

Characterizing the Plant-Pollinator Interactions of *Bombus* in Santa Cruz County

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Introduction

The Randall Morgan insect collection, housed at the University of California Santa Cruz, consists of 70,000+ insect specimens collected in Santa Cruz county between 1989 and 1999. Randy Morgan collected in numerous habitat types and often revisited sample sites over several years. Every insect was given a detailed data label, including plant association data if the insect was caught on a plant. The presence of plant species names alongside their insect visitors is an extremely unique feature in a collection this size. It allows a rare glimpse into macroscopic plant-pollinator interactions and patterns over a wide variety of habitats.

This sizable dataset contains important information regarding study systems that have experienced change since the 1990s. All information related to sandhill chaparral habitat is crucial, as this is an increasingly rare habitat type that is giving way to development (Griffin 1978). Similarly, the species *Bombus occidentalis* was classified as vulnerable soon after Randy's collecting ended. This means the collection contains information useful for characterizing the natural history of *occidentalis* right before it experienced a significant decline.

Randy characterized the different habitats as the following: coastal prairie, dune/coastal scrub, chaparral, sandhill chaparral, riparian forest, grassland, and urban. While there are dozens of separate collection sites under each category, the data has been analyzed at the habitat level to get at broad characterizations of these habitat types. Every single site likely has individual variation, but this specificity is not within the scope of this project. Often, the urban category has been omitted from the results, as it both contains comparatively little information and has some blaring ambiguities in its definition that blur its usefulness.

Due to the nature of the sampling method, any conclusions based upon abundance data are significantly more challenging to determine. Therefore, it cannot currently be said conclusively whether the numbers of insects caught by Randy are any indicator for their relative abundance in the wild. Richness, however, can be used to reach conclusions. Thus, the following analysis is based upon the number of species present in the habitats, not the number of individuals.

The focus of this study is the bumblebee community of Santa Cruz. Bumblebees worldwide experienced a population drop sometime in the late 90s and into the 2000s (Cameron 2011). The cause of this is unconfirmed, although the role of a parasite is likely. Regardless, this places *Bombus* into unstable territory. Additionally, bumblebees and other native bees are considered higher efficiency pollinators than other groups of insects (Kremen 2002). This makes their decline extremely alarming both for the species themselves and the environments in which they pollinate. The following report is a general exploration into this massive dataset in order to characterize and understand how *Bombus* interacts with plant communities in different habitat types. It also explores differences between select species of *Bombus* to understand the level of variation within the genus. Hopefully this research will provide starting points to future, more in-depth research inquiries. The inferences and patterns presented here provide important, rare insight into the bumblebee community directly before the historic decline in their population. A largescale database of plant-pollinator interactions is extremely unique, and the following is merely a starting point in working with the unbelievable wealth of information left to the world by Randy Morgan.

Bombus Diversity

Habitat	Bombus Diversity (in species)
Coastal prairie	9
Dune/coastal scrub	8
Chaparral	7
Grassland	6
Riparian forest	6
Sandhill chaparral	4

Figure 1. The number of bumblebee species present in each habitat.

The total number of bumblebee species sampled across six habitat types reveals the differing *Bombus* diversity in these locations. Coastal prairie habitats contain every species of bumblebee that have been shown to be present in Santa Cruz by the Randy Morgan collection. The subsequent habitats contain subsets of this set of species. One species, *Bombus sonorus*, only appeared once during the entire ten-year sampling period, but as the data cannot attest to abundances, this outlier has not been removed from the data analysis. The species *Bombus caliginosus*, *Bombus melanopygus*, and *Bombus vosnesenskii* were the three species that were found within every single habitat type. Every other species was found in at least four different habitat types (excluding the single instance of *sonorus*). Coastal prairie had the highest total diversity of bumblebees, while sandhill chaparral had the lowest diversity at four species.

Plant Communities

Habitat	Plants visited by Bombus	Total Plant Community in Habitat	Percentage of total community visited by Bombus
Coastal prairie	93	395	24%
Dune/coastal scrub	57	195	29%
Sandhill chaparral	38	196	19%
Chaparral	34	208	16%
Grassland	31	160	19%
Riparian forest	24	130	18%

Figure 2. The number of plants visited by the genus *Bombus* versus the total number of plants recorded in that habitat.

