## Title

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# Wild Bee Communities in Grassland Habitats of the Central Valley of California: Drivers of Diversity and Community Structure

By

Jennifer Lynn Hernandez

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in

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Committee in charge:

Professor Gordon Frankie, Chair
Professor Claire Kremen
Professor Mathias Kondolf

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# Abstract

# Wild Bee Communities in Grassland Habitats of the Central Valley of California:

## Drivers of Diversity and Community Structure

by

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Recent research has revealed a trend of decreasing pollinator abundance and diversity in regions throughout the world. This highlights the need to understand factors influencing patterns in bee community structure and the drivers of bee diversity and abundance patterns. My dissertation uses several methods to determine factors structuring bee communities with regards to diversity and abundance. I selected 10 sites in different regions of the Central Valley of California that differ with regards to land use and floral diversity. Bee communities at each site were sampled for diversity, abundance, and bee-floral host relationships.

Sampling bee communities is often done using only bee bowls because netting is time consuming and prone to sampler bias. In chapter one the methods used in this study were detailed and the use of bee bowls and netting in capturing a representative sample of the bee community were compared using the Sørensen's similarity index and the Bray-Curtis dissimilarity index. It was determined that sampling using one method alone would miss approximately 40% of the species richness of the community. Further, there were biases in using bee bowls and nets; the bee bowls sampled certain species more than nets and vice versa. This chapter provides evidence that to adequately sample a bee community both bee bowls and netting must be used.

Chapter two focuses on bee biodiversity and the correlation between bee species richness and plant diversity. Patterns of diversity in bee communities of the Central Valley indicate that the family Apidae was more speciose than other families. However, on a species level, those from the family Halictidae far exceeded species from Apidae in abundance. This could have reflected a sampling bias given that pan traps tend to sample individual bees from Halictidae more than Apidae. Chapter two also focused on temporal variability. There was considerable temporal variability in the abundance of one of the more abundant species, *Lasioglossum incompletum*. This highlighted the need for studies of longer duration in order to account for natural stochasticity in bee populations. Several different diversity indices were used to assess the biodiversity of the different study locations; Putah Creek sites were found to be more diverse than the San Joaquin sites. A correlation analysis was used to determine that a positive

relationship between plant diversity and bee species richness did exist for 2005 but not 2006. This indicated that plant diversity may be one of the factors driving bee species richness and community structure.

Another factor possibly accounting for variation in bee species richness and abundance is land use. Chapter three used non-metric multidimensional scaling and generalized linear mixed effects model to test for associations between differences in land use patterns and bee species richness and abundance. While there was no direct association between these factors, the ordination did show that the Putah Creek sites, San Joaquin sites, and Cosumnes sites clustered together. Therefore, sites that shared similar land-use patterns were related along a gradient. These cluster patterns were used to group the study locations for the other analyses performed in this project. The Putah Creek sites were characterized by agriculture and urban land use whereas, San Joaquin was semi-natural and Cosumnes Preserve was semi-natural and agricultural.

Chapter four is an analysis of the pollinator networks of Putah Creek, San Joaquin, and the Cosumnes Preserve. Pollination webs, matrices, and gplots were used to visualize the networks, while network and species-level indices were used to assess asymmetry, specialization versus generalization, and connectance. It was determined through these analyses that the connectance of the network decreased with increasing species richness and the complexity and composition of the network varied between the three regions of the Central Valley. Further, the San Joaquin Refuge sites, which were characterized as seminatural land use, contained a higher number of oligolectic species than other sites dominated by agricultural and urban land use.

The focus of this project was to use different methods to determine drivers of bee species diversity and abundance in different bee communities of the Central Valley of California. Three conclusions can be drawn from the analyses presented; 1) Given temporal variability in bee populations, studies of longer duration must be conducted to determine factors affecting bee community structure from that of natural population variability, 2) Floral diversity is positively correlated with bee species diversity and abundance but it is not the only factor influencing bee community structure. and 3) Land use change may be a factor influencing bee-plant networks but studies that compare networks across space and time are needed to determine the nature of this relationship.

I would like to dedicate this manuscript to my husband, Ken. It was with all of your support and encouragement that I was able to pursue my dream.

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# Chapter 1

## Sampling bee fauna: Netting versus bee bowls

## Introduction

Insects are a rich resource in natural systems, providing pollination to approximately two-thirds of the 240,000 flowering plant species (National Resource Council 2007). In some communities it is estimated that insects pollinate up to 93 percent of the flowering plants (Bawa 1974). Bees rely solely on pollen and nectar for their energy requirements and provisioning of their nests making them frequent flower visitors and the most valuable of the insect pollinators. In agricultural settings, they are essential to production as they pollinate most crops responsible for our fruits, vegetables, seed crops, and crops that provide fiber, drugs, and fuels (National Research Council 2007). It is estimated that bees are responsible for production of approximately thirty percent of the human diet (Buchmann and Nabhan 1996).

Studies have indicated that we are facing a global decline in pollinator populations of vertebrate and invertebrate species (Allen-Wardell et al. 1998, Buchmann and Nabhan 1996, Potts et al. 2010). This has prompted an upsurge in pollinator monitoring programs and initiatives designed to assess the current status and future trajectory of these environmentally and agriculturally vital populations. The Convention on Biological Diversity (International Pollinator Initiative, http://www.cbd.int/decision/cop/?id=7147) calls for the conservation and sustainable use of pollinators by monitoring pollinator decline, addressing lack of taxonomic information, and restoring pollinator diversity in agricultural and natural ecosystem among other goals. The ALARM Project (Assessing Large Scale Risks for Biodiversity with Tested Methods) was designed and funded by the United Nations Food and Agriculture Organization. The project assessed bee and flower fly populations in the Netherlands and England before and after 1980 analyzing more than 500,000 records. The results of the comprehensive survey, (reported in Beismeijer et al. 2006), revealed a decline in these populations. Species richness of bee populations declined in approximately 40 percent and 60 percent of the grid cells used for sampling in the United States and the United Kingdom and Netherlands respectively. In the United States the North American Pollinator Protection Campaign (NAPPC) is instrumental in promoting the conservation and restoration of pollinator habitat and in constructing task forces that promote pollinator conservation.

These programs are linked by the common goal of pollinator conservation; however, effective conservation must be based on sound knowledge of the community dynamics driving pollinator populations. Bee populations, in particular, exhibit a high degree of spatiotemporal variation making detection of actual declines difficult. This is further hindered by the fact that a variety of methods have traditionally been used to collect data on bee populations. Williams et al. (2001) compiled surveys on bee fauna to assess patterns in abundance and richness. The authors determined that bee populations are highly variable in space and time and are comprised of a high percentage of rare species. This led to the conclusion that intense sampling is required to adequately characterize bee population dynamics. The authors further conclude that standardized sampling protocols using replicated designs are essential to this field of research to increase the value of data. The standardization of sampling methods will permit the cross-comparison of studies and produce data that can be tested using statistical techniques.

A technique that is often employed to sample bee diversity and relative abundance because it is inexpensive and relatively easy to use is bee bowls or pan traps (Cane et al.2000, Leong and Thorp 1999, Wilson et al. 2008). The use of pan traps involves setting out bowls filled with water mixed with dish soap. To simulate the flower colors most often visited by bees the pan traps are painted fluorescent blue and yellow, white pans are left untreated. Bowls are placed along transects or clumped in a web design.

The use of pan-traps has been incorporated into a standardized method for bee sampling. The Bee Inventory Plot was the result of a collaborative effort put forth to standardized methods for sampling bee populations (BI Plot, http://online.sfsu.edu/beeplot). In 2003, a group of bee researchers and pollination biologists met with the agenda to establish formalized methods for sampling bee communities in order to compile information on geographic patterns of bee diversity. Among the goals of the contributors was to establish a simple sampling protocol that could be used by researchers varying in experience and resources. The use of bee bowl monitoring techniques and the establishment of the bee inventory plot was the primary method developed by the contributors.

As many have adopted pan-trapping or bee bowls as the primary technique for sampling bees, there has been debate regarding the extent to which this technique, when used exclusively, samples the entire bee community. Westphal et al. (2008) tested six sampling methods in agricultural and semi-natural habitats and concluded that pan-traps were the best suited for inexpensive and unbiased sampling, in addition, they are easy to use for researchers with varying levels of entomological experience. However, others have questioned the efficacy of pan-traps for capturing an acceptable representation of the entire bee community and caution against using this method as a sole sampling technique. Leong and Thorp (1999), tested the use of pan traps to sample a floral community dominated by a floral host, *Limnanthes douglasii rosea*, visited primarily by an oligolectic bee species, *Andrena (Hesperandrena) limnanthis*. The authors concluded that color significantly influenced the numbers captured of the oligolege A.*limnanthis*, as well as other specialist and generalist bee species collected in the pan traps thereby biasing samples, particularly in communities with a higher proportion of oligolectic bees. Wilson et al. (2008) state that pan traps show a strong generic bias, attracting 85% of the Halictinae genera (e.g. *Agapostemon*, *Halictus*, *Lasioglossum*) while neglecting to attract *Bombus* or many species in the family Colletidae. The authors conclude that pan-trapping must be used in conjunction with aerial netting to accurately sample bee communities.

This study sampled habitats in the Central Valley of California. Diversity and abundance data were collected for bee communities at 10 sites in three different regions. Pan-trapping and aerial netting were conducted concurrently to facilitate comparison of the techniques with regards to their efficacy in sampling the bee communities. It was hypothesized that using one technique alone would not adequately sample the bee community necessitating a sampling approach that employs both bee bowls and netting.

## Methods

Bee communities were sampled grassland habitats in three regions of the Central Valley of California; Putah Creek, the Cosumnes River Preserve, and the San Joaquin National Wildlife Refuge in 2005 and 2006. Comparisons of net and pan samples in this study are based on bee surveys that were conducted to assess bee diversity and abundance patterns in communities that varied with regards to surrounding land use patterns and floral diversity. The Central Valley of

California is represented by a variety of habitat types including tule marshes, riparian forest, open prairies, oak woodland, and chaparral (Barbour et al. 1993). However, extensive cultivation has transformed the region allowing for the introduction of many non-native plant species that now dominate the landscape. The sites selected for this study were located within 500m of a primary waterway or tributary in grassland habitat (Barbour et al. 1993).

Bees were surveyed at eleven sample sites throughout the years 2005 (n=8) and 2006 (n=10). In 2005, surveys were conducted across the months June through August. In 2006, surveys occurred across the months May through October. The duration of the sample season increased in 2006 because of an increase in funding and site availability. In 2005, there was heavy precipitation in May which led to flooding across all locations restricting access until June.

Five sample sites were located along Putah Creek, a tributary of the Yolo Bypass. Putah Creek has its headwaters in the Mayacamas Mountains and flows into Lake Berryessa, 11.7km west of Winters, CA. The first sample site, Interdam is located 5.2 km east of Lake Berryessa and the Monticello Dam (38°30.456'N, 122°2.622'). Other sampling locations occurred within the cities of Winters and Davis with the fifth site in the lower reach of Putah Creek located 5.0 km southeast of the City of Davis (38°31.106'N, 121°41.583'W). Two sample sites were selected within the Cosumnes River Preserve, 9.2 km west of Galt, CA. (38°16.192'N, 121°24.176'W). Bees were also surveyed at four sites ( 3 in 2005, and 3 in 2006; 1 site was substituted for an alternative site in 2006) within the San Joaquin National Wildlife Refuge situated 4.6 km north of Westley, CA (37°35.413'N, 121°11.522'W).

Each sample site was a $100m^2$ plot established outside the riparian forest. The location of the sample sites were determined based on site availability as dictated by land ownership and funding agency requirements. Sites located along Putah Creek were administered primarily by the City of Davis or the University of California. The Cosumnes River Preserve is owned by the Nature Conservancy and the San Joaquin National Wildlife Refuge is administered by the United States Fish and Wildlife Service. Although, the site locations were predetermined, the $100m^2$ plots within each site were selected by overlaying a grid with $100m^2$ divisions on an aerial photo of the site and assigning numbers to each square. A random number generator was then used to select the actual site in which transects were located.

At each site, bees were collected by aerial netting and pan traps concurrently. There was concern that concurrent sampling using both methods would reduce the capture of bees by either net or pan, however, this has not been observed in at least one other study and preliminary observation in this study by sampling with net and pan on different days determined concurrent sampling to be acceptable (Roulston et al. 2007). Netting was conducted by myself. Two 100m transects were established in each sample site in an X pattern that traversed the study plot. Netting was conducted for one hour in the morning, before 12:00pm, and one hour in the afternoon, after 12:00pm. Aerial netting occurred in three phases during each 2-hour period; transects were sampled, the perimeter of the plot was sampled, attractive plant patches were revisited. Transects were walked and netting was conducted opportunistically meaning all observed bees, whether on a floral host or in flight, were collected. This was done to ensure the collection of parasitic species and male bees that do not forage as frequently. All flowering plants within 1m of either side of the transect were sampled, spending no more than 5 minutes at each plant. The perimeter of the plot was sampled using the same sampling protocol (i.e. plants were sampled for 5-minute durations). Finally, patches of flowering plants were revisited and sampled for a longer duration to ensure complete sampling of the bee fauna present in the plot.

Pan-trapping was conducted between the hours of 0800 and 1600 hours on the same day as netting was conducted. A total of 21 pan traps were placed on each 100m transect in the plot. The pans were fluorescent yellow, fluorescent blue, and white, these were left untreated. The pans were placed in an alternating color pattern (e.g. y, b, w) and placed 5m apart. Each 6oz Solo© brand bowl was filled 2/3 full with water mixed with Dawn© liquid detergent. The bees were attracted to the bowls and drown upon contact with the water. Specimens were collected at the end of each sample day, rinsed with distilled water and mounted for identification. All bee specimens were identified to the finest taxonomic level possible with extensive assistance from R. W. Thorp (University of California, Davis). All specimens were identified to species or morphospecies. For those specimens lacking in taxonomic treatment, an identification to morphospecies was used, with the assistance of R. W. Thorp, on a portion of the collection. All taxonomic determinations were conducted using Michener (2000). Oliver and Beattie (1996), conducted a comparison of α and βdiversity of for ants, beetles, and spiders in forest fragments and determined that for ants and spiders, the use of morphospecies resulted in estimates of richness that varied little from estimates using species identifications. Although they did not conduct their study on bees, their research does support the use of morphospecies as a surrogate for species identifications in ecosystem inventories. Except for a synoptic collection, specimens are to be housed in the Bohart Museum of Entomology at the University of California, Davis.

In 2005, sampling occurred on 17 days. Netting was conducted for a total of 34 hours during this time, pan traps for a total collection time of 136 hours.

In 2006, sampling was conducted for a total of 34 days. Netting was conducted for 68 hours and pan traps were employed for a total of 328 hours during this sample season. Sampling effort was increased in 2006 because an increase in funding and site availability allowed for more intense sampling of the selected regions. The difference in sampling effort between 2005 and 2006 makes comparisons between the years difficult.

To estimate the species richness of the bee community sampled by bee bowls versus netting, the program Specrich was used; this program utilizes a jackknife estimator developed by Burnham and Overton (1979) to obtain species richness estimates. This online biological statistics program is available at: http:/www.mbr-pwrc.usgs.gov/software.html (Date of access: May 12, 2013). To compare the similarity of samples collected in bowls and by netting the Chao version of the Sørensen's similarity index, in which undetected species are taken into account, was calculated for each site per year (Chao et al. 2005). The index is calculated based on the number of species shared by each site, or in this case, collection method, and by the number of species that are unique to each site or method. The classic Sørensen's similarity index is based on presence/absence data; therefore, abundance has no effect on the index. Values close to 1 indicate greater similarity. A modified Sørensen's similarity index was used, also referred to as the Bray-Curtis dissimilarity index to determine the probability that individuals selected from two samples, i.e. those collected by net and pan, are species shared between the two collection methods. The Bray-Curtis dissimilarity index accounts for relative abundance of the species sampled and provides a value between 0 and 1 with values closer to 0 indicating greater similarity in species composition between the two methods (Magurran 2004). The Magurran (2004) modification to the Bray-Curtis dissimilarity index was used. The indices were calculated using the program EstimateS, version 9.0 (Colwell 2013)

## Results

In 2005, the estimated species richness for collections using aerial netting was 42 ±3.7 and for pan collections it was 50±5.1 with an overall estimated richness of 45±3.1 (Table 1). In 2006, the collection methods yielded similarly close species richness estimates to one another: net collections yielded 117±13.6 species and pan produced 122±12.4 species with total estimated richness equal to 206±24.8 (Table 1).

In 2005, a total of 40 unique species were identified across all sites for this study. Of the 40 species, 33 species (83%) were collected using both pan traps and netting techniques, 5 species (13%) were collected using only pan traps, and 2 species (4%) were collected by net alone (see Appendix A for species list separated by pan and net). Of the species sampled by one method alone, either pan or net, all were singletons or doubletons with the exception of *Megachile angelarum*, of which 7 individuals were collected by net.

In 2006, 104 species were collected across all sites with 45 species (43%) collected in both pans and net. Using aerial netting 24 unique species (23%) were collected and using pan-trapping 35 unique species (34%) of the 104 species were collected.

The bees that were collected over 5 times during 2005 were *Agapostemon texanus, Ceratina dallatorreana, Halictus tripartitus, Lasioglossum incompletum, Osmia nemoris,* and *Svastra obliqua.* The most common species were collected using pan-trapping and aerial netting. Abundance of the most commonly collected species was greater in the pan samples than the net; *A. texanus* (90% captured by pan), *C. dallatorreana* (91%), *H. tripartitus* (97%), *L. incompletum* (94%), and *O. nemoris* (92%). The exception was *S. obliqua* which was captured primarily by net (61% by net).

In 2006, the most common species were classified as those collected over 25 times throughout the year. The most common species were *Diadasia enavata, Halictus ligatus, Halictus tripartitus, Hylaeus mesillae, Lasioglossum incompletum,* and *Melissodes lupina.* These species were collected using both pan and net. The pan collected a greater abundance of *Halictus tripartitus* (96%), *Lasioglossum incompletum* (97%), and *Melissodes lupina* (86%) than net. This trend was not as evident in the following species; *Diadasia enavata* (56% pan) and *Halictus ligatus* (58% pan) were collected only slightly more in pan traps than by net; whereas, *Hylaeus mesillae* (61% net) was captured primarily by net.

The Sørensen's similarity values calculated using presence/absence data demonstrate shared species between pan and net collections and the Bray-Curtis dissimilarity index factors in relative abundance when determining similarity in species richness between techniques. In 2005, the Sørensen's Classic Similarity index indicates that the Dry Creek Confluence (0.518), South Fork Preserve (0.647), and San Joaquin Refuge 1 (0.571), had a moderate degree of species overlap between the pan and net collections at each site. There was little species overlap in collection methods for Russell Ranch (0.285), San Joaquin Refuge 2 (0.333) and San Joaquin Refuge 4 (0.296) (Table 2). The Bray-Curtis Dissimilarity index revealed a different pattern when relative abundance was factored into dissimilarity measurements. Across all sites the index revealed a high number of shared species between sampling techniques (Table 2). Table 2 indicates that for pan traps, a high percentage of the species sampled were unique to pan-trapping, yet this is not reflected in the Bray-Curtis Dissimilarity index. Many of the species sampled in the pans and by net were singletons or doubletons which means they are weighted less in the index based on abundance.

In 2006, the Sørensen's Similarity index again revealed only a moderate level of similarity between techniques with the highest values occurring for Cosumnes Preserve 1 (0.595), Cosumnes Preserve (0.549), Restoria (0.484), and Russell Ranch (0.489) (Table 3). The Bray-Curtis Dissimilarity index calculated for pan and net collections at each site returned low values for all sites indicating that when bee species relative abundance was factored into the index, the techniques were similar with regards to shared species. Similar to 2005, the pan trap collected a high percentage of unique species but returned low dissimilarity index values. This can be attributed to the high number of singleton and doubleton species represented in the pan collections.

## Discussion

Several findings resulting from the comparison of pan trapping and aerial netting can be used to guide the design of future bee sampling protocols. The 2006 data are used to discuss the findings because they included a larger sample and are therefore more robust than the 2005 data for illustrating patterns of interest. Sampling for three or more consecutive years is desirable but was not feasible for this study (Williams et al. 2001). An initial finding in this study was that pan traps and nets sampled similar portions of the estimated species richness in the bee communities when considered across all study sites. Estimated species richness values indicated that pan traps alone would sample 59% of the bee community compared to net collections which would account for 57% of the estimated species richness. This finding indicates that using either technique alone would miss ≥ 40% of the species estimated to be present in the bee community.

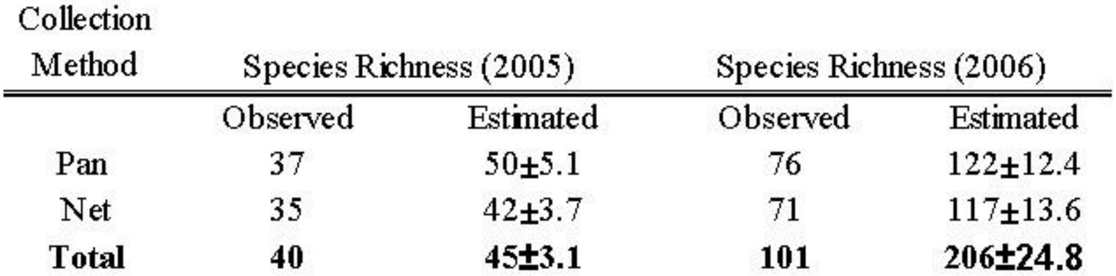
In this study, pan traps and net collections had complementarity that resulted in sampling a greater percentage of the bee community than estimated. Pans found 75% of the total observed species and nets sampled 69% of the total observed species. Estimated species richness from pans was 59% of the total species richness and estimated species richness from net was 57% of the total estimated species richness. In conclusion, this study indicated that using either technique alone would have missed ≥ 31% of the species present in the communities sampled rather than the estimated 40%.

There were some biases inherent in the pan and net sampling. In 2005 and 2006, bees from the family Halictidae were sampled in both pan and net but at much higher abundance in the pan traps. *Halictus tripartitus* and *Lasioglossum incompletum* were found in pan traps over 90% of the time for both species and rarely in net collections. This is similar to findings by Roulston et al. (2007) in which 1ha plots in open fields were sampled revealing that species in the genus *Lasioglossum* were more likely to be caught by pan than net. *Svastra obliqua* was one of the few bee species to be collected primarily by net in 2005. This species is a large robust bee that was often found foraging on yellow star thistle (*Centaurea solstitialis*), one of the few abundant floral hosts in the study sites. The prevalence of a suitable floral host, may explain why *Svastra obliqua* was captured by net more readily than by pan. In 2006, *Halictus tripartitus* and *Lasioglossum incompletum* were again heavily represented in pan collections along with *Melissodes lupina*. *Diadasia enavata* and *Halictus ligatus* were sampled evenly from pan and net, this may because these bee species are often found foraging on sunflower (*Helianthus annuus*) which was in greater abundance during the 2006 sample season. Evidence suggests that pan trap collection abundance and richness is inversely proportional to floral abundance and richness (Baum and Wallen 2011). *Hylaeus mesillae* was the only common species that was collected primarily by net in 2006. Wilson et al. (2008) found that *Colletes*, another genus in the family Colletidae, was also collected primarily by net. These findings indicate that need to use both collecting methods when sampling the bee community as there are biases inherent in both techniques.

The Bray-Curtis Dissimilarity Index accounted for the relative abundance of species when determining the similarity in species richness between pan and net collections. These values indicated that the probability was very high that if an individual was chosen from a net or bowl collection it will belong to a species shared by both set of samples. This was true for all sample sites. This indicates that the pan and nets sampled abundant species similarly. It is rare species that tended to be sampled by either pan or net alone. Bee communities often have a high percentage of singleton and doubleton species (Williams et al. 2001). This lends further support to the assertion that both pan and net techniques should be used in bee sampling protocols.

Pan trapping has been endorsed as an inexpensive and easily utilized method of bee sampling that eliminates sampler bias prompting many to use it as a sole means of sampling bee communities. This study demonstrates that there are biases inherent in the types of bees sampled by pan traps and nets and that a combined sampling approach is most effective at ensuring compete sampling of the bee fauna.

Table 1. Estimated species richness for net collections and pan collections in 2005 and 2006 across all sites.



| Collection Method | Species Richness (2005) | | Species Richness (2006) | |
|---|---|---|---|---|
| | Observed | Estimated | Observed | Estimated |
| Pan | 37 | 50±5.1 | 76 | 122±12.4 |
| Net | 35 | 42±3.7 | 71 | 117±13.6 |
| **Total** | **40** | **45±3.1** | **101** | **206±24.8** |

Table 2. 2005 similarity values for presence/absence data (Sørensen’s Classic) and abundance data (Bray-Curtis dissimilarity index) across sites. Cosumnes Preserve was sampled in 2005 and is therefore not present in this analysis.

| Site | Abundance | | Total Species | Total Species Collected (% Unique Spp.) | | Sørensen's Similarity Index | Bray-Curtis Dissimilarity Index |
|---|---|---|---|---|---|---|---|
| | pan | net | | pan | net | | |
| Dry Creek Confluence | 65 | 35 | 20 | 13 (6) | 14 (7) | 0.518 | 0.320 |
| Interdam | 94 | 13 | 21 | 18 (12) | 9 (3) | 0.444 | 0.112 |
| South Fork Preserve | 145 | 56 | 23 | 18 (7) | 16 (5) | 0.647 | 0.248 |
| Russell Ranch | 57 | 18 | 12 | 5 (3) | 9 (7) | 0.285 | 0.160 |
| San Joaquin Refuge 1 | 345 | 52 | 25 | 20 (10) | 15 (5) | 0.571 | 0.186 |
| San Joaquin Refuge 2 | 31 | 13 | 10 | 6 (4) | 6 (4) | 0.333 | 0.136 |
| San Joaquin Refuge 3 | 75 | 4 | 8 | 7 (5) | 3 (1) | 0.400 | 0.075 |
| San Joaquin Refuge 4 | 378 | 26 | 23 | 14 (10) | 13 (9) | 0.296 | 0.039 |

Table 3. 2006 similarity values for presence/absence data (Sørensen’s Classic) and abundance data (Bray-Curtis dissimilarity index) across sites.

| Site | Abundance | | Total Species | Total Species Collected (Unique Spp.) | | Sørensen's Similarity Index | Bray-Curtis Dissimilarity Index |
|---|---|---|---|---|---|---|---|
| | pan | net | | pan | net | | |
| Cosumnes Preserve 1 | 287 | 99 | 33 | 25 (11) | 22 (8) | 0.595 | 0.207 |
| Cosumnes Preserve 2 | 736 | 59 | 37 | 33 (19) | 18 (4) | 0.549 | 0.125 |
| San Joaquin Refuge 1 | 234 | 62 | 25 | 22 (16) | 9 (3) | 0.387 | 0.378 |
| San Joaquin Refuge 2 | 261 | 66 | 31 | 24 (19) | 12 (7) | 0.277 | 0.238 |
| San Joaquin Refuge 3 | 264 | 27 | 31 | 27 (20) | 11 (4) | 0.368 | 0.144 |
| Dry Creek Confluence | 212 | 79 | 29 | 15 (7) | 21 (11) | 0.388 | 0.164 |
| Interdam | 122 | 43 | 28 | 15 (11) | 22 (5) | 0.486 | 0.206 |
| South Fork Preserve | 381 | 50 | 45 | 35 (27) | 18 (10) | 0.301 | 0.111 |
| Restoria | 1194 | 131 | 50 | 42 (26) | 24 (8) | 0.484 | 0.125 |
| Russell Ranch | 679 | 130 | 37 | 26 (14) | 23 (11) | 0.489 | 0.155 |

# Chapter 2

# Wild bee species richness and abundance in communities of the Central Valley of California

## Introduction

Bee species richness and abundance values are parameters of interest in pollination studies because they provide a means by which to compare communities and they enable us to detect changes in populations, which is of particular importance in light of the putative global decline in pollinators. The primary question underlying most studies of bee species richness and abundance is what drives changes in these community parameters. This question increases in importance as anthropogenic disturbance becomes ever more present in natural areas.

Bees are closely linked to flowers because they are one of the few animals that depend entirely on angiosperms to meet their nutritional requirements; consequently, floral diversity and abundance have been cited as major determinants in structuring bee communities. Heithaus (1974) selected four different plant communities in Costa Rica monitoring pollinator visitation over a given period. He determined that floral abundance and diversity positively correlated with pollinator diversity and abundance. Banaszak (1996) also notes that there is a relationship between diversity of Apoidea and floral diversity. Potts et al. (2003) monitored bee populations in Israel and found a strong association between diversity in Andrenidae and Megachilidae and floral diversity. It was further determined that, in their study region, the availability of pollen was the factor correlated with species diversity in the families Megachilidae and Halictidae. Petanidou and Ellis (1996) documented a correlation between diversity in the family Andrenidae and diversity of annual flower species. Similarly, Gathmann et al. (1994) report that habitats with greater floral diversity support more species of bees in the family Megachilidae because of a corresponding increase in nesting availability. Despite the seemingly conclusive evidence linking bee and floral diversity and abundance contradictory studies cite examples in which a relationship is not evident.

