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Biodiversity and Foraging Preferences of Bee Communities at Pinnacles National Park Over Time

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BIODIVERSITY AND FORAGING PREFERENCES OF BEE COMMUNITIES AT PINNACLES NATIONAL PARK OVER TIME

by

Abigail M. E. Lehner

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

of

MASTER OF SCIENCE

in

Biology

Approved:

Edward W. Evans, Ph.D. Major Professor	Terry L. Griswold, Ph.D. Committee Member
Shannon Wing Belmont, M.S. Committee Member	D. Richard Cutler, Ph.D. Interim Vice Provost of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2022

ABSTRACT

Biodiversity and foraging preferences of bee communities at Pinnacles National Park over time

by

Abigail M. E. Lehner, Master of Science

Utah State University, 2022

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

Like many other animals, bees are facing biodiversity losses due to habitat loss, pesticide use, and climate change. Despite much research delving into potential losses to bee diversity, long-term pollinator monitoring programs have been implemented in few areas. Moreover, little is known about what factors may be influencing bee species presence, foraging and nesting behaviors. In chapter two, we compare historical and current datasets on bees at Pinnacles National Park in California in order to understand how bee communities in the park have changed over time. We found that overall bee richness hasn't changed much from 2002 to now, but bee community composition has significantly changed. These results point to species turnover, but not biodiversity loss. In chapter three, we discuss issues in current bee monitoring techniques and provide recommendations to combat these issues. We used the small carpenter bee species, *Ceratina sequoiae* Michener, to develop a framework for modeling suitable habitat at Pinnacles using citizen science records. The suitability modeling indicated that considering the required nesting and floral resources for *C. sequoiae* as well as elevation better predicted *C. sequoiae* presence. These techniques could have utility for selecting sites or finding areas that could be of importance to oligolectic bee species, for example. In the fourth chapter, we present a novel foraging behavior observed at Pinnacles National Park during the early part of the sampling season. A variety of bee species were found feeding on aphid-produced pine honeydew, a behavior rarely noted for native bees.

(176 pages)

PUBLIC ABSTRACT

Biodiversity and Foraging Preferences of Bee Communities Over Time at Pinnacles National Park

Abigail Lehner

Bees are considered to be the most important animal pollinator, providing billions of dollars in pollination services each year. Despite their importance in both natural and agricultural settings, the status of most native bees is unknown. Native bees are subject to a variety of threats including habitat loss, pesticide use, and climate change. Yet, monitoring programs have been implemented in few natural areas. Pinnacles National Park, PNP, in California is one of the only natural areas to have a large historical dataset on bees across decades with surveys conducted in 1996, 1997, 1998, 1999, 2002, 2011, and 2012. These surveys have found PNP to house an exceptionally diverse community of bees. To determine how the bee community at PNP has changed over time we returned to survey bees in 2020 and compare the current collection to historical collections. We found that overall diversity levels remained at similar levels across years, but community composition changed among years, suggesting that the bee community experiences species turnover, but has not experienced over diversity losses. Using our bee survey as a framework, we discuss some issues with current bee monitoring practices and recommend creative solutions. To provide better techniques for site selection or monitoring monolectic species habitat we used *Ceratina sequoiae* Michener abundance at PNP, as a framework to model suitable habitat using citizen science records. We selected six topographic factors to model in conjunction with the required floral and nesting resources of *C. sequoiae*. The suitability modeling indicated that considering elevation in addition to the required floral and nesting resources could better predict *C. sequoiae* abundance. Throughout the duration of our bee survey at PNP, we also observed a novel foraging behavior. We discovered tens of bees feeding on aphid-produced pine honeydew, a seemingly rare behavior among native bees. The culmination of our findings highlight the importance of long term pollinator monitoring studies, not only to detect diversity shifts over time, but also to determine the diversity of behaviors exhibited by bees.

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CHAPTER 1

INTRODUCTION

Insect and plant biodiversity is crucial both to maintain natural ecosystems (Cardinale et al., 2012; Hooper et al., 2012; Tilman et al., 2014) and to provide food security (Losey & Vaugh, 2006; Ollerton et al., 2011; Reilly et al., 2020). Approximately 90% of flowering plant species (*Angiospermae*) rely on pollination by animals (Ollerton et al., 2011), including many non-grain crops. Of these animal pollinators, bees (*Anthophila*) are most important (Thapa, 2006).

Bees provide multiple ecosystem services. They prevent soil erosion by maintaining floral populations (Greene et al., 1994; Ingels, 1998), provide food for other animals (Roman-Palacios et al., 2019), promote nutrient cycling (Tilman et al., 2014), and renew water sources (Brockerhoff et al., 2017). Flowering plants have developed complex relationships with their pollinators (Johnson, 2010; Keister et al., 1984; Willmer, 2011). Plants have evolved intricate morphologies to foster bee preferences, and have established highly specialized relationships with pollinators (Johnson, 2010; Keister et al., 1984; Willmer, 2011). There are many bee and plant species that rely almost exclusively on each other (Danforth, 2007). Global populations of pollinators and plants have been declining in parallel, particularly within specialist species (Biesmeijer et al., 2020, Mathiasson & Rehan, 2020). Therefore, conserving both bee biodiversity and abundance plays a key role in habitat maintenance and sustaining complex pollination networks (Mathiasson & Rehan, 2020).

Insects pollinate a considerable amount of the food we eat (Losey & Vaugh, 2006; National Research Council, 2007). Insects, particularly native and managed bees, provide up to $177 billion annually in pollination services to agricultural production globally (Gallai et al., 2009). European honey bees (Apoidea: *Apis mellifera*) were introduced to the United States for agricultural purposes, as they produce honey and wax and are easy to manage (Bohart, 1952; Moritz et al., 2005). The European honey bee became important for agriculture because of its ability to provide pollination services in monocultural areas and on nonnative plants (Bohart, 1952; Calderone, 2012). Without access to plant diversity and natural habitat, native bees alone are not able to fulfill the heavy pollination requirements of monocultural areas (Kremen et al., 2004; Kremen et al., 2002; Paterson et al., 2019). Yet, native bees contribute as much as honey bees to crop pollination in the United States (Reilly et al., 2020). About half of all bee species have been observed to buzz pollinate, a requirement of several crop species such as cranberries or tomatoes, a service the European honey bee cannot provide (Cardinal et al., 2018; Pritchard & Vallejo-Marín, 2020). With continued European honey bee declines in the United States, farms are relying more on native bees for pollination and to provide food security (Rader et al., 2013; Winfree et al., 2007). Moreover, native bees, when present in agricultural areas, increase crop yields regardless of honey bee abundance (Garibaldi et al., 2013). Diverse pollinator communities result in increased fruit yield and seed set in many crops (Bllitzer et al., 2016; Hoehn et al., 2008). In addition to pollinating food crops, managed populations of leaf-cutter bees (Megachilidae: *Megachile rotundata*) pollinate alfalfa, a primary food source for cows (Wilson & Carril, 2016). Without their pollination service there would likely be a significant loss of dairy products (Wilson & Carril, 2016). Native bees may also increase yields of crops that self-pollinate, such as cotton and canola (Ali et al., 2011; Esquival et al., 2020; Stein et al., 2017). Generally, in the United States, crop yield is currently limited by pollinator availability (Reilly et al., 2020) and pollinator declines could directly result in a decline in crop production (Calderone, 2012; Reilly et al., 2020).

Despite their importance in ecosystem maintenance and economic services, the 4,000 native bee species in the United States are frequently overlooked (Kopec & Burd, 2017; Potts et al., 2010; Sanchez-Bayo & Wyckhuys, 2019; Winfree, 2010). While honey bee population declines have been well documented (Genersch, 2010; National Research Council, 2007), the current status of most native bee species is unknown (Kopec & Burd, 2017; Potts et al., 2010; Sanchez-Bayo & Wyckhuys, 2019). It has been suggested that anywhere from 25% to 50% of native bee species may be in decline (Kopec & Burd, 2017; Zattara & Aizen, 2021), and there have been worldwide declines in bee species richness (Zattara & Aizen, 2021). Native bees face declines for a variety of reasons, including habitat loss, agricultural intensification, pesticide use, pathogens, climate change, and trophic mismatch (Goulson et al., 2015; Kerr et al., 2015; Kopec & Burd, 2017; Mathiasson & Rehan, 2020; Potts et al., 2010; Sanchez-Bayo & Wyckhuys, 2019; Wilcove et al., 1998; Winfree, 2010).

Approximately 75% of the terrestrial environment has been intensely altered by humans; more specifically, about 33% of land on Earth is dedicated to livestock and crop production (Díaz et al., 2021). The growing agricultural industries are resulting in devastating losses in biodiversity, including pollinators (Díaz et al., 2021). Native bees are significantly less abundant in monocultures and need wild areas adjacent to crop fields for alternate forage (Kremen et al., 2004; Kremen et al., 2002). Native bees can be highly affected by pesticide use, commonplace in agricultural areas (Goulson et al., 2015; Main et al., 2020). In particular, bumblebee (*Bombus*) learning and memory is degraded by neonicotinoid pesticide use, if they survive the chemicals at all (Hatfield et al., 2021; Stanley et al., 2015). Native bees are significantly less likely to nest underground in areas where there is a higher pesticide concentration (Main et al., 2020). In addition to agricultural intensification and pesticide use, native bees can be harmed by European honey bees, which are frequently found in agricultural areas (Angelella et al., 2021; Paini & Roberts, 2005; Thomson, 2004). The honey bee can pass along harmful pathogens to native bees (Fürst et al., 2014; Murray et al., 2019; Nanetti et al., 2021). Honey bees can also push native bees out of their foraging areas, as native bees are significantly less likely to be found on plants that honey bees are foraging on (Thomson, 2004). Poor agricultural practices are likely one of the largest threats to native bee populations.

Native bees are known to be closely tied to seasonal characteristics, with soil humidity as an important indicator (Danforth et al., 2019). Climate change disrupts seasonal characteristics, with both an overall warming and an increase in extreme climate events. Extreme climate events such as droughts or wildfires negatively impact insect populations (Filazzola et al., 2021). With climate change occurring worldwide, there have been shifts in floral bloom time, causing potential disturbance to native bee foraging and emergence (Fisogni et al., 2020, Forrest & Thomson, 2011; Inouye, 2008; Robbirt et al., 2014). Solitary bee emergence typically overlaps with peak host plant blooms and emergence can be delayed to avoid high mortality rates during drought years (Danforth et al., 2019). However, as most solitary bees only forage as adults for 10-14 days, temporal cues caused by extreme climatic events that trigger emergence could result in trophic mismatch (Danforth et al., 2019). A study conducted in the Rocky Mountains found bee phenology was affected by climatic factors such as early snowmelt (Stemkovski et al., 2020). However, bee phenology was less sensitive to climatic disruptions than floral phenology indicating the potential for a mismatch (Stemkovski et al., 2020). An example of this phenomenon was previously observed in California in the 1950s when heavy rainfall in the late summer resulted in a fall emergence of *Hesperapis fulvipes*, typically a spring species (Hurd, 1957). Warming temperatures worldwide have also resulted in bumblebee species moving north and to higher elevations, out of their historic range (Kerr et al., 2015). Heat waves are extreme climatic events and their increasing occurrence is known to negatively affect bumblebees because queens die before entering winter diapause due to warm autumnal temperatures (Filazzola et al., 2021; Soroye et al., 2020). Different bee species likely have varied reactions to environmental pressures, with considerations like floral and nesting preferences as factors. With continued climate change it is unclear how bees and plant-pollinator networks could be affected (Filazzola et al., 2021).

The importance of bees in both natural and agricultural systems, combined with an increasing concern regarding pesticide use, habitat loss, and climate change, underscore the value of monitoring native bee populations. However, few natural areas have implemented such a program and fewer still for non-*Apis* and non-*Bombus* species. There is a pressing need to carry out long-term studies on bees to provide information on their population trends and habitat requirements.

Pinnacles National Park (PNP) in California is one of the most densely diverse locations for bees in the world, housing nearly 500 species in just 109 km^2 (Meiners et al., 2019). PNP boasts a semi-pristine habitat supporting a diverse range of flowering plants (Kittel et al., 2012). The park covers an array of elevations, soil types, microclimates, and lies along several fault lines (Kittel et al., 2012; Matthews, 1976). Extensive sampling of bees was completed in the park in 2011 and 2012 (Meiners et al., 2019). Amid widespread concerns regarding bee declines and a growing need for repeated survey work, we set out to re-sample the bees at PNP ten years after this previous sampling. We followed the methodology of the 2011-2012 study identically in order to directly compare the historic bee community to the present. In 2020, we sampled bees at nine plots established by Meiners et al. (2019) and two plots that had undergone restoration in the early 2000s. One-hectare sites were sampled biweekly using both aerial netting and pan trapping techniques. The diversity of bees at PNP was a primary motivation for the National Park Service funding this project.

Chapter 2 compares the diversity and community composition of bees collected across nearly a decade (2011, 2012, and 2020). It examines the community dynamics over years and among habitat types to hopefully ascertain patterns that may be applied to similar areas of interest. Chapter 3 uses our bee collection data combined with citizen science data from iNaturalist, to model suitable habitat for the small carpenter bee *Ceratina sequoiae* at PNP. Our goal was to use the combined data to determine if *C. sequoiae* is found where the habitat is predicted to be suitable, and if not, what landscape factors may be accounting for their absence. Finally, Chapter 4 is a short remark about novel foraging practices noted during the survey of PNP. We observed native bees, primarily *Andrena*, feeding on aphid-produced pine honeydew. There are no other recorded instances of such a behavior from *Andrena* and we suggest bees foraging on non-floral resources may be more common than previously thought. These chapters delve into both temporal and spatial relationships of bees and their habitats that may guide pollinator conservation efforts both at PNP and in similar habitat settings.

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CHAPTER 2

COMPARING BEE DIVERSITY AND COMMUNITY COMPOSITION OVER TIME AT PINNACLES NATIONAL PARK

Abstract

Pinnacles National Park, PNP, in California is currently known to be one of the most densely diverse places for bees. Three pollinator surveys have previously been conducted at PNP beginning in 1996. In 2020, we aimed to re-sample the park to determine how bee diversity and community composition has changed over time. We collected over 20,000 specimens, bringing the total number of bee species observed at PNP to 511, including the first record of the non-native alfalfa leaf-cutter bee *Megachile rotundata*. Our examination of bee richness and community composition indicated that bee diversity levels have remained constant over time. We also found that bee community composition is distinct among years, which is indicative of species turnover. This study highlights the importance of monitoring native bees over time to determine areas and species of conservation need.

Introduction

Native bees (*Anthophila*) are vital to preserve flowering plant (*Angiospermae*) communities (Mathiasson & Rehan, 2020). Bees and plants have evolved complex relationships and many species depend almost solely on the other (Danforth et al., 2019). Many experiments have shown the importance of biodiversity in ecosystem functions including pollination (Winfree et al., 2018). Recent research finds that the importance of biodiversity has been underestimated and higher bee diversity is needed for pollination in nature than previously thought, due to species turnover (Winfree et al., 2018). This emphasizes the need to monitor bee communities, as many bee species, including rare ones, are needed to maintain flowering plant species and pollinate crops (Winfree et al., 2018). Diverse bee communities support complex plant-pollinator networks (Danforth et al., 2019). With continued climatic change, invasive species introductions, and habitat loss there is potential to lose pollinator and plant species (Matthiasson & Rehan, 2020; Winfree, 2010). Additionally, approximately 67% of flowering plants worldwide rely on pollination from insects (Axelrod, 1960). Therefore, it is of the utmost importance to monitor pollinators around the world to determine their conservation status and protect declining bee populations (Kopec & Burd, 2017). Despite the need for long-term pollinator studies, there are very few natural areas that have implemented such a program.

Pinnacles National Park, PNP, near Paicines, California, has been identified as a biodiversity hotspot for bees with over 450 bee species in only 10,767 hectares (Meiners et al., 2019). PNP is also one of the only natural areas to have conducted pollinator studies across decades with studies completed in 1996, 1997, 1998, 1999, 2002, 2011, and 2012 (Meiners et al., 2019). There are several reasons why PNP is suspected to have such a diverse bee community. Among these is the fact that PNP is home to nearly 650 flowering plant species. The diverse plant community at PNP is likely a leading factor in driving bee diversity. Moldenke (1976) found California chaparral habitats to house a particularly large diversity of bees, and a notably high abundance of those with co-evolved specialist relationships. This is attributed to the frequency of fires and lack of ground cover, providing excellent habitat for ground-nesting species (Moldenke, 1976). There are few studies of caliber similar to those done at PNP, but Petanidou et al. (2008) completed a bee survey on a 30 ha area of a botanical garden in Daphni, Greece from 1983-1986, which resulted in approximately 18,000 specimens representing 661 bee species. This suggests that a Mediterranean type climate, as seen in PNP, may promote diverse bee communities. In general, solitary bees are most diverse in Mediterranean and arid climate regions such as the Chihuahuan and Sonoran deserts of the southwestern United States and adjacent Mexico (Michener, 1979).

This research aims to resample the bee community at PNP and determine how bee diversity and community composition has changed over time. Natural areas with high levels of cover (75% or greater) have been seen to experience minimal insect biodiversity loss over time compared to more developed areas (Outhwaite et al., 2022). We hypothesize that bee diversity will not differ among years or habitat types due to the semi-pristine environment at PNP that supports bee diversity. However, diversity metrics alone may not fully describe patterns in bee biodiversity; relevant measures of bee biodiversity may rely on species compositional differences. Additionally, underlying patterns in community composition could indicate distinct habitats at PNP which may be of higher conservation need and worth further investigation. Therefore, we hypothesize bees at PNP will have distinct community compositions across years and between habitats. This is due to species turnover and complex phenological relationships between bees and flowers, dependent on temporal cues that shift from year to year and among habitat types. Overall, we hope to gauge if there may be cause for concern regarding bee biodiversity at Pinnacles National Park based on changes in diversity metrics or major pattern shifts in community composition.

Methods

Study Area

Pinnacles National Park contains 10,767 ha located in San Benito and Monterey Counties, south of Paicines, in the South Coast range of California, USA. PNP has a semi-arid Mediterranean climate which supports a variety of habitats, but the park is dominated by chaparral (Kittel et al., 2012). PNP is distinctive in that it contains both granite-based soils and volcanic soils due to movement along the San Andreas Fault that runs through the park. Elevation ranges in the park from 219 m to 1,008 m. The park is an ecological island surrounded mostly by agricultural fields and cattle ranches.

Distribution of Sites

Nine one-hectare plots were sampled for this study; these plots were established in 2011 (Meiners et al., 2019). Eight plots were paired for logistical reasons to enable two plots to be sampled per day. Paired plots were spaced 400 m to 2.62 km apart, the remaining unpaired plot was approximately 2.2 km from the nearest plot. A tenth unpaired plot from 2011 was eliminated due to logistical challenges with the geographic layout of the plots. The nine selected plots include 14 vegetation types, with the most abundant being mediterranean California naturalized annual and perennial grassland herbaceous vegetation. The complete vegetation composition of these plots is available in Appendix A.

Additional sampling was completed at two restored plots used in Meiners et al. (2019). These plots were previously dominated by invasive yellow star thistle, *Centaurea solstitialis*, but through combined mechanical and chemical treatments, yellow star thistle was eradicated from these plots in the early 2000s. The plots resemble native grassland habitat, but are still dominated by other non-native species like *Hirschfeldia incana* and *Erodium cicutarium.* The park is actively continuing restoration efforts with both mechanical and chemical treatments. We excluded a third restored plot studied in earlier years, because PNP has built new recreational areas that impinge on the plot. Further aerial net sampling occurred opportunistically along trail segments, or other areas of interest in the park.

Collection Techniques

The collection methods and frequency of sampling over the growing season during 2011 and 2012 (Meiners et al., 2019) were repeated at the nine study plots in 2020. To successfully sample two plots in one day and visit each plot biweekly, two field collectors were employed. The sampling effort was identical across all plots. The study plots (and the two restored sites described below) were sampled from 24 February to 30 June in 2020, for a total of 54 sampling dates at approximately two-week intervals. In comparison, these plots had been sampled for 58 days from 21 February to June 24 in 2011 and 53 days from 24 February to June 27 in 2012 (Meiners et al., 2019).

Sampling was completed only if conditions were ideal (i.e., at least fairly sunny, calm winds, and 16º C or above). Two collection methods were engaged: pan traps and aerial netting. Pan traps attract bees and are ⅔-filled with soapy water, trapping bees for collection. Three different colored pan traps were used (Solo brand 96 ml plastic soufflé cups painted fluorescent blue, fluorescent yellow, or white). Bowls were active from approximately 09:00 to 15:00. We placed 30 pan traps in an 'X' at each plot, evenly spaced between opposite corners, and placed in a repeated color pattern (blue, yellow, white). Specimens caught in pan traps were strained, stored in 70% ethanol, and later washed and dried in preparation for pinning, labeling, and identification to species.

Additionally, aerial nets were deployed in the morning and afternoon to collect specimens not attracted to pan traps, as well as to determine floral preference for bees. To maximize aerial netting the two collectors took opposite halves of the plot and netted for 15 minutes, then switched for a second 15 minutes. The combined one hour of morning collection was repeated in the afternoon in each plot. Collectors attempted to walk at an even pace through the entire plot during the collection time rather than focusing on one or two areas within a plot. Collectors visually surveyed for and collected bees on a variety of substrates in addition to flowering plants, including bare ground, shrubs not in bloom, grasses, trees, mud, rocks, etc. Specimens caught in aerial nets were placed in separate kill jars based on the plant they visited. Non-plant captures were designated as ‘air/ground’. Specimens were frozen for later processing when they were thawed, pinned, labeled and identified to species.

Following the same methodology for the data collected in 2002, we collected at two restored plots in the park. These plots were also sampled biweekly, in ideal weather conditions, from 09:00 to 15:00. Four different colored pan traps were used (Great Value brand 592 ml plastic bowls colored dark blue, light blue, yellow, or white). The colors and pan traps used for collecting at the restored plots are different from those used in the primary plots described above. We placed 48 pan traps in a straight line, alternating colors in a sequence along the transect. Specimens collected in these plots were processed in the same fashion as bees collected from other pan traps. Aerial nets were not deployed at these plots.

Statistical Analysis

Passive sampling and collector bias may skew abundance, richness, and diversity data (Portman et al., 2020). Additionally, sampling cannot practically capture all bee species in a plot. Therefore, Hill-diversity estimates calculated directly from raw data cannot be used to compare species diversity across assemblages (Chao et al., 2020) To combat the above issues, we used coverage-based standardization, rather than rely on equal-effort or equal-sample size (e.g., as achieved by rarefaction), to make fair comparisons of Hill-diversity across assemblages. Hill-diversity was selected over traditional diversity metrics, such as Shannon or Simpson diversity indices, because Hill-diversity behaves in a way that is more logically reasonable for a diversity measurement (Roswell et al., 2021). Our data contain wide-ranging species abundances, so we opted to look at all three Hill-diversity metrics, as each weighs abundance differently. We used methodology developed by Chao and colleagues (Chao & Chiu, 2016; Chao et al., 2014) to calculate species diversity with a sample coverage of 0.978 utilizing the estimateD function in the iNEXT package in R (version 2.0.20, Hsieh et al., 2016) which determined Hill-diversity N0, N1, and N2. This sample coverage was selected because it was the point when about half of the samples were interpolated and half were extrapolated.

