Title

Does pollinator diversity loss affect pollination: a test with the California poppy and clustered tarweed

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Does pollinator diversity loss affect pollination: a test with the California poppy and
clustered tarweed

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

in

Biology

by

Henry Jiayin Cen

Committee in charge:

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

2015

The Thesis of Henry Jiayin Cen is approved and it is acceptable in quality and form for publication on microfilm and electronically:

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Chair

University of California, San Diego

2015

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ABSTRACT OF THE THESIS

Does pollinator diversity loss affect pollination: a test with the California poppy and
clustered tarweed

by

Henry Jiayin Cen

Master of Science in Biology

University of California, San Diego, 2015

Professor David Holway, Chair

Pollinators are in decline as a result of human activities such as habitat
fragmentation. This study examined the effects of habitat fragmentation and reduced bee
diversity on the reproductive performance of California poppy, *Eschscholzia californica*,
and clustered tarweed, *Deinandra fasciculata*, in the San Diego region. We
experimentally introduced potted poppy plants in to scrub fragment habitats and natural
reserves. We surveyed the potted poppy plants for floral visitors followed by *in situ*
tarweed plants in our field sites after the poppies senesced. Both poppy and tarweed

revealed no difference in reproductive performance between fragments and reserves. Pollinator surveys of poppy and tarweed in fragment and reserve sites also revealed no difference in overall visitor abundance or species richness. However, we found that of the tarweed visitors, reserve sites harbored higher bee species richness than fragment sites. Native pollinator assemblage composition of tarweed visitors also differed between fragment and reserve sites. Honey bees accounted for 61% of all floral visitors observed in all sites. Although we cannot conclude that pollinator diversity played a significant role in the reproduction of poppy and tarweed, results from this study suggest that visitation in fragmented habitats is still sufficient for some native plant species to reproduce successfully. Also, generalist pollinators like honey bees may potentially help buffer against the negative effects of habitat fragmentation on pollinator diversity by maintaining an adequate level of pollination services in the system.

Introduction

Many flowering plant species depend on insect pollination for successful reproduction (Ollerton et al. 2011). Pollination services benefit from diverse pollinator assemblages since higher pollinator diversity leads to higher degrees of floral fidelity (Brosi and Briggs 2013) and diverse pollinator assemblages often include more specialists (Brittain et al. 2013; Brosi and Briggs 2013; Fründ et al. 2013; Hoehn et al. 2008) which may enhance the quality of pollination (Schemske & Horvitz. 1984). Bees are the most important group of insect pollinators; however, both bee abundance and species richness may be negatively affected by human disturbances and habitat loss (Potts et al. 2010; Winfree et al. 2009). A decline in pollinator diversity may potentially have negative effects on pollination services.

Surprisingly, the relationship between pollinator diversity loss and the reproductive success of the plant species that rely on insect pollination has not been well studied, especially in natural ecosystems (Mayer et al. 2011). Studies investigating the relationship between pollinator declines and pollination services have mostly focused on agricultural systems (e.g., Brittain et al. 2013, Hoehn et al. 2008), or used model simulations (e.g., Abramson et al. 2011, Memmott et al. 2004). Agricultural systems may not provide a good representation of non-managed ecosystems, and crop species may often differ strongly from native plant species with respect to how they interact with pollinators. Thus it is important to study how native plant species respond to changes in pollinator diversity.

The introduction of non-native species, such as the European honey bee (*Apis mellifera* L.), may have positive and negative effects on the quality of pollination for

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native plants. There is evidence that honey bees may compete with native bees for floral

resources and reduce native bee visitation rates (Aizen et al. 2014; Paini 2004). However,

as generalist pollinators, honey bees may help mitigate the negative effects of habitat

fragmentation on pollination services (Abramson et al. 2011) by pollinating specialist

plants (i.e. plants that depend on specialist pollinators for successful reproduction). In

other systems, honey bee visitation to flowers increases with decreasing fragment size,

while native bee visitation to flowers and richness of native bees increases with larger

fragment size (Aizen and Feinsinger 1994). It is therefore relevant to compare visitation

frequencies of native bees and honey bees between different levels of habitat

fragmentation and determine whether visitor community composition has an effect on the

reproductive performance of native plant species.

To test the hypothesis that pollinator diversity loss negatively affects native plant

reproduction, we compared the reproductive performance of two native plant species:

California poppy (*Eschscholzia californica* Cham) and clustered tarweed (*Deinandra*

fasciculate (DC.) Greene) between fragment and reserve sites. Poppy is a common and

widespread native plant species in the San Diego region. California poppy is mostly self-

incompatible (e.g., Cook 1962, Becker et al. 2005); its reproductive success is thus highly

dependent on insect pollination (Cook 1962). California poppy is also a broadly attractive

plant species to pollinators and is visited by a variety of bees, flies, butterflies, and

beetles even in highly urbanized landscapes (Wojcik & McBride 2012, Frankie et al.

2009). Timberlake (1956) discovered five species of solitary bees belonging to the genus

Perdita that only gather pollen from California poppy, indicating that some pollinators of

California poppy exhibit a high degree of host-specialization. For these reasons,

California poppy represents a good plant species to use in a study on pollinator-plant interactions. Clustered tarweed is also a common native plant species in the San Diego region. Tarweed may also exhibit a low degree of self-compatibility (Tanowitz 1985), suggesting that it may heavily depend on insect pollination for successful reproduction. As with the California poppy, tarweed is also drought tolerant and can be common in open, coastal sage scrub habitats (Sawyer et al. 2009). Tarweed also blooms later compared to poppy and may provide an interesting comparison of potentially different pollinator assemblages present during different times of the season, making it an ideal plant species to study in conjunction with the poppy experiment.

The goals of this study are as follows: (1) to determine whether there is a difference in insect visitation frequencies and visitor richness between fragment and reserve habitats, and (2) to determine whether habitat fragmentation has an effect on the reproductive performance of two native plant species. By studying how poppy and tarweed reproduction are related to habitat fragmentation and declines in pollinator diversity, we can expand our knowledge for the conservation of insect-pollinated native plant species. This research also provides information about the effectiveness of larger natural reserves at maintaining adequate levels of native pollinator and plant diversity versus smaller open-space fragment reserves. Such knowledge may benefit future management strategies for native plant communities.

Materials and Methods

Study system

Coastal sage scrub (CSS) ecosystems are important habitats in coastal portions of Southern California, which harbor a diverse community of plant species. However, CSS is threatened by habitat loss, fragmentation and degradation as a result of human activities (Bowler 2000; Westman 1981). The area of CSS habitat in this region has been reduced to about 15% of its original extent (Westman 1981). Surveys of bees in the San Diego region have found that large natural reserves harbor an average of 35% more bee genera and 36% more bee species compared to scrub fragments (Hung et al. *In preparation*). This decline in pollinator diversity may disrupt pollen transfer and reduce the reproductive performance of native plants.