A consensus on whether a positive correlation exists between flowering plant and bee species diversity and abundance has yet to be reached in light of contradictory findings. Brosi et al. (2007) monitored bee populations in a tropical countryside in Costa Rica and found no correlation between bee diversity and abundance and floral diversity and abundance. Klein et al. (2003) sampled bee communities in 24 agroforestry coffee fields in Indonesia and found inconsistent results. For solitary bee species there was a correlation between species abundance only and plant species richness of all species (not just those in flower), which is inconsistent with other findings linking bee species to flowering plant diversity.

The link between plants and bees is undeniable as plants are the primary food source for bees. Yet, unraveling the interrelationship between bees and plants is complicated by several factors such as variability in the quality of floral rewards and temporal variability in floral diversity and abundance. Using floral diversity and abundance as a proxy for resource availability can be misleading because the availability of pollen and nectar varies between plants within a floral patch and throughout a 24 hour cycle. Further, temporal variability in plant communities is often observed in regions experiencing unpredictable fluctuations in climate such that floral diversity and abundance vary from year to year. Univoltine bees rely on floral resources within one season to provision their nest; the following year's bee community reflects the resource availability from the previous year. Regions characterized by temporal variation in floral resources will show a decoupling between bee and plant species diversity and abundance. Perhaps, a tight relationship between the structure of plant and bee communities only occurs in stable habitats with a constant floral resource base. There are other factors as well that complicate the study of bee species richness and abundance.

Spatial and temporal variation in bee species diversity and abundance are dominant forces shaping bee community structure. Yet, this variation presents a formidable obstacle when measuring changes in bee community composition; a necessity for bee conservation. Temporal variation in the presence of specialist and generalist species across seasons is common (Minckley et al. 1994) and there is little overlap between bee fauna in adjacent locations. This is confounded by the high turnover of rare species (Williams et al. 2001). Surveys in disturbed habitats possess the least predictability (Roubik 2001). Herrera (1988) showed that only one-third of the bee species collected on *Lavandula latifolia* were documented in every year of a five-year study. A study sampled bee species from sites containing creosote, spaced 1100km apart and found that the sites shared 18% of the bee species collected. Further sampling from sites spaced 1-5km apart only resulted in sharing 39% of the bee species (Minckley et al. 1999). Another interesting trend is that in some habitats the bee species collected from plant species in the same habitat represented different subsets of the bee population. For example, collections from creosote and sunflower in the southwestern United States contained different bee species and different average number of species (Hurd and Linsley 1975; Hurd et al. 1980). Increased research effort needs to be directed towards understanding the role of temporal and spatial variatbility in bee populations. It is possible that in a considerable number of studies, diversity patterns attributed to environmental factors such as floral diversity are the result of temporal and spatial variation within populations. Expanding research efforts over space and time would begin to separate natural variation from environmental drivers of diversity patterns.

This study was conducted in California as it is considered a hotspot for biodiversity due in part to its diverse climate and vegetative zones. The California bee fauna is rich with an estimated 1,500 to 2,000 bee species (Michener 2000; Moldenke 1975). However, there is much to learn about California bee ecology, including ranges, nesting habits, and bee-plant interactions. One of the first publications documenting CA bee populations was a 1974 technical report prepared by Moldenke and Neff. Since the 1974 study, other studies have yielded species lists and bee-plant association data for a variety of habitat types, including urban areas (Kremen et al. 2002a, Frankie et al. 2005, Love 2010, Messenger and Griswold 2002). What we do know about California bee species is that they are responsible for pollinating many of the state's multitude of endemic plant species. Native bee species also provide valuable pollination services in agricultural settings (Kremen et al. 2002b). Therefore, understanding bee community dynamics and contributing to their conservation is of paramount importance.

The objectives of this portion of the project were 1) to provide baseline species diversity data for regions of the Central Valley of California, 2) to determine if bee species richness differed between study regions, and 3) to determine if a correlation exists between floral diversity and bee species richness and abundance. The first objective is descriptive in nature but an important contribution if future changes in the bee communities are to be detected. The second and third objectives are questions focused on determining first, whether regions that differ in characteristics such as land use, floral diversity, and other environmental characteristics differ in bee species richness, and second, whether floral diversity correlated to bee species richness. It was hypothesized that bee species richness is different between regions of the Central Valley and that a positive relationship exists between floral diversity and bee species richness.

## Methods

### *Study Sites*

The 10 study sites selected for sampling in the Central Valley were located in three main locations; Putah Creek in the Sacramento Valley (Yolo Co. and Solano Co.), the Cosumnes River Preserve in the Sacramento Valley (Sacramento Co.), and the San Joaquin National Wildlife Refuge in the San Joaquin Valley (San Joaquin Co.) (Figure 1) (for location coordinates see Appendix B). Table 1 lists the study sites by region.

Putah Creek extends from Lake Berryessa, 11.7km west of Winters, CA to the Yolo Bypass Wildlife Area 12.8km southeast of Davis, CA (Figure 2). The creek flows through the town of Winters, CA. Winters has a population of approximately 6,624 as of the 2010 population census. According to the US census the population density is 2,255 people per square mile. The town is characterized by single family homes in the main town and agriculture on the outskirts. Putah Creek also flows through Davis, CA, passing through the UC Davis campus. Davis has a population of 65,622 people as of the 2010 census and a population density of 6,615 people per square mile. The city is characterized by dense urban development in the core and is surrounded by agriculture on the perimeter.

The Intdm site was located 5.3km east of Lake Berryessa. This location was represented by semi-natural habitat consisting of a mixed riparian forest. The zone outside the mature riparian forest consisted of a variety of forbs and small shrubs, both native and non native to California, including yellow star thistle (*Centaurea solstitialis*), chicory (*Cichorium intybus*), and blackberry (*Rubus* sp.). One transect was established in the lower region of the floodplain and the second transect in the upper region of the site separated by a steep bank. The area surrounding this study site is oak woodland/grassland and is used for a combination of limited grazing and recreation with limited agricultural use.

The Dryck site was located within the town of Winters on the property of Dr. Michael Barbour of the University of California, Davis. This site was the location of a major project to redirect the flow of Putah Creek where it meets the confluence of Dry Creek. The project commenced in 2005 and was completed in 2006. The main goal of the project was to move the main channel of Putah Creek away from Putah Creek Road because severe undercutting of the bank was threatening the integrity of the road. The project required the removal of riparian vegetation along the banks of Putah Creek as well as massive redistribution of soil. The area surrounding this study site was used for almond orchards and included the use of pesticides and herbicides. There was also urban development within close proximity of this site.

The site referred to as Russr was located 10.9km W of Davis. Russell Ranch was the property of the University of California, Davis and was the site of a mitigation project that began implementation in 2002. Areas of the UC Davis campus were developed under the 2003 UC Davis Long Range Development Plan. As part of this development plan mitigation for loss of habitat occurred on the Putah Creek Reserve lands belonging to the campus. UC Davis chose to locate the mitigation on campus lands close to the actual campus so that it may be used for teaching and research on restored ecosystems. Portions of the reserve are set aside as habitat for

Swainson's hawk, burrowing owl, and Valley elderberry longhorn beetle (VELB) (putahcreek.ucdavis.edu, Feb 18, 2012). The restoration of Russell Ranch included several phases. First, the site was disked to overturn the soil and disrupt weedy seed banks followed by spraying with glyphosate herbicide. Next, seeding on the elderberry savanna, the site where the bee sampling occurred, with desirable grass species such as creeping wildrye (*Elymus triticoides*), blue wildrye (*Elymus glaucus*), Yolo slender wheatgrass (*Elymus trachycaulus*), and meadow barley (*Hordeum brachyantherum*) was performed. Prior to germination of the desirable seeds, herbicide was applied to weedy species followed by a combination of grazing, mowing, and/or burning to rid the area of weedy grass and broadleaf species. The main plantings in the restoration area were elderberry shrubs (*Sambucus* spp.). In the third year of the restoration forbs were planted including Spanish lotus (*Lotus purshianus*), gum plant (*Grindelia camporum*), yarrow (*Achillea millefolium*), tomcat clover (*Trifolium wildenovii*), bull clover (*Trifolium fucatum*), and arroyo (*Lupinus succulentis*). The goal of the mitigation was to support sustaining populations of the species of interest mentioned previously and to have a self-maintaining habitat without the return of abundant populations of weedy species.

The Rest site was located 3.9km SW of Davis and 17.6km E of Winters. This site is under active management by the City of Davis. It was regularly mowed to keep down the spread of yellow star thistle (*Centaurea solstitialis*) and has been planted with valley oak (*Quercus lobata*) seedlings. The angiosperms found in this area included gumplant (*Grindelia camporum*), Spanish lotus (*Lotus purshianus*), and sweet clover (*Melilotus alba*) among others.

The SFrkPs site was located 5km SE of Davis. This site was actively restored in 1994 by US Army Corps of Engineers. The purpose of the restoration was to restore the riparian habitat as well as the oak woodland, and native grassland. The site is now used for the benefit of wildlife with limited recreational and agricultural use. The organisms targeted for preservation with this restoration plan were the Swainson's hawk and the valley elderberry longhorn beetle. The area surrounding the South Fork Preserve is agricultural with sunflower fields and urban development at low density.

The Cosumnes Preserve sites (CRP 1 and 2) were located 9.2km west of Galt, CA. The Cosumnes River is 80 miles long, originating from rain and snow melt in the Sierra Nevada mountains. It converges with the Mokelumne River and continues to flow into the Sacramento-San Joaquin Delta. The Cosumnes River plays an integral role in the biology of the Central Valley through which it flows because it is one of the last remaining unregulated rivers on the western slope of the Sierra Nevada. As a result, the river regularly overflows into adjacent floodplains contributing to the growth and maintenance of rich native vegetation which in turn supports diverse faunal communities. Currently, the preserve is home to more than 250 bird species, more than 40 fish species, and approximately 230 plant species (www.cosumnes.org).

The Cosumnes River Preserve was established in 1987 by The Nature Conservancy when they purchased a conservation easement of 85 acres with the goal of protecting valley oak riparian forest. The project grew with the purchase of an additional 1400 acres. In 1988, the Cosumnes River Project was joined by Ducks Unlimited and the U.S. Bureau of Land Management. The California Department of Fish and Game joined the project in 1990 with the purchase of additional oak woodland and seasonal sloughs. Also in the 1990s, the Sacramento County Department of Regional Parks and the California Department of Water Resources also became partners in the project. The overarching goal of the Cosumnes River Project is to protect the integrity of ecological systems on a watershed scale. The preserve has now grown to include more than 46,000 acres. The Cosumnes River Project was originally started with the goal of preserving valley oak woodland habitat but has now grown to encompass all major habitat types represented on the preserve (www.cosumnes.org).

The San Joaquin Refuge sites (SJR 1, 2, and 3) were located in San Joaquin County and were administered by the U.S. Fish and Wildlife Service. The refuge includes over 7,000 acres of riparian woodlands, wetlands, and grasslands. It is located where three rivers (San Joaquin, Tuolumne, Stanislaus) converge. The refuge was established in 1987 as required under the Endangered Species Act and the Migratory Bird Conservation Act. The refuge was the site of one of the largest restoration projects in the Central Valley of California. The restoration involved the planting of over 40,000 willows, cottonwoods, and oaks across 17,000 acres of floodplain (www.fws.gov). The restoration at the SJNWR was conducted by River Partners. The land was formerly used for a dryland grain ranch and other agriculture. Levees were constructed to move water from the San Joaquin into the fields. Other former uses of the refuge included farming of corn, oats, and alfalfa and some grazing (River Partners 2006).

### ***Sampling Methods***

The methods used for pan-trapping bees at all study sites were based on those outlined in the publication, "A standardized method for monitoring Bee Populations-The Bee Inventory (BI) Plot." The document, developed by a consortium of bee biologists in 2003, outlines techniques for establishing transects, preparing pan traps, and executing a sampling protocol. It is available online and, as of its original posting, had been implemented at over 100 sites across the United States and Canada (www.online.sfsu.edu/beeplot/). The primary goal of establishing the Bee Inventory Plot protocol was to promote the use of a standardized sampling method in studies sampling bee fauna thereby facilitating comparisons of bee diversity and abundance across data sets.

The pan traps used in my project were the same as those specified in the Bee Inventory protocol. The pan traps were 6oz Solo brand white bowls. I used 21 bowls for each transect, placed 5m apart. Three colors were used for the pan traps, fluorescent yellow, fluorescent blue, and white. The blue and yellow pans were painted with spray paint on the inside and top edges, the white bowls were left their natural color. Each pan trap was filled 2/3rd full with a solution made of 1tsp of blue Dawn liquid soap per 1 gallon of water. The bees were collected at the end of each day and stored in 95% ethanol.

I used aerial netting to supplement pan trap data, adding to diversity measurements and providing bee-plant host association information. The Bee Inventory (BI) Plot protocol includes specifications for netting including time requirements and sampling pattern. In accordance with the BI protocol I sampled alone for one hour in the morning before 12PM and 1 hour in the afternoon after 12:00PM. I moved throughout the entire 1ha plot not spending more than 5 minutes at any particular patch of plants. After moving throughout the plot I returned to patches that were exhibiting bee activity. While netting I focused on all bees including males, parasitic bees, and foraging females. Bees were collected while making contact with the reproductive parts of flowers, the plant species were identified either in the field or a specimen was collected for later identification. In 2005, 34 hours were spent netting over 17 days at study sites. In 2006, netting was conducted for 68 hours over the course of 34 days.

Bee specimens were curated by myself and labeled with the following information: state, county, latitude and longitude, elevation, site, date, floral host, collector. The specimens are currently stored in my personal collection; however, they will be donated to the Bohart Museum at the University of California, Davis and the Essig Museum at the University of California, Berkeley. Bee identification to the taxonomic level of species was conducted by myself and Dr. Robbin Thorp of the University of California, Davis. Identifications in which species names are provided were verified by Dr. Robbin Thorp. Specimens that could not be given a species identification with confidence were labeled as morphospecies. A morphospecies refers to specimens that are readily separable by morphological differences. The use of morphospecies in studies such as my own can be justified for two reasons; it allows researchers with limited resources and taxonomic experience to conduct diversity and abundance studies and it has been shown that the use of morphospecies can result in the same habitat rankings, based on diversity indices, as detailed taxonomic surveys (Oliver and Beattie 1996).

### *Analyses*

Bee biodiversity was compared between the Putah Creek sites, the Cosumnes sites, and the San Joaquin sites using a variety of diversity indices: the Simpson's Diversity Index, Gini-Simpson's Index, Inverse Simpson's Index, and the Shannon-Weiner Diversity Index. Multiple indices were calculated to provide a measure of accuracy. The Simpson's Diversity Index (D) is a measure of biodiversity in which small values indicate high diversity and high values indicate low diversity. The index measures whether two species taken from a population at random will be the same species. The more diverse the population the lower the chance the species will be the same. The Gini-Simpson's Index is the probability that two species taken at random from a population are different species. The Inverse Simpson's Index is the arithmetic mean of the average proportional abundance of species in a population. The Shannon-Weiner Diversity Index is a weighted geometric mean of the proportional abundances of species in a population.

A chi-square goodness of fit test was used to test for temporal variability between sample days at the different sites. This test was conducted using Excel. For the analysis of temporal variability, *Lasioglossum incompletum* was used because it was collected during all sample days at most of the study locations.

Correlation analyses using data from all sites combined were conducted for 2005 and 2006 separately. Analyses were conducted using the complete data set and using data subsets (net and pan). Both parametric (Pearson correlation) and nonparametric (Spearman's rho) were used to conduct the analyses.

## Results

### *Diversity Patterns*

Patterns in species diversity are presented to serve as a baseline for future comparisons of the Central Valley bee communities.

In 2005, a total of 1,427 bee specimens were collected from all sites combined. The 4 Putah Creek sites accounted for 35% (493 individuals) of the total number of bees collected in 2005, representing 15 genera and 35 species. A total of 934 individuals or 65% of specimens were collected from the San Joaquin Refuge in 2005 from 29 species (see Appendix C for 2005-2006 bee species list). The Cosumnes Preserve was not sampled in 2005, therefore, it is only included in the 2006 descriptions.

In 2006, a total of 5125 bees were collected from the Putah Creek, San Joaquin Refuge, and Cosumnes Preserve habitats. A total of 3030 bees, from 24 genera, and 81 species were sampled from the Putah Creek sites, accounting for 59% of the 2006 sample. The San Joaquin Refuge sites yielded fewer bees accounting for 18% (917 individuals) of the total bees from 18 genera and representing 48 species. The Cosumnes Preserve accounted for 23% (1178 individuals) from 19 genera and 47 species .

Species from the family Halictidae were the most abundant in the Putah Creek and San Joaquin sites in 2005. In Putah Creek (2005), *Halictus tripartitus* (n=141) and *Lasioglossum incompletum*(n=109) were the most abundant (Figure 3). In the San Joaquin Refuge sites (2005), the most abundant species was *Halictus tripartitus* (n=720) (Figure 4). The abundance of this species far exceeded that of any other species in the San Joaquin sites. The other 4 species that ranked high in relative abundance at the San Joaquin sites in 2005 were relatively low in abundance in comparison to *H. tripartitus*; for example, *Lasioglossum incompletum* was represented by 47 individuals and *Ceratina dallatorreana* by 30 individuals. It is important to note that Putah Creek and San Joaquin Refuge had the top three species in common indicating some degree of similarity in the composition of these two communities. Cosumnes was not sampled in 2005 and is therefore not included with the 2005 summary.

In 2006, the Putah Creek region was again dominated by *Halictus tripartitus* (n=1076) and *Lasioglossum incompletum* (n=1047)but the other top species were different from those sampled in 2005. *Agapostemon texanus* (n=154) was relatively abundant in 2006, as well as *Hylaeus mesillae* (n=71) and *Melissodes lupina* (n=73) (Figure 5). The San Joaquin Refuge again had species in common with Putah Creek; the top two most abundant species were *Diadasia enavata* (n=239) and *Lasioglossom incompletum* (n=271). The other top species were *Halictus tripartitus* (n=71), *Melissodes lupina* (n=44), and *Melissodes tepida* (n=51) (Figure 6). The Cosumnes Preserve, similar to the other two regions, was dominated by *Halictus tripartitus* (n=720) and *Lasioglossum incompletum* (n=47). *Diadasia enavata* (n=19) and *Halictus ligatus* (n=30) were also sampled from this region in higher numbers than other species (Figure 7).

These data were presented as a baseline from which to compare future community species composition data. Major shifts in species abundance data may be an indication of environmental shifts that are potentially affecting the bee communities. However, shifts in bee species abundance and species composition do vary temporally and we know little about long-term stability of bee populations. This highlights the need for baseline abundance and richness data such as these.

### ***Bee Biodiversity***

Biodiversity indices were used to determine if bee species richness differed between study regions (Putah Creek and the San Joaquin Refuge) in 2006. The Cosumnes Preserve was not used in the biodiversity analysis because it included only two study sites; a correlation analysis could only be applied to study regions with three or more study sites. It was hypothesized that since the study regions differ with regards to land use, floral diversity, and other factors that may affect bee communities that bee biodiversity would be different between study regions. If differences in biodiversity existed between regions then investigation into the drivers of variation in bee species richness could be explored.

Bee diversity was compared between Putah Creek and San Joaquin Refuge for 2005 and 2006. The Cosumnes Preserve was not included in the biodiversity comparisons as it only contained two sites. To calculate the biodiversity indices the sites for each region were used as data points; at least 3 sites were required to calculate a biodiversity index for a region.

Total bee species diversity and bee species diversity based on data subsets (pan and net) were used to compare locations (Table 2). For 2005, from the pan data there was a difference in diversity between the Putah Creek and the San Joaquin sites (p=0.002, 0.010, 0.013), with Putah Creek having higher species richness. The diversity indices also indicated a difference for the total set of data in 2005 as well (p= 0.003, 0.017, 0.004). Similarly, in 2006, there was a difference in diversity of bees by pan (p= 0.014, 0.020, 0.023), net (p= 0.023, 0.015) and with both pan and net together (p= 0.033), again with Putah Creek showing higher species richness.

### *Bees and Flowers.*

Correlation analyses using data from all regions did not show significant correlations between total bee species richness, pan bee species richness, or net bee species richness and total plant diversity using a nonparametric Spearman's rho test (Table 3a), or a parametric Pearson correlation (Table 3b). In addition, the Pearson correlation showed no relationship between native or introduced plant species diversity and total bee species richness or the net/pan subset data (Table 3c).

## Discussion

The goals of this study were, 1) to provide baseline bee species richness and abundance data for regions in the Central Valley of California, 3) to determine if bee species richness differed between study regions as a basis for continued investigation into the drivers of bee community composition, and 4) to determine if there was a correlation between floral diversity and bee species richness and abundance.

### *Bee Biodiversity*

In 2005 and 2006, Putah Creek had higher bee species richness than the San Joaquin region. Cosumnes Preserve was not included in the biodiversity comparisons as it was not statistically feasible. The data indicated that bee species richness was higher in Putah Creek regardless of whether pan bee species or net bee species richness were assessed together or separate.

Evaluation of trends in bee biodiversity is complicated by the fact that we lack a unified working definition of this concept. Biodiversity can refer to diversity of ecosystems, habitats, communities, species, and even genes (Yoccoz et al. 2001). Noss (1983) classifies diversity as alpha (number of species within a habitat), beta (number of species between habitats), or gamma (number of species within a large geographic area). He states that most diversity measurements refer to alpha diversity or simple species counts within a community. Other biodiversity indices, such as Shannon-Weiner or Simpson's, utilize weighted sums of the relative abundances of species. It has been proposed that biodiversity indices should account for parameters such as economic value, ecosystem value, and taxonomic distinctness (Yoccoz et al. 2001). Some object to the use of biodiversity measurements as a means of attributing value to species or for modeling biological processes and prefer they be used primarily as empirical measures of change over time (Buckland et al. 2005). Given the multitude of opinions on the definition of biodiversity it is necessary to clearly define the goals of a study a priori so that the appropriate experimental design can be drafted to measure parameters of interest. Regardless, the biodiversity results in this study can be loosely interpreted to guide future work in this area.

An ecosystem is an open system that exchanges nutrients, energy, and, most importantly, species with other systems. In heterogenous environments it is beneficial to evaluate the ecosystem from a landscape perspective—a mosaic of interconnected ecosystems with different ecological characteristics. The importance of the landscape concept to the measurement of population diversity is the acknowledgement that ecosystems interact thereby generating edge effects (Noss 1983). An edge is defined as part of the habitat at which different plant communities meet or where successional stages come together. Along an edge animals from each type of vegetative community mix, thereby increasing alpha diversity. The concept of habitat ‘edges’ has long been important to wildlife managers as a method to increase local species diversity (Noss 1983). In the Putah Creek habitats sampled in this project the edge habitats likely brought together bee populations differing in species diversity based on their utilization of urban, agricultural, or semi-natural/floodplain habitat. This may have accounted for higher species diversity values for these sites.

Although, human land use may be associated with changes in bee biodiversity and other population parameters, the nature of the relationships are still poorly understood. Indices and measurements that treat each species as interchangeable units cannot capture shifts in species composition; which is necessary for evaluating ecological processes. As well, bee populations have inherent spatial and temporal variability that must be considered when trying to assess biodiversity in this group.

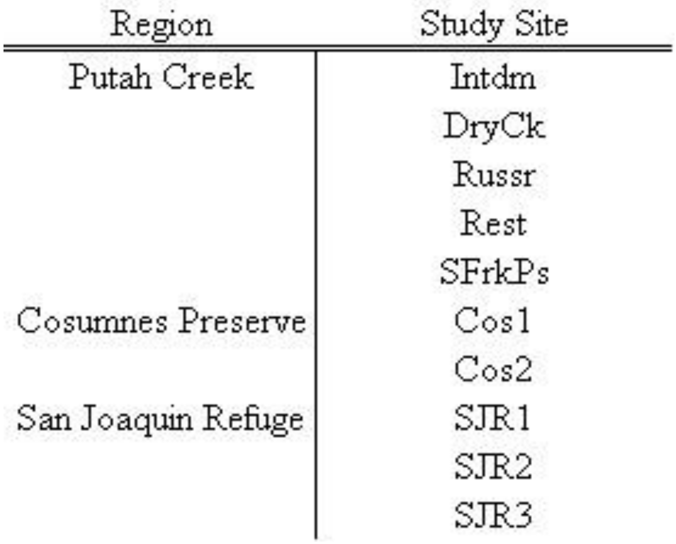
### ***Floral Diversity and Bee Species Richness***

Floral diversity was not correlated with bee species diversity or abundance. All sites were analyzed together. Total plant diversity as well as native plant species and introduced plants were correlated with bee species richness, all failed to show significant correlations. Bee species richness was evaluated with collections from both pan and net and with pan and net separately, again correlations with floral diversity were not apparent.

Other studies such as Brosi et al. (2007) similarly found that bee species richness in a Costa Rican agricultural region did not correlate with floral diversity. It has been proposed that bee species richness may be related to floral diversity from the year prior as it is the year that served as provisions for adults in the present community (Potts et al. 2003). It is also possible that nesting resources have an equal effect on bee species richness making detection of the relationship between flowers and bee diversity difficult. Further work is needed before one can conclusively determine whether floral diversity structures bee communities in this region, this is particularly true in light of temporal and spatial variability in bee populations.

The need to understand the effects of human land use on bee populations is critically important as the human population continues to grow and natural and semi-natural areas decrease. We are facing a global decline in pollinators brought on by habitat fragmentation and loss, pesticide use, and other factors. We do not know what may happen in the face of global warming as habitat ranges begin to shift and plant communities are altered. The better we understand the drivers of bee biodiversity the more prepared we will be to preserve, manage, or supplement the habitats upon which bees rely. This study evaluated associations between plant diversity and bee biodiversity. Temporal and spatial variation were present in the bee populations and require the extension of study duration to multiple seasons and years.

Table 1. 10 study sites sampled in 2005 and 2006. In 2005 the following sites were sampled Intdm, Dryck, Russr, SFrkPs, SJR1, SJR2, SJR3. In 2006, the Cosumnes sites (CRP1 and CRP2) were added to the project.



| Region | Study Site |
|---|---|
| Putah Creek | Intdm |
| | DryCk |
| | Russr |
| | Rest |
| | SFrkPs |
| Cosumnes Preserve | Cos1 |
| | Cos2 |
| San Joaquin Refuge | SJR1 |
| | SJR2 |
| | SJR3 |

Figure 1.  Map of study site locations in the Central Valley of California.

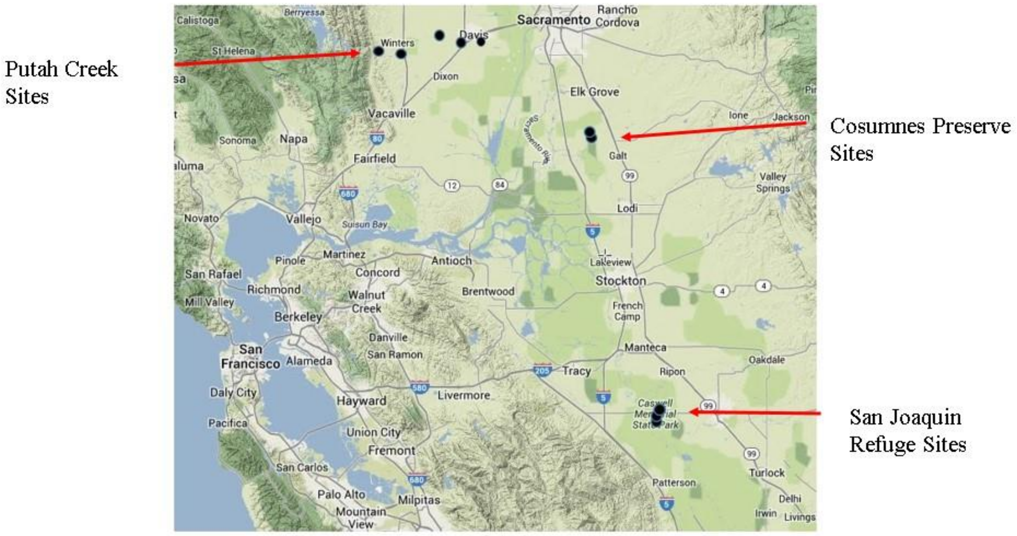


Figure 2.  The location of the 5 study sites along Putah Creek.

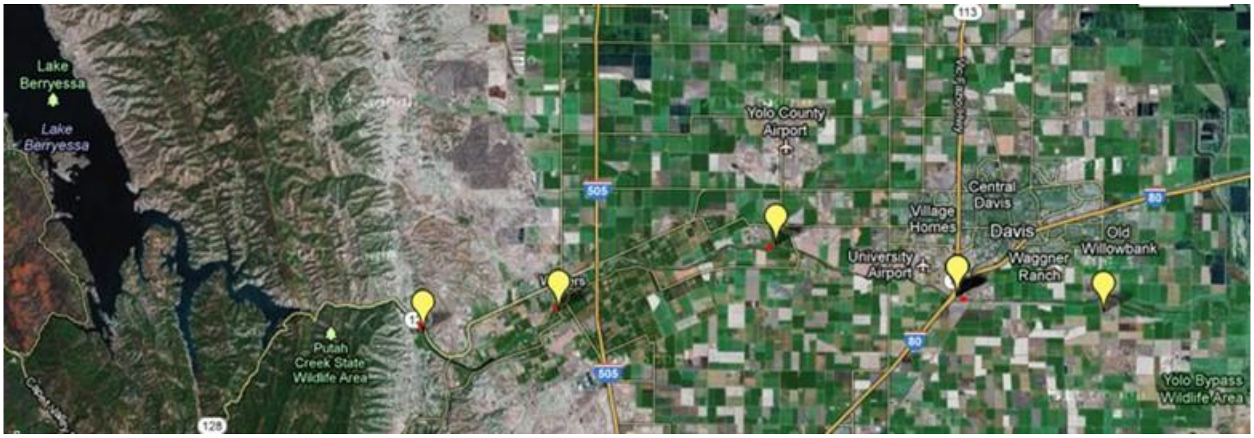


Figure 3. Relative abundance of the top 6 most abundant species in the Putah Creek sites in 2005.

