How do the pollinators' flower preferences affect the features of the pollination network?

How is the ecological health of the pollinator network in a montane meadow ecosystem, in terms of sustaining biodiversity and stability and resistance to species extinction, affected by the composition of generalist and specialist pollinators: when the pollinator species are all generalists, all specialists, or the particular mix of specialists and generalists that reflects reality?

Disa Yu, Vanderbilt University
Eco-Informatics Summer Institute, Summer 2014
Pollinators Research Project
HJ Andrews Experimental Forest and Oregon State University

Abstract

All pollinators are classified as either generalists or specialists, depending on the variety of flower species that they pollinate. This research project strives to understand how these generalist and specialist pollinators' flower preferences affect the features of the resulting pollination network. More specifically, it aims to quantify and compare the ecological health of the pollination network that results from different compositions of generalists and specialists, by connecting the ecological concepts of sustaining biodiversity, stability, and resistance to species extinction to the network indices of links per species, nestedness, weighted nestedness, niche overlap, and extinction slope. Many R programs were written to compute flower abundances, pollinator abundances, pollinators' flower preferences, and the pollinator-flower interaction networks based on preferences and abundances. The Bipartite package in R was used to compute the specified indices of the pollination interaction networks. Based on an analysis and interpretation of the indices, it was concluded that the pollination network containing all generalist pollinators is the most ecologically healthy network.

Introduction

The purpose of the plant-pollinator network research project is to study the interactions between pollinators and flowering plants in the montane meadows of the western Cascades mountain range in Oregon. The four specific research aims of this study, according to the Master's thesis work of Vera Pfeiffer, are:

1. How are the abundance and diversity of plant-pollinator interactions related to pollinator network complexity?
2. How are meadow size and surrounding area related to the density and diversity of flowering plants and plant-pollinator interactions in montane meadows?
3. How is soil moisture related to the density of flowering plants and plant-pollinator interactions over the summer?
4. How are phenology and soil moisture related to the abundance of flowers, pollinators, and specific pollinator guilds (Lecturer Pfeiffer)?

The ecological motivations of the plant-pollinator network project include aspects from both a public interest perspective and a scientific interest perspective (Lecturer Pfeiffer). From a public interest perspective, there has been scientific evidence of recent widespread pollinator declines and pollinator limitations (Lecturer Pfeiffer). This research project may offer insight into the effects of these two worrying phenomena on the overall pollination network of montane meadows. From a scientific interest perspective, this study's value lays in its well-defined study system of montane meadows, its examination of the highly dynamic nature of pollinator populations, and in the opportunity to analyze pollinator network complexity (Lecturer Pfeiffer).

For the purposes of the 2014 Eco-Informatics Summer Institute (EISI), we have chosen to focus on addressing the first research aim. We plan to analyze the pollination network from the perspective and knowledge-foundations of our studies in mathematics, statistics, computer science, and ecology.

In particular, for my individual research project, I plan to examine how the pollinators' flower preferences affect the features of the pollination network. I would like to discover how the pollination network and the quantitative features of the network are affected by the generalist or specialist natures of the pollinators with respect to particular flower species. How is the ecological health of the pollination network in a montane meadow ecosystem, in terms of sustaining biodiversity and stability and resistance to species extinction, affected by the composition of generalist and specialist pollinators: when the pollinator species are all generalists, all specialists, or the particular mix of specialists and generalists that reflects reality? I hypothesize that the pollination network of a montane meadow ecosystem will be the most sustainably biodiverse and stable and resistant to species extinction when all of the species are generalists, since then all of the flowers will potentially have an equal chance of being pollinated (given that they are equally abundant).

Study Site

The data collection of the pollination network study took place at various montane meadows in the HJ Andrews Experimental Forest, which is situated in the Western Cascades mountain range of Oregon. Data was collected during the summer months of 2011-2014. The EISI 2014 students collected data for the summer of 2014. During our period of data collection, the weather was typically sunny with still winds and temperatures ranging from 70-90 degrees Fahrenheit; no data was collected on rainy days or excessively cloudy days. The pollinator species and flower species observed during data collection are reasonably representative of the flora and fauna of the Western Cascades montane meadows.

Methods

The data collection portion of the plant-pollinator network study occurred in 5 montane meadow complexes during the study years of 2011-2013, and 3 montane meadow complexes during the study year of 2014 (Lecturer Pfeiffer). Each meadow complex consisted of 3-4 meadows (Lecturer Pfeiffer). The 3 meadow complexes in which we collected data during the summer of 2014 all consisted of 4 meadows per complex. Each meadow had ten 3-meter by 3-meter plots spaced 15-meters apart, equally divided into two transects that ran either vertically or horizontally along the face of the meadow (Lecturer Pfeiffer). Data was collected by performing 15-minute "plot-watches" in each of the plots, once per week (Lecturer Pfeiffer). During the plot-watches that we conducted over the summer of 2014, we first performed an exhaustive flower survey of the flowers that were blooming in the plot, noting the flower species, number of flower stems, and number of flowers per stem. Then, we recorded some statistics relating to the current weather and temperature conditions. Finally, we observed the plot for 15-minutes. During the plot-watch, we recorded the number of flower-pollinator interactions that occurred during each discrete minute. For each interaction, we noted the flower species, the pollinator species, the number of interactions between the two species, and caught the pollinator (to be identified later) if its species was uncertain.

Data entry was conducted using Microsoft Excel, and was performed on a weekly basis, for the data that we collected during the summer of 2014.

My individual research project within the larger ongoing research project of the plant-pollinator network study involves examining how the pollinators' flower preferences affect the features of the pollination network. More specifically, I would like to discover how the composition of generalist and specialist pollinators-- when all of the pollinators are generalists, all of the pollinators are specialists, or a reality-reflecting intermediate case-- affects the ecological health of the pollination network in a montane meadow ecosystem, in terms of sustaining biodiversity and stability and resistance to species extinction.

The scope of my research project encompasses the data collected during the 2011, 2012, and 2013 summers of the study. The flower survey dataset and interactions dataset for those years contained a total of 147 flower species and 466 pollinator species.

To address my research question, I wrote several programs in R. The main R program took in the four inputs of flower abundance, pollinator abundance, pollinators' flower preferences, and the total number of pollinators, and produced a quantitative matrix of pollinator-flower interactions. The flower abundances were derived from the 2011-2013 flower survey data. The pollinator abundances were estimated from the 2011-2013 interactions data. The pollinators' flower preferences was a matrix that contained probability values that represented the probability that the pollinator would prefer that flower; the preference probabilities for each pollinator species across all of the flower species summed to 1. To generate the matrix of flower preferences when all of the pollinator species are generalists, I divided 1 by the total number of flower species in the dataset. To generate the flower preference matrix when all of the pollinator species are specialists, for each pollinator species I generated a probability of 1 for a randomly selected flower species, and assigned probabilities of 0 elsewhere. To generate the flower preference matrix for the reality-reflecting intermediate case, I met with our entomology mentor Andy Moldenky to discuss which pollinators were specialists and what flowers they specialized on. The total number of pollinators was a numeric integer value that represented the total number of pollinator individuals across all of the pollinator species. I also wrote other R programs that took-in the flower survey data and interactions data to produce the tables of flower abundances and pollinator abundances.

Provided below is a table of the specialists that Andy Moldenky identified, along with the flowers that they specialize on. A total of 31 pollinator species were identified as specialists.

