

Observing pollinator trait variation in relation to niche breadth in seasons of high and low precipitation

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Independent Research and Course

2019

Abstract

Interactions between plants and pollinators are complex and a change to one can cause a significant impact on the other. Environmental perturbations like drought can alter plant-pollinator systems, changing the relative abundance of flower species, shifting species distribution, and decreasing floral resources. As a result of these drought-induced changes, pollinators, particularly insect pollinators, may be forced to change their foraging behavior. Pollinators' foraging behavior is greatly defined by their niche breadth, which is the set of flower species that they can and will visit. A niche breadth is influenced by multiple factors such as the phenology of flowers, geography, and both the morphology of flowers and pollinators. Pollination events are more likely to occur if the morphological traits of the pollinator and the flower “match” in such a way as to make the interaction most efficient and beneficial for both partners: the pollinator needs to be able to reach nectar and the plant must be able to deposit its pollen on the pollinator for transport to another flower. In this way trait matching helps to define pollinator niche breadths. In this project I examined the impact of a drought in 2018 on the foraging patterns and niche breadth of pollinator species in the area around Gothic, Colorado. I predicted that because of the drought and resulting decrease or shift in floral resources, flower abundance, and flower species distribution, pollinating insect species will be forced to alter their foraging behavior and widen their niche breadth. As a result of this increase in generalist foraging behavior, bee traits and floral traits would likely match less frequently during the drought year. I found this hypothesis to be mostly rejected; trait matching was essentially nonexistent in the compared traits in the drought year and the next non-drought year. Floral abundance did decrease during the drought, but floral species richness did not significantly decrease. There was no clear decrease in pollinator abundance during the drought, however there was a decrease in pollinator abundance in the following year. This shows that a pollinator group's niche breadth is highly variable and likely impacted by multiple factors including, but not limited by, floral abundance, floral species richness, abundance of other pollinators, and the quantity and quality of floral resources.

Introduction

Climate change is projected to greatly increase the severity and frequency of droughts in the American southwest and Great Plains region as a consequence of decreased snow pack levels (Dai 2013; Spinoni et al 2013; Hanson & Weltzin 2000; Trenberth et al. 2014). Droughts have a large impact on ecosystems and can have a particularly negative impact on floral communities, such as altering the abundance and distribution of flowers, and decreasing floral resources (Alqudah et al. 2011). As droughts become more frequent and more severe, pollinators could be negatively impacted due to the changes in floral communities, triggering declines in pollinator populations. (Goulson et al. 2015; Phillips et al. 2018). In addition to population declines, changes to floral resources would likely impact pollinators in other ways, such as altering foraging patterns or niche breadths as floral communities changed.

The niche breadth of a pollinator is the range of flower species that it chooses to visit and pollinate. Pollinators are rarely exclusive to one flower species; instead many different pollinators may visit one flower species, and one species of pollinator may visit many different flower species. Some pollinators are generalists, in that they visit a wide variety of flower species. Other pollinators are specialists, in that they visit only a few different flower species. This specialization is influenced by trait-matching, where the morphological characteristics of the pollinator match with those of the flower (Junker et al 2013). For example, a bee with a long proboscis will be able to reach the nectar in a flower with a deep corolla, but a bee with a short proboscis will have trouble obtaining nectar from such a flower. Pollinators will likely interact with flowers that best match their traits to make their foraging most efficient in terms of resources and time. (Waddington & Holden 1979). Pollinators that maximize trait matching during foraging bouts are likely to be more efficient pollinators, as they will visit more of the same flowers in succession, transferring greater quantities of pollen to the correct flower species.

In this project I explored plant-pollinator trait matching and niche breadth dynamics in years of high and low precipitation. By analyzing data from 2016 – 2019, I examined (1) whether drought causes a decrease in floral abundance and richness, (2) if pollinator abundance decreases during drought, (3) if there is a significant change in pollinators' niche breadth during drought and whether it expands or contracts, and (4) whether the drought causes a lower frequency of pollinator-flower trait matching.

I hypothesize that there will be a decrease in flower and pollinator abundance during the drought. Pollinators will be more generalist during the drought year because there are fewer floral resources and altered flower species distribution and abundance, and pollinators will deviate from their expected foraging behavior. I expect trait matching between pollinators and flowers to decrease due to this increased generalization as they are forced to expand their niche breadth.

