AN ABSTRACT OF THE THESIS OF

Edward Helderop for the degree of Master of Science in Geography presented on June 9, 2015.

Title: Diversity, Generalization, and Specialization in Plant-Pollinator Networks of Montane Meadows, Western Cascades, Oregon.

Abstract approved:

Julia A. Jones

Despite the importance of plant-pollinator interactions for ecological communities, few long-term observational studies have been conducted of plant-pollinator networks. Using four years of plant-pollinator interaction data from 18 meadows in the Willamette National Forest, Oregon, this thesis examined how meadow size, the amount of nearby meadow habitat, weather, degree days, and soil moisture are related to the frequency of plant-pollinator interactions. Spatial and temporal turnover of plant and pollinator assemblages (based on the Jaccard dissimilarity index) were compared between meadows in a given year and within a meadow in different years. The degree distributions of these plant-pollinator networks were constructed, and analyses were conducted to determine the prevalence of generalization in the component species, and the possible presence of modularity in some of the meadows. Pollinator assemblages varied little in space: pollinator communities were very similar in the 18 study meadows in a given year, but pollinator communities differed dramatically between years. In contrast, plant assemblages had high turnover: plants differed dramatically between nearby meadows in the same year, and plant turnover was also high within meadows between years. Network structures were dominated by species that were very well connected, and they contained more well-connected species than would occur in a randomly-assembled network. Plant and pollinator assemblages in interaction networks also were dominated by generalist species. Some evidence of modularity occurred in small meadows in the network. The results of this study are consistent with many published studies that have found that generalization in plant-pollinator networks promotes their resilience over time in spite of the high component species turnover occurring between growing seasons. These results provide little support for the hypothesis that pollinator networks in fragmented habitats are fragile and highly sensitive to the loss of individual species. However, the high spatial heterogeneity among the meadows in this study, shown by dissimilarity in flowering plants, and the high permeability of the forest separating the meadow habitats, shown by the similarity among pollinators, both contribute to the generalization and resilience of these networks. Future work on plant-pollinator networks should focus on naturally fragmented, heterogeneous habitats, and continue to observe long-term changes in pollinator assemblages.

Diversity, Generalization, and Specialization in Plant-Pollinator Networks of Montane Meadows, Western Cascades, Oregon

by
Edward Helderop

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented June 9, 2015
Commencement June 2016

Master of Science thesis of Edward Helderop presented on June 9, 2015.

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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.

Edward Helderop, Author

ACKNOWLEDGEMENTS

I would like to begin by acknowledging the enormous amount of support and guidance received from my major professor, Dr. Julia Jones. I could not have accomplished any of this without her help; it was through her excellent mentorship throughout my tenure here at Oregon State University that I grew professionally as a developing scientist. In addition, I would like to thank Dr. Andy Moldenke for his invaluable contribution to the data collection necessary for this work. I also acknowledge Dr. Leah Minc, Dr. Mary Santelmann, and Dr. Andy Jones for serving on my committee and helping to improve this thesis.

This work was supported by the National Science Foundation grants 0755511 (S. Rao and S DeBano, co-PIs), 0823380 (B. Bond, M. Harmon, S. Johnson, J. Jones, T. Spies, PIs), 1005175 (D. Tullos and J.A. Jones, co-PIs), 1261550 (D. Tullos and J.A. Jones, co-PIs). In particular I would like to thank Vera Pfeiffer for teaching me the field protocol and helping me develop novel research questions; and the students who helped me collect data during the 2014 field season: Jacob Lambert, Kaitlin Horan, Ivan Pyzow, Lauren Beatty, Ruth Mares, Disa Yu, and Ryan DeMuse. The following students contributed to data collection in 2013: Noelle Patterson, Kyra Stillman, Scott Nordstrom, Fabian Ochoa, and Amanda Reinholtz (graduate mentor). These students contributed to data collection in 2012: Jeremiah Schmidt, Linnet Vacha, and Carolyn Whitlock, and Vera Pfeiffer (graduate mentor). These students contributed to data collection in 2011: Tiffany Harper, Alina Kanaski, Tim Luttermoser, and Samantha Monier, Vera Pfeiffer (graduate mentor). I would like to thank Peggy Lee for her help in organizing the logistics of each field season. For help in writing and troubleshooting my analysis code, I would like to acknowledge the support of Anna Currey and Rebecca Hutchinson.

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CHAPTER 1 INTRODUCTION

In the past two decades, the study of ecological networks has blossomed (Ings et al., 2008). Ecologists have long recognized the importance of understanding the complexity that arises from the countless interactions that occur among organisms in a network, and the persistence of networks in the face of their apparent fragility (McCann, 2000; Montoya et al., 2006). With the advent of increased computing power and the adaptation of network algorithms from other fields, networks can be better quantified and more comprehensively studied (Strogatz, 2001; Dorogovtsev et al., 2003). Plant-pollinator networks are no exception, with many authors utilizing long-term and spatially comprehensive datasets to explore their spatial and temporal dynamics (Olesen and Jordano, 2002; Price et al., 2005; Moeller, 2005; Petanidou et al., 2008; Olesen et al., 2008; Dupont et al., 2009; Burkle and Alarcón, 2010). These studies all highlight the importance of spatially extensive, long-term data collection in order to better understand pollination networks and their behaviors.

Plant-pollinator networks are highly variable in time. Many flowering plants are in anthesis (available for pollinators) for only a short time during a growing season (Petanidou et al., 2008). Most pollinators are insects, and the working individuals of most insect species rarely survive an entire pollination season (Münch et al., 2008). Honeybee workers, for example, may live for only five to six weeks, while pollination may occur for 10 to 12 weeks, depending on latitude and elevation (Woyciechowski and Morón, 2009). In addition, plant and insect phenology are dramatically affected by environmental factors such as temperature and humidity (Potts et al., 2010), and dry or wet winters can affect the structure of the pollination network during the subsequent growing season (Dupont et al., 2009; Lázaro et al., 2009). Despite very high turnover of plant and pollinators species within and between seasons (Waser et al., 1996; Memmott et al., 2004; Olesen et al., 2008; Burkle and Alarcón, 2010), pollination networks tend to be resilient, retaining a similar network structure over time (Waser et al., 1996; Memmott et al., 2007; Petanidou et al., 2008; Okuyama and Holland, 2008).

Plant-pollinator networks also vary in space. In a landscape containing a matrix of suitable habitat, the primary cause of spatial variation in plant-pollinator networks arises from heterogeneity in environmental and physical characteristics of the landscape (Steffan-Dewenter et al., 2002). These characteristics determine which plant species can be found in a particular patch of habitat, in turn affecting pollinator communities (Potts et al., 2003; Steffan-Dewenter and Westphal, 2008). In spite of the innate differences in plant assemblages between patches of habitat, each individual habitat patch usually contains more plant genetic diversity than would otherwise be expected based on patch size alone (Fortuna et al., 2009). Pollinators that are able to move between the habitat patches increase the functional genetic population size of plant species (Chapman et al., 2003; Fortuna et al., 2008). This pollinator-mediated movement of genetic material allows individual habitat patches to support a high level of plant diversity, further increasing the potential for nearby or adjacent habitat patches to differ in the compositions of their plant communities

(Steffan-Dewenter and Westphal, 2008; Luque et al., 2012). Finally, besides being affected by available plant species, pollinator communities differ between meadows due to differences among insect guilds in foraging distances (Steffan-Dewenter et al., 2002), which lead them to respond to spatial pattern in a landscape at different spatial scales (Steffan-Dewenter and Tscharntke, 1999; Jauker et al., 2009). Thus, the plant-pollinator network at any given location may depend as much upon the habitat matrix in a landscape as on the characteristics of individual habitat patches (Jules and Shahani, 2003).

Both spatial and temporal turnover in plant-pollinator networks are commonly measured with similarity indices (Basilio et al., 2006; Olesen et al., 2008; Dormann et al., 2009). In a landscape that has experienced some habitat fragmentation, these indices are used to measure how the plant and pollinator communities differ between patches in the habitat matrix to determine how the component species change in space; and between years to determine how the component species change over time (Fang and Huang, 2012; Díaz-Castelazo et al., 2013). Additionally, when combined with network characteristic statistics (such as nestedness or modularity) similarity indices provide for comprehensive measurements of plant-pollinator network resilience or vulnerability in the face of habitat fragmentation (Montoya et al., 2006; Petanidou et al., 2008; Alarcón et al., 2008).

Many network analysis techniques have been adapted to study a variety of characteristics of plant-pollinator networks in particular. Network analysis can reveal the centrality – often defined as the importance -- of component species (González et al., 2010; Jordano et al., 2006). By quantifying component species turnover and changes in component species importance, network analysis also reveals the structural similarity among networks sampled in different locations or times (Petanidou et al., 2008; Weiner et al., 2011). Modularity -- defined as clustering within a network -- is a common feature of observed plant-pollinator networks that are large (more than 150 component species), but a rare feature of networks that are small (fewer than 50 component species) (Olesen et al., 2007; Fortuna et al., 2010).

When examining the importance of individual species in a particular network, a common measurement is the 'degree' (or degree centrality) of a particular vertex in the network (Dormann et al., 2009). A vertex's degree is the number of edges leading from that vertex, and the degree distribution is the probability distribution of all the degrees of all vertices of a network (Saavedra et al., 2009; Ramos-Jiliberto et al., 2009). Networks that are assembled randomly have degree distributions that follow a random (Poisson) distribution (Barabási, 2009; Newman, 2009). Real pollination networks often have power-law distributed degree distributions (Dormann et al., 2009; Bosch et al., 2009; Vázquez et al., 2009) indicating that the network contains a higher-than-expected (by random assembly) number of vertices with a large number of edges. However, some pollination networks have exponentially distributed degree distributions, usually in smaller or more isolated networks (Dormann et al., 2009, Kallimanis et al., 2009).

Degree centrality measurements for a particular vertex examine only the edges connecting that vertex to its neighbors. Other centrality measurements take into account a particular vertex's position within the network. Eigenvector centrality, for example, is used in some studies of ecological networks, including plant-pollinator networks (Alarcón et al., 2008; Estrada and Bodin, 2008; Dupont et al., 2009). The eigenvector centrality for a particular vertex is the eigenvector of the interaction matrix of the original plant-pollinator network (Jordano et al., 2006). A vertex's eigenvector centrality is proportional to the sum of all of its neighbors' centrality measurements, where a neighbor is defined as the nearest connected vertex. Therefore, vertices that are connected to other well-connected vertices have a higher eigenvector centrality than a vertex that is connected to poorly-connected vertices (even if the number of edges in both cases is the same) (Jordano et al., 2006). Eigenvector centrality is a good indicator of generalization in networks because eigenvector centrality quantifies the extent to which a species is connected to other species that also have many connections (Bascompte and Jordano, 2007; Fang and Huang, 2013). Species in plant-pollinator networks that are generalists will have higher eigenvector centralities, while those that are specialists will have lower eigenvector centralities (Sazima et al., 2010).

Network modularity measures the strength of clusters, or subnetworks within a network (Hofman and Wiggins, 2008). Several studies have examined modularity in plant-pollinator networks (Olesen et al., 2007; Fortuna et al., 2010; Danieli-Silva et al., 2011). Most studies have found that plant-pollinator networks are significantly modular (Danieli-Silva et al., 2011) while others have found that significant modularity only emerges when there are more than 50 component species (Olesen et al., 2007). In larger networks, the modules emerge around functional groups of plants and pollinators (Danieli-Silva et al., 2011). Modularity and nestedness (a measure of organization of a network against a randomly assembled network) have also been found to be correlated, and modularity is often positively related to a network's resilience, with many modules able to adapt to the loss of some of their members (Fortuna et al., 2010).

This thesis aims to combine similarity indices that quantify spatial and temporal turnover in a matrix of suitable habitat in a broader landscape with network analysis techniques that quantify the importance of different species to the overall network structure. Together, the analyses here provide tools to understand how plant-pollinator networks are organized at different scales, and the roles that different component species play in maintaining that network structure.

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CHAPTER 2 SPATIAL AND TEMPORAL TURNOVER IN PLANT-POLLINATOR NETWORKS IN THE WESTERN CASCADES, OREGON

2.1 Abstract

Despite the importance of plant-pollinator interactions for ecological communities, few long-term observational studies have been conducted of plant-pollinator networks. Using four years of plant-pollinator interaction data from 18 meadows in the Willamette National Forest, this study examined how meadow size, the amount of nearby meadow habitat, weather, degree days, and soil moisture were related to the frequency of interactions. In addition, spatial and temporal turnover of plant and pollinator assemblages (based on the Jaccard dissimilarity index) were compared between meadows in a given year and within a meadow in different years. Pollinator assemblages varied little in space: pollinator communities were very similar in the 18 study meadows in a given year, but pollinator communities differed dramatically between years. In contrast, plant assemblages had high turnover: plants differed dramatically between nearby meadows in the same year, and plant turnover was also high within meadows between years. Collectively these findings indicate that most pollinators are likely able to travel between patches of meadow habitat in this fragmented landscape and have a tendency to be generalist foragers, pollinating whatever plant species are available. Continued long-term monitoring of plant-pollinator networks is important to understand the causes and consequences of interannual variations in relative abundance of plant and pollinator species.

2.2 Introduction and objectives

Mutualistic relationships between species, especially plant-pollinator interactions, are widely studied (Winfree et al., 2009; Chamorro et al., 2012; Davila et al., 2012). Plant-pollinator networks are bipartite interaction networks linking plant and animal species. These interactions are commonly identified in the field, when a pollinator is observed to visit a flower in anthesis (Olesen et al., 2008). Many plant-pollinator studies have examined interactions among specific species or species pairs (Knight et al., 2005; Lopezaraiza-Mikel et al., 2007), but in the past 15 years, plant-pollinator studies have increasingly examined whole networks in a specific location over time (Olesen et al., 2008; Alarcón et al., 2008; Dupont et al., 2009; Díaz-Castelazo et al., 2010) and/or compared networks among locations (Price et al., 2005; Moeller, 2005; Dupont et al., 2009; Burkle and Alarcón, 2010). These studies all highlight the importance of spatially extensive and long-term data collection required in order to capture the complete pollination network and its behavior.

Plant-pollinator networks are highly variable in time. Many flowering plants are in anthesis (available for pollinators) for only a short time during a growing season (Petanidou et al., 2008). Most pollinators are insects, and the working individuals of most insect species rarely survive an entire pollination season (Münch et al., 2008). Honeybee workers, for example, may live for only five to six weeks, while pollination may occur for 10 to 12 weeks, depending on latitude and elevation (Woyciechowski and Morón, 2009). In addition, plant and insect phenology are dramatically affected by environmental factors such as temperature and humidity

(Potts et al., 2010), and dry or wet winters can affect the structure of the pollination network during the subsequent growing season (Dupont et al., 2009; Lázaro et al., 2009). Despite very high turnover of plant and pollinators species within and between seasons (Waser et al., 1996, Memmott et al., 2004, Olesen et al., 2008, Burkle and Alarcón, 2010), pollination networks tend to be resilient, retaining a similar network structure over time (Waser et al., 1996; Memmott et al., 2007; Petanidou et al., 2008; Okuyama and Holland, 2008).

Plant-pollinator networks also vary in space. In a landscape containing a matrix of suitable habitat, the primary cause of spatial variation in plant-pollinator networks arises from heterogeneity in environmental and physical characteristics of the landscape (Steffan-Dewenter et al., 2002). These characteristics determine which plant species can be found in a particular patch of habitat, in turn affecting pollinator communities (Potts et al., 2003; Steffan-Dewenter and Westphal, 2008). In spite of the innate differences in plant assemblages between patches of habitat, each individual habitat patch usually contains more plant genetic diversity than would otherwise be expected based on patch size alone (Fortuna et al., 2009). Pollinators that are able to move between the habitat patches increase the functional genetic population size of plant species (Chapman et al., 2003; Fortuna et al., 2008). This pollinator-mediated movement of genetic material allows individual habitat patches to support a high level of plant diversity, further increasing the potential for nearby or adjacent habitat patches to differ in their plant communities (Steffan-Dewenter and Westphal, 2008; Luque et al., 2012). Finally, besides being affected by available plant species, pollinator communities differ between meadows due to differences among insect guilds in foraging distances (Steffan-Dewenter et al., 2002), which lead them to respond to spatial pattern in a landscape at different spatial scales (Steffan-Dewenter and Tscharntke, 1999; Jauker et al., 2009). Thus, the plant-pollinator network at any given location may depend as much upon the habitat matrix in a landscape as on the characteristics of individual habitat patches (Jules and Shahani, 2003).

Component species of plant-pollinator networks experience high turnover (Olesen et al., 2008) often due to the effects of habitat fragmentation (Kremen and Ricketts, 2000; Klein et al., 2007). Over time, loss and fragmentation of suitable habitat reduce connectivity, and associated declines in dispersal and genetic exchange may reduce biodiversity (Fahrig, 2003). Habitat fragmentation produces a complicated cascade of consequences for plant-pollinator networks (Kremen et al., 2007; Potts et al., 2010). In theory, a decline in abundance of one species may affect all of the species with which it is linked, potentially affecting much of the network (Fortuna and Bascompte, 2006). However in practice, most plant-pollinator networks are especially resistant to the loss of component species (Memmott et al., 2004; Rezende et al., 2007).

Both spatial and temporal turnover in plant-pollinator networks are commonly measured with similarity indices (Basilio et al., 2006; Olesen et al., 2008; Dormann et al., 2009). In a landscape that has experienced some habitat fragmentation, these indices are used to measure how the plant and pollinator communities differ between patches in the habitat matrix to determine how the component species change in space; and between years to determine how the component species change over time (Fang and Huang, 2012; Díaz-Castelazo et al., 2013). Finally, when combined with network characteristic statistics (such as nestedness or modularity) similarity indices provide for comprehensive measurements of plant-pollinator network resilience or vulnerability in the face of habitat fragmentation (Montoya et al., 2006; Petanidou et al., 2008; Alarcón et al., 2008).

2.2.1 Research questions

This study took advantage of a dataset of plant-pollinator observations, collected from 2011 to 2014 in 18 montane meadows located in the western Cascades, Oregon to answer the following questions:

> **Q1**. How do meadow size, the amount of nearby meadow habitat in a landscape, and weather at time of sampling affect the surveyed number of interactions?

H1. The observed number of interactions will be positively related to meadow size, which influences suitable habitat for plant species, and to surrounding meadow habitat area, which permits pollinators to move between meadow patches in the landscape (Jauker et al., 2009; Diekötter et al., 2007). The presence of clouds and wind is expected to be negatively related to the number of interactions surveyed because pollinators tend to spend less time foraging when the weather is inclement (Arroyo et al., 1982; Heard and Hendrikz, 1993).

Q2. How similar are surveyed plant and pollinator assemblages between meadows in a single year? In the same meadow between years?

H2. Plant assemblages in different meadows over the course of a season will differ between meadows, because of the varying phenologies of the different flowering plant species in the meadows and the fact that interactions are recorded only with flowers in anthesis. Many rare plant species can self-pollinate and many (both perennial and annual) species are able to persist at low numbers, essentially waiting for the rare pollination opportunity (Moldenke, pers. comm., 2015). This reproductive strategy allows for significant plant species diversity between meadows during the same growing season.

Relative to plants, species turnover will be relatively low over the course of a season for pollinator species participating in plant-pollinator interactions, because most pollinator species must continue foraging for an entire growing season to survive. Although individual pollinating insects often have a short lifespan, many individuals may survive for the entire short growing season in the study meadows (Moldenke, pers. comm., 2015). Individuals of social species, like bumblebees, have staggered lifespans, such that workers live for about six weeks of foraging, and individuals from a colony (and thus the species in our interaction data) will always be present in the network as long as foraging is possible.

Unlike plants, however, inter-annual turnover is likely to be higher than intra-seasonal turnover in pollinator species participating in plant-pollinator interactions. Pollinators, particularly insects, are especially sensitive to minor environmental changes and are generally prone to higher variability in abundance than plants (Dupont et al., 2009; Potts et al., 2010). Furthermore, there is no seed bank equivalent to function as a reserve to replenish pollinating species after a disturbance that reduces their numbers.

2.3 Background

Very few long-term and large-scale plant-pollinator network datasets exist. One of the most widely used dates from 1991 and consists of a four-year, year-round study of plants and pollinators in Greece. These data have been used in a number of publications (Petanidou and Ellis, 1993; Olesen and Jordano, 2002; Medan et al., 2006; Potts et al., 2006; Petanidou et al., 2008). The plant-pollinator network observed by Petanidou et al. (2008) experienced high temporal dynamism: most interaction pairings between plants and pollinators did not persist over time, and very few species were present in all four years. In spite of high temporal turnover, network structure (as measured by degree centralization, connectance, and nestedness) was stable. Petanidou et al. (2008) concluded that most component species in these networks act opportunistically, pollinating (or being pollinated by) whatever species are available at any given time.

Opportunistic behavior is likely, because most component species in plant-pollinator networks are generalists. Pollination syndrome theory (Waser et al., 1996; Fenster et al., 2004) states that most flowers have traits limiting pollinator access to their reproductive organs. Although some specialist relationships do exist in tropical pollination networks, the most common plant and pollinator species are generalists (Johnson and Steiner 2000). On oceanic islands, the most common endemic species (‘super-generalists') were able to pollinate or be pollinated by exotic species almost immediately following introduction of the exotic species (Olesen et al., 2002). The pollination of three common plant species in North America and Europe also did not conform to pollination syndrome theory (Ollerton et al., 2009).

A tendency for most component species of plant-pollinator networks to be generalists may enable networks to persist in a fragmented landscape. Although habitat fragmentation decreased the number of observed interactions of a network, fewer losses occurred because of the plasticity of pollination partner preferences among species in the networks (Steffan-Dewenter and Westphal, 2008). In some landscapes, habitat fragmentation may increase pollen and gene flow, minimizing or even negating the consequences of inbreeding depression among plants (White et al., 2002).

2.4 Methods

2.4.1 Study site

The study was conducted in 18 meadows located in five meadow complexes found between Lookout Mountain and Cone Peak in the western Cascades of Oregon, within or adjacent to the HJ Andrews Experimental Forest (Figures 1 and 2) (all meadows located near 44.2° N and 122.2° W). Study meadow size varied from 0.26 ha to 4.44 ha as of 2005. Elevation ranged from 1,308 to 1,536 m, and slope ranged from 0 to 55 percent. The climate of the region is maritime, with wet winters, and warm and dry summers. Mean annual precipitation is 2,221 mm and the mean annual temperature is 6.7°C. Mean annual snow water equivalent (at Vanilla Leaf MET station, 1,273 m) is 370 mm.

Vegetation communities in these meadows tend to be xeric or mesic (Miller and Halpern, 1998). Soils are shallow and bedrock is exposed in some locations, especially in xeric meadows. The meadows may have been maintained by Native American burning over at least the past 6,000 years (Highland, 2012). Decimation of Native Americans by the late 1700s and fire suppression since arrival of Europeans in the 1800s is associated with significant contraction of meadow habitat throughout the Cascade Range of Oregon (Miller and Halpern, 1998). In the Andrews Forest, montane meadows have contracted by 45% from 1948 to 2005 (Rice, 2009, Highland, 2012).

A total of 18 meadows has been surveyed since the study began in 2011. Fifteen meadows were selected initially (in 2011) in five meadow complexes (three in the Andrews Forest, one on Cone Peak, and one on Bunchgrass Ridge), using a stratified-random design based on meadow complex and meadow size. In each complex except Lookout, one large and two small meadows were chosen. In 2013, one mesic meadow was added to the three already being sampled in the three complexes in the Andrews Forest, and the Bunchgrass and Cone Peak meadow complexes were dropped from the survey protocol. Therefore, in 2014, 12 total meadows were surveyed, four located in each of three complexes.

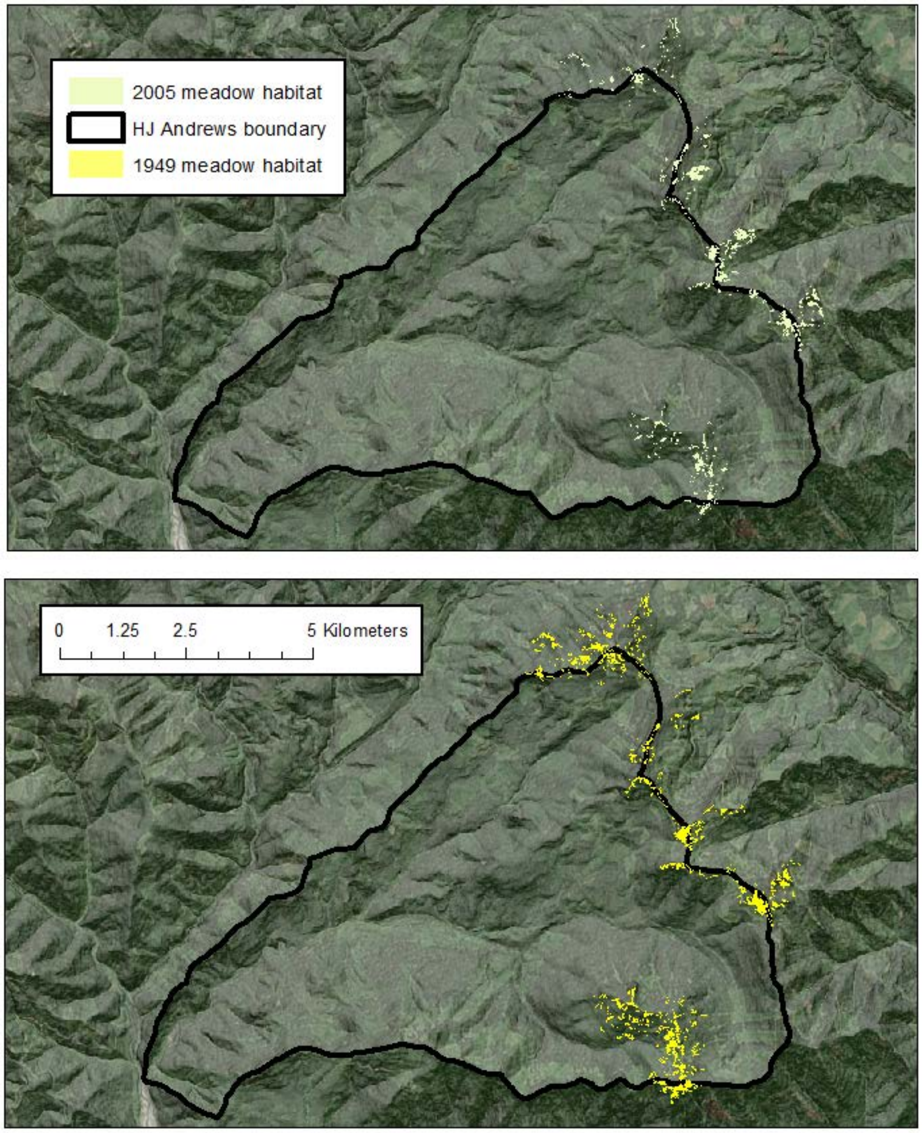


Figure 1. Meadow habitat along the eastern edge of the HJ Andrews experimental forest. Digitized from aerial photographs taken in 2005 (top image) and 1949 (bottom image). This figure does not show the meadow complexes that were surveyed outside the HJ Andrews (Cone Peak and Bunchgrass Ridge).

