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Honey bees as pollinators in natural communities

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Honey bees as pollinators in natural communities

A thesis submitted in satisfaction of the requirements for the degree of Masters of Science

in

Biology

by

Jennifer Marie Kingston

Committee in Charge:

Professor Joshua Kohn, Chair
Professor David Holway
Professor James Nieh

2017

The thesis of Jennifer Marie Kingston is approved, and is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2017

DEDICATION

To my mother and best friend, Joan Kingston, whose personal sacrifices throughout my childhood and teen years have made me the person I am today. I will always be grateful.

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I would like to acknowledge Professor Joshua Kohn for his role as the chair of my thesis committee, as well as the countless hours he has spent advising and revising the work within this thesis.

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Chapter 1, in part is currently being prepared for submission for publication of the material. Hung, Keng-Lou James; Kingston, Jennifer M.; Albrecht, Matthias; Holway, David A.; Kohn, Joshua R. Keng-Lou James Hung was the primary investigator and author for this paper.

Lastly I would like to acknowledge the contribution of my wonderful team of volunteers and BISP 199 students: Lauren Hansen, Victoria S Apaldetti, and Yifei Wang without whom the data collected for Chapter 2 would not have been possible.

ABSTRACT OF THE THESIS

Honey bees as pollinators in natural communities

by

Jennifer Marie Kingston

Master of Science in Biology

University of California, San Diego 2017

Professor Joshua Kohn, Chair

Honey bees are the most widespread pollinating animal species in natural plant communities worldwide, and in San Diego, California, despite high native bee diversity, the introduced honey bee is responsible for over 75% of flower visits. We performed a) a meta-analysis of published studies which report the per-visit efficiency of honey bees as pollinators relative to other floral visitors and b) a field survey documenting seasonal change in floral abundances and pollinator visitation in a coastal sage scrub (CSS) system in San Diego, in

order to better understand the importance of honey bees as pollinators in natural communities. We found that, although honey bees were less efficient than the top non-honey bee pollinator, their efficiency did not differ from the average of non-honey bee floral visitors, and after factoring in visitation frequency, honey bees were no less important. Furthermore, in a San Diego system where honey bees are the numerically dominant floral visitor, we found that honey bees almost exclusively visit the most abundantly flowering species and increase their numbers rapidly as floral abundance increases. By contrast, non-honey bees were fairly indiscriminate floral visitors and only responded to the changes in floral abundance of some plant species with low overall floral abundance. Therefore, although in natural communities honey bees generally provide average pollination services for the plant species they visit, preference for, and recruitment to species with abundant flowers may mean that plant species with lower floral abundance within these systems depend on the pollination services of non-honey bee floral visitors.

CHAPTER 1

Effectiveness of honey bees (*Apis mellifera*) as pollinators of naturally occurring plants

ABSTRACT

Honey bees are the world's most widespread pollinating animal species in both agriculture and natural plant communities. Nevertheless, their efficiency and importance as pollinators relative to other floral visitors has never been comprehensively reviewed. We performed a meta-analysis of published studies that report the per-visit efficiency of honey bees as pollinators relative to other floral visitors. Efficiency is defined as the seed set, probability of fruit set, or the number of pollen grains deposited on the stigma by a single visit of a particular species of pollinator. The importance of pollinators, defined as per-visit efficiency times relative visitation rate, was calculated for studies that additionally reported pollinator visitation rates. From the 32 studies surveyed, we gathered efficiency data on 34 plant species from 22 different families. Of these studies, 13 reported visitation rates that were then used to calculate importance. We found that, on average, honey bees were less efficient than the top non-honey bee pollinator within a system, but their efficiency did not differ from the average of non-honey bee floral visitors. After factoring in visitation, we found that, for plant species studied, honey bees did not differ from either the average or top non-honey bee pollinators in terms of importance. Of the 34 plant species, 20 were undomesticated and 14 were domesticated. We found no difference in relative honey bee efficiency and importance between undomesticated and domesticated plants. The findings of our study suggest that on average, floral visitation rates by honey bees to plant species within

a community can serve as an estimate of their overall importance, though for any particular species, the efficiency of honey bees as pollinators can vary widely.

INTRODUCTION

The honey bee (*Apis mellifera*) is the most prevalent single species of floral visitor worldwide both in agricultural fields and natural plant communities (Garibaldi et al. 2013; Rader et al. 2016; Hung et al. in review). In natural habitats where the honey bee is present, it accounts for nearly 13% of total floral visits and visits 37% of all plants present, on average, as documented in plant-pollinator network studies, which report the identity and frequency of pollinators that visit flowers of each plant species in a given study area (Hung et al. in review). While plant-pollinator network studies usually gauge pollinator importance solely by interaction frequency (Ballantyne et al. 2015) due to the strong correlation between plant-pollinator interaction frequency and overall reproductive impact (Vazquez et al. 2005), there are cases where visitation frequency does not reflect importance, due to the low pollinator efficiency of some frequent floral visitors (Fumero-Caban and Melendez-Ackerman 2007). The importance of a pollinator to plant reproduction is often defined as the product of interaction frequency and per-interaction effect (Schemske and Horvitz 1984, Herrera 1987, Vazquez et al. 2005). Despite the ubiquity of honey bee presence in natural systems worldwide, their relative performance as pollinators is largely unknown because of the difficulty of assessing pollinator efficiencies over a wide range of species. Our goal here is to assess whether visitation frequency adequately reflects average honey bee importance as a pollinator by determining whether the pollination efficiencies of honey bees on various species differ systematically from those of other floral visitors. We also assess the importance of honey bees as pollinators of species where both the per-visit efficiencies and visitation frequencies of various floral visitors were measured.

To that purpose, we conducted a meta-analysis of published studies that report the efficiency of honey bees as pollinators relative to other floral visitors for both domesticated and undomesticated plants. Pollinator efficiency is the average result of a single visit by a particular species of floral visitor to a flower of a particular species (Fumero-Caban and Melendez-Ackerman 2007). Currency of pollinator efficiency varies among studies as either the number of seeds set, the probability of fruit set, or the number of pollen grains deposited on the stigma resulting from a single visit. Additionally, for the subset of studies which report visitation data for honey bees and other pollinators, we analyzed the relative pollination importance where importance is the product of the relative pollination efficiencies of each pollinator type studied and that pollinator's relative visitation frequency. Because pollinator efficiencies of honey bees are often measured in agricultural systems, we also assess whether the relative efficiency and importance of honey bees as pollinators differs between domesticated (agricultural) and undomesticated (naturally occurring) plant species

The pollination efficiency of honey bees is of interest for several reasons. First, the honey bee might be expected to be less efficient compared to native pollinators (Gross 2001, Bruckman and Campbell 2014) in regions of the world where it has been introduced, though specialist and native pollinators don't necessarily have higher pollinator efficiencies (Stoepler et al. 2012, Horvitz and Schemske 1994, Dieringer 1992). Second, worldwide habitat fragmentation and climate change threaten to decrease pollinator diversity and abundance. As resource availability decreases with habitat fragmentation more sharply for specialist pollinators than generalist pollinators, specialists may experience greater population declines than generalists (Aizen and Feinsinger 2002). Furthermore, in South America for example, populations of non-native honey bee and bumblebee species increase in abundance with habitat fragmentation and disturbance relative to native species (Aizen and Feinsinger 2002). Therefore, evaluating the efficiency and importance of honey bees as pollinators to a variety of plant species, could provide crucial information about how well honey bees might fill the void as pollinator diversity decreases.

MATERIALS AND METHODS

Data for efficiency analysis consist of single-visit pollination efficiency trials for single plant species, in which researchers investigated the efficiency of both honey bees and at least one other floral visitor. We used two approaches to compile our data set. First, we performed a literature search using the ISI Web of Science database with the search term [pollinat*] in combination with one of the following terms: [efficiency], [effectiveness], ["pollen deposition], [seed set], [fruit set], or ["pollination biology of"], from October 2014 to August 2016. Second, we examined the literature cited sections of each of the studies found through the first approach for additional studies that were not captured in the initial literature search. The most recent study was used when more than one study was found for the same plant species. Selected papers experimentally compared pollinator efficiency of two or more pollinators using at least one of the following metrics: average pollen deposition, seed set, or fruit set resulting from a single visit by an individual pollinator species. If necessary, seed set was calculated as the number of seeds per fruit times percent fruit set. When multiple metrics were available from the same study, we chose seed set when reported, and fruit set if seed set was not reported, as seed set is the most accurate metric of fitness (Schemske and Horvitz 1984, Cane and Schiffhauer 2003). Pollen deposition was used only when no other efficiency metric was available. In a small number of cases, we used Image-J to extract data from figures when raw data were not available.

For every plant species in each study, we calculated the average single-visit pollination efficiency of non-honey bee pollinators by taking the mean efficiency metric of all non-honey bee pollinators studied. Single-visit pollination efficiency of the top non-honey bee pollinator was taken at the lowest taxanomic class provided by study (where "top pollinator" ranged from a single species, genus, or morpho-group). When there was a single non-honey bee pollinator studied, the efficiency measure for average and top non-honey bee pollinator was the same. Next, we calculated the relative single-visit pollination efficiency of honey bees by dividing honey bee efficiency by the average pollination efficiency of all non-honey bee pollinators or by the efficiency of the top non-honey bee pollinator. We then used one-sample *t*-tests to examine whether the relative efficiency of honey bees differed from that of the average or top non-honey bee pollinator, where the null hypothesis was honey bee relative pollination efficiency equals one.

