Relationship Between Pollination Behavior of Invasive Honeybees and Native Bumblebees in Montane Meadows

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Abstract

Data on plant-pollinator interactions collected over six summers in montane meadows of the HJ Andrews Experimental Forest provided an opportunity to explore the association between two genera of generalist pollinators: Apis and Bombus. Ten plots in each meadow were "watched" for fifteen minutes five times every summer, and each flower species in a meadow-watch was assigned a class based on the ratio of Apis to Bombus interactions. Flowers were also designated expected classes based on flower traits and prior knowledge about the plant and pollinator species at play. The study found that Apis and Bombus rarely visited a single flower species equally in a given meadow-watch, even when flower traits suggested that the number of interactions should be uniformly divided between the two pollinators. A predictive modeling approach, which took advantage of an ensemble method for tree classification called AdaBoost, found that this partitioning of interactions was best explained by a combination of environmental covariates and flower traits. The proportion of Apis to all social bees in the meadow-watch was the most important predictor variable in the classification task. This finding suggests that there is a significant relationship between pollinator presence and the flower preferences of other pollinator species in a meadow.

1. Introduction

Most plant-pollinator network analyses have focused on bipartite networks, dividing the data into two non-overlapping sections, plants and pollinators, and ignoring the possible relationships within each group. While some studies have investigated competition for pollination amongst flower species, notably Levin and Anderson's work in 1970, the literature is limited when it comes to the relationship between pollinator species in a network. Colony Collapse Disorder has been a recent popular topic of conversation and study, but it is equally worth investigating the impact of invasive honeybees on the pollination behavior of native bumblebees and solitary bees. There could also be implications for the flowers in the network. One study on male and female hummingbirds found that pollinator competition could drive a flower species to evolve into multiple forms (Temeles *et al*., 2016).

This study sets out to determine how pollinator species relate to one another in the meadows of the HJ Andrews Experimental Forest. I will focus on two genera of pollinators: Apis and Bombus. The only species of Apis present in the Andrews' meadows is *Apis mellifera*, but it accounts for more than a fifth of all recorded interactions. It is also an invasive honeybee, so it is of interest to understand how it competes with native pollinators for flower resources. There are ten species of Bombus in the Andrews, all of which are native bumblebees.

The two genera are conducive to comparative analysis. Both are generalist pollinators, and they interact with many of the

same flower species. Additionally, the total number of recorded Apis interactions is approximately equal to the number of Bombus interactions in the aggregate data set across all years.

All flower species have traits that make Apis and Bombus pollinators more or less likely to interact with them. Based on these attributes, each flower involved in Apis and/or Bombus interactions has been given an expected class that indicates whether the visits will be dominated by Apis, Bombus, or neither.

This project will explore how actual observations deviate from these expectations and how flower traits and environmental factors relate to the Apis/Bombus partitioning of interactions.

2. Methods

2.1 Field Methods

The data for this study were collected by Eco-Informatics Summer Institute participants in the HJ Andrews Experimental Forest between 2011 and 2015. During the summer of each year, fieldwork was conducted in three meadow complexes (an additional two complexes were included in 2011 and 2012). Each complex is composed of three to four meadows with ten $3x3m^2$ plots. Data were collected in each meadow five to seven times over the course of a summer.

Field sampling for each plot consisted of a flower abundance survey and a 15-minute watch, during which all plant-pollinator interactions were recorded. For the purposes of this study, an interaction is defined as a pollinator touching down on the reproductive parts of a flower. There is no differentiation between successful and unsuccessful pollination since this information was not available for all years.

Furthermore, an interaction is bounded by a one-minute period. If a pollinator visited multiple flowers of the same species during a single minute, the visit is still considered a single interaction. If a single flower visit persisted for more than one minute, it is counted as an additional interaction.

2.2 Definitions and Notation

This study will focus on data at the watch level for each meadow sampled during a given year. Let mwy denote a unique meadow-watch-year combination in the data set (e.g. M2 Watch 1 2013). In this study, 178 meadow-watch-years were analyzed.

For each mwy, only a subset of the total flowers in the meadow were involved in social bee interactions, where a social bee is defined to be either Apis or Bombus. In order to remove noise from the data set, I will refer to F_{mwy} as the set of flowers in a given mwy with at least 10 social bee interactions. Next, f is a single flower species in the meadow-watch-year, with $f \in F_{mwy}$. Finally, A_f is defined as the number of Apis interactions with f, while B_f is the number of Bombus interactions.

Now, each f observation can be classified in one of three ways based on the ratio of Apis to Bombus interactions:

Class A := at least 2:1 A_f to B_f
Class B := at least 2:1 B_f to A_f
Class E := approximately 1:1 A_f to B_f

More specifically, Class E (Equal) flowers include all $f \in F_{mwy}$ that do not meet the criteria for Class A (Apis) or Class B (Bombus).

Lastly, let A_T and B_T denote the total number of respective Apis and Bombus interactions in a mwy (including flowers with <10 social bee interactions). This metric is used to indicate the total number of Apis and Bombus pollinators present in a meadow-watch-year.

2.3 Flower Traits

Each f has an observed class from the field data and an expected class provided by Professor Andy Moldenke of Oregon State University. The expectations were based on flower traits, including size/biomass, tube depth, color, orientation, flower platform (vertical or horizontal), time of year in anthesis, amount of nectar, and openness of flower.

These traits often favor one pollinator genus over the other. For instance, Bombus have longer tongues, so they can reach the nectar of flowers with deep tubes more easily than Apis. They also have a stronger entry to closed flowers, and their flying skill allows them to interact with flowers that are suspended upside-down in the air. Additionally, Bombus are expected to have more interactions with flowers that bloom later in

the year when Apis have mostly shut down for the season. Blue color favors Bombus over Apis, as well.

Apis, on the other hand, are expected to dominate interactions with small flowers and those with less nectar. This is because Bombus are much heavier than Apis, and the effort of interacting with species that have little nectar is not worth the reward. Finally, Apis are often more attracted to flowers with umbels (multiple flowers stemming from a single stalk like an umbrella).

It is worth noting that many flower species do not have traits that give an advantage to Apis or Bombus. These are the expected Class E flowers. From here on out, the expected class based on the aforementioned flower traits will be referred to as the "Andy" class.