Each plot was categorized as belonging to one of four generalized habitat types: grassland, live oak woodland, blue oak woodland, or alluvial (Appendix A). Despite the two restored plots resemblance to grassland habitat, we opted to categorize these plots in particular as belonging to a fifth generalized habitat type, restored. For each combination of diversity metric (N0, N1, or N2) and collection method (aerial net, pan trap, or combined effort), we assessed differences in diversity among habitats (blue oak woodland, live oak woodland, alluvial, grassland, and restored) and years (2002, 2011, 2012, and 2020) as fixed effects factors using a completely randomized design with repeated measurements, omitting inclusion of potential interactions (for which there was no evidence) between the fixed effect factors, habitats and years. No aerial netting occurred in 2002, and therefore 2002 is only included in analyses examining pan trap diversity. Plots were a random effects factor associated with levels of habitat; repeated measurements on plots was a random effects factor associated with levels of year. We assumed a normal distribution and checked assumptions using the DHARMa package in R (version 0.4.5. Hartig, 2022). Means and comparisons among means were estimated using the estimated marginal means function in the emmeans package in R (version 1.7.2 Lenth, 2022).

Community composition at individual plots each year and habitat was visualized using nonmetric multidimensional scaling (NMDS) in the vegan package in R (version 2.5-7, Oksanen et al., 2020). NMDS was selected over other ordination methods because it ranks distances between samples. To account for differences in sampling between years such as collector biases, and variable weather or sampling days, as well as to suppress any overly dominant species collected in pan traps, we applied a square root transformation of species abundance data before performing the NMDS. Using Bray-Curtis distance to calculate dissimilarity between plots, we created the initial configuration with principal coordinate analysis applying a maximum of 20 random starts. We utilized modified Kruskal's stress to determine the match between ordination distances and ecological distances. Then, we determined whether the configurations converged using procrustes rotation, centered the axes scores, and rotated points to display the greatest plane of variation. We tested employing NMDS with different dimensions (k=1, 2, 3, 4) to optimize stress. We intended to use the fewest number of dimensions to represent the original position of the data in ordination space as accurately as possible in visualizations and minimize stress. Ultimately, we opted to run NMDS with three dimensions which had the lowest stress values and therefore best fit. We ran separate ordinations for aerial netting, pan trapping, and the combined effort using each combination of site and year as a sample. For any genera that could not be identified in 2020, we matched taxonomic levels in previous years to prevent discrepancies in the ordinations.

We performed a permutational ANOVA on the Bray-Curtis dissimilarity matrix to determine the statistical significance of dissimilarity of community composition between years and habitats in the *vegan* package in R (adonis, version 2.5-7, Oksanen et al., 2020). We incorporated a block design to accommodate our plots into the permutational ANOVA, to determine if the centroids of each treatment, year or habitat, in ordination space, differed significantly from each other. We analyzed data from aerial netting, pan trapping, and the combined effort separately. We opted to exclude the two restored plots from the ordinations as they followed a different methodology.

Additionally, to gauge if the plants bees were collected from were different among years and habitats we performed an NMDS ordination and permutational ANOVA for the floral associations of netted bees. We did not have abundance data on these plants, so we used presence-absence to create a Sorensen dissimilarity. We used the same parameters as the above ordinations: 20 random starts, procrustes rotation, centering, rotation, and three dimensions.

Bees that were collected opportunistically were not considered in any analyses, but were added to the species list. All analyses were conducted in R version 4.1.2 (R Core Team, 2021).

Results

Our collection efforts resulted in 23,170 bee specimens representing 50 genera and 281 species. Eight genera: *Andrena, Ceratina, Halictus, Hesperapis, Lasioglossum, Melissodes, Osmia,* and *Panurginus* accounted for 83% of the specimens collected, with the remaining 42 genera accounting for 17% of specimens. Twenty-nine species had not been previously observed at PNP, an additional 19 species had not been observed since 2002 or earlier. With the addition of these bees to the inventory, 511 bee species have been documented at PNP. Of particular note, the 2020 inventory contains the first record of the non-native alfalfa leafcutting bee *Megachile rotundata* in the park. A full list of species from the current survey and all related surveys in previous years is available in Appendix B. Bees have been collected on 287 plant species in the park (Appendix C).

Hill-Richness, N0, which weights species equally regardless of abundance, did not differ significantly for aerial net, pan trap, or bees from the combined effort by year or habitat (Table 2-1, Figure 2-1). Hill-Shannon, N1, which weights species in proportion to their abundance individually, did not not differ significantly between years for the combined collection effort (Table 2-1, Figure 2-2). However, aerial net and pan trap specimens showed individual differences among years (Table 2-1, Figure 2-2). N1 diversity of aerial net specimens was higher in 2020 than in 2012, but there were no other differences in N1 diversity among years (Table 2-1, Figure 2-2). Mean N1 diversity for pan trap specimens in 2012 was higher than in 2002, but there were no other differences among years (Table 2-1, Figure 2-2). There was no evidence of differences in N1 diversity among habitats (Table 2-1, Figure 2-2). Hill-Simpson, N2, which gives more weight to more abundant species, was not shown to differ among years or habitat types for the combined collection efforts (Table 2-1, Figure 2-3). N2 for aerial net specimens differed among years, but not habitat (Table 2-1, Figure 2-3). For aerial netting, diversity in 2020 was higher than in 2012; no other differences were detected among years (Table 2-1, Figure 2-3). There were no differences in N2 for pan trap specimens among years or habitats (Table 2-1, Figure 2-3).

Separate ordinations were run for pan collected bees, aerial net bees, and the combined effort. The bee communities collected from the combined collection methods were significantly different by year and not by habitat (Figure 2-4, 2-5, 2-6, 2-7). The bee communities collected in pan traps were significantly different by year and not by habitat (Figures 2-8, 2-9). Lastly, the bee communities aerial netted were also significantly different by year and not by habitat (Figures 2-10, 2-11). The general pattern of sites in ordination space can be examined in Figure 2-12. The bee-visited floral communities in 2011, 2012, and 2020 were ordinated using presence-absence. The floral communities differed significantly by year and not by habitat (Figure 2-13, 2-14).

Figures and Tables

Table 2-1

Probability Values for Each Combination of Hill-Diversity Metric and Collection Method in Plots at Pinnacles National Park

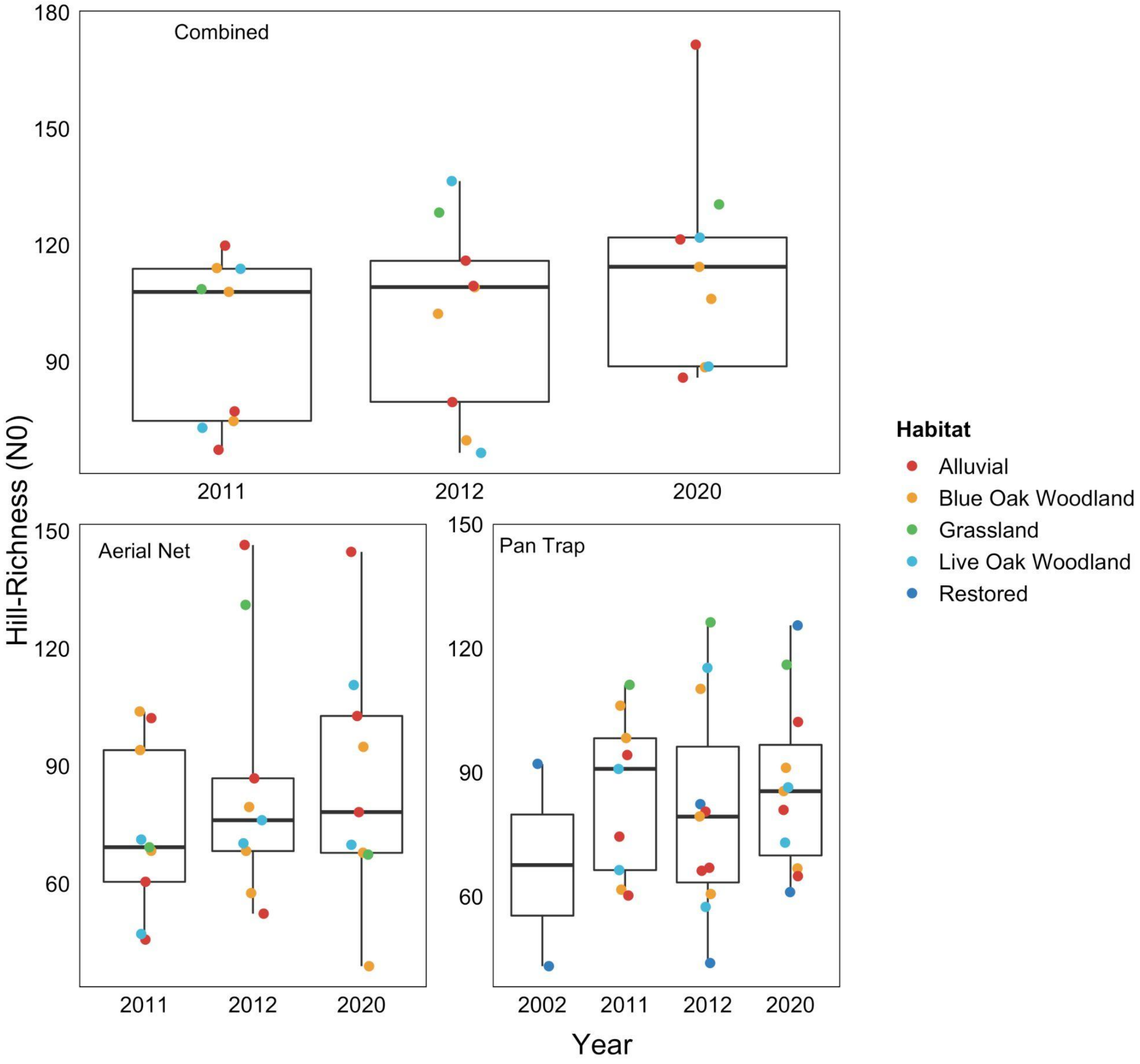
Hill-diversity	Fixed effect	Collection method	Probability value (p)
N0	Year	Combined	0.126
		Aerial Net	0.535
		Pan Trap	0.731
	Habitat	Combined	0.813
		Aerial Net	0.757
		Pan Trap	0.488
N1	Year	Combined	0.095
		Aerial Net	0.019 *
		Pan Trap	0.037 *
	Habitat	Combined	0.55
		Aerial Net	0.568
		Pan Trap	0.529
N2	Year	Combined	0.158
		Aerial Net	0.019 *
		Pan Trap	0.106
	Habitat	Combined	0.689
		Aerial Net	0.435
		Pan Trap	0.621

Note. We assessed differences in diversity across habitats and years. The full results of these statistical tests are available in Appendix D.

$^{*}p < .05$.

Figure 2-1

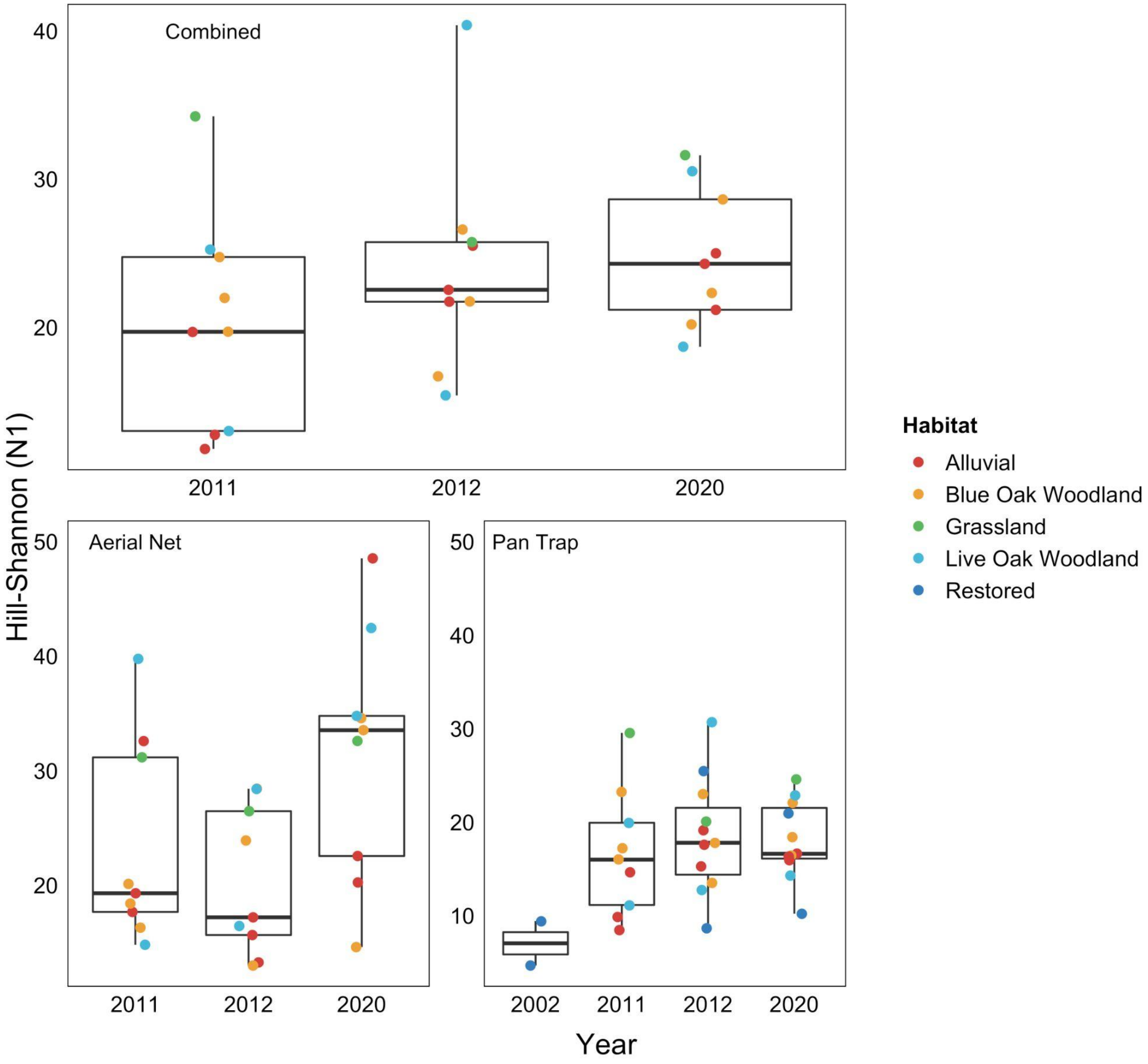
Hill-Richness, N0, by Collection Type and Habitat for 2002, 2011, 2012, and 2020 at Pinnacles National Park



Note. There were no significant differences in N0 between years or habitat type (Table 2-1).

Figure 2-2

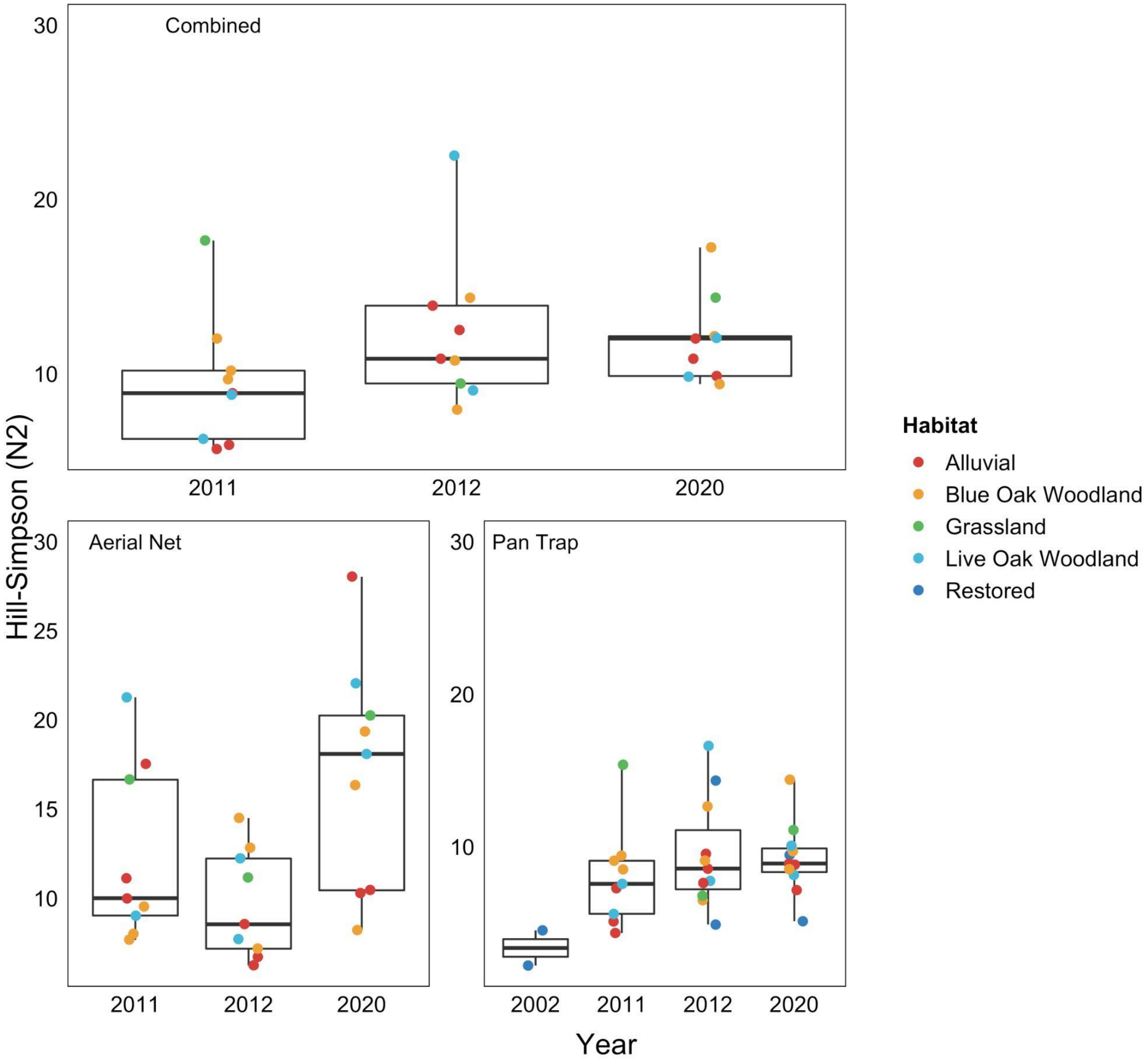
Hill-Shannon, N1, by Collection Type and Habitat for 2002, 2011, 2012, and 2020 at Pinnacles National Park



Note. N1 diversity for aerial net specimens in 2020 was higher than in 2012 (p=0.019), but mean diversity in 2011 was not different from 2012 (p=0.689) or 2020 (p=0.093). Mean diversity for pan tap specimens in 2012 was higher than in 2002 (p=0.042), but there were no other differences among years or habitats (Table 2-1).

Figure 2-3

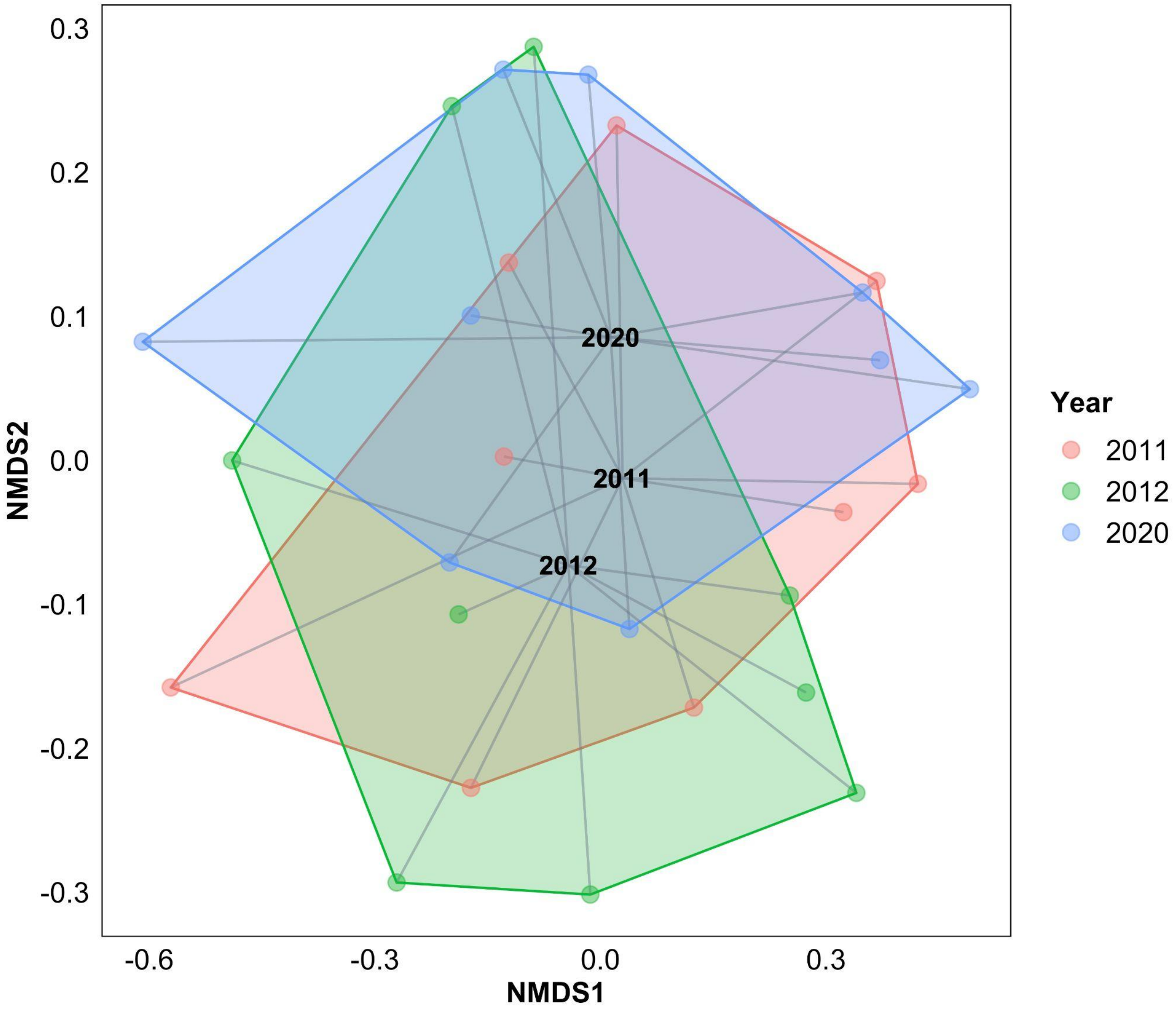
Hill-Simpson, N2, by Collection Type and Habitat for 2002, 2011, 2012, and 2020 at Pinnacles National Park



Note. N2 for aerial net specimens differed; mean diversity in 2020 was higher than in 2012 (p=0.016); no other differences were detected among years or habitats (Table 2-1).

