualists. In recent, community-wide studies of pollination dynamics, pervasive generalization has emerged over and over through results which indicate interaction neutrality may be used to describe the majority of link presence/absence, along with phenological overlap, although interaction neutrality patterns do not describe overall network structure (Waser et al. 1996, Vazquez 2005, Olesen et al. 2010). Phenophase overlap boosted the probability of links between plant and pollinator pairs in interaction networks, however, an extensively long period of overlap was required reach a high probability of linkage (Olesen et al. 2010). This result emphasizes the importance of the spatial and temporal distribution of plants and pollinators.

Interesting structural parameters of plant-pollinator networks have begun to emerge over the past two decades, with the movement of resources towards investigation of these communities. Contrasting the finding that connectance decreases with network size, occasional instances of increasing connectance with network size have been explained by generalization and optimal foraging theory, or more flexible use of resources with increased competition (Sabatino et al. 2010).

Lazaro et al. (2010) found no relationship between network size and connectance. A skewed distribution of links per species with many specialists and few generalists has been observed by several authors (Waser et al. 1996, Vazquez and Aizen 2003). It is unclear how much this finding is influence by the incredible richness of pollinators which characterizes datasets with a high proportion of visitors observed only once. Asymmetric connections between specialists to generalists is another frequent characteristic also described as the nestedness of networks where high degree species are more often linked with low degree species (Vazquez and Aizen, 2004, Bascompte et al. 2006). This structure is often overlayed by a compartmentalized or modular structure of clearly defined groups of species with many intragroup links and few intergroup links (Dicks et al. 2002, Guimaraes et al. 2007, Olesen et al. 2007). This finding at least emphasizes the low probability that tight co-evolutionary coupling is prevalent, an assumption once taken for granted. Robust behavior following extinctions based on redundancy inherent in generalized behavioral patterns has been inferred many times in recent literature. These later characteristics may be explained by sampling effects, though generalist rare species have often been identified in observed interaction networks (Bascompte et al. 2006). This “nested” network structure, characterized by asymmetric interaction strength and low connectance could occur as a result of probability where rare species are observed interacting with more common species (Dorado et al. 2011, Bluthgen et al. 2008). While generalization may be hypothesized to be defined by the number of plant species present, Frund et al. (2010) found that specialization did not differ across a gradient of flower diversity in

meadows in southern Germany. The interpretation of “nested networks” as robust and resistant to extinction was strongly criticized by Bluthgen et al. (2008) who concluded that most mutualistic networks show a higher degree of specialization and trait matching than expected based on neutral conditions when sampling effects are better controlled. Bluthgen et al. (2008) developed a revised statistical metric called specialization asymmetry to replace interaction strength asymmetry without such strong dependence on network size and sampling limitations. The apparent structure of pollinator networks might be expected to vary depending upon (1) the amount of time spent observing/counting interactions; (2) the sizes of the networks examined; and (3) seasonal, phenological changes in the composition of the community.

Multi-annual temporal variability is another pervasive characteristic of plant-pollinator networks. Several research programs have maintained monitoring programs for several years or more to better understand the temporal variability of plant-pollinator networks (Basilio et al. 2006, Alarcon et al. 2008, Olesen et al. 2008, Olesen et al. 2011, Petanidou et al. 2008, Vazquez et al. 2009). While some structural network properties such as network nestedness and connectance remained stable, there was high variability between the actual links present in networks or pairwise interactions. Petanidou et al. (2008) found 5% of interactions were present during all four years of a network interaction study, and Alarcon et al. (2008) found that 31% of links were present in 3 years of a network interaction study. Chacoff and Vazquez (unpublished) found that 15% of links were present in 3 years of a study (Vazquez et al. 2009). While abundance and temporal distribution allowed prediction of some

aggregate network properties, these characteristics did not predict the occurrence of pairwise interactions between years (Vazquez et al. 2009), contrasting results are described by Olesen et al. (2011). In Petanidou et al. (2008), through four years of year-round qualitative pollinator network data collection from a Mediterranean scrub community in Greece between 661 pollinators an 133 plant species, pollinator community was twice as variable as the plant community between years. In Olesen et al. (2011), rare specialist link turnover appeared driven by species turnover. For generalists, link turnover was driven by reshuffling of existing interactions accounting for 81% of link turnover, while only 19% of link turnover was driven by species turnover (Olesen et al. 2011).

Historical events are known to influence local community composition and structure (Ricklefs 1987, Herrera 1992). It has been shown that historical events act upon network structure as well as species presence/absence. As evidenced by temporal variability in plant-pollinator networks it is possible that colonization and extinction processes and dispersal significantly impact richness, evenness and network structural parameters. Albrecht et al. (2010) surveyed pollinator networks in subalpine meadows along a glacial foreland in the Swiss Alps to better understand network assembly. Bees were found at the younger sites, while flies dominated the older mature areas. The study showed an increase in generalization of pollinators but not plants with time. Authors cited optimal foraging theory to explain increasing pollinator generalization with higher plant diversity and increased pollinator density.

Pradal et al. (2009) described the phenological dynamics of an arctic plant-pollinator network throughout the season during two consecutive years. As plants and pollinators entered, established and exited the system, they obtained one or two links then gradually increased linkage, and after an average phenophase of 17 days, species lost links rapidly. Pollinators were removed with probability inversely proportion to their linkage level in a model that fit the observed patterns within a 95% confidence limit in both years despite high species turnover. Pollinators are empirically portrayed with high temporal variability based upon investigated plant-pollinator networks. Spatial variability is also expected because incredibly diverse pollinator species possess different life-history patterns and dispersal abilities, which we predict will cause them to respond to habitat, defined by unique species-specific parameters at different spatial scales.

Spatial distribution of habitat is known to affect species absence and presence, however, effects of landscape composition upon plant-pollinator network structure are emerging. In the Argentine sierra system, Aizen et al. (2012) found evidence for non-random loss of links in isolated sierras. Links that occurred with low frequency between interaction partners with low degree (i.e. high specialization) were found most vulnerable to disruption. Common, generalist interactions present in all sierras lost their central structural role in plant pollinator networks in the smaller sierras (Aizen et al. 2012).

In this study, we compared plant-pollinator networks across fifteen montane meadows in the western cascades to compare differences in network structure across a

gradient of meadow size, meadow complex size, and meadow moisture. Pollinator network structure was assessed using various structural statistics as well as some effects of species composition.

## METHODS

### *Study site description*

Fire is a major influential factor over the past millennium. The influence of native people on burns before 1850 is not well understood for this area, however, there is evidence for increased fire occurrence from European settlers along the Santiam wagon trail (Burke 1979; Hadley 1999). Halpern et al. (in press) conducted manipulative experiments on meadow restoration techniques in the Bunchgrass meadow complex. Tree removal with or without fire was shown to increase meadow species dramatically, at the expense of forest herbs. Fire dramatically decreased meadow herbs for at least 3 years after the treatment, but much diversity was restored following these treatments. Establishment of meadow species diversity was even faster in older forest patches than young forest patches contradicting hypotheses that forest soil changes would prevent reestablishment of meadow herbs (Halpern et al. in press).

### *Plant-pollinator surveys*

Plant-pollinator networks were surveyed in fifteen western Cascades montane meadows six times between 13 July and 13 September. Exhaustive floral surveys and 15 minute plant-pollinator interaction watches were conducted at ten permanent plots during each visit. Full sampling design, field methods, and data processing are described in Part II methods.

#### *Plant-pollinator network structure statistics*

Plant-pollinator networks are described as a matrix of interactions between plants and pollinators. In past studies, networks have been described by both qualitative link presence/absence, and quantitative links where each cell equals the frequency with which the link was realized. Full season networks for each study meadow were described using a variety of network statistics defined as follows.

Network Size is the product of the total number of plant and pollinator species, or the number of potential links within the network.

Link density is a quantitative measure based on abundance/distribution of interactions incurred. Link density is defined as the mean number of interactions per species or the total number of interactions divided by the total number of species (Tylianakis et al. 2007).

Species degree is one of the most basic descriptions of plant species and pollinator species behavior within the network. It is the “degree of generalization” exhibited by the species. The degree of an individual species is defined as the number of

interaction partners it obtains within the network. For pollinators, the degree equals the number of plants visited by each pollinator; and for plants, the degree equals the number of visiting pollinators.

*Network connectance* is defined as the realized proportion of possible links, or the number of links present divided by the size of the interaction network (number of links / plant species \* pollinator species) (Dunne et al. 2002). Network connectance discussed in the introduction section generally decreased with increasing network size.

*Nestedness* measures describe the topology of network structure, by measuring how species with low degree most often link to species with high degree, and species with high degree are often connected to many species with low degree. The weighted nestedness is calculated here, or nestedness based on the weight or frequency of interactions. The weighted nestedness measure approaches zero when the nestedness is similar to nestedness values for a similar randomly generated network. It approaches one as it nears a maximally nested arrangement. Negative weighted nestedness values are possible.

Nestedness measures first used to describe plant-pollinator networks were quickly found to be highly dependent upon network size and fill (Bascompte et al. 2003). Several qualitative nestedness measures emerged to correct for such biases, however, a weighted nestedness measure was not developed until 2009 to account for interaction abundance (Galeano et al. 2009).

*Robustness* is calculated as the area under the secondary extinction curve. When the modeled effect of secondary extinctions increases, robustness decreases. The

secondary extinction curve is modeled very simply by the subsequent removal of pollinator species from the network. As pollinator species are removed based on low abundance, then chosen randomly, plants only visited by the extinct pollinator are removed from the system. When extinctions incur only a slight effect on the total plant and pollinator populations, robustness is considered high (Memmott 2004).

#### *Plant-pollinator network visualization*

Plant-pollinator network visualizations were conducted using the Bipartite package implemented in R software (Dorman et al. 2009, R Development Core Team 2006).

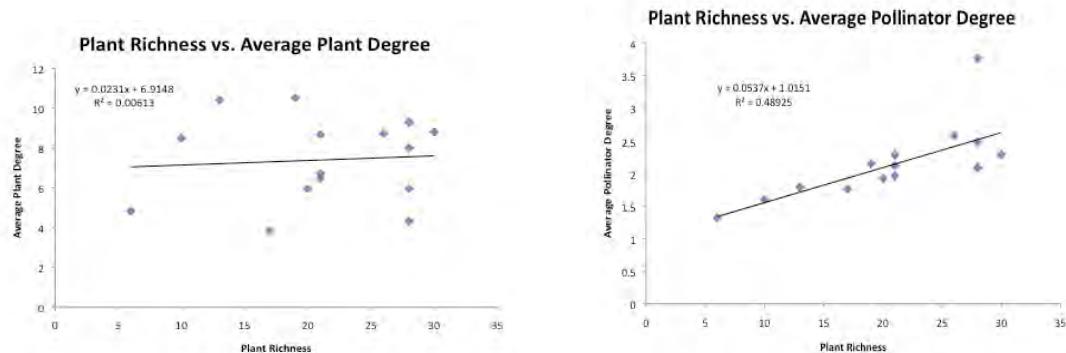
## RESULTS

#### *Network statistics and widespread generalization*

Plant-pollinator networks were described by various structural statistics developed in past studies. In past studies, qualitative networks have been described by link presence/absence and degree distributions while quantitative networks where interactions are weighted by frequency have been described by link asymmetry, link density, various measures of evenness and more complicated statistical models such as network “robustness” against secondary extinctions.

Some common results such as low overall connectance, an overlaid compartmentalized or modular structure, and network “nestedness” were observed. These structural conditions are all expected based on sampling artifacts, though they have been interpreted to represent ecologically meaningful mechanisms in recent literature.

Comparison of species richness to average degree showed that increased species richness was positively correlated with increased degree of the opposite group. Network plant richness did not have an effect on average plant degree. Increased pollinator richness was positively correlated with increased pollinator degree.

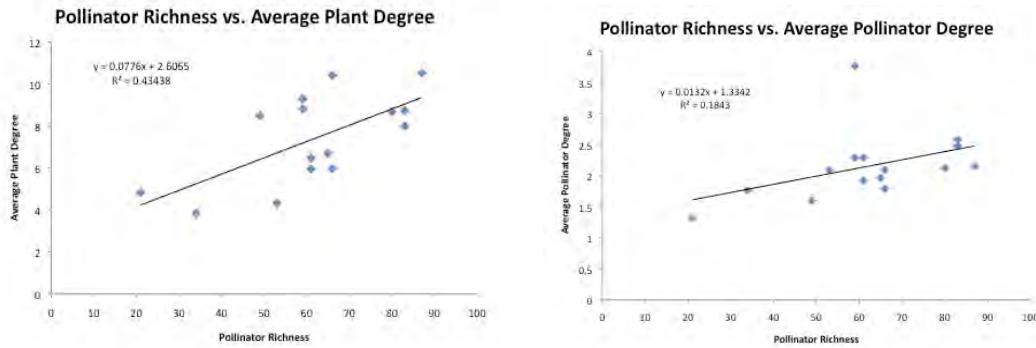


**Figure 11 Plant richness vs. average plant and pollinator species degree within each meadow network.** This figure shows comparisons between the plant richness and average species degree for each full season meadow network.

#### Plant Richness

Plant richness does not explain variation in plant degree ( $R^2 = 0.004$ ,  $p = 0.82$ ), which would have represented a pattern of pollinators choosing to visit a plant species of maximum benefit when provided the opportunity with increased plant richness. As expected, an increase in plant richness is significantly related to an increase in

pollinator degree and explains a large part of the variation in pollinator degree ( $R^2 = 0.48$ ,  $p = 0.004^{**}$ ). The linear slope is maintained even through the highest plant richness values for each full season meadow, indicating that increased degree did not level off at a certain threshold plant richness value in this system. Average pollinator degree increases by 5% with a 1% increase in network plant richness and 1% increase in pollinator richness over the extent of the dataset.



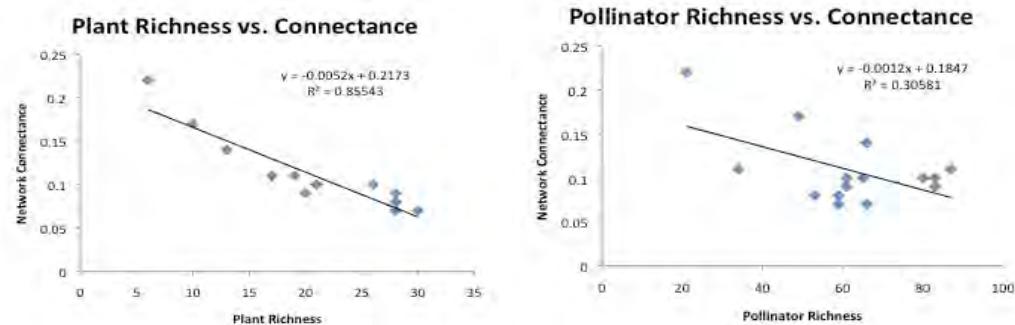
**Figure 12 Pollinator richness on average plant and pollinator species degree within each meadow network.** This figure shows comparisons between the pollinator richness and average species degree for each full season meadow network.

#### Pollinator Richness

Plant degree increased by 7% of pollinator richness, and pollinator degree increased by 5% of plant richness with rise in pollinator richness over the extent of the dataset. This growth differed dramatically in actual degree changes for plant and pollinator individuals because pollinator richness ranged between 20-100 while plant richness ranged between 5-35. Pollinator richness explains a significant amount of variation in plant degree ( $R^2 = 0.42$ ,  $p = 0.009$ ). Pollinator richness is not significantly

correlated to pollinator degree, but this correlation was almost significant ( $R^2 = 0.23$ ,  $p=0.07$ ).

### *Network Connectance*



**Figure 13 Plant and pollinator richness vs. network connectance.** This figure shows comparisons between the plant and pollinator richness and network connectance for each full season meadow network.

Network connectance is defined as the realized proportion of possible links, or the number of links present divided by the size of the interaction network (plant species \* pollinator species) (Dunne et al. 2002). Network connectance discussed in the introduction section decreased with increasing network size. Both positive and negative relationships have been described from this relationship in other systems. A positive relationship has been explained by optimal foraging theory or more flexible use of resources with increased competition. A negative relationship is the more common and intuitive result. Plant species richness and pollinator species richness are positively correlated, and both responded similarly, although plant species richness explained much more of the variation in the network connectance decline than

pollinator species richness. Plant richness explained connectance with high significance ( $R^2 = 0.84$ ,  $p = 1.45e-06$  \*\*\*). Pollinator richness explained connectance significantly ( $R^2 = 0.28$ ,  $p = 0.042*$ ).

### *Nested Networks*

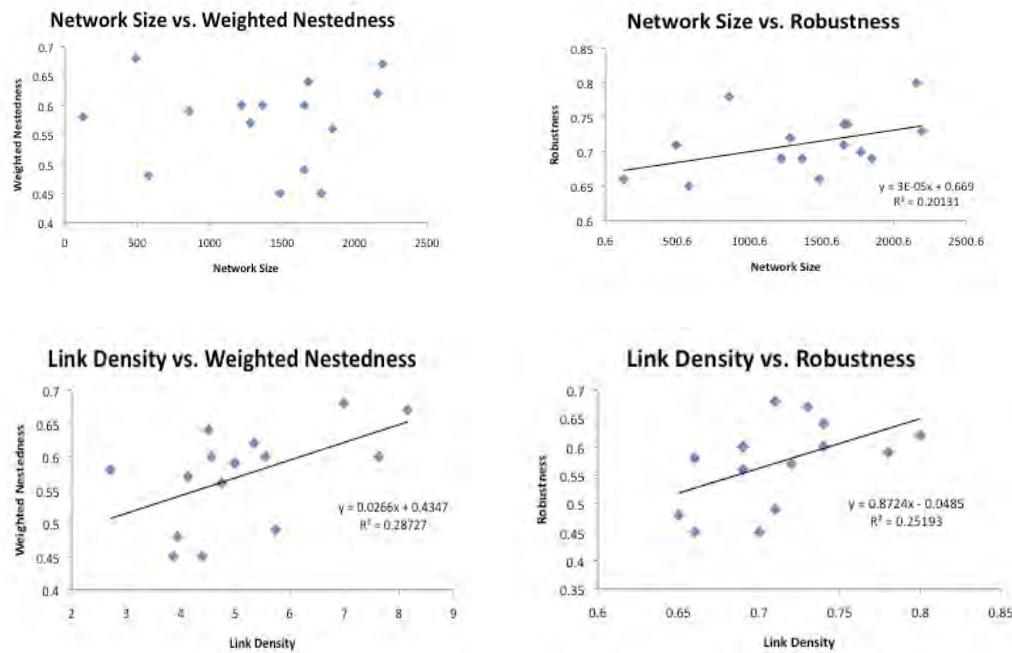
Networks were all found to be highly significantly nested when compared to null models of similar size and fill. Past literature has associated nested network structure with increased resilience to perturbation caused by local extinctions.

**Table 6 Full season meadow network statistics.** This table shows several network statistics of interest for all study meadows based on full season data.

Meadow	Size	Network Nestedness	p value	Robustness	Link density
BD	490	0.68	0.0	0.71	6.99
BH	858	0.59	0.0	0.78	4.99
BS	126	0.58	1.56E-09	0.66	2.71
CNE	1652	0.49	0.0	0.71	5.74
CNM	1680	0.64	0.0	0.74	4.51
CNT	1848	0.56	0.0	0.69	4.75
CPB	1484	0.45	0.0	0.66	3.87
CPM	1770	0.45	0.0	0.70	4.39
CPR	578	0.48	2.22E-16	0.65	3.94
CPS	1365	0.60	0.0	0.69	4.56
LM	2194	0.67	0.0	0.73	8.16
LO	1653	0.60	0.0	0.74	7.63
M2	2158	0.62	0.0	0.80	5.34
RP1	1220	0.60	0.0	0.69	5.55
RP2	1281	0.57	0.0	0.72	4.13

While network size is not a predictor of nestedness or network robustness (following sequential extinction of pollinators based on linkage), link density is a

significant predictor of weighted nestedness and likely robustness as well. Link density and network size show only a slight positive relationship ( $R^2 = 0.16$ )



**Figure 14 Network size and link density vs. network nestedness and robustness.** This figure illustrates the effect of network size and link density upon network weighted nestedness and network robustness following sequential pollinator extinctions

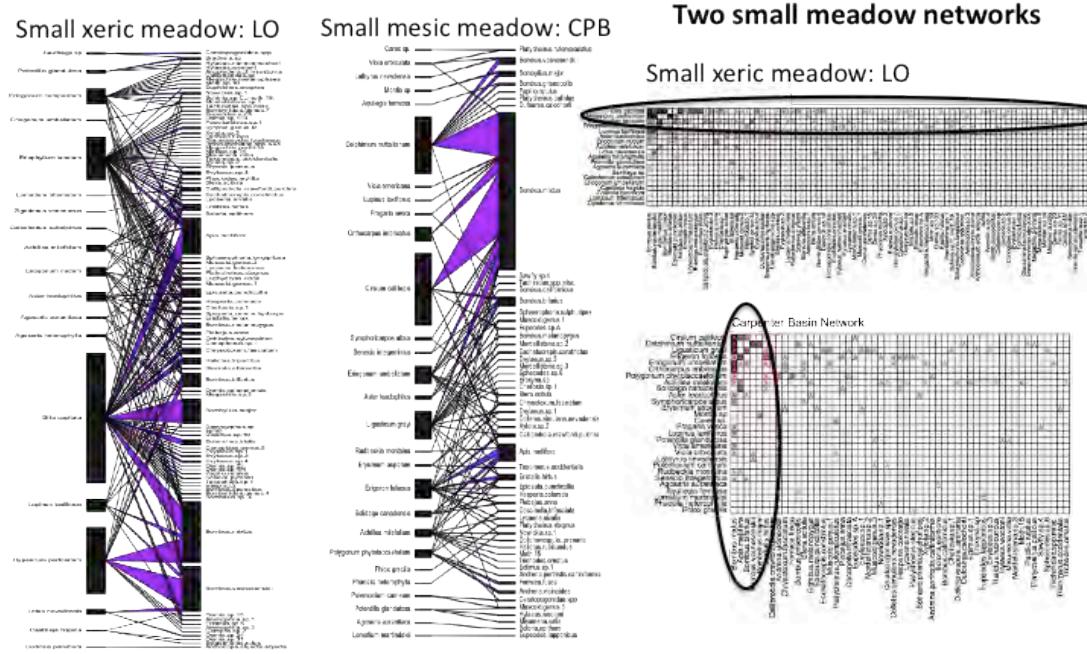
#### *Impacts of major generalists in the network*

The impact of major generalists differed between meadows based on the relative soil moisture of the meadow, a limitation to floral abundance at the beginning and end of the season.

Many of the very dry, xeric meadows exhibited very pronounced position of super generalist flowers in the network. The most moist meadows exhibited a more

pronounced position of the most generalist pollinators (often *Bombus* spp.) in the full season network.

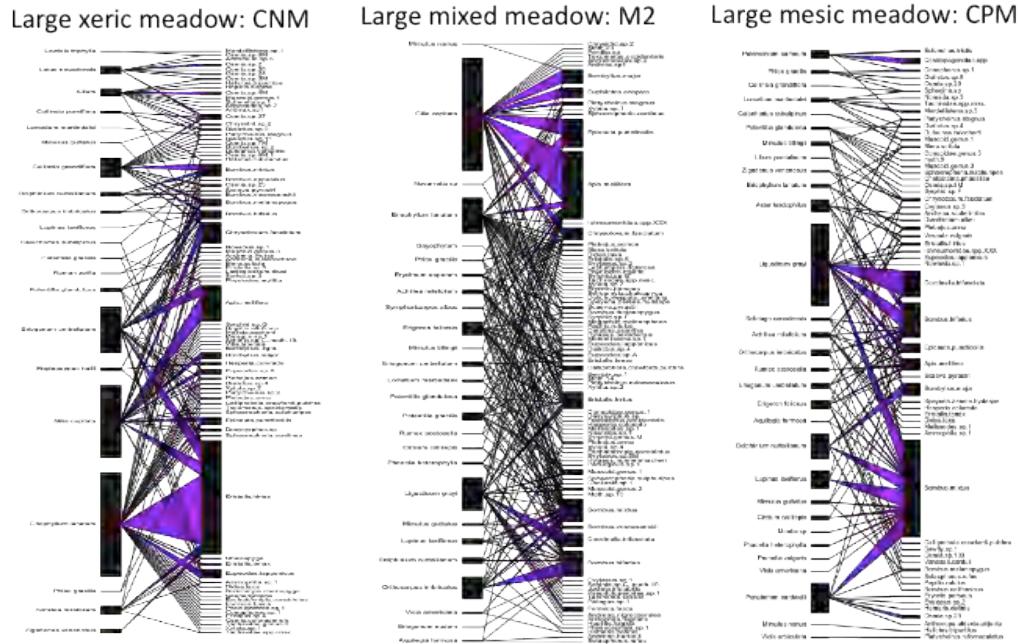
### Small Meadow Plant-pollinator Networks



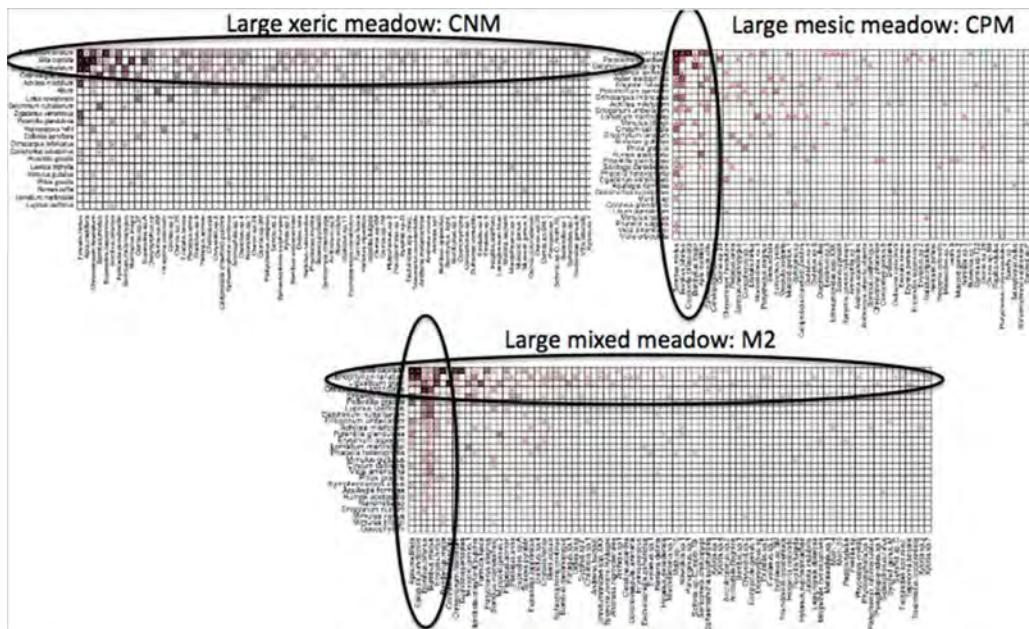
**Figure 15 Small meadow network generalists.** This figure shows the position of super-generalists within several small meadow networks

This trend was also exhibited not only in small meadows but in the large meadows as well. The large meadows were more likely to support mixed xeric and mesic habitat; some of these meadows exhibited both patterns of super-generalist plants and pollinators.

## Large Meadow Plant-Pollinator Networks



## Plant-Pollinator Network Matrices



**Figure 16 Large meadow network generalists.** This figure shows network visualizations with corresponding matrices exhibiting the impact of super-generalists in the network.

## DISCUSSION

Widespread generalization was also documented across the networks with significant linear models describing the correlated increase in species degree with increased richness of the interaction partner. Increased plant richness is, as expected, significantly related to an increase in pollinator degree and explains a large part of the variation in pollinator degree ( $R^2 = 0.48$ ,  $p = 0.00430^{**}$ ). Network plant richness did not cause a decline in average plant degree, which could have indicated that pollinators specialize when given the opportunity, in more abundant and rich systems due to parallel competitive advantages. Pollinator richness is not associated with a decline in pollinator degree, but rather an insignificant increase in degree. This also does not provide support a competitive exclusion hypothesis.

Plant-pollinator networks exhibited some structural patterns similar to networks assessed through similar methods. Significantly nested structure in all networks supported past documentation of this pervasive structural pattern. Despite improvement of index calculation techniques, further investigation is necessary to tease apart the identifiable sampling effects that may obscure our perception of the actual network structure.

While the significant association of network “nestedness” and robustness with link density is not unexpected it underscores the need to further examine the impact of sampling effects on weighted nestedness. It is likely that very rich networks may be

more undersampled than smaller networks, obscuring modeled results such as “robustness” statistics.

The effects of super-generalists in plant-pollinator networks have not been widely studies yet likely impact networks very strongly. Phenological limitations may well explain the prominence of generalist plants over generalist pollinators in very dry montane meadows, as all pollinators must use the same resources before they desiccate. This is likely an important area of study given that the most super-generalist pollinator in our study system has incurred serious population declines in the past few decades in some regions.

## CONCLUSIONS

While species richness of plant-pollinator interactions influenced the overall and species-specific linkage of plant-pollinator networks, meadow moisture, a physical environmental descriptor with implications for resource availability, exhibited structural implications for pollination networks as well. As pollinator richness increased, so did the number of interaction partners of each flower species, and linkage density within the network, while connectivity of the network decreased. However, linkage density and not network size resulted in stronger effects on network nestedness and robustness: two emerging network characteristics, that have been associated with highly ecologically significant interpretations. The effect of sampling effort is a question of upmost concern for more accurate assessment of plant-pollinator

network structure. Further assessment of actual network structure is likely to lead to interesting future questions regarding the response of plant-pollinator networks to environmental change.

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## CHAPTER 5 CONCLUSIONS

In the past two decades, energy intensive investigation of plant-pollinator networks across several continents have shed light on pervasive and variable network structural parameters. However, ecological mechanisms explaining network structure are still quite undefined, as are specific habitat requirements and natural history of most native pollinators. Long-term data regarding plant and pollinator phenology exists from very few, valuable research centers. Increased attention to pollination services, and increased awareness of their value for our culture and our society, will almost certainly improve our ability to undertake restoration and conservation strategies to improve the capacity of human dominated landscapes to support diverse pollination services.

In this study of fifteen 0.12 to 8.12 ha meadows in the Cascade Range of Oregon surrounded by a range of different meadow configurations, floral richness was found to be very high in both small and large meadows along the Western Cascades crest, but much lower in the more isolated Bunchgrass meadow complex. These patterns suggest that flowering species richness is the result of meta-population dynamics over very long temporal scales, as small and large meadows in the western cascades complexes were likely connected before the encroachment of conifer forest under fire suppression. Pollinator richness responded to closer scales of habitat, which have changed significantly in the past century, indicating a faster response to vegetation changes in the surrounding landscape.

The density of flowers and of flower-pollinator interactions were significantly positively correlated to meadow size (measured as the open area bounded by forest). Hence, flower and pollinator populations may decline not only due to increased meadow loss, but also due to increased meadow fragmentation. While floral species richness was almost significantly related to complex size (surrounding habitat within 3000m), the richness, evenness and diversity of pollinators and plant-pollinator interactions were best explained by the amount of meadow habitat at two different spatial scales: within 250/500m and 1000m/1500m of the sampled meadow. This is thought to be caused by different mobility limitations of pollinator species. Richness of pollinators and of flower species increased with abundance of pollinators and flower species, but pollinator richness increased at twice the rate of floral richness.

Western Cascades montane meadows are characterized by diverse conditions of meadow moisture which likely influence the dynamics and components of communities within a very short, seasonally-constrained system. Results suggest weak effects of soil moisture on individual species or guild abundance, due to unique habitat requirements, such as late season floral abundance. Flower and pollinator abundance were slightly associated with dry meadows at the beginning of the season and moist meadows at the end of the season. *Apis mellifera* occurred in large complexes, consistent with the longer dispersal ability, and colony life-history pattern of this guild. This species also exhibited reciprocal abundance patterns in some meadow complexes where bees appear to move between meadows based on floral abundance. Solitary bees were more abundant in dry meadow habitat with more

disturbed soil which they require for nesting . *Bombus* spp. were less abundant in meadows with low soil moisture and more abundant in moist habitat where floral resources persisted until the end of the season.

In full season pollination networks, species richness affected several structural aspects of network architecture. As pollinator richness increased, so did the number of interaction partners of each flower species, and linkage density within the network, while connectivity of the network decreased. However, linkage density and not network size resulted in the strongest effects on network nestedness and robustness, two emerging network characteristics that have been interpreted with ecologically significant implications. The effect of sampling effort is a question of upmost concern for more accurate assessment of plant-pollinator network structure. Further assessment of actual network structure is likely to lead to interesting future questions regarding the response of plant-pollinator networks to environmental change.

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## **APPENDICES**

## APPENDIX A SAMPLING

**Table A1 Sampling dates for each meadow.** Plant and pollinator interactions were surveyed within fifteen study meadows throughout the 2011 growing season. Meadows were visited 5-6 times during the summer between 13 July – 13 September. Visitation dates are shown below using ordinal dates (between 1-366 starting with 1 on 1 January) according to the schedule shown below. In all full season analyses, only data from day 196 was used from watch 1 at the Cone Peak sites, because Cone Peak sites were sampled an extra time on date 203.

Meadow	Watch 1	Watch 2	Watch 3	Watch 4	Watch 5	Watch 6
CPR	194	207	214	221	230	251**
CPB	194	207	214	221	230	251
CPM	194	205	217	221	230	256
CPS	194*	202	214	221	229	256**
M2	195	207	216	229	234	252
RP1	195	207/208	215	228	238	255
RP2	195	207/208	215	228	238	255**
LM	201	208	216	222	233	254
LO	204	210	216	223	233	254
BS	201	208	214	227	X**	255**
BH	201	208	214	227	X	255**
BD	X	206	215	226	234	255
CNT	196 & 203	209	217	224	232	250
CNE	196 & 203	209	217	224	232	250
CNM	196 & 203	209	217	224	232	250

**194-209 Early Season (15 days: 13 July - 28 July) - Watches 1, 2 -**

**214-229 Mid-Season (15 days: 2 Aug – 17 Aug) - Watches 3, 4 -**

**230-256 Late-Season (25 days: 18 Aug – 12 Sept) - Watches 5, 6 -**

**No visits 238-250**

\*Only flower plots were surveyed, but no pollinator watches

\*\*Upon plot observation no flowers were located in any of the 10 plots so no pollinator watches occurred.

**X indicates where no plots were visited**

## Study Meadow Details

*Cone Peak meadows* are located at the north edge of the study area, due east of Corvallis above highway 20 (44°24'32" N, 122°08'02" W). The Cone Peak meadow complex contains the largest amount of meadow habitat. This extensive complex spreads from Iron Mountain across the Cone Peak ridges. Vast expanses of dry, rocky xeric meadow area are characterized by very shallow soils and exposed bedrock. Occasional drainage paths and seeps support local patches of mesic meadow flora. Sparse forested corridors shelter shade-dwelling wildflowers and ferns.

CNE: Cone Meadow E is a small oblong basin meadow aligned with the contours of the mountain positioned about 200m downslope of Cone Main. The xeric meadow intersects a drainage path supporting a corridor of moist floral habitat and a *Rubus* thicket at its downslope exit point. Although a small portion of the meadow remained moist throughout the summer and supported mesic vegetation, most of the meadow consisted of exposed bedrock and very thin soil.

CNM: Cone Main Meadow is a large xeric meadow located at the top of Cone Peak. This extensive meadow is regionally acclaimed for its huge diversity and abundance of early season flowers in very shallow soils. The meadow is similar in size to the large meadows on Carpenter, Frissell, and Lookout Mountains. It is adjacent to other xeric meadows several times its size which extend across neighboring ridges. A peak on the east edge of the sampling site supplies snowmelt drainage passing through Cone Main meadow. This corridor and several nearby small basins provide small areas of mesic meadow habitat.

CNT: Cone Tip is a small “V” shaped meadow at the end of Cone Main. This little meadow is positioned on the upper plateau of Cone Mountain and is separated from the main meadow by a 25m wide stand of conifer forest.

*Carpenter Mountain meadows* are located due south of Cone Mountain at the North-eastern corner of H.J. Andrews Forest Long-term Ecological Research Forest (LTER) ( $44^{\circ}16'52''$  N,  $122^{\circ}08'37''$  W). This meadow complex consists of many isolated small- and medium-sized meadows with one large meadow on the south-west facing slope of the mountain. This complex contains less total but more mesic meadow habitat than Frissell Ridge or Lookout Mountain. Much of this complex has been colonized by coniferous forest in the past 60 years since 1946. Carpenter meadows have deeper soil which retains more moisture in the late summer compared to the other meadows.

CPB: Carpenter Basin is a small/medium-sized basin meadow located on the northwestern slope of Carpenter Mountain. The meadow lies at the bottom of a steep northern slope descending from the ridge protruding westward from Carpenter Mountain. The meadow is predominantly mesic vegetation. An ephemeral stream occupies the western side and the northern boundary of the meadow.

CPM: Carpenter Main Meadow is located on the western slope of Carpenter Mountain near the summit. The upper central meadow consists of xeric meadow with large areas of bare soil. Several drainage paths pass through the meadow. The

southern half of the meadows supports dense ferns which overtake the wildflowers near the end of the summer.

CPR: Carpenter Ridge meadow is a tiny meadow on the end of a ridge extending west from Carpenter Mountain. A bedrock bluff supports a very, very thin and patchy distribution of organic-rich soil.

CPS: Carpenter Saddle meadow is a long meadow located adjacent to the road leading to Carpenter Mountain on a broad saddle. Bedrock is exposed in the center of the meadow. The eastern slope of the meadow descends steeply into thick vegetation and brush. The western edge of the meadow was developed into a dirt and gravel forest road leading to Carpenter Main meadow.

*Frissell Ridge meadows* are located in the middle of Frissell Ridge, which forms the eastern edge of H.J. Andrews Forest, and links Carpenter Mountain to the north and Lookout Mountain to the south ( $44^{\circ}14'47''$  N,  $122^{\circ}07'38''$  W). Several other large meadows and medium to small meadows occur in neighboring meadow complexes on Frissell Ridge. A road corridor containing meadow plant species connects some of the meadows across the ridge. The Frissell Ridge meadows are predominantly, moderately sized and contain both mesic (wet) and xeric (dry) habitat supporting diverse plant species.

M2: M2 is a large, slightly convex west-facing meadow, centrally positioned in the middle of Frissell Ridge. The meadow crests the top of the ridge and descends

into more irregularly branching meadow on the east side of the ridge. This meadow also is adjacent to the unpaved forest road.

**RP1:** RP1 is a small southwest-facing xeric meadow located on a ridge extending west from M2 in the middle of Frissell Ridge. This oblong meadow extends down the south facing slope of the ridge, and it is located in the middle of a short string of small meadows.

**RP2:** RP2 is a small west-facing xeric meadow located on the ridge extending west from M2 in the middle of Frissell Ridge, adjacent to and slightly northwest of RP1. This steep xeric meadow is notable for a tall outcrop ridge-capping andesite/basalt formation.

*Lookout Mountain meadows* are located at the southeastern corner of H.J. Andrews Forest and the southern edge of the study extent ( $44^{\circ}12'15''$  N,  $122^{\circ}07'49''$  W). This complex consists of one large meadow and many small to medium sized meadows spread across a wide area. This complex has lost a roughly half of its area (Rice 2009, Takaoka and Swanson 2008) within the past 50 years, however it still remains quite large.

**LM:** Lookout Main meadow is a large meadow located on the western side of the north-south trending crest of Lookout Mountain. This very large meadow supports a wide range of moist and dry habitat, but the meadow dries quickly. Despite their similar sizes, LM meadow contains much more xeric habitat than M2. The LM meadow is convex and very open and exposed to prevailing winds. Clouds often hit

this most exposed mountain protruding westward from the main western Cascades Ridge: This meadow was considered to be the most exposed with the highest count of breezy watch minutes.

LO: Lookout Outcrop is a small very steep, rocky meadow located on the South side of Lookout Mountain. The meadow is surrounded by similar small xeric meadows, although a large amount of meadow habitat has been colonized by forest in the past 60 years. It is difficult to climb up and down this meadow due to the very steep terrain. The substrate for this xeric meadow consists of bare rock and thin very shallow soils. Small rocky outcrops and fractures in the steeply descending southern face catch and retain some water supporting thickets of berry bushes and occasional columbine.

*Bunchgrass Meadows* are located due east of Carpenter Mountain on the western slope of the High Cascades ( $44^{\circ}16'36''$  N,  $121^{\circ}57'32''$  W). The High Cascades are much younger (<2 m-yr), deep lava flows, compared to the western Cascades (25-35-m yrs) where all other study meadows are located. This complex consists of a very dense group of core meadows, and very little meadow habitat surrounding this core. The complex lies on a sloping high plateau surrounded by forest dominated by *Abies grandis* and *Pinus contorta* (Halpern et al. in press). Bunchgrass Ridge may have formed by glacial reworking of a lava flow, producing a long, very gently sloping, truncated plateau-like feature (F.J. Swanson, personal communication). Soil profiles indicate that grassland has dominated this site for centuries (Haugo and Halpern

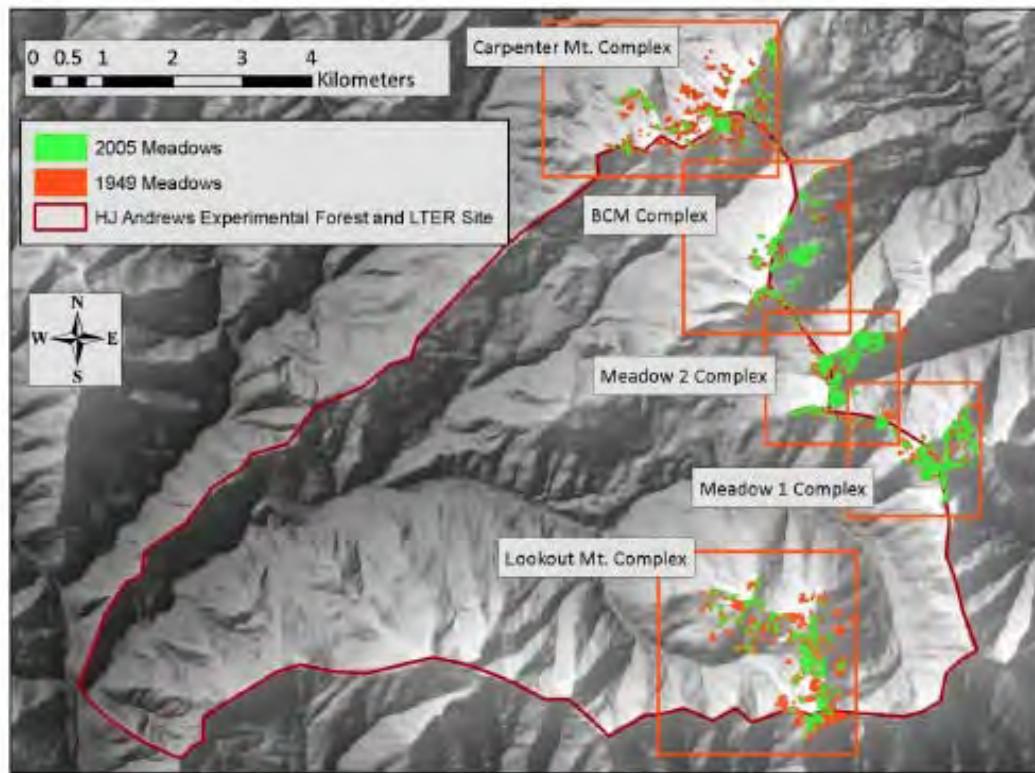
2007). Soils are deep (>1.7m), well-drained, fine to very fine sandy loams, with dense grass cover. Parts of these meadows retained water from snowmelt very early in the season, but plant-available soil moisture throughout the season was low (despite high values of the topographic convergence index).

**BD:** Bunchgrass Dragon is a small flat meadow on the western periphery of the complex. The meadow is adjacent to other large and small similar meadows.

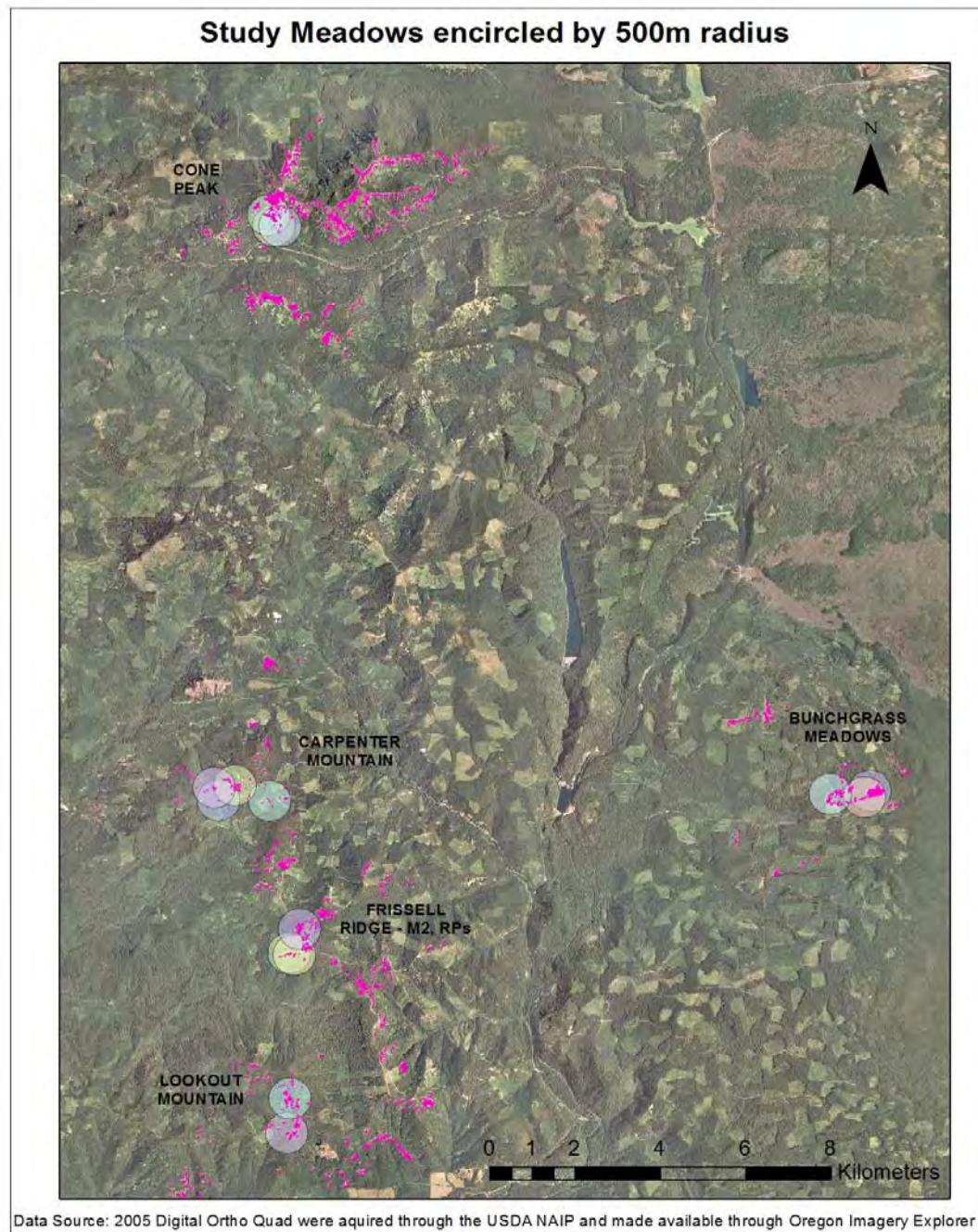
**BH:** Bunchgrass Hall is a small, flat, long, narrow meadow. The eastern end of the meadow is adjacent to the largest meadow in the complex, Bunchgrass Summit. This meadow stretches west toward the middle of the complex and supported the most diverse floral and pollinator populations within the Bunchgrass complex.

**BS:** Bunchgrass Summit is a very, very large meadow at the eastern edge of the Bunchgrass complex. It is the biggest meadow in this complex, and its easternmost edge is the highest area in the complex. The meadow is underlain by deep, well-drained, fine-textured soils, and covered with and dense grass cover, and very low pollinator and especially floral diversity.

## MEADOW CONTRACTION 1949-2005



**Figure A1 Meadow contraction 1949-2005 in H.J. Andrews forest meadow complexes.** This figure, created by Steven Highland (2009), shows the loss of natural meadow between 1949 and 2005 based on digitized montane meadows surrounding Frissell ridge at the H.J. Andrews Forest, OR observed from aerial photos.



