Floral Insect Visitation to California Native Flowers and their Exotic Counterparts at the UC Berkeley Botanical Garden

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ABSTRACT

The introduction of non-native plant species to the urban landscape has altered historic plant-insect interactions and raised concern regarding the conservation of native pollinators. Little research has investigated the potential of specific exotic flower species to attract pollinators compared to taxonomically-related native flowers. I investigated the attraction of honey bees and native insect visitors to three species of California native flowers (*Symphyotrichum chilense, Eriogonum fasciculatum and solidago californica*) and three exotic but taxonomically-similar species of flowers (*Symphyotrichum oblongifolium, Eriogonum fagopyrum, Solidago speciosa*) at the University of California botanical garden to examine differences in abundance, visitation rates over time, and diversity of floral insect visitors as measured by the Gini-Simpson coefficient. The California native flowers attracted a similar species richness and diversity of insects as their taxonomically-related floral counterparts. Pairwise comparisons showed that the native aster attracted greater numbers of honey bees, but fewer native insect visitors compared to the aromatic aster. The California buckwheat attracted more honey bees and native insects than the exotic buckwheat, but a species-specific attraction of syrphid fly to the exotic flower suggests that nonative flowers can fill an important niche in plant-pollinator networks. Honey bee visitation was independent of time of day for all floral pairs and visitation rates of native insects were only significantly different in the evening sessions, suggesting that other predictors such as floral density, temperature, pollen availability, or shading better predict insect visitor abundance.

KEYWORDS

INTRODUCTION

Bees and other pollinating insects contribute to the production of almost two-thirds of the world's crops and 90% of flowering plants including tomatoes, almonds, squash, strawberries, coffee and even cocoa (Kremen et al. 2002, Ollerton et al. 2011). Pollinators fulfill an essential regulating ecosystem service that humans depend upon for a stable food supply. Estimates placed the economic value of pollination services by insects around $14 billion in the year 2000 (Greenleaf and Kremen 2006). California alone is home to nearly 1,600 species of native bees, including bumble bees (*Bombus spp.)*, digger bees (*Habropoda* and *Anthophora spp.),* and mason bees (*Osmia spp.*) (Frankie et al. 2009), representing 40 percent of all bee species in the U.S. Unfortunately, bees and other pollinators have experienced a startling population decline in recent years. The monarch butterfly, for instance, has experienced a 99 percent reduction in population size in the Western U.S. with now less than 30,000 individuals as of 2018 compared to more than 4.5 million pre-1980 (Pelton et al. 2019) and several native bumblebee species are nearly extinct ("Western Bumblebee and Native Pollinator Research" n.d., Simanonok et al. 2021).

There is growing concern that altered landscapes across the U.S. provide enough suitable forage and nesting space for native and introduced bee species (Frankie et al. 2005). Offering rich floral resources and habitat may help combat the decline in pollinators caused by the conversion of wildlands to cities, farmland, and other developed spaces. Agricultural plots of sunflowers near natural habitat contain much higher levels of average species richness compared to sites located far from natural habitat (Kim et al. 2009), demonstrating the positive correlation between proximity of native flowers and pollinator diversity. A bee survey conducted in the urban environment of the Berkeley, Albany, and Oakland area found that while the average species richness of bees between urban and wildland poppy patches did not differ, the California poppies in wildlands consistently attracted a higher abundance of bees -- meaning proximity to undisturbed habitat may explain greater pollinator presence (Wojcik and McBride 2012). Agricultural fields sown with annual and perennial wildflowers in three different ecoregions of the U.S. attracted significantly greater species richness and abundance of bees in California, Michigan, and Florida compared to weedy, undisturbed control plots (Williams et al. 2015). These case studies provide evidence that careful planning and execution of landscape

modifications has the potential to attract and host a variety of pollinator species compared to conventional agricultural or weedy settings.

The introduction of many nonnative species of flowers and plants to the U.S. may be a leading contributor to the bee decline. From a survey of nearly 950 exotic flowers and 50 native flowers in the bay area, nearly 78% of the native flower species showed measurable attraction to bees while only 9% of the surveyed exotic plants were attractive to bees and other insects (Frankie et al. 2005). This disparity reveals that a vast proportion of introduced species of flowers planted in the Berkeley-Albany area provide very little value to bees and other insects, while a greater proportion of California native plants attract pollinators. However, other surveys in the U.S. found no statistical difference in the species richness or abundance of insect visitors between the native and nonnative plants (Mach and Potter 2018), demonstrating that carefully chosen species of nonnative flowers and woody shrubs have the potential as pest-resistant and highly bee-attractive candidates for the urban landscape. The abundance of native versus nonnative flowers even affects the larvae of the monarch butterfly, who experience *greater* mortality in warmer temperatures when feeding on exotic species of tropical milkweed, such as *Asclepias currassiva,* compared to those feeding on native North American counterparts (Faldyn et al. 2018). Widespread distribution of non-native species of milkweed and other plants could spell disastrous consequences for the monarch butterfly and other species of insects in a changing climate. These examples stress the importance of native plant conservation and recommendations from land restoration experts when performing alterations to the landscape.

Some flower families, such as *Asteraceae, Lamiaceae,* and *Polygonaceae*, regardless of origin, contain highly bee-attractive flowers (Frankie et al. 2005). Species of native flowers such as California lilac, manzanitas, yarrow, and buckwheat, as well as exotic flowers such as pride of madeira, tickseed, lavender, and rosemary experience the greatest visitation by honey bees and native bees (Frankie et al. 2019). Although native versus nonnative identity is an important predictor of floral insect presence, other factors could include temperature, humidity, and lifeform (annual, perennial, or biennial). A study conducted in the United Kingdom found that while Simpson's diversity index did not differ between a selection of attractive annual, biennial or perennial flowers, floral insect diversity was significantly higher on native plants compared to non-natives (Rollings and Goulson 2019). Surprisingly, some plants with very similar floral structures attract different insect pollinator communities. For example, both *Helenium* cultivars

in the study attracted mainly honey bees, while other flowers in the same botanical family, *Asteraceae,* attracted far fewer honey bees despite being grown in the same environmental conditions and having similar flower structure suitable for short-proboscis insects (Rollings and Goulson 2019). Relatively few other studies have aimed to quantify differences in floral insect visitor diversity and changes in attractiveness over time of one native flower species compared to a nonnative relative in the same genus or botanical family.

The present study will expand upon the findings of Frankie (Frankie et al. 2005, Frankie et al. 2019) and other bee surveys (Mach and Potter 2018, Rollings and Goulson 2019) to compare the level of attractiveness of several California native flowers and a corresponding species of exotic flower that may be taxonomically or structurally similar to determine if both native and exotic flowers are valuable resources for pollinator conservation. I will investigate whether bees and other insects visit native California flower species more often than their closely related exotic counterparts in the same environmental conditions. First, I specifically ask: (1) how does floral insect abundance compare between three select species of California native flowers and their respective exotic counterparts, (2) how does species diversity of insect visitors compares between each native flower and its exotic counterpart, and (3) whether honey bee and native bee visitation change in a predictable manner over the course of the day considering each native flower and its nonnative counterpart. This third question will help answer whether visitation by native insects and honey bees follows a predictable trend from morning until evening in the native and nonnative flower groups. I conducted observations at the UC Berkeley Botanical Garden to investigate these questions in a semi-controlled study.

METHODS

Site description

The UC Berkeley Botanical Garden consists of 34 acres of land that spans in elevation from 600 to 900 feet situated approximately one half a mile west of the central UC Berkeley campus at coordinates 37.8751° N, 122.2387° W. The history of the UC Berkeley Botanical garden begins in 1925 when it was relocated from the main campus to where it now stands following a purchase of land in 1909 in the region of Strawberry Canyon. This garden contains

approximately 10,000 different species of plants in its collections separated into seven major "ecoregions" meant to resemble plant habitats from different parts of the world including California, Eastern North America, Asia, the tropical cloud forest, and more. While these spatial designations are apparent to the average visitor, the flowers growing in different sections are in close enough proximity to one another to help control the effects of climate variability, temperature, or topographic features that may vary heterogeneously between flowers sampled from distant study sites. Garden horticultural staff conduct regular watering schedules for each section in the garden, irrigating the plants in each ecoregion once a week on average in the spring, summer, and fall months when rainwater is unavailable.