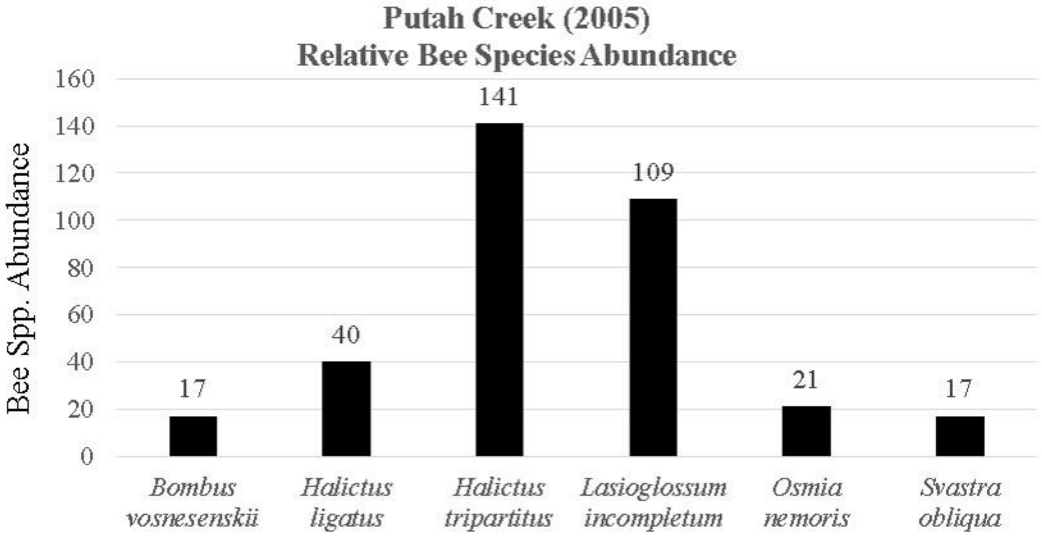


Figure 4. Relative abundance of the 5 most abundant species sampled at the San Joaquin sites in 2005.

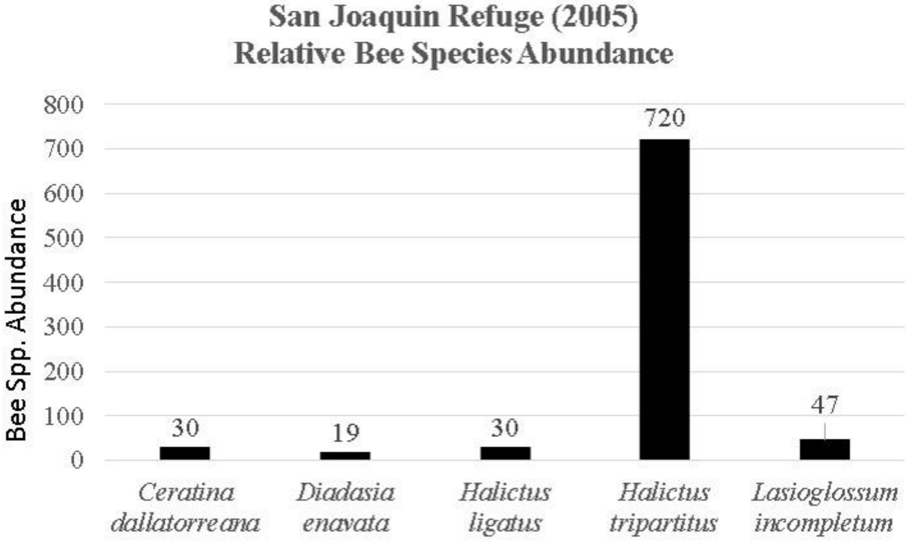


Figure 5. Relative bee species abundance for the 5 most abundant bee species at the Putah Creek sites (2006).

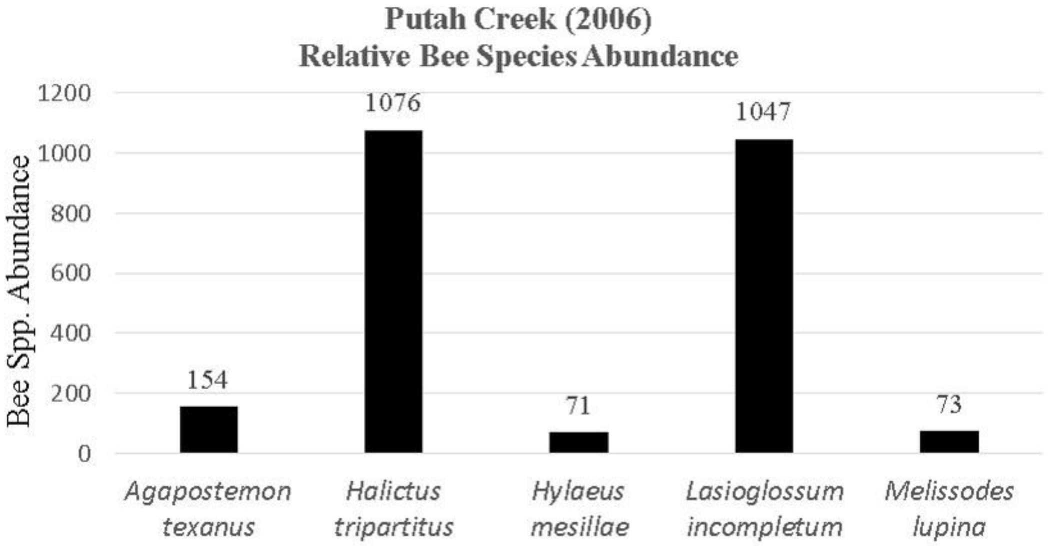


Figure 6. Relative bee species abundance for the 5 most abundant species sampled at the San Joaquin Refuge sites in 2006.

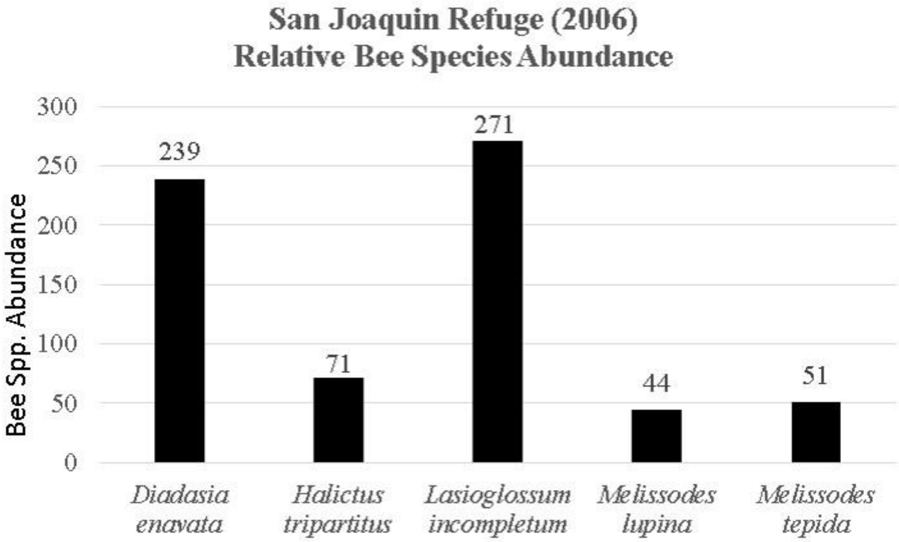


Figure 7. Relative bee species abundance for the 5 most abundant species sampled at the Cosumnes Preserve sites in 2006.

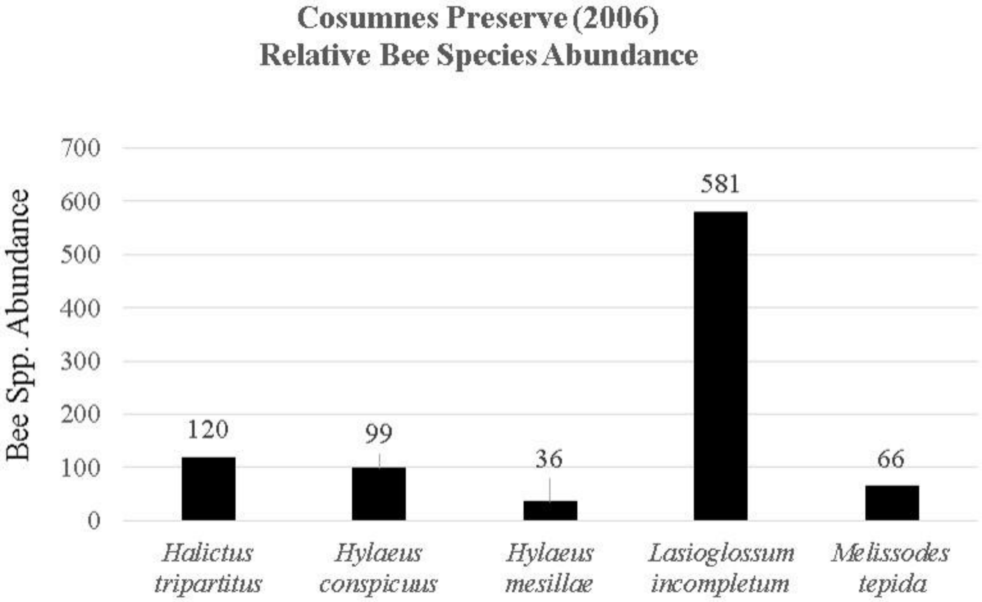
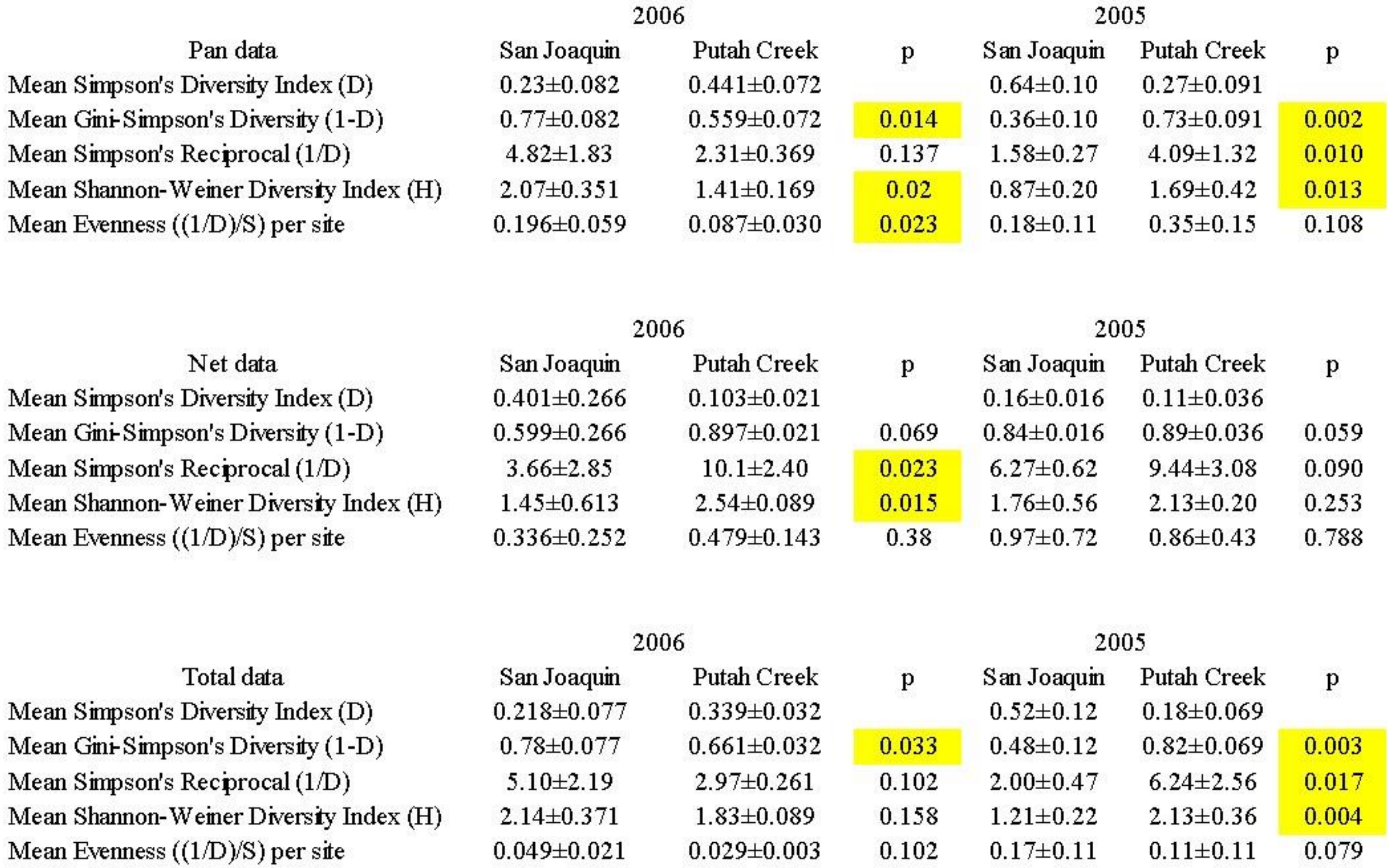


Table 2. Diversity indices for all sites (2005-2006). Data is presented for pan traps, netting, and total. Yellow bolding indicates significant results.



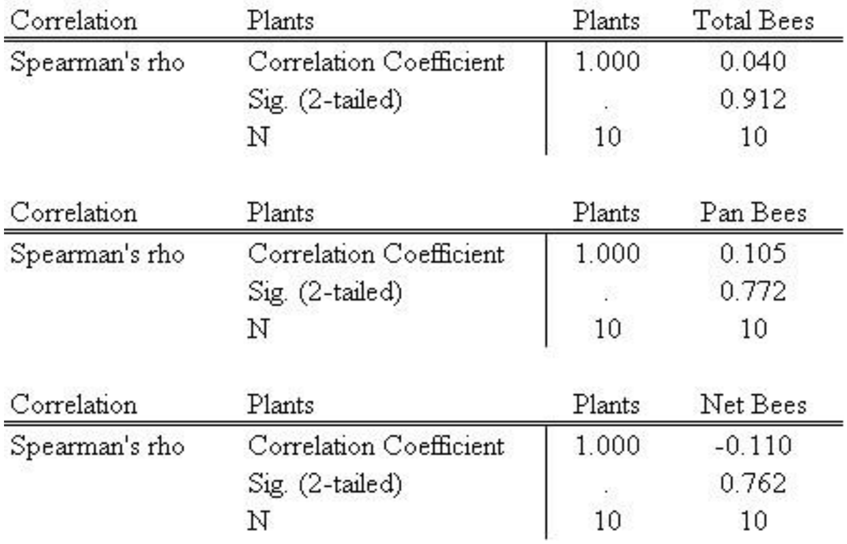
| | 2006 | | | 2005 | | |
|---|---|---|---|---|---|---|
| Pan data | San Joaquin | Putah Creek | p | San Joaquin | Putah Creek | p |
| Mean Simpson's Diversity Index (D) | 0.23±0.082 | 0.441±0.072 | | 0.64±0.10 | 0.27±0.091 | |
| Mean Gini-Simpson's Diversity (1-D) | 0.77±0.082 | 0.559±0.072 | 0.014 | 0.36±0.10 | 0.73±0.091 | 0.002 |
| Mean Simpson's Reciprocal (1/D) | 4.82±1.83 | 2.31±0.369 | 0.137 | 1.58±0.27 | 4.09±1.32 | 0.010 |
| Mean Shannon-Weiner Diversity Index (H) | 2.07±0.351 | 1.41±0.169 | 0.02 | 0.87±0.20 | 1.69±0.42 | 0.013 |
| Mean Evenness ((1/D)/S) per site | 0.196±0.059 | 0.087±0.030 | 0.023 | 0.18±0.11 | 0.35±0.15 | 0.108 |

| | 2006 | | | 2005 | | |
|---|---|---|---|---|---|---|
| Net data | San Joaquin | Putah Creek | p | San Joaquin | Putah Creek | p |
| Mean Simpson's Diversity Index (D) | 0.401±0.266 | 0.103±0.021 | | 0.16±0.016 | 0.11±0.036 | |
| Mean Gini-Simpson's Diversity (1-D) | 0.599±0.266 | 0.897±0.021 | 0.069 | 0.84±0.016 | 0.89±0.036 | 0.059 |
| Mean Simpson's Reciprocal (1/D) | 3.66±2.85 | 10.1±2.40 | 0.023 | 6.27±0.62 | 9.44±3.08 | 0.090 |
| Mean Shannon-Weiner Diversity Index (H) | 1.45±0.613 | 2.54±0.089 | 0.015 | 1.76±0.56 | 2.13±0.20 | 0.253 |
| Mean Evenness ((1/D)/S) per site | 0.336±0.252 | 0.479±0.143 | 0.38 | 0.97±0.72 | 0.86±0.43 | 0.788 |

| | 2006 | | | 2005 | | |
|---|---|---|---|---|---|---|
| Total data | San Joaquin | Putah Creek | p | San Joaquin | Putah Creek | p |
| Mean Simpson's Diversity Index (D) | 0.218±0.077 | 0.339±0.032 | | 0.52±0.12 | 0.18±0.069 | |
| Mean Gini-Simpson's Diversity (1-D) | 0.78±0.077 | 0.661±0.032 | 0.033 | 0.48±0.12 | 0.82±0.069 | 0.003 |
| Mean Simpson's Reciprocal (1/D) | 5.10±2.19 | 2.97±0.261 | 0.102 | 2.00±0.47 | 6.24±2.56 | 0.017 |
| Mean Shannon-Weiner Diversity Index (H) | 2.14±0.371 | 1.83±0.089 | 0.158 | 1.21±0.22 | 2.13±0.36 | 0.004 |
| Mean Evenness ((1/D)/S) per site | 0.049±0.021 | 0.029±0.003 | 0.102 | 0.17±0.11 | 0.11±0.11 | 0.079 |

Table 3. Correlation analysis of total, native, and introduced plant diversity and total, net and pan bee species richness. a) Nonparametric correlation analyses using Spearman’s rho. Plant species richness is correlated with total bee species richness, bee species richness collected by pan, and bee species richness collected by net.

a)

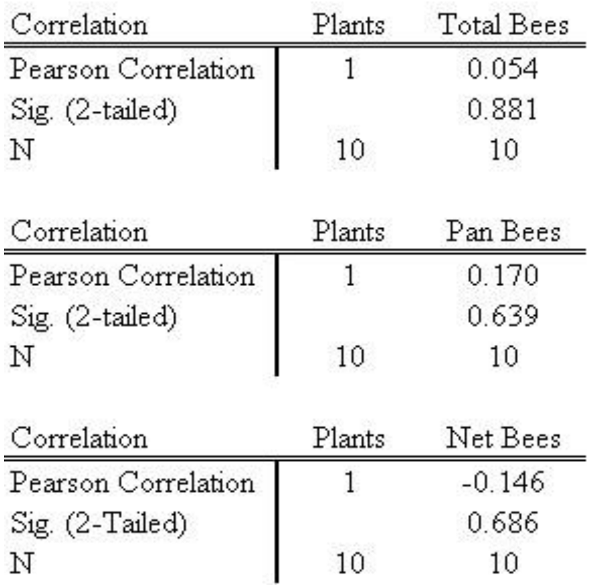


| Correlation | Plants | Plants | Total Bees |
|---|---|---|---|
| Spearman's rho | Correlation Coefficient | 1.000 | 0.040 |
| | Sig. (2-tailed) | . | 0.912 |
| | N | 10 | 10 |

| Correlation | Plants | Plants | Pan Bees |
|---|---|---|---|
| Spearman's rho | Correlation Coefficient | 1.000 | 0.105 |
| | Sig. (2-tailed) | . | 0.772 |
| | N | 10 | 10 |

| Correlation | Plants | Plants | Net Bees |
|---|---|---|---|
| Spearman's rho | Correlation Coefficient | 1.000 | -0.110 |
| | Sig. (2-tailed) | . | 0.762 |
| | N | 10 | 10 |

Table 3. b) Parametric correlation analysis using Pearson correlation between total plant species richness and total bee species richness, bee species richness collected by pan, and bee species richness collected by net.



| Correlation | Plants | Total Bees |
|---|---|---|
| Pearson Correlation | 1 | 0.054 |
| Sig. (2-tailed) | | 0.881 |
| N | 10 | 10 |

| Correlation | Plants | Pan Bees |
|---|---|---|
| Pearson Correlation | 1 | 0.170 |
| Sig. (2-tailed) | | 0.639 |
| N | 10 | 10 |

| Correlation | Plants | Net Bees |
|---|---|---|
| Pearson Correlation | 1 | -0.146 |
| Sig. (2-Tailed) | | 0.686 |
| N | 10 | 10 |

Table 3. c) Parametric correlation analysis using Pearson’s correlation between native and introduced plant species and a) total bee species richness, b) bee species richness by pan traps, and c) bee species richness collected by net.

| Correlation | Native Plants | Total Bees |
|---|---|---|
| Pearson Correlation | 1 | -0.416 |
| Sig. (2-tailed) | | 0.232 |
| N | 10 | 10 |

| Correlation | Introduced Plants | Total Bees |
|---|---|---|
| Pearson Correlation | 1 | -0.068 |
| Sig. (2-tailed) | | 0.852 |
| N | 10 | 10 |

| Correlation | Native Plants | Pan Bees |
|---|---|---|
| Pearson Correlation | 1 | -0.094 |
| Sig. (2-tailed) | | 0.795 |
| N | 10 | 10 |

| Correlation | Introduced Plants | Pan Bees |
|---|---|---|
| Pearson Correlation | 1 | -0.134 |
| Sig. (2-tailed) | | 0.713 |
| N | 10 | 10 |

| Correlation | Native Plants | Net Bees |
|---|---|---|
| Pearson Correlation | 1 | -0.491 |
| Sig. (2-Tailed) | | 0.150 |
| N | 10 | 10 |

| Correlation | Introduced Plants | Net Bees |
|---|---|---|
| Pearson Correlation | 1 | 0.299 |
| Sig. (2-Tailed) | | 0.402 |
| N | 10 | 10 |

# Chapter 3

## The effects of land-use on bee communities in the Central Valley, California.

## Introduction

Pollination is one of the more important ecosystem services because it influences habitat integrity and human food supply. Animal pollinators are responsible for enabling sexual reproduction of approximately 90% of all angiosperms. Further, 70% of the world's most important crop species experience improved yield with cross pollination mediated through animal pollinators (124 crop species from 200 surveyed countries). It is estimated that 35% of the global food supply is dependent on pollination (Klein et al. 2007, Gallai et al. 2009, Garibaldi et al. 2011).

Many have expressed concern over a decline in pollinators, documented most thoroughly for the EU, and a subsequent reduction of the critical ecosystem service that they provide (Allen-Wardell et al. 1998, Beismeijer et al. 2006, Kearns et al. 1998, Potts et al. 2010). Insects are the primary pollinators of wild and agricultural plants and bees are a predominant taxa in this group because they depend entirely on pollen and nectar for energy and provisioning of larvae. A survey of records documenting bee and hoverfly populations over a period of time before and after 1980 in the UK and Netherlands determined that bee diversity declined in both countries with communities now disproportionately dominated by fewer species. Perhaps more importantly, species with narrow habitat requirements, such as oligolectic or long-tongued foragers showed greater declines (Beismeijer et al. 2006). Bumble bees (*Bombus*) are important pollinators of wild and cultivated plants. Cameron et al. (2011) recently reported a 96% reduction in the abundance of four North American bumble bee species, B. *occidentalis*, B. *pensylvanicus*, B. *affinis*, and B. *terricola* coinciding with a 23-87% reduction in their geographic ranges. The causes of the declines in North America were not definitively reached; however, they seemed to coincide with reduced genetic diversity and higher prevalence of the pathogen *Nosema bombi*. Regardless, there seems to be an emerging pattern in the U.S. and Europe of declining abundance and range of bumble bee populations. It has been proposed in Europe that a reduction in habitat availability combined with climatic shifts have been key factors in the population trends (Williams and Osborne 2009). Studies such as these are numerous. It is important to understand the drivers of pollinator declines, particularly for bees, whether on a local or global scale so that we may mitigate the effects whenever possible.

The drivers of pollinator population declines are numerous and thought to be synergistic; however they have yet to be clearly characterized owing to geographically sporadic and temporally limited studies (Potts et al. 2010). This has led to varied findings regarding the effects of land-use change and fragmentation on bee populations (Winfree et al. 2011). Studies documenting bee communities exposed to agricultural intensification and habitat loss suggest declines in species richness and abundance are correlated with increased land conversion (Aizen and Feinsinger 1994, Greenleaf and Kremen 2006, Klein et al. 2007, Kremen et al. 2002b, Potts et al. 2010). Whereas, other studies reported certain types of land conversion as neutral to beneficial for some bee species when certain conditions are met (Cane et al. 2006, Ricketts et al. 2008, Winfree et al. 2007).

Anthropogenic modification of the land is widespread accompanying a boom in human population growth. The growth in infrastructure and the conversion of natural lands to agriculture needed to support an ever-increasing human population has contributed to global land degradation and habitat loss.  It is estimated that humans have modified greater than 50% of the Earth's land surface and this is but one change, others include changes in composition of air and water, and loss of overall biodiversity (Hook and Martín-Duque 2012, Vitousek 1992).  Studies documenting a negative relationship between anthropogenic land change and bee species richness and abundance have largely focused on agriculture.  One such study, Kremen et al. (2002b), determined that the native bee community could provide pollination services comparable to those of managed honey bees.  However, in farms that were isolated from wildlands, there was a decline in bee abundance and diversity thought to be in response to a loss of floral and nesting resources critical for native bees.  Similarly, Greenleaf and Kremen (2006), monitored native bee populations responsible for pollination of tomato and discovered that *Bombus vosnesenskii* was present more often in farms proximate to natural habitats.

Anthropogenic land-use in non-agricultural settings has a similar effect on bee populations to that of agricultural intensification in that bee species richness and abundance can be reduced.  McIntyre and Hostetler (2001), measured wild bee species richness and abundance in four urban habitat types (xeriscaped residential yards, mesiscaped residential yards, urban desert-remnant parks, and natural desert parks).  The residential yards contained the lowest diversity and abundance of bees indicating a negative response to urban development.  Aizen and Feinsinger (1994), monitored bee visitation to two flowering trees in the subtropical dry forest of Argentina and consequently documented a decrease in species richness and frequency of visits of native bees as forest fragment size decreases.  Yet, not all responses to land conversion are negative.

A meta-analysis of studies evaluating the relationship between bee species richness, bee abundance, and human disturbance reported mixed responses in bee communities to land use intensification (Winfree et al. 2009).  Although species richness and abundance of wild bees were negatively correlated with human disturbance, this trend was most notable in habitats experiencing extreme habitat loss, in areas with modest loss, the effects were not significant (Winfree et al. 2009).  Similarly, solitary bees experience less deleterious effects of human disturbance than social bees, particularly in tropical ecosystems (Ricketts et al. 2008); yet, solitary bees are more sensitive in temperate grasslands (Steffan-Dewenter et al. 2006).  It is thought that the composition of the social bee groups in comparison to solitary bee species may play a role in community response to human disturbance (Winfree et al. 2009).  In a study sampling bee fauna in forested, agricultural, urban and suburban habitats results indicated that bee abundance and species richness decreased in the forested ecosystem with increased forest cover.  Further, bee abundance and species richness was greater in the agricultural, urban, and suburban sample sites than in the surrounding forested sites (Winfree et al. 2007).  Cane et al. (2006), sampled bees visiting *Larrea tridentata* at 59 habitat fragments of desert scrub in the Tucson, AZ basin.  Some species declined in abundance in small desert fragments whereas others increased.  The authors concluded that species-specific traits such as nesting and dietary preference influenced response to habitat fragmentation.

In this study, bee communities at 10 sites were sampled and species richness and abundance were recorded.  The proportions of urban, agricultural, and semi-natural land at each site were measured at a 500m, 1000m, and 1500m radius.  Based on much of the previous research, it was hypothesized that bee species richness and abundance would be lower in sites with higher proportions of urban and agricultural land in the surrounding matrix.

## Methods

### *Study Sites*

Sampling for the study occurred in 2005 and 2006 in the Central Valley, California. Ten study sites were sampled in 3 regions Putah Creek (Intdm, Dryck, Russr, Rest, SFrkPs), Cosumnes Preserve (Cos1, Cos2), and the San Joaquin Refuge (SJR1, SJR2, SJR3) (Figure 1). The Central Valley is a 60 mile wide by 400 mile long stretch through the center of California. It once contained tule marshes, riparian forests, grasslands, and vernal pools. Because of agriculture and urban development the Central Valley natural ecosystems have been greatly reduced and altered by land conversion and the introduction of invasive species. This region of California is responsible for supplying approximately one-quarter of the food consumed by Americans. Farms produce tomatoes, almonds, pistachios and alfalfa and are used for grazing. This is also one of the largest regions in the country for vineyards and wine production. Agriculture and development dominate the landscape of the Central Valley and characterize land-use in this region (Barbour et al. 1993).