Table 1. Specialist pollinators and their flower species of specialization

Specialist Pollinator	*Flower Species of Specialization*
Andrena (Micrandrena) sp 3	Fragaria virginiana
Andrena birtwelli	Potentilla glandulosa, Potentilla gracilis
Andrena columbiana	Haplopappus hallii, Solidago canadensis
Bombus appositus	Delphinium nuttallianum
Chelostoma phaceliae	Phacelia hastata
Chrysolina quadrigeminata	Hypericum perforatum
Dianthidium ulkei	Erigeron foliosus, Eriophyllum lanatum
Dufourea bernardina	Gilia capitata
Dufourea calochorti	Calochortus subalpinus
Dufourea campanulae	Campanula scouleri
Dufourea scabricornis	Gayophytum humile
Dufourea trochantera	Phacelia hastata
Dufourea versatilis rubriventris	Castilleja hispida, Castilleja miniata, Mimulus guttatus, Mimulus nanus, Mimulus tilingii
Hylaeus nunnenmacheri	Potentilla glandulosa, Potentilla gracilis
Judiola instabilis	Lupinus laxiflorus
Judiola monticola	Lupinus laxiflorus
Megachile melanophaea	Lupinus laxiflorus, Vicia americana, Lathyrus nevadensis
Megachile perihirta	Erigeron foliosus, Eriophyllum lanatum, Haplopappus hallii, Solidago canadensis
Megachile pugnata	Erigeron foliosus, Eriophyllum lanatum, Haplopappus hallii, Solidago canadensis
Melissodes rivalis	Cirsium callilepis
Melissodes sp 1	Erigeron foliosus, Eriophyllum lanatum, Haplopappus hallii, Solidago canadensis

Osmia (Acanthosmoides) male	Lupinus laxiflorus
Osmia coloradensis	Erigeron foliosus, Eriophyllum lanatum
Osmia subaustralis	Erigeron foliosus, Eriophyllum lanatum
Panurginus sp 1	Potentilla glandulosa, Potentilla gracilis
Perdita rivalis	Aster ledophyllus, Aster oregonensis, Erigeron foliosus
Pseudomasaris zonalis	Phacelia hastata
Saxinis saucia	Eriogonum nudum
Speyeria sp 2	Cirsium callilepis
Speyeria zerene	Cirsium callilepis
Villa lateralis	Erigeron foliosus, Eriophyllum lanatum, Haplopappus hallii, Solidago canadensis

Subsets of the flower abundance table and the pollinator abundance table are provided below. The flower abundance table contains 147 flower species and the pollinator abundance table contains 466 pollinator species. The sum of the abundances in each abundance table equals one.

Table 2. Fifteen flower species and their abundances

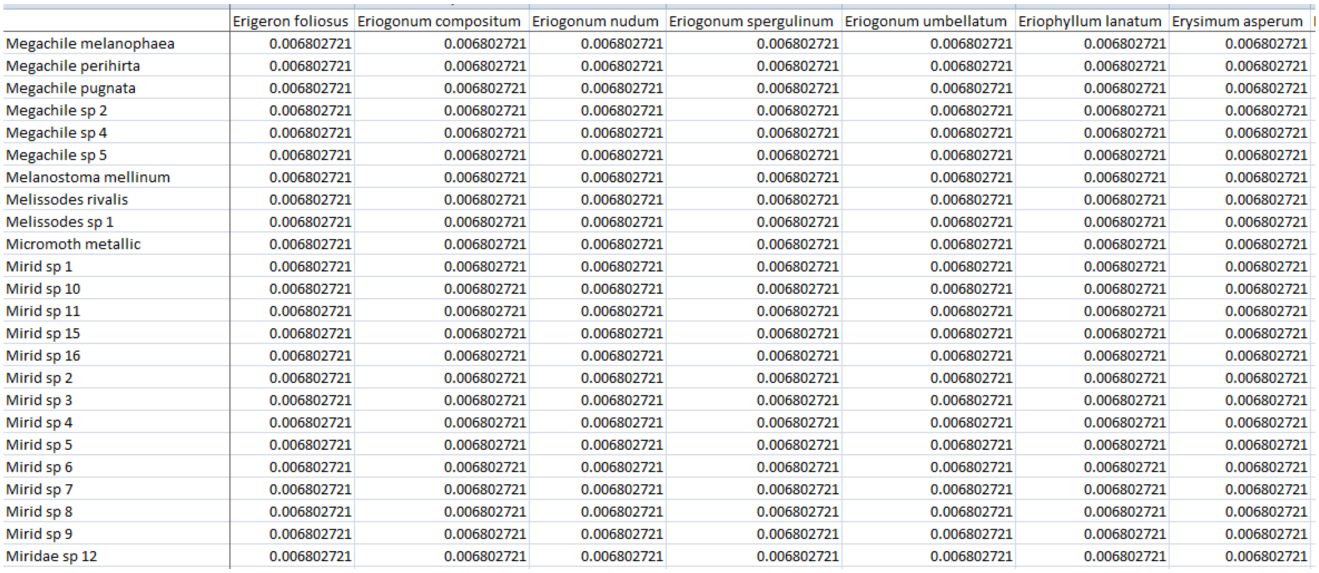
Flower Species	*Abundance*
Erigeron foliosus	0.010614275
Eriogonum compositum	0.052788104
Eriogonum nudum	0.020095111
Eriogonum spergulinum	0.000122809
Eriogonum umbellatum	0.151870882
Eriophyllum lanatum	0.026198132
Erysimum asperum	0.001258285
Erythronium grandiflorum	8.99E-05
Fragaria virginiana	0.00053413
Galium aparine	0.000320382
Galium oreganum	0.014033251
Gayophytum humile	0.003249889
Gilia capitata	0.058668116
Haplopappus hallii	0.000333082
Heracleum lanatum	0.00015456

Table 3. Fifteen pollinator species and their abundances

Pollinator Species	*Abundance*
Apis mellifera	0.185977801
Araniella displicata	3.99E-05
Arctophila flagrans	3.99E-05
Asemosyrphus polygrammus	0.002116106
Ashmeadiella sp 1	0.000279486
Asilid genus 1	0.000399265
Beetle unknown sp 1	3.99E-05
Beetle unknown sp 2	3.99E-05
Beetle unknown sp 3	3.99E-05
Beetle unknown sp 5	7.99E-05
Bembix amoena	7.99E-05
Blera scitula	0.002914637
Boloria epithore	0.000758604
Bombus appositus	7.99E-05
Bombus bifarius	0.040924699

Provided below are subsets of the three pollinators' flower preference matrix. Each complete preference matrix contains 147 flower species on the columns and 466 pollinator species on the rows. Each row of preference for a particular pollinator species sums to one.

Table 4. A subset of the pollinators' flower preference matrix, when all of the pollinators are generalists

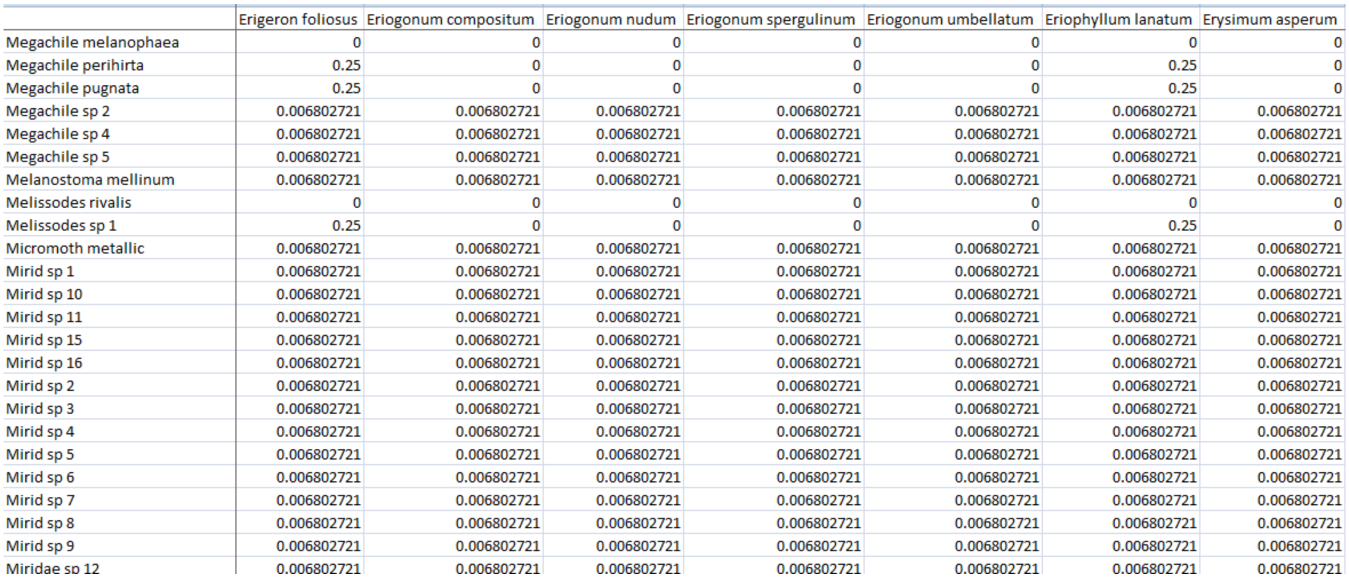


	Erigeron foliosus	Eriogonum compositum	Eriogonum nudum	Eriogonum spergulinum	Eriogonum umbellatum	Eriophyllum lanatum	Erysimum asperum
Megachile melanophaea	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Megachile perihirta	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Megachile pugnata	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Megachile sp 2	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Megachile sp 4	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Megachile sp 5	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Melanostoma mellinum	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Melissodes rivalis	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Melissodes sp 1	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Micromoth metallic	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 1	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 10	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 11	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 15	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 16	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 2	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 3	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 4	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 5	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 6	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 7	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 8	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 9	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Miridae sp 12	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721