Figure 2-4

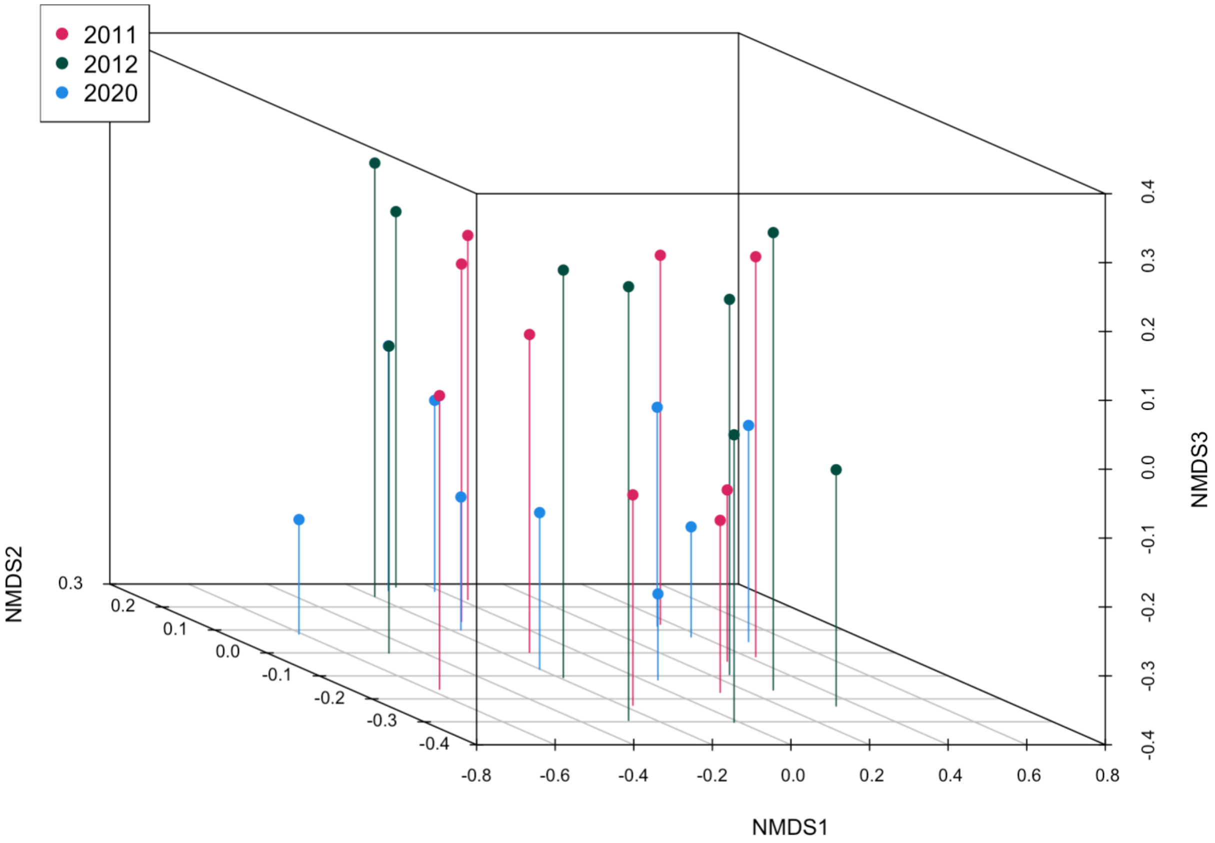
NMDS of the Bee Communities in 2011, 2012, and 2020 at Pinnacles National Park



Note. This is a Bray-Curtis ordination using nonmetric multidimensional scaling (NMDS, k=3, stress=0.16691). Points represent bee communities at individual plots. There is a significant difference in the centroids between the bee communities each year (p~0.01). This ordination represents the bees collected from the combined effort of aerial netting and pan trapping.

Figure 2-5

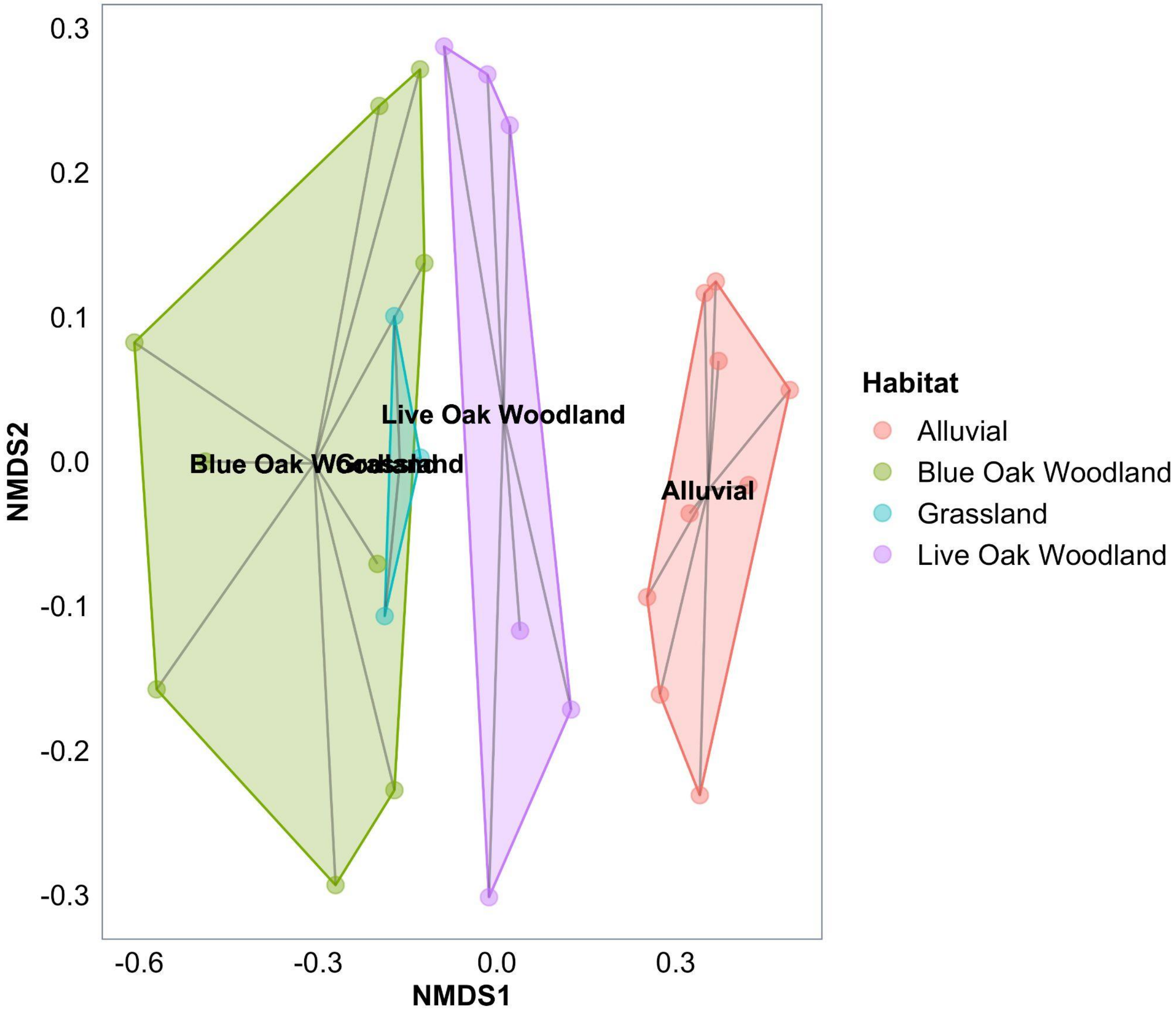
3-D NMDS of the Bee Communities in 2011, 2012, and 2020 at Pinnacles National Park



Note. This ordination is identical to that found in Figure 2-4 (NMDS, k=3, stress=0.16691), but is visualized in 3-D to show the layout of points in ordination space. There is a significant difference in the centroids between the bee communities among years (p~0.01).

Figure 2-6

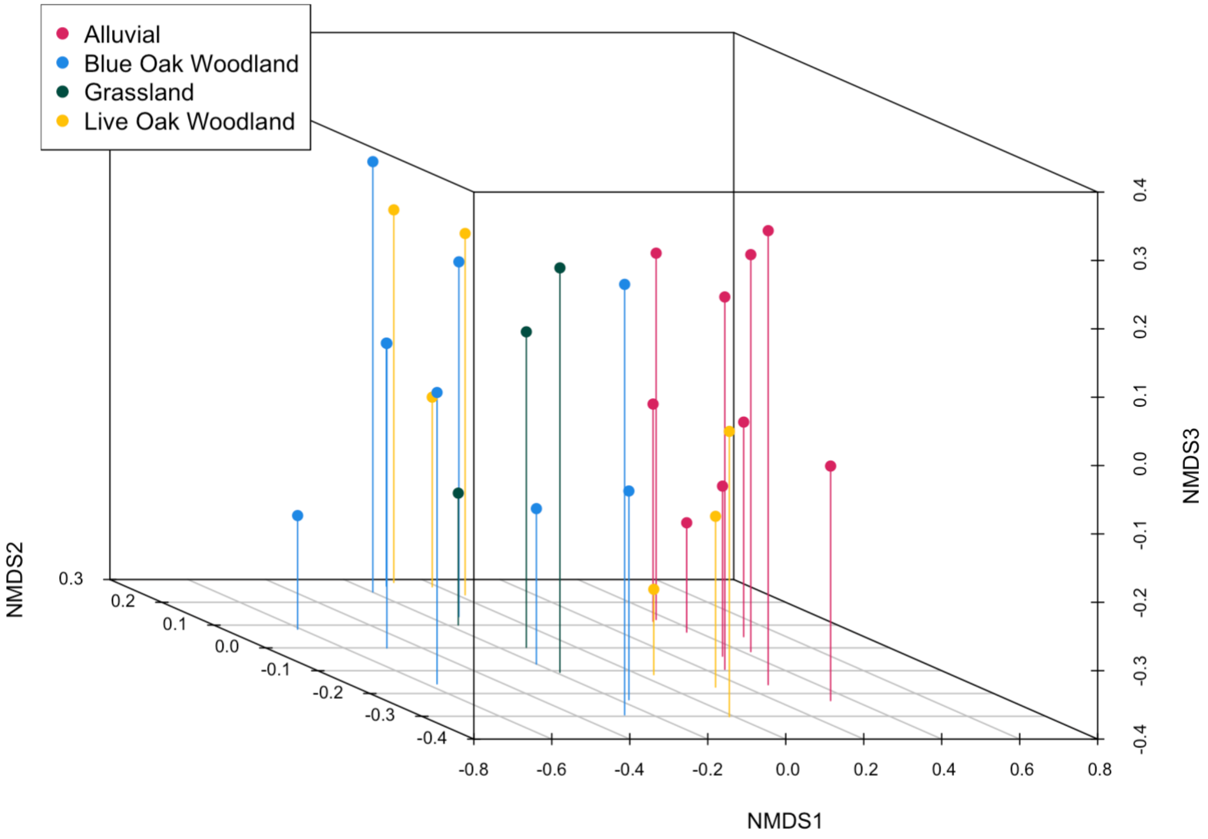
NMDS of the Bee Communities by Habitat Type at Pinnacles National Park from 2011, 2012, and 2020



Note. This is a Bray-Curtis ordination using nonmetric multidimensional scaling (NMDS, k=3, stress=0.16691). There is not a significant difference in the centroids between the bee communities in each habitat (p~1). This ordination represents the bees collected from the combined effort of aerial netting and pan trapping.

Figure 2-7

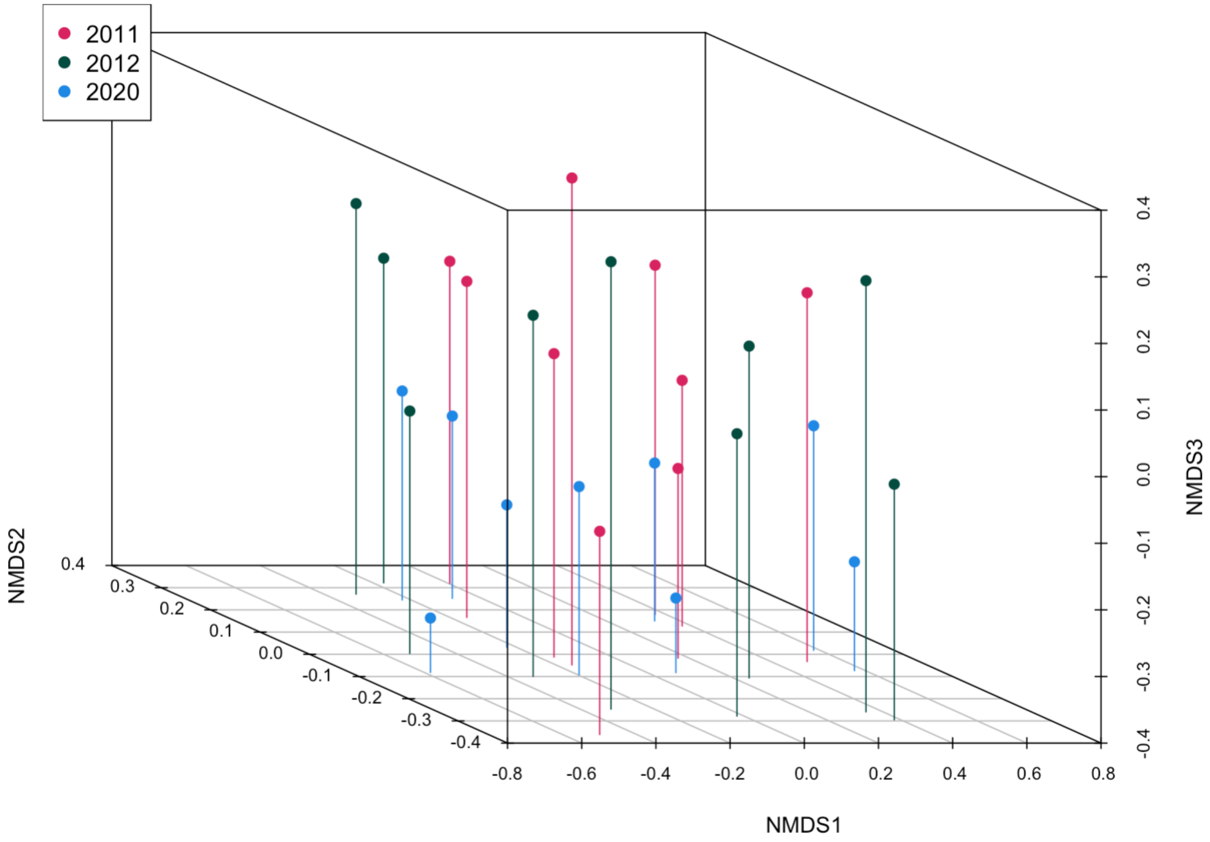
3-D NMDS of the Bee Communities in 2011, 2012, and 2020 by Habitat Type at Pinnacles National Park



Note. This ordination is identical to that found in Figure 2-6 (NMDS, k=3, stress=0.16691), but is visualized in 3-D to show the layout of points in ordination space. There is not a significant difference in the centroids between the bee communities among habitats (p~1).

Figure 2-8

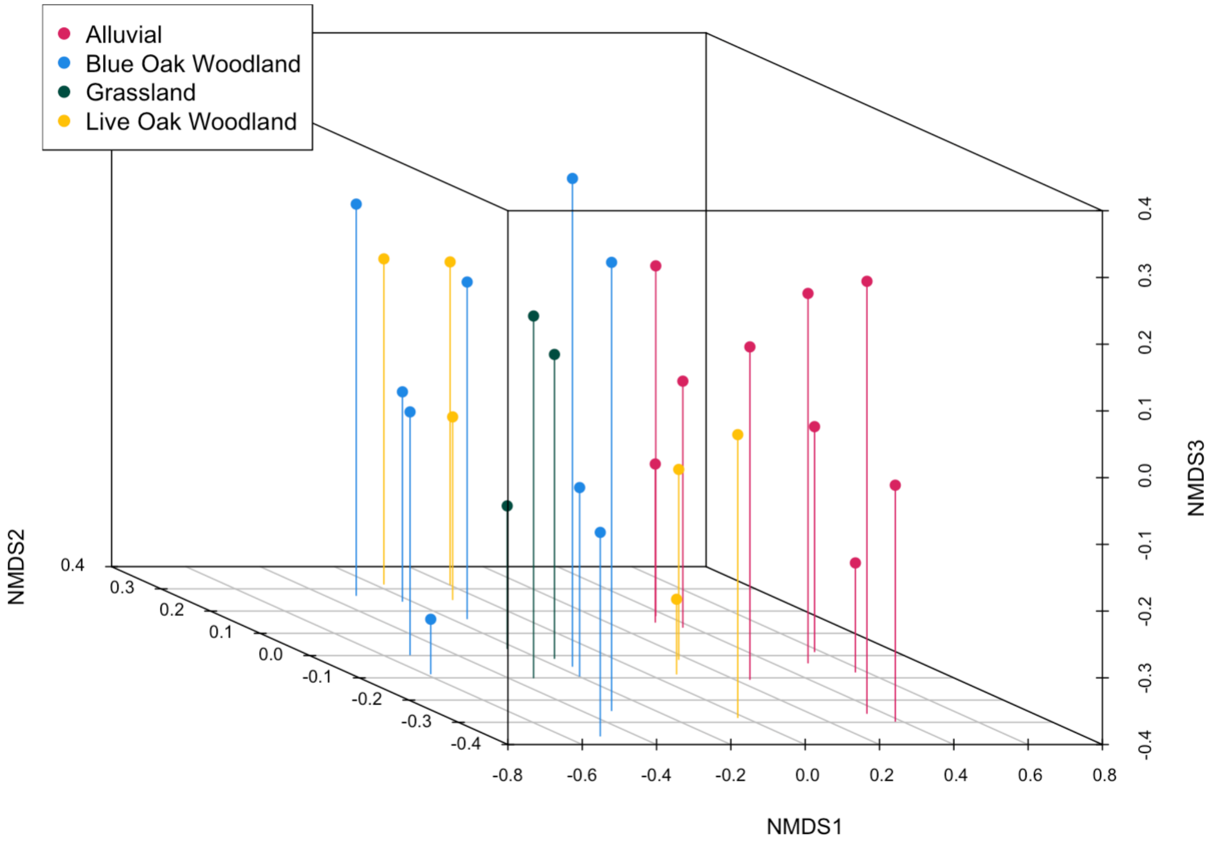
NMDS of the Bee Communities Collected in Pan Traps in 2011, 2012, and 2020 at Pinnacles National Park



Note. This is a Bray-Curtis ordination using nonmetric multidimensional scaling (NMDS, k=3, stress=0.1047785). There is a significant difference in the centroids between the bee communities each year (p~0.01).

Figure 2-9

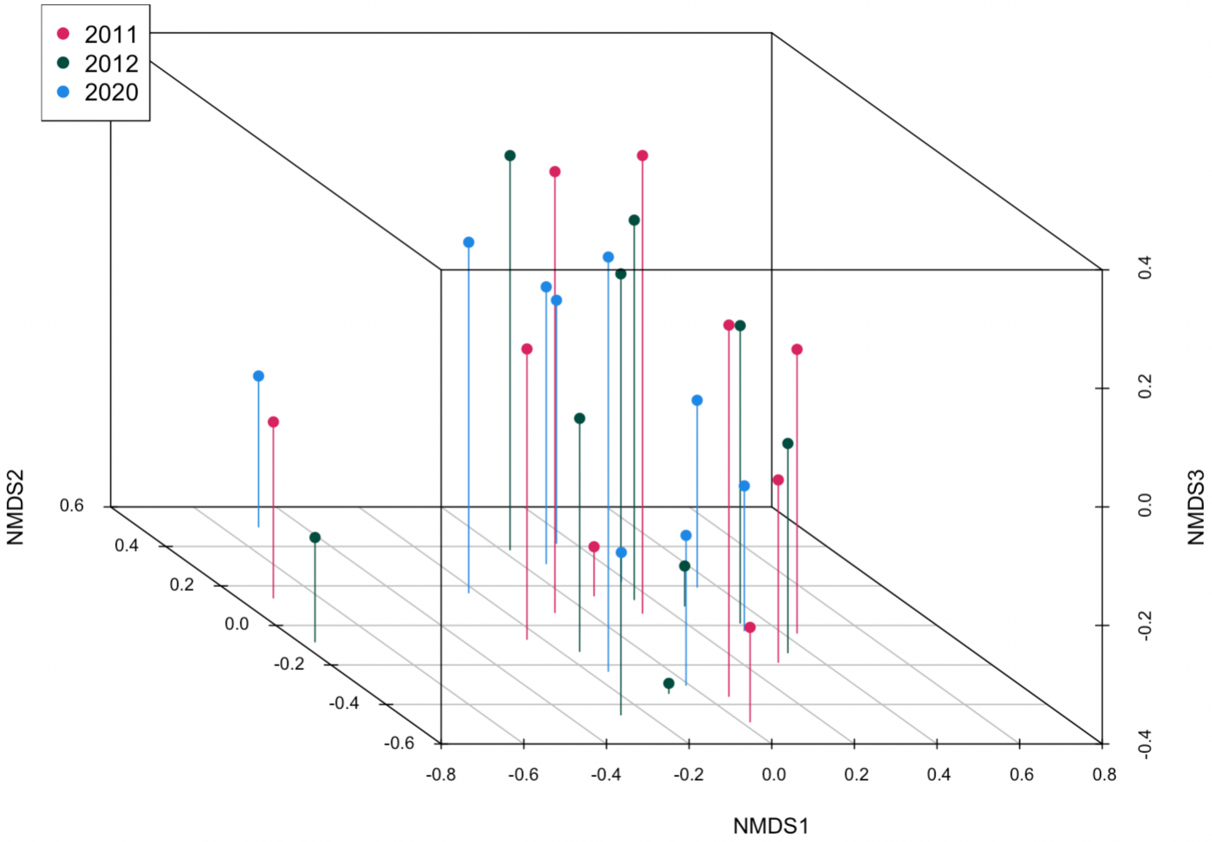
NMDS of the Bee Communities Collected in Pan Traps by Habitat Type at Pinnacles National Park from 2011, 2012, and 2020



Note. This is a Bray-Curtis ordination using nonmetric multidimensional scaling (NMDS, k=3, stress=0.1047785). There is not a significant difference in the centroids between the bee communities in each habitat (p~1).