Methods

I used data collected from three subalpine meadows around Gothic, CO: Gothic Town (2871m elevation), Avery Picnic (2967m), and Virginia Basin (3492m) These sites were established in 2016 by the Brosi lab and have been sampled each subsequent year. At each of the three sites the lab established four 1 x 20 meter transects which were sampled on a weekly basis. Pollinators that came in contact with the reproductive structures of a flower were captured via aerial netting and identified, and the flower species they pollinated were identified. We destructively sampled all insect pollinators except *Bombus* and butterfly species. After returning to the lab we measured the following traits of collected insects: proboscis length, body length, and intertegular span. We also measured the following traits of 29 flower species: corolla depth and width, flower height, and nectar volume. Trait measurements were done on 5 individuals of each flower species, and an average measurement for each species was calculated. In addition to the data collected this summer, I used data from 2016 – 2018. 2016, 2017, and 2019 represent years of normal snowpack levels, whereas 2018 was considered a drought year with roughly half as much snowpack as the other years.

I conducted data analysis using RStudio and the *lme4*, *ggplot2*, and *dplyr* packages. First, I analyzed pollinator abundance in the form of the raw number of observations. To analyze the pollinator populations I created 6 functional groups: other flies, Bombyliidae, Syrphidae, other bees, *Bombus spp.*, and small black solitary bees. All insect pollinators besides bees and flies, such as Lepidoptera and Hemiptera were excluded from all data analysis. For the abundance of flowers I did not make any distinction between species but calculated total seasonal flower abundance for each of the 3 sites for each year, 2016-19. To determine pollinator niche breadth I used the metric of number of unique interactions: the number of different flower species that a pollinator group visited. The number of unique interactions was found for each of the 6 pollinator groups for each year. Floral species richness was also calculated for each year, but did not include sites. Two sets of traits were compared: corolla depth and proboscis depth, and corolla width and body length. The trait matching was evaluated using a scatter plot, the pollinator trait measurement was the y-value of the point and the flower measurement was the x-value. A linear regression was conducted on both sets of traits to determine if there was a trend or difference between 2018 and 2019. Trait data was not collected in 2016 or 2017. All other graphs representing abundances and unique interactions were line graphs. To determine what had a significant impact on the number of the unique interactions I ran a generalized linear mixed model (GLMM) where the fixed effects were flower abundance, pollinator abundance, pollinator gross ID (group), and precipitation in the form of snowpack; and the random effects were year and site.

Results

Flower abundance was found to have decreased in 2018 by 22%, from 21956 flowers counted across the entire season in all three sites in 2017, to 22711 flowers in 2018. Then in 2019 the flower count increased to 44243 flowers across the three sites. There was 990cm of snowpack in 2017, 490cm in 2018, and 967cm in 2019. Insect abundance did not follow a clear trend in response to the drought in 2018: the observed numbers of *Bombus spp.* and syrphids decreased by 43% and 26% respectively. The number of small black solitary bees observed increased by 108% from 2017 to 2018. The observed number of Bombyliidae and other bees did not change significantly between 2017, 2018, and 2019. The observed numbers of all pollinator groups decreased in 2019, despite the increase in flower abundance and precipitation compared to 2018. The number of unique interactions for all pollinator groups except Bombyliidae decreased at least 50%. This reduced the number of flower species visited by the collective pollinator groups from 34 in 2017 to just 8 in 2018. The 8 flower species visited in 2018 were *Achillea millefolium*, *Agoseris glauca*, *Erigeron elatior*, *Erigeron speciosus*, *Heliomeris multiflora*, *Hymenoxys hoopesii*, *Potentilla pulcherrima*, and *Solidago parryi*. In 2019 the number of unique interactions increased substantially for all pollinator groups except Bombyliidae. The analysis of trait matching showed no clear trend in either 2018 or 2019. The R^2 value of the linear regressions for proboscis length and corolla depth was 0.000536, and 0.00877 for body length and corolla depth. The GLMM showed that 4 of the fixed factors had a significant impact on the number of unique interactions: gross ID other bee ($p = 0.000243$), snowpack depth ($p =$

0.000843), gross ID *Bombyliidae* ($p = 0.000976$), and gross ID other fly ($p = 0.001885$). The meaning of a gross ID being significant is that the identity of that pollinator group has a significant impact on the number of unique interactions. Figures representing flower abundance, pollinator observed abundance, unique interactions, and trait matching are located after the discussion and references.