The ten sites selected for this study were located in three regions of the Central Valley; the cities of Winters and Davis in Yolo and Solano Counties, Cosumnes River Preserve in Sacramento County, and the San Joaquin National Wildlife Refuge in Stanislaus County (Figure 1). All sites were located within 500m of a waterways and in grassland habitat outside the boundaries of riparian forests, in locations where they occurred.

The five study sites located near the cities of Winters and Davis were along Putah Creek. Each of these sites were actively managed in some manner either before or during sampling for this study. The control site (Intdm) was regularly mowed to prevent yellow star thistle (*Centaurea solstitialis*) from overtaking the landscape as this is a popular fishing location for local residents; this occurred during the 2006 sample season. The site managed by UC Davis as a long-term agricultural research station (Russr) underwent a prescribed burn and was planted with supplemental vegetation such as blue elderberry (*Sambucus mexicana*) and valley oak (*Quercus lobata*); this occurred in 2005. The site at the confluence of Dry Creek and Putah Creek (DryCrk) underwent a reconstruction project in which the flow of the Putah Creek main channel was redirected; this occurred in 2005. The site (Rest), was mowed to control the growth of the invasive yellow star thistle (*Centaurea solstitialis*); this occurred in 2005.

The study sites at the San Joaquin National Wildlife Refuge and the Cosumnes River Preserve were located within nature reserves. The San Joaquin National Wildlife Refuge was in various stages of a restoration conducted by River Partners; the stages were located in different parcels of land throughout the reserve. The study locations were located in 3 parcels; 1) restored in 2002, 2) restored in 2004, and 3) not yet restored. The restoration involved revegetation with plants such as gum weed (*Grindelia camporum*), California rose (*Rosa californica*) and coyote bush *(Baccharis pilularis*). The overriding goal of the River Partner's project was to restore habitat for the critically endangered riparian brush rabbit (*Sylvilagus bachmani riparius*). The Cosumnes River Preserve is managed by a consortium of organizations including The Nature Conservancy. The goal of the preserve is to maintain a variety of habitats in the riparian corridor that extends from the Cosumnes headwaters to the Delta. The preserve is mixed use in that is combines agricultural uses with preservation.

### ***Bee Sampling***

Two 100m transects were established at each study site. When possible, the transects intercepted forming an X. When this was not possible because of terrain, the transects were established parallel to one another, separated by 100m. Bees were sampled using bee bowls or pan traps following the protocol outlined in the the Bee Inventory Plot (http://online.sfsu.edu/beeplot/). Six-ounce Solo brand bowls were painted blue and yellow using fluorescent spray paint; white bowls were left untreated. Twenty-one bowls were placed on each transect spaced 5m apart. A color pattern was followed when placing the bowls such that each color was represented before the pattern repeated (e.g. white, yellow, blue; white, yellow, blue; …). Bowls were filled approximately to the ¾ mark with water combined with Dawn brand liquid soap. The soap disrupted the surface tension of the water, when a bee contacted the water/soap combination it quickly drowned. Bowls were placed on the ground, following each transect, between 7:00am-8:00am and retrieved between 1500 and 1600 hrs for a sampling duration of approximately 8-9 hours.

Netting was used to collect bees as they were foraging on floral resources. Floral hosts were recorded when bees were netted while collecting pollen and nectar. Netting was conducted for 2 hours during a sample day. One hour of netting was conducted before 12:00pm, usually between 9:00-10:00am. The second hour of netting was conducted after 12:00pm, usually occurring between 1200-1300hrs. In order to sample using this technique in an unbiased manner an established protocol was followed for every sample site. The perimeter of the study site was walked with no more than 5 minutes spent at any one resource. Following this, transects forming an X through the middle of the study site were walked while sampling at all floral hosts that occurred within 5 m of the transects. Finally any floral patches at which there were high numbers of foraging bees were revisited for 10 minute periods to ensure adequate sampling of bee diversity. All bees, with the exception of honey bees (*Apis mellifera*) were collected for identification to species and morphospecies by myself and Robbin Thorp, Professor, University of California, Davis.

### ***Land Use***

The land surrounding each site was quantified according to the proportions of urban, agricultural, and semi-natural land present at 3 distances from the center of the site. Urban land was classified as land with houses, businesses, landscaping associated with urban establishments, and roads. Agricultural land included any land with crops, orchards, fallow fields or tilled land and levee roads. Semi-natural land was any land that was not in use for a human designated purposes (i.e. agricultural or urban) and that contained native or non-native vegetation.

The land surrounding and including each study site was measured at a 500m radius, 1000m radius, and a 1500m radius from the center of the site. To measure land use, images of each study site were obtained using Google Earth Pro. A circle was delineated around the image at the proper radius. A grid with uniform squares was overlaid on the image. The number of squares in the grid representing each land use type (urban, agricultural, semi-natural) were then tallied and their proportions calculated (Figure 2).

### ***Analyses***

A generalized linear model was used to evaluate the effect of land use on total species diversity and average bee abundance at the study sites for the 2006 sample season alone. Generalized linear models use a function *F* to linearize the data while calculating the expected variance on the untransformed scale to enable correction for the distortions that linearization induces. The non-normal errors are grouped into the *exponential family*, including Poisson, binomial, gamma, and Gaussian distributions. In this analysis, the Poisson distribution was used with the log link function. The model is fit by iteratively reweighted least squares which overcomes the problem of changing variance upon data transformation (McCullagh and Nelder 1989). A generalized linear model was conducted in R to determine the effects of land use on total bee species richness. Total bee species richness was the response variable and urban and agricultural land use at 1500m were used as predictor variables with ‘Site’ as a random effect in the model.

Species composition at the study sites was compared using nonmetric multidimensional scaling. Dissimilarity coefficients for each pair of samples are summarized in a matrix and non-metric methods are then used to rank-order the pairs. The purpose of this technique is to reduce the number of dimensions needed to show the relationship between habitats and species. With presence/absence data the samples are placed such that those with more distance between them have fewer species in common (Prentice 1977). For this analysis the Bray-Curtis Dissimilarity Index was used and the model was conducted with 2 dimensions and 100 random iterations until 2 of the same stress solutions were reached. The ordination was performed using the (**vegan**) package in R.

## Results

A total of 6512 bees were collected representing 109 species for 2005 and 2006 (See Chapter 1, Appendix A for species list). In 2005, the most abundant genera between the sample months of June-August were *Halictus* representing 65% of the bees sampled and *Lasioglossum*, which comprised 12% of the sample. In 2006, between the sample months of May-Sept, *Halictus* (28%) and *Lasioglossum* (40%) were the dominant genera. *Lasioglossum* was dominated by one species, *Lasioglossum incompletum;* similarly, *Halictus* was largely comprised of the species *Halictus tripartitus*. Species rarity is a common occurrence in bee communities (Williams et al. 2001). Rare species are those that occur as singletons, i.e. represented by only one individual. The bee communities sampled had percentages of rare species that ranged from 24% to 59%.

### ***Land Use***

Table 1 lists the percentage of urban, agricultural, and semi-natural land at a 1500m radius surrounding each study site. In the Putah Creek Region, agricultural land was the predominant land type in the sites DryCk (4), Rest (5),Russr (6), and SFrkPs (10). The Intdm (1) site was dominated by semi-natural land at the 1500m radius. This was considered a control site for the Putah Creek region. In the Cosumnes River Preserve Region, site 1 was surrounded by approximately an even proportion of agricultural and semi-natural land at a 1500m radius. Site 2 in the Cosumnes River Preserve had an approximately 50% distribution each of semi-natural and agricultural land at the same radius. The three sites in the San Joaquin Natural Wildlife Refuge were surrounded entirely by semi-natural land.

To test whether there was a significant relationship between species richness and urban, agricultural, or seminatural land surrounding each study site a generalized linear model was used. The tests were conducted at the 1500m radius distance from the center of the study site. The response variable was total bee species richness, predictor variables were percentage of urban and agricultural land. The variable 'site' was included as a random effects variable. The percentage of agricultural land at the 1500m radius was significantly associated with bee species richness (p=0.014). The coefficient for percentage of agricultural land was 0.427.

The ordination conducted with non-metric multidimensional scaling was conducted with 2 dimensions which produced a stress value of 0.117. The Shepard plot is shown to provide a goodness of fit estimate (Figure 3). It plots the ordination distances against the original dissimilarities calculated by the Bray-Curtis. The $R^2$ value obtained from the Shepard plot is $R^2=0.986$.

The ordination produced several clusters; one main cluster of Putah Creek sites, SFrkPs (10), Rest (5), Russr (6), DryCk(4); one main cluster of Cosumnes Preserve sites, Cos2 (3), Cos1(2), and one main cluster of San Joaquin Refuge sites, SJR2 (8), SJR3 (9) (Figure 4). The clusters are based on how similar the species composition is between sites. Sites that are closer together share more species than sites located farther apart. Sites Intdm (1) and SJR 1 (7) have unique species assemblages, being located on the outer areas of the graph. Site Intdm (1) is located along Putah Creek, downstream from Lake Berryessa. There is remnant riparian forest at this site and semi-natural grassland. This site is unique from the other sites located along Putah Creek (DryCk 4, Rest 5, Russr 6, SFrkPrs 10) in that they were dominated by agricultural land in the surrounding matrix. Site SJR1 (7) is located in the San Joaquin National Wildlife Refuge. Its species assemblage differs from sites SJR2 (8) and SJR3 (9) because Site 7 was unique structurally; it was restored prior to the other sites and thus had a more well-developed forest and canopy. From a land use perspective, the Putah Creek sites were dominated by agricultural and urban land, the San Joaquin Refuge sites by seminatural land, and the Cosumnes Preserve by agricultural and seminatural land.

## Discussion

The objective of this study was to determine whether land-use in the landscape surrounding sampling sites had an effect on bee species richness or community composition. Based on other findings it was hypothesized that species richness would decrease with an increase in human disturbance in the form of agricultural intensification or urbanization. Analyses using generalized linear model indicated that bee species richness had a positive relationship with agricultural land-use. An ordination using non-metric multidimensional scaling did show an association between some species and certain sites yet trends based on natural history traits were difficult to identify.

Analyses revealed a positive relationship between agricultural land-use and bee species richness. A meta-analysis performed by Winfree et al. (2009) suggests that habitat loss is the primary factor affecting bee communities negatively and that factors relating to anthropogenic disturbance have mixed to neutral effects on bee communities. In some ecosystems, there is evidence that some forms of anthropogenic disturbance are not detrimental to pollinators and may even be advantageous (Winfree et al. 2007). The Putah Creek sites were heavily dominated by agricultural land-use and consequently were species rich. It is possible that the presence of weedy plant species in and surrounding the agricultural fields provided ample forage for bee species resulting in a species rich community. The abundance of such plant species may have been higher in agricultural setting compared to semi-natural and urban settings leading to greater species abundance as well.

The analyses indicated that there was no relationship between urban land use and bee species richness. A neutral response from the bee communities to land-use on a landscape scale is similar to results reported in other studies (Winfree et al. 2011). There are several factors that may have attributed to the neutral response, the first of which being the temporal and spatial variability that is inherent in bee populations. Williams et al. (2001), conducted a survey of published studies that evaluated bee communities from locations around the world to identify patterns of bee species richness and abundance. The authors identified two traits of bee faunas that are of particular relevance to this study; bee communities vary in richness and abundance in space and time, and are often rich in rare species. That bee communities often exhibit spatial and temporal variability can obscure the relationship between species richness and land-use. Minckley et al. (1999) sampled bee communities at creosote (*Larrea tridentata*) and found that even within a distance of 5km, communities shared less than 40% of their species. Williams et al. (2001), also reported similar temporal variability in abundance, concluding that abundance within species is particularly high within and among years. Frankie et al. (1993), monitored seven species in the genus *Centris* using wooden sampling units in Costa Rica. Although the overall abundance of the bee community did not change, there was significant fluctuation in individual species throughout the course of the 5-year study.

The 2006 data was evaluated for spatial variability as it was the more robust sampling year. Sites that were nearer in location and similar in landscape composition were compared. The Cosumnes River Preserve sites 2 and 3 were within 520m of one another; these sites had slightly less than 50% of their species in common. The San Joaquin National Wildlife Refuge sites were within 1.5km and also shared approximately 50% of the species found in each community. Similarly, abundance in the most common species fluctuated within and among years. *Lasioglossum incompletum* was the most abundant species in 2006. In 2006, the species was almost 3 times more abundant at some sites than it was in 2005. The variation in this data set could have made it difficult to detect patterns from land-use.

Species rarity is common in bee fauna making the detection of community level patterns in richness and abundance difficult. Williams et al. (2001), determined that many studies documenting bee fauna reported high proportions of singletons and doubletons. A high proportion of singletons and doubletons leads to high estimates of species richness but low species evenness. Michener (1979), discusses the rarity of species in most bee communities as well. Even with intensive sampling bee species rarity can still reach high levels and comprise a significant portion of the population (16-42%) (Timberlake, cited in Michener 1979). One interpretation of species rarity is that regardless of heavy sampling, a significant portion of the population remains undersampled. If bee communities are undersampled, what we perceive as differences in composition of communities may actually be differences in species evenness that because of undersampling are being misinterpreted. In this study, the bee fauna sampled at site 1 in the Cosumnes River Preserve contained 33 species, 15 of which were singletons or doubletons (45%). At the SFrkPrs, 62% of the bee fauna was represented by 1or 2 individuals. The differences between sites in species richness, may diminish, with further sampling of these sites.

A second reason that may lead to a neutral response to urban land use in this study is that the response of bees to land-use change may depend on the natural history traits of the bee species. Bee species vary in nesting preferences, phenologies, sociality, and floral specialization, all of which may influence how a species utilizes available habitat. Typically, nesting substrate and foraging resources are spatially disparate (Cane 2001). For example, ground nesting bees require exposed soil for nesting and patches of floral resources for foraging, often these do not occur in the same area. Bees are forced to traverse a patchwork of unsuitable habitat in order to access desired resources (Cane 2001). Therefore, assessments of anthropogenic effects on bee communities must take into account the patchy matrix that is likely being utilized.

There are several types of nesting preferences in bees that can affect how they utilize their habitat; most bees nest underground, some nest above ground in pre-existing cavities in deadwood or in stems in which they excavate tunnels (Cane 1991). Most studies documenting the effects of habitat change on native bees focus on losses of foraging resources; neglecting to factor in the effect of anthropogenic land-use on nesting habitat. Species specific differences in nesting biology could explain some of the variation and lack of a clear relationship between land-use and bee species richness. Aizen and Feinsinger (1994), provide an example of species specific response to land-use. In their Argentinian study of the genera *Dialictus* and *Augochlora*. The genus, *Augochlora*, composed of two subgenera, nest in rotting wood and were determined to be less abundant in small fragments and farmer’s fields than *Dialictus*, composed of ground-nesting species. It was reasoned that the farmer’s fields and small forest fragments contained fewer rotting logs to serve as nesting sites for *Augochlora*, leading to the decrease in abundance of this genus. To further support the concept that nesting requirements determine bee responses to landscape, Cane et al. (2006), sampled the bee fauna visiting *Larrea tridentata* in desert habitat fragments throughout the urban matrix in Tucson, AZ. A heterogenous response was documented for the 62 bee species visiting the floral host. While some ground-nesting specialists were less abundant in the older and smaller fragments, cavity-nesting species were more abundant in fragments within the urban matrix possible due to increased availability of nesting substrate.

In this study the ordination did show that different study site groups had different species assemblages. However, it was difficult to discern a trend in species distributions based on land-use. The Putah Creek sites 10, 5, 6, and 4 were characterized by agriculture and urban development and had a cluster of species around them on the ordination. However, the species were not clustered by a natural history trait such as nesting preference or socialization. It is likely that the sites with different species assemblages had different floral resources and that the species were responding to this resource in addition to proximity to nesting habitat. It seems that bee species response to land-use is complex and not easy to isolate to one factor.

This study asked the question, how does land-use effect bee species richness, abundance, and composition in bee communities of the Central Valley, California? Although a negative relationship was expected, the results for agricultural land-use were positive and for urban land-use, there was a neutral relationship. The proportions of urban and semi-natural land in the surrounding landscape did not seem to affect the bee communities sampled at 10 sites throughout the Central Valley. The duration of this study was 2 years, 2006 was used for the NMDS. Williams et al. (2001) recommend a study duration of 5 years in order to accurately assess the natural variability in the population. This study needed to be longer to assess temporal variability. In addition, an increase in sampling effort may have decreased the collection of rare species at each providing more accurate of species richness and community composition. There is a need to understand how land-use effects bee populations and whether it is one of the drivers of change in bee populations.  In the face of human population growth it is essential that we understand bee community response to anthropogenic change so that we may mitigate its effect on bees and the ecosystem service they provide.

Figure 1. Partial map of California Central Valley with approximate locations of study sites.

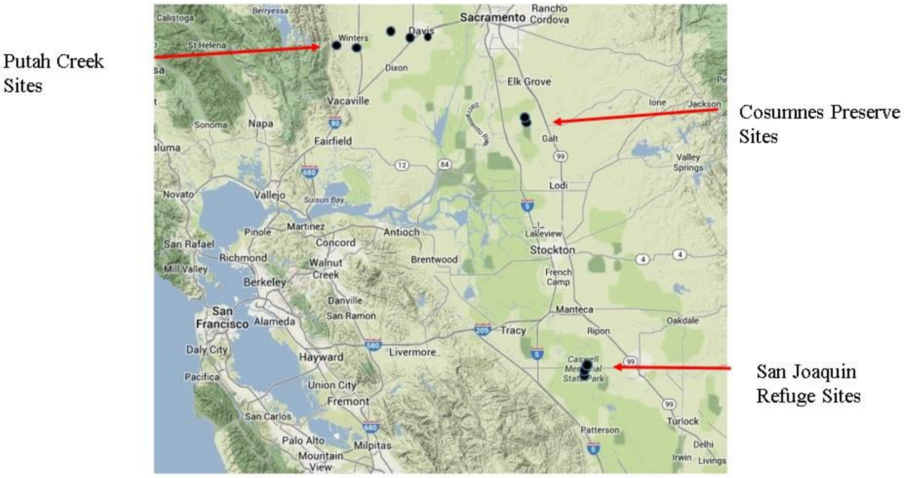


Figure 2. Study site with a grid overlaid on the photo to use in the quantification of land use as urban, agricultural, and semi-natural. The proportion of squares within the diameter of the circle representing each land use type are tallied to provide a proportion of each land type in the matrix surrounding the study site.

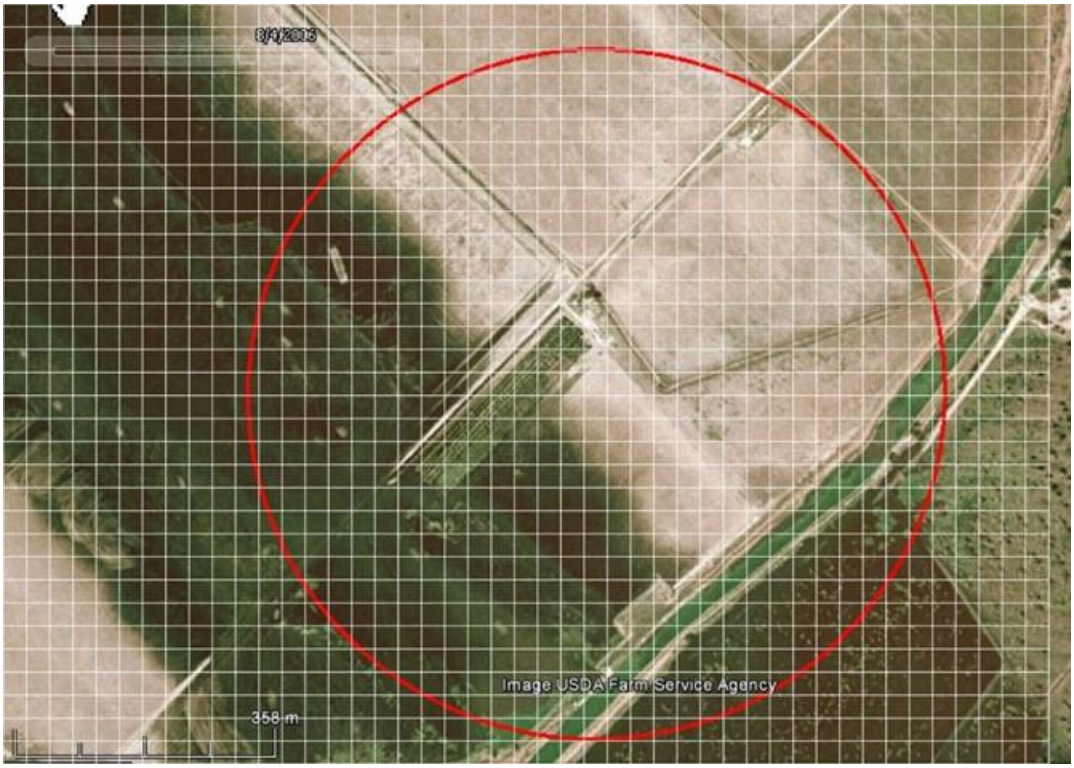
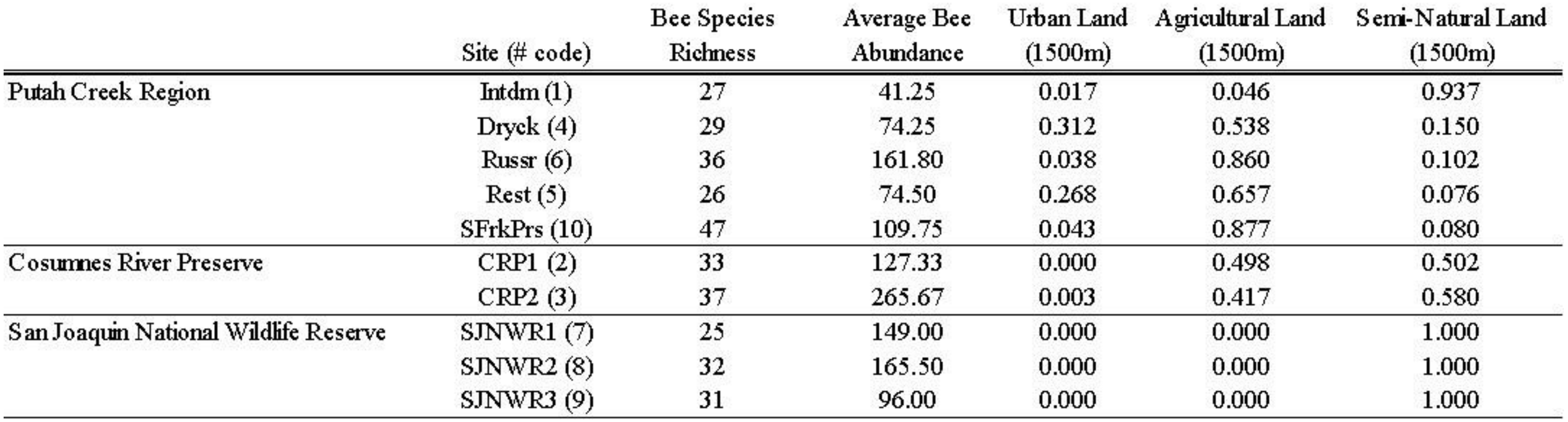


Table 1. Proportion of urban, agricultural, and semi-natural land surrounding study sites at a 1500m radius.



| | Site (# code) | Bee Species Richness | Average Bee Abundance | Urban Land (1500m) | Agricultural Land (1500m) | Semi-Natural Land (1500m) |
|---|---|---|---|---|---|---|
| Putah Creek Region | Intdm (1) | 27 | 41.25 | 0.017 | 0.046 | 0.937 |
| | Dryck (4) | 29 | 74.25 | 0.312 | 0.538 | 0.150 |
| | Russr (6) | 36 | 161.80 | 0.038 | 0.860 | 0.102 |
| | Rest (5) | 26 | 74.50 | 0.268 | 0.657 | 0.076 |
| | SFrkPrs (10) | 47 | 109.75 | 0.043 | 0.877 | 0.080 |
| Cosumnes River Preserve | CRP1 (2) | 33 | 127.33 | 0.000 | 0.498 | 0.502 |
| | CRP2 (3) | 37 | 265.67 | 0.003 | 0.417 | 0.580 |
| San Joaquin National Wildlife Reserve | SJNWR1 (7) | 25 | 149.00 | 0.000 | 0.000 | 1.000 |
| | SJNWR2 (8) | 32 | 165.50 | 0.000 | 0.000 | 1.000 |
| | SJNWR3 (9) | 31 | 96.00 | 0.000 | 0.000 | 1.000 |

Figure 3.  Shepard Plot of ordination distances against original dissimilarities for species and sites.

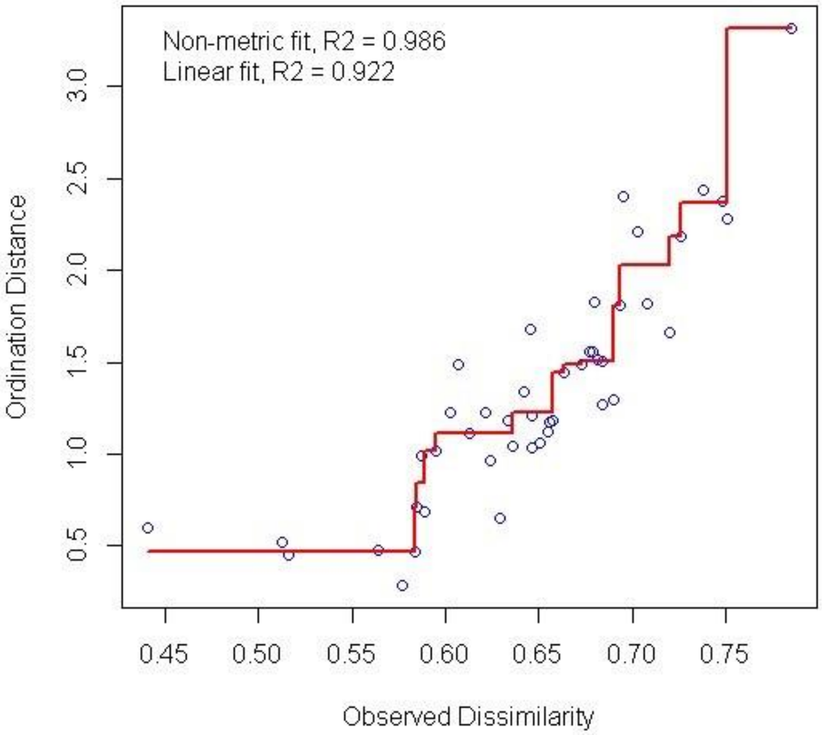
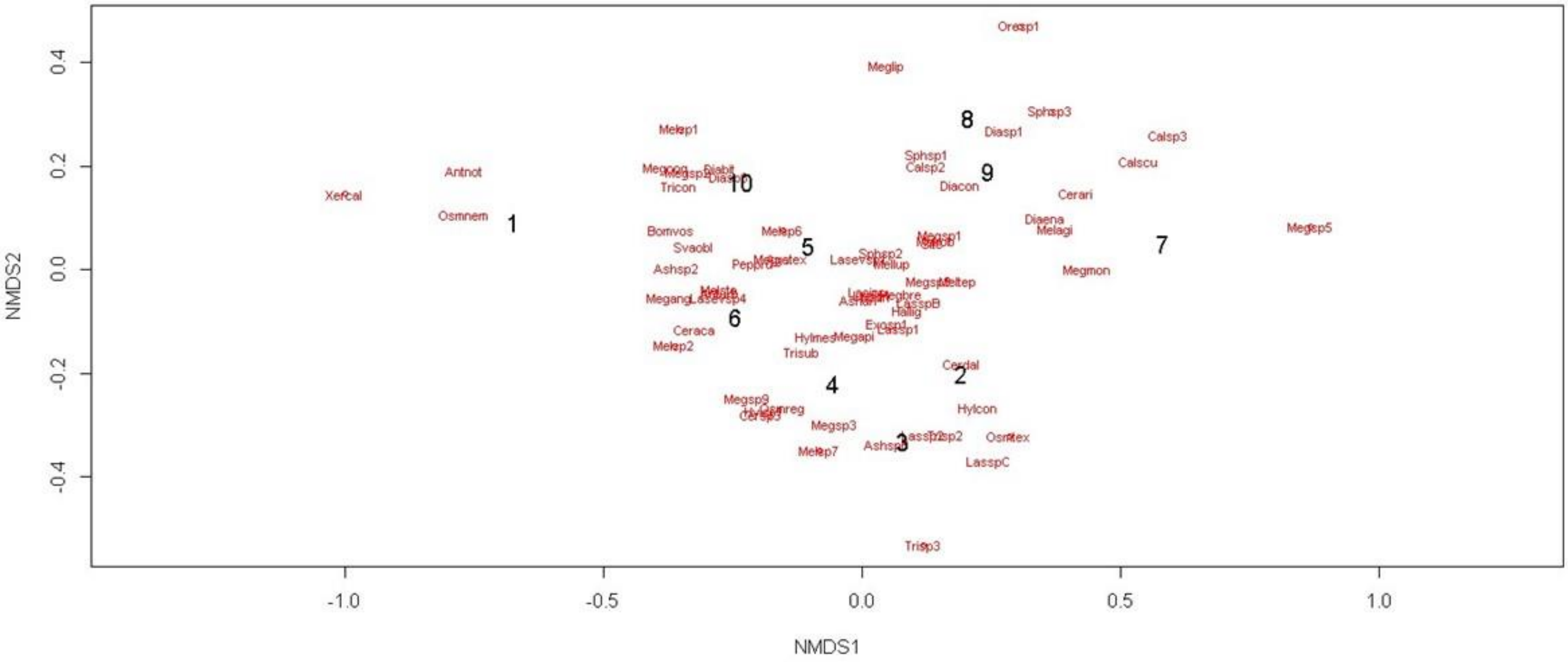


Figure 4. Non-metric multidimensional scaling used to produce ordination of species and sites.