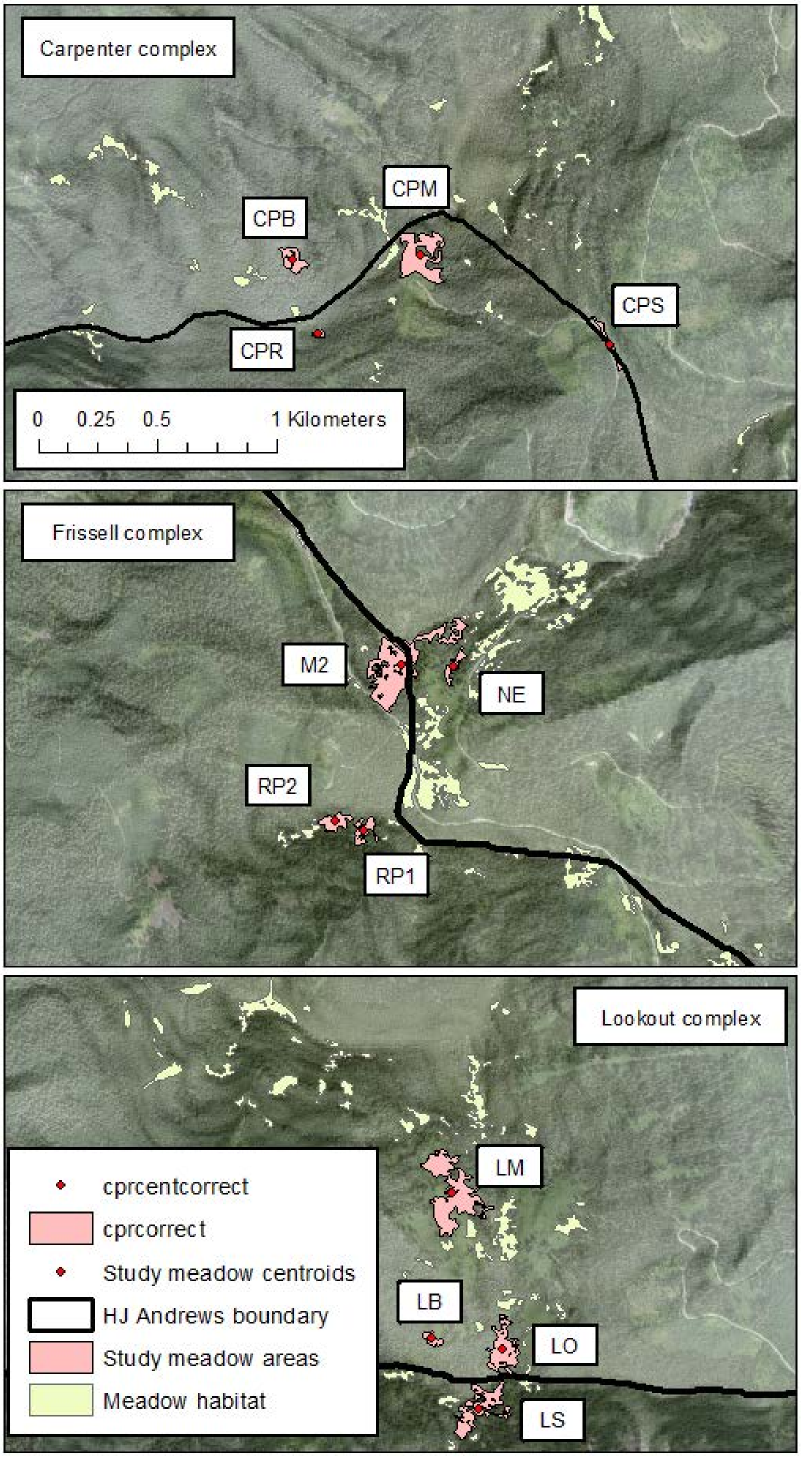


Figure 2. The three meadow complexes within or adjacent to the HJ Andrews (Lookout, Frissell, and Carpenter), each with four surveyed meadows (indicated by the pink polygons above). The four meadows in the Lookout complex are: Lookout Main (LM), Lookout Bog (LB),

Lookout Outcrop (LO), and Lookout Steep (LS); the four meadows in the Frissell complex are: Frissell Main (M2), Northern Exposure (NE), RP1, and RP2; the four meadows in the Carpenter complex are: Carpenter Main (CPM), Carpenter Saddle (CPS), Carpenter Basin (CPB), and Carpenter Ridge (CPR). Note that one meadow in the Carpenter complex is on the watershed boundary. The remaining meadow habitat in each complex as of 2005 is shown in yellow.

2.4.2 Field methods

Plant-pollinator interactions were sampled at each plot in each meadow using 15-minute 'watches' on each of five days in each summer (mid-June to mid-August) from 2011 to 2014. Each meadow contained ten 3 x 3 m plots, spaced along two parallel transects, with five plots along each transect. The plots were spaced 15 meters apart along each transect, and transects were spaced 20 meters apart. The two transects were aligned along the major axis of each meadow, near the center of each meadow. Transects in some of the small meadows were curved slightly to avoid proximity to forest edges. Thus, 90 m^2 were surveyed in each meadow regardless of meadow size.

Each meadow was visited five times approximately weekly over the course of the 2014 season, and a ‘watch’ was conducted at each plot. To reduce effects on pollinator behavior, watches were conducted between 0900 and 1700 hours, on days that were sunny or partly cloudy, had little to no wind, and experienced no precipitation. At the beginning of each watch, every flowering plant in the plot was identified to species, the number of stalks (that contained at least one flower) was counted, and the numbers of flowers on each stalk were counted for each species (up to ten stalks per species). Thus, flower abundance of each species was counted or (in the cases of species with more than ten stalks) estimated based on the average number of flowers per stalk multiplied by the number of stalks present. Compound flowers and inflorescences were counted as a single flower. Individual plants that could not be identified were photographed from outside the plot, harvested, pressed in the meadow, and transported to the lab for identification later in the day.

Each 'watch' consisted of pollinator observations for a period of 15 minutes. At each minute, the observer recorded the weather (sunny or party cloudy and still or breezy), whether the plot was in the shade or not, the air temperature, and all visits by a pollinator species to each flower species. An 'interaction' consisted of an individual pollinator making contact with the reproductive parts of a flower. If a particular individual visited different plant species in a given minute or different individuals of the same species, each visit was recorded as a separate interaction for that sampled minute. If multiple pollinator individuals of the same or different species in the plot visited a flower in the plot during the same minute, each interaction was recorded separately. If a particular pollinator individual visited multiple flowers of the same species (but of the same individual) during the same minute, those visits were counted and recorded as a single interaction, and the number of visits was recorded in a separate column.

Pollinators that could not be visibly identified in the field were captured using a net after the first visit and euthanized in the field using a small jar of ammonium carbonate and a small amount of moisture (to generate carbon dioxide). From the field they were transported to the lab, given unique ID numbers, pinned, and sent to an expert entomologist for identification (Andy Moldenke). During the capture and euthanization process, the 15 minute timer was stopped, and no observations were made. When the observer was ready to continue the watch, the timer was restarted and the 15 minute watch continued from the point where it stopped.

2.4.3 Data analyses

At the end of each day, the data from the day's watches were entered into Excel and checked for potential errors by the field crew leader. At the end of the field season, the entire dataset (2011 to 2014) was checked for several types of errors with help from Andrew Moldenke and Rebecca Hutchinson. These included: discrepancies between the interaction dataset and the flower survey dataset (for example, a flower that appeared in the interaction dataset but not the flower survey), abnormally high numbers of stalks or flowers (for example, an observer attempting to count the individual flowers of an inflorescence), and data entry errors (incorrectly entered temperature, incorrectly coded weather, etc.). These errors were corrected when possible, and affected data were omitted from analysis when errors could not be corrected. In all, 4,870 interactions were recorded in 2014, of which 202 (<5%) were omitted from analysis. These cases were omitted either due to an egregious error (no pollinator species recorded for an interaction, due to a failed capture attempt) or due to an entirely nonsensical error (recording a plant species absent from the flower survey and not present in this area of the world).

Three variables were used in analyses in this study: plants, pollinators, and interactions. The number of interactions was defined as the number of occurrences of each unique pairing (one pollinator species and one plant species) for each plot and watch date. The number of plant species was defined as the number of plant species participating in the interactions, and the number of pollinator species was defined as the number of pollinator species participating in the interactions.

Shapefiles and plot location shapefiles of the meadow complexes, and aerial photos of the landscape from 1949 and 2005 were obtained from Stephen Highland (pers. comm.). Elevation data and climate data were obtained from the HJ Andrews data repository. Elevation data were obtained from the GI002 dataset, consisting of a 30 m digital elevation model of the HJ Andrews site. Climate data were obtained from the Vanilla Meteorological Station, and the daily maximum and minimum temperatures were used for each day from 1 March to 31 October of each year from 2011 to 2014.

The following spatial metrics were calculated for each meadow using the Arcpy module from ArcGIS version 10.2.2 in Python version 2.7.9: size (using the field calculator function), distance to all other meadows (using the near function), and meadow proximity indices (MPI). The MPI was calculated as the percentage of meadow area at varying distances from the centroid of each meadow (centroids were produced with the feature to point tool, while the ring distances were calculated with the multiple ring buffer tool). The distances were rings rather than cumulative distances, and ranged from 50 to 3000 m (50, 100, 150, 200, 300, 500, 750, 1,000, 1,500, 2,000, 2,500, and 3,000 m). The surrounding meadow habitat and MPI values were calculated from digitized aerial orthophotographs obtained in 2005 and 1949.

For statistical analyses, data were obtained at three scales: the 'plot-watch', the 'meadow-watch' and the 'meadow' scale (Table 1). In 2014, 600 plot-watches were sampled (12 meadows x 5 dates x 10 plots). In 2011, 2012, and 2013, 900, 750, and

840 plot-watches were sampled. For some analyses, data were aggregated to 'meadow-watches' (n = 12 meadows x 5 watches = 60 for 2014) and in some analyses data were aggregated to the season (n = 12 meadows for 2014).

Table 1. The numbers of plot-watches, meadow-watches, and meadows surveyed for all complexes and then for the three complexes within the HJ Andrews.

All Complexes	**2011**	**2012**	**2013**	**2014**	**All years**
Plot-watches	900	750	840	600	3090
Meadow-watches	90	75	84	60	309
Meadows	15	15	12	12	18

HJ Andrews	**2011**	**2012**	**2013**	**2014**	**All years**
Plot-watches	540	450	840	600	2430
Meadow-watches	54	45	84	60	243
Meadows	9	9	12	12	12

The Jaccard distance (or Jaccard dissimilarity index) was used to calculate the similarity between pairs of meadows at various dates and locations. When comparing two network datasets from different meadows in the same year, the Jaccard index is a measure of spatial turnover. When comparing a meadow in two different years, the index is a measurement of temporal turnover. The Jaccard dissimilarity index (J) measures the similarity of two sets:

$$J(A,B) = 1 - (|A \cap B| / |A \cup B|) \tag{1}$$

where A and B are the two sets being tested. The index J is the inverse of the intersection of the two sets divided by the union of the two sets (Levandowsky and Winter, 1971). J ranges between 0 and 1, where a value of 0 indicates that the two sets are completely similar, and a value of 1 indicates that the two sets are completely dissimilar. Jaccard values were calculated for plants, pollinators, and interactions for all pairwise comparisons of meadows. Jaccard indices were computed using the Vegdist function in the Vegan package of R version 3.1.1.

The response of plant-pollinator interactions to meadow size, distance, and meadow proximity was tested by correlation analysis. The number of interactions was correlated with meadow size and meadow proximity for each ring buffer distance for each meadow using Pearson's r. Resulting correlation coefficients were plotted as a function of distance to test how the amount of meadow habitat at different distances around the study meadows was related to interaction frequency.

The diversity of plant-pollinator interactions was related to three environmental factors: cumulative temperature, weather on the day of the watch, and soil moisture.

Cumulative degree days (CDDs) were calculated for the HJ Andrews Forest study site for each year (2011-2014). The degree days for a particular day were calculated as:

$$\mathrm{DD}_d = ((\mathrm{T}_{max} - \mathrm{T}_{min}) / 2) - \mathrm{T}_{base} \qquad (2)$$
$$\mathrm{CDD}_d = \sum_1^d DD_d$$

where T_{max} is the daily maximum temperature, T_{min} is the daily minimum temperature, and T_{base} is the base temperature, 10°C in this case. Degree day calculations began March 1. The base temperature (10°C) and the day that degree days were first calculated (March 1) were selected based on consultation with an expert in plant phenology in this area and prior work in the literature (Moldenke, pers. comm.; McMaster 1997). Negative degree days were set to zero. The value of CDD at day d was the sum of that day's DD and each prior day's degree day, starting from March 1.

In addition, in 2011 and 2013 soil moisture data were collected every other week during the field season. Composite soil samples were collected from near each plot and taken to the lab where they were weighed and air-dried. After air-drying, soil samples were sieved through a 2-mm sieve, the >2-mm and <2-mm fractions were weighed, and the >2-mm gravel and organic matter subfractions were sorted and weighed. A 10-g subsample of the <2-mm fraction was weighed and oven-dried overnight. Field moisture content was determined as the percent change between the field sample and the air-dried sample. Oven-dry moisture content was determined as the field moisture content (in percent) plus the percent change in the air-dried and oven-dried sample. Oven-dry moisture contents were very low, so field moisture contents were used in regression analyses described below.

Weather was noted for each minute of each meadow watch including wind (still or breezy), and sun (sunny, partly cloudy, or cloudy). These minute-by-minute weather measurements were aggregated to the meadow-watch scale for the regression analysis.

A multiple linear regression was performed to test the response of the number of interactions to cumulative degree days and the weather on the day of the watch. Regressions were fitted separately for each of the ten meadows that had been surveyed for four years. Multiple linear regressions were also fitted for data from 2011 and 2013. The number of interactions was the dependent variable and CDD, weather, soil moisture, and the interactions between CDD, weather, and soil moisture were independent variables. Regressions were performed using the base functions available in R version 3.1.1. For regressions for 2012 and 2013, soil moisture was used as an additional independent variable.

2.5 Results

Only four of the top ten pollinator and plant species identified in plant-pollinator networks from 2011 to 2014 appeared in the top ten in all four years (Tables 2 and 3).

A few very common plant and pollinator species are abundant every year (e.g., *Apis mellifera* and *Gilia capitata*). Other seemingly common species (such as *Bombus mixtus* or *Erigeron foliosus*) are very abundant most of the time, but in some years they decline in abundance. Still other species can drop in abundance between years, only to resurge later. *Eristalus hirtus*, for example, ranked third in 2011, eighth in 2012, below ten in 2013, and seventh in 2014.

Table 2. The ten most abundant pollinator species surveyed each year, ranked in order. An asterisk denotes species found in all four years.

2011	**2012**	**2013**	**2014**
*Bombus mixtus**	*Apis mellifera**	*Apis mellifera**	*Apis mellifera**
*Apis mellifera**	*Epicauta puncticollis**	*Bombus mixtus**	*Bombus mixtus**
Eristalis hirtus	*Muscoid sp.*	*Epicauta puncticollis**	*Epicauta puncticollis**
Bombus bifarius	*Coccinella septempunctata*	*Bombus bifarius*	*Bombus bifarius*
*Epicauta puncticollis**	*Bombylius major**	*Muscoid sp.*	*Bombus flavifrons*
*Bombylius major**	*Tapinoma sessile*	*Bombus vosnesenskii*	*Bombylius major**
Chrystotoxum fasciatum	*Nowickia sp.*	*Bombylius major**	*Eristalis hirtus*
Bombus vosnesenskii	*Eristalis hirtus*	*Syrphus opinator*	*Bombus vosnesenskii*
Eschatocrepis constrictus	*Bombus mixtus**	*Evylaeus sp.*	*Nowickia sp.*
Coccinella trifasciata	*Evylaeus sp.*	*Bradysia sp.*	*Chrystotoxum fasciatum*

Table 3. The ten most abundant plant species surveyed each year, ranked in order. An asterisk denotes species found in all four years.

2011	**2012**	**2013**	**2014**
*Gilia capitata**	*Gilia capitata**	*Gilia capitata**	*Eriophyllum lanatum**
*Eriophyllum lanatum**	*Erigeron foliosus**	*Eriophyllum lanatum**	*Gilia capitata**
*Erigeron foliosus**	*Eriophyllum lanatum**	*Orthocarpus imbricatus*	*Cirsium callilepis*
*Ligusticum grayi**	*Calochortus subalpinus*	*Sedum oreganum*	*Ligusticum grayi**
Sedum oreganum	*Ligusticum grayi**	*Ligusticum grayi**	*Eriogonum compositum*
Penstemon procerus	*Angelica arguta*	*Erigeron foliosus**	*Hypericum perforatum*
Achillea millefolium	*Agoseris aurantiaca*	*Hypericum perforatum*	*Achillea millefolium*
Lupinus laxiflorus	*Cirsium callilepis*	*Potentilla gracilis*	*Sedum oreganum*
Delphinium nuttallianum	*Lupinus laxiflorus*	*Dodecatheon alpinum*	*Erigeron foliosus**
Orthocarpus imbricatus	*Eriogonum umbellatum*	*Solidago canadensis*	*Boykinia major*

Of the total of 29,686 interactions observed in all meadows surveyed from 2011 to 2014, 2,863 were unique, involving 109 plant species and 492 pollinator species (Table 4). Of these, 22,939 total interactions, 2,393 unique interactions (84%), 96 plant species (88%) and 447 pollinator species (91%) were observed in the Andrews Forest (Table 5). The observations from 2014 represented 16% of total interactions and 21% of unique interactions but just over half of the total plant (53%) and about one third of the total pollinator (32%) species observed over the four-year period in all meadows (Table 4). Considering meadows in the Andrews Forest only, the observations from 2014 represented 20% of total interactions and 25% of unique interactions but 60% of the total plant and 35% of the total pollinator species observed at the Andrews Forest over the four-year period (Table 5).

Pollinator species were about 2.7 times more frequent than plant species in 2014 but 4.5 times more frequent in all years (Table 4). Each unique interaction was observed on average 10.4 times in the four years, but only 7.6 times in 2014 (Table 4). For just the meadows within the HJ Andrews, pollinator species were 4.7 times more frequent than plant species in all years (Table 5). Also, there were more than 150 unique interactions per meadow for all 18 meadows and all four years, but only 51 unique interactions per meadow for 2014 (Table 4). In the HJ Andrews alone for all years, there were 199 unique interactions per meadow (Table 5). The number of unique interactions was very weakly related to meadow size ($r^2 = 0.16$) (Table 6, Figure 3). Table 7 lists the distances between each meadow sampled in the HJ Andrews.

Table 4. Total and unique interactions, and the numbers of plant and pollinator species surveyed for each year for 18 meadows in the Andrews Forest, Bunchgrass Ridge, and Cone Peak, in the central western Cascades of Oregon.

	2011		**2012**		**2013**		**2014**		**all years**	
	no.	*% of all*	*no.*	*% of all*	*no.*	*% of all*	*no.*	*% of all*	*no.*	*% of all*
Total interactions	10285	35	8177	28	6558	22	4666	16	29686	100
Unique interactions	1174	41	1187	41	1132	40	610	21	2863	100
Plant species	80	73	76	70	72	66	58	53	109	100
Pollinator species	238	48	271	55	248	50	156	32	492	100
No. of meadows	15		15		12		12		18	
No. of watches/meadow	6	26	5	22	7	30	5	22	23	100
No. of plots/meadow	10		10		10		10		40	
Total plot-watches	900	29	750	24	840	27	600	19	3090	100
Total interactions/meadow	686		545		547		389		1649	
Unique interactions/meadow	78		79		94		51		159	
Total/unique interactions	8.8		6.9		5.8		7.6		10.4	
Pollinator/plant species	3.0		3.6		3.5		2.7		4.5	

Table 5. Total and unique interactions, and the numbers of plant and pollinator species surveyed for each year in just the meadows within the Andrews Forest in the central western Cascades of Oregon.

	2011		**2012**		**2013**		**2014**		**all years**	
	no.	*% of all*	*no.*	*% of all*	*no.*	*% of all*	*no.*	*% of all*	*no.*	*% of all*
Total interactions	6825	30	4890	21	6558	29	4666	20	22939	100
Unique interactions	872	36	829	35	1132	47	610	25	2393	100
Plant species	65	68	64	67	72	75	58	60	96	100
Pollinator species	194	43	223	50	248	55	156	35	447	100
No. of meadows	9		9		12		12		12	
No. of watches/meadow	6	26	5	22	7	30	5	22	23	100
No. of plots/meadow	10		10		10		10		40	
Total plot-watches	540	22	450	19	840	35	600	25	2430	100
Total interactions/meadow	758		543		547		389		1912	
Unique interactions/meadow	97		92		94		51		199	
Total/unique interactions	7.8		5.9		5.8		7.6		9.6	
Pollinator/plant species	3.0		3.5		3.5		2.7		4.7	

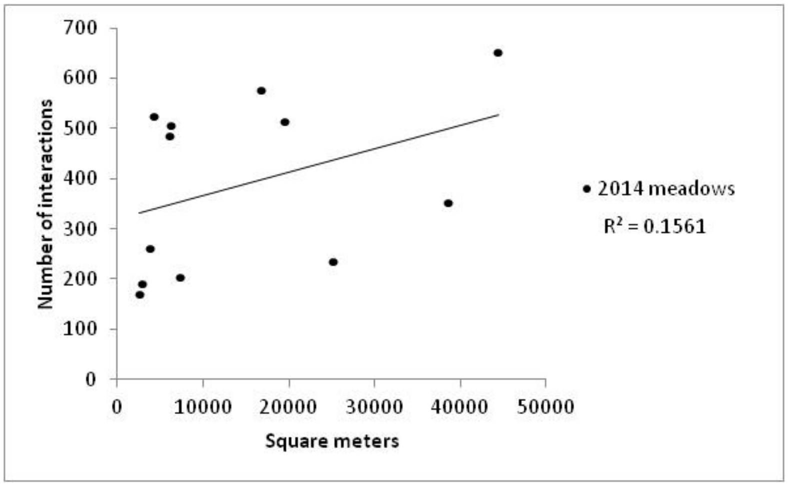
Table 6. The sizes in square kilometers of each of the 12 meadows surveyed in 2014 as well as the total number of interactions recorded over the field season.

Meadow	**Size (ha)**	**Interactions**
CPB	0.72	203
CPM	2.52	234
CPR	0.26	170
CPS	0.39	260
LB	0.29	190
LM	3.89	352
LO	1.95	514
LS	1.68	577
M2	4.44	651
NE	0.43	525
RP1	0.61	484
RP2	0.63	506

Table 7. Pairwise distances between meadow centroids in kilometers.

	CPB	CPM	CPS	CPR	LO	LM	LS	LB	NE	RP1	RP2
CPM	0.5										
CPS	1.4	0.9									
CPR	0.2	0.8	1.6								
LO	8.7	8.6	8.1	8.6							
LM	7.8	7.7	7.2	7.7	0.9						
LS	8.5	8.4	7.9	8.4	0.3	0.7					
LB	8.4	8.3	7.8	8.3	0.4	0.6	0.3				
NE	4.8	3.8	3.2	4.1	5.1	4.2	4.8	4.8			
RP1	4.5	4.3	3.8	4.5	4.4	3.5	4.1	4.1	0.8		
RP2	4.4	4.3	3.7	4.4	4.4	3.5	4.2	4.1	0.8	0.1	
M2	4.0	3.7	3.1	4.0	5.1	4.2	4.8	4.8	0.2	0.7	0.7

a.



