

Niche breadth changes in response to environmental perturbation: the impact of early snowmelt on subalpine plant-pollinator specialization

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Abstract

With global climate change, we observe phenological changes across all ecosystems. In the Colorado Rocky Mountains, warming is resulting in lower snowpack and earlier spring melt. Since plants use snow melt timing as a cue to start growing, climate change is implicated in accelerated bloom time and thus has the potential to cause a phenological mismatch between plants and their pollinators. To account for this mismatch, pollinators may change the plant species they interact with (i.e. their niche breadth) to account for the difference in timing of floral resources. This could include wholesale switching to a new resource, changing the number of species they visit, or instead could change the frequency of their visits to different plants. In this study, we investigated the impact of an environmental perturbation on plant-pollinator niche breadth, focusing on if and how niche breadth changes. We perturbed the system by inducing a phenological change by manipulating the timing of snowmelt which in turn accelerated bloom time by approximately two weeks. Our study thus tested for a phenological mismatch between plants and pollinators. Under this manipulation, in accelerated-snowmelt plots, we found that pollinators foraged on more diverse plants while maintaining the number of plant species they visited. We expect pollinators to expand their niche breadth in order to receive enough floral resources. In changing their own niche breadth, pollinators also broaden plant niche breadth. Consequently, we expect both plants and pollinators to face uncertainties and challenges due to phenological change.

Introduction

Phenology describes the timing of seasonal or cyclical life events and influences many life history traits. Across all ecosystems, climate change has been observed to alter phenology (Parmesan and Yohe 2003). Climate change is impacting ecosystems in the Colorado Rocky Mountains through microhabitat differences in snow accumulation and melting patterns; lower snowpack results in earlier snowmelt, which initiates the growing season (Inouye 2008). Early snowmelt is one key driver that is expected to cause phenological change (Sparks and Menzel 2002, Parmesan and Yohe 2003) by altering temperature and water availability, and triggering earlier flowering events (Fitter and Fitter 2002, Visser and Both 2005). Significant changes in flower phenology due to climate change have been well documented (CaraDonna et al. 2014, Inouye 2008, Livensperger et al. 2016, Sparks and Menzel 2002). However, it is relatively unknown how phenological change will impact pollinators, and if the phenological changes observed in plants will be commensurate in pollinators (Fitter and Fitter 2002, Visser and Both 2005).

Temperature strongly impacts both plant and pollinator development, but through different mechanisms (Forrest and Thomson 2011). Therefore, plant-pollinator communities may be affected when the abiotic cues that influence plant phenology, such as timing of snowmelt, and cues that influence pollinator emergence timing, such as number of degree-days, shift differentially due to climate change. However it remains unknown if these cues will decouple

enough to result in a phenological mismatch (Forrest and Thomson 2011). A phenological mismatch shifts the life events of plants and pollinators to a point where flowers bloom out of sync from their pollinators and limits plant reproduction (Kudo and Ida 2013). The degree and direction of phenological change has been observed to be highly species-specific in both plants and pollinators (Forrest and Thomson 2011, CaraDonna et al. 2014) yet we do not know the consequences on the community-level. Here I investigate the impacts of phenological change to whole communities of plants and pollinators since most systems are networks of many interacting species and thus phenological mismatch on the community level has implications for network structure, function, and stability.