Discussion

My analysis showed that during times of environmental stress such as drought, pollinators will contract their niche breadth. This was evident by the decrease in unique interactions in nearly every pollinator group during the drought year of 2018. A contraction of niche breadth was contrary to what I expected to have occurred. The drought caused a decrease in floral abundance, though not as drastic a decrease as what would be expected considering the collective pollinator niche breadth decrease from 34 flower species in 2017 to 8 in 2018. If flower abundance is not the main driver of unique interactions, then could it be flower species richness? This is not likely, as in 2017 there were 63 flower species observed at the sites, and 61 in 2018. A drop in two flower species did not likely cause the significant decrease in unique interactions in 2018. A possible explanation is that while there were less flowers in bloom, even fewer flowers were producing nectar in amounts or quality that would warrant a pollinator to visit and pollinate. There is data on nectar measurements of flowers from 2018 and 2019, but there was not enough time to examine the validity of this hypothesis.

When looking at the figures of flower abundance and pollinator observations, there are obvious outliers, particularly the 2016 Virginia Basin flower count and the number of observed other flies in 2016 – 2018. The flower abundance is likely explained by the fact that in 2016 the individual flowers on the species *Achillea millefolium* and *Valeriana edulis* were counted, and in 2017 – 2019 the number of flower umbels were counted instead. If there was a higher frequency of these flower species at the Virginia Basin site than at Gothic Town or Avery Picnic there could easily have been thousands more flowers recorded at Virginia Basin. The high number of observed other flies in 2016 – 2018 could be due to misidentification, such as labeling syrphids as other flies, or including bycatch of other flies and recording the flies as if they had been pollinating, or due to an actual decrease in fly abundance (Hallmann et al 2017). Another outlier is visible in Figure 3; in 2018 all pollinator groups declined or had a small increase except small black solitary bees, which more than doubled in number. A possible explanation for this is that if flowers had less or lower quality nectar during the drought a bee would need to visit more flowers to obtain the necessary amount of nectar (Waser et al 2016). If more flowers are being visited by an individual bee, there is a higher chance that the bee would land within a transect and be observed, and the number of observed bees would increase. This may not have happened to the other pollinator groups due to compounding effects of their true abundance and how many flowers they need to visit during a foraging bout. For example, if other flies had roughly the same abundance as small black solitary bees but required less nectar than bees to survive, they would visit less flowers, resulting in a smaller observed number than the bees.

While flowers did poorly during the drought in 2018, and all pollinators did not thrive in the drought, there are lasting effects of the drought in 2019. All pollinator groups decreased in number in 2019, while flower abundances increased substantially; Avery Picnic and Gothic Town had record flower abundances in 2019. The pollinator abundance decrease is likely due to a drought legacy effect, meaning that the insects in 2018 could have had lower fecundity due to fewer floral resources: fewer eggs might have been laid in 2018, and fewer insects developed to adulthood in 2019. 2019 also had a late snowmelt, and there was a frost in June, which could have killed or weakened insects that had emerged earlier in the season, further reducing their numbers.

While the analysis of trait matching between corolla depth and proboscis length, and corolla width and body length did not yield significant results, this does not mean that traits have no impact on pollinator niche breadth. Instead of clearly defining a niche breadth like I originally thought, traits could still play a role in niche breadth by setting upper limits on what flower species a pollinator can visit. For instance, *Bombus spp.* have a relatively long proboscis, which allows them to feed from most flowers. There is nothing preventing them from feeding from flowers with very small corolla depths except that it may be inefficient. Body size and flower size also likely set limits on a niche breadth, as a very large insect would have difficulty feeding from a small flower. This said, pollinator-flower trait matching could still be a driving force in determining niche breadth, but with traits other than those that were analyzed and measured (Lázaro 2008). It is also possible that the traits we took into consideration are significant, but due to problems with measurement and data collection they yielded insignificant results. Proboscis measurements were likely very inaccurate as we did not manipulate the dead insects to fully extend their proboscis, and only measured what was visible. Flower traits were also found from an average of 5 flowers for each species; if we measured the traits of the flower that was observed being pollinated by the collected insect there potentially could have been a more significant trend. This would allow trait matching to be on the individual scale, and then related to the species level niche breadth.