# Chapter 4

## Bee-plant network structure in the Central Valley of California

## Introduction

Complex plant-animal interactions are the evolutionary drivers of Earth's biodiversity (Ehrlich and Raven 1964). Pollination is arguably the most important of these interactions; it is estimated that approximately 78% of angiosperms in temperate-zone communities and 94% in tropical communities rely on animal pollinators (Ollerton et al. 2011). The plant-pollinator relationship is usually mutualistic; the pollinator receives energy-rich nectar, and for some species other resources, and the pollen of the plant is transported to conspecifics (Proctor et al. 1996). Bees are the predominant animal pollinator as they are entirely dependent on the resources provided by angiosperms. There are > 16,000 identified bee species worldwide and all are obligate foragers on angiosperms (Michener 2000). Plant-pollinator interactions have been studied within the context of coevolution with an emphasis on whether interactions tend towards specialization or generalization and identification of the mechanistic drivers of such interactions (Crepet 1983, Gilbert and Raven 1975, Stebbins 1970). However, as evidence mounts of declines in pollinator populations, the number of studies evaluating the complexity of plant-pollinator interactions and their contribution to community stability and biodiversity are increasing (Rathcke and Jules 1993, Memmott and Waser 2002, Memmott et al. 2004, Steffan-Dewenter et al. 2006).

Plant-pollinator networks are modeled after food webs and built using principles of network theory; their main purpose is to allow the visualization of complex interactions in species rich communities (Bascompte and Jordano 2007). There are network and species-level indices to aid in the understanding of plant-pollinator mutualisms but their interpretation and application to community ecology remains an active field of investigation, as such there are conflicting views regarding the interpretation of trends.

A loss of pollinators has the potential to disrupt ecosystem function by effecting changes in the plant community (Lundberg and Moberg 2003). The risk of pollinator and/or plant extinction caused by the decline of one participant in a mutualism depends on the degree of specialization in the plant-pollinator interaction. In a close relationship between pollinator and plant the extinction of one will inevitably result in the extinction of the other. However, ecosystems characterized by generalists, pollinators that visit several hosts and plants that are visited by multiple pollinators, are resilient against plant and pollinator loss (Steffan-Dewenter et al. 2006). Determination of the degree of specialization versus generalization in plant-pollinator communities has now become a focus in community ecology.

The study of plant-pollinator mutualisms has traditionally focused on whether most interactions are dominated by specialists or generalists. The concept of specialization in plant-pollinator mutualisms is typified by "pollination syndromes" or suites of floral traits that reflect adaptations to certain pollinators at the level of order or above (Grant 1949, Baker 1963, Stebbins 1970, Crepet 1983). Pollination syndromes have gained much popularity over the years but accumulating evidence indicates that generalization is more prevalent in plant-pollinator systems. Generalized pollination systems have been identified in tropical and temperate ecosystems indicating that evolution may be a more diffuse process than earlier suggestions of coevolution would suggest (Roubik 1992, Waser and Price 1993). In fact, Waser et al. (1996) evaluated the plant pollinator network of a community and although the colors of the flowers clustered in “phenotypic space” there was not strong association between flower color and pollinator group. As analyses on plant-pollinator networks continue, generalization between floral host and pollinators seem to be the rule rather than the exception. The prevalence of generalization in plant-pollinator networks is thought to convey resilience to these systems (Waser et al. 1996).

An interpretation of the measurement of connectance would seem to differ with the popular held belief that generalization dominates in plant-pollinator communities. One of the earliest studies applying network theory to plant-animal mutualisms compared plant-pollinator and plant-seed disperser systems (Jordano 1987). For both mutualisms, it was determined that as species richness of the system increased the absolute number of interactions also increased but the connectance decreased (i.e. the proportion of all possible interactions that actually occur). An interpretation of this characteristic is that generalization decreased with species richness (Bosch et al. 2009). This contrasts with the assertion that pollinator communities are dominated by generalist species (Waser et al. 1996). It is estimated that 67-74% of bee species are polylectic (Minckley and Roulston 2006), supporting generalization in pollinator communities. However, Bosch et al. (2009), sampled a Mediterranean scrubland community, observing pollinator visitation and analyzing pollen load. They determined that pollinators in the community are undersampled in studies using only standard sampling, consequently, many rare specialist species are missed.

Another characteristic of plant-pollinator systems is they are often found to be asymmetrical and characterized by an abundance of weak interactions. (Jordano 1987). Asymmetry occurs when specialist species are linked to generalists and vice versa (Olesen et al. 2008). Bascompte et al. (2003), analyzed 52 mutualistic networks and determined that complex networks are highly nested and asymmetrical providing the system response routes for dealing with perturbations. It is thought that asymmetry in mutualistic networks allows for the persistence of rare species (Jordano 1987).

Connectivity, the number of links per species, increases slowly with species richness. Bosch et al. (2009), interpret this characteristic as creating a community with many specialists and few generalists. Another characteristic of plant-pollinator communities is that they generally have a core of species with high connectivity to which many specialist species are peripherally connected. This property increases as connectivity between species increases (de Nooy et al. 2005).

The extent to which the characteristics discussed above vary by land use is an area that has not been explored to a large extent. This study was conducted over a two-year period from 2005-2006 at 10 sites in the Central Valley, California. Using non-metric multidimensional scaling with land use data it was determined that the 10 study sites formed clusters based on region (Putah Creek, Cosumnes River Preserve, San Joaquin Wildlife Refuge). The purpose of this analysis was to address questions regarding community structure in the three regions of the Central Valley. 1) Were the communities in the Central Valley dominated by generalist or specialist bee species and did the structure vary according to land use? 2) Did network structure (i.e. asymmetry and connectivity) vary with land use? and 3) Was there temporal variability in network structure? It was hypothesized that the study sites surrounded by semi-natural land would have a more complex network structure with a higher degree of specialization and asymmetry than the study sites surrounded by agricultural and/or urban land.

## Methods

### *Study Sites*

Ten study sites selected for sampling were located in the Central Valley of California. Five sites were selected in habitats along Putah Creek, in Yolo and Solano Counties. Two sites were located in the Cosumnes River Preserve in Sacramento County. Three sites were placed within the San Joaquin National Wildlife Refuge in San Joaquin County (For a detailed description of study site locations and characteristics see Chapter 1: Methods).

The landscape surrounding each study location at a 1500m radius was quantified according to the proportion of urban, agricultural, and semi-natural land present. Using the generalized linear model it was determined that land use did not affect bee species richness or abundance. However, an ordination of the study sites using non-metric multidimensional scaling indicated that they formed 3 main clusters; 4 Putah Creek sites (Intdm(1) was different from the other Putah Creek sites), 3 San Joaquin Refuge sites, and 2 Cosumnes Preserve sites. The Putah Creek sites were dominated by agriculture and urban land use. The San Joaquin Wildife Refuge contained only semi-natural land, and the Cosumnes River Preserve was comprised of a mix of agricultural and semi-natural land (for details see chapter 2 and Appendix A). Landscape proportions were used to group study sites into clusters based on land use.

### *Sampling*

Wild bees were sampled while foraging and making contact with the reproductive organs of the floral host. In 2005, sampling was conducted June through August. In 2006, sampling effort increased, occurring from May through September. Each site was 1ha, inside of which were located two-100m transects. The transects formed an X through the middle of the study site. Netting was conducted for one-hour before and after 1200 hours. Sampling was conducted at all flowering plants within the plot. The two transects were walked and any plant occurring within 5m of either side of the transect was sampled. Next, the periphery of the plot was sampled, followed by a random walk to survey for missed plants. Bees were identified to the level of species with the assistance of R.W. Thorp. Species that could not be clearly identified to species were sorted to morphospecies.

### *Network Analysis*

The bee species-floral host data was combined for the sites that clustered using the non-metric multidimensional scaling technique. Therefore, for the network analysis data was analyzed for two groups of sites in 2005 (Putah Creek and San Joaquin Refuge) and three groups for 2006 (Putah Creek, San Joaquin Refuge, Cosumnes Preserve). It was reasoned that since they formed clusters in the ordination they likely shared characteristics that may influence their pollination networks, such as soil, climate, topography, and land use.

The network analysis was conducted using the bipartite package in R (Dormann 2011). The first component of the analysis is a comparison of network indices. Following the network comparison is a group level analysis including plots and species level indices. The analyses for each group of sites consisted of several components. For each group of sites the analysis contained the following: 1) pollination web, 2) pollination matrix, 3) two-mode gplot, and 4) one-mode gplot. The species level analysis includes several indices that were selected to indicate level of specialization among species.

The following indices were selected to assess the similarity of the networks in the Central Valley: connectance, $H_2$, and specialization asymmetry. Connectance is the proportion of actual links between pollinator and plant divided by the potential number of links in a network. Connectance is used to assess the generalization of a network (Medan et al. 2006). This index is known to decrease with sample size and species richness. This occurs because the denominator (the number of possible interactions) increases geometrically, whereas the numerator (the number of realized interactions) decreases at a slower rate (Oleson and Jordano 2002). Low connectance indicates greater specialization in the network.

The $H_2'$ index is another network level measure of specialization. Blüthgen et al. (2006), defined $H_2'$ as the deviation of a species' realized number of interactions from what is expected based on the species' total number of interactions. An $H_2'$ of 0 indicates no specialization or no deviation from the expected distribution of interactions. An $H_2'$ of 1 indicates perfect specialization for the network.

Specialization asymmetry was proposed by Blüthgen et al. (2006), to measure mean dependence asymmetry at the network level. This is a modification to another asymmetry index that corrects for the influence of singletons. The specialization asymmetry measures the interaction strength asymmetry of a network and is a good gauge of specialization. Positive values indicate a higher level of specialization and low positive and negative values indicate generalization.

Pollination webs were used to illustrate the strength of the interactions between plants and bee species and connectivity (the number of interaction partners of a species). A pollination matrix representation of each web displays squares for interactions. The greater the number of interactions between bee species and plant, the darker the square. The matrix can be used to evaluate nestedness and to identify specialist versus generalist bee species. Two-mode and one-mode gplots are provided for each group of sites. The two-mode gplots contain pollinators (blue squares) and plant species (red circles) with arrows showing all interactions between species. The length of the arrows correspond to the strength of the interactions. The one-mode gplot represents pollinators only. The number of links between pollinators is illustrated with arrows. If a bee species forages on the same floral host as another species there is 1 link between them. If two bee species do not visit the same plant but have a third pollinator in common the path length for their connection is two. The links between all pollinators are illustrated so that patterns of generalization versus specialization can be identified and centrality can be visually assessed. Centrality is the measure of how many bee species make up the core of the networks interactions.

### *Species-level indices*

The species level indices were calculated using the specieslevel function from the bipartite package in R (Dormann 2011). The following indices are included in the calculations; degree, node specialization index (NSI), strength, pollination service index (PSI), and d' index. The degree is the number of plant links observed for each bee species. This is one method in the species indices chart used to evaluate whether a species is a specialist (D=1) or generalist (D ≥2), the higher the degree value the higher the level of generalism (Blüthgen et al. 2006).

The node specialization index (NSI) is calculated in a one-mode network as mean path length between each pollinator and every other pollinator. When two pollinators visit the same floral host the path length between them is NS=1 and they are represented in the one-mode network with one link. Two pollinators that do not visit the same plant but are linked by a third pollinator have an NSI of 2. A pollinator with a low NSI is thought not to contribute much to the network because it pollinates plant species that are directly pollinated by other bees, whereas a bee species with an NSI of on average 3, is 3 links away from all other pollinators and of higher importance to the network. NSI allows for species to be ranked according to the degree of node specialization but as a measurement of overall specialization it is inferior to d' and PSI. NSI is based on the position of species within the network and is therefore not based on species characteristics (Dormann 2011).

Strength is a quantitative index that measures the dependence of the plant community on a specific bee species (Jordano 1987). The strength is calculated as the proportion of visits a plant receives from each pollinator out of the total number of interactions for that plant. The meaning of strength with regards to specialization versus generalization of the pollinator is unclear. A pollinator may be of high importance to a particular plant species without being a specialist (Dormann 2011).

Pollination service index (PSI) is considered a good indicator of specialization in pollinators. The index is based on the idea that a pollinator is more important for a plant species when it is common and specialized. This based on the premise that generalist pollinators may deliver pollen to non-target plant species. PSI is the product of the dependency of the pollinator on the plant and the dependency of the plant on the pollinator.

The final value in the species indices is the d' index. This measure indicates how a species utilizes available niches in the environment. A species that utilizes available niches in the same proportion as their availability in the environment can be considered a generalist, whereas a species that utilizes primarily rare resources may be considered a specialist (Blüthgen et al. 2006). High d' values indicate that a species is primarily visiting a rare plant and is possibly a specialist.

An assessment of oligolectic versus polylectic bee species was conducted for each bee community. Oligolecty is defined as conspecific bees that exhibit foraging specialization on one or a few plant species, generally within the same plant genus or family (Cane and Sipes 2006). Identification of oligolectic species for the purpose of this study was conducted using the Catalog of Hymenoptera (Krombein and Hurd Jr. 1979) and species monographs.

## Results

### *Network Indices*

The network indices are presented in Table 1 and include connectance, $H_2'$, and specialization asymmetry. The connectance for the site groups ranged from 0.129 to 0.190 (Table 1). Connectance is the proportion of actual links in a network divided by all possible links. This index was lowest for Putah Creek in 2006 with a value of C=0.129. This was a decrease from the Putah Creek value in 2005, C=0.132. The decrease in connectance for Putah Creek between the two sample years corresponds to an increase in species richness in the community. In 2006, there were 38 species recorded in the Putah Creek network and in 2005 there were 26 species. The connectance was highest for San Joaquin Refuge in 2005 (C=0.190). The Cosumnes Preserve also had a high connectance with C=0.183. Both of these communities had similar species numbers with the San Joaquin Refuge at 19 species and the Cosumnes Preserve at 21 species. Whether connectance corresponds to levels of generalization versus specialization can be assessed through the other indices as well as with connectance.

The $H_2'$ index, a measure of specialization, indicates generalization when it is close to 0 and specialization as it moves towards 1. Of the networks evaluated, $H_2'$ was lowest for San Joaquin Refuge ($H_2' = 0.383$) in 2005 and highest for San Joaquin Refuge ($H_2' = 0.693$) in 2006. The increase in this value indicates an increase in specialization in the network from 2005 to 2006. The 2006 sample year was more robust and included more species, this may have affected this index value. For 2006, the Cosumnes Preserve had an $H_2' = 0.529$ and Putah Creek exhibited a value of $H_2' = 0.453$. When separating the sites by land use, San Joaquin sites are all semi-natural, Cosumnes Preserve sites are primarily semi-natural with some agriculture, and Putah Creek contain primarily agriculture and urban.

For specialization asymmetry, which is different from $H_2'$, the values closer to zero indicate more specialization. The San Joaquin Refuge in 2005 and 2006 had a value of -0.62, which although a negative number, is quite small. The Cosumnes Preserve had a specialization index of -0.126 and the Putah Creek sites had an index of -0.115 in 2005. Given that these values are all negative numbers they indicate that all the networks have a certain degree of generalization in their structure.

### ***Putah Creek (2005-2006)***

The 2005 pollination web illustrates a community in which the plant species *Brassica nigra* attracted the greatest variety of bee species (Figure 1). Many of the plant species in this network were generalists meaning that they attracted a several species of pollinators. The exceptions were *Lepidium latifolium*, *Marrubium vulgare*, and *Sambucus nigra* which attracted only one bee species each. However, the pollination web indicates that 58% of the bee species in the network visited only one species of plant. The exceptions are the following bee species that visited many plant species and could be considered extreme generalists: *Bombus vosnesenskii*, *Halictus ligatus*, *Megachile apicalis*, and *Svastra obliqua*.

The 2005 pollination matrix displays shaded boxes according to the strength of bee-host interactions, it is a method of visualizing the most significant interactions in a network (Figure 2). The matrix indicates that *Halictus ligatus* and *Brassica nigra* have a strong interaction as well as *Hylaeus morphospecies 2* and *Brassica nigra*. Also strongly linked in this network are *Bombus vosnesenskii* with *Brassica nigra* and *B. vosnesenskii* with *Lotus corniculatus*. Evaluation of the pollination web and matrix illustrate a network that was characterized by asymmetry; the plant species demonstrated generalization in that they attracted multiple bee species yet over half of the bee species were recorded foraging on only one plant species.

The 2005 two-mode gplot for the Putah Creek sites shows that this network is composed of 3 compartments. The large compartment has 1 plant species with many pollinators connected to it. It is evident from the gplot that there are several bee species linked to the generalist plant species centered in the largest compartment. The one-mode gplot for Putah Creek 2005, depicts pollinators linked to one another. There is high centrality shown in this plot. The core of the plot is occupied by generalist bee species with many links to other species through their common use of resources.

The species-level indices for Putah Creek in 2005 indicated a core of specialists by evaluating the degree of each species. Those with a degree of one visited only one plant species and those with higher degrees visited multiple plant species (Table 2). The degree index indicates that there is a core of specialists in this community with 15 species that were collected visiting only one plant species (i.e. degree=1). Specialization of individual bee species in the network can also be assessed by evaluating the NSI index. The NSI value will be high for specialists; the value was highest for *Ashmeadiella* morphospecies 1 and 2 for Putah Creek in 2005. Another species-level index, the d' value, is particularly robust for determining how a species utilizes resources, a high value indicates specialist species. Both *Ashmeadiella* species had the highest values in the network with d'=0.708. The strength measurement, calculates the dependence of the plant community on a particular plant species. The strength was highest for *Bombus vosnesenskii*, *Halictus ligatus*, and *Megachile apicalis* which indicated that the plant community is more dependent on bee species visiting multiple plant species rather than species visiting only one plant species.

The 2006 pollination web (Figure 5) for Putah Creek contrasted with the 2005 web in that there are many generalist bee and plant species. In addition, in the 2006 web there were many weak interactions as is evident by the thin interaction lines in the web. This is different from 2005 in which most of the interactions formed stronger links. The 2006 matrix (Figure 6), indicates that the strongest interaction is between *Halictus tripartitus* and *Brassica nigra.*

The two-mode (Figure 7) and one-mode (Figure 8) gplots indicated a well-developed core of generalists in the 2006 Putah Creek network and a periphery of bee species that visited few plant species. The two-mode gplot showed that there are both pollinator and plant species that were important to the stability of the network because they were found in the middle of the plot with many links attached to them. The one-mode gplot showed a large core of generalist pollinators with many links to other pollinators through shared resources. The pollinators on the outside of the graph were the specialists. The complexity of the graphs was greater than the 2005 graphs which could be a reflection of an increase in community size.

The degree measurement on the species-level indices showed that 15 out of 38 bee species or 39% were found to have visited only one plant species. The NSI index identifies *Melissodes stearnsi* as the species with the highest specialization. This species also has a high d' = 0.759 making it one of the more important specialists in the network. However, if the PSI is taken into account, which is the measurement of how important a pollinator is to the network, *Melissodes coquiletti* is also important. This species has a high d' = 0.690 and would be considered close to *Melissodes stearnsi* based on those two indices.

### *San Joaquin Refuge (2005-2006)*

The pollination web for San Joaquin Refuge showed 53% of the bee species foraging on more than one plant species (Figure 9). *Halictus tripartitus*, H. *ligatus*, and *Diadasia enavata* were had the highest degree measurements in the web (10, 6, and 4 respectively). With the exception of *Convolvulus arvensis* and *Datura wrightii*, all plants were visited by more than one pollinator. The pollination matrix showed the strongest interaction to be between *Halictus tripartitus* and *Brassica nigra* (Figure 10). The interaction between *Diadasia enavata* and *Helianthus annuus* was similarly strong. The two-mode gplot (Figure 11) and one-mode gplot

(Figure 12) indicated that this network was centered around 2-3 main pollinators and was comprised of many bee species with 1-2 links rather than a core of generalists with many links as seen in Figure 4 for Putah Creek.

The species-level indices showed through the degree measure that 9 out of 19 bee species or 47% were collected from only one plant species (Table 4). The NSI value was highest for *Calliopsis* morphospecies 3, however, it was also high for *Ceratina arizonensis*. The PSI index and d' value are much higher for *Ceratina arizonensis* indicating that it is more important in this network than the *Calliopsis* species. *Ceratina arizonensis* was found foraging on *Heliotropium curassavicum* and was shown as having a strong interaction whereas, *Calliopsis* morphospecies 3 had a weak relationship with *Frankenia salina.*

The pollination web for the San Joaquin Refuge in 2006 (Figure 13) showed asymmetry between bee species and plant species. *Diadasia enavata* was found visiting many plant species but the remaining bee species visited 1-2 plant species only. The plant species were generalists in that they have many pollinators visiting each of them with the exception of *Brassica nigra* and *Lepidium latifolium*. The pollination matrix showed that the two strongest interactions were *Diadasia enavata* and *Helianthus annuus* and *Ceratina arizonensis* with *Heliotropium curassavicum* (Figure 14).

The two-mode gplot (Figure 15) shows that there were three compartments in the network for San Joaquin Refuge in 2006. The compartments were centered around generalist plant species. It was also evident from the two-mode plot that there were many specialist pollinators that visited only one plant species. The one-mode gplot (Figure 16**)** showed that one compartment had a tightly linked core of pollinators whereas the larger compartment centered around one main pollinator.

The species-level indices showed that 13 out of 16 (81%) bee species were collected on only one plant species (Table 5). The NSI value was high for *Ceratina dallatorreana* and *Megachile prosopidis*. However, the PSI and d' values were high for *Ceratina arizonensis.* As with the 2005 network, *Ceratina arizonensis* had a strong interaction with *Heliotropium curassavicum. Megachile prosopidis* was recorded once on *Cephalanthus occidentalis* and *Ceratina dallatorreana* was recorded once on *Convolvulus arvensis* but both interactions were weaker than that of C. *arizonensis.*

### ***Cosumnes River Preserve (2006)***

The pollination web for the Cosumnes River Preserve (2006) showed a community with mostly generalist plants visited by generalist bee species (Figure 17). There appeared to be 6 bee species that only visited one plant species in the community but there was asymmetry in the relationship in that the plants visited by those species were generalists. The pollination matrix showed a nested community with the most common interaction being *Megachile apicalis* and *Grindelia stricta* (Figure18). The next most common interaction was *Osmia texana* and *Grindelia stricta*.

The two-mode gplot (Figure 19) showed a loosely structured network with both pollinators and plant species in the core of the network. The upper right corner indicated there was one plant species with several pollinators that visited only that plant species. Comparing the two-mode gplot to the pollination web it was *Helianthus annuus* that created the pattern seen in the gplot. The one-mode gplot (Figure 20) showed 2 cores of generalists with several bee species with fewer connections forming the outer periphery of the network. The cores that were visible in Figure 19 formed the more complex part of the network as they had the most links to other pollinators through their use of multiple resources.

The species-level indices for Cosumnes River Preserve (Table 6) showed by the degree category that 7 out of 21 or 33% of the bee species visited only one plant species. The node specialization index (NSI) was highest, NSI = 2.900, for *Lasioglossum* (*Dialictus*) morphospecies 1. The PSI = 0.500 and d' = 0.787 showed that this species was the most important specialist for this network. It was collected foraging on *Lotus unifoliolatus* which had only one other pollinator, *Megachile brevis.* Both pollinators had a fairly weak relationship with their host plant.

## Discussion

The structure of the bee-plant communities for Putah Creek, San Joaquin Refuge, and the Cosumnes Preserve were presented in several ways to visualize properties of the networks: specialization versus generalization, asymmetry, and connectivity. These properties may be predictive of a community's ability to withstand anthropogenic disturbance, furthermore, land use may influence the plant-pollinator communities in such a way that these properties are affected in a predictive manner. It was hypothesized that a community surrounded by semi-natural land would have a higher complexity and level of specialization than a community surrounded by agricultural and/or urban land. The results of the analyses were mixed but overall trends did support this hypothesis.

### *Network Analyses*

Several trends were evident regarding network structure and land use. Connectance varied in a somewhat predictable manner. The connectance value was lowest for Putah Creek because it had the highest species richness value. Putah Creek is surrounded primarily by agricultural and urban land with a low percentage of semi-natural land. However, the agricultural land had a high number of weedy plant species growing in and around the fields. Weedy plant species often provide forage to a variety of bee species and can sustain diverse populations (Tscharntke et al. 2005). The San Joaquin Refuge was surrounded by semi-natural land and also had a high species richness as was evident with a low connectance value but it was not as species rich as Putah Creek. This may be indicative of a trend towards increased species richness in moderately disturbed regions. Holzschuh et al. (2007), studied agricultural areas in Germany and concluded that the number and diversity of flowering weed species in the fields and surrounding landscape was positively related to bee diversity. Therefore, although Putah Creek contained many weedy and non native species in the surrounding habitat it still seems to have supported a diverse bee community.

Asymmetry refers to the interaction of specialist species with generalist species. Since specialist species are usually rare and generalist species are abundant, this property provides a mechanism for the persistence of rare species. The core of interactions creates a system that is impervious to perturbations after an elimination of a species. This occurs because the redundancy of interactions in the core of the network provides alternative routes for system responses after a perturbation (Jordano et al. 2006).

The $H_2'$ index is a measure of specialization. The highest value, H2' = 0.693, occurred for the San Joaquin Refuge. This separated the community with semi-natural land from the other communities. The discussion of asymmetry is related to one of specialization versus generalization.

### *Specialization versus generalization*

The species-level indices were used in this study to determine the level of specialization in the networks that were evaluated from the Central Valley. The term specialization can take on different meanings depending on the perspective from which it is being discussed. A plant can be specialized if it attracts one or a few pollinator species as visitors (Armbruster and Baldwin 1998). A plant may also be considered specialized if there appears to be strong directional selection on floral traits such that certain pollinators seem particularly well-suited to pollinate the flowers (van der Pijl 1961). Pollinators can be specialized or generalized based on their foraging preference without reference to adaptive traits. For the purpose of this discussion a specialist bee is one that is typically referred to as oligolectic.

There are two trends worthy of noting, the network with more semi-natural land contains a greater percentage of rare species and a greater percentage of oligoleges. The term oligolectic is used to refer to bee species that restrict foraging to the same few pollen hosts (Cane and Sipes 2006). Bee species defined as oligolectic for the purpose of this study were categorized as such using published literature, primarily the Catalog of Hymenoptera (Krombein and Hurd Jr. 1979) and species monographs.

The species-level indices were useful in that they identified the rare bee species that was the most specialized and valuable to the network. Although the many ‘specialized’ bee species were not necessarily oligoleges they were rare in the sample and important for the pollination of the one or two plant species they were visiting. The indices indicated that their removal would have a greater impact on the network than the removal of other rare species. Although, it is important to note that the removal of bee species that visited a multitude of plant species would have a higher impact on the bee community than removal of rare species according to the strength index.

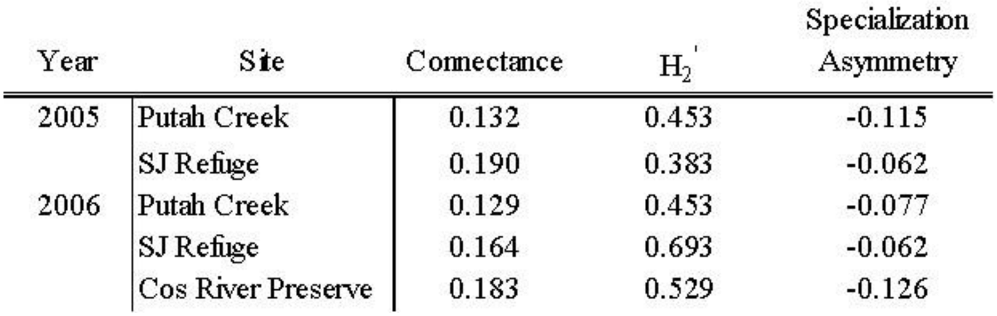
The percentage of true oligoleges was highest for the San Joaquin Refuge sites in 2006; these sites were characterized by semi-natural land. The other networks were composed of approximately 30% oligoleges whereas the San Joaquin Refuge in 2006 was comprised of approximately 54% oligolectic bee species. This is in agreement with the prediction that generalization will increase with species richness. The Putah Creek site had greater species richness than the San Joaquin sites and consequently had a higher degree of polylectic bee species (Bosch et al. 2009). This could indicate a difference between semi-natural networks and those characterized by agricultural land. The pollination web and matrix for San Joaquin 2006 showed a network that had a more equal distribution of strong interactions with many plant species visited by more than one bee species but many oligolectic bee species that visited only one or a few plant species indicating a high degree of asymmetry. This may be a characteristic of more intact ecosystems. Perhaps, in more intact ecosystems, in the absence of weedy plant species, there is less chance for weedy species to dominate the community allowing oligolectic bee species to exist in the available niches.

