

Comparing Plant-Pollinator Network Structure between Drought and Non-Drought Years

Aidan Fife

Emory University

Dr. Berry Brosi

Full-time Independent Research

2018

Abstract

Network analyses can be used to examine multi-species interactions and have been applied to many ecological interactions such as food webs, antagonistic relationships such as plant-herbivory, and mutualistic relationships. A particular focus has been on plant-pollinator interactions given their importance in driving terrestrial ecosystem functions. These networks can be structured with various attributes, which have been measured with network indices to describe the interactions. The indices of interest for this study are connectance, diversity of interactions, generality, vulnerability, nestedness, and specialization. Natural perturbations, such as drought or climate change, have the potential to alter the structure of these networks. We compared network structure between 2017, a year with normal precipitation and 2018, a year with extreme drought conditions in East River Valley in western Colorado, USA. Phenological mismatch and the decrease in relative abundances as a result of drought were predicted to cause changes in network structure. We constructed quantitative networks were built at three sites by collecting floral visitation data through capturing of pollinators. We compared the indices from 2017 and 2018 and the network structures showed a significant difference in diversity of interactions, meanwhile showing visible differences in connectance, nestedness, and specialization.

Introduction

Understanding the organization of ecosystems and how particular species interact has long been an objective of studying ecological systems (Ings et al. 2009). Using developments in theoretical modelling, ecologists now employ network analyses to investigate multi-species interactions. A network analysis is a tool to examine links between species to understand the broader patterns of the system (Brosi et al. 2017). This tool has grown more sophisticated and can be analyzed mathematically to evaluate various metrics that correspond to network stability and ecosystem function (Blüthgen et al. 2008; Ings et al. 2009).

Investigating natural perturbations of networks is a subsequent concern of network analyses and heightens their relevance. In particular, the mutualistic relationship between plants and pollinators has been subject to changes, specifically in climate (Post & Inouye 2008; Rosenzweig et al. 2008). Many ecosystems are affected by climate change, particularly an increase in temperature (IPCC 2007). In the last 20-50 years, plants in many systems have begun to flower earlier (Fitter & Fitter 2002). Some studies have found that plants and pollinators have different phenological environmental cues and therefore may respond differently to climate change (Visser & Both 2005). Therefore, climate warming may cause temporal mismatches in pollinator and plant interactions, potentially altering the structure of plant-pollinator networks (Hegland et al., 2009).

One prediction of climate change in the western United States is increased frequency and severity of drought as a consequence of decreased snow pack levels (Hanson & Weltzin 2000; Trenberth et al. 2014). While the effects of widespread temperature changes on plant-pollinator networks have been studied (Hegland et al. 2009; Forrest et al. 2010; Potts et al. 2010), the impact of drought on these networks had not been specifically examined. Generally, in agricultural systems, drought has been shown to negatively affect pollination by decreasing the amount of pollen and nectar produced by flowers, making them less attractive to pollinators (Alqudah et al. 2011). In a specific study drought caused significant negative responses for nectar volume and flower size in *Epilobium angustifolium* (Carroll et al. 2001). Furthermore, low levels of snow that melt out more quickly can advance phenological development (Wipf et al. 2009). Broadly, the temporal, phenological, and physiological changes induced by drought may cause organisms to shift their niches within a mutualistic network, altering its structure.

This investigation asks: How do plant-pollinator network structures differ between drought and non-drought years? We compared the plant pollinator network structure of high alpine communities in a normal precipitation year (2017) and a severe drought year (2018).

The specific structural indices that were compared were connectance, Shannon diversity of interactions, generality, vulnerability, nestedness, and specialization. Connectance is defined as the number of links realized out of the possible interactions within a network (Dunne et al. 2002). Diversity of interactions accounts for the richness and evenness of the interactions within the network (Fabian et al. 2013). Generality is concerned with the number of plant species per type of pollinator, while vulnerability pertains to the number of different pollinators per plant species. Nestedness is the degree to which specialists interact with proper subsets of the species interacting with generalists (Dormann et al. 2009). Finally, specialization is the dependency of each species on a few exclusive partners (Blüthgen et al. 2006).

I predicted that floral phenology will shift earlier in the drought year with less snow pack (Forrest et al. 2010; Caradonna et al. 2014), causing structural changes to the plant-pollinator network when compared to a non-drought year. An advanced shift in floral phenology during a drought year may have implications for plant-pollinator network structure. Hypothesized changes in network indices were listed below:

H₁: Connectance was hypothesized to decrease during a drought, with temporal links being disrupted and specialization being increased. Additionally, a decrease in flower attractiveness could have resulted in fewer connections between pollinators and plants (Alqudah et al. 2011; Carroll et al. 2001).

H₂: Shannon diversity of interactions was hypothesized to decrease as a result of disturbance of temporal links (Blüthgen et al 2008).

H₃: Generality is hypothesized to decrease because of the disruption of temporal links.

H₄: Vulnerability is hypothesized to increase because of fewer flowers available.

H₅: Nestedness was hypothesized to decrease as a result of diminishing community stability (Blüthgen et al 2008).

H₆: Specialization was hypothesized to increase with greater competition between species. (Blüthgen & Klein 2011).

Methods

Experimental Design

We conducted this investigation at three subalpine meadow sites around Gothic, CO (38.9 564° N, 107.0106° W): Avery Picnic, Gothic Town, and Virginia Basin (Figure 1).

Replicating the experimental methodology in 2017 and 2018, we collected data to build quantitative networks using four 20 x 1 meter transects at each site. At each 2 x 1 meter section, we surveyed and counted all flowering plants each week, recording number of flowers per individual. We sampled floral visitation along transects weekly. We observed each section for 3 minutes, totaling 120 minutes of observation of the transect area per week. When we observed a pollinator come into contact with reproductive structures of plants in anthesis, or fully open, we captured these pollinators and immediately identified them to one of 30 categories of gross identification. We destructively sampled the pollinators, except birds, species of bumblebees (*Bombus spp.*), and butterflies, to preserve those populations. We noted the species of plant and will later identify the destructively sampled pollinator species in the lab. We recorded hummingbird interactions and we released the captured bumble bees and butterflies after being uniquely marked with a paint pen.