In conclusion, drought has a significant impact on plant-pollinator networks. While the impact on insect pollinator abundance is not fully clear, there is a negative impact on flower abundance. The legacy effect of the 2018 drought and potentially the late snowmelt and frost in 2019 compounded to decrease the number of pollinator insects in 2019. In 2018 the number of flower species visited by all the pollinator categories decreased to just 8, so the niche breadth of pollinators contracted due to the drought. These 8 flower species anchored the survival of the pollinator community, and were also the species most resistant to drought, in that they could bloom and provide enough resources for pollinators to visit them. By seeing which flower species are essential to pollinators in times of environmental stress, conservation efforts can be focused to maintain the stability of plant-pollinator systems.

References

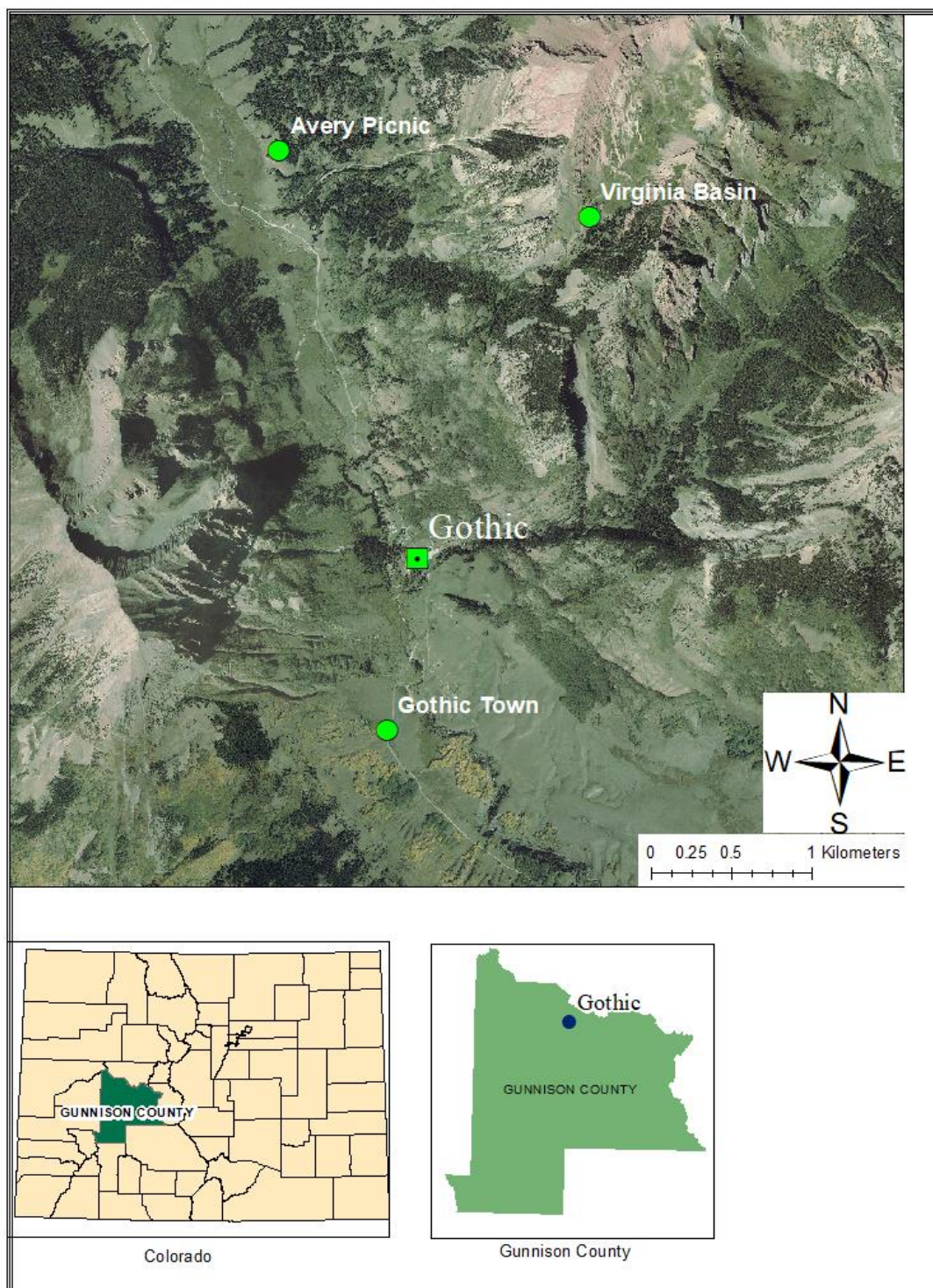
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Figures