The plant community visited by *Bombus* in different habitat types is presented both by number of plant species visited, as well as percentage of total plant community recorded in that habitat. The total number of plants is drawn from all of the plant data across Randy's records. This community represents every plant species visited by any insect over the course of Randy's sampling. It provides an idea of all the plants that are receptive to insect pollination. The percentage of *Bombus* pollinated plants is given by dividing the *Bombus* plant community with the total plant community for each habitat. Coastal prairie has the highest total number of insect receptive plants, yet bumblebees in dune/coastal scrub habitats use the highest percentage of the plant community available to them. Interestingly, Sandhill chaparral has the lowest diversity of bumblebee species, yet a relatively high plant percentage use at 19%. This could indicate that the few species present in that habitat have developed a more generalist pollination procedure, or simply that sandhill chaparral contains more plants usable to bumblebees, and that any amount of *Bombus* species will always maximize the number of plants they visit. Pollinators have been shown to switch between generalist and specialist pollination behavior over as short a time period as a single year (Pentanidou 2008). Despite this plasticity, all of this data has been pooled together from the ten-year sampling period and therefore represents the total average plant visitation patterns. The unpredictability of year to year changes is reduced by grouping multiple years of data together, providing a clearer picture. Also of note here is the extremely high number of plants present in coastal prairie, and the low number of plants in the riparian forest and grassland communities, indicating a higher concentration of pollinating insects in coastal prairie versus the other habitats.