2.4 Observed Class vs Andy Class

To determine the relationship between the two classes of each f, the results were compiled into a contingency table, with rows representing Andy classes and columns representing recorded classes. The table contains every $f \in F_{mwy}$ for all unique meadow-watch-years. Additionally, the proportions by row of the contingency table were calculated to show the match rate for each class and the percentages of each type of mismatch error.

A chi-squared test determined whether there was significant association between the observed class and the Andy class. The chi-square test statistic is defined as follows:

$$\chi^2 = \sum \sum \frac{(O_{ij} - E_{ij})^2}{E_{ij}}$$

where:
$E_{ij} = R_i \times C_j / N$
R_i = row marginal total
C_j = column marginal total
N = grand total

The resulting p-value of the test is the probability of observing a value at least as extreme as the test statistic for a chi-square distribution with (row - 1)(col - 1) degrees of freedom. A significant p-value for this test would indicate that there is association between the observed class and the Andy class.

2.5 Influence of flower traits and environmental factors

Initially, different environmental covariates were plotted against the proportion of Apis to all social bees in the meadow-watch-year to determine the relationship between each factor and the class of f. However, clear patterns were difficult to find (see Appendix). Instead, a predictive modeling approach was utilized. This approach took advantage of machine learning techniques to train a classifier that could predict the class of unseen data. By comparing different models, an ordering of the importance of predictor variables was obtained.

i) Classification Method: AdaBoost

AdaBoost—short for Adaptive Boosting—is an ensemble method for classification. It uses a linear combination of weighted "weak learners," which perform somewhat better than average on training data, to create a strong classifier. This study used the AdaBoost.M1 algorithm (Freund and Schapire, 1996) from the **adabag** R package. The algorithm is shown in Figure 1. We start with a training set $T_n = \{(x_1,y_1),...,(x_i,y_i),...,(x_n,y_n)\}$, where x_i is the feature vector and y_i is the observed class, taking values 1, 2, …, k. Each observation x_i is assigned an initial weight $w_b(i) = 1/n$, which is updated after each iteration. Let B equal the total number of basic classifiers (or weak learners).

On each iteration of step 2, a new weak learner $C_b(x_i)$ is built on the weighted training set (T_b) and applied to every example. Then, the training error of the classifier is calculated by summing the weights of the misclassified data points (step 2b). The constant α_b is considered the learning rate, and it is used in the final decision rule to weight the vote of the b-th classifier. It is calculated in step 2b as a function of the error rate.

Finally, the weight of each data point is updated for the (b+1)-th iteration based on how it was classified by the b-th weak learner (step 2c). Misclassified points are given a larger weight so that they are more likely to be correctly classified in the next iteration. The calculated weights $w_b(i)$ are normalized to sum to 1.

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1. Start with $w_b(i) = 1/n$, $i = 1, 2, \ldots, n$

2. Repeat for $b = 1, 2, \ldots, B$
   a) Fit the classifier $C_b(\mathbf{x}_i) = \{1, 2, \ldots, k\}$ using weights $w_b(i)$ on $\mathbf{T}_b$
   b) Compute: $e_b = \sum_{i=1}^{n} w_b(i)\mathbf{I}(C_b(\mathbf{x}_i) \neq y_i)$ and $\alpha_b = 1/2 \ln((1 - e_b)/e_b)$
   c) Update the weights $w_{b+1}(i) = w_b(i) \exp(\alpha_b \mathbf{I}(C_b(\mathbf{x}_i) \neq y_i))$ and normalize them

3. Output the final classifier $C_f(\mathbf{x}_i) = \arg\max_{j \in Y} \sum_{b=1}^{B} \alpha_b \mathbf{I}(C_b(\mathbf{x}_i) = j)$

Figure 1: AdaBoost pseudocode implemented by the `boosting` function in the adabag R package

The final ensemble classifier determines the class of a data point by calculating the weighted sum of votes for each class and assigning the class with the highest vote. Figure 2 shows a very basic visual representation of the AdaBoost algorithm.
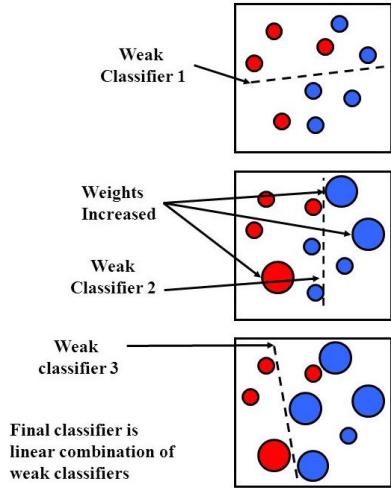
Figure 2 (by Paul Viola): a visual representation of the AdaBoost algorithm

Points misclassified by Weak Classifier1 are given greater weight in the second iteration. The final classifier is a linear combination of all weak learners, where each is weighted by its performance on the training data. Here, the weak learners are linear classifiers.

An important addition to the **adabag** package's implementation of AdaBoost is the inclusion of an importance vector in the model output. This vector contains the numerical value assigned to each variable, indicating its relative importance to the classification task. The measure takes into account the gain of the Gini index, as well as the weight of the weak learner (α_b). The Gini index is calculated by the `varImp` function of the **caret** package.

ii) Choice of Weak Learners

Rather than using simple linear classifiers as depicted in Figure 2, this study implemented AdaBoost with decision trees as weak learners. Figure 3 shows an example of a decision tree for the data set. The leaves represent class labels and the branches represent conjunctions of features that lead to the final labels. Additionally, the leaves display the probability of the data point belonging to each class, which tells us the certainty of the classification tree in its final decision. This method is preferred to linear classification because it can handle multiple classes (E, A, B) and draw non-linear decision boundaries in order to classify the data more accurately.

iii) Approach

In this study, a total of 6 classifiers were trained using AdaBoost—3 each for the observed class and the Andy class. Model 1 took three environmental covariates into account: day, flower abundance and presence of Apis in the meadow-watch as compared to all social bees. They are defined as follows:

Day = day of year
Abund := #staks * #flws/stalk
ApisProp := $A_T / (A_T + B_T)$

Model 2 only incorporated flower traits to build the classifier and make predictions about the flower class. The predictors are biom.flwr, tube, and visibility, where:

Biom.flwr = biomass per flower
Tube = one of 10 levels indicating the
extent of tube exclusivity
Visibility = bright or red/dark

