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Joan M. Meiners  
*Utah State University*

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BIODIVERSITY, COMMUNITY DYNAMICS, AND NOVEL FORAGING  
BEHAVIORS OF A RICH NATIVE BEE FAUNA ACROSS HABITATS  
AT PINNACLES NATIONAL PARK, CALIFORNIA

by

Joan M. Meiners

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

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Dr. Edward W. Evans  
Major Professor

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UTAH STATE UNIVERSITY  
Logan, Utah

2016

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## ABSTRACT

BIODIVERSITY, COMMUNITY DYNAMICS, AND NOVEL FORAGING  
BEHAVIORS OF A RICH NATIVE BEE FAUNA ACROSS HABITATS  
AT PINNACLES NATIONAL PARK, CALIFORNIA

by

Joan M. Meiners

Utah State University, 2016

Major Professor: Dr. Edward W. Evans  
Department: Biology

Wild, native bees (Hymenoptera: Apoidea) provide pollination services valued at nearly \$3 billion to U.S. agriculture annually, and are the primary pollinators maintaining plant communities in natural landscapes, an ecosystem service of incalculable worth. Global concern over widespread honeybee declines has spurred research to save that single species, while knowledge of the health and habitat requirements of 20,000 native bee species worldwide lags behind. Understanding dynamics and habitat associations of pristine native bee communities may help inform conservation priorities and restoration goals to ensure the widespread longevity of native bees. We surveyed the bee and plant communities over two flowering seasons and across four distinct habitat types (Alluvial, Live Oak Woodland, Blue Oak Woodland, and Grassland) at Pinnacles National Park, a protected biodiversity hotspot, and a pristine, heterogeneous environment. We collected 52,853 bee specimens over 308 collector days, and increased the species inventory to 479,

from the previous 398 recorded as of the late 1990s. This statistic ranks Pinnacles as likely the most densely diverse area for native bees currently known.

Spatially, no relationship between habitat type and bee abundance or richness was observed. Bee species composition in Alluvial habitats, however, was more unique and showed lower dispersal, suggesting this habitat may serve as a nesting refugia for a core community of resident species. Temporally, we evaluated potential resilience of solitary bees to anticipated disruptions in bloom availability via novel, community-wide foraging on honeydew sugars produced by scale insects. We observed 56 native bee species using honeydew sugars during the early season low bloom, and determined that they locate this resource without visual cues. Overall, these findings suggest that native bee communities at Pinnacles National Park may be buffered against temporal resource shifts and may benefit from protection of the Alluvial habitat type. The patterns observed here should be evaluated in other locations to determine their value towards forecasting and managing widespread risks to native bees.

(143 pages)

## PUBLIC ABSTRACT

BIODIVERSITY, COMMUNITY DYNAMICS, AND NOVEL FORAGING  
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AT PINNACLES NATIONAL PARK, CALIFORNIA

Joan M. Meiners

Global concern about honeybee declines has spurred feverish research about the status and protection of this single species, yet our understanding of the ecology and issues impacting thousands of species of native bees lags behind. Pinnacles National Park, America's newest, near Salinas, California, is currently the most densely biodiverse area for native bees known on the planet. Recent work by researchers at Utah State University and the USDA-ARS has documented 479 species of native bees in only 42 square miles of this park. During two years of field studies and 308 collector days, we assembled data on 52,853 bee specimens to determine natural patterns in thriving bee communities and how they relate to climate and habitat variables. We found that the 'alluvial' habitat type, low in elevation and dominated by woody shrubs and sparse grass, had a unique composition of bee species that may depend on their local resources more than bees in 'woodland' and 'grassland' habitat types. We also evaluated novel, early-season foraging behaviors of 56 native bee species locating scale insect honeydew sugars without visual aid of flowers or color. Overall, these findings suggest that native bees at Pinnacles National Park may be resilient to temporal bloom shifts, but may be negatively affected by loss of 'alluvial' habitat. If similar patterns are found in other locations, these results may have widespread value in guiding native bee conservation priorities.

## DEDICATION

For Barbara Kingsolver (beauty), Alice Sebold (guts), and David Quammen (humor),  
and for Marilyn Meiners, who would have actually read this.

RIP Sylvester

## FRONTISPIECE



Photo Credits (from top to bottom, left to right): Joan Meiners (1,5,8,10,11), Pete Lamperty (2,9,12), and Therese Lamperty (3,4,6,7).



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I would like to thank my committee (Ted Evans, Terry Griswold, and Geno Schupp) and funders (NPS, USDA-PIRU) for dedicating time and funds to exploring the bee diversity at Pinnacles National Park, for their trust in me to conquer this task, and for their patience with my intellectual and global wanderings along the way. I especially appreciate Terry's energetic curiosity, Ted's warmth, and Geno's biting humor.

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I am extremely fortunate that Therese Lamperty was hired to help me in the field my first year, and very grateful that she elected to return for a second year of grueling, hot, underpaid, mountain-lion-infested field work. I consider it one of the best outcomes of this project that she remains a good friend, and still decided to pursue ecology in her own graduate studies. I will always think fondly of our lunchtime, heat-coma field naps.

I am indebted to Harold Ikerd and Skyler Burrows for helping me wade through 50,000 bee specimens and a foreign database, and to Jordan Frank for his meticulous lab work. Nancy Huntly, Al Savitzky, Kami McNeil, Glenda Yenni, and Susan Durham all improved my project and/or university experience. I appreciate Dr. Yael Mandelik for hosting me in her lab for a semester adventure in Israel. Finally, thank you to Morgan for believing, Suzanne for cheering, my bike racing teammates for balance, my family and Laila for taking care of each other, and Jereme for always picking me up when I crash.

Joan M. Meiners

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## CHAPTER 1

### INTRODUCTION

#### **Context and Importance**

Recent widespread honeybee declines have raised awareness about the immense economic importance of bees, whose pollination services to U.S. agriculture are valued at up to \$14.6 billion per year (*Morse and Calderone, 2001; Potts et al., 2010*). Whereas the imported European honeybee raised and transported around the U.S. for rent in crop pollination represents only one species, *Apis mellifera*, there are approximately four thousand species of native bees recorded in North America (*Michener, 2007*). Due to the abundance of solitary and ground-nesting species, however, few native bee species have been successfully managed for agricultural purposes (*James and Pitts-Singer, 2008*). Nevertheless, wild native bees have been shown to be capable of providing adequate pollination for a majority of crop species in the absence of honeybees, and enhancing fruit yield and seed set when active in conjunction with honeybees (*Garibaldi et al., 2013, 2013; Greenleaf and Kremen, 2006; Kremen et al., 2004; Winfree et al., 2007*). Alone, the value to U.S. agriculture of native bees has been estimated at \$3.07 billion annually and up to 30% of the U.S. diet, with most of this activity attributed to wild pollinators persisting in remnant patches of semi-natural habitat (*Losey and Vaughan, 2006*). The magnitude and quality of this service, however, is strongly dependent on the amount of surrounding natural habitat, a resource that is rapidly disappearing with increasing agricultural intensification, habitat fragmentation, and urban development (*Cane et al., 2006; Kremen et al., 2004; Tscharntke et al., 2002*).



Not only do diverse, wild native bees play an underappreciated role in agriculture, but the ecosystem services they provide in natural landscapes are of almost immeasurable value to global wellbeing (*Buchmann and Nabhan, 1996; Foley et al., 2005; Kremen, 2005*). Angiosperms, the flowering plants, are known to be intricately linked to their pollinators, having evolved elaborate floral colors and morphologies in response to pollinator preferences (*Ohashi and Yahara, 2001; Willmer, 2011*). Ninety-two percent of flowering plants that require a pollen vector are pollinated by animals, while only eight percent rely on abiotic forces like wind and water to transport pollens (*Nabhan and Buchmann, 2012*). Animal pollinators, of which bees are the most important, thereby play a key role in maintaining plant communities in natural landscapes, which stabilize the soil against catastrophic erosion and provide habitat and forage, at some trophic level, for nearly all other living creatures (*Ollerton et al., 2011; Potts et al., 2003; Tepedino, 1979*). But it is not only an abundance of bees that are required for this service. The biodiversity of native bee communities, with each species contributing a slightly different service depending on its size and foraging, nesting, and social behaviors, is thought to be a critical stabilizing component of mutualistic pollination networks (*Kremen, 2005; Larsen et al., 2005*).

### **State of Knowledge**

Despite the critical importance of diverse communities of native bees to both sustainable agriculture and the maintenance of natural plant communities, research on their current health, habitat requirements, and vulnerability to environmental change lags far behind that being conducted for the managed honeybee (*Cane, 2001; Kearns et al.,*

1998; Kremen, 2005; Winfree, 2010). The biology of many native bees is known to be tied closely to the bloom of particular floral groups, which in turn are tied to seasonal and habitat characteristics such as temperature, moisture levels, and elevations (Linsley, 1958). Recent observations of shifts in floral bloom time in relation to timing of native bee emergence have caused concern about a temporal decoupling of specialist bees from their host plants or a dearth of resources for bees emerging early or late in the season when bloom may be unreliable (Forrest and Thomson, 2011; Inouye, 2008; Robbirt *et al.*, 2014). Furthermore, evidence that bee species respond differently to environmental disturbance and habitat loss depending on traits like body size and foraging specialization threatens an impending pattern of non-random species loss that has been shown to be particularly disruptive to ecosystem stability in mutualistic networks (Aizen *et al.*, 2012; Bartomeus *et al.*, 2013; Bommarco *et al.*, 2010; Cane *et al.*, 2006; Larsen *et al.*, 2005; Memmott *et al.*, 2007; Williams *et al.*, 2010). However, other studies indicate that, in general, biodiverse native bee and plant communities may be buffered to impacts from environmental, habitat, and resource disruptions due to redundant functional diversity, ability to delay emergence in poor resource years, and flexibility in pollinator networks when necessary (Bartomeus *et al.*, 2011; Campbell *et al.*, 2011; Fontaine *et al.*, 2005, 2008; Johnson and Steiner, 2000; Minckley *et al.*, 2013; Waser, 2006; Waser *et al.*, 1996; Williams, 2003; Williams and Kremen, 2007).

One thing these authors all agree on is the need for more research on community-level responses of native bees to environmental perturbations across a range of ecosystems, as much uncertainty remains in broad forecasts of native bee health status (Kearns *et al.*, 1998). Several large surveys of native bee fauna, particularly in the

western United States, have added to current knowledge of diversity and variability (Griswold *et al.*, 1999; Marlin and LaBerge, 2007; Messinger, 2006; Messinger and Griswold, 2003; Roubik, 2001; Wilson *et al.*, 2009). Additional widespread efforts are hampered by the high cost and man-power required to thoroughly sample and catalog native bee communities, and the ‘taxonomic impediment,’ the dearth of expertise required to identify specimens once they are collected to determine sample diversity (Cardoso *et al.*, 2011; Gonzalez *et al.*, 2013). Limiting collecting methodology to less costly, passive pan traps to enable broader sampling has merit, but is known to produce biased, incomplete samples of the bee community (Cane *et al.*, 2000; Droege *et al.*, 2010; Roulston *et al.*, 2007).

Efforts to truly capture ecological patterns in an area must also contend, statistically, with the immense spatiotemporal variability inherent to native bee communities (Cane and Tepedino, 2001; Williams *et al.*, 2001). Since native bee flight time can be shorter than a month per year for a solitary species, temporal turnover in a location is extremely high over a flowering season (Linsley, 1958; Petanidou *et al.*, 2008). On top of that, spatial variability, combined with uncertainty about bee flight and home ranges, limits our ability to generalize and extrapolate findings to areas not sampled (Cane and Tepedino, 2001; Greenleaf *et al.*, 2007; Roubik, 2001; Waddington, 1980). Targeted research on responses of diverse native bees to manipulated or measurable degrees of disturbance in urban, agricultural, and fragmented habitats are making important strides towards understanding bee community dynamics (Cane *et al.*, 2006; Foley *et al.*, 2005; James and Pitts-Singer, 2008; Kremen *et al.*, 2002; Matteson *et al.*, 2008; Minckley *et al.*, 2013; Park *et al.*, 2015; Tonietto *et al.*, 2011; Winfree *et al.*,

2008). However, a foundational understanding of what native bee health looks like in the absence of human disturbance is still murky and confounded by variability, compromising assessments of community health and integrity (*Buchmann and Ascher, 2005*). Evaluation of a thriving native bee community that includes systematic, frequent sampling over large areas to enable detection of changes over time, and identification of community patterns over space as they relate to generalizable habitat characteristics may have particular value in advancing our understanding and goals for preservation of native bees.

### **Research Objectives**

Broadly, the present study aims to survey a rich native bee fauna in a semi-pristine habitat, where the establishment of a monitoring baseline for a thriving bee community may aid detection of future shifts in bee health, and where identification of general community patterns may help inform restoration goals for native bee communities in degraded habitats. We chose to work in Pinnacles National Park in the Inner South Coast Range of California, a protected, heterogeneous landscape documented in the late 1990s as being more species-rich per unit area than any place studied for native bees (*Messinger and Griswold, 2003*). Pinnacles lies along several fault lines, has strong environmental gradients in elevation, moisture, soil types and microclimates, and boasts a huge diversity of wildflowers across several distinct habitat types (*Matthews, 1976; Tucker et al., 2006*), making it an ideal place to investigate relationships between native bee community health and environmental habitat characteristics.

We sampled the bee and floral communities in ten different locations that spanned diverse habitats and regions of the park, over the flowering seasons of two consecutive years. In order to promote comparability of bee community samples across space and time, a standardized procedure was defined and adopted by the native bee research community in 2003 that sets the ideal at biweekly sampling in hectare-sized plots using passive pan trapping and aerial net collecting, both of which are lethal methods necessary for viewing specimens under a microscope to obtain essential laboratory species-level determinations (*LeBuhn et al., 2003*). A recent evaluation of the effect of this repeated, lethal sampling procedure found native bee communities to be robust to such sampling efforts, which extract only a small temporal slice of the community each biweekly visit (*Gezon et al., 2015*).

The high bee species richness is a subject of pride for Pinnacles National Park, and a central motivation behind the National Park Service funding of this thesis work. Chapter 2 reviews the updated bee species inventory across the park, with the full list and relative abundances over all seven years of sampling included as an Appendix. It then evaluates community dynamics at Pinnacles by testing correlations between bee abundance and richness across space and time with environmental characteristics such as floral diversity and elevation. Finally, in Chapter 2, the relationship between habitat type and native bee communities via metrics of abundance, richness, and species composition are explored with an aim to identify generalizable, predictable, ecologically relevant community patterns that may be used to improve our understanding of bee health in similar habitat types without the need to collect, process, identify and analyze 50,000 specimens in each location of interest.

Chapter 3 is a departure from the above a priori analyses in that it describes an experimental manipulation undertaken to explore unusual early season native bee foraging on honeydew sugars observed during systematic plot sampling. This behavior has been recorded in select species of social bees in disparate ecosystems (*Batra, 1993; Bishop, 1994; Crane and Walker, 1985*), but never evaluated as a resource used by an entire community of solitary bees. This behavior may also have implications for native bee community interactions, health, and resilience to seasonal fluctuations in the availability of nectar resources threatened by climate change. Together, these two data chapters explore spatial and temporal interactions between diverse native bee communities and their habitats that provide insight to the operations of a thriving bee community at Pinnacles National Park that may inform expectations for assessments and predictions about native bees elsewhere.

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## CHAPTER 2

LANDSCAPE-SCALE HABITAT TYPES AS PREDICTORS OF NATIVE BEE  
DIVERSITY AND COMMUNITY DYNAMICS IN A SEMI-PRISTINE ECOSYSTEM

## ABSTRACT

Native bees (Hymenoptera: Apoidea) are diverse and effective pollinators, responsible for the majority of plant pollination in natural and degraded ecosystems. Despite this critical role, little is known about patterns in native bee biodiversity, community dynamics, and expected variation between habitat types, particularly in the absence of human disturbance. Such knowledge could help detect population trends and guide conservation in natural and altered landscapes. We surveyed the bee and plant communities over two flowering seasons across four distinct habitat types (Alluvial, Live Oak Woodland, Blue Oak Woodland, and Grassland) at Pinnacles National Park, a protected hotspot of native bee diversity, to 1) update the inventory of park bee biodiversity; 2) identify patterns in bee abundance, richness and community composition; and 3) evaluate whether habitat type is an indicator of native bee dynamics. We collected 52,853 bee specimens, and increased the Pinnacles species inventory from 398 to 479. While habitat type was not related to bee abundance, richness, or even floral richness over a season, species composition varied significantly among habitat types. In alluvial habitat, bee species composition was more unique, tightly defined, and related to distance between sites than in other habitat types, suggesting these areas may serve as nesting refugia, particularly for some oligolectic species. Further examination of these patterns may clarify the value of protecting alluvial habitats at Pinnacles and beyond.

## INTRODUCTION

Bees perform the vast majority of animal-mediated pollination services, which are required for reproduction in 85% of wild and cultivated plants worldwide (*Ollerton et al., 2011*). The honey bee has historically received much of the credit for this key ecosystem service, especially within agricultural settings. However, diverse assemblages of native bees have been found to not only greatly enhance fruit set and yield in the presence of imported honey bees, but to also be capable of providing adequate pollination for the majority of crops in their absence (*Garibaldi et al., 2013; Greenleaf and Kremen, 2006; Park et al., 2010; Winfree et al., 2007*). In natural areas, without the manpower of imported, managed honey bee hives, native bees play a key role in maintaining the plant communities that structure the soil, shelter other invertebrate ecosystem service providers, and sustain wildlife all the way up the food chain (*Tepedino, 1979*). Yet, compared to the managed honey bee, little is known about native bee ecology, habitat requirements, or sensitivity to environmental disturbances (*Winfree, 2010*). Recent concerns about global honey bee declines have highlighted the challenges and dearth of native bee monitoring efforts, which are often insufficient to detect or evaluate parallel declines among native bee communities similarly exposed to widespread threats such as habitat loss, fragmentation, pesticides, pathogens, alien species, climate change, and the synergistic effect of these factors (*Kremen and Ricketts, 2000; Memmott et al., 2007; Potts et al., 2010*). Indeed, the potential cascading impact of native bee decline on the stability of plant-pollinator mutualisms and the integrity of natural and managed landscapes, is fraught with uncertainty (*Kearns et al., 1998*).

A central cause of uncertainty in the status and implications of native bee declines, especially in natural areas, is the lack of systematic, repeatable monitoring efforts to establish historical baselines with which to compare current measures of abundance and richness (*Winfree, 2010*). This is largely due to the inherently high variability of diverse bee communities over space and time, which complicate the discovery of useful, predictable indicators for native bee health (*Williams et al., 2001a; Wilson et al., 2009*). Native bees are a rich group with over twenty thousand species worldwide and approximately four thousand species documented in North America (*Michener, 2007*). They are particularly diverse in xeric and Mediterranean environments, owing to strong seasonal blooms and well-drained soils that support a diversity of foraging specializations and high temporal turnover of solitary, ground-nesting bees in these areas (*Linsley, 1958; Michener, 1979; Minckley, 2008*). A comparison of bee faunas from several Mediterranean climate zones found the chaparral habitats of California to represent perhaps the greatest of global biodiversity hotspots for native bees (*Moldenke, 1976a, 1976b*). In the late 1990s, Messinger and Griswold (2003) found Pinnacles National Monument in California's Inner South Coast Range to be one of the most densely diverse areas known for bees on the planet, with nearly 400 bees discovered in what was then a 65 square kilometer area.

Pinnacles, made a National Park in 2013 and currently 108 square kilometers, lies along several California fault lines, is bisected by a high rocky ridge running north-south, and is known for its wildflower diversity and highly heterogeneous landscape (*Matthews, 1976; NPS, 2015; Tucker et al., 2006*). The floral diversity and complex landscape make Pinnacles National Park an ideal place to study the natural complex dynamics and habitat

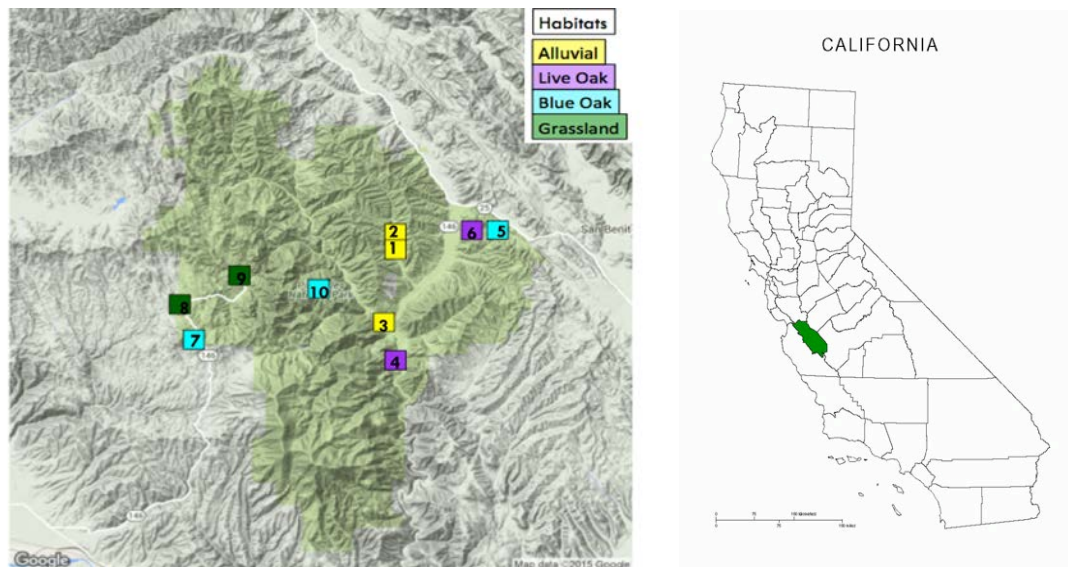
associations of thriving native bee communities. We took advantage of the strong, albeit geographically-constrained, gradients of habitat, elevation, and floral diversity at Pinnacles National Park to accomplish two goals: establish a baseline for current and repeatable assessment of a thriving native bee fauna; and identify associations between habitat type and bee metrics, such as richness, that may be broadly useful in evaluating native bee status in similar areas. We collected biweekly bee and plant community samples from 10 one-hectare plots over two flowering seasons to address the following three objectives: 1) update the inventory of park bee biodiversity; 2) identify patterns in bee abundance, diversity, and community composition across habitats; and 3) evaluate whether habitat type (Alluvial, Live Oak Woodland, Blue Oak Woodland, or Grassland) could be a useful predictor of native bee dynamics. Tracking and evaluating patterns and fluctuations among native bee communities in semi-pristine habitat types, such as those at Pinnacles National Park, may fill a much-needed gap in our understanding of the dynamics of a thriving native bee community, which may help identify conservation priorities and restoration goals. Being able to associate these metrics with easily-identifiable, Mediterranean habitat types may facilitate our ability to detect and manage native bee decline at Pinnacles and beyond.



## MATERIALS & METHODS

### Study Site

We began the current study on site in February of 2011 by establishing ten one-hectare-sized plots for repeated, systematic bee sampling (**Fig. 2-1**). Given the time, funding, and two full-time collectors allotted, we determined ten to be the number of plots feasible to sample biweekly on foot, while also leaving time for opportunistic trail collecting to capture the full bee diversity in further reaches of the park. We surveyed the available landscapes and selected plot sites that occurred along gradients in elevation, grass cover, and microclimates and which were spread across both sides of the steep, dividing ridge of namesake “Pinnacles” rock, which separates the drier, lower, eastern side of the park from the higher, more coastal-influenced, western side.



**Figure 2-1** Pinnacles National Park Map of 2011-2012 study plots (left), and park location within California on the western coast of the United States (right). Plots are numbered and colored corresponding to habitat type.

The location description, coordinates, elevation, dimensions, and habitat type of each of ten plots are given in **Table 2-1**. We identified four main, visually distinctive habitat types at the plot-sized (hectare) scale across the park, and endeavored to distribute sampling effort (plots) among them. These four habitat types are pictured and described below, roughly ordered by their position east to west across the park, and by increasing grass cover, elevation, moisture, and decreasing woody shrub and bare ground cover:

1. **Alluvial** (N=3) plots are rocky, fan-shaped deposits at the outlet or lowest part of a canyon drainage or flow area where bloom tends to be highly seasonal, variable, and moisture-dependent. Overall vegetation cover is low and composed of short, woody shrubs, and herbaceous annuals. These plots occur typically at lower elevations and drier microclimates, and are all found on the east side of the park.



Plot 1: McCabe Upper Alluvial



Plot 2: McCabe Canyon Lower Alluvial



Plot 3: Peaks View Alluvial

2. **Live Oak Woodland** (N=2) plots have more grass cover than Alluvial plots, but more gravel cover than Blue Oak woodland or grassland plots. They are shaded across approximately 50% of their ground surface, with deep shade provided by clustered live oak trees (*Quercus agrifolia* var. *agrifolia*) interspersed with open grassland areas composed of thick, invasive grasses. Woody shrub presence is higher, and fairly rich, in these plots compared with Blue Oak woodlands or open grasslands, but lower and more homogenous than in Alluvial plots. At Pinnacles National Park, this habitat type occurs at lower elevations, often near ephemeral stream flow and is restricted to the east side of the park.



Plot 4: S. Wilderness Live Oak Woodland  
(Photo by Paul Johnson)



Plot 6: Needlegrass Live Oak Woodland

3. **Blue Oak Woodland** (N=3) plots also have approximately 50% shade cover across their ground surface area, but it is more evenly dispersed across the landscape of dispersed blue oak (*Quercus douglassii*), creating a mottled shade effect. Below the canopy, they have high

vegetation cover of mostly homogenous, invasive grasses, and fairly rich, if short-lived, herbaceous bloom, but little woody shrub presence or bare ground. These areas are typically drier than Live Oak or Alluvial sites, but span a range of elevations and are the only habitat type to occur on both east and west sides of the park.



Plot 5: Needlegrass Blue Oak Woodland



Plot 7: West Gate Blue Oak Woodland



Plot 10: High Peaks Blue Oak Woodland

4. **Grassland** (N=2) plots are found on the west side of the park, at fairly high elevations and variable moisture regimes. Vegetation cover is nearly complete, and is composed primarily of invasive grasses and sparse woody shrubs, with rich ephemeral herbaceous bloom as well.





Plot 8: Double Gates Grassland



Plot 9: W N. Wilderness Grassland

To ensure that all plots would yield abundant bee samples, enable meaningful comparisons of bee metrics between plots, maintain consistency with other bee sampling projects across the country, and support practical, safe, and repeatable sampling, we also employed a number of other criteria for plot establishment, as follows: 1) Plots had to be one hectare in area, and roughly rectangular in shape; 2) The area within a plot had to fit into only one of the four outlined habitat types, be fairly homogenous in vegetation within its boundaries, and not immediately bordered by any contrasting habitat type; 3) Plots had to be fairly flat to enable use of passive bee collection by pan traps (colored bowls with soapy water placed on the ground); 4) Plots had to be in fairly low-human-use areas so as to be considered relatively natural and undisturbed; 5) Approximately half of the area in a plot had to be sunny, and the majority terrestrial; 6) Plots had to be easy to walk through, and reasonably free of risks (*e.g.* poison oak, running water, thick brush, etc.); 7) For logistical reasons, most plots should be paired so that two could be sampled in one day, separated by no more than a fifteen-minute walk; 8) Plots needed to span the diversity of elevations, coastal influences (west side vs. east side), and habitat types available.

**Table 2-1 Names, locations, and descriptions of study plots sampled in 2011-2012 at Pinnacles National Park**

<b>Site/Plot Number</b>	<b>Site/Plot Name</b>	<b>GPS lat/long</b>	<b>Elevation</b>	<b>Dimensions</b>	<b>Habitat "Type"</b>
1	McCabe Canyon Upper	36.5081, -121.156	410m	175 m x 57m	Alluvial
2	McCabe Canyon Lower	36.503, -121.156	395m	175m x 57m	Alluvial
3	Peaks View	36.4802, -121.16	290m	200m x 50m	Alluvial
4	South Wilderness	36.4683, -121.156	280m	250m x 40m	Live Oak Woodland
5	Needlegrass BOW	36.5091, -121.12	385m	200m x 50m	Blue Oak Woodland
6	Needlegrass LOW	36.509, -121.129	365m	200m x 50m	Live Oak Woodland
7	West Gate	36.4747, -121.227	610m	175m x 57m	Blue Oak Woodland
8	Double Gates	36.4858, -121.232	535m	200m x 50m	Grassland
9	W. North Wilderness	36.4949, -121.211	430m	200m x 50m	Grassland
10	High Peaks	36.4907, -121.183	595m	175m x 50m	Blue Oak Woodland

### **Field Methods**

The field sampling protocol for the project required two full-time collectors in order to sample two plots in one day and cycle through ten plots in a two-week period. Two regular collectors is also ideal to ensure safety in remote areas, to distribute and control for potential collector biases, to get pan traps set out and picked up at the same time in both plots simultaneously, and to capture diurnal bee diversity by sampling in pairs at specific times of the morning and afternoon. See **Appendix A** for a full list of supplies used (from plot establishment to field sampling to collection management) to conduct the bee survey in 2011-2012, including a sample data collection card.

We began our field seasons in both 2011 and 2012 in mid-February before most bloom had commenced, and ended the season in late June after most bloom had faded.

We sampled ten plots in six days over a period of two weeks using the daily schedule included in **Appendix A**, then started the cycle over for a total of eight sampling cycles of ten plots in 2011 and seven in 2012. Days deemed appropriate for sampling were fairly sunny, without high winds, and over 15 degrees Celsius if possible. Weather permitting, we typically sampled two pairs of plots per day Monday through Wednesday, and included additional trail collecting and work on side projects where possible. Thursdays and Fridays were spent collecting bees in other areas of the park for the diversity inventory, processing bee and plant samples, and entering data.

Each sampling day began and ended on site with the placement of pan traps (aka “bowls”). Pan traps were made from 2-ounce plastic Solo cups, spray painted one of three colors known to be attractive to bees (white, fluorescent blue, and fluorescent yellow). We placed 30 pan traps, ten of each color, evenly spaced in an “X” shape connecting the four corners of the rectangular plots at 9 am each sampling morning. Pan trap bowls were placed directly on the ground and filled  $\frac{3}{4}$  full of soapy water (using a small squirt of blue Dawn dish soap, standardized within the bee research community to control for influences of soap scent or color). In grassland habitats, we made an effort to flatten an area in the grass on which to place bowls so that they were easily visible to bees from the air. We placed bowls in approximately the same position each time we sampled a plot because the bowl locations served as sample points for a companion vegetation monitoring protocol (*see Meiners et al., 2015*). At 4pm, after all net sampling had been completed, each collector picked up bowls in the same order in which they were placed out, straining the bee contents into three labeled mesh tea strainers, one for each pan trap bowl color, then emptying the strainers into separate plastic Whirl packs, filled with 75%

ethanol until all bees were fully submerged in liquid, and stored in the freezer until specimens could be removed, washed, and individually pinned.

On days with sufficiently good conditions to anticipate bee activity, we began plot net sampling in the two plots at 10am and 11:15am, respectively. Immediately before these times, we recorded the cloud cover category (full sun, partly cloudy, cloudy, or mostly cloudy), and used a Kestrel monitoring device to record the ambient temperature (in the sun), wind speed, humidity, and barometric pressure at the plot. We began net sampling with the two collectors starting at opposite corners of the rectangular plot, then systematically working their way through one long half of the plot towards the opposite end for fifteen minutes, before switching sides to spend another 15 minutes covering the area on the other side, such that each collector evenly paced themselves through the entire plot area over 30 minutes and were not sampling in the same location at the same time. Because the study goal was to capture and record the plot bee community and relate it to measured habitat characteristics, we focused on moving consistently throughout the plot, rather than spending inordinate amounts of time in richly floral patches promising higher bee captures.

Net sampling involved visual and auditory-focused collecting of bee individuals encountered, rather than sweep-netting or otherwise randomized sampling methods. We quickly learned to visually distinguish and avoid collecting wasps and flies, but attempted to avoid bias in collecting certain bees, such as larger more charismatic fliers, by actively keeping our search images broad. Specimens were placed into cyanide killing vials immediately after net capture, and without stopping the clock, as it is possible to efficiently put bees into vials with practice, and thereby avoid the human error and



schedule setbacks inherent with starting and stopping the sampling timer. Bee collections from different floral hosts or surface category (i.e. “ground” or “air”) were kept in separate vials during sampling in order to associate each bee with the plant species or surface on which it was collected. We took and pressed vouchers of all unknown flowering species, regardless of whether or not bees were collected from them, for later identification using keys and herbarium collections. Once the plot sampling period was over, we labeled each vial with the unique number of the corresponding data card and plant voucher, and moved bees into plastic storage containers.