Bombus-Plant Interactions

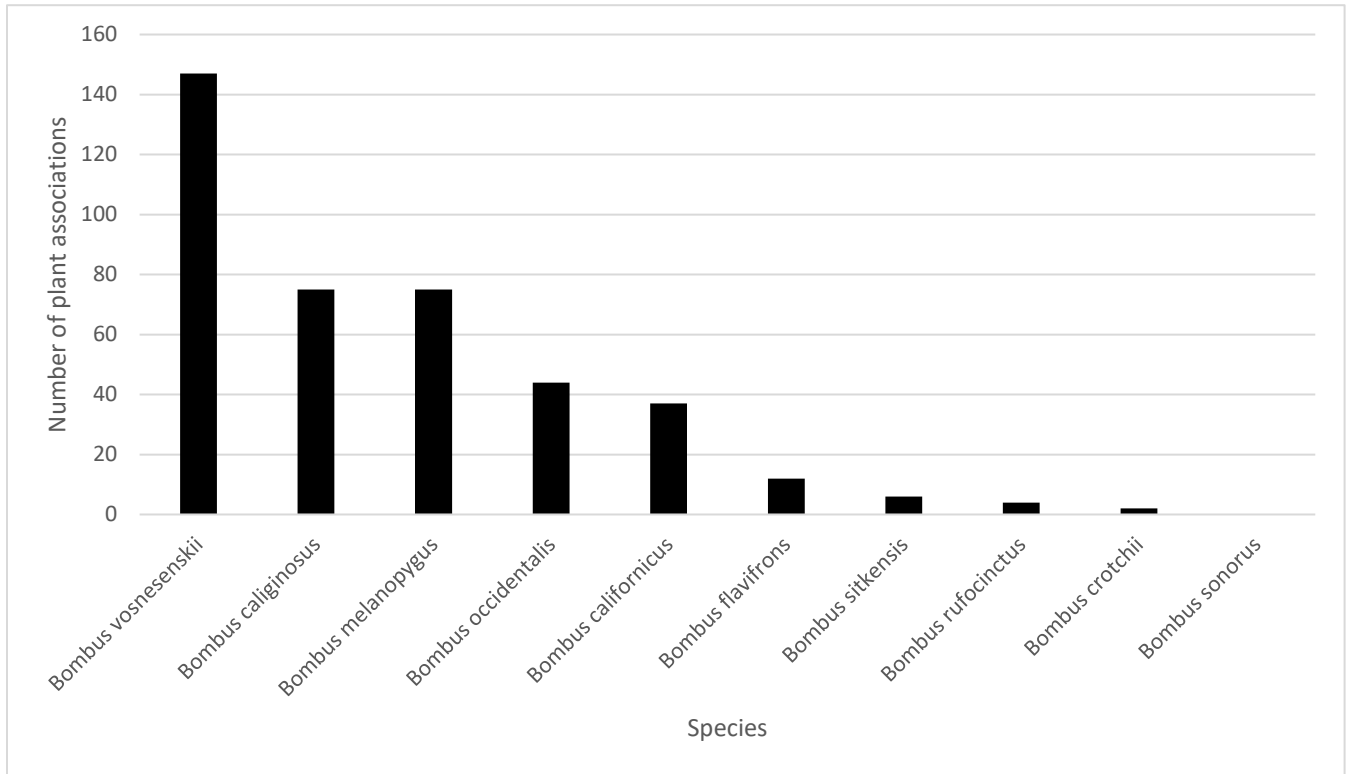


Figure 3. The total number of plant associations per *Bombus* species.

	Coastal prairie	Sandhill chaparral	Dune/coastal scrub	Grassland	Riparian forest	Chaparral
<i>Bombus vosnesenskii</i>	13%	15%	22%	9%	5%	7%
<i>Bombus caliginosus</i>	4%	8%	9%	6%	7%	7%
<i>Bombus melanopygus</i>	5%	7%	6%	8%	8%	6%
<i>Bombus occidentalis</i>	6%	0%	10%	3%	3%	0%
<i>Bombus californicus</i>	4%	0%	4%	4%	0%	3%
<i>Bombus flavifrons</i>	1%	1%	0%	1%	5%	0%
<i>Bombus sitkensis</i>	1%	0%	1%	0%	1%	1%
<i>Bombus rufocinctus</i>	0%	0%	2%	0%	0%	0%
<i>Bombus crotchii</i>	0%	0%	0%	0%	0%	1%
<i>Bombus sonorus</i>	0%	0%	0%	0%	0%	0%

Figure 4. A breakdown of plant visitations per *Bombus* species by percentage of total plant community.

Figure 3 shows the number of plant species visited by each *Bombus* species. Figure 4 shows a more detailed breakdown by habitat type and percentage of total plant community. *Bombus vosnesenskii* visited the highest diversity of plant species, at almost double the next highest species. *Caliginosus* and *melanopygus* have comparably sized plant communities, as do *occidentalis* and *californicus*. *Vosnesenskii* visits the highest percentage of the total plant community in three habitats, with chaparral, riparian forest, and grasslands having more even numbers of plant percentage use across every bumblebee species. These habitats all likely have similarly sized plant communities that are receptive to bumblebee pollination. Within grasslands, twenty-one plant species are unique to one bumblebee, while ten plant species are visited by at least two bumblebee species. This means that most of the plant-pollinator interactions within grasslands are specialist interactions. In riparian forest fifteen species of plant are unique to one bumblebee species, while nine species of plant overlap between at least two bumblebee species. While a majority of the plant interactions here are specialist, there is a higher amount of overlap than in grassland. In chaparral habitats, twenty-five plant species are specific to one species of *Bombus* and nine species are visited by at least two species of bee.

Understanding *Bombus occidentalis*

Bombus occidentalis was a common species until recent decades, when its numbers began to dramatically decline (Hatfield 2005). The time period of this dataset allows a pre-drop natural history characterization of *occidentalis* to be made. *Occidentalis* was present in five habitat types (every habitat except sandhill chaparral) but was mostly concentrated in coastal prairie and dune/coastal scrub. *Bombus vosnesenskii* is also present in significant number in these habitats and exists in the unique position of being one of the few bumblebee species that has remained common even after the historic decade long bumblebee decline (Hatfield 2005). While bumblebees on a whole seem to be declining, it is important to understand the differences of decline within the genus *Bombus*. Thus, a comparison between the plant communities that both species visit provides an insight both into the generalist/specialist leanings of these species, but also the pollination redundancy available to the plants in those habitats. If both species visit one plant, then the common *vosnesenskii* can continue pollinating the plant after *occidentalis* has

declined. The plants that only have *occidentalis* as their primary pollinators, however, are at risk of decline as well (Miñarro 2018).