**Figure A2 Aerial imagery of all study meadow complexes.** This figure shows the 2005 aerial photo of the study landscape with naturally occurring meadows in the 3000m vicinity of study meadows shaded in pink. The 500m landscape sector is shown with transparent tint around each study meadow.

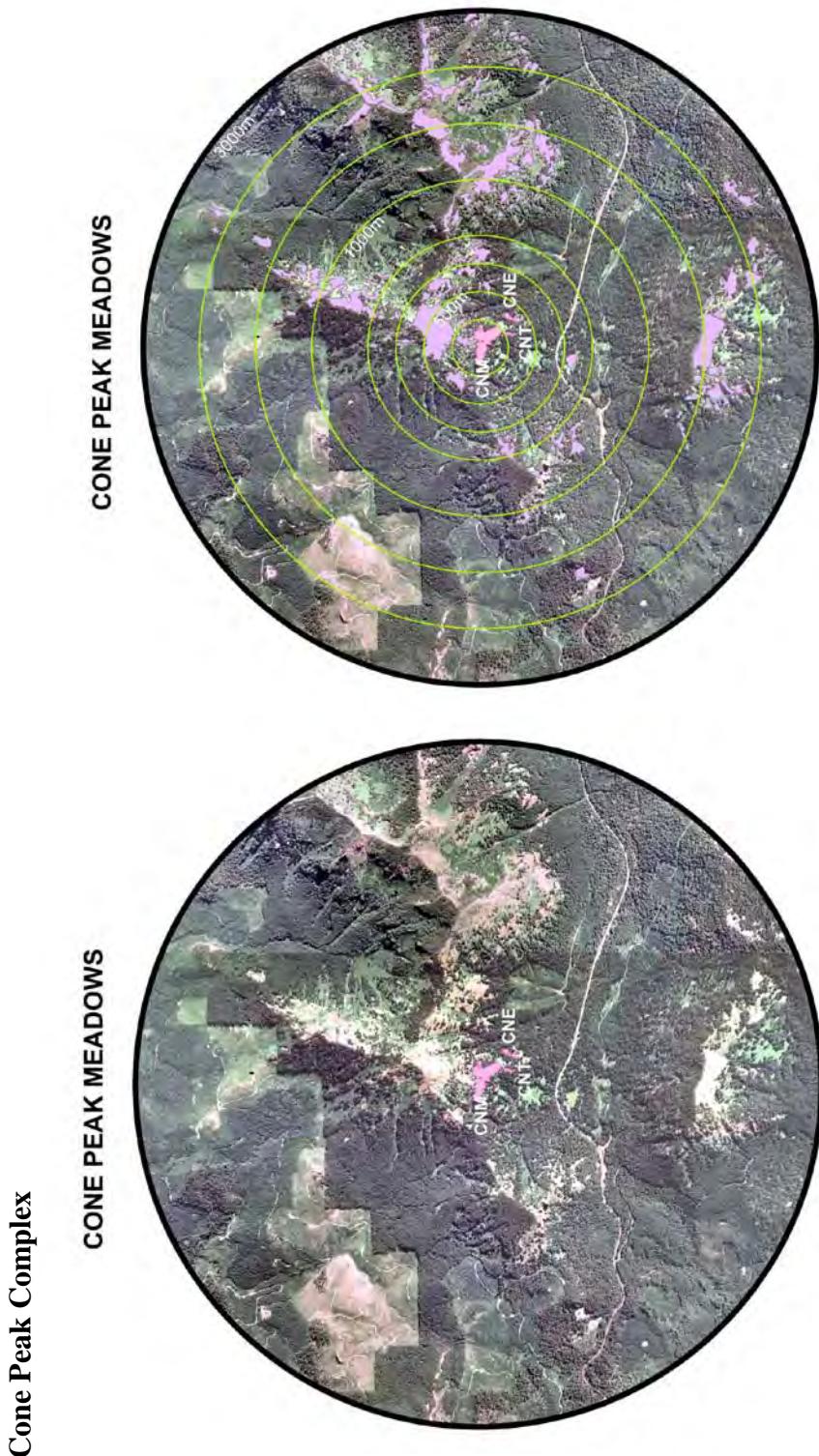
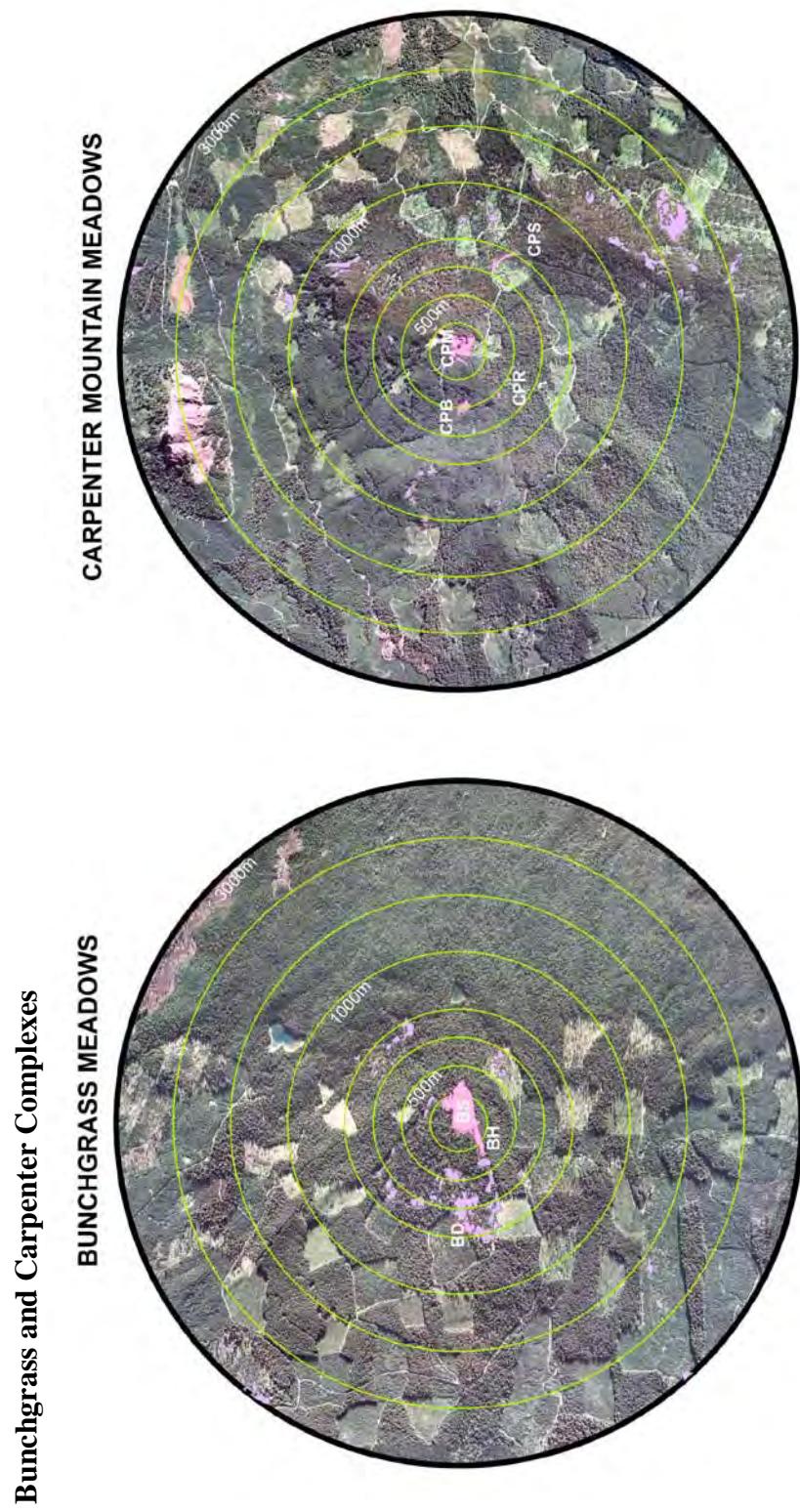


Figure A3 Meadow area within the 3000m landscape sector surrounding Cone Peak main meadow. This figure shows the three Cone Peak study meadows in pink on 2005 aerial imagery. In the figure on the right, natural meadow area identified by light brown or green shade, homogeneous texture, and irregular boarders is shown in purple within the 3000 m landscape sector surrounding Cone Main.



**Figure A4 Meadow area within the 3000m landscape sectors surrounding Bunchgrass Summit and Carpenter Main meadows.** This figure shows the three Bunchgrass study meadows and four Carpenter meadows in pink inside the 3000m landscape sectors surrounding Bunchgrass Summit and Carpenter Main meadows on 2005 aerial imagery. Natural meadow area designated by lavender polygons, were digitized based on their light brown or green, homogeneous appearance and irregular boarders.

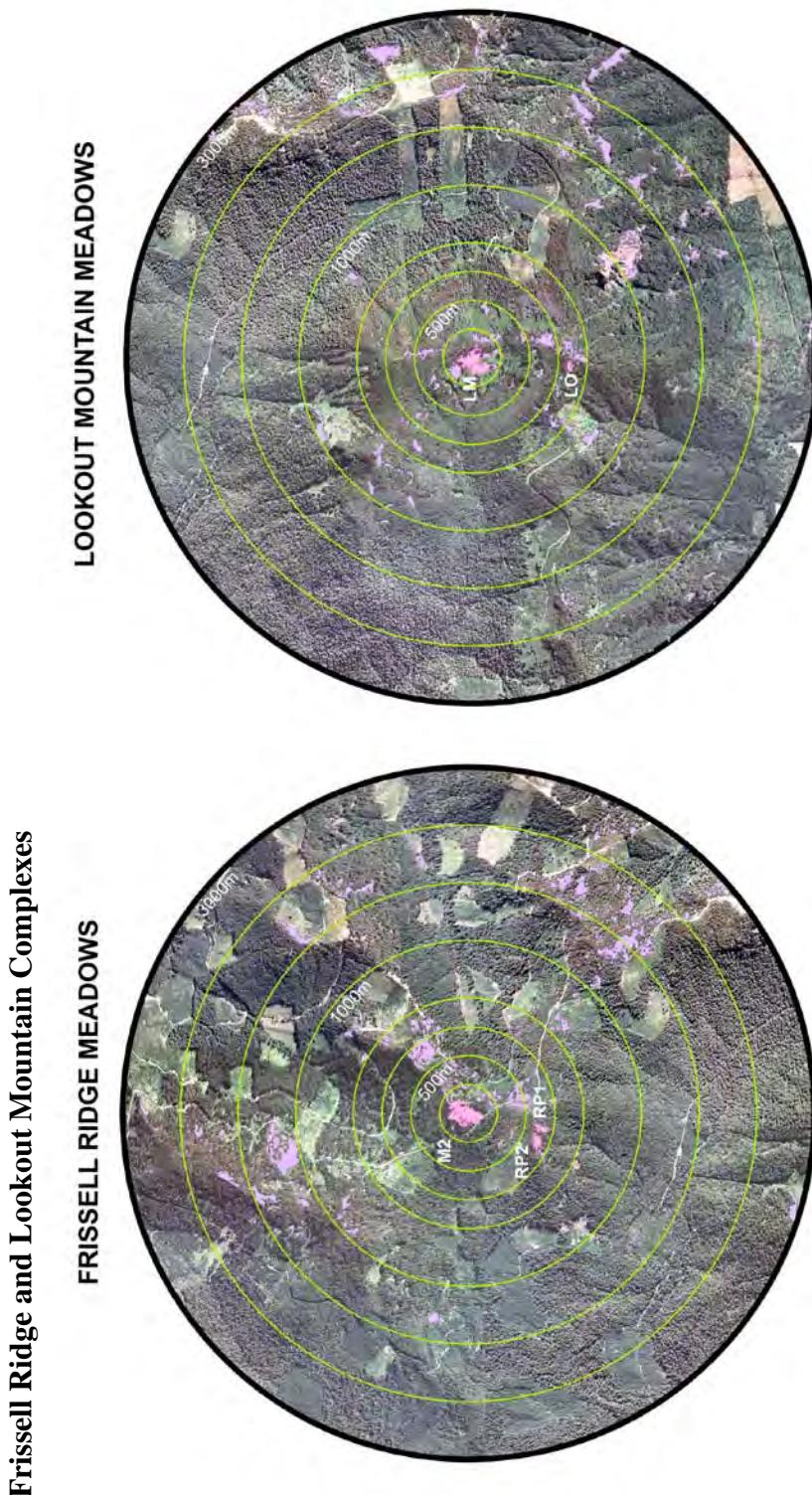
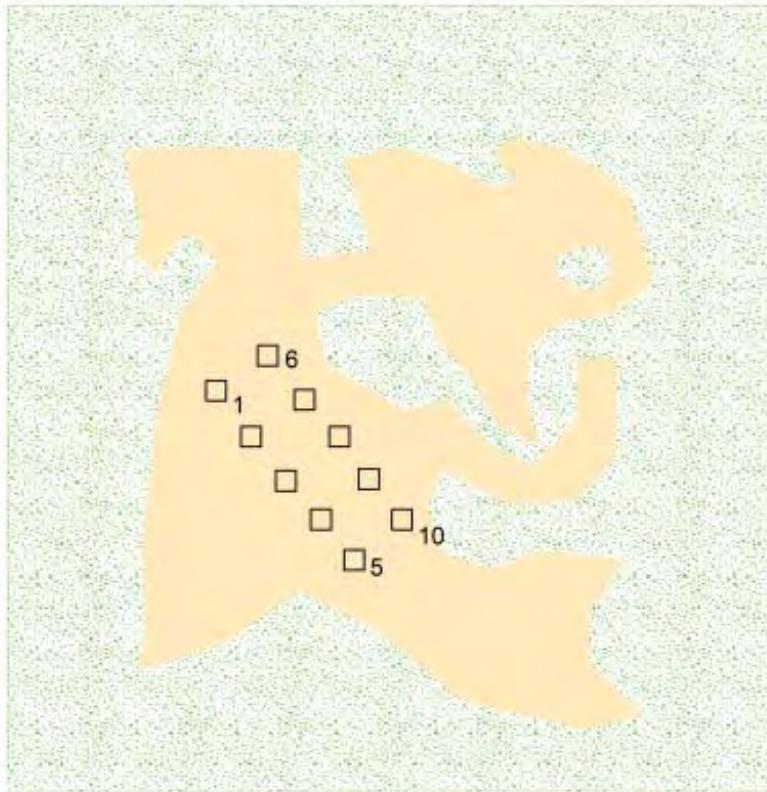


Figure A5 Meadow area within the 3000m landscape sectors surrounding M2 and Lookout Main meadows. This figure shows the three Bunchgrass study meadows and four Carpenter meadows in pink inside the 3000m landscape sectors surrounding Bunchgrass Summit and Carpenter Main meadows on 2005 aerial imagery. Natural meadow area designated by lavender polygons, were digitized based on their light brown or green, homogeneous appearance and irregular borders.

## Sample plot layout



**Figure A6 Plot survey design.** This figure presents the sample layout of the ten permanent plots along two parallel transects. Plot layout was structured similarly in each study meadow. The beige shape represents Carpenter Main meadow area and the two 60 m plot transects are oriented parallel to each other, 20 m apart, along the longest meadow diameter. Five plots are spaced 15m apart along each transect.

**Table A2 Weather conditions recorded in each study meadow.** This table shows the number of total observation minutes recorded from each weather category from all visits throughout the season and the interaction rate during these minutes. The interaction rate is the number of observations that occurred during the recorded minutes divided by the number of minutes recorded. No minutes were recorded in plots where no flowers were in anthesis. Fifty-one additional minutes were removed because it was unclear if an interaction had occurred or the visitor observation not identifiable to order.

	Sunny		Cloudy		Sunny, Breezy		Cloudy, Breezy		Shady	
Meadow	MIN	IR	MIN	IR	MIN	IR	MIN	IR	MIN	IR
<b>BD</b>	253	0.75	20	0.30	185	0.53	12	0.17	0	X
<b>BH</b>	296	1.76	30	1.00	209	0.97	2	1.00	0	X
<b>BS</b>	266	0.45	0	X	152	0.37	0	X	0	X
<b>CPB</b>	672	0.74	58	0.24	85	1.11	14	0.14	22	0.00
<b>CPM</b>	412	0.88	5	0.00	334	0.93	15	0.00	0	X
<b>CPR</b>	400	0.65	3	0.00	113	0.60	0	X	20	0.30
<b>CPS</b>	432	1.59	0	X	78	0.62	0	X	0	X
<b>CNE</b>	505	0.51	5	0.00	227	0.25	10	0.00	15	X
<b>CNM</b>	590	1.87	0	X	204	0.52	10	X	0	X
<b>CNT</b>	518	0.93	17	1.00	214	0.59	6	X	122	0.40
<b>M2</b>	660	1.97	29	0.55	161	2.66	3	1.67	0	X
<b>RP1</b>	603	0.76	5	0.00	107	0.50	20	0.10	0	X
<b>RP2</b>	355	0.60	1	0.00	342	1.25	37	0.30	0	X
<b>LM</b>	225	0.64	2	1.00	537	1.02	29	0.14	0	X
<b>LO</b>	427	1.33	30	0.13	269	0.91	0	X	0	X

**Table A3 Weather conditions in each observation round.** This table shows the number of minutes recorded under each weather condition during each observation round and the interaction rate in interactions per minute from each weather pattern/sampling round combination.

	Sunny		Cloudy		Sunny, Breezy		Cloudy, Breezy		Shady	
Meadow	MIN	IR	MIN	IR	MIN	IR	MIN	IR	MIN	IR
<b>W1</b>	897	0.62	135	0.34	509	0.27	93	0.18	62	0.13
<b>W2</b>	987	1.75	50	0.52	813	0.97	35	0.31	57	0.32
<b>W3</b>	1021	1.19	3	1.00	975	0.99	6	0.00	5	0.80
<b>W4</b>	1202	1.49	0		764	1.20	0		10	1.30
<b>W5</b>	1674	0.89	0		0		0		0	
<b>W6</b>	673	0.32	0		13	0.08	0		0	

**Table A4 Weather conditions of minutes observed during each meadow watch.**

This table shows the number of minutes observed under each weather condition broken down by watch date in each meadow. The two additional right columns note the total number of minutes observed per watch in each meadow and the number of plots in which no flowers were in anthesis (plots in which no pollinator watch was initiated).

Meadow	Sunny Still	Cloudy Still	Sunny Breezy	Cloudy Breezy	Shady	Total Minutes	Plots w/o flowers
BD 1						0	
BD 2		20	47	12		79	1
BD 3	103		33			136	1
BD 4			105			105	3
BD 5	120					120	2
BD 6	30					30	8
BH 1	116	30	2	2		150	
BH 2	114		4			118	2
BH 3	66		54			120	2
BH 4			149			149	
BH 5						0	
BH 6						0	
BS 1	117		31			148	
BS 2	86		34			120	2
BS 3	63		27			90	4
BS 4			60			60	6
BS 5						0	
BS 6						0	
CPB 1	85	34	1		15	135	2
CPB 2	47	24	55	14	7	147	1
CPB 3	105		29			134	1
CPB 4	135					135	1
CPB 5	150					150	
CPB 6	150					150	
CPM 1	24	5	60	15		104	3
CPM 2			138			138	2
CPM 3	148		2			150	
CPM 4	15		134			149	
CPM 5	150					150	
CPM 6	75					75	5
CPR 1	87	3				90	4
CPR 2	43		27		20	90	4
CPR 3	60		86			146	
CPR 4	120					120	2

CPR 5	90				90	4
CPR 6					0	
CPS 1					0	
CPS 2	135				135	1
CPS 3	60	60			120	2
CPS 4	103		18		121	2
CPS 5	134				134	1
CPS 6					0	
CNE 1	74	2	11	2	89	4
CNE 2	43		76		119	
CNE 3	44		90		134	1
CNE 4	120				120	2
CNE 5	120				120	2
CNE 6	60				60	6
CNM 1	36		110		146	
CNM 2	105				105	2
CNM 3	98		22		120	2
CNM 4	134				134	1
CNM 5	104				104	3
CNM 6	75				75	5
CNT 1	59		28	47	134	1
CNT 2	57		77	30	164	
CNT 3	23	3	88	5	119	2
CNT 4	140			10	150	
CNT 5	116				116	2
CNT 6	45				45	7
M2 1	114	23			137	
M2 2	70	6	72	3	151	
M2 3	60		89		149	
M2 4	135				135	
M2 5	150				150	
M2 6	131				131	
RP1 1	63	5	62	20	150	
RP1 2	105		45		150	
RP1 3	150				150	
RP1 4	150				150	
RP1 5	105				105	
RP1 6	30				30	
RP2 1	12	1	104	32	149	
RP2 2	29		107	5	141	
RP2 3	14		131		145	
RP2 4	150				150	
RP2 5	150				150	

RP2 6	0				0	
LM 1	10	2	100	22	134	1
LM 2	3		131	1	135	1
LM 3			144	6	150	
LM 4			149		149	
LM 5	150				150	
LM 6	62		13		75	5
LO 1	100	30			130	3
LO 2	150				150	
LO 3	27		120		147	
LO 4			149		149	
LO 5	135				135	1
LO 6	15				15	9

**Table A5 Interaction abundance and interaction rates for all minutes observed under each weather condition during each observation round.** This set of tables shows the number of minutes observed under each weather condition per site visit followed by the number of visits which occurred during that visit and the interaction rate for that time period. Part A includes the still minutes and Part B includes the breezy minutes.

Part A: Still Minutes

Meadow	Sunny Min	S Visits	Sunny IR	Cloudy Min	C Visits	Cloudy IR
BD 1						
BD 2				20	6	0.3
BD 3	103	100	0.97			
BD 4						
BD 5	120	86	0.72			
BD 6	30	3	0.10			
BH 1	116	85	0.73	30	30	1
BH 2	114	373	3.27			
BH 3	66	64	0.97			
BH 4						
BH 5						
BH 6						
BS 1	117	33	0.28			
BS 2	86	63	0.73			
BS 3	63	25	0.40			
BS 4						
BS 5						
BS 6						
CPB 1	85	5	0.06	34	0	0
CPB 2	47	16	0.34	24	14	0.58
CPB 3	105	95	0.90			
CPB 4	135	108	0.80			
CPB 5	150	234	1.56			
CPB 6	150	42	0.28			
CPM 1	24	12	0.50	5	0	0
CPM 2						
CPM 3	148	159	1.07			
CPM 4	15	40	2.67			
CPM 5	150	101	0.67			
CPM 6	75	49	0.65			
CPR 1	87	11	0.13	3	0	0
CPR 2	43	74	1.72			
CPR 3	60	28	0.47			

CPR 4	120	76	0.63			
CPR 5	90	70	0.78			
CPR 6						
CPS 1						
CPS 2	135	60	0.44			
CPS 3	60	50	0.83			
CPS 4	103	351	3.41			
CPS 5	134	227	1.69			
CPS 6						
CNE 1	74	8	0.11	2	0	0
CNE 2	43	7	0.16			
CNE 3	44	26	0.59			
CNE 4	120	90	0.75			
CNE 5	120	86	0.72			
CNE 6	60	16	0.27			
CNM 1	36	47	1.31			
CNM 2	105	208	1.98			
CNM 3	98	215	2.19			
CNM 4	134	414	3.09			
CNM 5	104	131	1.26			
CNM 6	75	17	0.23			
CNT 1	59	24	0.41			
CNT 2	57	136	2.39			
CNT 3	23	69	3.00	3	3	1
CNT 4	140	106	0.76			
CNT 5	116	56	0.48			
CNT 6	45	16	0.36			
M2 1	114	51	0.45	23	10	0.43
M2 2	70	509	7.27	6	6	1
M2 3	60	248	4.13			
M2 4	135	296	2.19			
M2 5	150	171	1.14			
M2 6	131	22	0.17			
RP1 1	63	15	0.24	5	0	0
RP1 2	105	126	1.20			
RP1 3	150	77	0.51			
RP1 4	150	201	1.34			
RP1 5	105	33	0.31			
RP1 6	30	7	0.23			
RP2 1	12	8	0.67	1	0	0
RP2 2	29	48	1.66			
RP2 3	14	29	2.07			
RP2 4	150	112	0.75			

RP2 5	150	15	0.10				
RP2 6	0						
LM 1	10	10	1.00	2	2		1
LM 2	3	5	1.67				
LM 3							
LM 4							
LM 5	150	90	0.60				
LM 6	62	38	0.61				
LO 1	100	249	2.49	30	4		0.13
LO 2	150	99	0.66				
LO 3	27	29	1.07				
LO 4							
LO 5	135	186	1.38				
LO 6	15	4	0.27				

#### Part B: Breezy Minutes

Meadow	Sunny Min	S Visits	Sunny IR	Cloudy Min	C Visits	Cloudy IR
BD 1						
BD 2	47	15	0.32	12	2	0.17
BD 3	33	22	0.67			
BD 4	105	61	0.58			
BD 5						
BD 6						
BH 1	2	3	1.50	2	2	1
BH 2	4	4	1.00			
BH 3	54	28	0.52			
BH 4	149	168	1.13			
BH 5						
BH 6						
BS 1	31	14	0.45			
BS 2	34	10	0.29			
BS 3	27	12	0.44			
BS 4	60	20	0.33			
BS 5						
BS 6						
CPB 1	1	1	1.00			
CPB 2	55	50	0.91	14	2	0.14
CPB 3	29	43	1.48			
CPB 4						
CPB 5						
CPB 6						
CPM 1	60	2	0.03	15	0	0

CPM 2	138	49	0.36			
CPM 3	2	8	4.00			
CPM 4	134	253	1.89			
CPM 5						
CPM 6						
CPR 1						
CPR 2	27	41	1.52			
CPR 3	86	27	0.31			
CPR 4						
CPR 5						
CPR 6						
CPS 1						
CPS 2						
CPS 3	60	13	0.22			
CPS 4	18	35	1.94			
CPS 5						
CPS 6						
CNE 1	11	1	0.09	2	0	0
CNE 2	76	9	0.12			
CNE 3	90	34	0.38			
CNE 4						
CNE 5						
CNE 6						
CNM 1	110	30	0.27			
CNM 2						
CNM 3	22	38	1.73			
CNM 4						
CNM 5						
CNM 6						
CNT 1	28	7	0.25			
CNT 2	77	47	0.61			
CNT 3	88	60	0.68			
CNT 4						
CNT 5						
CNT 6						
M2 1						
M2 2	72	307	4.26	3	5	1.67
M2 3	89	122	1.37			
M2 4						
M2 5						
M2 6						
RP1 1	62	10	0.16	20	2	0.10
RP1 2	45	43	0.96			

RP1 3						
RP1 4						
RP1 5						
RP1 6						
RP2 1	104	67	0.64	32	10	0.31
RP2 2	107	53	0.50	5	1	0.20
RP2 3	131	306	2.34			
RP2 4						
RP2 5						
RP2 6						
LM 1	100		0.00	22	3	0.14
LM 2	131	160	1.22	1	1	1.00
LM 3	144	162	1.13	6	0	0.00
LM 4	149	223	1.50			
LM 5						
LM 6	13	1	0.08			
LO 1						
LO 2						
LO 3	120	89	0.74			
LO 4	149	156	1.05			
LO 5						
LO 6						

### **Effects of weather on plant-pollinator interaction sampling**

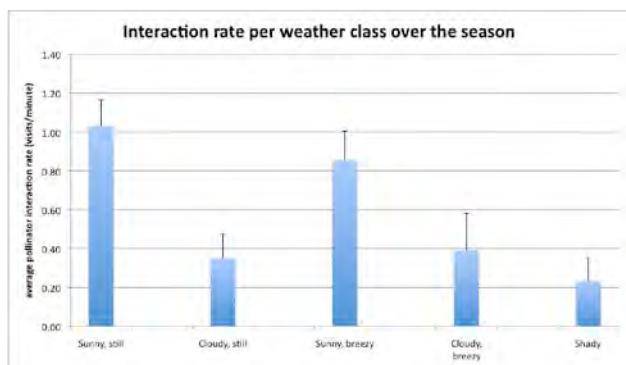
Weather is known to influence the activity level and foraging ability of pollinators. Many pollinators use the polarization of ultra-violet radiation for navigation. When clouds obscure direct solar radiation through refraction from water vapor, non-navigable conditions prevent most central-place foragers from foraging. Temperature must also remain high enough to warm pollinator's body temperature and enable physical activity. Meadow visitation times were varied to limit compounding weather conditions with field observations at particular meadows. No visitations were conducted when the weather was cold, cloudy, or windy. Weather conditions could not be held constant throughout visitation periods, so weather patterns were recorded

each minute during observations, in order to better understand potential affects, or compare weather trends with pollination rates and identify potential sources of significant environmental variability.

Across all meadows, pollination interactions under “cloudy,” “cloudy, breezy,” and “shady” weather conditions showed significantly lower average interaction rates per meadow than “sunny” and “sunny breezy” weather conditions. These weather conditions were concentrated during weeks 1 and 2.

Overall, the number of cloudy or cloudy breezy minutes recorded in the dataset is very low (Figure A5). Significant differences in breezy conditions were more likely a factor between different meadows due to differences in exposure. However during sunny periods over the whole summer, differences in interaction rates were not shown to be significant. Breezy conditions likely had a greater effect on interaction rate during week 1 and 2. This effect may be associated with decreased temperature.

### **Full season interaction rates under each weather condition**



**Figure A7 Full season interaction rates under each weather condition.** This table shows bar charts of average interaction rates based on all minutes surveyed under each weather condition.

**APPENDIX B STUDY MEADOW AREA, MEADOW PROXIMITY, AND MEADOW AREA IN SURROUNDING LANDSCAPE SECTORS**

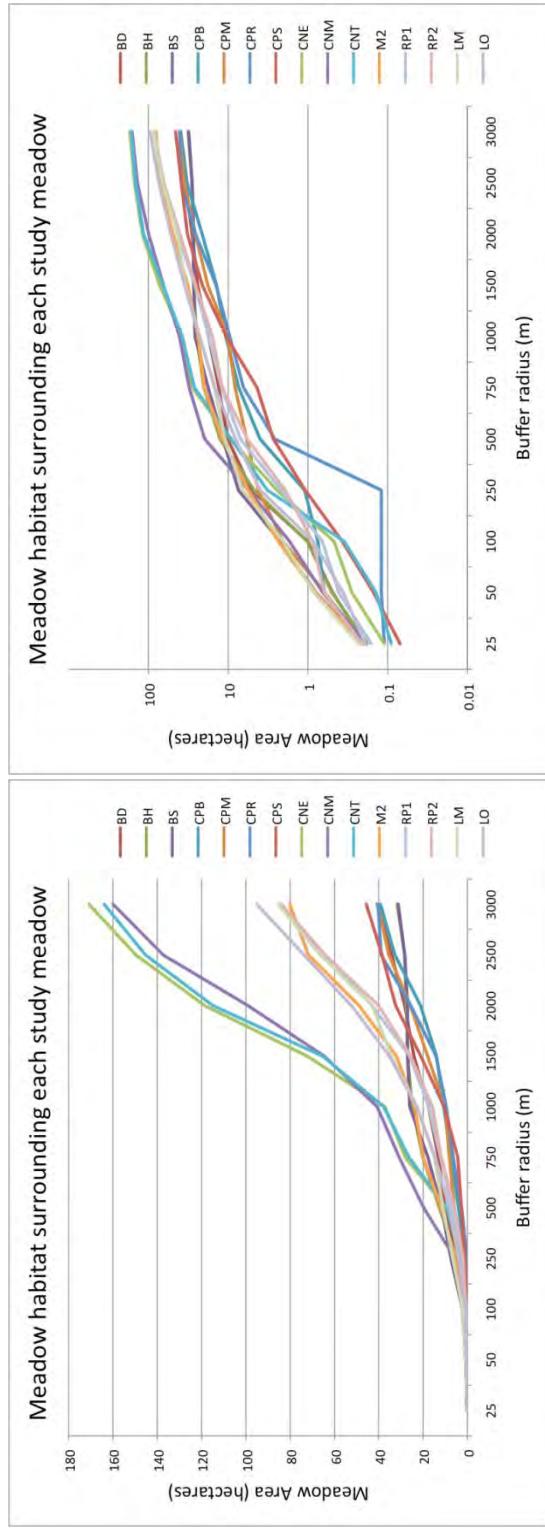
**Table B1 Study meadow area and weighted-patch meadow proximity values.** The following table shows the meadow surface area, surface area of meadow with TCI below 2, surface area of meadow with TCI between 4 and 9, and meadow proximity index values based on three different dispersal factors.

Study Meadow	Surface Area (hectares)	Mdw Prox B= 1	Mdw Prox B= 0.46	Mdw Prox B= 0.2
BD	0.62	16.85	25.06	32.34
BH	1.08	19.06	23.95	27.68
BS	8.12	18.73	23.58	27.27
CPB	0.75	10.79	20.01	28.80
CPM	2.89	12.88	22.04	30.60
CPR	0.12	10.92	20.84	29.91
CPS	0.50	12.68	23.95	34.04
CNE	0.35	48.72	90.11	127.57
CNM	3.60	49.13	85.97	120.05
CNT	0.14	47.05	86.73	163.95
M2	4.80	26.18	44.02	60.64
RP1	0.47	21.37	41.42	61.25
RP2	0.74	20.37	40.21	59.91
LM	3.24	24.18	43.34	62.30
LO	0.36	24.95	47.23	68.90

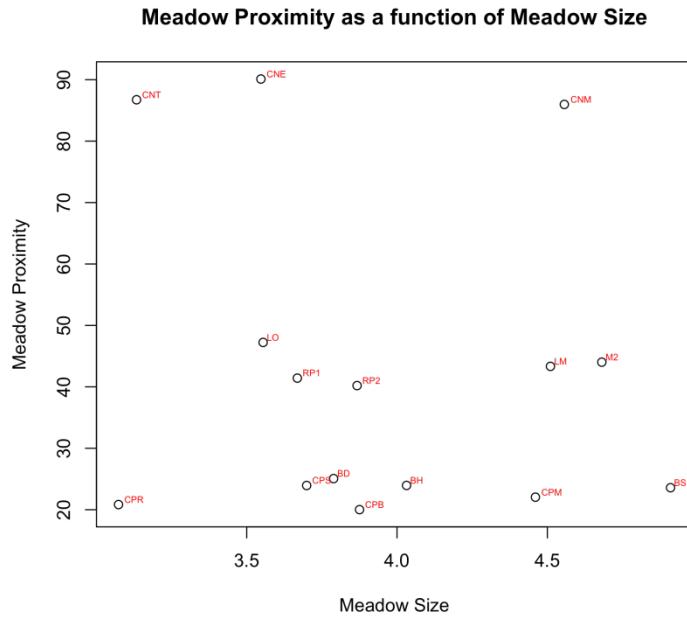
**Table B2 Surrounding meadow surface area in hectares.** Three-dimensional surface area of meadow habitat, measured in hectares, located within a circular buffer or “landscape sector”. The landscape sectors constructed with radii of 250m to 3000m were centered at the middle point of the permanent meadow study plots.

	25m	50m	100m	250m	500m	750m	1000m	1500m	2000m	2500m	3000m
BD	0.19	0.49	1.00	5.10	10.10	13.09	17.59	24.12	28.28	34.18	40.76
BH	0.18	0.50	1.02	4.72	12.64	20.11	24.89	27.02	27.58	28.35	31.69
BS	0.20	0.79	2.22	7.43	11.62	17.79	26.01	27.02	27.02	28.28	31.24
CPB	0.19	0.62	0.75	1.10	3.98	7.35	10.71	13.95	21.16	32.73	39.24
CPM	0.21	0.61	2.05	4.19	5.85	8.17	10.05	17.95	25.75	35.44	40.60
CPR	0.11	0.12	0.12	2.60	6.41	9.53	14.14	25.53	38.93	40.36	
CPS	0.07	0.15	0.37	1.08	2.71	4.33	10.53	21.04	32.37	38.56	45.62
CNE	0.11	0.28	0.47	2.44	9.33	28.06	37.19	72.21	118.60	149.62	170.79
CNM	0.19	0.65	1.70	5.51	19.67	30.77	40.73	64.59	99.09	137.31	159.91
CNT	0.09	0.14	0.35	3.22	9.17	26.38	37.79	65.32	114.90	145.28	163.95
M2	0.21	0.80	2.35	5.60	11.74	19.85	23.84	32.00	48.92	71.79	80.16
RP1	0.16	0.41	0.66	2.15	7.02	12.04	17.51	26.03	43.15	64.12	85.43
RP2	0.21	0.62	0.87	1.93	5.77	11.79	15.71	25.63	40.14	64.30	83.99
LM	0.23	0.84	2.04	6.55	11.01	14.87	22.68	34.34	42.94	66.46	85.51
LO	0.19	0.36	0.86	3.94	8.09	14.56	22.84	35.17	52.33	73.73	95.04

## Surrounding Meadow Area



**Figure B1 Surrounding meadow habitat for each study meadow measured in hectares and log-transformed.** This figure displays surrounding meadow habitat in hectares within each landscape sector for each study meadow (left). The amount of meadow habitat was measured within fixed circular landscape sectors defined by the radii shown on the x-axis and centered around the mid-point of the permanent plots. The same chart with log transformed meadow area is shown (right); using a log scale y-axis.



**Figure B2 Meadow Size vs. Meadow Proximity.** This graph shows the results of the stratified-random sampling design for a distribution of meadow size and surrounding meadow habitat. A meadow proximity index based on distance weighted meadow patch area shows the relative amount of surrounding habitat for each study meadow. Meadow complexes were chosen stratified by contagion, then one large meadow and two small meadows were selected from each complex at random, except in the cases of Lookout Mountain and Carpenter Mountain as described in the methods section.

### APPENDIX C RICHNESS, EVENNESS, AND DIVERSITY STATISTICS

**Table C1 Surveyed flower and network flower full season diversity statistics.** This table shows the following full season metrics for flowers summed across all plots/watchers and each visitation round: Richness, log-transformed richness, evenness, Shannon diversity, and abundance. Calculations are described in the methods. These values are based on observations including singletons from a maximum of six watch dates limited to observations identified to species or genus for network flowers n= 10,019 (interactions from which pollinators were only identified to order were not excluded because the flower was identified to species).

Meadows	Flowers					Network Flowers				
	Richness	log(Rich)	PIE Even	Shan	Abundance	Richness	log(Rich)	PIE Even	Shan	Abundance
BD	14	1.15	0.39	0.83	8310	10	1.00	0.65	1.42	330
BH	28	1.45	0.47	1.23	24386	13	1.11	0.76	1.78	746
BS	8	0.90	0.18	0.42	6151	6	0.78	0.55	1.1	175
CNE	40	1.60	0.92	2.83	6945	28	1.45	0.88	2.72	263
CNM	31	1.49	0.87	2.37	42264	22	1.34	0.78	1.9	1072
CNT	34	1.53	0.77	2.12	18088	28	1.45	0.75	2.08	552
CPB	38	1.58	0.87	2.41	9193	28	1.45	0.84	2.26	600
CPM	39	1.59	0.85	2.5	14126	31	1.49	0.84	2.45	677
CPR	23	1.36	0.87	2.41	4434	18	1.26	0.84	2.16	317
CPS	36	1.56	0.86	2.36	9752	22	1.34	0.72	1.83	717
LM	30	1.48	0.91	2.67	24254	28	1.45	0.86	2.44	728
LO	30	1.48	0.83	2.10	12153	19	1.28	0.76	1.87	808
M2	40	1.6	0.82	2.19	44040	26	1.41	0.77	2.05	1732
RP1	27	1.43	0.79	2.03	14016	20	1.3	0.82	2.09	501
RP2	29	1.46	0.78	1.92	19312	21	1.32	0.74	1.9	626

**Table C2 Pollinator and interaction full season diversity statistics.** This table shows the following full season metrics for pollinators and interactions summed across all plots/watches and each visitation round: Richness (Richness), log-transformed richness (log(Rich)), evenness (PIE Even), Shannon diversity (Shan), and abundance (Abund). Calculations are described in the methods. These values are based on observations including singletons from a maximum of six watch dates limited to observations identified to species or genus (n=9844, excluding pollinator observations categorized by order).

Meadows	Pollinators			Interactions						
	Richness	log(Rich)	PIE Even	Shan	Abundance	Richness	log(Rich)	PIE Even	Shan	Abundance
BD	49	1.69	0.91	2.91	330	82	1.91	0.96	3.67	330
BH	66	1.82	0.89	2.76	746	121	2.08	0.94	3.63	746
BS	21	1.32	0.77	1.99	175	28	1.45	0.83	2.40	175
CNE	59	1.77	0.93	3.20	263	125	2.10	0.98	4.41	263
CNM	80	1.90	0.82	2.68	1072	164	2.21	0.92	3.65	1072
CNT	66	1.82	0.90	3.02	552	135	2.13	0.94	3.87	552
CPB	53	1.72	0.59	1.87	600	113	2.05	0.89	3.24	600
CPM	59	1.77	0.79	2.35	677	128	2.11	0.95	3.69	677
CPR	34	1.53	0.63	1.88	317	62	1.79	0.92	3.18	317
CPS	65	1.81	0.87	2.84	717	131	2.12	0.92	3.59	717
LM	83	1.92	0.92	3.21	728	184	2.26	0.98	4.63	728
LO	87	1.94	0.91	3.21	808	222	2.35	0.96	4.11	808
M2	83	1.92	0.89	2.82	1732	114	2.06	0.94	3.91	1732
RP1	61	1.79	0.88	2.86	501	134	2.13	0.96	3.9	501
RP2	61	1.79	0.83	2.61	626	207	2.32	0.91	3.5	626

**Table C3 Surveyed flower and network flower peak season diversity statistics.** This table shows the following full season metrics for flowers summed across all plots during week 2, 3, and 4 visitation rounds: Richness (Richness), log-transformed richness (log(Rich)), evenness (PIE Even), Shannon diversity (Shan), and abundance (Abund). Calculations are described in the methods. These values are based on peak season observations including singletons from three watch dates limited to observations identified to species or genus (richness, evenness, and Shannon diversity calculations included interaction abundance derived from pollinators only identified to order (n=7757).

Meadows	Flowers					Network Flowers				
	Richness	log(Rich)	PIE Even	Shan	Abundance	Richness	log(Rich)	PIE Even	Shan	Abundance
BD	13	1.11	0.45	0.96	5028	9	0.95	0.67	1.46	242
BH	23	1.36	0.44	1.10	20579	10	1.00	0.75	1.65	631
BS	6	0.78	0.29	0.56	3052	5	0.70	0.39	0.76	128
CNE	34	1.53	0.90	2.61	4080	20	1.30	0.89	2.58	156
CNM	26	1.41	0.85	2.18	27956	17	1.23	0.73	1.66	869
CNT	31	1.49	0.76	2.01	13445	24	1.38	0.67	1.78	446
CPB	26	1.41	0.79	2.17	4737	21	1.32	0.78	1.99	323
CPM	33	1.52	0.80	2.15	11872	20	1.30	0.74	1.86	517
CPR	18	1.26	0.88	2.32	3221	15	1.18	0.84	2.15	243
CPS	30	1.48	0.83	2.20	5232	19	1.28	0.72	1.85	493
LM	28	1.45	0.90	2.57	17835	25	1.40	0.81	2.20	538
LO	25	1.40	0.82	2.07	6977	16	1.20	0.69	1.69	599
M2	33	1.52	0.77	2.13	27117	24	1.38	0.73	1.89	1482
RP1	24	1.38	0.81	2.05	8668	17	1.23	0.79	1.93	440
RP2	22	1.34	0.72	1.66	16388	19	1.28	0.67	1.68	537

**Table C4 Pollinator and interaction peak season diversity statistics.** This table shows the following full season metrics for pollinators and interactions summed across all plots during week 2, 3, and 4 visitation rounds: Richness (Richness), log-transformed richness (log(Rich)), evenness (PIE Even), Shannon diversity (Shan), and abundance (Abund). Calculations are described in the methods. These values are based on observations including singletons from three watch dates limited to observations identified to species or genus (n= 7644, excluding general order categories).

Meadows	Pollinators				Interactions					
	Richness	log(Rich)	PIE Even	Shan	Abundance	Richness	log(Rich)	PIE Even	Shan	Abundance
BD	43	1.63	0.91	2.91	242	72	1.86	0.96	3.62	242
BH	58	1.76	0.88	2.66	631	98	1.99	0.93	3.41	631
BS	15	1.18	0.68	1.69	128	19	1.28	0.75	2.00	128
CNE	43	1.63	0.91	3.04	156	81	1.91	0.97	4.05	156
CNM	62	1.79	0.79	2.45	869	122	2.09	0.90	3.32	869
CNT	54	1.73	0.88	2.78	446	106	2.03	0.92	3.57	446
CPB	44	1.64	0.63	1.99	323	74	1.87	0.88	3.08	323
CPM	39	1.59	0.76	2.09	517	74	1.87	0.92	3.07	517
CPR	29	1.46	0.56	1.62	243	51	1.71	0.90	2.91	243
CPS	57	1.76	0.85	2.76	493	104	2.02	0.91	3.47	493
LM	66	1.82	0.90	3.01	538	151	2.18	0.98	4.32	538
LO	81	1.91	0.92	3.27	599	155	2.19	0.96	4.07	599
M2	71	1.85	0.88	2.73	1482	192	2.28	0.93	3.72	1482
RP1	52	1.72	0.85	2.63	440	93	1.97	0.95	3.67	440
RP2	49	1.69	0.80	2.32	537	106	2.03	0.89	3.21	537

## Rarefaction

Rarefaction is most widely known as a technique for comparing observed richness among sampled sites. A rarefied curve results from averaging species richness from a random assortment of  $i$  individuals calculated statistically, or from reoccurring iterations. From rarefaction curves, species richness at a certain number of samples (increasing along the x-axis) may be read so that a richness value standardized by individuals rather than area or time can be derived.

Rarefaction methods provide a meaningful standardized way to compare species richness based on individuals captured through construction of taxon sampling curves. Species richness based on area sampled, sampling effort, or individuals captured can provide very different pictures of community richness. While species accumulation curves plot the specific number of species represented in a pool of individuals as individuals are gradually accumulated on the x-axis, rarefaction averages this accumulation of richness per individual sampled over many interactions. Rarefaction curves are constructed by re-sampling a pool of N individuals (or N samples in sample based rarefaction) without replacement tabulating expected richness for each subset of N individuals. Sample-based curves almost always lie below individual-based curves because there is almost always some degree of spatial autocorrelation between plots. In sample-based rarefaction, plots are accumulated rather than individuals to account for spatial autocorrelation, however the curves are still based on individual abundance plotted on the x-axis. In this thesis individual-based rarefaction curves were used instead of sample-based rarefaction curves,

because such great differences in relative abundance between meadows made sample-based rarefaction curves difficult to compare.

In this study, non-rarified richness of plants and pollinators in plots are actually a measure of species density because species richness is determined within a fixed area. Plant and pollinator species richness is originally determined as richness density within fixed space and time. This method for richness calculation lends itself to the assumption that communities compared for richness alone are drawn from communities with similar density. Species density depends not only on species richness but also upon mean density of individuals. Richness, or species density is of importance especially for conservation or landscape oriented methods, because this direct measurement gauges the richness of species in a given area. However, individual-based species richness should be considered separately using rarefaction to assess the degree to which patterns of species density are formed by patterns of individual abundance.

In this case, meadow plots supported very different densities of floral resources, which in effect change the sampling intensity for the ten permanent plots during the 30 minutes watch period. Slight changes in environmental conditions may also influence individual abundance. So estimating mean richness over the season for each plot based on network abundance of flowers, pollinators, and interactions, may be useful. In this case, the very low abundance in a few plots or meadows makes it difficult to compare all rarefaction curves uniformly.

### **Chao Species Richness Estimates**

Unlike rarefaction, which is used to compare differences in measured species richness between sampled plots, species richness estimators are non-parametric statistics that were developed to extrapolate estimations of total community species richness based on the proportion of singletons and doubletons in the dataset. Species richness estimators are used to estimate the total richness of a community based on observed species counts.

While rarefaction is a techniques used for interpolating species richness of larger samples based on abundance present in smaller samples, estimators extrapolate beyond sampled data. Statistical research has produced a variety of species richness estimators. Some non-parametric estimators based on the proportion of singletons and doubletons in the dataset have exhibited very encouraging results (Colwell & Coddington, 1994). In species rich communities where taxon accumulation curves do not come close to any asymptote, it is thought that estimators should be used as a lower bound for species richness (Chao, EstimateS).