We conducted fieldwork in the spring and summer of 2015 at thirteen different sites in San Diego County, CA: seven scrub fragments and six natural reserves (Table 1). The natural reserves used for this study consist of expanses of relatively undisturbed coastal sage scrub habitats more than 640 ha in area. Fragments consist of sites with less than 40 ha of scrub habitats that are surrounded by urban development. At each of these thirteen sites, we worked in 1-ha plots (n=6 reserves, n=7 fragments). We selected these sites because there were no poppies found in any of the sites, thus we can avoid pollination bias and all poppy sites have the same level of genetic diversity.

Poppy introduction experiment

In spring 2014 we collected California poppy seeds from two sites in Rose Canyon Open Space Park and from one site in Mission Trails Regional Park. We collected about twenty fruits from each site. In fall 2014 we incubated and germinated the

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poppy seeds in the laboratory. We randomly selected 300 seeds from each collection site for planting.

Poppy seeds were planted in 281, 4-liter pots at the UC San Diego Biological Field Station in November 2014. The soil in the pots was stratified into three different layers: silty loam soil at the base, sandy loam soil in the center, and loam soil at the surface. We left a 0.5-cm depression in the soil where each seed was planted to help channel water down towards the seed. Six seeds from the same seed origin site (i.e. Mission Trails site or Rose Canyon sites 1 or 2) were planted into each pot; seeds were spread out an equal distance from each other within each pot. We watered the pots three times a week until the poppies germinated, grew, and produced their first floral bud. We thinned poppies in each pot such that only one plant was present.

Prior to transplanting potted poppies into the field, we put them in a nested pot setup to protect them from drought conditions. The setup consisted of the pot containing the poppy placed in an outer 8-liter pot with all the drainage holes taped. The space between the two pots was filled with 50-ml of hydration crystals. Hydration crystals retained water and allowed plants to obtain water in between weekly manual watering.

In early March 2015 we transported the potted poppies to our study plots. For each of our twelve sites, we selected four poppies from Rose Canyon site 1, three poppies from Rose Canyon site 2, and three poppies from the Mission Trails site for a total of ten plants for each study plot. We selected poppies that were at comparable life stages (i.e., each bud will bloom at approximately the same time as all the other plants within the same study plot) to transfer to each site. At each plot, pots were arranged in a cluster situated in an open space but far enough from walking trails to remain hidden. To prevent

human tampering, we taped warning placards on five pots in fragment study plots and on two pots in reserve study plots. Each poppy patch was watered with approximately 4 liters of water each week using a watering backpack.

In late March 2015 we monitored experimentally introduced poppies for floral visitors every 3-5 days for 45 min total at each plot on a rotating basis between study plots. During each monitoring session, we recorded the identity (to genus for bees based on morphology, and to family for other floral visitors) and behavior (number of flowers visited per plant, and duration of contact with each flower) of each floral visitor. We collected at least one visitor that we believed to be a different species to keep as a reference specimen for identification.

We compared poppy reproductive performance between fragment sites and reserve sites as follows. After poppy flowers senesced, we brought the potted plants back to the UC Biological Field Station and allowed fruit to mature. For each fruit, seeds were counted and categorized into developed and undeveloped groups based on coloration (e.g., dark brown and round seeds were considered developed, light brown and disfigured seeds were considered undeveloped). To compare reproductive performance between reserves and fragments, we used two-way analyses of variance with seed origin and site type as factors using the program RStudio Version 0.98.1091. We conducted separate two-way ANOVAs on each of three response variables: flower number, fruit number, and mature seeds per fruit.

Floral visitation on tarweed

To test whether there was a difference in pollinator visitation and reproductive performance between *in situ* plants in reserves versus fragments, we surveyed tarweed in

each study plot from April 8 to May 23. We estimated the number of tarweed plants

within each plot. Because one of our fragment study plots (Harry Griffin Memorial Park)

did not harbor tarweed, we selected Scripps Coastal Reserve to be a substitute plot for

this portion of the study (Table 1). We monitored tarweed found within each study plot

for a total of 45 min at each plot every 3-5 days on a rotating basis and recorded the

identity and behavior of each floral visitor. To assess whether tarweed is autogamous, we

selected five immature tarweed inflorescences at each study plot to be enclosed in mesh

bags to prevent pollinators from visiting.

After most of the tarweed in the study plot senesced, we collected five floral

clumps, which consisted of a branch of a tarweed plant containing approximately 30

capitula (composite flowers), from similar sized tarweed individuals. At this time, we

also collected individuals bagged earlier for autogamy. We counted the number of

capitula and number of ray seeds produced in each floral clump and weighed the seeds.

We also categorized seeds into developed and undeveloped groups based on seed mass

(seed mass < 0.2mg = undeveloped seed). We calculated the average mass of developed

seeds collected from each site. We used a two-sample t-test to compare average seed

mass per site and visitor abundance between fragment and reserves. After sorting all of

our specimens into morphospecies, we used a two-sample t-test to compare overall visitor

richness and native bee richness between reserves and fragments; we used a one-tailed

test because we expected reserves to have greater bee richness compared to fragments.

Using the raw visitor abundance data, we performed a multivariate analysis

(PERMANOVA) and produced an NMDS ordination plot using the Bray-Curtis

dissimilarity index with 1000 permutations to compare assemblage composition of native

floral visitors between fragments and reserves using the VEGAN package (Oksanen et al. 2015). We also performed an indicator species analysis using the LABDSV package (Roberts 2015). All analyses were conducted in RStudio Version 0.98.1091. We excluded the Otay-Sweetwater Unit, Trace Road site from the visitor abundance and richness analyses because there was very little tarweed present. We decided that if the number of tarweed in a site is less than 100 per hectare, we would exclude visitation data because there would be little visitation.

Results

Poppy introduction experiment

We detected no significant difference in poppy visitor abundance (Table 2; two-sample *t*-test: $t_7 = 0.293$, $P = 0.778$) or morphospecies richness (Table 2; two-sample *t*-test: $t_9 = 0.161$, $P = 0.876$) between fragment and reserve sites. Over the course of five days of surveying poppies at our different field sites, we observed a total of 96 floral visitors (Table 2). The average number of visitors at each site equaled nine individuals. Halictid bees (n = 84 observations) such as *Lasioglossum* spp. and *Halictus* spp. spent an average of 22 seconds in flowers, whereas *Apis* spent an average of 6 seconds in flowers (n = 8 *Apis*).