To affirm and record the difference in levels of drought between 2017 and 2018, the two years of data comparison, the winter weather data indicates snowpack of 2017 being 977.9 cm compared to 490.2 cm in 2018. Additionally, the snow melted out in May 24th of 2017 compared to May 5th in 2018 (Gothic Weather Station)

Data Analysis

Pollinator visitation data was analyzed using the *bipartite* package in the R statistical programming language (Dormann et al. 2009). Connectance was measured as “realised proportion of possible links” $C = L/(IJ)$ (Dunne et al. 2002) which was calculated as the sum of links divided by number of cells in the matrix (Gotelli & Graves 1996). Diversity of interactions was calculated, taking into account species richness and evenness (Dormann et al. 2009). Nestedness was calculated on a scale from 0 to 100, with 0 representing maximum nestedness when pollinators and plants are ordered in decreasing number of links (Dormann et al. 2009). We used null models to ensure that the nestedness metrics represented significant data. Specialization on the network-level was calculated as H2’ which can range from 0 (no specialization) to 1 (complete specialization) (Blüthgen et al. 2006). These indices, calculated by R, were the dependent variables for the project, affected by the independent variable of drought. A paired t-test was used to determine the variation between years for each metric.

Results

Figure 1: Network metrics across three sites from 2017 and 2018

	Connectance		Diversity of interactions		Generality		Vulnerability		Nestedness		Specialization	
	2017	2018	2017	2018	2017	2018	2018	2018	2017	2018	2017	2018
Avery Picnic	0.178	0.275	2.81	3.46	5.87	6.87	2.15	3.35	0.28	0.28	0.24	0.24
Gothic Town	0.175	0.213	2.72	3.00	2.78	2.89	4.49	5.68	0.17	0.17	0.23	0.23
Virginia Basin	0.178	0.179	2.44	3.01	5.02	4.00	2.05	3.04	0.23	0.23	0.32	0.32
<i>Paired t-test results</i>	p = 0.123		p = 0.024		p = 0.482		p = 0.002		p = 0.194		p = 0.251	

Figure 2: Numbers of observed plants and pollinators in each site

	Avery Picnic		Gothic Town		Virginia Basin	
	2017	2018	2017	2018	2017	2017
Number of Observed Pollinators	16	15	19	17	21	17
Number of Observed Plants	20	16	18	16	23	20