Table 5. A subset of the pollinators' flower preference matrix, when all of the pollinators are specialists

	Saxifraga oregona	Saxifraga sp	Sedum oreganum	Sedum spathulifolium	Sedum stenopetalum	Senecio integerrimus	Senecio triangularis
Megachile melanophaea	0	0	0	0	0	0	0
Megachile perihirta	0	0	0	0	0	0	0
Megachile pugnata	0	0	0	0	0	0	0
Megachile sp 2	0	0	0	0	0	0	0
Megachile sp 4	0	0	0	0	0	0	1
Megachile sp 5	0	0	0	0	0	0	0
Melanostoma mellinum	0	0	0	0	0	1	0
Melissodes rivalis	0	0	0	0	0	0	0
Melissodes sp 1	0	0	0	0	0	0	0
Micromoth metallic	0	0	0	0	0	0	0
Mirid sp 1	0	1	0	0	0	0	0
Mirid sp 10	0	0	0	0	0	0	0
Mirid sp 11	0	0	0	0	0	0	0
Mirid sp 15	0	0	0	0	0	0	0
Mirid sp 16	0	0	0	0	0	0	0
Mirid sp 2	0	0	0	0	0	0	0
Mirid sp 3	0	0	0	0	0	0	0
Mirid sp 4	0	0	0	0	0	0	0
Mirid sp 5	0	0	0	0	0	0	0
Mirid sp 6	0	0	0	0	0	0	0
Mirid sp 7	1	0	0	0	0	0	0
Mirid sp 8	0	0	0	0	0	0	0
Mirid sp 9	0	0	0	0	0	0	0
Miridae sp 12	0	0	0	0	0	0	0

Table 6. A subset of the pollinators' flower preference matrix, when the pollinators are both generalists and specialists



	Erigeron foliosus	Eriogonum compositum	Eriogonum nudum	Eriogonum spergulinum	Eriogonum umbellatum	Eriophyllum lanatum	Erysimum asperum
Megachile melanophaea	0	0	0	0	0	0	0
Megachile perihirta	0.25	0	0	0	0	0.25	0
Megachile pugnata	0.25	0	0	0	0	0.25	0
Megachile sp 2	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Megachile sp 4	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Megachile sp 5	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Melanostoma mellinum	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Melissodes rivalis	0	0	0	0	0	0	0
Melissodes sp 1	0.25	0	0	0	0	0.25	0
Micromoth metallic	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 1	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 10	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 11	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 15	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 16	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 2	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 3	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 4	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 5	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 6	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 7	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 8	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Mirid sp 9	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721
Miridae sp 12	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721	0.006802721

To calculate the quantitative matrix of pollinator-flower interactions, I multiplied together the corresponding probabilities of flower abundance and pollinator preference, normalized the resulting probabilities to sum to 1, and multiplied those probabilities by the product of the pollinator abundances and the total number of pollinators. These calculations occurred in the main R program, and produced an interactions matrix with 466 rows and 147 columns. The 466 rows correspond to the species of pollinators and the 147 columns correspond to the species of flowers. Each cell in the interactions matrix contained an integer number that represents the number of interactions that would occur between that particular pollinator species and flower species. I generated three such interactions matrices-- one corresponding to the case where all of the pollinator species are generalists, one corresponding to the case where all of the pollinator species are specialists, and one corresponding to the case where the pollinator species are both generalists and specialists.

I used the bipartite package in R to visualize my data. I also used the bipartite package to compute the indices of the three pollination networks. The five indices that I computed are: links per species, nestedness, weighted nestedness, niche overlap, and extinction slope.

Links per species is the average number of links per species, and is calculated by dividing the sum of the links by the number of species (Inside R). In the context of pollination interactions, links per species represents the average number of interactions between a pollinator species and a flower species.

Nestedness represents the extent to which generalists interact with generalists only and specialists interact with generalists only. The concept of nestedness is thought to represent the promotion of biodiversity in mutualistic systems such as pollination systems (Staniczenko et al., 2013). Weighted nestedness is a nestedness estimator that accounts for the weight of the interactions (Galeano et al., 2009). For the nestedness index, 0 represents high nestedness and 100 represents chaos; for the weighted nestedness index, 1 represents perfect nestedness and 0 represents perfect chaos (Inside R).

Niche overlap represents the "mean similarity in interaction pattern between species of the same trophic level," where a value of 0 indicates no common niches and a value of 1 indicates perfect niche overlap (Dormann et al., 2009).

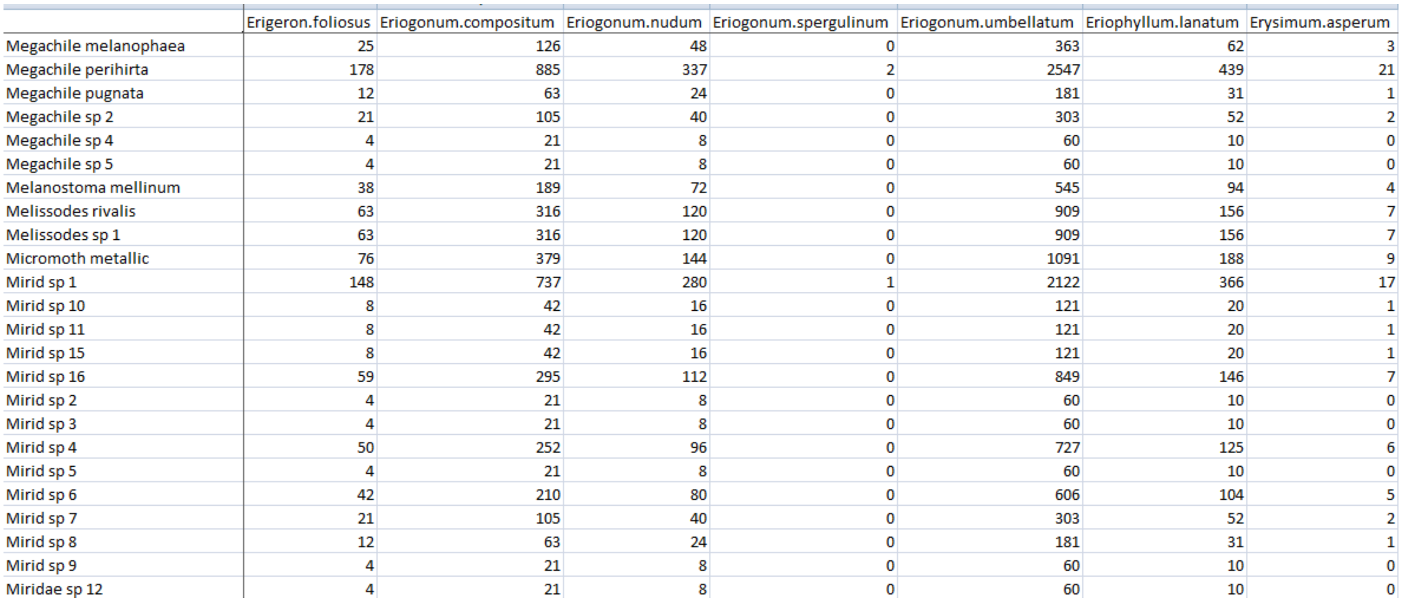
The extinction slope value measures the vulnerability of the network to species extinctions. Higher extinction slope values indicate that the network is less affected by species extinctions (Dormann et al., 2009).

I plan to measure my three criteria for ecological health-- sustaining biodiversity, stability, and resistance to species extinction-- using these five indices. I plan to draw conclusions about sustaining biodiversity from the links per species, nestedness, and weighted nestedness values. I plan to draw conclusions about stability from the links per species and niche overlap values. I plan to draw conclusions about resistance to species extinction from the extinction slope value.