Plants visited by <i>Bombus vosnesenskii</i>	Plants shared between <i>vosnesenskii</i> and <i>occidentalis</i>	Plants visited by <i>Bombus occidentalis</i>
<i>Aesculus californica</i>	<i>Acmispon glaber</i> var. <i>glaber</i>	<i>Acmispon americanus</i> var. <i>americanus</i>
<i>Alisma triviale</i>	<i>Baccharis glutinosa</i>	<i>Bidens laevis</i>
<i>Anthemis cotula</i>	<i>Cirsium vulgare</i>	<i>Brassica nigra</i>
<i>Calochortus luteus</i>	<i>Eschscholzia californica</i>	<i>Daucus carota</i>
<i>Carduus pycnocephalus</i> subsp. <i>pycnocephalus</i>	<i>Hirschfeldia incana</i>	<i>Grindelia camporum</i>
<i>Castilleja densiflora</i> subsp. <i>densiflora</i>	<i>Hypochaeris radicata</i>	<i>Grindelia</i> sp.
<i>Chorizanthe pungens</i> var. <i>hartwegiana</i>	<i>Melilotus albus</i>	<i>Juncus</i> sp.
<i>Cichorium intybus</i>	<i>Mentha pulegium</i>	<i>Leontodon saxatilis</i> subsp. <i>longirostris</i>
<i>Collinsia heterophylla</i>	<i>Plantago lanceolata</i>	<i>Lotus corniculatus</i>
<i>Corethrogyne filaginifolia</i>	<i>Rubus armeniacus</i>	male <i>Baccharis pilularis</i> subsp. <i>consanguinea</i>
<i>Deinandra corymbosa</i>	<i>Symphotrichum chilense</i>	<i>Persicaria punctata</i>
<i>Genista monspessulana</i>	<i>Trifolium fragiferum</i>	<i>Triphysaria versicolor</i> subsp. <i>versicolor</i>
<i>Grindelia hirsutula</i>	TOTAL: 12	TOTAL: 12
<i>Heliotropium curassavicum</i> var. <i>oculatum</i>		
<i>Helminthotheca echioides</i>		
<i>Heteromeles arbutifolia</i>		
<i>Holocarpha macradenia</i>		
<i>Holodiscus discolor</i> var. <i>discolor</i>		
<i>Lagophylla ramosissima</i>		
<i>Layia gaillardiioides</i>		
<i>Lupinus nanus</i>		
<i>Lupinus variicolor</i>		
male <i>Salix lasiolepis</i>		
<i>Perideridia gairdneri</i> subsp. <i>gairdneri</i>		
<i>Perideridia kelloggii</i>		
<i>Persicaria amphibia</i>		
<i>Persicaria hydropiperoides</i>		

<i>Plagiobothrys chorisianus</i> <i>var. hickmanii</i>		
<i>Primula clevelandii</i> <i>var.</i> <i>gracilis</i>		
<i>Prunus cerasifera</i>		
<i>Rosa californica</i>		
<i>Rupertia physodes</i>		
<i>Salix laevigata</i>		
<i>Stachys ajugoides</i>		
<i>Toxicodendron</i> <i>diversilobum</i>		
<i>Trichostema lanceolatum</i>		
<i>Trifolium grayi</i>		
<i>Trifolium microcephalum</i>		
<i>Trifolium willdenovii</i>		
TOTAL: 39		

Figure 5. Comparison between the plant communities of *vosnesenskii* and *occidentalis* within coastal prairie.