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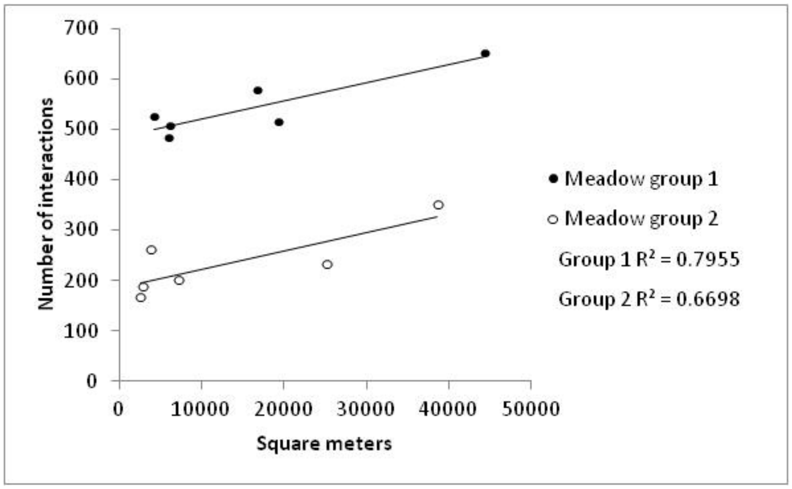
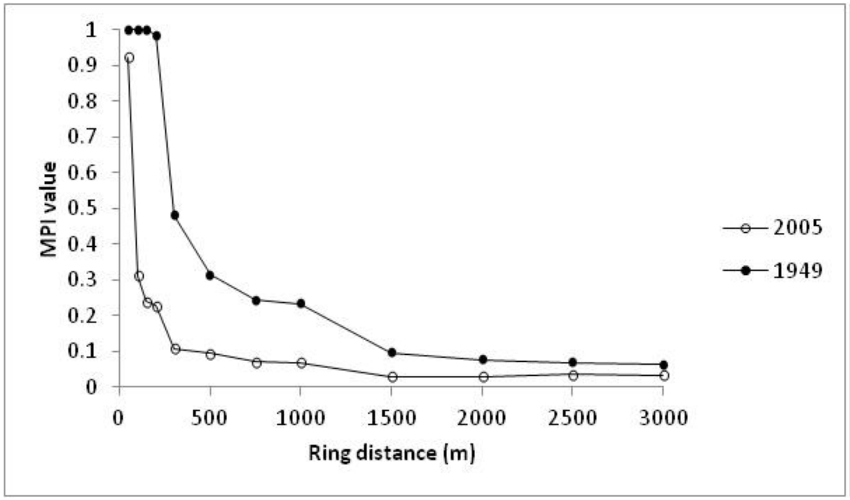


Figure 3. The number of interactions in 2014 in a particular meadow plotted against meadow size, with linear regression lines (data from Table 6). (a) linear fit for all 12 meadows from 2014 (b) linear fit for two groups: meadow group 1 contained the four meadows from the Frissell complex, plus two meadows from the Lookout complex (LO and LS). Meadow group 2 contained the meadows from the Carpenter complex plus LM and LB. Controlling for meadow size, meadow group 1 had a much higher number of interactions than meadow group 2.

a.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2000
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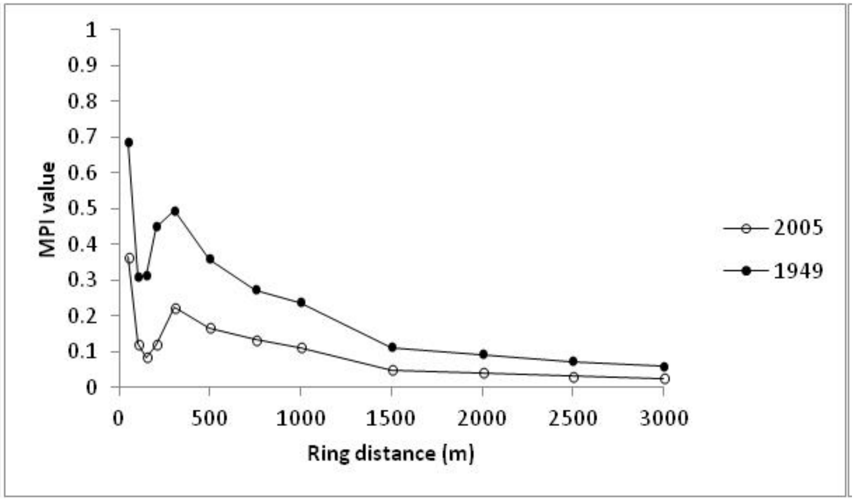
Ring distance (m)
2005
1949

b.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Ring distance (m)
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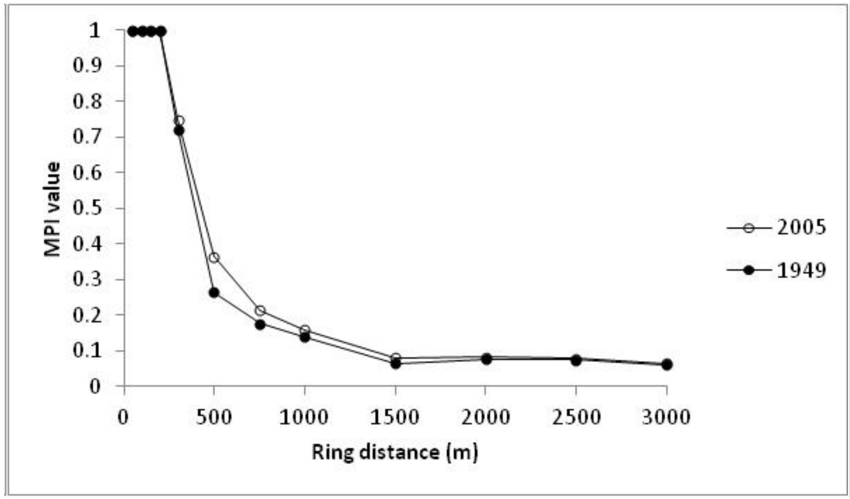
c.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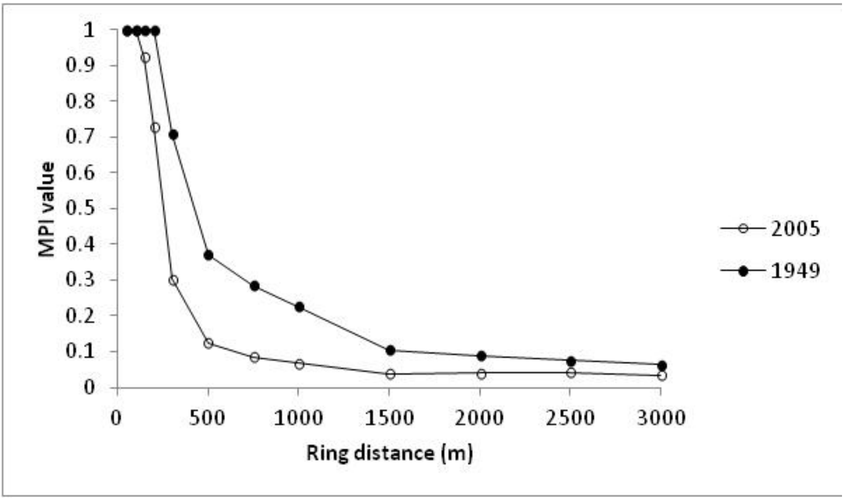
3000
Ring distance (m)
2005
1949

d.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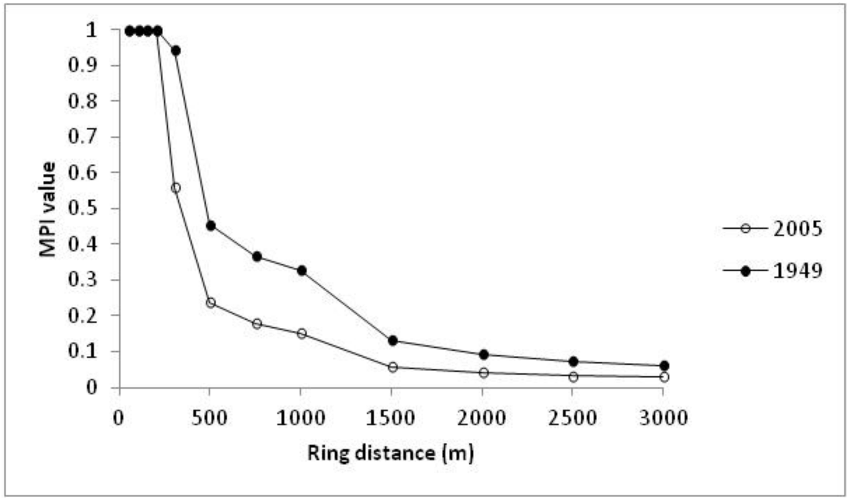
2000
2500
3000
Ring distance (m)
2005
1949

e.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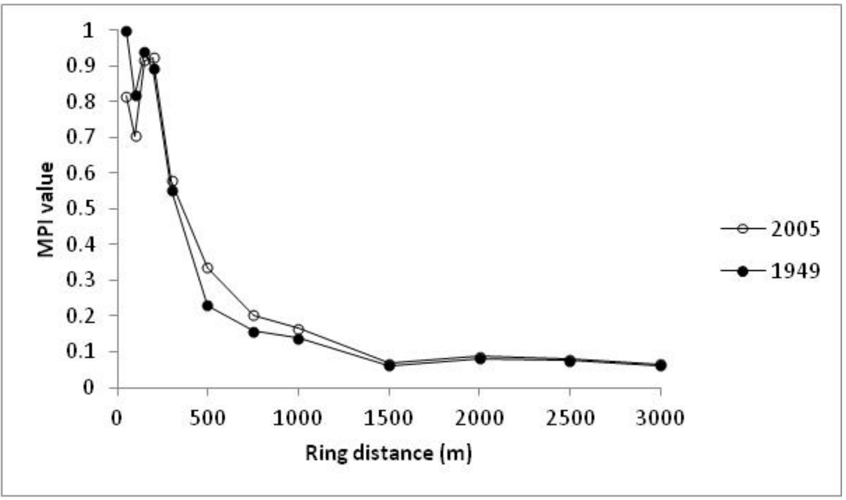
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
500
1000
1500
2000
2500
3000
Ring distance (m)
2005
1949

f.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0
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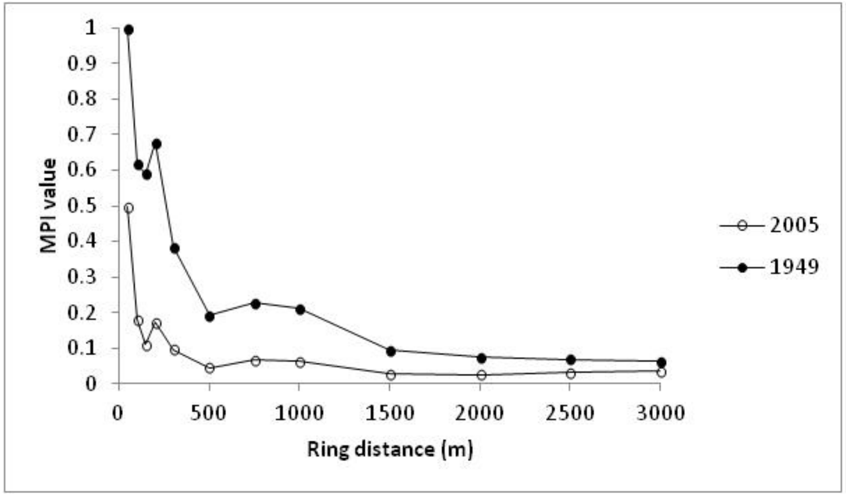
1000
1500
2000
2500
3000
Ring distance (m)
2005
1949

g.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0.1
0
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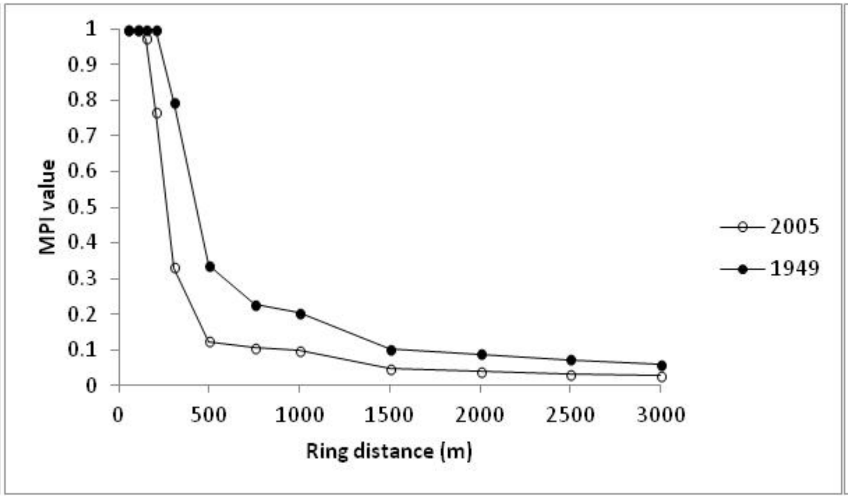
1500
2000
2500
3000
Ring distance (m)
2005
1949

h.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0
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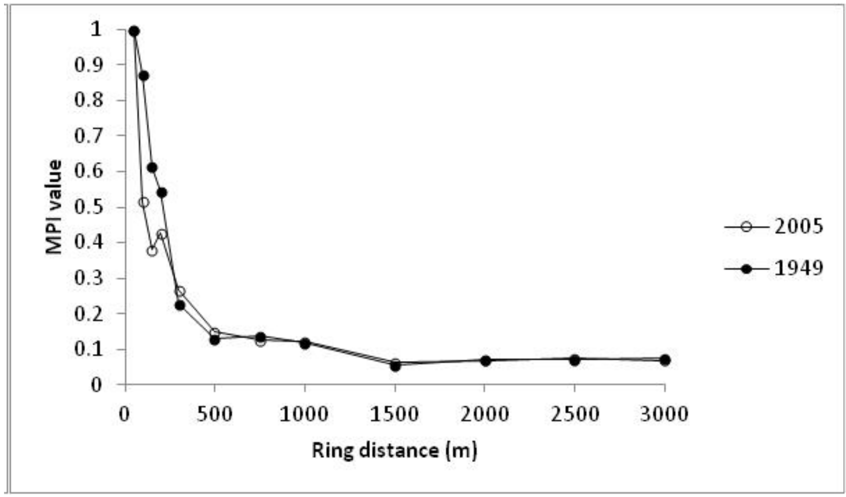
1500
2000
2500
3000
Ring distance (m)
2005
1949

i.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0.7
0.6
0.5
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0.3
0.2
0.1
0
0
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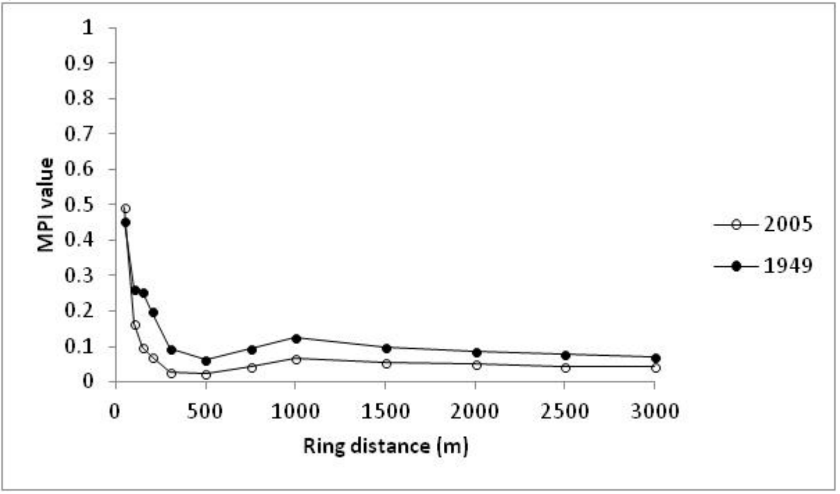
1000
1500
2000
2500
3000
Ring distance (m)
2005
1949

j.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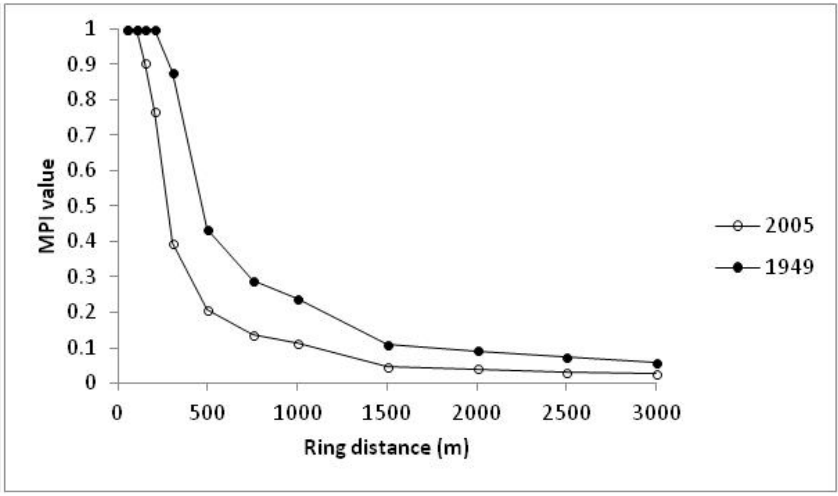
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
500
1000
1500
2000
2500
3000
Ring distance (m)
2005
1949

k.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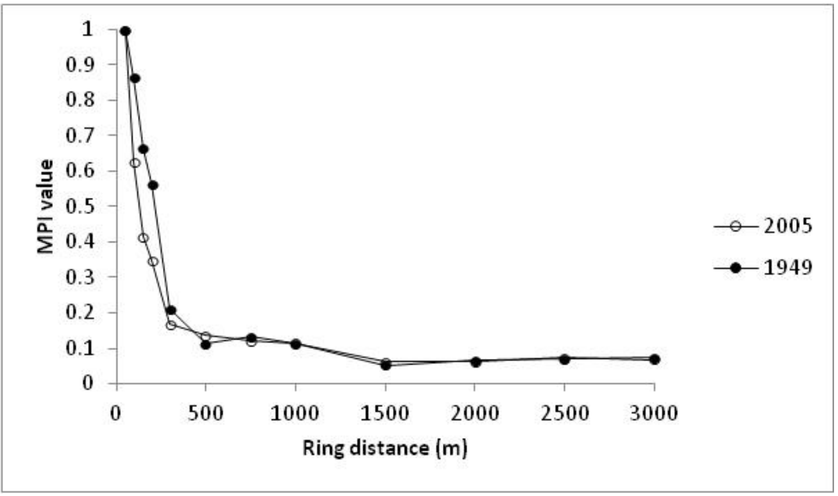
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
500
1000
1500
2000
2500
3000
Ring distance (m)
2005
1949

l.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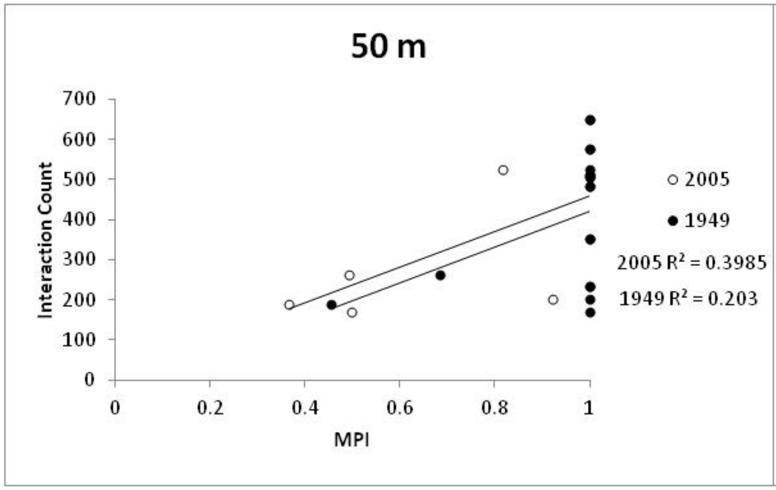
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
500
1000
1500
2000
2500
3000
Ring distance (m)
2005
1949

Figure 4. Meadow proximity index values at varying distances around the centroid of each study meadow; (a) CPB, (b) LB, (c) M2, (d) CPM, (e) LM, (f) NE, (g) CPR, (h) LO, (i) RP1, (j) CPS, (k) LS, and (l) RP2. The index is calculated based on the meadows visible in 2005 and 1949 air photos.

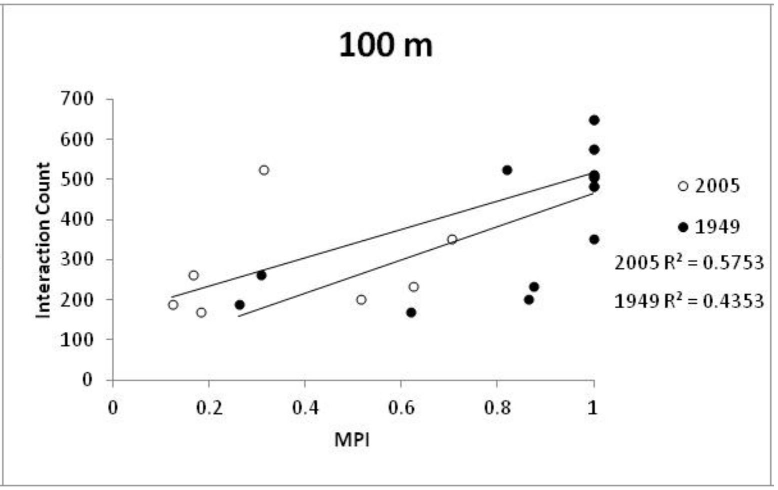
Meadow proximity indices (proportion of meadow area to total area in concentric rings around each meadow centroid) ranged from 0.25 to 1 (Figure 4). High values of MPI at 100 to 300 meters from meadow centroids show the accumulation of other meadows within a meadow complex. MPI values were higher for 1949 than for 2005 in almost all cases, indicating the loss of meadow area surrounding each study meadow from 1949 to 2005 (Figure 4).

The number of total interactions observed in 2014 was most closely related to the accumulated meadow area beyond 50 m from meadow centroids ($r^2 > 0.4$ at MPI > 50 m) (Figure 5). The total number of interactions was most strongly correlated to the amount of 2005 meadow 500 meters from meadow centroids ($r^2 = 0.631$) (Figure 5 f). The MPI at 100 m to 3000 m explained about 40 to 60% of the total interactions observed in 2014, and this explanatory power did not differ by distance or between 1949 and 2005 (Figure 6).

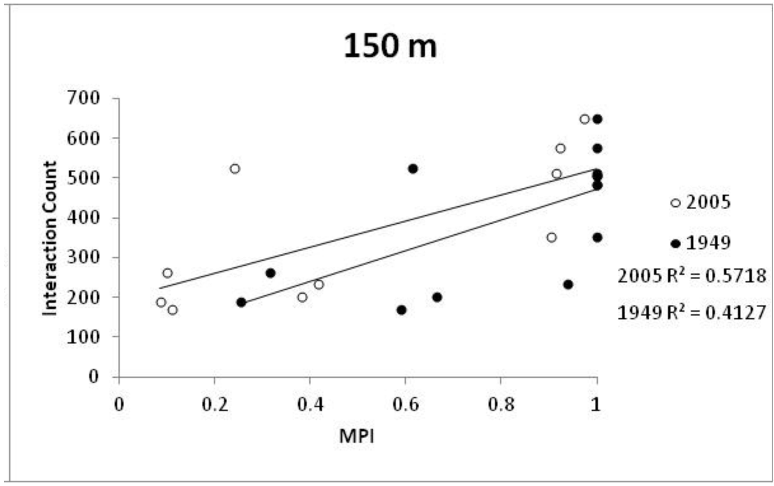
a.


50 m
Interaction Count
700
600
500
400
300
200
100
0
0
0.2
0.4
0.6
0.8
1
MPI
○ 2005
● 1949
2005 R² = 0.3985
1949 R² = 0.203

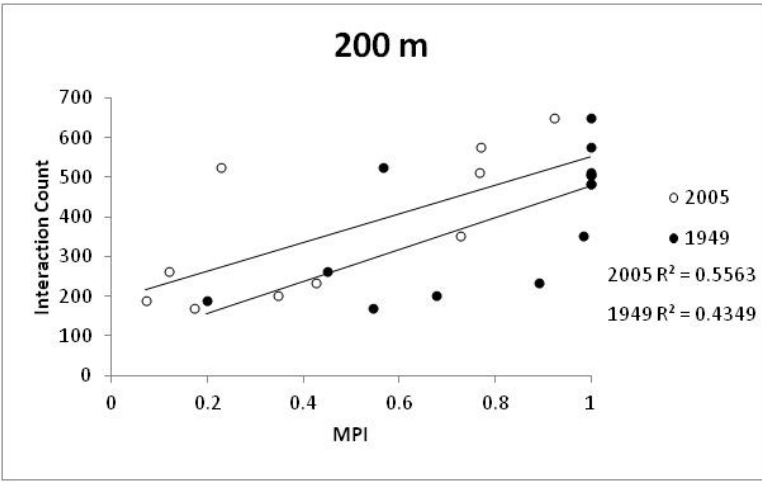
b.


100 m
Interaction Count
700
600
500
400
300
200
100
0
0
0.2
0.4
0.6
0.8
1
MPI
○ 2005
● 1949
2005 R² = 0.5753
1949 R² = 0.4353

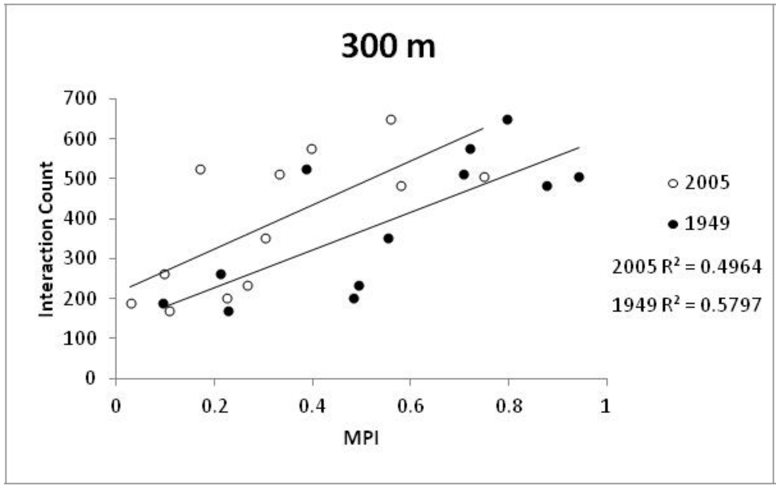
c.


150 m
Interaction Count
700
600
500
400
300
200
100
0
0
0.2
0.4
0.6
0.8
1
MPI
○ 2005
● 1949
2005 R² = 0.5718
1949 R² = 0.4127

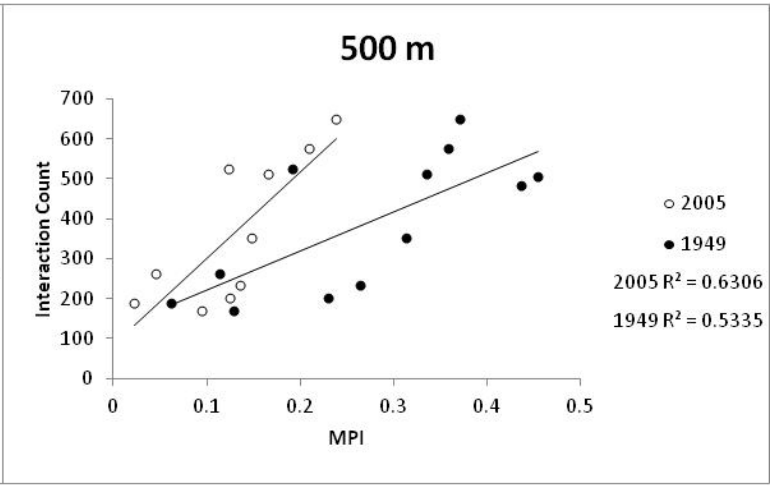
d.


200 m
Interaction Count
700
600
500
400
300
200
100
0
0
0.2
0.4
0.6
0.8
1
MPI
○ 2005
● 1949
2005 R² = 0.5563
1949 R² = 0.4349

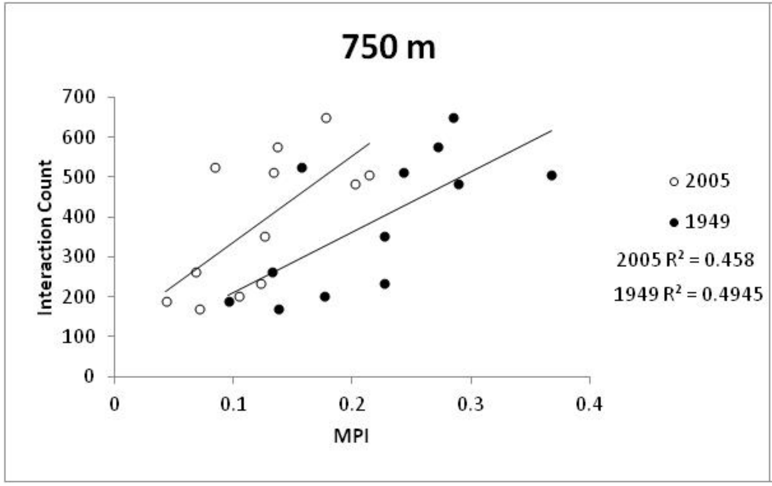
e.