**Table C5 Flower, pollinator and interaction full season richness estimate statistics.** This table shows the following full season metrics based on all data including richness estimates for flowers, pollinators and interactions summed across all plots/witches and all visitation rounds (5 to 7 rounds): Total abundance, total richness (richness), rarified-richness (4434 individuals) for survey plants, and total abundance, total richness (richness), rarified-richness (176 individuals) and Chao estimates for network flowers, pollinators, and interactions. Calculations are described in the methods. These values are based on observations from all collected survey and plot watch data.

Meadows	BD	8310	14	13.73	337	10	14.43	8.50	337	49	88.75	37.63	337	82	149.49	58.55
BH	24386	28	24.19	756	13	13	11.08	756	66	129.5	31.53	756	121	228.29	54.96	
BS	6151	8	7.97	176	6	7.11	6	176	21	36.43	21	176	28	43.65	28	
CNE	6945	40	39.03	305	28	31	26.36	305	59	129.3	47.65	305	125	418.13	94.46	
CNM	42264	31	27.42	1207	22	24.25	14.92	1207	80	126.91	36.20	1207	164	307.87	58.73	
CNT	18088	34	32.05	658	28	34	21.35	658	66	141	38.79	658	135	373.11	68.35	
CPB	9193	38	36.79	610	28	30.13	19.88	610	53	101.64	29.39	610	113	283.04	52.40	
CPM	14126	39	38.12	691	31	43.25	23.34	691	59	122.06	28.80	691	128	350.15	57.52	
CPR	4434	23	23	328	18	18.25	16.16	328	34	62.6	26.01	328	62	114.5	45.51	
CPS	9752	36	35.17	733	22	40	15.29	733	65	98.41	36.44	733	131	279.78	59.08	
LM	24254	30	27.72	745	28	60	20.16	745	83	125.89	43.17	745	207	441.48	88.61	
LO	12153	30	28.59	834	19	22	14.60	834	87	114.78	45.52	834	184	360.03	72.75	
M2	44040	40	36.98	1740	26	26	18.17	1740	83	139.57	30.05	1740	222	417.16	62.36	
RP1	14016	27	26.61	513	20	30	15.78	513	61	90.45	38.33	513	114	206.24	65.21	
RP2	19312	29	27.39	645	21	25.5	16.67	645	61	80.4	35.86	645	134	339.03	59.54	

*Plot Flower Rarefaction per Meadow*

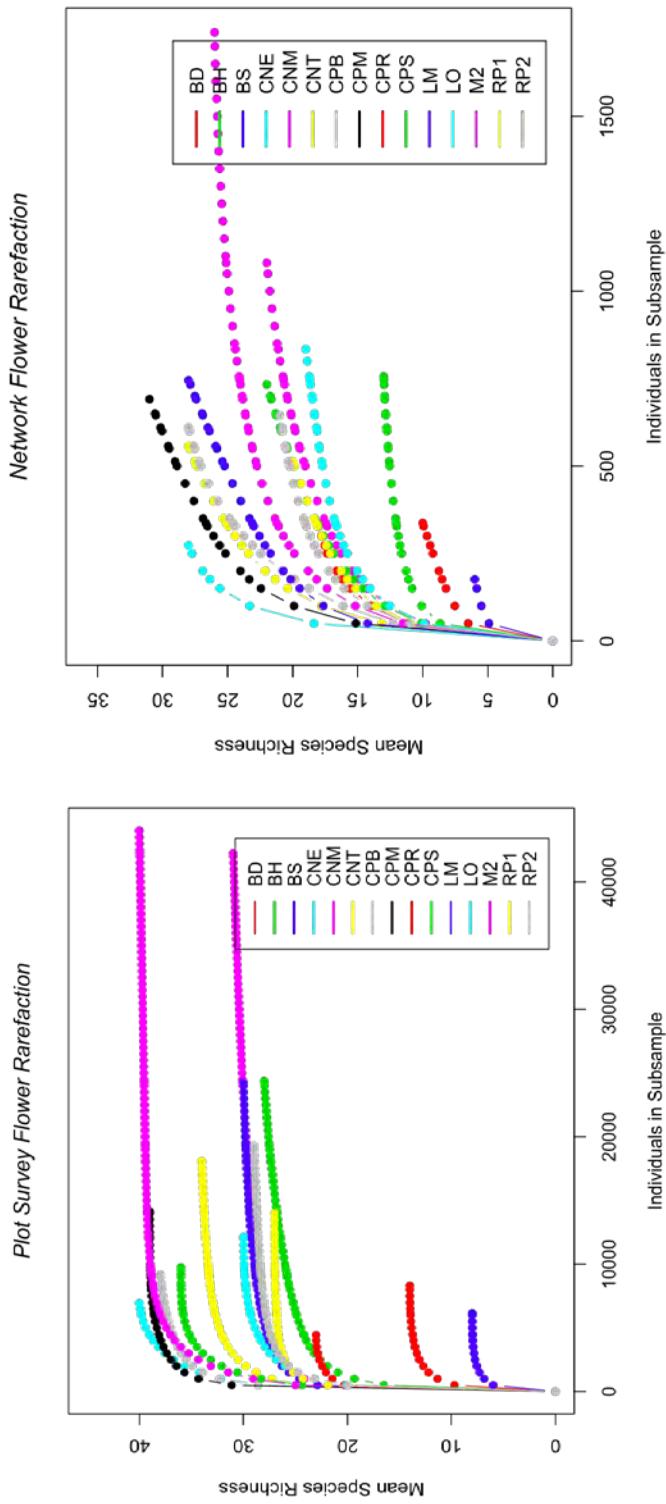
Rarefaction curves for surveyed floral communities calculated at the meadow scale increased rapidly and reached an asymptote in almost every meadow. Flower surveys provided a complete account of all flower species within all plots on each visit. Plot floral communities exhibited high abundance relative to low accumulation of new species and there weren't any singletons. Due to the exhaustive nature of this survey data, and lack of singleton observations, Chao abundance-based flower richness estimators were not thought necessary for this survey flower data. Network plant rarefaction curves all reached an asymptote near 600 interactions per site. CPS continued to climb after 600 interactions and CNE, CPR, and BD never reached 600 interactions observed, these meadows continued to increase in richness throughout the interactions observed.

*Pollinator and Interaction Rarefaction per meadow*

Pollinator and plant-pollinator interaction data were assessed using individual-based rarified richness for plot level and meadow level data. These analyses provide additional information at study sites where frequency of visitation differs and at sites where sampling coverage was decreased relative to potential site richness due to high abundance and diversity. Rarefaction is best used to estimate individual-based richness of a place when rarefaction curves have reached an asymptote, but the analysis is still useful to evaluate relative richness between plots on the upslope of the curve. Pollinator and interaction richness did not approach asymptotes during the

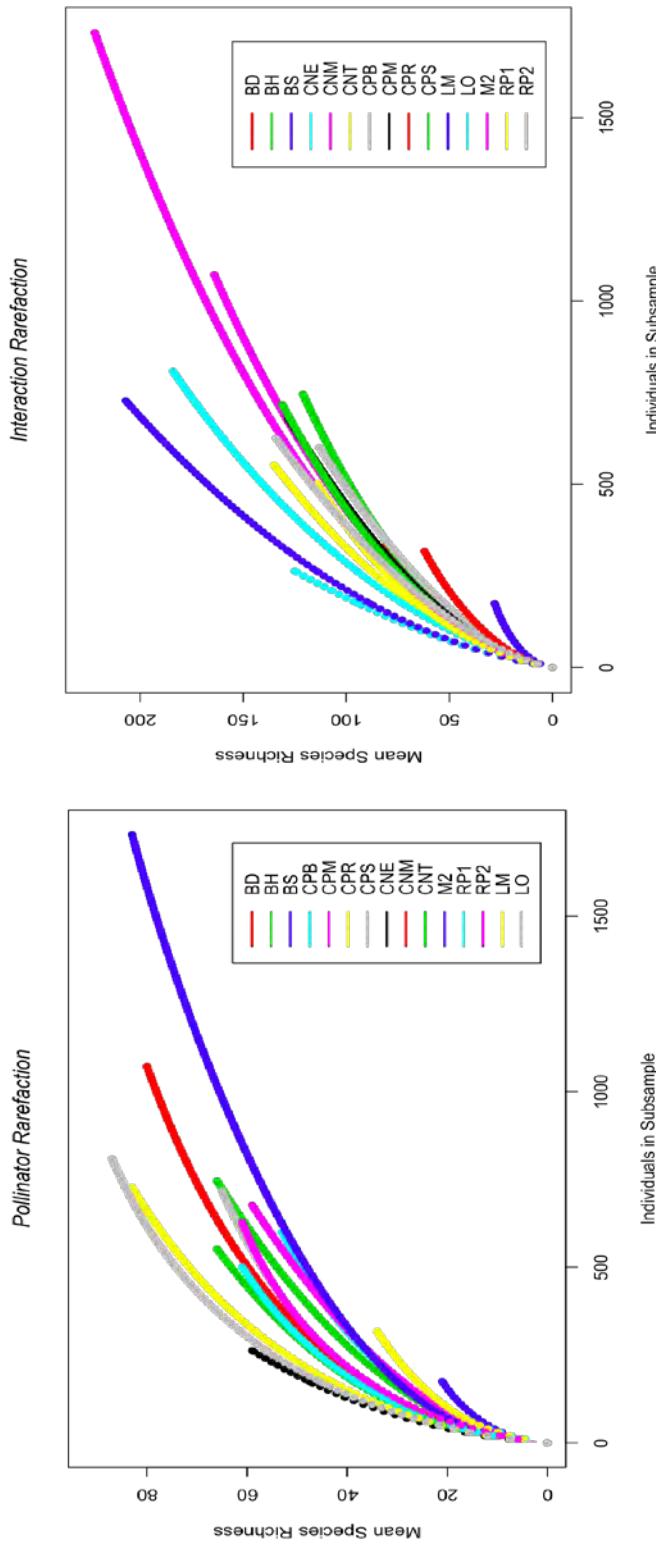
extent of interactions observed. Very high overall arthropod richness explains this pattern.

### Survey flower and Network interaction flower rarefaction curves



**Figure C1 Meadow-scale flower rarefaction curves.** Individual-based rarefaction was used to evaluate the full season richness of floral, pollinator, and interaction surveys normalized by a standard number of individuals. This technique isolates richness per standardized count of individuals from richness density (referred to here as richness) standardized by plot area and sampling effort. This figure shows individual-based rarefaction of survey floral richness and network floral richness for each meadow.

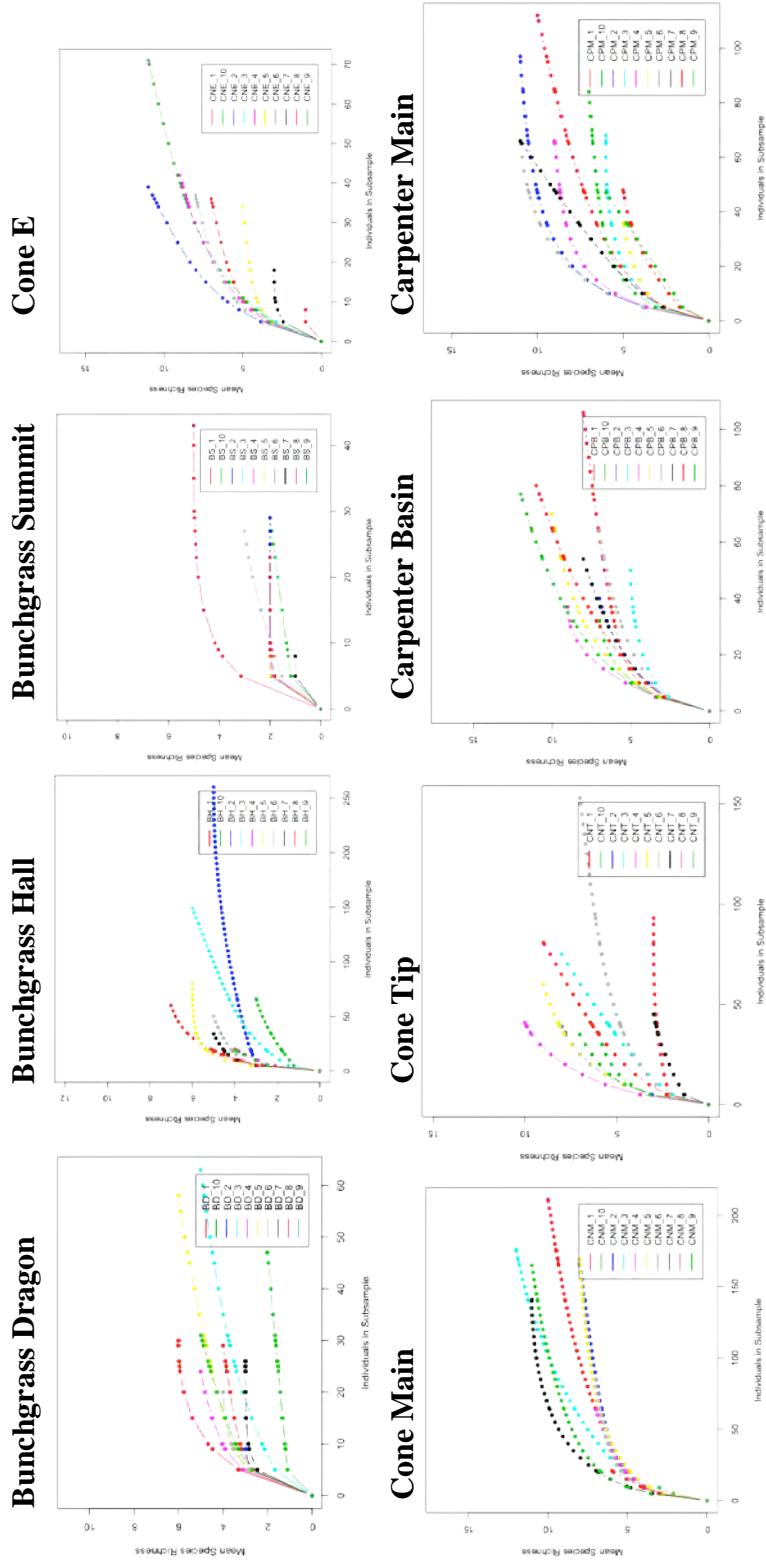
### Network pollinator and interaction rarefaction curves

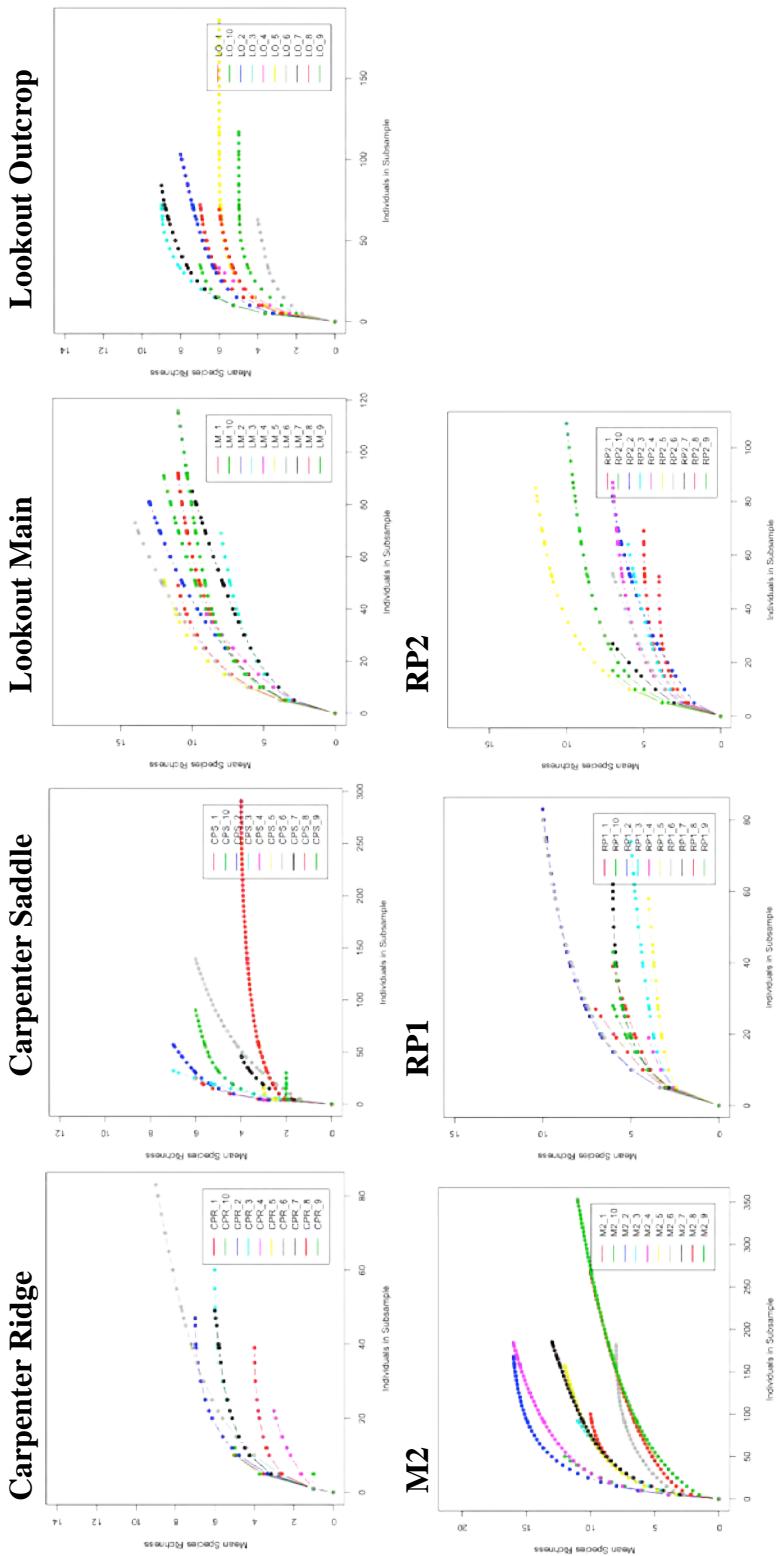


**Figure C2 Meadow-scale pollinator and interaction rarefaction curves.** Individual-based rarefaction was used to evaluate the full season richness of floral, pollinator, and interaction surveys normalized by a standard number of individuals. This technique isolates richness per standardized count of individuals from richness density (referred to here as richness) standardized by plot area and sampling effort. This figure shows individual-based rarefaction of pollinator richness and interaction richness for each meadow

**Figure C3 Plot level network flower rarefaction curves.** Individual-based rarefaction analyses were conducted in order to calculate average richness at the plot level based on a standardized number of observed individuals in the network.

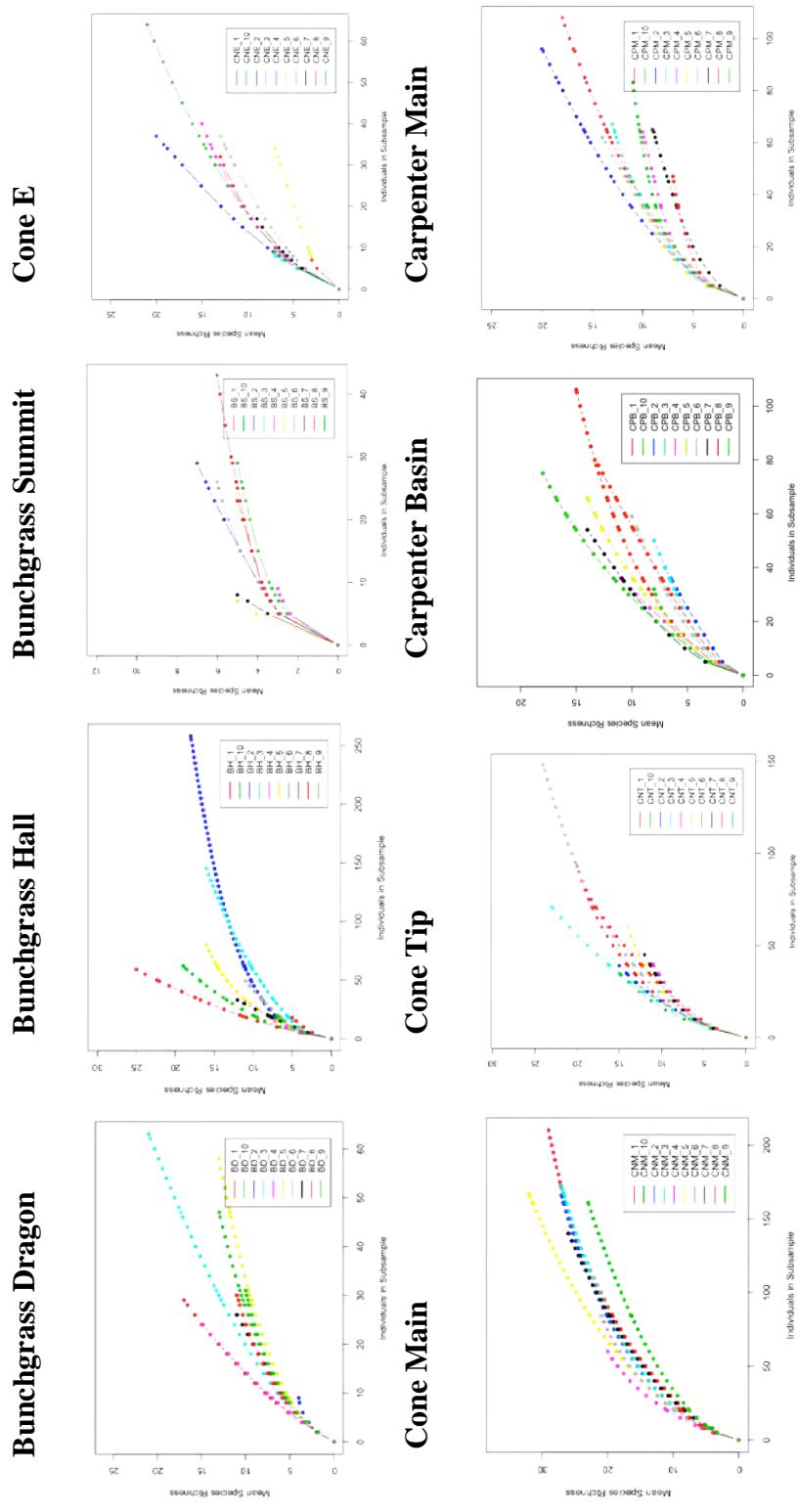
### Plot-level network flower rarefaction curves

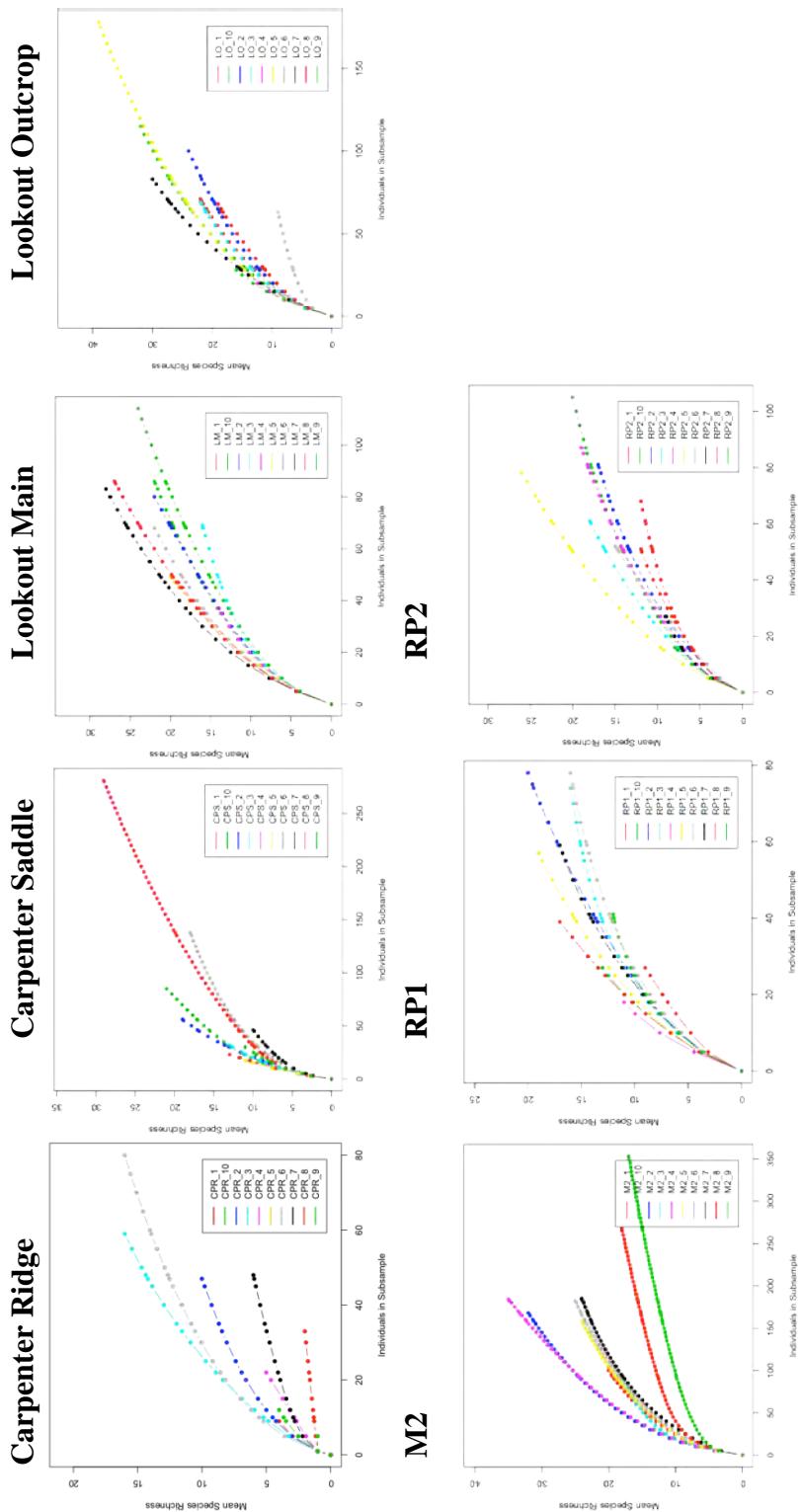




**Figure C4 Plot level network pollinator rarefaction curves.** Individual-based rarefaction analyses were conducted in order to calculate average richness at the plot level based on a standardized number of observed individuals in the network.

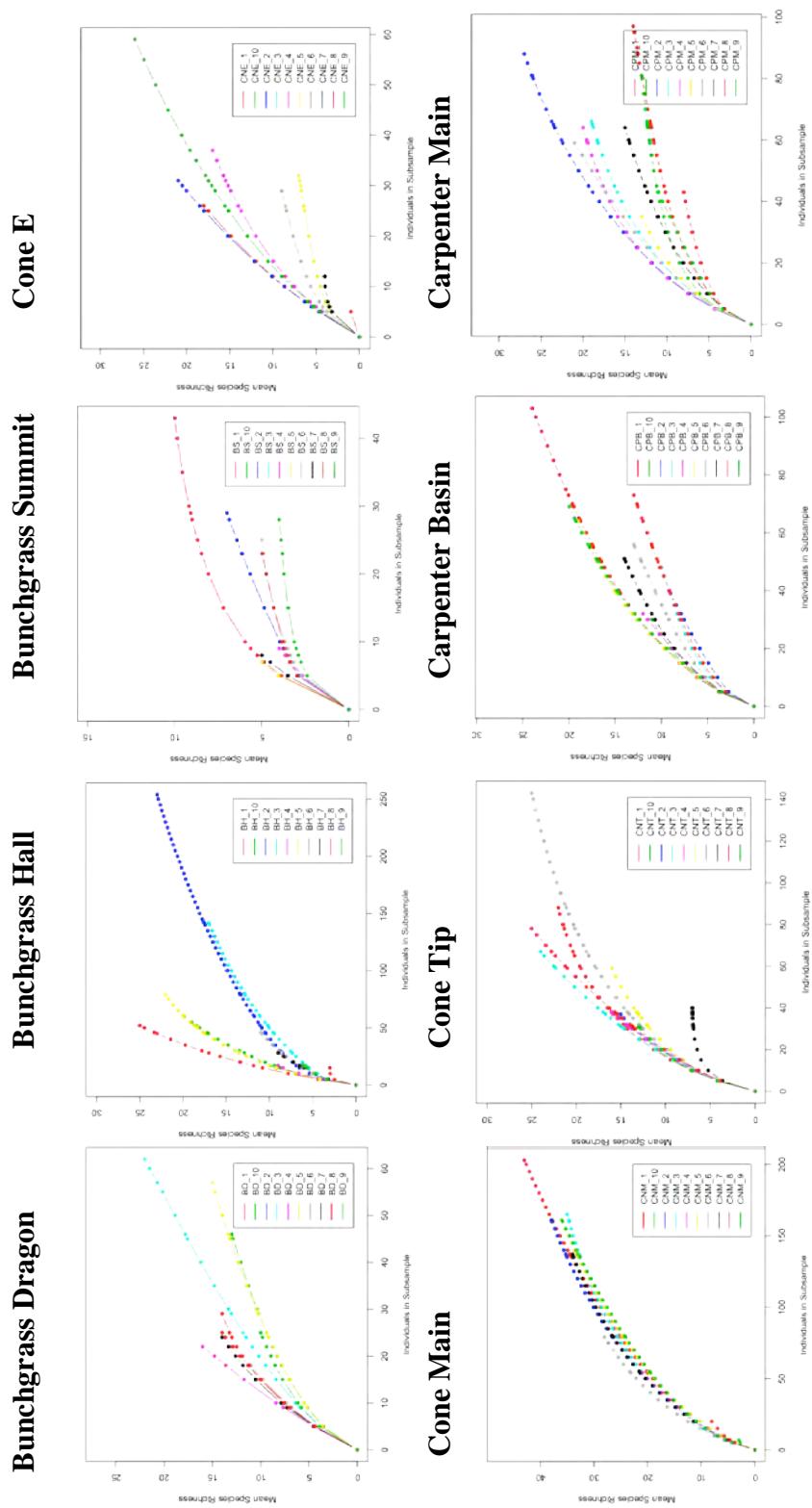
### Plot-level network pollinator rarefaction curves

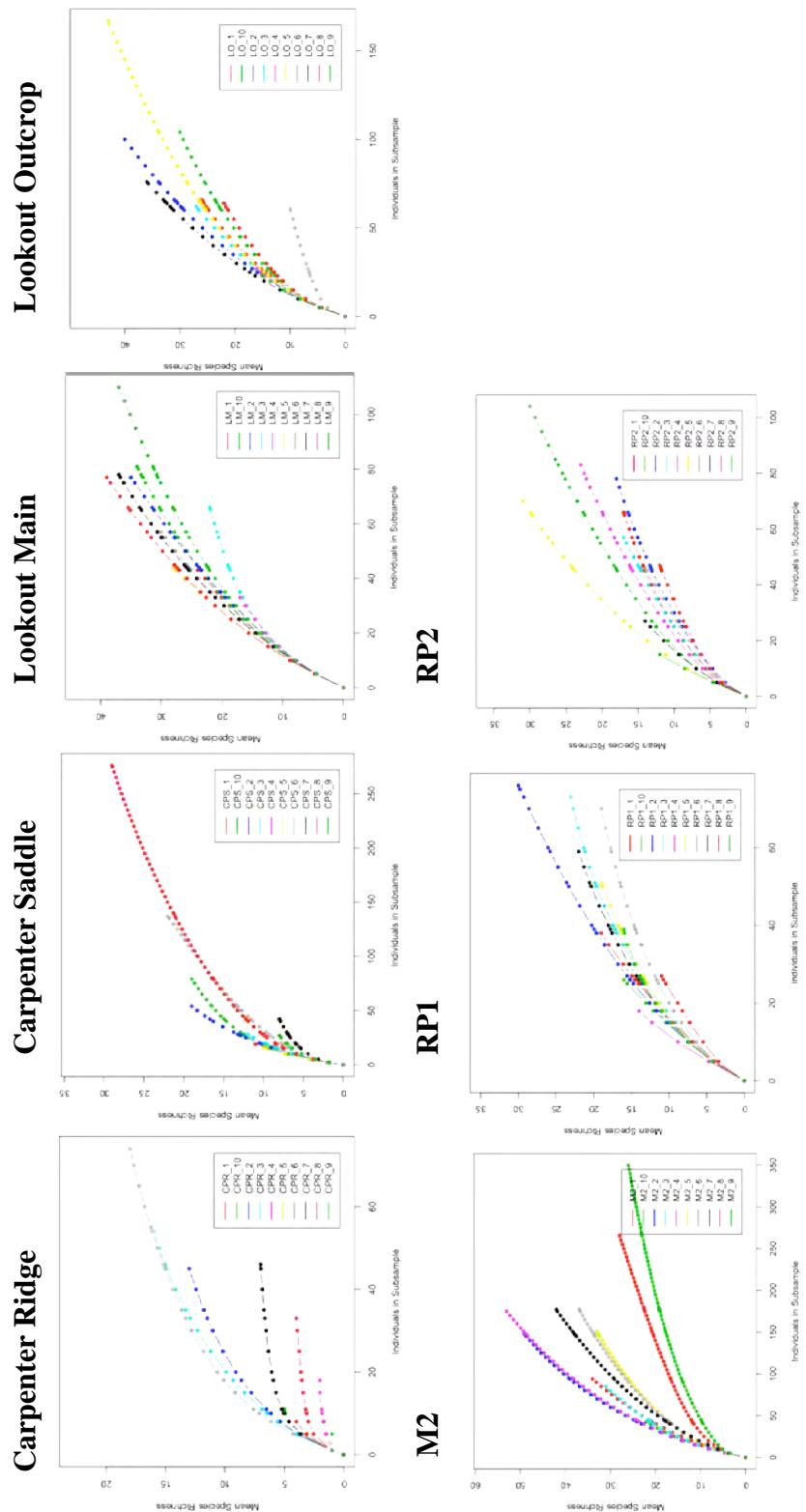




**Figure C5 Plot level network interaction rarefaction curves.** Individual-based rarefaction analyses were conducted in order to calculate average richness at the plot level based on a standardized number of observed individuals in the network.

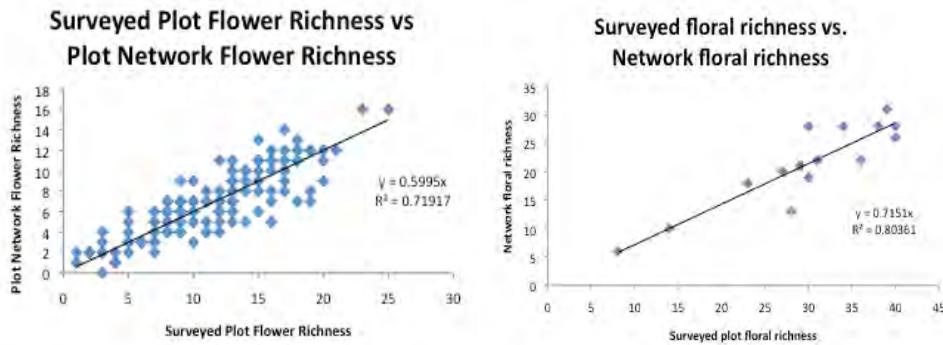
### Plot-level network interaction rarefaction curves





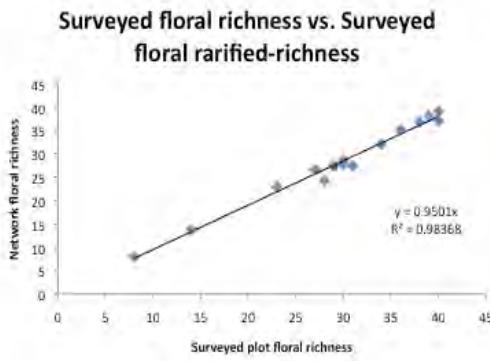
## APPENDIX D RELATIONSHIPS BETWEEN RICHNESS, EVENNESS, DIVERSITY

### Surveyed flower richness vs. network flower richness



**Figure D1 Surveyed flower richness vs. network flower richness.** Flower richness tallied as the number of species represented by all individuals surveyed in the permanent plots, was summed over the whole season and compared to floral richness observed in the full season interaction networks. One point represents each permanent plot in the first figure and each meadow in the second figure. The flower richness of the visited flowers (or network flower richness of each plot) increased by 60% of the plot flower species richness and 72% for meadow level species richness.

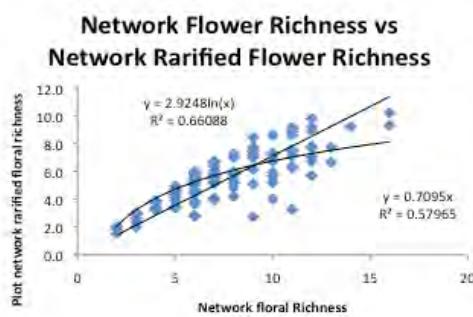
### Surveyed flower richness vs. rarified richness



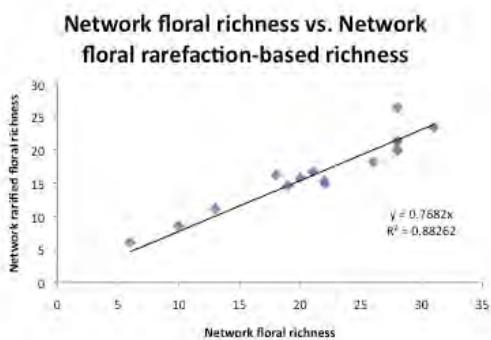
**Figure D2 Surveyed flower richness vs. rarified richness.** This chart shows the rarified-richness based on rarefaction curves (normalized to a sample size of 176 individuals) compared to the observed total flower richness in the plots. Normalized flower richness increased at 95% the rate of surveyed floral richness.

### Network flower richness vs. rarified richness

#### Plots



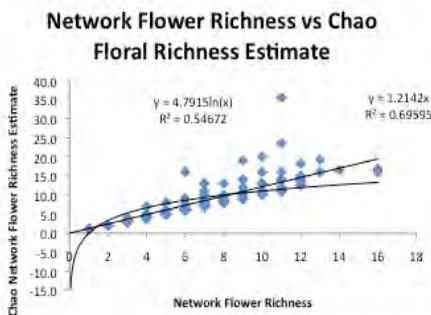
#### Meadows



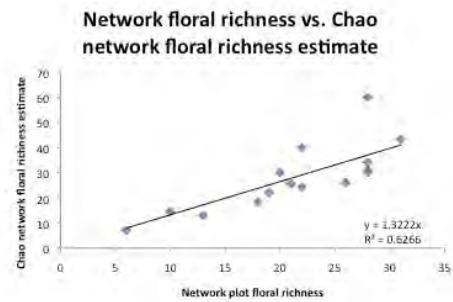
**Figure D3 Network flower richness vs. rarified richness.** Network flower rarified richness at 25 individuals increased by 71% of network plant richness based on plot level data ( $n = 150$ ) and 77% of network plant richness at 176 individuals based on meadow level data ( $n = 15$ )

### Network flower richness vs. Chao abundance-based richness estimate

#### Plots



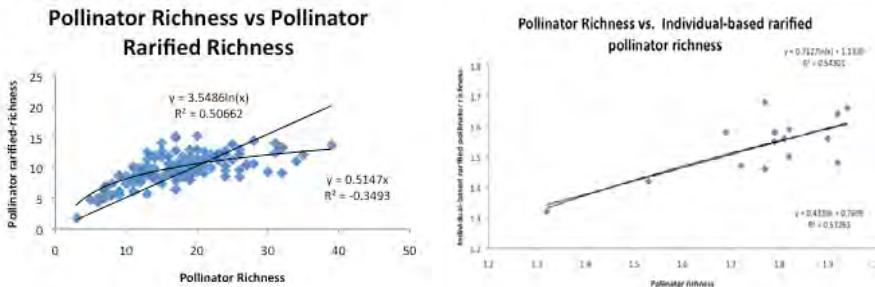
#### Meadows



**Figure D4 Network floral richness vs. Chao abundance-based richness estimates.** Chao richness estimates increased 1.3 times faster than network floral richness with based on plot level data ( $n = 150$ ) and 1.3 times faster than natural log network floral richness based on meadow level data ( $n = 15$ ). The highest observed Chao richness estimate surpasses surveyed floral richness at the site, invalidating the estimate.

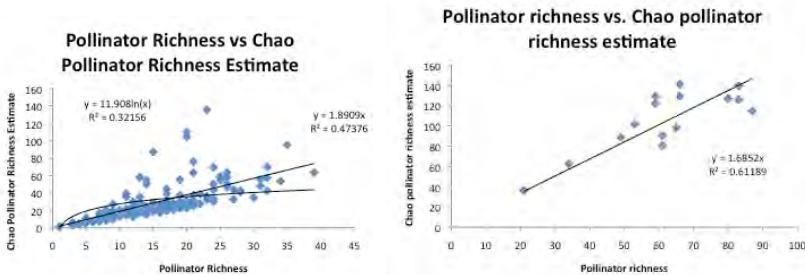
### Pollinator richness vs. rarified richness

#### Plots



**Figure D5 Pollinator richness vs. rarified richness.** Individual-based richness increased by 3.5 times the natural log of pollinator richness at 25 individuals ( $R^2 = 0.51$ ) based on the plot level data ( $n = 150$ ) and 43% of the observed pollinator richness at 176 individuals ( $R^2 = 0.53$ ) based on the meadow level data ( $n = 15$ ). Pollinator rarified-richness was highly correlated to measured richness.

### Pollinator richness vs. Chao abundance-based richness estimates

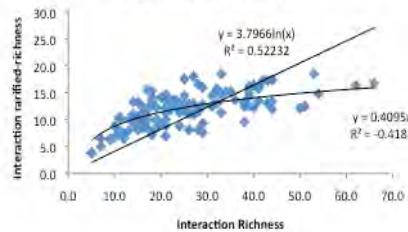


**Figure D6 Pollinator richness vs. Chao abundance-based richness estimates.** Chao estimates exhibit more high values with pollinators than plants where singleton abundance boosts permanent plots to several times the richness observed. One plot shows an estimate more than five times greater. Chao abundance estimates increased 1.89 times faster than measured pollinator richness ( $R^2 = 0.47$ ) based on permanent plots ( $n=150$ ). Chao pollinator richness estimates 1.69 times the increase of pollinator richness ( $R^2 = 0.61$ ) based on meadow level data ( $n = 15$ ).

### Interaction richness vs. rarified richness

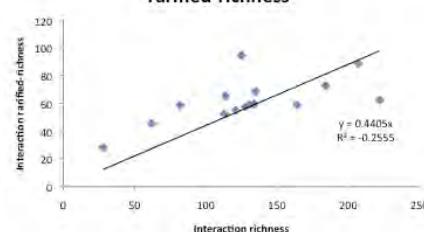
#### Plots

**Interaction Richness vs Interaction Rarified Richness**



#### Meadows

**Interaction richness vs Interaction rarified-richness**

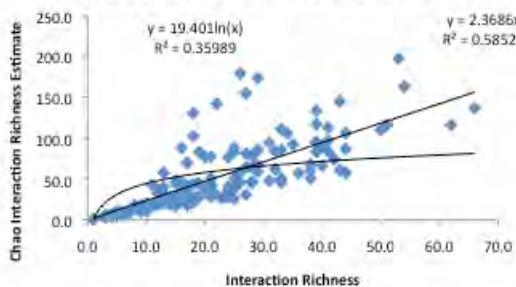


**Figure D7 Interaction richness vs. rarified richness.** Meadow level individual-based rarefaction calculated at 176 individuals increased by 44% on average while plot based individual-based rarefaction at 25 individuals increased by 40% observed richness on average or 3.8 times the natural log value of interaction richness ( $R^2 = 0.52$ )

### Interaction richness vs. Chao abundance-based richness estimate

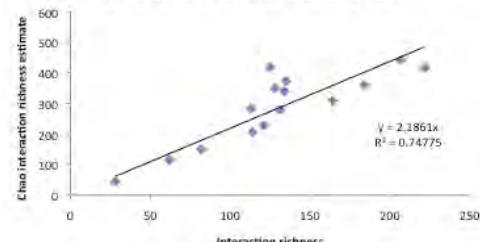
#### Plots

**Interaction Richness vs Chao Interaction Richness Estimate**



#### Meadows

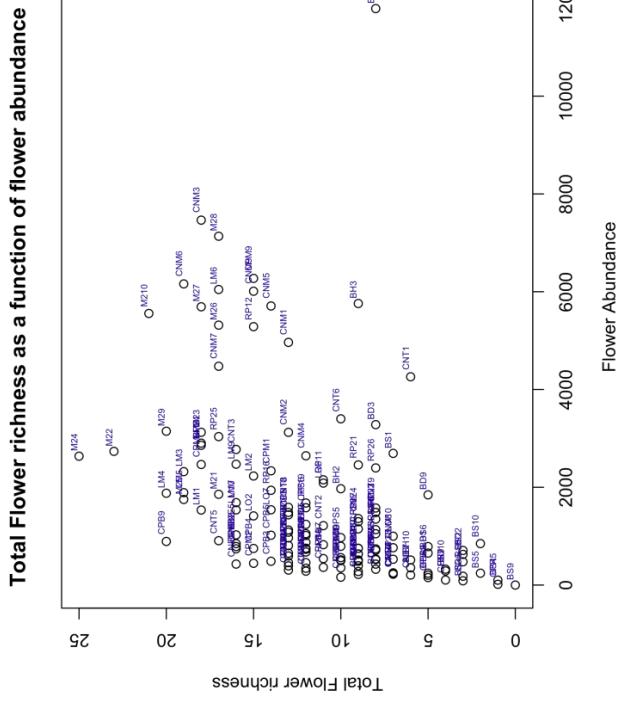
**Interaction richness vs. Chao interaction richness estimate**



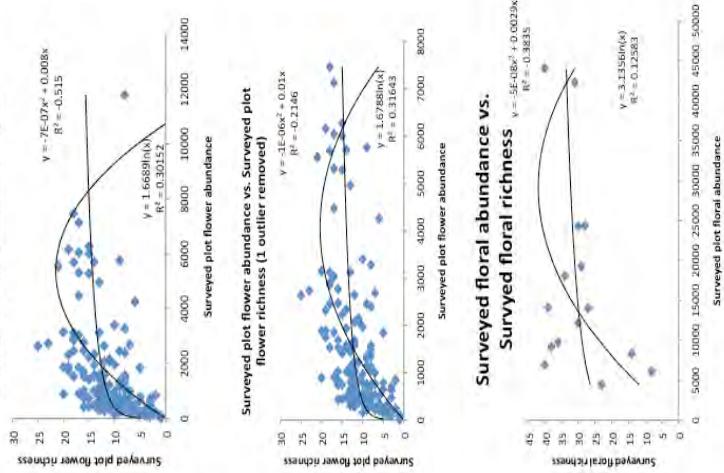
**Figure D8 Interaction richness vs. Chao abundance-based richness estimates.** Greater variability and frequent high Chao values in the interaction data compared to the pollinator data are caused by increased singletons in the dataset. Meadow level Chao estimates constrain some variability in plots by decreasing singletons through greater coverage of site diversity. At the plot level Chao estimates for interaction richness increased by 2.37 times measured richness ( $R^2 = 0.59$ ). At the meadow level, Chao richness estimate increased by 2.19 times the measured richness; and the linear model describes the data well ( $R^2 = 0.75$ ) indicating a similar proportion of singletons across the sites.