We finished each plot sampling day by mounting all net-caught specimens on size 1 or 2 pins into field boxes with associated vial field labels. Medium to large bees were pinned through the right mesosoma; bees too small to pin were glued directly to size 2 pins by carefully placing a tiny dab of Elmer’s washable glue directly on the pin and then cleanly attaching it to the right side of the bee mesosoma. We froze full field boxes for at least 48 hours and then sealed them into giant Ziplock bags to prevent contamination and beetle infestation. Bees from pan traps were stored in the freezer in whirl packs to pin on rainy days or at the Logan Bee Lab, before which they were briefly rinsed with 90% ethanol, and thoroughly dried by placing on paper towels and/or ‘fluffed’ with a hair drier. Plant vouchers were pressed with collection information in a large wooden plant press, separated by cardboard sheets and newspaper to blot moisture from plants.

### **Specimens & Data Management**

All bee and plant specimens were transported to Logan, Utah and incorporated into the USDA-ARS Pollinating Insect Research Unit collection except for reference and

display collections housed at Pinnacles National Park. Students and experts at the Logan Bee Lab collaborated to identify all bees to the species level wherever possible. Bee identifications were completed using high quality Leica dissecting microscopes, one of the best collections of reference specimens in the world (the Logan Bee Lab houses approximately 1.5 million curated bee specimen), and the appropriate taxonomic literature. Plants were identified on rainy field days using ‘The Jepson Manual’ (*Baldwin and Goldman, 2012*) and help from Pinnacles botanists, or were transported to the Logan Bee Lab and identified with help from the reference collection and experts at the Utah State University Intermountain Herbarium.

All collection information from data cards was entered into the Logan Bee Lab’s existing relational database using SQL and Microsoft Access as a front end. Corresponding individual ID numbers and barcodes were assigned to each specimen, and labels with this information were printed, double-checked, and pinned below each bee. Once each of the tens of thousands of bees for each sampling year were entered into the database and labeled, bees were moved into permanent museum storage unit drawers and sorted to morphotype by the naked eye. After species identification, all specimens were re-scanned, updated with their species and sex in the database, then organized in glass drawers by taxonomic group. The various iterations of the work described in the above two paragraphs took approximately two years.

### **Statistical Analyses**

Statistical analyses were performed at the  $p < 0.05$  significance level using the R-Cran statistical package and guidance from accompanying documents (*R Core*

*Development Team 2014 version 3.1.1; package “vegan” version 2.2-1; package “lmer” version 1.1-7*). Initial exploratory analyses were performed using the software PC-ORD version 6.0, with guidance from an associated book and instruction manual on multivariate methods (*McCune et al., 2002; Peck, 2010*).

Data were tested for normality and to ensure assumptions were met before appropriate tests were applied. Bee richness, measured as counts of distinct species or higher-level taxa, was verified as normally distributed by a Shapiro fit test in R before running parametric statistics (ANOVA, regression, generalized linear mixed models) to test for differences between habitat types and relationships to habitat variables. Floral richness, here defined as the number of distinct plant taxa from which bee specimens were collected in a sample, was also normally distributed via a Shapiro fit test. Bee abundance, calculated as the number of individual bee specimens collected in a given sample or set of samples, was square root transformed to meet assumptions of normality before running aforementioned parametric statistics. Elevation and longitude were non-normally distributed, and were therefore evaluated using the Friedman nonparametric alternative to ANOVA. Differences in bee abundance and richness among habitat types and sides of the park were evaluated using a mixed-effects ANOVA with habitat as the fixed effect grouping and the random effects of sample plot and day nested within year (*Gelman and Hill, 2006*). Cross-tab matrices of bee or flower taxa abundances per sample unit were used to calculate indices of diversity or to produce NMDS ordinations to evaluate compositional similarity between habitats using functions in the *vegan* package in R. Data for ordinations were relativized in R using the Wisconsin standardization procedure, and tested to assure assumptions of homogeneity of beta dispersions were met.

## RESULTS

### **Biodiversity**

Over the flowering seasons of 2011 and 2012 we conducted fifteen sampling rounds for each of the ten plots (8 rounds in 2011 and 7 rounds in 2012) resulting in 32,440 bee specimens from plots. Approximately 19% of these bees were collected using an aerial handheld net, 33% were collected in fluorescent blue pan traps, 20% in fluorescent yellow pan traps, and 28% in white pan traps. Ninety-nine percent of specimens were identified by experts at the Logan Bee Lab to generic level, with the vast majority of those determined to species. Over the two years we detected 283 species from 51 genera in plots, and expanded the known geographic range of three genera (*Brachynomada*, *Neopasites*, and *Peponapis*), none of which had previously been detected in the area.

Including opportunistic trail sampling outside of plots and sampling for two side projects, collection totals for the 2011-12 study include 52,853 bee specimens, 354 species, and 52 genera, with 72 new species records for the park and 3 new genera (listed above). The seventy-two new species records were split evenly between the two years of collections, but the three new park genera were all only collected in 2012. Nineteen species were unique to 2011, never collected in any of the six other years in which bees have been sampled at Pinnacles, and 36 species were unique to 2012. A full species list and relative abundances per year can be found in **Appendix B**.

The current study was precipitated by five years of bee inventory sampling efforts along trails across the previous, smaller area of Pinnacles National Park (1996-9), and using passive pan traps to sample the central bottomlands (2002). Delving into trends in

sampling effort and species accumulation between past and present projects, the overall number of specimens collected per new species record across the seven years is 177, with 1668 specimens required to detect a new genus, on average. By 2012, however, we collected 903 specimens for every new species we discovered, and 10,839 specimens for every new genus, indicating that the species accumulation rate has plateaued and the majority of diversity at Pinnacles has already been detected. Including the overall park collection from all seven years of sampling, the specimen total comes to 85,075 (average 25.4 specimens/species/year) and the current inventory for all bees recorded within Pinnacles National Park boundaries lists 479 distinct species. More details on the collection and its diversity are included in **Table 2-2**.

**Table 2-2 Summary results of sampling efforts for bees 1996-2012 at Pinnacles National Park.** See Appendix B for full bee species list and relative abundances by year.

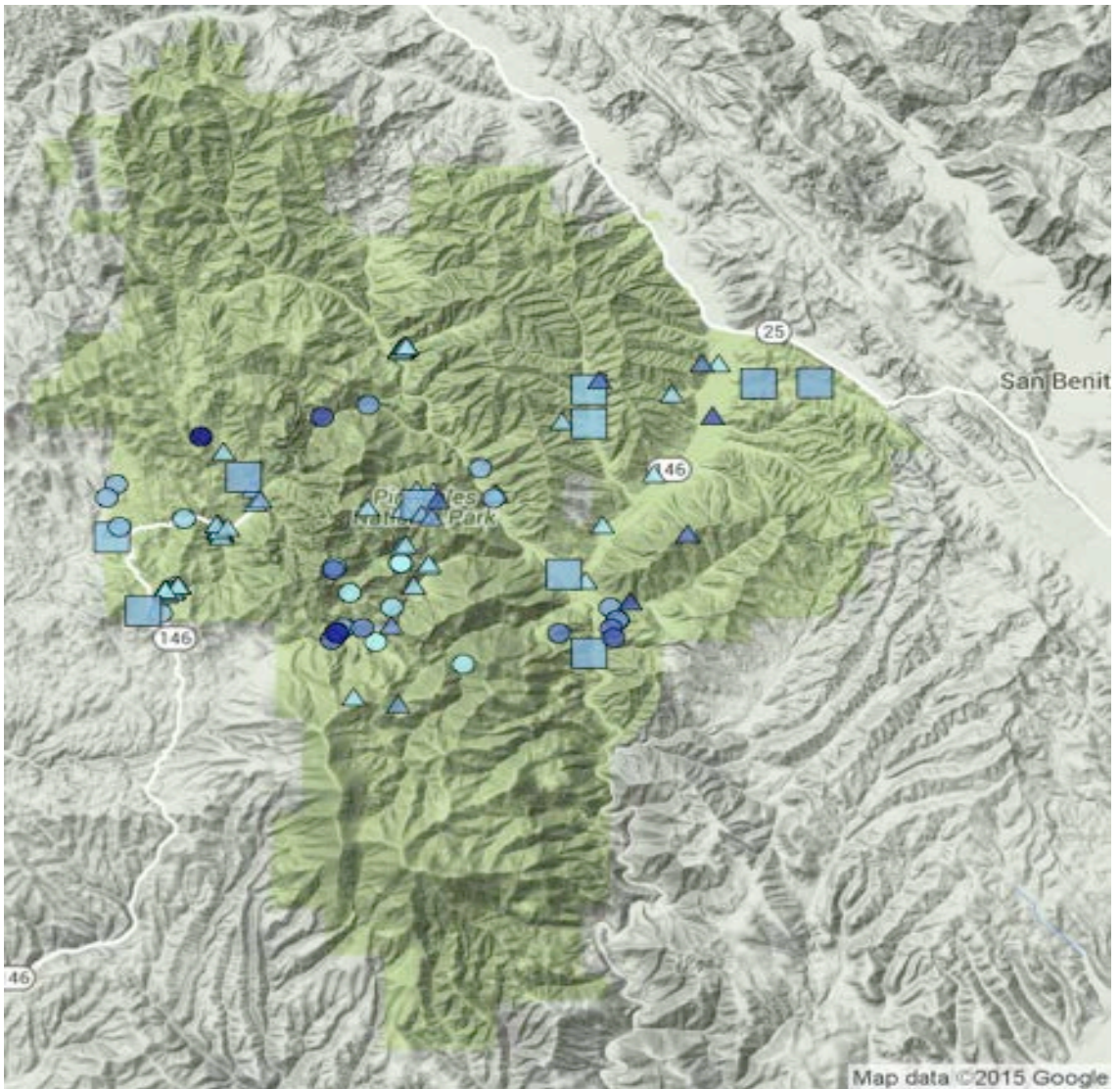
**A. By year sampled**

Bees at Pinnacles National Park By Year	Grand Totals	Individual Years						
		1996	1997	1998	1999	2002	2011	2012
Number of Specimen Collected	<b>85075</b>	1362	8077	9383	8234	5166	20336	32517
Number of Species Collected	<b>479</b>	174	302	320	213	76	285	283
Number of Genera Collected	<b>53</b>	38	48	49	43	23	45	49
Number of New Species Records	<b>480</b>	174	145	66	11	11	36	36
Number of New Genus Records	<b>52</b>	38	11	1	0	0	0	3
Bees / new species record	<b>177</b>	8	56	142	749	470	565	903
Bees / new Genus record	<b>1668</b>	36	734	9383	\	\	\	10839
Species unique to that year/project		9	25	23	4	5	19	36
Genera unique to that year/project		1	0	0	0	0	0	3
<b>Methodology (equipment):</b> <i>Since methodology and sampling effort vary widely between years and projects, comparisons should be interpreted with caution.</i>		Opportunistic trail collecting (aerial handheld net)				Passive collecting (pan trap bowls)	Plot (N=10) sampling (aerial nets + pan traps); Trail collecting (nets); Resample of 2002 bowl sites (pan traps)	
Primary Collectors/Contacts		O. Messinger & T. Griswold				A. Fesnock	J. Meiners & T. Lamperty	

**B. By project**

Bees at Pinnacles National Park By Project	Grand Totals	Projects		
		1996- 1999 Pilot Trail Inventory	Pre-2011 (Pilot Trail Inventory + 2002 Bottomlands Bowls (BB))	All 2011-12 Projects: Plot-based Community Study + Trails + Honeydew + BB Resample
Number of Specimen Collected	<b>85075</b>	27056	32222	52853
Number of Species Collected	<b>479</b>	396	407	354
Number of Genera Collected	<b>53</b>	51	51	52
Number of New Species Records	<b>480</b>	396 (all)	407	72
Number of New Genus Records	<b>52</b>	51 (all)	51	3
Bees / new species record	<b>177</b>	68	2929	734
Bees / new Genus record	<b>1668</b>	531	632	17618
Species unique to that year/project		116	126	72
Genera unique to that year/project		1	1	3
<b>Methodology (equipment):</b> <i>Since methodology and sampling effort vary widely between years and projects, comparisons should be interpreted with caution.</i>		Opportunistic trail collecting (aerial handheld net)	Passive collecting (pan trap bowls)	Plot (N=10) sampling (aerial nets + pan traps); Trail collecting (nets); Resample of 2002 bowl sites (pan traps)
Primary Collectors/Contacts		O. Messinger & T. Griswold	A. Fesnock	J. Meiners & T. Lamperty

The current study expanded collecting efforts into areas of Pinnacles National Park not previously sampled in the 1996-99 inventories by Messinger and Griswold inventories or the 2002 pan trap study by Fesnock. Thus, part of the motivation for the current study, other than establishing a systematic, repeatable, plot-based sample of bee community dynamics, was to inventory these additional new park lands. A map of collecting efforts over all these years shows the distribution of plots, trail sampling locations, and previous sampling locations recorded prior to this study, the specimens for which were also processed and are housed at the Logan Bee Lab (**Fig. 2-2**). The current study established four plots for repeated, systematic sampling in the upper right (NE) quadrant of the map that lie in park lands acquired since the previous decades' sampling efforts (plots are represented by squares in **Fig. 2-2** below). The current study also attempted to expand trail sampling efforts (represented by circles in **Fig. 2-2** below) beyond those covered during earlier inventories (the position of which are represented by triangles in **Fig. 2-2** below) to capture more of the biodiversity present within Pinnacles National Park both within and beyond previous boundaries. Biodiversity yield per sampling effort (or its position along a species accumulation curve, presented in subsequent sections) is indicated on the map by the shade of blue of all points, which is a function of the number of bee species collected in that area, divided by the number of days spent sampling at that location. Plots (squares) were heavily sampled compared to other locations, making their light shade not entirely reflective of the high species richness recorded in those areas (a species accumulation curve plateau). Further inventory efforts may wish to concentrate sampling in areas not represented by points in **Fig. 2-2**, or those which are darkest indicating there may be more diversity there yet to detect.



**Figure 2-2 Map of the current boundary of Pinnacles National Park (shown in green), and all sites sampled between 1996-2012 (shown in blue).** Squares represent the location of plots systematically sampled during the current study over the flowering seasons of 2011 and 2012 (See Table 1 for plot locations, dimensions, and habitat types). Triangles represent locations of opportunistic collecting in 2011 and 2012, and circles represent previous collecting locations (1996-2002). The shade of blue is a function of the bee species richness per days spent sampling at that location, with dark blue indicating a higher return of diversity per sampling effort and light blue indicating either less rich or more heavily sampled areas where new species records have begun to slow. Darker points and regions not yet sampled may indicate areas most worthy of additional sampling if further inventory efforts occur.



The 25 most abundantly collected bee species in 2011 and 2012, representing 81% of all bee specimens collected in those years though they represent only 7.5% of bee species diversity, are listed by abundance rank and year in **Table 2-3**. Variability in dominant bee taxa at Pinnacles (eight of 25 absent in alternate year) may have strong influences on community dynamics at different times and locations throughout the park. A testament to the well-known, high spatiotemporal variability among native bees from year to year (*Williams et al., 2001a*), *Hesperapis regularis* was the most abundant species over both years combined (16.6% of all specimens), and the most abundant in 2011 (23.6% of all specimens), but ranked only fourth in abundance in 2012 (9% of all specimens). Conversely, *Osmia nemoris* was most abundant in 2012 (12.6% of all specimens), having been ranked fifth in 2011 (6% of all specimens), while *Lasioglossum nigrescens* fluctuated less in time (ranked 3<sup>rd</sup> at 12.6% in 2011 and ranked 6<sup>th</sup> at 9.1% in 2012) though it was highly variable in its abundance across plots both years.

Whether driven by the ever-fluctuating abundances of their pollinators or by their own temporal fluctuations in abundance, similar interannual variability in rank abundance can be seen among plant species popular with bees at Pinnacles National Park (**Table 2-4**). *Clarkia unguiculata*, for example, attracted more bees than any other plant in 2011, but was only the fourth most popular plant with bees in 2012. *Eriogonum fasciculatum* var. *foliosolum* was the foraging source of more bee species in 2012 than any other plant, though it had been ranked eighth in number of bee-plant records the year before. This type of information may be useful to managers wishing to support specific aspects of Pinnacles' bee or wildflower diversity, a topic discussed at greater length in an associated project report submitted to the National Park Service (*Meiners et al., 2015*).

**Table 2-3 Twenty-five most commonly collected bee species at Pinnacles National Park in 2011-12, by rank abundance per year. See Appendix B for the complete bee species list.**

During the 2011 flowering season				During the 2012 flowering season		
Bee Family	Genus	Species	Rank Abun.	Bee Family	Genus	Species
Melittidae	<i>Hesperapis</i>	<i>regularis</i>	1	Megachilidae	<i>Osmia</i>	<i>nemoris</i>
Halictidae	<i>Halictus</i>	<i>tripartitus</i>	2	Halictidae	<i>Halictus</i>	<i>tripartitus</i>
Halictidae	<i>Lasioglossum</i>	<i>nigrescens</i>	3	Halictidae	<i>Lasioglossum</i>	<i>incompletum</i>
Halictidae	<i>Lasioglossum</i>	<i>brunneiventre</i>	4	Melittidae	<i>Hesperapis</i>	<i>regularis</i>
Megachilidae	<i>Osmia</i>	<i>nemoris</i>	5	Halictidae	<i>Halictus</i>	<i>farinosus</i>
Halictidae	<i>Lasioglossum</i>	<i>incompletum</i>	6	Halictidae	<i>Lasioglossum</i>	<i>nigrescens</i>
Apidae	<i>Apis</i>	<i>mellifera</i>	7	Apidae	<i>Melissodes</i>	<i>stearnsi</i>
Halictidae	<i>Lasioglossum</i>	<i>punctatoventre</i>	8	Apidae	<i>Apis</i>	<i>mellifera</i>
Halictidae	<i>Halictus</i>	<i>farinosus</i>	9	Halictidae	<i>Lasioglossum</i>	<i>brunneiventre</i>
Halictidae	<i>Lasioglossum</i>	<i>sp. 9</i>	10	Halictidae	<i>Lasioglossum</i>	<i>punctatoventre</i>
Halictidae	<i>Lasioglossum</i>	<i>imbrex</i>	11	Apidae	<i>Eucera</i>	<i>actiosa</i>
Apidae	<i>Ceratina</i>	<i>arizonensis</i>	12	Andrenidae	<i>Panurginus</i>	<i>gracilis</i>
Andrenidae	<i>Andrena</i>	<i>aff. cerasifolii</i>	13	Halictidae	<i>Agapostemon</i>	<i>angelicus / texanus</i>
Andrenidae	<i>Andrena</i>	<i>sp.</i>	14	Halictidae	<i>Lasioglossum</i>	<i>sp. 9</i>
Halictidae	<i>Agapostemon</i>	<i>angelicus / texanus</i>	15	Apidae	<i>Diadasia</i>	<i>bituberculata</i>
Andrenidae	<i>Andrena</i>	<i>crudeni</i>	16	Apidae	<i>Melissodes</i>	<i>sp.</i>
Halictidae	<i>Lasioglossum</i>	<i>nevadense</i>	17	Andrenidae	<i>Perdita</i>	<i>distropica</i>
Megachilidae	<i>Protosmia</i>	<i>rubifloris</i>	18	Halictidae	<i>Lasioglossum</i>	<i>sp.</i>
Apidae	<i>Eucera</i>	<i>actiosa</i>	19	Andrenidae	<i>Andrena</i>	<i>aff. cerasifolii</i>
Megachilidae	<i>Osmia</i>	<i>brevis</i>	20	Megachilidae	<i>Osmia</i>	<i>aglaia</i>
Andrenidae	<i>Panurginus</i>	<i>gracilis</i>	21	Megachilidae	<i>Osmia</i>	<i>regulina</i>
Halictidae	<i>Lasioglossum</i>	<i>sisymbrii</i>	22	Halictidae	<i>Lasioglossum</i>	<i>nevadense</i>
Apidae	<i>Diadasia</i>	<i>angusticeps</i>	23	Andrenidae	<i>Andrena</i>	<i>macrocephala</i>
Megachilidae	<i>Trachusa</i>	<i>perdita</i>	24	Andrenidae	<i>Andrena</i>	<i>w-scripta</i>
Megachilidae	<i>Osmia</i>	<i>regulina</i>	25	Apidae	<i>Ceratina</i>	<i>arizonensis</i>

**Table 2-4 Twenty-five most commonly recorded plants visited by bees in 2011-12 at Pinnacles National Park, ranked by popularity per year. See Appendix C for a complete 2011-2012 Bee-Plant list, with years collected and relative bee popularity.**

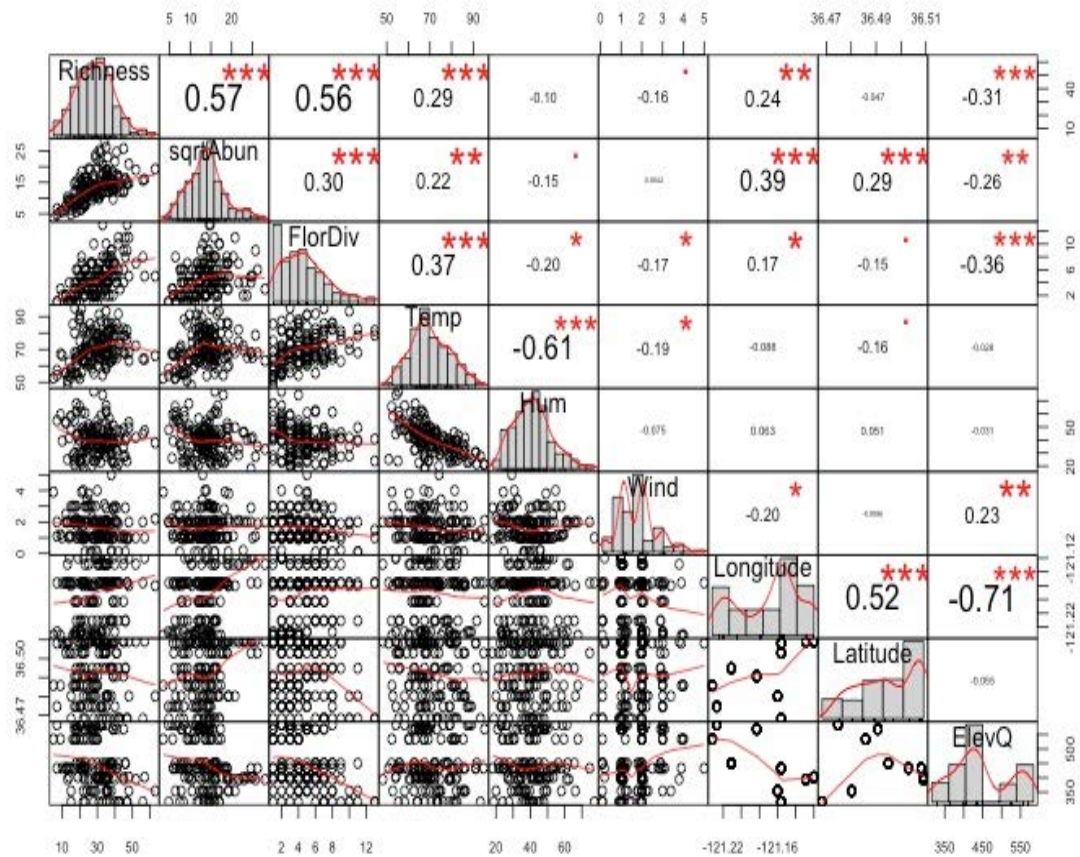
During the 2011 flowering season			During the 2012 flowering season	
<i>Plant Latin Name</i>	Plant Family	Popul. Rank	<i>Plant Latin Name</i>	Plant Family
<i>Clarkia unguiculata</i>	Onagraceae	1	<i>Eriogonum fasciculatum</i> <i>var.foliolosum</i>	Polygonaceae
<i>Adenostoma fasciculatum</i>	Rosaceae	2	<i>Adenostoma fasciculatum</i>	Rosaceae
<i>Eschscholzia californica</i>	Papaveraceae	3	<i>Eschscholzia californica</i>	Papaveraceae
<i>Clarkia purpurea</i>	Onagraceae	4	<i>Clarkia unguiculata</i>	Onagraceae
<i>Chaenactis glabriuscula</i>	Asteraceae	5	<i>Hirschfeldia incana</i>	Brassicaceae
<i>Lotus scoparius</i> <i>var.scoparius</i>	Fabaceae	6	<i>Marrubium vulgare</i>	Lamiaceae
<i>Ranunculus californicus</i>	Ranunculaceae	7	<i>Eriodictyon tomentosum</i>	Boraginaceae
<i>Eriogonum fasciculatum</i> <i>var.foliolosum</i>	Polygonaceae	8	<i>Chaenactis glabriuscula</i>	Asteraceae
<i>Hirschfeldia incana</i>	Brassicaceae	9	<i>Amsinckia menziesii</i>	Boraginaceae
<i>Salix exigua</i>	Salicaceae	10	<i>Salix lasiolepis</i>	Salicaceae
<i>Lupinus albifrons</i>	Fabaceae	11	<i>Clarkia purpurea</i>	Onagraceae
<i>Vicia villosa</i>	Fabaceae	12	<i>Lasthenia californica</i>	Asteraceae
<i>Eriodictyon tomentosum</i>	Boraginaceae	13	<i>Lupinus albifrons</i>	Fabaceae
<i>Viola pedunculata</i>	Violaceae	14	<i>Calochortus venustus</i>	Liliaceae
<i>Quercus agrifolia</i> <i>var.agrifolia</i>	Fagaceae	15	<i>Ceanothus cuneatus</i> <i>var.cuneatus</i>	Rhamnaceae
<i>Lasthenia californica</i>	Asteraceae	16	<i>Chorizanthe douglasii</i>	Polygonaceae
<i>Marrubium vulgare</i>	Lamiaceae	17	<i>Erodium cicutarium</i>	Geraniaceae
<i>Pholistoma auritum</i> <i>var.auritum</i>	Boraginaceae	18	<i>Salix exigua</i>	Salicaceae
<i>Arctostaphylos pungens</i>	Ericaceae	19	<i>Penstemon heterophyllus</i>	Plantaginaceae
<i>Amsinckia menziesii</i>	Boraginaceae	20	<i>Lotus scoparius</i> <i>var.scoparius</i>	Fabaceae
<i>Ceanothus cuneatus</i> <i>var.cuneatus</i>	Rhamnaceae	21	<i>Baccharis salicifolia</i>	Asteraceae
<i>Bloomeria crocea</i>	Liliaceae	22	<i>Vicia villosa</i>	Fabaceae
<i>Heliotropium curassavicum</i>	Boraginaceae	23	<i>Malacothamnus aboriginum</i>	Malvaceae
<i>Erodium brachycarpum</i>	Geraniaceae	24	<i>Ranunculus californicus</i>	Ranunculaceae
<i>Salix lasiolepis</i>	Salicaceae	25	<i>Heliotropium curassavicum</i>	Boraginaceae

### Community Dynamics

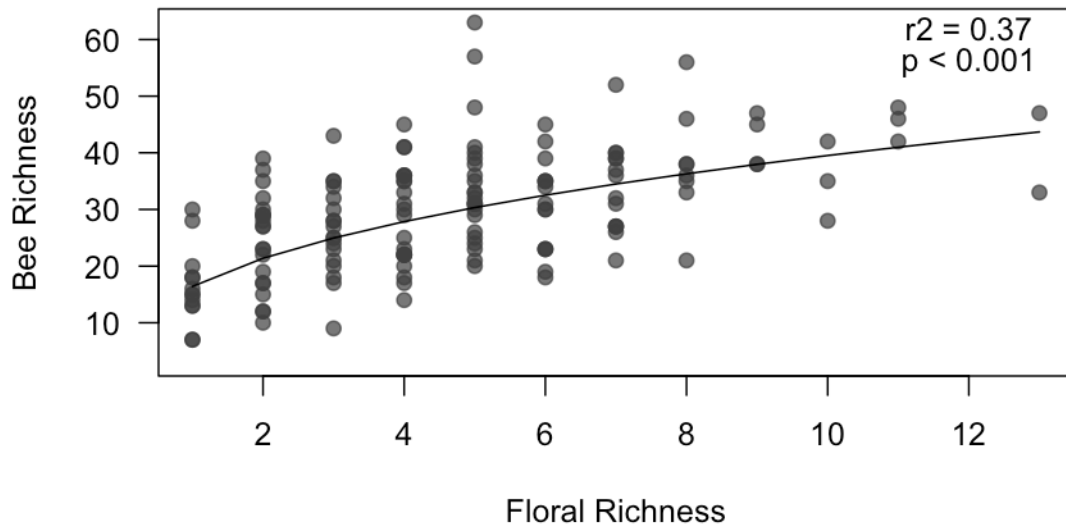
The overall bee richness (count of species) at Pinnacles National Park was normally distributed (Shapiro-Wilk normality test,  $p=0.8$ ), strongly correlated with the number of floral taxa on which all bees were collected ( $R^2=0.57$ ,  $p<0.001$ , **Fig. 2-3**), and positively related to floral richness of bee-visited plants by a power-law linear regression model (Bee Richness =  $\exp(2.79 + 0.38 \cdot \log(\text{FR}))$ ;  $R^2=0.37$ ,  $p<0.01$ , **Fig. 2-4**). Bee abundance (sum of all bee individuals collected by net and pan traps, square root transformed to normalize distribution) was also, though to a lesser extent, significantly positively correlated with the floral diversity of bee-visited plants, considering both the overall dataset ( $R^2=0.30$ ,  $p<0.001$ , **Fig. 2-3**) and in a linear power-law regression model (Bee Abundance =  $\exp(2.26 + 0.23 \cdot \log(\text{FR}))$ ;  $R^2 = 0.16$ ,  $p<0.01$ , **Fig. 2-5**).

Bee richness and abundance were also both positively correlated with the ambient temperature at the time of sampling and the longitude of the sample plot, and negatively correlated with the elevation of the sample plot (Richness:  $\text{BR} = \exp(1.14 \cdot \log(\text{Temp}) - 1.52)$ ,  $R^2 = 0.17$ ,  $p<0.01$ . Abundance:  $\text{BA} = \exp(0.85 \cdot \log(\text{Temp}) - 1.03)$ ,  $R^2 = 0.10$ ,  $p<0.01$ ,  $R^2=0.07 - 0.15$ ,  $p<0.001$ , **Figs. 2-6 & 2-7**). Bee abundance, but not bee richness, was positively correlated with the relatively small range of latitudes across sample plots ( $R^2=0.29$ ,  $p<0.001$ , **Fig. 2-3**), while humidity and wind speed showed no relationship to either bee richness or bee abundance in the Pinnacles data. Floral diversity was significantly positively correlated with the ambient temperature of a sample plot ( $R^2=0.378$ ,  $p<0.001$ , **Fig. 2-3**) and to a lesser degree with its longitude ( $R^2=0.17$ ,  $p<0.1$ , **Fig. 2-3**), and significantly negatively correlated with humidity ( $R^2= -0.20$ ,  $p<0.1$ , **Fig. 2-3**) and wind speed ( $R^2= -0.17$ ,  $p<0.1$ , **Fig. 2-3**) of sample plot. Temperature and humidity

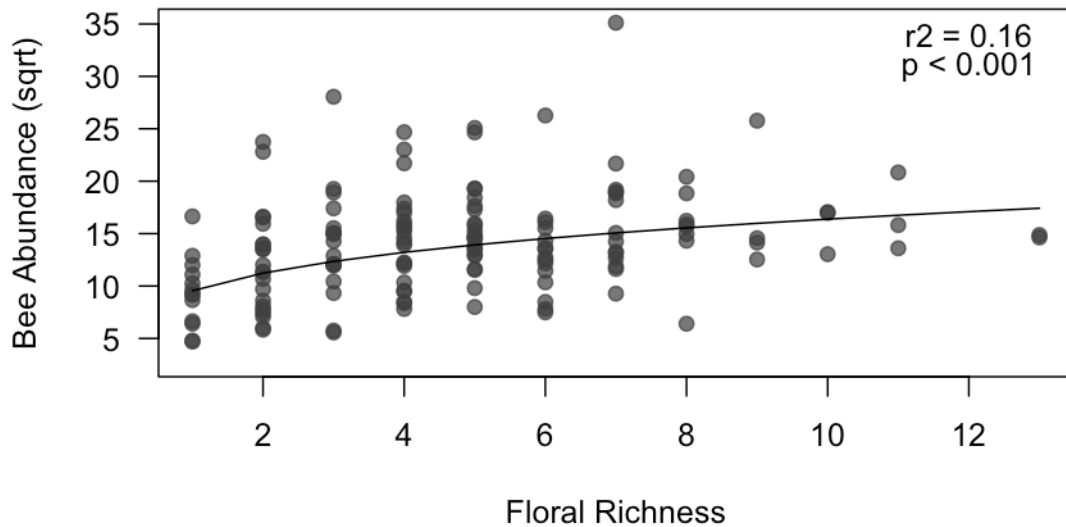
were inversely related ( $R^2 = -0.61$ ,  $p < 0.001$ , **Fig. 2-3**), and wind speed was higher at higher elevations ( $R^2 = 0.23$ ,  $p < 0.01$ , **Fig. 2-3**).