These were the attributes that seemed most important in the assignment of the Andy class. As previously mentioned, a smaller biomass is
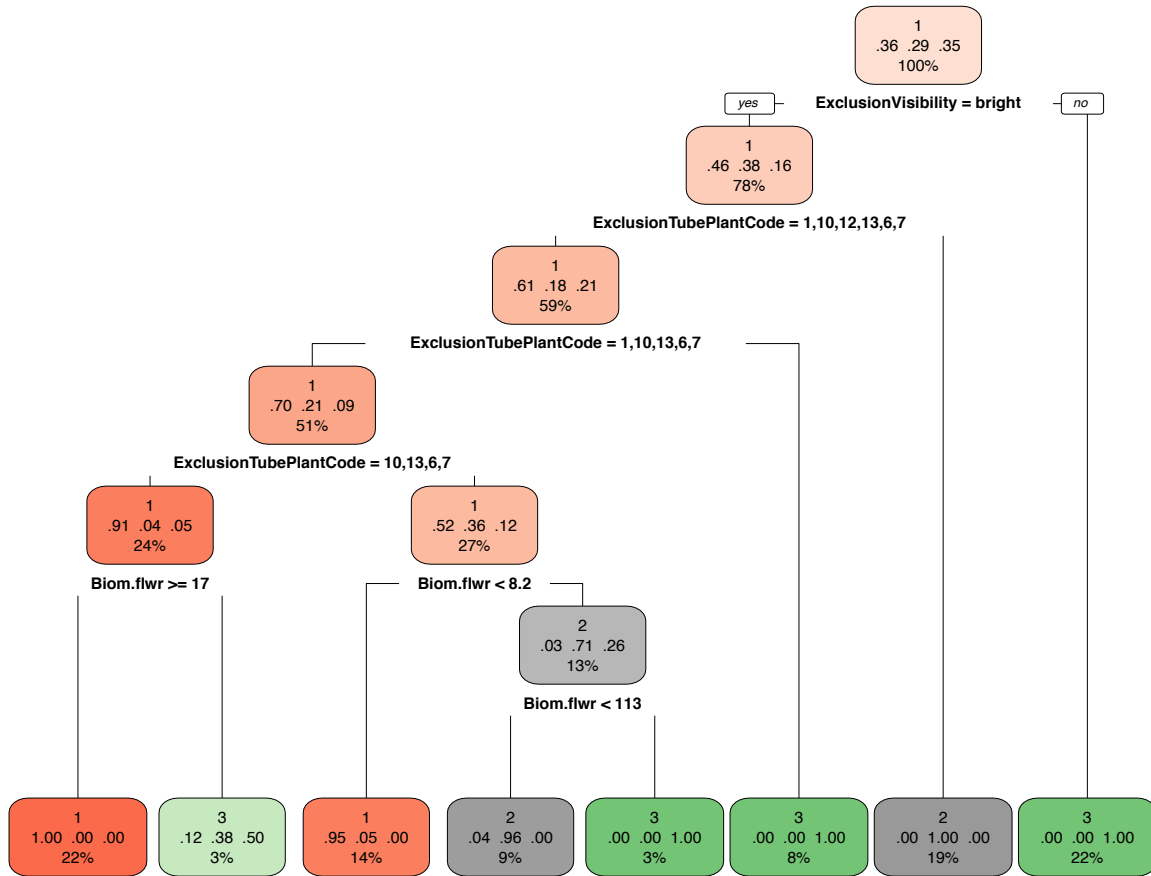
Figure 3: Classification tree for Andy Class based on flower traits

The objective of a decision tree is to assign every data point a class label based on the predictor variables in the model. Here the labels 1, 2 and 3 are equivalent to Class E, Class A, and Class B. Each interior node divides the branch into two parts based on one of the predictor variables in the model. For example, the first node considers visibility: if the flower is dark, it is immediately classified as Bombus dominated, and if it is bright, it continues on to the next node on the left. This process is repeated until every data point has been assigned a class. Each node also displays the probability of the data point belonging to each class based on the prior decisions.

expected to favor Apis, while a flower with a long tube or blue color will go to Bombus. Finally, Model 3 combined both flower traits and environmental covariates for a total of 6 predictor variables.

  For each model, two classifiers were trained using AdaBoost; the first predicted the Andy class, while the second predicted the observed class. In order to prune the ensembles and avoid overfitting to the training data, each classifier used only five weak learners. This number was chosen by plotting the boosting error against the number of tree classifiers, which is equivalent to the number of iterations of the

AdaBoost algorithm (Figure 4). No limit was placed on tree-depth for the weak learners because it did not improve the accuracy of the classifiers during test runs.

  The estimated prediction error of each classifier was obtained using k-fold cross-validation with k=50. Figure 6 shows how cross-validation generates the estimated misclassification rate. Rather than dividing the data into one test set and one training set, the entire data set is broken up into k-folds and the classifier is trained k times.
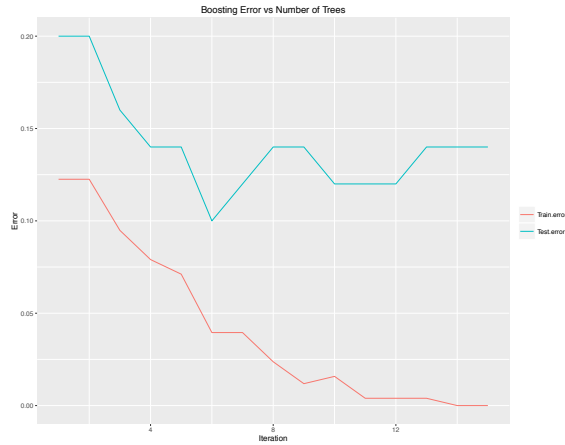
Figure 4: Evolution of error with # of weak learners

After iteration 5, the test error (blue) stops decreasing, while the training error (red) continues to improve. This is indicative of overfitting.
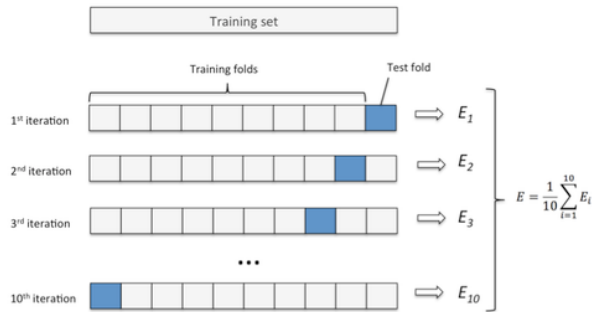

Figure 5: Cross-Validation Ex. by Sebastian Raschka

The data set is broken up into k-folds. A classifier is trained on (k-1)-folds and the kth is used for testing. Each fold is left out for testing once, and the estimated misclassification error is the average test error of each iteration.