Connectance

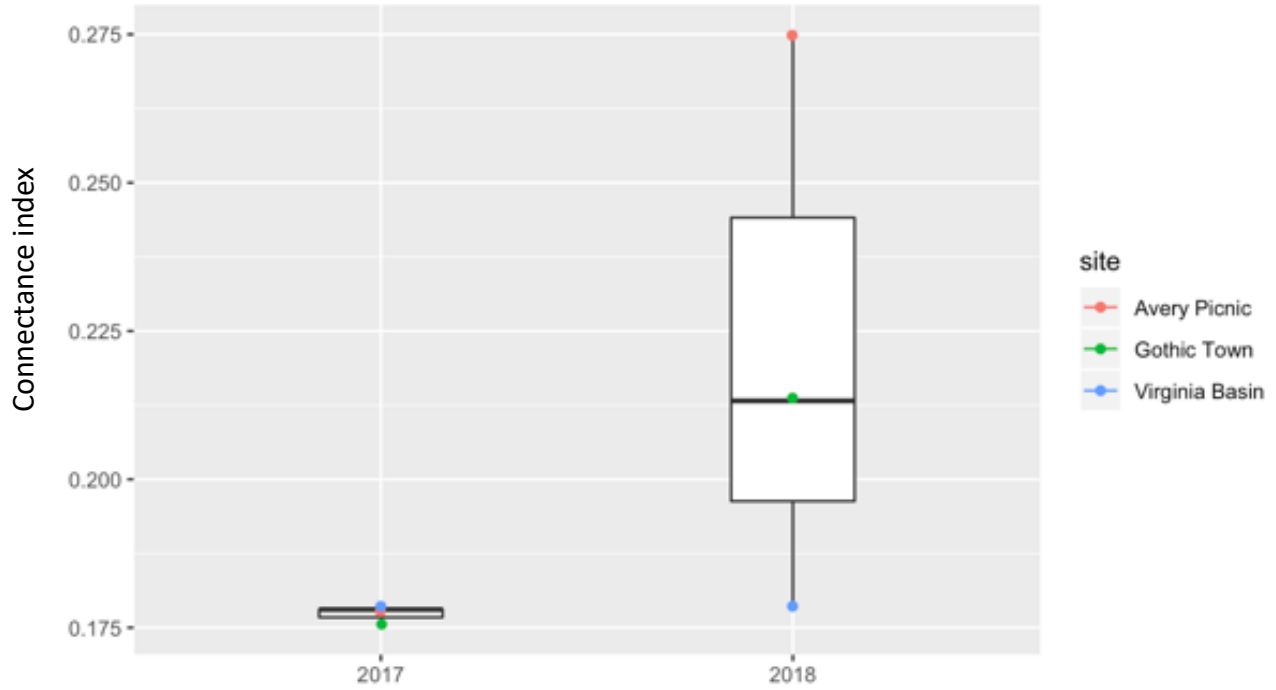


Figure 3: Connectance comparison of 2017 and 2018 between three sites

Diversity of interactions

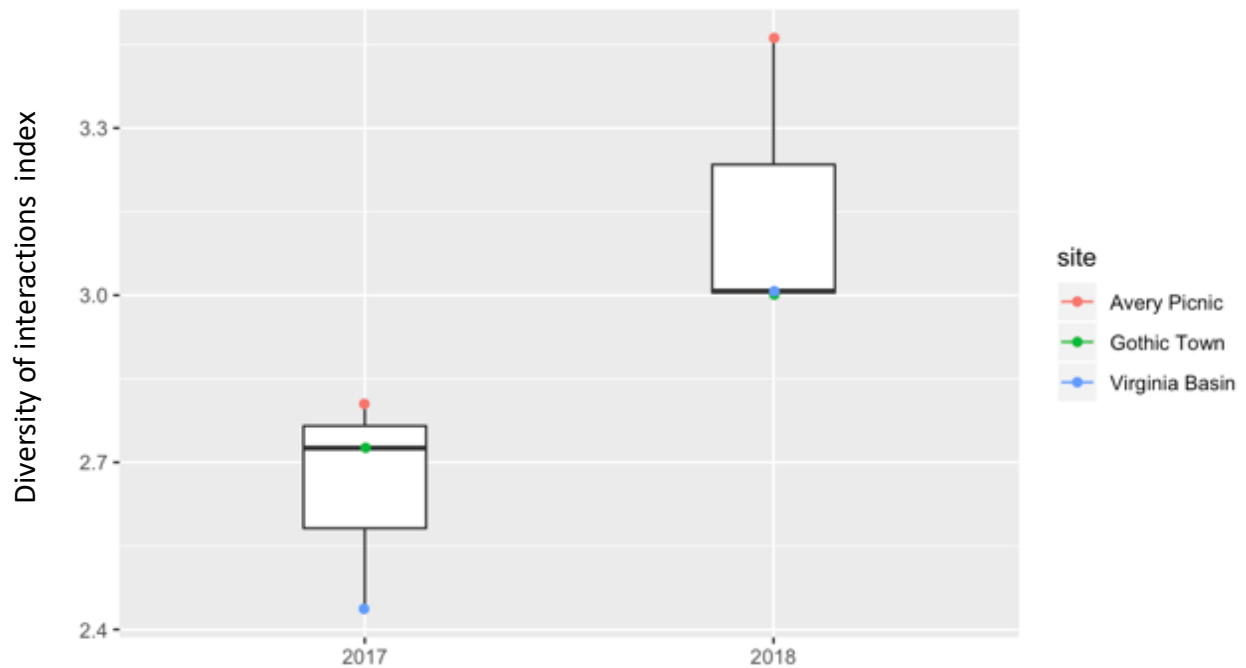


Figure 4: Shannon diversity of interactions comparison of 2017 and 2018 between three sites