Within plant-pollinator systems, the decoupling of plant and pollinator timing cues may result in pollinators foraging on different or unfamiliar plants. The extent to which pollinators can adapt to future climate change conditions remains largely unknown and exploring whether changes in pollinators' niche breadth occur after environmental perturbation can provide valuable insight into the potential consequences for phenological mismatch. Most plant-pollinator communities contain both generalist and specialist species, where generalists interact with many partners and specialists interact with few. Generalist pollinators take advantage of many floral resources, but may experience more competition while specialist pollinators have less competition, but access to fewer floral resources that may make them more prone to collapse if their one resource fails to provide. Specialist pollinators can also be more efficient foragers because they may spend less time per flower (Strickler 1979). In plants, generalist species are pollinated by many different pollinator individuals and species and may be more likely to receive heterospecific pollen (Brosi and Briggs 2013). While this is less likely to occur for specialist species, they are visited by fewer pollinators and are therefore more vulnerable to species collapse (Brosi and Briggs 2013). Broadly, generalists may have a higher quantity of interactions at the expense of quality, while specialists may instead focus on higher quality interactions at the expense of quantity (Brosi 2016). Here, we define a species' niche as the number and identity of its interaction partners. Accordingly, a generalist would have a broad niche breadth with many partners and a specialist would have a narrower niche breadth comprised of fewer species. There is evidence of declines in specialist bees, most likely due to phenological mismatch, with generalist bees replacing them in networks, despite generalists being less efficient foragers and more likely to compete for the same resources (Miller-Struttmann et al. 2015). Given our lack of understanding on how plant-pollinator interactions may shift, especially after perturbation, it is important that we explore ways to predict the nature of these shifts.

Here, we compare pollinator visitation in control and accelerated snowmelt plots to address the impact of early snowmelt on plant-pollinator niche breadth. Specifically, we studied how a pollinator's niche breadth changes after accelerated snowmelt and if a change in flower phenology impacted pollinator niche breadth. We expected pollinators to expand their niche

breadth and exhibit more generalist foraging behavior to accommodate the altered floral resources available due to early snowmelt.

Methods

Study area

We studied 16 plots across 8 subalpine meadow sites with similar plant composition around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (38°57' N, 106°59' W; Figure 1). Sites were at least 0.5km apart within the East River Valley and Washington Gulch Valley. Meadows were selected for similar plant composition across the sites.

Snowmelt manipulation

We induced a phenological change by staking a black shade cloth within 10m x 14m plots about 5-6 weeks before the expected melt date, accelerating snowmelt by approximately 2 weeks (*sensu* Steltzer et al. 2009). We assessed the impact of accelerated snowmelt with paired control and manipulated plots at each site (paired for slope, aspect, and plant community similarity). We removed shade cloth once 80% of the manipulated plot was melted out. The control plot was allowed to melt out ambiently.

Plant-pollinator interaction sampling

We observed floral visitation of all animals (hereafter pollinators) within three 10m x 1m transects in each plot and sample each site once a week. We only recorded legitimate visits when the pollinator came into contact with reproductive parts of a fresh flower in anthesis. We used timed targeted netting and transects were divided into 2m segments. To minimize bias, each observer was given a randomized order in which to sample segments for 3 minutes; 1.5 minutes on each side of the transect. We aimed to sample on clear, warm days with minimal wind when pollinators are most likely to be active and weather data was noted for each sampling period. We performed two rounds of sampling for each plot and randomized which treatment was sampled first. We destructively sampled all pollinators that came into contact with reproductive surfaces of plants during observation, except bumble bees, ladybugs, hummingbirds and butterflies which could be identified to species without destructive sampling. We also noted what plant species all insects were interacting with.

Data Analysis

To analyze the differences in niche breadth between pollinators in control and manipulated plots, we used a measure of community richness. To look at richness, we used rarefaction curves comparing the rate of species richness change over the number of observations. Richness is usually the number of species present in a community, however, for my analysis, it is the niche breadth (the number of interaction partners) for each pollinator. Given that we see more interactions and richness increases as we sample a community more, we estimated niche breadth where the number of interaction partners saturates. We rarified and extrapolated pollinator niche breadth using the iNEXT package in R (Hsieh et al. 2016). We completed all data analyses using the statistical program R (R Core Team 2018).