### *Future directions*

There is much to be learned from the use of pollination networks in the study of plant-pollinator communities.  Future direction of the study of these networks should focus on the quantification of spatial and temporal variability.  Most analyses to date have looked at these networks in a static time frame.  An understanding of how these networks vary in space and time will help us better understand whether networks are responding to perturbations or whether they are undergoing natural stochasticity.

A better understanding of generalization versus specialization in mutualistic networks and whether these definitions are referring to rarity versus oligolecty is another area that is in need of clarification, particularly in the study of bee-plant mutualisms.  In this study, specialization did not correspond to oligolecty, rather, it reflected rarity of, often times, polylectic species.  What does this mean for the stability of the network?  For the San Joaquin network, the species richness was less than for the Putah Creek network but specialist, i.e. they visited only one plant species, and oligolectic species were greater in abundance than in the Putah Creek network.  Perhaps this indicates that with less non-native weedy species in a more intact semi-natural habitat, there is greater capability for species to diversify.  Comparison of networks in different landscapes is also an area that would yield information that could then be applied to conservation.

Table 1. Network indices for 2005-2006. Includes Putah Creek and San Joaquin Refuge sites for 2005. For 2006, Putah Creek, San Joaquin Refuge, and Cosumnes Preserve sites are included.



| Year | Site | Connectance | $H_2'$ | Specialization Asymmetry |
|---|---|---|---|---|
| 2005 | Putah Creek | 0.132 | 0.453 | -0.115 |
| | SJ Refuge | 0.190 | 0.383 | -0.062 |
| 2006 | Putah Creek | 0.129 | 0.453 | -0.077 |
| | SJ Refuge | 0.164 | 0.693 | -0.062 |
| | Cos River Preserve | 0.183 | 0.529 | -0.126 |

Figure 1. Putah Creek (2005) bee pollination web of sites Dryck(4), Russr(6), and SFrkPs(10). Bees were sampled from June through August. The following is a list of plant species corresponding to the lower level of the web: a)*Brassica nigra*, b) *Centauria solstitialis*, c)*Cephalanthus occidentalus*, d)*Lepidium latifolium*, e)*Marrubium vulgare*, f)*Rubus discolor*, g)*Centromadia pungens*, h)*Cichorium intybus*, i)*Glychyrriza lepidota*, j)*Grindelia camporum*, k)*Lotus corniculatus*, l)*Raphanus sativus*, m)*Sambucus nigra*, n)*Heliotropium curassavicum.*

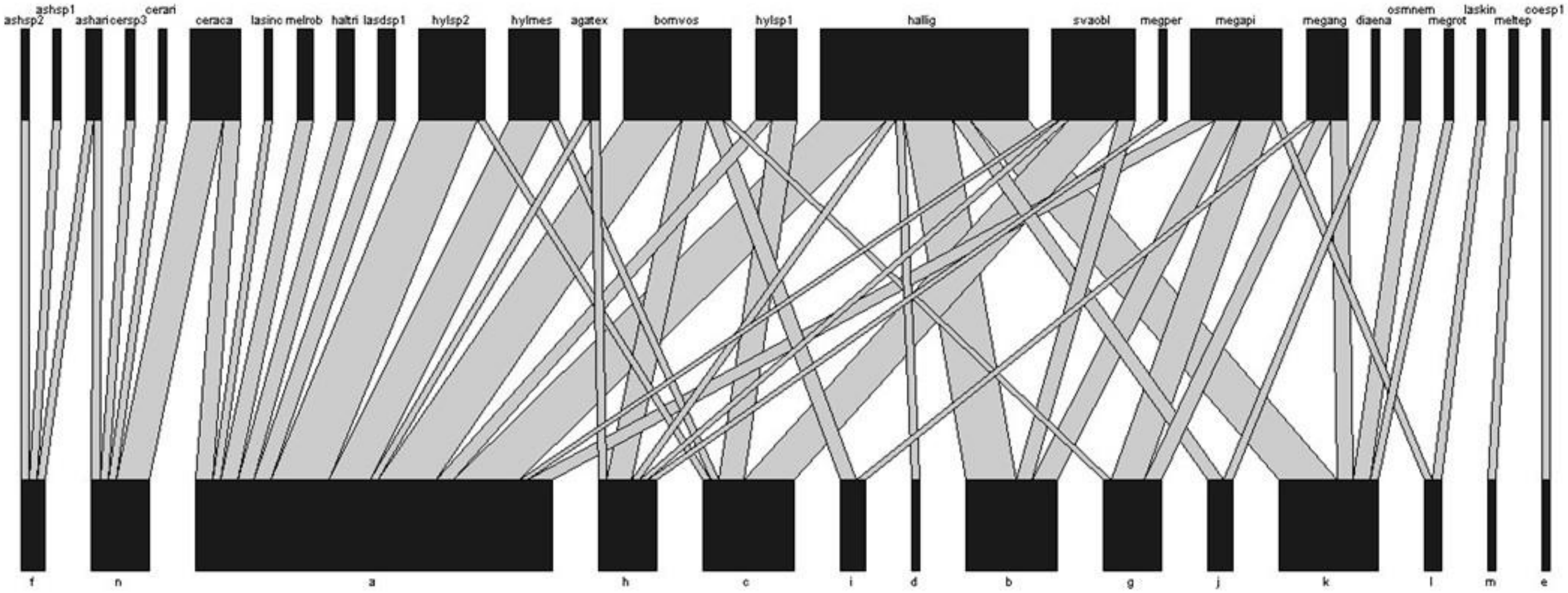


Figure 2. A pollination matrix of Putah Creek (2005) sites; Dryck(4), Russr(6), and SFrkPs(10). X-axis represents bee species and Y-axis represents plant species. Each square represents a potential bee-plant interaction. The shade of the box indicates the strength of the interaction with the darker squares indicating a greater number of visitations. : a)*Brassica nigra*, b) *Centauria solstitialis*, c)*Cephalanthus occidentalus*, d)*Lepidium latifolium*, e)*Marrubium vulgare*, f)*Rubus discolor*, g)*Centromadia pungens*, h)*Cichorium intybus*, i)*Glychyrriza lepidota*, j)*Grindelia camporum*, k)*Lotus corniculatus*, l)*Raphanus sativus*, m)*Sambucus nigra*, n)*Heliotropium curassavicum.*

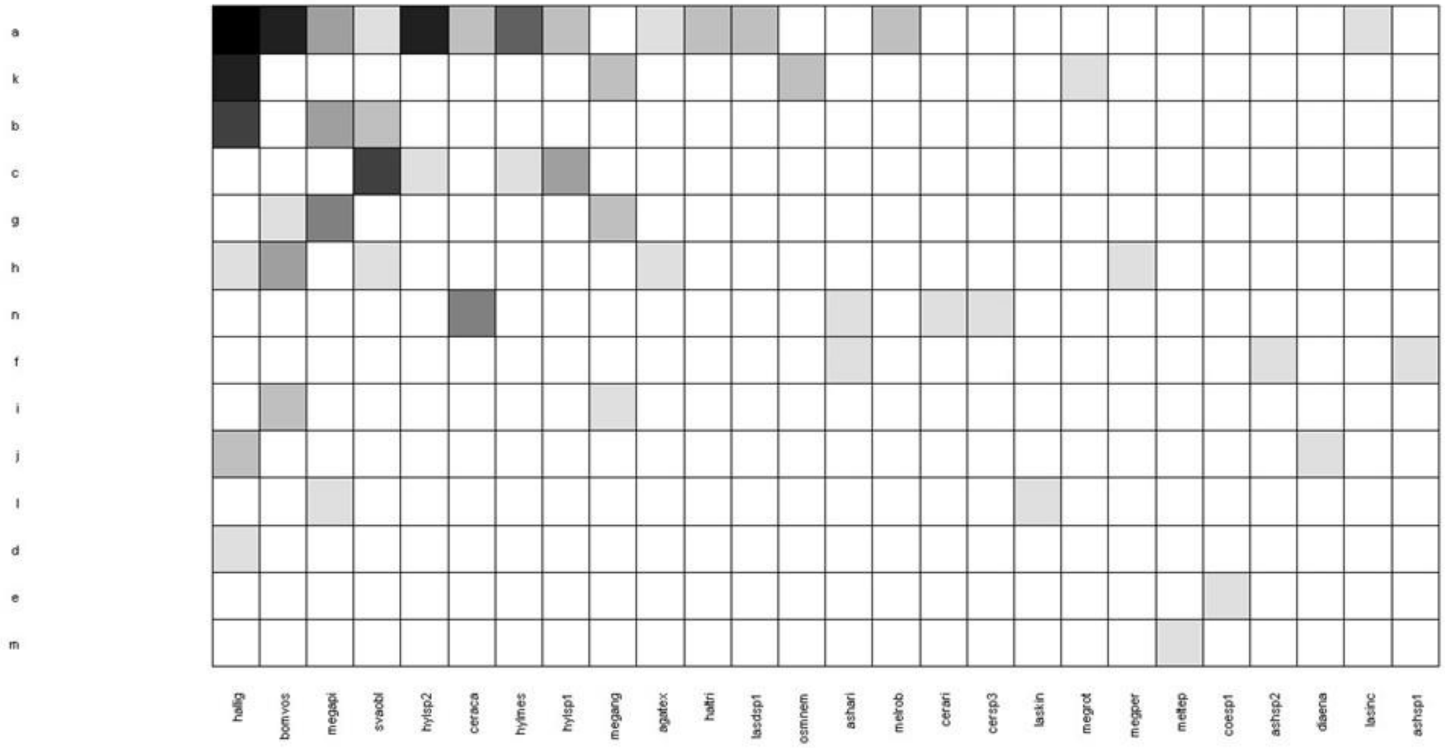


Figure 3. Putah Creek (2005). Two mode gplot illustrating links between pollinators (blue) and plants (red). The distance of the arrows indicates the strength of the relationship.

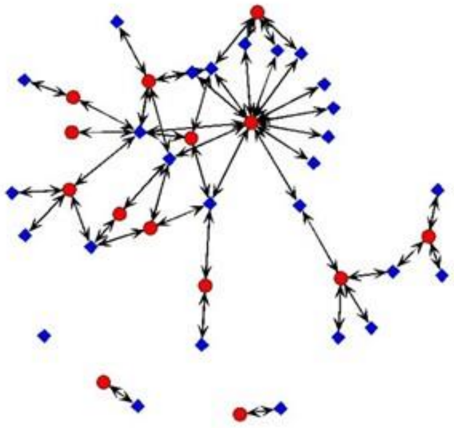


Figure 4. Putah Creek (2005). One-mode gplot illustrating links between pollinators based on shared resources.

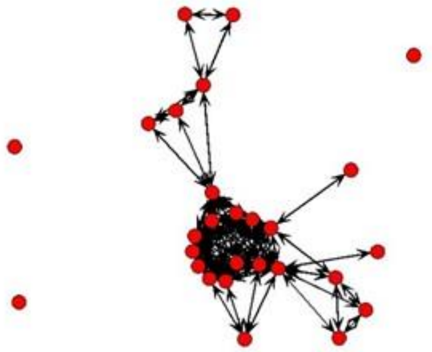
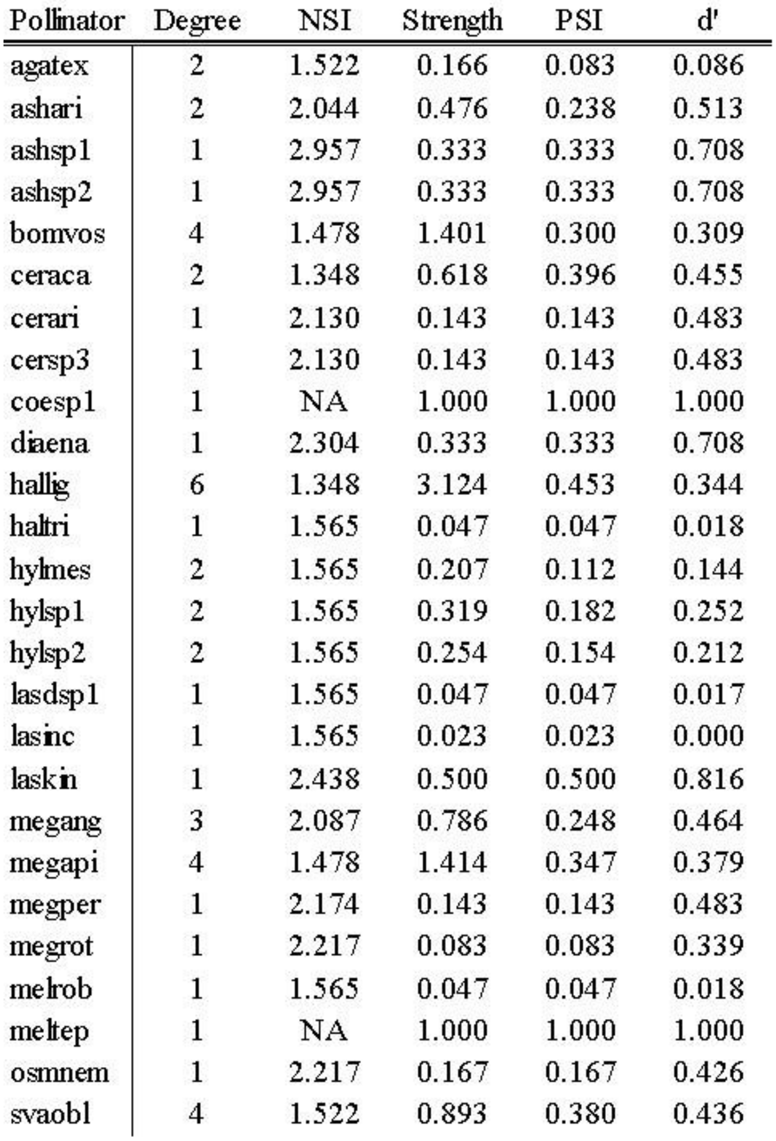


Table 2. Putach Creek (2005). Species level indices.



| Pollinator | Degree | NSI | Strength | PSI | d' |
|---|---|---|---|---|---|
| agatex | 2 | 1.522 | 0.166 | 0.083 | 0.086 |
| ashari | 2 | 2.044 | 0.476 | 0.238 | 0.513 |
| ashsp1 | 1 | 2.957 | 0.333 | 0.333 | 0.708 |
| ashsp2 | 1 | 2.957 | 0.333 | 0.333 | 0.708 |
| bomvos | 4 | 1.478 | 1.401 | 0.300 | 0.309 |
| ceraca | 2 | 1.348 | 0.618 | 0.396 | 0.455 |
| cerari | 1 | 2.130 | 0.143 | 0.143 | 0.483 |
| cersp3 | 1 | 2.130 | 0.143 | 0.143 | 0.483 |
| coesp1 | 1 | NA | 1.000 | 1.000 | 1.000 |
| diaena | 1 | 2.304 | 0.333 | 0.333 | 0.708 |
| hallig | 6 | 1.348 | 3.124 | 0.453 | 0.344 |
| haltri | 1 | 1.565 | 0.047 | 0.047 | 0.018 |
| hylmes | 2 | 1.565 | 0.207 | 0.112 | 0.144 |
| hylsp1 | 2 | 1.565 | 0.319 | 0.182 | 0.252 |
| hylsp2 | 2 | 1.565 | 0.254 | 0.154 | 0.212 |
| lasdsp1 | 1 | 1.565 | 0.047 | 0.047 | 0.017 |
| lasinc | 1 | 1.565 | 0.023 | 0.023 | 0.000 |
| laskin | 1 | 2.438 | 0.500 | 0.500 | 0.816 |
| megang | 3 | 2.087 | 0.786 | 0.248 | 0.464 |
| megapi | 4 | 1.478 | 1.414 | 0.347 | 0.379 |
| megper | 1 | 2.174 | 0.143 | 0.143 | 0.483 |
| megrot | 1 | 2.217 | 0.083 | 0.083 | 0.339 |
| melrob | 1 | 1.565 | 0.047 | 0.047 | 0.018 |
| meltep | 1 | NA | 1.000 | 1.000 | 1.000 |
| osmnem | 1 | 2.217 | 0.167 | 0.167 | 0.426 |
| svaobl | 4 | 1.522 | 0.893 | 0.380 | 0.436 |

Figure 5. Putah Creek 2006. The plant species list is as follows: a) *Brassica nigra*, b) *Centauria solstitialis* c) *Centromadia pungens*, d) *Helianthus annuus*, e) *Melilotus alba*, f) *Polygonum hydropiperoides*, g) *Raphanus sativus*, h) *Trichostema lanceolatum*, i) *Vicia sativa*, j) *Cephalanthus occidentalis*, k) *Cichorium intybus*, l) *Convolvulus arvensis*, m) *Glycyrrhiza lepidota*, n) *Lactuca serriola* o) *Phyla nodiflora*, p) *Rosa californica*, q) *Sylibum marianum*, r) *Eschscholzia californica*, s) *Grindelia camporum*, t) *Heliotropium curassavicum*, u) *Lepidium latifolium*, v) *Datura wrightii*, w) *Lotus corniculatus.*

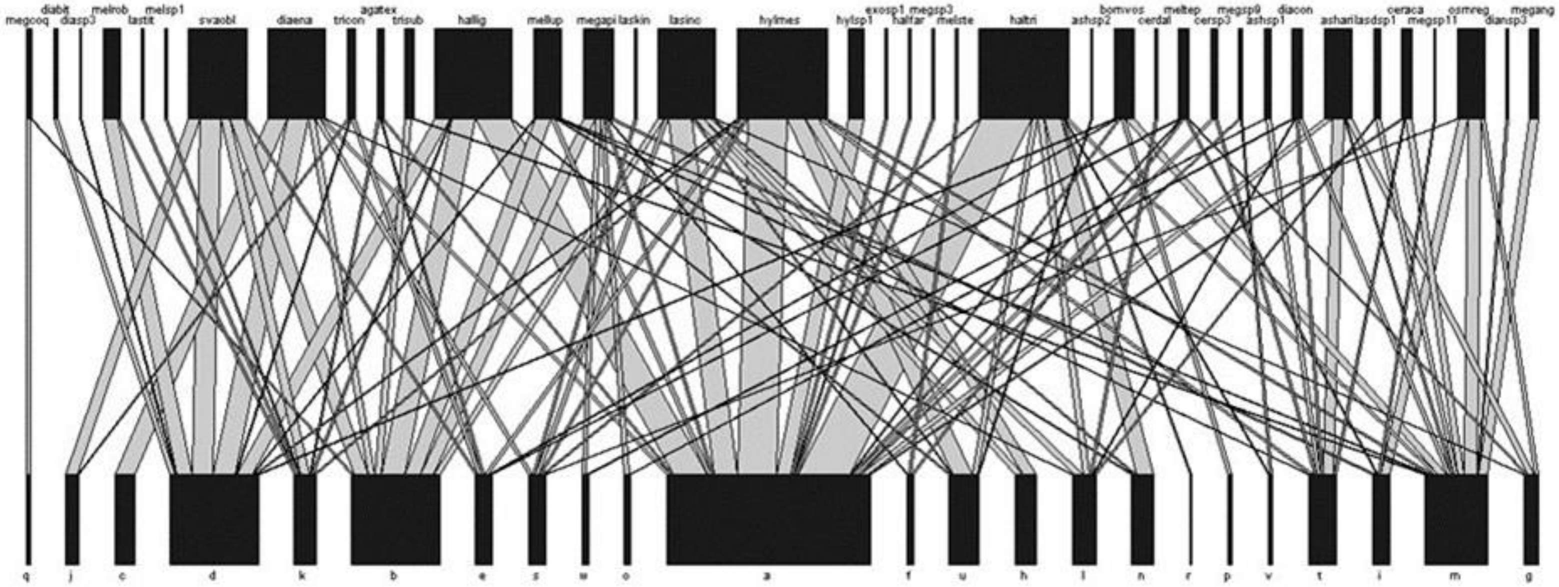


Figure 6. Putah Creek 2006. Pollination Matrix. a) *Brassica nigra*, b) *Centauria solstitialis* c) *Centromadia pungens*, d) *Helianthus annuus*, e) *Melilotus alba*, f) *Polygonum hydropiperoides*, g) *Raphanus sativus*, h) *Trichostema lanceolatum*, i) *Vicia sativa*, j) *Cephalanthus occidentalis*, k) *Cichorium intybus*, l) *Convolvulus arvensis*, m) *Glycyrrhiza lepidota*, n) *Lactuca serriola* o) *Phyla nodiflora*, p) *Rosa californica*, q) *Sylibum marianum*, r) *Eschscholzia californica*, s) *Grindelia camporum*, t) *Heliotropium curassavicum*,u) *Lepidium latifolium*, v) *Datura wrightii*, w) *Lotus corniculatus.*

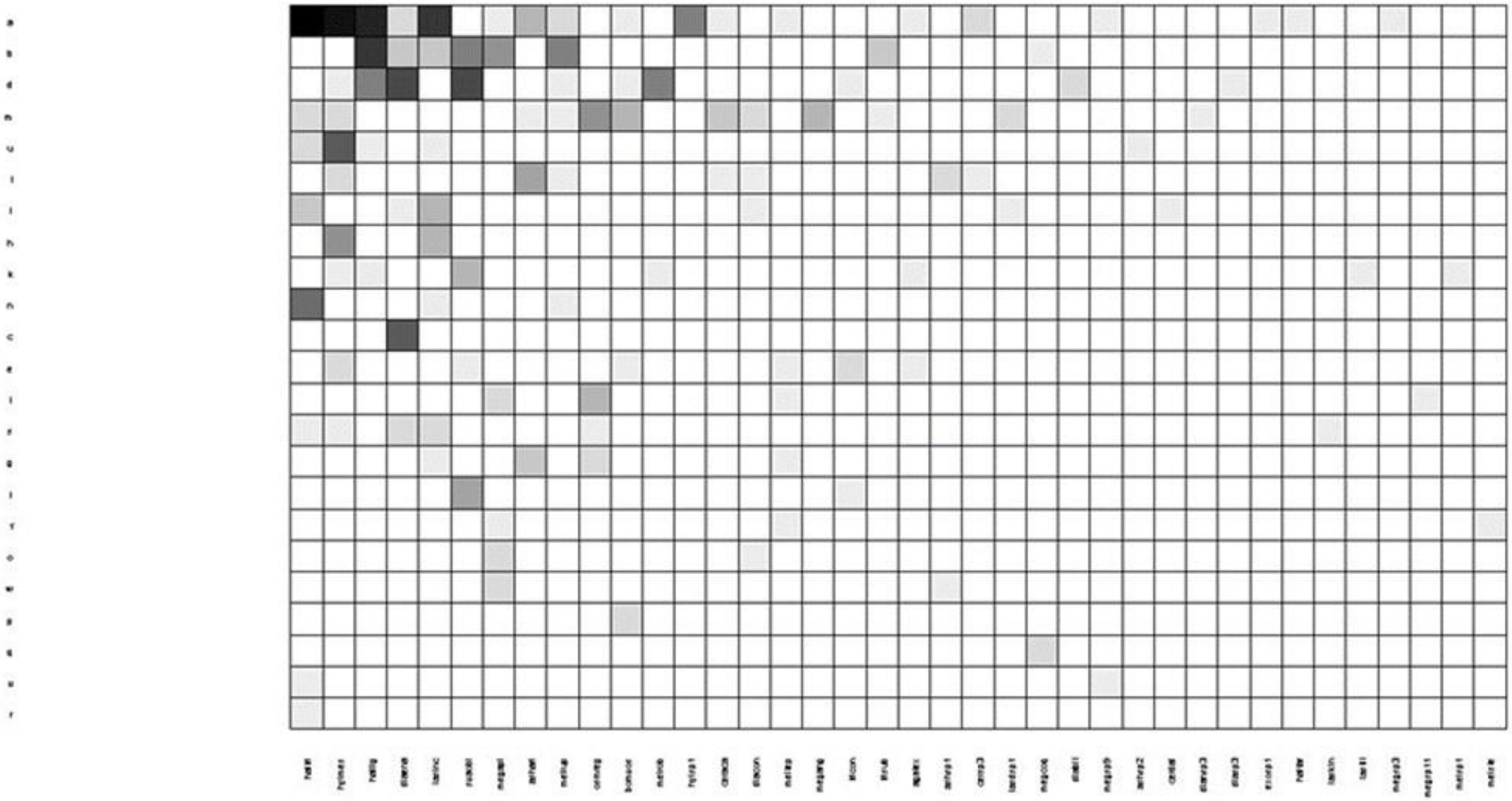


Figure 7.  Putah Creek 2006.  Two-mode gplot.

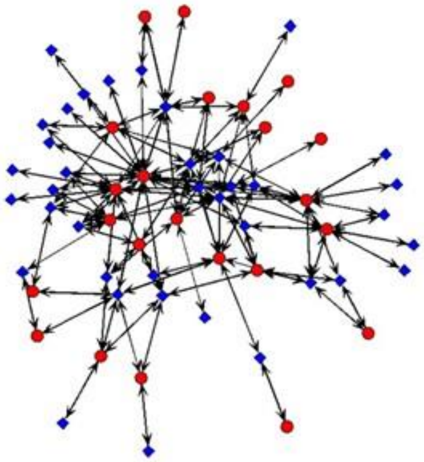
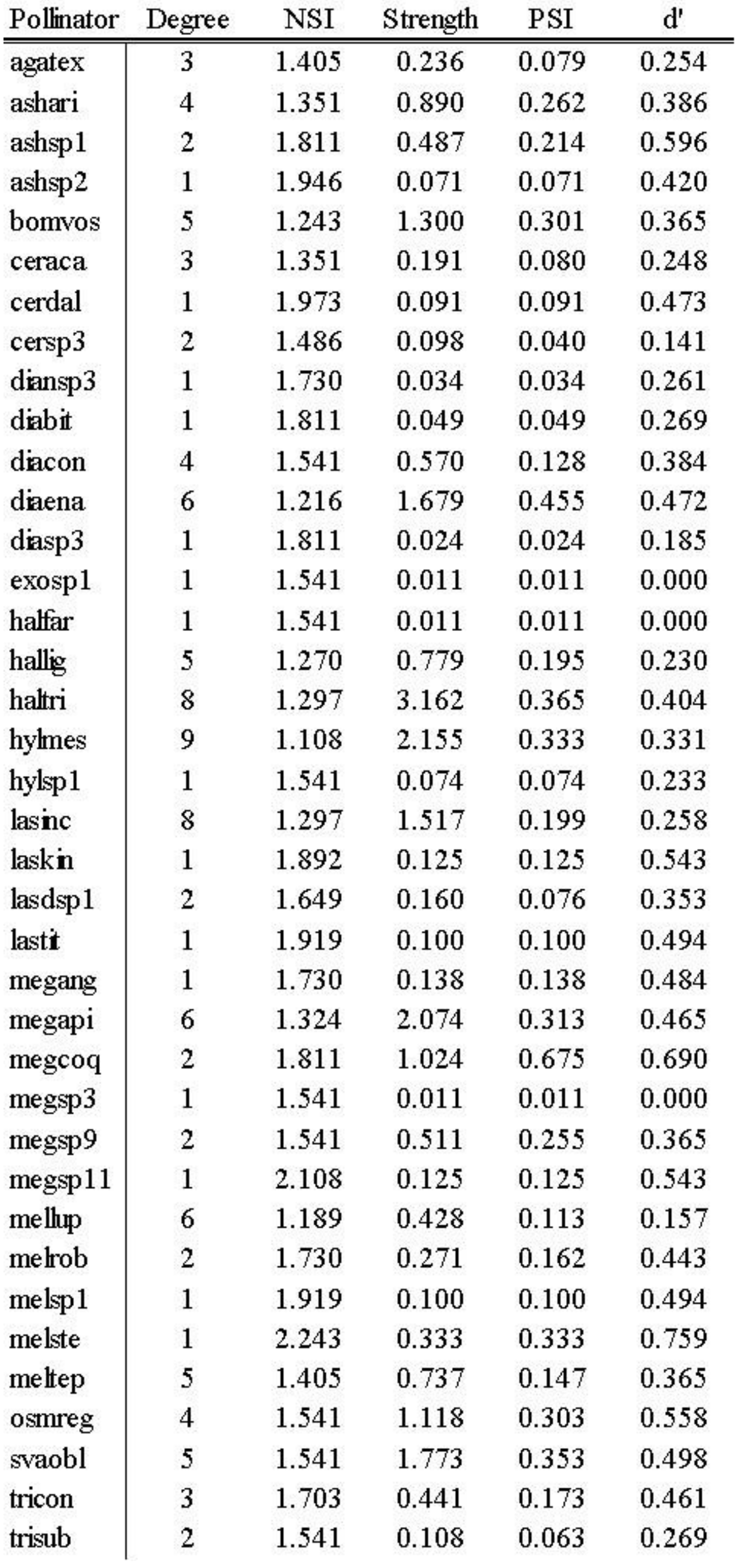


Figure 8.  Putah Creek 2006.  One-mode gplot

Table 3. Putah Creek 2006. Species-level indices.