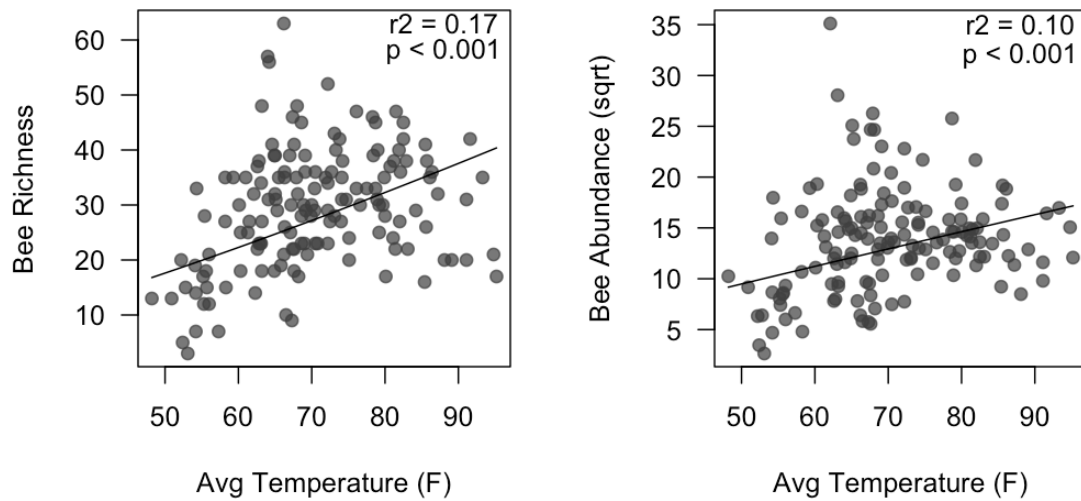
**Figure 2-3 Correlation matrix of collection results from all 149 positive plot samples.** Bee species richness, square root abundance, and environmental variables (floral diversity, ambient temperature, humidity, wind speed, longitude, latitude, and elevation) are plotted to show data distributions along the diagonal and scatterplots of compared variables in the lower triangle. Absolute correlations are shown in the upper triangle, with larger correlation values in bigger fonts and noted by more significance asterisks (\*= $0.05$ , \*\*= $0.01$ , \*\*\*= $0.001$ ). Note that some correlations are likely to occur by chance, and that this figure is intended to aid in visualizing distributions of major variables used in analyses.



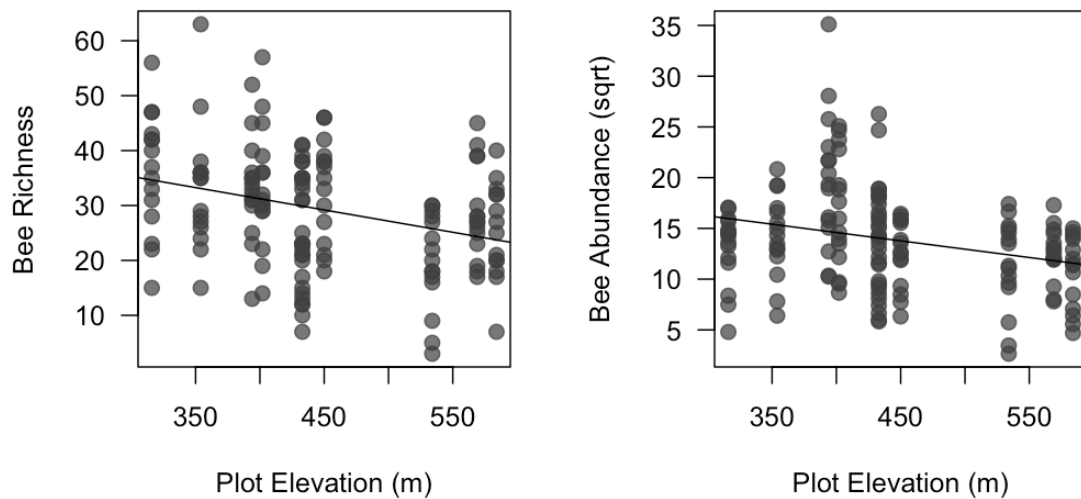
**Figure 2-4 Relationship between bee richness (BR) and floral richness (FR) at the plot-sample level (N=149) within Pinnacles National Park (2011-12).** Shown with power-law model (black line;  $BR = \exp(2.79 + 0.38 \cdot \log(FR))$ ;  $R^2=0.37$ ,  $p<0.01$ ).



**Figure 2-5 Relationship between bee abundance (square-root transformed; BA) and floral richness (FR) at the plot-sample level (N=149) at Pinnacles National Park (2011-12).** Shown with power-law model (black line;  $BA = \exp(2.26 + 0.23 \cdot \log(FR))$ ;  $R^2 = 0.16$ ,  $p<0.01$ ).

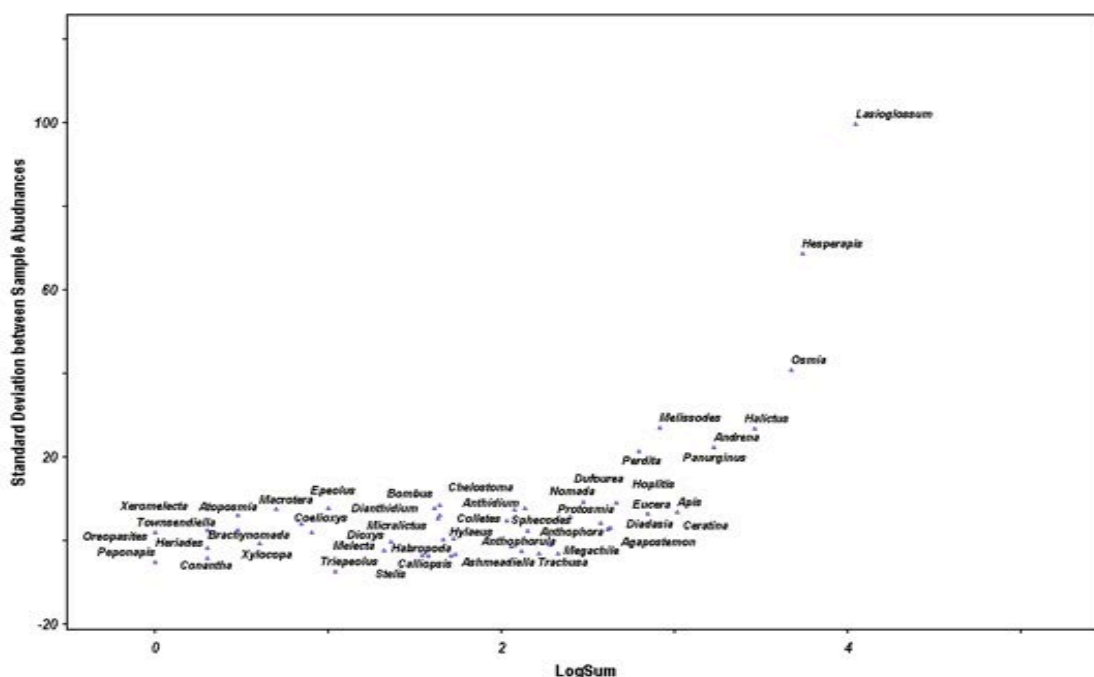


**Figure 2-6 Relationship between bee richness (left; BR) or bee abundance (square-root transformed, right; BA) and average ambient plot temperature (F) from 149 plot samples at Pinnacles National Park (2011-12).** Shown with power-law models (black line; Richness:  $BR = \exp(1.14 \cdot \log(\text{Temp}) - 1.52)$ ,  $R^2 = 0.17$ ,  $p < 0.01$ . Abundance:  $BA = \exp(0.85 \cdot \log(\text{Temp}) - 1.03)$ ,  $R^2 = 0.10$ ,  $p < 0.01$ ).



**Figure 2-7 Relationship between bee richness (left) or bee abundance (square-root transformed, right) and elevation from 149 plot samples at Pinnacles National Park (2011-12).** Trend lines are plotted for clarity in interpreting correlation, but results of linear regressions are not reported as elevation is not normally distributed.

Bee richness and abundance were significantly correlated with each other ( $R^2=0.57$ ,  $p<0.001$ , **Fig. 2-3**), despite a high unevenness of particular species' abundances within and across samples, with some plot bee communities composed of very high numbers of a few common species. *Lasioglossum*, for example, was the most abundant of all genera collected in plots at Pinnacles, followed by *Hesperapis*, *Osmia*, *Halictus*, and *Andrena* (**Fig. 2-8**). *Lasioglossum* and *Hesperapis*, in particular, were highly variable in their abundances between plot samples, whereas *Osmia*, *Halictus*, and *Andrena*, had standard deviations of abundance between samples more similar to that of less abundant genera.



**Figure 2-8** Logsum of bee abundance (x-axis) vs. standard deviation of abundance in 150 plot samples (y-axis) for all bee genera captured in plots in 2011-12.

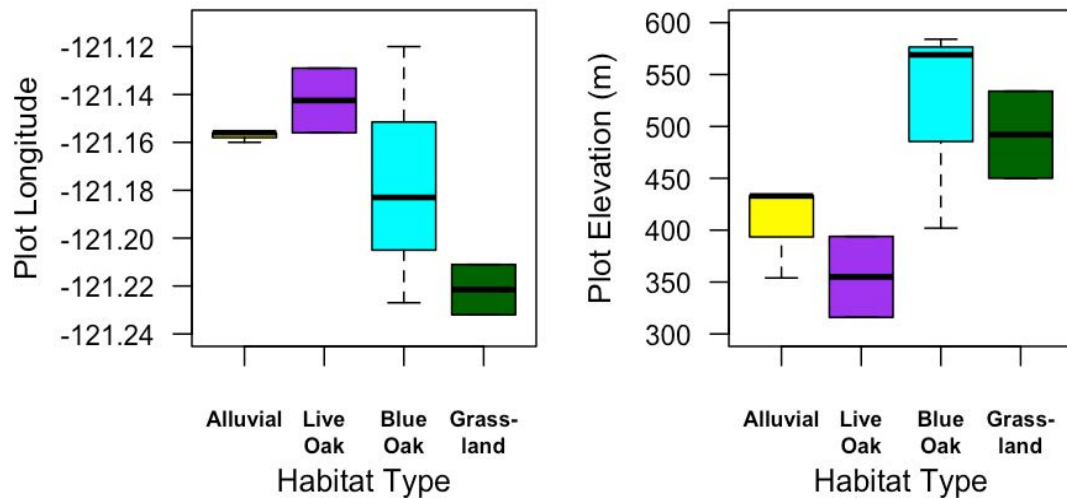
Comparison of position between genera along these axes gives a measure of both abundance and evenness of genera across samples. The y-axis is jittered at 15% to make labels visible; close vertical comparisons are not intended.



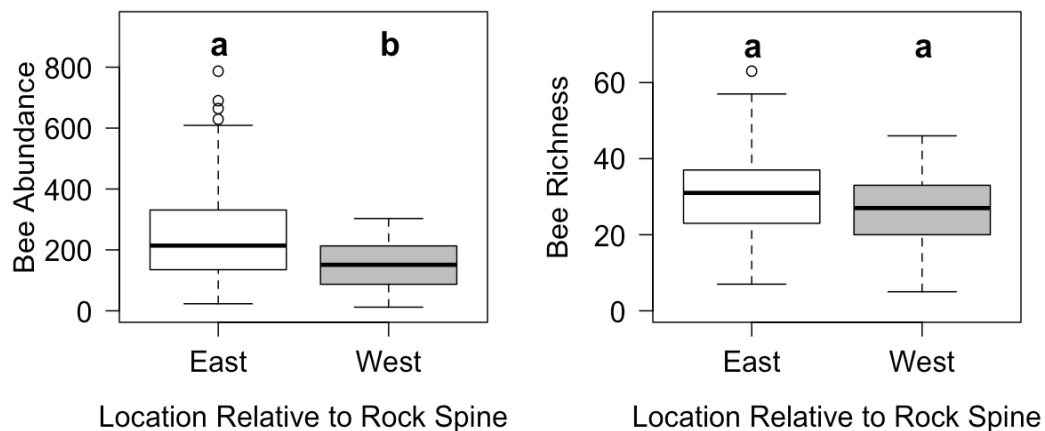
## **The Role of Habitat Type**

### **Geography and Floral Resources**

Ten plots were distributed between four visually distinct habitat types across Pinnacles National Park. Though these habitat types do not naturally occur in all areas of the park, every attempt was made to spatially distribute plot replicates for each habitat type evenly across environmental gradients (see **Fig. 2-1**). The west side of the park is prone to coastal influences while the drier, more climate-stable east side is not, for example. As a result, plots on the west side can be foggier, cloudier, windier, and colder than those on the east side. Though plots on the west side are also slightly higher in elevation than those on the east side due to the natural slope of the landscape, there were no significant differences in elevation between habitat types (KW chi-sq = 5.561, df=3, p=0.135, **Fig. 2-9**). Furthermore, while Blue Oak Woodland and Grassland habitat types naturally occur, on average, somewhat further west in longitude and higher in elevation than either Alluvial or Live Oak habitats at Pinnacles, there were also no significant differences in longitude between any of the four habitat types (KW chi-sq = 4.379, df=3, p=0.2234, **Fig. 2-9**). Still, there are some apparent differences between the east and west sides of the park in bee measures. Biotic differences across the east-west geographical barrier and elevation gradient in the park are reflected in the result of a mixed-effects ANOVA that determined bee abundance, as measured on individual days (N=149) at individual plots (N=10) across two years of sampling (2011-12), to be somewhat higher on the east side than the west side of the park ( $F(1,147)=5.033$ ,  $p=0.046$ , **Fig. 2-10**). Bee species richness, however, was similar across the Pinnacles dividing rock ridge according to a mixed-effects ANOVA ( $F(1,147)=0.8216$ ,  $p=0.38$ , **Fig. 2-10**).

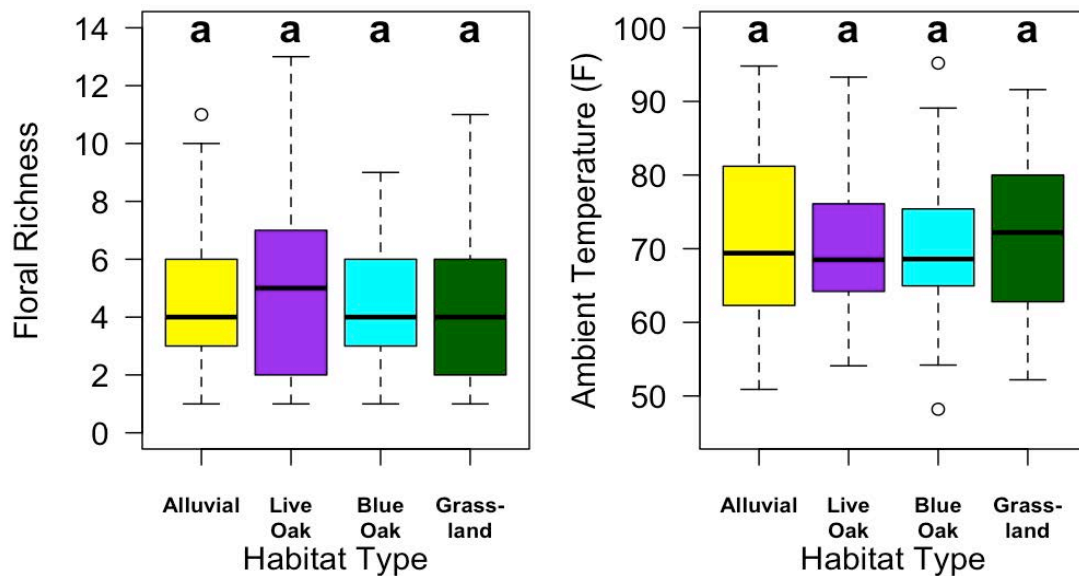


**Figure 2-9** Range of longitudes (left) and elevations (right) of four habitat types observed from 10 plots repeatedly sampled at Pinnacles National Park (2011-12). Nonparametric Kruskal-Wallis tests showed no significant differences in longitude or elevation between the four habitat types at the  $p < 0.05$  level. Box plots are shown with medians, first and third quartiles, and a range of 1.5 times the interquartile range. (Long.: KW chi-sq = 4.379, df=3,  $p=0.2234$ ; Elev.: KW chi-sq = 5.561, df=3,  $p=0.135$ ).



**Figure 2-10** Bee abundance (left) and richness (right) in 149 plot samples across the east (white) vs. west (gray) sides of Pinnacles National Park (2011-12). Habitat types with the same letter are not significantly different at the  $p < 0.05$  level. Box plots are shown with medians, first and third quartiles, and a range of 1.5 times the interquartile range. Outliers are represented as circles. Mixed-effects ANOVAs found bee abundance (square root transformed) was higher on the east side of the park ( $F(1,147)=5.033$ ,  $p=0.046$ ), but bee species richness did not differ ( $F(1,147)=0.822$ ,  $p=0.38$ ).

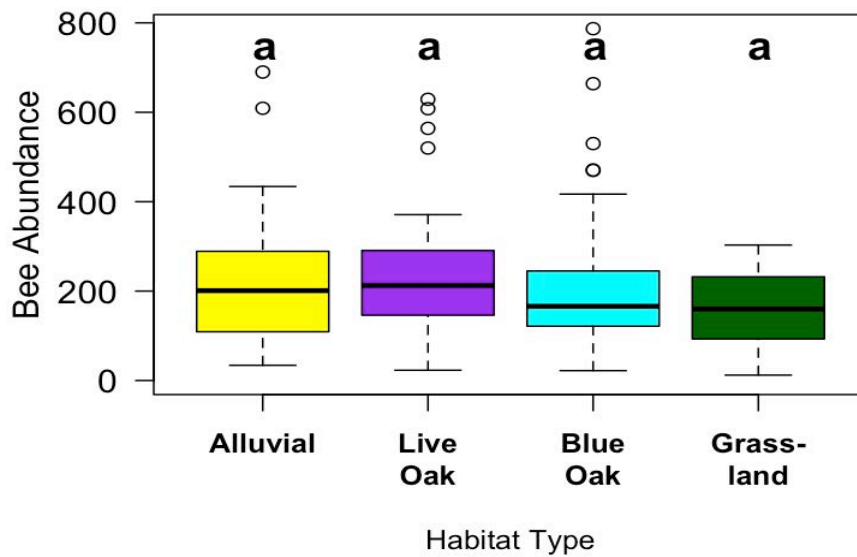
Despite the visual distinction between habitat types, their somewhat uneven distribution across various environmental gradients at Pinnacles, and their varying exposure to the influences of coastal weather patterns, the distinction between habitat types in other measures relevant to the bee community are minimal. A mixed-effects ANOVA identified no differences between habitat types in sample-level floral richness in either 2011 or 2012 ( $F(3,145)=2.093$ ,  $p=0.20$ , **Fig. 2-11**). Sample ambient temperatures, which are strongly correlated with floral diversity at the time of plot samples and known to vary with relevant habitat characteristics like shade cover and moisture levels, did not depend on habitat type across a season either ( $F(3,145)=0.1377$ ,  $p=0.93$ , **Fig. 2-11**).



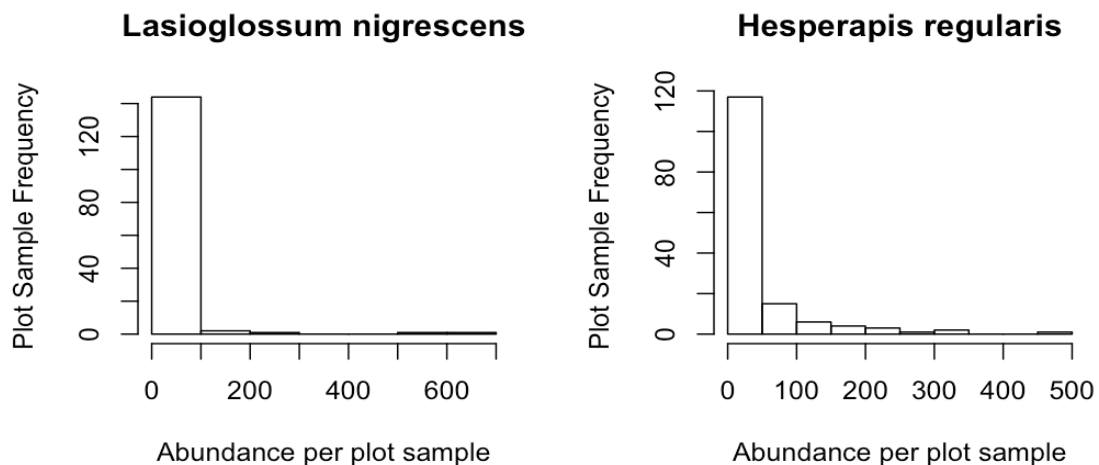
**Figure 2-11 Sample floral richness (left) and sample average temperature (right) across four habitat types observed from 149 plot samples at Pinnacles National Park (2011-12).** Habitat types with the same letter are not significantly different at the  $p < 0.05$  level. Box plots are shown with medians, first and third quartiles, and a range of 1.5 times the interquartile range. Outliers beyond the range are represented as circles. Over a whole season, neither sample floral richness ( $F(3,145)=2.093$ ,  $p=0.20$ ) nor sample ambient temperature differed between habitat types ( $F(3,145)=0.1377$ ,  $p=0.93$ ).

### Bee Abundance

Bee abundance at individual plot samples, while wildly variable across space and time, was also, surprisingly, not significantly different between habitat types ( $F(3,145)=0.7763$ ,  $p=0.55$ , abundance square-root transformed, **Fig. 2-12**). Variance in bee abundances across a season, as expected, was very high. The average number of bees collected per plot was 208, but individual plot sample abundances ranged from 7 to 1233 bees collected at a single plot in a single day (one sample with zero bees was omitted from all analyses due to poor environmental conditions for bees that day, thus plot sample N=149 as 15 replicates of 10 plots minus one zero record). High spatial variation, common among diverse native bee communities, also contributed to the lack of pattern between habitat types in bee abundances. A single extremely high outlier from one of the Live Oak habitat plots, for example, illustrates how variable bee abundance can be. A single plot sample collected on May 9, 2011 contained 1233 bees. The next three most abundant samples tallied just over half that number, at 787, 690, and 664 specimens. Ecologically, this outlier could be explained by emergence events of two very abundant species, *Hesperapis regularis* (N=343 on that day, third highest abundance record for this species) and *Lasioglossum nigriscens* (N=690 on that day, highest abundance record for this species, **Fig. 2-13**). To test for undue influence of these events on the results of bee abundance differences between habitat types, this sample was removed from the dataset, and all analyses in this section were repeated, with no changes in significance. It is therefore included in results presented here, but serves to illustrate the difficulty of identifying ecological patterns in native bee data due to very high spatiotemporal variability in abundances.



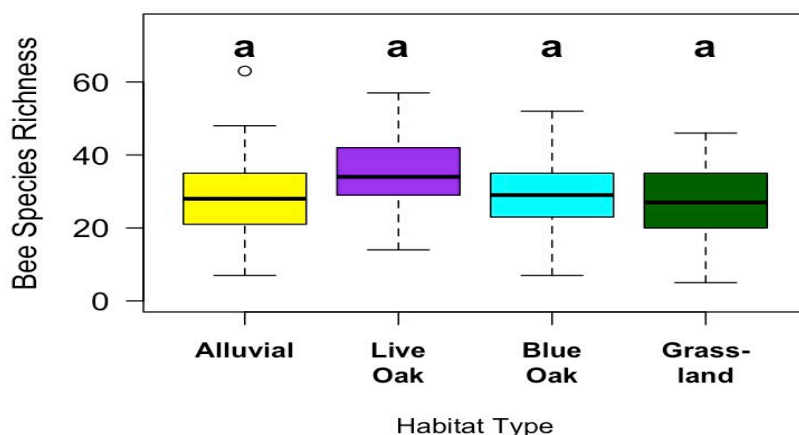
**Figure 2-12 Bee abundance (square root transformed) across four habitat types observed from 149 plots samples at Pinnacles National Park (2011-12).** Habitat types with the same letter are not significantly different at the  $p < 0.05$  level. Box plots are shown with medians, first and third quantiles, and a range of 1.5 times the interquartile range. Outliers beyond the range are represented as circles. A mixed-effects ANOVA concluded that bee abundance does not vary with habitat type ( $F(3,145)=0.7763$ ,  $p=0.55$ , abundance square-root transformed).



**Figure 2-13 Distribution of abundances across all 150 plot samples from 2011-12 at Pinnacles National Park for two species of bees with extreme outliers (outlying peak abundances for both species occurred at the Live Oak Plot 6 on May 9, 2011).**

### Bee Richness

Bee species richness, or the number of distinct species recorded in a given plot sample, varies less across the landscapes or timeframes sampled at Pinnacles National Park than bee abundance, and could be a useful measure for natural resource managers looking to prioritize protection of habitats with high biodiversity value. In 149 plot samples taken over the 2011-12 season at ten plots across Pinnacles, however, bee richness was not found to vary between any of the four habitat types by a mixed-effects ANOVA ( $F(3,145)=0.8327$ ,  $p=0.52$ , **Fig. 2-14**).

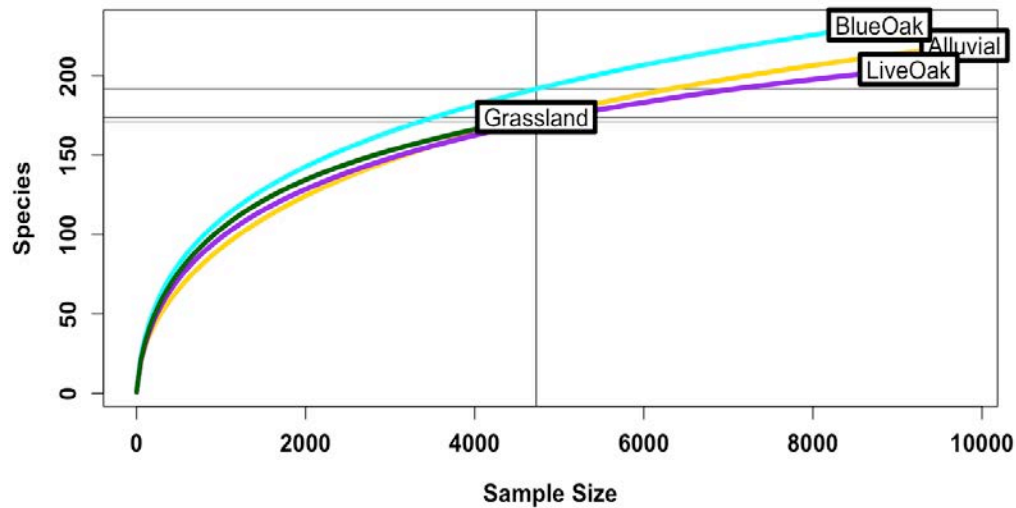


**Figure 2-14 Bee richness (count of species) across four main habitat types observed from 149 plot samples at Pinnacles National Park (2011-12).** Habitat types with the same letter are not significantly different at the  $p < 0.05$  level. Box plots are shown with medians, first and third quantiles, and a range of 1.5 times the interquartile range. Outliers beyond the range are represented as circles. A mixed-effects ANOVA found no relationship between habitat type and bee species ( $F(3,145)=0.8327$ ,  $p=0.52$ ).

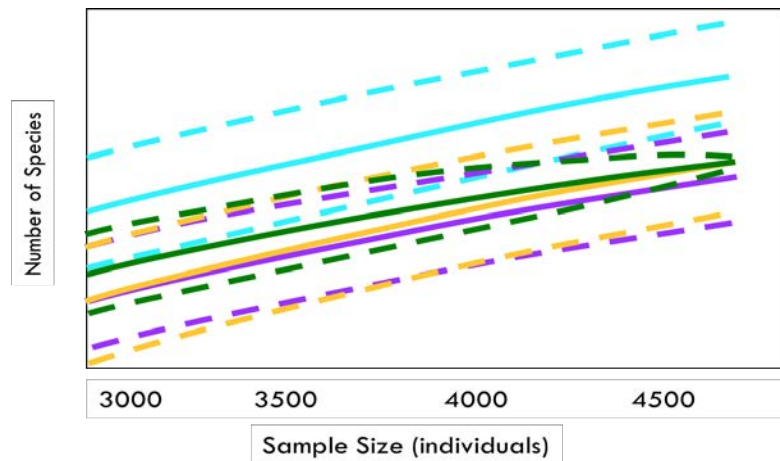
There are additional, potentially superior methods than a simple tally of species to measure the richness of an area, which deserve attention before the role of habitat type in estimating simple bee metrics is disregarded entirely. A species rarefaction curve

evaluates differences in species richness between habitat types by first standardizing uneven abundances or sampling efforts. This method of quantifying biodiversity takes statistical averages of the number of species in increasingly large samples of randomly selected individuals, and rarefies these values to match the smallest sample size of the groups for comparison, or that of the least abundant habitat type, for example, so that habitat types can be compared as if the bee collections from each were equal (*Gotelli and Colwell, 2001*). This eliminates confounding of species richness values due to some habitat types simply yielding more specimens (though, in this case, bee abundances did not vary between habitat types, **Fig. 2-12**), and allows a more even statistical comparison of differences between habitat types (**Fig. 2-15**).

In the Pinnacles dataset, the Grassland habitat type has the lowest sample size (N=4728 bees), thus richness values for all habitat types were compared at this number of individuals. Lack of overlap of 95% CIs at the vertical line, equal to the maximum Grassland sample size, suggests that Blue Oak Woodlands have higher species richness than other habitat types when sample sizes are standardized (**Fig. 2-16**). This conclusion, however, is highly dependent on how extensively the Grassland habitat type was sampled. For example, the estimated rarefied bee species richness values at a sample size of 3000 would have entirely overlapping CIs indicating no difference between habitat types, but at the maximum grassland sample size of 4728 bees, the CIs for this habitat type have narrowed around this exact, known value. In this way, species rarefaction curves help determine whether sampling effort was sufficient to reach an asymptote in detecting new species, but offer a somewhat inconclusive answer about richness differences between habitat types when confidence intervals are closely aligned.



**Figure 2-15** Rarefaction curves by habitat type of bee species richness estimated from random samples of individuals collected in 149 plot samples at Pinnacles National Park (2011-12). The vertical line in the center marks the point of appropriate comparison between the four habitat types, determined by the smallest sample size among habitat types (in Grassland), to which all other habitat type curves are rarefied.



**Figure 2-16** Rarefaction curves (solid lines, color-coded by habitat type as in Fig. 15) of bee species richness in 149 plot samples at Pinnacles National Park (2011-12), with 95% confidence intervals (dotted lines) estimating the species richness for each habitat type at continuous simulated sample sizes. The CI for grasslands (green dotted lines) converges on its main effect line (solid green) at the far right of the plot (aligned with the vertical line in the middle of Fig. 15) because this is an exact count of species at the maximum sample size, complicating comparison of curves.