300 m
Interaction Count
700
600
500
400
300
200
100
0
0
0.2
0.4
0.6
0.8
1
MPI
○ 2005
● 1949
2005 R² = 0.4964
1949 R² = 0.5797

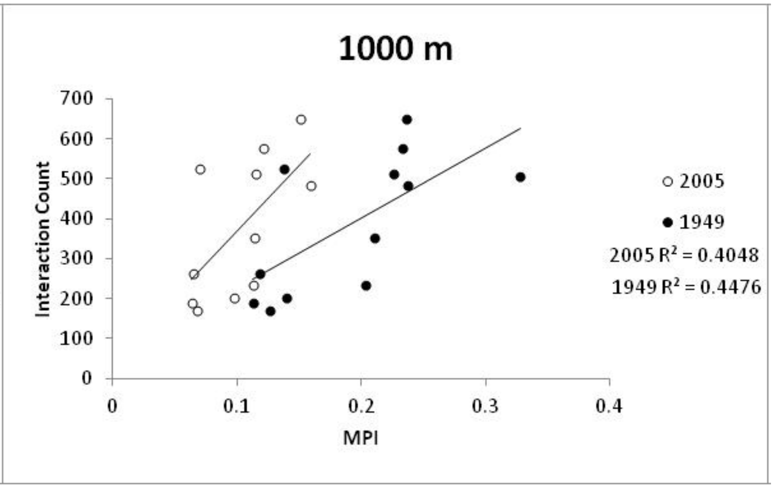
f.


500 m
Interaction Count
700
600
500
400
300
200
100
0
0
0.1
0.2
0.3
0.4
0.5
MPI
○ 2005
● 1949
2005 R² = 0.6306
1949 R² = 0.5335

g.


750 m
Interaction Count
700
600
500
400
300
200
100
0
0
0.1
0.2
0.3
0.4
MPI
○ 2005
● 1949
2005 R² = 0.458
1949 R² = 0.4945

h.


1000 m
Interaction Count
700
600
500
400
300
200
100
0
0
0.1
0.2
0.3
0.4
MPI
○ 2005
● 1949
2005 R² = 0.4048
1949 R² = 0.4476

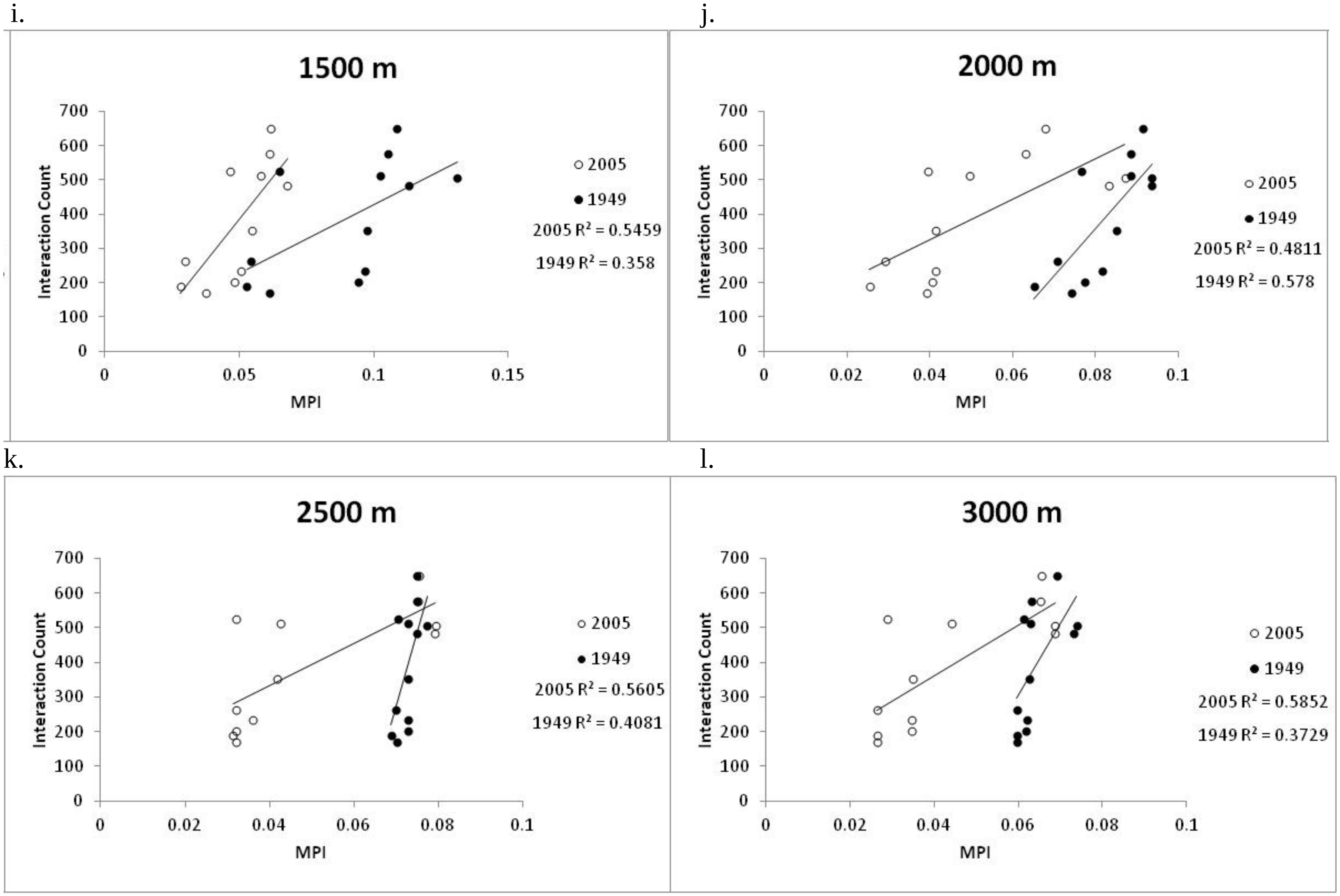


Figure 5. Interactions for each meadow graphed against each meadow’s MPI values at the varying ring distances.

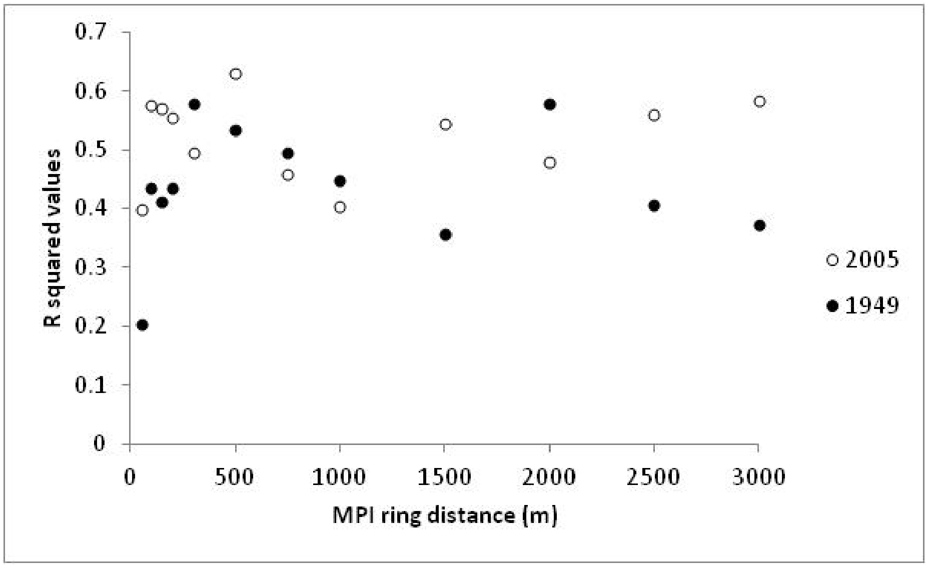


Figure 6. Correlation coefficients of meadow interaction number against meadow MPI value for each ring distance with the 2014 data.

Jaccard values for plants ranged from low to high (indicating both similarity and difference) between pairs of meadows within the HJ Andrews, for all years (Table 8, Figure 7). In contrast, Jaccard values for pollinators were quite low (indicating similarity) between pairs of meadows within each year. Thus, pollinator assemblages were much more similar than plant assemblages among meadows within a year. Within each year, the pairwise Jaccard values for pollinators were not related to the pairwise Jaccard values for plants (Figure 7).

Although Jaccard values for pollinators were low (indicating similarity) among the meadows in the HJ Andrews for a given year (Figure 7, Table 9), the Jaccard values for pollinators are quite high (indicating difference) within a meadow, between years (Figure 8). Jaccard values for plants, however, range from low to high (indicating similarity and difference) for pairs of meadows within a year (Figure 7), as well as for single meadows between years (Figure 8). This indicates that plant assemblage differences are approximately the same between two meadows of the same year and of the same meadow in two different years. The larger pollinator Jaccard values indicate that the pollinator assemblages in the same meadow between two years are much more different than the pollinator assemblages in two different meadows in the same year. Two meadows (LM and CPS) are identified in each of the cross-year comparisons in Figure 8. Their positions shift relative to the cloud of points in the different cross-year comparisons. No meadow has consistent plant Jaccard values between different years for each of the cross-year comparisons (Figure 8). In other words, the plant assemblages participating in plant-pollinator networks in a given meadow may change a great deal, or only a little, from one year to another; they do not change predictably.

Table 8. Jaccard dissimilarity index values for each pair of meadows using just the plants that had been surveyed as participating in a pollination interaction in the meadows within the HJ Andrews for each year; (a) 2011, (b) 2012, (c) 2013, and (d) 2014. Values range from 0 to 1, with low values indicating similarity and high values indicating dissimilarity.

a.

Plants	CPB	CPM	CPR	CPS	LM	LO	M2	RP1
CPM	0.45							
CPR	0.42	0.80						
CPS	0.59	0.79	0.44					
LM	0.15	0.86	0.75	0.21				
LO	0.22	0.67	0.26	0.80	0.18			
M2	0.33	0.48	0.44	0.31	0.23	0.64		
RP1	0.23	0.47	0.08	0.30	0.32	0.41	0.58	
RP2	0.22	0.42	0.34	0.43	0.15	0.65	0.18	0.53

b.

Plants	CPB	CPM	CPR	CPS	LM	LO	LS	M2	RP1
CPM	0.37								
CPR	0.79	0.70							
CPS	0.86	0.46	0.51						
LM	0.80	0.73	0.32	0.64					
LO	0.75	0.28	0.57	0.49	0.48				
LS	0.49	0.43	0.81	0.79	0.60	0.72			
M2	0.68	0.26	0.62	0.66	0.85	0.57	0.25		
RP1	0.90	0.72	0.29	0.65	0.53	0.62	0.34	0.44	
RP2	0.64	0.34	0.79	0.47	0.45	0.74	0.30	0.60	0.48

c.

Plants	CPB	CPM	CPR	CPS	LB	LM	LO	LS	M2	NE	RP1
CPM	0.70										
CPR	0.77	0.48									
CPS	0.74	0.89	0.70								
LB	0.69	0.88	0.90	0.19							
LM	0.77	0.74	0.89	0.72	0.66						
LO	0.49	0.62	0.79	0.90	0.89	0.83					
LS	0.26	0.60	0.39	0.82	0.80	0.60	0.30				
M2	0.76	0.67	0.59	0.74	0.70	0.42	0.60	0.76			
NE	0.32	0.57	0.65	0.89	0.88	0.82	0.64	0.75	0.74		
RP1	0.41	0.57	0.40	0.79	0.75	0.72	0.45	0.49	0.40	0.75	
RP2	0.27	0.76	0.66	0.59	0.52	0.43	0.71	0.30	0.25	0.52	0.67

d.

Plants	CPB	CPM	CPR	CPS	LB	LM	LO	LS	M2	NE	RP1
CPM	0.46										
CPR	0.83	0.76									
CPS	0.79	0.73	0.33								
LB	0.79	0.71	0.53	0.34							
LM	0.62	0.50	0.81	0.77	0.78						
LO	0.59	0.53	0.82	0.78	0.80	0.48					
LS	0.60	0.46	0.71	0.61	0.58	0.51	0.41				
M2	0.55	0.43	0.73	0.69	0.70	0.42	0.47	0.44			
NE	0.42	0.45	0.83	0.80	0.79	0.55	0.44	0.50	0.47		
RP1	0.59	0.54	0.84	0.80	0.80	0.47	0.26	0.41	0.52	0.42	
RP2	0.59	0.46	0.80	0.74	0.75	0.47	0.31	0.34	0.47	0.45	0.28

Table 9. Jaccard dissimilarity index values for each pair of meadows using just the pollinators that had been surveyed as participating in a pollination interaction in the meadows within the HJ Andrews for each year; (a) 2011, (b) 2012, (c) 2013, and (d) 2014. Values range from 0 to 1, with low values indicating similarity and high values indicating dissimilarity.

a.

Poll	CPB	CPM	CPR	CPS	LM	LO	M2	RP1
CPM	0.01							
CPR	0.06	0.33						
CPS	0.05	0.03	0.12					
LM	0.08	0.10	0.28	0.25				
LO	0.15	0.02	0.01	0.11	0.35			
M2	0.11	0.19	0.08	0.01	0.15	0.15		
RP1	0.21	0.43	0.13	0.12	0.15	0.04	0.05	
RP2	0.06	0.21	0.20	0.01	0.18	0.29	0.04	0.17

b.

Poll	CPB	CPM	CPR	CPS	LM	LO	LS	M2	RP1
CPM	0.02								
CPR	0.16	0.03							
CPS	0.08	0.07	0.03						
LM	0.04	0.16	0.10	0.27					
LO	0.12	0.24	0.11	0.21	0.07				
LS	0.01	0.04	0.16	0.04	0.02	0.24			
M2	0.35	0.29	0.01	0.12	0.22	0.35	0.10		
RP1	0.12	0.12	0.07	0.11	0.10	0.37	0.06	0.17	
RP2	0.22	0.15	0.04	0.24	0.01	0.05	0.20	0.01	0.14

c.

Poll	CPB	CPM	CPR	CPS	LB	LM	LO	LS	M2	NE	RP1
CPM	0.05										
CPR	0.01	0.11									
CPS	0.02	0.35	0.08								
LB	0.29	0.01	0.01	0.01							
LM	0.02	0.04	0.13	0.02	0.20						
LO	0.05	0.08	0.39	0.15	0.14	0.27					
LS	0.05	0.14	0.32	0.03	0.21	0.02	0.20				
M2	0.04	0.11	0.19	0.02	0.02	0.09	0.18	0.01			
NE	0.17	0.07	0.12	0.18	0.18	0.07	0.10	0.08	0.02		
RP1	0.04	0.16	0.09	0.08	0.15	0.03	0.16	0.11	0.20	0.08	
RP2	0.10	0.09	0.06	0.16	0.01	0.01	0.14	0.10	0.18	0.18	0.10

d.

Poll	CPB	CPM	CPR	CPS	LB	LM	LO	LS	M2	NE	RP1
CPM	0.12										
CPR	0.04	0.12									
CPS	0.03	0.11	0.01								
LB	0.01	0.08	0.04	0.03							
LM	0.11	0.03	0.14	0.13	0.10						
LO	0.36	0.30	0.38	0.37	0.35	0.28					
LS	0.25	0.18	0.28	0.27	0.24	0.16	0.15				
M2	0.35	0.29	0.37	0.37	0.35	0.27	0.02	0.14			
NE	0.24	0.17	0.27	0.3	0.24	0.15	0.15	0.01	0.15		
RP1	0.18	0.11	0.21	0.20	0.18	0.09	0.21	0.07	0.21	0.26	
RP2	0.18	0.10	0.21	0.20	0.17	0.08	0.22	0.09	0.21	0.08	0.01

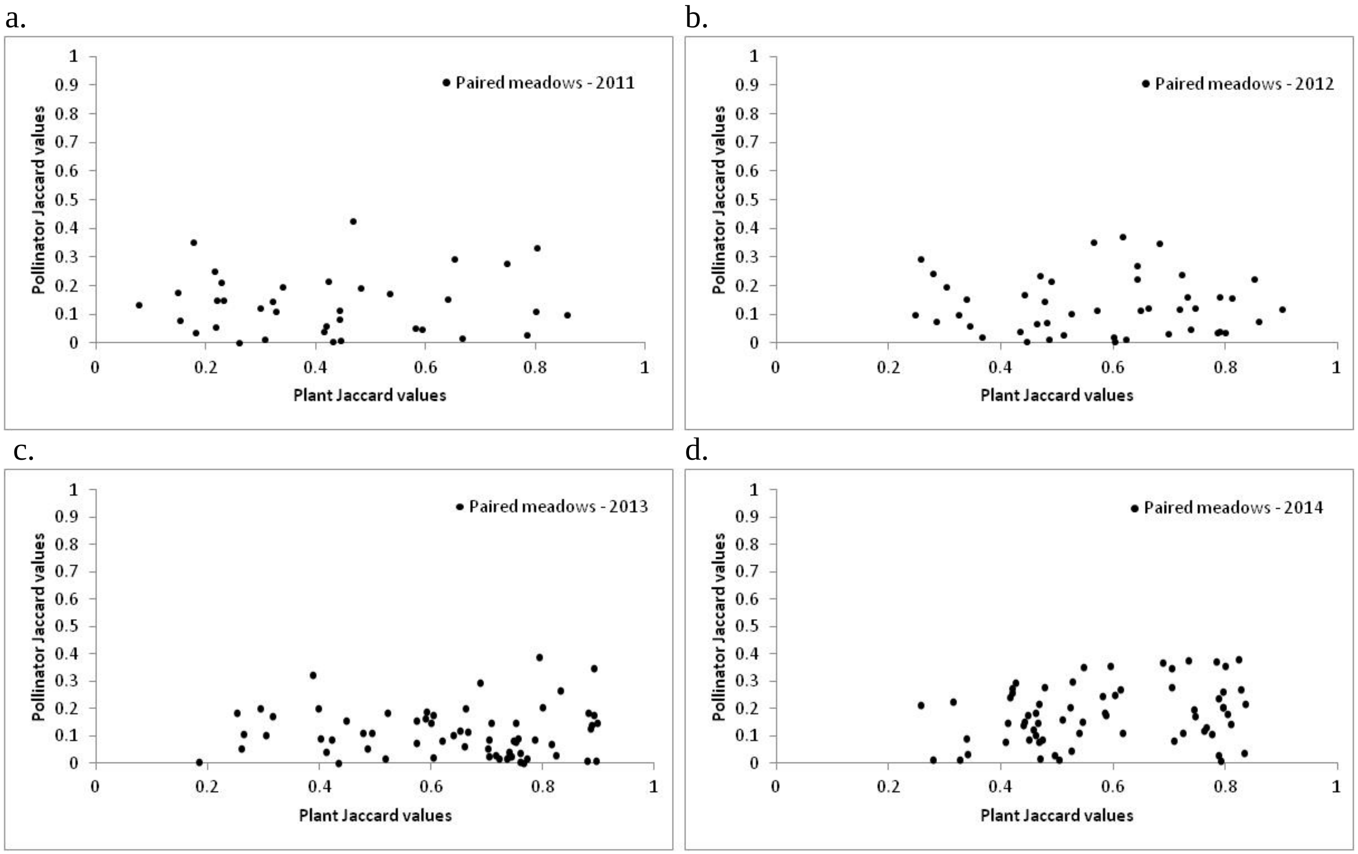
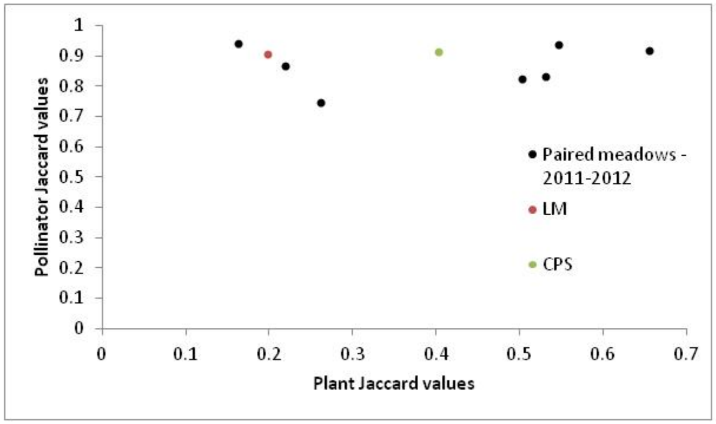
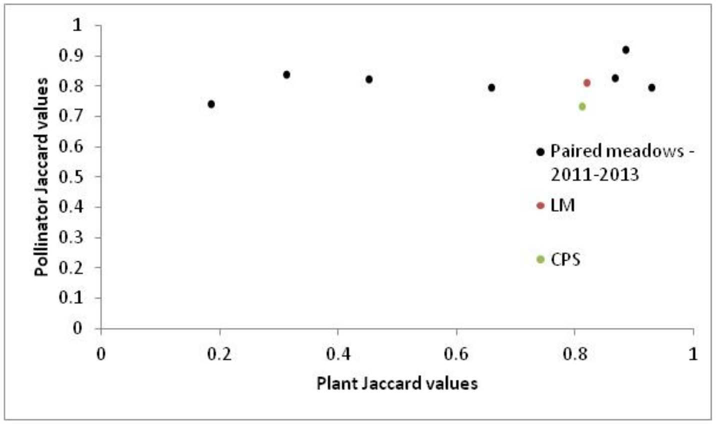


Figure 7. Pollinator assemblage Jaccard values plotted against plant values for each pair of meadows from the HJ Andrews surveyed each year, (a) 2011, (b) 2012, (c) 2013, and (d) 2014. Each point represents the pairwise Jaccard value for plants (x-axis) and pollinators (y-axis) for a pair of meadows, in a single year.

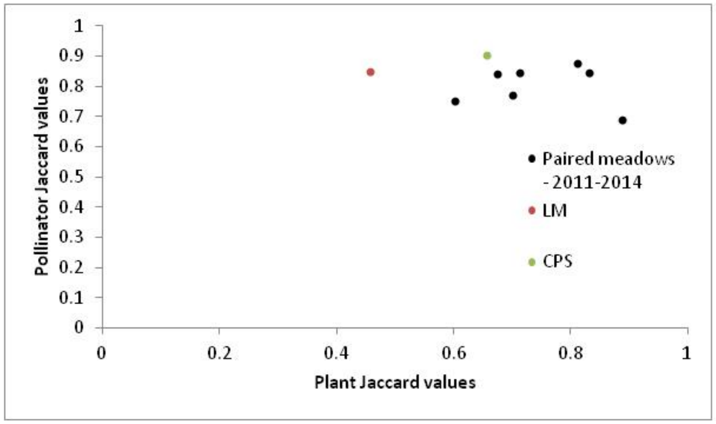
a.


Pollinator Jaccard values
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Plant Jaccard values
Paired meadows - 2011-2012
LM
CPS

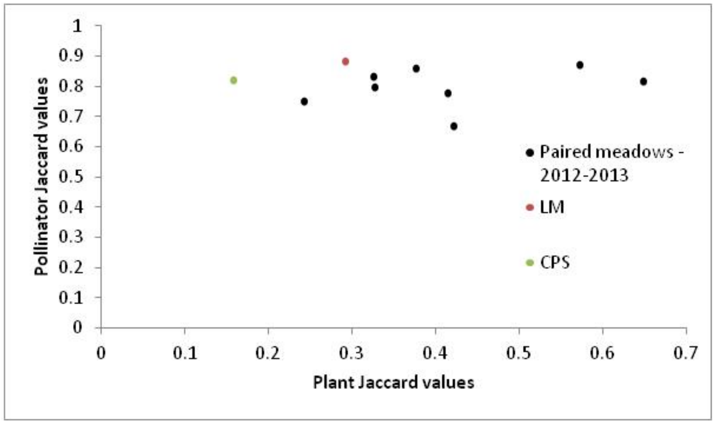
b.


Pollinator Jaccard values
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
1
Plant Jaccard values
Paired meadows - 2011-2013
LM
CPS

c.


Pollinator Jaccard values
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
1
Plant Jaccard values
Paired meadows - 2011-2014
LM
CPS

d.


Pollinator Jaccard values
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Plant Jaccard values
Paired meadows - 2012-2013
LM
CPS

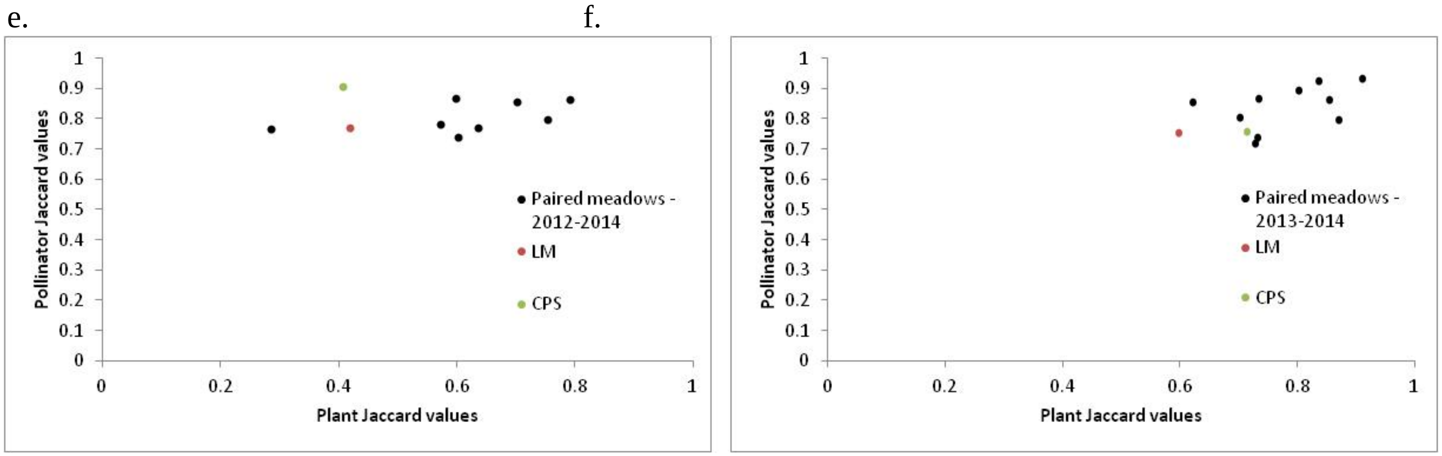


Figure 8. Pollinator assemblage Jaccard values plotted against plant values for meadow pairings of the same meadows in different years, with just the meadows located in the HJ Andrews; (a) 2011 vs. 2012, (b) 2011 vs. 2013, (c) 2011 vs. 2014, (d) 2012 vs. 2013, (e) 2012 vs. 2014, and (f) 2013 vs. 2014. Each point represents the pairwise Jaccard value for plants (x-axis) and pollinators (y-axis) for a single meadow, compared between two years. Two meadows (LM and CPS) are identified as colored points; their positions shift relative to the other meadows in the various year-to-year comparisons. These two meadows were chosen just for the sake of comparison.