We found that poppies in fragment sites produced more flowers than those at reserve sites (Table 3, Fig. 1A) and that seed origin also affected flower number. Poppies at fragment sites also produced more fruit than those at reserve sites (Table 3). Fruit production also varied as a function of seed origin. However, developed seeds produced per flower did not differ between fragment and reserve sites; this quantity was also independent of seed origin (Table 3, Fig. 1B). We did not find any significant relationship between floral visitor abundance and developed seeds per flower (linear regression: $F_{1,9} = 3.335$, $P = 0.1011$, $R^2 = 0.2704$).

Floral visitation on tarweed

We observed a total of 2,883 floral visitors to tarweed belonging to 97 different morphospecies (Appendix A). Reserves had higher bee species richness compared to fragments (Fig. 2C; two-sample *t*-test: $t_9 = 2.033$, $P = 0.0363$). Honey bees accounted for

61% of tarweed visitors; however, there was no significant difference in honey bee visitor abundance between fragment and reserve sites (Fig. 3A; two-sample t-test: $t_9 = 1.301$, $P = 0.2257$). Overall, 58% of non-honey bee visitors in fragments were hover flies and 50% of non-honey bee visitors in reserves were bee flies. Excluding honey bees from the data, we found a significant difference in the assemblage composition of tarweed floral visitors between fragments and reserves (Fig. 4; PERMANOVA: $F_{(1,10)} = 2.514$, $P = 0.002$). Indicator taxon analysis revealed *Copestylum marginatum* to be associated with fragments (indicator value = 0.9333, $P = 0.006$) and *Conophorus* spp. are associated with reserves (indicator value = 0.9375, $P = 0.011$). After excluding honey bees from the data, there was no significant difference in tarweed visitor abundance on tarweed between fragment and reserve sites (Fig. 3B; two-sample t-test: $t_9 = 1.207$, $P = 0.2584$) and there was no significant difference in overall tarweed visitor abundance between fragment and reserve sites (Fig. 2A; two-sample t-test: $t_9 = 1.501$, $P = 0.1677$). Overall species richness of floral visitors also did not differ between fragments and reserves (Fig. 2B; two-sample t-test: $t_9 = 0.6523$, $P = 0.2652$).

We found no statistical difference in the average developed seed mass of tarweed per site between fragments and reserves (Fig. 5; two-sample t-test: $t_{57} = 0.6971$, $P = 0.4886$). Number of developed seeds per site also did not differ between fragment sites and reserve sites (two-sample t-test: $t_{57} = 1.154$, $P = 0.2533$). We found that tarweed has a low degree of autogamy. Although ray seeds were present in the bagged tarweed inflorescences, they were undeveloped and weighed significantly less than ray seeds collected from open pollinated flowers (two-sample t-test: $t_{38} = 12.212$, $P < 0.0001$). The mean seed masses of bagged and open pollinated flowers were 0.18mg $\pm$ 0.02 SE and

0.35mg $\pm$ 0.02 SE respectively. The number of developed ray seeds per capitulum was also significantly lower in bagged tarweed inflorescences (two-sample t-test: $t_{60} = 8.9397$, $P < 0.0001$).

A strong positive relationship was observed between tarweed density and the number of floral visitors (linear regression: $F_{1,10} = 92.32$, $P < 0.0001$, $R^2 = 0.9023$) but no significant relationship between tarweed density and floral visitor species richness (linear regression: $F_{1,10} = 1.205$, $P = 0.298$, $R^2 = 0.1076$). We only found a strong positive relationship between tarweed density and number of honey bee visits (Fig.6B; linear regression: $F_{1,10} = 57.11$, $P < 0.0001$, $R^2 = 0.851$) but not with non-honey bee visits (Fig. 6C; linear regression: $F_{1,10} = 2.7$, $P = 0.1314$, $R^2 = 0.2126$). No relationship existed between the density of tarweed plants and average developed seed mass per site (Fig. 6A; linear regression: $F_{1,10} = 0.7526$, $P = 0.406$, $R^2 = 0.0699$). There was no significant difference in tarweed density between fragments and reserves (two-sample t-test: $t_7 = 2.128$, $P = 0.0708$).

Discussion

The results from this study suggest that despite documented declines in bee diversity in fragmented coastal sage scrub habitats (Hung et al. 2015), key pollinators still persistently forage in fragments resulting in no discernible change to the quality of pollination services. An abundance of generalist pollinators such as honey bees and sweat bees, both of which occur in fragments, also appear sufficient to perform pollination for the two plant species we studied. Pollination services may saturate with increasing pollinator abundance or diversity such that additional pollinators may be ecologically redundant (Fründ et al. 2013).

It has been suggested that fragment sites may function as "resource oases" (Bock et al. 2008; Slagle and Hendrix 2009) for pollinators in landscapes affected by urbanization, which may explain why we found similar levels of visitor abundance and richness in fragment sites and reserve sites similar to previous studies (Davis et al. 2008; Slagle and Hendrix 2009; Wojcik and McBride 2012). However, we did find that reserves have higher bee species richness than fragments, supporting recent findings (Hung et al. 2015), and the assemblage compositions differ in fragments and reserves similar to the findings of a previous study (Wojcik and McBride 2012). This suggests that despite higher bee species richness in reserves, non-bee pollinators or a different community of bees in fragments may be just as efficient at pollinating poppy and tarweed as bees found at reserves.

Because of the generalist behavior of honey bees, it is possible that a high abundance of honey bees is sufficient to effectively pollinate poppies and tarweed despite a dearth of visitor richness (Abramson et al. 2011). Although honey bees may carry more

incompatible pollen and transfer less pollen per flower compared to native pollinators (Adler 2005; Brittain et al. 2013; Young et al. 2007), native plants do not necessarily experience pollen limitation despite decreased conspecific pollen deposition (Bjerknes et al. 2007; Moragues and Traveset 2005). This indicates that generalist pollinators, like honey bees, may transfer sufficient pollen for many plant species and fill the niche gaps of disappearing specialist bees. However, the relationships we found among honey bee visitation, tarweed density and tarweed seed set suggests that although dense patches of tarweed attract large numbers of honey bees, greater numbers of honey bees do not significantly affect the reproductive performance of tarweed. Perhaps the effectiveness of honey bees saturates after a certain level of abundance since net benefits from pollination peak at intermediate levels of visitation (Finer and Morgan 2003; Klinkhamer and de Jong 1993), or honey bees may stress or damage flowers with high frequency visitation (Aizen et al. 2014).