Results

On average, we observed a two week advance in melt date in manipulated plots. We found differences in plant and pollinator niche breadth between control and manipulated plots. When looking at the change in plant niche breadth between control and manipulated plots, we found that on average 4 pollinator categories visited plants in both control and manipulated plots (Figure 3). The visitation range in between plots spanned from five fewer to eight more pollinator categories. Some species, such as *Linum lewisii*, increased their niche breadth from five to eleven pollinator categories. Other species saw no change in interaction partners such as *Ligusticum porteri*, *Draba aurea*, and *Arenaria congesta*. While some lost interaction partners from the control to the manipulated plots such as *Androsace septentrionalis* and *Delphinium barbeyi*. Early species such as *Claytonia lanceolata* and *Mertensia fusiformis* maintained similar numbers of pollinator categories. Late species such as *Erigeron speciosus* and *Solidago multiradiata* experienced a gain in number of pollinator categories.

To analyze niche breadth change weighted by frequency of interactions between manipulated and control plots, we did an individual-based rarefaction of observed plant-pollinator interactions. We measured overall richness of pollinator niche breadth as the total number of flower species each pollinator category was observed visiting. We found no difference in richness, meaning pollinators visited roughly the same number of flower species in control and manipulated plots (Figure 2). However, when comparing the Shannon's diversity between the two plots, we found that pollinators observed in manipulated plots visited a greater diversity of flower species in comparison with control plots. Since richness was unchanged and Shannon's diversity was higher in the manipulated plots, evenness of interactions was thus higher in the manipulated plots.

Discussion

Given that plants and pollinators respond differently and at different rates to climate change (Fitter and Fitter 2002), we aimed to explore the impacts of this phenological mismatch, in this case induced by early snowmelt, on plant and pollinator niche breadth. We hypothesized that niche breadth would broaden to include earlier blooming flowers and pollinators would show more generalist foraging behavior.

We did not see a change in richness between pollinator niche breadth in control and manipulated plots, however, we did see a difference in Shannon's diversity (Figure 2). Since this index is a measure of richness and evenness, this reflects a difference in evenness; higher Shannon's diversity means higher evenness in manipulated plots. This translates to pollinators visiting a greater number of flower species and concentrating less on the same resources which is consistent with more generalist foraging behavior. Given these results, after a phenological change like early snowmelt, we might expect pollinators to expand their niche breadth in order to receive enough floral resources. However, in changing their niche breadth, pollinators also

change the niche breadth of the flowers (Figure 3). While we found that on average 4 pollinator categories visited plants in both control and manipulated plots, the change in visitation between plots ranged from five fewer to eight more pollinator categories. More specialist species such as *Delphinium barbeyi* showed a dramatic increase in visitor category. This may have been due to the flower's more complex morphology, making it much more specialist without phenological change. Some early species such as *Claytonia lanceolata* and *Mertensia fusiformis* maintained similar numbers of pollinator categories while some late species such as *Solidago multiradiata* and *Erigeron speciosus* experienced a gain in number of pollinator categories. Since our manipulation accelerated snowmelt, a cue that initiates the growing season, plants in manipulated plots were phenologically advanced in comparison to control plots. These distinct responses between early and late plants to phenological change suggest that early species were not visited by fewer pollinator categories, despite blooming earlier in manipulated plots. Late species were visited by more pollinator categories likely due to novel interactions from the phenological shift. Early species were not able to expand their niche breadth in manipulated plots because they were not exposed to any new pollinators because of the shift in phenology. Although mutualism's positive feedback loop is maintained through generalization (niche broadening), both plants and pollinators face consequences in the wake of phenological change.

For pollinators, the most apparent consequence of the manipulation was the difference in floral resources. Generalization to include these flowers benefits pollinators and ensures they receive the nectar and pollen they need to survive, but also has negative impacts on pollination efficiency, handling time, competition, and parasitization rates (Brosi 2016, Brosi and Briggs 2013). Interacting with a different flower with its own set of interaction partners exposes a pollinator to a new set of competitors that may limit its access to floral resources. In addition to new competitors, a new flower presents nectar and pollen in a way that is unique to that flower. Figuring out how to interact with an unfamiliar flower increases handling time and decreases the pollinator's foraging and pollination efficiency, therefore limiting the number of flowers the pollinator can visit and the quality of pollination it can provide to the flower. Additionally, changes in niche breadth of specialist bees that feed on specific plant families can impact parasitization rates; a 2016 study noted the effects of Asteraceae pollen on parasitization rates of Aster-specialist *Osmia* (mason bees) and found lower rates of parasitization and decreased reproductive success of parasitic wasps when they preyed on these *Osmia* (Spear et al. 2016). More broadly, expanding diet breadth impacts nutrition, especially considering the nutritional value of pollen varies widely.