Plants visited by <i>Bombus vosnesenskii</i>	Plants shared between <i>vosnesenskii</i> and <i>occidentalis</i>	Plants visited by <i>Bombus occidentalis</i>
<i>Acmispon heermannii</i> <i>var.</i> <i>orbicularis</i>	<i>Acmispon glaber</i> <i>var. glaber</i>	<i>Baccharis glutinosa</i>
<i>Amsinckia spectabilis</i> <i>var.</i> <i>spectabilis</i>	<i>Chorizanthe robusta</i> <i>var. robusta</i>	<i>Brassica rapa</i>
<i>Cakile</i> <i>sp.</i>	<i>Cirsium vulgare</i>	<i>Euthamia occidentalis</i>
<i>Calystegia purpurata</i> <i>subsp.</i> <i>purpurata</i>	<i>Ericameria ericoides</i>	<i>Helminthotheca</i> <i>echiodes</i>
<i>Carduus pycnocephalus</i> <i>subsp.</i> <i>pycnocephalus</i>	<i>Erigeron glaucus</i>	<i>Persicaria amphibia</i>
<i>Carpobrotus chilensis</i>	<i>Eriogonum latifolium</i>	TOTAL: 5
<i>Carpobrotus edulis</i>	<i>Eriophyllum staechadifolium</i>	
<i>Cirsium occidentale</i> <i>var.</i> <i>occidentale</i>	<i>Eschscholzia californica</i>	
<i>Conium maculatum</i>	<i>Hirschfeldia incana</i>	
<i>Corethrogyne filaginifolia</i>	<i>Oenanthe sarmentosa</i>	
<i>Dudleya caespitosa</i>	<i>Potentilla anserina</i> <i>subsp.</i> <i>pacifica</i>	
<i>Epilobium ciliatum</i> <i>subsp.</i> <i>ciliatum</i>	<i>Raphanus sativus</i>	
<i>Erysimum ammophilum</i>	<i>Rosa californica</i>	
<i>Frangula californica</i> <i>subsp.</i> <i>californica</i>	<i>Solanum douglasii</i>	

<i>Grindelia sticta</i> var. <i>platyphylla</i>	<i>Stachys bullata</i>	
<i>Lupinus arboreus</i>	TOTAL: 15	
<i>Mimulus guttatus</i>		
<i>Phacelia distans</i>		
<i>Phacelia ramosissima</i>		
<i>Prunella vulgaris</i> var. <i>lanceolata</i>		
<i>Pteridium aquilinum</i> var. <i>pubescens</i>		
<i>Rubus ursinus</i>		
<i>Scrophularia californica</i>		
<i>Senecio elegans</i>		
<i>Silybum marianum</i>		
<i>Vicia gigantea</i>		
<i>Vicia villosa</i> subsp. <i>villosa</i>		
TOTAL: 27		

Figure 6. Comparison between the plant communities of *vosnesenskii* and *occidentalis* within dune/coastal scrub.

In coastal prairie (Figure 5) half of the total plants *occidentalis* visits overlap with the much larger *vosnesenskii* plant community, but twelve plant species are visited by *occidentalis* and not *vosnesenskii*. In dune/coastal scrub habitats, only five plants are visited by *occidentalis* but not *vosnesenskii*. In both habitats, the total plant community visited by *vosnesenskii* is almost double that of *occidentalis*. There are four plants that are visited by both species of bee in *both* habitats: *Acmispon glaber* var. *glaber*, *Cirsium vulgare*, *Eschscholzia californica*, and *Hirschfeldia incana*. These are comparisons solely between *vosnesenskii* and *occidentalis* and are useful in providing direct contrast between a robust, common species and a more vulnerable one.

Coastal prairie	Dune/coastal scrub
<i>Acmispon americanus</i> var. <i>americanus</i>	<i>Brassica rapa</i>
<i>Bidens laevis</i>	<i>Euthamia occidentalis</i>
<i>Daucus carota</i>	<i>Helminthotheca echiodes</i>
<i>Grindelia</i> sp.	<i>Persicaria amphibia</i>
<i>Juncus</i> sp.	TOTAL: 4
<i>Leontodon saxatilis</i> subsp. <i>longirostris</i>	
<i>Lotus corniculatus</i>	
male <i>Baccharis pilularis</i> subsp. <i>consanguinea</i>	
<i>Persicaria punctata</i>	
TOTAL: 9	

Figure 7. The plants that were exclusively visited by *Bombus occidentalis* in coastal prairie and dune/coastal scrub habitats.

In the context of the total bumblebee community, Figure 7 shows which plants, in both coastal prairie and dune/coastal scrub, were exclusively visited by *occidentalis*, meaning there is zero overlap between any other *Bombus* pollination network.