Additionally, for the subset of studies which report visitation rate data for honey bees and other pollinators, pollinator importance was calculated for each pollinator as [pollination efficiency * visitation rate]. Relative pollination importance of honey bees was then compared against the importance of the average or top non-honey bee pollinator as above.

Plants were categorized as domesticated or undomesticated based on whether the species has been cultivated and grown by humans for a specific use (food, biofuels, medicine). A plant species that has been cultivated, but was studied in its native habitat where it is a naturally occurring species was considered undomesticated. We ran four one-way anova tests, to determine whether there was a difference between domesticated and undomesticated plants in terms of relative honey bee efficiency and importance, compared to the average or top non-honey bee pollinator. All statistical tests were conducted on JMP version 11 software.

RESULTS

Pollinator efficiency study data spanned 34 plant species in 32 papers, covering 22 plant families. Of these, 20 plant species in 17 families were undomesticated, and 14 plant species in 5 families were domesticated. The number of pollinator groups, including honey bees, ranged from 2 to 8 pollinator groups studied, the median was 2.5 and average was 3.29 pollinator groups (Figure 1.1).

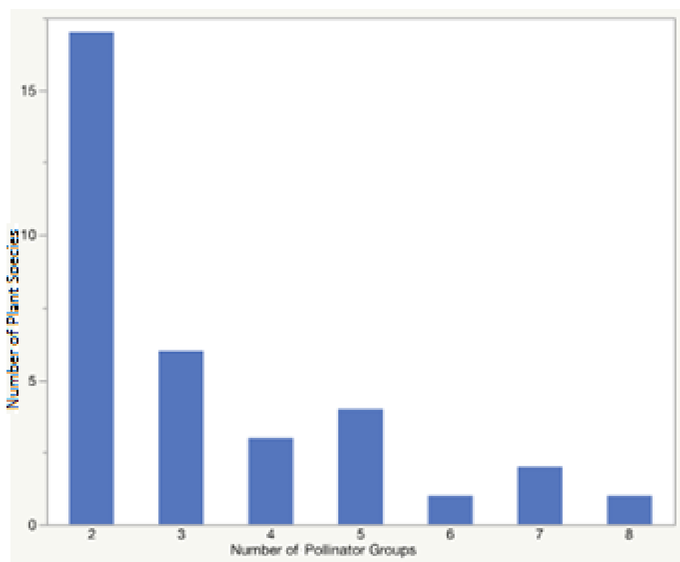

Figure 1.1: Distribution of the number of pollinators groups compared with honey bees in the efficiency studies analyzed for meta-analysis. Study authors varied in the lowest taxanomic classification provided for pollinators observed, ranging from species to genus to morph-group.

The single-visit pollination efficiency of honey bees did not differ from that of the average pollinator species measured (Figure 1.2; one sample t-test, $t_{33} = -0.89$, $P = 0.38$, n=34;

mean efficiency of honey bee / average non-honey bee = 0.92). However, honey bees' single-visit pollination efficiency was lower than the top non-honey bee pollinator visiting these plants (Figure 1.2; one sample t-test, $t_{33} = -2.66$, $P = 0.012$, n=34; mean efficiency of honey bee / top non-honey bee = 0.79). Meanwhile, the pollination importance of honey bees did not differ from that of the average pollinator species measured (Figure 1.2; one sample t-test, $t_{12} = 1.24$, $P = 0.24$, n=13; mean importance of honey bee / average non-honey bee = 1.63). The pollination importance of honey bees also did not differ from that of the top non-honey bee pollinator (Figure 1.2; one sample t-test, $t_{12} = -1.53$, $P = 0.16$, n=13; mean importance of honey bee / top non-honey bee = 0.73).

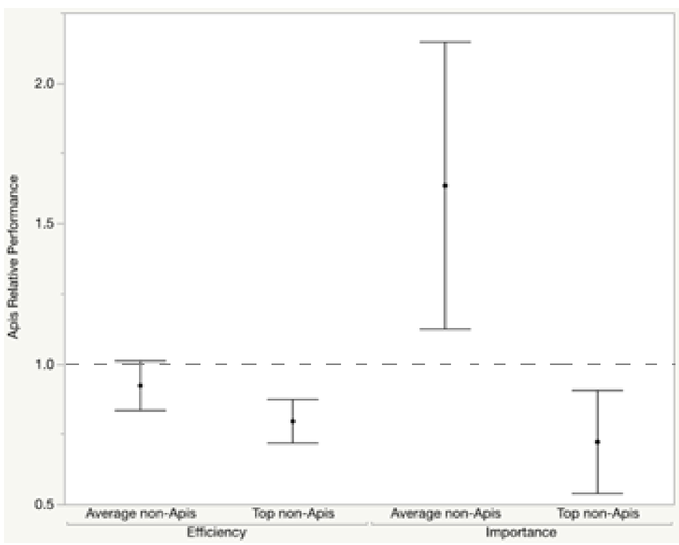

Figure 1.2: Performance of the honey bee (mean ± SE) relative to the average or the top non-honey bee pollinator across all plant species (efficiency n=35; importance n =13). A value of 1 means that honey bee performance equals that of comparison pollinators.

Honey bee pollination efficiency relative to average or top non-honey bee pollinators did not differ between domesticated and undomesticated plant species (Figure 1.3; average non-honey bee, $F_{(1,32)} = 1.53$, $P = 0.23$, n=34; top non-honey bee $F_{(1,32)} = 0.50$, $P = 0.49$, n=34).

Similarly, honey bee importance relative to the average or top non-honey bee pollinators did not differ significantly between domesticated and undomesticated plant species (Figure 1.4; average non-honey bee, $F_{(1,11)} = 3.67$, $P = 0.08$, n=13; top non-honey bee, $F_{(1,11)} = 4.88$, $P = 0.052$, n=13), though the sample size for domesticated plants was small (N=4 species).

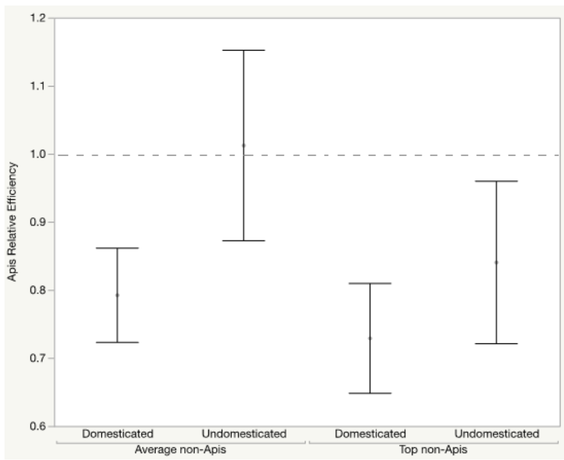

Figure 1.3: Honey bee efficiency (mean +/-SE) relative to the average and top non-honey bee pollinator for domesticated (n=15) and undomesticated plant species (n=20). A value of 1 means that honey bee performance equals that of comparison pollinators.

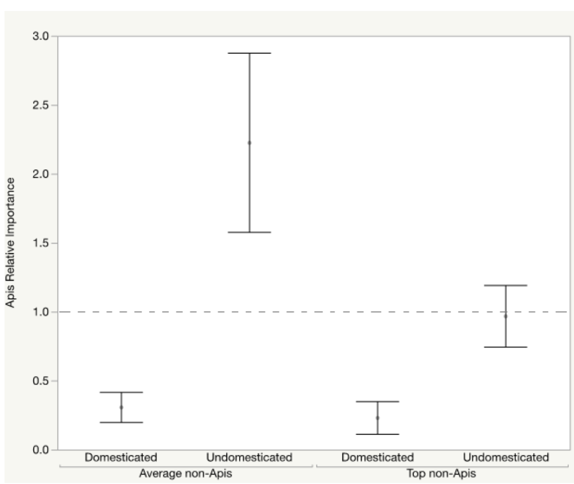

Figure 1.4: Honey bee importance (mean +/-SE) relative to the average and top non-honey bee pollinator for domesticated (n=4) and undomesticated plant species (n=9). A value of 1 means that honey bee performance equals that of comparison pollinators.

DISCUSSION

Among the wide diversity of plant species studied, honey bees did not differ in efficiency from the average floral visitor, though they were somewhat less efficient than the most efficient non-honey bee species. In addition, there was no difference between efficiency of honey bees relative to the average floral visitor on domesticated versus undomesticated species. Therefore our total dataset of 35 plant species provides a broad sample with which to compare the efficiency of honey bees to those of other common floral visitors to these widely varied plant species. Our findings that honey bees perform as well as the average non-honey bee floral visitor imply that, while the relative efficiency of honey bees varies widely across species, their community-wide effect as pollinators may be reasonably approximated by their visitation frequency.