The summer of 2011 was much cooler than summers of 2012 to 2014, which were similar (Figure 9). The number of interactions observed in meadow watches from 2011 to 2014 was not consistently related to degree days, weather during the watch, or soil moisture ($r^2 < 0.34$, Tables 10-13). In 2011, interactions were significantly positively related to the presence of sun ($r^2 = 0.24$, $p < 0.048$); the interactions per meadow-watch increased by 179 when it was sunny compared to other weather conditions (Table 10). In 2012, the number of interactions in each meadow-watch was not related to any of the independent variables ($r^2 = 0.07$, Table 11). In 2013 and 2014, the number of observed interactions was significantly negatively related to cumulative degree days ($r^2 = 0.28$ for 2013, $r^2 =0.34$ for 2014, $p < 0.01$). Three fewer interactions were observed for each 10 degree increase in cumulative degree days (Table 12, M). In 2013, the number of interactions was also weakly positively related to the presence of sun ($p < 0.07$) (Table 12).

Table 10. Results of the multiple linear regression analysis for interactions (dependent variable) as a function of sun, wind, CDD, and moisture (independent variables) for the 2011 plant-pollinator network data.

Residuals		**Deg. of Freedom:**	94
Min:	-145.05	**Residual std. error:**	111.8
1Q:	-60.21	**Multiple R-squared:**	0.24
Median:	-6.01	**Adjusted R-squared:**	0.16
3Q:	0.00	**F-statistic:**	3.04
Max:	680.06	**p-value:**	0.0022

Coefficients

	Estimate	**Std. Error**	**t-value**	**p-value**
Intercept	7.41	80.91	0.092	0.93
Sun	179.35	89.51	2.004	0.048
Wind	-21.32	105.27	-0.20	0.84
Moisture	34.05	194.74	0.18	0.86
CDD	-0.22	0.29	-0.77	0.44
SunCDD	0.14	1.19	0.12	0.90
SunMoist	120.48	751.68	0.16	0.87
CDDMoist	-0.54	11.83	-0.30	0.77
SunWind	85.73	417.73	0.21	0.84
WindCDD	-0.34	0.51	-0.67	0.50
WindMoist	-92.99	296.85	-0.31	0.76

Table 11. Results of the multiple linear regression analysis for interactions (dependent variable) as a function of sun, wind, CDD, and moisture (independent variables) for the 2012 plant-pollinator network data.

Residuals		**Deg. of Freedom:**	73
Min:	-134.12	**Residual std. error:**	121.8
1Q:	-73.61	**Multiple R-squared:**	0.068
Median:	-25.80	**Adjusted R-squared:**	-0.0088
3Q:	27.51	**F-statistic:**	0.89
Max:	545.36	**p-value:**	0.51

Coefficients

	Estimate	**Std. Error**	**t-value**	**p-value**
Intercept	149.46	71.92	2.08	0.041
Sun	17.44	39.24	0.44	0.66
Wind	9.40	66.13	0.14	0.89
CDD	-0.27	0.16	-1.62	0.11
SunWind	3.39	119.70	0.028	0.98
SunCDD	0.28	0.40	0.71	0.48
WindCDD	0.058	0.67	0.085	0.93

Table 12. Results of the multiple linear regression analysis for interactions (dependent variable) as a function of sun, wind, CDD, and moisture (independent variables) for the 2013 plant-pollinator network data.

Residuals		**Deg. of Freedom:**	77
Min:	-122.51	**Residual std. error:**	59.96
1Q:	-33.96	**Multiple R-squared:**	0.28
Median:	-15.74	**Adjusted R-squared:**	0.23
3Q:	24.02	**F-statistic:**	5.11
Max:	166.65	**p-value:**	0.00018

Coefficients

	Estimate	**Std. Error**	**t-value**	**p-value**
Intercept	157.34	25.88	6.08	<< 0.01
Sun	27.55	15.01	1.84	0.07
Moisture	-0.27	0.59	-0.46	0.65
CDD	-0.30	0.064	-4.65	<< 0.01
SunCDD	0.16	0.16	1.028	0.31
SunMoist	0.27	1.024	0.27	0.79
CDDMoist	0.0052	0.0038	1.35	0.18

Table 13. Results of the multiple linear regression analysis for interactions (dependent variable) as a function of sun, wind, CDD, and moisture (independent variables) for the 2014 plant-pollinator network data.

Residuals		**Deg. of Freedom:**	53
Min:	-127.02	**Residual std. error:**	56.21
1Q:	-32.23	**Multiple R-squared:**	0.34
Median:	-11.11	**Adjusted R-squared:**	0.26
3Q:	40.04	**F-statistic:**	4.48
Max:	157.26	**p-value:**	0.00098

Coefficients

	Estimate	**Std. Error**	**t-value**	**p-value**
Intercept	170.95	40.76	4.19	<< 0.01
Sun	12.67	21.72	0.58	0.56
Wind	-19.22	21.18	-0.91	0.37
CDD	-0.33	0.08	-4.23	<<0.01
SunWind	24.52	62.59	0.39	0.70
SunCDD	-0.28	0.19	-1.49	0.14
WindCDD	0.15	0.19	0.80	0.43

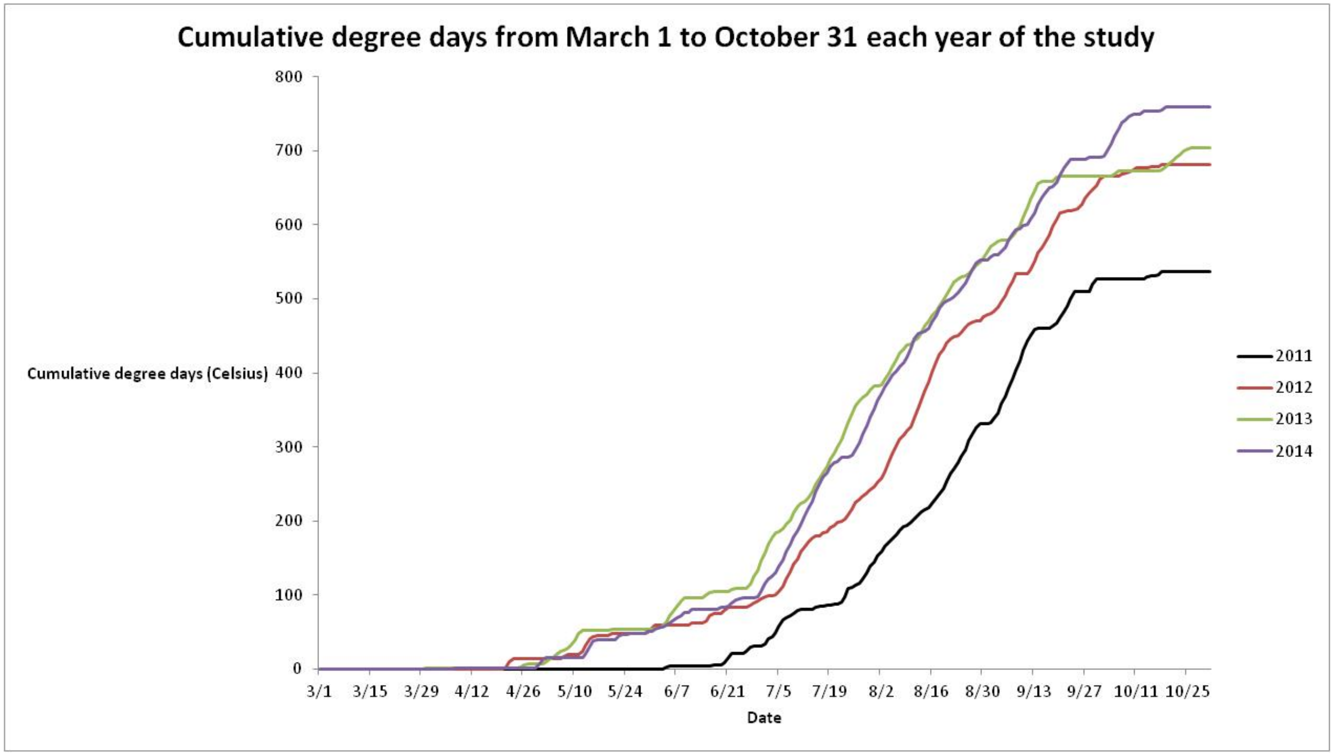


Figure 9. Cumulative degree days for each year from March 1 to October 31 for the four summer sampling periods in 2011 to 2014.

2.6 Discussion

There are several possible sources of error in this study. It is unlikely that rare pollinator species were adequately sampled, because each meadow was surveyed for only 750 to 1050 minutes (depending on the year) over the course of a field season. However, undersampling of rare species could not have produced the observed results of high similarity of pollinators within years, but low similarity between years. Even if they were perfectly sampled, rare species interactions would be low enough in abundance that they would not dramatically change the results.

In addition, some error likely arose from the survey protocol. The experimental plots in each meadow probably moved between 2011 and 2012, and again from 2012 to 2013, because of uncertainty associated with GPS point locations, but they were monumented in 2013 and 2014. Moving plot locations could have increased the amount of dissimilarity in plants between meadows in different years, but the fact that the dissimilarity was similar between each pair of years (including 2013 and 2014, when the plots had not moved) means that these differences are not attributable to changes in plot locations between years. Rather, it appears that most of the meadow is experiencing similar turnover across its entire area fairly consistently. Finally, there is certainly some bias in observers’ abilities to see pollinators and identify them to the species level in the field. However, one person trained all observers in all four years in the same way, and the observers surveyed different plots at different times during each watch. A final source of potential sampling error is that all the plant-pollinator interactions were observed only during the day; the activity of crepuscular (e.g., hummingbirds) or nocturnal (e.g., moth) pollinators was not observed.

We found some weak support for our first hypothesis: the number of interactions was positively related to meadow size and surrounding meadow habitat, but negatively related to inclement weather, in the form of clouds or wind. Although we found a positive relationship between interactions surveyed and meadow size, some other factor appears to produce a split between two groups of meadows, one of which has much higher interactions controlling for meadow size. The number of interactions was related consistently (i.e., the same r^2 values) to surrounding meadow area at all distances from 50 to 3000 m. This indicates that pollinators sense suitable foraging areas (meadows) at scales larger than individual study meadows, in other words, pollinators move between patches of meadows in the landscape. This finding is consistent with previous studies that show pollinator movement between patches of habitat in a landscape (Kremen et al., 2007; Potts et al., 2010; Menz et al., 2011). There was little evidence of a negative relationship between interaction numbers and weather, but that is not surprising, because the survey protocol controlled for weather: sampling occurs only on primarily sunny days with little to no wind. It is somewhat surprising that the number of plant-pollinator interactions observed in meadow-watches was not related to soil moisture in the two years when soil moisture was sampled; this finding may indicate that turnover of plant species in anthesis is controlled by more factors than moisture. For example, plant diversity may depend on pollinator abundance and behavior from the previous year (Fontaine et al., 2005).

Multiple environmental characteristics, including soil type, may interact to explain plant assemblages (Basilio et al., 2006).

This study provides evidence that pollinators sense meadow habitat at a scale larger than an individual meadow, consistent with previous studies (Ghazoul, 2005; Garcia and Chacoff, 2007; Mitchell et al., 2009). In 2014, meadow size alone did not explain the number of interactions surveyed, although when the sample of meadows was divided into two groups, meadow size was more closely related to the numbers of interactions. The amount of meadow habitat surrounding a particular study meadow up to a radius of 3 km was consistently positively related to the number of interactions observed. The finding that the number of interactions was most highly correlated with the meadow area within 500 meters may indicate that 500 m is a mean foraging range for the entire pollinator assemblage surveyed in these meadows in the HJ Andrews. Pollinator species vary in their foraging areas, and colony-based pollinating insects such as *A. mellifera* and *B. mixtus* (the most common species surveyed) can travel up to five or six kilometers to forage in a single day (Ribands, 1951). The most common pollinator species may forage over an area larger than an entire meadow complex. However, some solitary pollinators may range only up to a kilometer, and many species may be confined to a single meadow, or even to part of a large meadow (A. Moldenke, pers. comm.). The meadow complexes in this study may not necessarily be biologically distinct units, from the perspective of a pollinator.

The second hypothesis was much more strongly supported: pollinator assemblages were very similar within a given year, but quite dissimilar between years. Within-year similarity of pollinator assemblages is consistent with the notion that most common pollinators are generalists and are able to move between meadow patches freely. Even when plants differ between meadows, their pollinator assemblages are similar. Individual study meadows may have some rare, locally-confined pollinator species, but apparently generalist, far-foraging pollinator species dominate the assemblages in these meadows. While some previous studies have suggested that pollinator assemblages are primarily determined by plant assemblages at the individual meadow scale, these results show otherwise (Potts et al., 2003; Steffan-Dewenter and Westphal, 2008). However, the high dissimilarity between pollinator assemblages in different years may reflect the fact that pollinator species are sensitive to environmental factors like moisture and temperature during the winter preceding a field season (Petanidou et al., 2008).

In a single year (e.g., 2014), some meadow pairs had very different plant assemblages but very similar pollinator assemblages. Similarities in plants or pollinators were not related to the distance between meadows: some meadows that were almost adjacent had plant assemblages that were as different as two meadows that were separated by more than 8 km. This suggests that meadow plant assemblages depend on physical characteristics of the meadow (such as soil type, available moisture, aspect, or slope) while pollinators move freely between the meadows and forage for available flowers (Basilio et al., 2006; Petanidou et al., 2008).

These results indicate that plant diversity in a given meadow is probably not limited by locally-confined pollinators, but instead is supplemented by genetic exchange occurring between widely separated meadows via pollen transported by abundant, far-ranging generalist pollinators, supporting conclusions from previous studies (Steffan-Dewenter et al., 2002; Fortuna et al., 2008). Further work focusing on the genetic diversity of plant species in these meadows could examine long-distance pollen transport. If parent and seed (before they dispersed) material were collected from individuals of a particular species across several meadow patches in a landscape, the genetic lineage could be traced for the seeds to determine how frequently one of their parents is outside the meadow, and, depending on how exhaustively surrounding meadows were sampled, exactly how far pollen was being transported.

Further studies could also examine the impacts of fragmentation on plant-pollinator networks in greater detail. While it appears that many pollinators are not limited by the apparent fragmentation occurring in this study landscape, it is possible that rarer species remain locally confined, and are negatively impacted by fragmentation. To the extent that pollinators are competing for floral resources in a particular place, habitat fragmentation could upset the balance between a ‘traveling’ module of pollinators and a ‘local,’ confined module (Dupont and Olesen, 2009; Bosch et al., 2009).

2.7 Conclusion

The results of this study seem to indicate that although the montane meadows of the central western Cascade Range appear fragmented, pollinators travel between meadows despite intervening areas of coniferous forest. Further studies that look at individual pollinator movement, or more spatially comprehensive studies, are needed to confirm this. At the same time, meadows have quite distinctive plant communities whose differences are not related to their isolation or to meadow size, and the meadows support plant assemblages that vary from one year to another but still participate in landscape-wide plant-pollinator interactions. Genetic analysis of connectivity between meadows among individuals of a given plant species would provide a more comprehensive understanding of how pollinators influence plant populations in these meadows.

This study showed that pollinator assemblages vary from year to year. Insects are especially sensitive to environmental cues, like a wet or cold winter. These conditions may dramatically affect insect populations for a given year, thus changing the dominant species during a field season. Future studies could quantify the specific environmental cues to which the pollinators respond in an attempt to predict how their abundances or frequencies might change in a given year. It is crucial to continue these long-term observations of plant-pollinator networks in order to identify possible multi-year patterns of change in the pollinator assemblages.

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CHAPTER 3 PLANT-POLLINATOR NETWORK STRUCTURE IN MONTANE MEADOWS OF WESTERN OREGON: EVIDENCE FOR GENERALIZATION AND MODULARITY

3.1 Abstract

Using four years of plant-pollinator interaction data from 18 montane meadows in the Willamette National Forest, this study created the degree distributions of the plant-pollinator networks, quantified the prevalence of generalization in the component species, and sought evidence of modularity in some of the meadows. Network structures were dominated by species that were very well-connected, and they contain more well-connected species than would occur in a randomly-assembled network. The assemblages also were dominated by generalist species, and modularity was observed in some small meadows in the network. These results are consistent with the finding from other studies that generalization may contribute resilience to plant-pollinator networks in spite of high temporal turnover of component species.

3.2 Introduction and objectives

Mutualistic relationships between species, especially plant-pollinator interactions, are widely studied (Winfree et al., 2009; Chamorro et al., 2012; Davila et al., 2012). Plant-pollinator networks are bipartite interaction networks (or ‘two-mode’ networks) linking plant and animal species. These interactions are commonly identified in the field, when a pollinator is observed to visit a flower in anthesis (Olesen et al., 2008). A bipartite plant-pollinator network can be represented as two unipartite networks (or ‘one-mode’ networks), one for the plants and one for the pollinators. Each species participating in interactions is a vertex in the unipartite network, with each edge between vertices representing one shared pollination partner species (Suzuki and Wakita, 2009). Many network analyses require that bipartite networks be divided into their two component unipartite networks (Murata, 2009; Liu and Murata, 2009).

Network analysis of plant-pollinator networks has been used to study a variety of network characteristics. Network analysis can reveal the centrality – often defined as the importance -- of component species (Jordano et al., 2006; González et al., 2010). By quantifying component species turnover and changes in component species importance, network analysis also permits analysis of the similarity among networks sampled in different locations or times (Petanidou et al., 2008; Weiner et al., 2011). Modularity -- defined as clustering within a network -- is a common feature of observed plant-pollinator networks that are large (more than 150 component species), but a rare feature of networks that are small (fewer than 50 component species) (Olesen et al., 2007; Fortuna et al., 2010).

When examining the importance of individual species in a particular network, a common measurement is the ‘degree’ (or degree centrality) of a particular vertex in the network (Dormann et al., 2009). A vertex’s degree is the number of edges leading from that vertex, and the degree distribution is the probability distribution of all the degrees of all vertices of a network (Saavedra et al., 2009; Ramos-Jiliberto et al., 2009). Networks that are assembled randomly have degree distributions that follow a random (Poisson) distribution (Barabási, 2009; Newman, 2009). Real pollination networks often have power-law distributed degree distributions (Dormann et al., 2009; Bosch et al., 2009; Vázquez et al., 2009) indicating that the network contains a higher-than-expected (by random assembly) number of vertices with a large number of edges. However, some pollination networks have exponentially distributed degree distributions, usually in smaller or more isolated networks (Dormann et al., 2009; Kallimanis et al., 2009).

Degree centrality measurements for a particular vertex examine only the edges connecting that vertex to its neighbors. Other centrality measurements take into account a particular vertex's position within the network. Eigenvector centrality, for example, is used in some studies of ecological networks, including plant-pollinator networks (Alarcón et al., 2008; Estrada and Bodin, 2008; Dupont et al., 2009). The eigenvector centrality for a particular vertex is the eigenvector of the interaction matrix of the original plant-pollinator network (Jordano et al., 2006). A vertex's eigenvector centrality is proportional to the sum of all of its neighbors' centrality measurements, where a neighbor is defined as the nearest connected vertex. Therefore, vertices that are connected to other well-connected vertices have a higher eigenvector centrality than a vertex that is connected to poorly-connected vertices (even if the number of edges in both cases is the same) (Jordano et al., 2006). Eigenvector centrality is a good indicator of how much of a generalist a particular species in a network is, because eigenvector centrality quantifies the extent to which a species is connected to other species that also have many connections (Bascompte and Jordano, 2007; Fang and Huang, 2013). Species in plant-pollinator networks that are generalists have high eigenvector centralities, while those that are specialists have low eigenvector centralities (Sazima et al., 2010).

Early research on plant-pollinator networks tested how network structure might be determined by ‘pollination syndrome,’ the theory that plant floral traits have evolved to limit pollinator access to their reproductive organs (Ollerton et al., 2009). Pollination syndrome assumes that limiting pollinator access increases the pollination success rate of a flowering species (Fenster et al., 2004). However, observational studies of plant-pollinator networks have found that most component species are generalists (Waser et al., 1996). Species generality may increase the resilience of plant-pollinator networks in the face of extinctions of component species (Memmottet al., 2004).

Network modularity measures the strength of clusters, or subnetworks within a network (Hofman and Wiggins, 2008). Several studies have examined modularity in plant-pollinator networks (Olesen et al., 2007; Fortuna et al., 2010; Danieli-Silva et al., 2011). Most studies have found that plant-pollinator networks are significantly modular (Danieli-Silva et al., 2011) while others have found that significant modularity only emerges when there are more than 50 component species (Olesen et al., 2007). In larger networks, the modules emerge around functional groups of plants and pollinators (Danieli-Silva et al., 2011). Modularity and nestedness (a measure of organization of a network against a randomly assembled network) are correlated, and modularity is often positively related to network resilience, with many modules able to adapt to the loss of some of their members (Fortuna et al., 2010).

3.2.1 Research questions

Q1. How are the degrees of component species distributed in plant-pollinator networks?

H1. We hypothesize that the degree distributions of the species in plant-pollinator networks of montane meadows follow a power-law curve. A power law curve for the distributions would indicate that there are more vertices than expected with a large number of edges. Ecologically, this would mean that the networks tend to be dominated by highly generalist species. Alternatively, if the hypothesis is not supported, it would imply that the network's vertices are connected randomly, and the network is not dominated by a few highly generalist and well-connected species.

Q2. How is a species' eigenvector centrality (importance) related to its relative abundance in plant-pollinator networks?

H2. We expect a positive relationship between the relative abundance of a species in a network and its eigenvector centrality. Abundance in this analysis is defined as the frequency of appearance of a species in observed interactions, while eigenvector centrality is a measure of the number of partners of a species, its partner's partners, and each of those partners' importances (number of edges) etc. A positive relationship between these two variables for the component species of a plant-pollinator network would indicate that the network is dominated by generalist species. In other words, species with many partners are abundant, and commonly occurring pollinator species pollinate commonly occurring plant species. Alternatively, if the hypothesis is not supported, plant-pollinator pairings are not based on abundance, but rather some other factor determines network structure, such as specialization caused by pollination syndrome.

> **Q3**. What do eigenvector centrality measures indicate about modularity in these networks?

H3. We expect eigenvector centrality to be unimodally distributed, indicating that all species belong to a single module. Alternatively, if eigenvector centrality is bimodally distributed, this may indicate the presence of two modules in the network.

3.3 Background

González et al. (2010) used several centrality measurements to study the relationship between the generalization level of a species (as measured by the number of partners it interacts with out of the total possible number of partners) and its importance to the network (as measured by their centrality indices). Centrality scores were positively related to generalization levels in nearly all of the 34 pollination networks they examined. They concluded that in most plant-pollinator networks, most species are generalists, and the more generalist a species is, the more important it is to the overall network structure. Generalist species pollinate or are pollinated by more partners, and their partners are more important, than less generalist species (Gonzalez et al., 2010).

Species' centrality scores and network structure change over time. Alarcón et al. (2008) used eigenvector centrality scores to measure a species' importance to its network, and network nestedness to measure a network's resilience. The plant-pollinator networks that they studied had a core group of species every year that were generalists and were very important (well-connected in the network). However, the membership of that core group of generalists varied significantly between years, meaning the importance of many species rose and fell dramatically between years, and because the species were generalists, the important species contributed to network structure in very similar ways in every year. Each year, the network was similarly nested and similarly connected overall, meaning its resilience and structure did not change significantly over time. Alarcon et al. (2008) speculated that environmental cues may trigger large changes in the abundance of the component species of plant-pollinator networks, but that the overwhelming trend toward generalization for nearly all species in the network means that the overall network structure remains stable over time.

Olesen et al. (2007) performed a meta-analysis on 51 pollination networks looking for evidence of modularity. They found significant modularity in all networks that consisted of at least 150 component species, and no modularity in networks that consisted of fewer than 50 component species. For networks with species numbers between 50 and 150, the degree of modularity was positively related to the number of component species. Modularity and nestedness go hand-in-hand, and modular networks are significantly nested and tend to be resilient and have stable network structure over time (Olesen et al. 2007; Fortuna et al., 2010). As networks become larger, modules are increasingly organized according to functional traits; hence, many plants and pollinators may have preferred partners based on their functional traits, but they are readily able to become generalists if the network structure demands it (Olesen et al. 2007).

3.4 Methods

3.4.1 Study site

The study was conducted in 18 meadows located in five meadow complexes located between Lookout Mountain and Cone Peak in the western Cascades of Oregon, within or adjacent to the HJ Andrews Experimental Forest (Figures 1 and 2). Study meadows ranged in size from 0.26 to 4.44 ha as of 2005. Meadow elevation ranged from 1,308 to 1,536 m and slope ranged from 0 to 55 percent. The climate is maritime, with wet winters and warm and dry summers. Mean annual precipitation is 2,221 mm, mean annual temperature of 6.7°C. Mean annual snow water equivalent (at Vanilla Leaf met station, 1,273 m) is 370 mm.

Vegetation communities in these meadows tend to be xeric or mesic (Miller and Halpern, 1998). Soils are shallow and bedrock is exposed in some locations, especially in xeric meadows. These meadows may have been maintained by Native

American burning over at least the past 6,000 years (Highland, 2012). Decimation of Native Americans by the late 1700s and fire suppression since arrival of Europeans in the 1800s was associated with significant contraction of meadow habitat throughout the Cascade Range of Oregon (Miller and Halpern, 1998). In the Andrews Forest, montane meadows have contracted by 45% from 1948 to 2005 (Rice, 2012; Highland, 2012).

A total of 18 meadows have been surveyed since the study began in 2011. Fifteen meadows were selected initially (in 2011) in five meadow complexes (three in the Andrews Forest, one on Cone Peak, and one on Bunchgrass Ridge), using a stratified-random design based on meadow complex and meadow size. In each complex except Lookout, one large and two small meadows were chosen. In 2013, one mesic meadow was added to the three already being sampled in the three complexes in the Andrews Forest, and the Bunchgrass and Cone Peak meadow complexes were dropped from the survey protocol. Therefore, in 2014, 12 total meadows were surveyed, four located in each of three complexes.