Pollination by a wider variety of pollinators benefits plants by increasing the likelihood of pollination. However, while pollination by more generalist species brings a higher quantity of pollen to the flower, it may not bring the right species of pollen for germination. This would result in more competition for quality (conspecific) pollen among flowers and could limit pollination and reproduction of these flowers (Bell et al. 2005, Brosi 2016, Brosi and Briggs 2013, Feinsinger et al. 1988).

By taking a community ecology perspective, we are able to begin to look at implications for whole community stability and function. The changes in pollination and foraging interactions we observed has implications for network stability. Overall, the ability of an organism to adapt to climate change through flexible foraging might improve network stability by making pollinator species less prone to collapse, however a lack of conspecific pollen could also decrease plant reproductive success, consequently decreasing floral resources for their pollinators, and ultimately decreasing network stability (Brosi 2016). In addition, higher foraging evenness could result in more competition between pollinators for the same resources. Considering that we are currently seeing global pollinator decline due to a variety of factors, including climate change (Biesmeijer 2006, Matias et al. 2017), the findings of this study imply that phenological mismatch may play a major role in this relationship.

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References

- Bell, J. M., J. D. Karron, and R. J. Mitchell. 2005. Interspecific competition for pollination lowers seed production and outcrossing in *Mimulus ringens*. *Ecology* 86:762–771.
- Biesmeijer, J. C. 2006. Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313:351–354.
- Brosi, B. J. 2016. Pollinator specialization: from the individual to the community. *New Phytologist* 210:1190–1194.
- Brosi, B. J., and H. M. Briggs. 2013. Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proceedings of the National Academy of Sciences* 110:13044–13048.
- CaraDonna, P. J., A. M. Iler, and D. W. Inouye. 2014. Shifts in flowering phenology reshape a subalpine plant community. *PNAS* 111:4916–4921.
- Feinsinger, P., W. H. Busby, and H. M. Tiebout. 1988. Effects of indiscriminate foraging by tropical hummingbirds on pollination and plant reproductive success: experiments with two tropical treelets (Rubiaceae). *Oecologia* 76:471–474.
- Fitter, A. H., and R. S. R. Fitter. 2002. Rapid Changes in Flowering Time in British Plants. *Science* 296:1689–1691.
- Forrest, J. R. K., and J. D. Thomson. 2011. An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecological Monographs* 81:469–491.
- Gezon, Z. J., E. S. Wyman, J. S. Ascher, D. W. Inouye, and R. E. Irwin. 2015. The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology and*

- Evolution 6:1044–1054.
- Hsieh, T. C., K. H. Ma, and A. Chao. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7:1451–1456.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.
- Livensperger, C., H. Steltzer, A. Darrouzet-Nardi, P. F. Sullivan, M. Wallenstein, and M. N. Weintraub. 2016. Earlier snowmelt and warming lead to earlier but not necessarily more plant growth. *AoB Plants* 8:plw021.
- Matias, D. M. S., J. Leventon, A.-L. Rau, C. Borgemeister, and H. von Wehrden. 2017. A review of ecosystem service benefits from wild bees across social contexts. *Ambio* 46:456–467.
- Miller-Struttmann, N. E., J. C. Geib, J. D. Franklin, P. G. Kevan, R. M. Holdo, D. Ebert-May, A. M. Lynn, J. A. Kettenbach, E. Hedrick, and C. Galen. 2015. Functional mismatch in a bumble bee pollination mutualism under climate change. *Science* 349:1541–1544.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.
- URL <https://www.R-project.org/>.
- Sparks, T. H., and A. Menzel. 2002. Observed changes in seasons: an overview. *International Journal of Climatology* 22:1715–1725.
- Spear, D. M., S. Silverman, and J. R. K. Forrest. 2016. Asteraceae Pollen Provisions Protect