Results

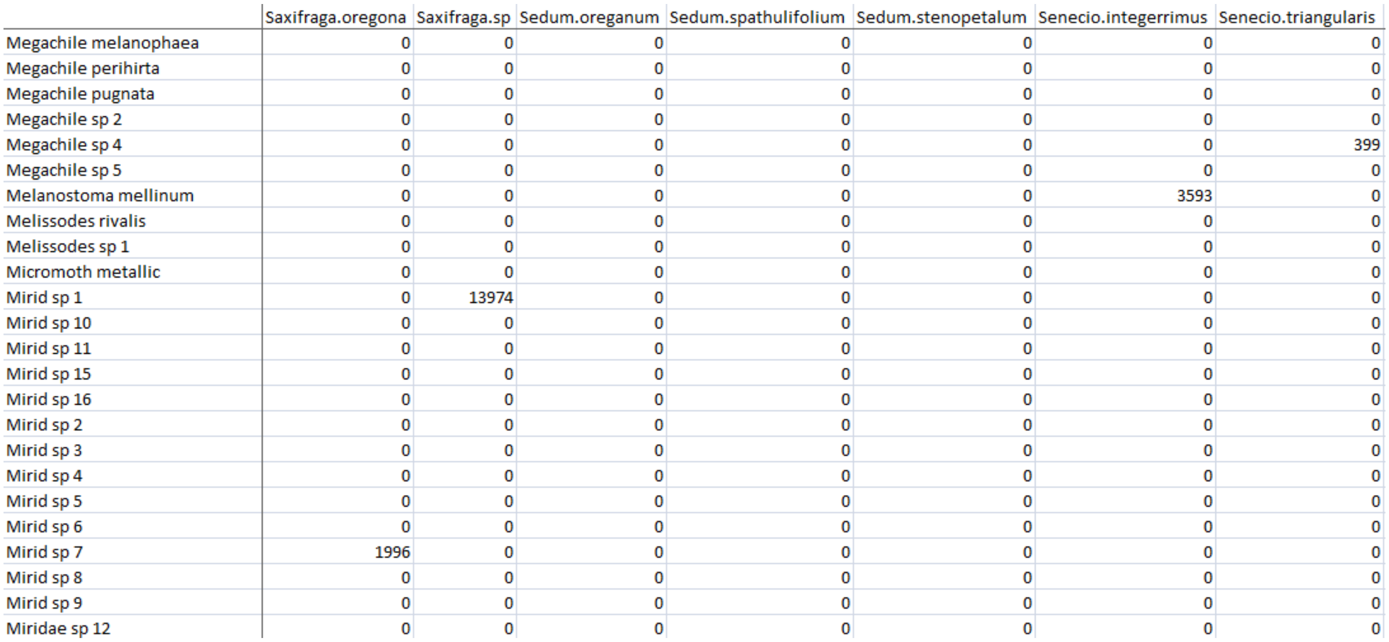
Three interaction matrices were generated from the R program; they represent the number of interactions between the flower species and pollinator species when all of the pollinators are generalists, when all of the pollinators are specialists, and when the pollinators are either generalists or specialists according to reality. Each of the interaction matrices contained 466 rows of pollinator species and 147 columns of flower species, reflecting the number of species contained in the original dataset. Due to the large size of the matrices, I have provided a subset of each of the matrices below.

Table 7. A subset of the interactions matrix when all of the pollinators are generalists



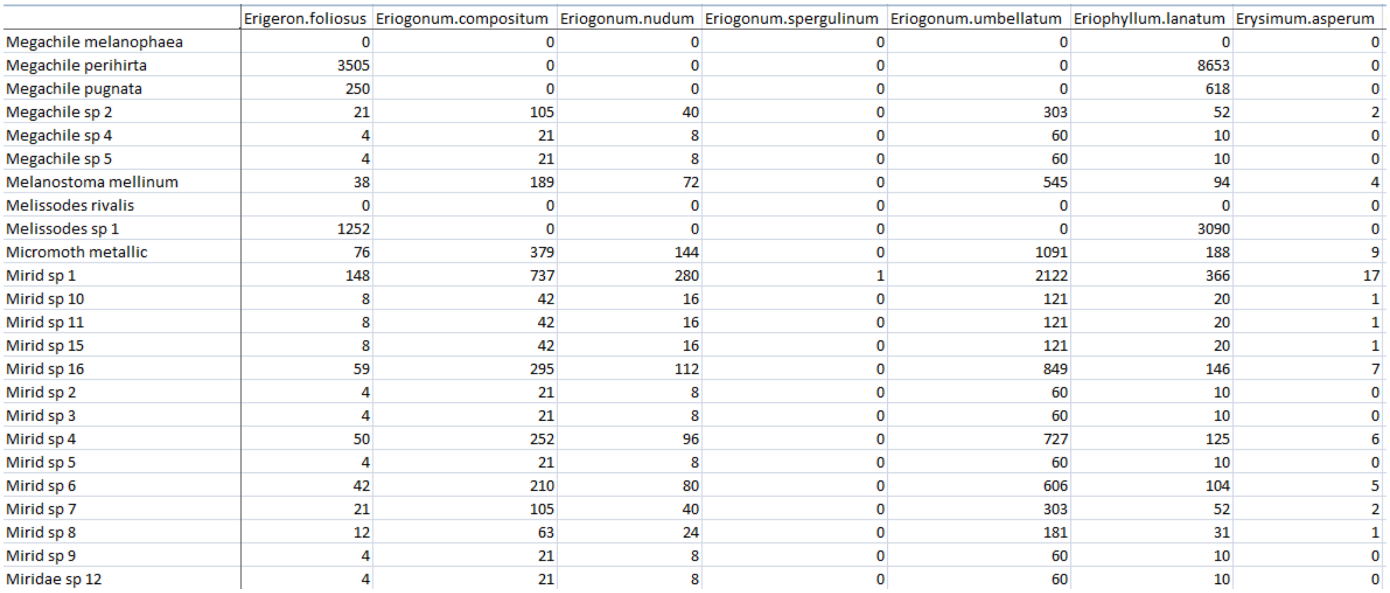
	Erigeron.foliosus	Eriogonum.compositum	Eriogonum.nudum	Eriogonum.spergulinum	Eriogonum.umbellatum	Eriophyllum.lanatum	Erysimum.asperum
Megachile melanophaea	25	126	48	0	363	62	3
Megachile perihirta	178	885	337	2	2547	439	21
Megachile pugnata	12	63	24	0	181	31	1
Megachile sp 2	21	105	40	0	303	52	2
Megachile sp 4	4	21	8	0	60	10	0
Megachile sp 5	4	21	8	0	60	10	0
Melanostoma mellinum	38	189	72	0	545	94	4
Melissodes rivalis	63	316	120	0	909	156	7
Melissodes sp 1	63	316	120	0	909	156	7
Micromoth metallic	76	379	144	0	1091	188	9
Mirid sp 1	148	737	280	1	2122	366	17
Mirid sp 10	8	42	16	0	121	20	1
Mirid sp 11	8	42	16	0	121	20	1
Mirid sp 15	8	42	16	0	121	20	1
Mirid sp 16	59	295	112	0	849	146	7
Mirid sp 2	4	21	8	0	60	10	0
Mirid sp 3	4	21	8	0	60	10	0
Mirid sp 4	50	252	96	0	727	125	6
Mirid sp 5	4	21	8	0	60	10	0
Mirid sp 6	42	210	80	0	606	104	5
Mirid sp 7	21	105	40	0	303	52	2
Mirid sp 8	12	63	24	0	181	31	1
Mirid sp 9	4	21	8	0	60	10	0
Miridae sp 12	4	21	8	0	60	10	0

Table 8. A subset of the interactions matrix when all of the pollinators are specialists



	Saxifraga.oregona	Saxifraga.sp	Sedum.oreganum	Sedum.spathulifolium	Sedum.stenopetalum	Senecio.integerrimus	Senecio.triangularis
Megachile melanophaea	0	0	0	0	0	0	0
Megachile perihirta	0	0	0	0	0	0	0
Megachile pugnata	0	0	0	0	0	0	0
Megachile sp 2	0	0	0	0	0	0	0
Megachile sp 4	0	0	0	0	0	0	399
Megachile sp 5	0	0	0	0	0	0	0
Melanostoma mellinum	0	0	0	0	0	3593	0
Melissodes rivalis	0	0	0	0	0	0	0
Melissodes sp 1	0	0	0	0	0	0	0
Micromoth metallic	0	0	0	0	0	0	0
Mirid sp 1	0	13974	0	0	0	0	0
Mirid sp 10	0	0	0	0	0	0	0
Mirid sp 11	0	0	0	0	0	0	0
Mirid sp 15	0	0	0	0	0	0	0
Mirid sp 16	0	0	0	0	0	0	0
Mirid sp 2	0	0	0	0	0	0	0
Mirid sp 3	0	0	0	0	0	0	0
Mirid sp 4	0	0	0	0	0	0	0
Mirid sp 5	0	0	0	0	0	0	0
Mirid sp 6	0	0	0	0	0	0	0
Mirid sp 7	1996	0	0	0	0	0	0
Mirid sp 8	0	0	0	0	0	0	0
Mirid sp 9	0	0	0	0	0	0	0
Miridae sp 12	0	0	0	0	0	0	0

Table 9. A subset of the interactions matrix when the pollinators are either generalists or specialists according to reality