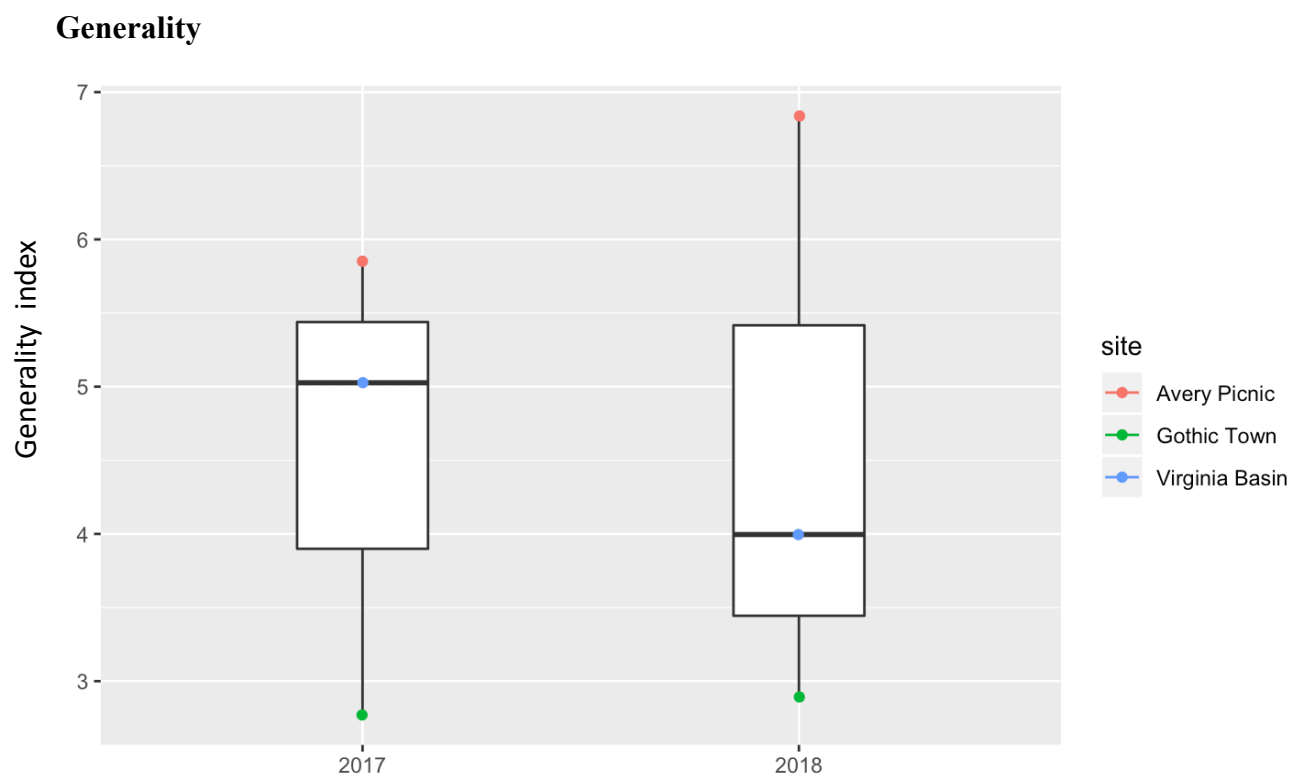


Figure 5: Generality comparison of 2017 and 2018 between three sites

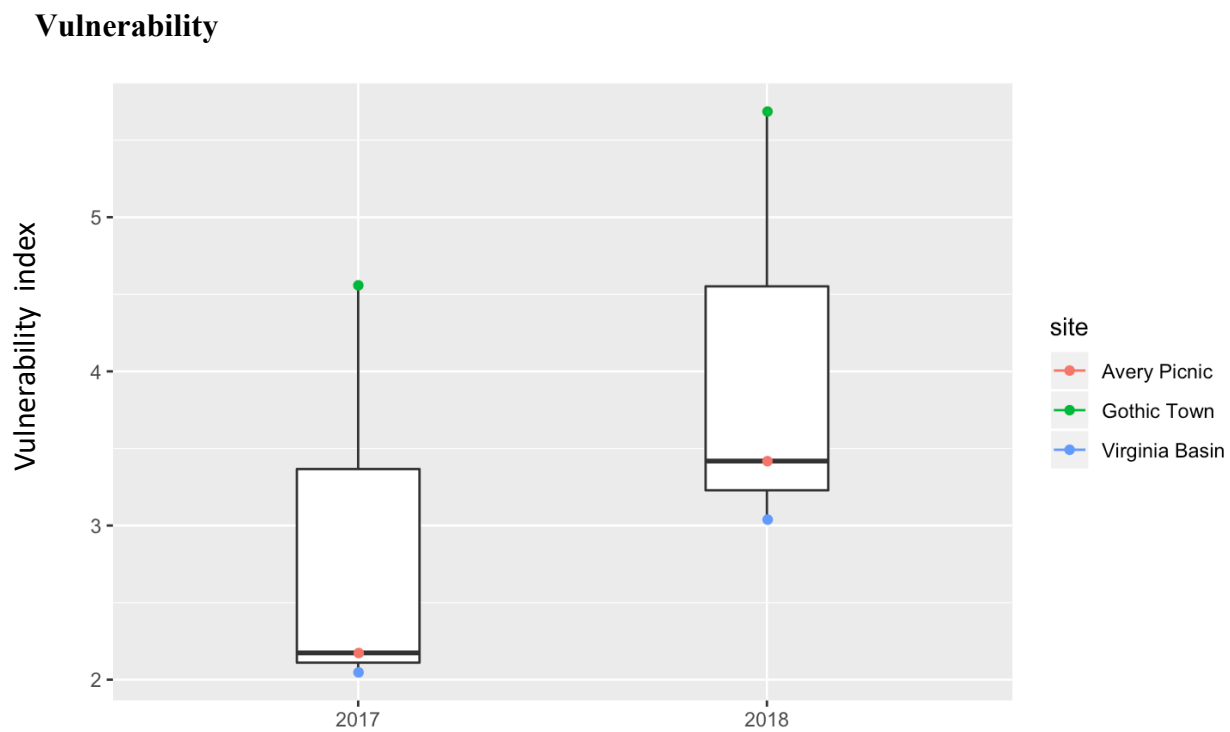


Figure 6: Vulnerability comparison of 2017 and 2018 between three sites

Nestedness

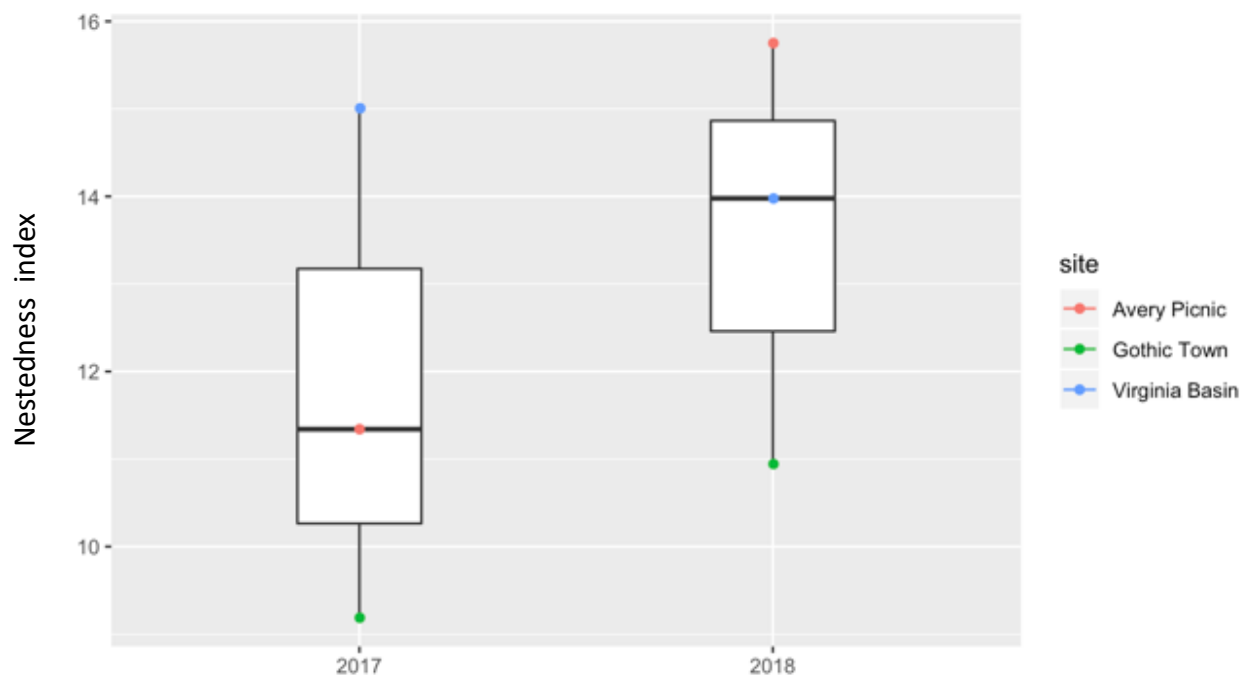


Figure 7: Connectance comparison of 2017 and 2018 between three sites

Specialization

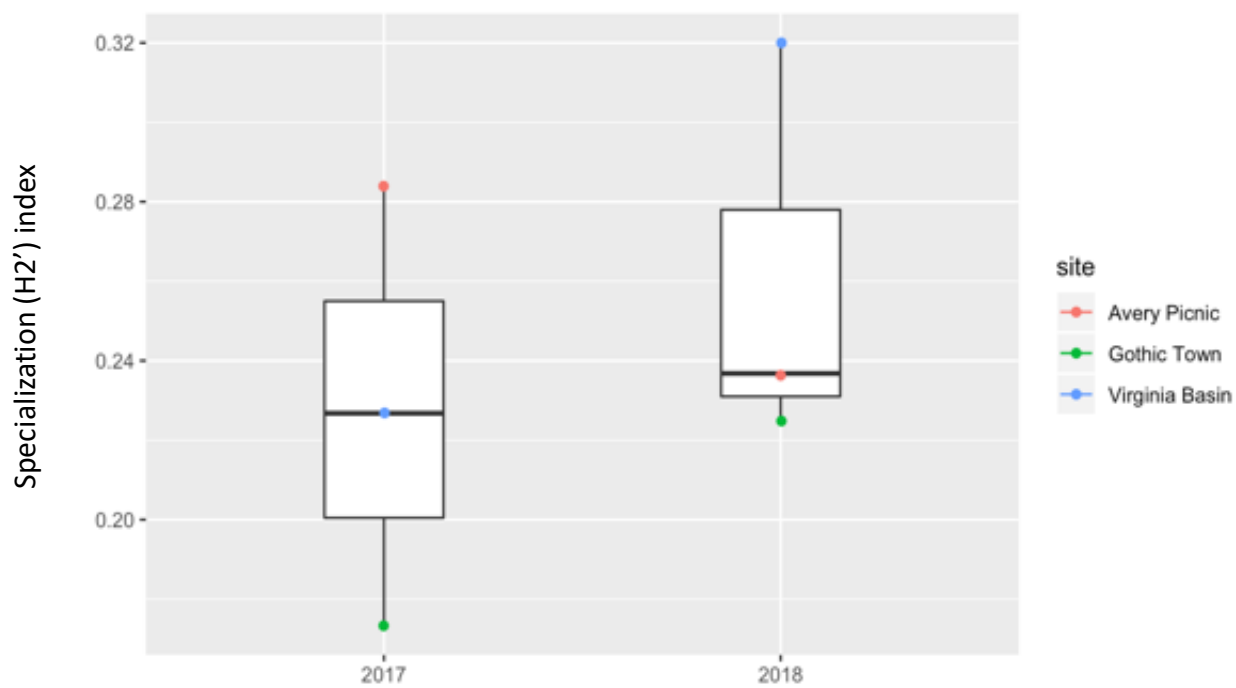


Figure 8: Specialization (H_2') comparison of 2017 and 2018 between three sites

Discussion

Connectance

Across all sites, the measure of connectance increased from 2017 to 2018 yet this was not significant ($p = 0.123$). The trends were towards greater proportions of realized links in 2018 compared to 2017. This was contrary to our predictions of decreased connectance in a drought year as a result of phenological mismatch and plants and pollinators being mistimed. However, the drought year showed greater connectance, meaning that there were proportionally more links realized.