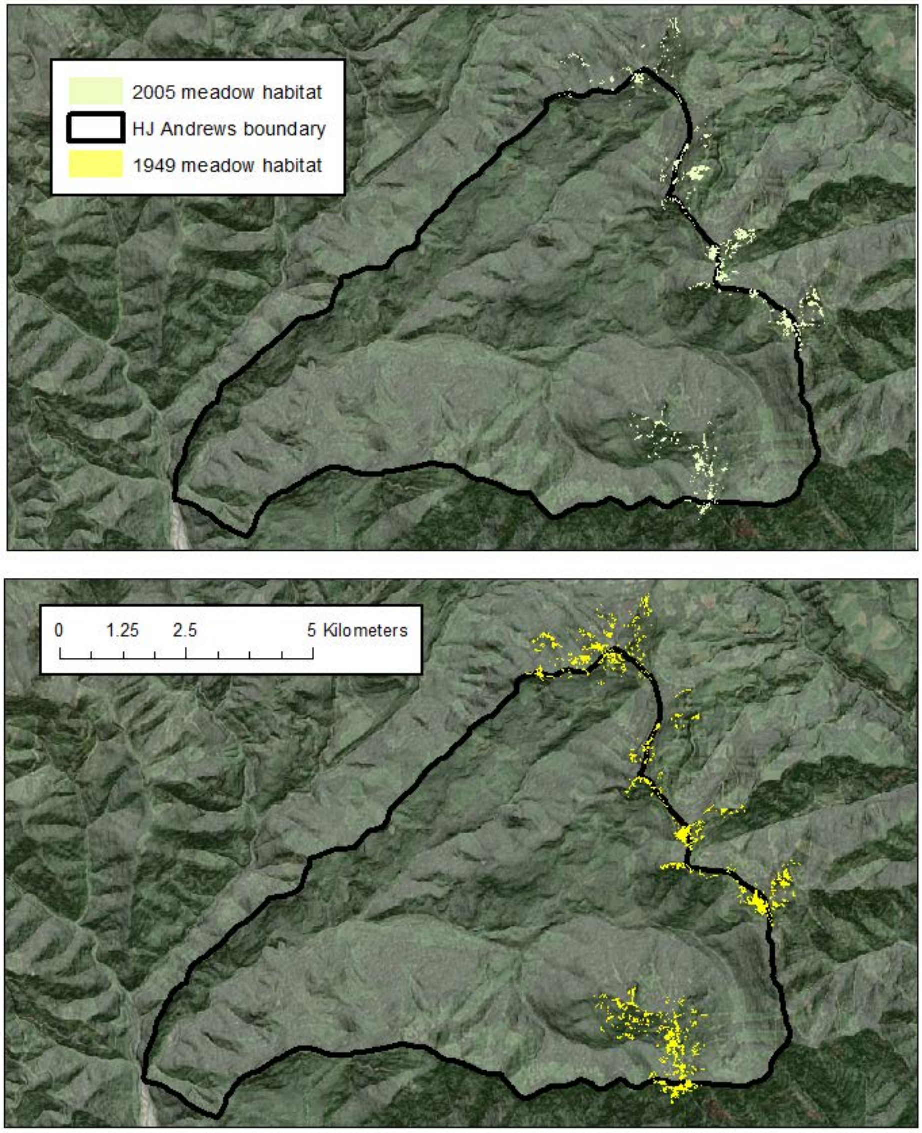


Figure 1. Meadow habitat along the eastern edge of the HJ Andrews experimental forest. Digitized from aerial photographs taken in 2005 (top image) and 1949 (bottom image). This figure does not show the meadow complexes that were surveyed outside the HJ Andrews (Cone Peak and Bunchgrass Ridge).

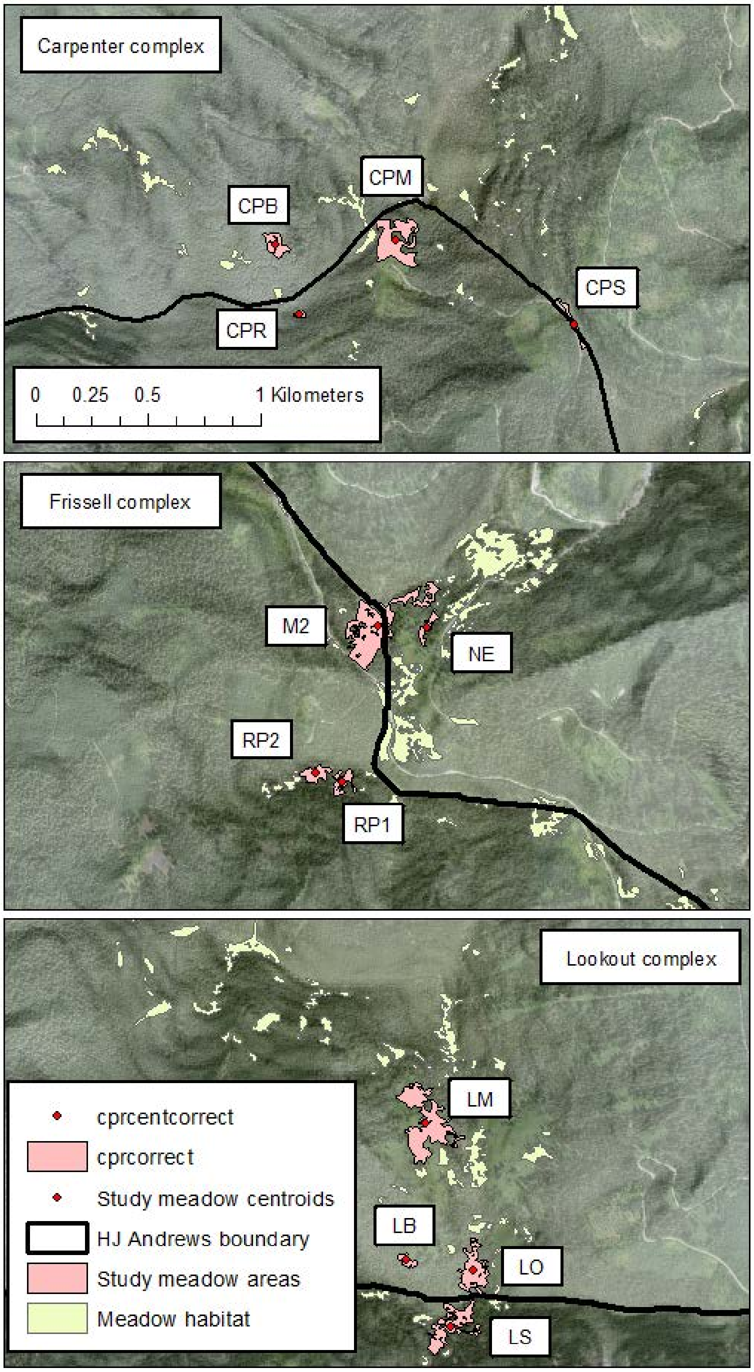


Figure 2. The three meadow complexes within or adjacent to the HJ Andrews (Lookout, Frissell, and Carpenter), each with four surveyed meadows (indicated by the pink polygons above). The four meadows in the Lookout complex are: Lookout Main (LM), Lookout Bog (LB),

Lookout Outcrop (LO), and Lookout Steep (LS); the four meadows in the Frissell complex are: Frissell Main (M2), Northern Exposure (NE), RP1, and RP2; the four meadows in the Carpenter complex are: Carpenter Main (CPM), Carpenter Saddle (CPS), Carpenter Basin (CPB), and Carpenter Ridge (CPR). Note one meadow in the Carpenter complex is on the watershed boundary. The remaining meadow habitat in each complex as of 2005 is shown in yellow.

3.4.2 Field methods

Plant-pollinator interactions were sampled at each plot in each meadow using 15-minute 'watches' on five days in each summer (mid-June to mid-August) from 2011 to 2014. Each meadow contained ten 3 x 3 m plots, spaced along two parallel transects, with five plots along each transect. The plots were spaced 15 meters apart along the transects, and the transects were spaced 20 meters apart. The two transects were aligned along the major axis of each meadow, near the center of each meadow. Transects in some of the small meadows are slightly curved to avoid proximity to forest edges. Thus, 90 m^2 were surveyed in each meadow regardless of meadow size.

Each meadow was visited five times over the course of the 2014 season, and a ‘watch’ was conducted at each plot. To reduce effects on pollinator behavior, watches were conducted between 0900 and 1700 hours, on days that were sunny or partly cloudy, had little to no wind, and experienced no precipitation. At the beginning of each watch, every flowering plant in the plot was identified to species, the number of stalks (that contained at least one flower) was counted, and the numbers of flowers on each stalk were counted for each species (up to ten stalks per species). Thus, the number of flowers of each species was counted or (in the cases of species with more than ten stalks) estimated based on the average number of flowers per stalk multiplied by the number of stalks present. Compound flowers and inflorescences were counted as a single flower. Individual plants that could not be identified were photographed from outside the plot, harvested, pressed in the meadow, and transported back to the lab for identification later in the day.

Each 'watch' consisted of pollinator observations for a period of 15 minutes. At each minute, the observer recorded the weather (sunny or party cloudy and still or breezy), whether the plot was in the shade or not, the temperature, and all visits by a pollinator species to each flower species. An 'interaction' consisted of an individual pollinator making contact with the reproductive parts of a flower. If a particular individual visited different plant species in a given minute or different individuals of the same species, each visit was recorded as a separate interaction for that sampled minute. If multiple pollinator individuals of the same or different species in the plot visited a flower in the plot during the same minute, each interaction was recorded separately. If a particular pollinator individual visited multiple flowers of the same species (but of the same individual) during the same minute, those visits were counted and recorded as a single interaction, and the number of visits was recorded in a separate column.

Pollinators that could not be visibly identified in the field were captured using a net and euthanized in the field using a small jar of ammonium carbonate and a small amount of moisture (to generate carbon dioxide). From the field they were transported back to the lab, given unique ID numbers, pinned, and sent to an expert entomologist for identification (Andy Moldenke). During the capture and euthanization process, the 15 minute timer was stopped, and no observations were made. When the observer was ready to continue the watch, the timer was restarted and the 15 minute watch continued from the point where it stopped.

At the end of each day, the data from the day's watches were entered into Excel and checked for potential errors by the field crew leader. At the end of the field season, the entire dataset (2011 to 2014) was checked for several types of errors. These included: discrepancies between the interaction dataset and the flower survey dataset (for example, a flower that appears in the interaction dataset but not the flower survey), abnormally high numbers of stalks or flowers (for example, an observer attempting to count the individual flowers of an inflorescence), and data entry errors (incorrectly entered temperature, incorrectly coded weather, etc.). These errors were corrected when possible, and affected data were omitted from analysis when errors could not be corrected. In all, 4,870 interactions were recorded in total in 2014, of which 202 (<5%) were omitted from analysis. These cases were omitted either due to an egregious error (no pollinator species recorded for an interaction, due to a failed capture attempt) or due to an entirely nonsensical error (recording a plant species absent from the flower survey and not present in this area of the world).

3.4.3 Data analyses

Plant-pollinator networks are bipartite interaction networks, meaning that all of the component species can be divided into two distinct subsets (plants and pollinators in this case). Edges in a bipartite network can only connect vertices of different sets. For plant-pollinator bipartite networks, edges can only connect a plant with a pollinator – not a plant with another plant or a pollinator with another pollinator. Bipartite interaction networks are also known as two-mode networks. Because many of the following analyses cannot be applied to two-mode networks, every two-mode network was first divided into two one-mode networks using R version 3.1.1. A one-mode network in this case consists of either plants or pollinators as vertices with connected edges when the two species share a partner in the two-mode network. For example, if both *Apis mellifera* and *Bombus mixtus* (two pollinator species) pollinate the same plant, they share an edge in the one-mode network of pollinators. If they both pollinate two plant species, they share two edges, and so on. One-mode networks were generated for each meadow, each complex, and the entire system using the 2014 data. Each one-mode network is a square matrix containing a 1 in each cell (vertex) *i*, *j* in which species *i* and species *j* share a plant (pollinator).

A vertex's degree is simply the number of edges it has in a particular network (i.e., the row or column sum in the one-mode network square matrix). This is one of the simplest vertex characteristics to measure, and it provides a limited understanding of the 'importance' of a vertex in a particular network. Using all of the data for all four years in every meadow surveyed, two one-mode network interaction matrices were constructed and a degree distribution was created for plants and for the pollinators. Power law and exponential lines were fitted to these data.

For each meadow in 2014 the numbers of unique species interactions were ranked for plant and pollinator species and plotted as a dominance-diversity curve. The shapes of these curves were estimated by fitting a negative exponential function of the form $y = Ae^{\alpha x}$. The parameters (A, α, and R^2) of these functions were compared between plants and pollinators, and among meadows. The steepness of the curve (indicated by high values of A and more negative values of α) is a measure of the dominance of a network by a few species that had many interactions during the 2014 field season. The α values from the exponential fits were plotted against meadow size to test how dominance was related to meadow size.

Eigenvector centrality is another measurement of characteristics of a vertex, but it incorporates more information than degree centrality (the number of edges of a particular vertex) (Bonacich, 2007). Eigenvector centrality incorporates the degree of the vertex, the degrees of its connected vertices, the degrees of their connected vertices, etc. using the following equation:

$$x_v = \frac{1}{\lambda}\sum_{t\in \mathrm{M(v)}}\frac{1}{\lambda}\sum_{t\in \mathrm{G}} a_{v,t} * x_t \qquad (1)$$

where x_v is the eigenvector centrality score of a vertex v, λ is the highest positive eigenvalue for its associated matrix (more on this below), $M(v)$ is the set of neighboring vertices of vertex v, and G is the entire matrix; $a_{v,t}$ is the number of edges connecting vertices v and t, and x_t is the eigenvector centrality score of vector t.

The eigenvalue λ for a given vertex is calculated from the eigenvector for the matrix in which that vertex is found. There are many valid eigenvectors for a square matrix, but the eigenvector centrality index only uses the dominant eigenvalues. An eigenvalue is considered dominant if it is larger than all other eigenvalues. The eigenvector containing the dominant eigenvalues for a particular matrix is calculated from:

$$\begin{aligned} x_1 &= A * x_0 \\ x_2 &= A * x_1 = A^2 * x_0 \end{aligned} \qquad (2)$$

$$\ldots$$
$$x_k = A * x_{k-1} = A^k * x_0$$

where χ_0 is a vector with magnitude equal to one, *A* is the square matrix (the one-mode network), and x_k is the dominant eigenvector. For the plant and pollinator one-mode networks of this study, the evcent function in the igraph package of R version 3.1.1 was used to calculate the eigenvector centrality values. The evcent function uses the equations described above except that the initial vector x_0 is the vector of degree centrality of the vertices. This step decreases the number of iterations *k* that need to be performed to arrive at the solution.

To test whether the majority of the component species of a given plant-pollinator network are generalists, eigenvector centrality values were plotted against the relative frequency of appearance of that species in the network. If the network is dominated by species that are generalists, we would expect a positive relationship between eigenvector centrality and species abundance, in other words, we would expect species with more centrality would be more frequent in our observations, and vice versa. Assemblages that departed from this relationship (either no relationship between eigenvector values and abundances or a multi-modal eigenvector centrality distribution) were examined for evidence of modularity.

For the assemblages in meadows for which evidence for modularity was found, common species were isolated and examined in more detail. The most common species in a particular module were identified, and their pollination partners were compared between modular meadows and meadows for which no modularity was detected.

3.5 Results

Degree distributions for pooled interaction data from all 18 meadows from 2011 to 2014 follow a power law more closely than an exponential line (plants: $R^2 = 0.92$ vs. $R^2 = 0.65$; pollinators: $R^2 = 0.65$ vs. $R^2 = 0.24$) (Figure 3).

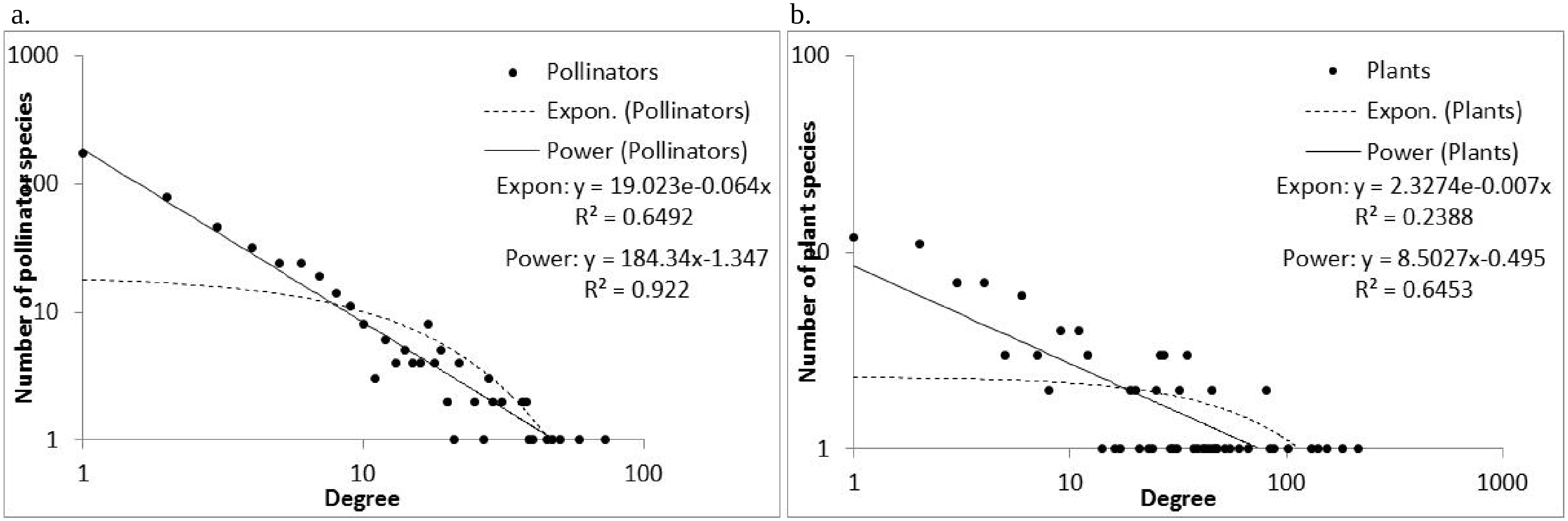
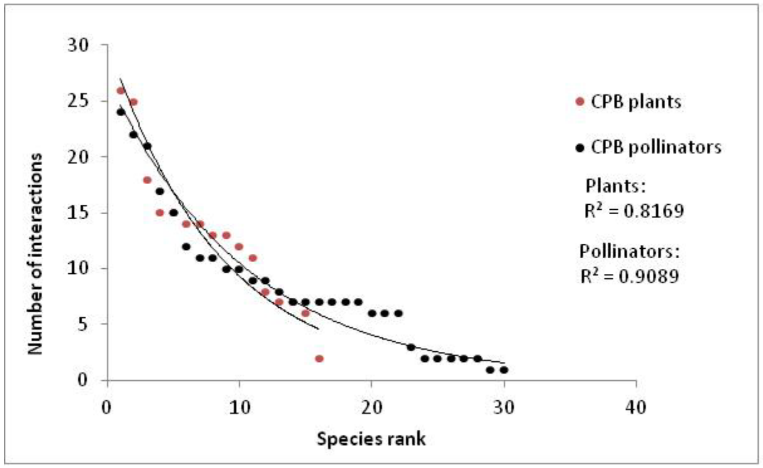


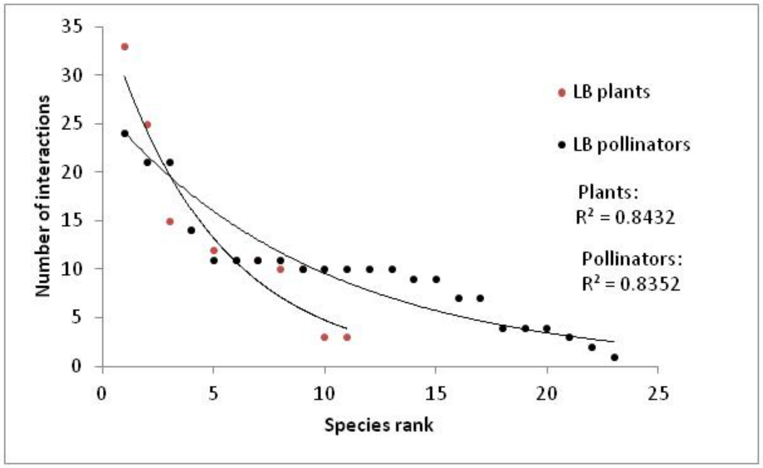
Figure 3. Degree distributions for (a) the pollinator one-mode network (n=109 species) and (b) the plant one-mode network (n=492 species) for 276 plot-watches in 18 meadows from 2011-2014 in montane meadows of the central Cascade Range, Oregon. The datasets are fitted with an exponential and a power law line.

For all meadows except one (LS) the dominance-diversity curves declined more steeply for plant species than for pollinator species in observed plant-pollinator networks, indicating that the plant assemblages observed were more strongly dominated than pollinator assemblages observed by species that had many interactions (Figure 4). The tails of the dominance diversity curves were longer for pollinators than for plants, representing the high number of pollinator species that were observed to participate in only a few interactions during the field season. The values of α for plant dominance-diversity curves were lowest in the smallest meadows (i.e., CPR, LB, NE, RP2), indicating that their plant-pollinator networks were more strongly dominated by a few species participating in many interactions (Table 1, Figure 5). The values of α for pollinator dominance-diversity curves were also low in some, but not all small meadows (i.e., CPB, CPR, LB) (Table 1, Figure 5).

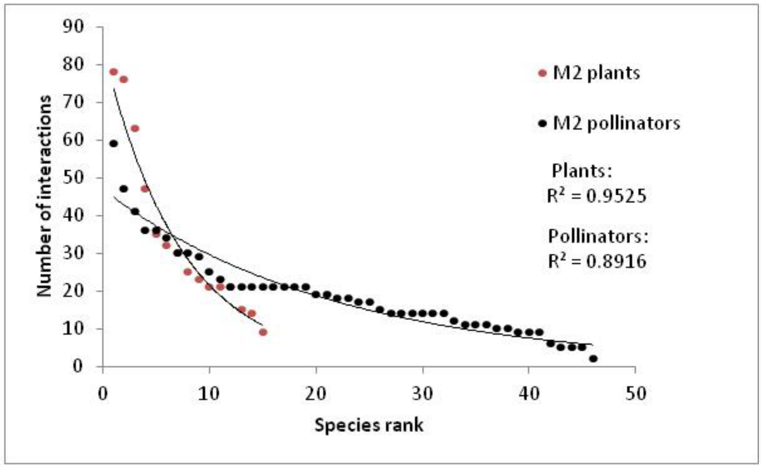
a.


Number of interactions
Species rank
CPB plants
CPB pollinators
Plants:
$R^2 = 0.8169$
Pollinators:
$R^2 = 0.9089$
0
5
10
15
20
25
30
0
10
20
30
40

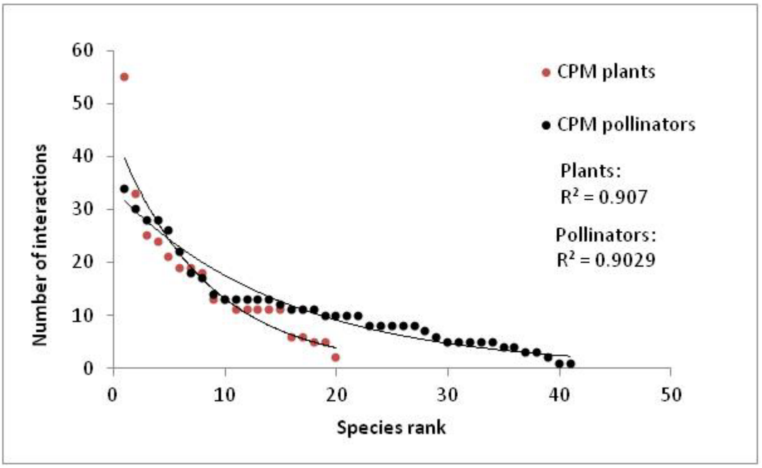
b.


Number of interactions
Species rank
LB plants
LB pollinators
Plants:
$R^2 = 0.8432$
Pollinators:
$R^2 = 0.8352$
0
5
10
15
20
25
30
35
0
5
10
15
20
25

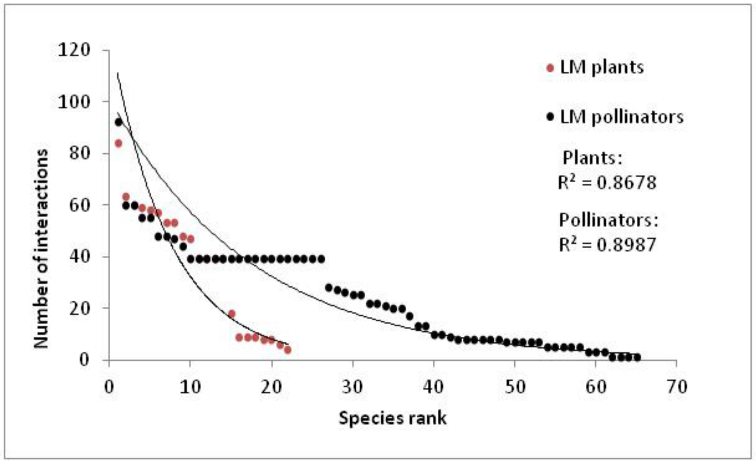
c.


Number of interactions
Species rank
M2 plants
M2 pollinators
Plants:
$R^2 = 0.9525$
Pollinators:
$R^2 = 0.8916$
0
10
20
30
40
50
60
70
80
90
0
10
20
30
40
50

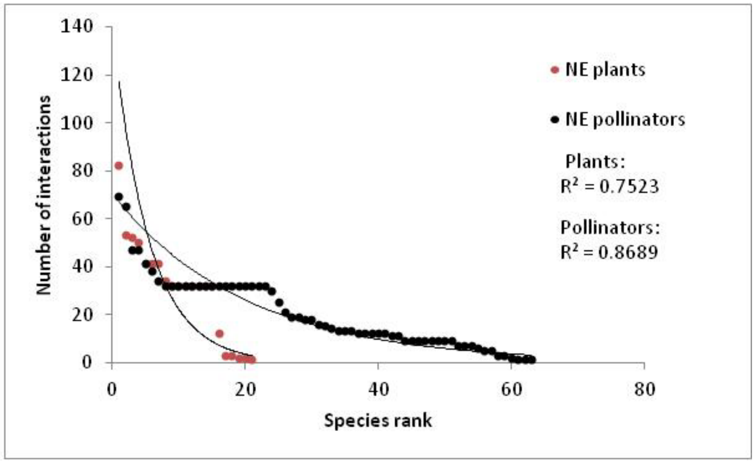
d.