Site map - made using GIS data and ArcMap, shows the 3 sites where data is collected in respect to the town of Gothic, CO

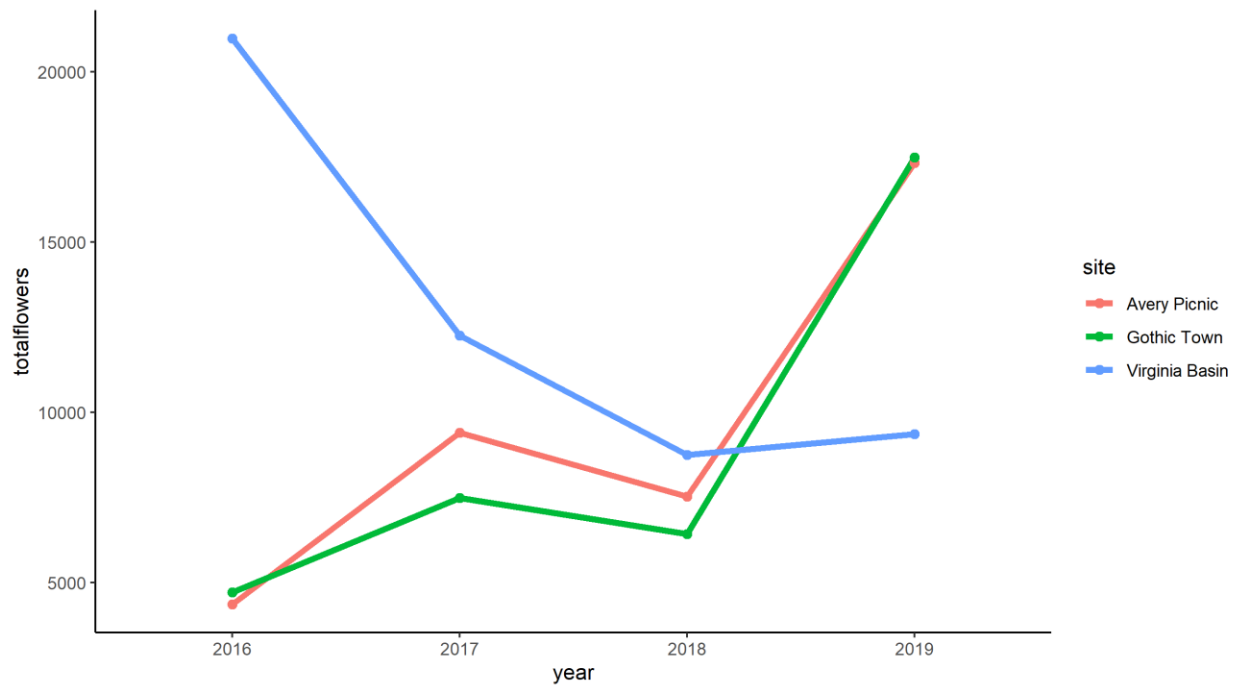


Figure 1. – Floral abundance at each site from 2016 – 2019

