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Complex effects of habitat fragmentation on the quantity and quality of pollination
services within a coastal sage scrub plant community

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Biology

by

Adrienne Lee

Committee in charge:

Professor David Holway, Chair
Professor Joshua Kohn
Professor James C. Nieh

2016

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The Thesis of Adrienne Lee is approved and it is acceptable in
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Chair

University of California, San Diego

2016

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ABSTRACT OF THE THESIS

Complex effects of habitat fragmentation on the quantity and quality of pollination services within a coastal sage scrub plant community

by

Adrienne Lee

Master of Science in Biology

University of California, San Diego, 2016

Professor David Holway, Chair

Habitat fragmentation due to human activity has led to pollinator declines worldwide, yet little is known about how this diversity loss affects pollination services in natural ecosystems. In this study, we investigate the mechanistic links between habitat fragmentation, a proxy for pollinator diversity loss, and the quantity (conspecific pollen deposition) and quality (heterospecific pollen proportion) of pollination services in coastal sage scrub habitats in the San Diego region. We documented pollinator visitation

and pollen deposition across ten focal plant species in six natural reserve and six scrub fragment plots. At the level of the community as a whole, habitat fragmentation *per se* was not a significant driver of conspecific pollen deposition nor was it a significant driver of heterospecific pollen proportion. However, habitat type (reserves vs. fragments) formed statistically significant interactions with other variables in both conspecific and heterospecific proportion models, suggesting that fragmentation can indirectly affect pollination services. The western honeybee, *Apis mellifera*, was the most numerically dominant floral visitor across all study plots. Due to its high abundance, *A. mellifera* could influence both conspecific pollen deposition and heterospecific pollen proportion among reserve and fragment plots, potentially altering pollination services within coastal sage scrub habitats. Overall, habitat fragmentation can impart complex effects within plant-pollinator networks, as habitat type was shown to affect plant species differently with regards to changing pollinator variables. These differences in responses from plant species and pollinators could potentially result in a restructuring of plant-pollinator networks.

Introduction

Ecosystems around the world are being altered by anthropogenic impacts. One of the most conspicuous alterations humans have on the environment is land transformations, such as agricultural conversion and urbanization (Vitousek et al. 1997). Land transformations have direct effects on the structure and function of ecosystems by eroding biodiversity, disrupting community dynamics, and altering ecosystem services, such as pollination (Tylianakis et al. 2008, Cardinale et al. 2012).

Pollination is arguably one of the most important ecosystem services in terrestrial ecosystems, as over 85% of the world's flowering plant species depend on animals (mainly insects) to provide pollination services (Ollerton et al. 2011). Unfortunately, this ecosystem function can be disrupted by anthropogenic disturbances such as habitat fragmentation and degradation (Kearns et al. 1998, Kremen & Ricketts 2000, Forup & Memmott 2005, Lomov et al. 2010). Habitat fragmentation can reduce population sizes of both pollinators and plants, and ultimately impact plant reproductive success and persistence of pollinators (Cunningham 2000). Additionally, fragmented habitats can accumulate introduced plants (Brown & Mitchell 2001, Vilà et al. 2011) and pollinators (Paton 1993, Roubik 2000, Lomov et al 2010) to a greater degree than in non-fragmented ecosystems due to human activity (Vitousek et al. 1997). Species introductions can restructure native plant-pollinator networks (Traveset & Richardson 2006) and further exacerbate the direct effects of habitat fragmentation on the persistence of native plant and pollinator communities.

A growing literature documents the effects altered ecosystems can have on pollinator diversity (reviewed in Winfree et al. 2009, Potts et al. 2010) and on plant species diversity (Vitousek et al. 1997). These studies have often implicated that pollinator diversity loss influences pollination services and will ultimately impact the persistence of native plants and pollinators. However, few studies have directly studied how declines in pollinator diversity alter interactions between plants and pollinators and influence the quality of pollination services. Studies relating pollinator diversity to plant reproduction have mostly focused on agricultural systems (e.g. Klein et al. 2003, Hoehn et al. 2008, Garibaldi et al. 2013), and are difficult to generalize to complex natural ecosystems. Similarly, experimental mesocosm studies investigating the link between pollinator diversity and pollination services (e.g., Fründ et al. 2013) often contain few plant and pollinator species, again making their results difficult to extrapolate towards more diverse natural ecosystems. To our knowledge, the study by Brosi & Briggs (2013) is the only published study that has mechanistically shown the effect of decreasing pollinator diversity on plant reproduction in a natural system by removing a single pollinator species. Despite the general consensus that human-modified environments affect pollinator diversity, which in turn affects the pollination services provided, no study has investigated how declines in pollinator diversity can impact the quantity and quality of pollination services in a natural ecosystem at the community level by directly measuring pollination services.