**Figure D9 Survey floral abundance vs. richness.** The first chart shows flower abundance vs. richness based on plot level data. The three charts on the right compare surveyed floral abundance to surveyed floral richness in plot level data, with and without singletons, and in meadow level data. Flower species richness in the plots increases by 1.7 times the natural log of total flower abundance in the plots or 3.1 times the floral abundance value based on the meadow level data. The relationships are best described using the logarithmic functions:  $y = 1.7 \ln(\text{abund})$ , ( $R^2 = 0.38$ ) and  $y = 3.1 \ln(\text{abund})$ , ( $R^2 = 0.13$ ). The quadratic equation had a worse fit for this relationship, though it better describes pollinator and interaction richness as a function of abundance matching the steeper initial increase. The removal of two outliers did not affect this relationship: the outlier was BS9. Floral richness in meadows increased by 3.12 times the log-transformed plot flower abundance value

### Survey flower abundance vs. richness

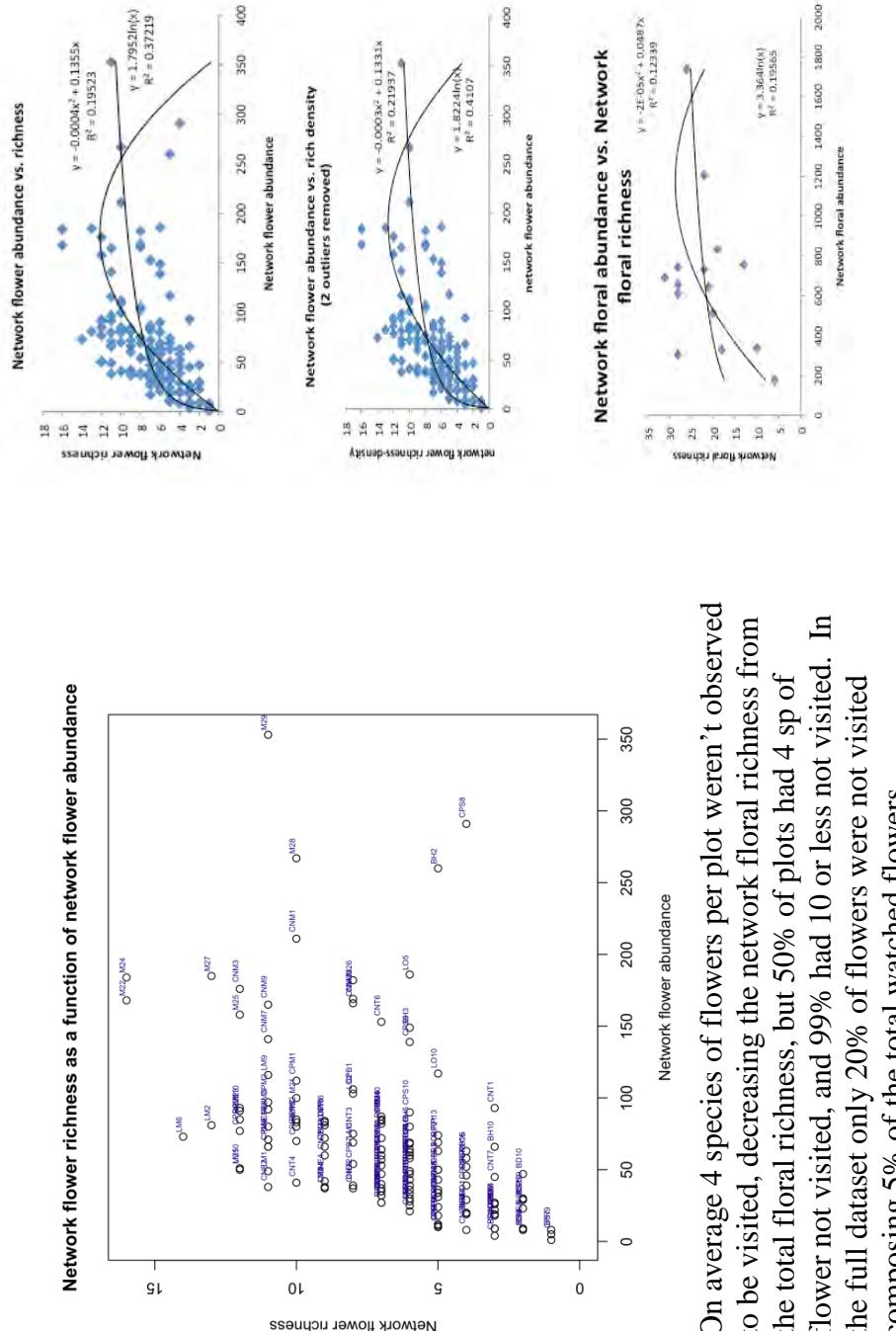


### Surveyed plot flower abundance vs. richness



**Figure D10 Network floral abundance vs. richness.** The first chart shows network floral richness as a function of network floral abundance based on plot-level data and the three charts on the right compare network floral abundance to network floral richness at the plot level with and without outliers, and at the meadow level. The relationship between network floral richness rises at 1.8 times the natural log value of network flower abundance based on the plot data and 3.4 times the natural log value of network flower abundance based on the meadow data. The curve dramatically rises, then tapers, leveling toward an asymptote. The logarithmic formula better fits this point distribution compared to the quadratic equation. The outliers removed were BH2 and CPS8

## Network flower abundance vs. richness



**Figure D11 Pollinator abundance vs. richness.** The first chart shows pollinator richness as a function of pollinator abundance based on plot-level data. The three charts on the right compare pollinator abundance to pollinator richness in the plot-level dataset with and without outliers, and in the meadow level dataset. Pollinator richness increases rapidly 4.1 times the natural log of pollinator abundance for the plot level ( $R^2 = 0.51$ ) and 9.8 times the natural log of pollinator abundance for the meadow level ( $R^2 = 0.44$ ), exhibiting a positive relationship. The dataset appears to exhibit an asymptote that is only reached by the most abundant plots. The models were fit with and without four outliers, but the model did not change significantly with these points omitted. The outlier removed were M28, M29, BH2, CPS8.

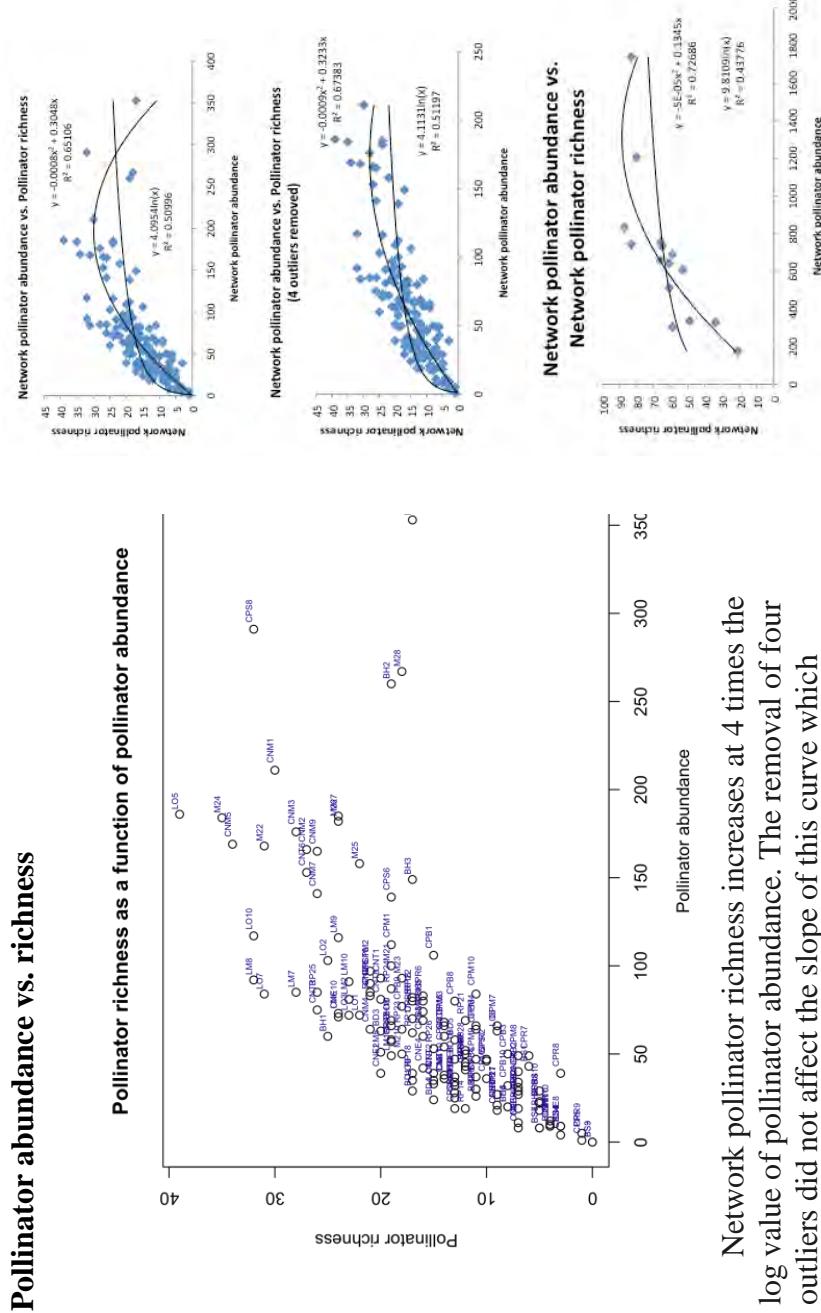
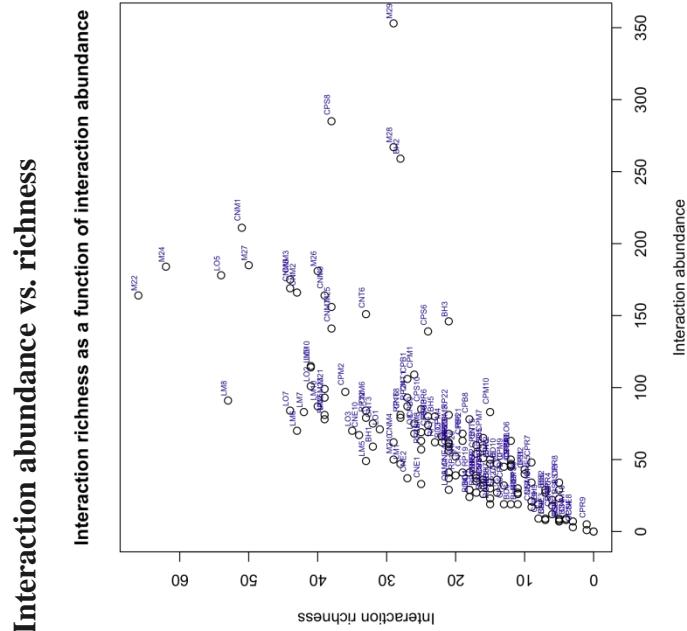
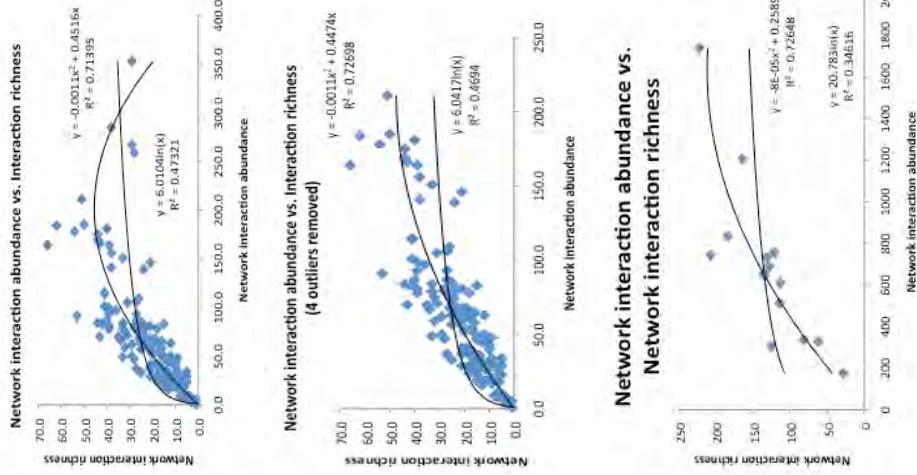


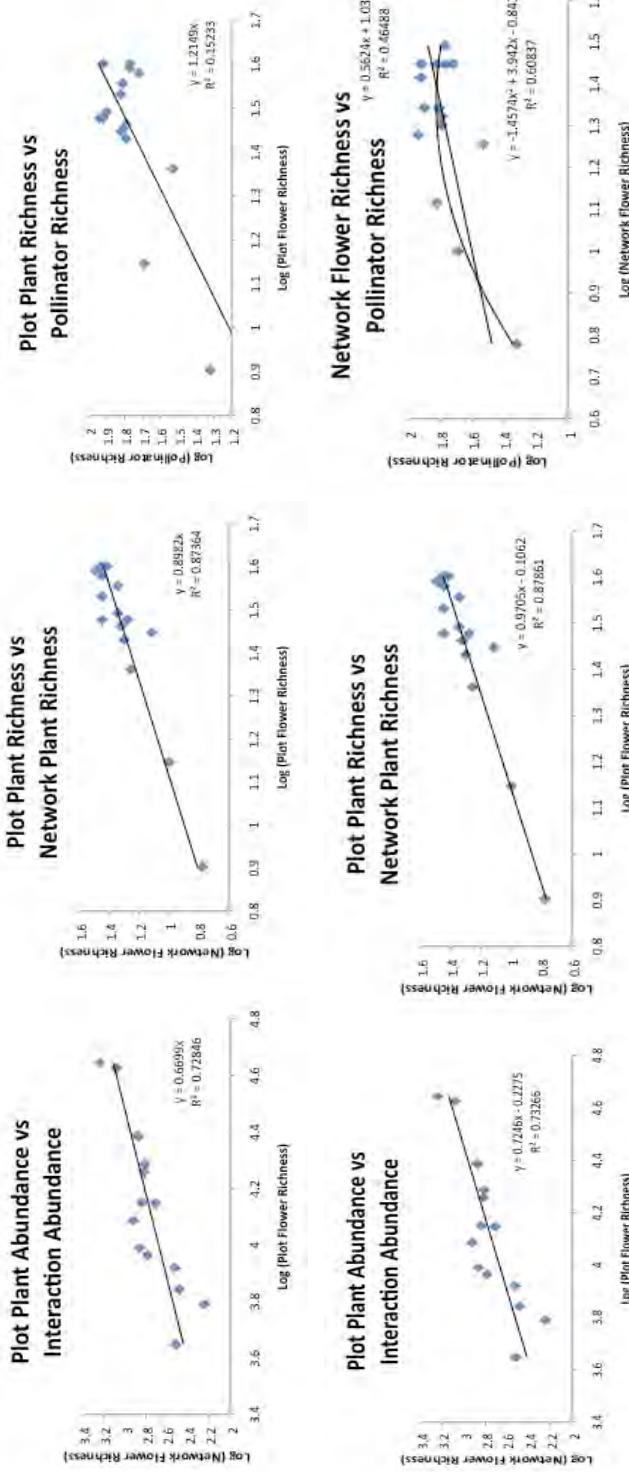
Figure D12 **Interaction abundance vs. richness.** The first chart shows interaction richness as a function of abundance based on plot-level data. The three charts on the right compare interaction abundance to interaction richness in the plot-level data with and without outliers, and in the meadow-level dataset. The relationship between interaction richness and interaction abundance increased very rapidly at 6 times the natural log of interaction abundance for the plot level data and 20.8 times the natural log of interaction abundance for meadow level data. An asymptote was not reached and interaction richness was remarkably high. This models was fit with and without four outliers, similar to the pollinator abundance vs. richness assessment. Again, the model did not change significantly with the points omitted (M28, M29, BH2, CPS8).



The plots show interaction richness as a function of interaction abundance from the network survey data.

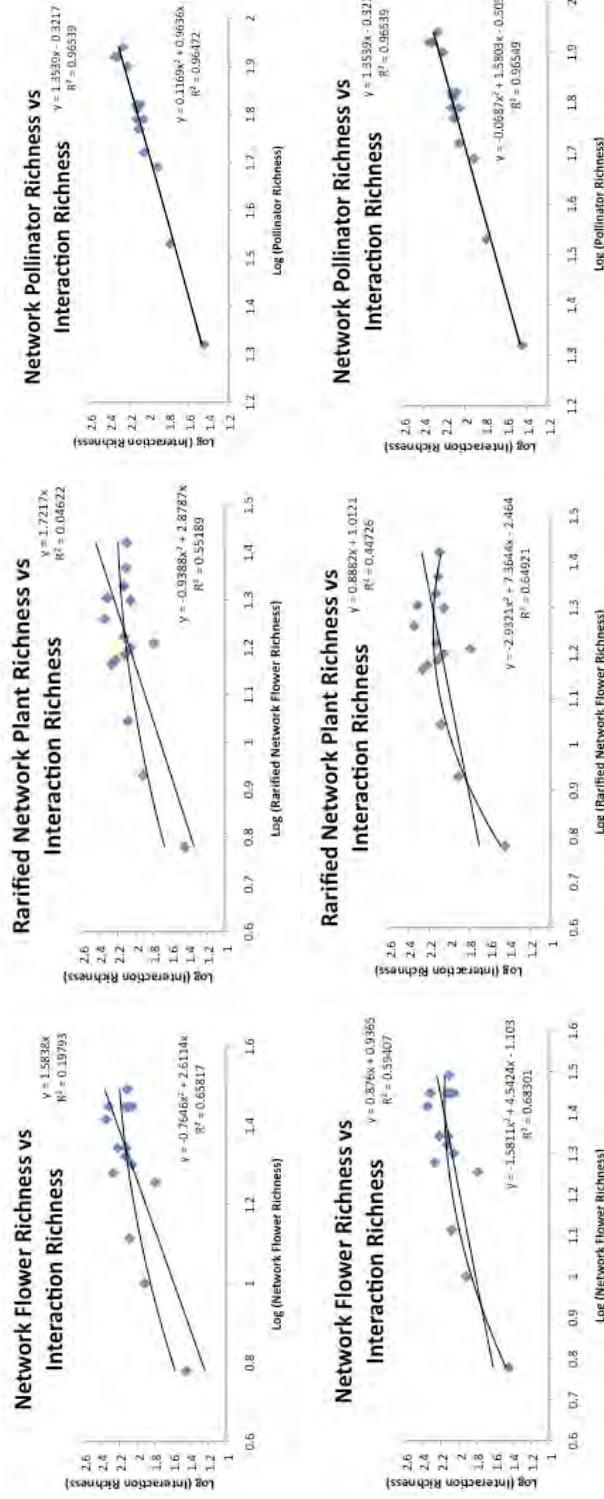


### Survey flower abundance and richness effects on interaction abundance and network flower and pollinator richness



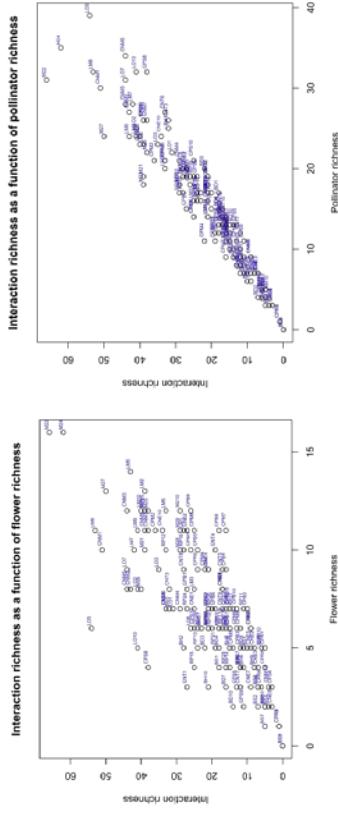
**Figure D13 The effects of survey flower abundance and richness on interaction abundance and network flower and pollinator richness.** Three plots compare surveyed floral abundance to interaction abundance, floral richness to network flora richness and floral richness to pollinator richness. Plots are shown two times with different linear models providing information from linear fits through the origin and fit to the data alone. Total interaction abundance increases by 67% the increase in total surveyed floral abundance. Total floral abundance explains a significant amount of variation in interaction abundance ( $R^2=0.73$ ). Total plant richness explains a significant amount of variation in network plant richness ( $R^2=0.88$ ), and network plant richness increases almost 1:1 (90%) with total plot flower richness. Log pollinator richness increases by 1.2 times of log surveyed flower richness ( $R^2$  value = 0.15), overall network pollinator richness is higher than plant richness.

### Network flower and pollinator richness vs. interaction richness.



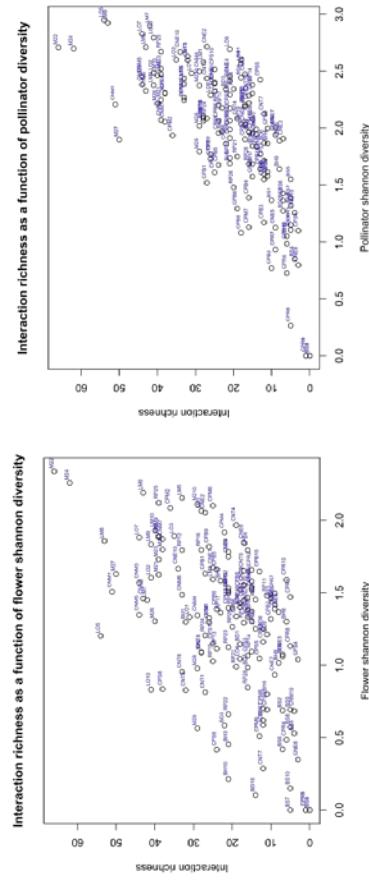
**Figure D14 Network flower and pollinator richness vs. interaction richness.** Three plots compare network floral richness to interaction richness, rarified network floral richness to interaction richness and pollinator richness to interaction richness. Plots are shown two times with different linear models providing information from linear fits through the origin and fit to the data alone. Interaction richness increases by 1.6 times of network flower richness (1.7 times rarified flower richness) and 1.4 times pollinator richness. Pollinator richness values were higher than plant richness values and pollinator richness explained a larger proportion of the variation in Interaction richness ( $R^2 = 0.97$  versus  $R^2 = 0.20$  or  $0.05$  for plants). Network flower richness and pollinator richness are positively correlated, however the relationship between interaction richness and plant richness is better explained by a quadratic function, due to the steep initial rise.

### Effects of flower and pollinator richness on interaction richness



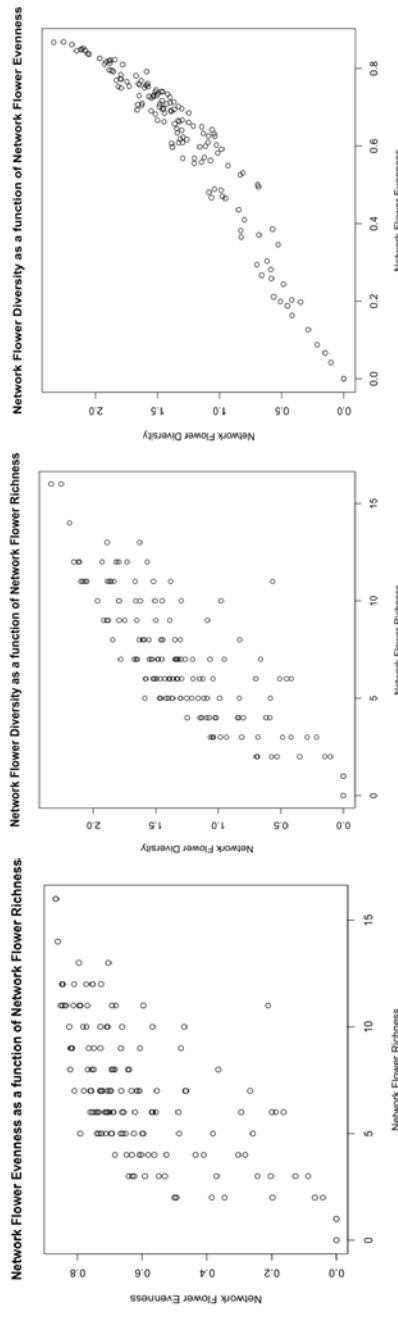
**Figure D15 Plant and pollinator richness vs. interaction richness at the plot level.** At the plot level the tight relationship between pollinator richness and interaction richness is even more visible. Interaction richness increases significantly with both groups, but a great deal more variability exists at plots with intermediate plant richness.

### Effects of flower and pollinator diversity on interaction richness



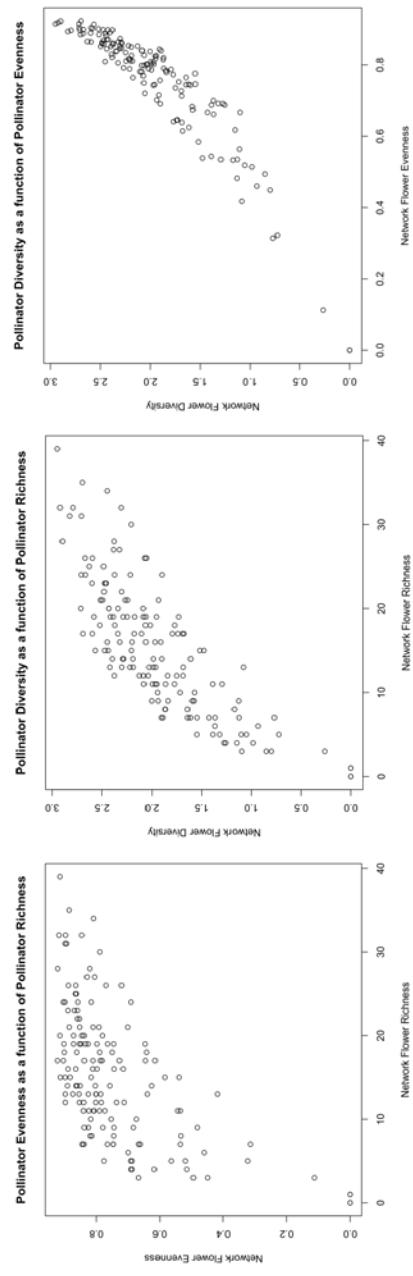
**Figure D16 Plant and pollinator Shannon diversity vs. interaction richness at the plot level.** These plots show a high degree of variability across these positive relationships. Again pollinator Shannon diversity is more significantly correlated to interaction richness than plant Shannon diversity.

### Relationships between flower richness, evenness and diversity



**Figure D17 Flower richness, evenness, and diversity.** These plots show relationships between floral richness, evenness and diversity at the plot scale.

### Relationships between pollinator richness, evenness, and diversity



**Figure D18 Pollinator richness, evenness, and diversity.** These plots show relationships between pollinator richness, evenness and diversity at the plot scale

### Relationships between interaction richness, evenness, and diversity

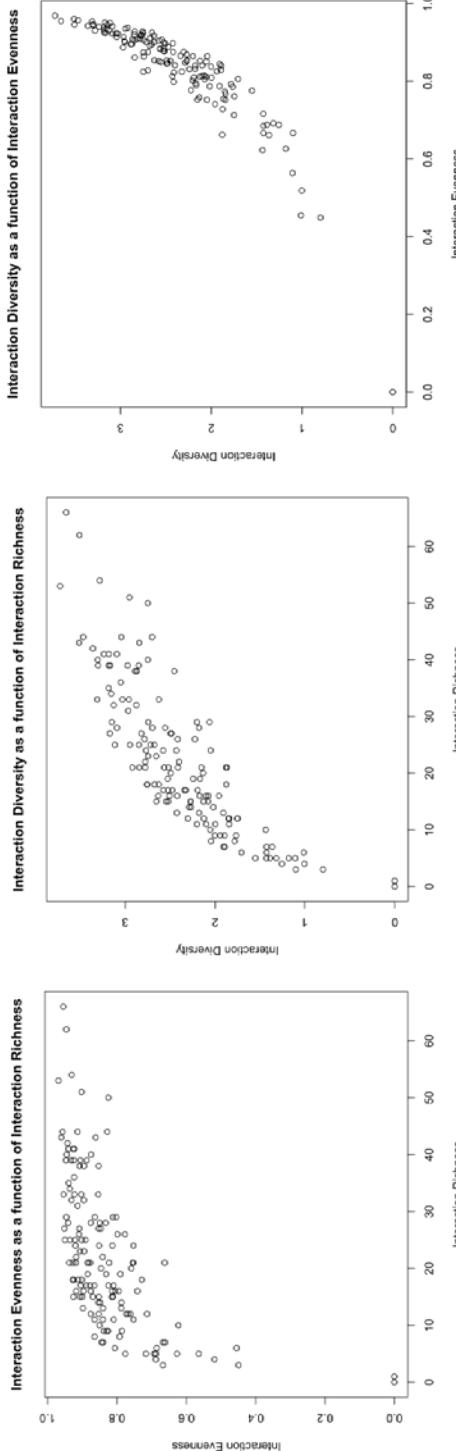
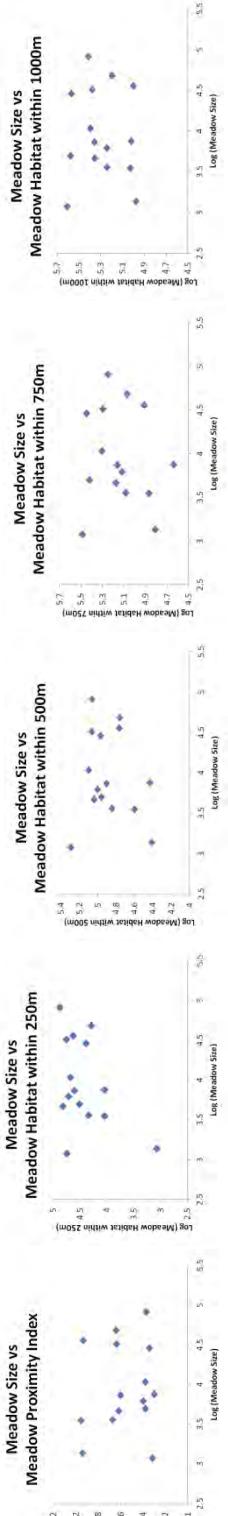


Figure D19 **Interaction richness, evenness, and diversity.** These plots show relationships between interaction richness, evenness and diversity at the plot scale.

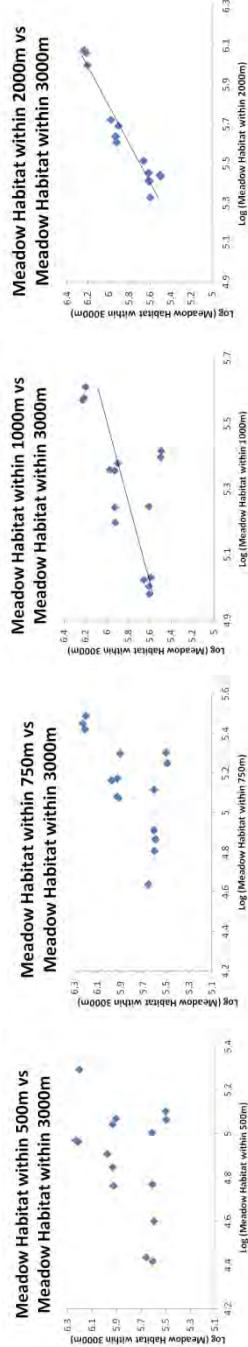
## APPENDIX E RICHNESS, EVENNESS, DIVERSITY VS. MEADOW SIZE AND SURROUNDING HABITAT

### Meadow size vs. surrounding meadow area at multiple scales



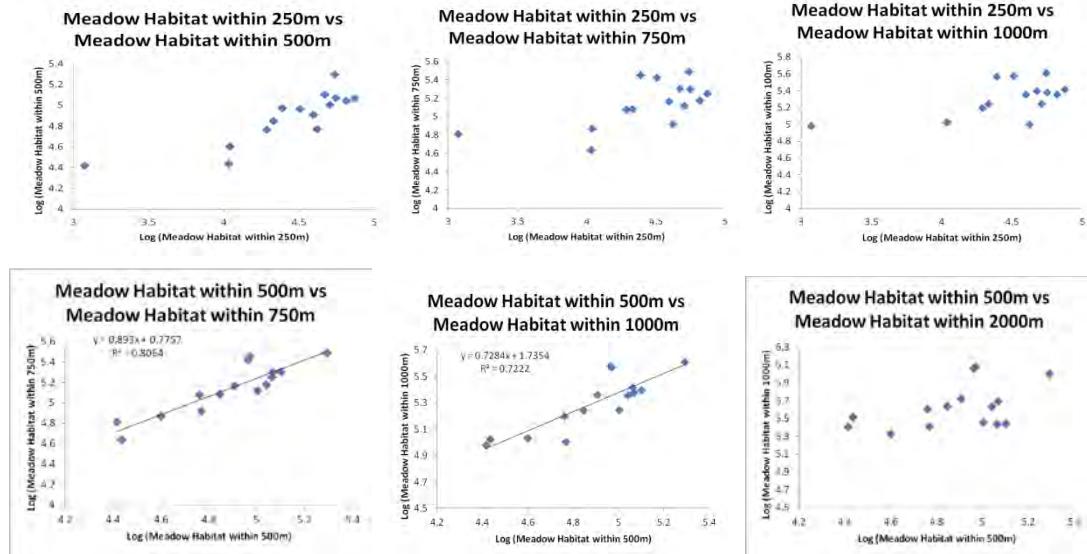
**Figure E1 Meadow size vs. surrounding meadow area at multiple scales.** These plot show meadow size compared to surrounding habitat at multiple scales: meadow proximity index; 250m; 500m; 750m; 1000m. These comparisons provide the context to understand the relationships between flower, pollinator, and interaction richness and diversity and habitat in the surrounding landscape.

### Surrounding meadow area at multiple scales vs. meadow area within 3000m



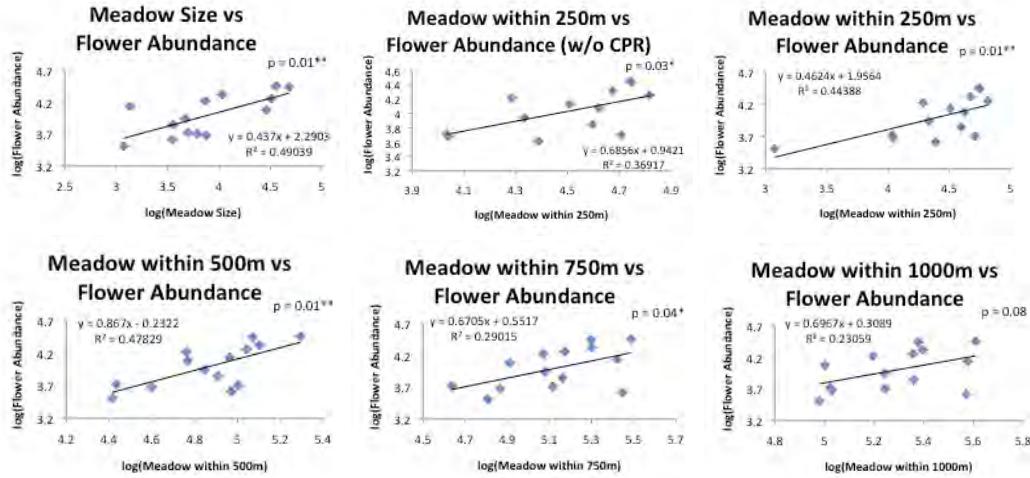
**Figure E2 Surrounding meadow area at multiple scales vs. meadow within 3000m.** These plot show surrounding meadow habitat at multiple scales compared to meadow habitat within 3000m, including: meadow habitat within 500m vs meadow habitat within 3000m; 1000m vs 3000m; and 2000m vs 3000m. These comparisons provide the context to understand the relationships between flower, pollinator, and interaction richness and diversity and habitat in the surrounding landscape.

### Variation between surrounding meadow area at different local scales



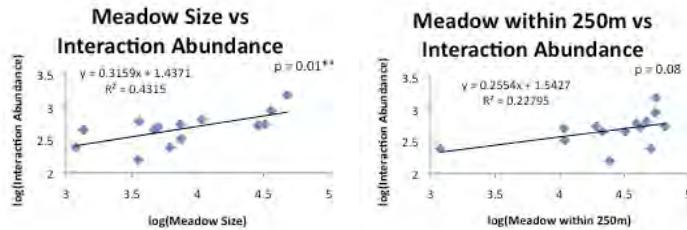
**Figure E3 Variation between surrounding meadow area at different local scales.** These plots show meadow size compared to surrounding habitat at multiple scales: meadow proximity index; 250m; 500m; 750m; 1000m. These comparisons provide the context to understand the relationships between flower, pollinator, and interaction richness and diversity and habitat in the surrounding landscape.

### Flower abundance: statistically significant regressions



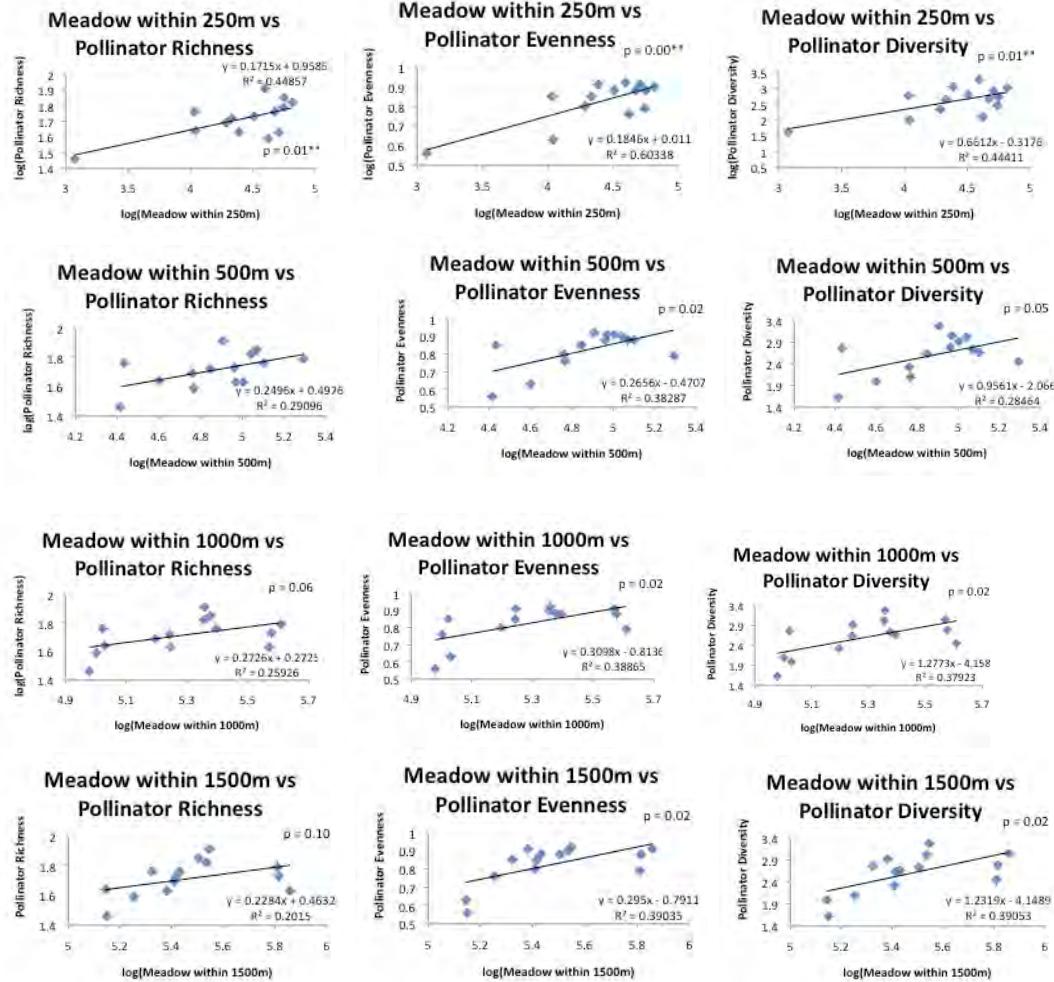
**Figure E4 Flower abundance: statistically significant regressions.** Charts describe the relationship between floral abundance and meadow size as well as surrounding meadow habitat at near scales. Bunchgrass Summit was omitted from all comparisons to meadow size due to its incredibly low abundance and diversity and huge size.

### Interaction abundance: statistically significant regressions



**Figure E5 Interaction abundance: statistically significant regressions.** Charts describe the relationship between interaction abundance and meadow size as well as surrounding meadow area within the 250m landscape sector. Bunchgrass Summit was omitted from all comparisons to meadow size due to its incredibly low abundance and diversity and its huge size.

### Pollinator richness, evenness, and diversity: statistically significant regressions



**Figure E6 Pollinator richness, evenness, and diversity: statistically significant regressions.** Charts describe the relationship between pollinator richness, evenness and diversity and meadow area within the surrounding 250m, 500m, 1000m, and 1500m landscape sectors. Bunchgrass Summit was omitted from all comparisons to meadow size due to its incredibly low abundance and diversity and its huge size.

## APPENDIX F MOISTURE ANALYSIS

**Table F1 Soil moisture measurements and moisture groups.** These tables show plant-available moisture measured in grams plant-available H<sub>2</sub>O per grams of oven dried soil for Week 3 and Week 5 and soil moisture decline between week 3 and week 5 in grams plant-available H<sub>2</sub>O per grams of oven dried soil. The tables on the right show the meadows classified as dry compared to the meadows classified as relatively moist.

### Plant-Available Moisture

Study Meadow	Week 3 (gH <sub>2</sub> O/ gSoil)	Week 5 (gH <sub>2</sub> O/ gSoil)	Decline (gH <sub>2</sub> O/ gSoil)
BD	0.11	0.12	0
BH	0.13	0.04	0.09
BS	0.16	0.06	0.1
CPB	0.29	0.17	0.12
CPM	0.32	0.12	0.2
CPR	0.39	0.13	0.26
CPS	0.09	0.07	0.02
CNE	0.44	0.17	0.27
CNM	0	0	0
CNT	0.07	0	0.07
M2	0.38	0.1	0.28
RP1	0.13	0.09	0.04
RP2	0.09	0.01	0.08
LM	0.41	0.03	0.38
LO	0.02	0	0.02

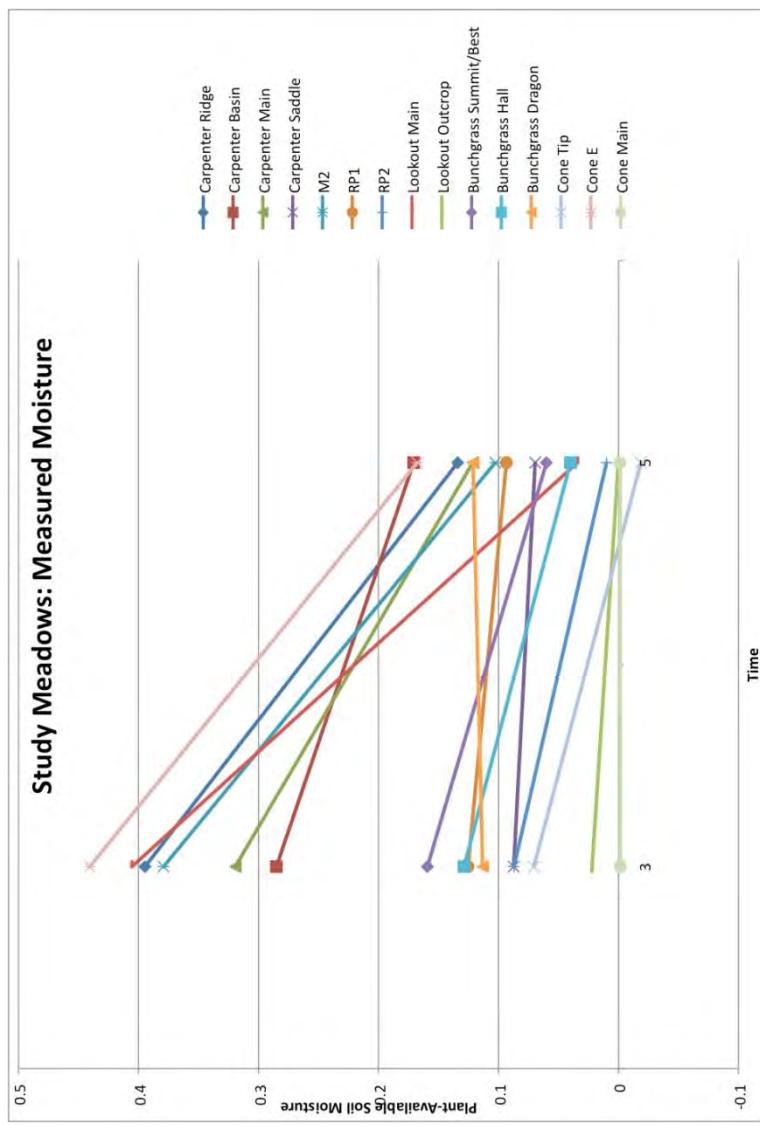
### DRY: Low DRY MEADOWS

Meadow	Week 3	Week 5	Decline
BD		0.11	0.12
BH		0.13	0.04
BS		0.16	0.06
CPS		0.09	0.07
CNM		0	0
CNT		0.07	0
RP1		0.13	0.09
RP2		0.09	0.01
LO		0.02	0

### RELATIVELY MOIST MEADOWS

Meadow	Week 3	Week 5	Decline
CPR		0.39	0.13
M2		0.38	0.1
LM		0.41	0.03
CNE		0.44	0.17
CPB		0.29	0.17
CPM		0.32	0.12

### Moisture decline through the season

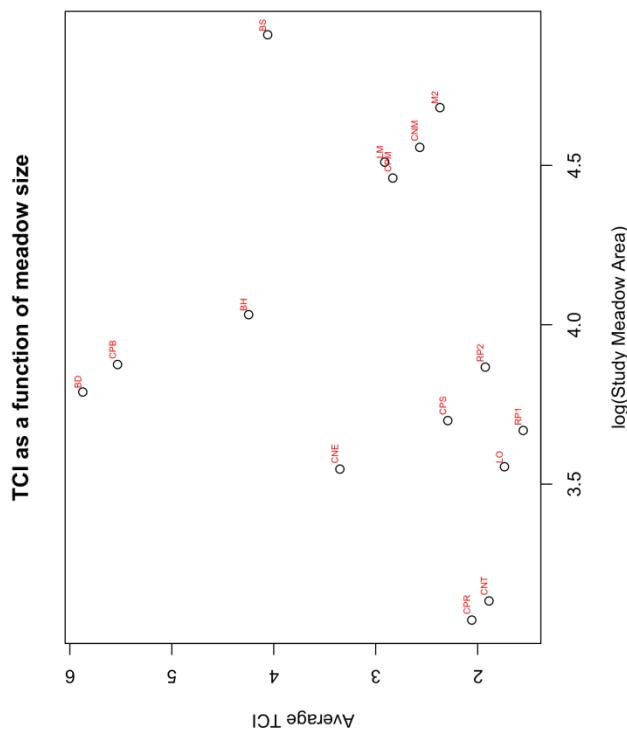


**Figure F1 Moisture decline through the season.** This figure shows the moisture decline between weeks 3 and 5 in all study meadows through the season.

Table F2 Measured soil moisture and Topographic Convergence Index (TCI) values. Average TCI values for each meadow, TCI Standard Deviation within each meadow

Study Meadow	Week 3		Week 5		Avg TCI	TCI St Dev	<2	Area TCI 4<9
	(gH <sub>2</sub> O/ gSoil)	(gH <sub>2</sub> O/ gSoil)						
BD	0.11	0.12	5.87	1.48	0.00	0.00	0.51	
BH	0.13	0.04	4.25	1.29	0.02	0.02	0.55	
BS	0.16	0.06	4.06	1.13	0.57	4.99		
CPB	0.29	0.17	5.53	1.11	0.02	0.72		
CPM	0.32	0.12	2.83	1.06	0.59	0.31		
CPR	0.39	0.13	2.06	0.68	0.07	0.00		
CPS	0.09	0.07	2.29	0.85	0.19	0.01		
CNE	0.44	0.17	3.35	1.18	0.05	0.08		
CNM	0	0	2.57	1.06	1.22	0.45		
CNT	0.07	0	1.89	1.05	0.06	0.00		
M2	0.38	0.1	2.37	0.88	1.65	0.14		
RP1	0.13	0.09	1.55	0.77	0.27	0.00		
RP2	0.09	0.01	1.93	0.62	0.37	0.00		
LM	0.41	0.03	2.91	1.22	0.69	0.54		
LO	0.02	0	1.74	0.27	0.33	0.00		

Figure F2 Meadow size vs. average TCI value. This figure shows the average meadow TCI as a function of log transformed study meadow size



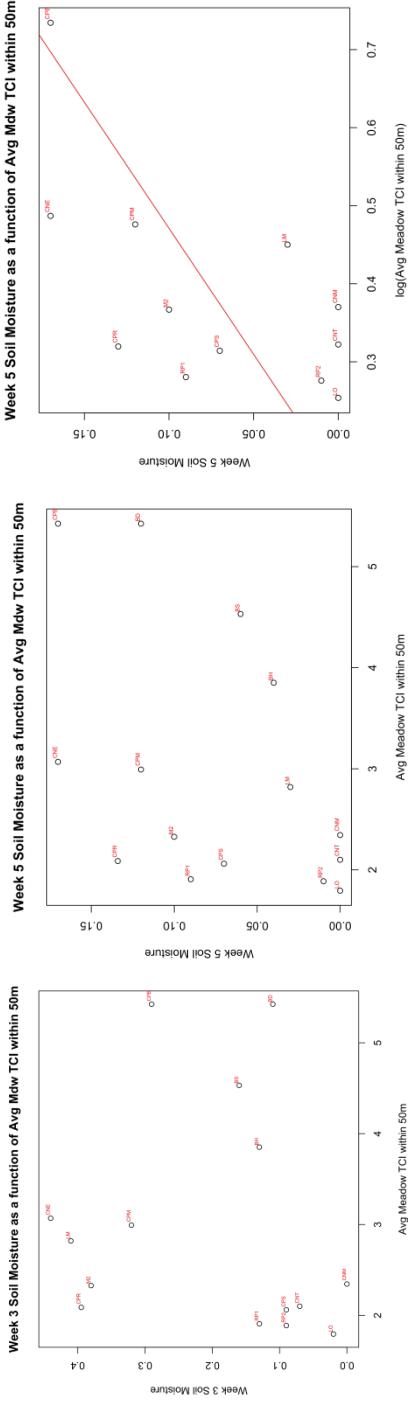
**Table F3 Surrounding meadow surface area where TCI<2 in hectares.** Three-dimensional surface area of meadow habitat where TCI value falls below 2 summed within a landscape sector and measured in hectares. The circular buffers constructed with radii of 250m to 3000m were centered at the middle point of the permanent meadow study plots.