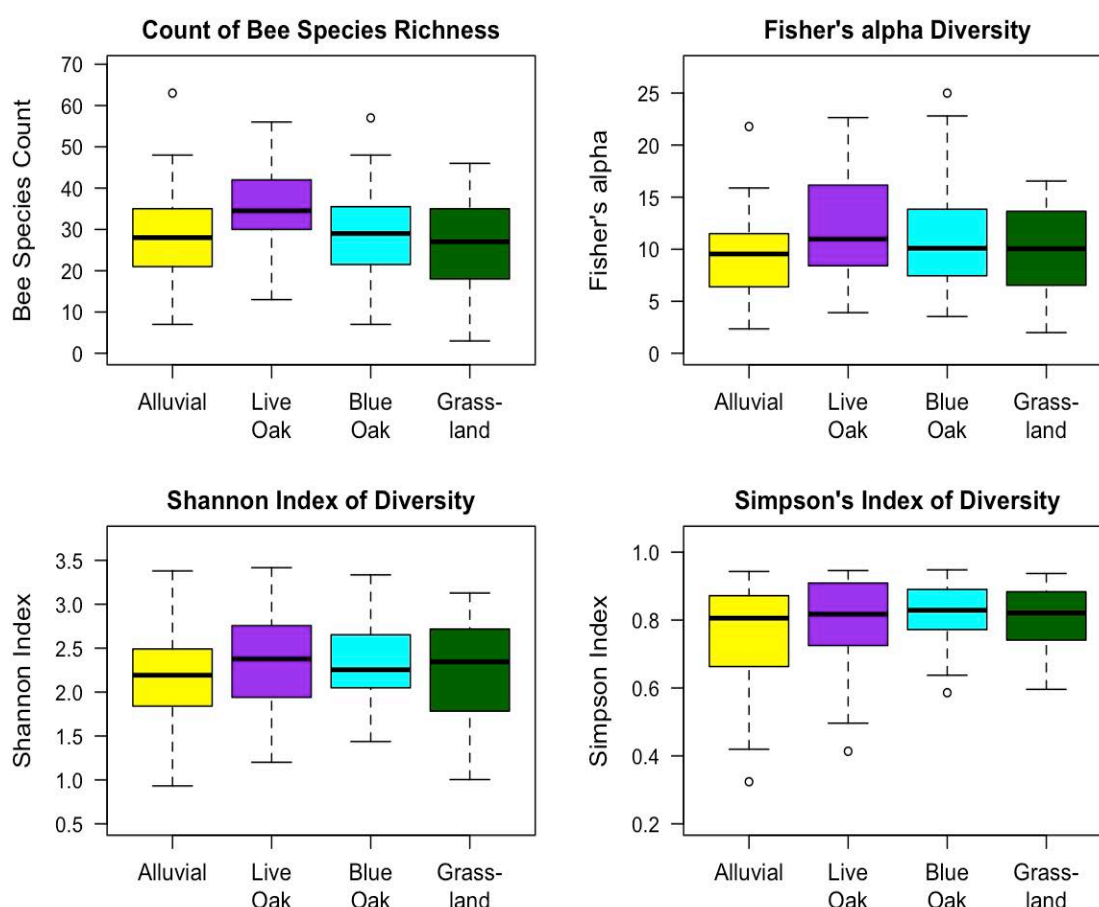


### Bee Diversity

A shortcoming of raw richness and species rarefaction as measures of biodiversity or ecosystem functioning is that they do not take variations in species abundances into account. We recorded 69 singleton species in Pinnacles plot samples, 30 of which were found in the Blue Oak woodland habitat type. Blue oak woodlands, therefore, had almost twice as many singleton species as any other habitat (Alluvial singletons = 16, Live Oak singletons = 15, Grassland singletons = 8), which alone could bump its species rarefaction curve above the other groups (**Fig. 2-15**), but may not have much ecological meaning. The Shannon's, Simpson's and Fisher's alpha indices of diversity are methods for estimating diversity that put varying emphases on the evenness of abundances between species and the sensitivity of variation across samples. Both the Shannon index of diversity and the Fisher's alpha metric tend to emphasize rare species more than the Simpson's index, which places more importance on evenness and dominance, and the Fisher's alpha stands out as having low sensitivity to sample-level variation (*Fisher et al., 1943; Hill, 1973; Nagendra, 2002*). All are used currently in ecological diversity assessments, and may sometimes produce conflicting interpretations of the concept of species richness in an ecosystem.

For the Pinnacles bee species data, habitat type once again does not sort out clearly according to any of these measures (**Fig. 2-17**), though we know evenness among samples to be highly variable at the generic level (**Fig. 2-8**). The Live Oak habitat type appears to be slightly higher in measures of raw bee species counts, mirroring trends of its slightly higher richness (**Fig. 2-14**). Live Oak also appears higher in Fisher's alpha measures for samples, though Blue Oak is high in this test as well, reflecting the

emphasis on rare species seen in the species rarefaction curve (**Fig. 2-15**). All four habitat types are nearly identical in mean sample Simpson's and Shannon's diversity indices, which place higher emphasis on evenness of abundances between species, with the Alluvial habitat type possibly having lower evenness of dominant species than the other three habitat types as reflected by the Simpson's index of diversity (**Fig. 2-17**).



**Figure 2-17 Diversity measures across habitat types for bees collected in 149 plot samples at Pinnacles National Park (2011-12).** Counts of bee species per plot sample produces one metric of richness (top left), whereas Fisher's alpha diversity incorporates a measure of evenness (top right). The Shannon's index of diversity (bottom left) measures evenness between samples while placing more emphasis on rare species than the Simpson's index of diversity, which places more weight on species dominance in samples (bottom right).

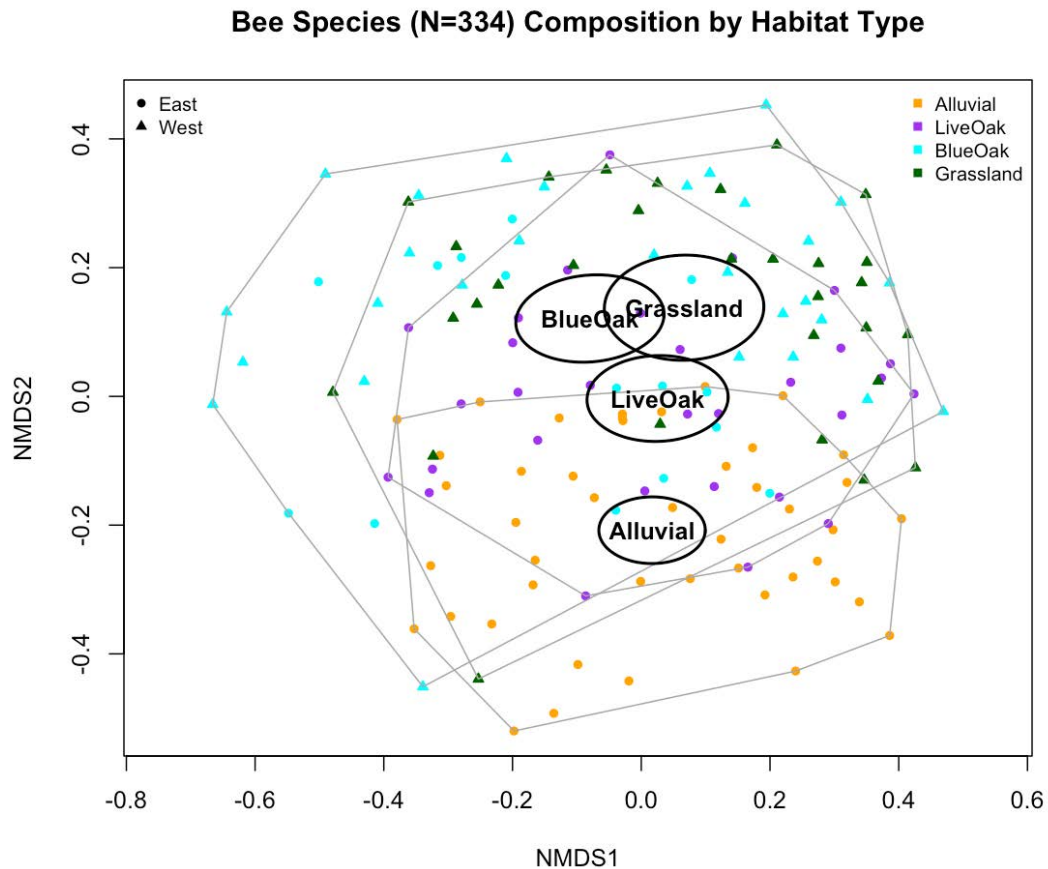
### Bee Community Composition

The number of different species and the evenness of their abundances may not be the most ecologically relevant measure of bee biodiversity for evaluating ecosystem functioning, which may depend more on the specific blends of species. Species composition differences between bee communities in different habitat types can be explored with Non-metric Multidimensional Scaling Ordinations, a technique which takes a matrix of species abundances across samples and uses a chosen distance measure to calculate and plot samples as points in ordination-space to visualize bee community similarity along two or sometimes three axes, depending on how the points can best be represented without overly stressing their ordination scores into too few dimensions. While NMDS ordinations do not assign specific variables to ordination axes, the *envfit* function in R (package “vegan”) can identify and plot scaled vectors representing environmental variables describing a significant amount of variance if they are included as an accompanying environmental dataset.

In this way, using a Bray Curtis distance measure and a Wisconsin standardization technique to reduce the influence of highly abundant species and peak sampling periods, the composition of 334 bee species collected in 149 plot samples are plotted and color-coded to show community similarity by habitat type (3-d NMDS, stress score = 0.20, **Fig. 2-18**). Elevation, longitude, latitude as well as day, temperature, humidity, and the floral diversity of plot samples all help explain the placement of these plot sample points into ordination space. Year and wind speed were not significant factors in plotting samples into the NMDS. Convex hulls connect all outlying points of each color-coded habitat type to show the spread of samples within a habitat type in

ordination space, while labels are plotted at the weighted average scores for each habitat type and surrounded by black 95% confidence ellipses (**Fig. 2-18**).

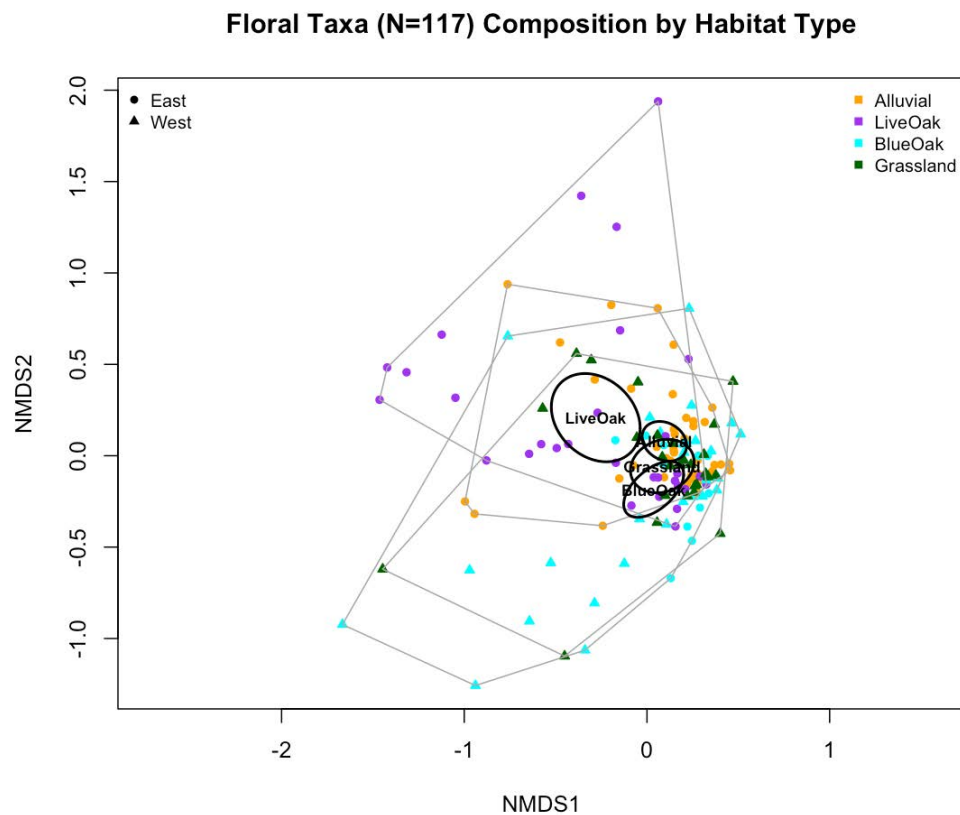
Unlike earlier results of tests for differences between habitat types for measures of bee abundance, richness, or diversity, in this NMDS ordination of 149 plot samples, the Alluvial habitat type clearly stands apart in bee species composition from the other three habitat types with overlapping 95% confidence ellipses (**Fig. 2-18**). This difference is supported by an analysis of similarity that confirms significant dissimilarity of bee species composition between habitat types (ANOSIM  $R=0.25$ ,  $p<0.001$ ). A permutational (per)MANOVA that can accommodate both categorical and continuous predictor variables, called the *adonis* function in R (*Kartzinel et al., 2015*), also finds habitat type to be a significant predictor of bee species sample composition (*adonis* pseudo  $F(3,145)=6.302$ ,  $R^2=0.12$ ,  $p<0.001$ ).



**Figure 2-18 NMDS ordination of bee species (N=334) community composition of non-zero plot samples (N=149), using a Bray-Curtis distance measure and a Wisconsin square-root transformation to relativize by species and samples (3-d, stress score =0.20).** Habitat type is emphasized by outlined convex hulls (gray lines) and 95% CI ellipses (black ovals) around the standard error of the weighted average of group scores. Points represent individual plot samples and are colored by habitat and shaped by location within the park. Analysis of similarity (ANOSIM) showed the Alluvial habitat type to be significantly dissimilar to the other habitats in bee community composition ( $R=0.25$ ,  $p<0.001$ ), and an *adonis* test of the predictive power of habitat on sample bee species composition was significant (*adonis* pseudo  $F(3,145)=6.302$ ,  $R^2=0.12$ ,  $p<0.001$ ).

An NMDS for the floral taxa (N=117 distinct taxa at species, genus, or sometimes family level) composition of all 149 plot samples shows a different result of separation between habitat types, however, indicating that the bee community composition is not simply a reflection of floral composition in those habitat types (**Fig. 2-19**). The Live Oak

Woodland stands out as the most dissimilar habitat type in floral composition, rather than the Alluvial as with the bee species composition, while the 95% confidence ellipsoids of the Blue Oak, Alluvial, and Grassland habitat types overlap in their floral composition. Only two environmental variables, floral diversity and day of each plot sample, have significant explanatory power of this ordination result according to the *envfit* function in R, suggesting a strong influence of temporal, seasonal variation in bloom.

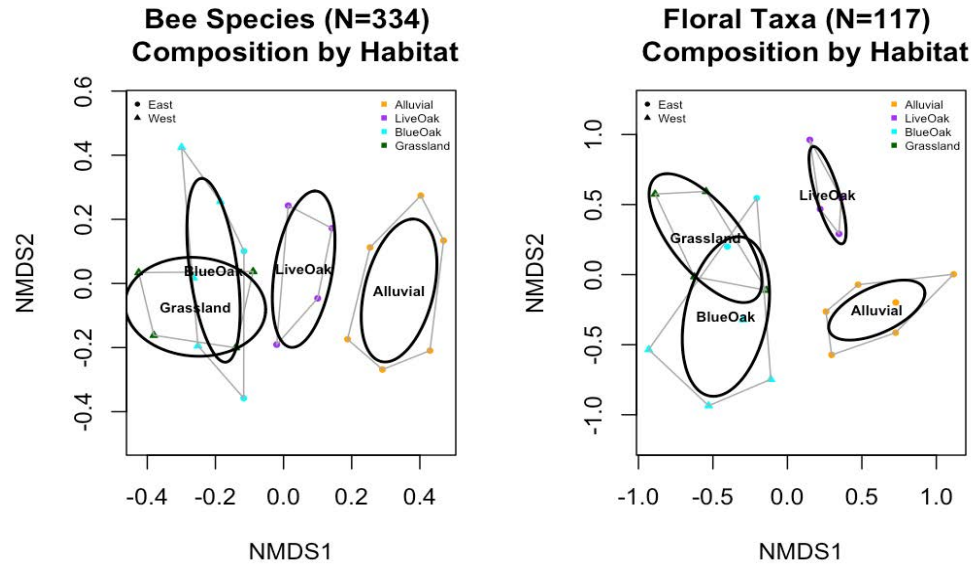


**Figure 2-19 NMDS ordination of floral taxa (N=117) community composition of non-zero plot samples (N=149) (2-d, stress score = 0.208).** Habitat type is emphasized by outlined convex hulls (gray lines) and 95% CI ellipses (black ovals) around the standard error of the weighted average of group scores. Points represent plot samples and are colored by habitat and shaped by location within the park. A permutation test for homogeneity of multivariate betadispersions found significant group differences ( $F(3,145)=5.091$ ,  $p=0.002$ ), thus further analysis is inappropriate. There is, however, a trend of Live Oak differing from other habitat types in floral composition.

### Temporal Variables in Species Composition

To examine the influence of temporal variables on composition, samples were condensed to generate NMDS ordinations for bee and floral community composition of just one point per plot per year in order to look at group separation of habitat type without seasonal noise. As with the ordination of all biweekly plot samples (N=149, **Fig. 2-18**), the separation of habitat type in annual plot bee species composition is clear for the Alluvial habitat type (N=20, **Fig. 2-20**). Considering the whole composition of plots over a season, the Live Oak habitat type also shows significant separation in bee species composition from all three other habitat types, while the Grassland and Blue Oak habitat types overlap in composition as they did in the biweekly plot sample ordination (ANOSIM  $R=0.53$ ,  $p<0.00$ ; *adonis* pseudo  $F(3,16)=3.631$ ,  $R^2=0.41$ ,  $p<0.001$ ). Latitude, Longitude, and elevation are significant variables in determining placement of annual plot samples in ordination space, while year, average temperature, wind speed, humidity, and floral richness at plots over a season are not (using the *envfit* function at  $p<0.05$ ).

Habitat type separation in the ordination of annual plot composition of floral taxa (N=20, **Fig. 2-20**) reflects a pattern more similar to that of the ordination for annual plot bee composition (N=20) than to the habitat type separation of floral taxa composition with all biweekly plot samples (N=149, **Fig. 2-19**). This suggests substantial seasonal noise in determining groupings of floral community composition by habitat type with all biweekly plot samples. *Adonis* perMANOVA test found habitat type to be predictive of annual floral plot sample composition (*adonis* pseudo  $F(3,16)=2.750$ ,  $R^2=0.34$ ,  $p<0.001$ ), and an analysis of similarity confirmed the differing composition of Alluvial and Live Oak habitat types for floral, as well as bee, community composition ( $R=0.54$ ,  $p<0.001$ ).

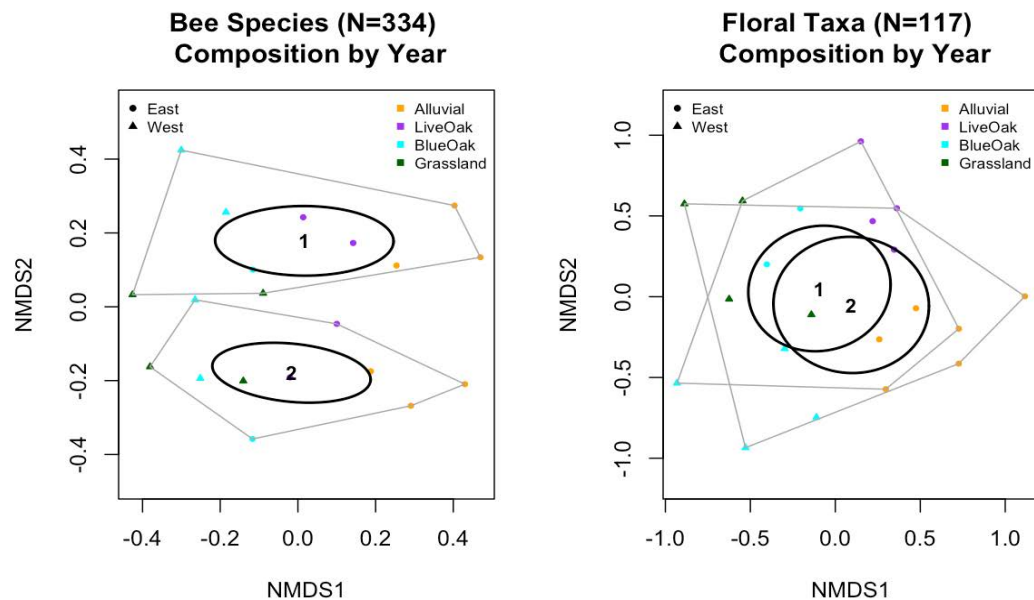


**Figure 2-20** NMDS ordinations of annual plot samples of bee species (left) and floral taxa (right) composition, with seasonal temporal variation of individual samples condensed into one point per plot per year (N samples=20) (2-d, stress score = 0.209 (bee), 0.214 (flora)). Habitat type is emphasized by outlined convex hulls (gray lines) and 95% CI ellipses (black ovals) around the standard error of the weighted average of group scores. ANOSIM showed the Alluvial and Live Oak habitat types to be significantly dissimilar to the other habitats in both bee and floral community composition ( $R=0.53$ ,  $p<0.001$ ;  $R=0.54$ ,  $p<0.001$ ), and an *adonis* perMANOVA test of the effect of habitat on annual plot sample composition was significant for both bees and flora (*adonis* pseudo  $F(3,16)=3.631$ ,  $R^2=0.41$ ,  $p<0.001$ ; *adonis* pseudo  $F(3,16)=2.750$ ,  $R^2=0.34$ ,  $p<0.001$ ).

High turnover of bee species between years is expected in native bee data, while the annual and perennial plants that support these bee communities are thought to be more stable (*Wilson et al., 2009*). Adding proof to this concept, NMDS ordinations of bee and floral taxa using the same points as above, but with the year of each annual plot sample as the grouping variable, show separation between years in bee but not floral community composition (**Fig. 2-21**). Lack of overlap of black ellipses representing the 95% CI boundaries around annual plot samples from 2011 or 2012 show weak separation for bee species composition, supported by significant results from ANOSIM and *adonis*



tests (ANOSIM  $R=0.18$ ,  $p=0.04$ ; *adonis* pseudo  $F(1,18)=2.241$ ,  $R^2=0.11$ ,  $p=0.03$ ). In contrast, no difference is indicated by ellipses or statistical tests for floral composition at annual plot samples between the two years of collecting (ANOSIM  $R=0.11$ ,  $p=0.08$ ; *adonis* pseudo  $F(1,18)=1.360$ ,  $R^2=0.07$ ,  $p=0.15$ ).

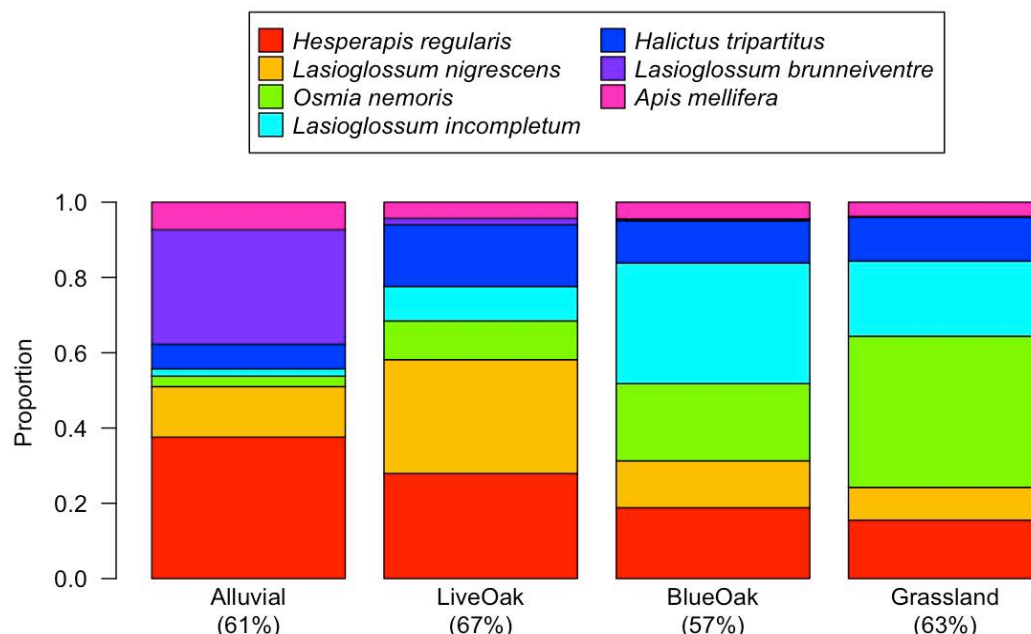


**Figure 2-21 NMDS ordinations** (same points as Fig. 20) **for composition of annual plot samples of all bee species (left) and floral taxa (right)** (2-d, stress score = 0.209 (bee), 0.214 (flora)). Year of plot sample is emphasized by outlined convex hulls (gray lines) and 95% CI ellipses (black ovals) around the standard error of the weighted average of group scores. ANOSIM showed a slight difference between years in bee but not floral plot composition ( $R=0.18$ ,  $p=0.04$ ;  $R=0.11$ ,  $p=0.08$ ), and an *adonis* perMANOVA test of the effect of sample year on plot composition was significant for bees but not for flora (*adonis* pseudo  $F(1,18)=2.241$ ,  $R^2=0.11$ ,  $p=0.03$ ;  $F(1,18)=1.360$ ,  $R^2=0.07$ ,  $p=0.15$ ).

### Dominant Bee Species

If the Alluvial habitat type is unique in bee species composition, but this is not a clear reflection of floral composition, and Alluvial habitats do not stand out in any other

measure of native bee biodiversity, it is reasonable to suspect that something about the bee traits present in different areas is driving this separation. The seven most abundant bee species in the plot dataset add up to 20,124 specimens, 62% of the entire collection of bees for the plot study (N=32,440 specimens). As a group of seven species, their abundance is fairly consistent across the four habitat types, representing between 57% and 67% of total specimens collected in each habitat type. The relative abundances of each of the seven species within each habitat type, however, varies considerably (**Fig. 2-22**). Alluvial habitats are dominated by *Hesperapis regularis*, a medium-sized, solitary specialist (oligolege) that forages for pollen almost exclusively on flowers of the genus *Clarkia* (Burdick and Torchio, 1959; Moeller, 2005). To a lesser degree, Live Oak and Blue Oak habitats are both dominated by species of the genus *Lasioglossum*, most of which are very small and thought to be generalist foragers (polyleges), aggregate ground nesters, and primitively eusocial (Danforth et al., 2003; Gibbs et al., 2012). Grassland habitats are dominated by *Osmia nemoris*, a medium-sized, stem-nesting bee, the foraging habits of which are not well understood (Rust and Clement, 1972). All seven species are present in each of the four habitats, though at very different abundances, with a third species of *Lasioglossum* also highly abundant in the Alluvial habitat type, but virtually absent in every other. There appears to be a higher similarity in the evenness and blend of species between the Live Oak, Blue Oak, and Grassland habitat types than for the Alluvial habitat type, which reflects bee species composition ordination results (**Fig. 2-18**). Ecological or functional trait differences between dominant species in different habitats may provide interesting clues as to the nature and ecological relevance of the community dissimilarity between Alluvial and the other three habitat types (**Table 2-5**).



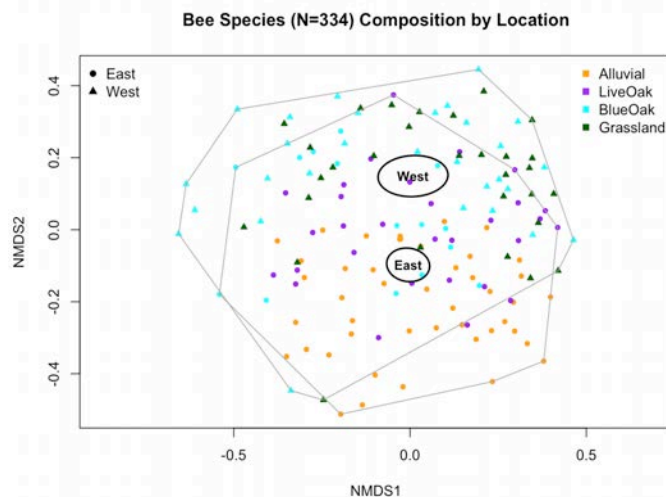
**Figure 2-22** Barplot of relative proportions in each habitat type of the seven most abundant bee species overall in 2011 and 2012 plot sampling at Pinnacles National Park, which together represent 62% of all specimens collected in plots for both years. Larger color blocks in each habitat bar represent the dominant species (by abundance) collected in that habitat type, listed by taxonomic name in top legend.

**Table 2-5** Top seven most abundant bee species collected in plots at Pinnacles National Park in 2011-12 combined (all species numbering over 1000 in total specimens count, ordered by rank abundance), count, and notes on their body size and functional traits. Specimen counts apply to both sexes of the species, but traits refer specifically to female characteristics.

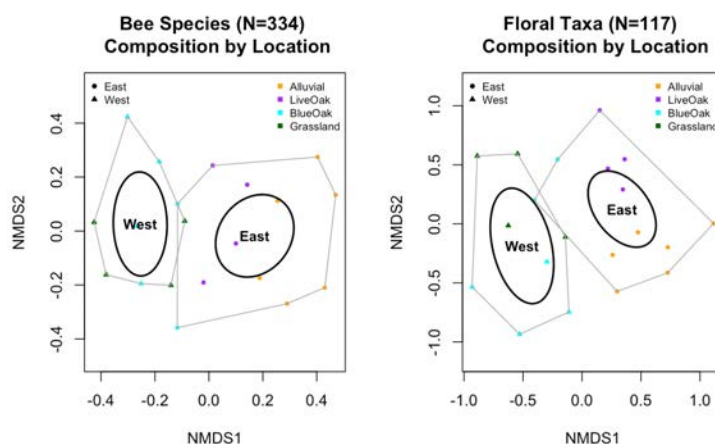
Bee species (Family)	Specimens collected in plots	Flight season at PINN	Size (inter-tegular distance)	Sociality	Nesting	Foraging style (# floral taxa recorded, % specimens with floral records)
<i>Hesperapis regularis</i> (Melittidae)	5372	Mar 12 – June 24	2.06mm	Solitary	Ground	Oligolectic (9; 14%)
<i>Lasioglossum (Evyllaes) nigrescens</i> (Halictidae)	3543	Feb 28 – June 23	1.15mm	Social	Ground	Polylectic (26; 4%)
<i>Osmia (Melanosmia) nemoris</i> (Megachilidae)	3027	Mar 15 – June 24	2.08mm	Solitary	Stem/wood	Polylectic (14; 1%)
<i>Lasioglossum (Dialictus) incompletum</i> (Halictidae)	2883	Feb 28 – June 24	0.89mm	Social	Ground	Polylectic (11; 2%)
<i>Halictus (Seladonia) tripartitus</i> (Halictidae)	2302	Mar 1 – June 24	1.22mm	Social	Ground	Polylectic (13; 1%)
<i>Lasioglossum (Dialictus) brunneiventris</i> (Halictidae)	1962	Mar 4 – June 23	0.79mm	Social	Ground	Polylectic (7; 1%)
<i>Apis mellifera</i> (Apidae)	1035	Feb 28 – June 24	2.80mm	Eusocial	Hive	Polylectic (43, 86%)

*Influence of Habitat Type vs. Geography*

Habitat type is a predictor of native bee community composition, and may be informative about the type and traits of bee species most likely to be found in those areas at Pinnacles. But it is difficult to attribute this result to habitat type alone without being able to separate this variable from the natural longitudinal and elevation gradients along which habitat types naturally occur, and which may have important influences on bee community composition due to dispersal limitation and geographical barriers. Without replicates of all habitat types on both sides of Pinnacles' central, high rock spine, questions about the mechanisms of historical bee community assembly are especially difficult to address. The same NMDS ordination presented earlier of bee community composition (**Fig. 2-18**), now shown with convex hulls and ellipses emphasizing the location on the east vs west side of the park instead of the habitat type of all biweekly plot samples, suggests that geography exerts an influence on bee species community composition (**Fig. 2-23**, *adonis* pseudo  $F=9.927$ ,  $R^2=0.06$ ,  $p<0.001$ ). Ordinations of the annual plot sample points (as in **Figs. 2-20 & 2-21**) also show strong dissimilarity between the west and east sides of the park for both bee species and floral taxa community composition (**Fig. 2-24**, *adonis* pseudo  $F(1,18)=5.658$ ,  $R^2=0.24$ ,  $p<0.001$ ;  $F(1,18)=3.106$ ,  $R^2=0.15$ ,  $p<0.001$ ).



**Figure 2-23 NMDS ordination of bee species community composition from 149 plot samples** (3-d, stress score = 0.20). Location (east vs. west) across Pinnacles National Park's dividing rock spine is emphasized by outlined convex hulls (gray lines) and 95% CI ellipses (black ovals) around the standard error of the weighted average of group scores. ANOSIM showed the west and east sides to be dissimilar in bee composition ( $R=0.22$ ,  $p<0.001$ ), and *adonis* found geographical location to be a significant predictor of bee composition (*adonis* pseudo  $F(1,147)=9.927$ ,  $R^2=0.06$ ,  $p<0.001$ ).