We did not find any significant correlation between poppy visitor abundance and the number of mature seeds produced per flower, similar to the findings of a previous study (Anic et al. 2015). Because our experimental poppies were likely suffering from environmental stress, it is possible that our transplanted poppies in reserves were not producing enough flowers to attract large numbers of pollinators since floral density may affect visitation rates of pollinators (Heinrich 1979; Hegland and Boeke 2006). In addition, other flowering plants present within our study sites may be out-competing the poppies for visitation by generalist pollinators. Honey bees were the most abundant pollinators documented in all of our study sites, and we observed that poppy patches in sites dominated by dense populations of flowering invasive mustard plants, *Brassica*

nigra, tended to be ignored by honey bees. Conspecific pollen in native plants can be reduced in landscapes infested with invasive plants (Larson et al. 2006). Perhaps native plants compensate for the lack of visitors by using other methods of pollination. It has been suggested that wind pollination may play a role in pollen receipt for poppies (Anic et al. 2015) because this phenomenon has been described in other insect-pollinated plants as well (Goodwillie 1999).

In 2015, there were atypical precipitation patterns and abnormally high temperatures between February and late March. These weather patterns and drought conditions may result in cascading effects on the quality of pollination services. Several key pollinators known to visit poppy, such as *Bombus vosnesenskii* Radoszkowski, were not observed during our surveys. Drought may have played a role in the absence of such pollinators (Franks et al. 2007). Drought-induced stress may have caused plants to bloom earlier than normal or to cease blooming prior to pollinators becoming active. This change in flowering phenology may have led to a decrease in native bee visitation in our field sites (Rafferty and Ives 2011) and since honey bees were found to be more abundant in smaller fragment habitats compared to larger reserve habitats (Aizen and Feinsinger 1994), perhaps our target plant species were not receiving enough floral visitation in reserve sites due to a lack of both native bees and honey bees.

Our findings from the poppy experiment suggest that poppies may still be able to persist in fragmented habitats previously documented to harbor lower bee diversity (Hung et al. 2015; Hung et al. *In preparation*). However, because of environmental stress, the lifespan of the poppy flowers may have decreased. Poppies located farther inland may have suffered from hotter and drier weather that prevailed during the field experiment,

and plants located on exposed slopes were also likely more prone to water loss due to evapotranspiration from convection. Since more fragment sites were closer to the coast, the poppies at those sites may have experienced more mist and cooler temperatures allowing them to produce more flowers than the poppies in some of the reserve sites farther inland where temperatures were higher. However, we did not have accurate measures of temperatures and weather conditions at each site so it is unknown why poppies in fragment sites produced more flowers. A decrease in poppy viability may account for lower flower production in reserve sites.

Similar to poppy, tarweed did not show any difference in reproductive performance between fragments and reserves. Because we surveyed *in situ* populations of tarweed at each of our sites, we had a larger number of plants to work with. However, atypical climate patterns still had effects on the tarweed experiment. We surveyed tarweed from April to May, but tarweed usually flowers from May to September (Munz and Keck 1968), and seeds typically mature in August (Stevens and O'Brien 2006). The temporal shift in flowering time may explain why we still found results similar to that of the poppy experiment.

In conclusion, our results indicate that although bee diversity in fragmented habitats is lower than in natural reserves, reproduction in certain plant species such as *Eschscholzia californica* and *Deinandra fasciculata* appear unaffected. Although we cannot conclude that visitor diversity played an important role in the reproductive performance of poppy and tarweed, results from this study suggest that visitation in fragment habitats is still sufficient for successful reproduction. This finding supports the idea that fragment habitats act as floral resource oases for pollinators in landscapes

affected by urbanization (Bock et al. 2008; Slagle and Hendrix 2009). Given the high abundance of honey bees we found in fragment sites, honey bee presence could help buffer against the negative effects of habitat degradation by maintaining an adequate level of pollination services in the system. However, we did not compare the pollination efficiency of generalist pollinators and specialists. Future studies may look into how effective generalist pollinators are compared to specialists in providing pollination services between fragment and reserve habitats. It is also possible that atypical climate patterns affect the reproduction of certain plant species such that the level of pollination received has little effect on the plants' reproductive performance. Despite our findings that native plants in fragments have similar levels of reproductive performance as reserves, fragments are fragile habitats that are unlikely to sustain healthy bee populations without other floral resources in the surrounding landscape (Kremen et al. 2004; Greenleaf and Kremen 2006). Since a large proportion of plants require bee-pollination to some extent, populations of native plants in fragments may diminish as a result of bee declines.

Tables

Table 1: Reserve and fragment sites used in this study

Site Type	Site Name	Latitude/Longitude
Fragment	Governor Street Fragment	N 32.85559, W 117.18837
Fragment	Juniper Canyon Open Space	N 32.721798, W 117.118225
Fragment	Eastridge High Street Fragment	N 32.7495, W 117.03147
Fragment	Harry Griffen Memorial Park *	N 32.786182, W 116.98899
Fragment	Pasatiempo West Open Space	N 32.792, W 117.075645
Fragment	Chollas Creek Open Space	N 32.719677, W 117.07809
Fragment	Scripps Coastal Reserve**	N 32.876389, W 117.248056
Reserve	Otay-Sweetwater Unit, San Diego National Wildlife Refuge (Millar Ranch)	N 32.728344, W 116.94002
Reserve	Otay-Sweetwater Unit, San Diego National Wildlife Refuge (Trace Road)	N 32.731876, W 116.955246
Reserve	Mission Trails Regional Park (Renovo Way)	N 32.834385, W 117.07441
Reserve	Mission Trails Regional Park (Colina Drive)	N 32.822292, W 117.075645
Reserve	UC NRS Elliott Chaparral Reserve (inner site)	N 32.89277, W 117.09172
Reserve	UC NRS Elliott Chaparral Reserve (outer site)	N 32.899723, W 117.07502

*Plot excluded from the tarweed portion of the study

**Plot only used for the tarweed portion of the study

Table 2: Number of poppy visitors observed at fragment and reserve sites in San Diego County.