Meadow	25m	50m	100m	250m	500m	750m	1000m	1500m	2000m	2500m	3000m
BD	0.00	0.00	0.00	0.05	0.11	0.19	0.26	0.67	0.81	0.80	0.79
BH	0.01	0.02	0.03	0.12	0.53	0.65	0.70	0.70	0.78	0.81	0.81
BS	0.00	0.00	0.00	0.09	0.55	0.62	0.67	0.70	0.70	0.81	0.80
CPB	0.00	0.02	0.02	0.05	0.62	1.70	2.81	4.05	5.94	9.95	12.00
CPM	0.00	0.06	0.39	0.86	1.17	1.50	2.21	4.86	7.58	10.76	12.19
CPR	0.03	0.04	0.04	0.01	0.37	1.49	2.23	4.59	7.97	12.12	12.54
CPS	0.05	0.06	0.15	0.27	0.34	0.85	2.32	6.38	9.03	11.90	14.88
CNE	0.04	0.07	0.07	1.00	2.65	9.12	13.87	27.21	47.91	63.95	74.59
CNM	0.04	0.15	0.31	1.23	7.70	11.83	16.18	25.72	40.09	59.90	70.28
CNT	0.04	0.06	0.16	1.75	2.94	9.54	14.05	25.15	48.17	63.80	71.87
M2	0.11	0.30	0.51	1.66	2.92	4.88	6.72	10.42	15.44	23.91	27.58
RP1	0.09	0.22	0.34	1.02	2.20	3.60	4.88	7.36	13.05	19.51	30.32
RP2	0.14	0.42	0.43	1.03	2.11	3.49	4.35	7.18	11.84	19.86	29.28
LM	0.06	0.16	0.40	1.53	2.84	3.47	6.67	11.14	15.06	27.03	35.46
LO	0.18	0.33	0.70	2.31	3.05	4.80	7.70	12.25	20.31	26.22	37.33

**Table F4 Surrounding meadow surface area where TCI values are >4, <9 in hectares.** Three-dimensional surface area of meadow habitat where TCI value falls between 4 and 9 summed within the landscape sector and measured in hectares. The landscape sectors constructed with radii of 250m to 3000m were centered at the middle point of the permanent meadow study plots.

Meadow	25m	50m	100m	250m	500m	750m	1000m	1500m	2000m	2500m	3000m
BD	0.19	0.37	0.62	4.49	9.03	11.29	14.16	18.60	21.02	25.79	30.57
BH	0.08	0.19	0.54	2.86	8.58	15.32	19.22	20.78	20.87	21.12	23.70
BS	0.16	0.62	1.72	5.02	7.63	13.16	19.90	20.78	20.78	21.02	23.31
CPB	0.19	0.58	0.67	0.68	1.11	1.30	2.05	2.57	5.46	7.75	9.17
CPM	0.00	0.03	0.21	0.44	1.16	2.12	2.17	3.99	6.47	8.44	9.43
CPR	0.00	0.00	0.00	0.05	0.65	1.30	1.96	2.61	4.86	8.97	8.03
CPS	0.00	0.00	0.00	0.17	1.39	1.59	2.67	4.93	8.44	9.06	9.63
CNE	0.00	0.05	0.07	0.16	1.29	3.09	3.55	5.88	8.23	9.19	10.03
CNM	0.00	0.00	0.13	0.80	1.54	2.09	3.27	4.90	7.20	8.41	9.36
CNT	0.00	0.00	0.00	0.09	1.17	2.64	3.31	5.00	7.63	8.73	9.57
M2	0.00	0.00	0.02	0.20	0.70	1.74	1.86	2.74	6.41	8.79	9.01
RP1	0.00	0.00	0.00	0.05	0.65	1.23	1.40	1.97	3.35	8.16	9.13
RP2	0.00	0.00	0.00	0.00	0.37	0.98	1.36	1.98	2.96	8.12	9.11
LM	0.04	0.08	0.25	0.78	1.52	2.00	2.20	3.08	4.07	5.22	6.63
LO	0.00	0.00	0.00	0.07	0.54	1.19	2.39	3.40	4.46	11.83	13.79

## Soil moisture vs. average TCI value around permanent plots



**Figure F3 Soil moisture vs. average TCI value around permanent plots.** The topographic convergence index (TCI) depicts meadows that retain moisture at the end of the season with very high index values, and meadows with very low values dried out very quickly. The relationship between actual meadow moisture and TCI moisture is described below. It is clear that the Bunchgrass meadows do not respond in a similar way to the other meadow complexes, and TCI cannot be used as a factor for those meadows relative to the rest of the study meadows. The chart on the far right does not include the three Bunchgrass meadows.

## APPENDIX G COMMUNITY STRUCTURE

### PART A FLOWER DENDROGRAMS

### PART B POLLINATOR COMMUNITY ORDINATION

#### Complex key

Complexes were grouped as follows

- 1 Cone Peak
- 2 Frissell Ridge
- 3 Lookout Mountain
- 4 Carpenter Mountain
- 5 Bunchgrass Meadows

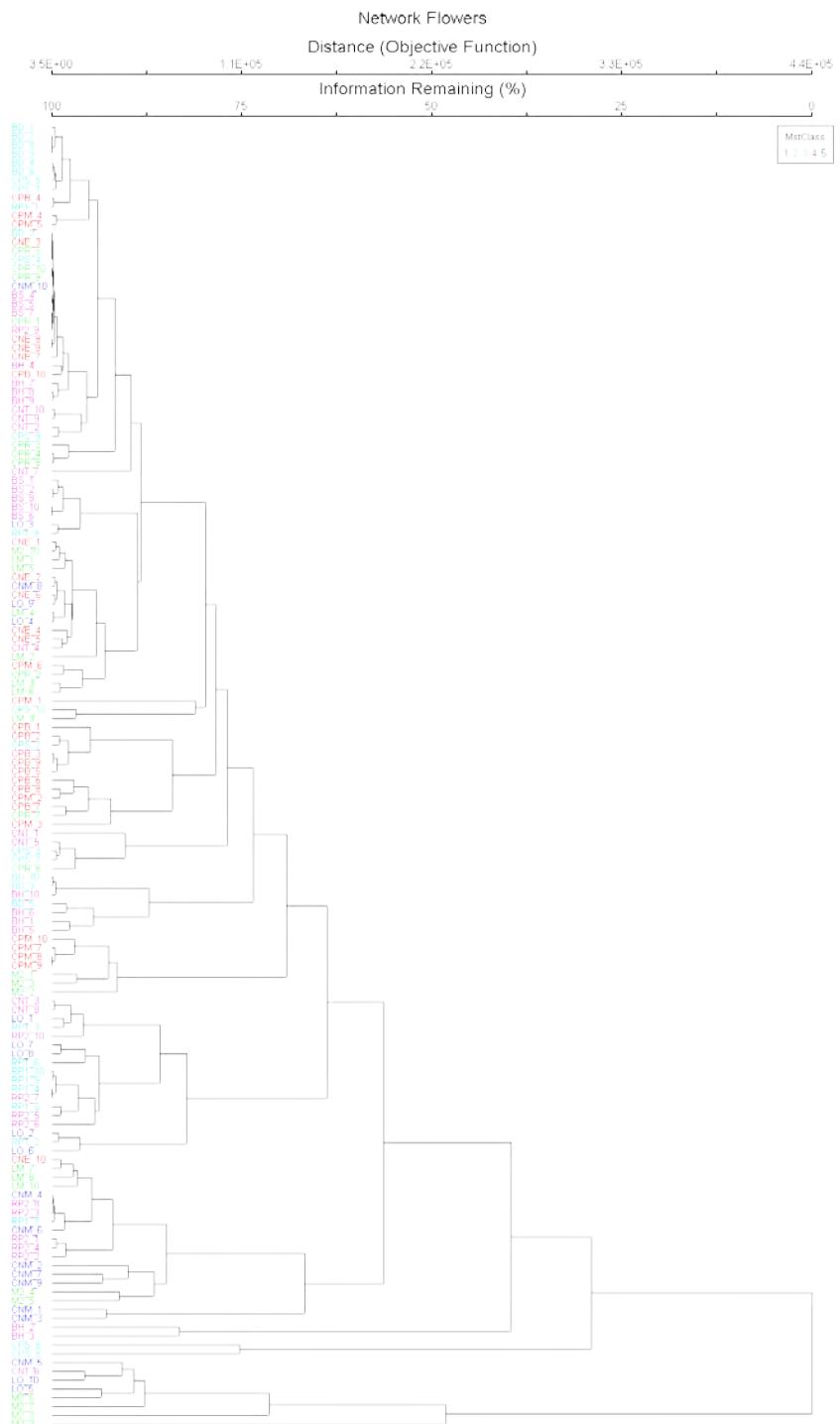
#### Moisture class key

Moisture classes were grouped according to the visual plot of the measured moisture in weeks 3 and 5. Classes were divided as follows.

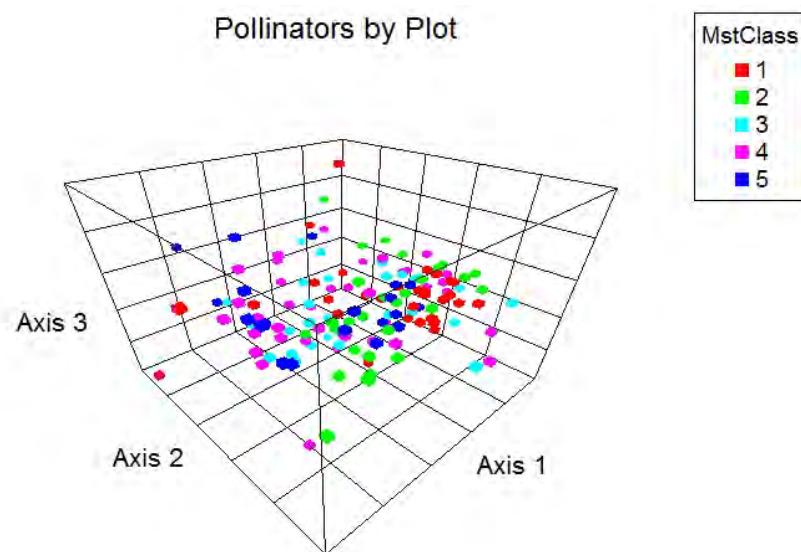
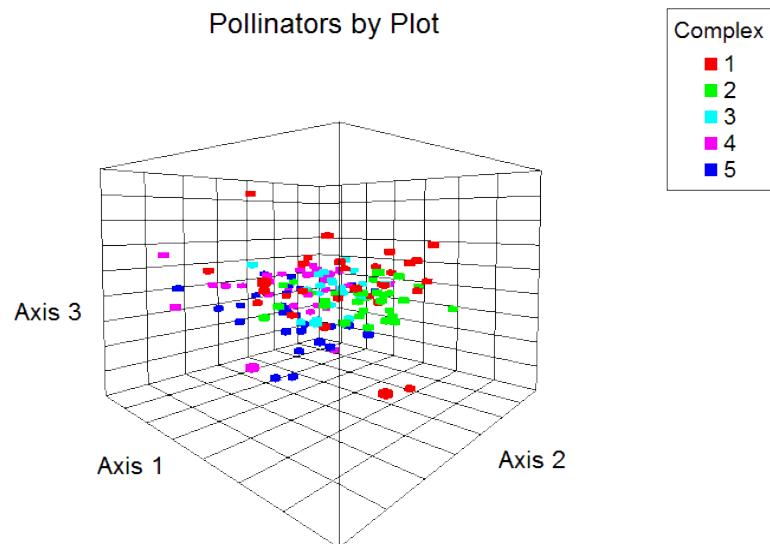
- 1 High moisture in weeks 3 and 5 (CNE, CPB, CPM)
- 2 High moisture with high decrease between week 3 and week 5 (CPR, LM, M2)
- 3 Moderate moisture, maintained through the season (BD, CPS, RP1)
- 4 Low moisture, but dried significantly (BH, BS, CNT, RP2)
- 5 Low moisture in weeks 3 and 5 (CNM, LO)

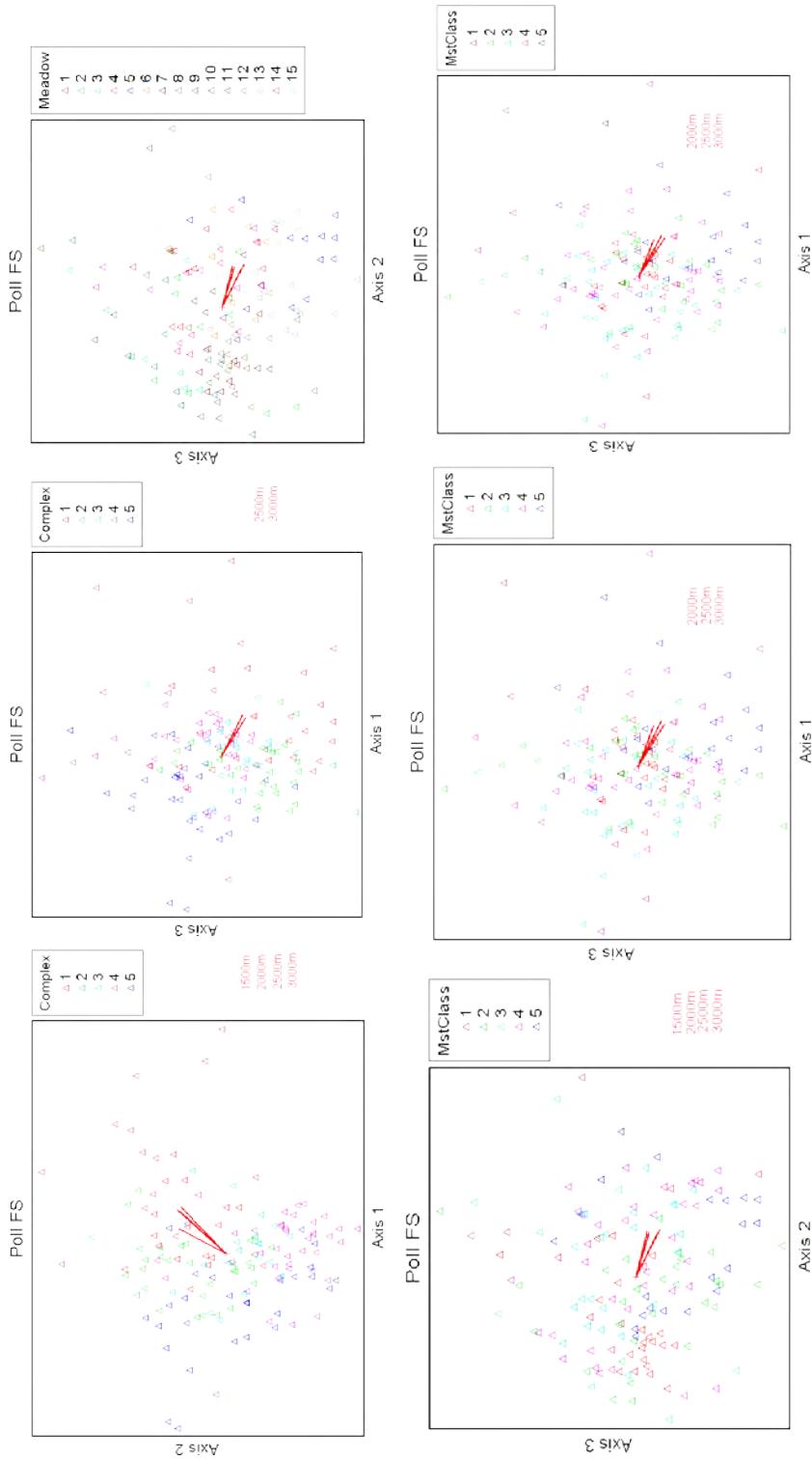
**Figure G1 Full season network flower cluster analysis results symbolized by meadow complex and soil moisture.** These two dendrogram images show the cluster analysis results for full season meadow plot floral communities symbolized (1) by meadow complex, and (2) by meadow moisture class.

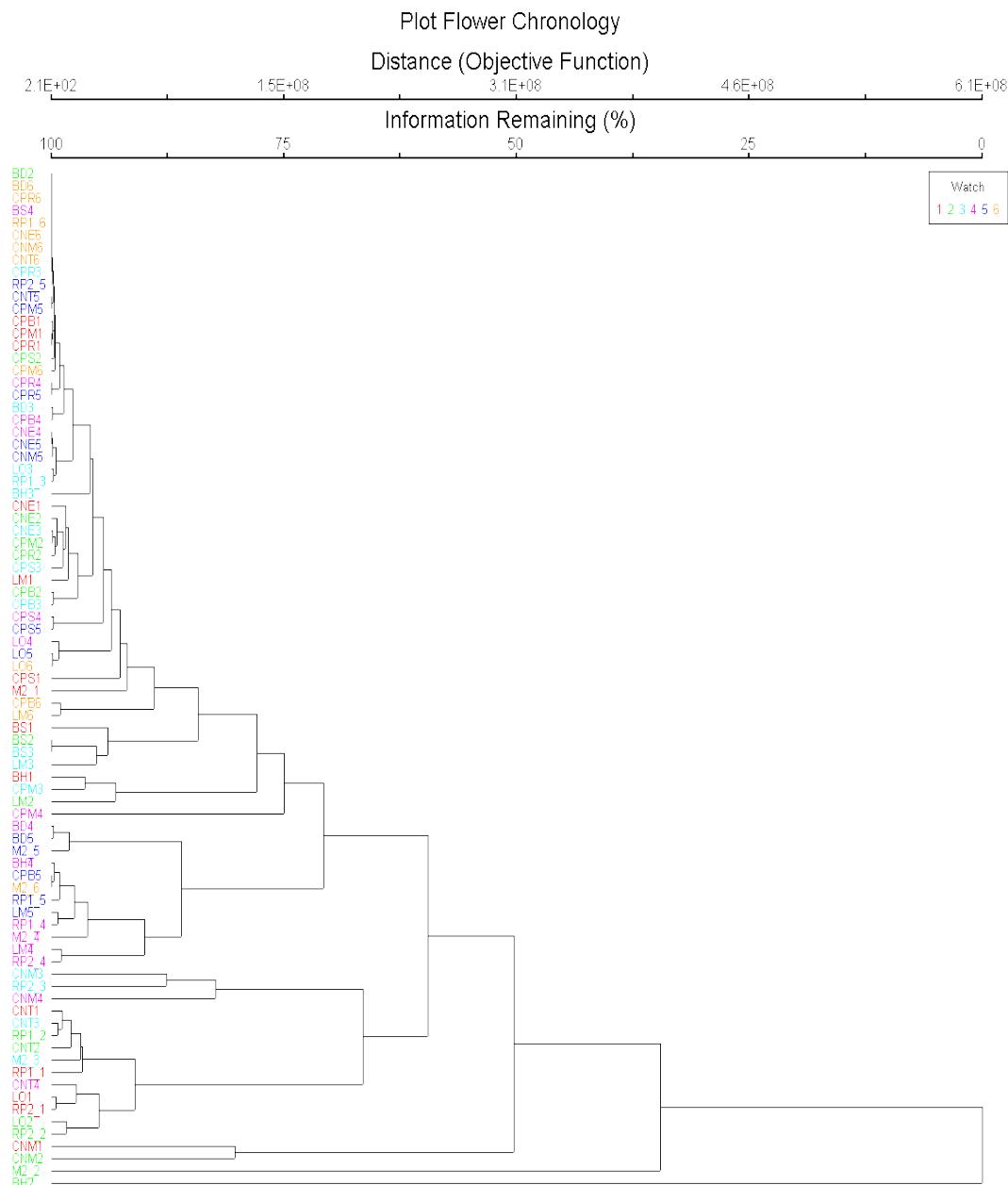




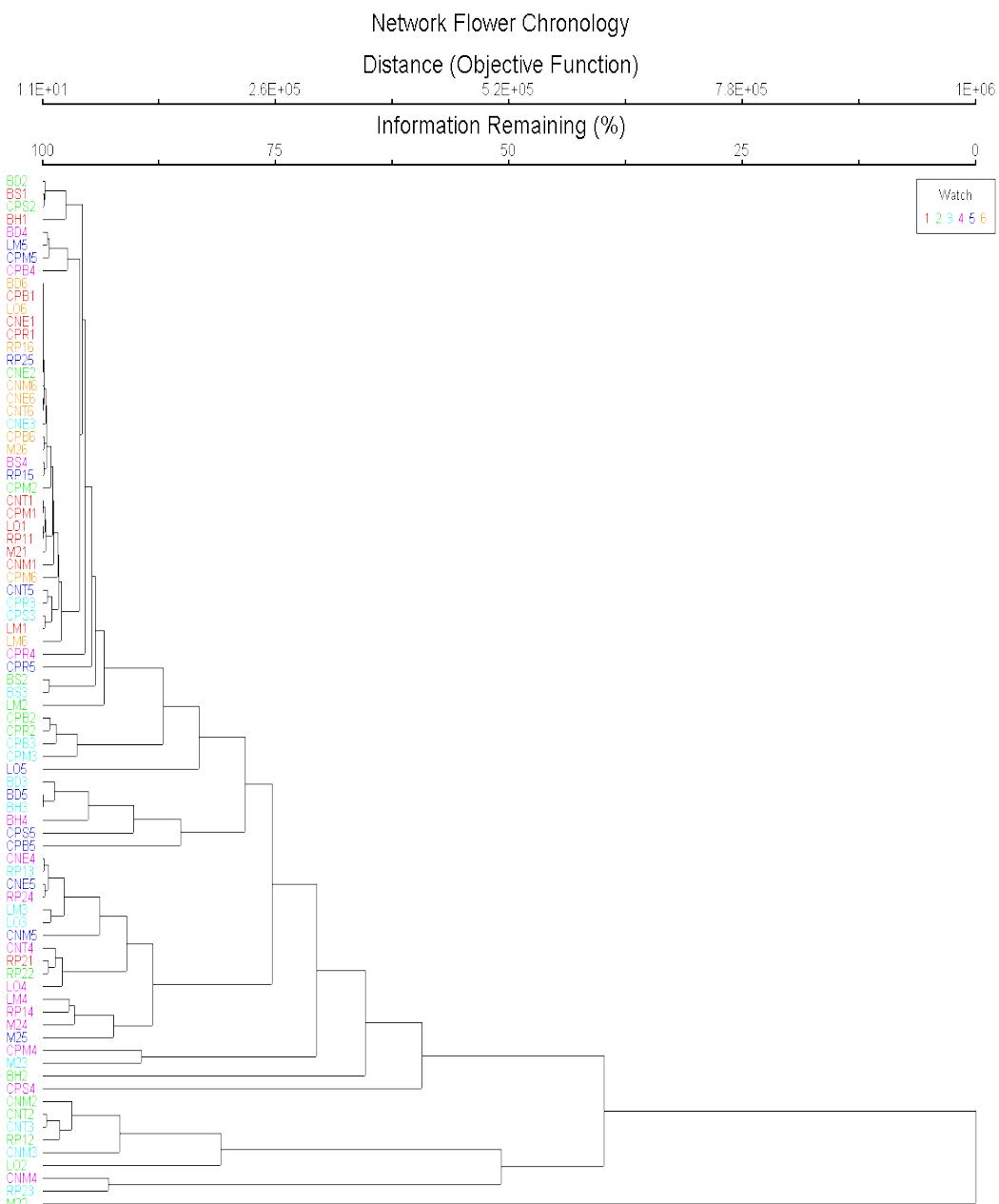
**Figure G2 Full season pollinator ordination results symbolized by meadow complex and soil moisture.** Permanent plot pollinator observations summed across the season did not show significant structure by complex or moisture class. Some sorting was visible when the full season plot points were symbolized by complex, however each complex mixes in the center of the ordinal space. Meadow complexes appeared slightly clumped, but no complex stood out from the others completely.





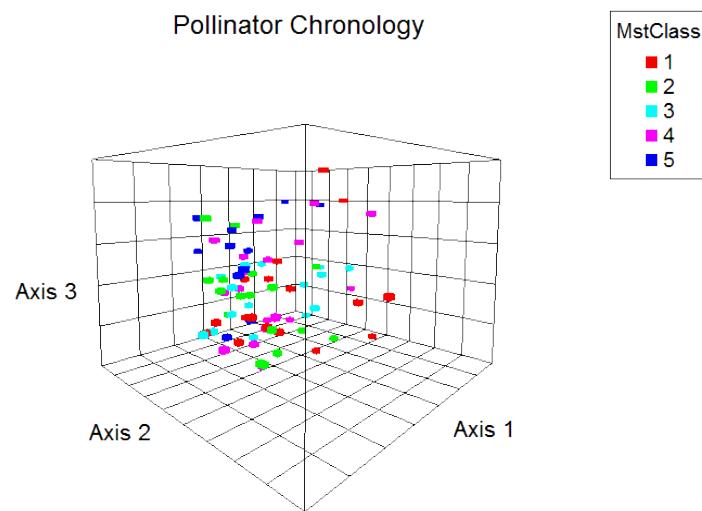
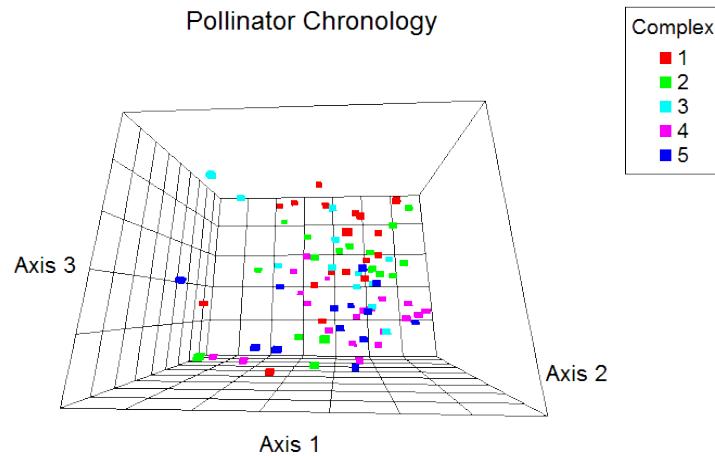


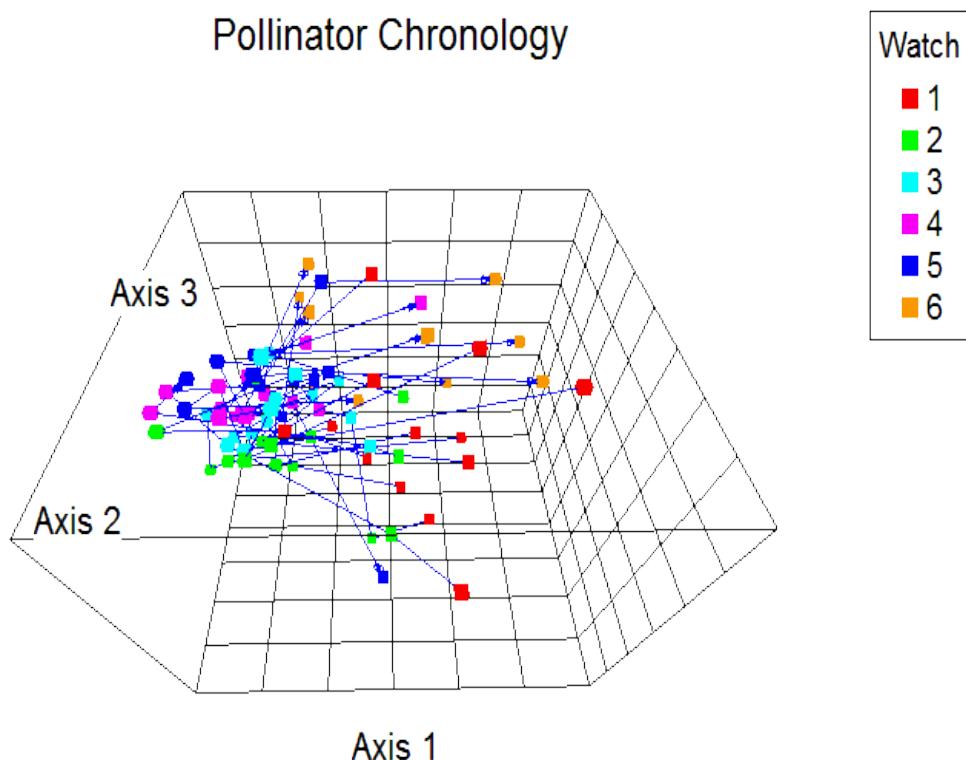
**Figure G3 Survey flower phenology cluster analysis results symbolized by watch date.** This dendrogram shows the cluster analysis results for meadow floral communities based on flower surveys summed across all ten plots for each visit. The communities are symbolized by visitation round.

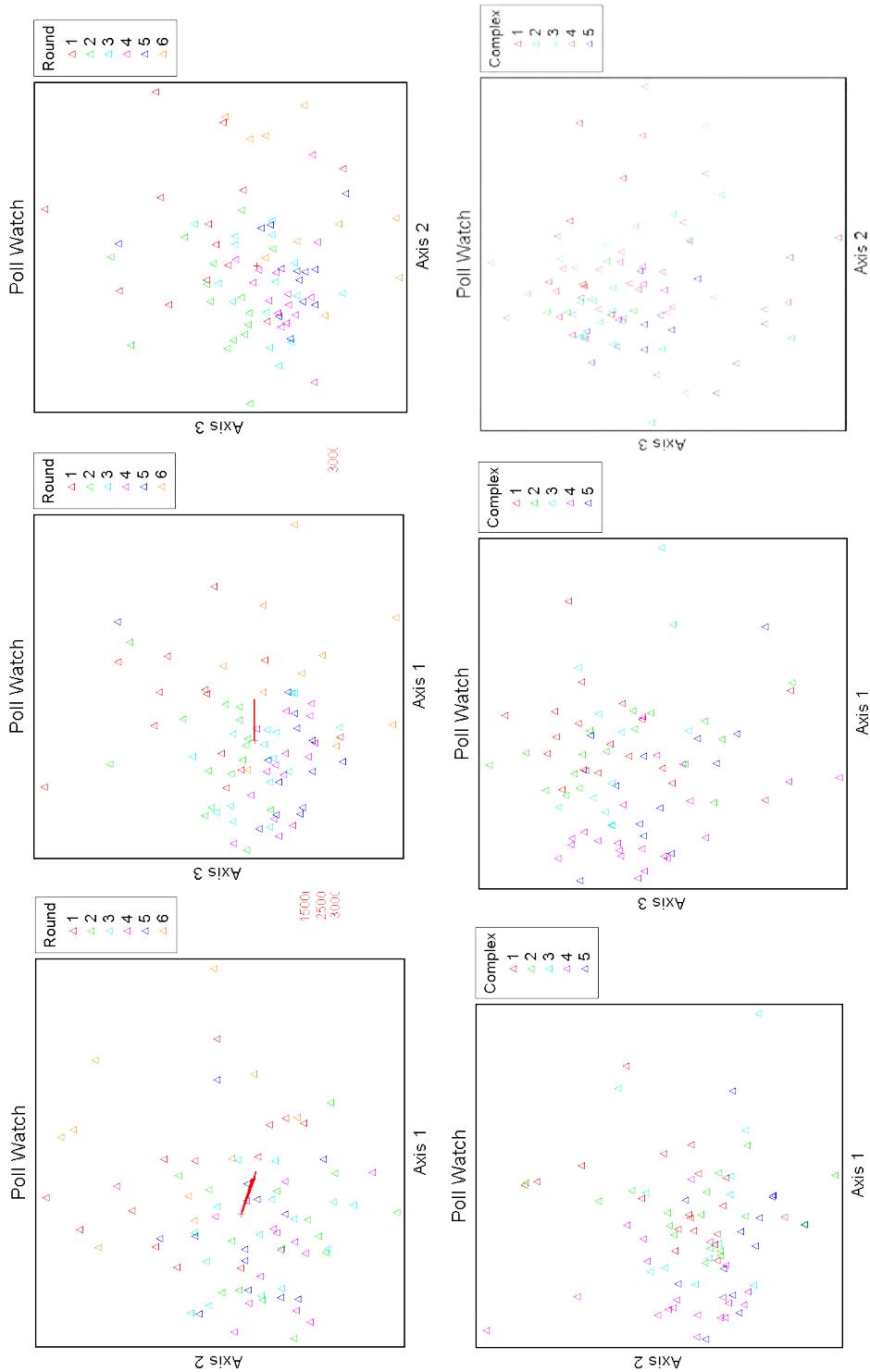


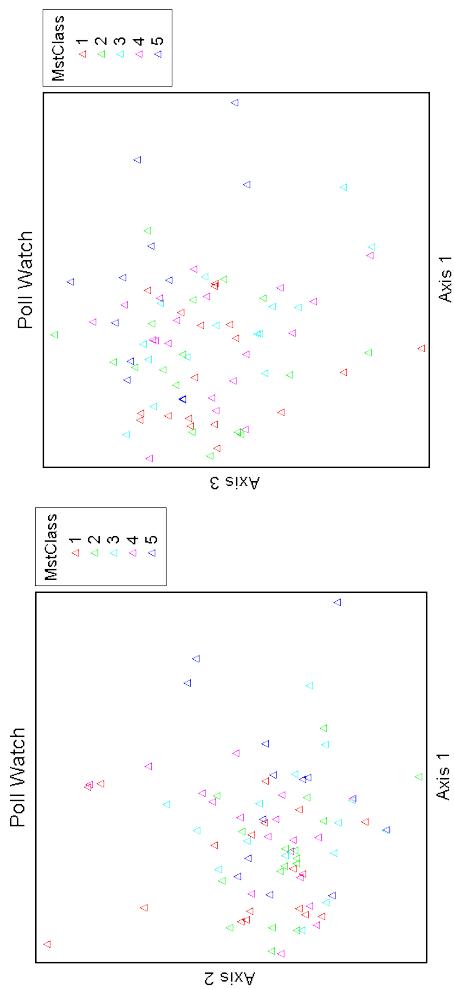
**Figure G4 Network flower phenology cluster analysis results symbolized by watch date.** This dendrogram shows the cluster analysis results for network floral communities based upon abundance in the network summed across all ten plots for each watch date. The communities are symbolized visitation round.

**Figure G5 Pollinator phenology ordinations symbolized by complex, moisture class, and watch date.** Meadow pollinator communities summed across all plot watches for each visitation round (watch date) are shown symbolized by meadow complex, moisture class, and meadow watch date. The communities did not show significant structure by complex or moisture class. Some sorting was visible when the full season plot points were symbolized by watch date and a phonological pattern emerged that is more easily viewed with added vector paths connecting subsequent watch date communities in each meadow.



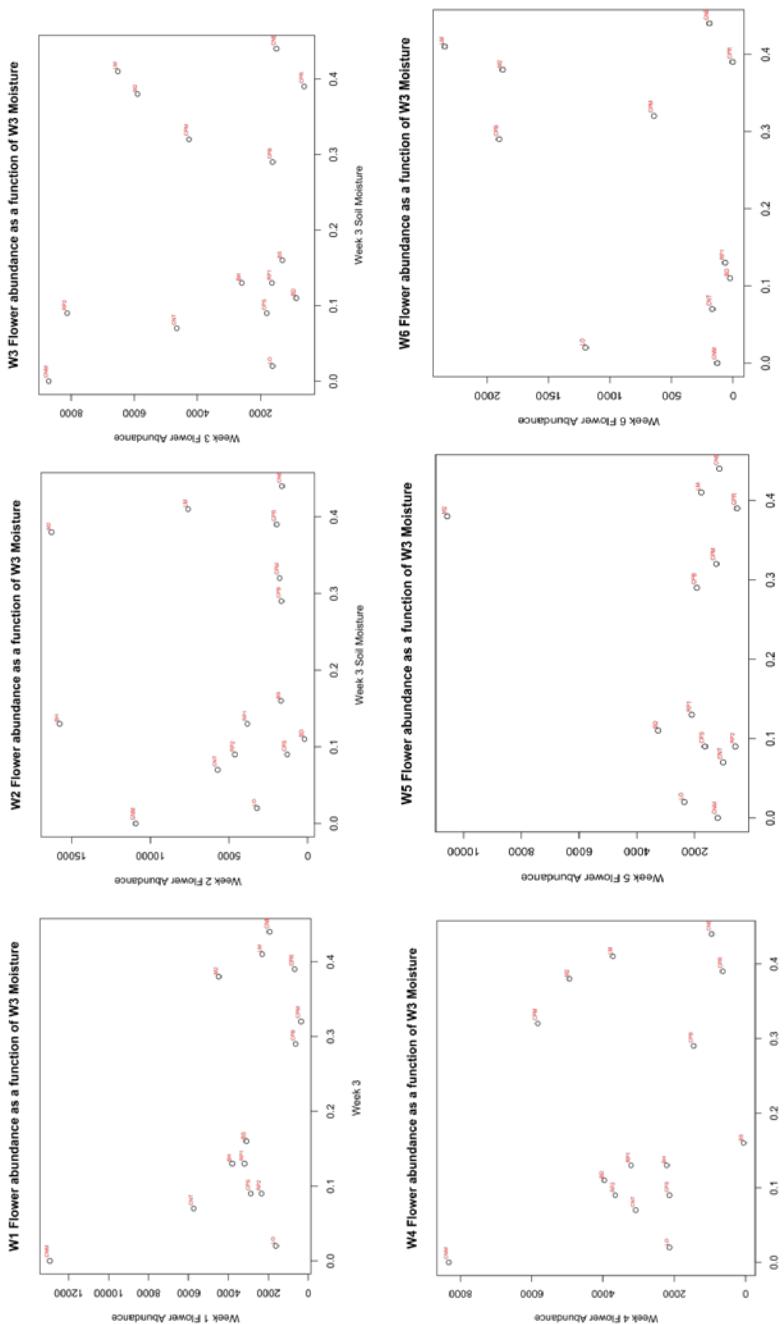






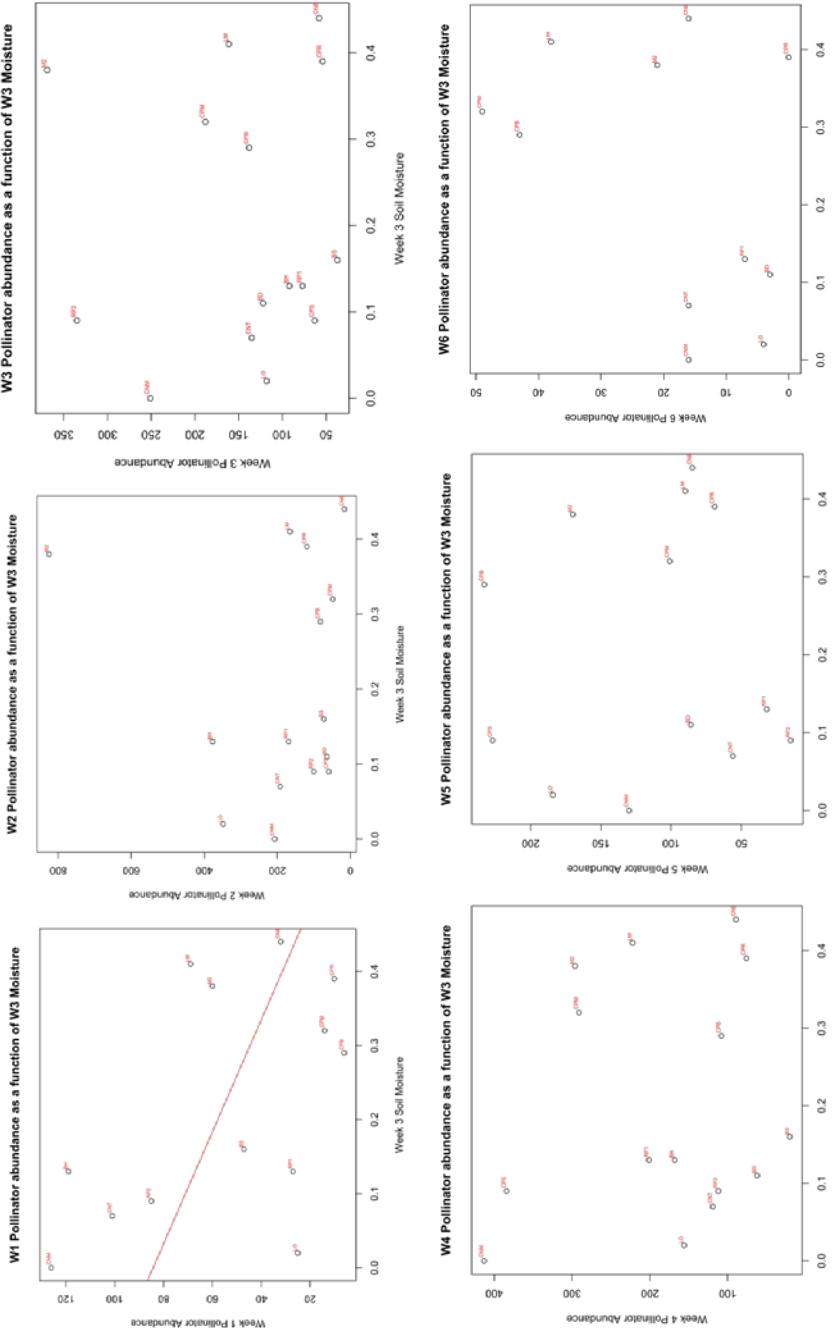
## APPENDIX H MOISTURE, PHENOLOGY, AND ABUNDANCE

### Peak season meadow moisture vs. floral abundance



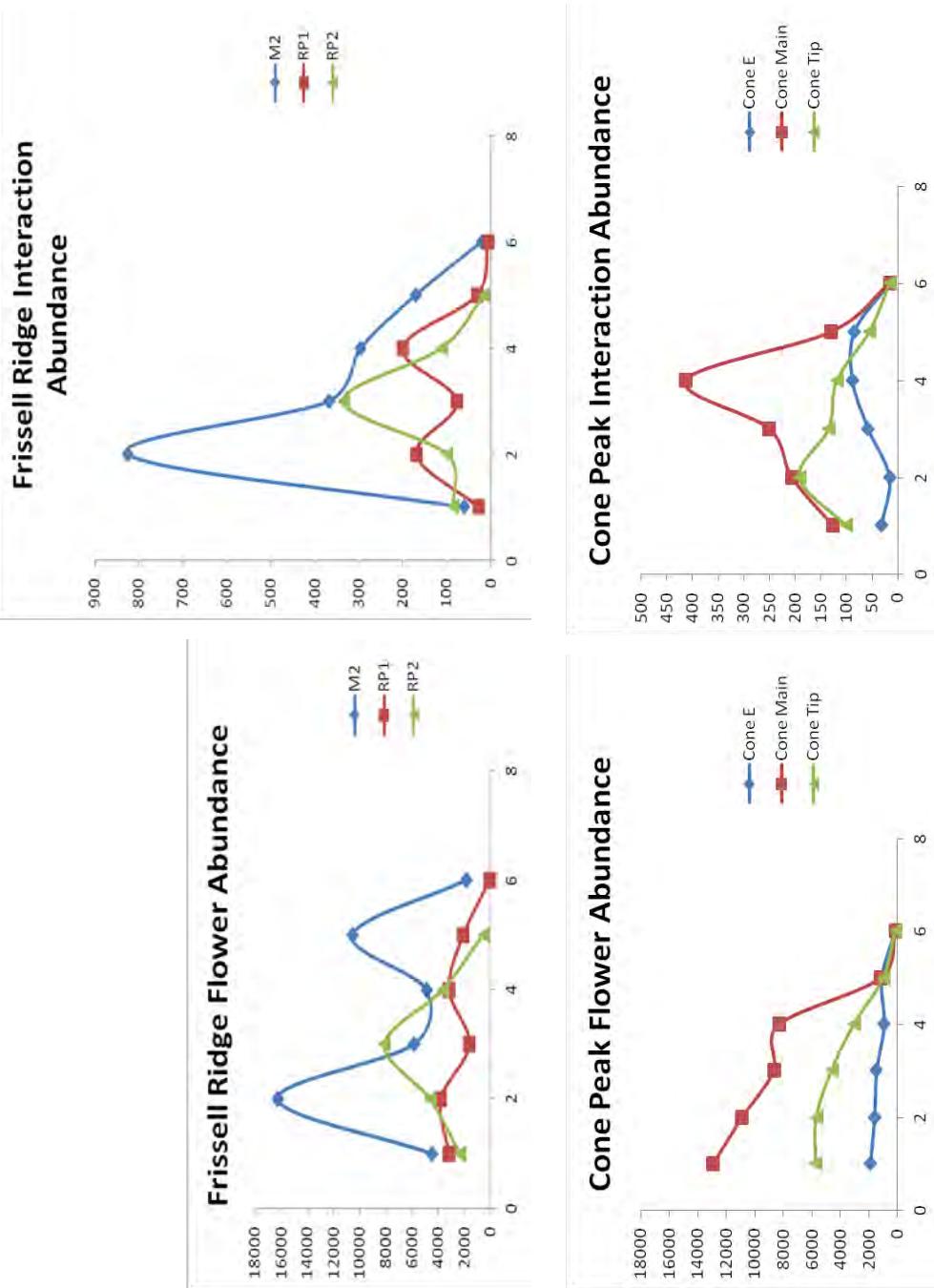
**Figure H1 Peak season meadow moisture vs. floral abundance.** Floral abundance from each meadow during watch period was plotted against measured soil moisture during week 3 and week 5. In the early season floral abundance appeared low where moisture was high and in the late season floral abundance appeared low where moisture was low.