On each iteration, one of the k-folds is left out of training and used as the test set to calculate the prediction error for that run. The operation is repeated until every fold has been left out as the test set once. The final estimated misclassification rate is the average test error of all k iterations.

In addition to the misclassification rate, the output of variable importance was obtained for each model. The relative importance of predictors and the accuracy of the classifiers were compared in order to determine which models best predicted the observed class and the Andy class.

3. Results

3.1 Observed Class vs. Andy Class

The contingency table for the Andy class versus the observed class is displayed in Figure 6, and a histogram visualizing the frequencies of matches and mismatches is shown in Figure 7. Pearson's chi-squared test resulted in a p-value < 2.2e-16, which indicates an association between the Andy class and the observed class.

Andy Class	Observed Class			
	E	A	B	Total
E	13	68	27	108
A	3	70	10	83
B	6	10	96	112
Total	22	148	133	303

Figure 6: Contingency table for Andy Class and Recorded Class
X-squared = 140.4, df = 4, p-value < 2.2e-16

In the contingency table, there are large numbers along the diagonal for Class A and Class B. Thus, flowers expected to be dominated by either Apis or Bombus according to Andy's assumptions met those expectations in the recorded data set. However, the small number of flowers with observed equal interactions (Class E) deviated drastically from the number expected by Andy (22 compared to 108).
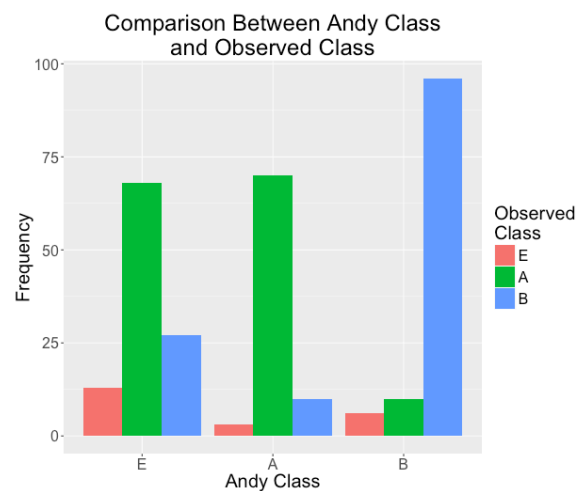

Figure 7: Histogram of contingency table results

The frequency of recorded Class E interactions is very low compared to the number of Andy Class E interactions. These visits are most often dominated by Apis.

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The proportions by row of the contingency table are displayed in Figure 8. Only 12% of Andy Class E interactions were observed to be equal. Instead, 63% of these interactions were dominated by Apis, while 25% were dominated by Bombus.

Andy Class	Observed Class		
	E	A	B
E	0.12	0.63	0.25
A	0.04	0.84	0.12
B	0.05	0.09	0.86

Figure 8: Proportions by row of contingency table for Andy Class and Recorded Class

3.2 Classification Model Results

The results of the 3 classification models, including misclassification rate (MR) and variable importance, are reported in Figures 9, 10, and 11. Additionally, Figure 12 shows the confusion matrix for Model 3 of the observed class.

The model that only considered environmental covariates performed badly on the Andy class (47.2% MR), while the model with 3 flower traits performed very well on it (1.3% MR). This is consistent with the fact that the Andy class is based only on flower traits. The model combining flower traits and environmental covariates was able to best predict the observed class (MR 14.9%); however, it still performed poorly on observed Class E interactions (Figure 12). It is important to note that in this model, Apis proportion was by far the most important predictor variable in the classification task.

Figures for Classification Model Results

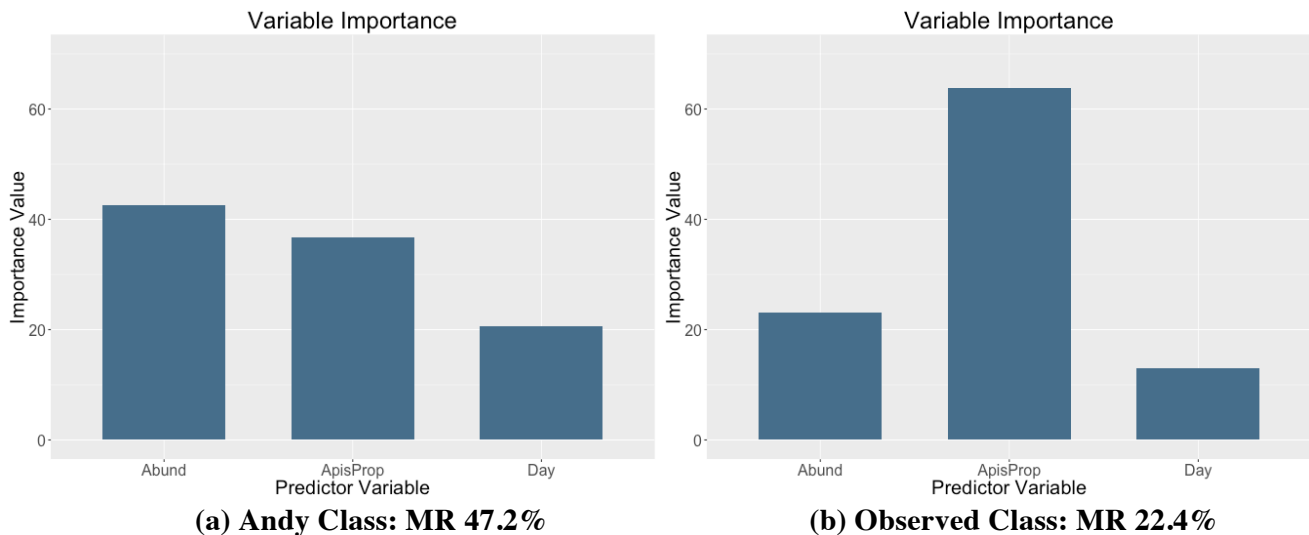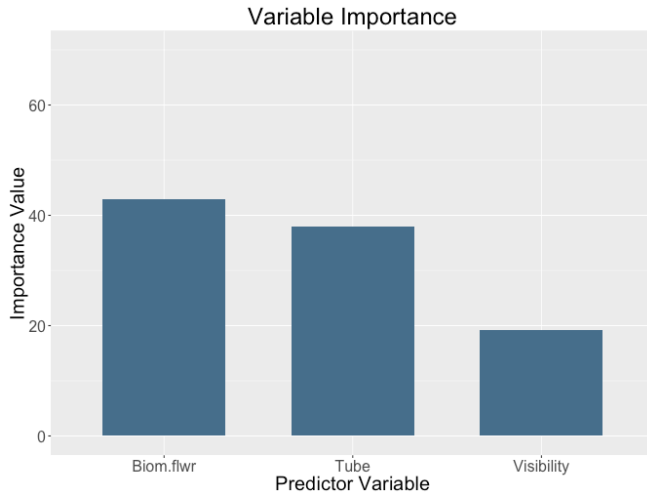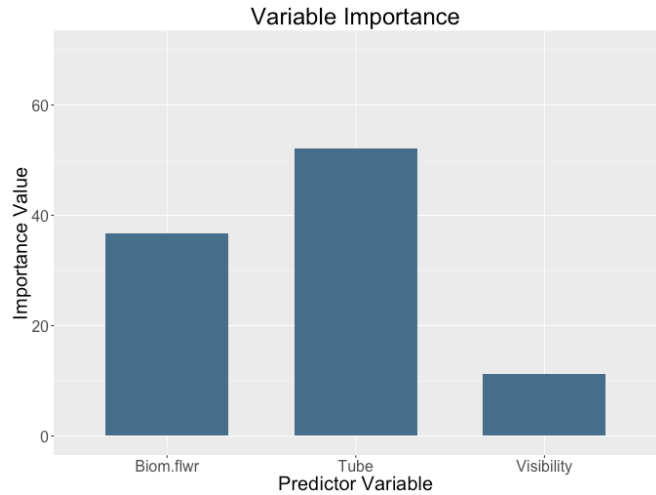**(a) Andy Class: MR 47.2%**   **(b) Observed Class: MR 22.4%**