	Erigeron.foliosus	Eriogonum.compositum	Eriogonum.nudum	Eriogonum.spergulinum	Eriogonum.umbellatum	Eriophyllum.lanatum	Erysimum.asperum
Megachile melanophaea	0	0	0	0	0	0	0
Megachile perihirta	3505	0	0	0	0	8653	0
Megachile pugnata	250	0	0	0	0	618	0
Megachile sp 2	21	105	40	0	303	52	2
Megachile sp 4	4	21	8	0	60	10	0
Megachile sp 5	4	21	8	0	60	10	0
Melanostoma mellinum	38	189	72	0	545	94	4
Melissodes rivalis	0	0	0	0	0	0	0
Melissodes sp 1	1252	0	0	0	0	3090	0
Micromoth metallic	76	379	144	0	1091	188	9
Mirid sp 1	148	737	280	1	2122	366	17
Mirid sp 10	8	42	16	0	121	20	1
Mirid sp 11	8	42	16	0	121	20	1
Mirid sp 15	8	42	16	0	121	20	1
Mirid sp 16	59	295	112	0	849	146	7
Mirid sp 2	4	21	8	0	60	10	0
Mirid sp 3	4	21	8	0	60	10	0
Mirid sp 4	50	252	96	0	727	125	6
Mirid sp 5	4	21	8	0	60	10	0
Mirid sp 6	42	210	80	0	606	104	5
Mirid sp 7	21	105	40	0	303	52	2
Mirid sp 8	12	63	24	0	181	31	1
Mirid sp 9	4	21	8	0	60	10	0
Miridae sp 12	4	21	8	0	60	10	0

The three interaction matrices visualized as bipartite graphs are provided below.

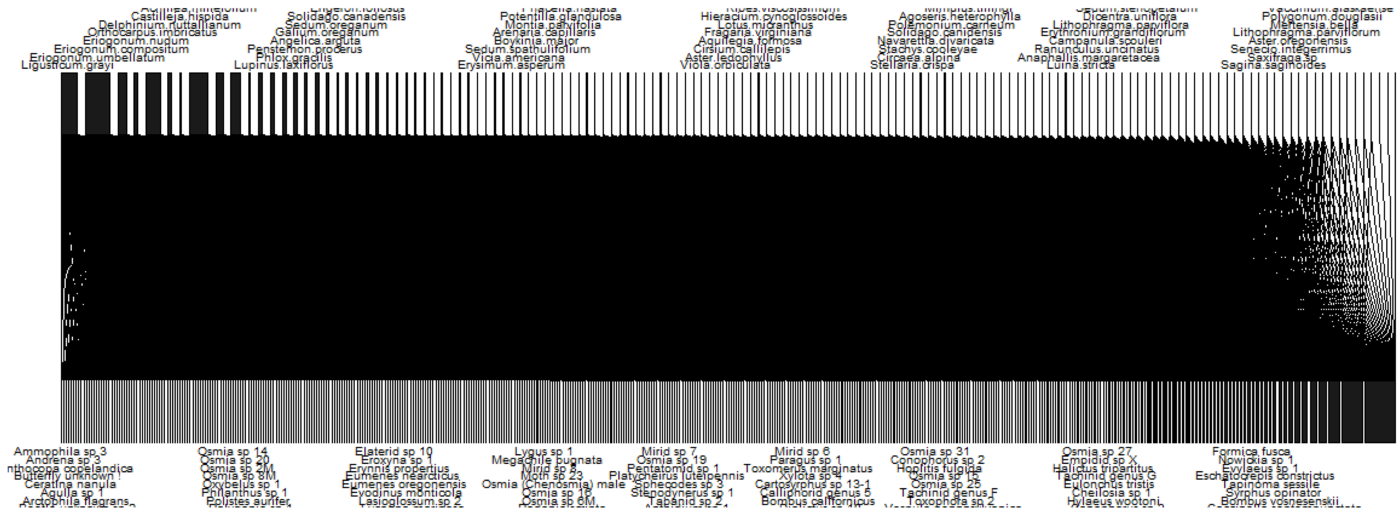


Figure 1. The bipartite graph visualization of the interaction matrix when all of the pollinators are generalists

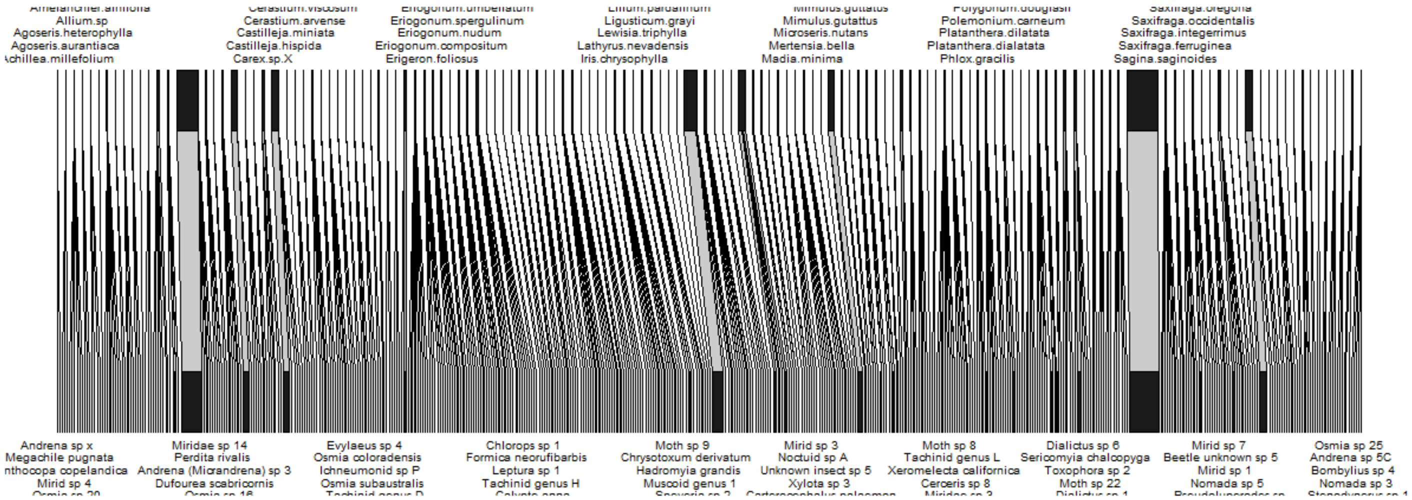


Figure 2. The bipartite graph visualization of the interaction matrix when all of the pollinators are specialists

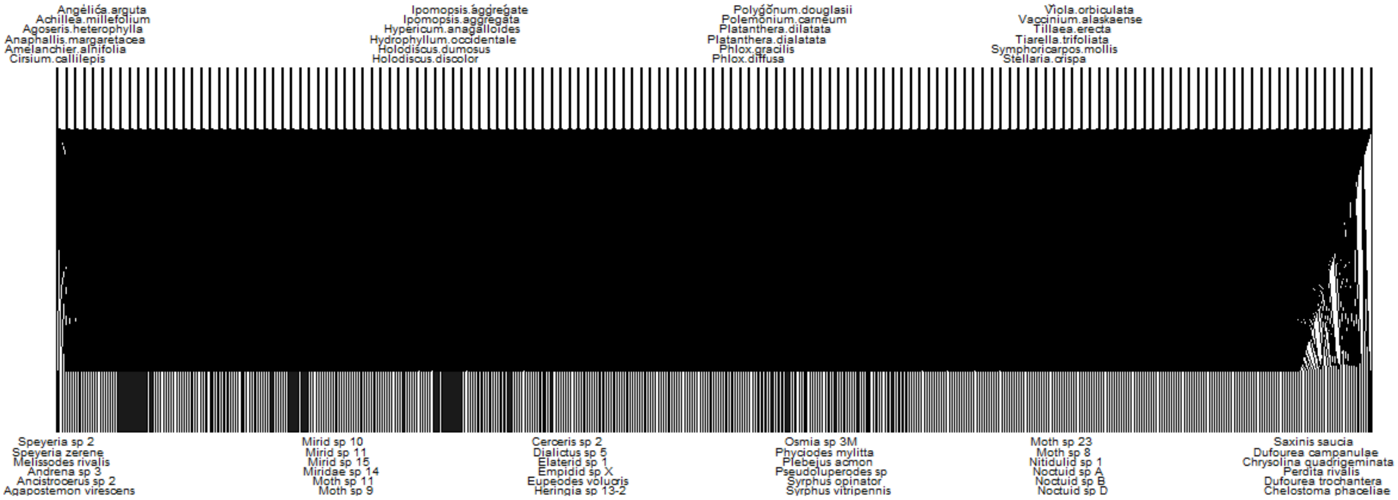


Figure 3. The bipartite graph visualization of the interaction matrix when the pollinators are either generalists or specialists according to reality

The network indices of links per species, nestedness, weighted nestedness, niche overlap, and extinction slope were computed from the three pollination networks. The table below displays the results.