I chose this study site to conduct this semi-controlled observational study because one of the major limitations of this study is the availability and accessibility of bee-attracting flowers in urban gardens. Choosing sites elsewhere or at random within the city of Berkeley introduced several confounding variables such as topographic variation, wind variability, and heterogeneous distribution of possible insect visitors to the floral pairs. One of the advantages of selecting only a single site is that it helps to control topographic variation, elevation, and unequal local distribution of native bee/ honey bee nesting sites that may vary over the course of the city of Berkeley. This means that I assume that the bees that are present in the small geographic area of the garden have equal access to all the plants in the collection, and that I cannot attribute a higher frequency of one species of bee to the native aster versus the exotic aster due to physical distance or separation.

The flowers of study are located in three particular sections or "ecoregions" of the botanical garden: California section, Eastern North America, and the Crops of the World. The California aster (*Symphyotrichum chilense*), and California goldenrod (*Solidago californica*) flower patches used in this study are located in beds 19 and 4, respectively, in the California ecoregion. The California buckwheat (*Eriogonum fasciculatum*) is located in bed, 171B, part of the deserts of the world garden. The aromatic aster (*Symphyotrichum oblongifolium*), and showy goldenrod (*Solidago speciosa*) are located in bed 307 of Eastern North America section. Finally, the cultivated buckwheat (*Eriogonum fagopyrum*) is located in bed 802 of the crops of the world garden. The greatest distance between any two plants of this study is no more than 500 feet. I recorded the sun exposure and direction of each patch of flowers was noted and analyzed for potential influence to the expected results as will be described in more detail.

Pairwise floral selection

To determine the differences in attraction between California native flowers and their nonnative counterparts, I have selected the following pairs of flowers shown below in response to several limiting factors including bloom seasonality, structural similarity, and accessibility. As described before, I found it difficult to locate a California native flower and a taxonomically-related exotic species growing in the same geographic location in bloom during the same time of year. The flowers listed below comprise those that are in bloom from August-September during and belong either to the same genus or botanical family.

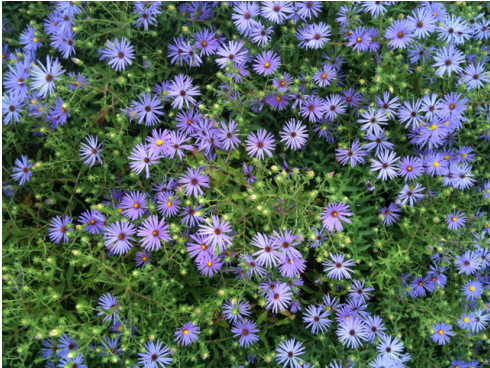**Table 1. Comparison of selected plant species for study on bee abundance/visitation.**

Native Flower	Exotic Counterpart
Pair #1	
California Aster- *Symphyotrichum chilense* (Family: *Asteraceae*)	Aromatic aster-*Symphyotrichum oblongifolium* (Family: *Asteraceae*) (Eastern U.S. native flower)

Photo by: Taylor Rein
(Flower type: Ray)

Photo by: Lee Page
(Flower type: Ray)

Pair #2

Eriogonum fasciculatum (Family: *Polygonaceae*) California Buckwheat	*Polygonum fagopyrum*- (Family: *Polygonaceae*) Cultivated form of buckwheat- European native

Photo by: Taylor Rein

(Flower type: Raceme of cymes)

Photo by: Taylor Rein

(Flower type: Raceme of cymes)

Pair #3

California Goldenrod - *Solidago velutina*

Photo by: Stan Shebs

(Flower type: Panicle)

Showy Goldenrod - *Solidago speciosa* (Eastern U.S. native)

Photo by: Janet Davis

(Flower type: Panicle)

It is important to understand the structural parts of a plant to evaluate these pairwise comparisons. Upon visual inspection, flowers such as those in the *Asteraceae* family appear to have a very similar floral structure with sunflowers, which are categorized as disk flowers. Buckwheats, for instance, in both native and exotic species have a cyme-like inflorescence structure as their flowers (Jacquemart et al. 2007). While some California native flowers may share structural characteristics and perhaps even evolutionary relatedness to species of flowers native elsewhere in North America or other regions of the world, the value to pollinators may not be comparable. Hence, this study aimed to discern differences in floral insect visitor attraction in attraction between a native flower matched with an exotic flower in the same family or genus to control for evolutionary relatedness.

I incorporated into the plant selection recommendations by Dr. Peter Oboyski from the Essig museum of entomology and the aid of casual observations conducted prior to this formal

study that observed insect visitors at the UC Berkeley Botanical Garden. The plant choices included in Table 1 reflects my attempt to select a native California flower and a nonnative counterpart that are both attractive to insects, in the same botanical family, and ideally have similar flower structures or morphology. I used The University and Jepson Herbarium online resource which is useful for distinguishing taxonomy and flower type of California native flowers (Jepson Flora Project, 2021).

My total sample size was N=3, which is 3 species of native flowers and 3 species of exotic flowers. For the purpose of this study, the term "native" refers to any and all plants indigenous to the state of California, as these are the plants of most interest for inclusion on planting diverse landscapes with plants well adapted to the Mediterranean climate, soil, and water availability. Plants that originated from other parts of North America or other countries, but have been introduced into the California landscape are considered *nonnative* or *exotic* and I may use these two terms interchangeably in this paper. I consider the presence of honey bees, native wild bees, syrphid flies, and butterflies as the primary insect visitors of interest for this study. I did not represent hummingbirds, flesh flies, beetles, or other potential animal pollinators, as they were either not present on the flowers in this study or so rare in occurrence that I did not find their contribution to this study meaningful.

Data collection methods

To establish my observation plots, I examined a single flower patch containing each species of flower listed above at the botanical garden and marked a 1.5 by 1.5 meter amount of space using a tape measure from which I observed all insect visitors during the course of the study. I tried to sample when temperatures were above 12.7° Celsius (65° Fahrenheit) and the weather was sunny-- optimal conditions for insect activity. These sampling conditions follow a regime similar to that of Frankie et al. (2005). Fortunately, each flower of this study nearly homogeneously occupied a two-dimensional area of soil and either completely occupied the boundaries of this 1.5 by 1.5 square meter of arbitrary space or exceeded those boundaries not more than a meter. This makes the pairwise comparison more reliable and helps to control for an overly abundant number of flowers within a single patch.

To quantify insect visitors to the flowers selected in this study, I recorded the number of bees, syrphid flies, wasps, and butterflies visiting one of the species of flowers of each floral pair during a 10 minute sampling session using a stopwatch to record time. I then walked to the part of the garden containing the other member of the flower pair (within 5 minutes) and repeated the 10 minute sampling session, recording all insect visitors. Samples were collected between the hours of 11:30 am at the earliest and 4:45 pm at the latest (the garden closes at 5pm sharp) over the course of several weeks while the flowers were in bloom. I repeated this procedure for a total of 110 sampling sessions over five weeks during the months of September-October. Although temperature and atmospheric pressure varied day by day, these changes would not be expected to impact the comparative abundance of bees on one flower in each pair because if one member of the floral pair was sampled on a particular day, its native or nonnative counterpart was subsequently sampled within a half-hour period. I alternated which flower I sampled first in each floral pair to avoid systematic bias from observing the same flower a few minutes earlier in the day than its counterpart.

For the identification of native bees, I performed visual observation in the field using the reference manual *Common Bees of California Gardens* (Frankie et al. 2017). I sent photographs of unknown species of syrphid flies or butterflies to the director of the Essig Museum of Entomology or local community member experts for further help in insect identification of unfamiliar insects. I also referred to online field guides (Correa 2019) or the database iNaturalist to confirm any uncertainties in insect identity for both syrphid flies and butterflies. Classifications of some insects were made only to the genus when species identification was impossible.

Because temperature, sunlight, time of day, and humidity all served as potential features that can help predict the number of insects present during a given sampling session, I recorded the temperature and relative humidity during each observation period using a sling psychrometer (Appendix A). I estimated the relative portion of the flower patch that experienced shading using a tape measure expressed as a fraction of the total flower patch. Finally, I recorded the direction of exposure of a flower patch by using a compass on a cell phone.