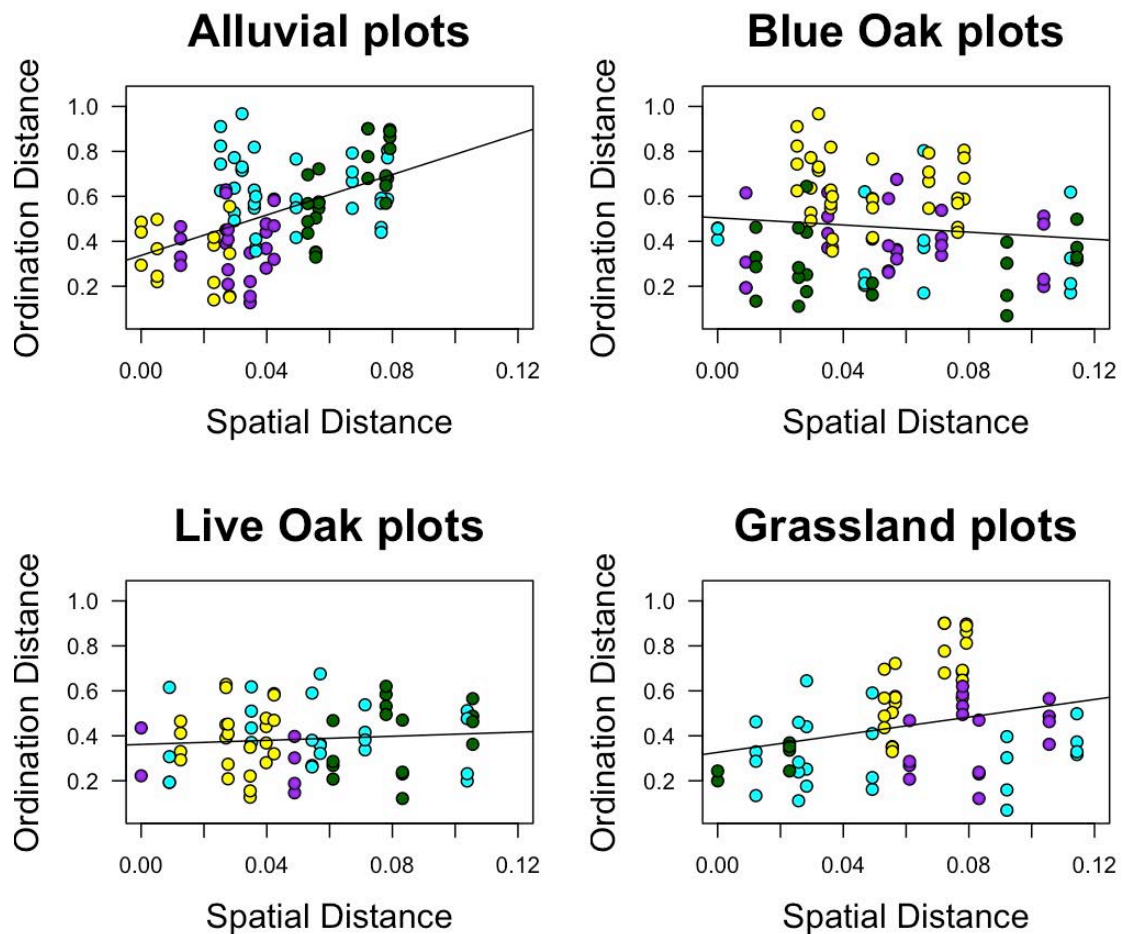
**Figure 2-24 NMDS ordinations of annual plot samples of all bee species (left) and floral taxa (right) compositions** (2-d, stress score = 0.209 (bee), 0.214 (flora)). Location (east vs. west) across Pinnacles National Park's dividing rock spine is emphasized by outlined convex hulls (gray lines) and 95% CI ellipses (black ovals) around the standard error of the weighted average of group scores. ANOSIM showed the sides of the park to be dissimilar to each other in annual plot bee and floral community composition ( $R=0.51$ ,  $p<0.001$ ;  $R=0.49$ ,  $p<0.001$ ), and an *adonis* test of effect of side of the park on annual plot composition was significant for both bees and flora (*adonis* pseudo  $F(1,18)=5.658$ ,  $R^2=0.24$ ,  $p<0.001$ ;  $F(1,18)=3.106$ ,  $R^2=0.15$ ,  $p<0.001$ ).

In an attempt to further tease apart the relative influences of habitat type and dispersal distance as determinants of bee species community composition, a final experimental analysis is included below. Using the annual plot ordination (as in **Figs. 2-20, 2-21, 2-24**) to eliminate temporal variation in bee species composition, ordination distances between all possible pairs of annual sampling plots (N=20) was calculated and plotted against a measure of the physical distance, based on GPS data, between each pair of plots (**Fig. 2-25**). The y-axis (ordination distance) coordinates of points plotted at the 0.00 coordinate on the x-axis (physical distance), therefore, reflect the ordination distance between the same plot in two different years, where the physical distance between them is zero on the x-axis. Each habitat type is represented in its own panel to highlight paired comparisons between annual plot points in that habitat type and points from all others (**Fig. 2-25**). Data points within each panel are color-coded for the habitat type with which each of the annual plots from the panel habitat type are paired. For example, points compared with Alluvial plots are yellow in all panels (including in the Alluvial panel when Alluvial plots are compared to each other), those compared with Live Oak plots are always purple, with Blue Oak plots are blue, and with Grassland plots are green, consistent with habitat type color-coding throughout the chapter.

Trend lines show a relationship between the ordination distance and the spatial distance between two plots, though these data do not meet the assumptions of regression so no correlation values are reported (**Fig. 2-25**). Nevertheless, this figure suggests a stronger relationship (a steeper slope) between bee community similarity and the physical distance between plots for comparisons with Alluvial plots than with any other habitat type (top left panel, **Fig. 2-25**). Bee community similarity and the distance between two

plots shows a weak pattern for Live Oak and Grassland plots, and no association for Blue Oak plots (nearly flat trend line in top right panel, **Fig. 2-25**), which is the only habitat type represented by plots on both sides of the park.

The stronger relationship between ordination distance and spatial distance for comparisons with Alluvial plots is also evidenced by the fact that the majority of yellow dots lie above the trend line in every habitat panel. No clear pattern is seen in the alignment of purple, blue, or green-colored dots signifying the relationship of ordination distance to spatial distance for any other habitat type in any of the three non-Alluvial panels. As with ordination results, there appears to be something about the Alluvial habitat type that produces unique patterns in native bee species community composition, if not in raw abundances or measures of richness or diversity, that is not simply due to its geographical location within the park.



**Figure 2-25** Comparisons of the spatial distance and NMDS ordination distance between all possible pairs of ten plots, with color indicating with which habitat each plot is paired in the four panel habitat categories (see text above for additional explanation). Simple linear model fits give regression lines showing trends. Alluvial plots show the strongest relationship with bee community similarity depending on the distance between plots, while there seems to be no relationship between the distance between plots and the similarity of the bee community composition in comparisons with blue oak habitats.



## DISCUSSION

### **Biodiversity**

Pinnacles National Park may harbor the highest density of bee species currently known anywhere in the world. Surveys conducted in Clark County, Nevada, Grand Staircase Escalante National Monument, Utah, around Riverside, California, and in a plot study near the Arizona-Mexico border also each recorded high numbers of bee species, though likely across substantially larger areas (study site size was not always specified) (*Griswold et al., 1999; Linsley, 1958; Messinger, 2006; Minckley, 2008*). Furthermore, after five years of prior sampling at Pinnacles, we still recorded three new bee genera, seventy-two new species, and sixty-nine singleton species in the two years of this study. While rarity and a high interannual turnover is expected among native bees (*Lennon et al., 2004; Petanidou et al., 2008; Williams et al., 2001a*), these numbers suggest that the inventory at Pinnacles has not been fully realized, though the leveling off of the species accumulation curve and the order of magnitude increase since the 1990s in the collection effort necessary to record a new species indicates a slowing of new species detection. Still, expanded sampling into areas and months not previously sampled is expected to be particularly fruitful.

Pinnacles' rich bee fauna can be attributed broadly to its Mediterranean climate, strong environmental gradients, and high habitat heterogeneity, the latter of which has been found in other research to be a stronger predictor of species richness than the species-area relationship (*Báldi, 2008; Tews et al., 2004*). Habitat heterogeneity can occur over both space and time. Mediterranean habitats, like those at Pinnacles, are known for their rich 'flash-bloom' cycles during spring months, followed by hot, dry

summers and mild, wet winters, an environment that tends to support a high biodiversity of many taxa (*Klausmeyer and Shaw, 2009; Potts et al., 2003*). Among bees, the rapid turnover of floral resources in these areas may favor solitary species, whose shorter flight periods and often specialized foraging behaviors may allow more species to coexist in a single area, as each can occupy a narrower temporal and foraging niche space than can longer-lived social or generalist species, which are more common in temperate areas (*Linsley, 1958; Minckley, 2008*).

Across space, habitats at Pinnacles change rapidly from the western, coastally-influenced slopes, up the 500m elevational gradient to the rock ridge, and down the different aspects and microclimates of the drier east side. This heterogeneity has likely arisen from the existence of several fault lines across Pinnacles, the geologic movements of which may have resulted in the elevational gradient, variety in aspect, and broader array of soil types and plant species than would typically be found in such a small area (*Matthews, 1976*). Perhaps because of this soil heterogeneity, Pinnacles is also considered to be a transitional zone between the floral ecotones of northern and southern California (*Tucker et al., 2006*). Consequently, the park boasts a list of nearly 700 plant taxa, many of them flowering species, which is extraordinarily biodiverse for a 42 square mile area (*NPS, 2015*). We found bee richness to be highly correlated with the richness of bee-visited angiosperms on any given day and site of sampling at Pinnacles, which corroborates results from previous studies (*Messinger, 2006; Potts et al., 2003*) Indeed, the overall diversity of native bees at Pinnacles seems to be a function of both the rich wildflower flora and the patchiness of the landscape. These factors seemingly allow for

more diverse bee communities to coexist within a smaller area than has been found in any other study.

### **Community Dynamics**

The variation between Pinnacles' plot samples in measures of bee abundance and richness with temporal, seasonally influenced variables like floral diversity and temperature, and along spatial gradients like longitude and elevation is consistent with known spatiotemporal variability widely found to be common to native bees (*Williams et al., 2001b; Wilson et al., 2009*). Fewer studies have assessed composition as a measure of native bee activity. Plot samples at Pinnacles also varied in composition, with some dominant genera displaying very high patchiness over space and/or time and others more consistently abundant. The composition of a bee community at a particular point in space and time, in terms of phylogenetics, functional traits, and relative abundances of specific bees, may be a product of competition for floral and nesting resources interacting with stochastic influences on community assembly (*Chase, 2007; Cody and Diamond, 1975; Diamond, 1978; Leibold et al., 2004*). These processes are difficult to disentangle, but may result in communities with very different ecosystem services and resilience to environmental change, thus an attempt to tease apart dominance patterns may be worthwhile, albeit challenging (*Bommarco et al., 2010; Williams et al., 2010*).

The high spatial variability of native bee communities at Pinnacles suggests an ecological limitation in niche breadth and/or dispersal ability of species (*Blackburn and Gaston, 2003; Bommarco et al., 2010*). Bee flight ranges, which may indicate the accessibility of distant areas to a species, are difficult to determine since technology to

follow foraging flights is currently only suitable for the largest of bee species (*He et al., 2012; Streit et al., 2003; Wikelski et al., 2010*). Radio frequency tagging methods have recorded honeybees, a relatively large species, returning to their hives in a single flight from as far as 11km away (*Pahl et al., 2011*). Indirect methods of estimating home ranges for smaller bees have recorded single foraging flights of several hundred to several thousand meters, though foraging distance is also highly dependent on nectar availability in the immediate area (*Roubik and Aluja, 1983; Waddington, 1980; Zurbuchen et al., 2010*). Building upon these studies, bee body size has been shown to correlate fairly well with flight distance, and might be useful for estimating home ranges or dispersal capabilities of diverse native bee species (*Cane, 1987; Greenleaf et al., 2007; Guédot et al., 2009*). Across larger areas, these calculations may help inform community turnover, as distance between areas sampled becomes large enough to limit dispersal of bee species into new suitable areas.

At Pinnacles, however, even with the geographic barrier of a bisecting rock spine, this 42-square-mile area is unlikely to be outside the range of potential colonization for any bee species collected, especially across multiple generations (*T. Griswold, pers. comm.*). Therefore, since bee communities differ across the park, it follows that compositional variation is likely to be a reflection of species' niche requirements being met by particular local habitat characteristics, combined with some influence of priority effects, competition, and chance in community assembly (*Chase, 2007*). Being able to relate habitat types that are easily distinguished by the human eye to specific predictable characteristics of bee community dynamics would aid conservation efforts where a rapid assessment of habitat type is possible, but extensive local bee sampling is not.

### **The Role of Habitat Type**

The four discrete categories of habitat type identified for this study (Alluvial, Live Oak Woodland, Blue Oak Woodland, Grassland) are easily distinguished by human visitors. However, native bee activity at Pinnacles, whether measured as numbers of individuals, numbers of species, species rarefactions, or various diversity indices incorporating evenness, was not clearly or consistently related to the four main habitat types studied. In contrast, a similar study in Utah's bee biodiverse Escalante Grand Staircase National Monument did find a relationship between habitat type and these bee metrics (*Messinger, 2006*), though across a much larger spatial scale, with different habitat type designations, and in a semi-arid rather than Mediterranean biome, where the rules governing bee community assembly may differ.

Ecologically, the lack of a relationship between habitat type and bee richness does not in itself refute the utility of habitat type for rapidly assessing bee communities at Pinnacles. Richness, as measured by species counts, is sensitive to taxonomic revisions, weighs rare and singleton species as equal to very abundant species, and does not factor in phylogenetic nestedness, counting a sample with ten species all in the same genus and a sample with ten species from ten different genera as equally rich, for example. While these various scenarios may have equivalent richness measures, they potentially represent vastly different communities and, therefore, pollination results, likely with cascading effects up the entire ecosystem. Had there been detectable differences in bee richness, as assessed by taxonomic determination, between the four habitat types in this study they still may have represented little in terms of functional richness, or inherent and consistent biodiversity or ecosystem service value of bees in a given habitat type. Once bee

specimens have been counted and identified, other measures of the community may be assessed as easily as richness, and may have more ecological meaning and generalizable connection to habitat type.

The foraging behaviors and interactions of different groups of bees can strongly influence the effectiveness and nature of pollination services. Abundance and evenness may not actually reflect the quality or quantity of pollination services in an area. For example, a dominant bee species focusing on a particular floral element to the exclusion of others, for example by enhancing pollination of invasive flora, may result in a negative ecosystem outcome of raw bee abundance (*King and Sargent, 2012; Tepedino et al., 2008*). Comparisons of richness, abundance, and evenness between habitat types may also be meaningless if the species involved have very different traits and impacts on the habitat, such as bees that excavate their own nests versus those who occupy preexisting cavities (*O'Toole and Raw, 1991*). Likewise, these metrics may fail to indicate real change in a community if shifts in bee species composition result in equivalent abundance, richness, and evenness values. Therefore, the use of such measures should be aligned with specific conservation goals and accompanied by knowledge of the taxa. Abundance, species richness, and evenness measures alone may not adequately reflect status or changes in the health or ecosystem services of discrete bee communities.

Comparing the species composition of a bee community over time, space, and habitat type may offer another, more ecologically informative view of native bee dynamics. The Alluvial habitat type, despite being indistinguishable from the other three habitat types in measures of abundance, richness, and evenness, was unique in several other ways at Pinnacles. In Bray-Curtis distance calculations of bee community

similarity, samples from the Alluvial habitat type were relatively constrained and distanced from the other three habitat types, while much more spread and overlap was observed for sample points in Live Oak, Blue Oak, and Grassland habitat types. This dissimilarity of Alluvial bee communities was not explained by differences in floral community composition between habitat types, as one might expect from strong correlations between bee and floral richness and from previous work relating bee community similarity to similarity of floral communities in discrete, post-fire, Mediterranean habitat types (*Potts et al., 2003*).

The compositional distinction of the Alluvial bee communities may instead be best explained by the dominance of a solitary, oligolectic (specialist) bee species. The notably high relative abundance in Alluvial habitats of the ground-nesting, *Clarkia* specialist, *Hesperapis regularis*, may point to subtle but influential differences in internal community dynamics related to intra- and interspecific bee interactions and competition for resources different from those at play in areas dominated by social or polylectic (generalist) species, as is the case for all three other habitat types. The resulting pollination services and, therefore, plant community composition may thereby differ between habitat types with contrasting patterns of dominance by bees with different lifestyle traits. Williams et al. (2010) recognized the importance to large-scale bee conservation of using functional trait groups, which can be applied to any community regardless of genetics or taxonomic classification, to identify community patterns predictive of species responses to environmental change. Further investigation of functional ecology patterns driving compositional uniqueness in the Alluvial habitat type may help decipher the structure and processes of a model healthy, stable bee community.

It is an experimental complication that the Alluvial habitats studied were not only unique and constrained in their bee species composition, but also in their distribution across Pinnacles National Park, occurring only at lower elevations on the typically drier east side of the park. This makes it difficult to attribute the community distinction of this habitat type to its dominant specialist or any other single factor, when it is likely also a result of spatial gradients to some unknown degree. Having determined that most native bee species should be able to travel across the entire protected range of Pinnacles National Park to colonize any other desired location or habitat type, even crossing the dividing rock ridge where it descends at the northern edge of the park (*T. Griswold, pers comm.*), reduces concerns about the confounding element of the natural spatial distribution of different habitat types. But it does not elucidate the relative influence of geographical versus habitat type characteristics on local bee species composition.

Comparing the Bray-Curtis distance between an Alluvial plot and any other plot with the spatial distance between them helps clarify the relative importance of habitat type and geographical habitat location. The result that the closer a plot was to an Alluvial plot, the more similar the bee community composition suggests that, while bees may forage into other habitat types, there is less interchange of resident bee species to and from Alluvial habitats compared to other habitats. This implies that bee community composition would be more unique and conserved in Alluvial habitats overall regardless of geographical distance from other habitats. Blue Oak habitats, on the other hand, show no relationship (a flat trend line) between bee community similarity and the spatial distance to other plots, suggesting that there is higher mixing and lower fidelity of bee species to these areas. This idea is supported by a study that found habitat to exert a



stronger influence on bee community similarity than geographical location in Mediterranean habitat types differentiated by post-fire age, floral community, and grazing intensity (*Potts et al., 2003*). A more detailed spatial analysis that incorporates a measure of the surrounding habitats and potential travel corridors for bees between habitat types may be interesting to further explore ideas of habitat type fidelity and likelihood of dispersal movements.

In the meantime, attributing bee community differences between habitat types to the ecological alignment of habitat type characteristics and niche requirements of the dominant species has equal merit. Lower rates of bee species dispersal to or from Alluvial habitat types could be explained by a lower propensity of the dominant oligolege to disperse from an area where its preferred floral resource is abundant. Polyleges, which dominate all three other habitat types, would be less tied to one resource and may thereby be more mobile and travel further, visiting a variety of flowers along the way to colonizing a new habitat. Whether this is a result or a cause of the corresponding patchiness of specific floral resources would be an interesting avenue for future research, likely requiring long-term habitat manipulations. Another explanation may be that lower grass cover in Alluvial habitats means a higher availability of nesting resources for ground-nesting species, which may have difficulty burrowing through grass roots. If this is the case, offspring of those ground-nesting bees may also be more likely to establish a nest nearby, preserving the unique composition and low dispersal of Alluvial bee communities. It is interesting to note here that most of the grasses dominating non-Alluvial habitats at Pinnacles National Park are highly invasive, and influence bee community dynamics as they spread by obscuring ground nesting habitat and

outcompeting key floral resources. Management of invasive grasses in different habitat types and subsequent analysis of any bee community response may contribute valuable information to native bee ecology and conservation efforts.

In summary, while habitat type was not a useful predictor of bee abundance, richness, or evenness, Alluvial habitats in and around Pinnacles National Park may be important refugia for resident solitary, ground-nesting species, which maintain compositional uniqueness via low dispersal of a dominant oligolege tied to local floral resources. This identification of bee community uniqueness characterized by a solitary, ground-nesting, specialist in Alluvial habitats seems promising for the utility of habitat type in bee conservation initiatives. Future work should pay particular attention to differences in measures of resilience to influences like climate change and habitat degradation between Alluvial and other habitat types to determine if this protection is warranted. Furthermore, investigation of the role a dominant solitary specialist plays in its plant and bee community would be interesting and informative for prioritizing protection of areas in accordance with specific management goals. Because Alluvial habitats are more constrained in species composition, shifts observed in future samples may indicate real changes in native bee health rather than variance, and thus may have particular value for both monitoring and conservation of diverse native bees.

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## APPENDICES

### Appendix A. Field Methods Supplementary Material: Materials list, Daily detailed field plot sampling schedule, Data card template

#### A1. Full Study Materials List

<b>Plot Establishment (at least a two-person job, more is ideal)</b>	
	• Park map
	• 100' tape measure
	• Range finder to help estimate distances when positioning plot
	• GPS unit to record corners of plot and to check plot dimension distance measurements
	• Red flags to mark outside boundary of plot (good color for visibility and to minimize influence on bee activity)
	• Pink flags to quarter inside of plot to guide sampling walks (also good color)
	• Camera to record images of plot from all corner angles
<b>Net Collecting (designed for two regular collectors)</b>	
	• 4 complete nets (2 for regular use, 2 extra)
	• 2 extra net bags
	• Extra wire to repair nets (necessity depends on type of net ring)
	• 3 collection shoulder bags (2 for regular use, one for guest collector)
	• 40 cyanide/killing vials (12 per each of 3 collection bags, 4 extra)—only need this many if trying to keep collections on different flowers separate per area
	• 3 pair small scissors
	• String to tie scissors to bag
	• Kestrel or other device for measuring temperature, wind speed, other desired metrics
	• Ethanol resistant pens
	• Pre-printed data books (one sheet for each expected day and collecting location)
	• “Stackers” or other plastic container with lots of small divisions to keep bees separated out of vials
<b>Pan Trap Collecting (designed for sampling two sites at once)</b>	
	• 3 sets of 30 painted “pan traps” (one per site to be sampled simultaneously, plus an extra set to replace broken bowls). “Pan traps” are 2-oz clear ‘Solo’ brand plastic shallow cups, spray-painted fluorescent blue, fluorescent yellow, and white (10 of each color per set)
	• 4 gallon jugs (2 for regular use, 2 extra)
	• ‘Dawn’ Brand blue dish soap (this specific kind is used to control for influence of particular soap scent or appearance on bee catch)
	• 400 ‘Whirl’ packs, (4 for each time a site is sampled (one for each pan trap color, one to put all three bags in all together), plus extras)
	• 9 tea strainers (3 for each site to be sampled simultaneously (one for each pan trap color), 3 extra)
	• Masking tape to mark pan trap color on strainers
	• Sharpie to label masking tape and Whirl packs



• Ethanol-resistant pens
• Pre-printed labels for pan trap colors (incorporated into pre-printed data books above)
• 4 gal. 75% (Usually buy as 95% and dilute down) Ethanol (about 10 - 16 oz. per collection site between 3 Whirl packs)
• 2 16 oz. plastic soda bottles to carry Ethanol into field
• Funnels to use to pour pan trap liquid back into gallon jugs and to dilute Ethanol into empty plastic soda bottles

### **Vegetation Monitoring**

• Printed loose data sheets and binder to keep them organized
• Meter stick or piece of PVC with decimeter increments marked
• Homemade handy field guide with pictures for remembering common plants
• Ziploc bags for collecting plant vouchers
• Camera to record more plant detail if taking only a small section or voucher not possible
• Notebook with extra sheets or notecards to write more information about full plant size, location, etc to put in ziplocs with plant vouchers
• Pruning shears and/or small trowel for collecting woody plants (optional)
• Cooler for storing plant vouchers in car while continuing field work (optional)
• Plant press for vouchers (small one for field, then transfer into larger one at night)
• Newspaper and cardboard for blotting and absorbing voucher moisture
• Newspaper or loose-leaf sheets on which to tape vouchers when dried
• Masking tape to lightly tape down vouchers to paper
• Sharpie to mark collection number and information on voucher sheet
• Jepson Manual for identifying plants
• Herbarium reference collection and botanist experts to help with identification if possible!

### **Personal Field Gear (recommended)**

• Radio or other method of reliable communication in the event of an emergency
• First aid kit
• Durable, non-cotton, long-sleeve and long-pant field clothes
• Wide-brimmed hat
• Sunglasses
• Sunscreen
• Backpack
• Water bottles
• Snacks
• Camera (for fun or to help with plant vouchers)
• Multi tool knife
• Snake chaps, if relevant in area
• Durable footwear and hiking socks
• Duct tape, to keep grass seeds out of your socks, and because it's really cool

### **Specimen Pinning**

• Field pinning ('Schmidt') boxes
• Pins (#1, #2)

• ‘Elmers’ non-washable glue or wood glue for gluing bees too small to pin
• Large plastic bowls for rinsing pan trap bees in 90% Ethanol
• 90% (undiluted) Ethanol
• Paper towels for drying and fluffing pan trap bees out of Ethanol
• Pen for labeling pinning boxes with date, location, collectors, frozen status, etc
• Freezer to store pinned bees and Whirl packs for 48 hours after pinning, then repeatedly check for Dermestid invasion and re-freeze
• Very large Ziploc bags for storing Schmidt boxes after freezing to prevent contamination

<b>Collection and Database Management</b>	
•	Computer with Microsoft Office and Access Database software
•	ODBC database and entry form in Access for inputting field notes and assigning a unique ID accession number, with searchable collection information, to each specimen
•	Printer for producing specimen labels
•	Card stock paper for labels
•	Fine, sharp scissors for precisely cutting labels
•	Pinning block to mount labels evenly
•	Unit boxes to move pinned, labeled specimen into
•	Sealed wooden drawers for storing specimen in a museum collection safe from desiccation, mold, and attack by Dermestid beetles
•	High quality dissecting microscope
•	Light source for microscope
•	Identification guide for bee genera
•	Identification guides specific to each genera for species level determinations
•	Card stock species determination labels
•	Ethanol-resistant labeling pens
•	Experts in bee identification who are willing to train or help with species determinations!

## A2. Daily Field Plot Sampling Schedule

Time	Task	Equipment
8:45am	One collector arrives separately at each plot to be sampled that day Lay out pan traps in “X” shape across plot	One set of pan traps Gallon of soapy water
9:00am	Collectors meet at first plot to sample for day Vegetation monitoring protocol for the first sampling plot of the day (this will take the whole 45 min allotted)	Vegetation datasheets Ethanol-proof pen Meter stick with decimeter marks Plant voucher bags
9:45am	Record Kestrel weather measurements	Databook Ethanol-proof pen Kestrel monitoring device
10:00am	Each collector walks to opposite long corner of plot Start collecting timer, begin walking	Net, Collection bag & killing vials Watch
10:15am	Collectors reach long end of plot, switch sides, and walk back other side	
10:30am	Record plants on which bees were collected Make corresponding vial labels from databook	Databook Ethanol-proof pen

	Transfer bee groups with vial labels to stackers	Stackers or other small storage
10:45am	Hike to other paired plot for sampling that day <i>OR if only sampling one plot, collect bees in a new area to increase diversity until Noon</i>	Bring all gear except active pan traps
11:00am	Record Kestrel weather measurements at second plot	Databook Ethanol-proof pen Kestrel monitoring device
11:15am	Repeat protocol 10-10:30am to take morning sample of second plot	Net, Collection bag & killing vials Watch
11:45am	Finish collecting time for second plot Record flowers on which bees collected Store bees from vials with labels	Databook Ethanol-proof pen Stacks or other small storage
12:00pm	Lunch break	Food!
12:30pm	Walk back to first sampling plot of the day	Bring all gear except active pan traps
12:45pm	Take afternoon Kestrel measurements at first plot	Kestrel monitoring device Databook & pen
1:00pm	Repeat protocol 10-10:30am to take afternoon sample of first plot	Net, Collection bag & killing vials Watch
1:30pm	Finish collecting Record plants and label bees from vials	Databook & pen Stackers or other small storage
1:45pm	Walk back to second sampling plot <i>OR if only sampling one plot, collect bees in a new area to increase diversity until 3:30pm</i>	Bring all gear except active pan traps
2:00pm	Take afternoon Kestrel measurements at second plot	Kestrel monitoring device Databook & pen
2:15pm	Repeat protocol 10-10:30am to take afternoon sample of second plot	Net, Collection bag & killing vials Watch
2:45pm	Finish collecting Record plants and label bees from vials	Databook & pen Stacks or other small storage
3:00pm	Vegetation monitoring protocol for the second sampling plot of the day	Vegetation datasheets Ethanol-proof pen Meter stick with decimeter marks Plant voucher bags
3:45pm	Two collectors split up and walk to separate plots to pick up bowls	Tea strainers Gallon jug Funnel Whirl Packs (labeled on inside with ethanol-proof tag + on outside with Sharpie) Ethanol in plastic soda bottle
4:00pm	Each collector picks up pan traps at one plot	(all of immediately above)
4:45pm	Finish sampling day Collectors meet and return to car	All gear
5:00pm	Lay out gear for next day File datasheet	New Whirl packs Refill Ethanol Refill soapy water gallon jugs Replace useless vials, etc.
Evening	Pin all bees collected that day into field boxes	Field (Schmidt) boxes Pins (#1 & #2) Pinning blocks

### A3. Sample Data Collection Card Template

Collection ID#	START Date (like ## /JUN)	END Date (like ## / MAY)	Set Plot Collection Random Collection site See Notes on Back	
Other data card #'s		Collector(s):		
Plot/Location Name:				
DD.dddd°(start)	w/lon	N/lat Input into GPS as	Elev	
DD.dddd°(end)	w/lon	N/lat Input into GPS as	Elev	
DD.dddd°BOWL	w/lon	N/lat Input into GPS as	Elev	
# of bowls run	Bowls Spilled >>>	Yellow	Blue	White
startAM Time (24hrs ex10:00)	endAM Time (ex10:30)	AM Temp °F	AM Wind Speed	AM Humidity
startPM Time	endPM Time (ex17:00)	PM Temp °F	PM Wind Speed	PM Humidity
startBowl Time- (24hrs)	endBowl Time- (24hrs)	AVG Temp °F		Avg Wind
BAR: Other weatherNotes:				
Sunny AM PM		Partly Cloudy (>50% sun) AM PM	Cloudy (some Shadow cast; <50% sun) AM PM	Completely Cloudy (NO shadow cast) AM PM
Inclement Weather *see notes on back AM PM				
Radius of collection in(m): 10/ 25/ 50/ 100 / 200/ >200 / >1km				
«Card_Numb er»-A	Am Pm	Collector initials	Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: Plant Name/info Abundance	
«Card_Numb er»-B	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-A COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-C	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-B COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-D	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-C COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-E	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-D COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-F	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-E COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-G	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-F COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-H	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-G COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-I	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-H COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-J	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-I COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-K	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-J COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-L	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-K COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-M	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-L COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-N	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-M COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-P	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-N COL: Date- / /2012 am/pm LOC: plant-	
«Card_Numb er»-Q	Am Pm		Plant details _____ NOT-Flowering/ Voucher / Bee Not Foraging: «Card_Number»-P COL: Date- / /2012 am/pm LOC: plant-	
PAN TRAPS Y / N		Col.ID#~«Card_Number» Date - '2012 col- site/plot#	Col.ID#~«Card_Number» Date - 2012 col- site/plot#	Col.ID#~«Card_Number» Date - 2012 col- site/plot#

**Appendix B.** Full bee species list for Pinnacles National Park, with relative abundance per year of capture, and status as new or lost to the current study. Groups are marked "R" for Rare if  $N \leq 10$ , "U" for Uncommon if  $100 > N > 10$ , and "C" for Common if  $N > 100$ . Dashed line distinguishes 2002 collection as separate from the original 1996-9 inventory, but still prior to the current study (2011-12). Species highlighted in blue were newly discovered by the current study, and those highlighted in red were recorded in the park previously, but were not confirmed by the current study. See Table 3 in Results I for 25 most common in current study.