Figure 9: Model 1 Environmental Covariates

Model 1 took into account day of year, proportion of Apis to all social bees in the mwy, and flower abundance. The classifier for the observed class outperformed the classifier for the Andy class, although neither predicted the class of unseen data exceptionally well. Apis proportion was by far the most important predictor for the observed class, followed by flower abundance and then day.

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(a) Andy Class: MR 1.3%   **(b) Observed Class: MR 20.8%**

Figure 10: Model 2 Flower Traits

The second model focused on flower traits, namely biomass per flower, exclusion based on tube length, and visibility due to color brightness. This model performed very well on the Andy class, giving the largest importance weights to biomass and tube. The observed class also found biomass and tube exclusivity to be the most important variables, with tube receiving a slightly higher importance value. The overall performance of the model on the observed class (MR 20.8%) was much worse than it was for the Andy class (MR 1.3%), but it was somewhat better than Model 1 for the observed class (MR 22.4%).
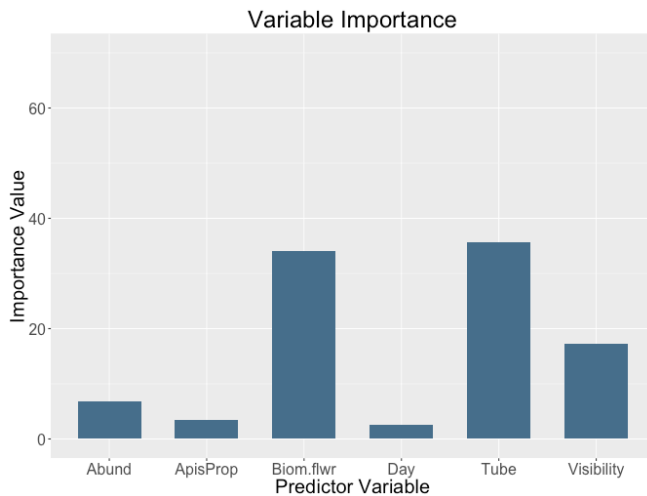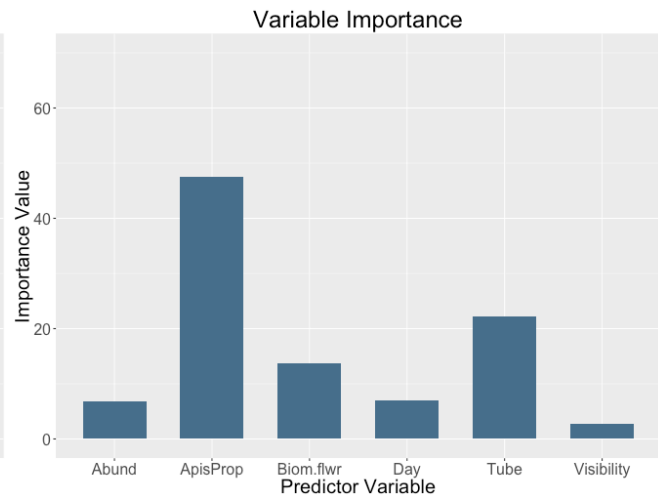
(a) Andy Class: MR 3.3%   **(b) Observed Class: MR 14.9%**

Figure 11: Model 3 Environmental Covariates and Flower Traits

The final model was a combination of Models 1 and 2. The noise of the environmental covariates caused the model to perform slightly worse on the Andy class than Model 2, but the misclassification rate of 3.3% was still low. This model was able to best predict the observed class out of the three models (MR 14.9%). Apis proportion was by far the most important variable in the classification task, followed by tube exclusivity and biomass.

Andy Class	Recorded Class		
	E	A	B
E	2	9	4
A	8	132	6
B	12	7	123

Figure 12: Confusion Matrix for Model 3 on the Observed Class

Only 2 observations in the entire training set were correctly classified for Class E interactions.

4. Discussion

4.1 Summary of Findings and Ecological Interpretation

This study found that Apis and Bombus rarely interacted equally with the same flower species in a given meadow-watch. While 35.6% of interactions were expected to be Class E based on flower traits, only 7.3% of observed interactions fell into this category. In general, Apis dominated Andy Class E interactions more often than Bombus with 63% of these interactions going to Apis and 25% going to Bombus. Many factors may have played a role in the observed partitioning, so I tested models with various predictor variables to gain insight.