Pollination Redundancy

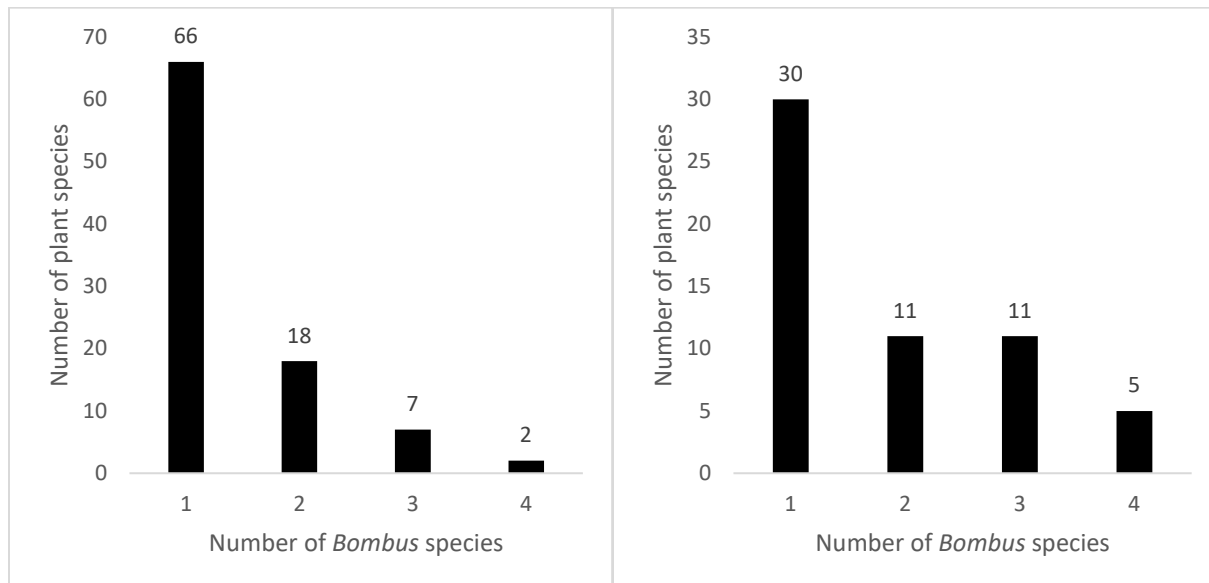


Figure 8 (left) and Figure 9 (right). The pollination redundancy present within *Bombus* pollination networks. Coastal prairie (left) and dune/coastal scrub (right).

Continuing with the directed comparisons between coastal prairie and dune/coastal scrub, Figures 8 and 9 show the level of pollination redundancy across every bumblebee present in those habitats. In coastal prairie (Figure 8), sixty-six plant species (~17% of total plant community) are only visited by one species of bumblebee, whereas only nine plant species (~3%) are pollinated by three or four bumblebee species. This pattern is present, although less extreme, in dune habitats (figure 9). Thirty plant species (~ 15%) are only visited by one bumblebee species, while the number of plant species that are visited by between two and four bumblebee species are closer together (between 3% and 6% of total plant community). This could indicate a higher level of plant-pollinator specificity in coastal prairie habitats versus other habitats. It could also indicate, based on the overall higher plant community diversity of coastal prairie that given more possible options bumblebees spread out and use every available resource, thus decreasing the possibility of an overlap between two pollination networks. Regardless, this information reveals a low degree of pollination redundancy in these habitats, indicating environmental vulnerability in the event of a reduction in bumblebee numbers.

Conclusion

The bumblebee community in Santa Cruz county was widely distributed across the multiple habitat types present in the area. Certain species were better able to adapt and utilize variety in their pollination preferences. *Bombus vosnesenskii* has been shown to be common and resilient to variation in plant community or habitat layout. Other species are more specialized in the habitat types they are able to proliferate within. *Bombus occidentalis*, before it was considered a vulnerable species, exhibited a relatively small, specialized pollination network. Overall the degree of specialization, meaning instances of only one species of bumblebee visiting a certain plant, in every habitat is quite high. This serves to highlight the absolute importance of high efficiency native hymenopteran pollinators in ecosystems, and the danger in their decline as a result of climate change or development projects. Future investigations that utilize the data of the Randy Morgan insect collection should look more at temporal variations of insect pollination over time, as this was outside the scope of this project. Future resampling efforts can visit the sites of Randy Morgan and use this data as a comparison point to draw conclusions about the *Bombus* community over a multi-decade period.

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