One possible reason for this phenomenon is that in all sites, there were a greater number of plants species and pollinator categories observed in pollination events in 2017, the non-drought year (Figure 2). With a greater number of species present in 2017, there had to be more interactions to have comparable connectance metrics to 2018 when there were fewer species present in the network. Regardless, the greater number of species present in the non-drought year compared to the drought year indicates a difference in the composition of species in the networks that changed during a variation in abiotic stress between 2017 and 2018.

Diversity of interactions

Like connectance, diversity of interactions increased at all sites. The differences between 2017 and 2018 were statistically significant ($p = 0.0235$).

At the Avery Picnic site, for example, the most dominant generalist species in a “typical” non-drought year had less of strong presence in the drought year of 2018. The category of pollinators that visited the most flower species in Avery Picnic was “Other fly” in both years. In 2017, however, the “Other fly” category dominated the network, while in 2018 the pollinators were more balanced, with hemipterans accounting for nearly an equal percentage of floral visitation at Avery Picnic. A similar phenomenon occurred amongst the flowering plants, with the generalist *Potentilla gracilis* being visited most in 2017 but only accounting for the fourth most visits in 2018 (Figure 7)

Likewise, at the Gothic Town site, the category of pollinators that vastly visited the most flower species at the Gothic Town site was “Other fly” in 2017, while hemipterans visited the most flower species in 2018 (Figure 8). Finally, at Virginia Basin, the category of pollinators that visited the most flower species in Virginia Basin was “Other fly” in both years. In 2017, the “Other fly” category of pollinators dominated the distribution of pollinator categories while in 2018, small black solitary bees, wasps, syrphidae flies, and hemipterans were more present. (Figure 9)

The general trend of the most dominant generalists in the network yielding to other species in a drought year could be representative of many factors. One possible reason for this occurrence could be the diminishing success of both the “Other fly” category of pollinators and *Potentilla gracilis* in drought conditions. However, it is additionally likely that both pollinators and plants had more generalized pollination strategies to account for abiotic stress.

Vulnerability / Generality

The metrics of vulnerability and generality have a larger narrative about plants and pollinators and their new temporal arrangement in a drought-year. The unchanging generality metric (Figure 5) indicates that pollinators did not change their niche breadth. The vulnerability metric (Figure 6) represents more visiting pollinators per flower species. From personal qualitative observation, we saw many pollinators visiting few plants during times when only a few flowers were in bloom. This supports the idea that phenological mismatch and changes in temporal relationships have had an effect on the networks. The sites consistently show a change in vulnerability and a significant p-value (0.002).

Nestedness

In general, the sites showed higher level of nestedness from 2017 to 2018 but this was not significant ($p = 0.194$). This metric was compared to null models to determine if the reported level of nestedness is significantly different from randomly generated networks of similar dimensions.

Specialization

Though not statistically significant, specialization ($H2'$) was greater in 2018 in comparison to 2017, offering some insight on network composition between the two years. The measure that was used ($H2'$) is intended to characterize the degree of specialization and partitioning among two parties in the network. Perhaps as a result of abiotic stress, both pollinators and plants became less specialized on the whole. While network size may affect other metrics, it has been shown not to affect specialization (Bluthgen et al., 2006)

Conclusions and Future Directions

Other studies have made generalizations about the combined occurrence of multiple changes in network metrics. More instability has been said to be generated by the simultaneous increase of connectance and diversity (May 1973; Gross 2009). Within this study, these two metrics showed the most visible changes, both increasing in the drought year. Based on this premise, the networks during the time of drought and abiotic stress could be experiencing more instability. The trends shown in the metrics of these networks may be attributed to phenology. The timings of maturation of plants and pollinators may produce the emergence of observable patterns in plant-pollinator networks (Encinas-Viso et al., 2012).

In the future, these metrics and network structures may gain even more clarity when the gross identifications of the pollinators are converted to fine identifications to the level of species. While gross identifications are helpful for visualizing larger trends in the network data, the fine identifications will get to the see the acute interactions between species. Additionally, these data may be analyzed to see temporal trends in phenology.

Literature Cited

- Alqudah, A. M., Samarah, N. H., & Mullen, R. E. (2010). Drought Stress Effect on Crop Pollination, Seed Set, Yield and Quality. *Alternative Farming Systems, Biotechnology, Drought Stress and Ecological Fertilisation*, 193-213. doi:10.1007/978-94-007-0186-1_6
- Blum, A. (1996). Crop responses to drought and the interpretation of adaptation. *Drought Tolerance in Higher Plants: Genetical, Physiological and Molecular Biological Analysis*, 57-70. doi:10.1007/978-94-017-1299-6_8
- Blüthgen, N., Fründ, J., Vázquez, D. P., & Menzel, F. (2008). What Do Interaction Network Metrics Tell Us About Specialization And Biological Traits. *Ecology*, 89(12), 3387-3399. doi:10.1890/07-2121.1
- Blüthgen, N., & Klein, A. (2011). Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology*, 12(4), 282-291. doi:10.1016/j.baae.2010.11.001
- Blüthgen N, Menzel F, Blüthgen N. (2006) Measuring specialization in species interaction networks. *BMC Ecology*. 2006;6(1):9. doi: 10.1186/1472-6785-6-9.
- Brosi, B. J., Niezgodá, K., & Briggs, H. M. (2017). Experimental species removals impact the architecture of pollination networks. *Biology Letters*, 13(6), 20170243. doi:10.1098/rsbl.2017.0243
- Caradonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences*, 111(13), 4916-4921. doi:10.1073/pnas.1323073111
- Carroll, A. B., Pallardy, S. G., & Galen, C. (2001). Drought Stress, Plant Water Status, and Floral Trait Expression in Fireweed, *Epilobium angustifolium* (Onagraceae). *American Journal of Botany*, 88(3), 438. doi:10.2307/2657108
- Dormann, C.F., Fruend, J., Bluethgen, N. & Gruber B. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7-24.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002 Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Science USA*
- Encinas-Viso, F., Revilla, T. A., & Etienne, R. S. (2012). Phenology drives mutualistic network structure and diversity. *Ecology Letters*, 15(3), 198-208. doi:10.1111/j.1461-0248.2011.01726.x
- Fabian, Yvonne, et al. “The Importance of Landscape and Spatial Structure for Hymenopteran-Based Food Webs in an Agro-Ecosystem.” *Journal of Animal Ecology*, vol. 82, no. 6, 2013, pp. 1203–1214., doi:10.1111/1365-2656.12103.