Analysis of insect visitor visitation rates

To quantify insect visitors, I first separated counts of insect visitors into distinct groups based on species or genera: counts of honey bees, native bees, syrphid flies, butterflies and wasps. I then aggregated (summed) the number of tally marks recorded on paper during the 10-minute sampling sessions, documenting each bee, syrphid fly, butterfly or other insect to produce a record of total insect visitors by species. For later analysis, I partitioned honey bees from other insect visitors to create two distinct groups: native pollinators and honey bees. I then conducted a pairwise t-test on the number of insect visitors recorded during a sampling period (# individuals/10 minutes) and checked for normality of the paired differences in insect visitors between each flower and its counterpart using the scipy stats version 1.7.1 in Jupyter Notebooks with Python version 3.9.7.

Analysis to determine changes in insect abundance over time

To quantify and predict the number of bees and other insect visitors for a particular sampling period, I first grouped together samples into three categories depending on the time of day. Any sample collected during the hour of 11:20-1:15pm, I grouped into the early afternoon session; any sample collected from 1:35pm-3:30pm as the mid afternoon session, and any insect observed from 3:45-5pm in the evening session. I then constructed box plots with time as a categorical variable and visualized the number of insect visitors on the y-axis. I conducted two-way ANOVA using stats models module version 0.13.1 (Seabold, Skipper, and Josef Perktold) to determine the effect of two categorical variables, time of day and native/nonnative plant identity, on the response variable of interest: insect visitation rates in numbers of individuals per 10 minute sampling session.

Analysis of species diversity

For analysis of species diversity during a particular sampling session, I calculated species diversity using the Gini-Simpson Diversity index. Ordinarily, the Simpson diversity index is calculated using the formula:

$$D = \sum_{i=1}^{S} (p_i)^2$$

where p_i represents the proportion of each species in the whole population (# individuals of species S)/(total number of individuals from all Species N). However, because this format usually produces higher numbers for less diverse communities and lower numbers for more diverse communities (counterintuitive to most scholars) I used the Gini–Simpson index, which is a simple modification in that it is 1-D :

$$Gini - Simpson\ Index = 1 - \sum_{i=1}^{S} (p_i)^2$$

which produces higher values for higher species diversity and lower values for lower species diversity. I calculated the Gini-simpson index using the scikit-bio package version 0.5.6, again in Jupyter Notebooks with Python version 3.9.7. and defined an original function to iterate through each row of the dataset and calculate the Gini-Simpson index for that session. As a second metric, I calculated the species richness of insect visitors for each sampling session as the number of nonzero recorded species of bees, syrphid flies, butterflies, or wasps. I then determined the mean species richness for each of the six flower species and the standard error range of that mean considering the entire study period.

RESULTS

Insect visitor abundance

During the multi-week study, I observed 2,669 insect visitors from nine different taxa. The dominant floral visitors included the European honey bee (*Apis mellifera*), sweat bee (*Halictus ligatus*), mining bee (*Adrenae spp.*), two species of *Lepidoptera* -fiery skipper and the mylitta crescent - and two species of syrphid (*Eristalis tenax and Toxmoerus spp.*). Considering all floral pairs, the European honey bee, mining bee and the sweat bee represent the three most abundant insect visitors, accounting for 28%, 23%, and 26%, respectively, of all insect visitors observed during the study amongst the floral pairs (Figure 1). The dominant visitor for the California buckwheat and the California aster was the mining bee (*Andrena sp.*) and European honey bee, respectively. The California aster attracted more honey bees, syrphid flies, and butterflies than its exotic counterpart, but not sweat bees or mining bees (Figure 1). Finally, the

nonative species of goldenrod attracted a greater or comparable number of insect visitors to its native counterpart, but comparisons for this floral pair are fewer as the sampling period was far shorter, lasting only a week, due to field conditions.
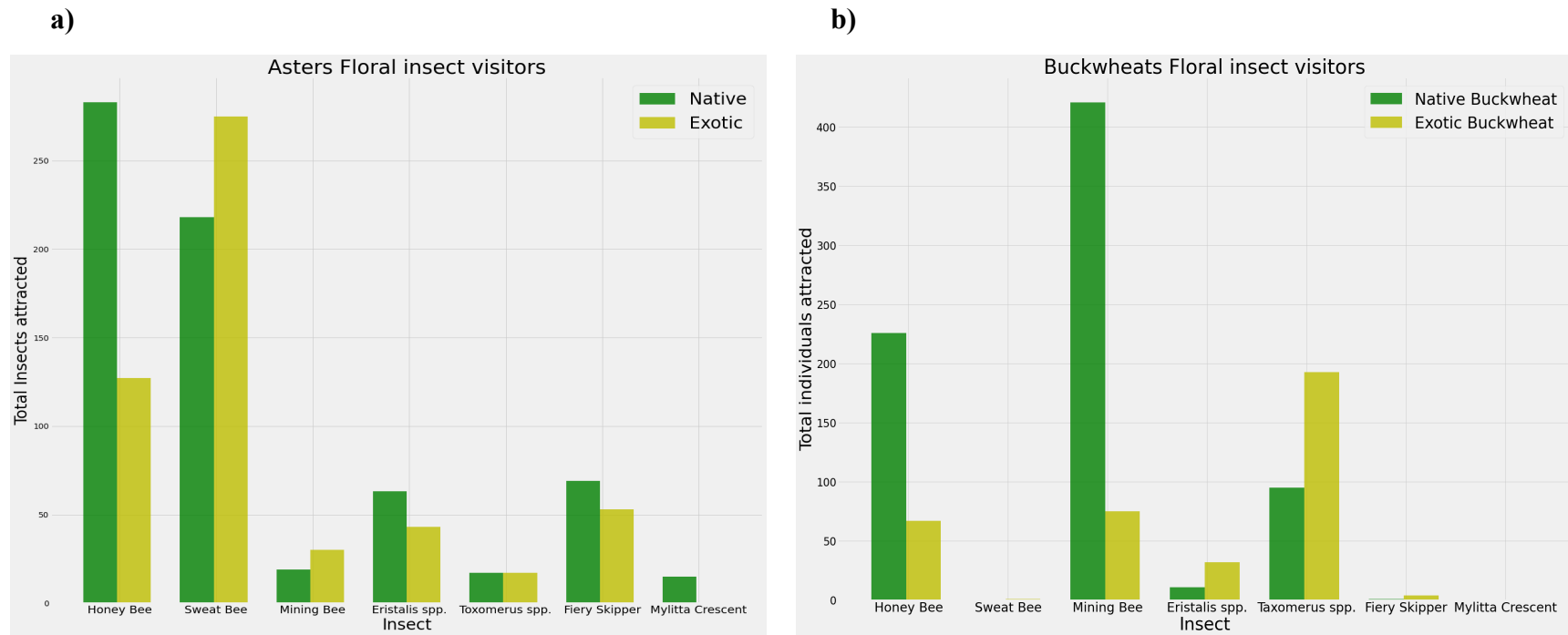
a)

b)

Figure 1: Total floral insect visitors by type at the a) California native and exotic aster and b) the naitve and exotic buckwheat. Note: I excluded the species *Bombus vosnesenskii, Anthidium manicatum*, vespula spp., gray hairstreak butterfly, syrphid in the genus *Spilomya,* and syrphid in the genus *Heilphous* from the calculations of summary statistics (Table 1), but not from statistical tests because I only observed these insects on rare occasions (less than five visits in any single session).

Pairwise comparison for abundance of Apis mellifera visitors

I first checked the normality of the paired differences for forty different sampling sessions which I conducted at the UC Berkeley botanical garden. I constructed a histogram plotting the number of honey bees observed at a particular exotic flower minus the number of bees observed at its respective native counterpart; negative differences hence mean that a greater number of bees visited the native flower compared to its exotic counterpart (Figure 2). The distribution of differences for both the aster floral pair and buckwheat floral pair resembles a bell-shaped curve with a mean of -4.9 and -7.1 respectively (Figure 2). A Shapiro test of normality was nonsignificant (p=0.91), meaning that the differences follow a nearly normal distribution.