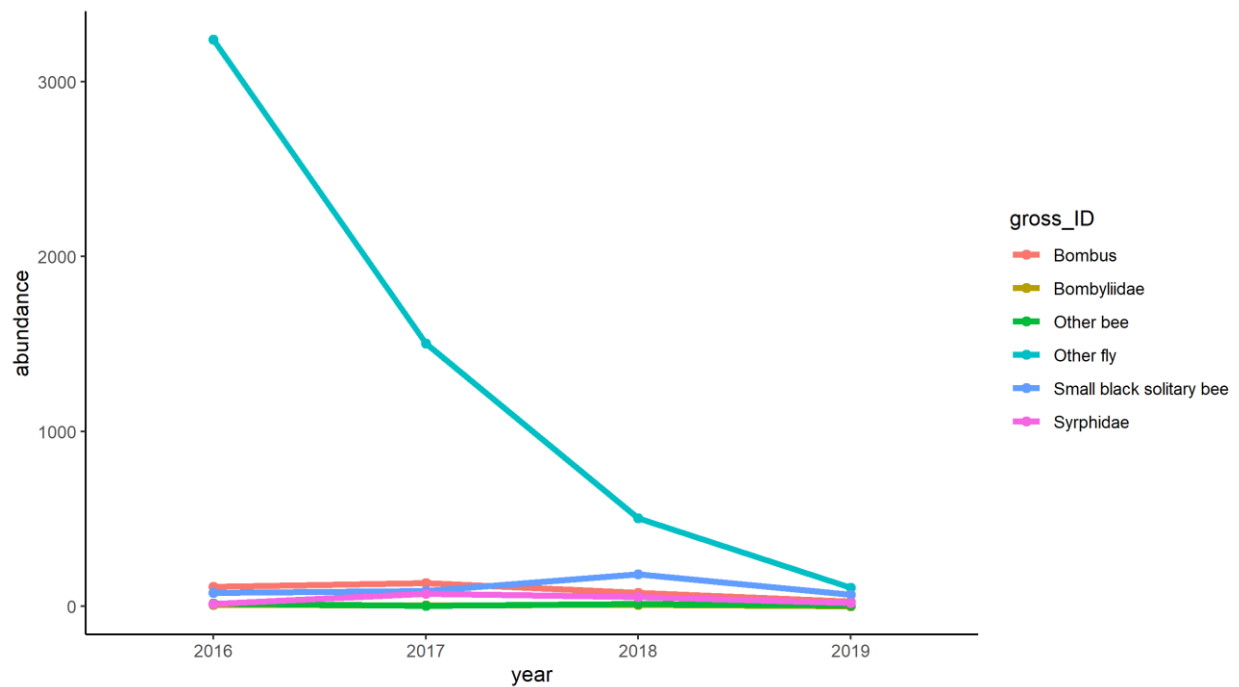


Figure 2. – Observed numbers of the 6 pollinator categories from 2016 – 2019

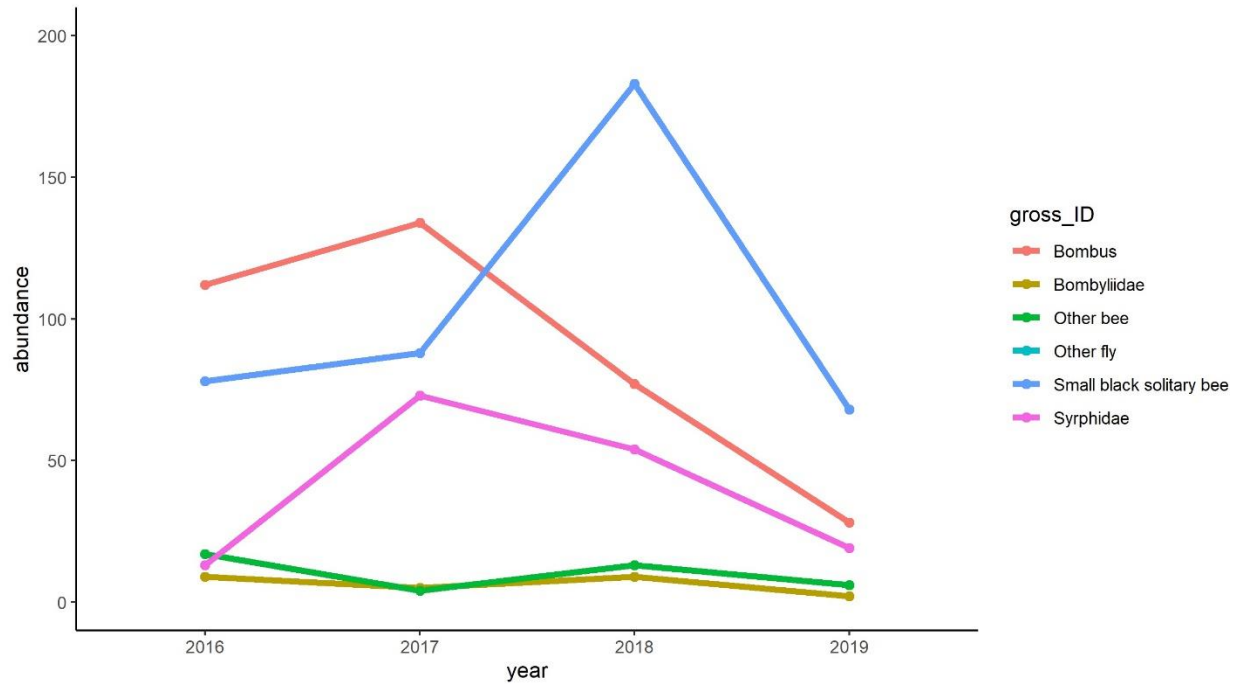