For many of the efficiency studies analyzed, per-visit pollination success was compared between honey bees and the one or two other most frequent flower visiting species. This occurs because frequent visitors are often deemed, *a priori*, the most significant pollinators and because of the difficulty of obtaining enough data to accurately estimate the average single-visit efficiency of infrequent floral visitors. By contrast, some efficiency studies lump non-honey bee pollinators to taxonomic groupings such as genus, order, or functional type rather than a single pollinating species, therefore the gap between honey bee relative efficiency and the top pollinator may be, in some cases, underestimated.

Honey bees are introduced to many areas of the world where they are currently abundant pollinators in natural ecosystems (Hung et al. in review). In fact, in our dataset of n=20 undomesticated plant species in which the efficiency of honey bees was assessed relative to other floral visitors, only one study was performed within the native range of honeybees while all plant species studied were in their native ranges. Despite being non-native in the great majority of places where they were studied, honey bees were as efficient, on average, as the native floral visitors studied. The fact that honey bees are as efficient as the average pollinator, even where non-native, is perhaps not surprising since they are a super-generalist pollinator. As super-generalists, the honey bee is adept at extracting pollen and/or nectar from many plant species within a landscape rather than being specialized on one or two plant species. Such a generalist will develop strategies to exploit many types of floral architectures, although efficient exploitation of a floral resource does not necessarily correspond to efficient pollination. Body size may help to explain why honey bees are relatively efficient pollinators of the majority of plants they visit, despite their floral diversity. Honey bees have fairly large bodies, which may better facilitate pollen transfer compared to small bodied pollinators; for example in commercial apple, larger body size of bumblebees was suggested to explain their higher pollen deposition rates relative to smaller pollinator taxa (Thomson and Goodell 2001).

Honey bees were however less efficient than the top pollinator. This pattern may be partially a statistical artifact. Whenever multiple floral visitors are studied, even if they are all in fact equally efficient, the estimate for the efficiency of honey bees is expected to be less than that of the top pollinator (1-n)/n of the time where n is the number of pollinating taxa studied. However, honey bees were significantly less efficient than the top pollinator measured in 15 of the 34 plants studied. Honey bee generalist pollinating behavior may make them as proficient as the average floral visitor. However their generalist strategy could also explain the gap in efficiency compared to the top pollinator, which may be more specialized, at least in some cases.

Although honey bees were less efficient than the top non-honey bee pollinator, honey bees were no less important. Lack of a statistical difference between pollinator types may partly be due to lower sample size. However, given the data at hand any lack of per-visit performance by honey bees in comparison to the top non-honey bee pollinator was made up for by relative visitation frequency. We conclude that for plant species where honey bees are the most frequent floral visitor, they may often account for the majority of pollination services.

Honey bee relative efficiency did not depend on whether or not a plant was domesticated, again suggesting that bees are reasonably efficient across species from a wide range of plant families and floral architectures. However, unlike undomesticated plants, honey bees were found to be less important for agricultural plants than the other pollinators studied though the sample size for domesticated plants is quite small (n = 4: *Cucurbita moschata*, *Pyrus communis*, *Solanum lycopersicon*, *Vaccinium angustifolium*). These plants may have been selected for study partially because of high visitation rates of non-honey bee species. Low relative honey bee importance in this small group of agricultural crops may also be due to special pollination systems for plant species studied; for example, tomato (Macias-Macias et al. 2009) is buzz pollinated, but honey bees don't perform buzz pollination and species of *Cucurbita* are visited by specialist bee species (squash bees) from the genera *Peponapis* and *Xenoglossa* that become locally abundant and move between flowers much more rapidly than honey bees, leading to high visitation rates.

In sum, for plants where honey bees are frequent floral visitors, we can generally expect them to provide adequate pollination services in natural communities. As a result of habitat fragmentation or climate change, the pollination services from specialist pollinators species may diminish or be lost (Aizen and Feinsinger 2003, Hung et al. in review). Where specialist pollinators have been lost, our results suggest that honey bees may be able to substitute for the pollination services formerly provided by the pool of diverse pollinators originally present, for the plants they visit. However, there may still be cases where, for particular plant species, the switch from one or more native pollinators to predominant visitation by honey bees could cause reproductive declines. Furthermore, given that, honey bees do not visit all plant species within natural communities (Hung et al. 2017), the integrity of plant reproduction on an ecosystem scale may still suffer with pollinator diversity loss, even where honey bees increase in abundance. Therefore, while honey bees, even where introduced, can provide important pollination services to naturally occurring plants, maintenance of a diverse pollinator assemblage may still be required to ensure adequate reproduction of entire plant communities. Further research is needed in order to more thoroughly understand community wide impact of changes to pollinator assemblages in response to current and future environmental stressors.

Chapter 1, in part is currently being prepared for submission for publication of the material. Hung, Keng-Lou James; Kingston, Jennifer M.; Albrecht, Matthias; Holway, David A.; Kohn, Joshua R. Keng-Lou James Hung was the primary investigator and author for this paper.

APPENDIX

Table A.1: Studies used for pollination efficiency meta-analysis.

Plant Species	Plant Family	Agricultural Species	Location	Reference
Agalinis strictifolia	Scrophulariaceae	No	Texas, US	Dieringer 1992
Anacardium occidentale	Anacardiaceae	No	Ceara, Brazil	Freitas 1998
Asclepias exaltata	Apocynaceae	No	Shenandoah NP, Virginia, US	Stoepler 2012
Capsicum chinense	Solanaceae	Yes	Xmatiul and Conkal, Mexico	Macias-Macias 2009
Citrullus lanatus	Curcubitaceae	Yes	New Jersey and Pennsylvannia, USA	Rader 2013
Cucurbita moshata	Curcubitaceae	Yes	Yucatan, Mexico	Canto-Aguillar 2000
Cucurbita pepo	Curcubitaceae	Yes	Utah, US	Tepedino 1981
Dillwynia juniperina	Fabaceae	No	Northern Tablelands, New South Wales	Gross 2001
Duranta mandonii	Verbanaceae	No	Mantanay, Peru	Watts 2012
Fragaria ananassa	Rosaceae	Yes	Lamarosa, Portugal	Albano 2009
Geranium sanguineum	Geraniaceae	No	Fife, Scotland	Willmer 2014
Hedysarum scoparium	Fabaceae	No	Gansu, China	Pan 2013
Impatiens capensis	Balsaminaceae	No	Vermont, US	Young 2007
Iris atropurpurea	Iridaceae	No	Yacum, Israel	Watts 2013
Jatropha curca	Euphorbaceae	Yes	Yucatan, Mexico	Romero 2013
Kallstroemia grandiflora	Zygophyllaceae	No	Chamela Biological Station, Mexico	Osorio-Beristain 1997
Malus domestica	Rosaceae	Yes	New York, US	Park 2016
Melastoma affine	Melastomataceae	No	Queensland, Australia	Gross 1998
Melocactus intortus	Cactaceae	No	Guánica FR, Puerto Rico	Fagua 2011
Metrosideros polymorpha	Mytraceae	No	Hawai'i Volcanoes NP, Hawaii, US	Junker 2010
Pedicularis densispica	Orobanchaceae	No	Hengduan Mtns, China	Sun 2013
Phacelia parryi	Boraginaceae	No	California, US	Bruckman 2014
Pitcairnia angustifolia	Bromeliaceae	No	Rı´o Abajo State FR, Puerto Rico	Fumero-Caban 2007
Prosopsis veluntia	Fabaceae	No	Arizona, US	Keys 1995
Prunus dulcis	Rosaceae	Yes	California, US	Thomson 2001
Prunus persica	Rosaceae	Yes	Bejing, China	Zhang 2015
Psychotria carthagenensis	Rubiaceae	No	Mato Grosso do Sul, Brazil	Faria 2015

Pyrus communis	Rosaceae	Yes	Girona, Spain	Monzon 2004
Rubus idaeus	Rosaceae	Yes	Invergowerie, Scotland	Willmer 1994
Solanum lycopersicon	Solanaceae	Yes	Xmatiul and Conkal, Mexico	Macias-Macias 2009
Vaccinium angustifolium	Ericaceae	Yes	Colchester, Novia Scotia, Canada	Javorek 2002
Vaccinium macrocarpon	Ericaceae	Yes	New Jersey, US	Cane 2003
Wahlenbergia cuspidata	Capanulaceae	No	KwaZulu-Natal, South Africa	Welsford 2012
Wahlenbergia krebsii	Capanulaceae	No	KwaZulu-Natal, South Africa	Welsford 2012

Table A.2: Study plants with their associated pollinator' efficiency values.