Figure 2-10

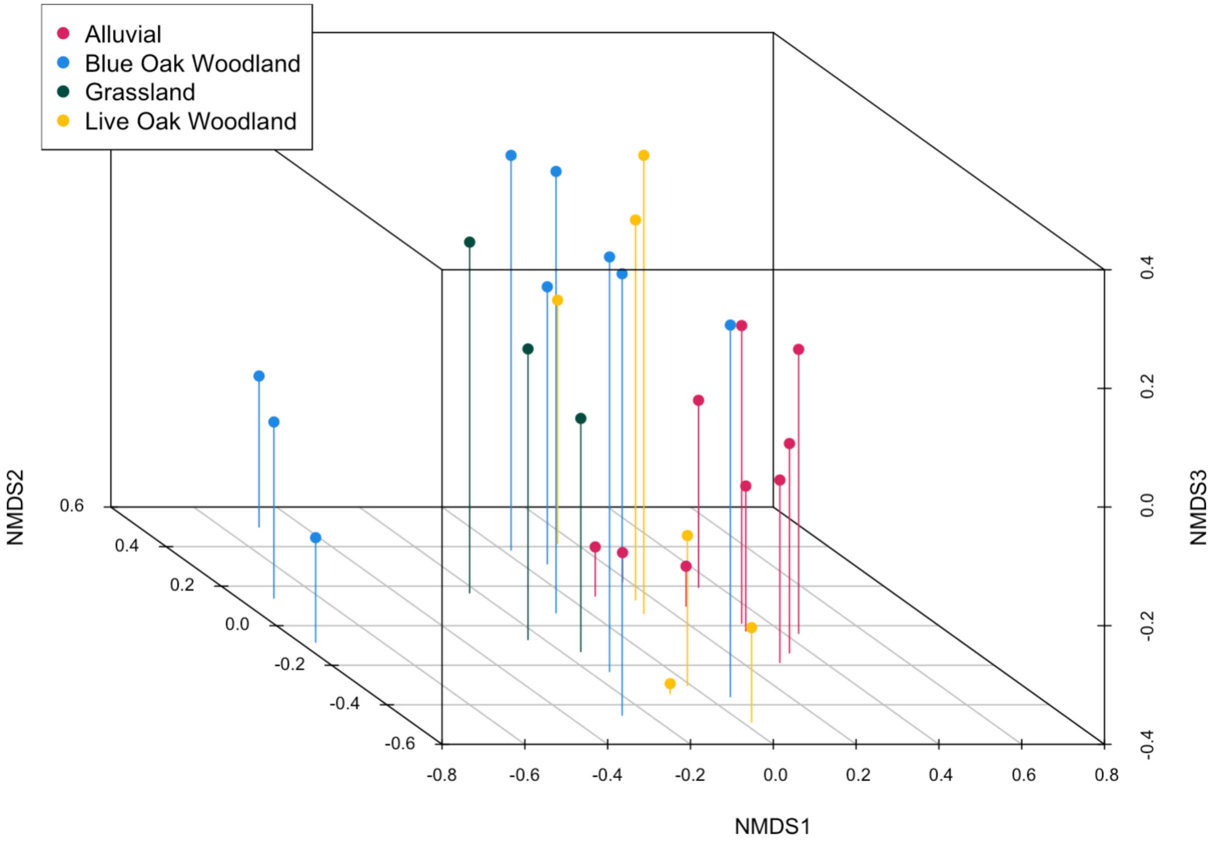
NMDS of the Bee Communities Collected via Aerial Netting in 2011, 2012, and 2020 at Pinnacles National Park



Note. This is a Bray-Curtis ordination using nonmetric multidimensional scaling (NMDS, k=3, stress=0.1423354). There is a significant difference in the centroids between the bee communities each year (p~0.01).

Figure 2-11

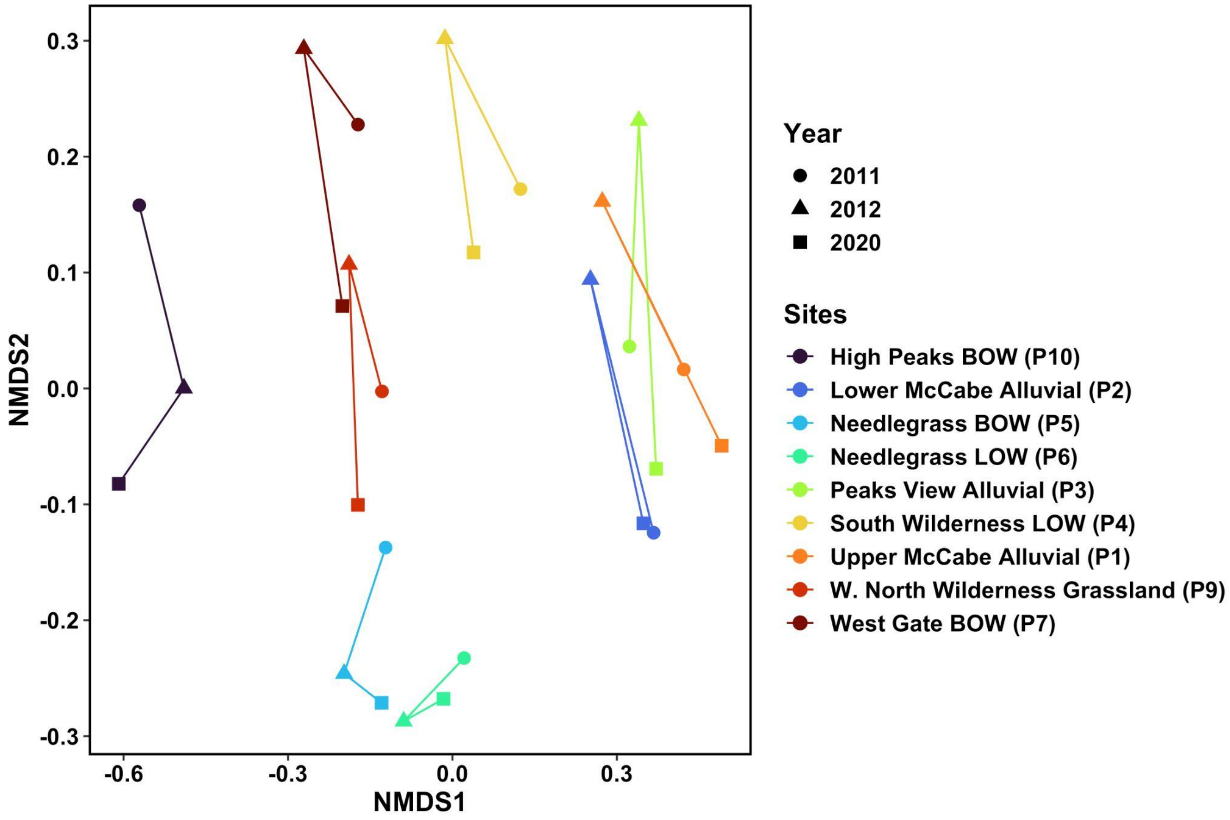
NMDS of the Bee Communities Collected via Aerial Netting by Habitat Type at Pinnacles National Park from 2011, 2012, and 2020



Note. This is a Bray-Curtis ordination using nonmetric multidimensional scaling (NMDS, k=3, stress=0.1423354). There is not a significant difference in the centroids between the bee communities in each habitat (p~1).

Figure 2-12

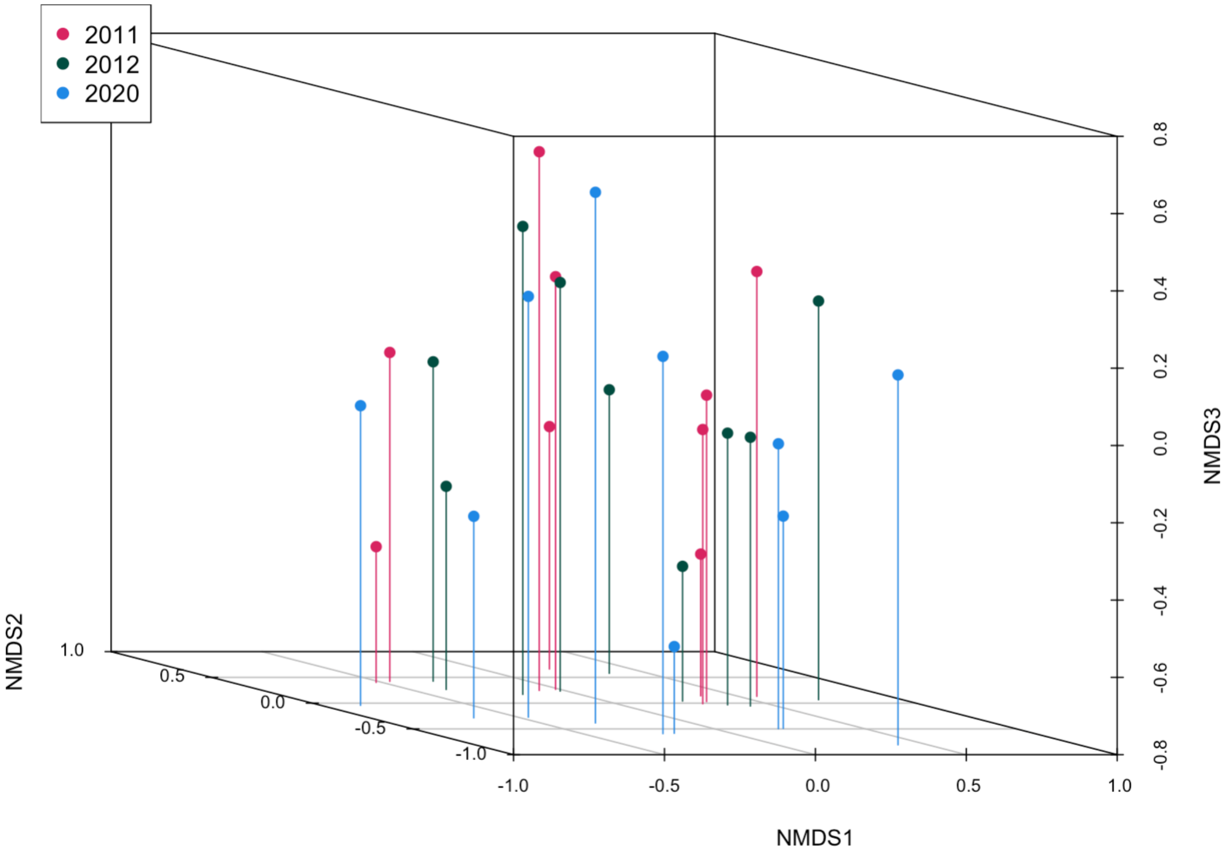
NMDS Connections Between the Bee Communities in 2011, 2012, and 2020 at Pinnacles National Park



Note. This ordination is identical to Figure 2-4 (NMDS, k=3, stress=0.16691), but demonstrates how the bee communities have shifted in ordination space each year.

Figure 2-13

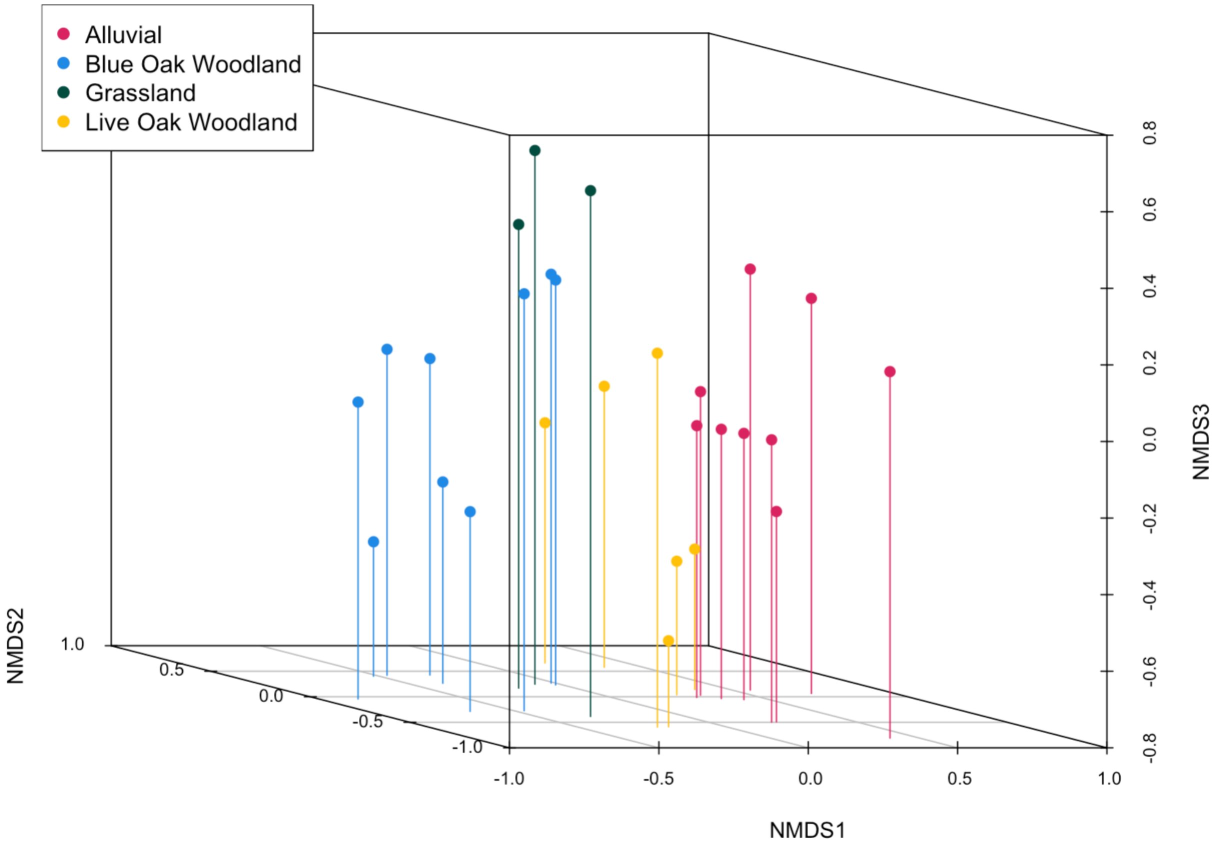
NMDS of the Floral Communities Bees were Collected from in 2011, 2012, and 2020 at Pinnacles National Park



Note. This is a Sorensen (presence-absence) ordination using nonmetric multidimensional scaling (NMDS, k=3, stress=0.14492). There is a significant difference in the centroids between the floral communities bees were collected from by year (p~0.01).

Figure 2-14

NMDS of the Floral Communities Bees were Collected from by Habitat Type at Pinnacles National Park from 2011, 2012, and 2020



Note. This is a Sorensen (presence-absence) ordination using nonmetric multidimensional scaling (NMDS, k=3, stress=0.14492). There is not a significant difference in the centroids between the floral communities bees were collected from in each habitat (p~1).

Discussion

Bees provide key ecosystem services in natural and agricultural areas (Danforth et al., 2019; Kopec & Burd 2017; Losey & Vaughn 2006). Despite the importance of bees, there are relatively few pollinator monitoring programs conducted that sufficiently replicate surveys to detect trends in bee diversity and community composition over time (Meiners et al., 2019). The ongoing surveys at Pinnacles National Park aim to fill this knowledge gap and explore patterns in bee diversity. The combined results of four bee surveys from 2002 to 2020 highlight the immense diversity at PNP and establish the park as a bee biodiversity hotspot, with one of the highest known densities of bee species in the United States, and likely globally. Five hundred eleven bee species have been observed in the 10,767 ha PNP encompasses. New species have been added to the bee inventory list with every survey, providing opportunities to monitor changes within the bee community.

We documented the first observation of the adventive *Megachile rotundata* in the park during the 2020 survey, which should be monitored closely. *Megachile rotundata* is one of the few introduced bees with empirical evidence suggesting they have a negative impact on native bees (Russo, 2016). Non-native bees can compete with native bees for resources, introduce pathogens, and disrupt native plant pollination (Goulson, 2003; Hedtke et al., 2015; Russo, 2016). Only one individual was collected, but the pervasiveness of *M. rotundata* in other natural areas in the United States suggests the potential to spread throughout the park (Barthell et al., 1998; Russo, 2016). While it is unclear how routinely farmers in the local area use *M. rotundata*, the Central Valley of California produces approximately two thirds of the state's alfalfa and likely use *M. rotundata* for pollination services through much of this area. *Megachile rotundata* is the world’s most intensively managed bee and triples alfalfa seed production (Pitts-Singer and

Cane, 2011). Future research should consider the impact *M. rotundata* invasion could have on the native bees of PNP.

We documented that bees at PNP are not experiencing diversity losses, but community composition is changing over time. Hill-diversity numbers were at overall similar levels across years or increased slightly in later years (Figure 2-1, 2-2, 2-3). When considering aerial net specimens or the combined collection efforts, Hill-diversity appeared to be stable across years or in some cases increased over time. Differences in Hill-diversity between pan trap collected bees in 2002 and later years may be due to the number of sampled plots and the vegetational character of those plots. There were only two plots sampled in 2002. These restored sites were sampled again in 2012 and 2020, but not 2011, which could lead to artificial differences in Hill-diversity for pan traps. N1 diversity was the only metric that differed significantly in the pan trap bee community composition among the four years of sampling, with lowest numbers in 2002 (Table 2-1). The addition of nine plots of varying habitat types in 2011, 2012, and 2020 likely contributed to the increased diversity as reflected in N1 diversity for those years. However, we opted to include this pan trap data from 2002 regardless, because differences in restored sites can still be visualized and inform some potential differences in diversity. For example, N1 diversity for restored plots visually appears higher in 2012 than 2002 when only the two restored sites are considered (*personal observation*). There are too few replicates, however, to test rigorously, for these two restored sites alone, whether this apparent difference over time in diversity at the two sites is significant. Interestingly, two models that examined aerial net diversity (N1 and N2) also found increases in 2020 compared with 2011 and 2012, which are not tied to the addition of plots or habitats.

Our findings suggest that the bee community at PNP is not facing diversity losses. Recent research suggests that natural areas mitigate the effects of climate change and the reduction of insect diversity seen in developed areas (Outhwaite et al., 2022). Protected areas act as carbon sinks, absorbing more carbon from the atmosphere than they release, minimizing the effects of climatic change (Melillo et al., 2016). Thus, adverse effects of global climate change may be less strongly expressed in natural areas than in more developed areas with factors such as extensive coverage of asphalt and concrete incorporated. Moreover, topographic variability, such as that found in natural areas, results in microclimatic buffering which has been seen to decrease extirpation risk from climate change for both plants and insects (Suggitt et al., 2018). This could be the case at PNP as well. PNP is considered a semi-pristine habitat, boasting thousands of hectares of undeveloped land, with only about 50 kilometers of trails, several kilometers of roads, a campground, and a handful of buildings. Overall, the majority of the park remains untouched, which could be protecting the diversity of bees over many years despite concerns of bee declines in other areas. This highlights the importance of both maintaining protected areas and alleviating consequences of climate change for biodiversity conservation.

Ordination indicated that community composition significantly differed between years (Figure 2-5). However, most plots followed a similar pattern of change in community composition from 2011 to 2012 to 2020, indicating a consistent shift across plots (Figure 2-12). For most plots, 2012 shifts to higher NMDS 2 values, then 2020 moves back down in NMDS 2 values toward 2011 (Figure 2-12). Our findings suggest that the bee community at PNP is variable, experiencing species turnover, but not facing diversity losses. It appears that high variability could be common among bee communities in natural areas, because of the intricately evolved relationship between flowering plants and bees (Leong et al., 2016). Bees in central

California may face drought and relatively scarce foraging opportunities provided by plants in flower in summer months, pushing for highly specialized phenological relationships between bees and their host plants. The chaparral habitat at PNP hosts a high number of specialized bees (Moldenke, 1976). Specialist bees have a narrow window to emerge and coincide with the peak bloom of their host plants (Danforth et al., 2019). If bees do not receive the right temporal cues, they may stay in diapause and delay emergence, particularly during drought conditions (Danforth et al., 2019). The fluctuation in bee emergence combined with the frequency of drought-like conditions in California could feasibly result in high community composition variability.

Contrary to our hypothesis that species composition of bees would vary among generalized habitat types, community composition seemingly was largely detached from generalized habitat type. We did not find significant differences in Hill-diversity or community composition among habitat types (Figure 2-1, 2-2, 2-3, 2-7). Even the plant communities bees were collected from differed by year rather than habitat (Figure 2-13, 2-14). Bees and their associated floral communities are changing together over time, suggesting that the bees at PNP are targeting specific plant species rather than generalized habitat types.

It is unclear whether sampling in additional generalized habitat types of PNP, beyond the five (including restored habitat) that were the focus in this study, would increase substantially the levels of bee diversity detected for PNP as a whole. The absence of significant differences in bee species composition among generalized habitat types, as found here, suggests that a large portion of the overall bee diversity of PNP is expressed within any given single generalized habitat type. The substantial number of specialist bee species at PNP could be driving these findings, because specialist bees rely on one or a few floral species and likely forage for their host plant in any habitat they are found. Many of these floral species for specialist bees occur in multiple habitat types. Bees, to avoid temporary declines of foraging sources in any one habitat type, will switch between habitat types and are easily able to move between habitat types within their flight range (Mandelik et al., 2012; Potts et al., 2005; Tscharntke et al., 2012). Sampling multiple habitat types as a standard element of a long-term survey, such has been done in this study, may increase the chances of sampling at those places in PNP where individual bee species are currently focusing their foraging in any given year.

Extending future surveys at PNP to include a variety of habitat types will allow more spatial comparisons to determine what areas may be at risk of biodiversity loss, and to address the issue of whether increasing the number of habitats also increases the estimate for overall bee diversity at PNP. Additionally, further research to explore the relationship between flowers and bees at PNP could identify other important factors to conserve bee communities, but maintaining the diverse floral community appears to be critical to protect bee biodiversity.

The spatial and temporal coverage of bee monitoring studies is sparse (Meiners et al., 2019). However, expanding long-term monitoring projects will allow areas and species of conservation concern to be discovered. Based on our results, the bees at Pinnacles National Park are not currently confronting diversity declines, but with increased climatic change and habitat loss this could change. By conducting surveys periodically over many years, we will be able to determine if there are pollinator declines in the future. We urge future studies in natural, agricultural, and urban areas to expand bee surveys beyond one or two year studies, which appears insufficient to monitor bee communities (Meiners et al., 2019). Assessing the status of native bees is a critical step in preserving agricultural stability and ecosystem services.

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CHAPTER 3

MODELING SUITABLE HABITAT FOR THE SMALL CARPENTER BEE, *CERATINA SEQUOIAE* (MICHENER 1936), AT PINNACLES NATIONAL PARK USING CITIZEN SCIENCE RECORDS: POTENTIAL SOLUTIONS TO CURRENT BEE MONITORING ISSUES

Abstract

Traditionally, bees have been monitored by passive trapping and aerial netting methods; however, these methods alone are likely not sufficient. By using the monolectic bee *Ceratina sequoiae* Michener in the pristine habitat offered by Pinnacles National Park, we provide potential techniques to supplement current bee monitoring protocols. We analyze the spatial spread of occurrence of *C. sequoiae*, its host plants (*Clarkia spp.*) and nesting resources (*Sambucus nigra spp. cerulea*), plus other landscape factors, by using existing citizen science records on iNaturalist, and the Habitat Suitability Modeler in ArcGIS Pro, as a case study for better informing bee monitoring work. Citizen science and geospatial tools in conjunction with museum data from bee monitoring efforts could improve site prioritization to monitor monolectic species ranges, such as *C. sequoiae*. However, these techniques have rarely been considered in previous monitoring work for solitary bees.