- Fitter, A.H. & Fitter, R.S.R. (2002). Rapid changes in flowering time in British plants. *Science*, 296, 1689–1691.
- Forrest, J., Inouye, D. W., & Thomson, J. D. (2010). Flowering phenology in subalpine meadows: Does climate variation influence community co-flowering patterns? *Ecology*, 91(2), 431-440. doi:10.1890/09-0099.1
- Gezon, Zachariah & Wyman, Eli & Ascher, John & Inouye, David & E. Irwin, Rebecca. (2015). The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology and Evolution*. 6. 10.1111/2041-210X.12375.
- Gross, T., Rudolf, L., Levin, S. & Dieckmann, U. (2009). Generalized models reveal stabilizing factors in food webs. *Science*, 325, 747–750.
- Gotelli, N. J., and G. R. Graves. 1996 Null Models in Ecology. *Smithsonian Institution Press*, Washington D.C.
- Gothic Weather Station. Barr, B. (2018). Retrieved from <http://www.gothicwx.org/>
- Hanson, P. J., & Weltzin, J. F. (2000). Drought disturbance from climate change: Response of United States forests. *Science of The Total Environment*, 262(3), 205-220. doi:10.1016/s0048-9697(00)00523-4
- Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, 12(2), 184-195. doi:10.1111/j.1461-0248.2008.01269.x
- Ings, T. C., Montoya, J. M., Bascompte, J. , Blüthgen, N. , Brown, L. , Dormann, C. F., Edwards, F. , Figueroa, D. , Jacob, U. , Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., Van Veen, F. F., Warren, P. H. and Woodward, G. (2009), Review: Ecological networks – beyond food webs. *Journal of Animal Ecology*, 78: 253-269. doi:[10.1111/j.1365-2656.2008.01460.x](https://doi.org/10.1111/j.1365-2656.2008.01460.x)
- IPCC (2007). *Intergovernmental Panel on Climate Change, Fourth Assessment Report, Climate Change 2007: Syntheses Report*. UNEP, Genève.
- Lance, R. F., Bailey, P., Lindsay, D. L., & Cobb, N. S. (2017). Precipitation and the robustness of a plant and flower-visiting insect network in a xeric ecosystem. *Journal of Arid Environments*, 144, 48-59. doi:10.1016/j.jaridenv.2017.03.015
- May, R. (1973). Stability and complexity in model ecosystems. *Princeton University Press*, Princeton, NJ.
- Post, E.S. & Inouye, D.W. (2008). Phenology: response, driver, and integrator. *Ecology*, 89, 319–320.

- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), 345-353. doi:10.1016/j.tree.2010.01.007
- Trenberth, K. E., Dai, A., Schrier, G. V., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, 4(1), 17-22. doi:10.1038/nclimate2067
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G. et al. (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature*, 453, 353–357.
- Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant-animal mutualistic networks: A review. *Annals of Botany*, 103(9), 1445–1457.
- Visser, M.E. & Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B-Biol. Sci.*, 272, 2561–2569.
- Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: Plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, 94(1-2), 105-121. doi:10.1007/s10584-009-9546-x