	Bee Family (SubFamily) Genus (Subgenus) Species	1996	1997	1998	1999	2000	2001	2002	2003	2004
1	Andrenidae (Andreninae) Ancylandrena atoposoma	R								
2	Andrenidae (Andreninae) Andrena sp. 17									R
3	Andrenidae (Andreninae) Andrena sp. 18									R
4	Andrenidae (Andreninae) Andrena sp. 19								R	R
5	Andrenidae (Andreninae) Andrena sp. 22									R
6	Andrenidae (Andreninae) Andrena sp. 25									R
7	Andrenidae (Andreninae) Andrena (Anchandrena) quercina			R						
8	Andrenidae (Andreninae) Andrena (Aporandrena) n. sp.	R								
9	Andrenidae (Andreninae) Andrena (Belandrena) nemophilae			R						
10	Andrenidae (Andreninae) Andrena (Belandrena) palpalis		R	R						
11	Andrenidae (Andreninae) Andrena (Cremnandrena) anisochlora			U					U	R
12	Andrenidae (Andreninae) Andrena (Dasyandrena) cristata			R						
13	Andrenidae (Andreninae) Andrena (Derandrena) arctostaphylae			R		R				
14	Andrenidae (Andreninae) Andrena (Derandrena) californiensis			R		R			R	R
15	Andrenidae (Andreninae) Andrena (Derandrena) n. sp.	R	R	R					R	U
16	Andrenidae (Andreninae) Andrena (Derandrena) vandykei			U		R				
17	Andrenidae (Andreninae) Andrena (Derandrena) viridissima								R	
18	Andrenidae (Andreninae) Andrena (Diandrena) chalybioides									R
19	Andrenidae (Andreninae) Andrena (Diandrena) cuneilabris									R
20	Andrenidae (Andreninae) Andrena (Diandrena) lewisorum	R	R	R	U				U	U
21	Andrenidae (Andreninae) Andrena (Diandrena) nothocalaidis			R						
22	Andrenidae (Andreninae) Andrena (Diandrena) puthua		R	U						R
23	Andrenidae (Andreninae) Andrena (Diandrena) sperryi								R	
24	Andrenidae (Andreninae) Andrena (Diandrena) subchalybea			R	R	R			U	C
25	Andrenidae (Andreninae) Andrena (Diandrena) submoesta					R				
26	Andrenidae (Andreninae) Andrena (Erandrena) principalis			R						
27	Andrenidae (Andreninae) Andrena (Euandrena) astragali		R	R					R	R
28	Andrenidae (Andreninae) Andrena (Euandrena) auricoma	R	R	U	R				U	
29	Andrenidae (Andreninae) Andrena (Euandrena) caerulea			U						R
30	Andrenidae (Andreninae) Andrena (Euandrena) chlorura		R	U		R			U	U
31	Andrenidae (Andreninae) Andrena (Euandrena) dissimulans			U					U	U
32	Andrenidae (Andreninae) Andrena (Euandrena) misella			R						
33	Andrenidae (Andreninae) Andrena (Euandrena) nigrocaerulea	R	R	R						
34	Andrenidae (Andreninae) Andrena (Euandrena) suavis			R					U	U

35	Andrenidae (Andreninae) Andrena (Euandrena) subdepressa			R			R	R
36	Andrenidae (Andreninae) Andrena (Genyandrena) mackieae		R	U			R	R
37	Andrenidae (Andreninae) Andrena (Hesperandrena) baeriae		R	R				
38	Andrenidae (Andreninae) Andrena (Hesperandrena) lativentris							R
39	Andrenidae (Andreninae) Andrena (Holandrena) cressonii		R					
40	Andrenidae (Andreninae) Andrena (Melandrena) aff. cerasifolii		U	U	U		C	C
41	Andrenidae (Andreninae) Andrena (Melandrena) cerasifolii	U	U	U	R		U	R
42	Andrenidae (Andreninae) Andrena (Melandrena) perimelas					R		
43	Andrenidae (Andreninae) Andrena (Melandrena) sola	R	U	U	U		U	U
44	Andrenidae (Andreninae) Andrena (Micrandrena) aff. ishii			U				
45	Andrenidae (Andreninae) Andrena (Micrandrena) annectens			R			R	
46	Andrenidae (Andreninae) Andrena (Micrandrena) chlorogaster		R	C		R	R	U
47	Andrenidae (Andreninae) Andrena (Micrandrena) microchlora		U	U	R	R	R	U
48	Andrenidae (Andreninae) Andrena (Micrandrena) piperi		R	R		R	R	R
49	Andrenidae (Andreninae) Andrena (Nemandrena) crudeni			U		R	C	C
50	Andrenidae (Andreninae) Andrena (Nemandrena) subnigripes			R				
51	Andrenidae (Andreninae) Andrena (Oligandrena) macrocephala	R	U	U		U	U	C
52	Andrenidae (Andreninae) Andrena (Parandrena) concinnula			R			R	
53	Andrenidae (Andreninae) Andrena (Pelicanandrena) atypica		R	C	R	R	U	R
54	Andrenidae (Andreninae) Andrena (Plastandrena) prunorum							R
55	Andrenidae (Andreninae) Andrena (Psammandrena) congrua		R	R			R	R
56	Andrenidae (Andreninae) Andrena (Ptilandrena) pallidiscopa			R				R
57	Andrenidae (Andreninae) Andrena (Scaphandrena) lomatii			R				
58	Andrenidae (Andreninae) Andrena (Scaphandrena) plana			R				
59	Andrenidae (Andreninae) Andrena (Scaphandrena) santaclarae		R	R				R
60	Andrenidae (Andreninae) Andrena (Scoliandrena) cryptanthae	R						
61	Andrenidae (Andreninae) Andrena (Scoliandrena) osmioides			R			R	R
62	Andrenidae (Andreninae) Andrena (Scapteropsis) biareola			R				
63	Andrenidae (Andreninae) Andrena (Simandrena) angustitarsata	R	R	C	U		U	U
64	Andrenidae (Andreninae) Andrena (Simandrena) hypoleuca						R	R
65	Andrenidae (Andreninae) Andrena (Simandrena) orthocarpi			R			R	
66	Andrenidae (Andreninae) Andrena (Simandrena) pallidifovea	R	R	R	R		R	R
67	Andrenidae (Andreninae) Andrena (Simandrena) pensilis							R
68	Andrenidae (Andreninae) Andrena (Thysandrena) aff. candida		R					R
69	Andrenidae (Andreninae) Andrena (Thysandrena) aff. lauta		R					
70	Andrenidae (Andreninae) Andrena (Thysandrena) candida	U	U	C	U	R	U	U
71	Andrenidae (Andreninae) Andrena (Thysandrena) vierecki		R	R				
72	Andrenidae (Andreninae) Andrena (Thysandrena) w-scripta	R	R	U	U	R	R	C
73	Andrenidae (Andreninae) Andrena (Trachandrena) fuscicauda			R	R			
74	Andrenidae (Andreninae) Andrena (Trachandrena) semipunctata		R	R			R	

75	Andrenidae (Andreninae) <i>Andrena</i> ( <i>Tylandrena</i> ) <i>subtilis</i>			R			R	
76	Andrenidae (Andreninae) <i>Andrena</i> ( <i>Tylandrena</i> ) <i>waldmeri</i>			R				
77	Andrenidae (Panurginae) <i>Calliopsis</i> <i>smithi</i>	U	U	U	U			R
78	Andrenidae (Panurginae) <i>Calliopsis</i> ( <i>Micronomadopsis</i> ) <i>fracta</i>	R	R	R			R	
79	Andrenidae (Panurginae) <i>Calliopsis</i> ( <i>Micronomadopsis</i> ) <i>helianthi</i>						R	
80	Andrenidae (Panurginae) <i>Calliopsis</i> ( <i>Micronomadopsis</i> ) <i>mellipes</i>		R				R	
81	Andrenidae (Panurginae) <i>Calliopsis</i> ( <i>Micronomadopsis</i> ) <i>trifolii</i>	R			R			
82	Andrenidae (Panurginae) <i>Calliopsis</i> ( <i>Nomadopsis</i> ) <i>anthidia</i>	R	R	R				
83	Andrenidae (Panurginae) <i>Calliopsis</i> ( <i>Nomadopsis</i> ) <i>obscura</i>	R	U	R	R		U	R
84	Andrenidae (Panurginae) <i>Calliopsis</i> ( <i>Nomadopsis</i> ) <i>zonalis</i>	R	R		R			
85	Andrenidae (Panurginae) <i>Macrotera</i> ( <i>Macroteropsis</i> ) <i>arcuata</i>			R			R	R
86	Andrenidae (Panurginae) <i>Panurginus</i> <i>gracilis</i>			C	R		C	C
87	Andrenidae (Panurginae) <i>Panurginus</i> <i>melanocephalus</i>		R	R			U	U
88	Andrenidae (Panurginae) <i>Panurginus</i> <i>morrisoni</i>		R					R
89	Andrenidae (Panurginae) <i>Panurginus</i> <i>nigrellus</i>	U	U	U			U	C
90	Andrenidae (Panurginae) <i>Panurginus</i> <i>occidentalis</i>					R		
91	Andrenidae (Panurginae) <i>Panurginus</i> <i>quadratus</i>			R	U			
92	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Hesperoperdita</i> ) <i>tresignata</i>	R	U	U	C		R	R
93	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>aff. linsleyi</i> n.sp.	R	R	R	R		R	
94	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>claypolei</i>		U	U				
95	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>hirticeps</i>							R
96	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>holoxantha</i>						R	
97	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>isocomae</i>		R					
98	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>jucunda</i>		R		R			
99	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>linsleyi</i>						R	
100	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>rhois</i>	U	C	C	R			R
101	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Perdita</i> ) <i>salicis</i>						R	
102	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Pygoperdita</i> ) <i>aureovittata</i>		R					
103	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Pygoperdita</i> ) <i>californica</i>			R				
104	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Pygoperdita</i> ) <i>distropica</i>	R	U	U	U		U	C
105	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Pygoperdita</i> ) <i>micheneri</i>			U	R		R	
106	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Pygoperdita</i> ) <i>montereyensis</i>	U	U	U	U		U	C
107	Andrenidae (Panurginae) <i>Perdita</i> ( <i>Pygoperdita</i> ) <i>nitens</i>	U	U	R			U	R
108	Apidae (Apinae) <i>Anthophora</i> ( <i>Anthophoroides</i> ) <i>californica</i>	R	U	R	R	R	R	R
109	Apidae (Apinae) <i>Anthophora</i> ( <i>Heliophila</i> ) <i>columbariae</i>			R				
110	Apidae (Apinae) <i>Anthophora</i> ( <i>Heliophila</i> ) <i>curta</i>	R	R	R	R		R	R
111	Apidae (Apinae) <i>Anthophora</i> ( <i>Heliophila</i> ) <i>estebana</i>		R					
112	Apidae (Apinae) <i>Anthophora</i> ( <i>Heliophila</i> ) <i>flavocincta</i>					R		
113	Apidae (Apinae) <i>Anthophora</i> ( <i>Lophanthophora</i> ) <i>pacifica</i>		R	U			R	
114	Apidae (Apinae) <i>Anthophora</i> ( <i>Melea</i> ) <i>bomboides</i>	R						
115	Apidae (Apinae) <i>Anthophora</i> ( <i>Mystacanthophora</i> ) <i>urbana</i>	R	U	U	U	R	U	U
116	Apidae (Apinae) <i>Anthophora</i> ( <i>Paramegilla</i> ) <i>centrifformis</i>	R	U	R	U		R	
117	Apidae (Apinae) <i>Anthophora</i> ( <i>Pyganthophora</i> ) <i>crotchii</i>	R	U	R	R	R	U	U
118	Apidae (Apinae) <i>Anthophora</i> ( <i>Pyganthophora</i> ) <i>edwardsii</i>	R	R	R			U	U
119	Apidae (Apinae) <i>Anthophora</i> ( <i>Pyganthophora</i> ) <i>platti</i>	U	U	U	R		U	U
120	Apidae (Apinae) <i>Anthophorula</i> ( <i>Anthophoriscia</i> ) <i>nitens</i>		U	U			U	U

121	Apidae (Apinae) Anthophorula (Anthophorula) albicans			U	U		R	R	R
122	Apidae (Apinae) Apis mellifera	R	C	C	U	U	C	C	
123	Apidae (Apinae) Bombus (Crotchiiibombus) crotchii		U	U	R				
124	Apidae (Apinae) Bombus (Fervidobombus) californicus	R	U	U	R	R	R	R	
125	Apidae (Apinae) Bombus (Pyrobombus) caliginosus		U				R	R	
126	Apidae (Apinae) Bombus (Pyrobombus) edwardsii							R	
127	Apidae (Apinae) Bombus (Pyrobombus) melanopygus	R	C	U	R	R	U		
128	Apidae (Apinae) Bombus (Pyrobombus) vandykei		R	R			R		
129	Apidae (Apinae) Bombus (Pyrobombus) vosnesenskii	R	C	C	R	R	U	R	
130	Apidae (Apinae) Centris (Paracentris) aff. californica		U	U	R				
131	Apidae (Apinae) Diadasia aff. ochracea		R	R		R	R	U	
132	Apidae (Apinae) Diadasia angusticeps		R	R	C	R	C	U	
133	Apidae (Apinae) Diadasia australis					R	R		
134	Apidae (Apinae) Diadasia bituberculata	R	U	R	U	U	U	C	
135	Apidae (Apinae) Diadasia consociata							R	
136	Apidae (Apinae) Diadasia laticauda		U	U	R	R	U	U	
137	Apidae (Apinae) Diadasia nigrifrons						R		
138	Apidae (Apinae) Diadasia nitidifrons		R	U	R	R	U	U	
139	Apidae (Apinae) Diadasia rinconis							R	
140	Apidae (Apinae) Eucera (Synhalonia) actiosa		R	R	R	U	C	C	
141	Apidae (Apinae) Eucera (Synhalonia) amsinckiae	R	R	R		R	R	R	
142	Apidae (Apinae) Eucera (Synhalonia) cordleyi		R	U		R	U	R	
143	Apidae (Apinae) Eucera (Synhalonia) delphinii		U	R	R	R	R	R	
144	Apidae (Apinae) Eucera (Synhalonia) dorsata		U	R	R	R	U	U	
145	Apidae (Apinae) Eucera (Synhalonia) edwardsii	R	R	R		R		R	
146	Apidae (Apinae) Eucera (Synhalonia) lunata			R			R	R	
147	Apidae (Apinae) Eucera (Synhalonia) venusta	U	U	U	R		R	R	
148	Apidae (Apinae) Eucera (Synhalonia) virgata			U	R	R	U	U	
149	Apidae (Apinae) Habropoda dammersi			R					
150	Apidae (Apinae) Habropoda depressa	R	U	U	R	R	U	U	
151	Apidae (Apinae) Habropoda tristissima	R	U	R	R	R	R	U	
152	Apidae (Apinae) Melecta (Melecta) pacifica		R	R			R		
153	Apidae (Apinae) Melecta (Melecta) separata			R	R	R	R	U	
154	Apidae (Apinae) Melecta (Melectomimus) edwardsii		R				R		
155	Apidae (Apinae) Melissodes sp. m1			R					
156	Apidae (Apinae) Melissodes (Callimelissodes) clarkiae		R				R	R	
157	Apidae (Apinae) Melissodes (Callimelissodes) composita							R	
158	Apidae (Apinae) Melissodes (Callimelissodes) lupina		R	U		R	U	C	
159	Apidae (Apinae) Melissodes (Callimelissodes) lustra		R						
160	Apidae (Apinae) Melissodes (Callimelissodes) n. sp.							R	
161	Apidae (Apinae) Melissodes (Callimelissodes) n. sp. 1		R	R	R				
162	Apidae (Apinae) Melissodes (Callimelissodes) n. sp. 2		R	R	R	R	R		
163	Apidae (Apinae) Melissodes (Callimelissodes) nigracauda			R					
164	Apidae (Apinae) Melissodes (Callimelissodes) plumosa		R				R	U	
165	Apidae (Apinae) Melissodes (Callimelissodes) stearnsi		R	R		C	U	C	
166	Apidae (Apinae) Melissodes (Eumelissodes) paulula		R						
167	Apidae (Apinae) Melissodes (Eumelissodes) velutina							R	
168	Apidae (Apinae) Melissodes (Melissodes) tepida							R	
169	Apidae (Apinae) Peponapis (Peponapis) pruinosa							R	
170	Apidae (Apinae) Xeromelecta (Melectomorpha) californica	R	U	R	U		R	R	
171	Apidae (Apinae) Xeromelecta (Xeromelecta) larreae	R							



172	Apidae (Nomadinae) Brachynomada (Melanomada) melanantha							R
173	Apidae (Nomadinae) Epeolus americanus	R	R			R	R	R
174	Apidae (Nomadinae) Epeolus compactus			R	R			R
175	Apidae (Nomadinae) Epeolus mesillae						R	R
176	Apidae (Nomadinae) Epeolus minimus				R	R		R
177	Apidae (Nomadinae) Neopasites (Micropasites) sp.							R
178	Apidae (Nomadinae) Nomada (Centrias) crotchii		R	U			R	R
179	Apidae (Nomadinae) Nomada (Centrias) sp. A	R	R					
180	Apidae (Nomadinae) Nomada (Holonomada) edwardsii		R	R				R
181	Apidae (Nomadinae) Nomada (Nomada) sp. A	R	R	R			R	R
182	Apidae (Nomadinae) Nomada (Nomada) sp. AA							R
183	Apidae (Nomadinae) Nomada (Nomada) sp. B	R	R	R			R	R
184	Apidae (Nomadinae) Nomada (Nomada) sp. BB					R	R	R
185	Apidae (Nomadinae) Nomada (Nomada) sp. CC					R		R
186	Apidae (Nomadinae) Nomada (Nomada) sp. D	U	U	U	R			
187	Apidae (Nomadinae) Nomada (Nomada) sp. DD						R	
188	Apidae (Nomadinae) Nomada (Nomada) sp. E	U	R	R	R		R	R
189	Apidae (Nomadinae) Nomada (Nomada) sp. EE						R	
190	Apidae (Nomadinae) Nomada (Nomada) sp. F	R		R				R
191	Apidae (Nomadinae) Nomada (Nomada) sp. FF							R
192	Apidae (Nomadinae) Nomada (Nomada) sp. G						R	R
193	Apidae (Nomadinae) Nomada (Nomada) sp. GG			R				R
194	Apidae (Nomadinae) Nomada (Nomada) sp. HH			R		R		
195	Apidae (Nomadinae) Nomada (Nomada) sp. I			R				
196	Apidae (Nomadinae) Nomada (Nomada) sp. II					R		
197	Apidae (Nomadinae) Nomada (Nomada) sp. J			R			R	
198	Apidae (Nomadinae) Nomada (Nomada) sp. Q		R	R			R	
199	Apidae (Nomadinae) Nomada (Nomada) sp. R		R	R				
200	Apidae (Nomadinae) Nomada (Nomada) sp. S		R					
201	Apidae (Nomadinae) Nomada (Nomada) sp. T		R					
202	Apidae (Nomadinae) Nomada (Nomada) sp. U		U	U			R	U
203	Apidae (Nomadinae) Nomada (Nomada) sp. V	R	R	R		R	R	R
204	Apidae (Nomadinae) Nomada (Nomada) sp. W		U	U			U	U
205	Apidae (Nomadinae) Nomada (Nomada) sp. X			R			R	R
206	Apidae (Nomadinae) Nomada (Nomada) sp. Y			R		R		
207	Apidae (Nomadinae) Nomada (Nomada) sp. Z			U				
208	Apidae (Nomadinae) Oreopasites aff. hurdi n.sp		R	R	R		R	R
209	Apidae (Nomadinae) Oreopasites vanduzeei	R	R	R	R		R	
210	Apidae (Nomadinae) Townsendiella ensifera		R	U	U			R
211	Apidae (Nomadinae) Townsendiella rufiventris			R				
212	Apidae (Nomadinae) Triepeolus sp. P1						R	R
213	Apidae (Nomadinae) Triepeolus sp. P2						R	
214	Apidae (Nomadinae) Triepeolus (Triepeolus) heterurus							R
215	Apidae (Nomadinae) Triepeolus (Triepeolus) sp. 1			R				
216	Apidae (Nomadinae) Triepeolus (Triepeolus) timberlakei		R	R	R		R	R
217	Apidae (Xylocopinae) Ceratina aff. nanula	R	R	R				
218	Apidae (Xylocopinae) Ceratina (Ceratina) arizonensis	U	C	U	U	U	C	C
219	Apidae (Xylocopinae) Ceratina (Euceratina) dallatorreana			R		R		
220	Apidae (Xylocopinae) Ceratina (Zadontomerus) acantha	R	U	R		R	U	R
221	Apidae (Xylocopinae) Ceratina (Zadontomerus) hurdi	R	R	R		R	U	U

222	Apidae (Xylocopinae) Ceratina (Zadontomerus) nanula	R	U	U	U	U	U	C
223	Apidae (Xylocopinae) Ceratina (Zadontomerus) pacifica		R	R			R	R
224	Apidae (Xylocopinae) Ceratina (Zadontomerus) punctigena	R	U	R	U		R	
225	Apidae (Xylocopinae) Ceratina (Zadontomerus) sequoiae	R	U	U	U	R	U	U
226	Apidae (Xylocopinae) Ceratina (Zadontomerus) tejonensis		U	R			R	R
227	Apidae (Xylocopinae) Ceratina (Zadontomerus) timberlakei		R	R	R	R	R	R
228	Apidae (Xylocopinae) Xylocopa (Notoxylocopa) tabaniformis	R	U	R	R	R	R	R
229	Colletidae (Colletinae) Colletes consors	U	U	R	R		U	R
230	Colletidae (Colletinae) Colletes aff. algarobiae	R	U	U	R		R	
231	Colletidae (Colletinae) Colletes algarobiae							U
232	Colletidae (Colletinae) Colletes fulgidus		R	R	R			R
233	Colletidae (Colletinae) Colletes simulans		R					
234	Colletidae (Colletinae) Colletes slevini	R	U	U	U		R	R
235	Colletidae (Hylaeinae) Hylaeus (Cephalylaeus) nunenmacheri			R	R			
236	Colletidae (Hylaeinae) Hylaeus (Hylaeus) bisinuatus		R					
237	Colletidae (Hylaeinae) Hylaeus (Hylaeus) conspicuus				R	R		R
238	Colletidae (Hylaeinae) Hylaeus (Hylaeus) granulatus		U	U	U		R	R
239	Colletidae (Hylaeinae) Hylaeus (Hylaeus) mesillae	R	C	U	U		U	R
240	Colletidae (Hylaeinae) Hylaeus (Hylaeus) rudbeckiae	R					R	R
241	Colletidae (Hylaeinae) Hylaeus (Hylaeus) verticalis	R	U	U	U		R	R
242	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) aff. cookii n.sp.		R	R	R			
243	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) calvus	R		U	U		R	U
244	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) coloradensis		U	U	R			
245	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) n. sp.2		U	R	R		R	
246	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) nevadensis	U	U	U	U		R	U
247	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) polifolii		U	U	U		R	
248	Colletidae (Hylaeinae) Hylaeus (Prosopis) episcopalis						R	R
249	Colletidae (Hylaeinae) Hylaeus (Prosopis) n. sp.	U	C	U	U			
250	Colletidae (Hylaeinae) Hylaeus (Spatulariella) punctatus				R			
251	Halictidae (Halictinae) Agapostemon (Agapostemon) angelicus / texanus					U	C	C
252	Halictidae (Halictinae) Agapostemon (Agapostemon) femoratus					R	R	
253	Halictidae (Halictinae) Agapostemon (Agapostemon) texanus	R	R	R	U			
254	Halictidae (Halictinae) Augochlorella (Augochlorella) pomoniella		R	R				R
255	Halictidae (Halictinae) Halictus (Nealictus) farinosus	U	C	C	C	C	C	C
256	Halictidae (Halictinae) Halictus (Odontalictus) ligatus				R	U	U	U
257	Halictidae (Halictinae) Halictus (Protohalictus) rubicundus					R	R	R
258	Halictidae (Halictinae) Halictus (Seladonia) tripartitus	U	U	C	C	C	C	C
259	Halictidae (Halictinae) Lasioglossum (Dialictus) aff. punctatovenre			R				
260	Halictidae (Halictinae) Lasioglossum (Dialictus) aff. ruidosense	R						
261	Halictidae (Halictinae) Lasioglossum (Dialictus) aff. tegulare	R	U	U	C			
262	Halictidae (Halictinae) Lasioglossum (Dialictus) albohirtum				R		R	R
263	Halictidae (Halictinae) Lasioglossum (Dialictus) brunneiventre		R	R	R		C	C
264	Halictidae (Halictinae) Lasioglossum (Dialictus)			R			R	

	diversopunctatum								
265	Halictidae (Halictinae) Lasioglossum (Dialictus) glabriventre							U	U
266	Halictidae (Halictinae) Lasioglossum (Dialictus) hudsoniellum							R	R
267	Halictidae (Halictinae) Lasioglossum (Dialictus) imbrex							C	U
268	Halictidae (Halictinae) Lasioglossum (Dialictus) impavidum								R
269	Halictidae (Halictinae) Lasioglossum (Dialictus) incompletum	R	R	U	C			C	C
270	Halictidae (Halictinae) Lasioglossum (Dialictus) megastictum			R				R	
271	Halictidae (Halictinae) Lasioglossum (Dialictus) n. sp. aff. nevadense			R	R				
272	Halictidae (Halictinae) Lasioglossum (Dialictus) nevadense	R	U	U	C			C	C
273	Halictidae (Halictinae) Lasioglossum (Dialictus) obscurior							R	U
274	Halictidae (Halictinae) Lasioglossum (Dialictus) perichlarum							R	
275	Halictidae (Halictinae) Lasioglossum (Dialictus) punctatoventre	U	U	C	C			C	C
276	Halictidae (Halictinae) Lasioglossum (Dialictus) sp. D	R							
277	Halictidae (Halictinae) Lasioglossum (Dialictus) sp. G				R				
278	Halictidae (Halictinae) Lasioglossum (Dialictus) sp. L			R	R				
279	Halictidae (Halictinae) Lasioglossum (Dialictus) tuolumnenie		R						
280	Halictidae (Halictinae) Lasioglossum (Evylaeus) allonotum			R				R	R
281	Halictidae (Halictinae) Lasioglossum (Evylaeus) argemonis	R	U	U	U	R		U	U
282	Halictidae (Halictinae) Lasioglossum (Evylaeus) aspilurum		R		R			R	R
283	Halictidae (Halictinae) Lasioglossum (Evylaeus) avalonense								R
284	Halictidae (Halictinae) Lasioglossum (Evylaeus) glabriventris	R	R	R	U			R	
285	Halictidae (Halictinae) Lasioglossum (Evylaeus) kincaidii	R	R	R	R			R	R
286	Halictidae (Halictinae) Lasioglossum (Evylaeus) miguelense		R		R				
287	Halictidae (Halictinae) Lasioglossum (Evylaeus) nigrescens	U	C	C	C			C	C
288	Halictidae (Halictinae) Lasioglossum (Evylaeus) ovaliceps							R	
289	Halictidae (Halictinae) Lasioglossum (Evylaeus) pulveris							U	R
290	Halictidae (Halictinae) Lasioglossum (Evylaeus) robustum		R	R	U			U	U
291	Halictidae (Halictinae) Lasioglossum (Evylaeus) ruficorne	R	R	U	U				
292	Halictidae (Halictinae) Lasioglossum (Evylaeus) sequoiae							U	U
293	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 1								R
294	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 10		R	R					
295	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 11		R						
296	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 12		R		R				
297	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 16				R			U	U
298	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 4	R		R	U				
299	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 9		R	R	U			C	C
300	Halictidae (Halictinae) Lasioglossum (Lasioglossum) egregium		R	R	R				U
301	Halictidae (Halictinae) Lasioglossum (Lasioglossum) sisymbrii	R	U	U	U	U		C	U
302	Halictidae (Halictinae) Lasioglossum (Lasioglossum) titusi			R	R			R	U
303	Halictidae (Halictinae) Lasioglossum (Sphecodogastra) sp.								R
304	Halictidae (Halictinae) Sphecodes arvensiformis	R	R						
305	Halictidae (Halictinae) Sphecodes sp. A		R					R	R
306	Halictidae (Halictinae) Sphecodes sp. B	R	U	U	R			R	R

307	Halictidae (Halictinae) Sphecodes sp. C	R						
308	Halictidae (Halictinae) Sphecodes sp. D	R		R	R		R	R
309	Halictidae (Halictinae) Sphecodes sp. E	R	R	R	U		U	U
310	Halictidae (Halictinae) Sphecodes sp. F	R	R					
311	Halictidae (Halictinae) Sphecodes sp. I		R	R				
312	Halictidae (Halictinae) Sphecodes sp. J		R					
313	Halictidae (Halictinae) Sphecodes sp. K		R					
314	Halictidae (Halictinae) Sphecodes sp. L		R	R	U		R	
315	Halictidae (Halictinae) Sphecodes sp. M							R
316	Halictidae (Rophitinae) Conanthalictus (Phaceliapis) bakeri		R	R	R		R	
317	Halictidae (Rophitinae) Conanthalictus (Phaceliapis) seminiger				R			
318	Halictidae (Rophitinae) Dufourea dentipes						R	
319	Halictidae (Rophitinae) Dufourea leachi	R	R	U	R		R	U
320	Halictidae (Rophitinae) Dufourea mulleri		R	R			R	
321	Halictidae (Rophitinae) Dufourea rhamni	R	R	R				R
322	Halictidae (Rophitinae) Dufourea sandhouseae		U	U			U	U
323	Halictidae (Rophitinae) Dufourea sparsipunctata	U	U	R	R		C	U
324	Halictidae (Rophitinae) Dufourea virgata	U	R	R	R		R	R
325	Halictidae (Rophitinae) Micralictoides altadenae		R				R	
326	Halictidae (Rophitinae) Micralictoides ruficaudus	R	R	R			U	R
327	Megachilidae (Megachilinae) Anthidiellum (Loyalanthidium) notatum						R	
328	Megachilidae (Megachilinae) Anthidiellum (Loyalanthidium) robertsoni		U	U				
329	Megachilidae (Megachilinae) Anthidium (Anthidium) collectum	R	U	U	U		R	R
330	Megachilidae (Megachilinae) Anthidium (Anthidium) edwardsii							R
331	Megachilidae (Megachilinae) Anthidium (Anthidium) jocosum							R
332	Megachilidae (Megachilinae) Anthidium (Anthidium) maculosum		R					
333	Megachilidae (Megachilinae) Anthidium (Anthidium) mormonum	R	R	R	R			
334	Megachilidae (Megachilinae) Anthidium (Anthidium) pallidiclypeum	R	R	R	R			
335	Megachilidae (Megachilinae) Anthidium (Anthidium) utahense	U	C	C	U		U	U
336	Megachilidae (Megachilinae) Anthidium (Callanthidium) illustre		U	R	R		R	R
337	Megachilidae (Megachilinae) Ashmeadiella aff. rufitarsis	R	R	R	R		R	
338	Megachilidae (Megachilinae) Ashmeadiella (Arogochila) aff. salviae n.sp.						R	
339	Megachilidae (Megachilinae) Ashmeadiella (Arogochila) australis		R	R	R			
340	Megachilidae (Megachilinae) Ashmeadiella (Arogochila) salviae	R	U	U	R		R	R
341	Megachilidae (Megachilinae) Ashmeadiella (Arogochila) timberlakei	U	C	U	U		R	R
342	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) buconis		U	R				R
343	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella)		R					

	cactorum								
344	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) californica	R	U	U	U			R	R
345	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) difugita		R	R				R	
346	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) femorata		R		U				
347	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) foveata	R	U	U	U			R	
348	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) gillettei		R	R					R
349	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) meliloti		U	U					R
350	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) pronitens		R						
351	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) rufitarsis								R
352	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) sonora		R	R					
353	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) titusi		U	R	R				
354	Megachilidae (Megachilinae) Atoposmia (Atoposmia) n. sp. 2	R	R	R				R	
355	Megachilidae (Megachilinae) Atoposmia (Atoposmia) pycnognatha		U	R	R				
356	Megachilidae (Megachilinae) Atoposmia (Eremosmia) hemizoniae							R	
357	Megachilidae (Megachilinae) Atoposmia (Hexosmia) copelandica	R	U	R	R			R	R
358	Megachilidae (Megachilinae) Chelostoma (Chelostoma) aff. minutum n.sp.		R	R	R				R
359	Megachilidae (Megachilinae) Chelostoma (Chelostoma) californicum	U	C	U	U			U	R
360	Megachilidae (Megachilinae) Chelostoma (Chelostoma) cockerelli	U	U	U	C			U	U
361	Megachilidae (Megachilinae) Chelostoma (Chelostoma) incisulum	U	U	U	U			U	R
362	Megachilidae (Megachilinae) Chelostoma (Chelostoma) marginatum	U	U	U	R			U	R
363	Megachilidae (Megachilinae) Chelostoma (Chelostoma) n. sp.	R	U	U	R				
364	Megachilidae (Megachilinae) Chelostoma (Chelostoma) phaceliae	U	C	U	U			U	R
365	Megachilidae (Megachilinae) Chelostoma (Chelostoma) tetramerum							R	R
366	Megachilidae (Megachilinae) Coelioxys (Boreocoelioxys) octodentata		R	R				R	
367	Megachilidae (Megachilinae) Coelioxys (Coelioxys) hirsutissima							R	
368	Megachilidae (Megachilinae) Coelioxys (Coelioxys) serricaudata	R	R	R	R			R	R
369	Megachilidae (Megachilinae) Coelioxys (Cyrtocoelioxys) gilensis		R						
370	Megachilidae (Megachilinae) Coelioxys (Cyrtocoelioxys) gonaspis		R						