Visitor	Fragment	Reserve
Skipper butterfly	1	0
Apis mellifera	7	1
Dufourea sp.	4	10
Lasioglossum spp.	34	36
Diptera	1	0
Micralictoides ruficaudus	0	1
Wasp	0	1

Table 3: Two-way ANOVA tables for three different comparisons of poppy reproduction

Number of flowers produced

Factors	df	Sum Sq	Mean Sq	F value	P value
Site type	1	242.53	242.53	10.077	**0.0037**
Seed origin	2	466.42	233.21	9.6903	**0.0007**
Interaction	2	0.2200	0.1100	0.0046	0.9954

Number of fruit produced

Factors	df	Sum Sq	Mean Sq	F value	P value
Site type	1	1.3520	1.3516	5.5504	**0.0191**
Seed origin	2	1.6530	0.8263	3.3931	**0.0348**
Interaction	2	0.1890	0.0946	0.3885	0.6783

Mature seeds per flower

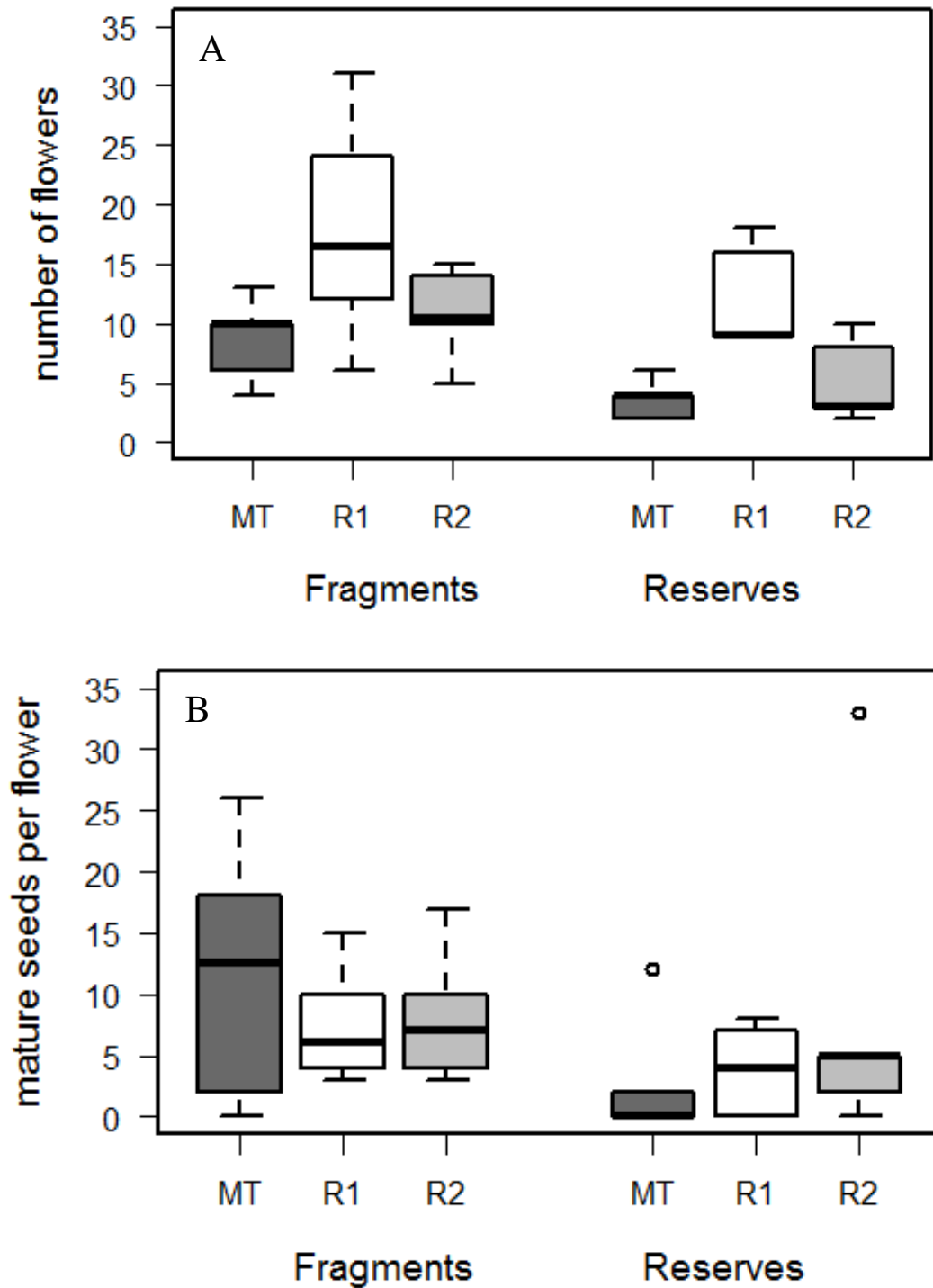| Factors	df	Sum Sq	Mean Sq	F value	P value
Site type	1	121.63	121.63	1.9905	0.1697
Seed origin	2	43.880	21.939	0.3591	0.7016
Interaction	2	137.70	68.849	1.1268	0.3388

Figure 1: Box plots of (A) poppy flowers and (B) mature seeds produced per flower between fragment and reserve sites in San Diego County by poppy seed source (MT, R1, R2). The center line is the median, box endpoints show the interquartile range, and the whiskers show the data range excluding outliers.