Tables and Figures

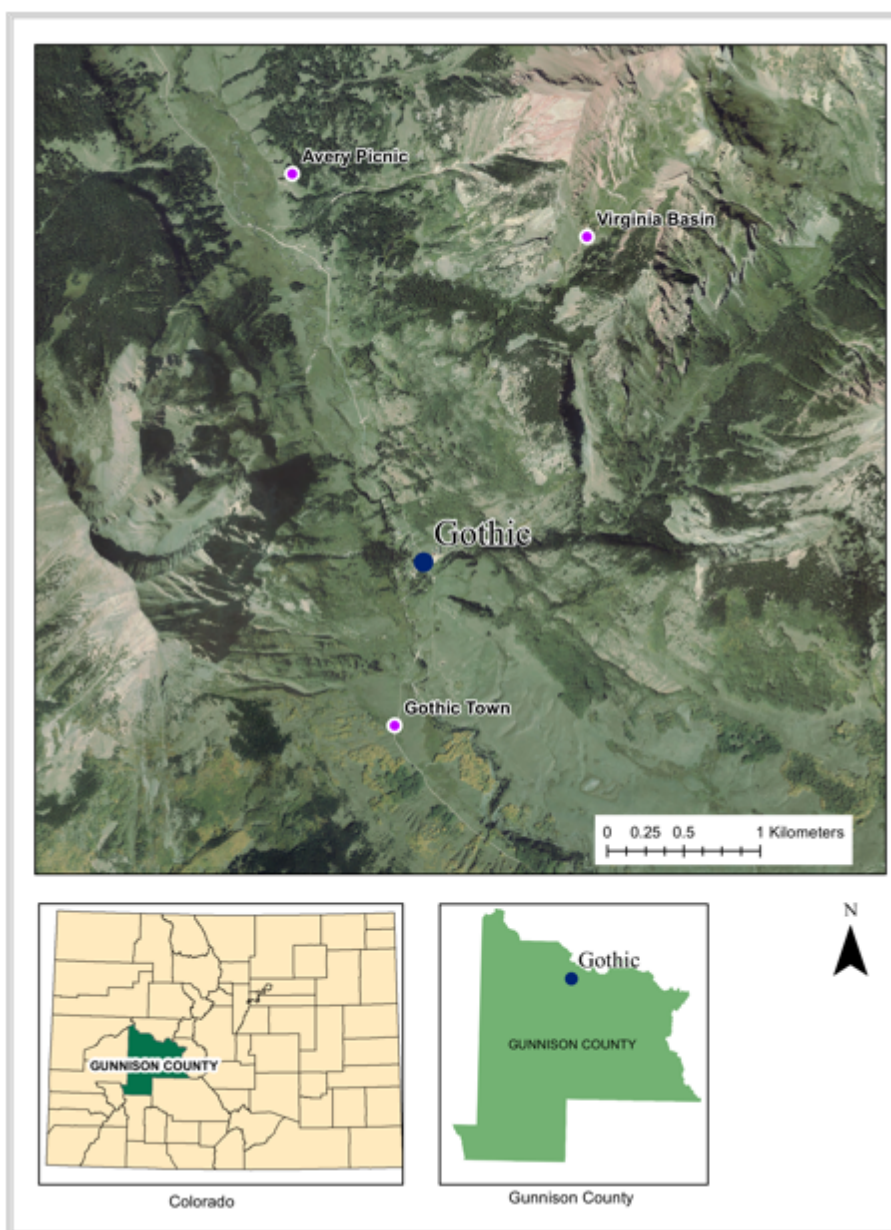


Figure 1: Map of three subalpine meadow sites (Avery Picnic, Virginia Basin, Gothic Town) in Gothic, Gunnison County, Colorado, USA.

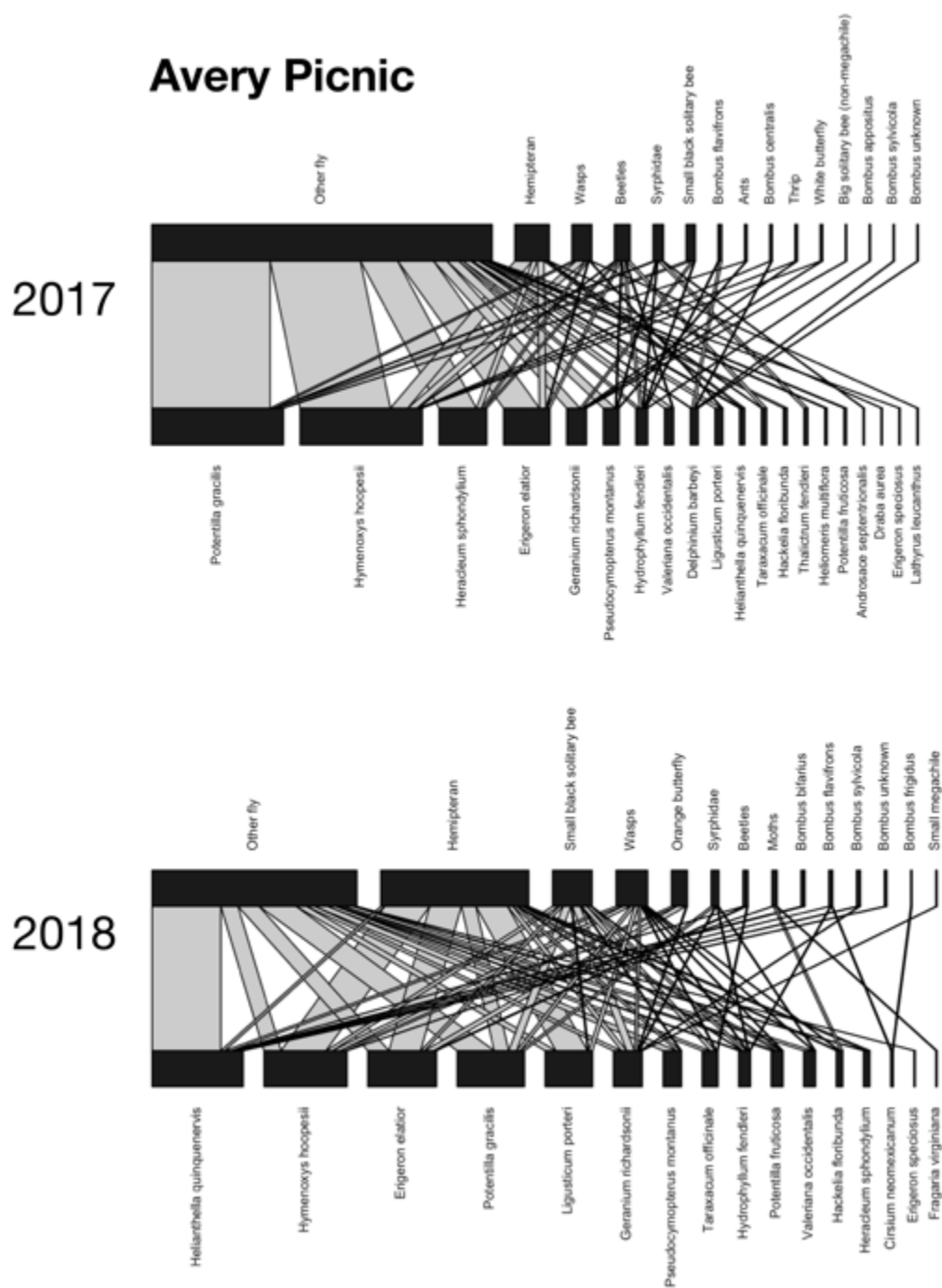


Figure 7: Bipartite graph comparing networks from 2017 and 2018 at Avery Picnic site