Number of interactions
Species rank
CPM plants
CPM pollinators
Plants:
$R^2 = 0.907$
Pollinators:
$R^2 = 0.9029$
0
10
20
30
40
50
60
0
10
20
30
40
50

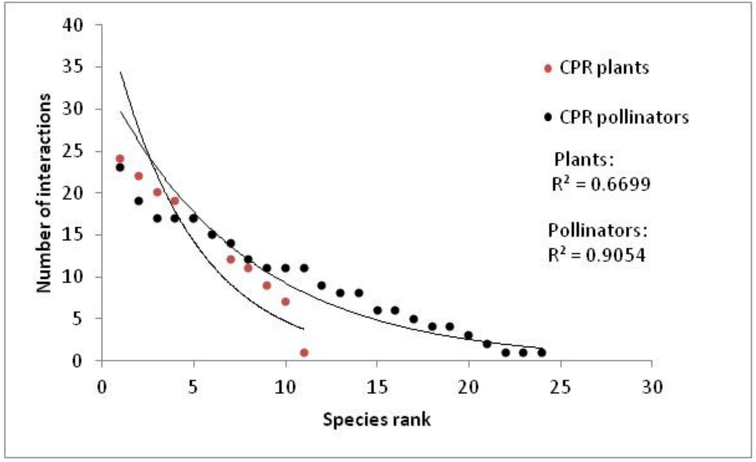
e.


● LM plants
● LM pollinators
Plants:
R^2 = 0.8678
Pollinators:
R^2 = 0.8987
Number of interactions
Species rank
0
20
40
60
80
100
120
0
10
20
30
40
50
60
70

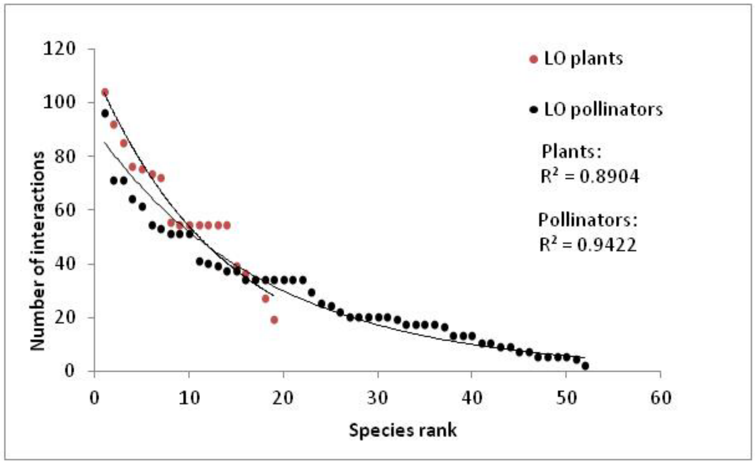
f.


● NE plants
● NE pollinators
Plants:
R^2 = 0.7523
Pollinators:
R^2 = 0.8689
Number of interactions
Species rank
0
20
40
60
80
100
120
140
0
20
40
60
80

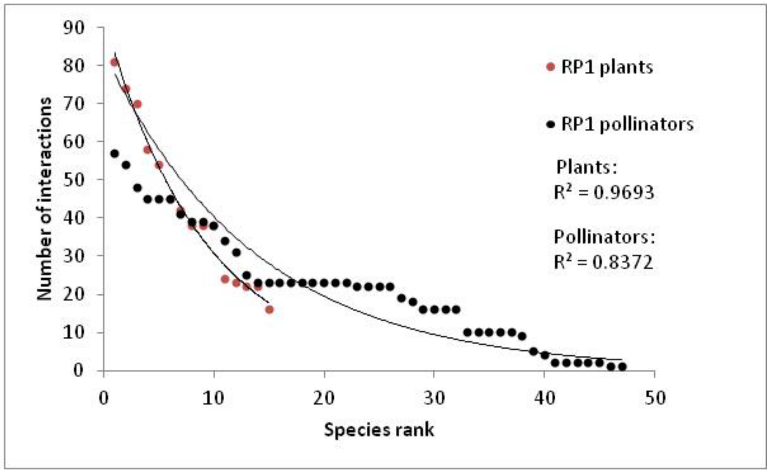
g.


● CPR plants
● CPR pollinators
Plants:
R^2 = 0.6699
Pollinators:
R^2 = 0.9054
Number of interactions
Species rank
0
5
10
15
20
25
30
35
40
0
5
10
15
20
25
30

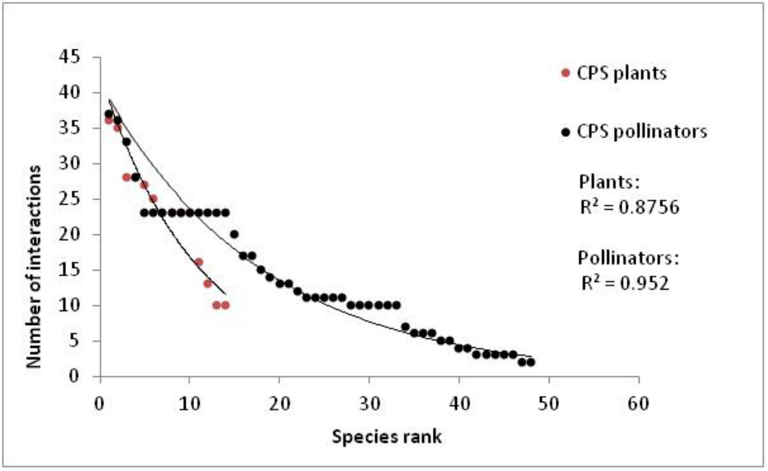
h.


● LO plants
● LO pollinators
Plants:
R^2 = 0.8904
Pollinators:
R^2 = 0.9422
Number of interactions
Species rank
0
20
40
60
80
100
120
0
10
20
30
40
50
60

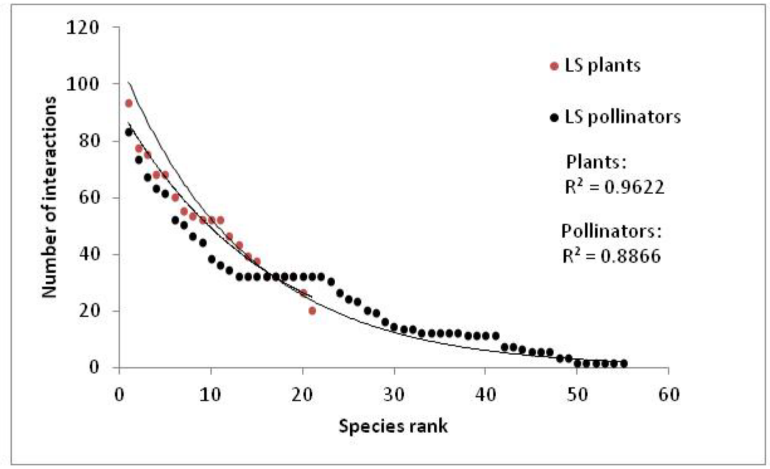
i.


90
80
70
60
50
40
30
20
10
0
Number of interactions
0
10
20
30
40
50
Species rank
● RP1 plants
● RP1 pollinators
Plants:
R² = 0.9693
Pollinators:
R² = 0.8372

j.


45
40
35
30
25
20
15
10
5
0
Number of interactions
0
10
20
30
40
50
60
Species rank
● CPS plants
● CPS pollinators
Plants:
R² = 0.8756
Pollinators:
R² = 0.952

k.


120
100
80
60
40
20
0
Number of interactions
0
10
20
30
40
50
60
Species rank
● LS plants
● LS pollinators
Plants:
R² = 0.9622
Pollinators:
R² = 0.8866

l.

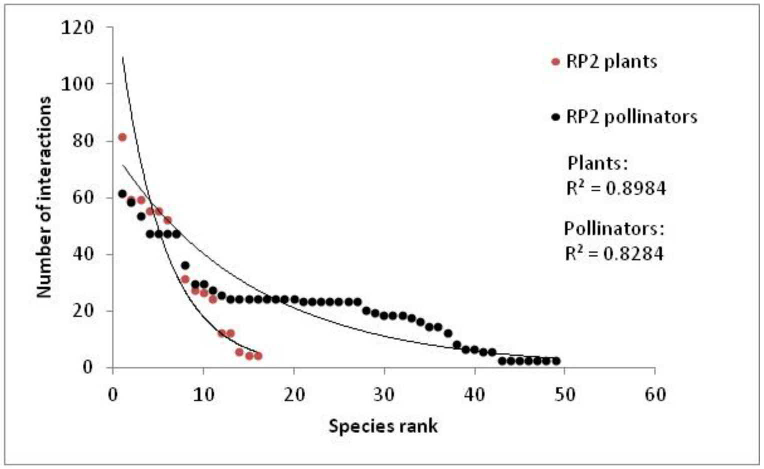

120
100
80
60
40
20
0
Number of interactions
0
10
20
30
40
50
60
Species rank
● RP2 plants
● RP2 pollinators
Plants:
R² = 0.8984
Pollinators:
R² = 0.8284

Figure 4. Dominance-diversity curves for the plant and pollinator assemblages in each of the 12 meadows surveyed in 2014, using the 2014 data; (a) CPB, (b) LB, (c) M2, (d) CPM, (e) LM, (f) NE, (g) CPR, (h) LO, (i) RP1, (j) CPS, (k) LS, and (l) RP2. Each dataset is fitted with an exponential function, whose parameters are reported below, in Table 1.

Table 1. Parameters from the exponential lines of fit to the dominance-diversity curves shown in Figure 4, of the form $y = Ae^{\alpha x}$. Curves that are steeper (have a more negative α) are more strongly dominated by a few species that had many interactions during the field season.

		Plants			***Pollinators***		
Meadow	**Size (m^2)**	**R^2**	**A**	**α**	**R^2**	**A**	**α**
CPB	7248	0.817	30.3	-0.12	0.909	27.1	-0.10
CPM	25207	0.907	44.8	-0.12	0.903	41.3	-0.06
CPR	2586	0.670	43.0	-0.22	0.905	33.8	-0.13
CPS	3869	0.876	42.7	-0.09	0.952	41.3	-0.06
LB	2869	0.843	36.6	-0.20	0.835	26.7	-0.10
LM	38633	0.868	127.3	-0.14	0.899	101.4	-0.06
LO	19465	0.890	111.5	-0.07	0.942	90.2	-0.06
LS	16786	0.962	91.8	-0.06	0.887	108.3	-0.07
M2	44396	0.953	84.5	-0.14	0.892	46.8	-0.05
NE	4303	0.752	141.1	-0.19	0.869	70.1	-0.05
RP1	6113	0.969	93.1	-0.11	0.837	83.7	-0.07
RP2	6263	0.898	134.0	-0.20	0.828	76.3	-0.06

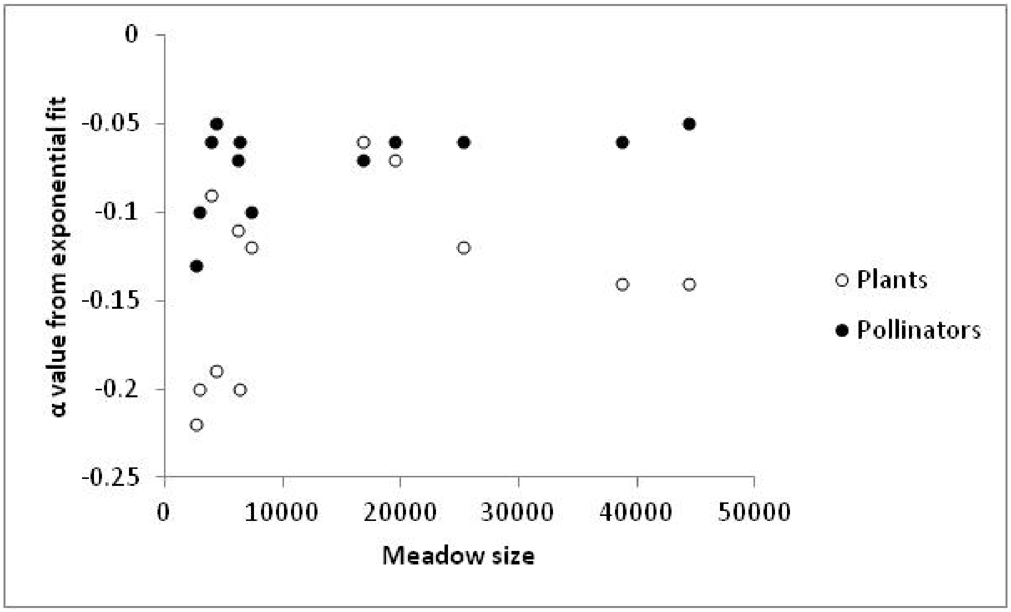
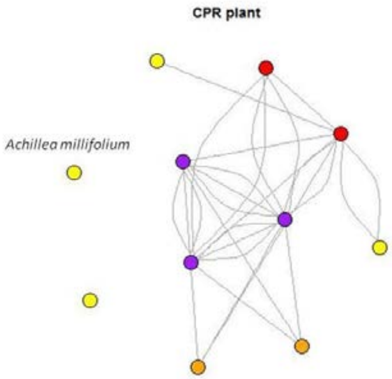


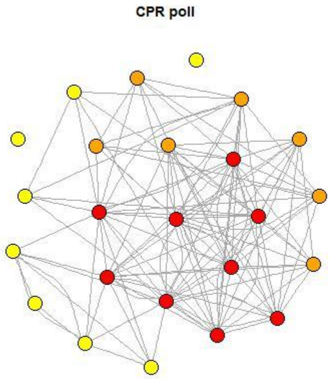
Figure 5. The α values from the exponential lines of best fit (from Figure 4) plotted against meadow size for the plant and pollinator datasets from 2014. A more negative α value indicates dominance by a few species that had frequent pollination interactions. A few small meadows were strongly dominated by a few species, particularly for plants. Plant assemblages were more strongly dominated by a few species than pollinator assemblages.

Visualizations of the one-mode networks generated for these meadows (Figure 6) illustrate the concept of eigenvector centrality. In the graphs, each vertex in a network is colored according to its eigenvector value, based on quartiles of the eigenvector distribution. In eight of the 12 meadows surveyed in 2014 (CPR, CPS, LM, LO, LS, NE, RP1, and RP2), the one-mode network of plants had one or more species with eigenvector centrality values in the upper quartile, whereas the corresponding one-mode pollinator networks lacked species with very high eigenvector centrality values (Figure 6). In contrast, two meadows (M2 and CPM) the pollinator networks had species with higher eigenvector centrality values than their plant networks. In two meadows (CPB and LB) both the plant and pollinator networks had species with very high eigenvector centrality values. Small meadows tended to have plant one-mode networks with very high eigenvector centrality. Three of four meadows with very high eigenvector centrality for pollinators were small, but one was large (Figure 6).

a.



b.



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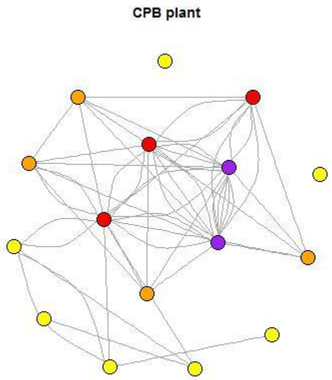
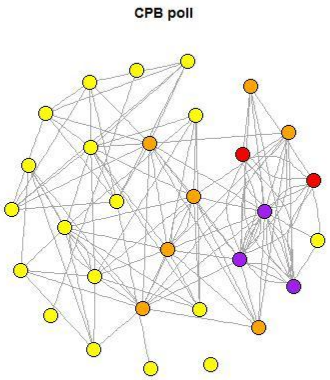
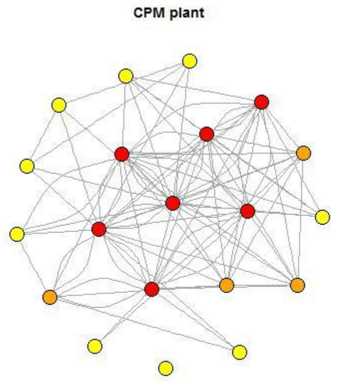


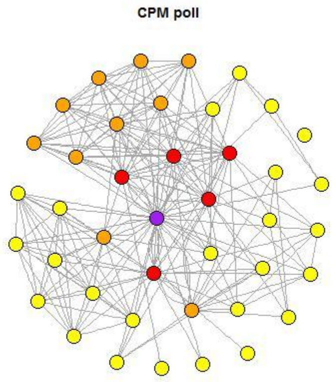
d.



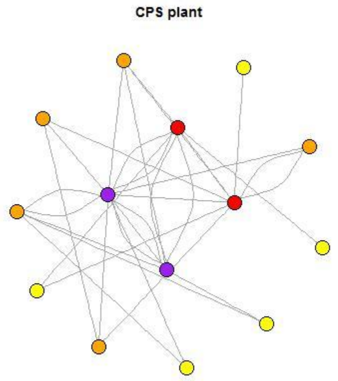
e.


CPM plant

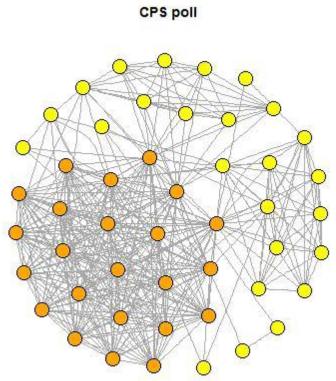
f.


CPM poll

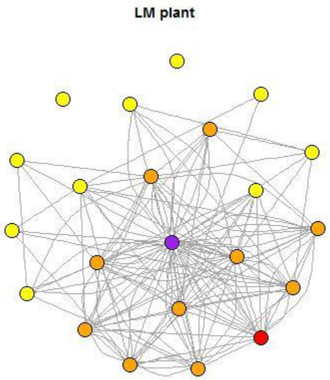
g.


CPS plant

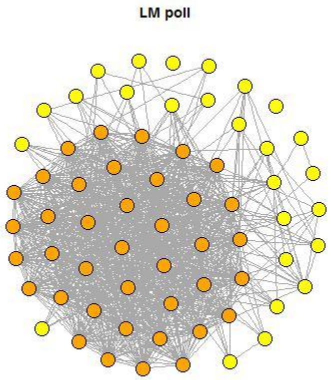
h.


CPS poll

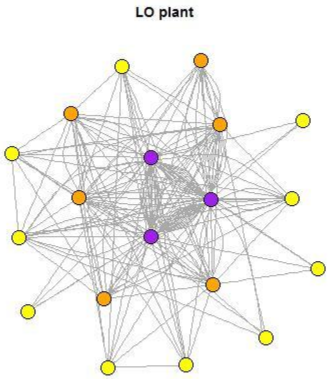
i.



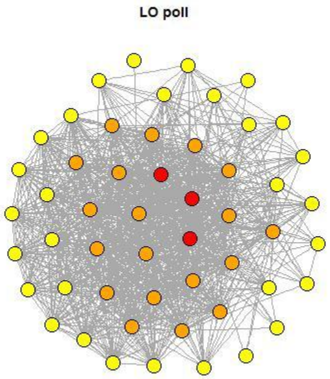
j.



k.



l.



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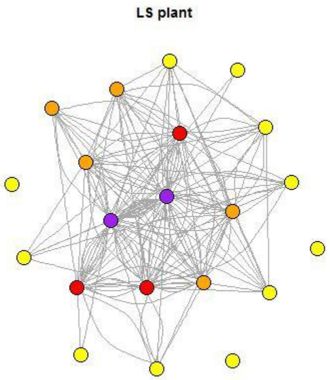
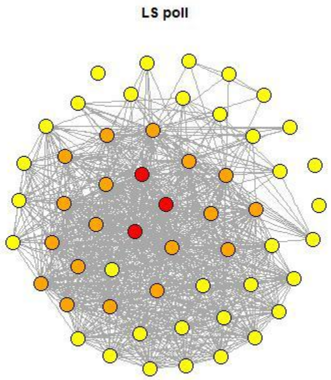
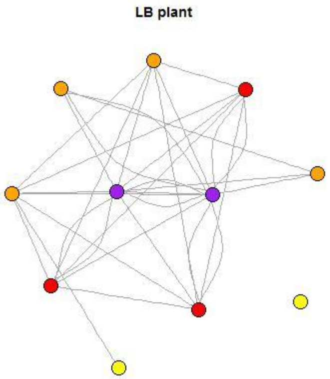


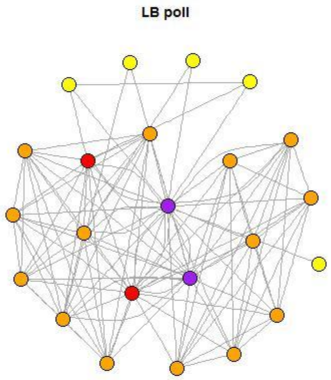
n.



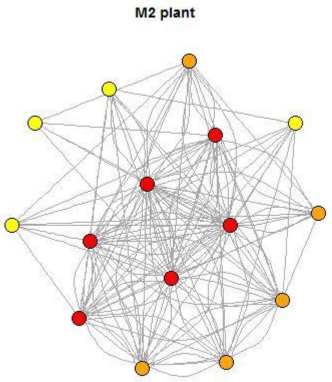
o.



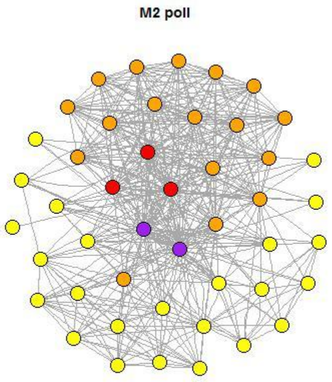
p.



q.



r.



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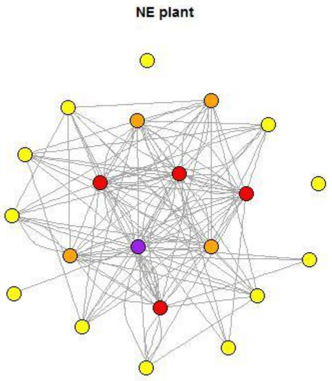
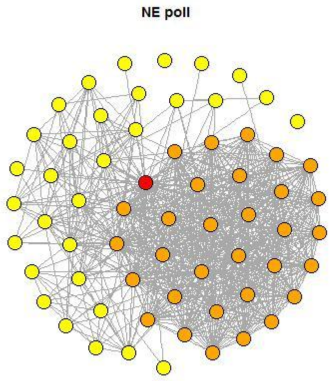
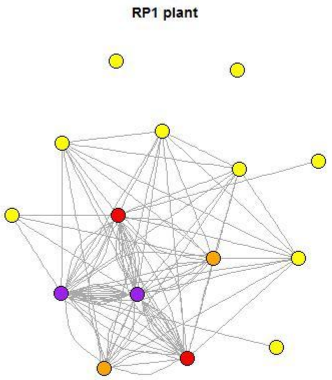


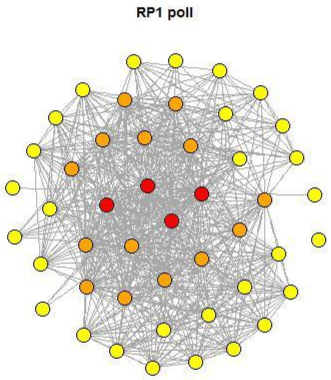
t.



u.



v.



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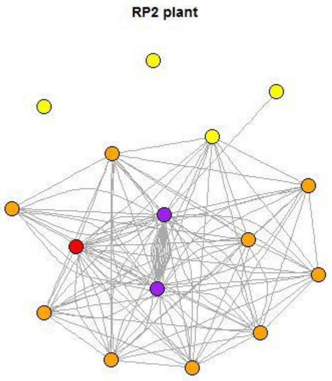


x.

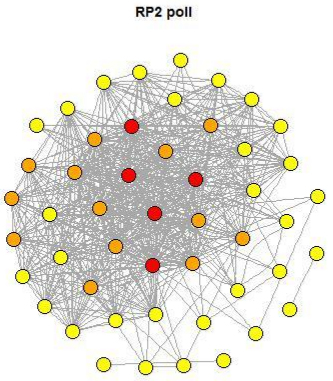
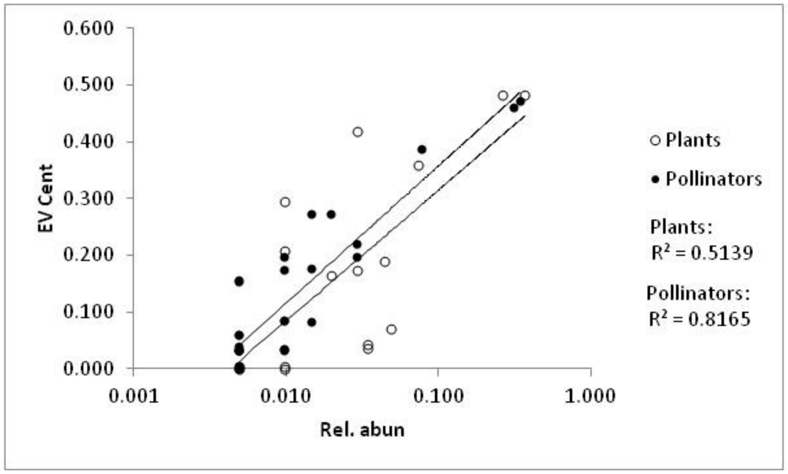


Figure 6. Plant and pollinator one-mode networks for each meadow surveyed in 2014, using the 2014 data. Edges connecting two vertices mean that those two species have a common pollination partner from the other set. Vertices that have no edges, e.g., the plant *Achillea millefolium* in Figure 7a, do not share pollinator partners (or, in the case of a pollinator, plant partners) with any other species in that meadow. The vertex color indicates the eigenvector centrality value of that node, based on the quartiles of the eigenvector centrality distribution for all networks. Yellow: 0-0.14, orange: 0.14-0.28, red: 0.28-0.42, purple: 0.42-0.56. Higher eigenvector values indicate that a vertex is more important to the overall network structure. Species labels were omitted from vertices due to the density of some of the networks.

In almost all meadows surveyed in 2014, eigenvector centrality of a species within the one-mode network was positively related to the frequency of interactions in which it participated (Figure 7). For each of the 12 meadows surveyed in 2014, the eigenvector centrality values of plant species were strongly positively related to the abundance of that species (defined as the number of times that species participated in an observed interaction). The eigenvector centrality values for pollinator species also were positively related to the abundance of the species, except in two meadows. In meadow CPS (Figure 7g) and to a lesser extent NE (Figure 7f) the eigenvector centrality values of pollinators were bimodally distributed. In CPS, the most abundant pollinators had very low eigenvector centrality values.