Table 10. The results of the network indices computed on the three networks

	All Generalists	*All Specialists*	*Both*
Links per Species	55.693	0.766	51.873
Nestedness	5.027	2.020	1.789
Weighted Nestedness	0.816	NaN	0.782
Niche Overlap	0.927 - 0.999	0.000 - 0.007	0.868- 0.875
Extinction Slope	144.972 - 82.324	2.784 - 0.991	134.009- 63.100

The generalist pollination network has the greatest number of links per species, 55.693; the mixed pollination network has a close-second number of links per species, 51.873; the specialist pollination network has the least number of links per species, 0.766. According to the nestedness index, all three cases are fairly nested, as they are all relatively close to the 0-value of high nestedness. The mixed pollination network is the most nested at a nestedness index of 1.789, the specialist network is the second most nested at 2.020, and the generalist network is the least nested of the three at 5.027. The weighted nestedness index indicates that the generalist network and mixed network are both fairly nested, with values close to the perfectly nested score of 1. The generalist network is the most nested at 0.816 and the mixed network follows at 0.782.

The weighted nestedness index fails to produce a numerical value for the specialist network. The two nestedness measures provide seemingly contradictory information. However, since the interaction matrices are weighted, it seems justified to place more significance on the weighted nestedness results. The interaction network with all specialists as very low niche overlap (0.000 - 0.007), the interaction network with both characteristics has high niche overlap (0.868- 0.875), and the interaction network with all generalists has almost perfect niche overlap (0.927 - 0.999). Lastly, for the extinction slope value, the generalist network has the highest extinction slope value, ranging from 144.972 - 82.324, which indicates the lowest vulnerability to species extinctions. The mixed network has comparably high extinction slope values of 134.009- 63.100, while the specialist interaction matrix has notably low extinction slope values of 2.784 - 0.991.

Discussion

The three cases of the composition of generalist and specialist pollinator species that I have considered represent the two extreme cases--the extreme generalist case where all of the pollinator species are generalists, the extreme specialist case where every pollinator species solely specializes in one flower species; as well as the case that most reflects reality, according to our entomology mentor-- where the majority of the pollinator species are generalists and a few pollinator species specialize in one to four flower species. It is important to note that when a pollinator species is a generalist-- that is, it displays equal preference for all of the flower species-- then flower abundance is the main deciding factor in which flower species it visits. In this case, a combination of flower abundance and pollinator abundance would largely determine the number of interactions between that pollinator species and a particular flower species. However, when a pollinator is a specialist, then pollinator preference and flower abundance have equal say in determining which flower species it visits (according to my methodology). And the combination of pollinator preference, flower abundance, and pollinator abundance would determine the number of interactions between the pollinator species and a particular flower species.

As I stated in the methods section, I plan to quantify my three criteria for the ecological health of the pollinator network-- sustaining biodiversity, stability, and resistance to species extinction--with the five indices that I have computed. More specifically, I plan to use the indices of links per species and weighted nestedness to make interpretations about the sustaining of biodiversity in the pollination network. I plan to use the indices of links per species and niche overlap to make interpretations about the stability of the pollination network. I plan to use the extinction slope value to make interpretations about resistance to species extinction in the pollination network. Admittedly, since the three concepts of sustaining biodiversity, stability, and resistance to species extinction are related and interdependent phenomena, all of the indices could be used to quantify all three concepts. However, for simplicity and ease of analysis, I have chosen the most apparently fitting indices to quantify each concept.

The pollinator-plant interaction network with all generalist pollinators has the highest value for links per species, which indicates that the greatest number of pollination interactions occur and consequentially, the greatest number of flowers get pollinated. A large number of pollination interactions occurring on a large number of flowers supports the continued biodiversity of the flowers in the montane meadow ecosystem. The generalist pollinator network also has the highest weighted nestedness value. The pollination network with both generalists and specialists has the second-highest links per species value and second-highest weighted nestedness value. The high weighted nestedness value suggests that in the generalist pollination network, generalist pollinators tend to interact with generalist flowers and specialist flowers, while specialist pollinators tend to only interact with generalist plants. According to a 2013 paper on nestedness by Staniczenko et al., the concept of nestedness is thought to represent the promotion of biodiversity in a mutualistic system. Thus, we can conclude that the pollination network comprising of all generalist pollinators sustains biodiversity to the greatest extent.

In terms of the stability of the pollination network, the generalist network has the greatest number of links per species, as discussed previously. The specialist network has the lowest number of links per species-- notably lower than the two other cases. However, the generalist network has the least favorable niche overlap value, indicating high niche overlap; while the specialist network has the most favorable niche overlap value, indicating low niche overlap. The pollination network with both types of preferences has the middle-value for both links per species and niche overlap. Gausse's competitive exclusion principle states that each species occupies its own unique niche and that no two species can occupy the same niche for an extended amount of time (Berkeley Department of Geography). It follows that the pollination network will be the most stable when there is low niche overlap. Since no pollinator preference case generates the most favorable combination of links per species and niche overlap, it is inconclusive as to which of the three pollination networks is the most stable, according to our decision to quantify stability using links per species and niche overlap.

The pollination network comprising of all generalists has the most favorable extinction slope value, which indicates that it is the least vulnerable to species extinction. The mixed pollination network has an extinction slope value that closely follows that of the generalist pollination network. However, the specialist pollination network has an extinction slope value that is notably smaller, and thus less favorable, than that of the other two networks. These comparative extinction slope values indicate that one extinction would likely cause several other extinctions to occur in the specialist pollination network, but not in the generalist or mixed networks. We can conclude that the generalist pollination network is the most resistant to species extinctions.

Conclusion

As discussed in the previous section, the generalist pollination network sustains biodiversity to the greatest comparative extent and was the most resistant to species extinction. The pollination network containing both generalists and specialists followed closely in both criteria. The relative stability of the three pollination networks was inconclusive. Overall, from an analysis and interpretation of the four indices--links per species, weighted nestedness, niche overlap, and extinction slope-- that were generated from the three pollination networks varying in pollinator preferences, we can conclude that the pollination network in which all of the pollinators are generalists is the most ecologically healthy because it sustains biodiversity to the greatest comparative extent and is the most resistant to species extinction. In addition, we can conclude that the pollination network containing both generalists and specialists is reasonably ecologically healthy because its ability to sustain biodiversity and its resistance to species extinction follow closely to that of the generalist network. .

Sources of possible uncertainty and error include possible misspellings of flower or pollinator species in the original data. This error would result in multiple entries of the same species in the resultant interactions matrix, which would definitely add a bit of uncertainty to my results. However, since all three interaction matrices were computed using the exact same data-set, all of the matrices would potentially contain the exact same errors, so it is unlikely that the error of species misspellings would significantly change my conclusions.

Further research could be conducted to determine the precise combination of generalist pollinator species and specialist pollinators species, along with their particular flowers of specialization, that would maximize particular desired indices. Although this result will be hypothetical rather than rooted in a changeable reality, the methods used to generate the result may be intriguing and novel. In addition, the result itself may be intriguing from the perspective of gaining knowledge about the world.

Acknowledgements

I am grateful to the following Eco-Informatics Summer Institute mentors for their lectures, advice, and support. They each assisted me in invaluable ways, both on my research project and throughout the entire summer experience in Oregon. Our mentors included: Jorge Ramirez, Julia Jones, Rebecca Hutchinson, Tom Dietterich, Andy Moldenke, Eddie Helderop, Vera Pfeiffer, and Peggy Lee.

References

Byrne, Roger. "Basic Concepts V: Niche Concepts and Ecological Valency." *Geography 148-Biogeography Lecture*. UNIVERSITY OF CALIFORNIA, BERKELEY. Web. 17 Aug. 2014.

Dormann, Carsten. "Networklevel {bipartite}." *Inside-R*. Revolution Analytics. Web. 17 Aug. 2014. <http://www.inside-r.org/packages/cran/bipartite/docs/.networklevel>.