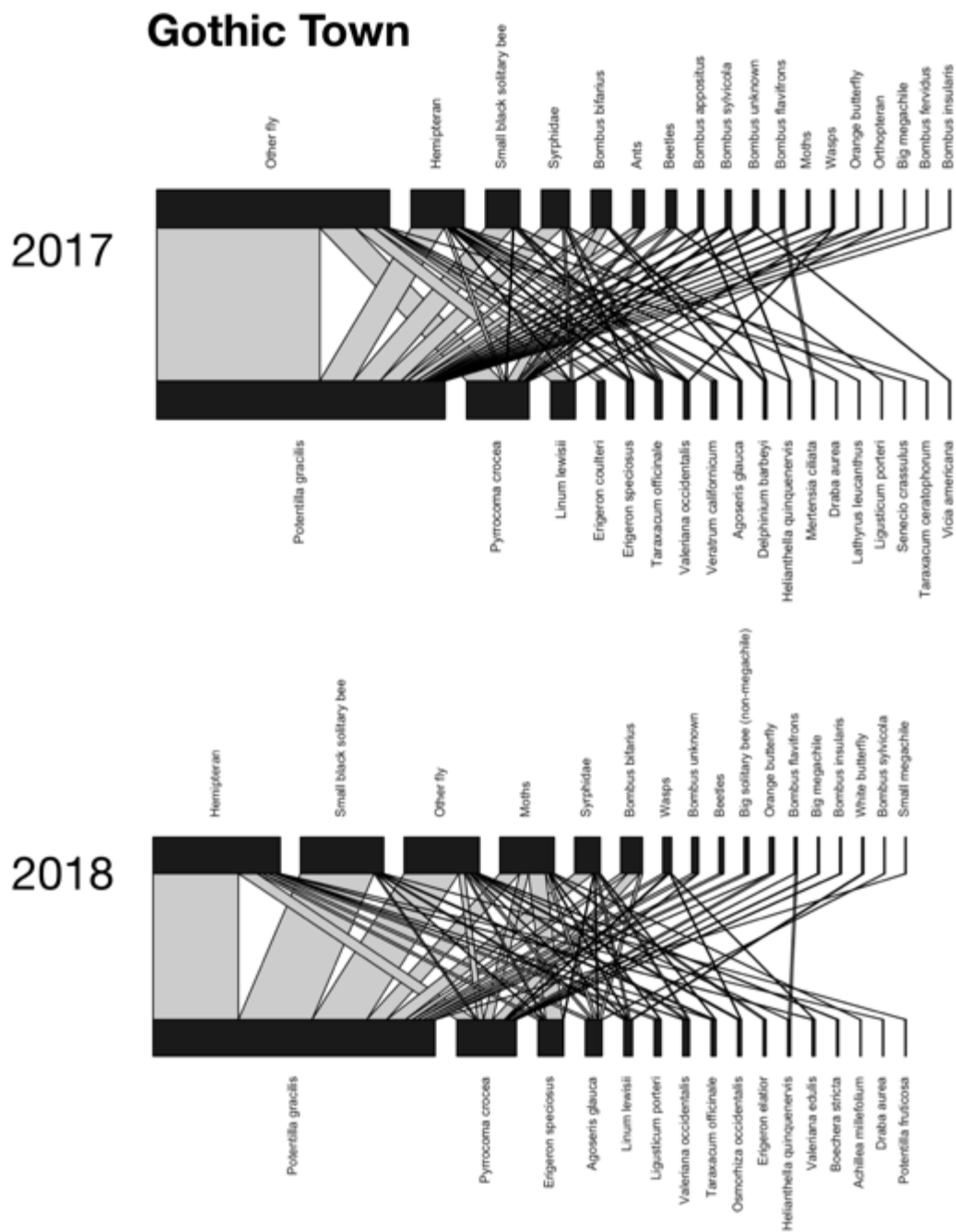


Figure 8: Bipartite graph comparing networks from 2017 and 2018 at Gothic Town site

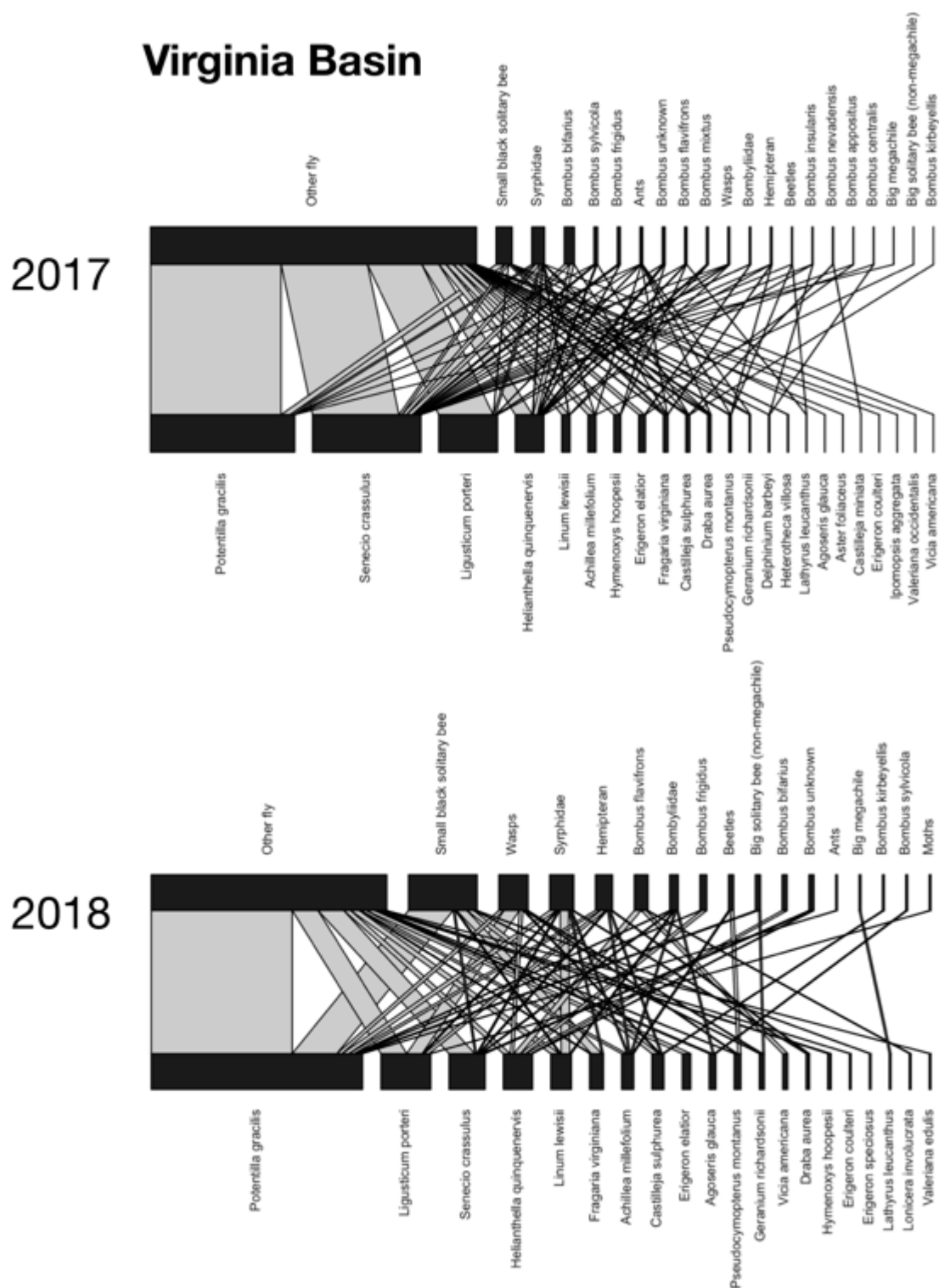


Figure 9: Bipartite graph comparing networks from 2017 and 2018 at Virginia Basin site