Through these models, I found that the Andy class was predicted very well by three flower traits (MR 1.3%). The most important factors in the classification task were tube exclusivity and biomass. Visibility also played a role in the division, but it was less important than the other two variables. Although the Andy class was based on many flower traits (approximately nine), only three variables were required to correctly classify nearly all of the data points. Perhaps this is indicative of a correlation between the different flower traits that favor one genus over the other. As an obvious example, take flower size and the amount of nectar in a flower: small flowers tend to have less nectar, so even though both of these traits will favor Apis, only one is needed to predict the class.

Next, I found that the observed class was predicted best by a combination of flower traits and environmental covariates. Flower traits alone could explain some, but not all, of the partitioning of interactions (MR 20.8%). Species

with more extreme traits, like long tubes or small flowers, always exclude one genus due to physiological limitations, while those without strong exclusionary characteristics do not show consistent favoritism.

Adding the environmental covariates to the model improved the prediction error significantly. Flower abundance and day of year had some influence—possibly because (1) the honeybee dance communication system has been shown to help honeybees hone in on the best flower resources quicker than other pollinators (Donaldson-Matasci *et al*., 2013) and (2) Apis, for the most part, stop foraging late in the season—but presence of Apis in the meadow had by far the greatest importance value. This result is not extremely surprising given that similar metrics were used to measure Apis presence (the proportion of Apis to all social bee interactions in the meadow-watch) and to classify the flower species based on the ratio of Apis to Bombus visits. Still, the implications of this finding must be emphasized: there is a significant relationship between the activity of a pollinator species and the presence of other pollinators in a meadow.

There may be many reasons behind this phenomenon, and I was unable to pinpoint precise causes. One explanation is that the pollinators avoided one another in a meadow, which led to a natural division; the two genera could exist harmoniously by finding their own niches within the same location. Alternatively, competition for flower resources may have led to the divide. If one genus got to a flower species first and took all of the nectar, the other genus would have been forced to interact with other flowers.

Finally, there is the question of how a pollinator's preference for certain flower species may have played a role. Both genera are considered generalist pollinators, but they have proven to be partial to certain flowers. For example, in our recorded data set, 43% of all *Apis mellifera* interactions were with *Gilia capitata*. It is conceivable that one genus dominated a certain flower interaction in a meadow-watch because the other genus was busy visiting flower species higher up on its preference list.

While the combined model of flower traits and environmental covariates performed best on the observed data, it still struggled to classify equal interactions correctly. There are multiple reasons for why the model performed poorly on Class E data. First, the number of observations was limited in the recorded data set (only 22 observed Class E flowers), which made it difficult to train an accurate classifier. Additionally, there may have been a lack of consistency in what caused a flower to be visited equally by Apis and Bombus based on the predictor variables.

4.2 Further Study

Although the total number of Apis and Bombus interactions were approximately equal in the aggregate data set, the abundance of the two genera varied significantly between meadow-watches. As the third model indicated, the presence of Apis compared to all social bees in the meadow-watch had a major impact on which genus dominated a given flower interaction. Moving forward, I propose two options to limit the influence of the ApisProp predictor variable on the overall model. This will allow us to test various hypotheses about competition and differences between Apis and Bombus presence in a meadow.

i) Option 1: Limit the data set so that $A_T = B_T$

The first method removes the presence of Apis from the model entirely by only looking at data from meadow-watch-years with approximately equal Apis and Bombus abundance. If similar results are obtained using this subset of data (i.e. very few equal interactions that cannot be explained by environmental covariates), we can be more certain that the strong partitioning of Apis/Bombus interactions is a result of pollinator competition or avoidance. The main drawback to this approach is the size of the data set; the number of observations may be too sparse to obtain meaningful results.

ii) Option 2: Replace presence of Apis by other explanatory variables

Another approach to limit the impact of Apis presence on the model is to determine what factors influence it. Perhaps ApisProp can be removed from the model and other predictor variables such as temperature, weather, and meadow location/size can be used instead. This will allow us to gain insights into why more Apis may be present in a meadow-watch compared to Bombus or vice versa.

iii) Application: Preference Modeling

The results of this study may have many applications to plant-pollinator network analyses, including flower preference models for single pollinator species. Most existing preference models only take into account flower abundance and flower traits (Kumaran, 2012), but I have begun to show that a pollinator's plant preference may also be impacted by the presence of other pollinator species in a meadow. Thus, the accuracy of predictions of existing models may improve by including pollinator abundance data.

5. Conclusion

This study indicates that the traditional method of studying plant-pollinator networks as bi-modal entities may be insufficient to fully understand the interactions within a network. My results show that abundance of other pollinators in a network may affect the pollination behavior of an insect, although more work must be conducted in order to determine the root causes. Other research has found that the relationship between plant species also plays a role in the larger pollination network. For example, competition with wind-pollinated plant species may negatively affect floral traits and attractiveness of insect-pollinated plants (Flacher *et al.*, 2015).

While this project focused on two abundant genera of generalist pollinators—Apis and Bombus—further research may be conducted to determine the effect of invasive honeybees on specialist native bees. Might dominant generalist pollinators such as *Apis mellifera* be displacing these already sparse native populations?