| Pollinator | Degree | NSI | Strength | PSI | d' |
|---|---|---|---|---|---|
| agatex | 3 | 1.405 | 0.236 | 0.079 | 0.254 |
| ashari | 4 | 1.351 | 0.890 | 0.262 | 0.386 |
| ashsp1 | 2 | 1.811 | 0.487 | 0.214 | 0.596 |
| ashsp2 | 1 | 1.946 | 0.071 | 0.071 | 0.420 |
| bomvos | 5 | 1.243 | 1.300 | 0.301 | 0.365 |
| ceraca | 3 | 1.351 | 0.191 | 0.080 | 0.248 |
| cerdal | 1 | 1.973 | 0.091 | 0.091 | 0.473 |
| cersp3 | 2 | 1.486 | 0.098 | 0.040 | 0.141 |
| diansp3 | 1 | 1.730 | 0.034 | 0.034 | 0.261 |
| diabit | 1 | 1.811 | 0.049 | 0.049 | 0.269 |
| diacon | 4 | 1.541 | 0.570 | 0.128 | 0.384 |
| diaena | 6 | 1.216 | 1.679 | 0.455 | 0.472 |
| diasp3 | 1 | 1.811 | 0.024 | 0.024 | 0.185 |
| exosp1 | 1 | 1.541 | 0.011 | 0.011 | 0.000 |
| halfar | 1 | 1.541 | 0.011 | 0.011 | 0.000 |
| hallig | 5 | 1.270 | 0.779 | 0.195 | 0.230 |
| haltri | 8 | 1.297 | 3.162 | 0.365 | 0.404 |
| hylmes | 9 | 1.108 | 2.155 | 0.333 | 0.331 |
| hylsp1 | 1 | 1.541 | 0.074 | 0.074 | 0.233 |
| lasinc | 8 | 1.297 | 1.517 | 0.199 | 0.258 |
| laskin | 1 | 1.892 | 0.125 | 0.125 | 0.543 |
| lasdsp1 | 2 | 1.649 | 0.160 | 0.076 | 0.353 |
| lastit | 1 | 1.919 | 0.100 | 0.100 | 0.494 |
| megang | 1 | 1.730 | 0.138 | 0.138 | 0.484 |
| megapi | 6 | 1.324 | 2.074 | 0.313 | 0.465 |
| megcoq | 2 | 1.811 | 1.024 | 0.675 | 0.690 |
| megsp3 | 1 | 1.541 | 0.011 | 0.011 | 0.000 |
| megsp9 | 2 | 1.541 | 0.511 | 0.255 | 0.365 |
| megsp11 | 1 | 2.108 | 0.125 | 0.125 | 0.543 |
| mellup | 6 | 1.189 | 0.428 | 0.113 | 0.157 |
| melrob | 2 | 1.730 | 0.271 | 0.162 | 0.443 |
| melsp1 | 1 | 1.919 | 0.100 | 0.100 | 0.494 |
| melste | 1 | 2.243 | 0.333 | 0.333 | 0.759 |
| meltep | 5 | 1.405 | 0.737 | 0.147 | 0.365 |
| osmreg | 4 | 1.541 | 1.118 | 0.303 | 0.558 |
| svaobl | 5 | 1.541 | 1.773 | 0.353 | 0.498 |
| tricon | 3 | 1.703 | 0.441 | 0.173 | 0.461 |
| trisub | 2 | 1.541 | 0.108 | 0.063 | 0.269 |

Figure 9. San Joaquin Refuge (2005). Pollination web combining data from 3 study sites within the refuge. The following are the plant species represented in the web: a)*Brassica nigra*, b) *Centromadia pungens* c) *Grindelia stricta*, d) *Helianthus annus*, e) *Heliotropium curassavicum*, f) *Lepidium latifolium*, g) *Lotus unifoliolatus*, h) *Melilotus alba*, i) *Phyla nodiflora*, j) *Sylibum marianum*, k) *Frankenia salina*, l) *Convolvulus arvensis*, m) *Datura wrightii*

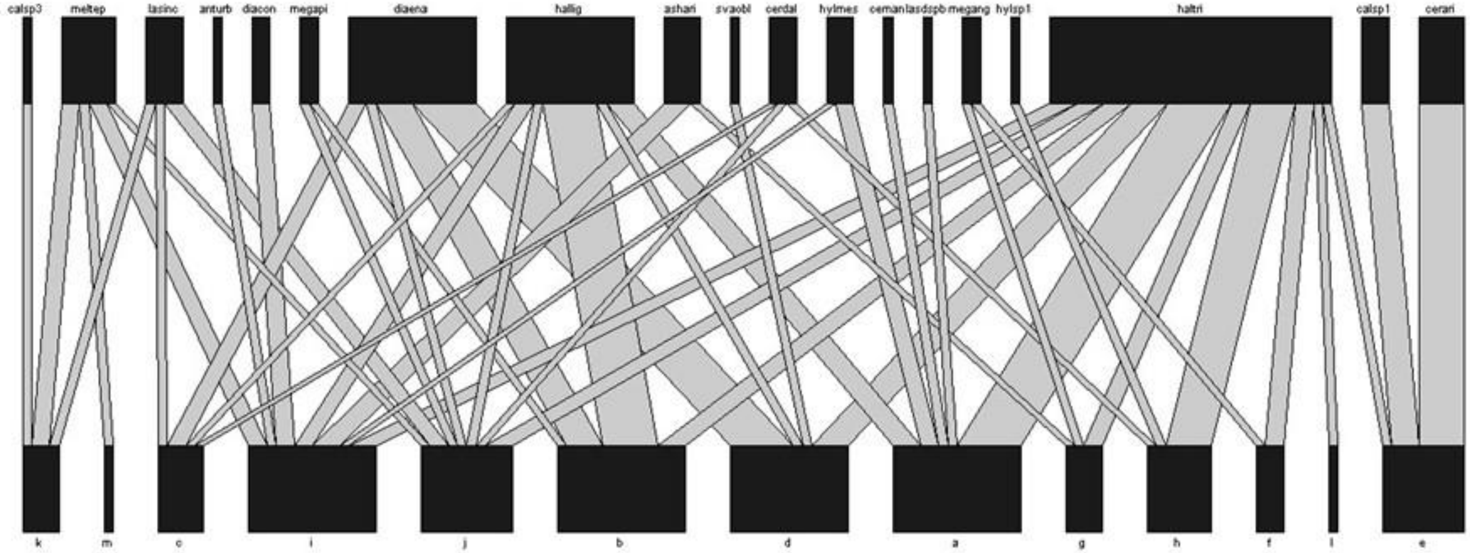


Figure 10. San Joaquin Refuge (2005). Pollination matrix with squares representing possible links between bee species (X-axis) and plant species (Y-axis). The shading of the box represents the interaction strength between species. a)*Brassica nigra*, b) *Centromadia pungens* c) *Grindelia stricta*, d) *Helianthus annus*, e) *Heliotropium curassavicum*, f) *Lepidium latifolium*, g) *Lotus unifoliolatus*, h) *Melilotus alba*, i) *Phyla nodiflora*, j) *Sylibum marianum*, k) *Frankenia salina*, l) *Convolvulus arvensis*, m) *Datura wrightii*

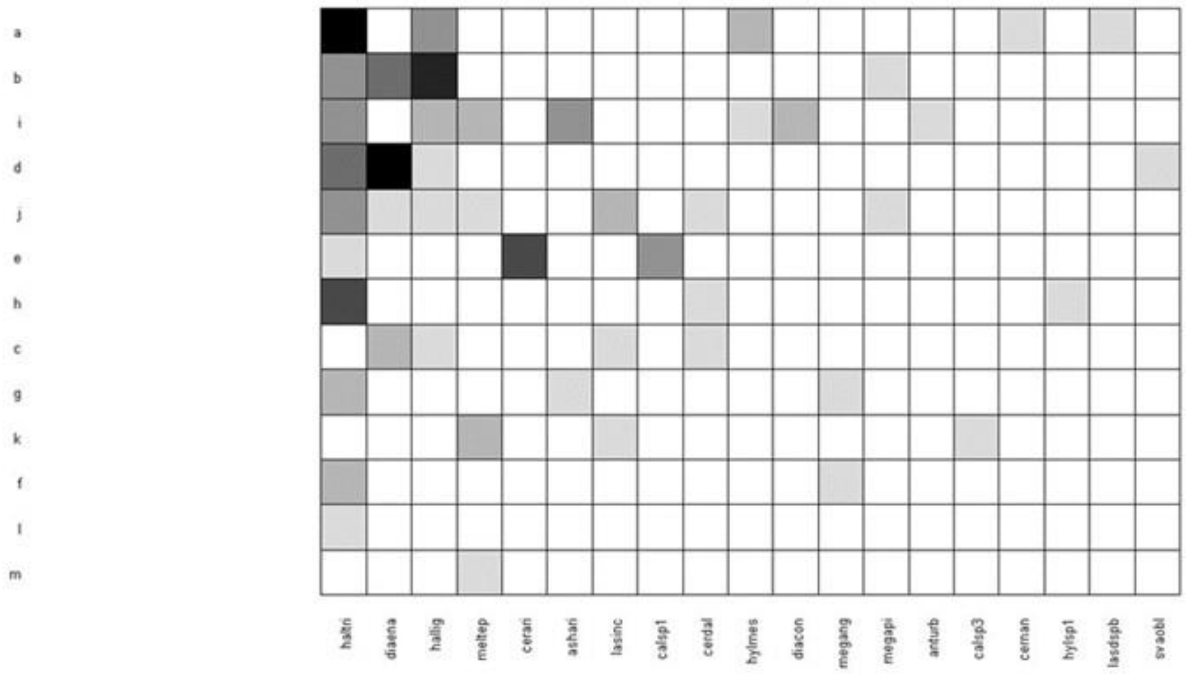


Figure 11. San Joaquin Wildlife Refuge (2005) two-mode gplot

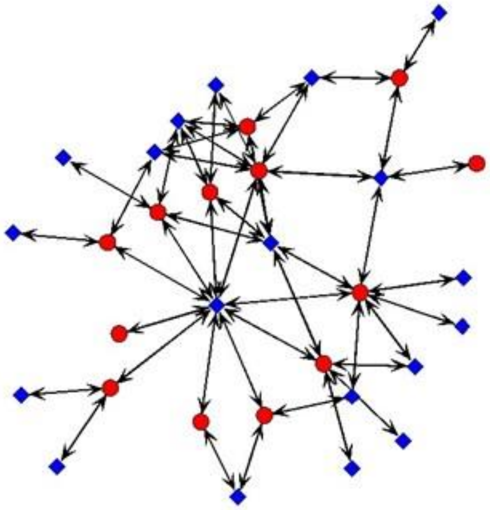


Figure 12. San Joaquin Refuge (2005). One-mode gplot

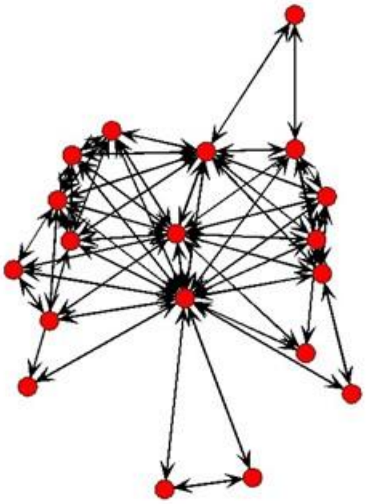
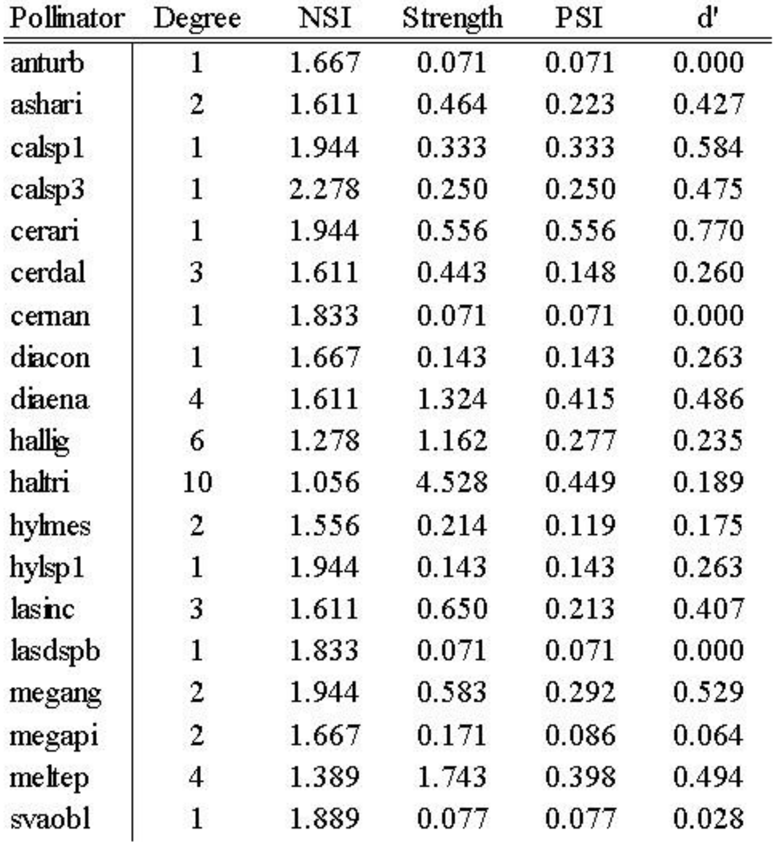


Table 4.  San Joaquin Refuge (2005).  Species-level indices for bee pollination network.



| Pollinator | Degree | NSI | Strength | PSI | d' |
|---|---|---|---|---|---|
| anturb | 1 | 1.667 | 0.071 | 0.071 | 0.000 |
| ashari | 2 | 1.611 | 0.464 | 0.223 | 0.427 |
| calsp1 | 1 | 1.944 | 0.333 | 0.333 | 0.584 |
| calsp3 | 1 | 2.278 | 0.250 | 0.250 | 0.475 |
| cerari | 1 | 1.944 | 0.556 | 0.556 | 0.770 |
| cerdal | 3 | 1.611 | 0.443 | 0.148 | 0.260 |
| cernan | 1 | 1.833 | 0.071 | 0.071 | 0.000 |
| diacon | 1 | 1.667 | 0.143 | 0.143 | 0.263 |
| diaena | 4 | 1.611 | 1.324 | 0.415 | 0.486 |
| hallig | 6 | 1.278 | 1.162 | 0.277 | 0.235 |
| haltri | 10 | 1.056 | 4.528 | 0.449 | 0.189 |
| hylmes | 2 | 1.556 | 0.214 | 0.119 | 0.175 |
| hylsp1 | 1 | 1.944 | 0.143 | 0.143 | 0.263 |
| lasinc | 3 | 1.611 | 0.650 | 0.213 | 0.407 |
| lasdspb | 1 | 1.833 | 0.071 | 0.071 | 0.000 |
| megang | 2 | 1.944 | 0.583 | 0.292 | 0.529 |
| megapi | 2 | 1.667 | 0.171 | 0.086 | 0.064 |
| meltep | 4 | 1.389 | 1.743 | 0.398 | 0.494 |
| svaobl | 1 | 1.889 | 0.077 | 0.077 | 0.028 |

Figure 13. San Joaquin Refuge (2006). Pollination web. The following is a plant list for this web:
a) *Convolvulus arvensis*, b) *Grindelia stricta*, c) *Lepidium latifolium*, d) *Brassica nigra*,
e) *Centramadia pungens*, f) *Helianthus annuus*, g) *Heliotropium curassavicum*, h) *Cephalanthus occidentalis.*

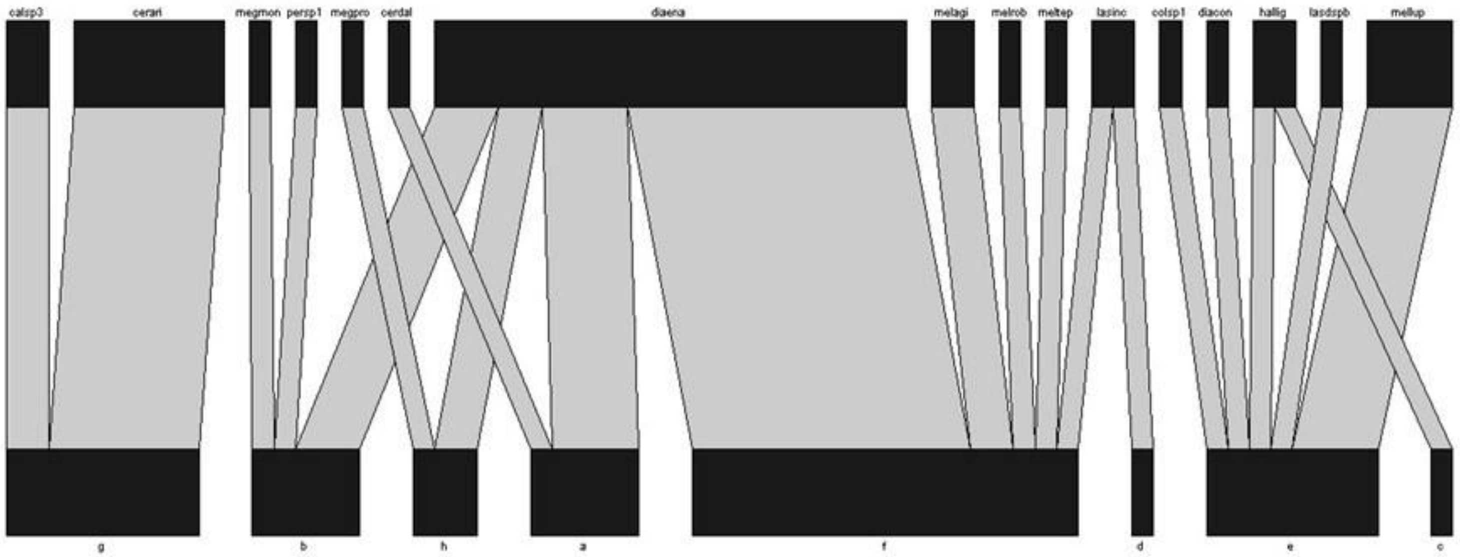


Figure 14. San Joaquin Refuge (2006) Pollination matrix
a) *Convolvulus arvensis*, b) *Grindelia stricta*, c) *Lepidium latifolium*, d) *Brassica nigra*,
e) *Centramadia pungens*, f) *Helianthus annuus*, g) *Heliotropium curassavicum*, h) *Cephalanthus occidentalis.*

Figure 14. San Joaquin Refuge (2006) Pollination matrix
a) *Convolvulus arvensis*, b) *Grindelia stricta*, c) *Lepidium latifolium*, d) *Brassica nigra*,
e) *Centramadia pungens*, f) *Helianthus annuus*, g) *Heliotropium curassavicum*, h) *Cephalanthus occidentalis.*

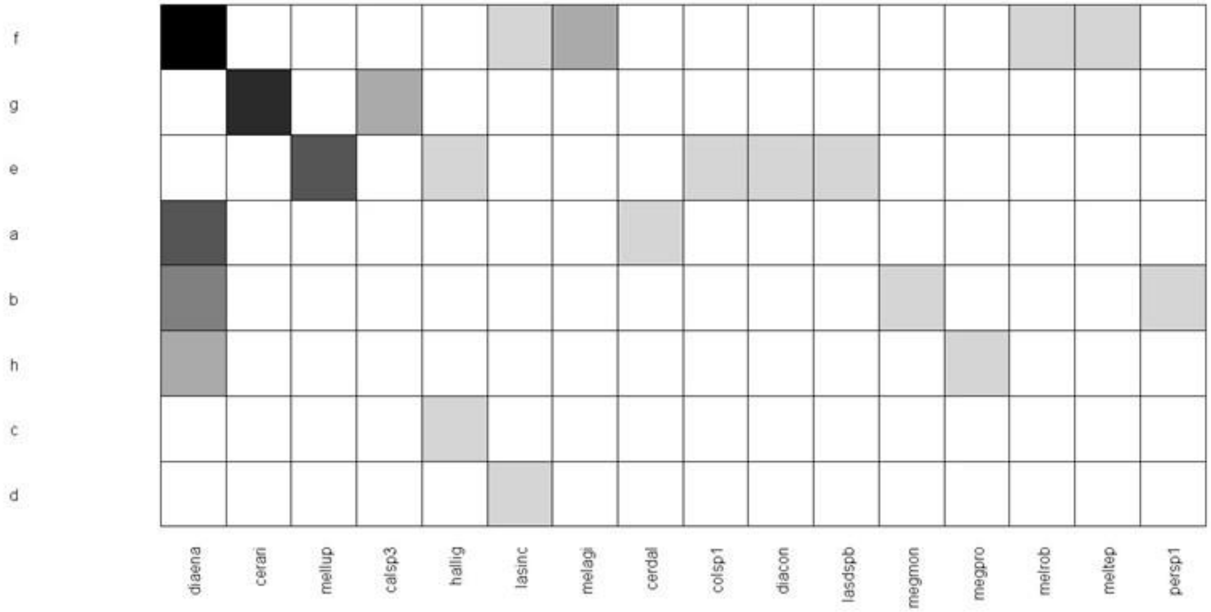


Figure 15. San Joaquin Refuge (2006). two-mode gplot

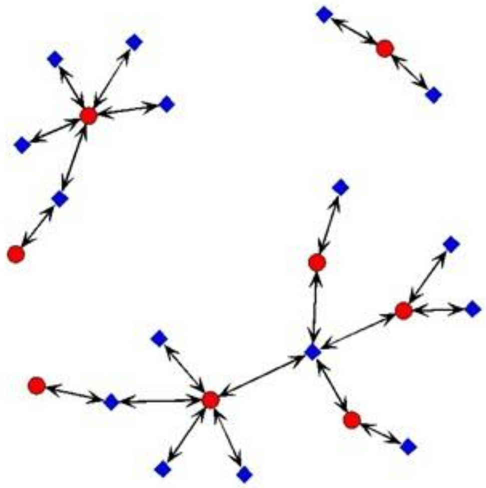


Figure 16. San Joaquin Refuge (2006).  One-mode gplot

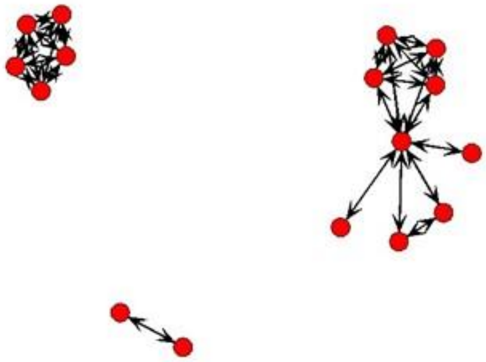
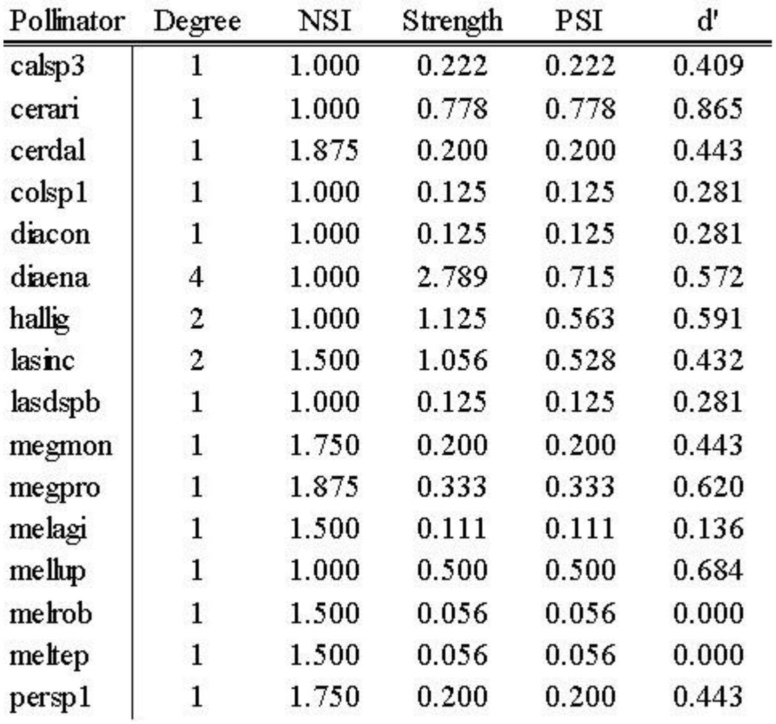


Table 5. San Joaquin Refuge (2006). Species-level indices.



| Pollinator | Degree | NSI | Strength | PSI | d' |
|---|---|---|---|---|---|
| calsp3 | 1 | 1.000 | 0.222 | 0.222 | 0.409 |
| cerari | 1 | 1.000 | 0.778 | 0.778 | 0.865 |
| cerdal | 1 | 1.875 | 0.200 | 0.200 | 0.443 |
| colsp1 | 1 | 1.000 | 0.125 | 0.125 | 0.281 |
| diacon | 1 | 1.000 | 0.125 | 0.125 | 0.281 |
| diaena | 4 | 1.000 | 2.789 | 0.715 | 0.572 |
| hallig | 2 | 1.000 | 1.125 | 0.563 | 0.591 |
| lasinc | 2 | 1.500 | 1.056 | 0.528 | 0.432 |
| lasdspb | 1 | 1.000 | 0.125 | 0.125 | 0.281 |
| megmon | 1 | 1.750 | 0.200 | 0.200 | 0.443 |
| megpro | 1 | 1.875 | 0.333 | 0.333 | 0.620 |
| melagi | 1 | 1.500 | 0.111 | 0.111 | 0.136 |
| mellup | 1 | 1.000 | 0.500 | 0.500 | 0.684 |
| melrob | 1 | 1.500 | 0.056 | 0.056 | 0.000 |
| meltep | 1 | 1.500 | 0.056 | 0.056 | 0.000 |
| persp1 | 1 | 1.750 | 0.200 | 0.200 | 0.443 |

Figure 17. Cosumnes River Preserve (2006). Pollination web. The following is a plant list for this web: a) *Brassica nigra*, b) *Centauria solstitialis*, c) *Centromadia pungens*, d) *Helianthus annuus*, e) *Helminthotheca echioides*, f) *Polygonum hydropiperoides*, g) *Rosa californica*, h) *Sylibum marianum*, i) *Convolvulus arvensis*, j) *Eryngium vaseyi*, k) *Lotus unifoliolatus*, l) *Mentha spicata*, m) *Phyla nodiflora*

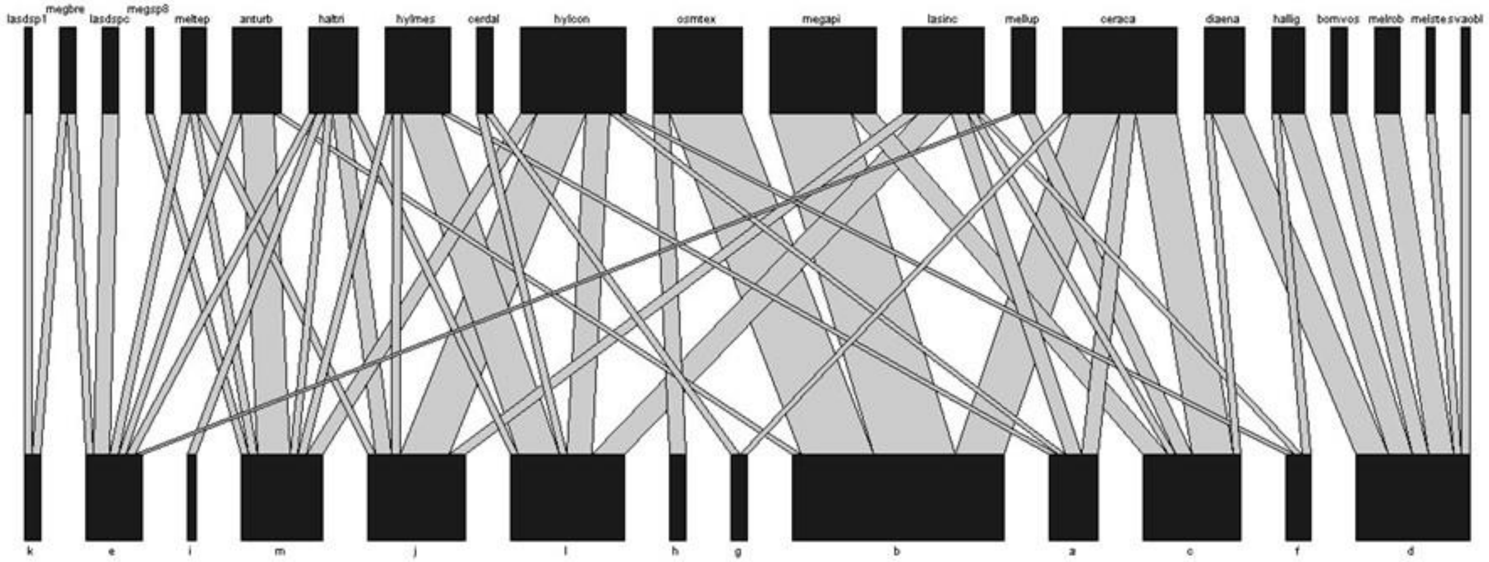


Figure 18. Cosumnes River Preserve (2006). Pollination matrix a) *Brassica nigra*, b) *Centauria solstitialis*, c) *Centromadia pungens*, d) *Helianthus annuus*, e) *Helminthotheca echioides*, f) *Polygonum hydropiperoides*, g) *Rosa californica*, h) *Sylibum marianum*, i) *Convolvulus arvensis*, j) *Eryngium vaseyi*, k) *Lotus unifoliolatus*, l) *Mentha spicata*, m) *Phyla nodiflora*