Introduction

Bee diversity is unique because it is not focused in the tropics. In fact, temperate and tropical zones have comparable levels of bee biodiversity. Michener (1979) asserts that warm, xeric regions of the world host the most bee biodiversity. Monolecty in bees also varies by climate, it is more common in desert regions than the tropics (Michener, 1979). Monolectic bees rely on pollen from one genus of flower (Cane, 2021). Monolectic bees can be the most effective pollinators of their host plant, because they often have higher visitation rates and carry large amounts of their host plant's pollen, but this is highly species dependent (Olsen, 1996; Parker, 1981; Parker et al., 2016; Schlindwein & Medeiros, 2006). The emergence of monolectic bees must coincide with the peak bloom of their host plants for successful foraging (Danforth et al., 2019). Aside from host plant availability, it is unclear what may be driving distributions of monolectic bee species. For most bee species, monolectic and oligolectic alike, it is difficult to determine suitable habitat, as most bees do not have described habitat requirements. If a bee species' floral and nesting preferences are known, there are rarely studies determining if topographic factors such as elevation, aspect, slope, or proximity to water are important. The lack of information on the topographic requirements of bees makes creating targeted studies to assess species status difficult.

There is a need to monitor populations of bees, particularly monolectic and other specialists, during this time of unprecedented climatic change (Kopec & Burd, 2017; National Research Council, 2007). Traditional monitoring protocols have typically consisted of passive trapping or passive trapping supplemented by aerial netting in areas of interest (Portman et al., 2020; Prendergast & Hogendoorn, 2021). However, researchers have questioned whether these methods alone are sufficient to assess bee populations (Portman et al., 2020; Prendergast & Hogendoorn, 2021). More strategic approaches to bee monitoring are likely needed to target species of interest (Portman et al., 2020).

Insect natural history collections have great potential to play a larger role in monitoring projects (Kharouba et al., 2019). Museum collections have documented information on both historic and recent bee locations. Museum data is underutilized, but should be used to help assess insect populations at this critical time (Kharouba et al., 2019). Additionally, citizen science is a growing interest in its applications for conservation work (Chandler et al., 2017). iNaturalist is a popular website and app to input observations of any organism that can be viewed, identified, and exported by the scientific community. iNaturalist has potential for research applications and can be of use in monitoring biodiversity (Chandler et al., 2017). Data available in iNaturalist has shown promising initial uses in bee monitoring projects (Brooks & Nocera, 2020; Wilson et al., 2020). Furthermore, the Suitability Modeler tool in ArcGIS Pro has been used to determine suitable habitats or locations in a wide variety of contexts (Goodspeed et al., 2022; Faisal et al., 2021; Mamatkulov et al., 2022). To our knowledge, the Suitability Modeler tool has not been used to assist in bee monitoring before, but has potentially useful applications in this context. The goal of this study is to provide a framework for utilizing museum data, iNaturalist records, and the Habitat Suitability Modeler in ArcGIS Pro to assist with the determination of suitable habitat of monolectic bees and to develop more ways to readily study bee populations of interest.

Small carpenter bees (Apidae: *Ceratina*) are a group of cavity-nesting bees that often live in pith, stems, or dead wood (Michener, 2007). Small carpenter bees are not typically monolectic bees, but *Ceratina sequoiae* Michener is the exception (MacSwain et al., 1973). *Ceratina sequoiae* is distributed throughout much of cismontane California and nests in pithy stems (MacSwain et al., 1973). Unlike other monolectic species, this bee often emerges a few weeks earlier than its host plant, *Clarkia*, with adults historically collected in the field in March and April (MacSwain et al., 1973). It should be noted that *C. sequoiae*, like many monolects, will nectar at a variety of plants, but rarely collect pollen from plants other than *Clarkia*. In addition to floral specialization, *C. sequoiae* may rely on one or a few species of plant for nesting sites. A common pithy stemmed plant at Pinnacles National Park (PNP) in the South Coast Range of

California is blue elderberry (*Sambucus nigra ssp. cerulea* (Raf.) R. bolli). *Ceratina sequoiae* is known to readily nest in elderberry plants (MacSwain et al., 1973). It is unclear if *C. sequoiae* nests in other plant species. Leong et al. (2016) determined that *C. sequoiae* in central California were found almost exclusively in natural landscapes as opposed to agricultural or urban environments. These natural areas were primarily oak woodlands and grassland habitats (Leong et al., 2016).

We aim to determine suitable habitat for *Ceratina sequoiae* at PNP using the Suitability Modeler tool in ArcGIS Pro, iNaturalist records, and museum data. By mapping suitable habitat based on required floral and nesting requirements, we hope to determine whether other landscape factors may be affecting where *C. sequoiae* is found in the park. We hypothesize that some landscape factors like aspect or slope will affect *C. sequoiae* presence. These protocols may be used in future studies to better target areas where monolectic bees are found and monitor their populations and habitats.

Methods

Collection

Pinnacles National Park is located in San Benito and Monterey counties, south of Paicines, California, USA. PNP encompasses 10,767 ha that supports a variety of habitats including oak woodlands and grassland, but the park is predominantly a chaparral habitat (Kittel et al., 2012). Elevation ranges in the park from 219 m to 1,008 m. The park contains both granite based and volcanic soils due to movement along the San Andreas Fault which runs through the park.

As part of a pollinator survey in 2020, nine one hectare plots previously established in 2011 (Meiners et al., 2019) were sampled for bees (Figure 3-1). The most abundant vegetation type was Mediterranean California naturalized annual and perennial grassland herbaceous vegetation, but the selected plots represented a total of 14 vegetation types. Appendix A describes the full vegetation composition of our plots. Our plots also contain eight different geologic units, but were dominated by alluvium-based units that often create fertile soils. The complete list of geologic units in these plots is available in Appendix E.

Pan trapping and aerial netting methods were implemented in these plots. Pan traps are a passive collection technique. Three different colored pan traps were employed (plastic soufflé cups painted fluorescent blue, fluorescent yellow, or white) to attract bees and are filled partially with soapy water, trapping bees for later collection. Specimens that were caught in pan traps were properly stored and cleaned for museum curation. In the morning and afternoon, collectors used aerial nets to capture bees and determine floral preferences in the plots. Collectors sampled bees on a variety of substrates including flowering plants, bare ground, grasses, trees, rocks, and mud. Specimens collected in aerial nets were separated based on the plant they visited and non-plant captures were labeled 'air/ground'. There was a combined 2 hours of aerial net collecting in the morning and afternoon in plots. Specimens collected via aerial netting were placed in kill jars then frozen until processing when they were thawed, pinned, labeled and identified to species. Additionally, as opportunity allowed, further aerial net sampling occurred opportunistically in other areas of interest at PNP. GPS locations were recorded at areas where opportunistic sampling occurred. All specimens were identified to species by researchers at the USDA-ARS Pollinating Insects Research Unit and curated into the USDA-ARS Pollinating Insects Research Unit museum collection, but remain property of the National Park Service.

Spatial Analysis

Sambucus and *Clarkia* are two plant resources that *Ceratina sequoiae* requires for nesting and provisions repectively. To determine where these plants are found at PNP, we opted to retrieve iNaturalist observations for the two genera. Using iNaturalist observations maximized the number of GPS locations for floral and nesting resources in the park. We included only observations with an accuracy of 100 m or less. All identifications were verified by us. A handful of observations by us while sampling plots were previously added to iNaturalist which ultimately provided more accurate observations specific to areas we collected specimens from. GPS coordinates of included iNaturalist plant observations were entered into ArcGIS Pro 2.8.6. All sampled plots had *Clarkia* observations and two plots had *Sambucus* observations. Foraging range for *C. sequoiae* is approximately 500 meters using intertegular distance (Greenleaf et al., 2007).

Using the Distance Accumulation tool in ArcGIS Pro, we created two rasters calculating distance from *Clarkia* and *Sambucus* individually. The Distance Accumulation rasters were then input into the Habitat Suitability Modeler tool. We classified distance from *Clarkia* and *Sambucus* categorically i.e., distances within 100 m of the plant were given a suitability value (SV) of ten, 200 m were assigned an SV of nine, etc. through a distance of 500 m. Distances over 500 m were deemed unsuitable and assigned an SV of one, the lowest suitability value. Additionally, the modeler can weigh input rasters, as some animal species have fixed weights for habitat factors. However, there are no known fixed weights for habitat factors that affect bee presence, so we opted to weigh distance to *Clarkia* and distance to *Sambucus* equally in this model. After the distance rasters were classified and weighted, the suitability modeler was run. The modeler outputs another raster where each 3 m cell is assigned a suitability value. For example, in this model, anywhere at PNP that is over 500 m away from a *Clarkia* observation and over 500 m away from a *Sambucus* observation was assigned an SV of two, the lowest possible score. A location that is 300 m away from a *Clarkia* observation and 100 m away from a *Sambucus* observation is assigned a much higher SV of 18. A visual representation of this process is shown in Appendix F.

In addition to proximity to floral and nesting resources, six topographic variables were selected as potential influences of *C. sequoiae* distribution: elevation, slope, aspect, vegetation type, proximity to water, and geologic unit. To describe the most suitable habitat attributes we used the landscape characteristics of two plots (South Wilderness and Needlegrass LOW) that yielded relatively high numbers of *C. sequoiae* (Figure 3-1, Table 3-1). For geologic unit and vegetation we used the type that accounted for the most coverage in the plot (Table 3-1). Following the same process as the first model, we input the six selected topographic factors into the Suitability Modeler tool in ArcGIS Pro. While we created a separate model for each topographic factor every model also included the rasters describing distance to *Clarkia* and distance to *Sambucus*. We designated areas within 500 meters of *Clarkia*, *Sambucus*, water, alluvium and quartz monzonite geologic units, or coast live oak and grassland habitat types as suitable, decreasing in suitability every 100 m, as done in the first model. Areas outside of 500 meters were considered unsuitable and assigned an SV of one. A table describing the SVs assigned to all topographic variables is available in Appendix G. In each of these six models, we opted to weigh distance to *Clarkia*, distance to *Sambucus*, and the selected topographic variable equally, meaning the lowest possible SV was 3 and the highest was 30.

Finally, we created an eighth model that input all the selected topographic factors and the distances to *Clarkia* and *Sambucus*. We attempted a model that weighted these eight variables equally. However, in contrast to the outputs for our models that included only a single additional topographic factor, areas that were not within 500 m of *Clarkia* and *Sambucus* could still be assigned very high suitability values. The plants are critical for *C. sequoiae,* so we needed to ensure these areas had higher suitability. For this final model, we chose to weight proximity to *Clarkia* and *Sambucus* twice as heavily as other factors, a reasonable value based on studies following similar methods (Buruso, 2017; Store & Jokimäki, 2003).

We assessed our modeling success by determining how many of the study plots were categorized correctly, i.e., as having entirely or partially habitat that was highly suitable (green) at plots where *C. sequoiae* was collected, or as not having such highly suitable habitat (yellow to red) at plots where *C. sequoiae* was not collected. We did not use the two plots that were used to categorize suitable habitat (South Wilderness and Needlegrass LOW). We calculated the percentage of these seven study plots that were categorized correctly, to estimate a percent prediction accuracy (PPA) for each model. Finally, we tested model predictions, for model confirmation, using opportunistic collections of *C. sequoiae*. We used the seven plots and the two places where opportunistic collections of *C. sequoiae* occurred to calculate a second PPA for each model.

Elevation was obtained from the USDA National Elevation Dataset. Slope and aspect were calculated in ArcGIS Pro 2.8.6. Vegetation type was acquired from Kittel et al. (2012). Geologic unit was provided by the NPS Geologic Resources Inventory Program. Proximity to water, park boundaries, and park developments were obtained from the National Geospatial Data Asset NPS National Parks Dataset. All datasets were converted to the projected coordinate system NAD 1983 UTM Zone 10N. Rasters had a resolution of $(3\ \mathrm{m})^2$ and were clipped to the extent of PNP.

Statistical Analysis

We elected to further confirm that the models created by the Habitat Suitability Modeler in ArcGIS Pro succeeded in predicting *Ceratina sequoiae* abundance in sampled plots by testing for significant positive associations of abundance with habitat suitability values. For each model, the suitability values were averaged in each plot to assign a singular SV to a plot. Then, we ran eight simple linear regressions with *C. sequoiae* abundance in plots against SVs calculated from *Clarkia* and *Sambucus* locations alone, *Clarkia* and *Sambucus* locations paired with a single additional topographic variable (i.e., elevation, aspect, slope, distance to water, vegetation type, or geologic unit), and *Clarkia* and *Sambucus* locations with all of the selected topographic features. Linear regressions (r^2) were performed with significance levels of 5%. All statistical analyses were implemented in R (version 4.1.2).

Results

Fifty-seven *Ceratina sequoiae* individuals were collected at PNP during the 2020 survey, of which 49 were associated with established plots and eight were collected opportunistically at two additional locations throughout the duration of the study. Fourteen individuals were collected in aerial nets on six flower species. The remaining 43 specimens were collected in pan traps. Of the nine plots involved in the survey, *C. sequoiae* was collected at seven and no *C. sequoiae* were found in two of the plots. We initially considered only the specimens collected in plots, where collection effort was equal among sampling locations. We then also considered specimens collected opportunistically to determine if *C. sequoiae* was found where habitat was considered suitable in other areas of the park.

Figures 3-3 and 3-4 show habitat suitability values for *C. sequoiae* across PNP for each of our eight models. Figure 3-3 focuses on the six selected topographic variables and Figure 3-4 shows all the combined topographic variables compared to only *Clarkia* and *Sambucus* locations. When considering only plots, all models achieved a percent prediction accuracy between 71% and 86%, correctly categorizing 5-6 of the seven plots (Table 3-2). When including the opportunistic *C. sequoiae* collections in addition to the plots (N = 9), percent prediction accuracy ranged from 56% to 89% for the models (Table 3-2). The lowest percent prediction accuracy of 56% came from the model only considering distance to *Clarkia* and distance to *Sambucus* (Table 3-2). The 89% prediction accuracy was achieved by four models that also included topographic variables: aspect, slope, distance to water, and all combined topographic variables (Table 3-2).

The simple linear regressions indicated that the most robust model considered *Clarkia* locations, *Sambucus* locations, and elevation (r^2=0.669, p=0.007) (Figure 3-5). Three other models indicated a significant positive relationship between *C. sequoiae* abundance and habitat suitability values determined by landscape factors paired with *Clarkia* and *Sambucus* locations: vegetation type (r^2=0.590, p=0.016), slope (r^2=0.542, p=0.024), and aspect (r^2=0.537, p=0.025) (Figure 3-5). These three models provided stronger results than the more complex model that included all additional topographic variables (r^2 = 0.416, p=0.061). The model that considered *Clarkia* and *Sambucus* locations alone was also significantly positively correlated with *C. sequoiae* abundance (r^2=0.590, p=0.016). Thus, this simplest model matched or exceeded in its prediction strength, all models that included a single additional topographic variable, except for the model incorporating elevation (Figure 3-5).

Figures and Tables

Table 3-1

Suitable Features for Ceratina sequoiae as Determined by South Wilderness and Needlegrass LOW Plots at Pinnacles National Park

Feature	Location	Description
Elevation	South Wilderness	280 m
	Needlegrass LOW	359 m
Aspect	South Wilderness	E / SE
	Needlegrass LOW	S / SW
Vegetation Type	South Wilderness	Coast Live Oak
	Needlegrass LOW	Grassland
Geologic Unit	South Wilderness	Quartz monzonite
	Needlegrass LOW	Alluvium
Slope	South Wilderness	~0.084º
	Needlegrass LOW	~0.75º

Note. The landscape features described in this table were used to determine suitable habitat for *C. sequoiae*, because these two plots returned the highest numbers of *C. sequoiae* specimens.

Table 3-2

Percent Prediction Accuracy (PPA) for Eight Habitat Suitability Models at Pinnacles National Park

Model	PPA 1 (%)	PPA 2 (%)
Aspect	86	89
Slope	86	89
Elevation	71	78
Vegetation Type	71	78
Distance to Water	86	89
Geologic Unit	71	78
All Landscape Factors	86	89
Clarkia and *Sambucus* only	71	56

Note. PPA 1 was calculated from the number of seven plots that the model corrected placed in suitable or unsuitable habitat based on if *Ceratina sequoiae* was observed in the plot or not. PPA 2 was calculated considering the seven plots as well as the locations of two opportunistic collections of *C. sequoiae*. The two plots that were used to describe suitable habitat were not included in these calculations (South Wilderness and Needlegrass LOW).

Figure 3-1

Map of Plots Used in the 2020 Bee Survey with iNaturalist Observations of Clarkia and Sambucus at Pinnacles National Park

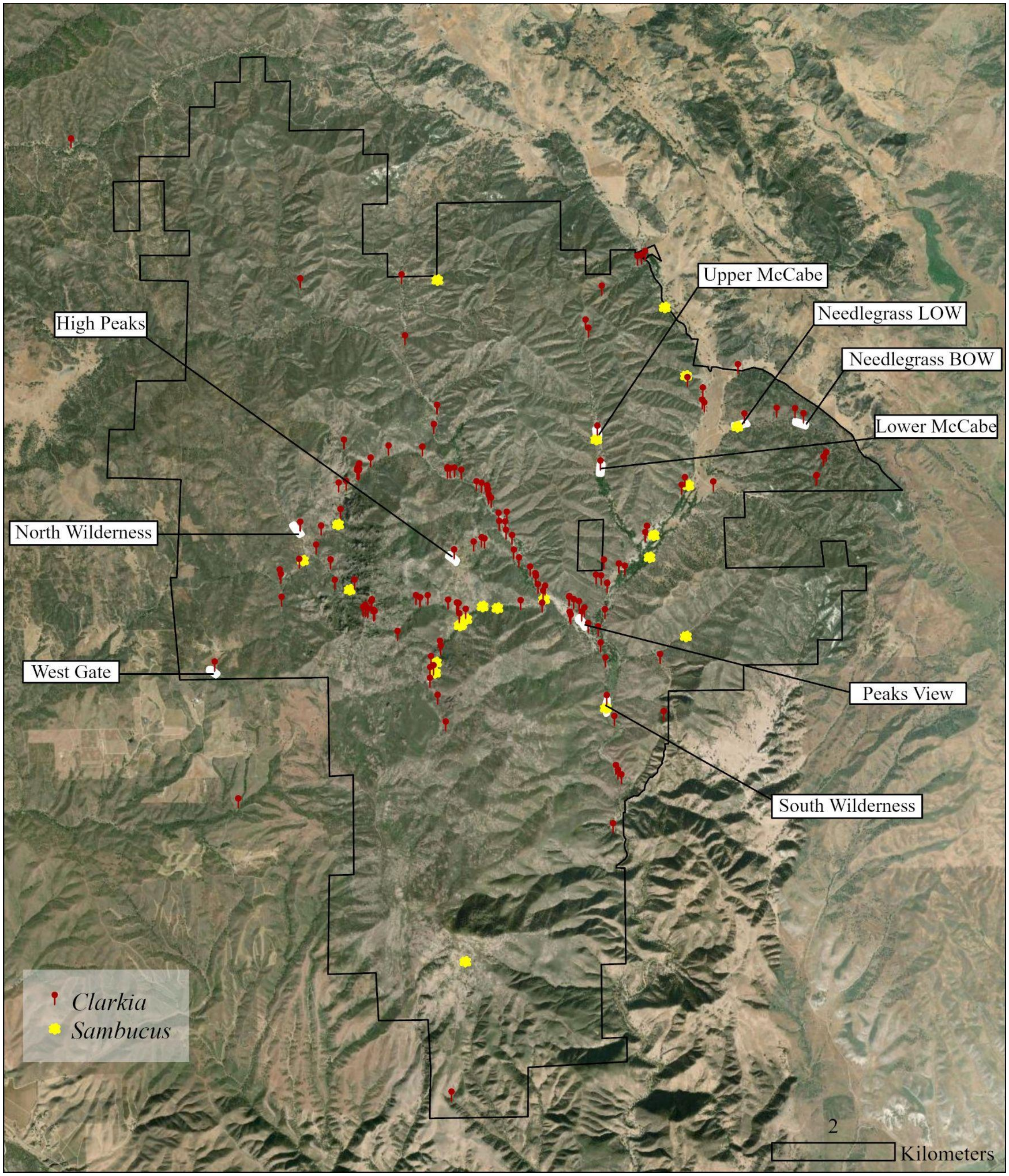
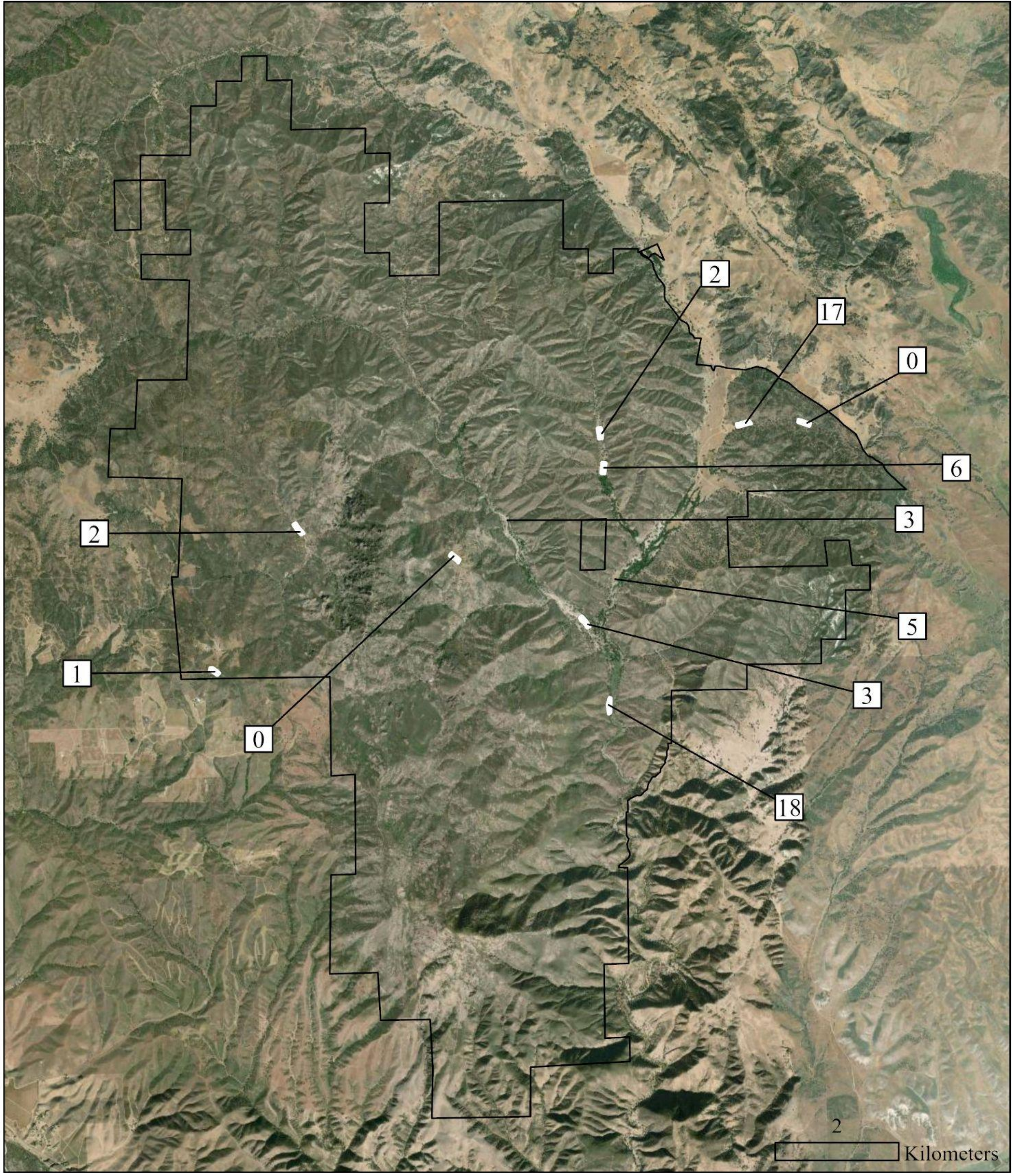