371	Megachilidae (Megachilinae) <i>Dianthidium</i> ( <i>Dianthidium</i> ) <i>dubium</i>		U	U	R		R	U
372	Megachilidae (Megachilinae) <i>Dianthidium</i> ( <i>Dianthidium</i> ) <i>parvum</i>						R	R
373	Megachilidae (Megachilinae) <i>Dianthidium</i> ( <i>Dianthidium</i> ) <i>pudicum</i>	R	R	R	R		R	R
374	Megachilidae (Megachilinae) <i>Dianthidium</i> ( <i>Dianthidium</i> ) <i>singulare</i>		R					
375	Megachilidae (Megachilinae) <i>Dianthidium</i> ( <i>Dianthidium</i> ) <i>ulkei</i>		R	R				R
376	Megachilidae (Megachilinae) <i>Dioxys</i> <i>aurifusca</i>		R					
377	Megachilidae (Megachilinae) <i>Dioxys</i> <i>pacifica</i>			R				R
378	Megachilidae (Megachilinae) <i>Dioxys</i> <i>pomonae</i>	R	R	R	R		U	R
379	Megachilidae (Megachilinae) <i>Dioxys</i> <i>producta</i>	R	R	R	R		R	R
380	Megachilidae (Megachilinae) <i>Heriades</i> ( <i>Heriades</i> ) <i>sp.</i>							R
381	Megachilidae (Megachilinae) <i>Heriades</i> ( <i>Neotrypetes</i> ) <i>occidentalis</i>		C	U				
382	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Acrosmia</i> ) <i>aff. emarginata</i>		U	R	R		R	
383	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>colei</i>	R	U	R	U		U	U
384	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>grinnelli</i>	R	U	R	R		R	R
385	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>producta</i>	U	U	U	U		U	R
386	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>sambuci</i>	R	U	R	R			
387	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Cyrtosmia</i> ) <i>hypocrita</i>	R	U	U	R		R	R
388	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Hoplitina</i> ) <i>bunocephala</i>	R		R				
389	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Hoplitina</i> ) <i>howardi</i>	U	C	U	U		R	R
390	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Monumetha</i> ) <i>albifrons</i>	U	C	U	U		U	U
391	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Monumetha</i> ) <i>fulgida</i>	U	U	U	U		U	R
392	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Penteriades</i> ) <i>remotula</i>	R	U	R			R	R
393	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Proteriades</i> ) <i>cryptanthae</i>	R	R					
394	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Proteriades</i> ) <i>jacintana</i>	U	U	R	R		R	
395	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Proteriades</i> ) <i>nanula</i>	R	U	R	R		R	
396	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Proteriades</i> ) <i>seminigra</i>	R	U	R	R		R	
397	Megachilidae (Megachilinae) <i>Hoplitis</i> ( <i>Proteriades</i> ) <i>semirubra</i>	R	R	R	R		R	R
398	Megachilidae (Megachilinae) <i>Megachile</i> ( <i>Argyropile</i> ) <i>parallela</i>		R					
399	Megachilidae (Megachilinae) <i>Megachile</i> ( <i>Chelostomoides</i> ) <i>angelarum</i>		U	U			R	R
400	Megachilidae (Megachilinae) <i>Megachile</i> ( <i>Chelostomoides</i> ) <i>davidsoni</i>		U				R	R
401	Megachilidae (Megachilinae) <i>Megachile</i> ( <i>Chelostomoides</i> ) <i>exilis</i>							R
402	Megachilidae (Megachilinae) <i>Megachile</i> ( <i>Chelostomoides</i> ) <i>spinotulata</i>		U	R				
403	Megachilidae (Megachilinae) <i>Megachile</i> ( <i>Eutricharaea</i> ) <i>apicalis</i>		U	R			R	U
404	Megachilidae (Megachilinae) <i>Megachile</i> ( <i>Litomegachile</i> ) <i>brevis</i>			R	R		R	

405	Megachilidae (Megachilinae) Megachile (Litomegachile) coquilletti	R	U	U			U	U
406	Megachilidae (Megachilinae) Megachile (Litomegachile) gentilis		R	R				R
407	Megachilidae (Megachilinae) Megachile (Litomegachile) lippiae							R
408	Megachilidae (Megachilinae) Megachile (Litomegachile) onobrychidis						R	R
409	Megachilidae (Megachilinae) Megachile (Litomegachile) texana	R	R	R	R			
410	Megachilidae (Megachilinae) Megachile (Megachile) montivaga		R				R	R
411	Megachilidae (Megachilinae) Megachile (Megachiloides) gravita		R		U		U	U
412	Megachilidae (Megachilinae) Megachile (Megachiloides) pascoensis	R	U	R	U		U	U
413	Megachilidae (Megachilinae) Megachile (Megachiloides) pseudonigra	R	R				R	
414	Megachilidae (Megachilinae) Megachile (Megachiloides) subnigra			R			U	R
415	Megachilidae (Megachilinae) Megachile (Sayapis) fidelis		R	R				R
416	Megachilidae (Megachilinae) Megachile (Sayapis) frugalis		C	U			R	R
417	Megachilidae (Megachilinae) Megachile (Sayapis) inimica		R					
418	Megachilidae (Megachilinae) Megachile (Sayapis) newberryae		R	R				
419	Megachilidae (Megachilinae) Osmia claremontensis	R	U	R	R		R	
420	Megachilidae (Megachilinae) Osmia (Acanthosmioides) nigrifrons		R		R			
421	Megachilidae (Megachilinae) Osmia (Acanthosmioides) nigrobarbata	R	R	R	R		R	R
422	Megachilidae (Megachilinae) Osmia (Acanthosmioides) odontogaster	R	U	U	R		R	R
423	Megachilidae (Megachilinae) Osmia (Acanthosmioides) sedula						R	
424	Megachilidae (Megachilinae) Osmia (Acanthosmioides) sp. A	R						
425	Megachilidae (Megachilinae) Osmia (Cephalosmia) californica	R	R	R	R		R	R
426	Megachilidae (Megachilinae) Osmia (Cephalosmia) montana	R	R	R	U	R	U	R
427	Megachilidae (Megachilinae) Osmia (Euthosmia) glauca	R	U	U	U		U	U
428	Megachilidae (Megachilinae) Osmia (Helicosmia) coloradensis		U	U	R		R	R
429	Megachilidae (Megachilinae) Osmia (Helicosmia) texana		U	R	R		R	R
430	Megachilidae (Megachilinae) Osmia (Melanosmia) aff. hesperos						R	
431	Megachilidae (Megachilinae) Osmia (Melanosmia) aglaia	R	C	U	U		U	C
432	Megachilidae (Megachilinae) Osmia (Melanosmia) atrocyanea	R	U	U	U		U	U
433	Megachilidae (Megachilinae) Osmia (Melanosmia) bakeri	U	U	U	U		U	R
434	Megachilidae (Megachilinae) Osmia (Melanosmia) brevis	U	C	U	U	R	C	U
435	Megachilidae (Megachilinae) Osmia (Melanosmia) calla	R	U	U	U		U	U
436	Megachilidae (Megachilinae) Osmia (Melanosmia) cara	U	U	U	U		U	U
437	Megachilidae (Megachilinae) Osmia (Melanosmia) clarescens	R	U	U	R		R	R



438	Megachilidae (Megachilinae) Osmia (Melanosmia) cyanella	U	U	U	U		U	U
439	Megachilidae (Megachilinae) Osmia (Melanosmia) cyanopoda	R	U	R	R			R
440	Megachilidae (Megachilinae) Osmia (Melanosmia) densa	U	U	U	R		U	U
441	Megachilidae (Megachilinae) Osmia (Melanosmia) gabrielis	U	U	U	U		U	U
442	Megachilidae (Megachilinae) Osmia (Melanosmia) gaudiosa						U	R
443	Megachilidae (Megachilinae) Osmia (Melanosmia) granulosa	R	U	U	U		U	U
444	Megachilidae (Megachilinae) Osmia (Melanosmia) inurbana			R			U	U
445	Megachilidae (Megachilinae) Osmia (Melanosmia) kincaidii	U	U	U	U		U	U
446	Megachilidae (Megachilinae) Osmia (Melanosmia) laeta	R	U	U	R		U	U
447	Megachilidae (Megachilinae) Osmia (Melanosmia) malina			R				
448	Megachilidae (Megachilinae) Osmia (Melanosmia) pusilla	R	U		R		R	R
449	Megachilidae (Megachilinae) Osmia (Melanosmia) raritatis	R	R	R	R		R	R
450	Megachilidae (Megachilinae) Osmia (Melanosmia) regulina	R	U	U	U		C	C
451	Megachilidae (Megachilinae) Osmia (Melanosmia) rostrata				R			
452	Megachilidae (Megachilinae) Osmia (Melanosmia) trevoris			R	R		U	U
453	Megachilidae (Megachilinae) Osmia (Melanosmia) tristella		R	R	R			
454	Megachilidae (Megachilinae) Osmia (Melanosmia) vandykei		R	R	R			
455	Megachilidae (Megachilinae) Osmia (Melanosmia) visenda	U	U	U	R		U	U
456	Megachilidae (Megachilinae) Osmia (Mystacosmia) nemoris		R	U	C	C	C	C
457	Megachilidae (Megachilinae) Osmia (Osmia) lignaria	R	U	C	R	R	U	U
458	Megachilidae (Megachilinae) Osmia (Osmia) ribifloris		R	R				
459	Megachilidae (Megachilinae) Osmia (Pyrosomia) nigricollis							R
460	Megachilidae (Megachilinae) Osmia (Trichinosmia) latisulcata		R	R	R		U	
461	Megachilidae (Megachilinae) Protosmia (Chelostomopsis) rubifloris	U	C	C	U		C	U
462	Megachilidae (Megachilinae) Stelis (Protostelis) anthidioides	R		R			R	
463	Megachilidae (Megachilinae) Stelis (Protostelis) hurdi		R	R	R		R	
464	Megachilidae (Megachilinae) Stelis (Stelis) aff. foederalis		R		R		R	
465	Megachilidae (Megachilinae) Stelis (Stelis) ashmeadiellae		R	R	R		R	R
466	Megachilidae (Megachilinae) Stelis (Stelis) calliphorina		R					
467	Megachilidae (Megachilinae) Stelis (Stelis) chemsaki							R
468	Megachilidae (Megachilinae) Stelis (Stelis) cockerelli				R		R	R
469	Megachilidae (Megachilinae) Stelis (Stelis) interrupta				R			R
470	Megachilidae (Megachilinae) Stelis (Stelis) lateralis		R	R	R		R	
471	Megachilidae (Megachilinae) Stelis (Stelis) micheneri	R	R		R		R	
472	Megachilidae (Megachilinae) Stelis (Stelis) montana	R	R	R	R		R	R
473	Megachilidae (Megachilinae) Stelis (Stelis) nigriventris		R	R				
474	Megachilidae (Megachilinae) Stelis (Stelis) occidentalis	R	R					R
475	Megachilidae (Megachilinae) Stelis (Stelis) submarginata	R	R	R	R		R	
476	Megachilidae (Megachilinae) Trachusa (Heteranthidium) timberlakei		R	U	U		R	R
477	Megachilidae (Megachilinae) Trachusa (Trachusomimus) perdita		U	C	U	U	C	R
478	Melittidae (Dasypodinae) Hesperapis (Amblyapis) ilicifoliae	U	C	C	C	R	U	U
479	Melittidae (Dasypodinae) Hesperapis (Panurgomia) regularis	U	C	C	C	C	C	C



**Appendix C.** Floral taxa visited by bees (unique groups, identified to lowest possible level), and their relative popularity by year at Pinnacles National Park, and status as new or lost to the current study.

Plants are marked with “R” for rare if bee visits were fewer than 10 in that year, with “U” for uncommon if bee visits ranged between 10-100, and “C” for common when over 100 bees were collected on that plant. The last row gives a count of plant taxa sampled on in each year. Dashed line distinguishes 2002 collection as separate from original 1996-9 study, but still prior to current study. Taxa highlighted in blue were newly collected on in the current study, and those highlighted in red had bees recorded on them in the park previously, but did not yield bees in the current study. Note that differences between red and blue highlighted taxa may only reflect the foci of the given study or the expertise of the plant identifications, rather than any measurable changes in park flora or attractiveness to bees. See **Table 4** in Results for 25 most popular in current study.

	Plant Name	1996	1997	1998	1999	2000	2001	2002
1	Alliaceae Allium fimbriatum						R	
2	Alliaceae Allium lacunosum		U	U	R			
3	Alliaceae Allium lacunosum var. micranthum							R
4	Alliaceae Allium sp.	U	U	R				
5	Anacardiaceae Toxicodendron diversilobum						R	
6	Apiaceae Anthriscus caucalis						R	
7	Apiaceae Apiaceae sp.		R	U				
8	Apiaceae Apiaceae sp. (yellow)			R			R	
9	Apiaceae Lomatium dasycarpum							R
10	Apiaceae Lomatium sp.		U	R				R
11	Apiaceae Lomatium utriculatum			R			U	R
12	Apiaceae Perideridia californica			R				
13	Apiaceae Sanicula crassicaulis						R	
14	Apiaceae Sanicula sp.		R					
15	Apiaceae Sanicula tuberosa						R	R
16	Asclepiadaceae Asclepias sp.			U				
17	Asteraceae Achillea millefolium		R				R	R
18	Asteraceae Agoseris grandiflora						R	
19	Asteraceae Agoseris sp.		R					
20	Asteraceae Anaphalis margaritacea		R					
21	Asteraceae Asteraceae sp.		R	U				
22	Asteraceae Asteraceae sp. (yellow)			R				
23	Asteraceae Baccharis pilularis		U	U				
24	Asteraceae Baccharis salicifolia	U	R		U		U	U
25	Asteraceae Carduus tenuiflorus		U					
26	Asteraceae Centaurea melitensis						R	R
27	Asteraceae Centaurea solstitialis		U	U		R		R
28	Asteraceae Chaenactis glabriuscula		R				C	U
29	Asteraceae Cirsium occidentale		R	U	R		R	R
30	Asteraceae Cirsium sp.		U	R				
31	Asteraceae Cirsium vulgare		R	R				
32	Asteraceae Erigeron foliosus		U					

33	Asteraceae Erigeron foliosus var.foliosus							R
34	Asteraceae Erigeron petrophilus		U					
35	Asteraceae Eriophyllum confertiflorum		U	U	U		R	R
36	Asteraceae Eriophyllum lanatum			R				
37	Asteraceae Eriophyllum multicaule							R
38	Asteraceae Eriophyllum sp.		U					
39	Asteraceae Euthamia occidentalis		R					
40	Asteraceae Gnaphalium bicolor						R	
41	Asteraceae Gnaphalium californicum						R	R
42	Asteraceae Hemizonia lobbii		U					
43	Asteraceae Heterotheca sessiliflora		U					
44	Asteraceae Hypochaeris glabra						R	
45	Asteraceae Hypochaeris radicata						U	R
46	Asteraceae Lasthenia californica	R	U	C			U	U
47	Asteraceae Layia hieracioides		R					
48	Asteraceae Lessingia tenuis				U			
49	Asteraceae Madia sp.		R					
50	Asteraceae Malacothrix californica						R	
51	Asteraceae Microseris douglasii						R	
52	Asteraceae Packera breweri						R	
53	Asteraceae Pectis papposa		R					
54	Asteraceae Senecio flaccidus		R					
55	Asteraceae Senecio sp.		U					
56	Asteraceae Stephanomeria virgata ssp.pleurocarpa			R				
57	Asteraceae Wyethia helenioides	R					U	U
58	Asteraceae Wyethia sp.				R			
59	Boraginaceae Amsinckia menziesii	U			R	R	U	U
60	Boraginaceae Amsinckia menziesii var.menziesii		U	U	R		R	
61	Boraginaceae Amsinckia sp.					U		
62	Boraginaceae Cryptantha sp.	U	C	U	R			R
63	Boraginaceae Emmenanthe penduliflora			R	U			
64	Boraginaceae Eriodictyon sp.			R				
65	Boraginaceae Eriodictyon tomentosum	U	C	U	C		U	U
66	Boraginaceae Heliotropium curassavicum		U				U	U
67	Boraginaceae Nemophila menziesii var.integrifolia		U	U				
68	Boraginaceae Nemophila menziesii var.menziesii						R	R
69	Boraginaceae Phacelia brachyloba		U					
70	Boraginaceae Phacelia californica		U					
71	Boraginaceae Phacelia distans		U	U				R
72	Boraginaceae Phacelia imbricata		U	U	U		R	
73	Boraginaceae Phacelia malvifolia			R	U			
74	Boraginaceae Phacelia ramosissima		U	U	R			
75	Boraginaceae Phacelia ramosissima var.ramosissima						R	
76	Boraginaceae Phacelia sp.	U	C	U	U			R
77	Boraginaceae Phacelia sp. (white)	U						
78	Boraginaceae Pholistoma auritum	U	C	C	R			R
79	Boraginaceae Pholistoma auritum var.auritum						U	R
80	Boraginaceae Pholistoma membranaceum			U			R	R
81	Boraginaceae Plagiobothrys canescens						U	
82	Boraginaceae Plagiobothrys nothofulvus			C				
83	Boraginaceae Plagiobothrys sp.		R	U		U		R

84	Brassicaceae Brassica nigra		C	U	U			
85	Brassicaceae Brassicaceae sp.					R		
86	Brassicaceae Cardamine californica			U				
87	Brassicaceae Cardamine californica var.californica			U			R	
88	Brassicaceae Erysimum capitatum var.capitatum						R	
89	Brassicaceae Erysimum sp.		R					
90	Brassicaceae Hirschfeldia incana						C	C
91	Brassicaceae Rorippa nasturtium-aquaticum		U		R			
92	Brassicaceae Thysanocarpus curvipes			C				
93	Brassicaceae Thysanocarpus laciniatus							R
94	Caprifoliaceae Lonicera hispidula			U				
95	Caprifoliaceae Lonicera sp.			U				R
96	Caprifoliaceae Lonicera subspicata var.denudata						R	
97	Caprifoliaceae Sambucus mexicana						R	U
98	Chenopodiaceae Chenopodium californicum						R	
99	Convolvulaceae Calystegia collina						R	U
100	Convolvulaceae Calystegia collina ssp.venusta						R	
101	Convolvulaceae Calystegia purpurata							R
102	Convolvulaceae Calystegia sp.			R				
103	Convolvulaceae Calystegia subacaulis	R	U					
104	Convolvulaceae Convolvulus arvensis						R	
105	Crassulaceae Dudleya cymosa		R	R	R			
106	Crassulaceae Dudleya sp.		R					
107	Crassulaceae Sedum spathulifolium		R					
108	Cuscutaceae Cuscuta californica		R					
109	Ericaceae Arctostaphylos pungens			C			U	
110	Ericaceae Arctostaphylos sp.			R		U		
111	Euphorbiaceae Euphorbia sp.			R				
112	Fabaceae Glycyrrhiza lepidota		R					
113	Fabaceae Lotus humistratus/wragelianus						R	
114	Fabaceae Lotus micranthus						R	
115	Fabaceae Lotus purshianus		U				R	
116	Fabaceae Lotus scoparius	U	C	C				
117	Fabaceae Lotus scoparius var.scoparius						C	U
118	Fabaceae Lotus sp.		U	U	R			
119	Fabaceae Lotus wrangelianus			U				
120	Fabaceae Lupinus albifrons	R	U	U			R	U
121	Fabaceae Lupinus albifrons var.albifrons						U	U
122	Fabaceae Lupinus bicolor		R					
123	Fabaceae Lupinus concinnus						R	
124	Fabaceae Lupinus microcarpus var.densiflorus						R	
125	Fabaceae Lupinus sp.	R	R	R				
126	Fabaceae Melilotus indicus		R				U	R
127	Fabaceae Trifolium albopurpureum						R	
128	Fabaceae Trifolium depauperatum						R	
129	Fabaceae Trifolium gracilentum var.gracilentum						R	
130	Fabaceae Trifolium microcephalum		R					R
131	Fabaceae Trifolium sp.	U	U	R				
132	Fabaceae Trifolium willdenovii			U			R	R
133	Fabaceae Vicia sp.			R				
134	Fabaceae Vicia villosa		U	R			U	U

135	Fagaceae Quercus agrifolia						R	R
136	Fagaceae Quercus agrifolia var. agrifolia						U	U
137	Fagaceae Quercus douglasii						R	R
138	Fagaceae Quercus lobata						R	
139	Fagaceae Quercus sp.	U	R	R			R	R
140	Fumariaceae Dicentra chrysantha		U	R	U			R
141	Fumariaceae Dicentra sp.			U				
142	Geraniaceae Erodium botrys						R	R
143	Geraniaceae Erodium brachycarpum						U	U
144	Geraniaceae Erodium cicutarium			R			U	U
145	Geraniaceae Erodium sp.		R					
146	Hippocastanaceae Aesculus californica		R	R			R	
147	Lamiaceae Lamium amplexicaule							R
148	Lamiaceae Lepechinia calycina		U	U	R		R	U
149	Lamiaceae Marrubium vulgare						U	U
150	Lamiaceae Mentha spicata		U					
151	Lamiaceae Mentha suaveolens		U					
152	Lamiaceae Monardella lanceolata		R					
153	Lamiaceae Monardella sp.			R				
154	Lamiaceae Monardella villosa		R				R	R
155	Lamiaceae Salvia columbariae						R	
156	Lamiaceae Salvia mellifera	R	U	U	U		U	R
157	Lamiaceae Stachys bullata		U	R	U		R	U
158	Lamiaceae Trichostema lanatum	R	U	U	R		R	R
159	Lamiaceae Trichostema lanceolatum	R	U					R
160	Liliaceae Bloomeria crocea		U	U			U	
161	Liliaceae Brodiaea sp.		R					
162	Liliaceae Brodiaea terrestris		R	U			R	R
163	Liliaceae Calochortus venustus		U	U	U		U	U
164	Liliaceae Dichelostemma capitatum		U				R	U
165	Liliaceae Tritoleia hyacinthina		R					
166	Liliaceae Tritoleia lugens		R	U				U
167	Liliaceae Zigadenus fremontii		R	R				
168	Liliaceae Zigadenus venenosus							R
169	Malvaceae Eremalche parryi				U			
170	Malvaceae Malacothamnus aboriginum		U	U			U	U
171	Oleaceae Fraxinus dipetala		R				R	
172	Onagraceae Camissonia sp.	R	U	R	R			R
173	Onagraceae Clarkia affinis		R				R	
174	Onagraceae Clarkia cylindrica		R	R				R
175	Onagraceae Clarkia modesta		R	R	R		R	
176	Onagraceae Clarkia purpurea	R	U	U	U		C	U
177	Onagraceae Clarkia similis		R					
178	Onagraceae Clarkia sp.	U	U	U	U			
179	Onagraceae Clarkia speciosa						R	R
180	Onagraceae Clarkia unguiculata		C	C	U		C	C
181	Onagraceae Epilobium canum			R				
182	Orobanchaceae Castilleja affinis			R			R	
183	Orobanchaceae Castilleja exserta		R	R			R	
184	Orobanchaceae Castilleja sp.		R	R				
185	Orobanchaceae Pedicularis densiflora						R	

186	Orobanchaceae Pedicularis sp.			R				
187	Orobanchaceae Triphysaria pusilla						R	
188	Papaveraceae Dendromecon rigida		U	R	R		R	
189	Papaveraceae Eschscholzia californica	U	C	U	C	R	C	C
190	Papaveraceae Eschscholzia sp.					R		
191	Papaveraceae Meconella linearis		R					
192	Papaveraceae Platystemon sp.			R				
193	Phrymaceae Mimulus aurantiacus	R	C	R	C		U	R
194	Phrymaceae Mimulus guttatus				R		U	R
195	Phrymaceae Mimulus pilosus		U					
196	Phrymaceae Mimulus sp.		R	R				
197	Pinaceae Pinus sabiniana						R	R
198	Plantaginaceae Antirrhinum multiflorum		U	R				
199	Plantaginaceae Antirrhinum sp.			R	R			
200	Plantaginaceae Collinsia heterophylla	U	C	C	U		R	U
201	Plantaginaceae Collinsia parviflora		U					
202	Plantaginaceae Keckiella breviflora		U	U				
203	Plantaginaceae Penstemon centranthifolius		U	R			U	U
204	Plantaginaceae Penstemon heterophyllus		R	U			U	U
205	Plantaginaceae Plantago erecta						R	
206	Plantaginaceae Veronica anagallis-aquatica		U				R	
207	Polemoniaceae Gilia achilleifolia			U				
208	Polemoniaceae Gilia angelensis		U					
209	Polemoniaceae Gilia capitata	R	R				R	
210	Polemoniaceae Gilia sp.		R	U				
211	Polemoniaceae Linanthus parviflorus						R	
212	Polemoniaceae Linanthus sp.		R	R				R
213	Polemoniaceae Navarretia hamata							U
214	Polemoniaceae Navarretia sp.			R				
215	Polygonaceae Chorizanthe douglasii	R	U		C		U	U
216	Polygonaceae Eriogonum elongatum		U					
217	Polygonaceae Eriogonum fasciculatum	U	C	C	U		R	
218	Polygonaceae Eriogonum fasciculatum var.foliolosum						C	C
219	Polygonaceae Eriogonum gracile		R					
220	Polygonaceae Eriogonum nortonii		R				R	
221	Polygonaceae Eriogonum sp.			U				
222	Polygonaceae Eriogonum vimineum		U					
223	Polygonaceae Polygonum punctatum		R					
224	Polygonaceae Polygonum sp.				U			
225	Portulacaceae Claytonia perfoliata		R	U			U	R
226	Portulacaceae Montia fontana		R					
227	Primulaceae Anagallis arvensis			R				R
228	Primulaceae Dodecatheon clevelandii							R
229	Primulaceae Dodecatheon clevelandii ssp.patulum						R	
230	Primulaceae Dodecatheon sp.		R					
231	Ranunculaceae Clematis lasiantha		R				R	R
232	Ranunculaceae Clematis sp.		R					
233	Ranunculaceae Delphinium hesperium							R
234	Ranunculaceae Delphinium hesperium ssp.pallescent						R	
235	Ranunculaceae Delphinium parryi						R	R
236	Ranunculaceae Delphinium parryi/patens						R	

237	Ranunculaceae Delphinium sp.		U	R	R			
238	Ranunculaceae Ranunculus californicus		R	U			C	U
239	Rhamnaceae Ceanothus cuneatus		R	C	U		U	
240	Rhamnaceae Ceanothus cuneatus var.cuneatus						U	U
241	Rhamnaceae Ceanothus sp.			R		R		
242	Rhamnaceae Rhamnus ilicifolia		R	U	C		R	R
243	Rhamnaceae Rhamnus sp.						R	
244	Rosaceae Adenostoma fasciculatum	U	U	C	R		C	C
245	Rosaceae Cercocarpus betuloides		R				R	R
246	Rosaceae Drymocallis glandulosa							R
247	Rosaceae Heteromeles arbutifolia		U				R	
248	Rosaceae Prunus ilicifolia		U	R	C		R	
249	Rosaceae Rosa californica		R				U	R
250	Rosaceae Rubus parviflorus				R			
251	Rosaceae Rubus sp.		R					
252	Rosaceae Rubus ursinus		U					
253	Rubiaceae Galium sp.		R					
254	Salicaceae Salix exigua						U	U
255	Salicaceae Salix laevigata						U	R
256	Salicaceae Salix lasiolepis						U	U
257	Salicaceae Salix sp.		U	C				
258	Saxifragaceae Lithophragma affine			R				
259	Saxifragaceae Saxifraga californica			U				
260	Scrophulariaceae Scrophularia californica		R		R			
261	Solanaceae Solanaceae sp.					R		
262	Solanaceae Solanum umbelliferum		U	R			U	U
263	Valerianaceae Plectritis ciliosa							R
264	Valerianaceae Plectritis macrocera			U			U	
265	Valerianaceae Plectritis sp.		R	U				
266	Verbenaceae Verbena lasiostachys var.scabrida						R	R
267	Verbenaceae Verbena sp.							R
268	Violaceae Viola pedunculata		R	U			U	U
	<b>Count of unique floral taxa on which bees were collected in each of seven years of Pinnacles study:</b>	<b>30</b>	<b>142</b>	<b>115</b>	<b>49</b>	<b>11</b>	<b>128</b>	<b>102</b>

## CHAPTER 3

NOVEL, WIDESPREAD USE OF HONEYDEW SUGARS AMONG  
A DIVERSE COMMUNITY OF SOLITARY BEES

## ABSTRACT

Bees are known to respond to visual cues, using floral colors and petal markings to locate nectar sources, but non-visual foraging is less well understood. Wild bees were observed visiting inconspicuous, pre-bloom *Adenostoma fasciculatum* shrubs across the Mediterranean landscapes of California's Pinnacles National Park. Many of these woody shrubs were covered with a 'sooty mold,' fueled by honeydew secretions of scale insects (Hemiptera: Coccoidea). While honeydew has been recorded as a resource visited by disparate social bees, knowledge of honeydew use by solitary bees or at a community-wide scale is lacking. We designed an experiment to evaluate the mechanism of attraction to this non-advertised resource, and to identify the bees involved. Collection results revealed that there is high bee visitation to moldy plants, but only in the presence of live scale insects, and that black paint, as a mold-like visual cue, did not enhance highly significant visitation to experimental honeydew-mimic sugars. The widespread ability of bees to locate unadvertised honeydew-mimic sugars suggests the existence of stochastic and socially-mediated foraging behaviors among a community of solitary bees that begs further study. Ongoing evaluations of functional-trait and taxonomic patterns among the particular bees engaging in honeydew foraging may have implications in predicting trait resilience to the increasing threat of climate-induced shifts in bloom predictability.

## INTRODUCTION

A variety of insects are known to forage on carbohydrate-rich honeydew excretions from scale insects (Hemiptera: Coccoidea) and aphids (Hemiptera: Aphididae) as a non-floral sugar source, which may be more nutrient-rich than floral nectar in some cases (Batra, 1993). Some insects, particularly ants, cultivate this resource in a mutualistic relationship with honeydew producers, offering protection from predators in exchange for reliable access to honeydew (Blatrix et al., 2009). In turn, access to honeydew as an additional sugar source has been shown to improve the life span and fitness of some forest insects (Zoebelein, 1957). Artificial honeydew is effective in recruiting wasp parasites of non-aphid pests when sprayed on alfalfa crops (Jacob, 1998).

In the 1960s, honeydew was thought to be toxic to some bees (Kirkwood et al., 1960), though its use among honeybees (*Apis mellifera*) has since been broadly recognized (Crane et al., 1984), and experiments have confirmed that the bee genera *Apis* and *Osmia* are able to obtain and digest honeydew sugars in the lab (Konrad et al., 2009). Documentation of honeydew use by other species of bees has been limited to isolated incidences involving social species in either forest or tropical habitats (Crane and Walker, 1985; Santas, 1983). Batra (1993) was among the first to record the behaviors of opportunistic bumble bees foraging on “rare, distant alpine honeydew bonanzas.” A year later, Bishop (1994) wrote about bumble bees visiting aphid honeydew in Russian boreal forests during two weeks in July. Less seasonal activity has been recorded among Malaysian stingless bees foraging year-round on honeydews in the tropics (Koch et al., 2011). Use of honeydew by solitary bees, bees in non-alpine or tropical habitats, or bees



at the community level, however, has never, to our knowledge, been experimentally examined.