Plant Species	Pollinator	Efficiency Measure	Efficiency
Agalinis strictifolia	*Apis mellifera*	Seed set	228.63
Agalinis strictifolia	*Bombus pennsylvanicus*	Seed set	162.63
Anacardium occidentale	*Apis mellifera*	Seed set	0.38
Anacardium occidentale	*Centris tarsata*	Seed set	0.52
Asclepias exaltata	*Apis mellifera*	Pollen deposition	65.96
Asclepias exaltata	Bombus	Pollen deposition	26.13
Asclepias exaltata	Epargyreus	Pollen deposition	59.58
Capsicum chinense	*Apis mellifera*	Seed set	35.20
Capsicum chinense	*Augochloropsis* spp.	Seed set	50.10
Capsicum chinense	*Exomalopsis* sp.	Seed set	52.50
Citrullus lanatus	*Apis mellifera*	Pollen deposition	17.92
Citrullus lanatus	*Bombus impatiens*	Pollen deposition	21.58
Citrullus lanatus	Ceratina	Pollen deposition	12.86
Citrullus lanatus	Green bees	Pollen deposition	12.41
Citrullus lanatus	*Melissodes bimaculata*	Pollen deposition	30.31
Citrullus lanatus	*Peponapis pruinosa*	Pollen deposition	33.52
Citrullus lanatus	Small dark bees	Pollen deposition	11.02
Citrullus lanatus	Tiny dark bees	Pollen deposition	11.95
Cucurbita moshata	*Apis mellifera*	Pollen deposition	253.40
Cucurbita moshata	*Peponapis limitaris,* female	Pollen deposition	481.40

Cucurbita moshata	*Peponapis limitaris,* male	Pollen deposition	177.00
Cucurbita pepo	*Apis mellifera*	Fruit set	56.20
Cucurbita pepo	*Peponapis pruinosa*	Fruit set	61.10
Dillwynia juniperina	*Apis mellifera*	Fruit set	14.50
Dillwynia juniperina	Native bees	Fruit set	25.00
Duranta mandonii	*Apis mellifera*	Fruit set	18.30
Duranta mandonii	*Metallura tyrianthina*	Fruit set	0
Duranta mandonii	Moths	Fruit set	3.80
Duranta mandonii	Native bees	Fruit set	18.30
Fragaria ananassa	*Apis mellifera*	Fruit set	274.00
Fragaria ananassa	Halictidae	Fruit set	273.00
Fragaria ananassa	Syriphidae - Eristalis spp.	Fruit set	297.00
Geranium sanguineum	*Apis mellifera*	Pollen deposition	34.40
Geranium sanguineum	*Bombus lapidarius*	Pollen deposition	44.00
Geranium sanguineum	*Bombus lucorum*	Pollen deposition	48.90
Geranium sanguineum	*Bombus pascuorum*	Pollen deposition	35.80
Geranium sanguineum	*Bombus pratorum*	Pollen deposition	34.40
Geranium sanguineum	*Bombus terrestris*	Pollen deposition	53.90
Hedysarum scoparium	*Amegilla* spp.	Pollen deposition	104.88
Hedysarum scoparium	*Apis mellifera*	Pollen deposition	110.97
Hedysarum scoparium	*Lasioglossum* spp.	Pollen deposition	113.00
Hedysarum scoparium	*Megachile spissula*	Pollen deposition	138.04
Hedysarum scoparium	*Megachile* spp.	Pollen deposition	117.06
Hedysarum scoparium	Syriphidae	Pollen deposition	23.02
Hedysarum scoparium	*Xylocopa nasalis*	Pollen deposition	98.11
Impatiens capensis	*Apis mellifera*	Seed set	162.52
Impatiens capensis	*Bombus impatiens*	Seed set	138.96
Iris atropurpurea	*Apis mellifera*	Pollen deposition	61.16
Iris atropurpurea	Sheltering bees	Pollen deposition	54.79
Jatropha curca	*Apis mellifera*	Fruit set	76.00
Jatropha curca	*Frieseomelitta nigra*	Fruit set	78.00
Kallstroemia grandiflora	*Apis mellifera*	Pollen deposition	39.90

Kallstroemia grandiflora	*Trigona nigra*	Pollen deposition	98.20
Malus domestica	*Apis mellifera*	Pollen deposition	16.44
Malus domestica	*Bombus* spp.	Pollen deposition	20.00
Malus domestica	*Melandrena* spp.	Pollen deposition	24.00
Melastoma affine	*Amegilla anomala*	Pollen deposition	272.70
Melastoma affine	*Apis mellifera*	Pollen deposition	8.41
Melastoma affine	*Lestis bombylans*	Pollen deposition	247.65
Melastoma affine	*Nomia* sp.	Pollen deposition	129.50
Melastoma affine	*Xylocopa nr gressitti*	Pollen deposition	548.78
Melocactus intortus	*Anthracothorax dominicus*	Seed set	140.70
Melocactus intortus	*Apis mellifera*	Seed set	119.40
Melocactus intortus	*Solenopsis* sp.	Seed set	135.20
Metrosideros polymorpha	*Apis mellifera*	Pollen deposition	161.84
Metrosideros polymorpha	*Hylaeus* sp.	Pollen deposition	65.49
Pedicularis densispica	*Apis cerana*	Pollen deposition	67.80
Pedicularis densispica	*Apis mellifera*	Pollen deposition	65.69
Pedicularis densispica	*Bombus atrocinctus*	Pollen deposition	207.12
Pedicularis densispica	*Bombus richardsi*, nectar	Pollen deposition	217.18
Pedicularis densispica	*Bombus richardsi*, pollen	Pollen deposition	164.74
Phacelia parryi	*Apis mellifera*	Seed set	110.35
Phacelia parryi	Native bees	Seed set	193.81
Pitcairnia angustifolia	*Anthracothorax viridis*	Pollen deposition	185.44
Pitcairnia angustifolia	*Apis mellifera*	Pollen deposition	59.84
Pitcairnia angustifolia	*Chlorostilbon maugaeus*	Pollen deposition	4.78
Pitcairnia angustifolia	*Coereba flaveola*	Pollen deposition	18.40
Prosopsis veluntia	*Apis mellifera*	Fruit set	0.11
Prosopsis veluntia	*Chalicodoma* spp.	Fruit set	0.23
Prosopsis veluntia	Colletidae	Fruit set	0.05
Prosopsis veluntia	*Perdita* spp.	Fruit set	0.10
Prosopsis veluntia	*Volucella* spp.	Fruit set	0.13
Prunus dulcis	*Apis mellifera*	Pollen deposition	62.56
Prunus dulcis	*Bombus occidentalis*	Pollen deposition	47.06

Prunus persica	*Apis mellifera*	Pollen deposition	34.25
Prunus persica	*Bombus patagiatus*	Pollen deposition	41.50
Psychotria carthagenensis	*Apis mellifera*	Fruit set	79.58
Psychotria carthagenensis	*Augochloropsis* spp.	Fruit set	90.89
Pyrus communis	*Apis mellifera*	Seed set	7.635
Pyrus communis	*Osmia cornuta*	Seed set	8.20
Rubus idaeus	*Apis mellifera*	Pollen deposition	47.00
Rubus idaeus	*Bombus lapidarius*	Pollen deposition	74.00
Rubus idaeus	*Bombus pascuorum*	Pollen deposition	70.00
Rubus idaeus	*Bombus pratorum*	Pollen deposition	68.00
Rubus idaeus	*Bombus terrestris*	Pollen deposition	82.00
Solanum lycopersicon	*Apis mellifera*	Seed set	91.20
Solanum lycopersicon	*Augochloropsis* spp.	Seed set	135.80
Solanum lycopersicon	*Exomalopsis* sp.	Seed set	131.30
Vaccinium angustifolium	*Andrena* spp.	Pollen deposition	46.20
Vaccinium angustifolium	*Apis mellifera*	Pollen deposition	11.70
Vaccinium angustifolium	*Bombus* spp., queens	Pollen deposition	50.60
Vaccinium angustifolium	*Bombus* spp., workers	Pollen deposition	34.30
Vaccinium angustifolium	*Halictus* spp.	Pollen deposition	25.80
Vaccinium angustifolium	*Megachile rotundata,* female, nectar	Pollen deposition	12.90
Vaccinium angustifolium	*Megachile rotundata,* female, pollen	Pollen deposition	27.80
Vaccinium angustifolium	*Megachile rotundata,* male	Pollen deposition	11.60
Vaccinium macrocarpon	*Apis mellifera*	Pollen deposition	10.00
Vaccinium macrocarpon	*Bombus affinis*	Pollen deposition	61.00
Vaccinium macrocarpon	*Megachile addenda*	Pollen deposition	28.00
Vaccinium macrocarpon	*Megachile rotundata*	Pollen deposition	15.00
Wahlenbergia cuspidata	*Apis mellifera*	Seed set	111.80
Wahlenbergia cuspidata	*Lipotriches* sp.	Seed set	79.08
Wahlenbergia krebsii	*Apis mellifera*	Seed set	57.27
Wahlenbergia krebsii	*Lipotriches* sp.	Seed set	104.31

Table A.3: Study plants with their associated pollinators' visitation rate.