Finally, additional studies may examine the consequences of pollinator relationships on the flowers within the network and on the overall network structure.
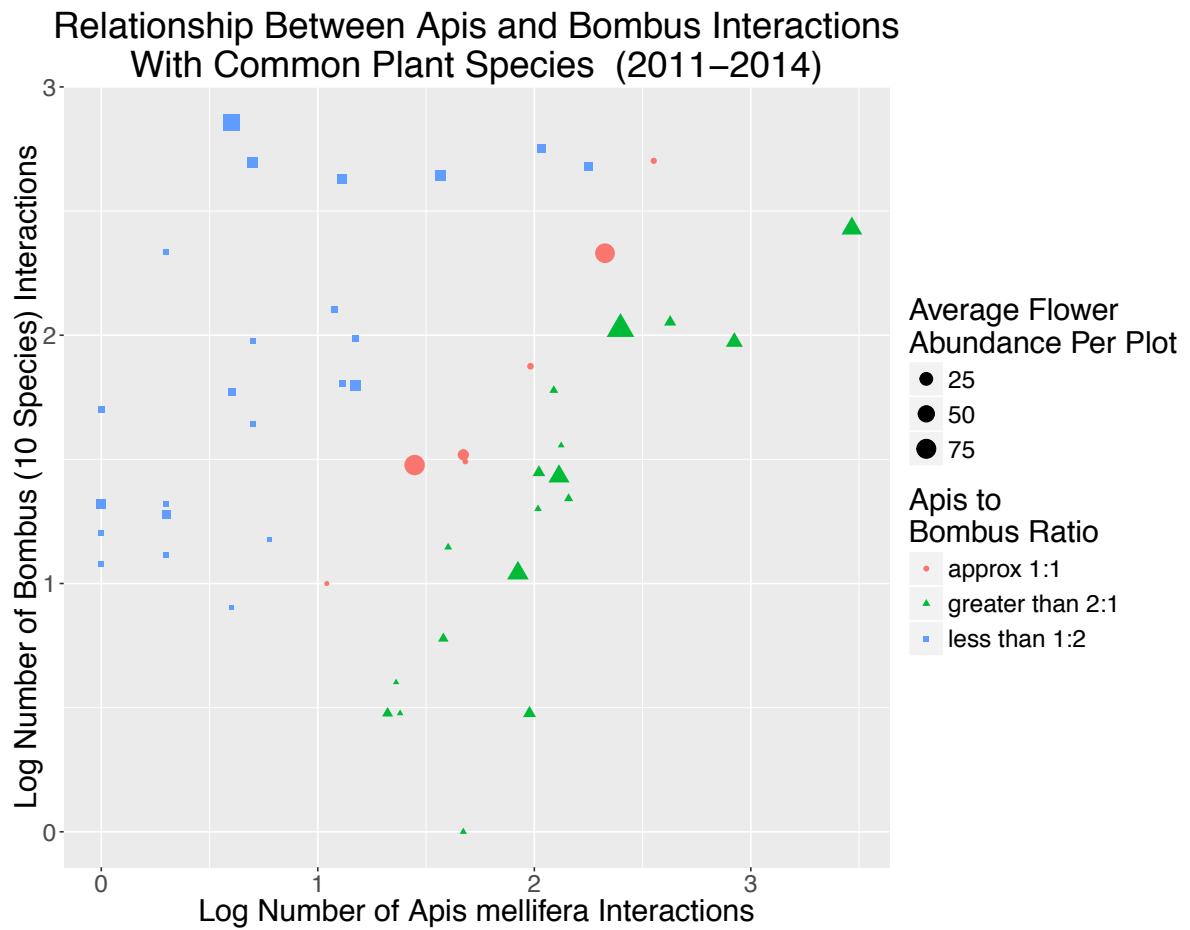
6. Acknowledgements

7. Appendix

Figure 13: Graph of the aggregate data set that shows the partition of Apis/Bombus interactions
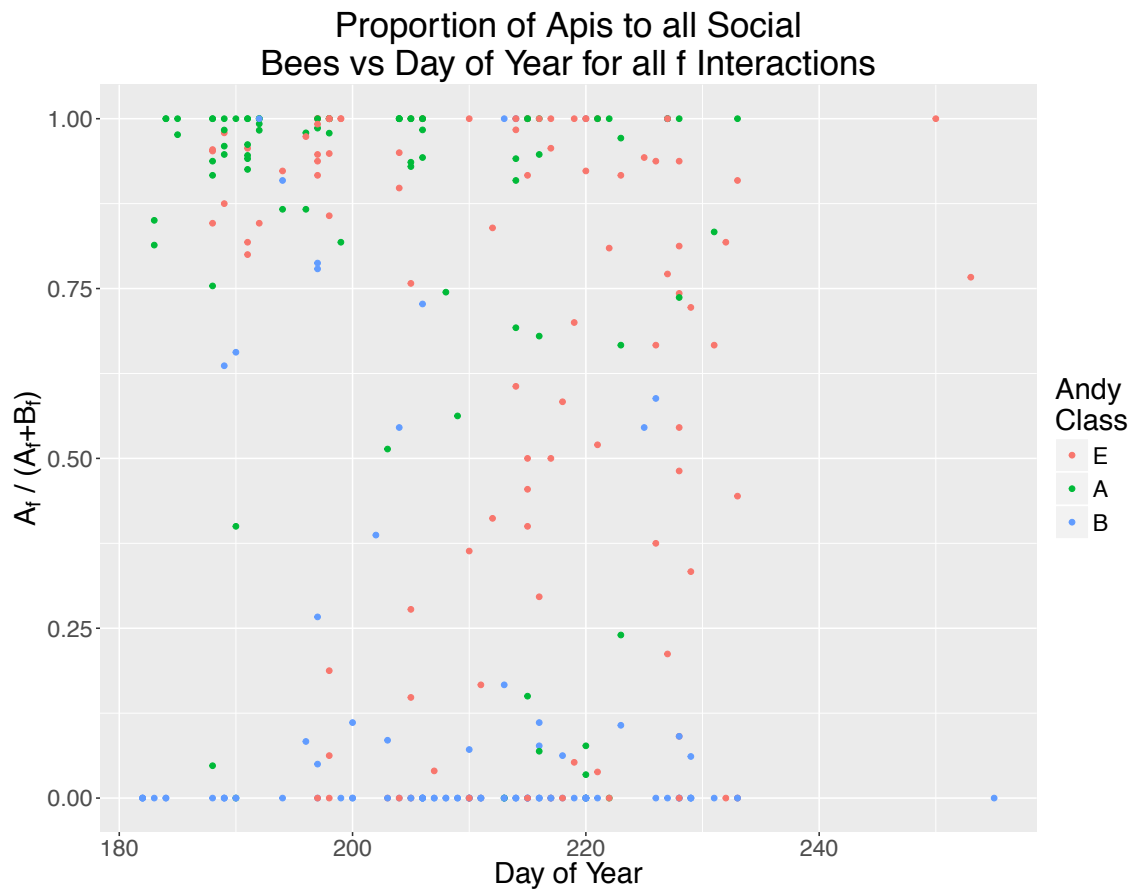
Environmental Covariate Plots