In 2011 and 2012, Hung et al. (*In revision*) revealed that fragmented habitats in San Diego County, California supported ca. 35% lower bee richness at both the genus and species level compared to large natural reserves, demonstrating the strong impact of habitat

fragmentation on bee assemblage structure. Additionally, this system is highly dominated by the widespread exotic generalist pollinator, the western honey bee (*Apis mellifera* L). With a near global distribution, *A. mellifera* alters native plant-pollinator networks both beneficially by substituting for extirpated native pollinators (Dick 2001, Hanna et al. 2013), and detrimentally by displacing native pollinators from the “core” of plant-pollinator interaction networks (Aizen et al. 2008). The strong contrast between reserves and fragments with respect to pollinator diversity, as well as the pervasiveness of *A. mellifera*, make this system ideal for examining the impacts of pollinator diversity loss on pollination services. Here, we performed *in-situ*, pollinator visitation observations and pollen deposition measurements to test the hypothesis that fragmentation can impact both the quantity (conspecific pollen deposition) and the quality (heterospecific pollen proportion) of pollination services within a plant community. This concept that quantity and quality of pollination services can be impacted independently of each other is still relatively new (reviewed in Morales & Traveset 2008, Ashman & Arceo-Gómez 2013, Arceo-Gómez & Ashman 2016) and is important for understanding how native communities will respond to disturbed landscapes.

Materials and Methods

Coastal sage scrub ecosystems, found along coastal portions of Southern California, support high bee diversity (Michener 1979) as well as a diversity of largely insect-pollinated, endemic plants (Minnich & Dezzani 1998). Yet, less than 15% of original coastal scrub ecosystem still remains intact due to urbanization and other forms of land-use intensification (Westman 1981, Minnich & Dezzani 1998). Additionally, much of the remaining coastal sage scrub habitat is fragmented due to human development, therefore, understanding the effects of fragmentation are extremely relevant towards the conservation of coastal sage scrub habitat and the functions that occur within it.

In the spring and summer of 2016, we studied pollinator visitation and pollen transfer in coastal sage scrub fragments and reserves in San Diego County, California, USA. We established twelve 1-hectare study plots (Table 1): 6 plots in scrub reserves (internal area \gg 500 ha) and 6 plots in well-preserved, scrub fragments (internal area $<$ 120 ha) embedded within the residential, urban matrix. These twelve study plots were established within the same system of reserve and fragment sites as in Hung et al. (*In revision*). We collected pollinator visitation and pollen deposition data from 10 focal plant species (8 native and 2 non-native): *Eriogonum fasciculatum*, *Calystegia macrostegia*, *Salvia mellifera*, *Deinandra fasciculata*, *Chlorogalum parviflorum*, *Malosma laurina*, *Bahiopsis laciniata*, *Gutierrezia sarothrae*, *Centaurea melitensis*, and *Brassica nigra*. The distribution of plant species across the twelve study sites is listed in

Table 2. Plant species were chosen based on their prevalence in reserves and fragments, and the feasibility of collecting pollen deposition data under field conditions.

We performed surveys of pollinator visitation and pollen deposition on clear days with light wind. Surveys were performed ca. every 2-3 weeks at each study plot (n = 6 survey days per plot) with two plots sampled per day. Data included in this thesis are a subset of the total data collected. Here, we focus on samples collected from each plant species during its peak bloom at each study plot. The peak bloom phase represents the time at which the quantity and quality of pollination services is likely to be most consequential for plant reproductive fitness (Willson & Burley 1983, Johnston 1991, Kearns & Inouye 1993). Table 1 lists the subset of total sample dates during which focal species' peak blooms occurred. During each visit to each plot, two researchers estimated floral abundances of focal plant species within study plots by estimating the number of blooming flowers on three individual plants (for large, woody shrubs) or three patches of individual plants (for forbs and sub-shrubs), and then counting the number of individuals or patches of each species within the study plots. Simultaneously, two researchers conducted pollinator visitation observations on focal plant species starting at 0900 h. During visitation observations, researchers recorded all putative insect pollinators that contacted the reproductive structures of flowers within an observational area. Insect species not identifiable in the field were collected for identification in the laboratory. For each plant species in bloom during a given survey, we performed 15 minutes of observations. Observations were performed on each observational unit (individual plant or patch of plants) for 1 min before moving on to the next observational unit, with the

exception of *C. macrostegia* for which we instead conducted five sets of 3-min observations because of low flower density.