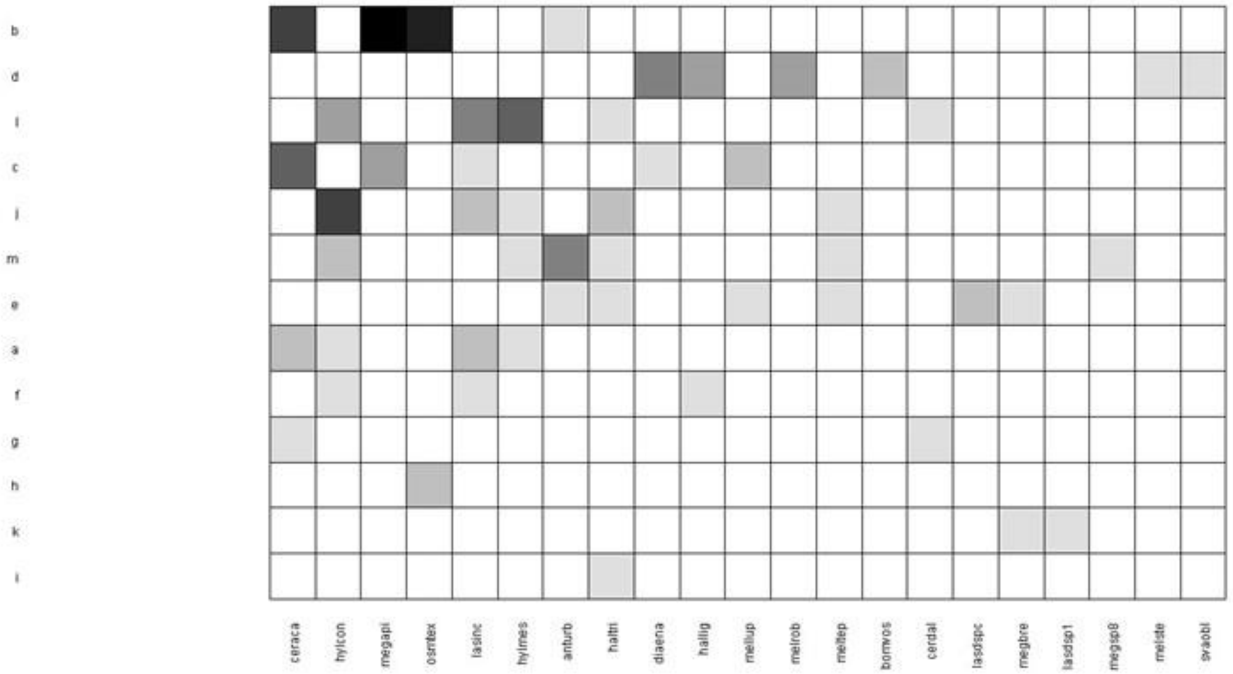


Figure 19. Cosumnes River Preserve (2006). two-mode gplot

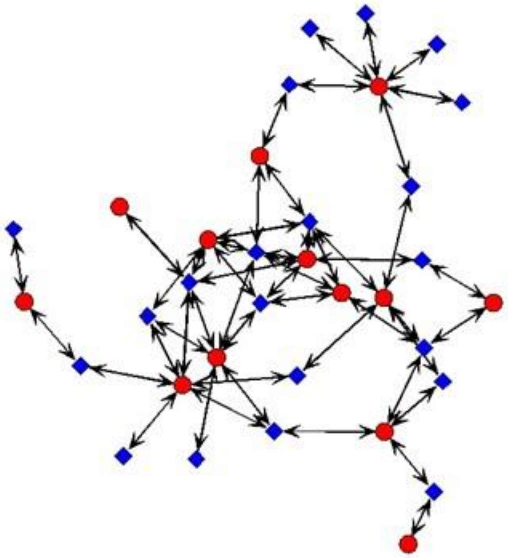


Figure 20. Cosumnes River Preserve (2006). one-mode gplot

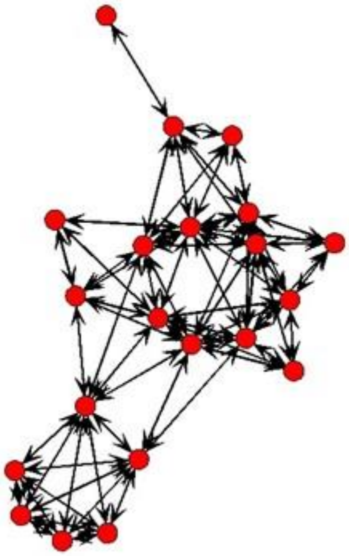
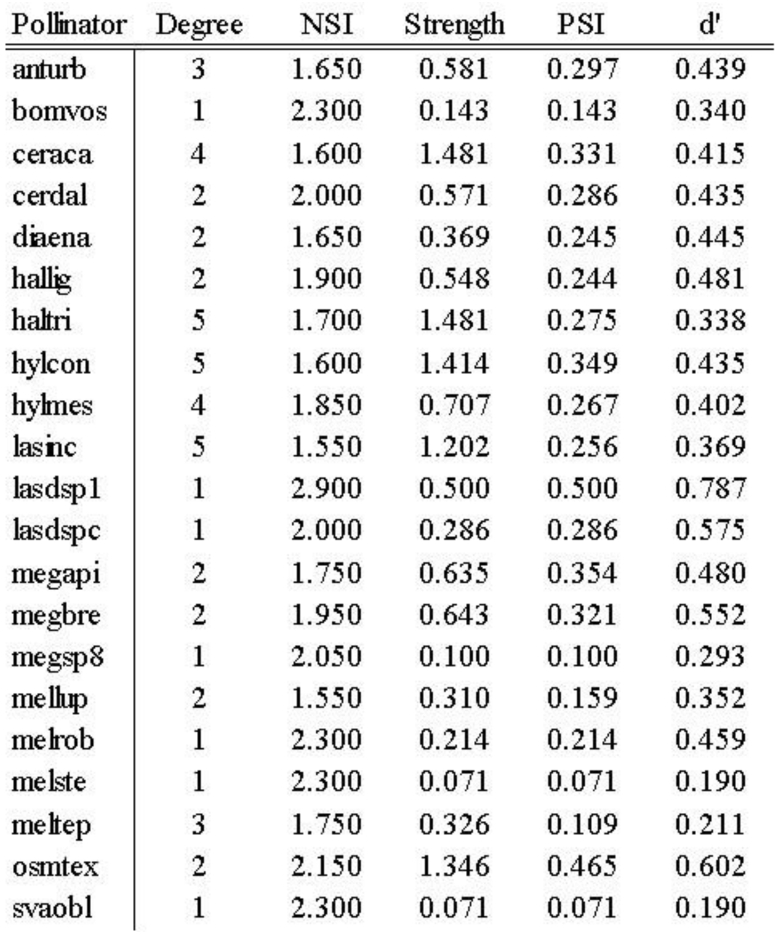


Table 6. Cosumnes River Preserve (2006). Species level indices



| Pollinator | Degree | NSI | Strength | PSI | d' |
|---|---|---|---|---|---|
| anturb | 3 | 1.650 | 0.581 | 0.297 | 0.439 |
| bomvos | 1 | 2.300 | 0.143 | 0.143 | 0.340 |
| ceraca | 4 | 1.600 | 1.481 | 0.331 | 0.415 |
| cerdal | 2 | 2.000 | 0.571 | 0.286 | 0.435 |
| diaena | 2 | 1.650 | 0.369 | 0.245 | 0.445 |
| hallig | 2 | 1.900 | 0.548 | 0.244 | 0.481 |
| haltri | 5 | 1.700 | 1.481 | 0.275 | 0.338 |
| hylcon | 5 | 1.600 | 1.414 | 0.349 | 0.435 |
| hylmes | 4 | 1.850 | 0.707 | 0.267 | 0.402 |
| lasinc | 5 | 1.550 | 1.202 | 0.256 | 0.369 |
| lasdsp1 | 1 | 2.900 | 0.500 | 0.500 | 0.787 |
| lasdspc | 1 | 2.000 | 0.286 | 0.286 | 0.575 |
| megapi | 2 | 1.750 | 0.635 | 0.354 | 0.480 |
| megbre | 2 | 1.950 | 0.643 | 0.321 | 0.552 |
| megsp8 | 1 | 2.050 | 0.100 | 0.100 | 0.293 |
| mellup | 2 | 1.550 | 0.310 | 0.159 | 0.352 |
| melrob | 1 | 2.300 | 0.214 | 0.214 | 0.459 |
| melste | 1 | 2.300 | 0.071 | 0.071 | 0.190 |
| meltep | 3 | 1.750 | 0.326 | 0.109 | 0.211 |
| osmtex | 2 | 2.150 | 1.346 | 0.465 | 0.602 |
| svaobl | 1 | 2.300 | 0.071 | 0.071 | 0.190 |

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## Appendix A

List of bee species with abundances provided for each method of collection. Collection methods are aerial netting and pan trapping. The pan traps were painted yellow and blue with fluorescent paint with one set remaining white.

| **Family** | **Bee Species** | **Net** | | **Pan** | |
|---|---|---|---|---|---|
| | | **2005** | **2006** | **2005** | **2006** |
| Andrenidae | *Andrena nigrocaerulea* Cockerell | | 1 | | |
| | *Andrena* sp. #1 | | 1 | | |
| | *Calliopsis scutellaris* Fowler | | 1 | | 10 |
| | *Calliopsis* sp. # 1 | 3 | | 4 | |
| | *Calliopsis* sp. #2 | | 1 | 1 | 4 |
| | *Calliopsis* sp. #3 | 1 | 3 | 1 | 17 |
| | *Perdita* sp. #1 | | 1 | | |
| | *Perdita* sp. #2 | | | | 1 |
| Apidae | *Anthophora urbana* Cresson | 1 | 13 | 4 | 21 |
| | *Bombus californicus* Smith | 1 | | | |
| | *Bombus crotchii* Cresson | | | 1 | |
| | *Bombus vosnesenskii* Radoszkowski | 16 | 17 | 1 | 3 |
| | *Ceratina acantha* Provancher | 6 | 27 | 1 | 4 |
| | *Ceratina arizonensis* Cockerell | 6 | 10 | 3 | 4 |
| | *Ceratina dallatorreana* Friese | 2 | 6 | 31 | 25 |
| | *Ceratina nanula* Cockerell | 2 | 1 | 3 | |
| | *Ceratina* sp.#3 | 4 | 4 | 1 | |
| | *Coelioxys* sp.#1 | 1 | | | |
| | *Diadasia bituberculata* (Cresson) | | 2 | | 1 |
| | *Diadasia consociata* Timberlake | 1 | 41 | 1 | 58 |
| | *Diadasia enavata* (Cresson) | 16 | 133 | 11 | 172 |
| | *Diadasia ochracea* (Cockerell) | | | | 1 |

| | | | | |
|---|---|---|---|---|
| *Diadasia* sp. #1 | | | | 21 |
| *Diadasia* sp. #2 | | 1 | | 6 |
| *Diadasia* sp. #3 | | 1 | | |
| *Diadasia* sp. #4 | | 5 | | |
| *Diadasia* sp. #5 | | | | 4 |
| *Diadasia* sp. #6 | | | | 2 |
| *Exomalopsis sp. #1* | | 1 | 1 | 6 |
| *Exomalopsis* sp. #2 | | | | 1 |
| *Exomalopsis* sp. #3 | | | | 1 |
| *Exomalopsis* sp. #4 | | | | 1 |
| *Melissodes agilis* Cresson | | 2 | | 10 |
| *Melissodes lupina* Cresson | | 24 | 10 | 116 |
| *Melissodes robustior* Cockerell | 2 | 14 | 4 | 25 |
| *Melissodes* sp. #1 | | 1 | | 1 |
| *Melissodes* sp. #2 | | | | 1 |
| *Melissodes* sp. #5 | | | | 1 |
| *Melissodes* sp. #6 | | | | 2 |
| *Melissodes* sp. #7 | | | | 1 |
| *Melissodes stearnsi* Cockerell | 3 | 3 | 10 | 37 |
| *Melissodes tepida* Cresson | 3 | 17 | 16 | 117 |
| *Oreopasites* sp. #1 | | | | |
| *Peponapis pruinosa* (Say) | | | | |
| *Svastra obliqua* (Say) | 11 | | 7 | |

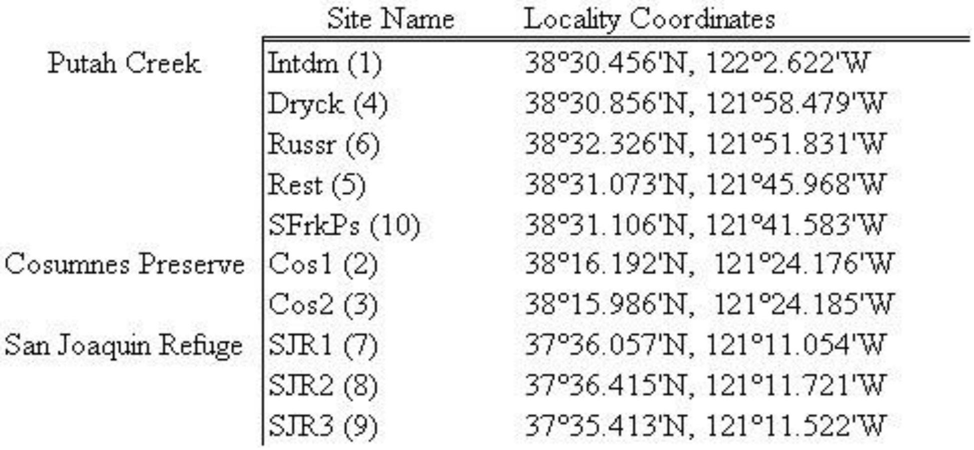
| | | | | | |
|---|---|---|---|---|---|
| | *Triepeolus concavus* (Cresson) | | 4 | | |
| | *Triepeolus* sp. #2 | | 1 | | 5 |
| | *Triepeolus* sp. #3 | | 1 | | |
| | *Triepeolus subnitens* Cockerell & Timberlake | | | | 5 |
| | *Xeromelecta californica* (Cresson) | | 4 | | |
| Colletidae | *Colletes* sp. #1 | | 1 | | |
| | *Colletes* sp. #2 | | 1 | | |
| | *Hylaeus conspicuus* (Metz) | | 14 | | 91 |
| | *Hylaeus mesillae* (Cockerell) | 8 | 69 | 7 | 41 |
| | *Hylaeus* sp #1 | 6 | 7 | 1 | |
| | *Hylaeus* sp. #2 | 8 | | 3 | |
| Halictidae | *Agapostemon texanus* Cresson | 2 | 5 | 17 | 170 |
| | *Halictus farinosus* Smith | | 1 | | 4 |
| | *Halictus ligatus* Say | 41 | 42 | 29 | 59 |
| | *Halictus tripartitus* Cockerell | 36 | 57 | 825 | 1210 |
| | *Lasioglossum incompletum* (Crawford) | 5 | 51 | 151 | 1848 |
| | *Lasioglossum (Dialictus)* sp. B | 1 | 1 | 2 | 24 |
| | *Lasioglossum (Dialictus)* sp. C | | 2 | | 6 |
| | *Lasioglossum (Dialictus)* sp.#1 | 3 | 9 | 7 | 65 |
| | *Lasioglossum kincaidii* (Cockerell) | 1 | 1 | 1 | 19 |
| | *Lasioglossum (Evylaeus)* sp. #1 | | 1 | 1 | 11 |
| | *Lasioglossum titusi* (Crawford) | | 1 | | |
| | *Lasioglossum (Evylaeus)* sp. #1 | | 1 | | 11 |
| | *Lasioglossum (Evylaeus)* sp. #2 | | 1 | | |
| | *Lasioglossum (Evylaeus)* sp. #4 | | | | 4 |

| | | | | | |
|---|---|---|---|---|---|
| | *Sphecodes* sp. #1 | | | | 6 |
| | *Sphecodes* sp. #2 | | | | 15 |
| | *Sphecodes* sp. #3 | | | | 1 |
| Megachilidae | *Anthidiellum notatum* (Latreille) | | 2 | | |
| | *Anthidium edwardsii* Cresson | | | | 1 |
| | *Anthidium* sp. #1 Fabricius | | | | 1 |
| | *Anthidium* sp. #2 Fabricius | | 1 | | |
| | *Ashmeadiella aridula* Cockerell | 6 | 22 | 5 | 7 |
| | *Ashmeadiella* sp. #1 Cockerell | 1 | 3 | 1 | 4 |
| | *Ashmeadiella* sp. #2 Cockerell | 2 | 1 | | 2 |
| | *Ashmeadiella* sp. #4 Cockerell | | | | 2 |
| | *Ashmeadiella* sp. #6 Cockerell | | 1 | | 2 |
| | *Dianthidium* sp. #1 Cockerell | | | | 1 |
| | *Dianthidium* sp. #2 Cockerell | | | | 1 |
| | *Dianthidium* sp. #3 Cockerell | | 1 | | |
| | *Megachile angelarum* Cockerell | 7 | 8 | 1 | |
| | *Megachile apicalis* Spinola | 13 | 37 | 4 | 29 |
| | *Megachile brevis* Say | | 3 | | 10 |
| | *Megachile coquilletti* Cockerell | | 4 | | 1 |
| | *Megachile lippiae* Cockerell | | | | 2 |
| | *Megachile montivaga* Cresson | | 1 | | 2 |
| | *Megachile parallela* Smith | | | | 1 |
| | *Megachile perihirta* Cockerell | 2 | 1 | 1 | |
| | *Megachile prosopidis* Cockerell | | 1 | | |
| | *Megachile rotundata* (Fabricius) | 1 | 2 | 5 | 7 |

| | | | | |
|---|---|---|---|---|
| *Megachile* sp. #1 Latreille | | | | 3 |
| *Megachile* sp. #2 Latreille | | | | 3 |
| *Megachile* sp. #3 Latreille | | 1 | | 4 |
| *Megachile* sp. #4 Latreille | | | | 1 |
| *Megachile* sp. #5 Latreille | | 1 | | |
| *Megachile* sp. #6 Latreille | | | | 1 |
| *Megachile* sp. #8 Latreille | | 1 | | 3 |
| *Megachile* sp. #9 Latreille | | 2 | | 1 |
| *Megachile* sp. #10 Latreille | | | | 1 |
| *Megachile* sp. #11 Latreille | | 1 | | |
| *Megachile* sp. #12 Latreille | | 1 | | |
| *Osmia nemoris* Sandhouse | 2 | | 24 | 7 |
| *Osmia regulina* Cockerell | | 13 | | 1 |
| *Osmia texana* Cresson | | 11 | | |
| **Total abundance** | **224** | **725** | **1196** | **4367** |
| **Total species** | **35** | **71** | **37** | **76** |

# Appendix B

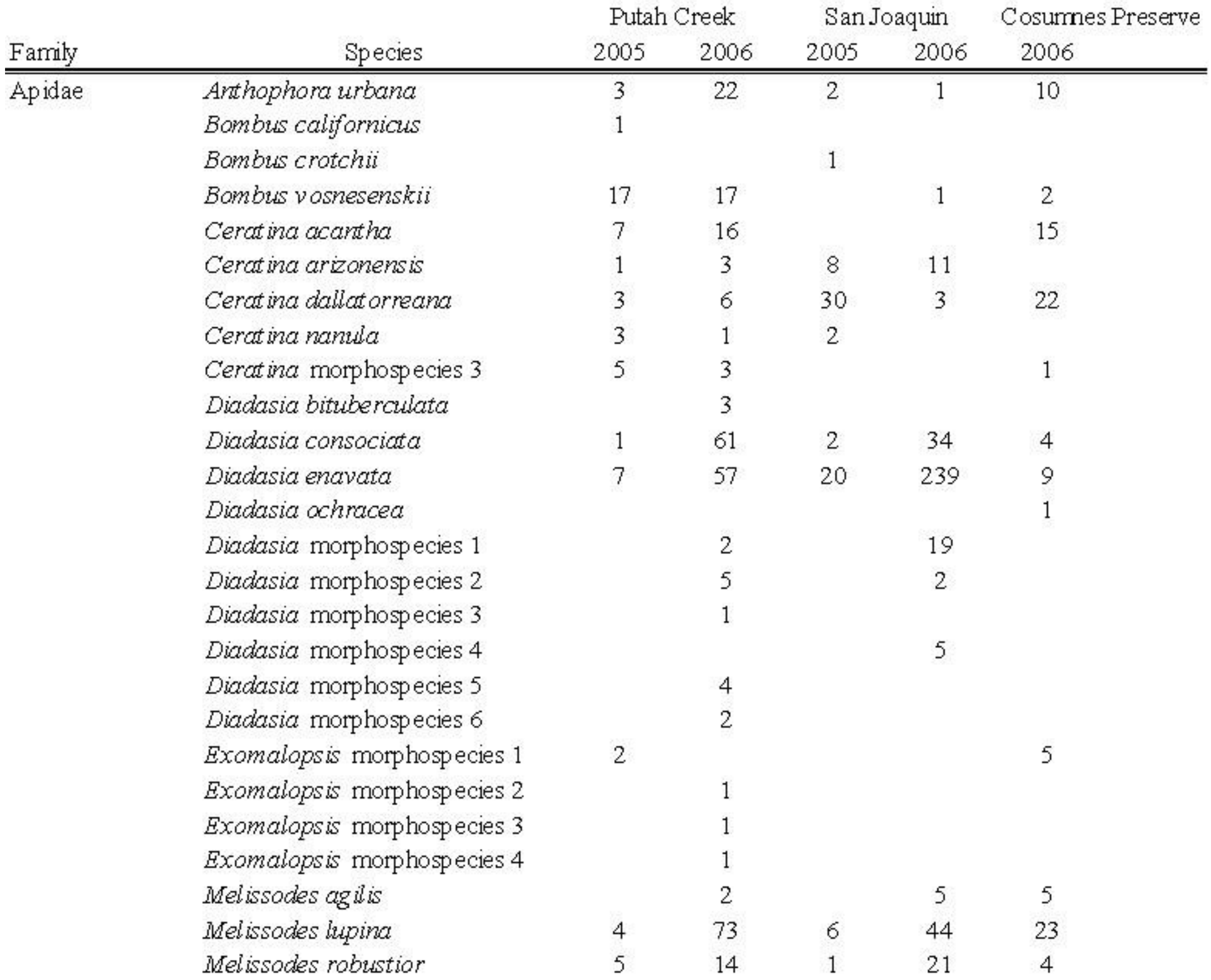
Location coordinates for study sites in the Putah Creek, San Joaquin Refuge, and Cosumnes Preserve regions.



|  | Site Name | Locality Coordinates |
|---|---|---|
| Putah Creek | Intdm (1) | 38°30.456'N, 122°2.622'W |
|  | Dryck (4) | 38°30.856'N, 121°58.479'W |
|  | Russr (6) | 38°32.326'N, 121°51.831'W |
|  | Rest (5) | 38°31.073'N, 121°45.968'W |
|  | SFrkPs (10) | 38°31.106'N, 121°41.583'W |
| Cosumnes Preserve | Cos1 (2) | 38°16.192'N, 121°24.176'W |
|  | Cos2 (3) | 38°15.986'N, 121°24.185'W |
| San Joaquin Refuge | SJR1 (7) | 37°36.057'N, 121°11.054'W |
|  | SJR2 (8) | 37°36.415'N, 121°11.721'W |
|  | SJR3 (9) | 37°35.413'N, 121°11.522'W |

# Appendix C

Bee species list for all study sites, 2006-2006.



| | | Putah Creek | | San Joaquin | | Cosumnes Preserve |
|---|---|---|---|---|---|---|
| Family | Species | 2005 | 2006 | 2005 | 2006 | 2006 |
| Apidae | *Anthophora urbana* | 3 | 22 | 2 | 1 | 10 |
| | *Bombus californicus* | 1 | | | | |
| | *Bombus crotchii* | | | 1 | | |
| | *Bombus vosnesenskii* | 17 | 17 | | 1 | 2 |
| | *Ceratina acantha* | 7 | 16 | | | 15 |
| | *Ceratina arizonensis* | 1 | 3 | 8 | 11 | |
| | *Ceratina dallatorreana* | 3 | 6 | 30 | 3 | 22 |
| | *Ceratina nanula* | 3 | 1 | 2 | | |
| | *Ceratina* morphospecies 3 | 5 | 3 | | | 1 |
| | *Diadasia bituberculata* | | 3 | | | |
| | *Diadasia consociata* | 1 | 61 | 2 | 34 | 4 |
| | *Diadasia enavata* | 7 | 57 | 20 | 239 | 9 |
| | *Diadasia ochracea* | | | | | 1 |
| | *Diadasia* morphospecies 1 | | 2 | | 19 | |
| | *Diadasia* morphospecies 2 | | 5 | | 2 | |
| | *Diadasia* morphospecies 3 | | 1 | | | |
| | *Diadasia* morphospecies 4 | | | | 5 | |
| | *Diadasia* morphospecies 5 | | 4 | | | |
| | *Diadasia* morphospecies 6 | | 2 | | | |
| | *Exomalopsis* morphospecies 1 | 2 | | | | 5 |
| | *Exomalopsis* morphospecies 2 | | 1 | | | |
| | *Exomalopsis* morphospecies 3 | | 1 | | | |
| | *Exomalopsis* morphospecies 4 | | 1 | | | |
| | *Melissodes agilis* | | 2 | | 5 | 5 |
| | *Melissodes lupina* | 4 | 73 | 6 | 44 | 23 |
| | *Melissodes robustior* | 5 | 14 | 1 | 21 | 4 |

| | | Putah Creek | | San Joaquin | | Cosumnes Preserve |
|---|---|---|---|---|---|---|
| Family | Species | 2005 | 2006 | 2005 | 2006 | 2006 |
| | *Melissodes stearnsi* | 13 | 35 | | 2 | 4 |
| | *Melissodes tepida* | 3 | 16 | 16 | 51 | 66 |
| | *Melissodes* morphospecies 1 | | 2 | | | |
| | *Melissodes* morphospecies 2 | | 1 | | | |
| | *Melissodes* morphospecies 5 | | | | 1 | |
| | *Melissodes* morphospecies 6 | | 2 | | | |
| | *Melissodes* morphospecies 7 | | 1 | | | |
| | *Oreopasites* morphospecies 1 | | | | 1 | |
| | *Peponapis pruinosa* | | 8 | | | |
| | *Svastra obliqua* | 17 | 38 | 1 | | 1 |
| | *Tripeolus concavus* | | 4 | | | |
| | *Triepeolus* morphospecies 2 | | 1 | | | 6 |
| | *Triepeolus* morphospecies 3 | | | | | 1 |
| | *Triepeolus subnitens* | | 4 | | | 1 |
| | *Xeromelecta californica* | | 4 | | | |
| Andrenidae | *Andrena* morphospecies 1 | | | | | 1 |
| | *Andrena nigrocaerulea* | | 1 | | | |
| | *Calliopsis* morphospecies 1 | | | 7 | | |
| | *Calliopsis* morphospecies 2 | | 4 | 1 | 2 | |
| | *Calliopsis* morphospecies 3 | | | 2 | 20 | |
| | *Calliopsis scutellaris* | | 1 | | 10 | |
| | *Perdita* morphospecies 1 | | | | 1 | |
| | *Perdita* morphospecies 2 | | | | | 1 |
| Colletidae | *Colletes* morphospecies 1 | | | | 1 | |
| | *Colletes* morphospecies 2 | | 1 | | | |
| | *Hylaeus conspicuus* | | 4 | | 2 | 99 |
| | *Hylaeus mesillae* | 12 | 71 | 3 | 3 | 36 |
| | *Hylaeus* morphospecies 1 | 6 | 7 | 1 | | |
| | *Hylaeus* morphospecies 2 | 11 | | | | |

| | | Putah Creek | | San Joaquin | | Cosumnes Preserve | |
|---|---|---|---|---|---|---|---|
| Family | Species | 2005 | 2006 | 2005 | 2006 | 2006 | |
| | *Dianthidium* morphospecies 1 | | | | | 1 | |
| | *Dianthidium* morphospecies 2 | | | | 1 | | |
| | *Dianthidium* morphospecies 3 | | 1 | | | | |
| | *Megachile angelarum* | 5 | 8 | 2 | | | |
| | *Megachile apicalis* | 15 | 30 | 2 | 2 | 34 | |
| | *Megachile brevis* | | 4 | | 2 | 7 | |
| | *Megachile coquelettii* | | 4 | | 1 | | |
| | *Megachile lippae* | | 1 | | 1 | | |
| | *Megachile montivaga* | | 1 | | 1 | 1 | |
| | *Megachile parallela* | | | | 1 | | |
| | *Megachile perihirta* | 3 | | | | 1 | |
| | *Megachile prosopidis* | | | | 1 | | |
| | *Megachile rotundata* | 2 | 6 | 4 | 2 | 1 | |
| | *Megachile* morphospecies 1 | | 1 | | 1 | 1 | |
| | *Megachile* morphospecies 2 | | 2 | | 1 | | |
| | *Megachile* morphospecies 3 | | 2 | | | 3 | |
| | *Megachile* morphospecies 4 | | | | | 1 | |
| | *Megachile* morphospecies 5 | | | | 1 | | |
| | *Megachile* morphospecies 6 | | | | 1 | | |
| | *Megachile* morphospecies 8 | | 1 | | 1 | 2 | |
| | *Megachile* morphospecies 9 | | 3 | | | | |
| | *Megachile* morphospecies 10 | | | | | 1 | |
| | *Megachile* morphospeces 11 | | 1 | | | | |
| | *Megachile* morphospecies 12 | | 1 | | | | |
| | *Osmia nemoris* | 21 | 7 | 5 | | | |
| | *Osmia regulina* | | 13 | | | 1 | |
| | *Osmia texana* | | | | | 11 | |
| | **Totals** | **493** | **3030** | **933** | **917** | **1178** | **6551** |