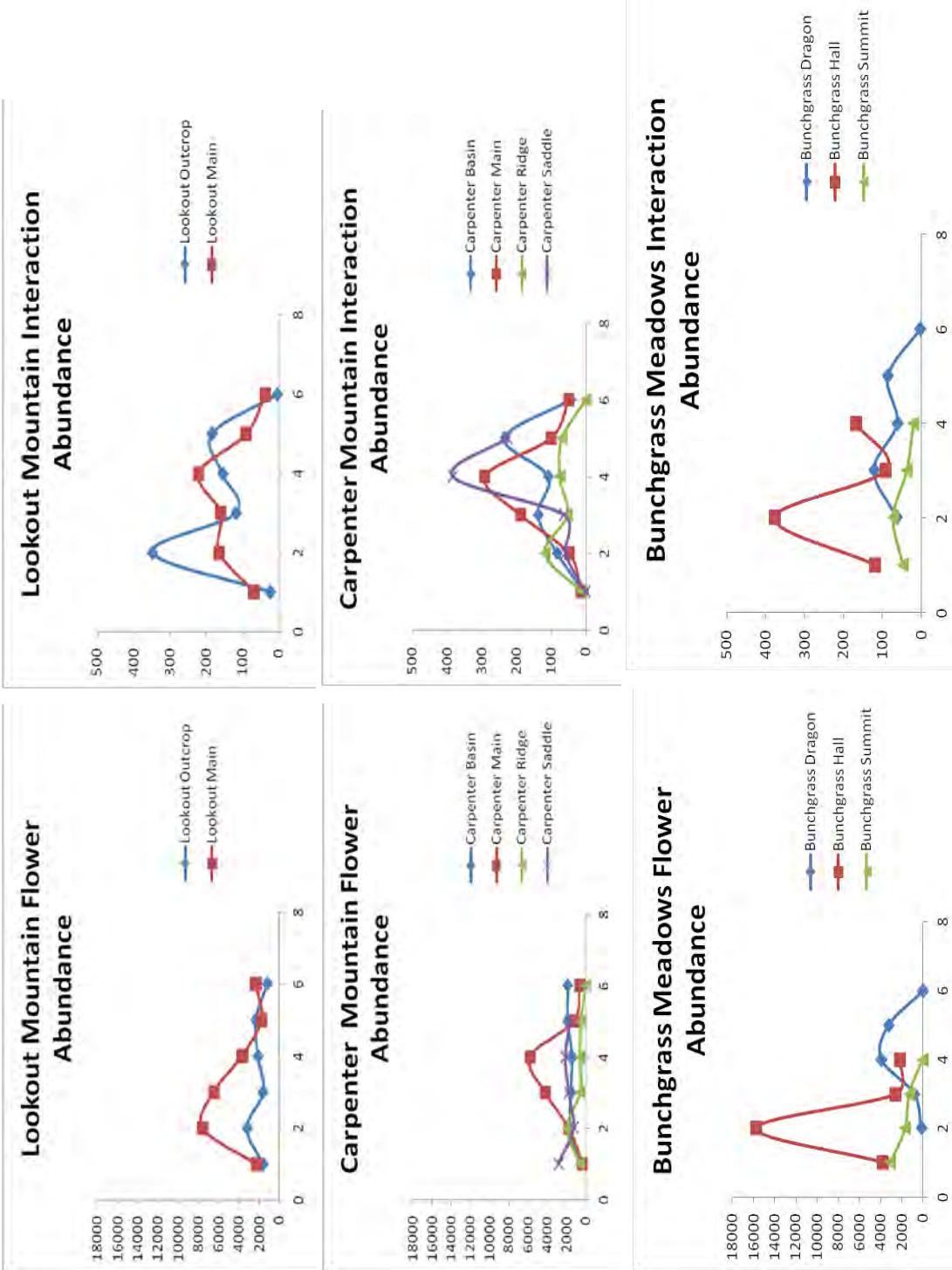
## Peak season meadow moisture vs. pollinator abundance



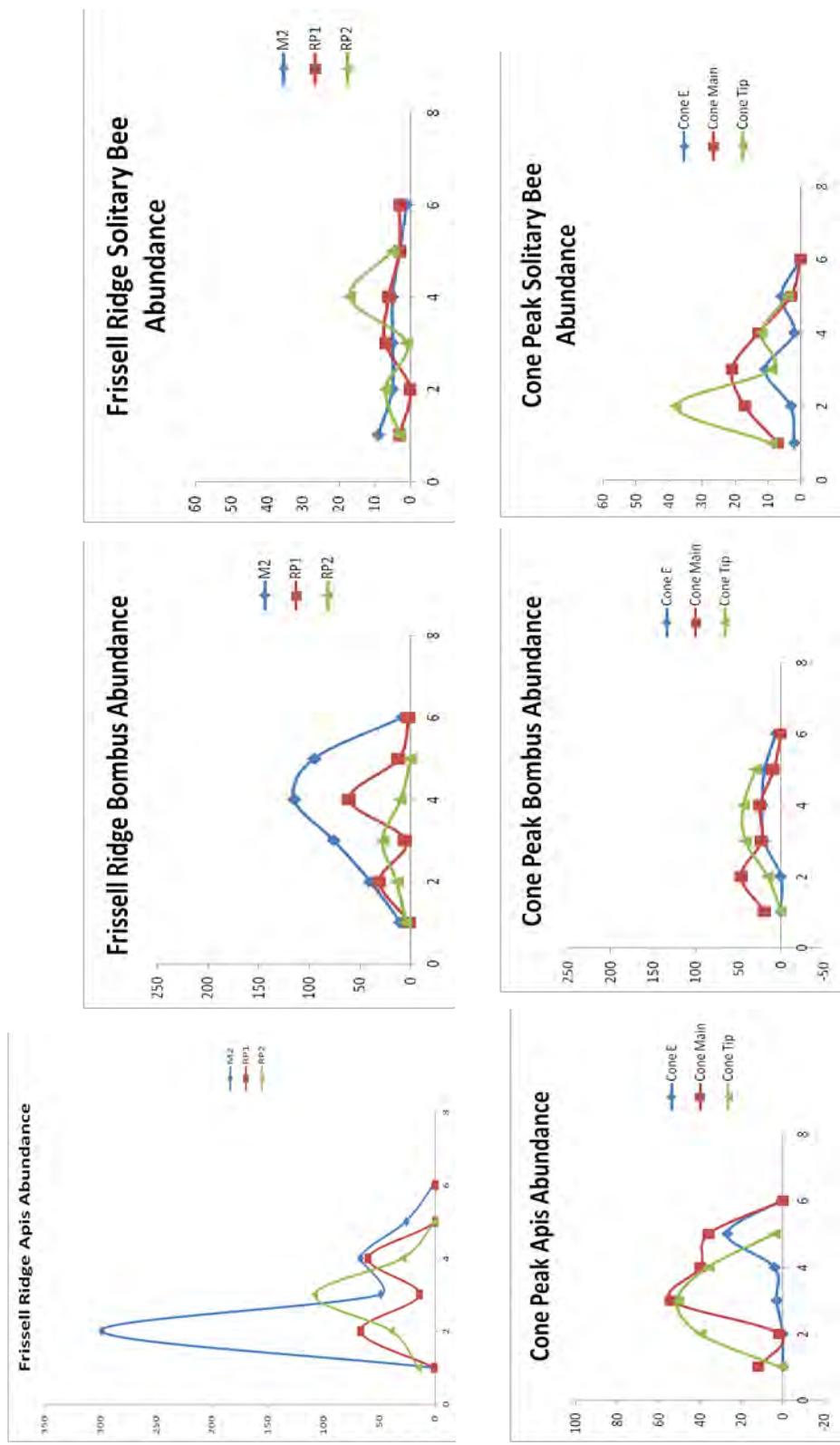
**Figure H2 Peak season meadow moisture vs. pollinator abundance.** Pollinators showed similar responses to moisture through the season. In the earliest watches, the highest pollinator abundance was observed in dry meadow habitat. At the end of the season, low moisture was associated with pollinator community decline.

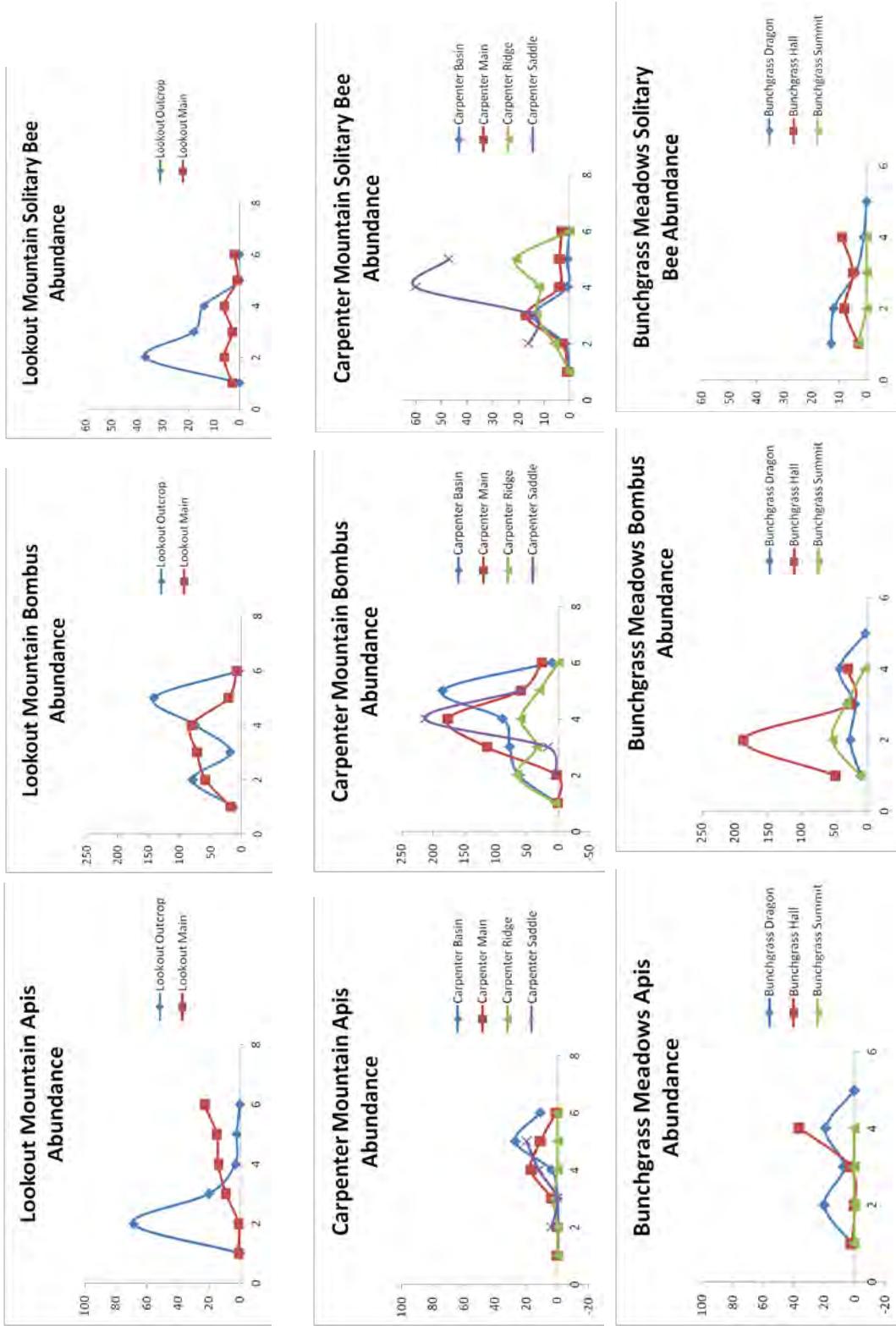
**Figure H3 Flower and pollinator abundance by sampling date.** These line graphs show flower and interaction abundance by sampling date. Peak interaction abundance occurred in concordance or following peak flower abundance.

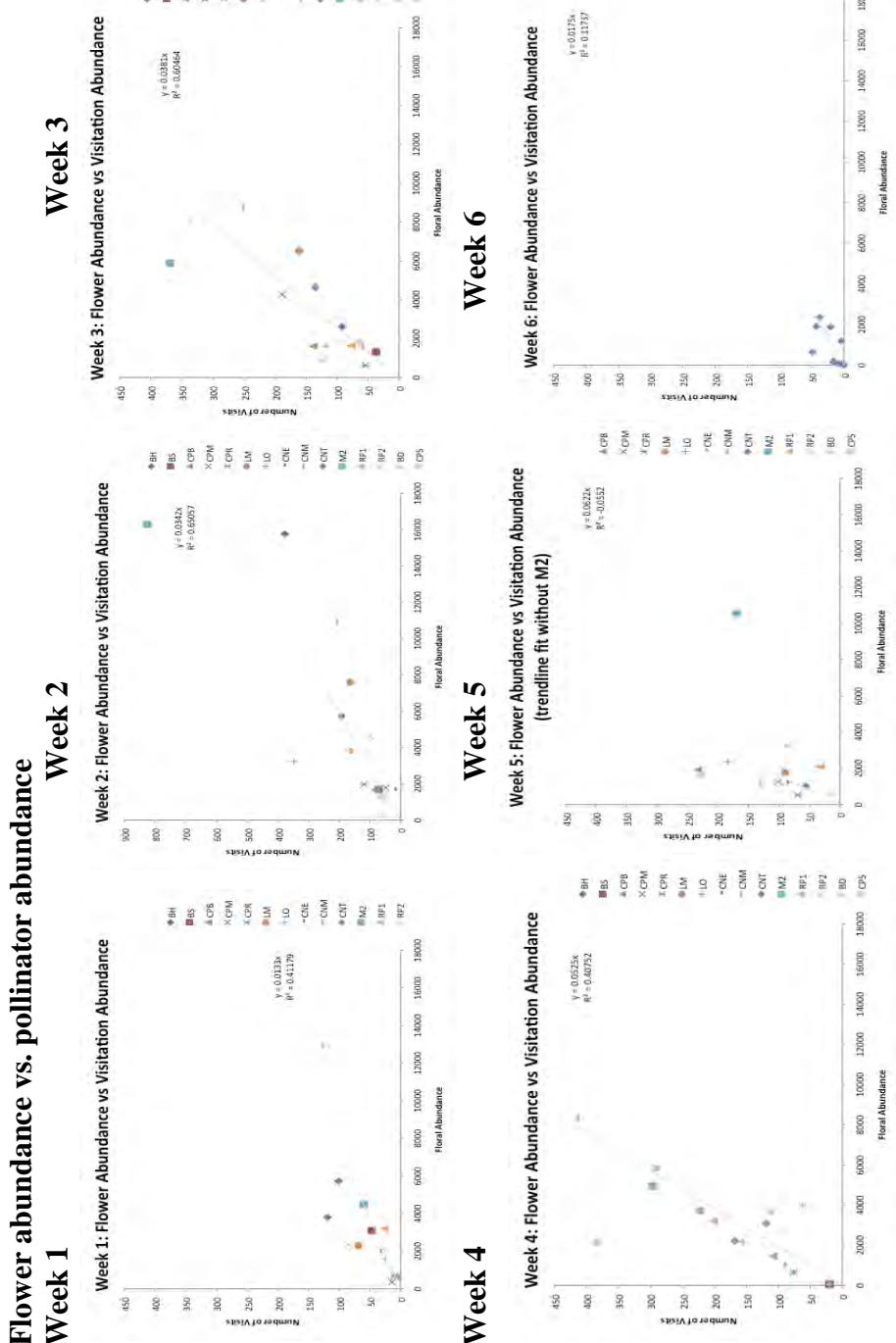




**Figure H4 Bee guild abundance by sampling date.** These charts show flower and interaction abundance by sampling date, then the relationship between floral abundance and pollinator abundance based on data from each meadow watch date. Lines will soon be added to better illustrate peak in floral and pollinator abundance during the season. It appears that pollinator abundance tends to lag behind flower abundance.







**Figure H5 Flower abundance vs. pollinator abundance.** Flower abundance was significantly correlated to pollinator abundance throughout the early and mid-summer; however, this trend was most significant during the peak season (weeks 3-4). Pollinator visitation continued to increase in relation to floral abundance throughout the peak season.

**Table H1 Pollinator distribution in percentage for each study meadow.** This table indicates the percent of pollinators from each order observed during the summer 2011.

Meadows	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Orthoptera	Thysanoptera	Trochiliformes	
BD	16.3	19.9	0.3	53.4	6.8	3.0	0	0.3
BH	12.2	24.1	1.2	47.0	5.6	0.4	9.5	0.1
BS	31.8	5.1	0.0	60.2	2.8	0	0	0
CNE	3.9	43.1	3.9	45.1	3.3	0	0	0.7
CNM	7.7	57.1	5.5	26.7	3.0	0	0	0
CNT	3.2	35.6	7.0	50.9	1.8	0	1.1	0.5
CPB	2.9	13.9	0.0	80.9	2.1	0	0	0
CPM	15.2	16.6	1.7	64.0	2.3	0	0	0.1
CPR	0.3	16.5	8.5	70.1	4.0	0	0	0.6
CPS	4.2	19.6	11.5	53.3	11.2	0	0	0.1
LM	18.8	29.7	0.7	46.9	3.3	0.4	0	0
LO	3.7	27.8	1.9	58.7	7.7	0	0	0.1
M2	16.2	28.4	0.0	49.0	6.3	0	0.1	0.1
RP1	9.9	25.7	0.6	53.7	9.7	0	0	0.4
RP2	6.2	44.0	0.6	43.6	4.5	0.8	0	0.3

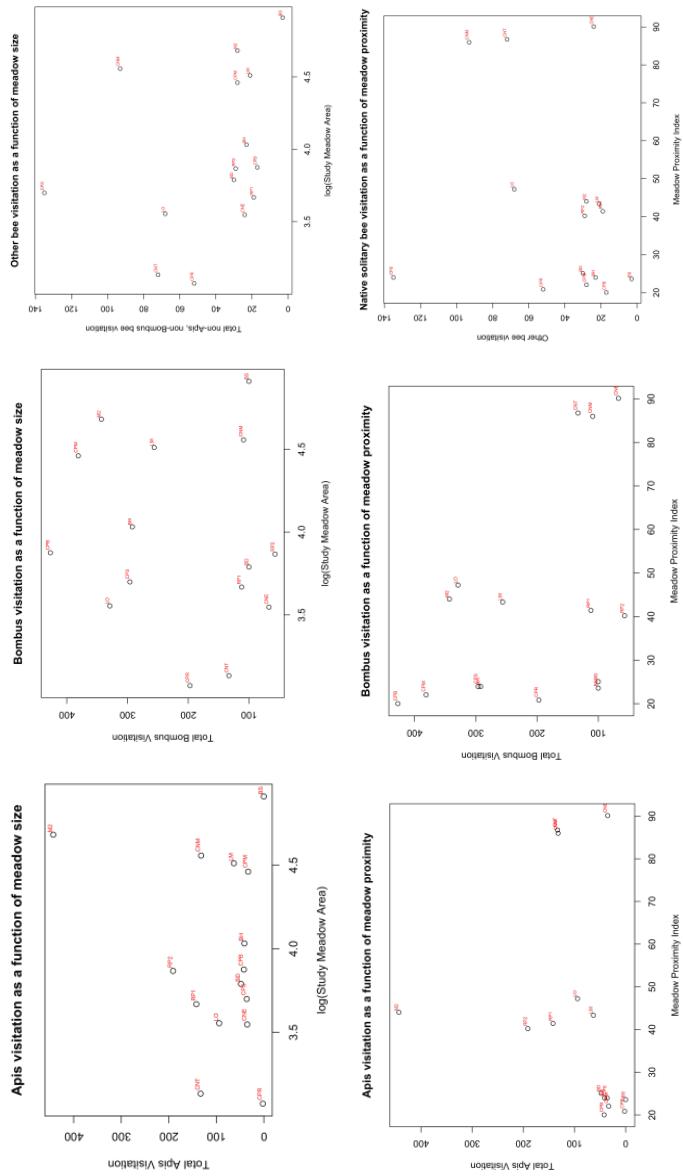
**Table H2 Bees by Family.** This table shows all bee species observed in the pollinator network study by family. In bee guild analyses, *Apis mellifera* (European honey bee) and all *Bombus* spp. (n = 9) are separated from all other native solitary bees. In bee family tables and analyses, *Apis mellifera* and *Bombus* spp. are assessed separately from “other Apidae bees” which include the remaining observed members of the family.

Andrenidae	Apidae	Colletidae	Halictidae	Megachilidae
<i>Andrena buckelli</i>	<i>Apis mellifera</i>	<i>Colletes simulans nevadensis</i>	<i>Dialictus</i> sp 10	<i>Anthidium</i> sp 2
<i>Andrena columbiana</i>	<i>Bombus appositus</i>	<i>Hylaeus nevadensis</i>	<i>Dialictus</i> sp 11	<i>Anthidium</i> sp 5
<i>Andrena melanochroa</i>	<i>Bombus bifarius</i>	<i>Hylaeus nummennacheri</i>	<i>Dialictus</i> sp 3M	<i>Anthocopa abjecta</i> <i>Osmia</i> sp 2
<i>Andrena nigrocaerulea</i>	<i>Bombus californicus</i>	<i>Hylaeus wootonii</i>	<i>Dialictus</i> sp 4	<i>Ashmeadiella</i> sp
<i>Andrena peritristis</i>	<i>Bombus griseocollis</i>		<i>Dialictus</i> sp 9	<i>Chelostoma phaeiae</i>
<i>Andrena scutellimitris</i>	<i>Bombus melanopygus</i>		<i>Dufourea bernardina</i>	<i>Dianthidium ulkei</i>
<i>Andrena</i> sp 19	<i>Bombus mixtus</i>		<i>Dufourea calochorti</i>	<i>Hoplitis albifrons</i>
<i>Andrena vicina</i>	<i>Bombus nevadensis</i>		<i>Dufourea versatilis</i>	<i>Hoplitis fulgida</i>
<i>Andrena vicinoides</i>	<i>Bombus occidentalis</i>		<i>Evylaeus</i> sp 1	<i>Megachile brevis</i>
<i>Panurginus</i> sp 1	<i>Bombus vosnesenskii</i>		<i>Evylaeus</i> sp 2	<i>Megachile melanophaea</i>
<i>Perdita</i> sp	<i>Ceratina acantha</i>		<i>Evylaeus</i> sp 3	<i>Megachile perihirta</i>
	<i>Melissodes</i> sp 1		<i>Evylaeus</i> sp 4	<i>Megachile pugnata</i>
	<i>Nomada</i> sp 3		<i>Evylaeus</i> sp 5M	<i>Megachile</i> sp 5
	<i>Nomada</i> sp 8		<i>Halictus rubicundus</i>	<i>Osmia coloradensis</i>
	<i>Psithyrus insularis</i>		<i>Halictus tripartitus</i>	<i>Osmia</i> sp 121
			<i>Lasioglossum titusi</i>	<i>Osmia</i> sp 13
			<i>Sphecodes</i> sp 1	<i>Osmia</i> sp 133
			<i>Sphecodes</i> sp 6	<i>Osmia</i> sp 15
			<i>Sphecodes</i> sp 7	<i>Osmia</i> sp 155
				<i>Osmia subaustralis</i>

**Table H3 Total bee visitation by guild.** This table summarizes the total number of visits observed and recorded by individuals of each bee guild in each meadow as well as the total number of visits observed in each meadow throughout the season.

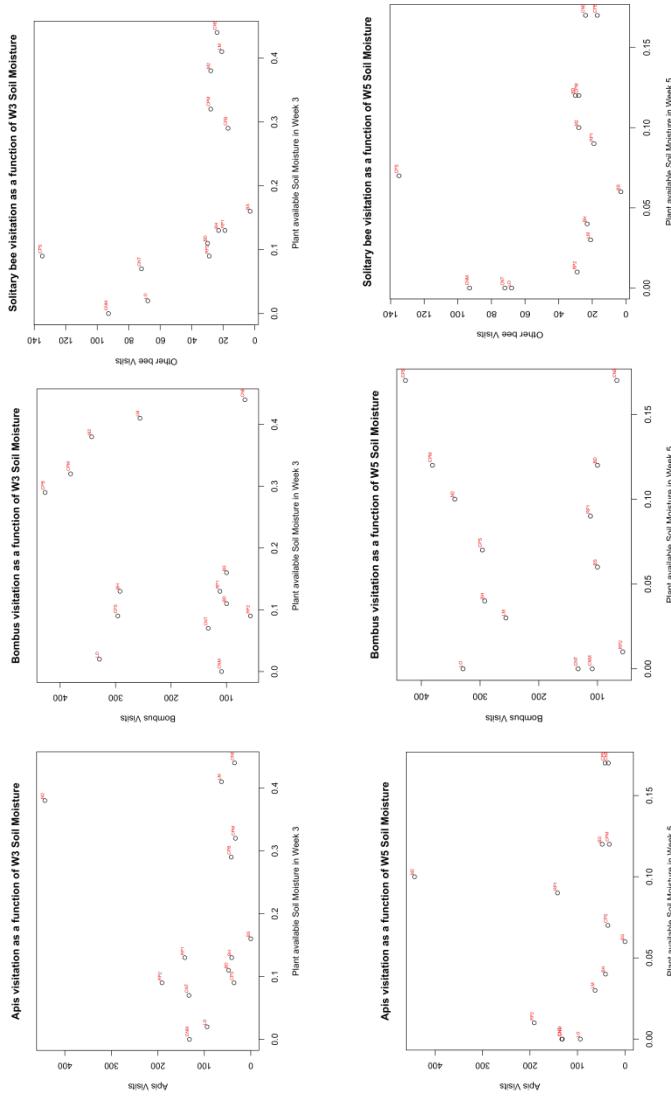
Meadow	Apis Visits	Bombus Visits	Solitary Bee Visits	Total Interactions
BD	48	100	30	330
BH	41	292	23	746
BS	0	100	3	175
CPB	42	427	17	600
CPM	33	381	28	677
CPR	2	197	52	317
CPS	36	296	135	717
CNE	35	67	24	263
CNM	132	109	93	1072
CNT	133	133	72	552
M2	443	343	28	1732
RP1	142	112	19	501
RP2	191	57	29	626
LM	63	256	21	728
LO	94	329	68	808

## Meadow size and meadow proximity vs. bee guild abundance



**Figure H6 Meadow size and meadow proximity vs. bee guild abundance.** *Apis mellifera* visitation is not clearly associated with meadow size, but high abundance is associated with a large amount of habitat within the surrounding complex (Cone, Frissell, Lookout, though Lookout is composed of smaller patches than the other two complexes and experienced lower *Apis mellifera* visitation). *Apis mellifera* visitation was very low in smaller complexes (Bunchgrass and Carpenter). *Bombus* visitation did not respond to meadow size, but experienced very low values in the more extensive meadow complexes. *Bombus* visitation was highly stratified within the smaller to mid-size complexes. Solitary bee visitation did not respond to meadow size in a constant manner, several small meadows, one mid-size meadow, and one large meadow exhibited very high values.

## Bee guild and meadow moisture during week 3 and week 5



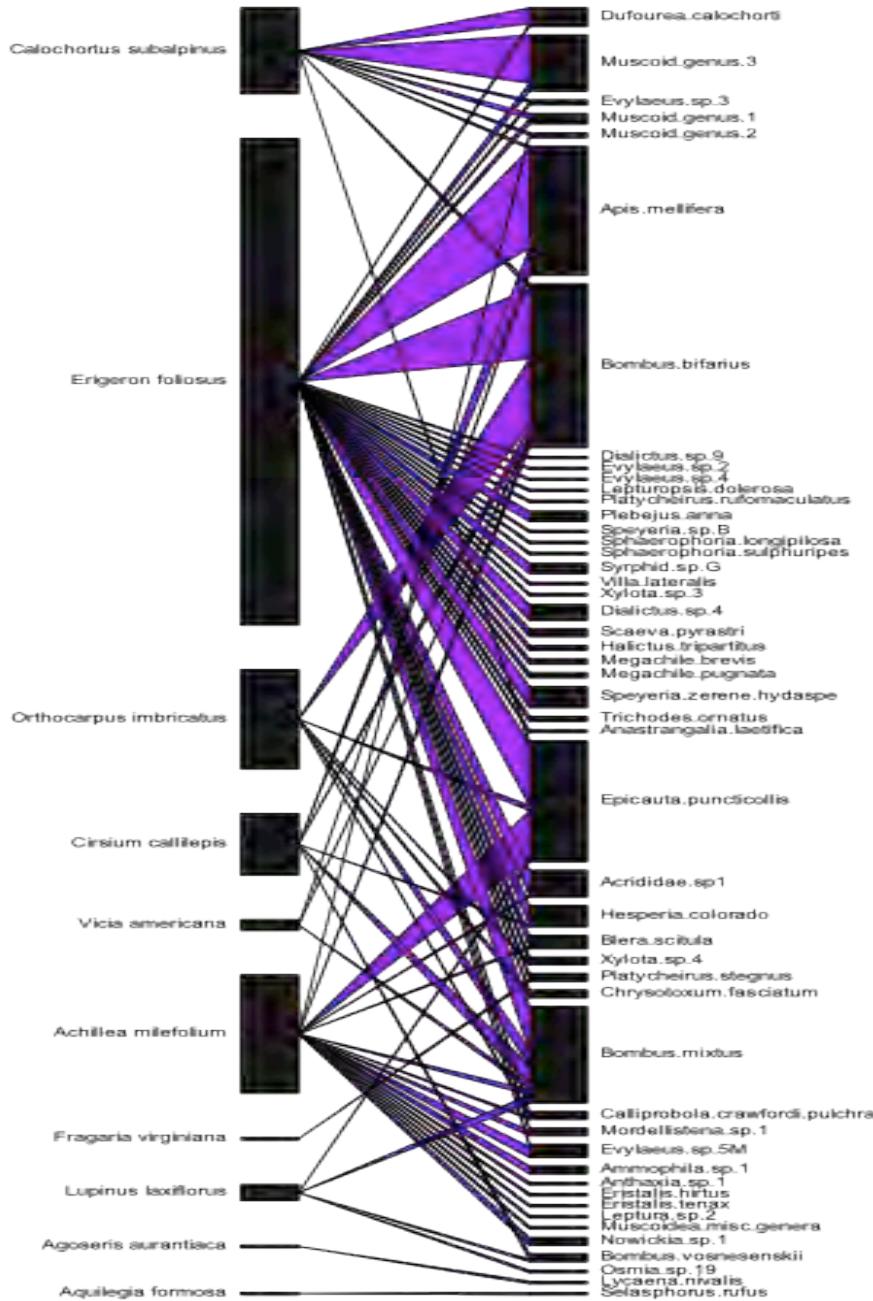
**Figure H7 Bee guild and meadow moisture during week 3 and week 5.** *Apis mellifera* did not show a clear response to soil moisture. *Bombus* spp. visitation was high in most of the meadows with high moisture, as well as several small meadows with low moisture during week 3. Solitary bees showed the strongest response to moisture, favoring dry meadows during week 3. The meadow with the highest solitary bee visitation experienced low soil moisture in week three, but maintained moderate moisture into the late summer season.

**Table H4 Bee guild distribution based on habitat area defined by TCI index values.** This table presents the p values for linear regressions explaining bee guild abundance by amount of meadow “habitat” within given landscape sectors. The regressions are conducted in a like manner to the chapter two analyses, however, habitat is narrowed to meadow area defined by a range of TCI values rather than total meadow area. The first two sections of the table describe univariate linear models conducted for “early season habitat” and “late season” habitat. The third section of the table describes multivariate linear regressions with terms for both “early” and “late season” habitat area within each landscape sector. Bunchgrass Summit and Hall were not included in the linear model due to their irregular relationship between soil moisture and TCI value.

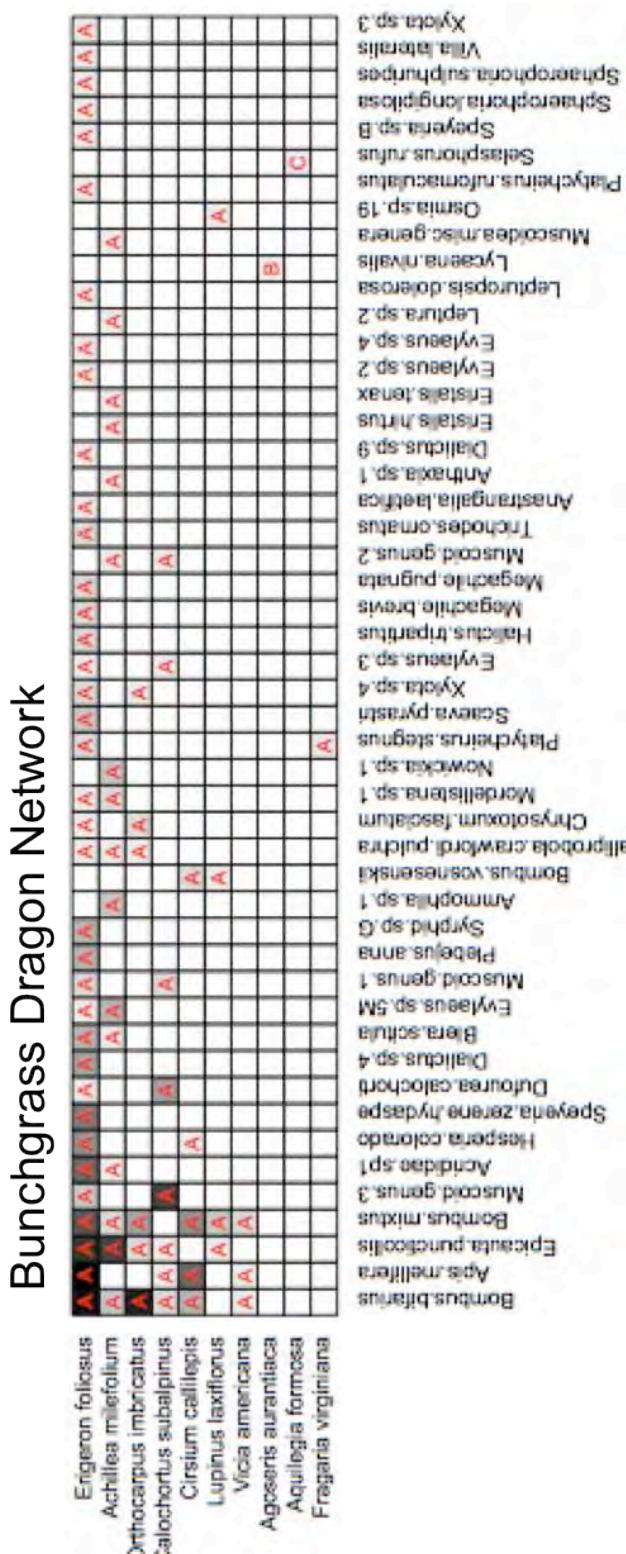
Landscape Sector (m)	Early Habitat (TCI < 2)			Late Habitat (4 < TCI < 9)			Apis Visitation	
	Apis Visitation	Bombus Solitary Bee Visitation	Apis Visitation	Bombus Visitation	Apis Visitation	Late and Early (TCI < 2) (4 < TCI < 9)		
25	0.1663	0.1151	0.1504	0.07892	0.0402	0.2094	0.507	
50	0.1577	0.01367	0.08043	0.1911	0.04097	(.)0.4896	0.0568	
100	0.128	0.007929	0.1098	0.007896	0.05004	0.2258	0.322	
250	0.2262	0.04035	0.02456	0.05894	0.106	0.2561	0.762	
500	0.1983	0.01606	0.005939	0.1109	0.0187	0.4108	0.1163	
750	0.1321	0.03662	0.03467	0.0327	0.09342	0.2914	0.190	
1000	0.09235	0.01347	0.08883	0.08171	0.07504	*0.0489	*0.0306	
1500	0.0579	0.02216	0.1606	0.03201	0.06624	*0.0452	*0.0420	
2000	0.05168	0.02907	0.156	0.03201	0.00956	0.09715	0.561	
2500	0.05986	0.0163	0.1317	0.01079	0.05076	0.06882	0.938	
3000	0.06481	0.0163	0.1252	0.01663	0.04135	0.08027	0.758	

## APPENDIX I POLLINATION NETWORKS

### Bunchgrass Dragon: Full Season Plant-Pollinator Interaction Network

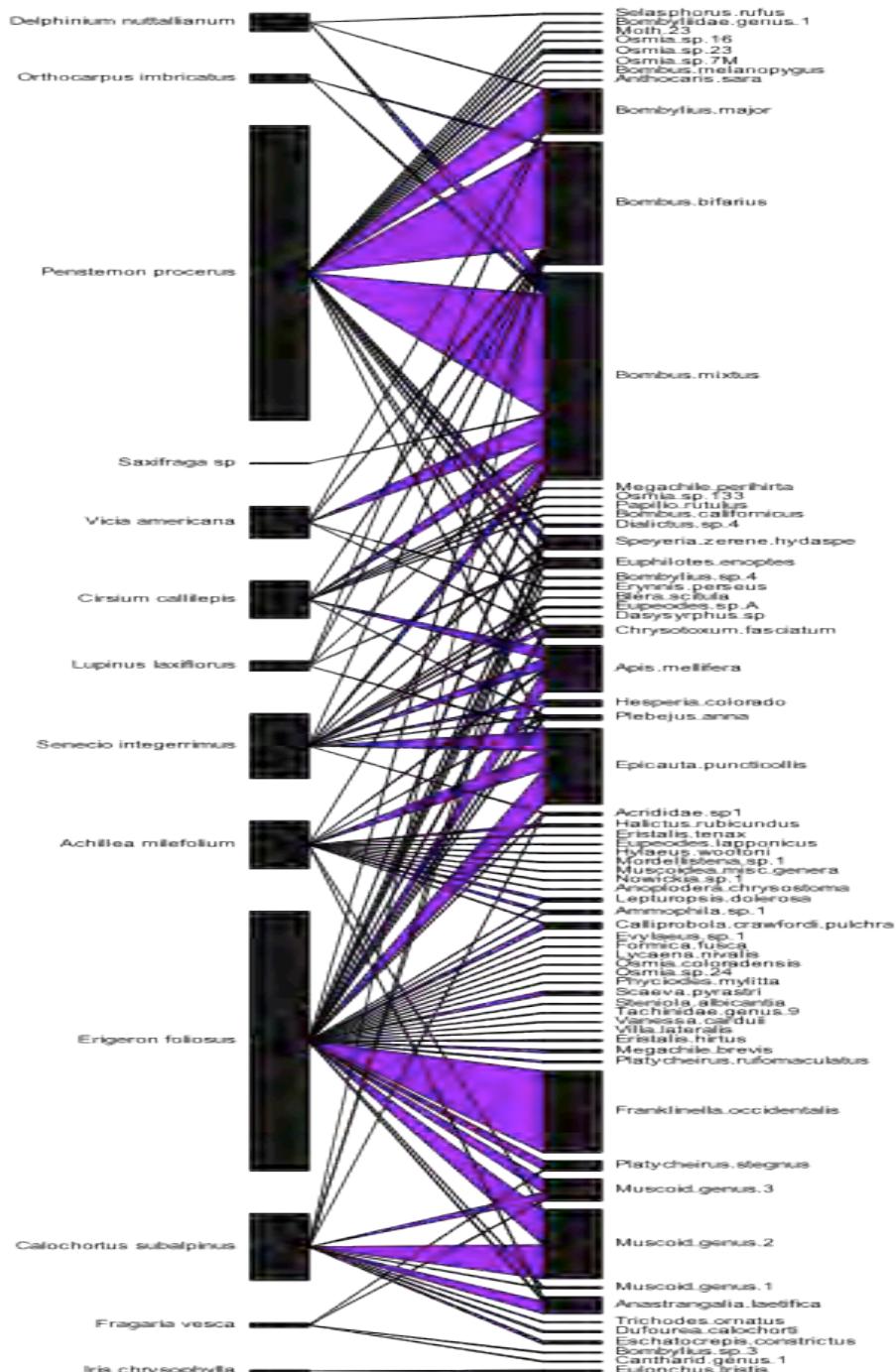


**Figure I1 Bunchgrass Dragon: Full Season Plant-Pollinator Interaction Network.** This figure shows the bipartite plant-pollinator network for Bunchgrass Dragon. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

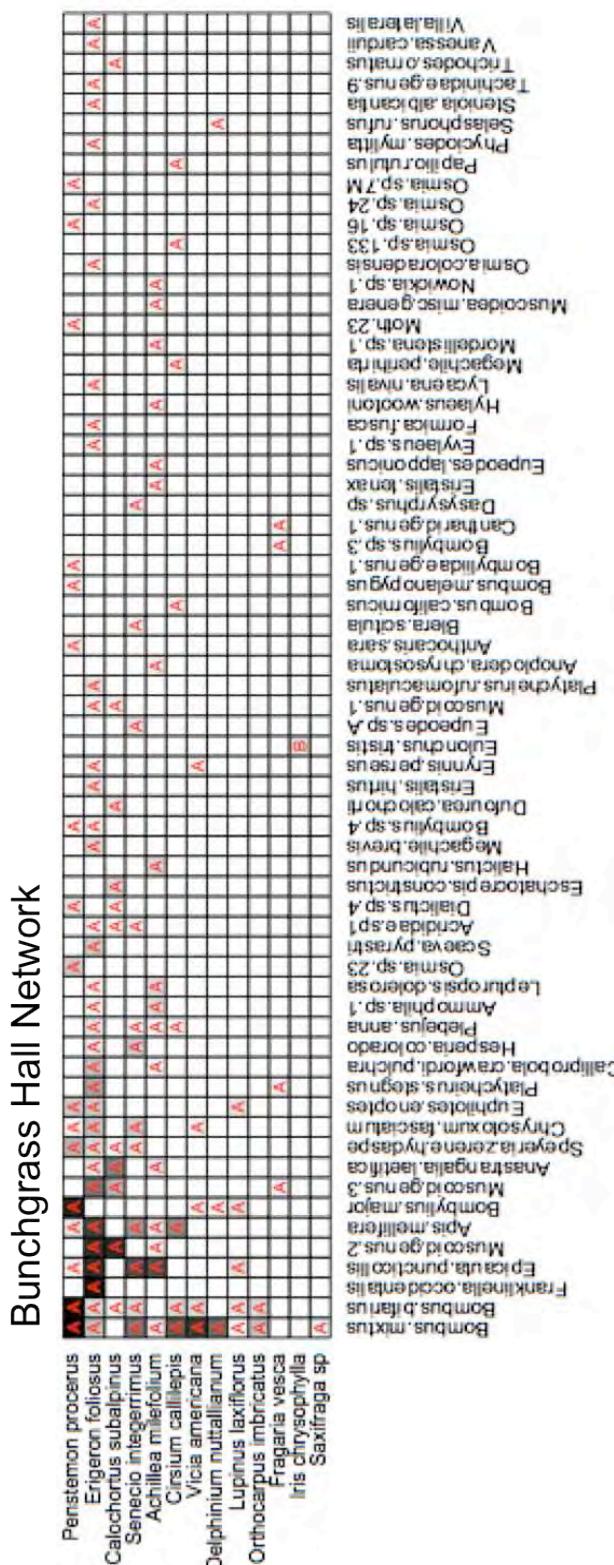


**Figure I2 Bunchgrass Dragon: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Bunchgrass Dragon. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Bunchgrass Hall: Full Season Plant-Pollinator Interaction Network

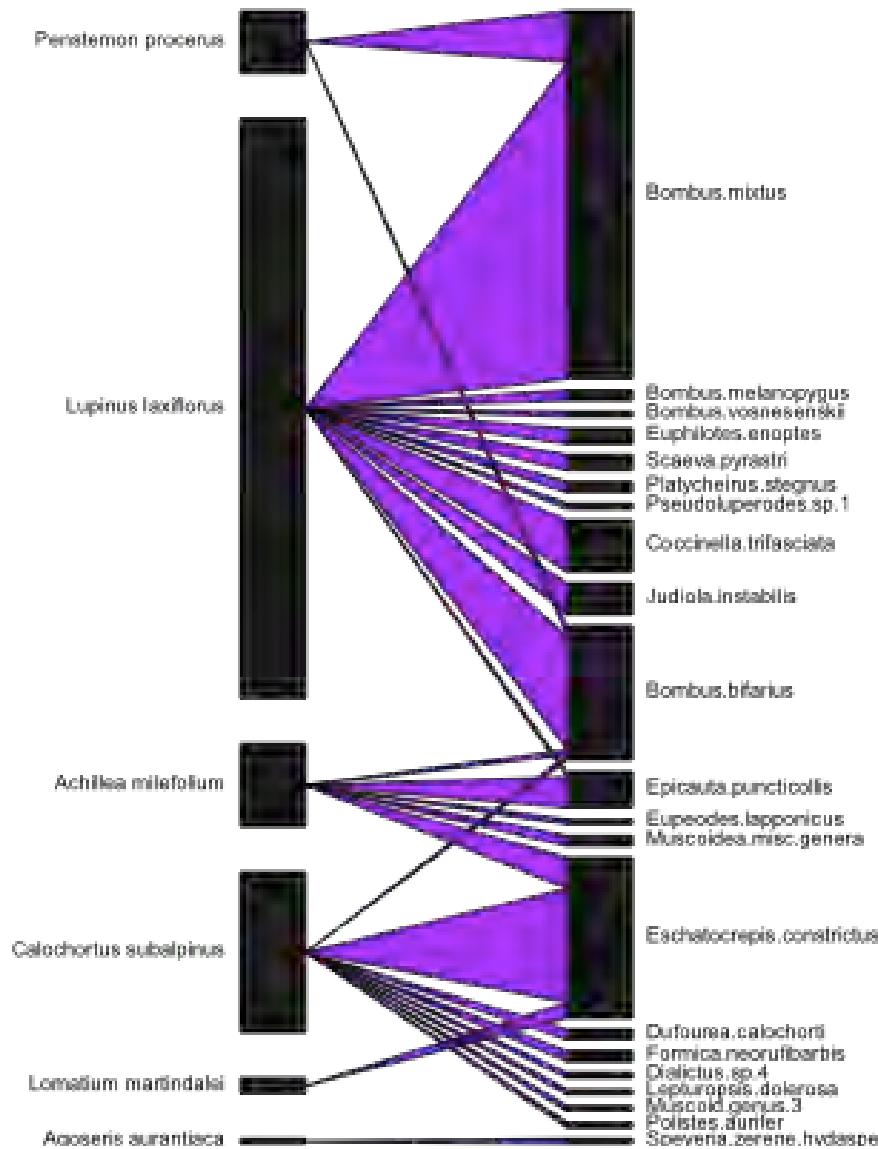


**Figure I3 Bunchgrass Hall: Full Season Plant-Pollinator Interaction Network.**  
This figure shows the bipartite plant-pollinator network for Bunchgrass Hall. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

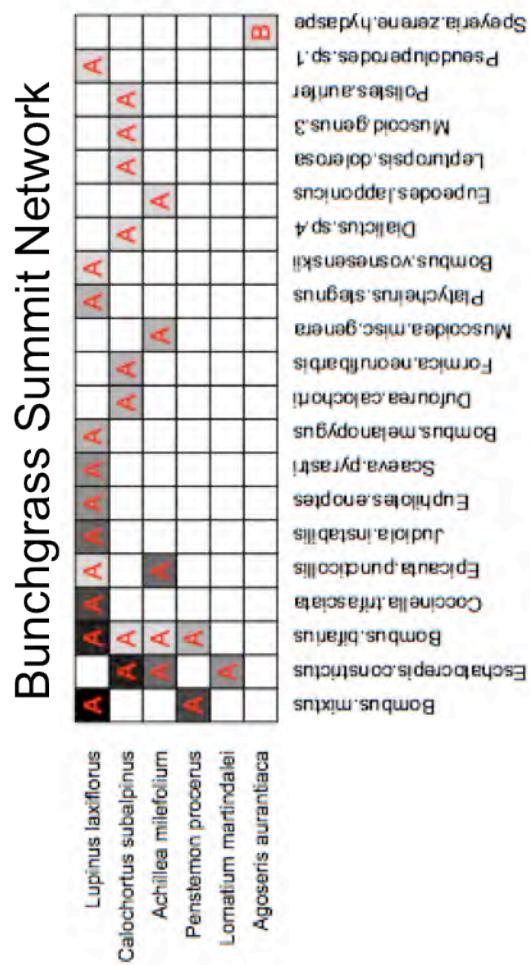


**Figure I4 Bunchgrass Hall: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Bunchgrass Hall. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Bunchgrass Summit: Full Season Plant-Pollinator Interaction Network

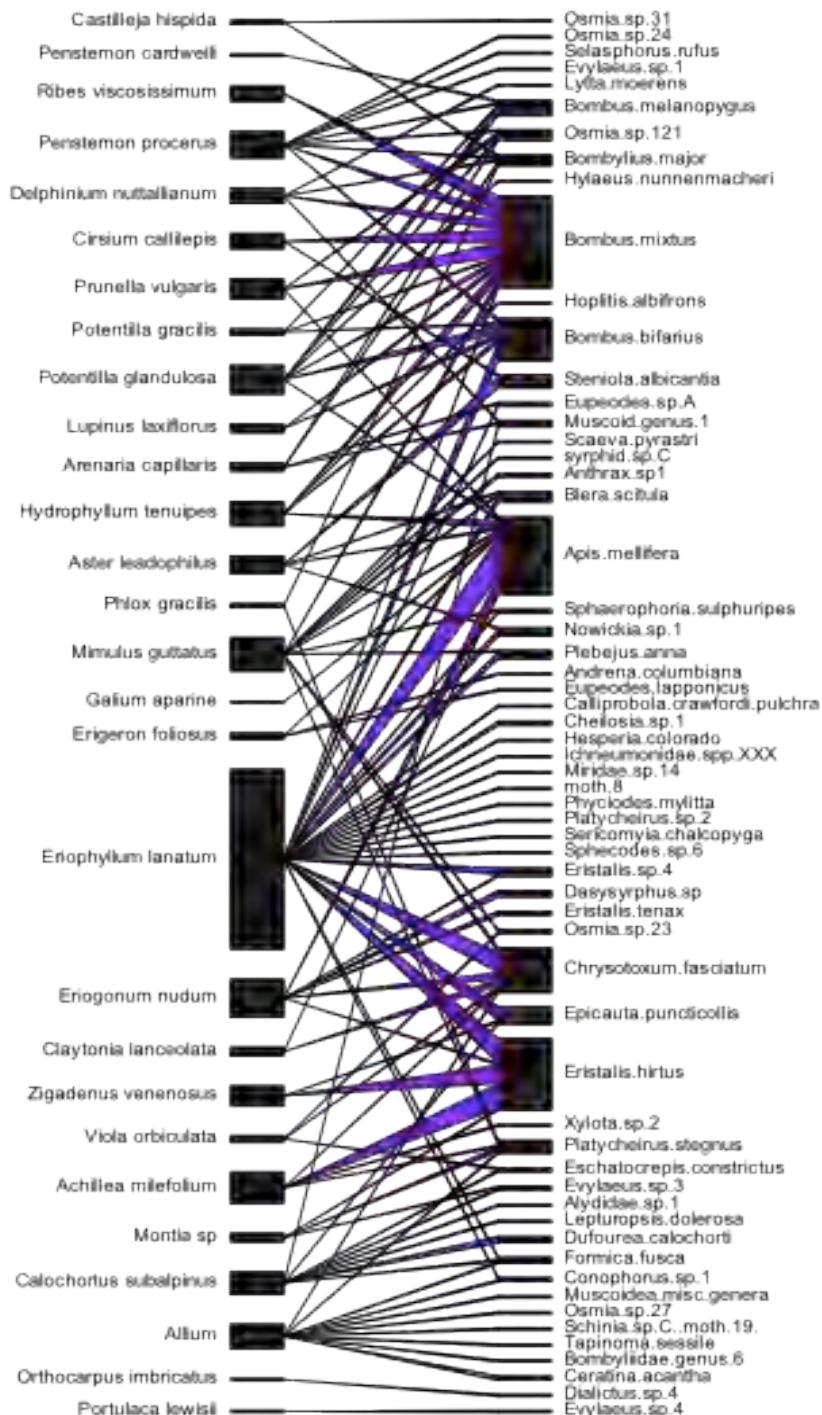


**Figure I5 Bunchgrass Summit: Full Season Plant-Pollinator Interaction Network.** This figure shows the bipartite plant-pollinator network for Bunchgrass Summit. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.