Pollen deposition data were collected for all 10 focal plant species. Three stigmas from each of four individuals per plant species per study plot were collected on each sample date. For *M. laurina* and *C. macrostegia*, we only collected one stigma per individual because of excessive handling time associated with small flowers (for *M. laurina*) or overall low flower density (for *C. macrostegia*). Stigmas were collected after 1400 h to allow plants to achieve maximum pollen receptivity. Stigmas were squashed on fuchsin-stained gelatin (Kearns & Inouye 1993) on microscope slides in the field.

To quantify the deposition of conspecific and heterospecific pollen, researchers examined stigmas under microscopes at 100x - 200x magnification. Pollen grains were classified and quantified as conspecific or heterospecific based on a reference pollen collection of flowering plants from our plots. Heterospecific pollen grains were not identified beyond the fact that they were heterospecific to the species from which the stigma was collected. Pollen grains were classified and counted by visually scanning the entire sample encapsulated in the fuchsin gel, as pollen grains could spread away from stigmas into the gel matrix during the collection process (Kearns & Inouye 1993). Each slide was counted twice (once each by two different researchers) in order to minimize counter bias; these counts were then averaged and means were used as data points in all analyses.

In order to address changes in quality and quantity of pollen deposition with habitat fragmentation, analyses were performed on two response variables: total number

of conspecific pollen grains and proportional representation of heterospecific pollen grains. We chose total conspecific pollen deposition as a proxy for the quantity of pollination services as it directly relates to pollination limitation for female reproductive success. We chose heterospecific pollen proportion as a proxy for the quality of pollination services (where higher heterospecific pollen proportion reflects lower quality of pollination services), as individual stigmas can have the same number of conspecific grains deposited (i.e., same quantity of pollination) but a different number of heterospecific grains being deposited. Heterospecific pollen receipt is ultimately detrimental to a plant as heterospecific pollen can interfere with the successful adhesion of conspecific pollen and inhibit conspecific pollen germination and pollen tube growth, thus reducing female reproductive success (Galen & Gregory 1989, Ashman & Arceo-Gómez 2013).

In our analyses, conspecific pollen grain count data were $\log(x+1)$ transformed, and heterospecific proportion data were logit transformed (with ± 0.0005 adjustment for values of 1 or 0), to improve normality. We also standardized each transformed dependent variable to its species-specific mean and standard deviation (mean = 0; SD = 1). In order to determine potential drivers of variation in pollen deposition, we examined seven explanatory variables (Table 3). Data were analyzed using linear mixed-effects (LME) models (using R package *nlme*; Pinheiro et al. 2016) with study plot included as a random effect to account for within-plot replication of plant species as well as individuals within plant species. We determined best-supported models of explanatory variables and their interactions on conspecific pollen deposition and heterospecific pollen proportion

via evaluating all possible models that may be constructed using the seven explanatory variables and their two-way interactions (using R package *glmulti*; Calcagno & Mazancourt 2010). We also constructed and evaluated all possible 3-variable models, with species always included, as our 10 focal species differed tremendously (e.g. in growth form, flower size, known specialist pollinators, etc.) and were therefore expected to exhibit divergent responses to each of the other explanatory variables. Each of our constructed 3-variable models was fully parameterized with all 2-way interactions and 3-way interactions. We selected the best model based on Akaike's information criterion (AIC). All analyses were performed using RStudio (version 3.1.3).

Results

A total of 16,300 pollinators were observed during peak bloom 15-min visitation surveys (45 reserve surveys and 39 fragment surveys), with the introduced *Apis mellifera* representing 80.3% of total pollinators (13,090 individuals). Despite having fewer visitation observational surveys in fragment plots, we observed 34.8% more *A. mellifera* in fragments than in reserves (5,576 in reserves and 7,514 in fragments) with an average of 31 *A. mellifera* per reserve survey and 48 per fragment survey. We observed, on average, 9 non-*A. mellifera* floral visitors per reserve survey and 10 per fragment survey. Scrub fragments overall were observed to have on average 45% more pollinator visitations per survey compared to scrub habitats (40 per reserve survey and 58 per fragment survey); this difference is largely driven by higher *A. mellifera* visitation in fragment plots.

We counted a total of 103,171 pollen grains (95,149 conspecific and 8,022 heterospecific) on 880 stigmas. Despite fragments having more observed pollinator visitations, scrub fragments had on average 104 conspecific grains per stigma, while reserves had on average 112 conspecific grains per stigma. For total pollen deposition per stigma, fragment plots had on average 112 grains and reserves had on average 122 grains. Total pollen deposition was extremely variable among species (range: 0-2,881 grains). Proportion of heterospecific pollen deposition ranged from 0-1.