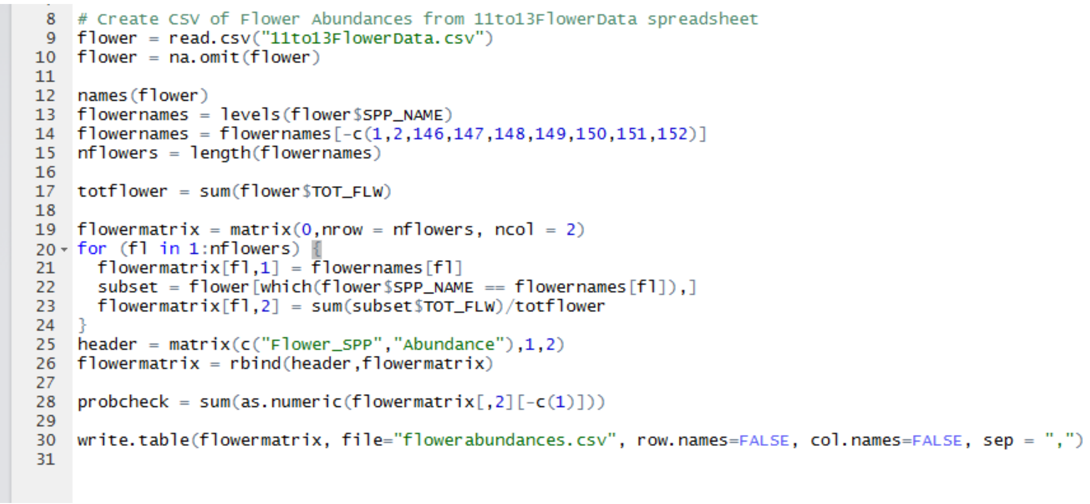
Dormann, Carsten F., Jochen Frund, Nico Bluthgen, and Bernd Gruber. "Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks." *The Open Ecology Journal* (2009): 7-24. Print.

Galeano, Javier, Juan M. Pastor, and Jose M. Iriondo. "Weighted-Interaction Nestedness Estimator (WINE): A New Estimator to Calculate over Frequency Matrices." *Environmental Modelling & Software* 24.11 (2009): 1342-346. Print.

Pfeiffer, Vera. "EISI Plant-Pollinator Network Project 2014." EISI REU Program. HJ Andrews Experimental Forest, Blue River, OR. 23 June 2014. Lecture.

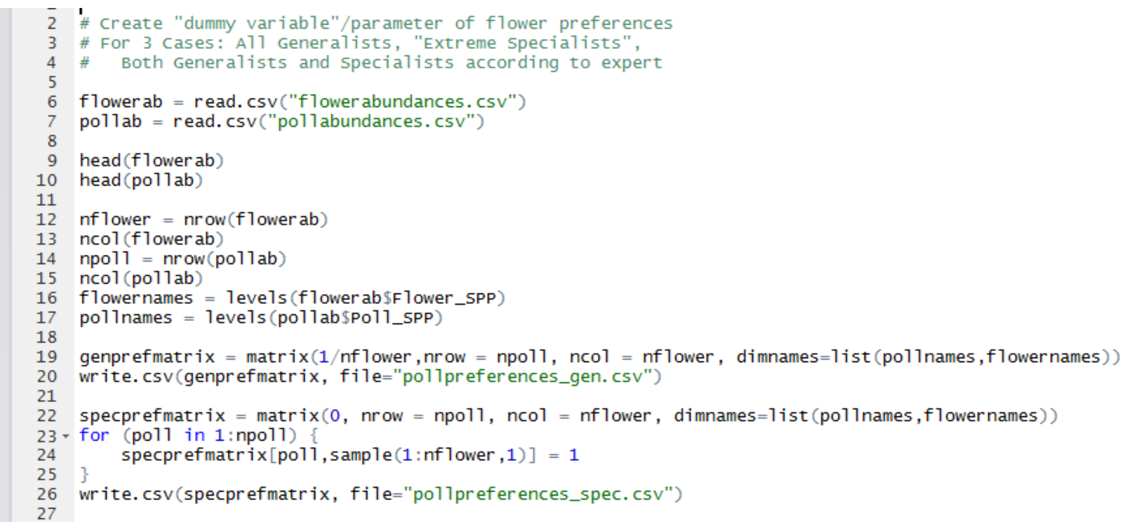
Staniczenko, Phillip P. A., Jason C. Kopp, and Stefano Allesina. "The Ghost of Nestedness in Ecological Networks." *Nature Communications*(2013): 1391. Print.

Appendix 1: R Code

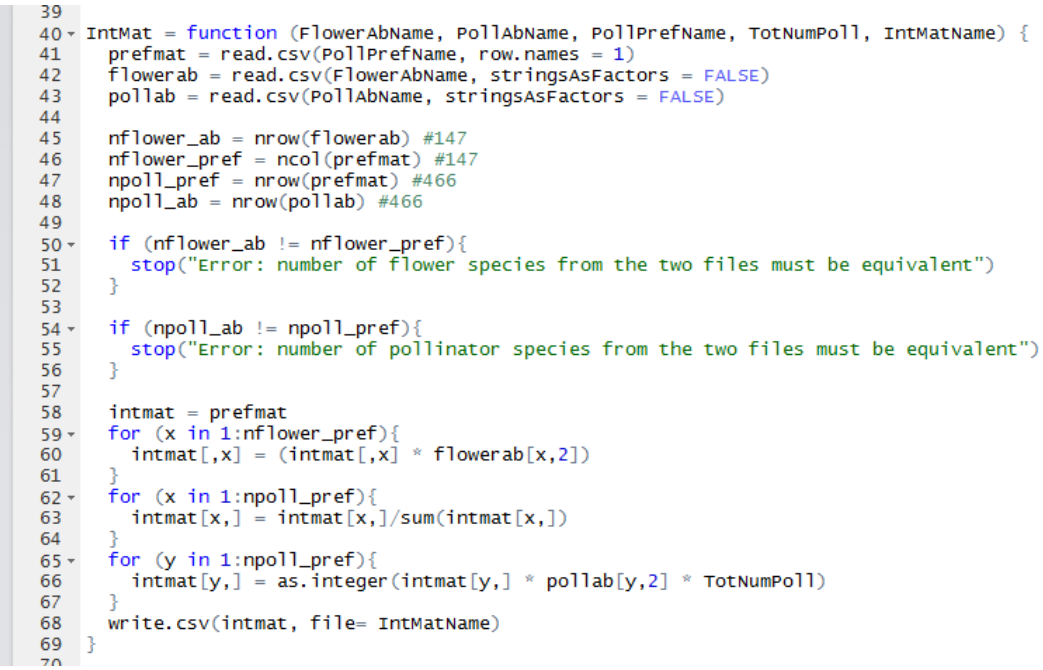


```r
# Create CSV of Flower Abundances from 11to13FlowerData spreadsheet
flower = read.csv("11to13FlowerData.csv")
flower = na.omit(flower)

names(flower)
flowernames = levels(flower$SPP_NAME)
flowernames = flowernames[-c(1,2,146,147,148,149,150,151,152)]
nflowers = length(flowernames)

totflower = sum(flower$TOT_FLW)

flowermatrix = matrix(0,nrow = nflowers, ncol = 2)
for (fl in 1:nflowers) {
  flowermatrix[fl,1] = flowernames[fl]
  subset = flower[which(flower$SPP_NAME == flowernames[fl]),]
  flowermatrix[fl,2] = sum(subset$TOT_FLW)/totflower
}
header = matrix(c("Flower_SPP","Abundance"),1,2)
flowermatrix = rbind(header,flowermatrix)

probcheck = sum(as.numeric(flowermatrix[,2][-c(1)]))

write.table(flowermatrix, file="flowerabundances.csv", row.names=FALSE, col.names=FALSE, sep = ",")

```

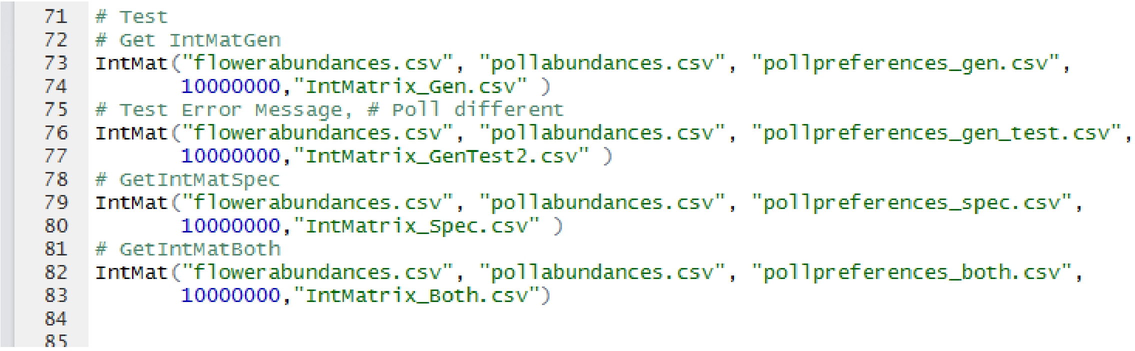
```r
# Create CSV of Pollinator Abundances (estimate) from 11to13Interactions spreadsheet

polldata = read.csv("11to13Interactions.csv")
pollspecies = levels(polldata$VISSP_NAME)
pollspecies = pollspecies[c(-1)]
npoll = length(pollspecies)

totalpoll = length(polldata$VISSP_NAME)

install.packages("hash")
library("hash")

pollhash = hash(keys = pollspecies, values = 0)
for (poll in 1:length(polldata$VISSP_NAME)) {
  if (nchar(as.character(polldata$VISSP_NAME[poll])) > 0) {
    pollname = as.character(polldata$VISSP_NAME[poll])
    pollhash[[pollname]] = pollhash[[pollname]] + 1
  }
}

pollmatrix = matrix(0,nrow = npoll, ncol = 2)
for (poll in 1:npoll){
  pollmatrix[poll,1] = pollspecies[poll]
  pollmatrix[poll,2] = pollhash[[pollspecies[poll]]] / totalpoll
}
header = matrix(c("Poll_SPP","Abundance"),1,2)
pollmatrix = rbind(header,pollmatrix)

sum(as.numeric(pollmatrix[,2][-c(1)]))

write.table(pollmatrix, file="pollabundances.csv", row.names=FALSE, col.names=FALSE, sep = ",")