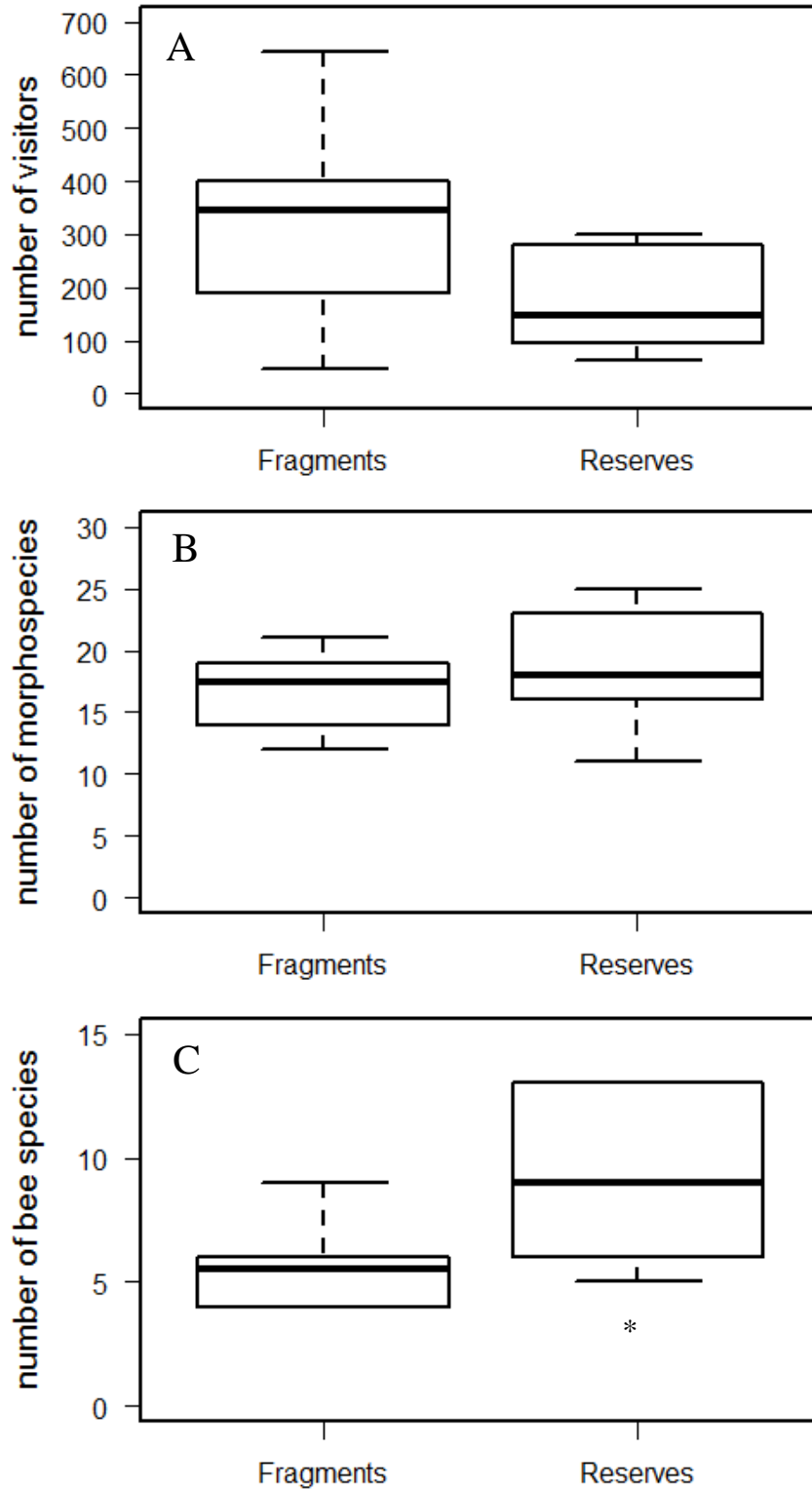**Figure 2:** Box plots of (A) abundance of floral visitors on tarweed, (B) species richness of visitors, and (C) bee species richness on tarweed between fragment and reserve coastal sage scrub habitats in San Diego County. Box plots as in Fig. 1.
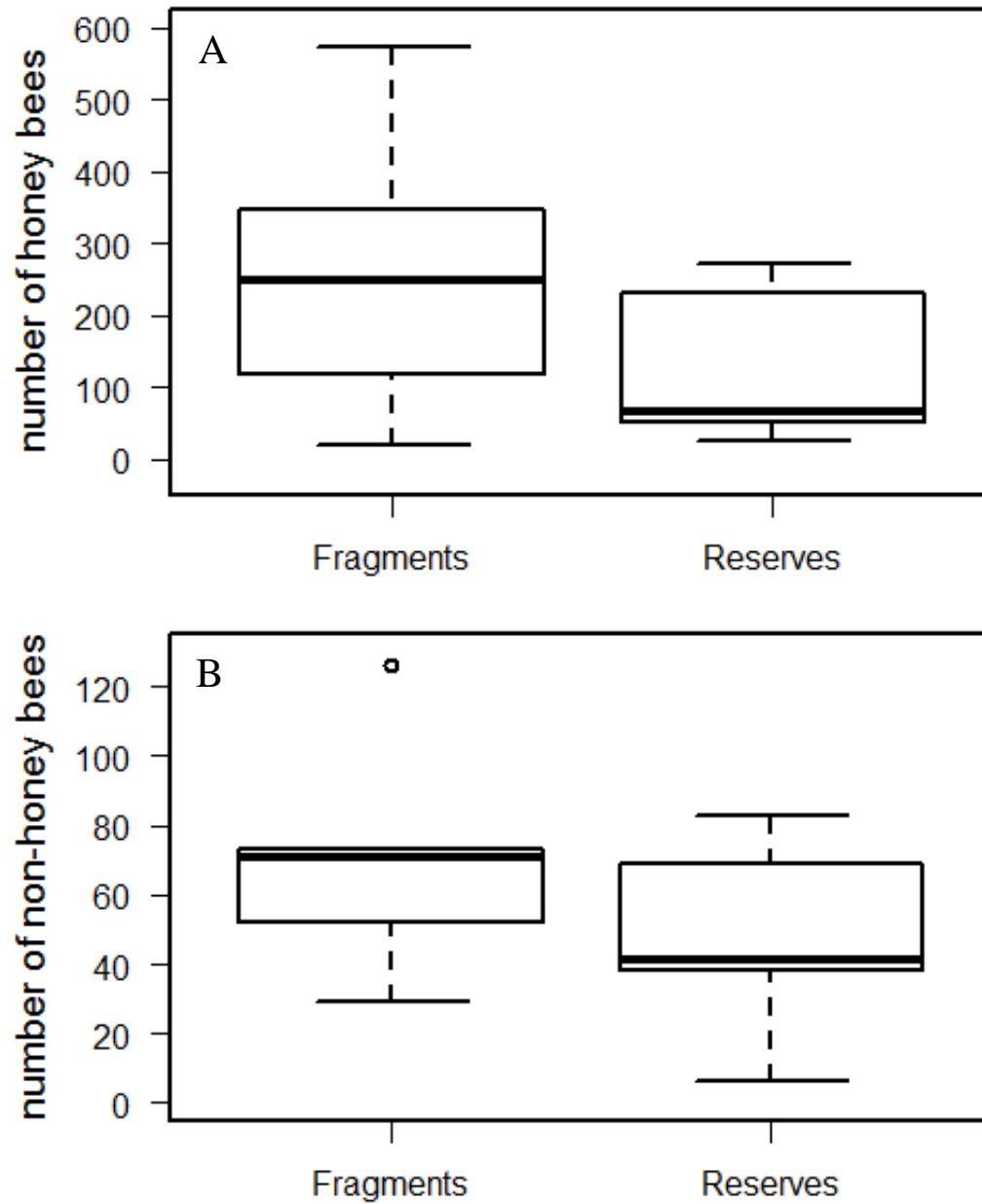
Figure 3: Box plots of (A) number of honey bee visits observed on tarweed, (B) number of non-honey bee visits observed on tarweed between fragmented and reserve coastal sage scrub habitats in San Diego County. Box plots as in Fig. 1.
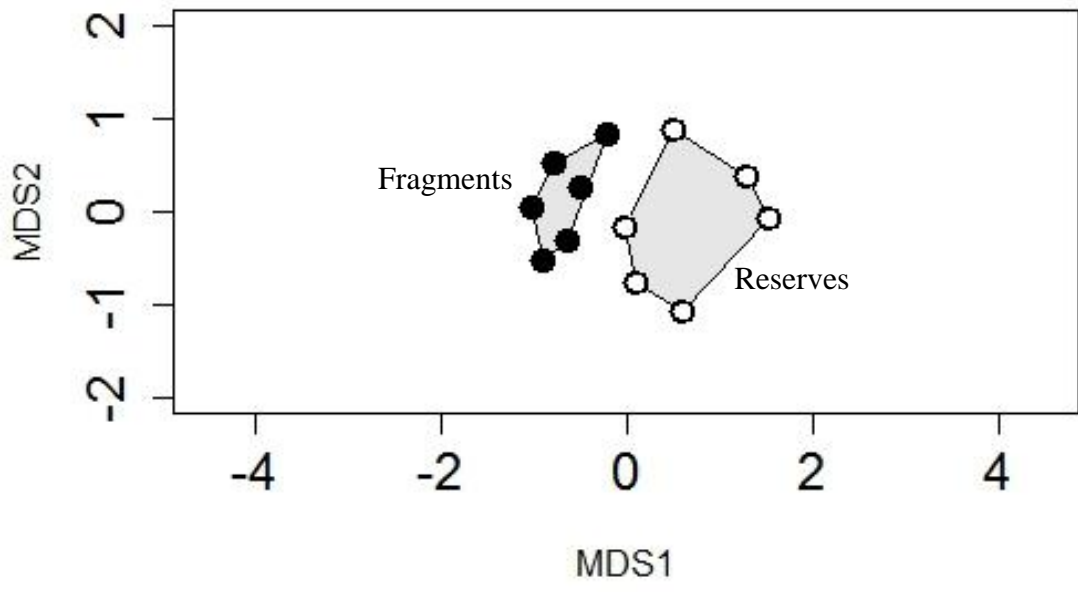
Figure 4: Non-metric multidimensional scaling plot based on the species composition of tarweed visitors in fragment sites versus reserve sites.