Plant Species	Pollinator	Visitation Measure	Visitation Rate
Cucurbita moshata	*Apis mellifera*	floral visit frequency	7.50
Cucurbita moshata	*Peponapis limitaris,* female	floral visit frequency	169.50
Cucurbita moshata	*Peponapis limitaris,* male	floral visit frequency	58.00
Dillwynia juniperina	*Apis mellifera*	bees/15min	3.35
Dillwynia juniperina	Native bees	bees/15min	0.99
Duranta mandonii	*Apis mellifera*	mean % of visits	7.40
Duranta mandonii	*Metallura tyrianthina*	mean % of visits	68.00
Duranta mandonii	Moths	mean % of visits	1.46
Duranta mandonii	Native bees	mean % of visits	5.17
Hedysarum scoparium	*Amegilla* spp.	flowers/hour	17.36
Hedysarum scoparium	*Apis mellifera*	flowers/hour	108.33
Hedysarum scoparium	*Lasioglossum* spp.	flowers/hour	3.36
Hedysarum scoparium	*Megachile spissula*	flowers/hour	3.64
Hedysarum scoparium	*Megachile* spp.	flowers/hour	45.07
Hedysarum scoparium	Syriphidae	flowers/hour	3.09
Hedysarum scoparium	*Xylocopa nasalis*	flowers/hour	1.12
Melastoma affine	*Amegilla anomala*	bees/15min	0.43
Melastoma affine	*Apis mellifera*	bees/15min	0.29
Melastoma affine	*Lestis bombylans*	bees/15min	0.49
Melastoma affine	*Nomia* sp.	bees/15min	1.3
Melastoma affine	*Xylocopa nr gressitti*	bees/15min	0.01
Melocactus intortus	*Anthracothorax dominicus*	no. of visits/(no. of flowers * time * no. of plants)	0.68
Melocactus intortus	*Apis mellifera*	no. of visits/(no. of flowers * time * no. of plants)	0.36
Melocactus intortus	*Solenopsis* sp.	no. of visits/(no. of flowers * time * no. of plants)	0.05
Phacelia parryi	*Agapostemon* sp.	% visits	0.50
Phacelia parryi	*Allograpta* spp.	% visits	0.10
Phacelia parryi	*Andrena* sp.	% visits	0.13

Phacelia parryi	*Anthophora californica*	% visits	0.26
Phacelia parryi	*Anthophora pacifica*	% visits	1.14
Phacelia parryi	*Apis mellifera*	% visits	83.90
Phacelia parryi	*Bombus vosnesenskii*	% visits	1.71
Phacelia parryi	*Bombylius* spp.	% visits	2.08
Phacelia parryi	*Ceratina arizonensis*	% visits	0.77
Phacelia parryi	*Chelostoma* sp.	% visits	1.30
Phacelia parryi	*Colletes* sp.	% visits	0.13
Phacelia parryi	*Copestylum* spp.	% visits	0.03
Phacelia parryi	*Eucera* sp.	% visits	0.10
Phacelia parryi	*Eupeodes* sp.	% visits	0.94
Phacelia parryi	*Hylaeus* sp.	% visits	0.23
Phacelia parryi	*Lasioglossum* spp.	% visits	5.30
Phacelia parryi	*Macrophya* sp.	% visits	0.23
Phacelia parryi	*Osmia* sp.	% visits	0.07
Phacelia parryi	*Pseudomasaris* sp.	% visits	0.10
Phacelia parryi	*Sphaerophoria* sp.	% visits	0.07
Phacelia parryi	*Sphecodes* sp.	% visits	0.23
Phacelia parryi	Unidentified syrphid flies	% visits	0.64
Pitcairnia angustifolia	*Anthracothorax viridis*	flower/hour/plant/patch	14.32
Pitcairnia angustifolia	*Apis mellifera*	flower/hour/plant/patch	66.23
Pitcairnia angustifolia	*Chlorostilbon maugaeus*	flower/hour/plant/patch	5.97
Pitcairnia angustifolia	*Coereba flaveola*	flower/hour/plant/patch	131.56
Pyrus communis	*Apis mellifera*	flowers/min	8.45
Pyrus communis	*Osmia cornuta*	flowers/min	13.80
Solanum lycopersicon	*Apis mellifera*	flowers/30min/plant	2.20
Solanum lycopersicon	*Augochloropsis* spp.	flowers/30min/plant	3.40
Solanum lycopersicon	*Exomalopsis* sp.	flowers/30min/plant	8.50
Vaccinium angustifolium	*Andrena* spp.	flowers/min	7.20
Vaccinium angustifolium	*Apis mellifera*	flowers/min	8.00
Vaccinium angustifolium	*Bombus* spp., queens	flowers/min	12.80
Vaccinium angustifolium	*Bombus* spp., workers	flowers/min	11.20

Vaccinium angustifolium	*Halictus* spp.	flowers/min	6.10
Vaccinium angustifolium	*Megachile rotundata,* female, nectar	flowers/min	4.30
Vaccinium angustifolium	*Megachile rotundata,* female, pollen	flowers/min	7.60
Vaccinium angustifolium	*Megachile rotundata, male*	flowers/min	4.10
Wahlenbergia cuspidata	*Apis mellifera*	no. visitors	92.00
Wahlenbergia cuspidata	*Lipotriches* sp.	no. visitors	157.00
Wahlenbergia krebsii	*Apis mellifera*	no. visitors	127.00
Wahlenbergia krebsii	*Lipotriches* sp.	no. visitors	86.00

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CHAPTER 2

Response of honey bees and native pollinators to variation in floral abundances in a San Diego coastal scrub system

ABSTRACT

San Diego county coastal sage scrub (CSS) communities have high native bee diversity but the introduced honey bee (*Apis mellifera*) is now numerically dominant as a floral visitor. We performed a field survey documenting seasonal changes in floral abundances and pollinator visitation across transects in a CSS system in San Diego, California in order to understand how honey bees and other pollinators respond to variation in the abundances of flowers of CSS plant species. The number of honey bee visits increased rapidly with increases in the floral abundance of the most abundantly flowering species, while the number of visits by non-honey bee pollinators was unaffected as these species floral resources changed. For plant species with low floral abundance, the reverse was often true; the number of honey bee visits was unaffected by increases in floral abundance while the number of visits by other insects, at least for some plant species, increased. Honey bees were numerically dominant floral visitors on plants with the highest overall floral abundances (*Eriogonum fasciculatum* and *Salvia mellifera*), while the plants where non-honey bees were the dominant floral visitor (*Centaurea melitensis*, *Deinandra fasciculata*, *Eriophyllum confertiflorum*) had relatively low floral abundances. Overall honey bee visitation was highly concentrated on the two plant species with the greatest season-long floral abundances, but non-honey bees were distributed more evenly across plant species whose flowers were either

abundant or rare. These patterns support the conclusion that non-native honey bees may be reducing resource availability for native pollinating insects.

INTRODUCTION

The coastal scrub ecosystems of San Diego California boast high native bee diversity (Hung et al. 2014, Hung unpublished dissertation 2017), however the non-native honey bee (*Apis mellifera*) accounts for over 75% of total floral visits and visits flowers of > 85% of plant species present within the San Diego CSS habitat (Hung et al. in review), most of which are native plant species. Though honey bees do not exhibit aggressive behavior, they have been observed in the tropics displacing stingless bees from nectar feeders (Roubik et al. 1980). Furthermore, in California a species of bumblebee experienced reduced reproductive success and changes to foraging behavior with increased proximity to introduced honey bee colonies (Thomson 2004), and research in Brazil found that honey bees may negatively affect eusocial *Melipona* sp. through exploitative competition due to resource overlap, although no direct evidence of competition was recorded (Wilms 1997). Because honey bees dominate the San Diego CSS landscape, we are interested in how this introduced species forages in natural habitats and the degree to which its feeding niche overlaps with that of the large community of other, mostly native, insect pollinators. From 2011-2016, drought conditions persisted in San Diego county, likely resulting in diminished floral resources and increased pressure on pollinators to obtain adequate food resources. Therefore, the question of resource partitioning and competitive exclusion between the dominant introduced honey bee and other pollinators is of timely importance.

In 2016, we conducted a survey documenting floral abundances and pollinator visitation across transects at a CSS system in San Diego in order to address these specific questions. 1) What factors affect the distribution of visits by honey bee and non-honey bee across different plant species? 2) How do honey-bees and non-honey bees respond to plant species in terms of the numbers of visitors as floral abundance changes? 3) What is the evidence for resource use overlap versus resource partitioning between honey bees and native pollinating insects?

MATERIALS AND METHODS

Field site and survey methods

Fieldwork was conducted in CSS habitat at Mission Trails Regional Park (MTRP; 32.830N, 117.055W) in San Diego County in 2016 from late February to early June (Julian dates 64-174). Five 50 m by 2 m transects were established, separated by 30-50 m. Pollinator and flower abundance surveys were conducted on the same day 1-2 times per week, weather permitting. Surveys were only conducted on days where temperatures were above 19^{o}C and when there was less than 30% cloud cover, in order to standardize survey conditions. Pollinator surveys were conducted by walking each 50 m transect for a period of 10-15 minutes twice a day during peak pollination hours, once in the morning between 10:00-11:30 and once in the afternoon between 12:30-14:30. Any winged insects observed on flowers were considered pollinators. Observers visually distinguished between honey bee and non-honey bee "other" pollinators, which are almost entirely native species.

Flower count surveys were conducted by walking transects and recording the number of flowers of each plant species present, either before or after pollinator surveys. For plants in the Asteraceae family (*Bahiopsis laciniata*, *Deinandra fasciculata*, and *Eriophyllum confertiflorum*), a single "flower" consisted of a capitula in which 20% or more of its component flowers were in bloom. Flower counts were conducted using one of the following approximation methods, depending on species and floral abundance at the time of the survey: a) absolute count, for species with a small number of flowers (*Astragalus tricopodus*, *Centaurea melitensis*, *Deinandra fasciculata*, *Eriophyllum confertiflorum*, *Mimulus aurantiacus*, and *Rhus integrifolia*), b) counting the number of flowers in a 0.3 m x 0.3 m area and approximating the number of 0.3 m^2 regions occupied at that density (*Erodium* sp. and *Bahiopsis laciniata*), c) sampling the number of flowers on 4 random inflorescence stems and counting the number of inflorescence stems with flowers, to calculate a total flower count [average flower per stem * number of stems with flowers], for species with numerous inflorescences (*Acmispon glaber*, *Eriogonum fasciculatum*, *Salvia mellifera*, and *Malosma laurina*).