**Figure 16 Bunchgrass Summit: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Bunchgrass Summit. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Cone E: Full Season Plant-Pollinator Interaction Network

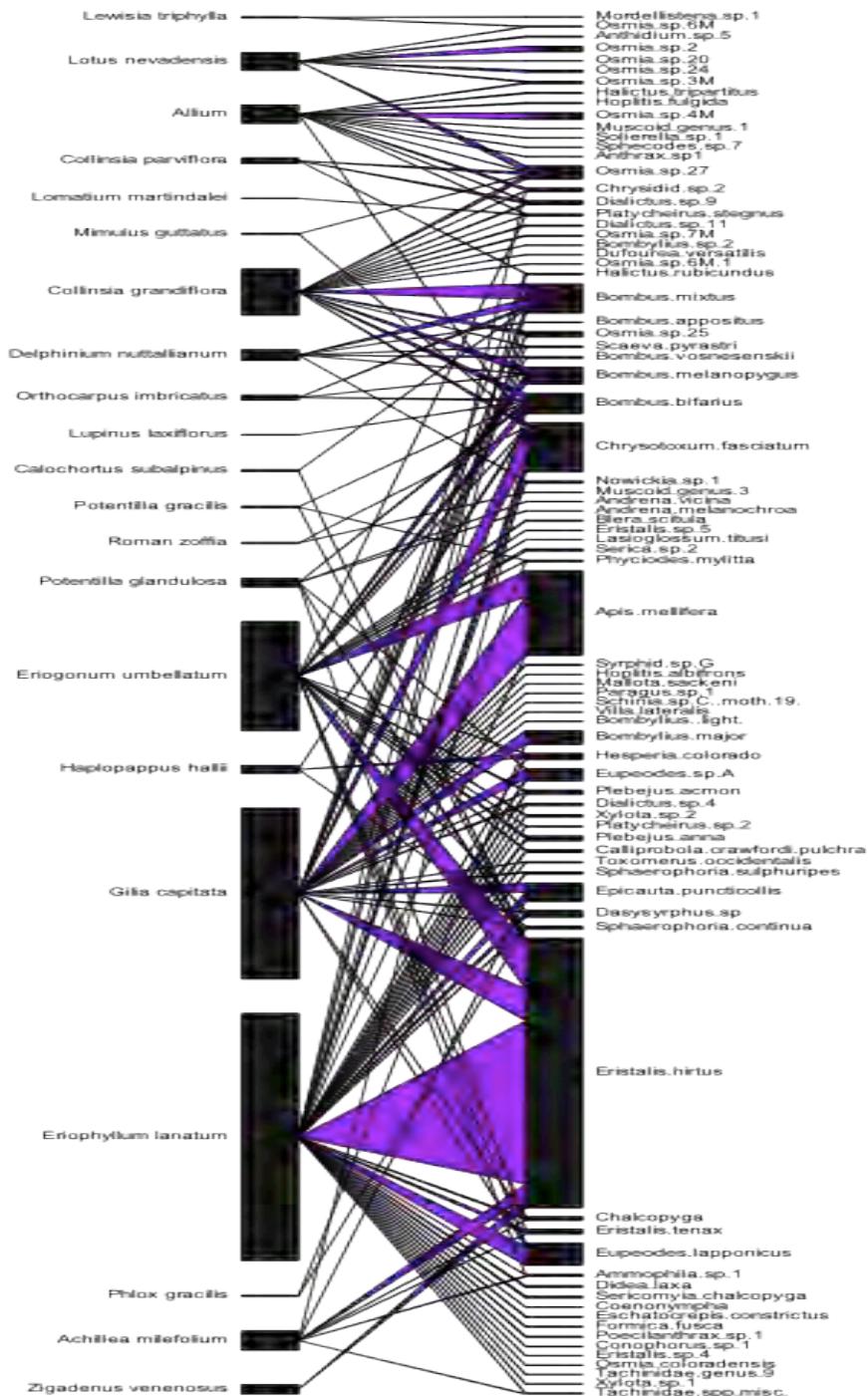


**Figure I7 Cone E: Full Season Plant-Pollinator Interaction Network.** This figure shows the bipartite plant-pollinator network for Cone E. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

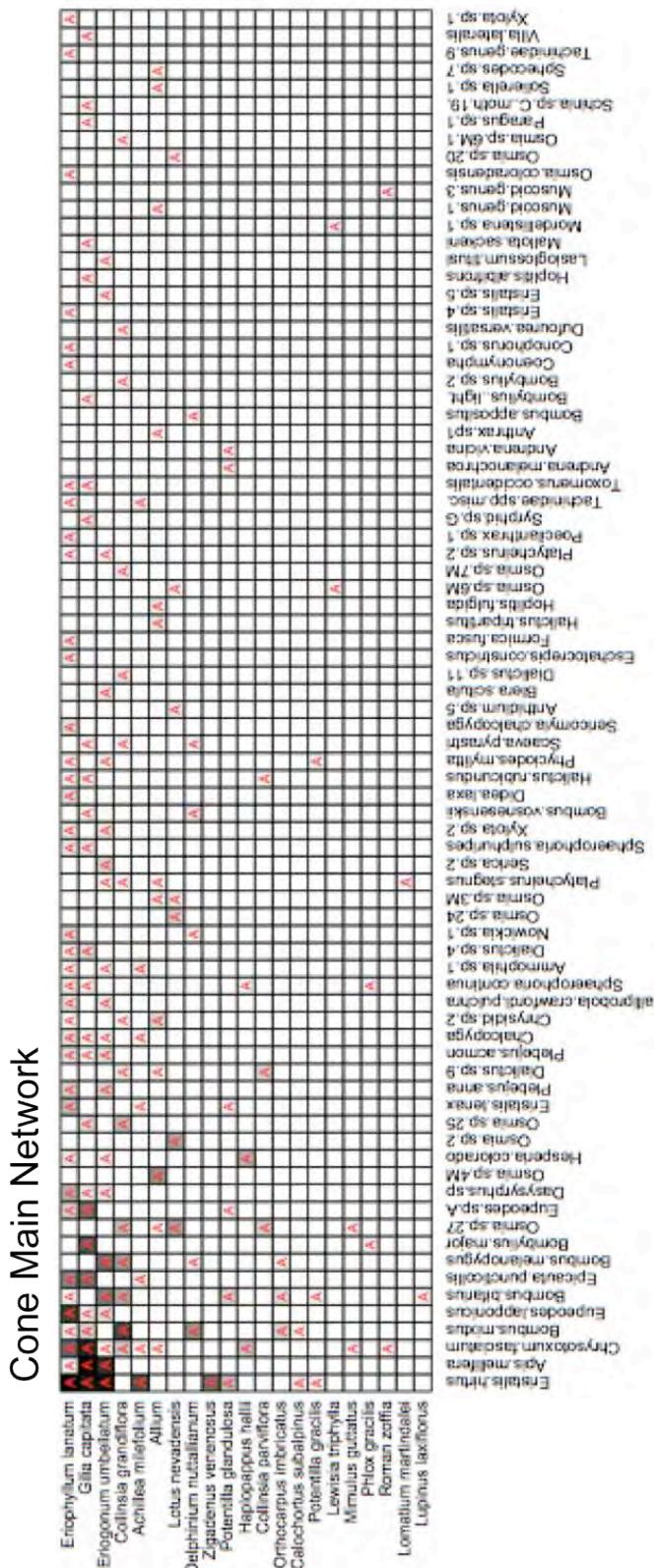
## Cone E: Full Season Plant-Pollinator Interaction Matrix

**Figure 18 Cone E: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Cone E. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Cone Main: Full Season Plant-Pollinator Interaction Network.

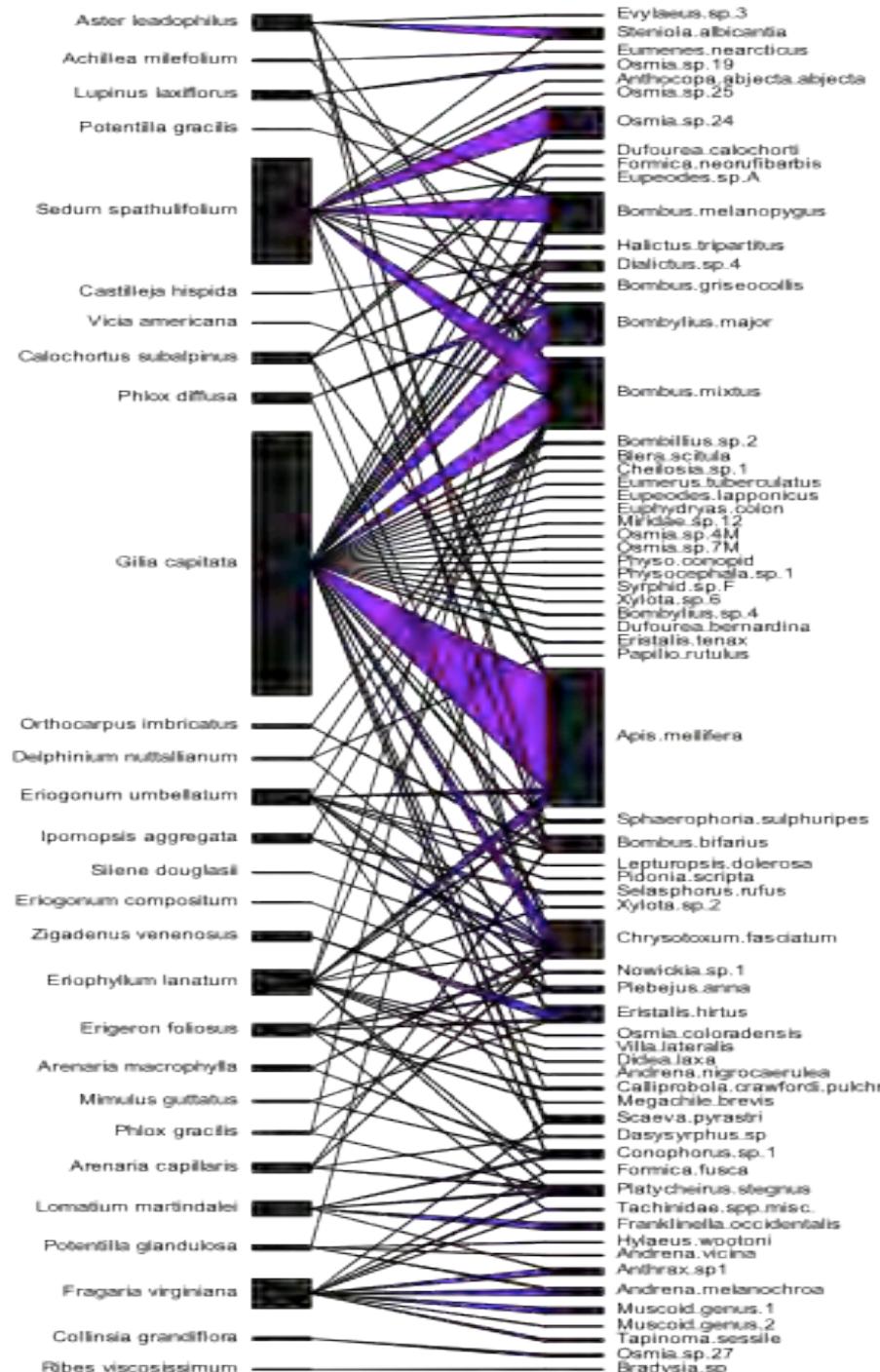


**Figure I9 Cone Main: Full Season Plant-Pollinator Interaction Network.** This figure shows the bipartite plant-pollinator network for Cone Main. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.



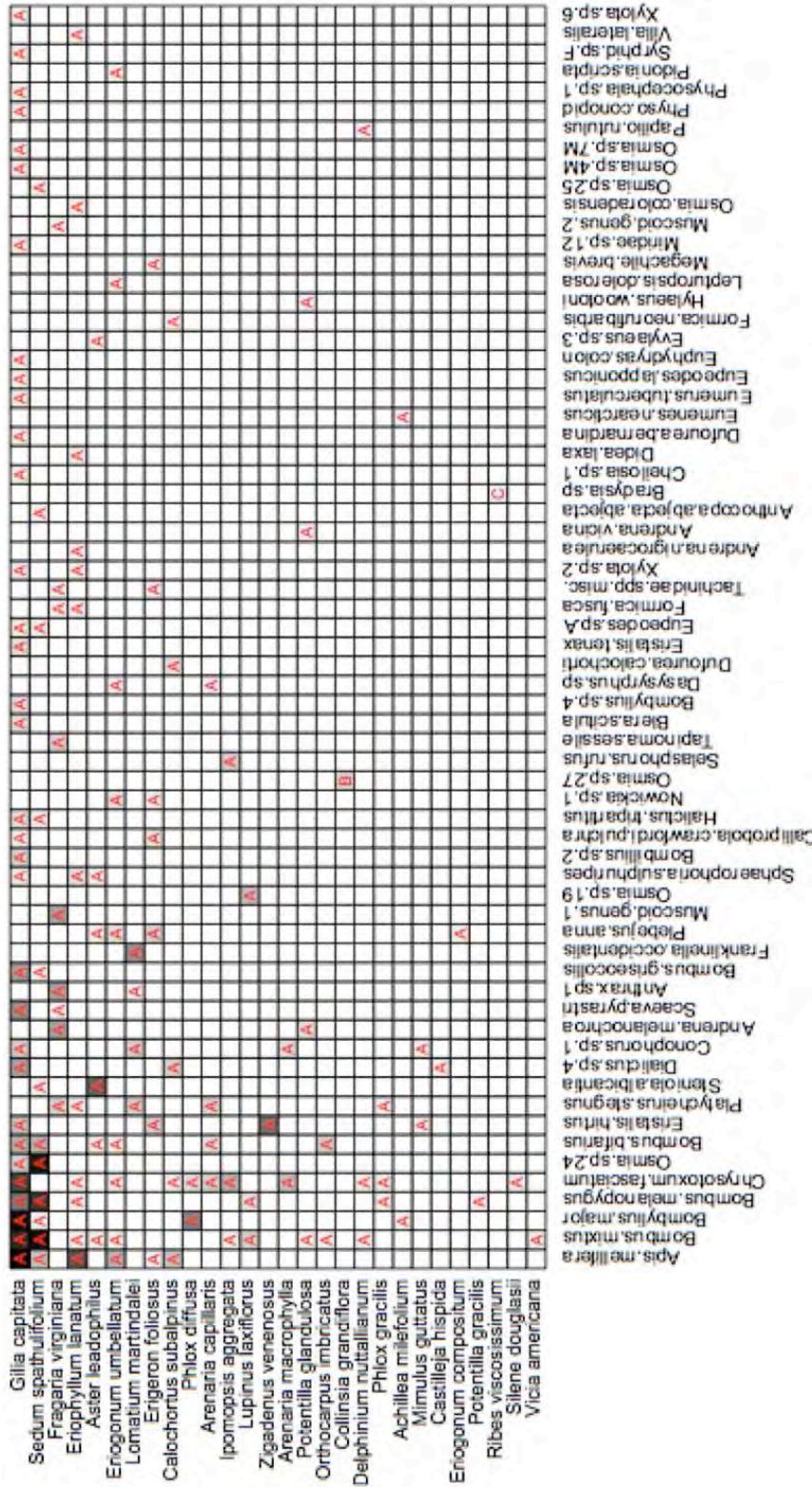
**Figure II0 Cone Main: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Cone Main. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Cone Tip: Full Season Plant-Pollinator Interaction Network



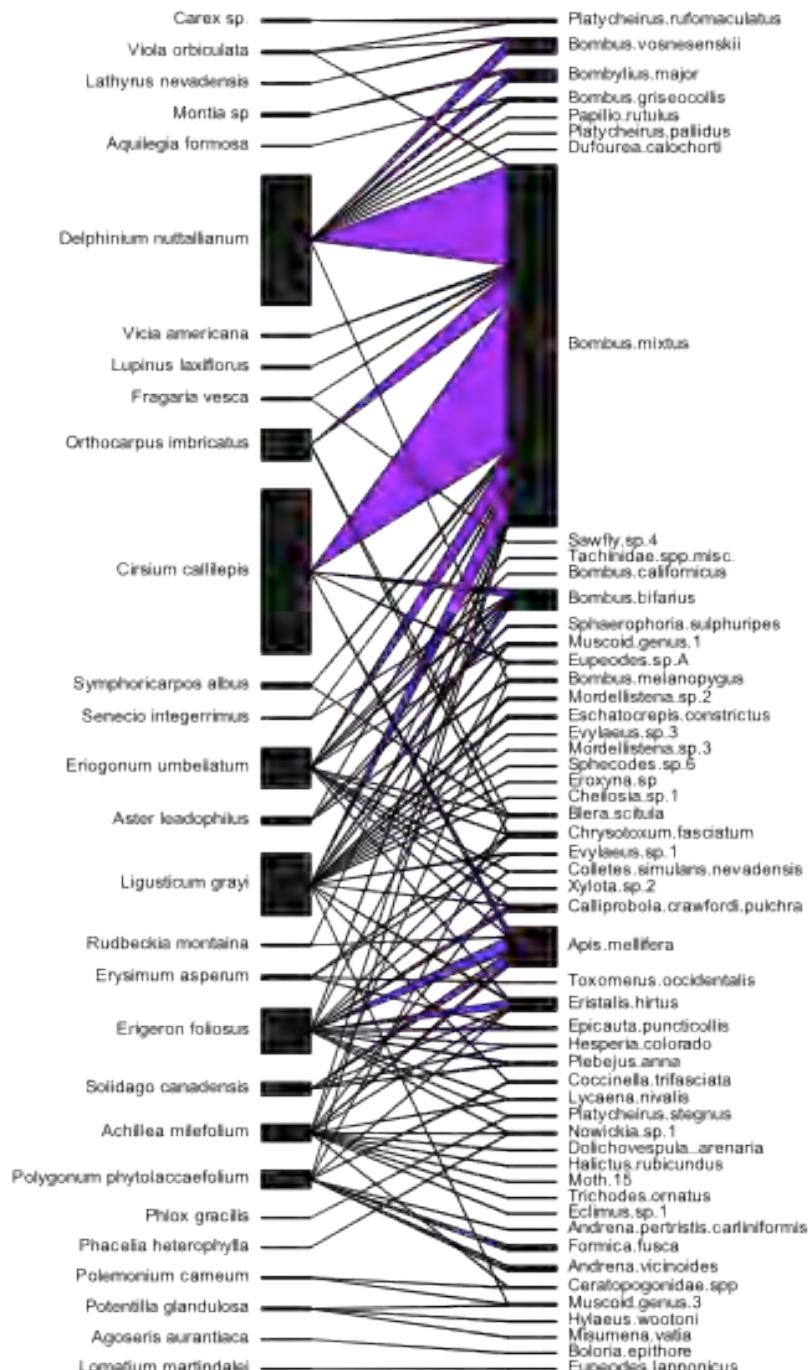
**Figure I11 Cone Tip: Full Season Plant-Pollinator Interaction Network.** This figure shows the bipartite plant-pollinator network for Cone Tip. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

### Cone Tip Network



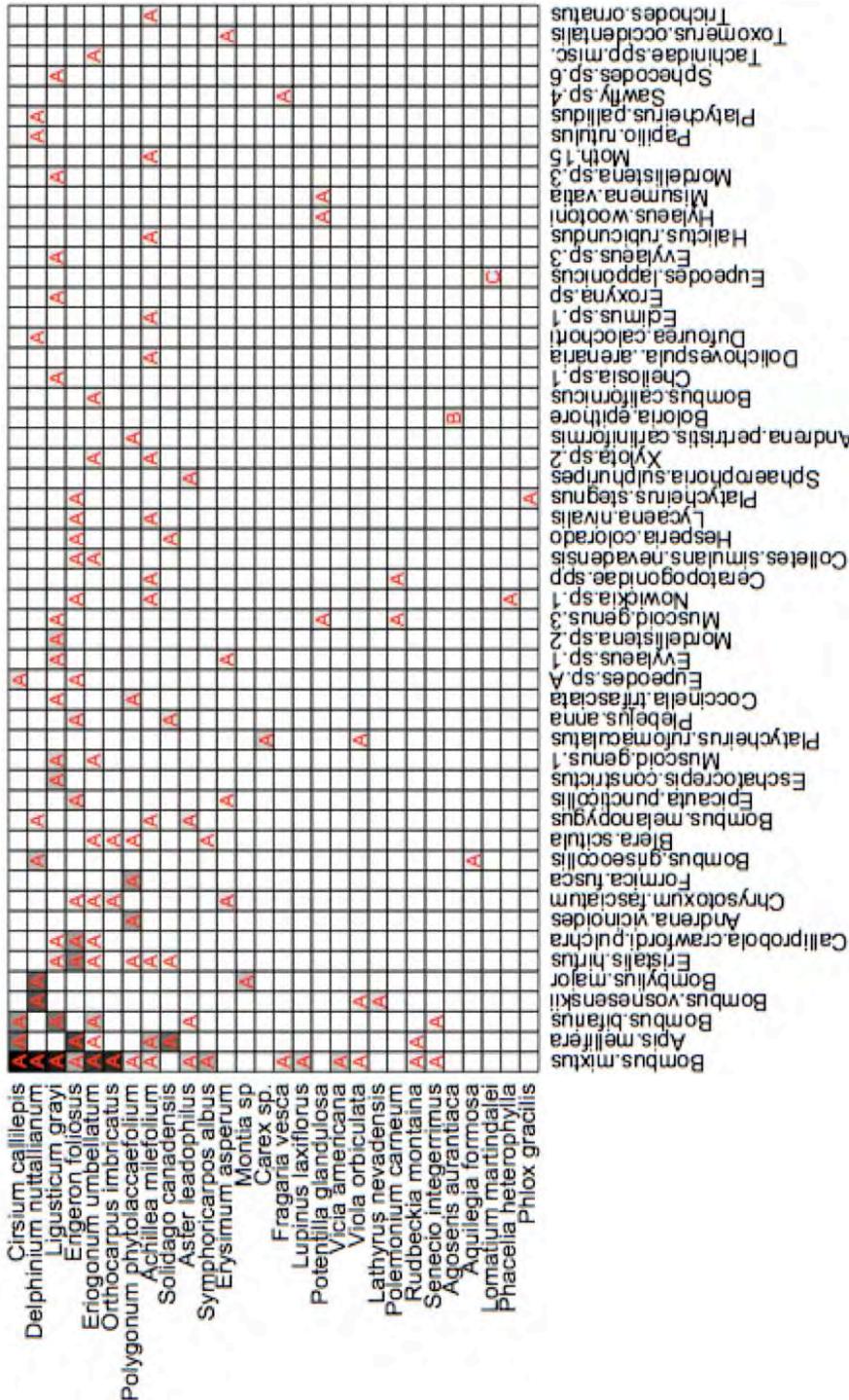
**Figure I12 Cone Tip: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Cone Tip. Plant species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Carpenter Basin: Full Season Plant-Pollinator Interaction Network

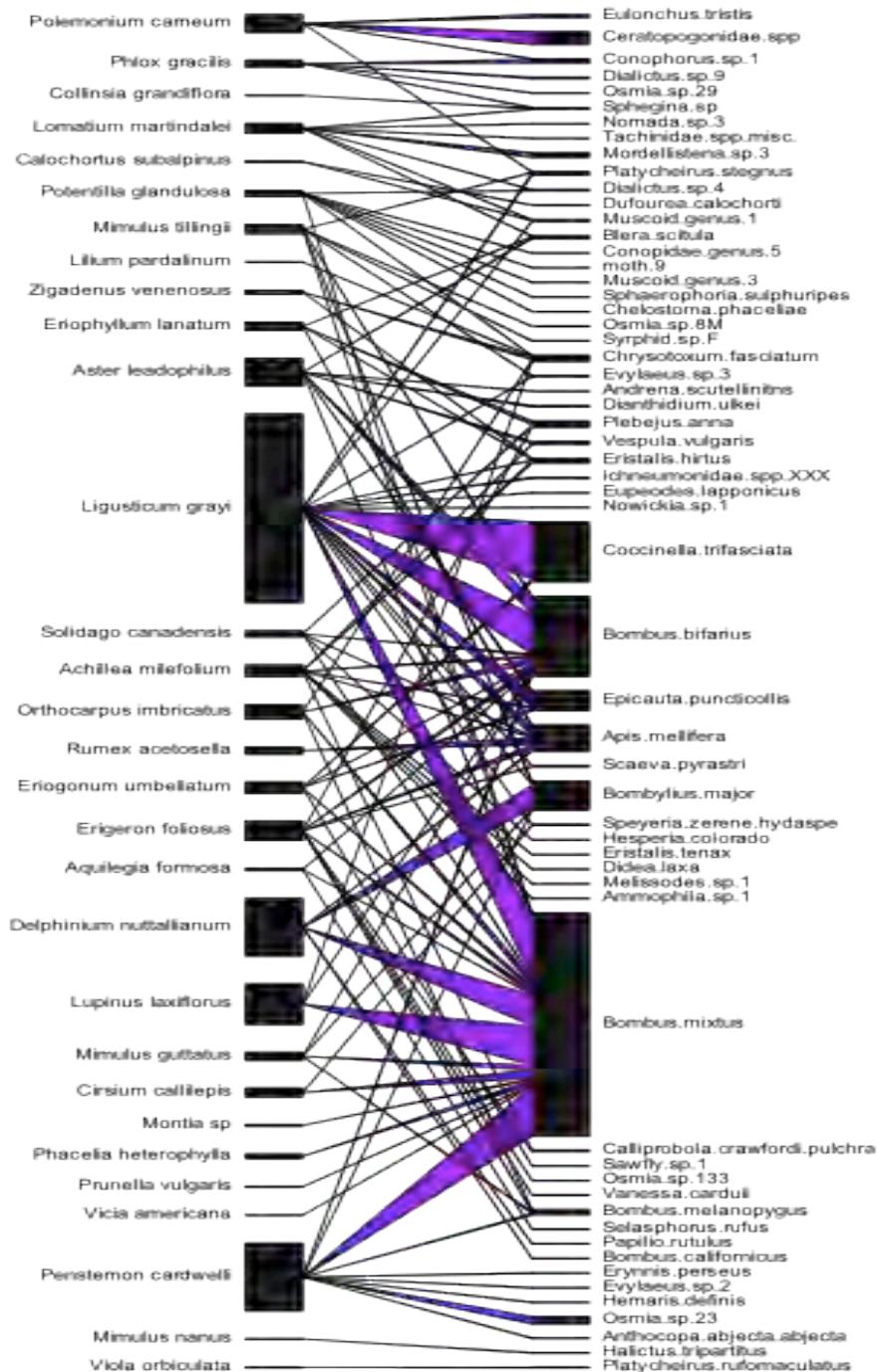


**Figure I13 Carpenter Basin: Full Season Plant-Pollinator Interaction Network.**  
This figure shows the bipartite plant-pollinator network for Carpenter Basin. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

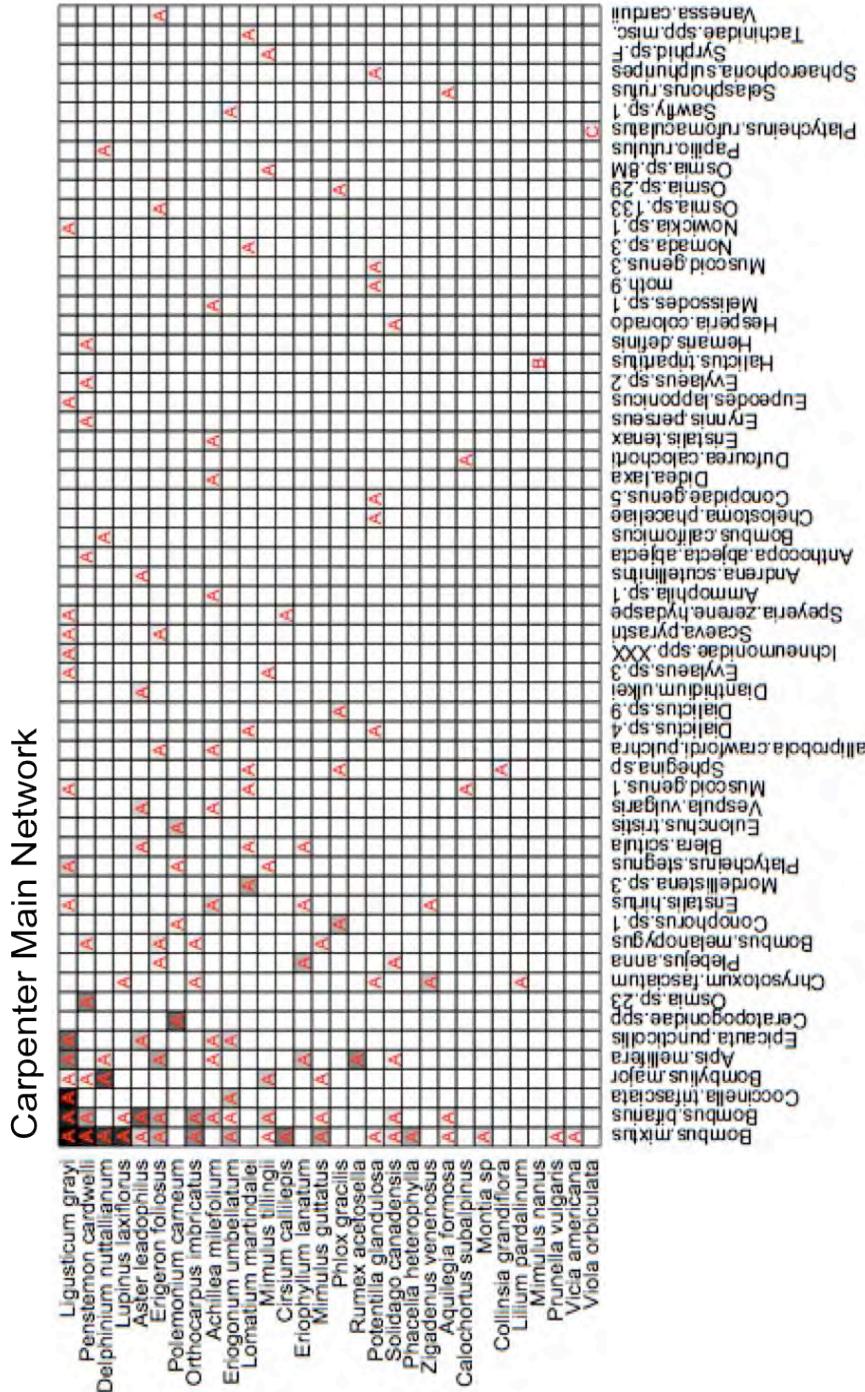
### Carpenter Basin Network



### Carpenter Main: Full Season Plant-Pollinator Interaction Network

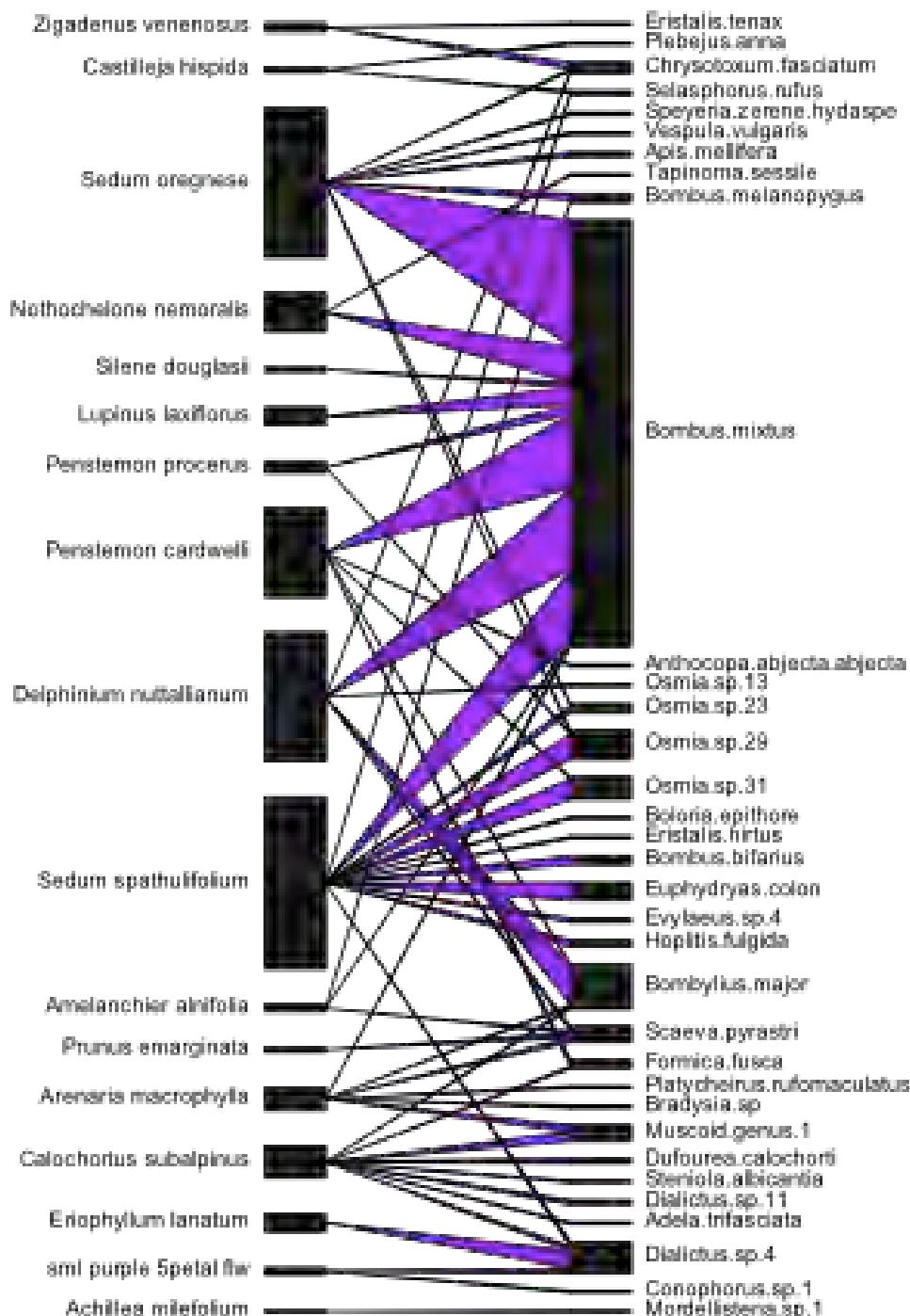


**Figure I15 Carpenter Main: Full Season Plant-Pollinator Interaction Network.**  
This figure shows the bipartite plant-pollinator network for Carpenter Main. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

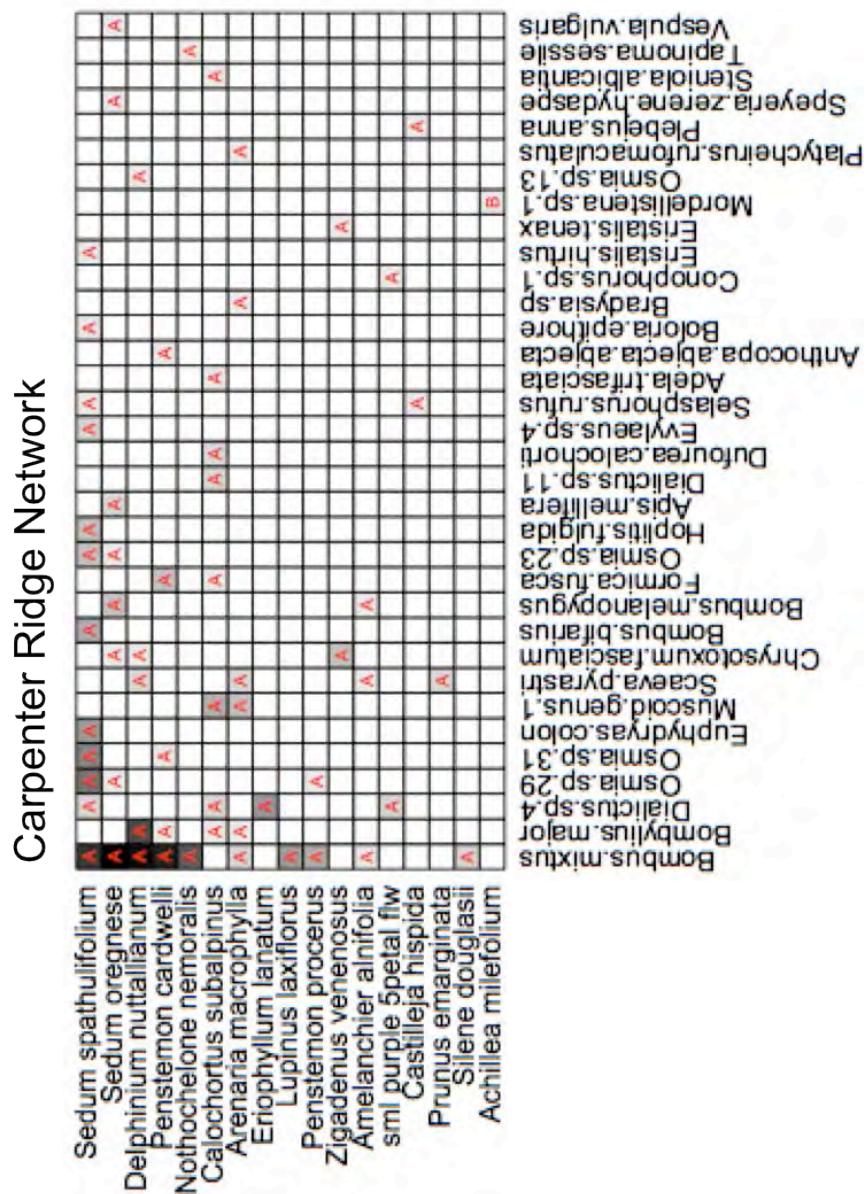


**Figure II6 Carpenter Main: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Carpenter Main. Plant species are listed as rows and pollinator species are listed in the columns. Box shading represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Carpenter Ridge: Full Season Plant-Pollinator Interaction Network

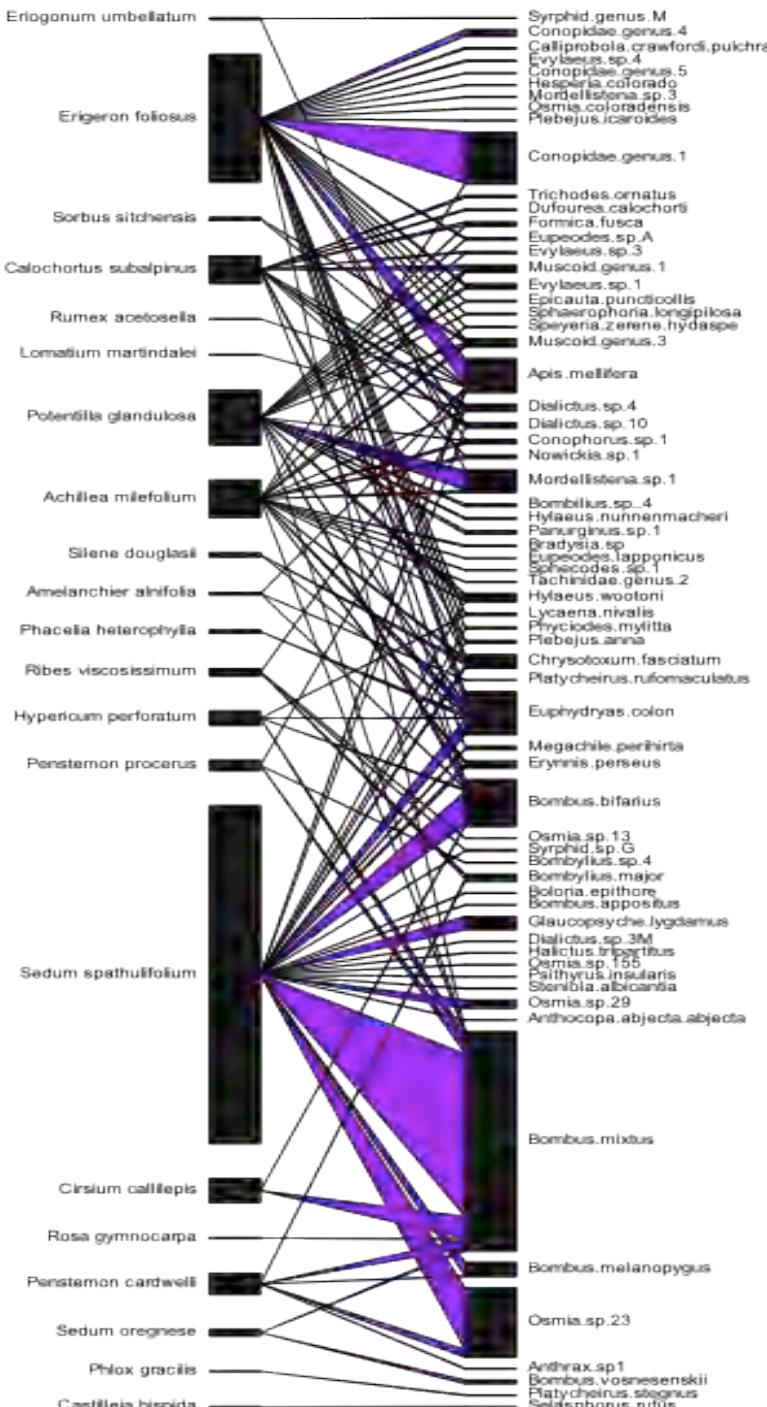


**Figure I17 Carpenter Ridge: Full Season Plant-Pollinator Interaction Network.**  
This figure shows the bipartite plant-pollinator network for Carpenter Ridge. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.