I performed a pairwise t-test to test whether the mean difference in number of honey bees from each native flower from its exotic counterpart was zero. There was a significant difference in the abundance of honey bees during each sampling session present at the California native aster and aromatic aster t(19) = -4.51, p=0.0002. More honey bees visited the California aster (M=10.5, SD= 5.22) than the exotic aster (M=5.61, SD=3.16). A pairwise t-test independently considering the buckwheat pair was significant: greater numbers of honey bees visited the native buckwheat (*Eriogonum fasciculatum)* (M=10.8, SD= 6.48) than the exotic counterpart (*Eriogonum fagopyrum)* (M=3.75, SD=2.57), t(15)=-4.61, p=0.003. Aggregating observations from all three floral pairs, including the few samples conducted on the goldenrods, fewer honey bees visited the exotic flower compared to the native counterpart with a mean difference of -5.22 honey bees between the exotic flower and the native counterpart, t(39)=5.665, p<<0.0001. I did not perform analysis independently on the goldenrods as I only obtained three matched sampling sessions for this floral pair and the sample size was too small to feel confident in applying statistical analysis.

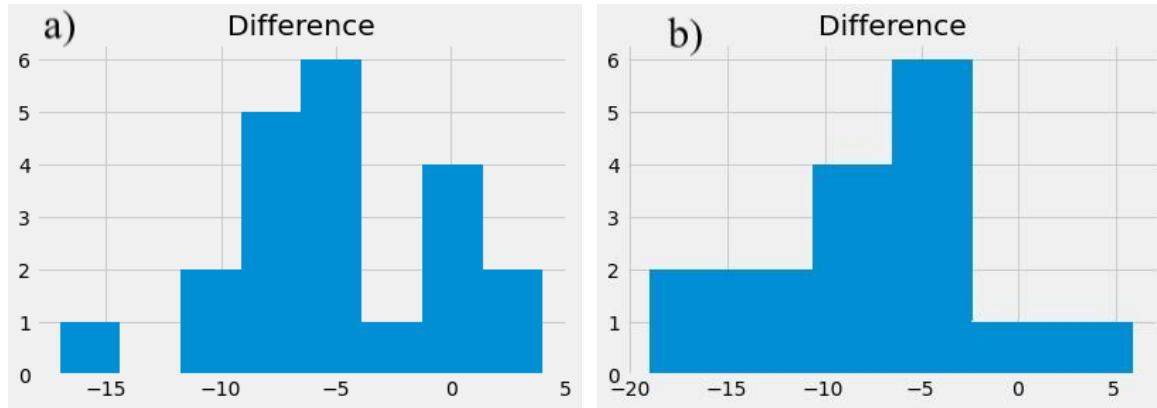a)   b)

Figure 2. Histograms of the paired differences in honey bee visitors (*Apis mellifera*) to the a) California aster and aromatic aster (Mean = -4.9, N= 20 sampling sessions) and b) buckwheats (Mean=-7.1, N= 16 sampling sessions). Negative differences indicate more visitors to the native flower than the exotic flower.

Pairwise comparison for abundance of native floral insect visitors

I checked for normality on the paired differences for only native insect visitors (all non-*Apis mellifera* insects). The paired differences follow a nearly normal distribution and a Shapiro Wilk test was insignificant (p=0.37) (Figure 3). When excluding honey bee visitors, a pairwise comparison revealed that although the California aster attracted a greater total number of insects overall during the study period (Table 1), *more* native insects visited the aromatic aster (M=20.809, SD=10.77) on average during each sampling session than the California aster (M=16.9, SD=8.37), t(19)=2.57, p=0.01. Considering native insect visitors of the buckwheats, pairwise comparison revealed a mean difference of d=-6.2, with a stronger preference for the native buckwheat (M= 22.6, SD=7.87) than the exotic counterpart (M=16.37, SD=8.76), t(13)=-2.8347415927785837, p=0.014. Surprisingly, if I combined the differences from the California aster, the buckwheats, and the goldenrods together and applied a single pairwise t-test, it produced a mean difference of 0.0, t(39)=0, p=1.0. Intuitively, one should apply pairwise comparisons of insect visitors separately for each floral pair because combining data from all three floral pairs effectively masked the preference of native insects for the California buckwheat and produced a nonsignificant result (p=1.0).

a)   **b)**
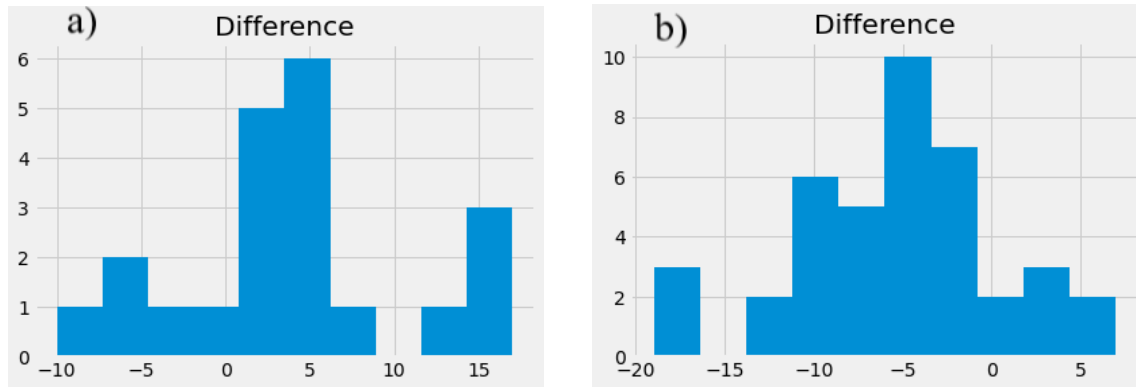
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Figure 3. Histogram of the paired differences in native insect visitors to the a) California aster and aromatic aster (Mean =3.9, N= 20 sampling sessions) and b) buckwheats (Mean=-6.2, N= 28 sampling sessions).

Changes in insect visitation rates over time

Total insect visitors- asters

I first checked for equal variance between each of the six groups using the Bartlett test when considering all insect visitors (honey bees and native insects) combined at the California aster and aromatic aster. Two-way ANOVA revealed no main effects between either time of day $F_{(2,43)}=2.596$, $p=0.086$ or native/nonnative status $F_{(1,42)}=0.88$, $p=0.35$. Visual inspection of the box and whisker plot confirms that total insect abundance was comparable between the three time periods of observation for the native and exotic aster (Figure 4a).
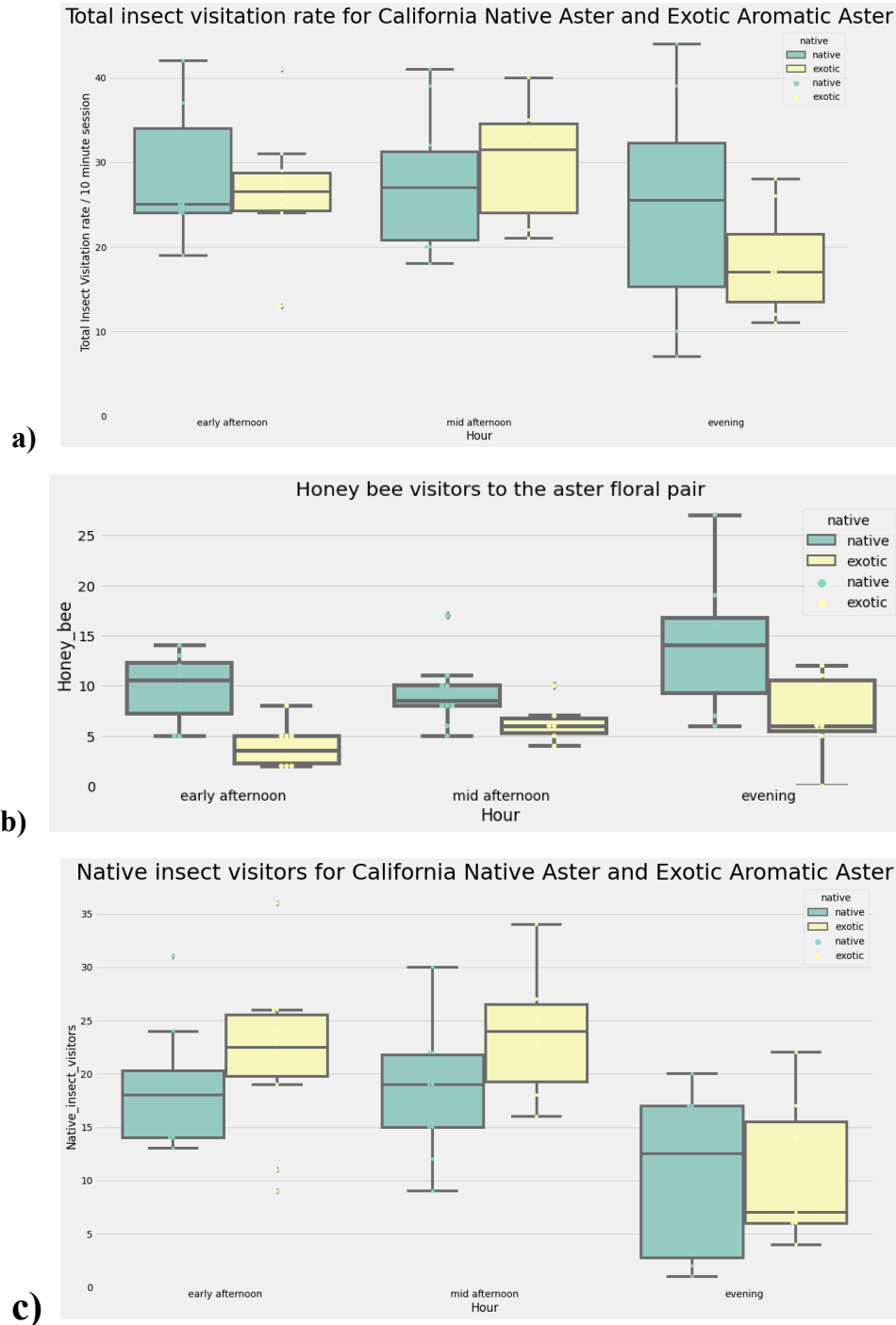
a)