- Osmia Mason Bees (Hymenoptera: Megachilidae) from Brood Parasitism. *The American Naturalist* 187:797–803.
- Steltzer, H., C. Landry, T. H. Painter, J. Anderson, and E. Ayres. 2009. Biological Consequences of Earlier Snowmelt from Desert Dust Deposition in Alpine Landscapes. *Proceedings of the National Academy of Sciences* 106(28): 11629–34.
- Strickler, K. 1979. Specialization and Foraging Efficiency of Solitary Bees - Strickler - 1979 - Ecology - Wiley Online Library. *Ecology* 60:998–1009.
- Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences* 272:2561–2569.

Appendix

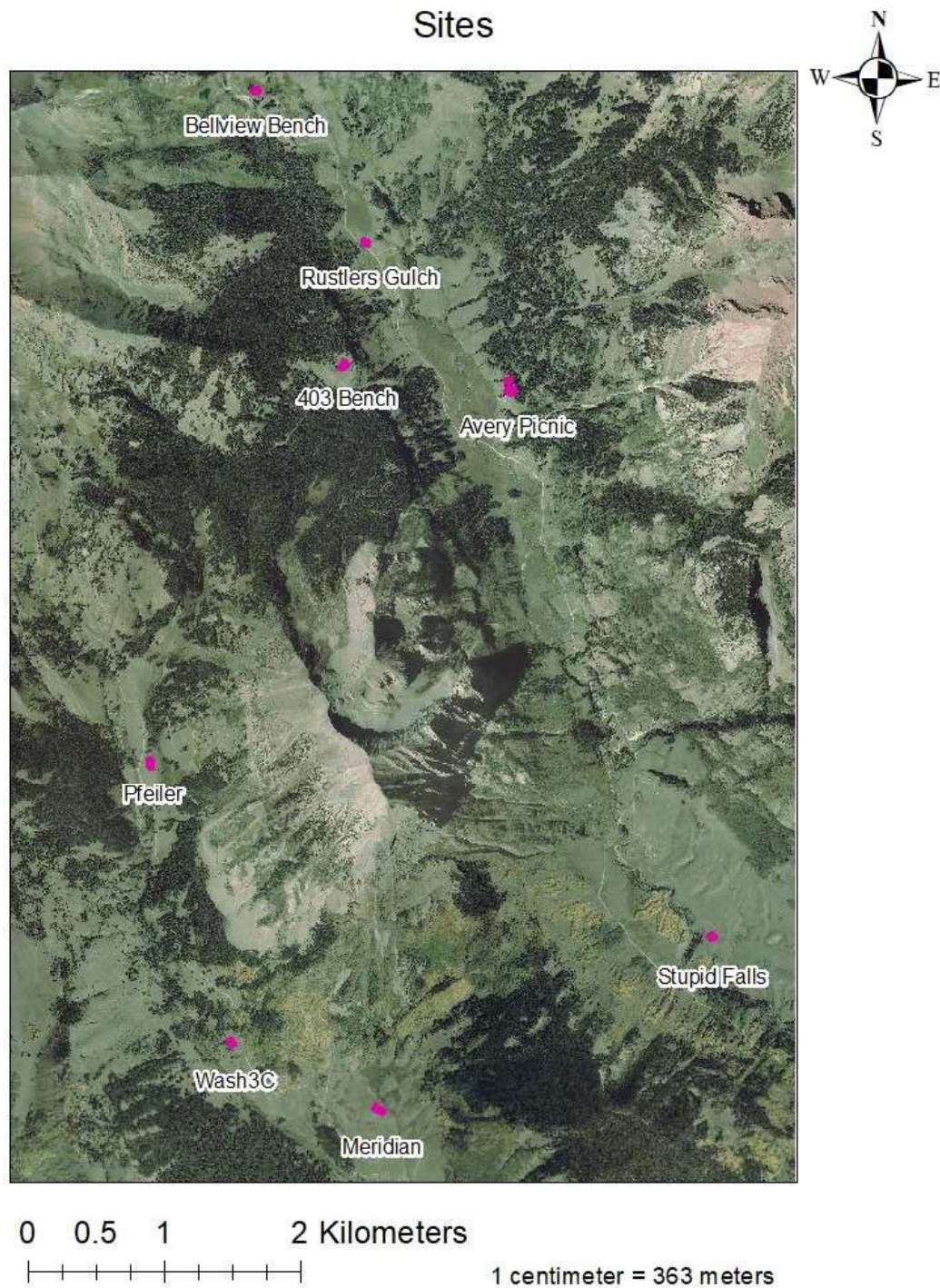


Figure (1): Aerial imagery of 8 sites in Washington Gulch and the East River Valley, Colorado, USA. Each site consisted of one 10x14m plot with three 10m transects split into 2m segments.