Eigenvector centrality increased about twice as fast relative to species abundance (based on the slopes of the relationships) for plants as for pollinators (Table 2). In some meadows, e.g., CPB and CPR, the slope of the relationship was similar for plants and for pollinators.

a.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EV Cent
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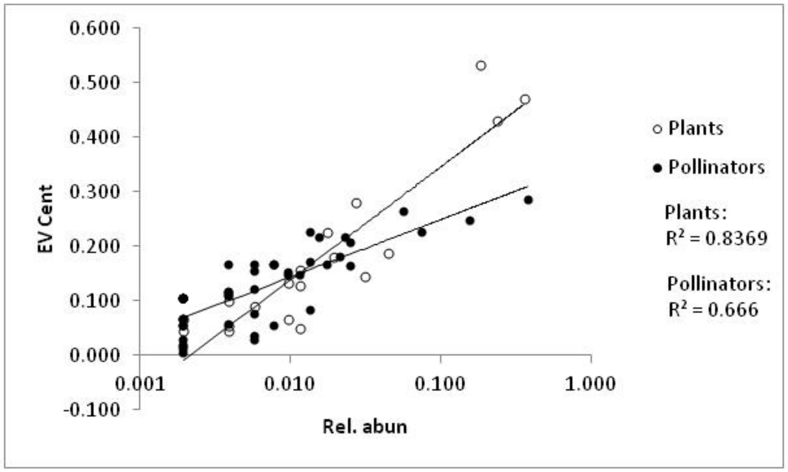
Rel. abun
○ Plants
● Pollinators
Plants:
$R^2 = 0.5139$
Pollinators:
$R^2 = 0.8165$

b.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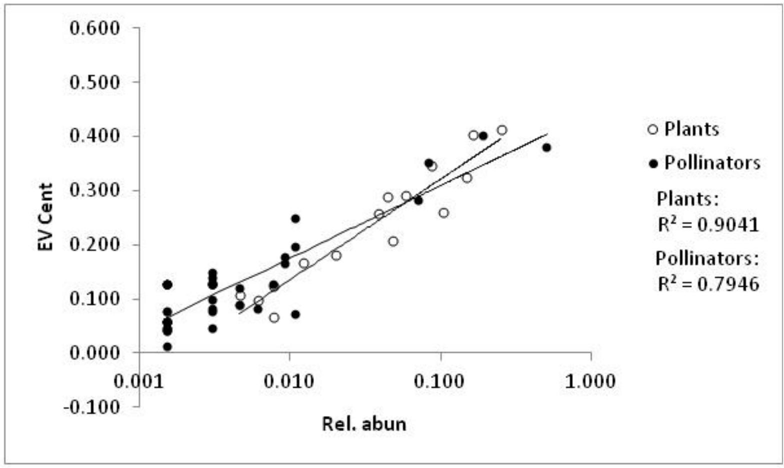
Rel. abun
○ Plants
● Pollinators
Plants:
$R^2 = 0.8369$
Pollinators:
$R^2 = 0.666$

c.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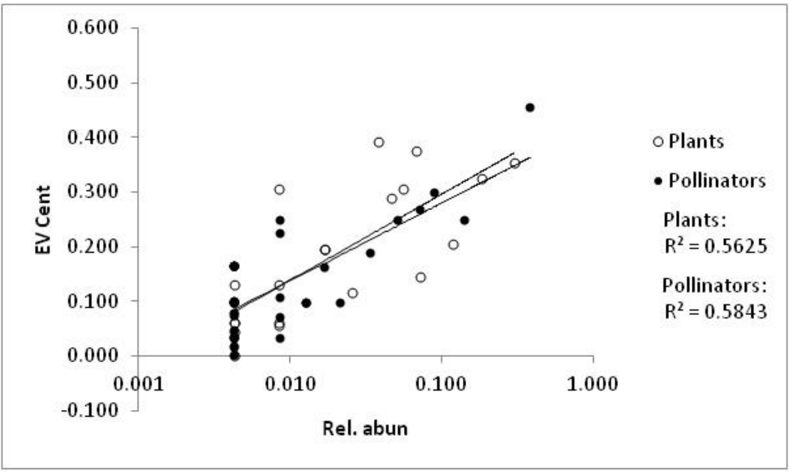
Rel. abun
○ Plants
● Pollinators
Plants:
$R^2 = 0.9041$
Pollinators:
$R^2 = 0.7946$

d.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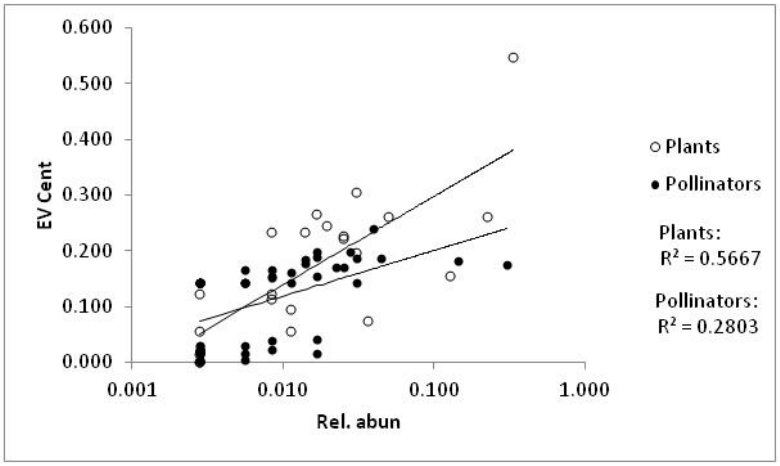
○ Plants
● Pollinators
Plants:
$R^2 = 0.5625$
Pollinators:
$R^2 = 0.5843$

e.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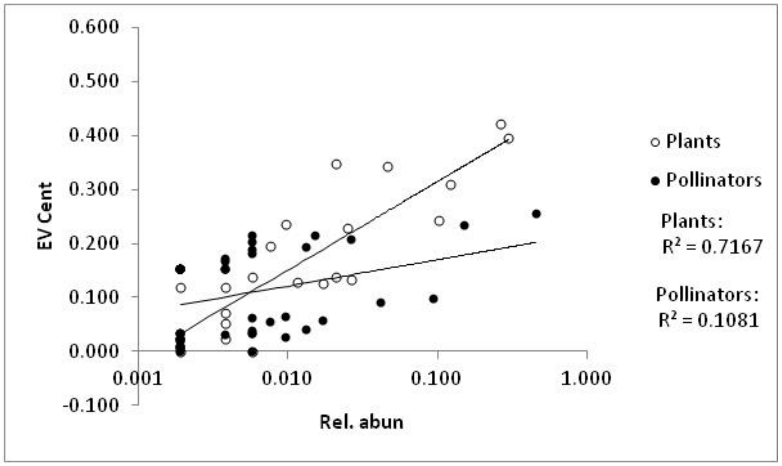
Rel. abun
Plants
Pollinators
Plants:
$R^2 = 0.5667$
Pollinators:
$R^2 = 0.2803$

f.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EV Cent
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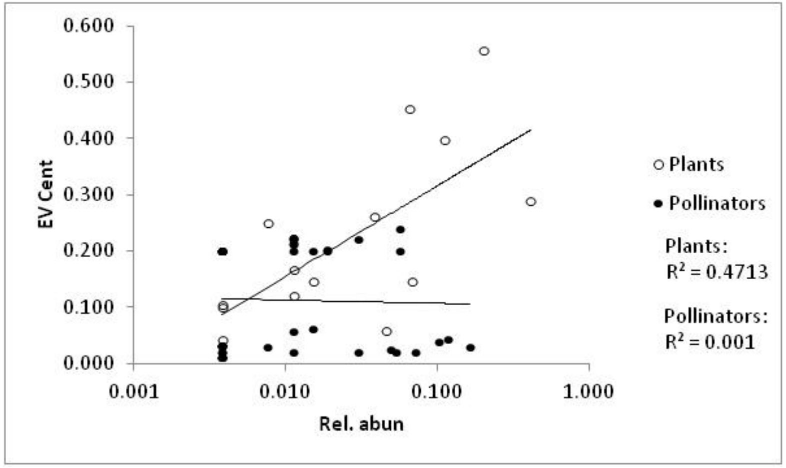
Rel. abun
Plants
Pollinators
Plants:
$R^2 = 0.7167$
Pollinators:
$R^2 = 0.1081$

g.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EV Cent
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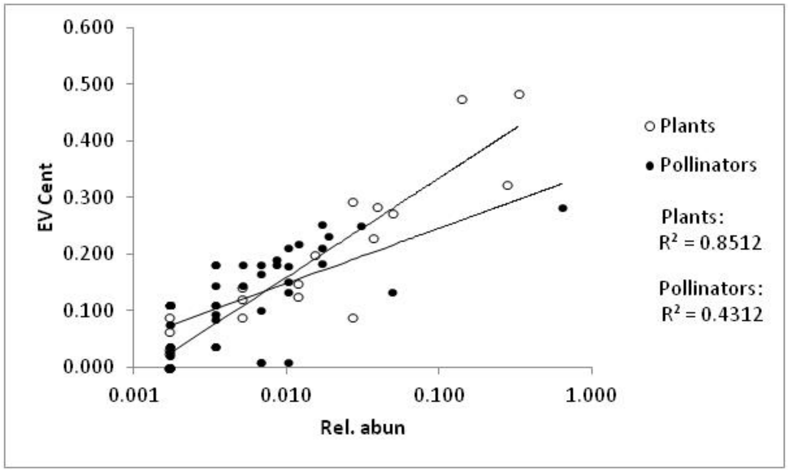
Rel. abun
Plants
Pollinators
Plants:
$R^2 = 0.4713$
Pollinators:
$R^2 = 0.001$

h.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EV Cent
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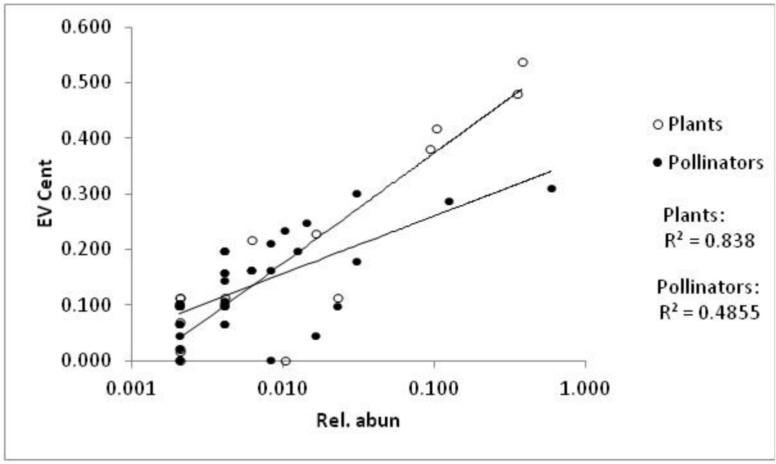
1.000
Rel. abun
Plants
Pollinators
Plants:
$R^2 = 0.8512$
Pollinators:
$R^2 = 0.4312$

i.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EV Cent
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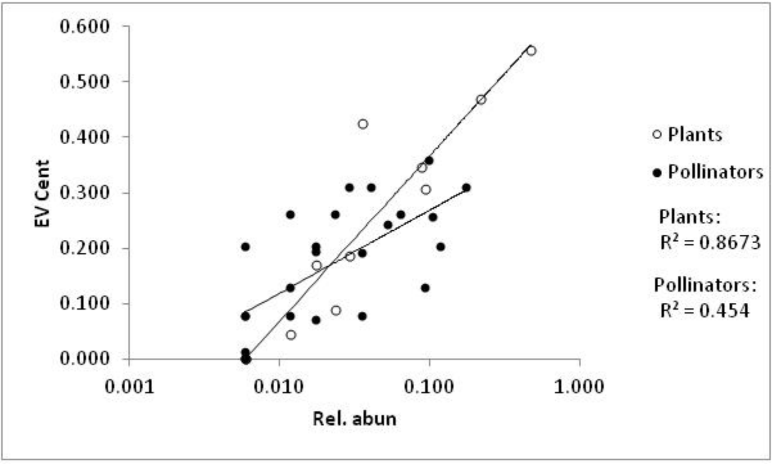
1.000
Rel. abun
○ Plants
● Pollinators
Plants:
$R^2 = 0.838$
Pollinators:
$R^2 = 0.4855$

j.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EV Cent
0.001
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0.100
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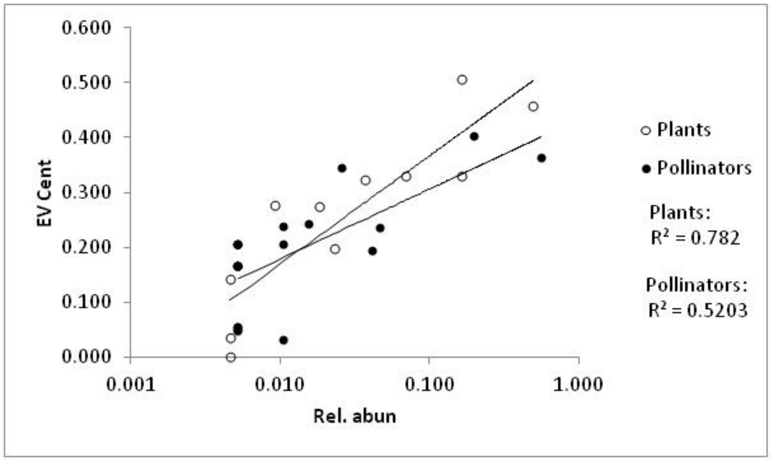
Rel. abun
○ Plants
● Pollinators
Plants:
$R^2 = 0.8673$
Pollinators:
$R^2 = 0.454$

k.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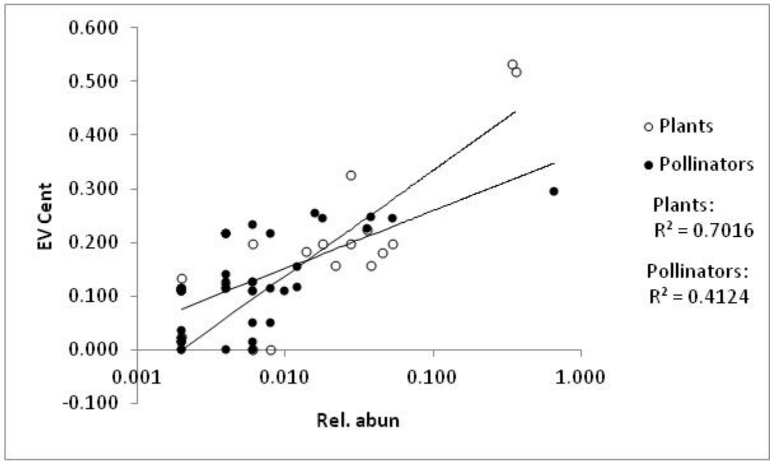
0.100
0.000
EV Cent
0.001
0.010
0.100
1.000
Rel. abun
○ Plants
● Pollinators
Plants:
$R^2 = 0.782$
Pollinators:
$R^2 = 0.5203$

l.


0.600
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-0.100
EV Cent
0.001
0.010
0.100
1.000
Rel. abun
○ Plants
● Pollinators
Plants:
$R^2 = 0.7016$
Pollinators:
$R^2 = 0.4124$

Figure 7. Eigenvector centrality values from the one-mode networks of plants and pollinators plotted against their relative abundances in each of the meadows sampled in 2014, using the 2014 data ((a) CPB, (b) LO, (c) M2, (d) CPM, (e) LM, (f) NE, (g) CPS, (h) LS, (i) RP1, (j) CPR, (k) LB, and (l) RP2). A positive relationship indicates that the component species tend to be generalists.

Table 2. Slope and correlation coefficients of the relationship of eigenvector centrality to the log of relative abundance for all species in the plant-pollinator networks of 12 meadows surveyed in 2014 (from Figure 7). A higher slope indicates a stronger tendency towards generalization for that network.

	Plant		***Pollinator***	
Meadow	**Slope**	**R^2**	**Slope**	**R^2**
CPB	0.100	0.514	0.105	0.817
CPM	0.068	0.563	0.062	0.584
CPS	0.070	0.471	-0.002	0.001
CPR	0.129	0.867	0.065	0.454
LO	0.090	0.837	0.046	0.666
LM	0.069	0.567	0.036	0.280
LS	0.076	0.851	0.042	0.431
LB	0.086	0.782	0.056	0.520
M2	0.081	0.904	0.058	0.795
NE	0.071	0.717	0.021	0.108
RP1	0.086	0.838	0.045	0.486
RP2	0.085	0.702	0.047	0.412
Mean	0.084		0.048	
Std. dev.	0.016		0.025	

In two of the 12 meadows surveyed in 2014, there was some evidence of pollinator modularity. In meadows CPS and NE (see Figure 7 f and g), the eigenvector centrality values for pollinators appeared to have a bimodal distribution, such that about half the species had values less than 0.05 and the other half had values of 0.15 to 0.2. The two most abundant pollinator species in CPS, *Apis mellifera* and *Bombus mixtus*, were abundant in all meadows, but in all but CPS they also had very high eigenvector centrality values, indicating their importance to the overall network in each location. In three contrasting meadows (CPS, NE, and CPM), *A. mellifera* and *B. mixtus* pollinated plant species that all had high eigenvector centrality. However, these pollinators had very low centrality in CPS, but high centrality in NE and CPM (Table 3). Thus *A. mellifera* and *B. mixtus* were pollinating fewer plant species in CPS than in the other two meadows. Table 4 further breaks down their partner species in the meadows CPS and CPM. In CPS, only four of the 14 plant species recorded in interactions also occur in CPM. Of those four shared plant species, both of *A. mellifera*'s pollinating partners can be found, and two of the three partners of *B. mixtus*.

Table 3. Abundances, eigenvector values, pollination partner numbers, available partners (number of flowering species recorded in a pollination interaction during the year) and pollination partner eigenvector values for *A. mellifera* and *B. mixtus* in three meadows. In CPS and NE some evidence was found suggesting there may be different pollinator modules in these networks, and the two pollinator species highlighted here were found in different modules in the two meadows. In CPM, no evidence of pollinator modularity was found. In each meadow, these two species are pollinating plant species of similar importance, but are simply pollinating fewer species in CPS, as indicated by their low eigenvector centrality values.

Meadow	**Pollinator species**	**Rel. abun.**	**Eigenvector value**	**Number of partner species**	**Available partners**	**Mean partner Eigenvector value**
CPS	*A. mellifera*	0.16	0.03	2	14	0.51
	B. mixtus	0.11	0.04	3		0.37
NE	*A. mellifera*	0.46	0.26	10	21	0.25
	B. mixtus	0.15	0.23	9		0.26
CPM	*A. mellifera*	0.09	0.30	7	20	0.27
	B. mixtus	0.39	0.45	10		0.23

Table 4. The 14 (CPS) and 21 (CPM) plant species recorded as participating in pollination interactions during the 2014 field season (listed alphabetically). The four species in bold are the four species shared by both meadows. *A. mellifera* pollinated two species in CPS, both also present in CPM (*A. mellifera*'s partners designated by *). *B. mixtus* pollinated three species in CPS, two of them also present in CPM (its partners designated by $^+$).

CPS		**CPM**	
Species	Eigenvector value	Species	Eigenvector value
Achillea millefolium* $^+$	0.56	*Eriophyllum lanatum** $^+$	0.39
Erigeron foliosus* $^+$	0.45	***Erigeron foliosus**** $^+$	0.38
Hypericum perforatum	0.4	*Penstemon procerus** $^+$	0.35
Sedum oreganum	0.29	*Ligusticum grayi** $^+$	0.33
Potentilla glandulosa	0.26	*Orthocarpus imbricatus*$^+$	0.31
Aster ledophyllus	0.25	*Rumex acetosella*	0.31
Rosa gymnocarpa	0.17	*Aquilegia formosa**	0.29
Eriogonum umbellatum	0.15	***Cirsium callilepis***	0.21
Lupinus laxiflorus	0.15	*Rubus parviflorus*$^+$	0.2
Gilia capitata	0.12	*Stachys cooleyae*	0.2
Vicia americana	0.11	*Delphinium nuttallianum*$^+$	0.15
Agoseris heterophylla$^+$	0.1	*Anaphalis margaritacea*	0.13
Cirsium callilepis	0.06	*Rudbeckia occidentalis*	0.13
Calochortus subalpinus	0.04	***Achillea millefolium**** $^+$	0.12
		Mimulus nanus	0.06
		Mimulus tilingii	0.06
		Phlox gracilis	0.06

*Zigadenus venenosus** $^{+}$	0.06
Eriogonum umbellatum^{+}	0.04
Mimulus moschatus	0

3.6 Discussion

There are several possible sources of error in this study. It is unlikely that rare pollinator species were adequately sampled, because each meadow was surveyed for only 750-1050 minutes (depending on the year) over the course of a field season. However, undersampling of rare species would not be expected to affect the eigenvector centrality and abundance numbers significantly, since rare species by definition appear in fewer interactions. In addition, the degree distribution shapes depended on species that had many partners – these were not rare species. The evidence for modularity was displayed by two of the most common pollinator species.

There is certainly some bias in observers' abilities to see pollinators and identify them to the species level in the field. However, one person trained all observers in all four years in the same way, and the observers surveyed different plots at different times during each watch.

The degree distributions generated using these data strongly support the hypothesis that networks tend to be dominated by highly generalist species. The degrees of both plant and pollinator data are power-law distributed, as opposed to exponentially. Most ecological networks (including plant-pollinator networks) have degree distributions that follow a power-law, especially for large datasets (Olesen et al., 2007; Dupont et al., 2009; Danieli-Silva et al., 2011). A power law degree distribution means that the plant-pollinator networks in montane meadows of the central Cascades have more species with many connections than would be expected by random chance. A few plant and pollinator species tend to interact with a lot of other partners in these networks.

The dominance-diversity curves provide further support for the hypothesis that plant-pollinator networks are dominated by a few species that interact with many partners. Super-generalist plants, indicated by very high eigenvector centrality values, occurred in 10 of 12 meadows. In contrast, super-generalist pollinators occurred in only 4 meadows. Thus, plant-pollinator networks, especially in the small meadows, were dominated by a few plant species participating in a large number of interactions. In combination with evidence (from Chapter 2) that pollinators move between meadows fairly freely in this landscape, the high dominance of a few plant species in networks of small meadows implies that pollinators may travel to these small meadows in search of particular plant species. Pollinators, on the other hand, which are able to move between patches of meadow, are less strongly dominated by individual species since they can spread out in the landscape more and select the flowers that they pollinate (Goulson, 1999; Gómez et al., 2007).

The fact that eigenvector centrality was positively related to species abundance provides additional evidence that networks are dominated by generalist plant and pollinator species. This finding is consistent with many other studies of plant-pollinator networks (Waser et al., 1996, Olesen et al., 2002; Olesen and Jordano, 2002; Memmott et al., 2004; Olesen et al., 2007; Petanidou et al., 2008). Generalization prevails because there is high turnover in the component species, and generalization makes networks resilient in response to high turnover (Memmott et al., 2004; Petanidou et al., 2008). With so many species changing in abundance and behavior so frequently during and between growing seasons, generalists come to dominate networks because they are able to participate opportunistically in plant-pollinator interactions. Generalists also are less vulnerable than specialists to extinction of their partners, since they have many partners.

This analysis also provides the first evidence of modularity in some of plant-pollinator networks in montane meadows of the central Cascade Range in Oregon. Previous studies have found that most large plant-pollinator networks tend to be highly modular (Olesen et al., 2007; Danieli-Silva et al., 2011). Two of the species that appeared to be modular, *A. mellifera* and *B. mixtus*, are well-known long-distance foragers (Ribands, 1951). Thus, in a landscape like this one, where pollinators can pick and choose from plant species in a matrix of habitat (meadow) patches separated by forest, less suitable habitat patches may contain two distinct modules of pollinators. A 'traveling module,' composed of colony-based insects that can forage long distances every day, may access these smaller meadow habitats but only pollinate a few preferred flower species (*Eriogeron foliosus* and *Achillea millefolium*, in this case). A 'local module,' consisting of primarily solitary insects that do not forage very far in a single day, may pollinate a larger number of locally occurring plant species, because they do not have access to a sufficient number of preferred plant species. The fact that *A. mellifera* (European honeybee) is a non-native pollinator raises intriguing questions about how the introduction of this species may have modified native plant-pollinator networks in this landscape. Future studies should seek further evidence of modularity, especially for networks in landscapes consisting of widely distributed meadow patches varying in size and isolation.

3.7 Conclusion

The results of this study indicate that, like many well-studied plant-pollinator networks around the world, these montane meadow networks are dominated by generalist component species. In addition, also like many previously studied networks, these networks are not assembled randomly, but are instead generally dominated by a higher than expected number of species that are very well-connected. These findings are consistent with the finding (from Chapter 2) that plant assemblages vary markedly among montane meadows, and pollinator assemblages experience very high turnover between years. Plant and pollinator species must be generalists if they are to find partners in a spatially and temporally variable environment.

This study also found some evidence for modularity in two small, isolated meadows. This finding suggests that, while the landscape as a whole is dominated by a few common, far-ranging pollinator species, locally-confined pollinators that pollinate opportunistically may dominate in small isolated meadows. Because they are unable to move between patches of suitable habitat, these species forage from whatever flowers happen to be in anthesis in their immediate neighborhood. Future studies should seek further evidence of modularity and attempt to determine which pollinator species belong to different modules and whether those modules are defined by functional differences, such as foraging distance.

3.7 References

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CHAPTER 4 CONCLUSION

This thesis has further highlighted the importance of using long-term and large-scale datasets when studying plant-pollinator networks. Pollinators' abilities to forage over very large distances makes studying an individual patch of suitable habitat difficult – instead, large scale studies that include a set of patches in a landscape are more appropriate to capture the activities of these pollinators. Further studies that look at individual pollinator movement, or more spatially comprehensive studies, are needed to confirm this. At the same time, montane meadows in this landscape in the central Cascade Range in Oregon have quite distinctive plant communities whose differences are not related to their isolation or to meadow size. This study showed that pollinator assemblages vary from year to year. Insects are especially sensitive to environmental cues, like a wetter or colder winter. These conditions may dramatically affect insect populations for a given year, thus changing the dominant species during a field season.

In spite of high spatial and temporal turnover of component species, most plant-pollinator networks are remarkably resilient. This study suggests that this resilience arises from the fact that these networks are dominated by generalist component species. These generalists pollinate or are pollinated opportunistically, with partner species according to their availabilty?. In addition, these networks are not assembled randomly, but are instead generally dominated by a higher than expected number of species that are very well-connected. This further supports the notion that plant species vary markedly in space, and pollinators vary in time. Plant and pollinator species must be generalists if they are to find partners in a spatially and temporally variable environment.

Finally, this thesis study also found some evidence for modularity in two small, isolated meadows. One explanation for this finding is that while the landscape as a whole is dominated by a few common, far-ranging pollinator species; locally-confined pollinators that pollinate opportunistically may dominate in small isolated meadows. Because they are unable to move between patches of suitable habitat, these species forage from whatever flowers happen to be in anthesis in their immediate neighborhood.

It remains crucial to continue these long-term and spatially comprehensive observations of plant-pollinator networks in order to capture the network structure and its response to environmental change and fragmentation of habitat in the landscape. These and many other results suggest that plant-pollinator networks are operating at a large scale, nearly always larger than a single patch of habitat. Genetic analysis and more advanced network analytical techniques also provide opportunities to further our understanding of how component species are linked through time and space, and should be considered for future studies.

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