b)

c)

Figure 4. Box plots for a) total insect visitors b) honey bees, and c) native insects to theCalifornia and exotic aster grouped into three times of day. Note that green box plots correspond to native flowers while yellow box plots correspond to the exotic flower. The horizontal line contained within the shaded boxes indicate the median of each group, not the mean. The top whisker indicates 1.5 times the interquartile range above the median while the bottom whisker indicates 1.5 times the interquartile range below the median.

Honey bees-asters

Although the variance of honey bees in the evening hour demonstrates a greater spread than that of the early and mid afternoon for both the California and aromatic aster, a Bartlett test to check for equal variance of California aster (spread of each of the three green boxplots) at the three times of the day revealed a nonsignificant result (p=0.07), indicating that the variation was not great enough to reject the null hypothesis that the spread of honey bee was the same over the course of the day. A repeated Bartlett test on the aromatic aster (spread of the three yellow box plots in Figure 4b) and between each flower at the three times of the day produced a low p-value (p=0.08), but still insignificant.

I then applied a two-way analysis of variance after confirming the assumptions of normality and equal variance to analyze the effect of two categorical variables: native/nonnative status and time of day (early afternoon, mid afternoon, and evening), and their effect on the number of honey bees present. Two-way ANOVA revealed a significant main effect of time of day $F(2,43)=4.41$, p=0.02 *and* native/nonnative flower status on honey bee visitors $F(1,43)=21.26$, $p << 0.01$. There was no significant interaction effect between the two independent variables $F(2,43)=1.09$, p=0.34.

According to the post-hoc test, the aromatic aster attracted fewer honey bees only during the early afternoon and evening sessions, but not mid-afternoon (Table 2). Time of day was not significant for the pairwise comparisons of interest. Honey bee visitation rates were independent of time of day for both of the asters

Table 2. Multiple Comparison of Means for Honey bees using Tukey post-hoc test.

group1	group2	p-value	Significant?
Aromatic Aster , early afternoon	Aromatic Aster , mid afternoon	0.8166	False
Aromatic Aster , early afternoon	Aromatic Aster , evening	0.5521	False
Aromatic Aster , evening	Aromatic Aster , mid afternoon	0.9	False
CA Aster , early afternoon	CA Aster , mid afternoon	0.9	False
CA Aster , early afternoon	CA Aster , evening	0.2507	False
CA Aster , evening	CA Aster , mid afternoon	0.1115	False
Aromatic Aster , early afternoon	**CA Aster , early afternoon**	**0.035**	**True**
Aromatic Aster , mid afternoon	CA Aster , mid afternoon	0.6978	False

Aromatic Aster , evening **CA Aster , evening** **0.0163** **True**

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Native insects-asters

Moreover, there was a main effect of time of day for the native pollinators present at the aster floral pairs $F(2,43)=10.6$, $p<0.05$, but native/nonnative status *did not* influence native pollinator abundance $F(1,43)=2.10$, $p=0.154118$) (Figure 3c). Native insect visitors were less abundant in the evening hours than the other times of day. The interaction effect was insignificant $F(2,43)=2.0$, $p=0.54$.

According to Tukey's post hoc test, there was *no* significant change in the mean number of native insects present at the three times of day for the California aster. However, native insect visitors were more abundant at the aromatic aster in the early afternoon and mid afternoon compared to the evening session (mean difference=10.9 insects and 13.0 insects respectively). As confirmed by two-way ANOVA, time of day had a main effect, but only for the exotic species. Pairwise comparisons revealed no significant difference in native bee visitation rates between the native and exotic flower species for the three time of day.

Table 3. Multiple Comparison of Means for Native Insects with Tukey's Post-hoc test. Note that all other unreported comparisons (six more total) were insignificant.

Group 1	Group 2	mean diff	p-value	Significant?
Aromatic Aster , early afternoon	Aromatic Aster , mid afternoon	2.0333	0.9	False
Aromatic Aster , evening	Aromatic Aster , mid afternoon	12.9762	0.0166	True
Aromatic Aster , early afternoon	Aromatic Aster , evening -10.9429		0.0256	True

Total insect visitors-buckwheats

Although the variance of total insect visitors between the three times of day was comparable for the native buckwheat (Bartlett's test, $p=0.19$) and the Cultivated Buckwheat ($p=0.82$), the evening hours for the California Buckwheat demonstrated a much wider spread than the exotic buckwheat, violating one of the assumptions of the two way analysis of variance

(Figure 5). Nonetheless, a two-way anova revealed a main effect between native/nonnative status and total insects present (F(1,43)=21.5, p<<0.05) but not time (F(2,43)=2.96, p=0.06). A post-hoc test reveals that the only significant pairwise comparison was between the California buckwheat and cultivated buckwheat in the evening session: the cultivated buckwheat had a lower total insect visitation rate in the evening compared to the California buckwheat. There were comparable numbers of total insect visitors at the other two times of day (Figure 5).
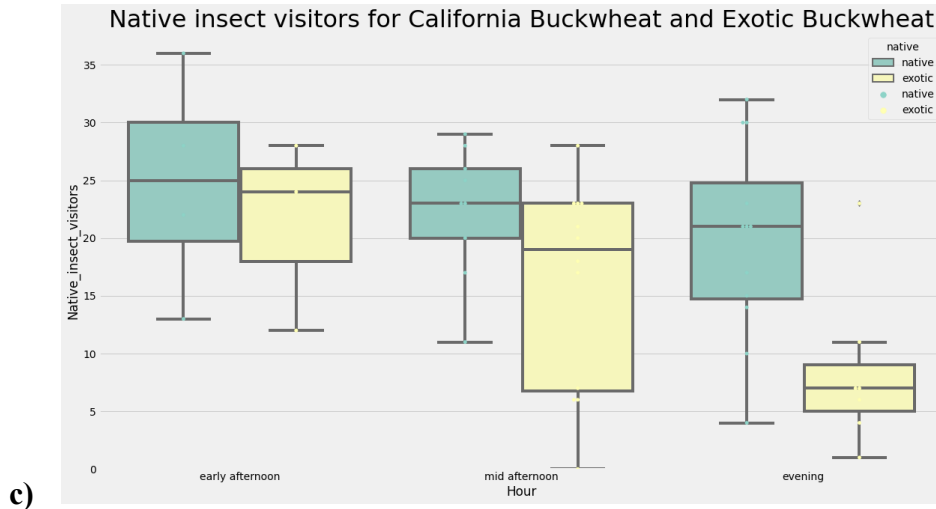