Analysis

Each plant species' daily flower abundance was calculated by taking the sum of flower counts across all five transects on a given day. A plant's total study flower abundance was calculated by taking a sum of flower counts across all transects and study dates. Floral visitors were broken into two pollinator type categories: honey bee or non-honey bee. The number of daily floral visitors of each type to a particular plant species was calculated by taking the sum of all honey bee or non-honey bee visitors across all transects where the plant was present, and summing the morning and afternoon survey events from a given day.

For the nine plant species with greater than five observation days and floral visitors, an individual ANOVA model was run to assess how the number of daily visits to that plant was affected by that species' daily total flower abundance, pollinator type, and their interaction. Additionally, a community- wide three-way fully factorial ANOVA model was run to test the effect of daily flower abundance, visitor type, and plant species (random effect) on daily total floral visitors for all 12 flowering plant species observed during our study. In addition to these three factors and their interactions, Julian date (random effect) was added to the model to account for repeated sampling of the same transects over time. All statistics were run on JMP version 13 software.

RESULTS

The following 12 plants were observed flowering along transects during our censuses: *Acmispon glaber*, *Astragalus tricopodus*, *Bahiopsis laciniata*, *Centaurea melitensis*, *Deinandra fasciculata*, *Eriogonum fasciculatum*, *Eriophyllum confertiflorum*, *Erodium* sp., *Malosma laurina*, *Mimulus aurantiacus*, *Rhus integrifolia*, and *Salvia mellifera* (Table 2.1).

Table 2.1: Plant species presence at five transects within Mission Trails Regional Park, where 0 is absent and 1 is present.

Plant Species	Transect1	Transect 2	Transect 3	Transect 4	Transect 5	Transects Present
Acmispon glaber	1	1	1	1	1	5
Astragalus tricopodus	0	1	1	1	0	3
Bahiopsis laciniata	1	1	1	1	1	5
Centaurea melitensis	1	1	1	1	1	5
Deinandra fasciculata	1	1	1	1	1	5
Eriogonum fasciculatum	1	1	1	1	1	5
Eriophyllum confertiflorum	0	1	1	1	0	3
Erodium sp.	1	1	1	1	1	5
Malosma laurina	1	0	0	0	1	2
Mimulus aurantiacus	0	0	1	0	0	1
Rhus integrifolia	0	0	0	0	1	1
Salvia mellifera	0	1	1	1	1	4
Total Plant Species Present	7	9	10	9	9	

The average transect had 8.8 plant species that flowered during our study (median 9, range 7-10). Both honey bee and non-honey bee pollinators were observed visiting all 12 plant species at least once during the study with the exception of hummingbird-pollinated

Mimulus aurantiacus, for which we observed no insect visitors. Meanwhile, *Rhus integrifolia* was rare and received too few visits for further analysis.

Summed across all transects, a total of 2159 visits by honey bees and 688 visits by non-honey bees were recorded throughout the study. On average, each day we observed a total of 117 honey bees (median 84.5, range 29-352), and 43 non-honey bee insect visitors (median 38.5, range 19-77). Summed across all transects, approximately 35105 flowers were observed on average per day (range 3970 - 65325).

The longest flowering cycle observed was for *Eriogonum fasciculatum* (over the entire study season, 110 days), followed by *Eriophyllum confertiflorum* (103 days). The average range in the number of days plant species were observed flowering was 67.8 days. The peak flowering period of *Salvia mellifera* and *Malosma laurina* may not have been captured as the full flowering cycle of these plants was not included in the study period (Figure 2.1).

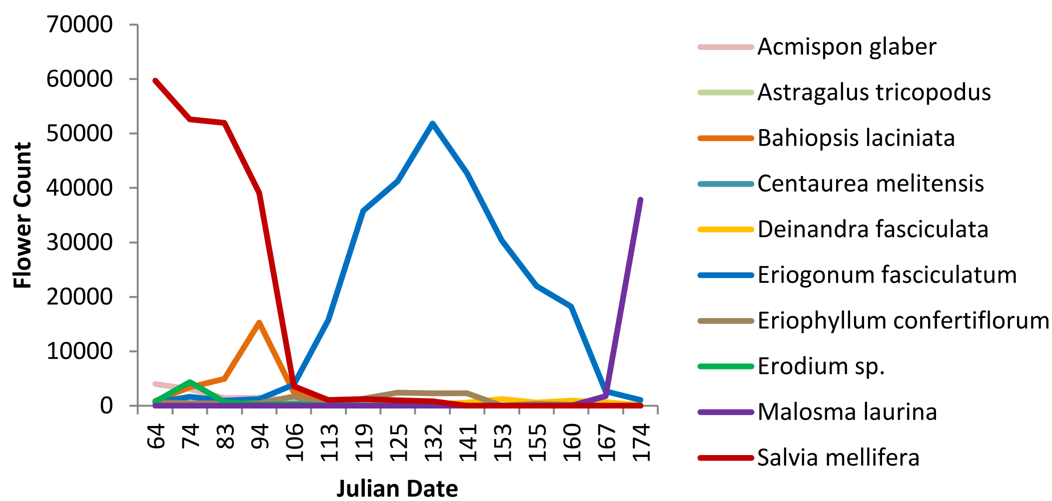

Figure 2.1: Change in daily flower count for main flowering species observed over 2016 study season.

Throughout the season, the two plants with the highest floral abundance were *Eriogonum fasciculatum* (45.8% of total site floral abundance) and *Salvia mellifera* (35.8% of total site floral abundance), while two plants with the next highest floral abundance had more intermediate floral resources: *Malosma laurina* (6.7% of total site floral abundance) and *Bahiopsis laciniata* (4.7% of total site floral abundance) (Figure 2.2a). The remaining eight plant species recorded across transects were relatively rare with only three species (*Acmispon glaber*, *Eriophyllum confertiflorum*, and *Erodium* sp.) responsible for more than 1% of site total floral abundance throughout the season (Figure 2.2a). The distribution of total floral visits throughout the season varied greatly in magnitude across plant species. The two plant species that received the most floral visits overall were as follows: *Salvia mellifera* (41.5% of total visits), *Eriogonum fasciculatum* (35.0 % of total visits), while *Bahiopsis laciniata* (8.9% of total visits) received the next most floral visits. The remaining nine plant species together accounted for 14.5% of total visits with no single species accounting for more than 3.3% of them. While honey bee visitation appeared to be concentrated on plant species with the highest floral abundance, visitation by non-honey bees appeared to be more evenly distributed among plant species regardless of their floral abundance (Figure 2.2b).

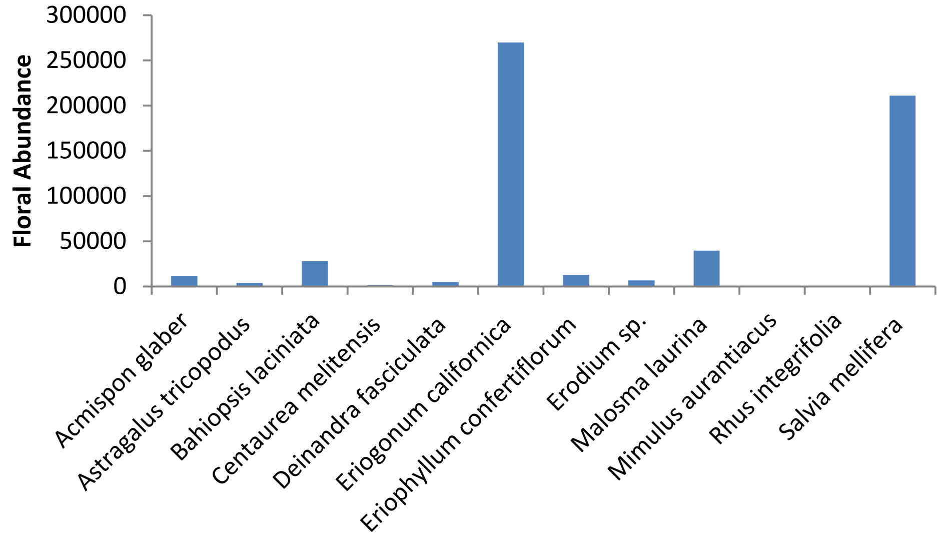

Figure 2.2a: Total observed floral abundance of plant species during the study period.