**Figure H18 Carpenter Ridge: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Carpenter Ridge. Plant species are listed as rows and pollinator species are listed in the columns. Box shading represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Carpenter Saddle: Full Season Plant-Pollinator Interaction Network

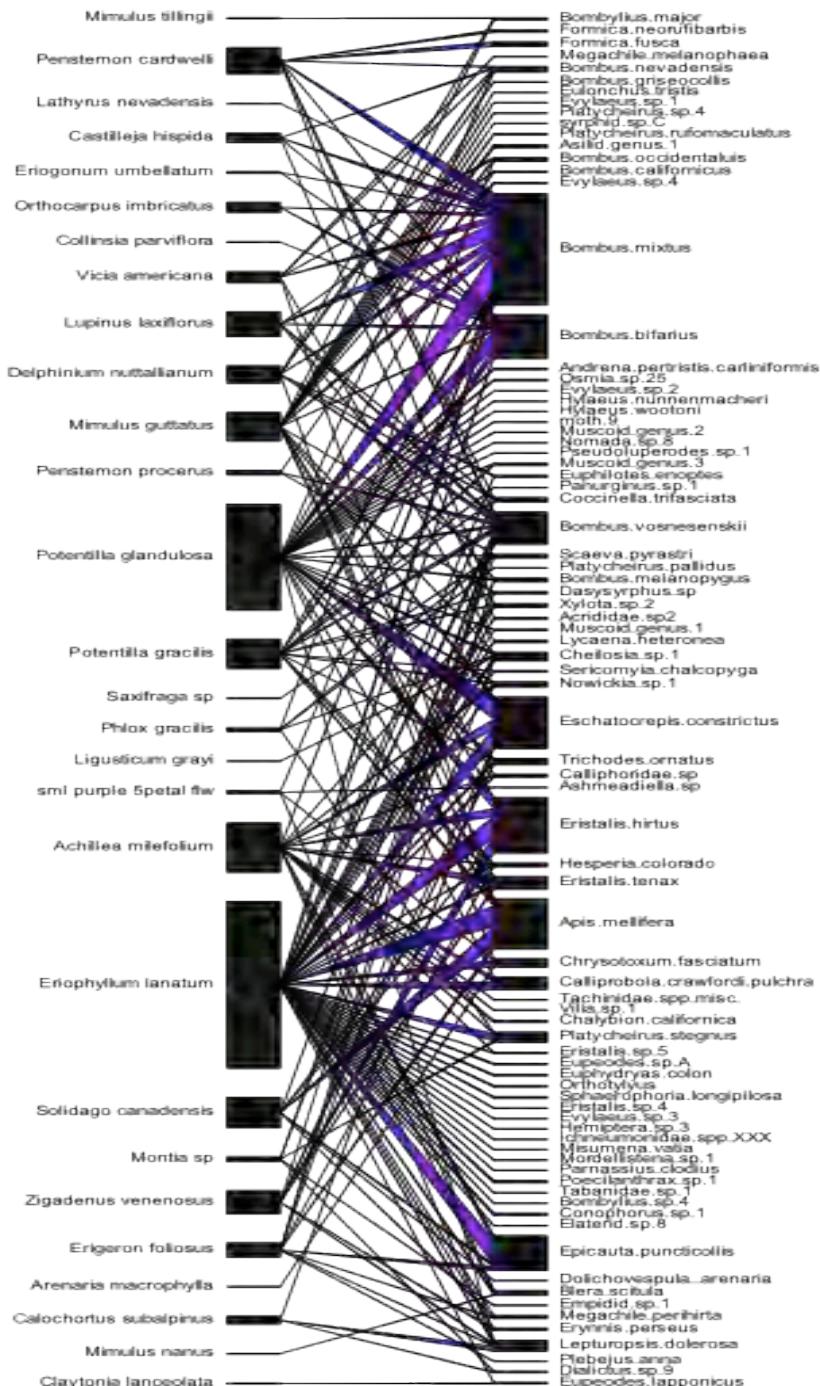


**Figure I19 Carpenter Saddle: Full Season Plant-Pollinator Interaction Network.**  
This figure shows the bipartite plant-pollinator network for Carpenter Saddle. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

Carpenter Saddle Network

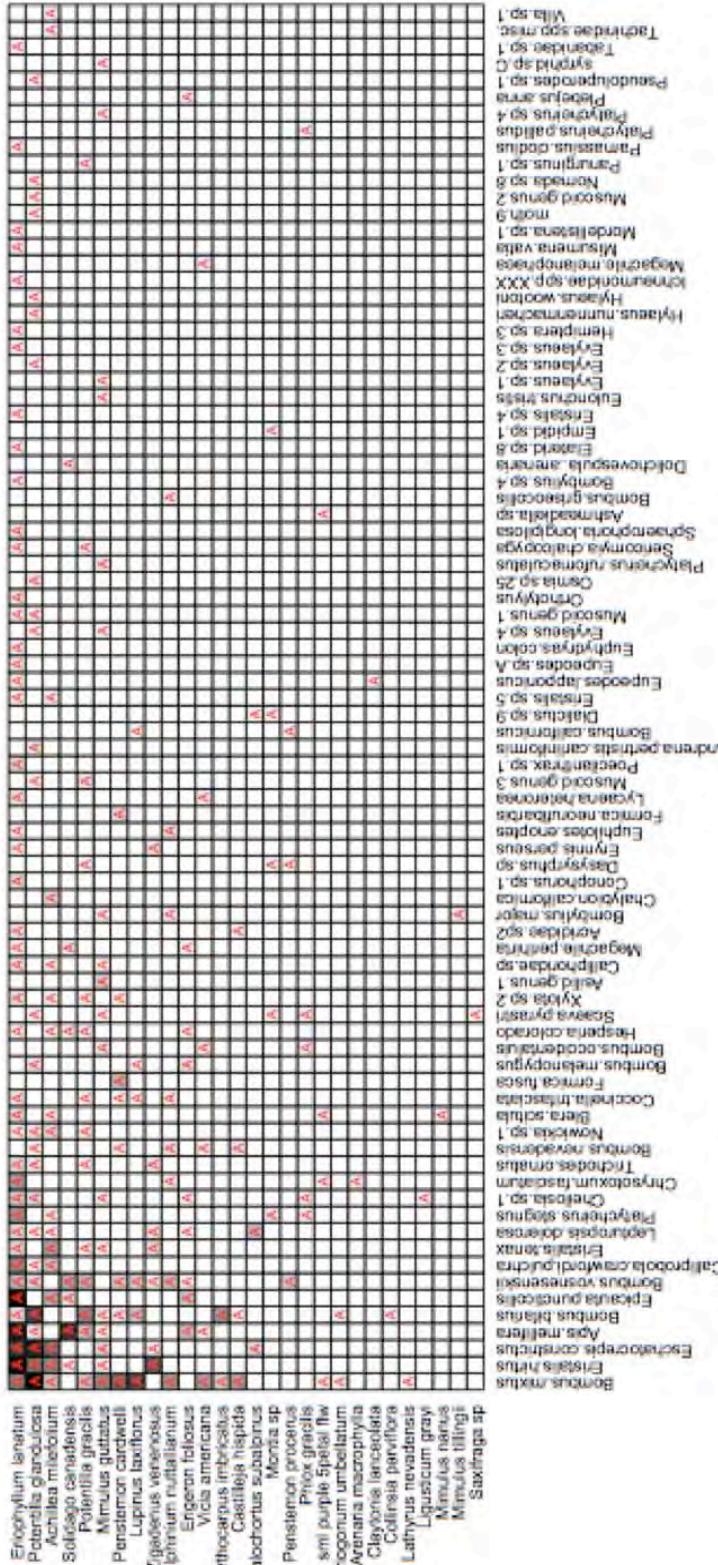
**Figure I20 Carpenter Saddle: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Carpenter Saddle. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

## Lookout Main: Full Season Plant-Pollinator Interaction Network



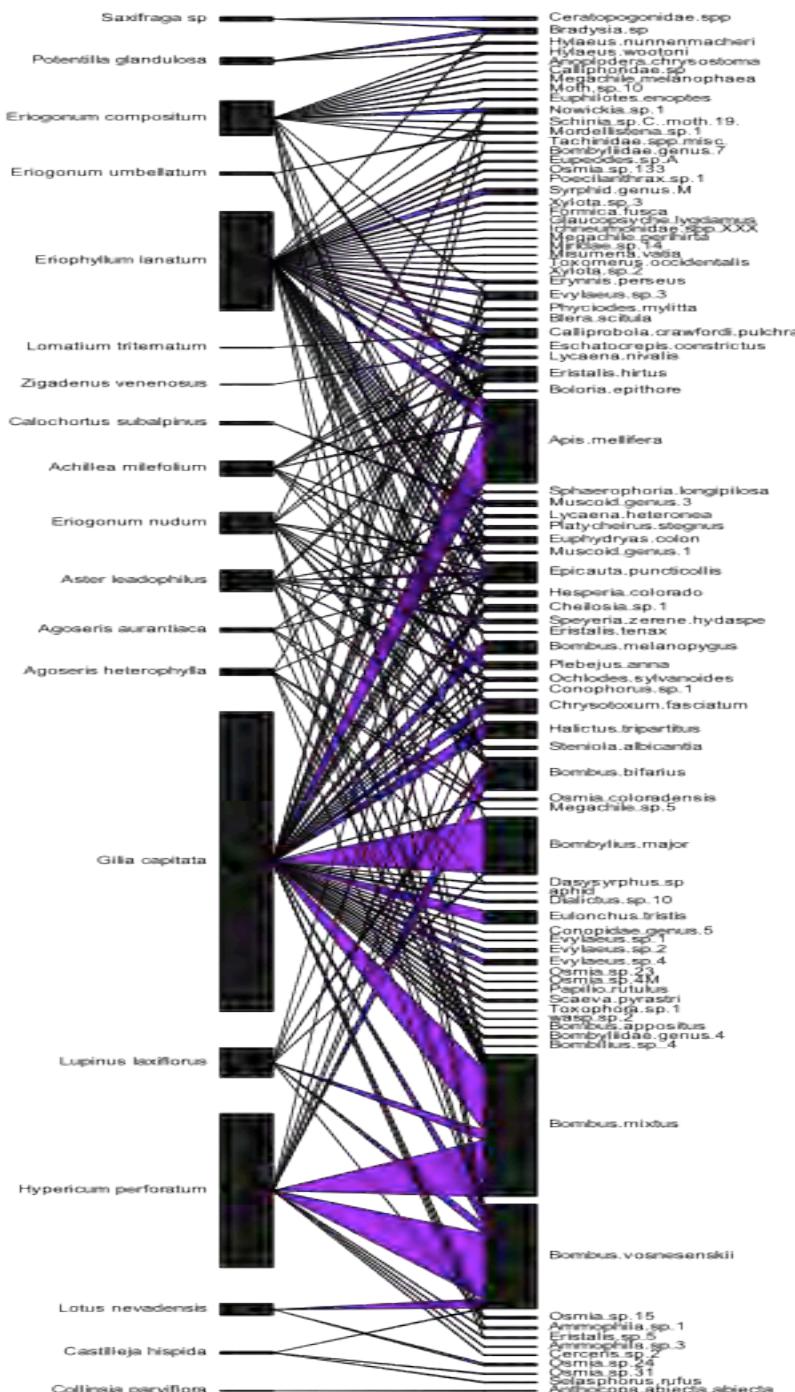
**Figure I21 Lookout Main: Full Season Plant-Pollinator Interaction Network.**  
 This figure shows the bipartite plant-pollinator network for Lookout Main. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

## Lookout Main Network

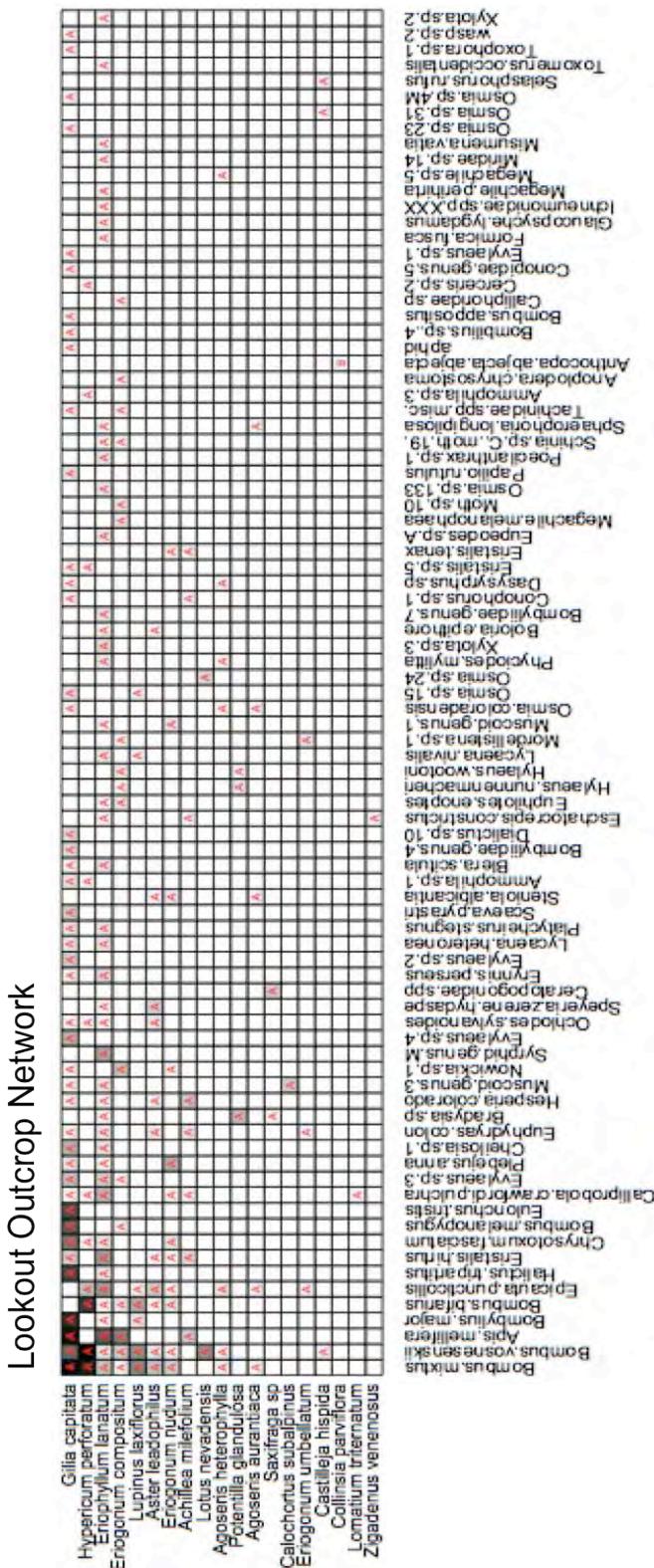


**Figure 122 Lookout Main: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Lookout Main. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### Lookout Outcrop: Full Season Plant-Pollinator Interaction Network



**Figure I23 Lookout Outcrop: Full Season Plant-Pollinator Interaction Network.**  
This figure shows the bipartite plant-pollinator network for Lookout Outcrop. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.



**Figure I24 Lookout Outcrop: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for Lookout Outcrop. Plant species are listed as rows and pollinator species are listed in the columns. Box shading represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

## M2: Full Season Plant-Pollinator Interaction Network

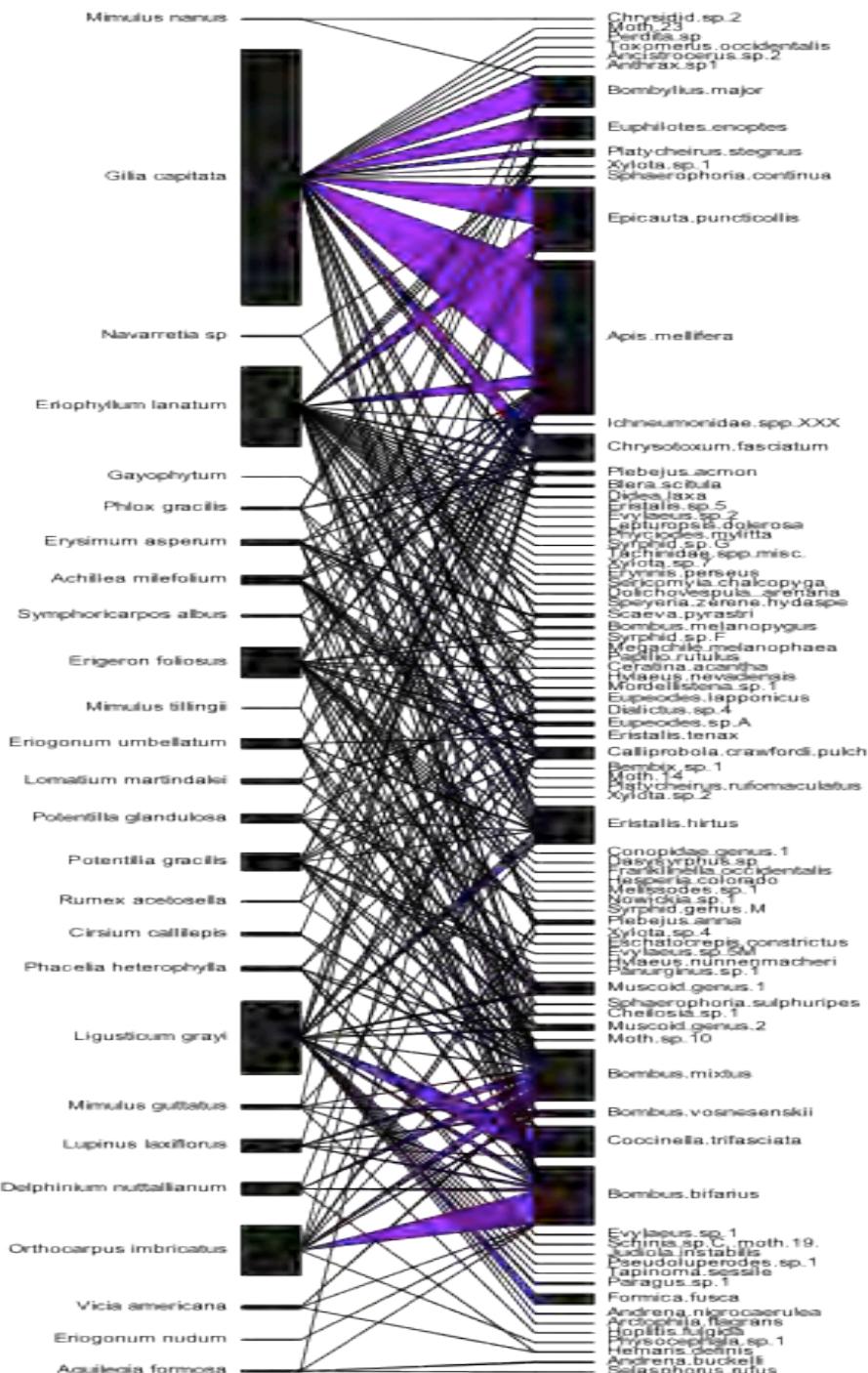
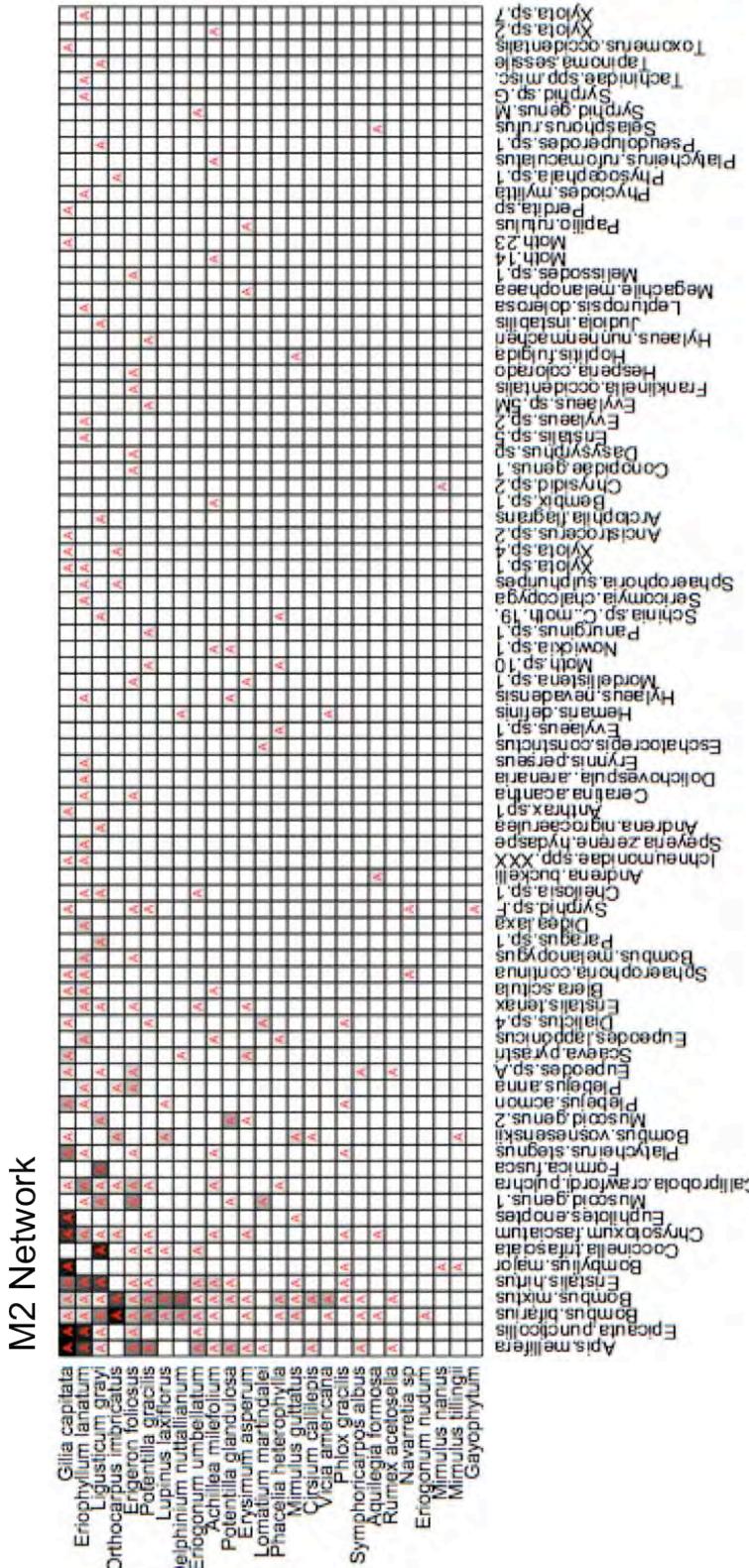
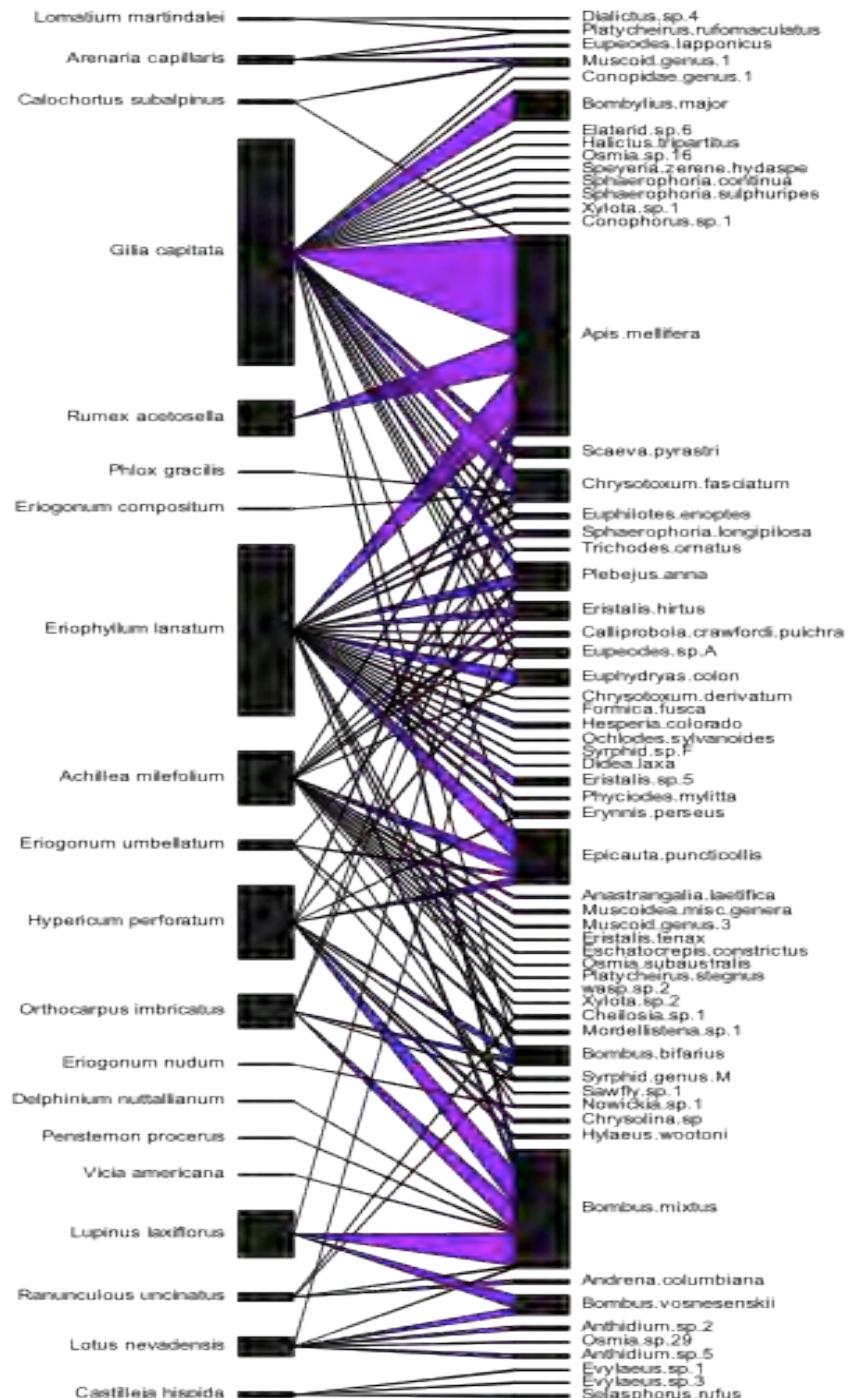


Figure I25 M2: Full Season Plant-Pollinator Interaction Network. This figure shows the bipartite plant-pollinator network for M2. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

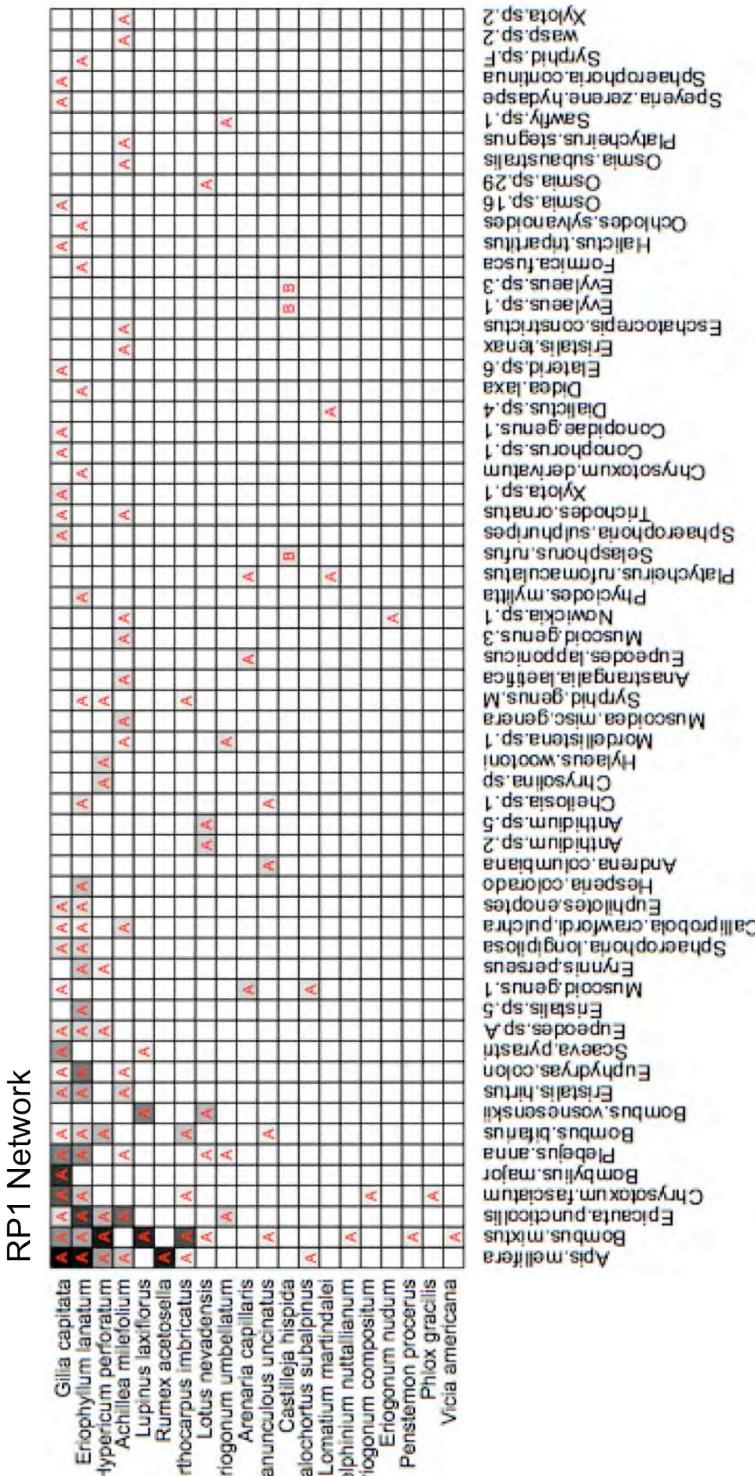


**Figure I26 M2: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for M2. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

### RP1: Full Season Plant-Pollinator Interaction Network

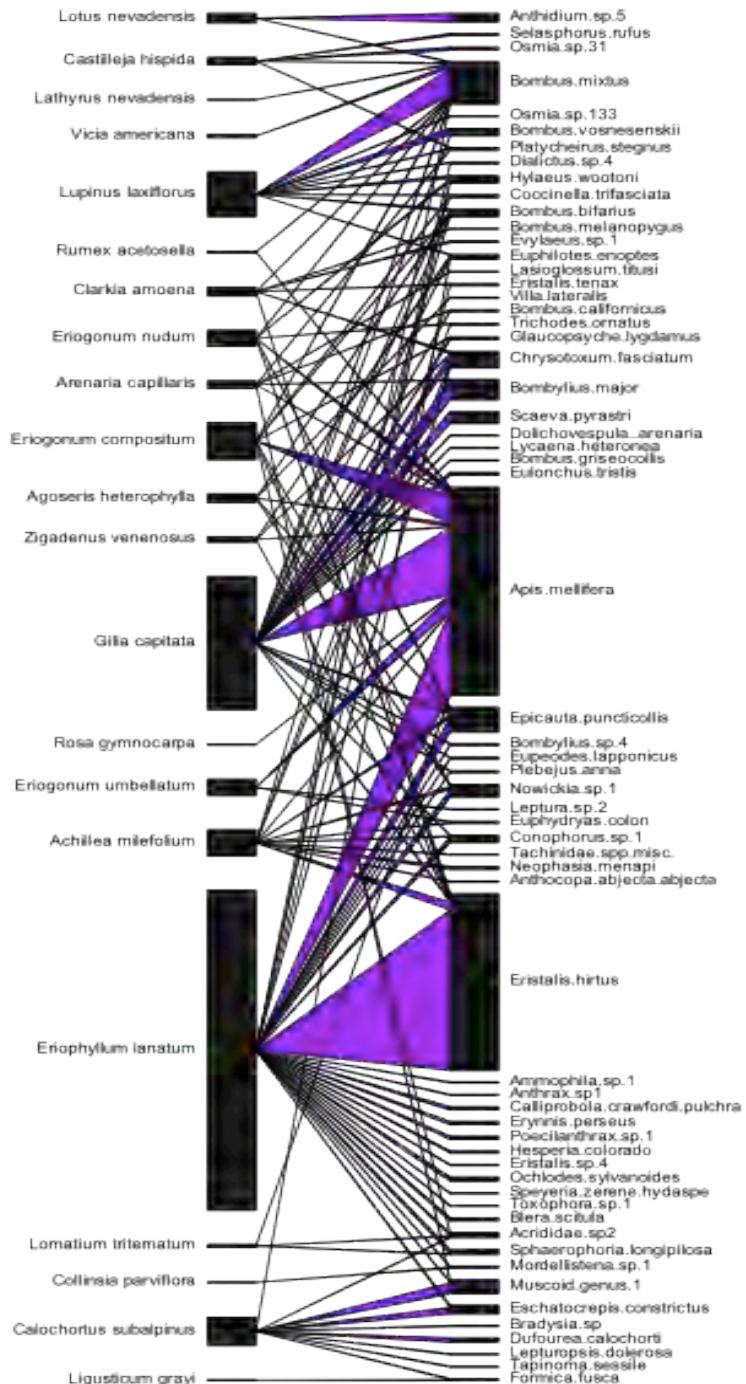


**Figure I27 RP1: Full Season Plant-Pollinator Interaction Network.** This figure shows the bipartite plant-pollinator network for RP1. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.

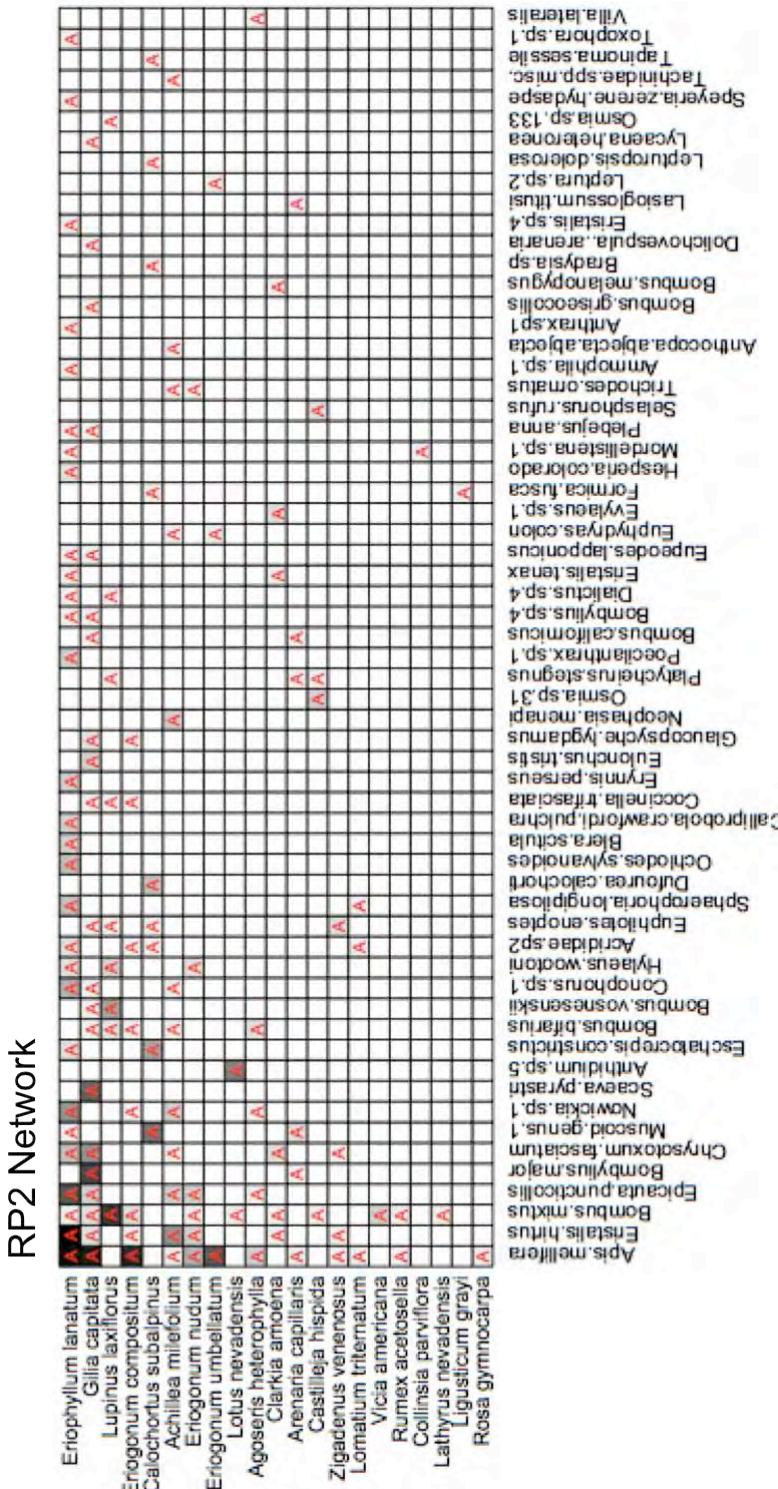


**Figure 128 RP1: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for RP1. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

## RP2: Full Season Plant-Pollinator Interaction Network



**Figure 29 RP2: Full Season Plant-Pollinator Interaction Network.** This figure shows the bipartite plant-pollinator network for RP2. Side boxes represent plant and pollinator abundance within the network, and triangle width represents interaction abundance.



**Figure I30 RP2: Full Season Plant-Pollinator Interaction Matrix.** This figure shows the plant-pollinator interaction matrix for RP2. Plant species are listed as rows and pollinator species are listed in the columns. Box shade represents interaction frequency. Letters designate network compartments, unconnected by any links to species outside the compartment.

**Table II Full Season Meadow Network Statistics by Meadow.** This table shows an assortment of bipartite network structural metrics calculated using the bipartite package in R. Calculation methods are described in the methods.

Meadow	Plants	Polinimators	Network Size	Connectance	Web asymmetry	Links per species	Number of compartments	Mean number of shared hosts	Mean number of shared visitors	Weighted nestedness	Interaction strength	Symmetry	Specialization	Plant niche overlap	Robustness (polinimators extremized)	Robustness (plants extremized)	Pollinators (polinimators exterminalted)	Linkage density
BD	49	10	490	0.17	0.66	1.39	3	1.40	0.72	0.68	0.30	-0.27	0.46	0.16	0.54	0.71	6.99	
BH	66	13	858	0.14	0.67	1.53	2	1.81	0.49	0.59	0.18	-0.23	0.24	0.27	0.53	0.78	4.99	
BS	21	6	126	0.22	0.56	1.04	2	0.73	0.45	0.58	0.41	-0.29	0.34	0.21	0.42	0.66	2.71	
CNE	59	28	1652	0.08	0.36	1.44	3	0.53	0.30	0.49	0.04	-0.07	0.16	0.13	0.57	0.71	5.74	
CNM	80	21	1680	0.10	0.58	1.62	1	0.90	0.48	0.64	0.20	-0.13	0.21	0.14	0.57	0.74	4.51	
CNT	66	28	1848	0.07	0.40	1.44	3	0.55	0.38	0.56	0.13	-0.17	0.20	0.09	0.55	0.69	4.75	
CPB	53	28	1484	0.08	0.31	1.40	3	0.53	0.30	0.45	0.02	0.13	0.12	0.19	0.59	0.66	3.87	
CPM	59	30	1770	0.07	0.33	1.44	3	0.69	0.22	0.45	0.00	0.01	0.08	0.21	0.57	0.70	4.39	
CPR	34	17	578	0.11	0.33	1.22	2	0.55	0.29	0.48	0.06	0.06	0.14	0.26	0.54	0.65	3.94	
CPS	65	21	1365	0.10	0.51	1.52	3	0.79	0.47	0.60	0.19	-0.23	0.21	0.11	0.56	0.69	4.56	
LM	83	28	2194	0.09	0.50	1.86	1	1.02	0.56	0.67	0.11	-0.10	0.23	0.16	0.60	0.73	8.16	
LO	87	19	1653	0.11	0.64	1.74	2	1.37	0.63	0.60	0.20	-0.29	0.26	0.12	0.58	0.74	7.63	
M2	83	26	2158	0.10	0.52	2.04	1	1.94	0.50	0.62	0.09	-0.21	0.16	0.22	0.57	0.80	5.34	
RP1	61	20	1220	0.09	0.51	1.41	2	0.71	0.43	0.60	0.24	-0.13	0.21	0.14	0.47	0.69	5.55	
RP2	61	21	1281	0.10	0.49	1.63	1	1.05	0.47	0.57	0.14	-0.16	0.21	0.19	0.58	0.72	4.13	

**Table I2 Average plant and pollinator degree and degree strength by meadow.** This table shows average degree and degree strength for plants and pollinators across the full season and during the peak season weeks.

Meadow	Avg degree	Avg Degree	Avg Strength	Avg Plant	Pollinator	Degree	Strength	Avg Plant	Peak Season	Avg Peak	Peak Season	Average	Peak
												Peak	Season
												Plant	Degree
BD	8.50	1.60	33.70	6.36	6.57	1.38	18.38	6.57	1.38	18.38	3.55	3.55	3.55
BH	10.42	1.79	62.92	10.79	6.65	1.43	31.29	7.58	1.43	31.29	7.58	7.58	7.58
BS	4.83	1.32	29.33	8.00	3.00	1.17	15.50	7.06	1.17	15.50	7.06	7.06	7.06
CPB	4.32	2.09	21.79	10.52	2.98	1.59	11.60	6.42	1.59	11.60	6.42	6.42	6.42
CPM	8.81	2.29	21.59	11.15	2.82	1.71	14.84	10.16	1.71	14.84	10.16	10.16	10.16
CPR	3.82	1.76	19.29	5.31	2.75	1.61	11.18	6.58	1.61	11.18	6.58	6.58	6.58
CPS	6.71	1.96	34.90	10.18	3.87	1.38	17.36	5.12	1.38	17.36	5.12	5.12	5.12
CNE	9.29	3.77	10.86	4.41	2.92	1.69	14.00	8.70	1.69	14.00	8.70	8.70	8.70
CNM	8.67	2.12	57.48	14.03	5.43	1.56	31.85	8.85	1.56	31.85	8.85	8.85	8.85
CNT	5.96	2.09	24.37	8.55	3.59	1.63	12.94	5.86	1.63	12.94	5.86	5.86	5.86
M2	8.73	2.58	66.92	19.77	4.80	2.26	29.83	13.97	4.80	2.26	29.83	13.97	13.97
RP1	5.95	1.92	24.43	7.89	4.26	1.52	16.08	5.51	4.26	1.52	16.08	5.51	5.51
RP2	6.48	2.29	28.04	9.92	4.38	1.71	17.21	6.97	4.38	1.71	17.21	6.97	6.97
LM	8.00	2.48	27.59	8.56	4.42	1.91	11.75	5.01	4.42	1.91	11.75	5.01	5.01
LO	10.53	2.15	43.89	8.97	6.41	1.62	19.97	4.53	6.41	1.62	19.97	4.53	4.53

**Table I3 Average plant and pollinator degree and degree strength by meadow per watch period.** This table presents average degree and degree strength for plants and pollinators for each meadow during each watch period.

Meadow	Plant Richness	Pollinator Richness	Average Plant Degree	Average Pollinator Degree	Average Plant Degree Strength	Average Pollinator Degree Strength
BD2	7	23	4.7	1.4	9.1	2.8
BD3	4	29	8.5	1.2	30.5	4.2
BD4	4	17	6.5	1.5	15.5	3.6
BD5	5	13	4	1.5	17	6.5
BD6	1	2	2	1	1.5	1.5
BH1	9	22	3.9	1.6	13.2	5.4
BH2	8	27	4.6	1.4	47.1	14.0
BH3	7	24	4.7	1.4	13.1	3.8
BH4	5	34	10.6	1.6	33.6	4.9
BS1	4	11	3.5	1.3	11.8	4.3
BS2	4	12	3.5	1.2	18	6
BS3	2	3	2	1.3	18.5	12.3
BS4	2	7	3.5	1	10	2.9
CPB1	4	3	1	1.3	1.5	2
CPB2	12	16	1.8	1.4	6.8	5.1
CPB3	11	32	3.8	1.3	12.5	4.3
CPB4	7	11	3.3	2.1	15.4	9.8
CPB5	11	15	2.7	2	21.2	15.5
CPB6	7	13	2.7	1.5	6.1	3.3
CPM1	5	7	1.8	1.3	2.8	2.0
CPM2	5	11	2.6	1.2	9.6	4.4
CPM3	15	28	3.4	1.8	12.5	6.7
CPM4	13	15	2.5	2.1	22.4	19.4
CPM5	14	19	2.8	2.1	7.2	5.3
CPM6	5	13	3.8	1.5	9.8	3.8
CPR1	3	3	2.0	2.0	3.3	3.3
CPR2	8	16	3.6	1.8	14.9	7.4
CPR3	9	14	2.4	1.6	6.0	3.9
CPR4	6	9	2.2	1.4	12.7	8.4

CPR5	2	12	6.0	1.0	34.5	5.8
CPS2	10	26	2.0	1.3	3.1	2.3
CPS3	10	26	3.4	1.3	6.3	2.4
CPS4	9	36	6.2	1.6	42.7	10.7
CPS5	9	31	5.3	1.5	25.2	7.3
CNE1	7	13	2.1	1.2	4.6	2.5
CNE2	5	9	1.8	1.0	3.2	1.8
CNE3	15	22	2.7	1.8	3.9	2.6
CNE4	11	30	4.1	1.5	8.1	3.0
CNE5	11	25	3.4	1.5	7.7	3.4
CNE6	3	6	2.3	1.2	5.3	2.7
CNM1	7	17	3.6	1.5	18.0	7.4
CNM2	11	32	4.5	1.6	18.8	6.5
CNM3	10	35	5.0	1.4	25.1	7.2
CNM4	8	32	6.8	1.7	51.6	12.9
CNM5	5	25	6.8	1.4	26.0	5.2
CNM6	1	4	4.0	1.0	16.0	4.0
CNT1	8	28	4.9	1.4	12.6	3.6
CNT2	15	33	3.7	1.7	12.8	5.8
CNT3	8	18	3.5	1.6	16.9	7.5
CNT4	13	28	3.5	1.6	9.2	4.3
CNT5	9	14	2.3	1.5	6.2	4.0
CNT6	2	8	4.0	1.0	8.0	2.0
LM1	10	32	4.3	1.3	6.9	2.2
LM2	17	34	4.1	2.1	9.7	4.9
LM3	15	33	4.1	1.8	10.7	4.9
LM4	15	42	5.1	1.8	14.8	5.3
LM5	7	23	5.4	1.7	12.9	3.9
LM6	1	7	7.0	1.0	38.0	5.4
LO1	3	9	3.7	1.2	8.0	2.7
LO2	10	59	7.5	1.3	34.8	5.9
LO3	9	40	6.1	1.4	13.1	3.0
LO4	13	33	5.6	2.2	12.0	4.7
LO5	8	21	4.1	1.6	23.0	8.8
LO6	1	1	1.0	1.0	4.0	4.0

M21	9	13	1.9	1.3	6.7	4.6
M22	16	35	3.7	1.7	51.6	23.6
M23	22	35	4.4	2.7	16.8	10.5
M24	14	38	6.4	2.3	21.1	7.8
M25	13	24	3.6	2.0	13.1	7.1
M26	4	10	2.5	1.0	5.3	2.1
RP11	5	14	3.4	1.2	5.4	1.9
RP12	8	25	4.1	1.3	21.1	6.8
RP13	11	25	3.5	1.5	7.0	3.1
RP14	10	30	5.2	1.7	20.1	6.7
RP15	3	10	4.3	1.3	10.7	3.2
RP16	1	5	5.0	1.0	7.0	1.4
RP21	7	28	5.3	1.3	11.9	3.0
RP22	8	23	3.8	1.3	12.5	4.3
RP23	12	27	4.5	2.0	27.9	12.4
RP24	10	27	4.9	1.8	11.2	4.1
RP25	6	10	1.7	1.0	2.5	1.5

Table I4 Number of realized network links filled by each bee guild or family. This table displays the number of network links filled by each bee family, *Apis mellifera* and *Bombus* spp. are removed from the Apidae family.

Meadow Watch	Potential Links	Links	Apis	Bombus	Apidae	Halictid	Megachilid	Colletidae	Andrena	All solitary native bees
BD	490	82	4	14	0	11	3	0	0	14
BH	858	121	5	20	0	5	8	1	0	14
BS	126	98	0	8	0	2	0	0	0	2
CPB	1484	113	6	30	0	6	0	3	2	11
CPM	1770	128	7	35	2	8	7	0	1	18
CPR	578	62	1	13	0	7	10	0	0	17
CPS	1365	131	7	21	1	16	9	4	1	31
CNE	1652	125	10	21	1	7	10	1	1	20
CNM	1680	164	3	20	0	13	21	0	2	36
CNT	1848	135	6	25	0	8	10	1	4	23
M2	2158	222	13	44	3	7	2	3	4	19
RP1	1220	114	7	17	0	4	5	1	1	11
RP2	1281	134	12	22	0	5	4	3	0	12
LM	2324	207	7	48	1	7	6	2	2	18
LO	1653	184	4	28	0	9	14	4	0	27

**Table I5 Proportional occupancy of network links.** This table shows the proportion of the total number of realized links comprised by each group of bees. Bees are grouped by family except *Apis mellifera* and *Bombus* spp. are removed from the Apidae family.

Meadow Watch	Potential Links	Link Density	Apis	Bombus	Apidae	Halictid	Megachilid	Colletidae	Andrena	All native solitary bees
BD	490	0.17	0.05	0.17	0.00	0.13	0.04	0.00	0.00	0.17
BH	858	0.14	0.04	0.17	0.00	0.04	0.07	0.01	0.00	0.12
BS	126	0.78	0.00	0.08	0.00	0.02	0.00	0.00	0.00	0.02
CPB	1484	0.08	0.05	0.27	0.00	0.05	0.00	0.03	0.02	0.10
CPM	1770	0.07	0.05	0.27	0.02	0.06	0.05	0.00	0.01	0.14
CPR	578	0.11	0.02	0.21	0.00	0.11	0.16	0.00	0.00	0.27
CPS	1365	0.10	0.05	0.16	0.01	0.12	0.07	0.03	0.01	0.24
CNE	1652	0.08	0.08	0.17	0.01	0.06	0.08	0.01	0.01	0.16
CNM	1680	0.10	0.02	0.12	0.00	0.08	0.13	0.00	0.01	0.22
CNT	1848	0.07	0.04	0.19	0.00	0.06	0.07	0.01	0.03	0.17
M2	2158	0.10	0.06	0.20	0.01	0.03	0.01	0.01	0.02	0.09
RP1	1220	0.09	0.06	0.15	0.00	0.04	0.04	0.01	0.01	0.10
RP2	1281	0.10	0.09	0.16	0.00	0.04	0.03	0.02	0.00	0.09
LM	2324	0.09	0.03	0.23	0.00	0.03	0.03	0.01	0.01	0.09
LO	1653	0.11	0.02	0.15	0.00	0.05	0.08	0.02	0.00	0.15

**Table I6 Full Season Bee Abundance and Degree.** This table shows bee species richness, network plant species richness; average plant and pollinator degree (number of species visited); as well as the full season visitation abundance and degree of each bee family.

Meadow Watch	Bee Species Richness	Network Plant Species Richness	Average Pollinator Degree	Average Pollinator Degree	Apis Count	Bombyx Degree	Bombyx Count	Andrena Degree	Andrena Count	Other Apidae Count	Other Apidae Degree	Colletidae Degree	Halictus Count	Halictus Degree	Megachilid Count	Megachilid Degree	Solitary Bee Count	Solitary Bee Degree	
BD	15	10	1.7	8.2	48	4	100	7	0	0	0	0	0	0	25	3	2	30	4
BH	18	13	1.8	9.3	41	5	292	11	0	0	0	1	1	9	4	13	3	25	5
BS	6	6	1.3	4.7	0	0	100	4	0	0	0	0	0	0	3	1	0	3	1
CPB	16	28	2.1	4.0	42	6	427	18	7	1	0	0	3	3	7	4	0	0	8
CPM	22	30	2.2	4.3	33	7	381	19	1	1	2	2	0	0	9	8	16	6	32
CPR	14	17	1.8	3.6	2	1	197	10	0	0	0	0	0	0	20	4	32	5	52
CPS	26	21	2.0	6.2	36	7	296	12	4	1	1	1	11	3	30	7	89	4	137
CNE	21	28	2.1	4.5	35	10	67	12	3	1	2	1	1	1	9	6	11	9	25
CNM	29	21	2.1	7.8	132	3	109	10	2	1	0	0	0	0	23	6	75	8	93
CNT	24	28	2.0	4.8	133	6	133	14	11	3	0	0	1	1	22	5	47	6	76
M2	20	26	2.7	8.5	443	13	344	22	8	4	3	2	3	3	12	6	2	2	28
RP1	15	20	1.9	5.7	142	7	112	10	3	1	0	0	3	1	4	3	9	3	22
RP2	16	21	2.2	6.4	191	12	57	14	0	0	0	0	7	3	9	5	13	4	33
LM	24	28	2.5	7.4	63	7	256	20	3	2	1	1	2	1	7	5	8	6	21
LO	26	19	2.1	9.7	94	4	330	11	0	0	0	0	6	2	43	3	19	9	69