a)

b)

c)
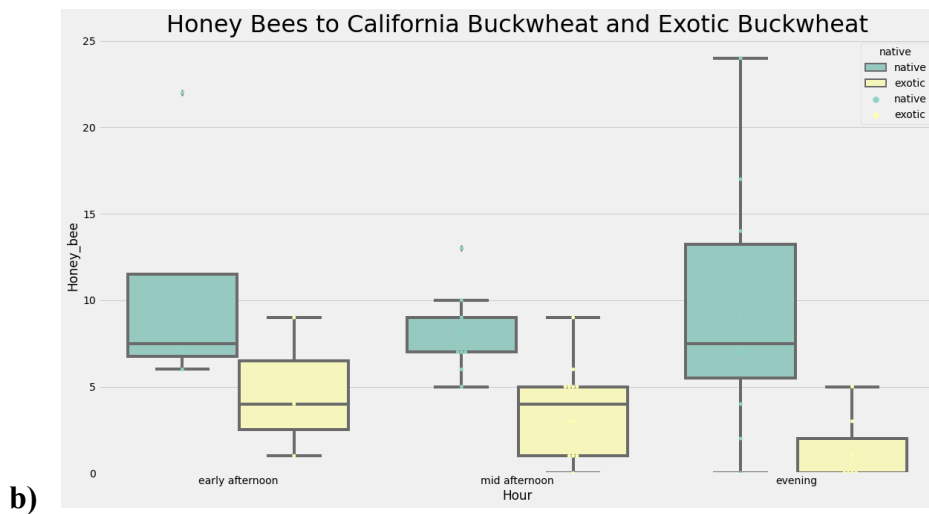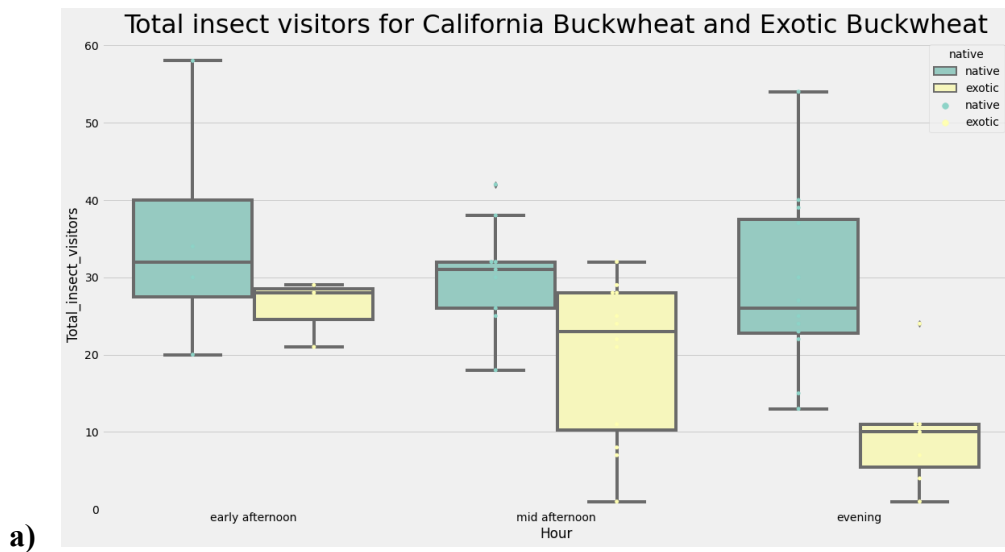
Figure 5. Box plots for a) total insect visitors b) honey bees, and c) native insects to California and exotic buckwheat grouped into three times of day. Note that green box plots correspond to native flowers while yellow box plots correspond to the exotic flower. The horizontal line contained within the shaded boxes indicate the median of each group, not the mean. The top whisker indicates 1.5 times the interquartile range above the median while the bottom whisker indicates 1.5 times the interquartile range below the median.

Honey bees-buckwheats

Although a Bartlett test of equal variance was significant for the honey bee visitors at the three times or day for the California buckwheat (p=0.019), I continued to apply two-way analysis of variance for the honey bees as a robust statistical test to violations of equal variance. Native/nonnative status *did* affect honey bee abundance $F(1,43)=19.7$, $p<<0.01$, but there was no main effect of hour or time of day for the buckwheat pair, $F(2,43)=0.597$, p=0.56, While the homogeneity of variance was violated in this sample, the p value for native/nonnative identity was far lower than 0.01, indicating a low likelihood of committing a type 1 error (false positive) for honey bee presence between the native and nonnative buckwheat. The evening session was the only time of the day during which the abundance of honey bees was significantly different between the native flower and its exotic counterpart (mean difference =-8.125, p=0.0037), with more visitors at the California Buckwheat.

Native insects-buckwheats

Bartlett's test for homogeneity of variance was insignificant for both the 3 times of day for the native buckwheat and nonnative buckwheat (p=0.44, p=0.82). The main effect of time of day was inconclusive $F_{(2,43)}=3.17$, p=0.05, but native/nonnative identity was significant $F_{(1,43)}=11.0$, p<0.0001 on the presence of native insect visitors.

A Tukey's post-hoc test revealed that the *only* significant difference in native bee visitation rates was in the evening hours between the native buckwheat and nonnative-- the native buckwheat attracted more native insects than the exotic flower species during this session (mean difference=-12.33, p=0.02). Time of day was not a significant predictor in any other circumstance, for either flower independently. I collected too few observations to feel confident applying statistical tests to the goldenrod pair, but the former analyses offer apt comparisons between the effectiveness and affinity for each native flower compared to its nonnative counterpart.

Floral insect visitor diversity

Considering the entire sampling period, there was no significant difference in the mean Gini-Simpson's diversity index between each native and nonnative flower in the aster pair using a two-sample t-test, t(48)==0.72, p=0.48, nor the buckwheat, t(47)=0.93, p=0.36, nor the goldenrod pair t(6)=-0.17, p=0.88 (Figure 5). Species diversity as measured by this metric was comparable for each native flower and its nonnative counterpart.

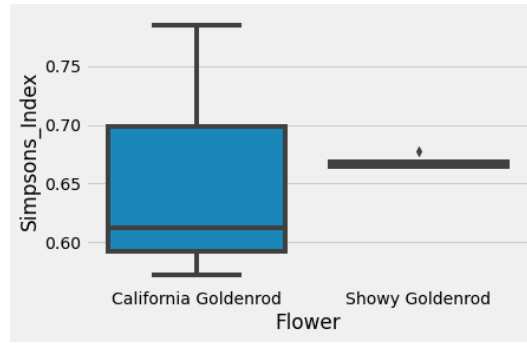a)   b)
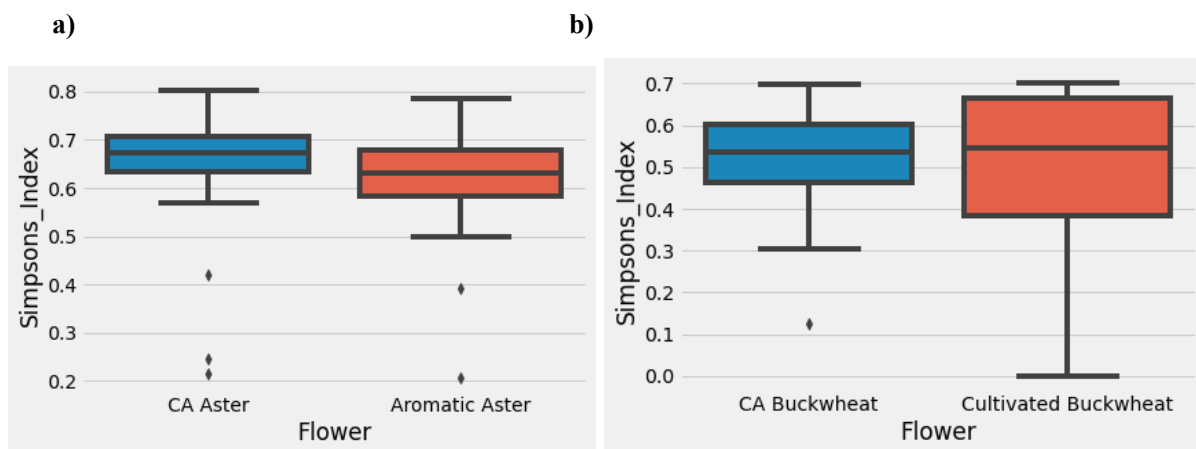
c)

Figure 5. Box and Whisker plots of the gini-Simpson coefficient for each flower species over the entire sampling period.