The best-supported model for total conspecific pollen deposition included main effects and interactions among plant species, habitat type (i.e., reserves vs. fragments),

and total visitation rate (Fig. 1). The main effect of total visitation rate was significant (Table 4). The two-way interaction of habitat type and total visitation rate and the three-way interaction of species, habitat type, and total visitation rate were significant as well (Table 4).

The best-supported model for proportion of heterospecific pollen deposition included main effects and interactions among plant species, habitat type, and proportional representation of visits by *Apis mellifera* (Fig. 2). The two-way interactions of plant species and proportion of *A. mellifera*, and habitat type and proportion of *A. mellifera* to total pollinators were significant (Table 5). The three-way interaction of species, habitat type, and proportion of *A. mellifera* was significant as well (Table 5).

The main effect of species was never significant in either model because we standardized within each species such that each plant species has a mean of 0.

Discussion

Our investigation of pollen deposition in coastal sage scrub reserve and fragment plots revealed substantial variation in conspecific pollen deposition and heterospecific pollen proportion both across and within plant species. Our results suggest that patterns of pollen deposition may be driven by multiple factors. Most notably, in both best-supported LME models, habitat type was not a significant main effect influencing overall patterns of pollen deposition. This finding suggests that, at the scale of the assemblage of studied focal plants, habitat fragmentation *per se* (and its associated declines in overall bee diversity) does not directly affect the overall quantity or quality of pollination services. However, for both conspecific pollen deposition and heterospecific pollen proportion models, the interaction between species and habitat type approached statistical significance ($p = 0.0850$ and 0.0935 , respectively), suggesting that pollen deposition of some plant species could be impacted by fragmentation. Potentially with more data (i.e., pollen deposition data for the entire time-series of each plant species, or data from more plant species or more sites), we may gain the statistical power to detect a significant interaction between species and habitat type as a driver for both conspecific pollen deposition and heterospecific pollen proportion models.

Pollen quantity: conspecific pollen deposition

The best-supported model for conspecific pollen deposition revealed that the main effect of total pollinator visitation rate was a significant driver of the quantity of conspecific pollen deposited. While we do see an overall negative trend in conspecific

pollen deposition with respect to increasing total visitation rates, this appears to be driven by two plant species: *Centaurea melitensis* and *Chlorogalum parviflorum*. One potential reason for the lack of any positive relationships between conspecific pollen deposition and total visitation rate could be that pollen deposition saturates at levels of visitation lower than those observed in our study, such that the variation in total visitation that we observed is not meaningful for pollen deposition. Previous studies have suggested that with increasing pollinator visitation, pollen limitation should be reduced and plant reproductive fitness should increase through increasing seed set or fruit development (Burd 1994, Ashman et al. 2004, Knight et al. 2005). Yet, more recent studies have suggested that the relationship between increasing visitation and plant reproductive fitness is not always positively linear. Pollen limitation can occur in situations of both low visitation and high visitation (Klinkhamer & de Jong 1993, Harder et al. 2001, Hargreaves et al. 2008, Morris et al. 2010, Aizen et al. 2014). In high visitation situations, pollinators can act more as pollen thieves by removing pollen from the system for consumption, rather than acting as successful pollinators (Hargreaves et al. 2008). One taxon known for pollen theft is *Apis mellifera* (Parker et al. 2015), an introduced and highly prevalent species throughout our study plots. *Apis mellifera* is a corbiculate bee species that removes pollen from anthers and compresses pollen grains into packets by moistening them with nectar (Parker et al. 2015). These moistened pollen packets make pollen less likely to fall off during subsequent flower visits, thus effectively removing pollen from the potential pollination environment (Parker et al. 2015). This effect could reduce male reproductive fitness and increase pollen limitation at the plant population level due to the overall depletion of male gametes in the system (Hargreaves 2007). In

addition to pollen theft from anthers, it is possible for pollinators to remove ungerminated pollen directly from the stigma (Hargreaves et al. 2008). Pollen removal from stigmas should directly reduce both male and female reproductive success (Gross & Mackay 1998) because theft reduces siring opportunities for male gametes and can potentially cause pollen limitation by reducing the overall number of male gametes available for successful fertilization of the female stigma (Hargreaves et al. 2008). These previous findings may explain the negative relationships for *C. melitensis* and *C. parviflorum* with respect to conspecific pollen deposition versus increasing total visitation rate.