Figure 3. – same data as Figure 2 but with the ‘other fly’ category removed

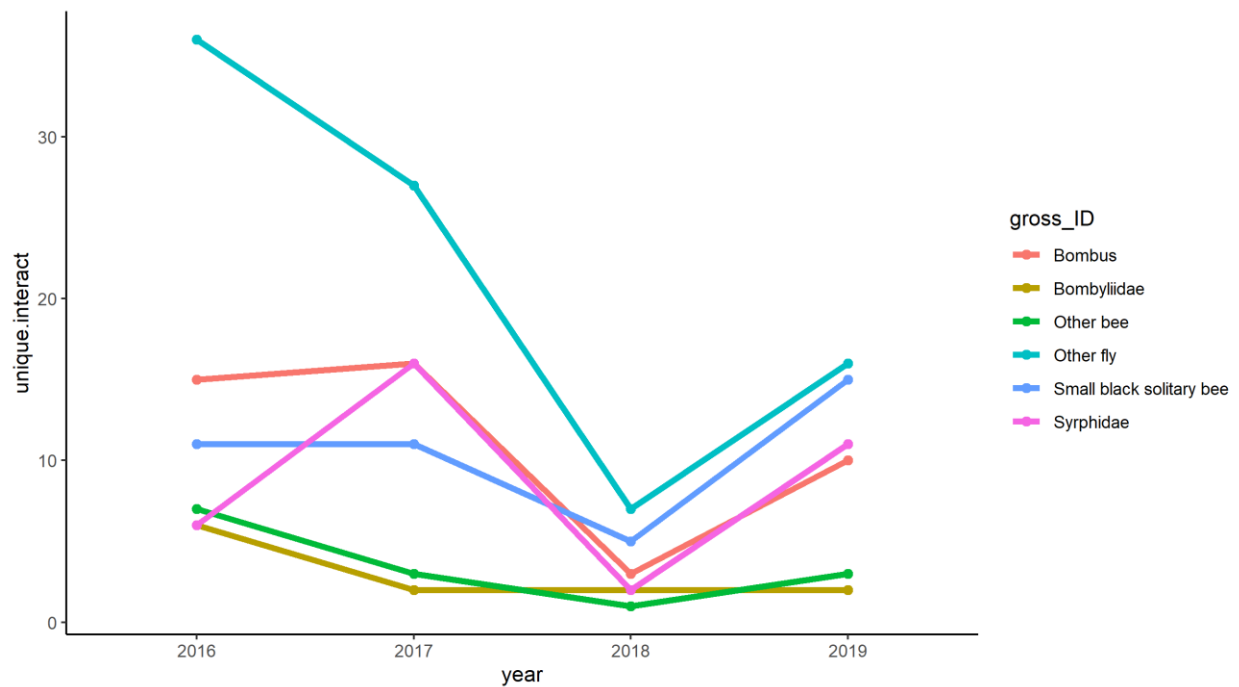


Figure 4. – the number of unique interactions (flower species) visited by each pollinator group from 2016 – 2019