The mean floral insect visitor species richness to each native flower was not significantly different compared to its exotic counterpart ($p > 0.05$) for the entire study period. The mean species richness was 5.57 insect species/10 minutes for the aromatic aster, 4.30 insects/10 minute sampling session at the exotic buckwheat and highest at the goldenrod of 6.67 species/10 minute sampling session (Figure 6). Mean floral species richness did not significantly differ between each floral pair, although the insect visitor richness to the aster pairs was higher than the buckwheat pair. The goldenrod pair only included three sampling sessions, so I have low confidence in the accuracy of the mean.
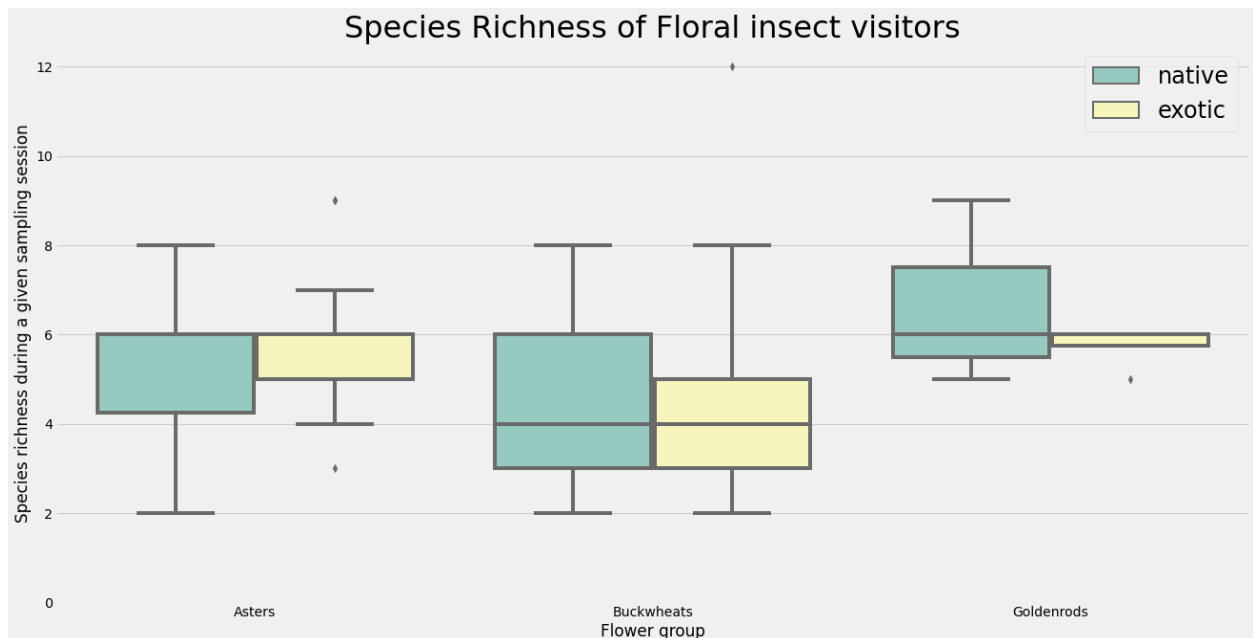
Figure 6. Box plots demonstrating insect visitor species richness for each floral pair. The mean species richness of each flower from left to right are: 5.5 +/-0.56, 5.6 +/- 0.58, 4.64 +/- 0.64, 4.30 +/- 0.96, 6.67 +/- 2.4, and 5.75 +/- 0.5. The means are reported with a confidence interval of +/- 2 standard errors.

DISCUSSION

Understanding differences in insect pollinator abundance and diversity between California native flowers and closely related exotic species will help determine whether nonnative plants offer valuable resources to native bees, hoverflies, and other insect pollinators. Changes in insect visitor presence over time between each native flower and its exotic counterpart were generally similar, although the evening sessions experienced suggesting other variables may better explain insect visitation rate. Species richness and diversity metrics were comparable within each floral pair for the entire study period, but two instances of species-specific attraction to one flower within a floral pair suggests unequal attractiveness of a native flower versus its counterpart. Although I hypothesized that native flowers would attract more pollinators, this study revealed that floral insect visitation rate depended upon the flower species and that species-specific insect attraction to the exotic flower trends in pollinator visitation rates

Pairwise Comparisons

Average honey bee abundance per sampling was greater for the California native aster and the California buckwheat which means that honey bees found both native flowers more attractive than their exotic counterparts. The initial hypothesis of this study that native flowers would attract more insect visitors per sampling session was supported by the buckwheat pair, but not by the aster pair. Surprisingly, the pairwise comparison revealed higher *native* floral insect visitation rates per sampling session at the exotic aster compared to the California aster. The California aster attracted greater numbers of honey bees, but I observed more sweat bees (*Halictus ligatus*) and mining bees on the aromatic aster (Table 1) during the study period. Other factors such as resource overlap or exploitative competition could explain this phenomenon.

Honey bee presence may induce a reduction in native bee visitation to a shared flower resource (Matthews 1984, Pyke 1990). In Southern California, honey bees disproportionately represent the dominant floral insect visitor at high abundance native flowers (Hung et. al 2019). Honey bees accounted for the most abundant insect visitor only at the California aster, while it was the second most abundant at aromatic aster and both buckwheats. As generalist feeders, honey bees forage from many different flowers but prioritize high abundance resources through their ability to recruit nest mates. Honey bees are abundant in the landscape, but other specialist native insects with fewer possible host flowers can easily outnumber honey bees at both native and nonnative flowers. A single honey bee colony collects enough pollen equivalent to feed 110,000 solitary bee progeny, indicating that exploitative competition from honey bees could reduce resources available to native bees (Cane and Tependino 2016). However, major shortcomings with most studies suggesting that honey bee density reduces native bee visitation rates include lack of experimental replication, scale, confounding variables, and no clear metrics on impact of native bee fecundity or fitness (Paini 2004).

Fine scale features of landscape composition could also influence visitation rates unequally to the native and nonnative flowers of this study. For instance, the visitation rate of honey bees to a single native flower species (*Phacelia parryi*) is more sensitive to changes in the floral neighborhood composition than native bees (Bruckman and Campbell (2017). Greater numbers of attractive flowers (both native and nonnative) in close proximity to the native *phacelia* led to reductions in honey bee visitation, but not native bee visitation, suggesting the unique preference of specialist native bees who forage for nectar or pollen from only specific species of flowers, regardless of the presence of other nearby native or nonnative flowers (Campbell 2017). If this were the case, then the greater number of native flowers in close proximity to the California aster in bloom should have led to a reduction in the numbers of honey bees I saw at the California aster compared to the exotic counterpart (due to greater availability or presence of comparatively valued resources). However, a pairwise comparison revealed a higher visitation rate of honey bees at the native aster than the exotic aster. Hence, some other unmeasured variable must explain why the exotic aseter experienced fewer honey bees- either due to inferior quality, location, or shading. Further research should investigate the influence of other floral neighbors on visitation rates as a variable that influences pollinator visitation rates in a field setting.

Temporal effects

Time of day had mixed effects on insect visitation rates depending on the flower species. I only observed significant changes over time for native bee visitation for the aromatic aster, suggesting that native insects were more sensitive to changes in the exotic flower's environmental conditions or nutritional quality compared to the California native aster. Native bee activity may be higher during the early parts of the day. Several species of native bees collecting pollen from wild sunflower species depleted resources of pollen by late morning, leaving none for forage by honey bees later in the day (Cane and Topedino 2016). However, the results of this study did not support that honey bee activity peaks at mid-day and declines in morning and evening (Barthell et al 2001) but rather was constant from early afternoon to evening. Honey bee visitation rates were higher, however, for the California aster compared to its exotic counterpart during the early afternoon and evening which implies that the California aster was more attractive to honey bees than the exotic aromatic aster. In this study, the aromatic aster, but not the native aster, confirmed the observation that native bee activity was highest in morning and declined predictably over the course of the day (Barthell et al. 2001).