The significant interaction between habitat type and total visitation rate suggests that visitation rates impact conspecific pollen deposition in different ways between reserves and fragment plots. Several species appear to have notably divergent slopes between reserves and fragment plots. This pattern is unexpected but has been documented in at least one other study. Waser & Price (2016) found a similar pattern between higher pollinator visitation rates but lower conspecific pollen deposition and concluded that a complex interplay of abiotic conditions such as drought and biotic factors such as plant physiology and pollinator behavior could impact pollination services. Similar processes might be occurring within our system but more data are needed. Future studies should address these potential abiotic and biotic influences by incorporating measurements such as soil moisture, length of visitation per flower over time, and conspecific pollen trends over multiple blooming seasons to give insight into how biotic and abiotic covariates can potentially influence pollen deposition. Moreover, there is the possibility that conspecific pollen deposition is more strongly influenced by

another variable that we failed to measure, which could correlate negatively with total visitation rate. This would mean that although the best model supported total visitation rate, it may be an insufficient model if it is picking up signals from an unmeasured variable that is negatively correlated with total visitation rate.

Pollen quality: heterospecific pollen proportion

As with the non-significant main effect of habitat, the main effect of *Apis mellifera* visitation proportion was not a significant driver for heterospecific pollen proportion. This finding is surprising, as *A. mellifera* workers are documented as being highly floral constant during their foraging trips (Ribbands 1949, Grant 1950, Free 1963, Waser 1986, Grüter et al. 2010). One would expect that increasing *A. mellifera* proportion should generally correspond with decreasing amounts of heterospecific pollen deposition; our results fail to agree with this expectation. However, despite this main effect not being significant, the interaction terms of plant species and habitat with *A. mellifera* visitation proportion are both significant. The interaction between plant species and *A. mellifera* visitation proportion suggests that the effect of *A. mellifera* proportion on heterospecific pollen proportion differs across plant species. Examining *A. mellifera* proportions as predicted by plant species and habitat type via a LME model shows that the main effect of species is significant ($p < 0.0001$), supporting previous reports that *A. mellifera* prefers to visit some plant species over others (Ballantyne et al. 2015). This variation in the foraging preferences of *A. mellifera* should ultimately impact how much pollen (both conspecific and heterospecific) *A. mellifera* would deposit per plant species. Plant species more frequented by *A. mellifera* would have a higher probability of pollen

exportation and pollen deposition, which should increase their chances of conspecific pollination, while less frequented plant species could incur more heterospecific pollen deposition. Out of the ten focal plant species, five showed that the proportion of *A. mellifera* had similar effects on heterospecific pollen proportion in reserve and fragments, suggesting that *A. mellifera* are behaving similarly with regards to their floral constancy between the two habitat types. The remaining five plant species show differing effects depending on habitat type. One possible explanation could be that the floral constancy of *A. mellifera* is not as intrinsic to the species as previously thought, but rather, more dependent on the environmental conditions in which individual workers forage. Another possibility is that the numerical dominance of *A. mellifera* on a particular plant species could impact the floral constancy of other pollinators associated with said plant species; similar effects of dominant species on the floral constancy of other pollinators has been reported in other systems (Brosi & Briggs 2013).

Both best-supported models for conspecific pollen deposition and heterospecific pollen proportion showed a significant three-way interaction for their respective main effect variables. These significant interactions suggest that plant species differ from one another with respect to the degree to which total visitation rate and *A. mellifera* proportion impacts pollen deposition differently in reserve and fragment plots.

Complex interactions driving pollen deposition trends

Pollinators are in decline worldwide in human-disturbed environments (Potts et al. 2010). Yet there are few studies that investigate how pollinator diversity loss affects the structure and function of pollination networks. Despite being the most abundant

generalist pollinator in our system, *A. mellifera*, was not a driver for the best-supported model for conspecific pollen deposition. However, the following four best LME models for conspecific pollen deposition all have some variable of *A. mellifera* as a main effect (either *A. mellifera* proportion or *A. mellifera* visitation rate). Our results suggests that the role of *A. mellifera* is stronger as an influencer of total visitation rate than directly on conspecific pollen deposition.

In eight out of ten plant species, increasing pollinator visitation rates appeared to have opposing effects on total conspecific pollen deposition patterns between reserve and fragment plots. Similarly, in four out of ten species, increasing the proportion of *A. mellifera* visitation appeared to have opposing effects on the proportion of heterospecific pollen being deposited in reserve and fragment plots. We speculate that these opposing results could be due to other pollination network structural properties such as modularity (Spiesman & Inouye 2013), which may influence pollination services and may respond to fragmentation in complex ways.

In conclusion, our results indicate that habitat fragmentation *per se* does not directly drive changes in pollen deposition patterns at a community level. However, three plant species did show higher baseline proportions of heterospecific pollen in fragment plots. This suggests that for some plant species, habitat fragmentation can increase the overall probability of receiving heterospecific pollen. Overall, fragmentation can alter the ways in which total pollinator visitation and *A. mellifera* proportions affect pollen deposition. These findings suggest that effects of fragmentation on pollination ecosystem

function are more subtle and complex than previously thought and support the further investigation of community-level pollen deposition networks.