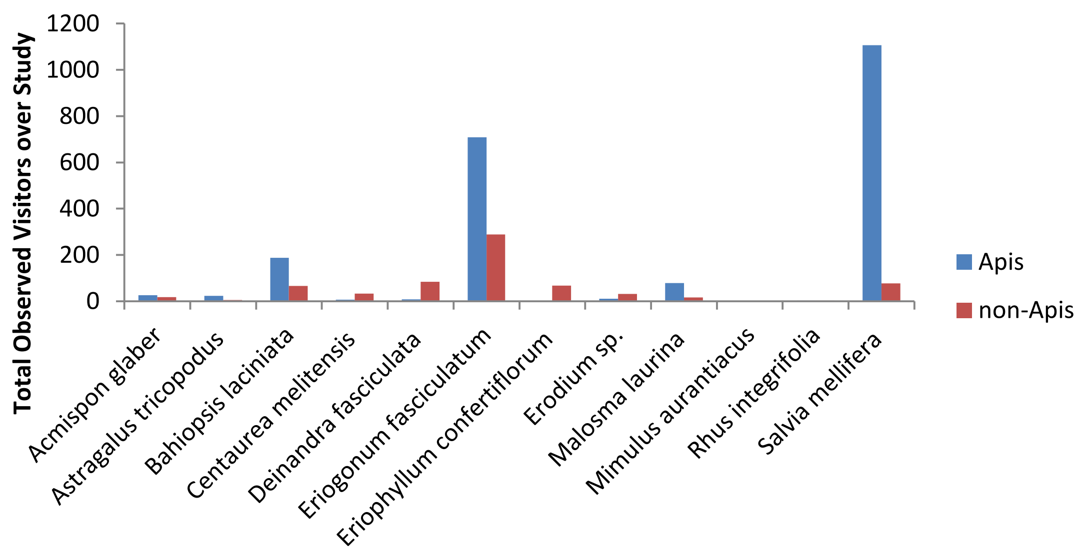

Figure 2.2b Distribution of honey bee and non-honey bee floral visits to plant species observed during the study period.

For the two plant species with the highest floral abundance, *Eriogonum fasciculatum* and *Salvia mellifera* (Figure 2.2a), there were significantly more floral visits by honey bees than non-honey bees, and there was also a significantly different response between honey bees and non-honey bees to the changes in flower abundance, where the number of honey bees increased more than non-honey bees as flower abundance increased (Fig. 2.3a,b; Table 2.2). Additionally, for both plant species, days with higher floral abundance resulted in more floral visitors (Table 2.2).

Although *Malosma laurina* produced the third highest floral output of all plant species studied, flowering began at the end of our study effort, amassing just two days of observation, such that not enough data exist for this species to examine the joint effects of flower number, visitor type, and their interaction. However, *Malosma laurina* received 79 honey bee visits and 16 non-honey bees overall; additionally, honey bee visits increased five fold as floral abundance increased while non-honey bee visitors increased less than twofold. The daily floral visitors of *Bahiopsis laciniata*, the plant with the fourth highest floral output, were not significantly different on days with high or low floral abundance, and did not differ by visitor type (Figure 2.3c, Table 2.2).

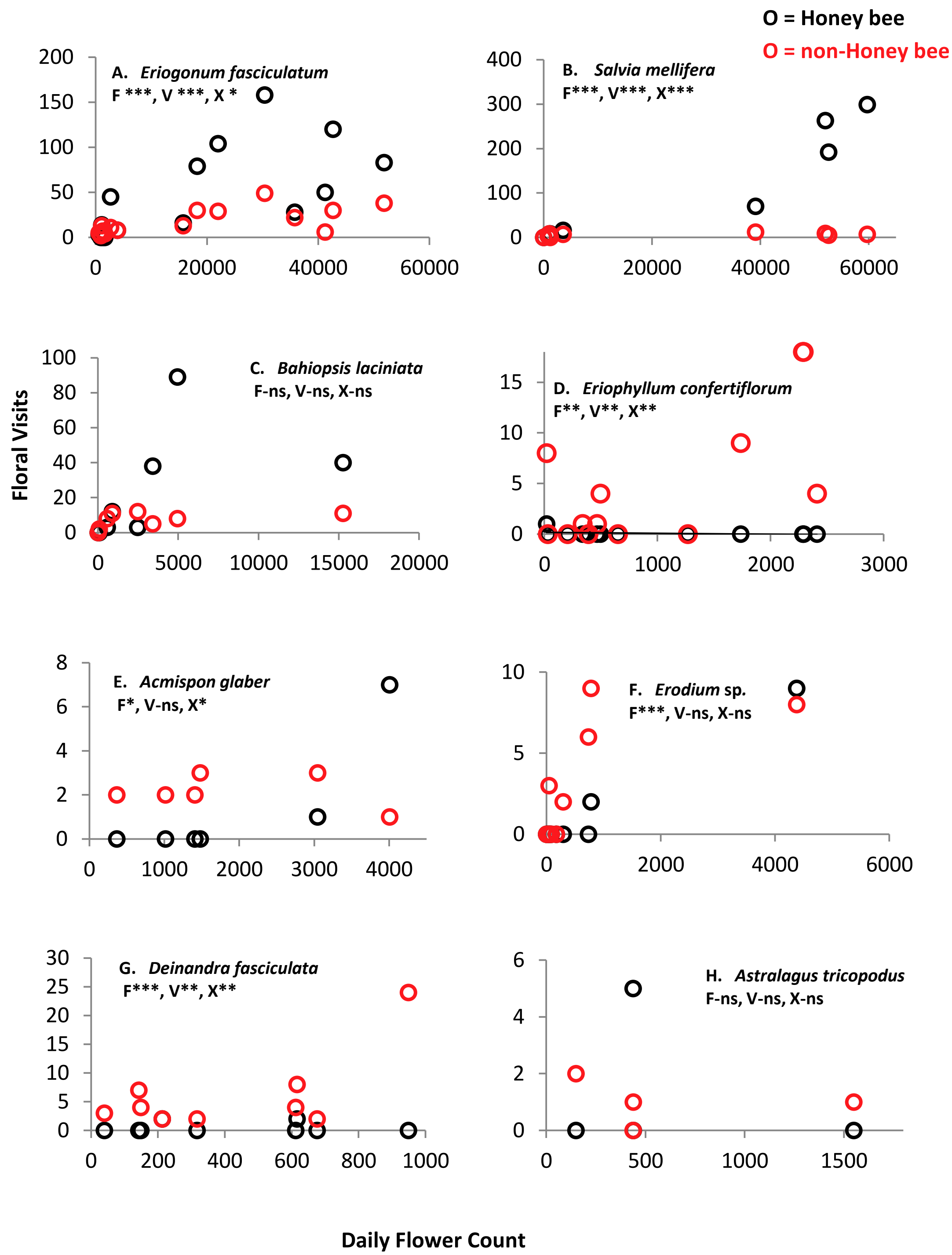

Figure 2.3: Daily flower count and visitors across all transects for plant species (in order of floral abundance): A. *Eriogonum fasciculatum* and B. *Salvia mellifera*, C. *Bahiopsis laciniata*, D. *Eriophyllum confertiflorum*, E. *Acmispon glaber*, F. *Erodium* sp., G. *Deinandra fasciculata*, H. *Astragalus tricopodus*, and I. *Centaurea melitensis*. Asterisks indicate significance levels for the effects of daily floral abundance (F), visitor type (V), and their interaction (X) (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns $P > 0.05$).

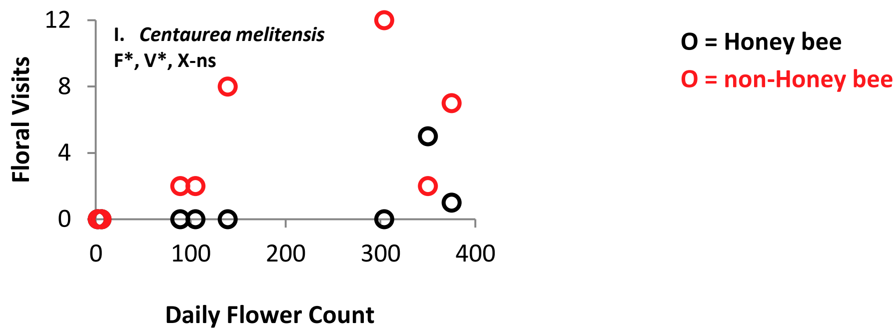

Figure 2.3, continued: Daily flower count and visitors across all transects for plant species (in order of floral abundance): A. *Eriogonum fasciculatum* and B. *Salvia mellifera*, C. *Bahiopsis laciniata*, D. *Eriophyllum confertiflorum*, E. *Acmispon glaber*, F. *Erodium* sp., G. *Deinandra fasciculata*, H. *Astragalus tricopodus*, and I. *Centaurea melitensis*. Graphs contain significance asterisks for daily floral abundance (F), visitor type (V), and their interaction (X), where denoted as *<0.05, **<0.01, ***<0.001, or ns for not significant.

Generally, plant species with low floral abundance had different visitation patterns compared to the two most abundantly flowering plant species (i.e. *Eriogonum fasciculatum* and *Salvia mellifera*). For the six plant species with the lowest floral abundances (*Eriophyllum confertiflorum*, *Acmispon glaber*, *Erodium* sp., *Deinandra fasciculata*, *Astragalus tricopodus*, and *Centaurea melitensis*), none were visited more frequently by honey bees than non-honey bees and in three of these species (*Eriophyllum confertiflorum*, *Deinandra fasciculata,* and *Centaurea melitensis)* honey bee visitors were significantly less frequent than non-honey bee visitors. In addition, where there were significant interactions between flower number and visitor type (*Eriophyllum confertiflorum, Acmispon glaber*, and *Deinandra fasciculata*) these were in the opposite direction of those observed for the two abundantly flowering species, with greater increases in non-honey bee than honey bee visitors as flower number increased (Figure 2.3, Table 2.2).