Although changes in insect visitation rates over time were either insignificant or inconclusive for the buckwheat pair, there were fewer visitors at the exotic buckwheat compared to the native buckwheat during the evening session. The cultivated buckwheat likely experienced reduced insect visitor visitation due to unfavorable environmental conditions of the cultivated buckwheat. The buckwheat floral pair does not support the that native bees forage primarily in the morning findings of (Cane and Topendino 2016) because time of day had no main effect on visitation rates to this floral pair.

Although time of day was not a significant factor in this study, these results confirmed other research that found temperature, flower shape, and color were all strong predictors of pollinator abundance (McCall and Primack 1992). I attribute the reduced native insect visitation rates in the evening hours at the aromatic aster either to a pronounced effect of shading of the exotic flower patch compared to the native flower patch which remained in better sun exposure and hence temperature. If I had better quantified changes in temperature, I might find that the minimal temperature changes from early afternoon to mid afternoon would better explain the

consistency of pollinator visitations during these times of day, while the more severe temperature changes in the evening contributed to reduced insect visitors. I also did not consider in this study how differences in color between the cultivated buckwheat flower and its native counterpart could contribute to differences in pollinator attraction. Floral density or number of flowerheads per unit area could have also influenced the abundance and visitation of insect pollinators between each native and nonnative counterpart.

Floral Insect Diversity

Although both honey bees and native bees are generally more attracted to California native plants on a percentage basis (Frankie et al. 2005) exotic flowers in a similar family or genera have the potential to attract a diversity of bees and other floral visitors. I found no significant difference in the Gini-Simpson coefficient or species richness between the native flower and nonnative counterpart aggregated over the entire study period. The relative similarity in species diversity suggests that native and nonnative flowers attract a similar community of insects. While the pairwise comparisons using two diversity metrics were nonsignificant, each flower may have attracted a greater abundance of a select few insect species compared to its counterpart. For instance, the nonnative buckwheat attracted disproportionate numbers of syrphid in the genus *Toxomerus spp.*, suggesting that the floral resources provided by the exotic flower were either superior or more accessible to this species of syrphid compared to the native buckwheat.

Flower phenology and morphology are important predictors of insect visitor composition. Bees with longer flight seasons encounter more resource turnover, flower choices, than bees with shorter and tend to be generalists in nature, foraging from many different plant species (Ogilvie and Forrest 2017). In this study, honey bees, some syrphid flies, and mining bees were found at all the native and exotic species of flowers, but sweat bees and fiery skipper butterflies demonstrated specificity of forage at the asters. The lower resource overlap of the sweat bees and butterflies could in part be explained by evolutionary histories of these species,and how shorter season bees tend to be solitary, specialist insects that feed from one or few pollen sources (Ogilvie and Forrest 2017). The abundance of mining bees to the California Buckwheat, but

relative absence of this species at the aster and goldenrod pair further supports the specificity of insect-host flower interactions.

Diversity metrics like the Gini-Simpson coefficient or species richness calculations can mask fine-scale features of community composition caused by other environmental agents. Similar to the discussion of the pairwise analysis, community composition of insects could influence syrphid fly and other insect visitation rates. I did not test whether honey bee presence in my study would affect diversity or abundance of native insect species at the flowers, but a study of resource overlap in Europe found no significant correlation between distance to honey bee apiary or and wild bee visitation rates (Steffan-Dewenter and Tscharntke 2000). However, bumblebees foraging from pasture rose (*Rosa carolina*) led to a reduction in foraging from syrphid in the genus *Melanostoma*, but favored foraging by the syrphid, *Toxomerus marginatus* who returned rapidly to the flower following dispersal of *Melanostoma* syrphid by the bumblebees (Morse 1981). The dominance of mining bees at the California buckwheat could explain the absence of other syrphid flies at this plant species due to interference competition.

Plant floral neighborhood composition could again serve as a confounding variable affecting the species diversity of insect visitors. Native plants grown in proximity to other native plants typically attract a greater abundance or diversity of pollinators and hence benefit from increased fitness (Patton and Agrawal 2014). At the botanical garden, both the California aster and California buckwheat are located in the California native plant section with closer proximity to other native flowers in bloom than the exotic counterparts. However, I observed more native insects at the exotic aster than its native counterpart which challenges the notion that proximity to native flowers correlates with greater native insect abundance. Hence, though this was ideally a controlled experimental study, landscape characteristics were heterogeneous in nature

Broader implications

This study offers only limited insight on the relative value of native flowers versus nonnative plants. While I sought to describe generalizations in affinity of native California plants to attract insects compared to their exotic counterparts, studying only three native/nonative pairs does not represent the entirety of California native plants compared to taxonomically related counterparts. Nonetheless, the pairwise results of this study indicated that the two focus native

California flowers (*Symphyotrichum chilense* and *Eriogonum fasciculatum*) attract a greater abundance of honey bee visitors compared to their exotic counterparts, but the nonnative aster actually attracted more native insects which challenged my initial hypothesis. I expected the native buckwheat to attract more insects during all times of day, but the only significantly higher session was in the evening, suggesting that the exotic buckwheat does have the potential to sustain insect visitors during the other parts of the day.

Though generally far lower in attraction to insect visitors, the cultivated buckwheat attracted an overwhelming number of the syrphid fly in the genus *Toxomerus* compared to the California buckwheat despite the poor sun exposure for the exotic flower. I speculate this species-specific niche provided by the nonnative flower to either superior nectar or pollen resources to this syrphid fly, avoidance of competition at other nearby flowers, the pink color of the exotic buckwheat, or differences in the floral structure that rendered the California buckwheat less suitable for forage by this small insect. Hoverflies have "sponging" mouthparts which may explain the reason they are unable to access more tubular flowers accessible to bees with a longer proboscis such as honey bees (Tasker et al. 2020). In any case, this opens the opportunity to investigate the reason why some species of exotic flowers demonstrate very specific attraction of native insects.

Flower color, floral neighborhood composition, temperature, flowerhead density, and shading all contribute as potential covariables influencing floral insect visitor attraction more than time of day. While diversity metrics and species richness values were comparable, fine-scale comparisons revealed species-specific trends not explained well by these metrics: including the affinity of the cultivated buckwheat to attract *Toxomerus* hoverfly and California aster to attract mylitta crescent butterfly. Late-season blooming exotic plants support pollinator diversity and even substitute limited resources provided by fewer native plants flowering in the late summer-fall (Staab 2020). Hence, carefully selected exotic flowers taxonomically-related to native flowers have the potential to fill important gaps in urban gardens. This study opens the opportunity to investigate other species of flowers not native to the California region that attract native specialist insects as these may serve as important tools to incorporate into the landscape where other species of flowers fail to provide adequate forage opportunities.

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APPENDIX A: Sling Psychrometer
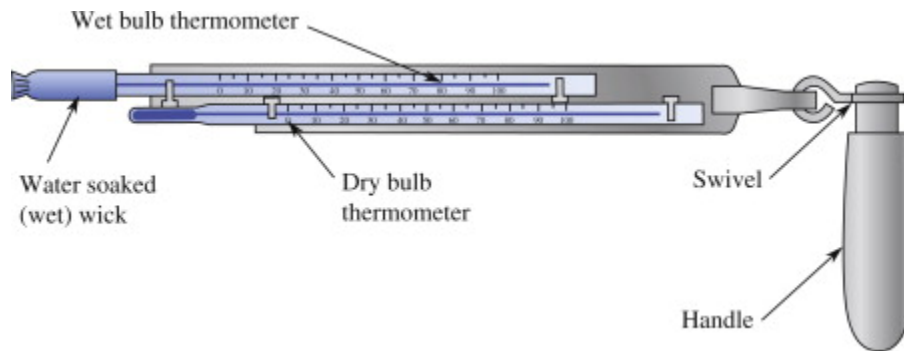
Figure A1: Sling psychrometer

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