Figure 3-2

Locations Where Ceratina sequoiae was Collected at Pinnacles National Park

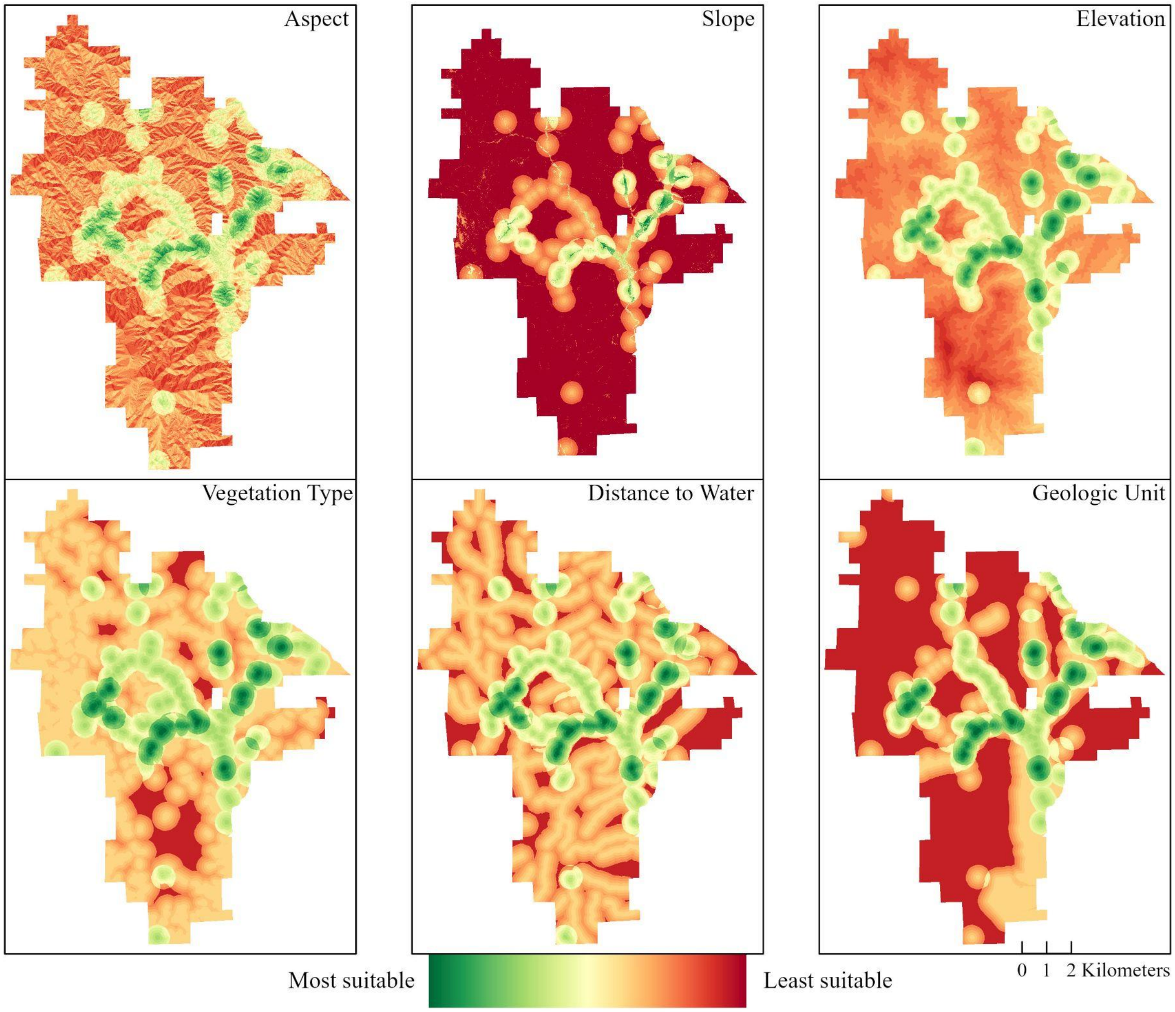


Note. Plots are displayed in white. Plots where *C. sequoiae* was not found are marked with zeros.

Two places where *C. sequoiae* were collected opportunistically are also included.

Figure 3-3

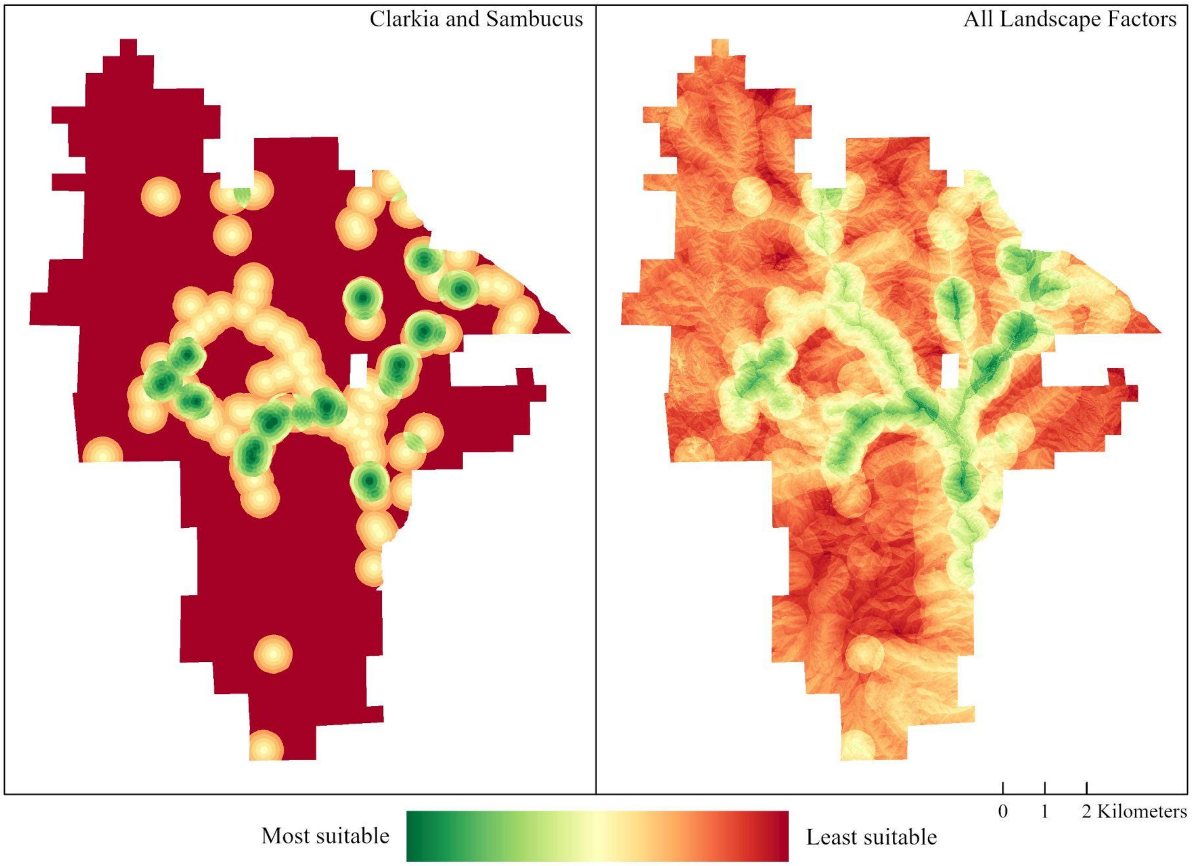
Suitable Habitat for Ceratina sequoiae at Pinnacles National Park if Considering Clarkia and Sambucus Locations and Aspect, Slope, Elevation, Vegetation Type, Distance to Water, or Geologic Unit



Note. More suitable habitat has a high suitability value and is represented in green. Less suitable habitat has a lower suitability value and is represented in red.

Figure 3-4

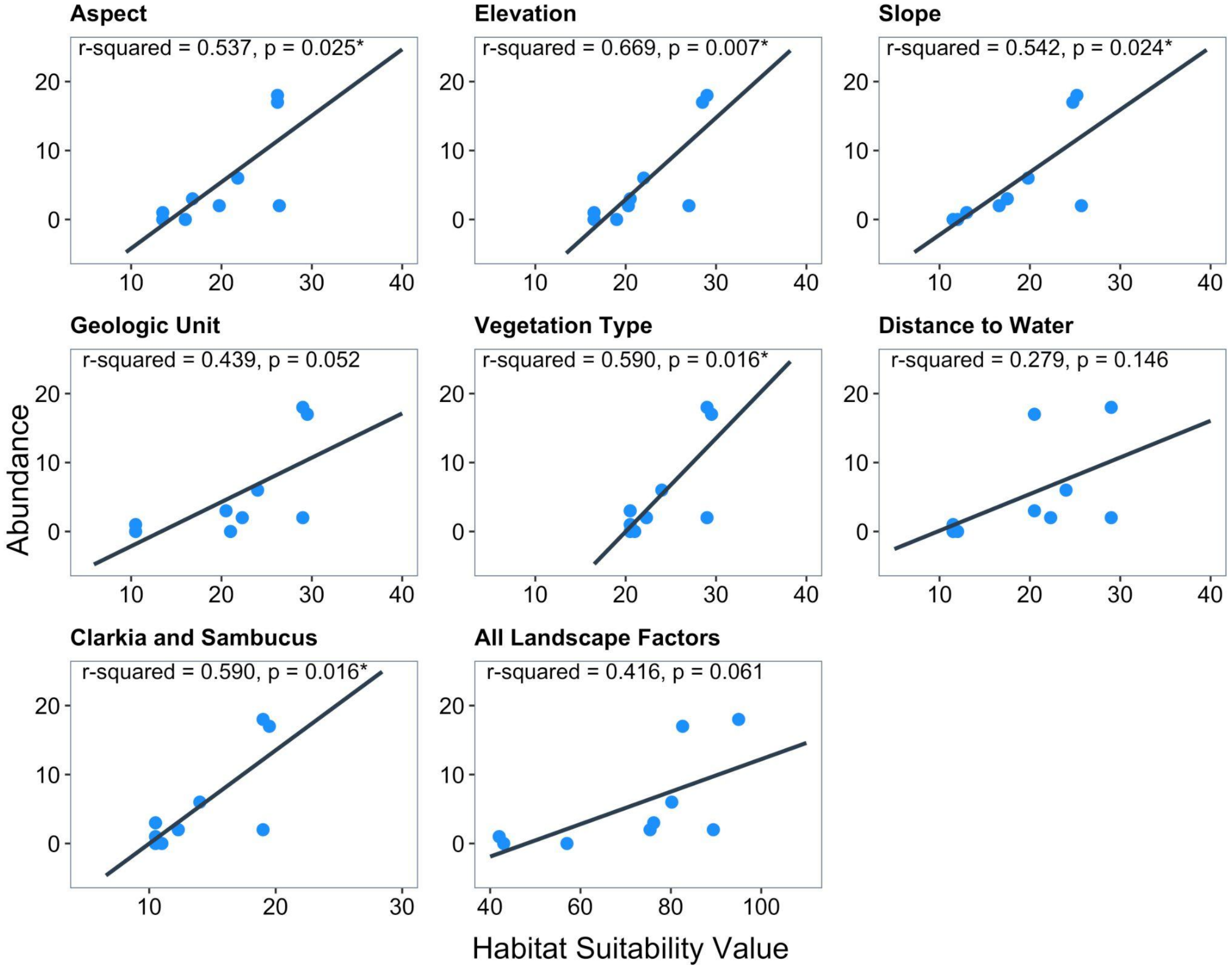
Suitable Habitat for Ceratina sequoiae at Pinnacles National Park if Considering Only Clarkia and Sambucus Locations or the Plant Locations and All Selected Landscape Factors



Note. More suitable habitat has a high suitability value and is represented in green. Less suitable habitat has a lower suitability value and is represented in red.

Figure 3-5

Ceratina sequoiae Abundance Explained by Habitat Suitability Value for Each Landscape Factor at Pinnacles National Park



Note. The habitat suitability values were calculated by the Habitat Suitability Modeler in ArcGIS Pro. Models considered the selected landscape factor, distance to *Clarkia*, and distance to *Sambucus*. Aspect, elevation, slope, geologic unit, vegetation type, and distance to water were all weighted equally with distance to *Clarkia* and *Sambucus*. The model that considered all landscape factors weighted distance to *Clarkia* and distance to *Sambucus* twice as heavily as other factors. A simple linear regression was developed to explain the differences in *C. sequoiae* abundance as a result of these landscape factors.

$^*p < .05$.

Discussion

While there is a need for pollinator monitoring programs, current protocols using passive trapping and/or aerial netting in areas of interest alone are likely not sufficient to successfully assess bee populations (Portman et al., 2020; Prendergast & Hogendoorn, 2021). We set out to employ a variety of tools available to researchers that exemplify simple adjustments which can be used to improve current bee monitoring techniques. We mapped suitable habitat for the small carpenter bee species, *Ceratina sequoiae*, at Pinnacles National Park using the Suitability Modeler tool in ArcGIS Pro, iNaturalist records, and museum data. The methods we applied have potential for site prioritization to better target areas where monolectic bees are expected, but the limitations of these tools must be considered.

Using iNaturalist observations is clearly only effective in developed areas, where the public has access for photos. In our maps, much of the northern and southern areas of the park appear unsuitable, but there are few observations of *Clarkia* or *Sambucus* in these areas which may not reflect the true frequency of these plants due to a lack of trails and public access (Figure 3-3, 3-4). The data are much stronger in the central area of the park, where our plots are located, and the park is fairly well developed. Furthermore, iNaturalist observations have varying levels of accuracy, while some points have 3 m accuracy others have 500 m accuracy, which could potentially disrupt the analysis. We opted for a maximum of 100 m accuracy as this seemed to be a reasonable range considering the estimated foraging distance of *C. sequoiae*. Consideration needs to be taken to determine what accuracy is reasonable for one's study species. To examine monolectic bee habitat in developed areas like urban parks, using existing iNaturalist observations could be very effective. Urban areas typically have improved public access for photographs and better cell phone service for refined spatial accuracy on iNaturalist observations than a national park.

There are also limitations within the abilities of ArcGIS Pro to represent landscape realistically. For example, the pixels of the digital elevation models (DEM) used represent a $(3\ \mathrm{m})^2$ area. When considering an organism as small as a bee, the microclimates created within a $(3\ \mathrm{m})^2$ area could have implications for the species habitat preferences. Subsequently, the DEM affects the determination of slope and aspect. Moreover, spatial objects such as lines or points do not accurately represent the area of a plant or stream.

Our results indicate that *C. sequoiae* may be dependent on a variety of landscape factors rather than just the presence or absence of required floral and nesting resources. The Suitability Modeler generally had a high percent prediction accuracy, 71% or greater in every model except one (Table 3-2). The highest PPAs were achieved for both only plots and plots paired with opportunistic collections when considering aspect, slope, distance to water, and all selected topographic variables in addition to the distances to *Clarkia* and *Sambucus* (Table 3-2). The lowest PPA (59%) was calculated from plots and opportunistic collections for the model that only considered *Clarkia* and *Sambucus* locations (Table 3-2).

To further confirm suitability model success, we tested for significant positive correlations between the suitability value calculated by the modeler and *C. sequoiae* abundance. All eight models had a positive correlation, and five were significant: elevation, vegetation type, slope, aspect, and *Clarkia* and *Sambucus* locations alone (Figure 3-5). The most robust model was the one that included elevation in addition to *Clarkia* and *Sambucus* locations (Figure 3-5). We utilized museum data from just nine plots, of which two were used to initially describe suitable habitat. Therefore, the regression results from the habitat suitability models are more suggestive than conclusive. However, the results from both the PPAs and the regressions indicate that topographic features aside from floral and nesting preferences could be affecting *C. sequoiae* presence. Future studies are needed to determine precisely how many sites are needed to successfully predict suitable habitat and create robust suitability models for a monolectic bee species. Topographic features have not been previously considered for this species and are rarely acknowledged in other bee monitoring studies. However, topographic information may be able to improve site prioritization and bee monitoring techniques (Doherty et al., 2021).

iNaturalist and the Suitability Modeler tool in ArcGIS Pro are potentially underutilized tools for monitoring bee populations and distribution. Future research could benefit from utilizing similar techniques to determine where to establish plots to study monolectic bees or for monitoring monolectic species habitat. Recent publications have also had success using citizen science to model where invasive bee species may spread throughout a country (Dart et al., 2022). Pre-existing data such as iNaturalist observations and museum data paired with a quick, user-friendly tool like the Suitability Modeler could be useful solutions to assist with issues in current wide-scale bee monitoring protocols.

The status of most native bees is unknown, but anywhere from 25 to 50% of bee species out of 20,000 worldwide may be at risk (Kopec & Burd, 2017; Zattara & Aizen, 2021). Despite these estimations, only 483 bee species are listed on the IUCN Red List, of which 316 are data deficient, and merely 9 are listed as critically endangered (IUCN, 2021). In general, insect conservation is lagging due to insufficient knowledge for listing species (Winfree, 2010). By providing creative solutions to bee monitoring practices, we aim to fill this knowledge gap and press future studies to consider topographic traits, citizen science, and geospatial analyses in partnership with traditional monitoring techniques to better assess bee status.

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CHAPTER 4

OBSERVATION OF A NOVEL FORAGING BEHAVIOR: MINING BEES (ANDRENIDAE: *ANDRENA*) UTILIZING APHID-PRODUCED PINE HONEYDEW

Abstract

How visual patterns, coloration, and nectar of flowers affects foraging by bees is well-studied, particularly in *Apis* and *Bombus* (Apidae) species. However, there are more emerging instances of bees utilizing non-floral food sources. While use of insect-produced honeydew as a food source by solitary bees has not been well-documented, it could be more common than previously thought. During a pollinator survey at Pinnacles National Park in California, we observed bees, primarily *Andrena* (Andrenidae) feeding on aphid-produced (Aphididae) pine honeydew before the onset of spring bloom. The survey sampling combined with historical records at the park suggests that feeding on insect-produced honeydew could be commonplace for the early spring bees found there. Such use of honeydew may arise from lack of floral resources, diversity in foraging behaviors, learning foraging behavior, or a combination of these.

Introduction

Nearly all Sternorrhyncha feed on phloem sap and excrete copious amounts of water and carbohydrates in the form of honeydew. The use of this honeydew as a food source has been well documented among diverse species of Hymenoptera, including various ant (Formicidae) and wasp species, and honeybees (*Apis mellifera*) (Crane, 1991; Moller & Tilley, 1988; Santas, 1983). However, there are relatively few records of non-*Apis* bees using honeydew as a food source. Herrmann et al. (2003) found *Lasioglossum pallens* regularly utilized aphid-produced honeydew from various tree and shrub species. Konrad et al. (2009) conducted both lab and semi-field experiments showing that *Osmia bicornis* collected honeydew from aphids, but foraging was dependent on what plant the honeydew was derived from and whether floral resources were available. These findings suggest that feeding on insect-produced honeydews could be situational.

Insects typically consume aphid-produced honeydew in two ways: directly from the terminalia of aphids (Aphididae) or from fallen droplets left on plants (Douglas, 2006). Ants often feed directly from the terminalia of aphids when tending them (Douglas, 2006). It is unclear how commonly and under what conditions bees forage on insect-produced honeydew. Cameron et al. (2019) observed large numbers of *Bombus terrestris* feeding on fallen aphid-produced honeydew droplets during drought conditions. Meiners et al. (2017) observed over 40 species of non-*Apis* bees foraging for residual honeydew left by scale insects (Coccoidea) on *Adenostoma fasciculatum* at Pinnacles National Park in California. These observations were during times of limited floral resources (Meiners et al., 2017).

While conducting research as part of a pollinator survey at Pinnacles National Park, we observed multiple bee species collecting honeydew from aphids on gray pine (*Pinus sabiniana* Douglas) in February and March of 2020. Particularly, there were high numbers of mining bees (Andrenidae: *Andrena*) consuming pine honeydew. To our knowledge, there are no published records of mining bees as opportunistic foragers on aphid-produced pine honeydew. The only other record of mining bees consuming insect-produced honeydew is by Meiners et al. (2017), who observed over 100 instances of mining bees feeding on honeydew excreted by scale insects. It is not clear whether this behavior is unique to the *Andrena* found at Pinnacles National Park, or whether it is a common behavior among mining bees that has been previously overlooked.

Methods

Pinnacles National Park, PNP, is a conserved area in the South Coast Range of California, located south of Paicines, California, USA, located in San Benito and Monterey Counties. The semi-arid Mediterranean climate at PNP cultivates 10,767 ha of predominantly chaparral habitat (Kittel et al., 2012). While sampling nine plots that were established in 2011 for a pollinator monitoring study (Meiners et al., 2019), we observed bees foraging for gray pine honeydew in three one hectare plots during February and March of 2020. This early in the season there were only a few species of plant in bloom at these plots. The survey took place from late February to early July. Sampling was completed only if conditions were ideal, i.e., at least fairly sunny, calm winds, and 16° C or above. Blooming plants at each plot were recorded at each sampling occasion, and quantified as ‘few’, ‘moderate’, or ‘abundant’. Bees were sampled morning and afternoon by aerial netting. Two collectors took opposite halves of the plot and netted for 15 minutes, then switched for a second 15 minutes. Collectors attempted to walk at an even pace through the entire plot during the collection time rather than focusing on one or two areas within a plot. Due to the observation of bees at Pinnacles National Park feeding on scale-produced honeydew on non-flowering *Adenostoma* by Meiners et al. (2017), collectors visually surveyed for bees on a variety of substrates in addition to flowering plants, including bare ground, shrubs not in bloom, grasses, trees, mud, rocks, etc. All sampling that occurred on tall shrubs and pines were on lower branches that could be reached by collectors on foot. Bees collected on flowers, trees, and shrubs were recorded in association with the respective plant species and bees collected in midair or on the ground were recorded as “Air/ground”. Bees caught in aerial nets were placed in kill jars. Specimens were frozen for later processing when they were thawed, pinned, labeled and identified to species by researchers at the USDA-ARS Pollinating Insects Research Unit. Specimens were curated into the USDA-ARS Pollinating

Insects Research Unit's US National Pollinating Insects Collection, but remain the property of the National Park Service.