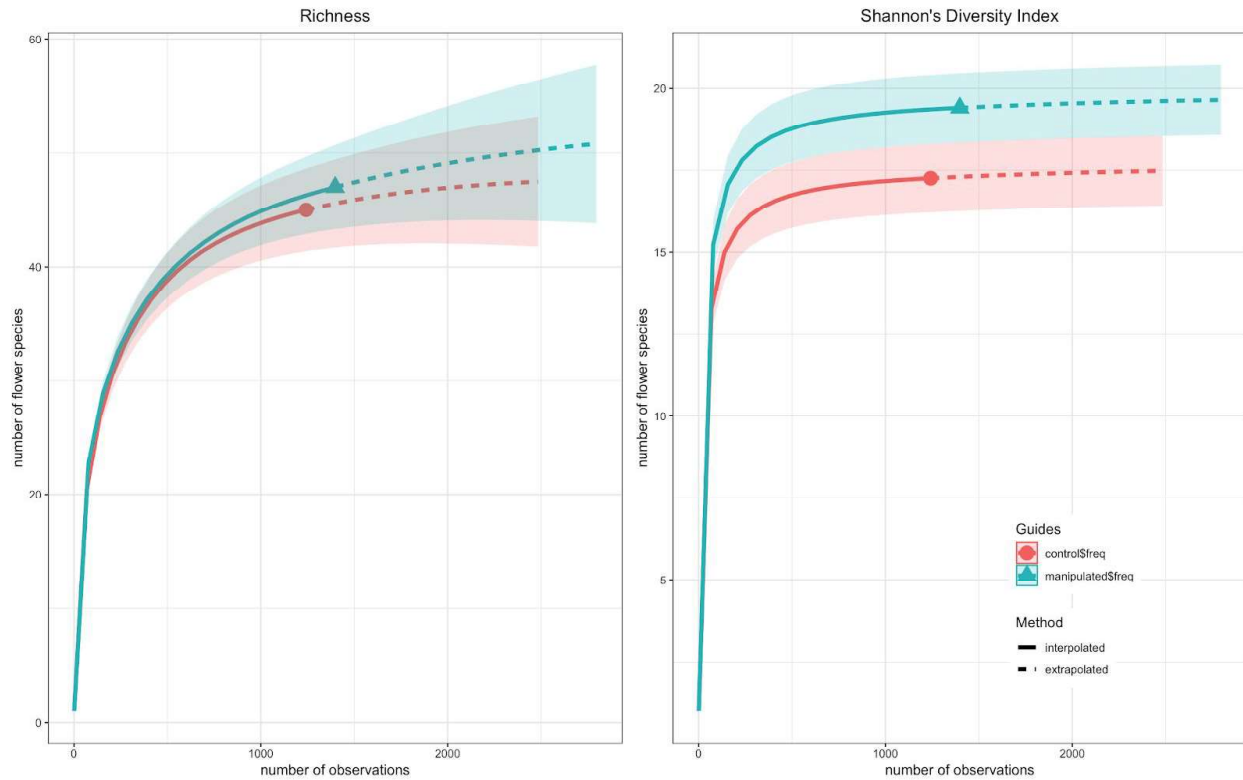


Figure (2): Individual-based rarefaction curves of observed plant-pollinator interactions. Solid lines represent flower species accumulated per visit and dashed lines represent extrapolated accumulation. The red line shows the richness or Shannon's diversity for pollinator niche breadth in control plots and the blue line shows richness and Shannon's