Figure 5: Box plot of average seed mass per site (mg) of tarweed between fragment and reserve coastal sage scrub habitats in San Diego County. Box plots as in Fig. 1.
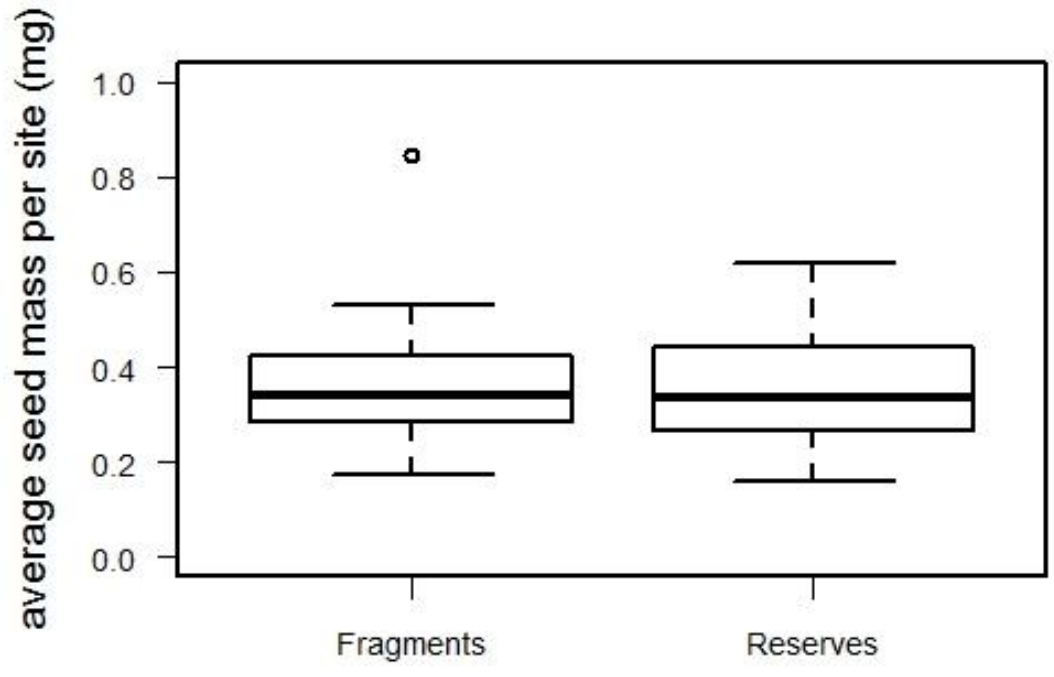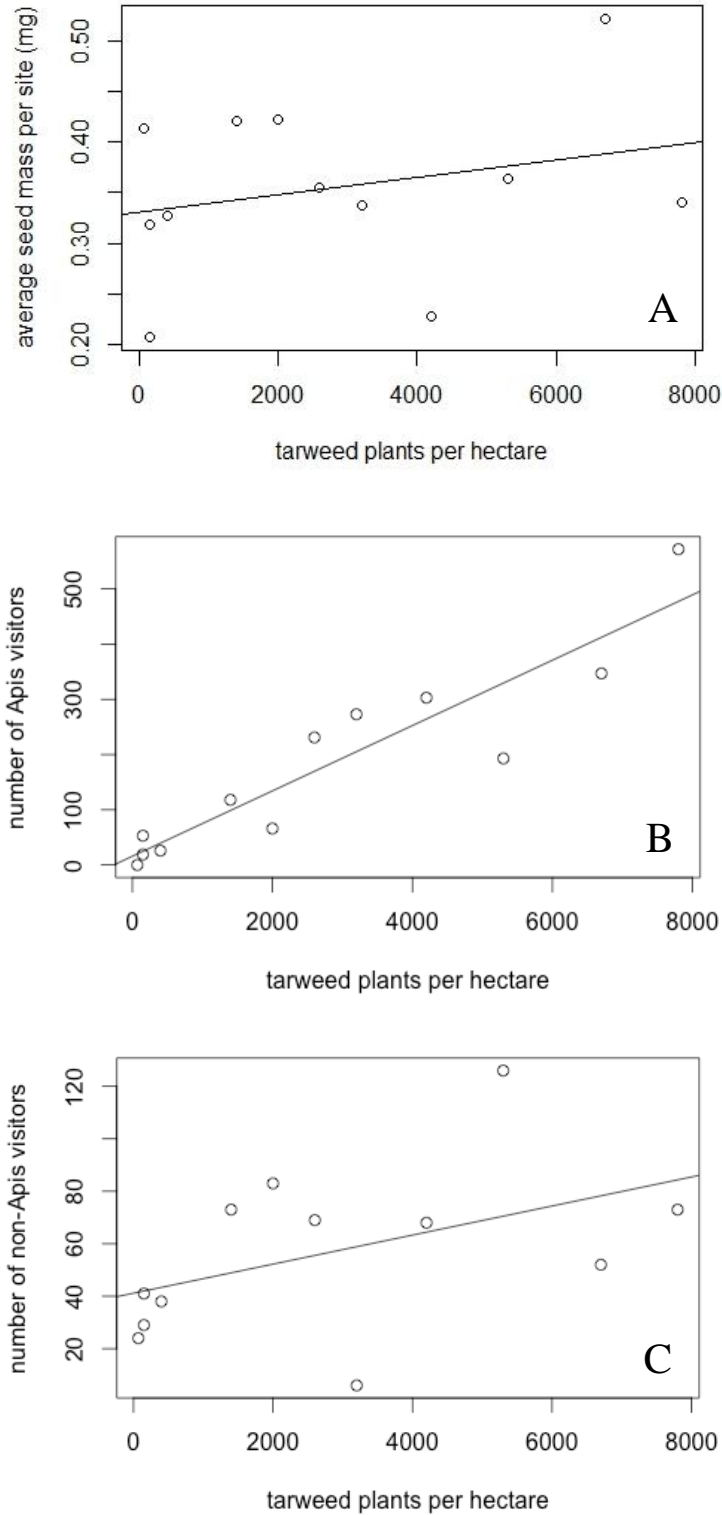
Figure 6: Linear regression models of the relationships between tarweed density and (A) average seed mass per site (mg), (B) number of honey bee visitors, and (C) number of non-honey bee visitors.