Figure 14. Relationship between Day of year and Apis dominance of flower interactions
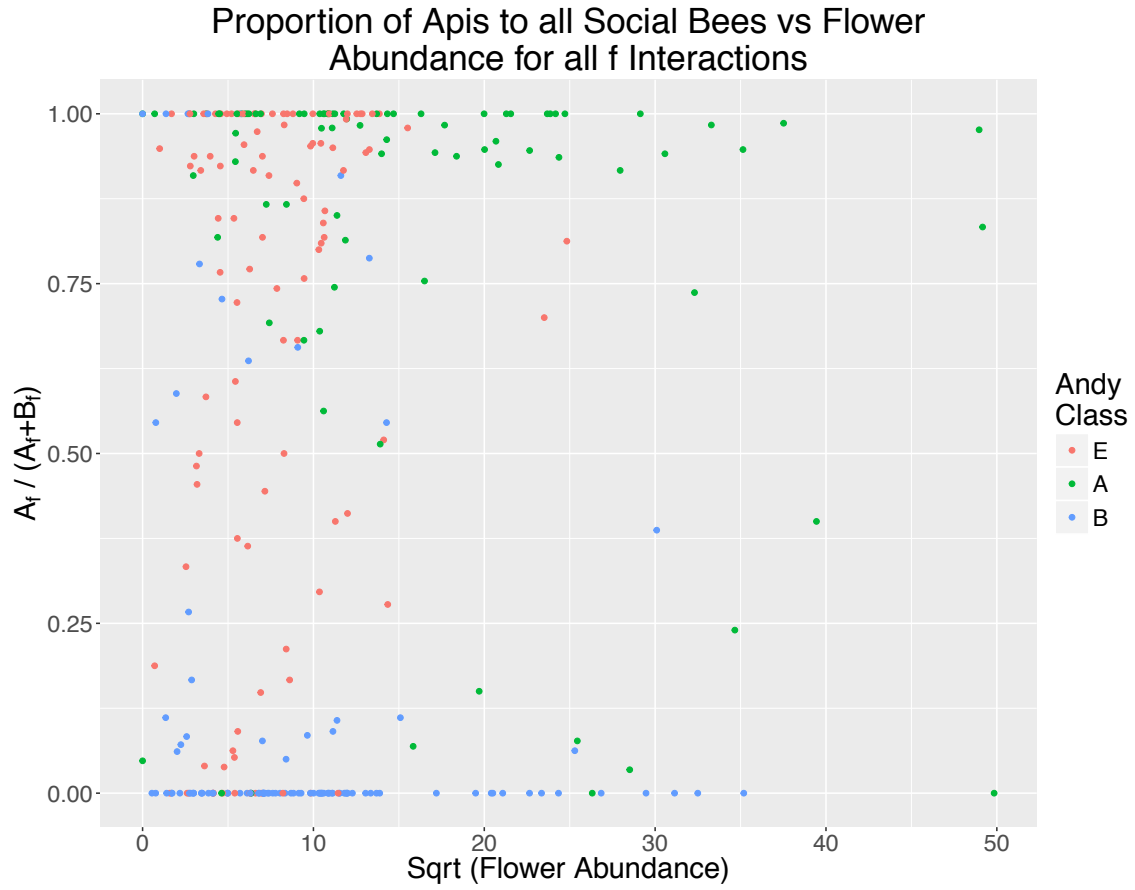
Figure 15 : Relationship between flower abundance and Apis dominance of flower interactions
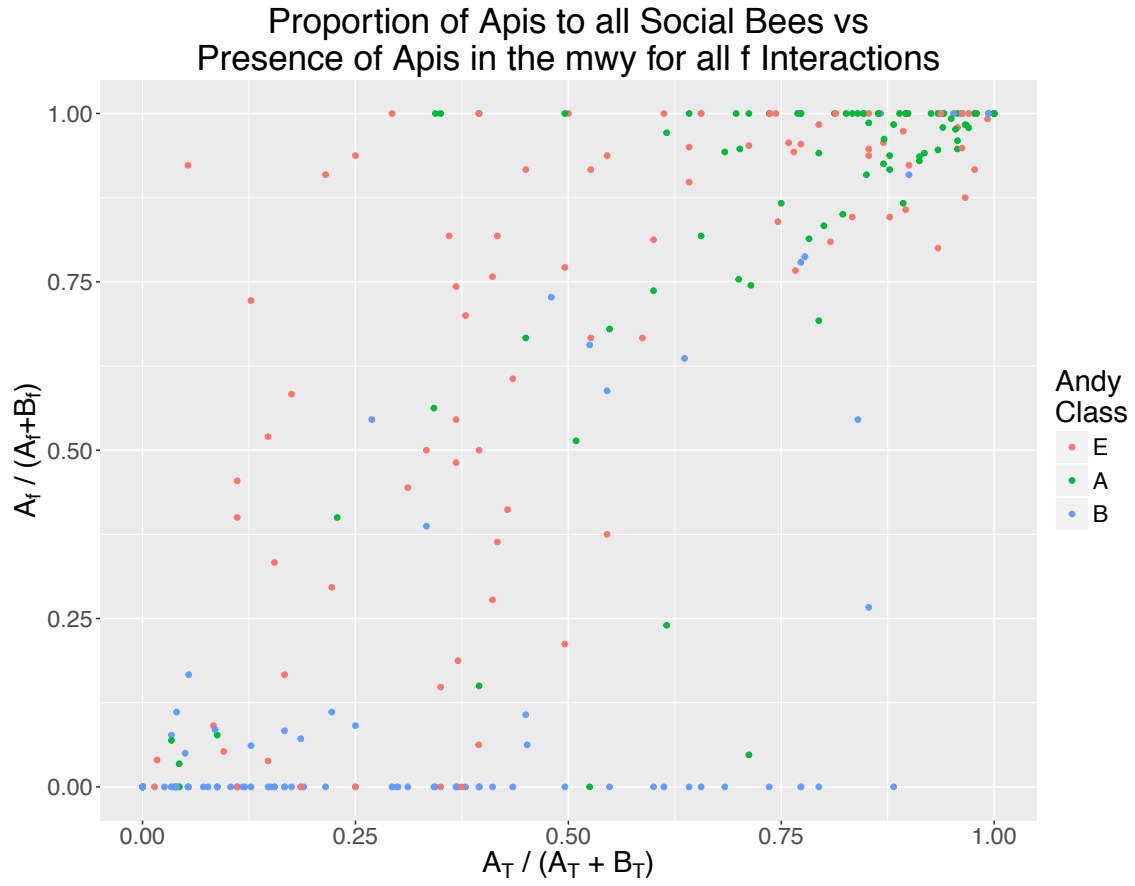
Figure 15 : Relationship between Apis presence in the mwy
and Apis dominance of flower interactions

8. References

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