Table 2.2: Results of ANOVAs on visits to individual plant species listed in order of floral abundance from highest to lowest. ANOVA models tested the fixed effects of floral abundance (flowers), visitor type (visitor), and their interaction on the number of floral visitors (significance levels: * P < 0.05; ** P < 0.01; *** P< 0.001). For each plant species, there are two rows of data per study date (one for *Apis* visitors and one for non-*Apis* visitors), so N = number of study dates * 2, for all study dates in which that plant species was observed flowering.

Plant species	N	Flowers	Visitor	Interaction	Dominant visitor
Eriogonum fasciculatum	30	16.52***	8.01**	5.18*	Apis
Salvia mellifera	20	65.45***	37.31***	61.03***	Apis
Bahiopsis laciniata	18	2.54	2.35	1.52	
Eriophyllum confertiflorum	28	9.57**	11.85**	10.33**	non-Apis
Acmispon glaber	14	8.06*	0.87	5.05*	
Erodium sp.	22	29.17***	3.48	0.18	
Deinandra fasciculata	20	4.18***	3.95**	3.45**	non-Apis
Astragalus tricopodus	10	1.53	0.02	0.05	
Centaurea melitensis	16	5.98*	5.65*	1.16	non-Apis

Overall, honey bees rarely visited and were never dominant for plant species with relatively low floral abundance, but focused the majority of pollination efforts on plants with relatively high floral abundance (Figure 2.4).

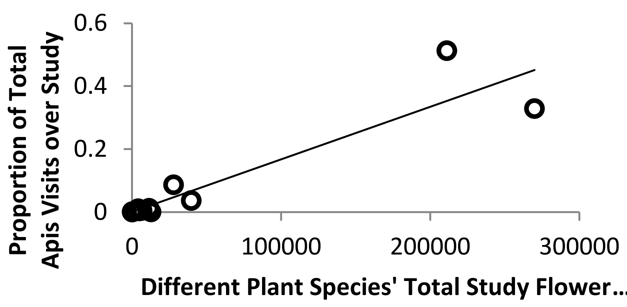

Figure 2.4: Total flower count for each plant species summed across all days of study and the proportion of all visits by honey bees (n=12 plants) throughout 2016 study season.

Results for all fixed effects in the three way full factorial ANOVA model that also included Julian date are given in Table 3. None of the random effects (I.e., species and its interactions with fixed factors, Julian date) had estimated variance components significantly greater than zero as evaluated by the Wald chi-square statistic. The model shows that plants with more flowers had more visits and that honey bees were overall more abundant than non-honey bees, but there is also a strong interaction between flower number and type of pollinator, with a greater proportion of honey bee visits to plants with more flowers on any particular day (Figure 2.5, Table 2.3).

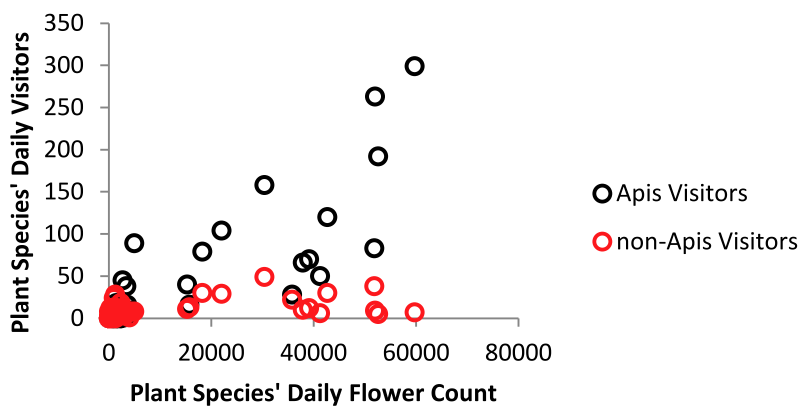

Figure 2.5: Daily flower count and floral visitors for each plant species (n=12 plants, n=14 study dates) throughout 2016 study season. Each data point represents a plant species' flower count on a given date and the corresponding number of honey bee or non-honey bee visitors to that plant species on that date.

Table 2.3: Fixed effects results from an ANOVA model testing the effects of daily flower abundance, visitor type, and plant species (random effect), plus all interactions among these factors. Julian date (random effect) was also added as a factor in the model to account for repeated sampling of the same site (significance levels: * P < 0.05; ** P < 0.01; *** P< 0.001). Variables and their interactions which are not listed in table (all random effects) were not significant (see text).

Effect	DF	DF Density	F ratio
Floral Abundance	1	5.08	46.71**
Visitor Type	1	2.48	25.65*
Floral Abundance*Visitor Type	1	8.04	25.66**

DISCUSSION

Honey bees and non-honey bees visited the same set of plant species but responded differently to variation in their floral abundances. Honey bees were responsible for 75% of all recorded floral visits, a level of numerical dominance recorded in other field studies in this area (Hung unpublished dissertation 2017, Hung et al. in review). However, patterns of floral visitation differed strongly between honey bees and non-honey bees. The number of honey bee visits increased rapidly with increases in the floral abundance of the most abundantly flowering species, while the number of visits by non-honey bee pollinators was unaffected. For species with low floral abundance, the reverse was often true; the number of honey bee visits was unaffected by increases in floral abundance while the number of non-honey bee visits, at least for some species, increased.

Honey bee visitation was highly concentrated on the plant species with the greatest floral abundance, whereas non-honey bee visits were more evenly distributed across plant species. Though non-honey bees visited the two honey-bee dominated plant species (*S. mellifera* and *E. californicum*) they accounted for a distinct minority of visits to flowers of these species. Conversely, honey bees rarely visited plants with low floral abundance and were frequently the minority visitor type to these species. Therefore, the feeding niches of honey bees differed strongly from those of non-honey bee pollinators taken as a group. Honey bees foraged primarily on abundantly flowering taxa while non-honey bees visited plants with high and low floral abundance at about the same frequency.

At least two factors may explain honey bee numerical dominance on abundant resources. First, the honey bee is the only flower visitor in this habitat that communicates resource distance, direction, and quality to nestmates (Gould et al. 1970, Gould et al. 1975, Nieh 2004). Communication allows honey bees to recruit nestmates to patches of high resource abundance. Bumblebees, though social, are not nearly as common as honey bees in our area, and are unable to communicate distance and direction of resources to nestmates. The remaining insect floral visitors are overwhelmingly solitary bees (Hung et al. 2014, Hung unpublished dissertation 2017) or other non-social, non-bee species and therefore not expected to recruit conspecifics to exploit a resource. Nestmate recruitment by honey bees may explain why they show a strong functional response to increases in floral abundance. Our findings across species mirror ones from at least one intraspecific study in which honey bees are found to be minority visitors in small patches and dominant visitors in large patches of *Impatiens glandulifera* (Sowig 1989). Similarly, Sih and Balthus (1987) showed that rates of visitation per-flower by honey bees were lower in small than in large patches of catnip (*Nepeta cataria*).

Second, it is possible that honey bees exclude non-honey bee floral visitors at high abundance resources through interference or exploitative competition. Honey bees are larger than most of the many solitary bee species found in San Diego County and tend to begin foraging earlier in the day. It is possible that through recruitment of workers and extended hours of exploitation honey bees can remove enough pollen and nectar from abundantly flowering species that non-honey bee pollinators find them a poorer resource compared to species rarely visited by honey bees. Honey bees might also actively exclude non-honey bees through interference competition, though active displacement of non-honey bees by honey bees has only rarely been observed.

Our method of quantifying floral resources was quite crude. Floral resources for some plant species were quantified using individual flowers while for others we counted capitula. Quantification of floral resources could be improved by measuring the pollen and nectar resources proffered by flowers of different species. Nevertheless, our methods captured resource variation that was important to the pollinator community, given the clear patterns of differential visitation shown by the pollinator types. Moreover, the plant species observed in our study, other than hummingbird pollinated *Mimulus aurantiacus*, all have relatively small flowers with pollen rewards that are easily accessed by honey bees and many other insects. Our model found that plant species identity was not a significant factor impacting visitation by pollinators, indicating that species-specific aspects of floral biology, other than abundance, had little effect on visitation patterns. That plant species identity was of little significance is perhaps not surprising given the super-generalist foraging behavior of honey bees and the fact that the species rich, non-honey bee pollinator community collectively is also quite generalized in its foraging.

Non-native honey bees are dominant floral visitors on the most abundant floral resources in natural habitats in San Diego County. Nevertheless, their effect, if any, on populations of native pollinators is unclear. It seems unlikely that, in the absence of honey bees, abundantly flowering species would be as poorly attended by the native pollinator assemblage as is currently observed, but we lack any method of removing honey bees from large enough areas for a long enough time period to determine their effect on population sizes of native pollinators. Meanwhile, these non-native pollinators appear to be important providers of pollination services, at least to high abundance flowering native plant species. Further studies of the effects of honey bees on both populations of native pollinators and on the reproductive biology of the plants which they visit are warranted.

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