Results

A total of 34 bee specimens were collected on gray pine on four different days (Table 4-1). The aphids, identified as *Essigella sp.,* were present on each occasion bees were collected on pine (Figure 4-1A, B, D). It is unclear if there was one aphid species or multiple, as *Essigella* is currently composed of approximately 25 pine-feeding cryptic species, of which six are part of species complexes (Théry et al., 2018). The bees appeared to be feeding on fallen honeydew droplets on pine needles (Figure 4-1A, C, D). These bees were almost exclusively mining bees (*Andrena*) (Table 4-2). Only four non-*Andrena* were collected, two *Lasioglossum sp.* and two *Apis mellifera* Linnaeus (Table 4-2). In addition, there were photographed instances of one *Colletes sp.* and one *Nomada sp.* on pine during the same time period provided by a National Park Service employee (Figure 4-1B, C).

We examined historical records in the park (1996-2012) and found five records of bees netted on grey pine, two in 2011 and three in 2012 (Table 4-1). These five historical records included one *Osmia gabrielis* Cockerell*,* one *Andrena chlorura* Cockerell, and three *Andrena knuthiana* Cockerell (Table 4-2). The majority of the bees were collected when few to no plants were blooming in the plot (Table 4-3).

Figures and Tables

Table 4-1

Bees Collected on Pinus sabiniana at Pinnacles National Park in 2020 by Date, Location, and Habitat Type

Date	Location	Habitat type	# Bees collected
25 February	Lower Needlegrass Canyon	Live Oak Woodland	5
25 February	Lower McCabe Canyon	Alluvial	4
3 March	Lower Needlegrass Canyon	Live Oak Woodland	8
4 March	Upper McCabe Canyon	Alluvial	1
4 March	Lower McCabe Canyon	Alluvial	15
31 March	Upper McCabe Canyon	Alluvial	1

Table 4-2

Faunal List and Count of Bees Collected on Pinus sabiniana at Pinnacles National Park

Taxa	Year	# Bees collected
Osmia gabrielis	2011	1
Andrena chlorura	2011	1
Andrena knuthiana	2012	3
Apis mellifera	2020	2
Lasioglossum nigrescens	2020	1
Lasioglossum punctatoventre	2020	1
Andrena cerasifolii	2020	9
Andrena spp.	2020	21

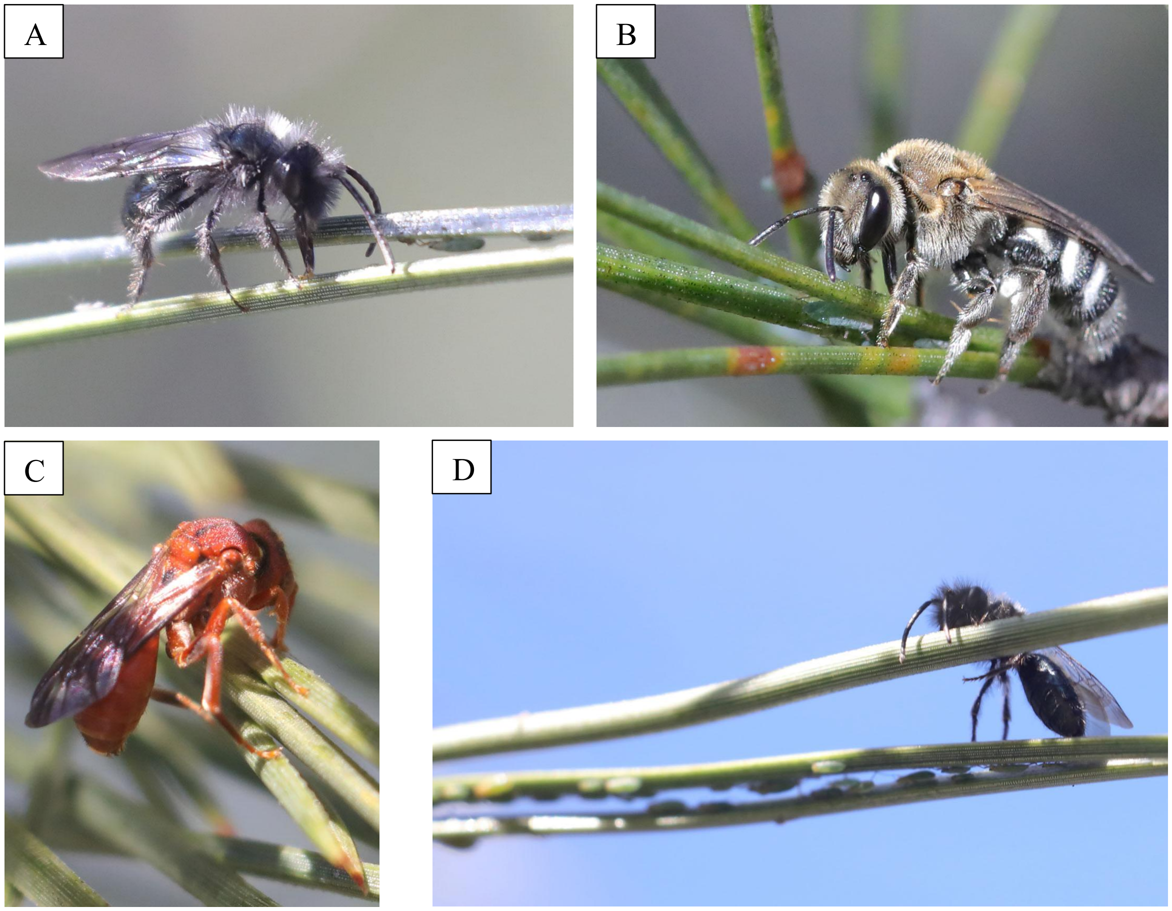
Table 4-3

Flowers in Bloom at Pinnacles National Park in 2020 by Date and Location Where Bees Were Found Foraging on Pinus sabiniana

Date	Location	Bloom	Quantity
25 February	Lower Needlegrass Canyon	None	NA
25 February	Lower McCabe Canyon	None	NA
3 March	Lower Needlegrass Canyon	*Solanum umbelliferum*	Few
4 March	Upper McCabe Canyon	None	NA
4 March	Lower McCabe Canyon	None	NA
31 March	Upper McCabe Canyon	*Lupinus albifrons var.albifrons*	Moderate
		Ceanothus cuneatus var.cuneatus	Few
		Eschscholzia californica	Few
		Erodium cicutarium	Few
		Amsinckia menziesii	Few

Figure 4-1

Examples of Bees Feeding on Aphid-produced Honeydew on Pinus sabiniana



Note. A. *Andena cerasifolii* male feeding on honeydew left behind on a pine needle near aphids. B. *Colletes sp.* female above an aphid feeding on honeydew. C. *Nomada sp.* female feeding on residual honeydew. D. *Andrena cerasifolii* male on pine among many aphids. Photo credits to NPS/Paul G. Johnson.

Discussion

There are several potential explanations as to why there were so many *Andrena* foraging on aphid-produced pine honeydew. It could be that non-*Apis* bees utilize insect-produced honeydew more often than previously thought. Such use of honeydew may arise from lack of floral resources, diversity in foraging behaviors, learned foraging behavior, or a combination of these reasons.

This foraging behavior was only observed at the beginning of the spring bloom when floral resources were very limited. Others have observed bees using insect-produced honeydew during times of limited floral resource availability. Cameron et al. (2019) found a bumblebee (*Bombus terrestris*) to be an opportunistic forager on aphid honeydew during drought conditions, likely due to diminished food rewards provided by temperature-stressed flowers. Meiners et al. (2017) noted that bees foraging on scale-produced honeydew occurred at a time of low floral availability. There have also been semi-field experiments showing that *Osmia bicornis* will only feed on aphid-produced honeydew in the absence of floral nectar (Konrad et al., 2009). At the dates and locations of our observations, there were few to no flowers in bloom, so there was likely a lack of sufficient floral nectar resources (Table 3). The bees may have been using the insect-produced honeydew as a way to cope with these conditions.

Andrena constitutes a diverse group with many polylectic species, feeding from a wide variety of flowers (Michener, 2007). Of the bee species previously observed foraging on scale-produced honeydew with known floral preferences, the majority were generalist species (Meiners et al., 2017). Generalist bees could be utilizing a variety of resources to obtain well-rounded provisions. Bees rely on varying levels of protein, carbohydrates, lipids, and fatty acids; flowers produce pollen with a range of nutritional and chemical profiles (Danforth et al., 2019). There are recorded instances of polylectic bees adjusting foraging behaviors based on pollen quality, floral resource availability, and chemical signaling (Cameron et al., 2019; Konrad et al., 2009; Ruedenauer et al., 2016; Wilson Rankin et al., 2020). Experiments done on female parasitoid wasps have shown that individuals fed aphid-produced honeydew live longer than individuals given sucrose or water (Faria et al., 2008), which could be the same case with bees. The diversity of foraging behaviors in generalist bee species may allow more flexibility in where nutrients are obtained.

Generalist species often use learning in foraging and selecting nutrients (Dukas 1998). Food rewards, both artificially and naturally produced, affect learning and memory in bees (Muth et al., 2018; Simcock et al., 2018). In honeybees (*Apis mellifera*), nutritional sugars with the correct taste and odor cues can restore robust 24 hour memories with the bees preferentially returning to the same locations to forage for these sugars (Mustard et al., 2018; Tsvetkov et al., 2019). Similar behavior has been observed in bumblebees (Chittka et al., 1999; Zhang et al., 2020). There are few studies investigating food rewards as motivation for modifying foraging behavior in solitary bees, but they could have similar learning behaviors to *Apis* and *Bombus*.

Bees feeding on non-floral resources, notably insect-produced honeydews, may be more commonplace than previously believed. *Andrena* are often among the first bees to emerge in the spring (Wilson & Carril, 2016). Early in the season, there are few flowers in bloom. Additionally, of the few plants that were in bloom, such as *Solanum umbelliferum* and *Lupinus albifrons,* most are not typically visited by *Andrena* at PNP. The lack of floral resources, the foraging behaviors of generalist bees, and learning foraging behavior from sugar rewards could all impact why we observed so many mining bees feeding on aphid-produced pine honeydew.

Studies delving into how non-floral sugar rewards affect learning and foraging behavior in solitary bees could provide more insights into why bee forage on non-floral sugars. Future research may also benefit from considering non-floral food sources for native bees when examining foraging behaviors or conducting surveys. Surveys should include investigation of other substrates in addition to flowering plants in order to develop a more robust understanding of bee foraging behavior.

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CHAPTER 5

CONCLUSION

Pinnacles National Park, PNP, is currently known to be one of the most diverse locations in the world for bees for areas of this size. Our survey brought the total number of bee species housed in the park to 511 in just 10,767 ha. The 2020 updated park inventory was also the first detection of the non-native alfalfa leaf-cutter bee, *Megachile rotundata*, at PNP, which could have a negative impact on native bees and should be closely monitored. We examined how bee diversity and community composition has changed at PNP over time. While 255 species that had been previously observed in the park were not found in 2020, we found 29 species were new to PNP and we collected 19 species that had not been observed since 2002 or earlier. Hill-diversity numbers showed small potential increases in bee richness over time, but overall were at similar levels across years. Ordination analyses indicated that community composition differed significantly between years. Neither Hill-diversity or ordination analyses found differences in bee diversity or community composition by habitat type. These findings are indicative of species turnover, but not of overall diversity losses in the park.

We used both passive trapping and aerial netting to collect bees for this survey. These methods alone have been critiqued as inadequate by researchers and may not be sufficient for large-scale monitoring. We supplemented our monitoring work by utilizing creative tools that are rarely used in bee monitoring studies. We modeled suitable habitat at PNP for the monolectic bee, *Ceratina sequoiae* Michener, using both citizen science records from iNaturalist and the Habitat Suitability Modeler in ArcGIS Pro. We selected six topographic factors that may affect *C. sequoiae* abundance in addition to their required floral and nesting resources. The model that included elevation as an influence on *C. sequoiae* abundance was more robust than only considering floral and nesting resources. Utilizing similar methods could be beneficial for future monitoring work by improving site prioritization, modeling bee range changes, or finding areas that may be of greater importance to specific monolectic bee species.

The distinctiveness of PNP lies not only in the diversity of bee species, but also in their foraging behavior. Early in this study, we observed bees, mostly *Andrena*, foraging on aphid-produced pine honeydew. Such behavior has rarely been noted in native bee studies and may result from a lack of floral resources, unique learned foraging behavior at PNP, an overall larger diversity in bee foraging behaviors than previously known, failure by researchers to notice non-floral feeding, or a combination of these reasons. This behavior would not have been observed if we did not purposefully sample non-floral areas within our plots. Therefore, we encourage future studies to consider non-floral honeydew as potential forage for bees.

Pinnacles National Park offers a rich native bee fauna and the semi-pristine habitat appears to be supporting bee diversity well over time. Continuing to monitor trends in innately variable bee populations is a critical step for protecting pollinators in a time of biodiversity loss and climate uncertainty. By conserving bees, the ecosystem services they provide are also conserved–sustaining flowering plant populations, preventing soil erosion, renewing water sources, and maintaining nutrient cycles, among other things. More natural areas would benefit from implementing long-term pollinator monitoring programs. Moreover, future research should consider the diversity of foraging behavior observed in bees and how topographic factors may be affecting bee species diversity and presence.

APPENDICES

Appendix A

Vegetation composition of sampled plots at Pinnacles National Park

Plot	Generalized Habitat	Vegetation Type	Area (m^2)
High Peaks	Blue Oak Woodland	Blue Oak/Mixed Herbaceous Woodland Association	3396.062
		Blue Oak Woodland Alliance	1001.467
		Californian Xeric Chaparral Shrubland Group	2.78902
		Mediterranean California Naturalized Annual and Perennial Grassland Herbaceous Vegetation	5225.691
Lower McCabe	Alluvial	Foothill Pine Woodland Alliance	2735.628
		Valley Oak Woodland Alliance	633.5415
		Mediterranean California Naturalized Annual and Perennial Grassland Herbaceous Vegetation	457.8689
		California Coastal Scrub Shrubland Macrogroup	6398.925
Needlegrass BOW	Blue Oak Woodland	Blue Oak/Mixed Herbaceous Woodland Association	9101.167
		Blue Oak Woodland Alliance	3.254127
		Mediterranean California Naturalized Annual and Perennial Grassland Herbaceous Vegetation	416.195
Needlegrass LOW	Live Oak Woodland	Valley Oak Woodland Alliance	1377.048
		Coast Live Oak Woodland Alliance	301.3984

		Blue Oak Woodland Alliance	5.455013
		Californian Xeric Chaparral Shrubland Group	585.0126
		Mediterranean California Naturalized Annual and Perennial Grassland Herbaceous Vegetation	9289.492
Peaks View	Alluvial	Valley Oak Woodland Alliance	159.0025
		Alluvial Herb and Shrub Vegetation	5930.156
		Foothill Pine Woodland Alliance	989.9205
		Southwestern North American Riparian/Wash Scrub Shrubland Group	3513.034
South Wilderness	Live Oak Woodland	Coast Live Oak Woodland Alliance	9913.035
		Southwestern North American Riparian Evergreen and Deciduous Forest Group	16.48252
		Post Burn and Post Disturbance Californian Xeric Chaparral Shrubland	0.008544
		Post Burn and Post Disturbance Californian Chaparral Shrubland	80.78388
Upper McCabe	Alluvial	Coast Live Oak Woodland Alliance	751.7512
		Alluvial Herb and Shrub Vegetation	9855.684
		California Coastal Scrub Shrubland Macrogroup	53.48747
W. North Wilderness	Grassland	Blue Oak Woodland Alliance	613.5114
		California Wild Buckwheat Shrubland Alliance	1973.789

		Californian Xeric Chaparral Shrubland Group	663.68
		Blue Oak/Mixed Herbaceous Woodland Association	1573.967
		Mediterranean California Naturalized Annual and Perennial Grassland Herbaceous Vegetation	5384.954
West Gate	Blue Oak Woodland	Blue Oak/Mixed Herbaceous Woodland Association	7851.451
		Mediterranean California Naturalized Annual and Perennial Grassland Herbaceous Vegetation	328.1059

Note. Vegetation data was obtained from Kittel et al. (2012). We categorized plots into generalized habitats based on the dominant vegetation type.

Appendix B

Species list for bees collected at Pinnacles National Park in 2020 and associated historic collections

	Bee Family (Subfamily) Genus (Subgenus) Species	1996	1997	1998	1999	2002	2011	2012	2020
1	Andrenidae (Andreninae) Ancylandrena atoposoma	R							
2	Andrenidae (Andreninae) Andrena sp.								C
3	Andrenidae (Andreninae) Andrena sp. 17							R	
4	Andrenidae (Andreninae) Andrena sp. 18							R	
5	Andrenidae (Andreninae) Andrena sp. 19						R	R	
6	Andrenidae (Andreninae) Andrena sp. 22							R	
7	Andrenidae (Andreninae) Andrena sp. 25							R	
8	Andrenidae (Andreninae) Andrena (Anchandrena) quercina			R					
9	Andrenidae (Andreninae) Andrena (Aporandrena) n. sp.	R							

10	Andrenidae (Andreninae) Andrena (Belandrena) nemophilae			R					
11	Andrenidae (Andreninae) Andrena (Belandrena) palpalis		R	R					
12	Andrenidae (Andreninae) Andrena (Cremnandrena) anisochlora			U			U	R	
13	Andrenidae (Andreninae) Andrena (Dasyandrena) cristata			R					
14	Andrenidae (Andreninae) Andrena (Derandrena) arctostaphylae			R		R			
15	Andrenidae (Andreninae) Andrena (Derandrena) californiensis			R		R	R	R	
16	Andrenidae (Andreninae) Andrena (Derandrena) n. sp.	R	R	R			R	U	
17	Andrenidae (Andreninae) Andrena (Derandrena) vandykei			U		R			
18	Andrenidae (Andreninae) Andrena (Derandrena) viridissima						R		
19	Andrenidae (Andreninae) Andrena (Diandrena) chalybioides							R	
20	Andrenidae (Andreninae) Andrena (Diandrena) cuneilabris							R	
21	Andrenidae (Andreninae) Andrena (Diandrena) lewisorum	R	R	R	U		U	U	R
22	Andrenidae (Andreninae) Andrena (Diandrena) nothocalaidis			R					

23	Andrenidae (Andreninae) Andrena (Diandrena) puthua		R	U				R	
24	Andrenidae (Andreninae) Andrena (Diandrena) sperryi						R		
25	Andrenidae (Andreninae) Andrena (Diandrena) subchalybea			R	R	R	U	C	U
26	Andrenidae (Andreninae) Andrena (Diandrena) submoesta					R			
27	Andrenidae (Andreninae) Andrena (Erandrena) principalis			R					
28	Andrenidae (Andreninae) Andrena (Euandrena) astragali		R	R			R	R	R
29	Andrenidae (Andreninae) Andrena (Euandrena) auricoma	R	R	U	R		U		
30	Andrenidae (Andreninae) Andrena (Euandrena) caerulea			U				R	
31	Andrenidae (Andreninae) Andrena (Euandrena) chlorura		R	U		R	U	U	
32	Andrenidae (Andreninae) Andrena (Euandrena) dissimulans			U			U	U	
33	Andrenidae (Andreninae) Andrena (Euandrena) misella			R					
34	Andrenidae (Andreninae) Andrena (Euandrena) nigrocaerulea	R	R	R					

35	Andrenidae (Andreninae) Andrena (Euandrena) suavis			R			U	U	
36	Andrenidae (Andreninae) Andrena (Euandrena) subdepressa			R			R	R	
37	Andrenidae (Andreninae) Andrena (Genyandrena) mackieae		R	U			R	R	
38	Andrenidae (Andreninae) Andrena (Hesperandrena) baeriae		R	R					
39	Andrenidae (Andreninae) Andrena (Hesperandrena) lativentris							R	
40	Andrenidae (Andreninae) Andrena (Holandrena) cressonii		R						
41	Andrenidae (Andreninae) Andrena (Melandrena) aff. cerasifolii		U	U	U		C	C	
42	Andrenidae (Andreninae) Andrena (Melandrena) cerasifolii	U	U	U	R		U	R	U
43	Andrenidae (Andreninae) Andrena (Melandrena) perimelas					R			
44	Andrenidae (Andreninae) Andrena (Melandrena) sola	R	U	U	U		U	U	
45	Andrenidae (Andreninae) Andrena (Micrandrena) aff. ishii			U					
46	Andrenidae (Andreninae) Andrena (Micrandrena) annectens			R			R		
47	Andrenidae (Andreninae) Andrena (Micrandrena) chlorogaster		R	C		R	R	U	

48	Andrenidae (Andreninae) Andrena (Micrandrena) microchlora		U	U	R	R	R	U	
49	Andrenidae (Andreninae) Andrena (Micrandrena) piperi		R	R		R	R	R	
50	Andrenidae (Andreninae) Andrena (Nemandrena) crudeni			U		R	C	C	C
51	Andrenidae (Andreninae) Andrena (Nemandrena) subnigripes			R					
52	Andrenidae (Andreninae) Andrena (Oligandrena) macrocephala	R	U	U		U	U	C	C
53	Andrenidae (Andreninae) Andrena (Parandrena) concinnula			R			R		
54	Andrenidae (Andreninae) Andrena (Pelicandrena) atypica		R	C	R	R	U	R	
55	Andrenidae (Andreninae) Andrena (Plastandrena) prunorum							R	
56	Andrenidae (Andreninae) Andrena (Psammandrena) congrua		R	R			R	R	
57	Andrenidae (Andreninae) Andrena (Ptilandrena) pallidiscopa			R				R	
58	Andrenidae (Andreninae) Andrena (Scaphandrena) lomatii			R					
59	Andrenidae (Andreninae) Andrena (Scaphandrena) plana			R					
60	Andrenidae (Andreninae) Andrena (Scaphandrena) santaclarae		R	R				R	

61	Andrenidae (Andreninae) Andrena (Scoliandrena) cryptanthae	R							
62	Andrenidae (Andreninae) Andrena (Scoliandrena) osmioides			R			R	R	
63	Andrenidae (Andreninae) Andrena (Scrapteropsis) biareola			R					
64	Andrenidae (Andreninae) Andrena (Simandrena) angustitarsata	R	R	C	U		U	U	
65	Andrenidae (Andreninae) Andrena (Simandrena) hypoleuca						R	R	
66	Andrenidae (Andreninae) Andrena (Simandrena) orthocarpi			R			R		
67	Andrenidae (Andreninae) Andrena (Simandrena) pallidifovea	R	R	R	R		R	R	
68	Andrenidae (Andreninae) Andrena (Simandrena) pensilis							R	
69	Andrenidae (Andreninae) Andrena (Thysandrena) aff. candida		R					R	
70	Andrenidae (Andreninae) Andrena (Thysandrena) aff. lauta		R						
71	Andrenidae (Andreninae) Andrena (Thysandrena) candida	U	U	C	U	R	U	U	
72	Andrenidae (Andreninae) Andrena (Thysandrena) vierecki		R	R					
73	Andrenidae (Andreninae) Andrena (Thysandrena) w-scripta	R	R	U	U	R	R	C	