Tables

Table 1: Name, type, location and subset of total sample dates on which focal species' peak blooms occurred within each site

Site Code	Type	Latitude/Longitude	Survey Dates
MTS1A	Fragment	N32.7922, W117.0605	4/19/16, 5/4/16, 6/16/16, 7/12/16
MTS2	Fragment	N32.8555, W117.1883	4/6/16, 4/26/16, 5/12/16, 6/3/16, 6/30/16
MTS6	Fragment	N32.7219, W117.1186	4/6/16, 4/26/16, 5/12/16, 6/22/16
SWS1	Fragment	N32.7496, W117.0316	3/31/16, 4/18/16, 5/18/16, 6/15/16, 6/29/16
SWS3	Fragment	N32.7201, W117.0778	3/31/16, 4/18/16, 5/3/16, 5/18/16, 6/15/16, 6/29/16
SWS10	Fragment	N32.7855, W116.9889	4/1/16, 4/19/16, 6/1/16, 6/29/16
ECR4	Reserve	N32.8929, W117.0916	4/4/16, 4/21/16, 5/13/16, 6/7/16, 6/23/16
ECR5	Reserve	N32.8996, W117.0752	4/21/16, 5/13/16, 6/7/16, 6/23/16
MTE3	Reserve	N32.8220, W117.0755	4/5/16, 4/20/16, 5/11/16, 6/2/16, 7/12/16
MTE4	Reserve	N32.8346, W117.0751	4/5/16, 4/20/16, 6/2/16, 6/20/16, 7/12/16
SWI4	Reserve	N32.7274, W116.9400	3/24/16, 4/14/16, 5/19/16, 6/8/16
SWEA	Reserve	N32.7319, W116.9557	3/24/16, 4/14/16, 5/2/16, 6/28/16

Table 2: Biological information and site presence of each focal plant species

Plant Species	Family Name	Native/Introduced
<i>Bahiopsis laciniata</i>	Asteraceae	Native
<i>Brassica nigra</i>	Brassicaceae	Introduced
<i>Calystegia macrostegia</i>	Convovulaceae	Native
<i>Centaurea melitensis</i>	Asteraceae	Introduced
<i>Chlorogalum parviflorum</i>	Agavaceae	Native
<i>Deinandra fasciculata</i>	Asteraceae	Native
<i>Eriogonum fasciculatum</i>	Polygonaceae	Native
<i>Gutierrezia sarothrae</i>	Asteraceae	Native
<i>Malosma laurina</i>	Anacardiaceae	Native
<i>Sabia mellifera</i>	Lamiaceae	Native

Table 2. Biological information and site presence of each focal plant species, Continued

PLANT SPECIES	SITES PRESENT													
	MTS1A	MTS2	MTS6	SWS1	SWS3	SWS10	ECR4	ECR5	MTE3	MTE4	SW14	SWEA		
<i>B. laciniata</i>	X			X					X	X	X	X		
<i>B. nigra</i>	X	X		X	X	X			X	X	X	X		
<i>C. macrostegia</i>				X		X	X		X	X				
<i>C. melitensis</i>	X	X		X	X	X	X		X	X	X	X		
<i>C. parviflorum</i>				X	X		X	X	X			X		
<i>D. fasciculata</i>	X	X		X	X		X	X	X	X	X	X		
<i>E. fasciculatum</i>	X	X		X	X	X	X	X	X	X	X	X		
<i>G. sarothrae</i>	X			X	X				X	X	X			
<i>M. laurina</i>	X	X		X		X	X	X	X	X	X	X		
<i>S. mellifera</i>		X			X		X	X	X					

Table 3: Independent and dependent variables for LME models

Variable	Description
Independent Variables	
Species	Identity of focal plant species
Habitat	Scrub reserve or scrub fragment plot
Flowers per plot	Total # of flowers of plant species in question within study plot
Apis visitation rate	Visitation rate of <i>Apis mellifera</i> (visits/flower/minute)
Other visitation rate	Visitation rate of all non- <i>Apis</i> pollinators (visits/flower/minute)
Total visitation rate	Visitation rate of all pollinators (visits/flower/minute)
Proportion of Apis	Proportion of <i>Apis mellifera</i> to total # of pollinators
Dependent Variables	
Total conspecific Proportion	Total conspecific pollen deposited per plant species
heterospecific	Proportion of heterospecific pollen out of total pollen deposited per species