Widespread use of honeydew by diverse solitary bees would have interesting implications for behavioral and landscape-scale bee ecology, namely because it would be a departure from the intricate dependence of bee foraging behaviors on floral morphology, a well-studied mutualism that has been widely credited with driving floral trait evolution. Honeydew is a non-volatile sugar source, and occurs independently of flowering resources. Angiosperms' globally elaborate and costly floral displays, however, are thought to serve a central purpose in attracting animal pollinators, of which bees make up about 85% (Ollerton et al., 2011). Support for this idea includes the fact that the floral structure of wind-pollinated plants is usually much more modest and drab than that of plants that rely on biotic pollination (Willmer, 2011), and that larger floral displays have been shown to attract more pollinators and increase the number of flowers visited on a plant (Ohashi and Yahara, 2001). Bees are known to visit colored objects placed in their habitat and to respond to complex visual cues, using petal markings to navigate to nectar sources (Roulston et al., 2007; Willmer, 2011). Their use of visual cues to locate floral resources and ability to learn to recognize floral color, shape, size and patterns to establish constancy and efficiency during foraging flights has been well established, and is suspected of shaping the assembly of flower colors within a plant community (Chittka and Thomson, 2001; de Jager et al., 2011). Research on the floral chemistry and olfactory signal in insect foraging strategies has also been gaining momentum in recent decades (Deisig et al., 2012; Wäckers, 1994; Wright and Schiestl, 2009). The ability of bees to

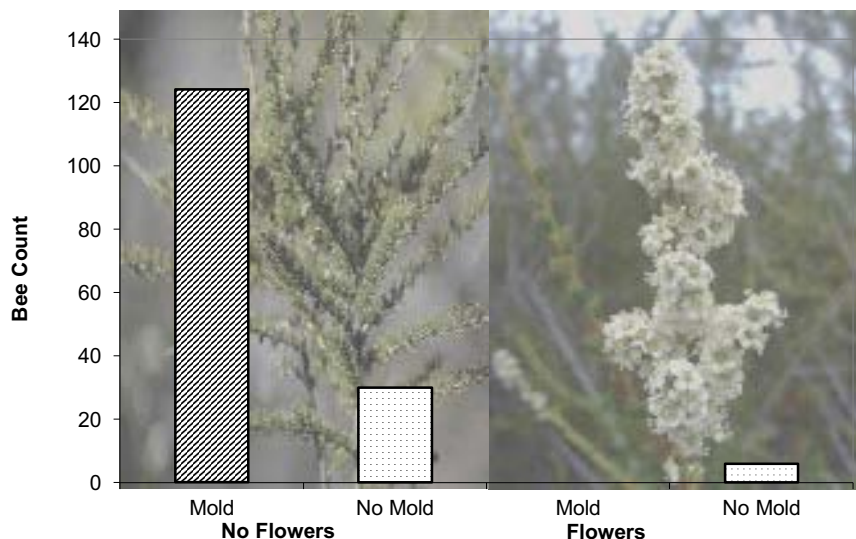
locate non-visually advertised, non-volatile, and non-floral resources, however, has not been thoroughly evaluated.

Working in the rich Mediterranean habitats of Pinnacles National Park in the Inner South Coast Range of California, we observed a diverse array of native, solitary bee species visiting pre-bloom *Adenostoma fasciculatum* shrubs during the early spring when floral resources are still very limited. Upon closer examination, we discovered many of these shrubs to be covered in a dark ‘sooty mold,’ known to grow on the honeydew excretions of colonized scale insects (Hemiptera:Coccoidea) (Crane and Walker, 1985; Santas, 1983). The unusual and abundant bee activity around these non-flowering shrubs prompted us to perform an experiment to evaluate three primary questions: 1) what are these bees finding at this otherwise inconspicuous shrub? (Are they interested in the honeydew residues, their scale-insect providers, or perhaps the mold itself?), 2) what is the role of potential visual, olfactory, or insect-insect cues in alerting bees to this resource?, and 3) which members of the native bee community are involved?

## MATERIALS & METHODS

### Pilot Study

Initial observations and collections were made in the spring of 2011 at Pinnacles National Park, California. While conducting routine plot sampling for another project tracking bee community phenology, we noted high bee activity on pre-bloom *Adenostoma fasciculatum* in Pinnacles' McCabe Canyon field sites, particularly those covered in a sooty mold thought to grow on the honeydew secretions of scale insects. By keeping track of bee collections on pre-bloom plants with or without sooty mold, we confirmed that, during the entire 2011 season at all plot sampling locations, many more bees were collected on pre-bloom *Adenostoma fasciculatum* shrubs with sooty mold than without it, even when compared with the same plants in flower (Fig. 3-1).



**Figure 3-1:** Bee counts from 2011 sampling of bees active on *Adenostoma fasciculatum* with and without flowers and with and without sooty mold. Numbers represent collections from all areas in the park and across the entire sampling season (Feb – June), during routine plot-based collections for another project, and are shown here to illustrate the incentive for the 2012 experimental investigation.

## **Experimental Design**

To explain the behavior of bees visiting these pre-bloom *Adenostoma fasciculatum* shrubs, we designed an experimental evaluation to tease apart the source and possible mechanisms of attraction. We located three experimental sites, each approximately a hectare in size, within Pinnacles National Park in San Benito County, California. Each site was dominated by the large, hardy, allelopathic *A. fasciculatum* shrubs and included several shrubs with obvious presence of scale insects and ‘sooty mold.’ We applied seven treatments, outlined below, to three woody shrubs of pre-bloom *A. fasciculatum* at each of the three sites, for a total of 63 experimental shrubs.

To examine whether the presence of scale insects was necessary for attracting bees to these non-flowering shrubs, we selected six shrubs at each site that were visibly coated on more than 50% of their branches by sooty mold, which grows on the honeydew excretions of scale insects (Crane and Walker, 1985; Santas, 1983). These moldy plants were tagged and randomly assigned to one of two treatments: 1) ‘natural mold’ which served as our control (sprayed only with 5 ounces of water) to provide data on normal visitation to these plants, or 2) ‘natural mold’ + insecticide, which were naturally occurring moldy plants to which 5 ounces of a natural, short-residual insecticide (*Orange Guard*) was applied at least one hour before each sampling event to remove the influence of live scale insects but leave sugars and mold intact (**Table 3-1**).

To differentiate between the attraction of the dark color of the mold, the mold itself, or simply the honeydew sugars to bees attending naturally moldy plants, we selected fifteen non-moldy shrubs of similar stature at each of the three sites and randomly assigned them to one of five remaining experimental treatments (**Table 3-1**).

To test the attraction of the natural honeydew as an isolated resource, we applied 5 ounces of a sugar spray of 20% equal mixture of chemical-grade Fructose and Sucrose similar to the formula used for laboratory research on insect honeydew (pers. comm. F. Waackers) to three shrubs at each site. At three other plants per site, a 5-ounce application of non-toxic black paint, sufficient to darken the appearance of the shrubs' branches, served as both a test of the darkened visual cue of mold, and as an evaluation of whether potentially increased surface temperatures of darkened branches might be attractive to bees in accordance with an established preference among bumble bees for warmer flowers during foraging bouts (Whitney et al., 2008). Three additional shrubs at each site were sprayed with both the sugar solution and the black paint mixture in order to simulate the complete attraction of natural mold, and examine interaction effects. To serve as controls for the possible influence of the *Orange Guard* insecticide applied to moldy shrubs in the 'natural mold + insecticide' treatments outlined above, three non-moldy shrubs at each site were sprayed with 5 ounces of *Orange Guard* at least an hour prior to all sampling events. Finally, we selected three shrubs at each site to serve as a baseline control for quantifying any normal, stochastic bee visitation to random plants in the environment. These control plants received a 5-ounce spray application of water before sampling events. In total, we had nine shrub replicates, three at each of three sites, for each of our seven experimental treatments (**Table 3-1**).

**Table 3-1:** Seven experimental treatments, outlined with plant condition and treatment spray used. Each treatment was replicated with three plants at three different sites, for a total of nine plants per treatment and sixty-three plants total.

Treatment Description	Condition of <i>A. fasciculatum</i>	Treatment Spray received
Natural Mold	Moldy	5ml distilled water
Natural Mold + Insecticide	Moldy	5ml Orange Guard® short-residual insecticide
Control	Not Moldy	5ml distilled water
Insecticide	Not Moldy	5ml Orange Guard® short-residual insecticide
Black Paint	Not Moldy	5ml non-toxic black paint
Sugar	Not Moldy	5ml 20% Chem-grade Fructose:Sucrose
Black Paint + Sugar	Not Moldy	5ml non-toxic black paint + 5ml 20% Chem-grade Fructose:Sucrose

### **Sampling Protocol**

All experimental collections took place during March and April, the period at Pinnacles National Park after which native bee activity has begun, but prior to peak bloom of the surrounding plant community. Sampling was conducted on sunny days over sixty degrees (F), to ensure adequate bee activity, at one of the three sites per week. Each site was visited three times, approximately once every three weeks over the nine-week study period. All plants were refreshed with their randomly assigned treatment spray, which remained the same throughout the experiment, at 9am on each sampling day. After waiting an hour for the effect of the insecticide to take place and for bee activity to approach peak levels for the day, a randomly ordered plant list was divided between two collectors, who spent five minutes sequentially netting all bees visiting each respective plant. Temperature, wind speed, humidity, barometric pressure, and an estimate of cloud cover were recorded every thirty minutes during sampling. This whole sampling procedure was conducted once in the morning, beginning around 10am, and once in the afternoon, around 1pm, to capture the full daily bee community. On sampling days, all

flowering species in bloom within the site, approximately a hectare in size, were listed to provide an estimate of floral richness and seasonal bloom progression. An infrared thermometer was used to record surface temperatures of three different external branches of each plant at noon on sampling days to test for effects of potentially warmer, darker plants.

### **Specimen Processing & Data Management**

All bees were labeled and pinned into field boxes each evening, then frozen for 48 hours to protect from insect infestations, and transported to Utah where they were identified to species by experts at the USDA-ARS Pollinating Insect Research Unit (“Logan Bee Lab”). Bee identifications were completed using high quality ‘Leica’ dissecting microscopes, one of the best collections of reference specimens in the world (the Logan Bee Lab houses approximately 2 million curated bee specimens), and a variety of generic and specific taxonomic keys. Bees were assigned individual barcode numbers, printed on labels affixed to each specimen pin and recorded along with all collection information into a relational database, which was then managed and queried for statistical analyses using Microsoft Access front end software.

### **Statistical Analyses**

Individual sample bee counts produced a zero-inflated negative binomial distribution of response variables, thus nonparametric methods were used to evaluate data. We compared the effect sizes of treatment means in bee abundance, relative to the

control treatment, using Cohen's  $d$  Effect Size (Cohen, 1992). We then employed a generalized linear mixed model to assess significance of differences in bee abundances between treatments, and interactions among them, coding relevant treatments as fixed effects and location and temporal variables as random effects. Statistical analyses were performed at the  $p < 0.05$  significance level using the R-Cran statistical package (R Development Core Team 2014 version 3.1.1; package "sciplot" version 1.1-0; package "lme4" version 1.1-7) (R Core Development Team 2014 version 3.1.1; package "vegan" version 2.2-1; package "lmer" version 1.1-7).



## RESULTS

### **Bee Collection**

Over three sampling days at each of three experimental sites, the 63 shrubs included in the experiment were each sampled six times for a total of 54 replicates per treatment in 378 plant samples. In total, 308 bees were collected on treated *Adenostoma fasciculatum* plants, representing 9 Genera and 56 species. The ratio of female to male bees overall was 3:1. Images of bees foraging on non-flowering *A. fasciculatum* shrubs are included below (**Fig. 3-2**). Several dozen wasps and flies were also collected during sampling, but were not included in analyses. The vast majority of bee specimens were collected on the two sprayed sugar treatments (*Sugar* N=119, and *Sugar + Paint*, N=101). Shrubs with naturally-occurring mold attracted more bees (N=41), than any of the four treatments not anticipated to be attractive to bees (*Control*, N=11; *Insecticide*, N=17; *Mold + Insecticide*, N=12; and *Black Paint*, N=7). **Table 3-2** gives a full faunal list, with taxonomic determinations, ordered by species abundance on treatment groups.



Photo Credit (above): Paul Johnson, Pinnacles National Park



**Figure 3-2:** *Andrena* sp. (top, and bottom left and center) foraging on a non-flowering *Adenostoma fasciculatum* shrub (right) sprayed with sugar treatment.

**Table 3-2:** Faunal list and specimens count of bees collected on experimental treatments over the duration of the study. Ordered by abundance in treatment groups (Mold, Sugar, then Other (all ‘Other’ treatments were not significantly distinguishable from control)).

<i>Genus</i>	<i>Subgenus</i>	<i>Species</i>	# Bees on Mold (1 Treatment)	# Bees on Sugar (2 Treatments)	# Bees on Other (4 Treatments)
<i>Andrena</i>	( <i>Derandrena</i> )	<i>n. sp.</i>	10	33	20
<i>Lasioglossum</i>	( <i>Evylaeus</i> )	<i>nigrescens</i>	5	15	1
<i>Lasioglossum</i>	( <i>Dialictus</i> )	<i>nevadense</i>	4	16	2
<i>Andrena</i>	( <i>Micrandrena</i> )	<i>chlorogaster</i>	4	9	3
<i>Lasioglossum</i>	( <i>Dialictus</i> )	<i>punctatoventre</i>	3	14	2
<i>Andrena</i>		<i>sp. 1</i>	3	4	
<i>Panurginus</i>		<i>gracilis</i>	3	1	
<i>Hylaeus</i>	( <i>Paraprosopis</i> )	<i>nevadensis</i>	2	9	
<i>Andrena</i>	( <i>Melandrena</i> )	<i>aff. cerasifolii</i>	1	12	2
<i>Nomada</i>		<i>sp. 2</i>	1	10	
<i>Andrena</i>	( <i>Euandrena</i> )	<i>chlorura</i>	1	7	1
<i>Andrena</i>		<i>sp. 19</i>	1	3	
<i>Lasioglossum</i>	( <i>Evylaeus</i> )	<i>pulveris</i>	1	1	
<i>Andrena</i>	( <i>Thysandrena</i> )	<i>candida</i>	1		
<i>Panurginus</i>		<i>morrisoni</i>	1		
<i>Andrena</i>		<i>sp. 20</i>	1		
<i>Lasioglossum</i>	( <i>Lasioglossum</i> )	<i>sisymbrii</i>		16	1
<i>Hylaeus</i>	( <i>Paraprosopis</i> )	<i>calvus</i>		10	
<i>Lasioglossum</i>	( <i>Evylaeus</i> )	<i>sp. 9</i>		9	
<i>Lasioglossum</i>	( <i>Lasioglossum</i> )	<i>egregium</i>		8	
<i>Lasioglossum</i>	( <i>Evylaeus</i> )	<i>argemonis</i>		5	1
<i>Andrena</i>		<i>sp. 9</i>		5	2
<i>Halictus</i>	( <i>Seladonia</i> )	<i>tripartitus</i>		5	1
<i>Lasioglossum</i>	( <i>Evylaeus</i> )	<i>sp. 9</i>		3	
<i>Halictus</i>	( <i>Nealictus</i> )	<i>farinosus</i>		2	
<i>Hylaeus</i>	( <i>Prosopis</i> )	<i>hinae</i>		2	
<i>Nomada</i>	( <i>Gnathias</i> )	<i>sp. 1</i>		2	
<i>Andrena</i>	( <i>Pelicanandrena</i> )	<i>atypica</i>		1	
<i>Hylaeus</i>	( <i>Hylaeus</i> )	<i>granulatus</i>		1	
<i>Apis</i>		<i>mellifera</i>		1	2
<i>Lasioglossum</i>	( <i>Evylaeus</i> )	<i>robustum</i>		1	
<i>Halictus</i>	( <i>Protohalictus</i> )	<i>rubicundus</i>		1	
<i>Andrena</i>	( <i>Melandrena</i> )	<i>sola</i>		1	
<i>Lasioglossum</i>	( <i>Evylaeus</i> )	<i>sp. 1</i>		1	
<i>Andrena</i>		<i>sp. 11</i>		1	
<i>Andrena</i>		<i>sp. 18</i>		1	
<i>Andrena</i>		<i>sp. 21</i>		1	
<i>Andrena</i>		<i>sp. 22</i>		1	
<i>Andrena</i>		<i>sp. 23</i>		1	
<i>Andrena</i>		<i>sp. 24</i>		1	1
<i>Andrena</i>		<i>sp. 25</i>		1	
<i>Andrena</i>		<i>sp. 6</i>		1	
<i>Sphecodes</i>		<i>sp. A</i>		1	
<i>Lasioglossum</i>	( <i>Evylaeus</i> )	<i>sp. A</i>		1	
<i>Sphecodes</i>		<i>sp. B</i>		1	
<i>Hylaeus</i>	( <i>Hylaeus</i> )	<i>verticalis</i>		1	
<i>Protosmia</i>	( <i>Chelostomopsis</i> )	<i>rubifloris</i>			2
<i>Andrena</i>		<i>sp. 17</i>			2
<i>Andrena</i>	( <i>Derandrena</i> )	<i>californiensis</i>			1
<i>Nomada</i>		<i>sp. 3</i>			1
<i>Andrena</i>	( <i>Thysandrena</i> )	<i>w-scripta</i>			1

### **Bee Visitation to Experimental Treatments**

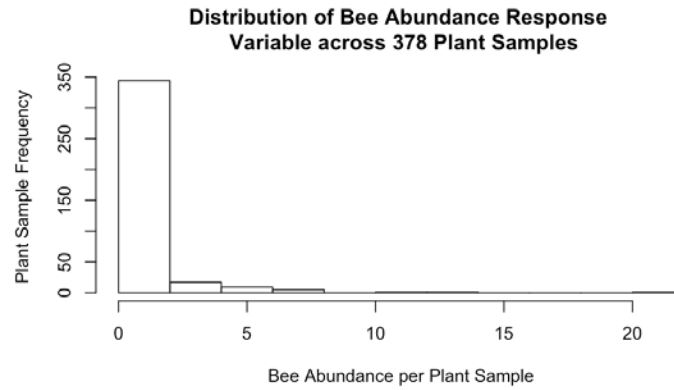
Bee counts at individual plant sampling events included many zeros, ones and twos, and a few values over ten (on sugar treatments), resulting in a zero-inflated negative binomial distribution of the response variable (**Fig. 3-3**). Nonparametric options for analysis of treatment means in bee visitation were complicated by very high daily variation in bee activity across sites and weeks of the study, an expected complication of such a spatiotemporally variable group as bees (Williams et al., 2001). To visualize differences between treatment means relative to the control we calculated Cohen's  $d$  Effect Size, a statistic thought to be minimally sensitive to non-normal distributions:

$$d = (M_{\text{treatment}} - M_{\text{control}}) / \sigma$$

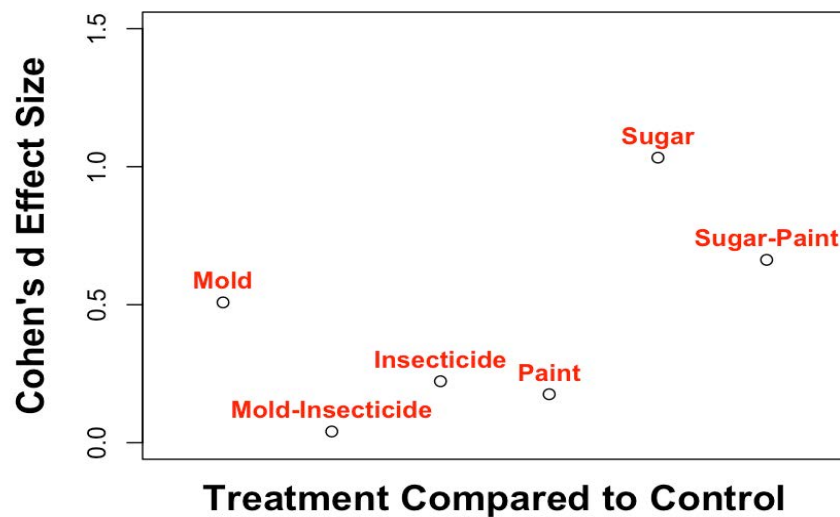
where

$$\sigma = (\sigma_{\text{treatment}} + \sigma_{\text{control}}) / 2.$$

Cohen (1992) provided suggested thresholds for interpretation, wherein an effect size over 0.8 signifies a large effect of that treatment relative to the control, 0.5 signifies a medium effect, and 0.2 constitutes a small effect (Cohen, 1992). Using Cohen's thresholds, the effect of *Sugar* treatment on bee visitation was large ( $d=1.03$ ), while the *Sugar + Black Paint* treatment ( $d=0.66$ ) had a medium-high effect on bee visitation (**Fig. 3-4**). The *Mold* treatment ( $d=0.51$ ) had a medium effect size of increased bee visitation over background control levels. Treatments not expected to increase bee visitation all had small effect sizes in terms of the mean number of bees they each attracted over the course of the experiment: *Insecticide* ( $d=0.22$ ), *Mold + Insecticide* ( $d=0.04$ ), and *Black Paint* ( $d=0.18$ ).



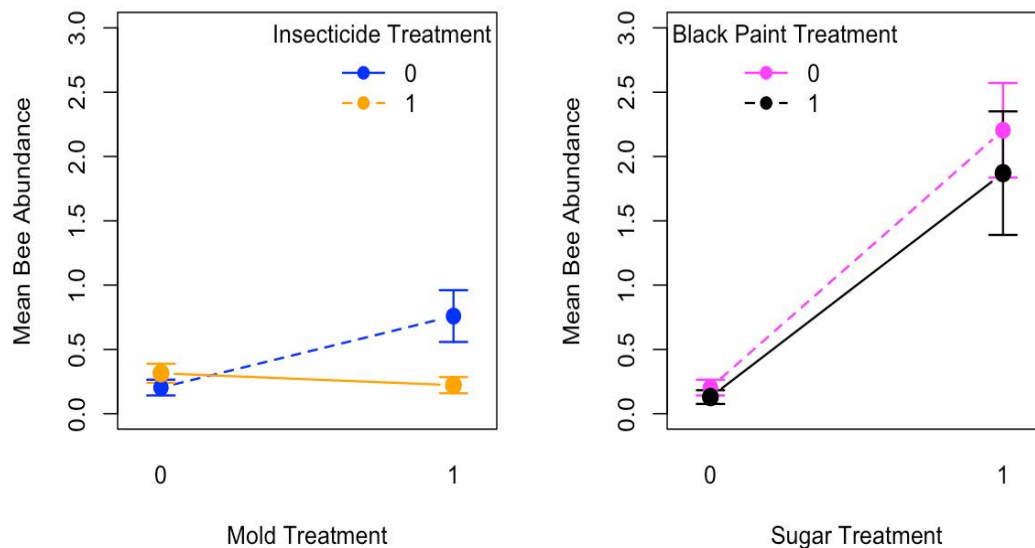
**Figure 3-3:** Negative binomial distribution of response variable: bee count data at treatment plants over 378 samples.



**Figure 3-4:** Cohen's d effect size of each experimental treatment (labeled in red) calculated as the standardized mean difference from the control (Becker, 1998). Cohen considered an effect size of 0.2 to be "small," of 0.5 to be "medium," and of 0.8 to be "large." The effect of *Sugar* and *Sugar-Paint* treatments are 'large,' and the effect size of the *Mold* treatment is 'medium' (Cohen, 1992; Nakagawa and Cuthill, 2007).

To further test for treatment significance and interactions on bee visitation while controlling for influences from abiotic variables, we also built a general linear mixed effects model with a negative binomial distribution in R, and performed a step-wise AIC

model selection procedure. The best-fit model included the treatments of primary interest (*Mold*, *Mold + Insecticide*, *Sugar*, and *Sugar + Paint*) as fixed effects, and the plant ID within the site (categorical), as well as the time of day within each sampling day (continuous) as random effects. Bee visitation to pre-bloom *Adenostoma fasciculatum* plants was significantly higher on plants with natural mold ( $p=0.019$ ) as well as on plants with sprayed sugar ( $p<0.001$ ) than on control plants. Bee visitation was not higher than controls to plants with Insecticide ( $p=0.38$ ) and plants with only black paint ( $p=0.39$ ). There was a significant interaction between the Mold and Insecticide treatments ( $p=0.03$ ), but not between the Sugar and Paint treatments ( $p=0.84$ ) (**Fig. 3-5**).



**Figure 3-5:** Two-way interactions of average sample bee abundance on *Mold* vs *Insecticide* Treatments (left) and *Sugar* vs *Black Paint* Treatments (right), with 95% se confidence intervals around points for each treatment combination. Treatment application to specified plants is represented by a “1” on x-axes and solid lines, while the absence of that treatment is shown by a “0” on x-axes and dotted lines, with the control treatments represented at 0,0. A negative binomial mixed model found *Mold* and *Sugar* to attract significantly more bees per sample than the *Insecticide*, *Paint*, or *Control* treatments, and significant interactions of *Mold & Insecticide*, but not of *Sugar & Black Paint*.

### **Environmental, Seasonal & Temperature Significance**

Floral richness increased linearly across the season and evenly across 1-hectare experimental sites as expected, from zero to thirteen species recorded in bloom during sampling, confirming the environmental context of the experiment as the period between beginning and peak-season bloom. Likewise, though somewhat less linearly, total bee specimens collected increased over the nine-week duration of the study, from the first sampling round (N=85), through some more variable weather over the second sampling period (N=77), to approaching peak bee activity during the third and final sampling round (N=146) of all three sites. Bee abundance differed between sites somewhat, with bee activity at sites C (N=125) and B (N=115) consistently higher than bee activity at site A (N=68). Treatment effects, however, remained significant with temporal and site variables included in the model. Similarly, none of the environmental variables recorded (e.g. cloud cover, ambient temperature, wind speed, humidity) influenced the significance of treatment results. Infrared thermometer temperature readings from plant branches did not differ between treatments and thus were not considered as a variable influencing bee visitation.

## DISCUSSION

Our finding that nearly fifty species of native, solitary bees are able to locate non-floral, non-volatile, non-visually advertised sugars within a few hours after application to inconspicuous shrubs is an interesting and understudied behavior, especially in the context of the costly and elaborate floral displays largely regarded as a fundamental strategy among angiosperms to attract visually-oriented pollinators. Additionally, current knowledge about the role of olfaction in insect foraging does not explain our result that a diverse community of bees were quickly and abundantly able to find non-volatile, simple sugars sprayed on plants without honeydew producers present (Tapia et al., 2010; Wright and Schiestl, 2009). Other research that has delved into non-visual flight patterns of bees has so far focused on such ideas as the use of magnetic fields in navigation (Chittka et al., 1999), and has included little discussion of other mechanisms by which bees may locate resources. While floral nectar is likely the primary source of sugar for bees in most habitats, the fact that bees are not dependent on floral displays to locate similar, non-volatile sugars, and can be found visiting non-floral sugars in high abundances is an interesting complication in the perception of bee-plant mutualisms as being tightly coupled relationships.

While our small experiment suggests that bees can locate non-advertised sugars, the responses (or lack thereof) to the other treatments also introduce intrigue into this novel community-wide behavior. The lack of any interaction between the *Sugar* and the *Sugar + Black Paint* treatments suggests that bees are not relying on any learned association between the visual cue of the darkened sooty mold and the honeydew reward. On the other hand, the significant interaction between the mold and insecticide treatment,



in which moldy plants were significantly more attractive to bees than the control, but only without the application of the insecticide targeted at scale insects, suggests that the presence of live honeydew-producing insects is appealing to bees, rather than simply the residual sugars on branches or other nutrients gleaned from the mold itself. Whether this reflects a limited ability of bees to detect or collect dried sugar, or potentially the existence of a bee-scale relationship is unclear, but worth further investigation. While the greater attraction of bees to the sugar spray suggests that the mold itself was not a main attractant for bees, ants mutualistic with honeydew-producers for sugars have been shown to collect and even cultivate fungus, and *Trigona spp.* bees have been documented collecting mold ‘in lieu of pollen’ (Eltz et al., 2002). Thus, further evaluation of the possible use of the sooty mold by bees may be also be fruitful. The lack of any significant effect of the insecticide itself compared to control plants confirms that it was effective in killing scale insects and removing the attraction of their live presence to bees, but that it did not deter bee visitation equivalent to that at control plants.

We propose that the rapid and highly significant increase in bee visitation to plants sprayed with a non-volatile, nectar-like sugar suggests that bee optimal foraging strategies are guided less by visual, floral-related cues than is commonly assumed. Rather, we believe that bee foraging is heavily influenced by a combination of stochastic exploration of resources across a habitat, and a strong reliance on social cues from the activity of other bee foragers, even among solitary bees. While bees did not show evidence of learning to associate the dark color of sooty mold with honeydew resources, bees are known to make repeat foraging trips to a location after discovering an abundant resource, and these return visits could account for the spike in bee visitation to plants

sprayed with honeydew-mimic sugars. If solitary bees are cueing off the activity of conspecifics in their habitat to opportunistically harvest unusual sugar resources, this implies the existence of complex, socially-mediated foraging dynamics within solitary bee communities that may be sensitive to non-random species loss, which may also impact pollination network stability.

Understanding more about the functional traits and relationships of the particular bee species accessing honeydew before peak bloom in this Mediterranean community may shed light on both novel foraging tactics and differential resilience within a bee community to nectar unpredictability. Mediterranean habitats have been identified as both hotspots for diversity, as well as being particularly vulnerable to the effects of climate change, invasions of exotic species, and urbanized habitat degradation (Klausmeyer and Shaw, 2009). In light of recent observations that warming temperatures have induced decoupling shifts in the emergence time of solitary bees in relation to their preferred host plants (Forrest and Thomson, 2011; Inouye, 2008; Robbirt et al., 2014), this may be an opportunity to study early-season bee foraging responses to habitat degradation and climate-induced phenological bloom shifts. For bees that emerge during the early season into a habitat of unexpectedly poor floral resources, the ability to locate alternate sugar sources before pollens become available could be critical to survival and production of offspring for the following season.

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## CHAPTER 4

### SUMMARY

Pinnacles National Park remains one of the most densely diverse areas for native bees studied. Our updated park inventory lists 479 distinct species in 53 genera from seven years of sampling and over 85,000 specimens collected. There were 126 species previously detected in Pinnacles during opportunistic sampling of the late 1990s and 2002 that we did not detect in 2011 or 2012, and 76 species that were new records for the park from our sampling. Whether this lower number of species recorded in 2011-12 compared to previous years signifies a decline in diversity, range shifts over the intervening decade, or simply the very high spatiotemporal variability expected within a rich native bee fauna is difficult to say. The total abundances and standard deviations between plot samples of bee genera, for example, show variation on several orders of magnitude from moderately abundant but ever-present genera to hugely dominant but patchily-distributed genera. This appears to be a stable, if highly dynamic, pattern. Thus, while sifting through the environmental noise of such a speciose and short-lived group remains a challenge, continuing to investigate expected fluctuations for a theoretically thriving native bee community in a semi-pristine ecosystem will be valuable in improving the ability to detect and determine the magnitude of species loss in degraded habitats where a pre-disturbance sample is available. In degraded habitats where no such baseline sample exists, patterns found at Pinnacles National Park could potentially serve as a restoration model for a healthy bee community. Looking at how the structure and dynamics of bee communities in the Mediterranean climate of Pinnacles compare to

thriving bee communities in other biomes would be an interesting exploration of expected variation between and within habitat types in different climates.

Unfortunately, habitat type was not a reliable predictor of easily-assessed native bee metrics. Between the four main habitat types identified for evaluation at Pinnacles National Park (Alluvial, Live Oak Woodland, Blue Oak Woodland, and Grassland) none were consistently or significantly different in native bee abundance or richness over an entire sampling season. Care must be taken to select the appropriate and ecologically relevant statistical methods for evaluating these questions, however, as different methods for measuring richness and controlling for random factors resulted in some disagreement over which habitat type appeared more species-rich for native bees. Regardless, descriptive statistics suggests that, ecologically, habitat type is not a useful guide for predicting the native bee abundance, richness, or evenness in an unsampled location.

Bee species composition, however, did vary significantly with habitat type at Pinnacles National Park. The Alluvial habitat type, which generally occurs at lower elevations, drier microclimates, and ranks low on percent grass cover, had a more unique and more tightly constrained species composition than the Live Oak, Blue Oak, and Grassland habitat types. This difference in bee community may be driven in part by the traits of the dominant bee species in each habitat, which is a solitary specialist in the Alluvial habitat type, and generalists in each of the other three habitat types. The Alluvial habitat type was also found to have a stronger relationship between community similarity and the distance between two plots, supporting the suggestion that Alluvial habitats may be important refugia that retain a more specialized taxon of bees due to abundant ground-nesting resources and preferred flora. Further exploration into this pattern, the

vulnerability and ecosystem role of this specialist species, and the value of the Alluvial habitat type to other bee species is necessary to determine whether Alluvial habitats may warrant conservation priority in the name of native bee conservation, or if similar habitats elsewhere also may serve as limited nesting refugia for more specialized, and therefore potentially more vulnerable, bee communities.

The vulnerability of a bee community to temporal resource fluctuations was experimentally tested during the second year of plot sampling at Pinnacles National Park. Fifty-six different species were found visiting seven treatments designed to test the attractiveness of honeydew sugars and the use of visual cues in locating this resource. Significantly more bees visited shrubs that had a ‘sooty mold’ associated with natural honeydew sugars than visited the control treatment, or similar shrubs after an insecticide removed the effect of live scale insect honeydew producers. No evidence of a visual cue for this behavior was detected, as responses to plants painted with black paint to mimic ‘sooty mold’ did not increase bee visitation to control plants or those sprayed with honeydew-like sugars. This behavior is interesting because it suggests a previously unstudied phenomenon of widespread, stochastic, and socially-influenced foraging strategies among a community of solitary bees, as well as implying some resilience of these groups to climate-induced changes in temporal bloom predictability. Along with spatial insights from the habitat type chapter, this result adds spatiotemporal insight to the biodiversity, community dynamics, and foraging behaviors of a rich native bee fauna in a semi-pristine ecosystem.