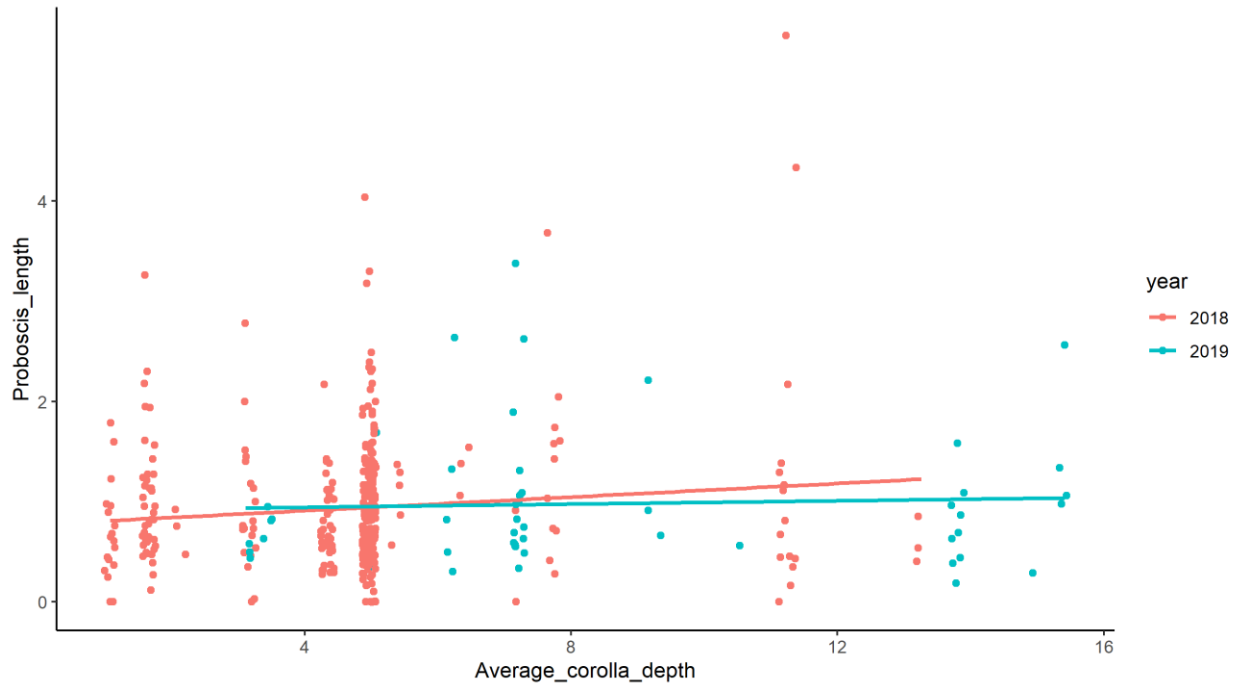


Figure 5. – Scatterplot and linear regression line of insect’s proboscis length as y-value and the average corolla depth of the flower species it visited as x-value from 2018 – 2019

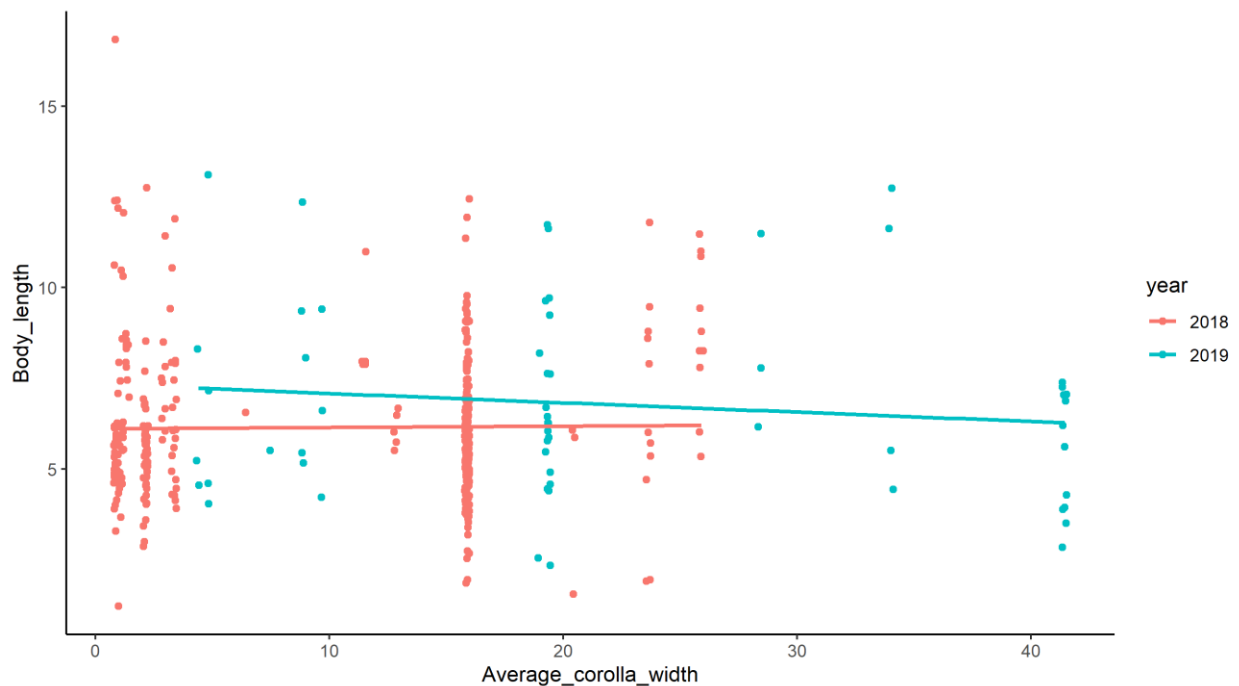


Figure 6. – Same as Figure 5 but using insect’s body length instead of proboscis length and average corolla width instead of average corolla depth