diversity in manipulated plots. The symbol between interpolated and extrapolated data shows the actual number of interactions observed.

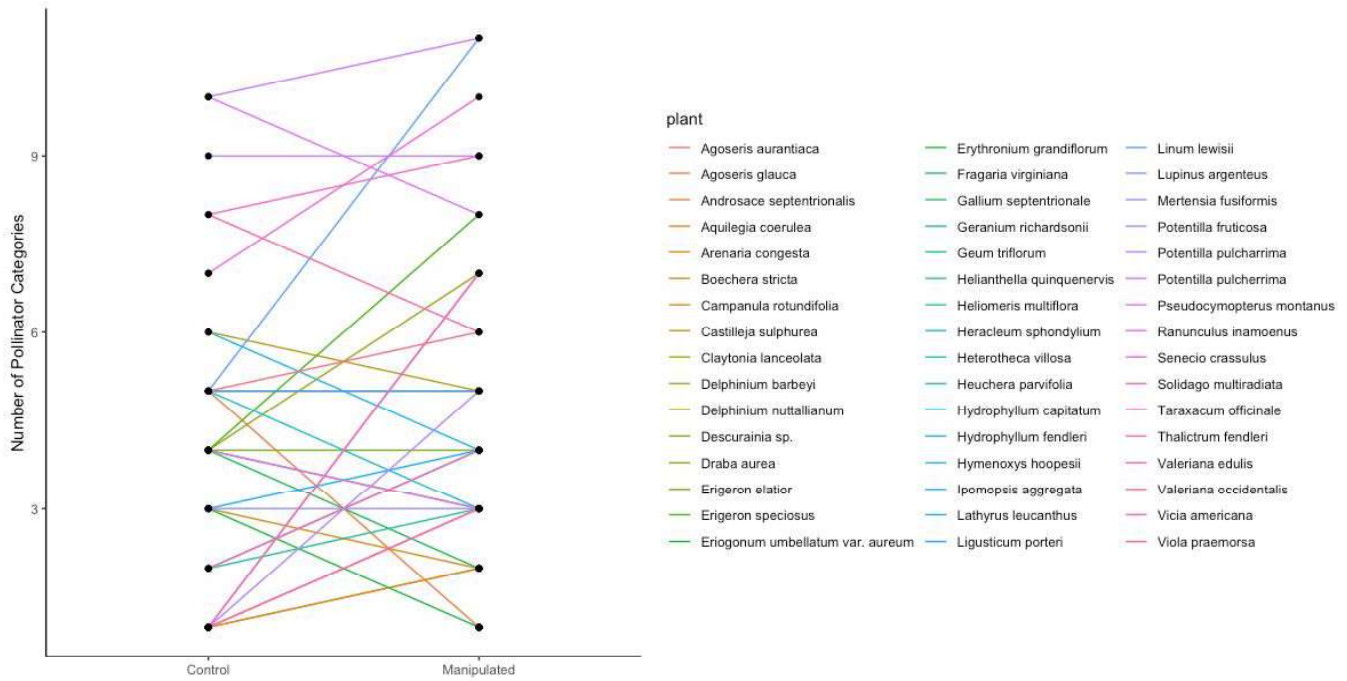


Figure (3): Change in plant niche breadth between control and manipulated plots. Each colored line represents a plant species found in both plots and each point represents a number of pollinator categories.