```



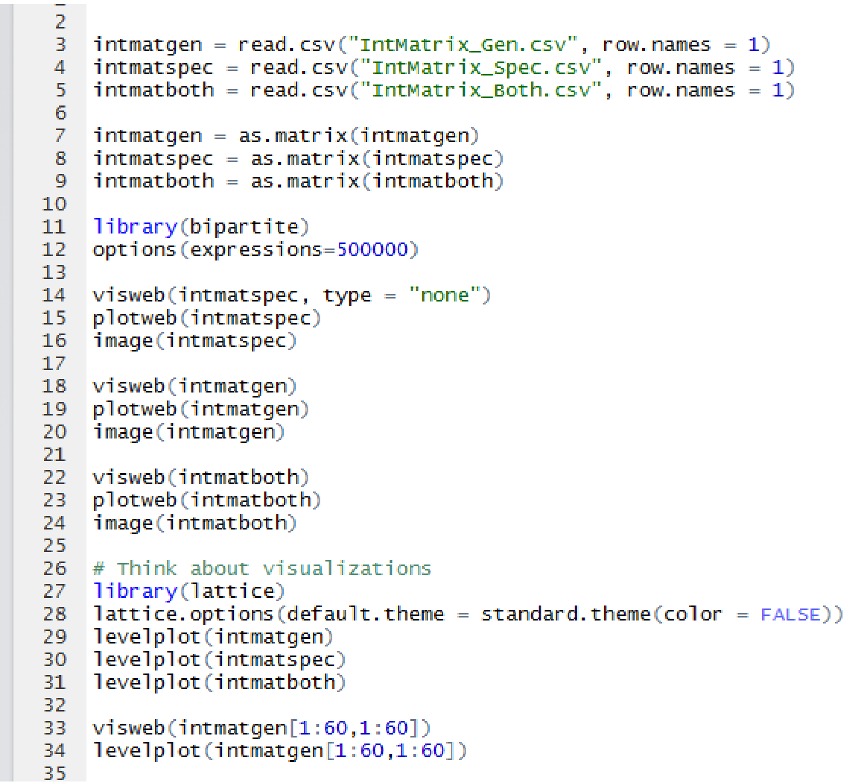
```r
# Create "dummy variable"/parameter of flower preferences
# For 3 Cases: All Generalists, "Extreme Specialists",
#   Both Generalists and Specialists according to expert

flowerab = read.csv("flowerabundances.csv")
pollab = read.csv("pollabundances.csv")

head(flowerab)
head(pollab)

nflower = nrow(flowerab)
ncol(flowerab)
npoll = nrow(pollab)
ncol(pollab)
flowernames = levels(flowerab$Flower_SPP)
pollnames = levels(pollab$Poll_SPP)

genprefmatrix = matrix(1/nflower,nrow = npoll, ncol = nflower, dimnames=list(pollnames,flowernames))
write.csv(genprefmatrix, file="pollpreferences_gen.csv")

specprefmatrix = matrix(0, nrow = npoll, ncol = nflower, dimnames=list(pollnames,flowernames))
for (poll in 1:npoll) {
    specprefmatrix[poll,sample(1:nflower,1)] = 1
}
write.csv(specprefmatrix, file="pollpreferences_spec.csv")

```



```r

IntMat = function (FlowerAbName, PollAbName, PollPrefName, TotNumPoll, IntMatName) {
  prefmat = read.csv(PollPrefName, row.names = 1)
  flowerab = read.csv(FlowerAbName, stringsAsFactors = FALSE)
  pollab = read.csv(PollAbName, stringsAsFactors = FALSE)

  nflower_ab = nrow(flowerab) #147
  nflower_pref = ncol(prefmat) #147
  npoll_pref = nrow(prefmat) #466
  npoll_ab = nrow(pollab) #466

  if (nflower_ab != nflower_pref){
    stop("Error: number of flower species from the two files must be equivalent")
  }

  if (npoll_ab != npoll_pref){
    stop("Error: number of pollinator species from the two files must be equivalent")
  }

  intmat = prefmat
  for (x in 1:nflower_pref){
    intmat[,x] = (intmat[,x] * flowerab[x,2])
  }
  for (x in 1:npoll_pref){
    intmat[x,] = intmat[x,]/sum(intmat[x,])
  }
  for (y in 1:npoll_pref){
    intmat[y,] = as.integer(intmat[y,] * pollab[y,2] * TotNumPoll)
  }
  write.csv(intmat, file= IntMatName)
}
```



```r
# Test
# Get IntMatGen
IntMat("flowerabundances.csv", "pollabundances.csv", "pollpreferences_gen.csv",
        10000000,"IntMatrix_Gen.csv" )
# Test Error Message, # Poll different
IntMat("flowerabundances.csv", "pollabundances.csv", "pollpreferences_gen_test.csv",
        10000000,"IntMatrix_GenTest2.csv" )
# GetIntMatSpec
IntMat("flowerabundances.csv", "pollabundances.csv", "pollpreferences_spec.csv",
        10000000,"IntMatrix_Spec.csv" )
# GetIntMatBoth
IntMat("flowerabundances.csv", "pollabundances.csv", "pollpreferences_both.csv",
        10000000,"IntMatrix_Both.csv")

```



```r

intmatgen = read.csv("IntMatrix_Gen.csv", row.names = 1)
intmatspec = read.csv("IntMatrix_Spec.csv", row.names = 1)
intmatboth = read.csv("IntMatrix_Both.csv", row.names = 1)

intmatgen = as.matrix(intmatgen)
intmatspec = as.matrix(intmatspec)
intmatboth = as.matrix(intmatboth)

library(bipartite)
options(expressions=500000)

visweb(intmatspec, type = "none")
plotweb(intmatspec)
image(intmatspec)

visweb(intmatgen)
plotweb(intmatgen)
image(intmatgen)

visweb(intmatboth)
plotweb(intmatboth)
image(intmatboth)

# Think about visualizations
library(lattice)
lattice.options(default.theme = standard.theme(color = FALSE))
levelplot(intmatgen)
levelplot(intmatspec)
levelplot(intmatboth)

visweb(intmatgen[1:60,1:60])
levelplot(intmatgen[1:60,1:60])

```

```r
# http://www.inside-r.org/packages/cran/bipartite/docs/.networklevel

networklevel(intmatspec,index = c("links per species", "nestedness", "weighted nestedness",
                                  "niche overlap", "extinction slope"))
# links per species          nestedness weighted nestedness    niche.overlap.HL    niche.overlap.LL
# 0.766447368         2.019611201                 NaN         0.000000000         0.006673128
# extinction.slope.HL extinction.slope.LL
# 2.784079121         0.990703001

networklevel(intmatgen,index = c("links per species", "nestedness", "weighted nestedness",
                                 "niche overlap", "extinction slope"))
# links per species          nestedness weighted nestedness    niche.overlap.HL    niche.overlap.LL
# 55.6933116           5.0265003           0.8159513           0.9270456           0.9990493
# extinction.slope.HL extinction.slope.LL
# 144.9721522          82.3241458

networklevel(intmatboth,index = c("links per species", "nestedness", "weighted nestedness",
                                  "niche overlap", "extinction slope"))
# links per species          nestedness weighted nestedness    niche.overlap.HL    niche.overlap.LL
# 51.8727569           1.7887376           0.7816295           0.8681998           0.8749648
# extinction.slope.HL extinction.slope.LL
# 134.0094497          63.9999371

```