Appendix

Appendix A. Insect taxa observed visiting clustered tarweed

Family	Species	frag	res
Andrenidae	*Andrena* (Sp.1)	✓	✓
	Andrena (Sp.2)		✓
	Calliopsis pugionis		✓
Apidae	*Anthophora curta*	✓	✓
	Anthophorula nitens	✓	✓
	Anthophorula torticornis	✓	✓
	Apis Mellifera	✓	✓
	Brachynomada annectens		✓
	Bombus melanopygus	✓	
	Ceratina acantha		✓
	Ceratina nanula		✓
	Diadasia nitidifrons		✓
	Diadasia ochracea	✓	
	Leiopodus singularis		✓
	Melissodes (Sp.1)	✓	✓
	Melissodes (Sp.2)	✓	✓
	Melissodes (Sp.3)	✓	
	Melissodes (Sp.A)		✓
	Melissodes (Sp.B)	✓	✓
	Tetraloniella davidsoni	✓	✓

Family	Species	frag	res
	Tetraloniella pomonae	✓	✓
	Triepeolus (Sp.1)		✓
	Triepeolus (Sp.2)	✓	
	Triepeolus matildae		✓
Bombyliidae	BOMBYLIIDAE (Sp.1)	✓	✓
	BOMBYLIIDAE (Sp.2)	✓	✓
	BOMBYLIIDAE (Sp.3)		✓
	BOMBYLIIDAE (Sp.4)		✓
	BOMBYLIIDAE (Sp.5)	✓	
	BOMBYLIIDAE (Sp.6)		✓
	BOMBYLIIDAE (Sp.7)	✓	
	BOMBYLIIDAE (Sp.8)		✓
	BOMBYLIIDAE (Sp.9)		✓
	Conophorus spp.	✓	✓
	Pantarbes spp.	✓	✓
Calliphoridae	CALLIPHORIDAE (Sp.1)	✓	
Colletidae	*Colletes* (Sp.1)	✓	
	Hylaeus (Sp.1)		✓
DIPTERA	DIPTERA (Sp.1)	✓	
Halictidae	*Augochlorella pomoniella*	✓	✓
	Halictus farinosus	✓	✓
	Halictus ligatus		✓

Family	Species	frag	res
	Halictus tripartitus	✓	✓
	Lasioglossum (*Dialictus* Sp.2)	✓	✓
	Lasioglossum (*Dialictus* Sp.3)		✓
	Lasioglossum (*Dialictus* Sp.4)		✓
	Lasioglossum brunneiventre	✓	
	Lasioglossum incompletum	✓	✓
	Lasioglossum microlepoides	✓	✓
	Lasioglossum nevadense		✓
Hesperiidae	*Erynnis* sp.	✓	✓
Lycaenidae	*Brephidium exile*		✓
	Strymon melinus	✓	
Megachilidae	*Anthidium* (Sp.1)		✓
	Ashmeadiella bucconis		✓
	Ashmeadiella californica	✓	✓
	Atoposmia (Sp.1)		✓
	Megachile (Sp.1)		✓
	Megachile (Sp.2)		✓
Pieridae	*Pontia protodice*	✓	✓
Riodinidae	*Apodemia mormo*		✓
Sarcophaginae	SARCOPHAGINAE (Sp.1)	✓	
Scenopinidae	SCENOPINIDAE (Sp.1)	✓	
Syrphidae	*Copestylum avidum*	✓	✓

Family	Species	frag	res
	Copestylum marginatum	✓	✓
	Copestylum mexicanum	✓	✓
	SYRPHID [unID]	✓	
	SYRPHID (sp.10)	✓	
	SYRPHID (sp.11)	✓	
	SYRPHID (sp.12)	✓	
	SYRPHID (sp.13)	✓	
	SYRPHID (sp.2)	✓	✓
	SYRPHID (sp.3)	✓	✓
	SYRPHID (sp.4)	✓	
	SYRPHID (sp.5)	✓	
	SYRPHID (sp.6)	✓	
	SYRPHID (sp.7)	✓	
	SYRPHID (sp.8)	✓	
	SYRPHID (sp.9)	✓	
Tachinidae	TACHINIDAE (Sp.1)	✓	
	TACHINIDAE (Sp.2)	✓	
	TACHINIDAE (Sp.3)	✓	
WASP	WASP (sp.1)	✓	✓
	WASP (sp.11)		✓
	WASP (sp.12)		✓
	WASP (sp.2)		✓

Family	Species	frag	res
	WASP (sp.3)	✓	
	WASP (sp.4)	✓	
	WASP (sp.5)	✓	✓
	WASP (sp.6)	✓	
	WASP (sp.7)		✓
	WASP (sp.8)		✓
	WASP (sp.9)	✓	
	WASP (sp.11)		✓
	WASP (sp.12)		✓
	WASP (sp.13)	✓	
	WASP (sp.14)	✓	

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