Table 4: ANOVA table for best-supported conspecific pollen deposition LME model

Model	numDF	denDF	F-value	p-value
Total conspecific pollen deposition				
(Intercept)	1	282	0.00	1.0000
Species	9	282	0.00	1.0000
Habitat	1	10	0.13	0.7283
Total visitation rate	1	282	6.11	0.0140*
Species:Habitat	9	282	1.72	0.0850
Species:Total visitation rate	9	282	1.27	0.2515
Habitat:Total visitation rate	1	282	8.35	0.0042***
Species:Habitat:Total visitation rate	9	282	2.74	0.0044**

Table 5: ANOVA table for best-supported heterospecific pollen proportion LME model

Model	numDF	denDF	F-value	p-value
Proportion of heterospecific pollen deposition				
(Intercept)	1	282	0.00	0.9957
Species	9	282	0.01	1.0000
Habitat	1	10	0.03	0.8559
Proportion Apis	1	282	0.94	0.3325
Species:Habitat	9	282	1.68	0.0935
Species:Proportion Apis	9	282	2.19	0.0227*
Habitat:Proportion Apis	1	282	7.59	0.0062**
Species:Habitat:Proportion Apis	9	282	3.15	0.0012***

Figures

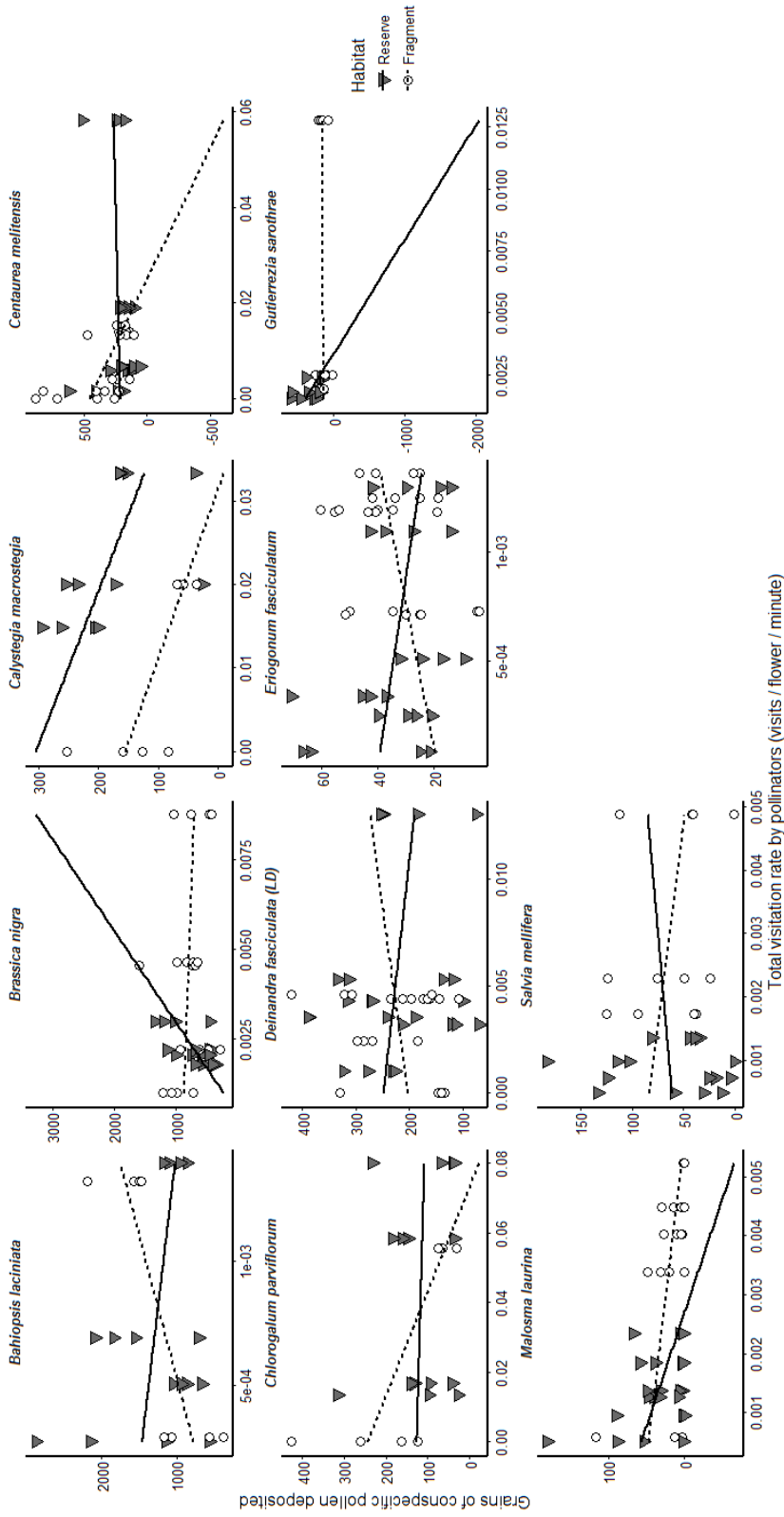


Figure 1: Total conspecific pollen deposition with respect to total pollinator visitation rate per species across scrub reserves and scrub fragments. Data are logged and ordinary least squares regression lines are drawn to help visualize trends.

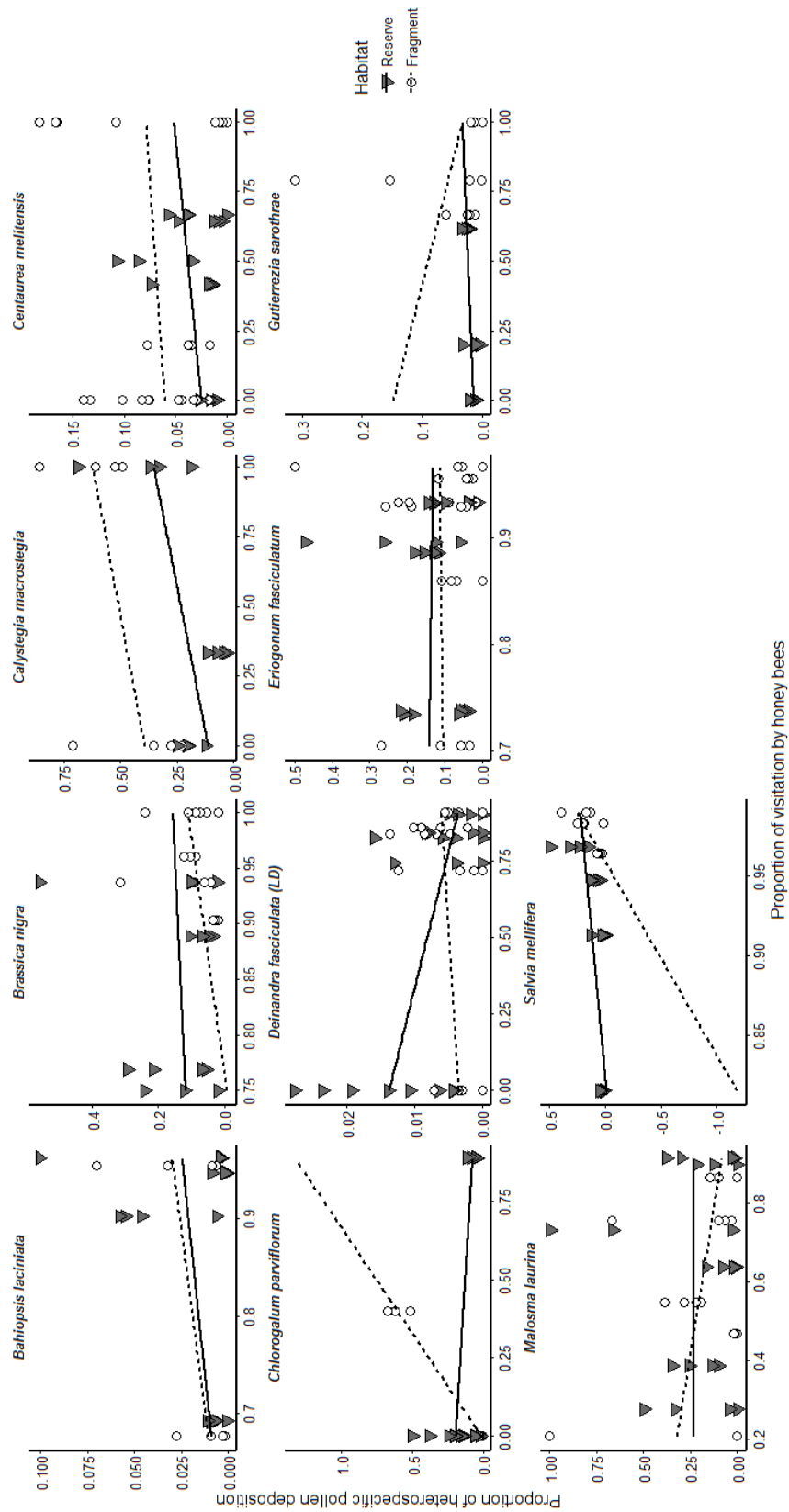


Figure 2: Heterospecific pollen proportion with respect to *Apis mellifera* proportion per species across scrub reserves and scrub fragments. Data are logged and ordinary squares regression lines are drawn to help visualize trends.

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