74	Andrenidae (Andreninae) Andrena (Trachandrena) fuscicauda			R	R				
75	Andrenidae (Andreninae) Andrena (Trachandrena) semipunctata		R	R			R		
76	Andrenidae (Andreninae) Andrena (Tylandrena) subtilis			R			R		
77	Andrenidae (Andreninae) Andrena (Tylandrena) waldmerei			R					
78	Andrenidae (Panurginae) Calliopsis smithi	U	U	U	U			R	
79	Andrenidae (Panurginae) Calliopsis (Micronomadopsis) fracta	R	R	R			R		
80	Andrenidae (Panurginae) Calliopsis (Micronomadopsis) helianthi						R		R
81	Andrenidae (Panurginae) Calliopsis (Micronomadopsis) mellipes		R				R		R
82	Andrenidae (Panurginae) Calliopsis (Micronomadopsis) trifolii	R			R				
83	Andrenidae (Panurginae) Calliopsis (Nomadopsis) anthidia	R	R	R					
84	Andrenidae (Panurginae) Calliopsis (Nomadopsis) obscurella	R	U	R	R		U	R	U
85	Andrenidae (Panurginae) Calliopsis (Nomadopsis) zonalis	R	R		R				
86	Andrenidae (Panurginae) Macrotera (Macroteropsis) arcuata			R			R	R	

87	Andrenidae (Panurginae) Panurginus gracilis			C	R		C	C	C
88	Andrenidae (Panurginae) Panurginus melanocephalus		R	R			U	U	U
89	Andrenidae (Panurginae) Panurginus morrisoni		R					R	
90	Andrenidae (Panurginae) Panurginus nigrellus	U	U	U			U	C	C
91	Andrenidae (Panurginae) Panurginus occidentalis					R			
92	Andrenidae (Panurginae) Panurginus quadratus			R	U				
93	Andrenidae (Panurginae) Panurginus sp. 1								R
94	Andrenidae (Panurginae) Perdita sp.								R
95	Andrenidae (Panurginae) Perdita (Hesperoperdita) trisignata	R	U	U	C		R	R	
96	Andrenidae (Panurginae) Perdita (Perdita) aff. linsleyi n.sp.	R	R	R	R		R		
97	Andrenidae (Panurginae) Perdita (Perdita) claypolei		U	U					R
98	Andrenidae (Panurginae) Perdita (Perdita) hirticeps							R	

99	Andrenidae (Panurginae) Perdita (Perdita) holoxantha						R		
100	Andrenidae (Panurginae) Perdita (Perdita) isocomae		R						
101	Andrenidae (Panurginae) Perdita (Perdita) aff. jucunda								R
102	Andrenidae (Panurginae) Perdita (Perdita) jucunda		R		R				R
103	Andrenidae (Panurginae) Perdita (Perdita) aff. linsleyi								R
104	Andrenidae (Panurginae) Perdita (Perdita) linsleyi						R		
105	Andrenidae (Panurginae) Perdita (Perdita) rhois	U	C	C	R			R	U
106	Andrenidae (Panurginae) Perdita (Perdita) salicis						R		
107	Andrenidae (Panurginae) Perdita (Pygoperdita) aureovittata		R						
108	Andrenidae (Panurginae) Perdita (Pygoperdita) californica			R					
109	Andrenidae (Panurginae) Perdita (Pygoperdita) distropica	R	U	U	U		U	C	C
110	Andrenidae (Panurginae) Perdita (Pygoperdita) micheneri			U	R		R		R

111	Andrenidae (Panurginae) Perdita (Pygoperdita) montereyensis	U	U	U	U		U	C	U
112	Andrenidae (Panurginae) Perdita (Pygoperdita) nitens	U	U	R			U	R	R
113	Apidae (Apinae) Anthophora (Anthophoroides) californica	R	U	R	R	R	R	R	R
114	Apidae (Apinae) Anthophora (Heliophila) columbariae			R					
115	Apidae (Apinae) Anthophora (Heliophila) curta	R	R	R	R		R	R	R
116	Apidae (Apinae) Anthophora (Heliophila) estebana		R						
117	Apidae (Apinae) Anthophora (Heliophila) flavocincta					R			
118	Apidae (Apinae) Anthophora (Lophanthophora) pacifica		R	U			R		R
119	Apidae (Apinae) Anthophora (Melea) bomboides	R							R
120	Apidae (Apinae) Anthophora (Mystacanthophora) urbana	R	U	U	U	R	U	U	U
121	Apidae (Apinae) Anthophora (Paramegilla) centriformis	R	U	R	U		R		R
122	Apidae (Apinae) Anthophora (Pyganthophora) crotchii	R	U	R	R	R	U	U	U

123	Apidae (Apinae) Anthophora (Pyganthophora) edwardsii	R	R	R			U	U	U
124	Apidae (Apinae) Anthophora (Pyganthophora) platti	U	U	U	R		U	U	U
125	Apidae (Apinae) Anthophorula (Anthophorisca) nitens		U	U			U	U	U
126	Apidae (Apinae) Anthophorula (Anthophorula) albicans		U	U		R	R	R	U
127	Apidae (Apinae) Apis mellifera	R	C	C	U	U	C	C	C
128	Apidae (Apinae) Bombus (Crotchiibombus) crotchii		U	U	R				
129	Apidae (Apinae) Bombus (Fervidobombus) californicus	R	U	U	R	R	R	R	U
130	Apidae (Apinae) Bombus (Pyrobombus) caliginosus		U				R	R	
131	Apidae (Apinae) Bombus (Pyrobombus) edwardsii							R	
132	Apidae (Apinae) Bombus (Pyrobombus) melanopygus	R	C	U	R	R	U		U
133	Apidae (Apinae) Bombus (Pyrobombus) vandykei		R	R			R		
134	Apidae (Apinae) Bombus (Pyrobombus) vosnesenskii	R	C	C	R	R	U	R	U

135	Apidae (Apinae) Centris (Paracentris) aff. californica		U	U	R				R
136	Apidae (Apinae) Diadasia aff. ochracea		R	R		R	R	U	U
137	Apidae (Apinae) Diadasia angusticeps		R	R	C	R	C	U	
138	Apidae (Apinae) Diadasia australis					R	R		
139	Apidae (Apinae) Diadasia bituberculata	R	U	R	U	U	U	C	U
140	Apidae (Apinae) Diadasia consociata							R	R
141	Apidae (Apinae) Diadasia diminuta								R
142	Apidae (Apinae) Diadasia laticauda		U	U	R	R	U	U	U
143	Apidae (Apinae) Diadasia lutzi								R
144	Apidae (Apinae) Diadasia nigrifrons						R		
145	Apidae (Apinae) Diadasia nitidifrons		R	U	R	R	U	U	U
146	Apidae (Apinae) Diadasia ochracea								R

147	Apidae (Apinae) Diadasia rinconis							R	R
148	Apidae (Apinae) Diadasia sp.								R
149	Apidae (Apinae) Eucera (Synhalonia) actuosa		R	R	R	U	C	C	C
150	Apidae (Apinae) Eucera (Synhalonia) amsinckiae	R	R	R		R	R	R	R
151	Apidae (Apinae) Eucera (Synhalonia) cordleyi		R	U		R	U	R	R
152	Apidae (Apinae) Eucera (Synhalonia) delphinii		U	R	R	R	R	R	R
153	Apidae (Apinae) Eucera (Synhalonia) dorsata		U	R	R	R	U	U	U
154	Apidae (Apinae) Eucera (Synhalonia) edwardsii	R	R	R		R		R	
155	Apidae (Apinae) Eucera (Synhalonia) frater								R
156	Apidae (Apinae) Eucera (Synhalonia) lunata			R			R	R	U
157	Apidae (Apinae) Eucera (Synhalonia) sp.								R
158	Apidae (Apinae) Eucera (Synhalonia) venusta	U	U	U	R		R	R	

159	Apidae (Apinae) Eucera (Synhalonia) virgata			U	R	R	U	U	U
160	Apidae (Apinae) Habropoda dammersi			R					
161	Apidae (Apinae) Habropoda depressa	R	U	U	R	R	U	U	R
162	Apidae (Apinae) Habropoda tristissima	R	U	R	R	R	R	U	R
163	Apidae (Apinae) Melecta (Melecta) pacifica		R	R			R		R
164	Apidae (Apinae) Melecta (Melecta) separata			R	R	R	R	U	U
165	Apidae (Apinae) Melecta (Melectomimus) edwardsii		R				R		
166	Apidae (Apinae) Melissodes sp.								U
167	Apidae (Apinae) Melissodes sp. m1			R					
168	Apidae (Apinae) Melissodes (Callimelissodes) clarkiae		R				R	R	R
169	Apidae (Apinae) Melissodes (Callimelissodes) composita							R	
170	Apidae (Apinae) Melissodes (Callimelissodes) lupinus		R	U		R	U	C	U

171	Apidae (Apinae) Melissodes (Callimelissodes) lustra		R						
172	Apidae (Apinae) Melissodes (Callimelissodes) n. sp.							R	
173	Apidae (Apinae) Melissodes (Callimelissodes) n. sp. 1		R	R	R				
174	Apidae (Apinae) Melissodes (Callimelissodes) n. sp. 2		R	R	R	R	R		R
175	Apidae (Apinae) Melissodes (Callimelissodes) nigracauda			R					
176	Apidae (Apinae) Melissodes (Callimelissodes) plumosus		R				R	U	U
177	Apidae (Apinae) Melissodes (Callimelissodes) stearnsi		R	R		C	U	C	C
178	Apidae (Apinae) Melissodes (Eumelissodes) paulula		R						
179	Apidae (Apinae) Melissodes (Eumelissodes) velutina							R	
180	Apidae (Apinae) Melissodes (Melissodes) tepida							R	
181	Apidae (Apinae) Peponapis (Peponapis) aff. pruinosa								R
182	Apidae (Apinae) Peponapis (Peponapis) pruinosa							R	

183	Apidae (Apinae) Xeromelecta (Melectomorpha) californica	R	U	R	U		R	R	R
184	Apidae (Apinae) Xeromelecta (Xeromelecta) larreae	R							
185	Apidae (Nomadinae) Brachynomada (Melanomada) melanantha							R	R
186	Apidae (Nomadinae) Epeolus americanus	R	R			R	R	R	R
187	Apidae (Nomadinae) Epeolus compactus			R	R			R	
188	Apidae (Nomadinae) Epeolus mesillae						R	R	
189	Apidae (Nomadinae) Epeolus minimus				R	R		R	R
190	Apidae (Nomadinae) Neopasites (Micropasites) sp.							R	
191	Apidae (Nomadinae) Neopasites (Micropasites) sp. 4								R
192	Apidae (Nomadinae) Nomada sp.								C
193	Apidae (Nomadinae) Nomada (Centrias) crotchii		R	U			R	R	R
194	Apidae (Nomadinae) Nomada (Centrias) sp. A	R	R						

195	Apidae (Nomadinae) Nomada (Holonomada) edwardsii		R	R				R	
196	Apidae (Nomadinae) Nomada (Nomada) sp. A	R	R	R			R	R	
197	Apidae (Nomadinae) Nomada (Nomada) sp. AA							R	
198	Apidae (Nomadinae) Nomada (Nomada) sp. B	R	R	R			R	R	U
199	Apidae (Nomadinae) Nomada (Nomada) sp. BB					R	R	R	
200	Apidae (Nomadinae) Nomada (Nomada) sp. CC					R		R	
201	Apidae (Nomadinae) Nomada (Nomada) sp. D	U	U	U	R				
202	Apidae (Nomadinae) Nomada (Nomada) sp. DD						R		
203	Apidae (Nomadinae) Nomada (Nomada) sp. E	U	R	R	R		R	R	
204	Apidae (Nomadinae) Nomada (Nomada) sp. EE						R		
205	Apidae (Nomadinae) Nomada (Nomada) sp. F	R		R				R	
206	Apidae (Nomadinae) Nomada (Nomada) sp. FF							R	

207	Apidae (Nomadinae) Nomada (Nomada) sp. G						R	R	
208	Apidae (Nomadinae) Nomada (Nomada) sp. GG			R				R	
209	Apidae (Nomadinae) Nomada (Nomada) sp. HH			R		R			
210	Apidae (Nomadinae) Nomada (Nomada) sp. I			R					
211	Apidae (Nomadinae) Nomada (Nomada) sp. II					R			
212	Apidae (Nomadinae) Nomada (Nomada) sp. J			R			R		
213	Apidae (Nomadinae) Nomada (Nomada) sp. Q		R	R			R		
214	Apidae (Nomadinae) Nomada (Nomada) sp. R		R	R					
215	Apidae (Nomadinae) Nomada (Nomada) sp. S		R						
216	Apidae (Nomadinae) Nomada (Nomada) sp. T		R						
217	Apidae (Nomadinae) Nomada (Nomada) sp. U		U	U			R	U	
218	Apidae (Nomadinae) Nomada (Nomada) sp. V	R	R	R		R	R	R	R

219	Apidae (Nomadinae) Nomada (Nomada) sp. W		U	U			U	U	R
220	Apidae (Nomadinae) Nomada (Nomada) sp. X			R			R	R	
221	Apidae (Nomadinae) Nomada (Nomada) sp. Y			R		R			
222	Apidae (Nomadinae) Nomada (Nomada) sp. Z			U					
223	Apidae (Nomadinae) Oreopasites aff. hurdi n.sp		R	R	R		R	R	R
224	Apidae (Nomadinae) Oreopasites powelli								R
225	Apidae (Nomadinae) Oreopasites vanduzeei	R	R	R	R		R		R
226	Apidae (Nomadinae) Townsendiella ensifera		R	U	U			R	R
227	Apidae (Nomadinae) Townsendiella rufiventris			R					
228	Apidae (Nomadinae) Triepeolus sp.								R
229	Apidae (Nomadinae) Triepeolus sp. P1						R	R	
230	Apidae (Nomadinae) Triepeolus sp. P2						R		

231	Apidae (Nomadinae) Triepeolus (Triepeolus) heterurus							R	
232	Apidae (Nomadinae) Triepeolus (Triepeolus) sp. 1			R					
233	Apidae (Nomadinae) Triepeolus (Triepeolus) timberlakei		R	R	R		R	R	
234	Apidae (Xylocopinae) Ceratina sp.								R
235	Apidae (Xylocopinae) Ceratina aff. nanula	R	R	R					
236	Apidae (Xylocopinae) Ceratina (Ceratina) arizonensis	U	C	U	U	U	C	C	C
237	Apidae (Xylocopinae) Ceratina (Euceratina) dallatorreana			R		R			U
238	Apidae (Xylocopinae) Ceratina (Zadontomerus) acantha	R	U	R		R	U	R	U
239	Apidae (Xylocopinae) Ceratina (Zadontomerus) hurdi	R	R	R		R	U	U	R
240	Apidae (Xylocopinae) Ceratina (Zadontomerus) nanula	R	U	U	U	U	U	C	U
241	Apidae (Xylocopinae) Ceratina (Zadontomerus) pacifica		R	R			R	R	U
242	Apidae (Xylocopinae) Ceratina (Zadontomerus) punctigena	R	U	R	U		R		R

243	Apidae (Xylocopinae) Ceratina (Zadontomerus) sequoiae	R	U	U	U	R	U	U	U
244	Apidae (Xylocopinae) Ceratina (Zadontomerus) tejonensis		U	R			R	R	R
245	Apidae (Xylocopinae) Ceratina (Zadontomerus) timberlakei		R	R	R	R	R	R	R
246	Apidae (Xylocopinae) Xylocopa (Notoxylocopa) tabaniformis	R	U	R	R	R	R	R	R
247	Colletidae (Colletinae) Colletes aff. algarobiae								U
248	Colletidae (Colletinae) Colletes californicus								R
249	Colletidae (Colletinae) Colletes consors consors	U	U	R	R		U	R	
250	Colletidae (Colletinae) Colletes consors pascoensis								R
251	Colletidae (Colletinae) Colletes daleae aff. algarobiae	R	U	U	R		R		
252	Colletidae (Colletinae) Colletes daleae algarobiae							U	
253	Colletidae (Colletinae) Colletes fulgidus fulgidus								R
254	Colletidae (Colletinae) Colletes simulans fulgidus		R	R	R			R	

255	Colletidae (Colletinae) Colletes simulans simulans		R						
256	Colletidae (Colletinae) Colletes simulans slevini	R	U	U	U		R	R	R
257	Colletidae (Hylaeinae) Hylaeus sp.								R
258	Colletidae (Hylaeinae) Hylaeus (Cephalylaeus) nunenmacheri			R	R				
259	Colletidae (Hylaeinae) Hylaeus (Hylaeus) bisinuatus		R						
260	Colletidae (Hylaeinae) Hylaeus (Hylaeus) conspicuus				R	R		R	R
261	Colletidae (Hylaeinae) Hylaeus (Hylaeus) granulatus		U	U	U		R	R	R
262	Colletidae (Hylaeinae) Hylaeus (Hylaeus) mesillae	R	C	U	U		U	R	U
263	Colletidae (Hylaeinae) Hylaeus (Hylaeus) rudbeckiae	R					R	R	U
264	Colletidae (Hylaeinae) Hylaeus (Hylaeus) verticalis	R	U	U	U		R	R	R
265	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) aff. cookii n.sp.		R	R	R				
266	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) calvus	R		U	U		R	U	R

267	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) coloradensis		U	U	R				R
268	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) n. sp.2		U	R	R		R		
269	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) nevadensis	U	U	U	U		R	U	U
270	Colletidae (Hylaeinae) Hylaeus (Paraprosopis) polifolii		U	U	U		R		U
271	Colletidae (Hylaeinae) Hylaeus (Prosopis) aff. episcopalis								U
272	Colletidae (Hylaeinae) Hylaeus (Prosopis) episcopalis						R	R	
273	Colletidae (Hylaeinae) Hylaeus (Prosopis) hinae	U	C	U	U				
274	Colletidae (Hylaeinae) Hylaeus (Spatulariella) punctatus				R				
275	Halictidae (Halictinae) Agapostemon (Agapostemon) angelicus / texanus					U	C	C	U
276	Halictidae (Halictinae) Agapostemon (Agapostemon) femoratus					R	R		
277	Halictidae (Halictinae) Agapostemon (Agapostemon) texanus	R	R	R	U				
278	Halictidae (Halictinae) Augochlorella (Augochlorella) pomoniella		R	R				R	R

279	Halictidae (Halictinae) Halictus (Nealictus) farinosus	U	C	C	C	C	C	C	C
280	Halictidae (Halictinae) Halictus (Odontalictus) ligatus				R	U	U	U	U
281	Halictidae (Halictinae) Halictus (Protohalictus) rubicundus					R	R	R	
282	Halictidae (Halictinae) Halictus (Seladonia) tripartitus	U	U	C	C	C	C	C	C
283	Halictidae (Halictinae) Lasioglossum sp.								C
284	Halictidae (Halictinae) Lasioglossum (Dialictus) aff. punctatoventre			R					
285	Halictidae (Halictinae) Lasioglossum (Dialictus) aff. ruidosense	R							
286	Halictidae (Halictinae) Lasioglossum (Dialictus) aff. tegulare	R	U	U	C				
287	Halictidae (Halictinae) Lasioglossum (Dialictus) albohirtum				R		R	R	R
288	Halictidae (Halictinae) Lasioglossum (Dialictus) brunneiventre		R	R	R		C	C	C
289	Halictidae (Halictinae) Lasioglossum (Dialictus) diversopunctatum			R			R		R
290	Halictidae (Halictinae) Lasioglossum (Dialictus) glabriventre						U	U	
291	Halictidae (Halictinae) Lasioglossum (Dialictus) hudsoniellum						R	R	R

292	Halictidae (Halictinae) Lasioglossum (Dialictus) imbrex						C	U	C
293	Halictidae (Halictinae) Lasioglossum (Dialictus) impavidum							R	
294	Halictidae (Halictinae) Lasioglossum (Dialictus) incompletum	R	R	U	C		C	C	C
295	Halictidae (Halictinae) Lasioglossum (Dialictus) megastictum			R			R		R
296	Halictidae (Halictinae) Lasioglossum (Dialictus) n. sp. aff. nevadense			R	R				
297	Halictidae (Halictinae) Lasioglossum (Dialictus) nevadense	R	U	U	C		C	C	C
298	Halictidae (Halictinae) Lasioglossum (Dialictus) obscurior						R	U	
299	Halictidae (Halictinae) Lasioglossum (Dialictus) perichlarum						R		
300	Halictidae (Halictinae) Lasioglossum (Dialictus) punctatoventre	U	U	C	C		C	C	C
301	Halictidae (Halictinae) Lasioglossum (Dialictus) sp. D	R							
302	Halictidae (Halictinae) Lasioglossum (Dialictus) sp. G				R				
303	Halictidae (Halictinae) Lasioglossum (Dialictus) sp. L			R	R				

304	Halictidae (Halictinae) Lasioglossum (Dialictus) tuolumnenie		R						
305	Halictidae (Halictinae) Lasioglossum (Evylaeus) allonotum			R			R	R	R
306	Halictidae (Halictinae) Lasioglossum (Evylaeus) argemonis	R	U	U	U	R	U	U	U
307	Halictidae (Halictinae) Lasioglossum (Evylaeus) aspilurum		R		R		R	R	R
308	Halictidae (Halictinae) Lasioglossum (Evylaeus) aff. avalonense								C
309	Halictidae (Halictinae) Lasioglossum (Evylaeus) avalonense							R	
310	Halictidae (Halictinae) Lasioglossum (Evylaeus) glabriventre	R	R	R	U		R		U
311	Halictidae (Halictinae) Lasioglossum (Evylaeus) kincaidii	R	R	R	R		R	R	R
312	Halictidae (Halictinae) Lasioglossum (Evylaeus) miguelense		R		R				
313	Halictidae (Halictinae) Lasioglossum (Evylaeus) nigrescens	U	C	C	C		C	C	C

314	Halictidae (Halictinae) Lasioglossum (Evylaeus) ovaliceps						R		R
315	Halictidae (Halictinae) Lasioglossum (Evylaeus) pulveris						U	R	
316	Halictidae (Halictinae) Lasioglossum (Evylaeus) robustum		R	R	U		U	U	R
317	Halictidae (Halictinae) Lasioglossum (Evylaeus) ruficorne	R	R	U	U				
318	Halictidae (Halictinae) Lasioglossum (Evylaeus) sequoiae						U	U	U
319	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 1							R	
320	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 10		R	R					
321	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 11		R						
322	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 12		R		R				
323	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 16				R		U	U	
324	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 4	R		R	U				
325	Halictidae (Halictinae) Lasioglossum (Evylaeus) sp. 9		R	R	U		C	C	

326	Halictidae (Halictinae) Lasioglossum (Lasioglossum) egregium		R	R	R			U	U
327	Halictidae (Halictinae) Lasioglossum (Lasioglossum) mellipes								R
328	Halictidae (Halictinae) Lasioglossum (Lasioglossum) sisymbrii	R	U	U	U	U	C	U	C
329	Halictidae (Halictinae) Lasioglossum (Lasioglossum) titusi			R	R		R	U	U
330	Halictidae (Halictinae) Lasioglossum (Sphecodogastra) sp.							R	
331	Halictidae (Halictinae) Sphecodes arvensiformis	R	R						R
332	Halictidae (Halictinae) Sphecodes sp.								U
333	Halictidae (Halictinae) Sphecodes sp. A		R				R	R	
334	Halictidae (Halictinae) Sphecodes sp. B	R	U	U	R		R	R	R
335	Halictidae (Halictinae) Sphecodes sp. C	R							
336	Halictidae (Halictinae) Sphecodes sp. D	R		R	R		R	R	R

337	Halictidae (Halictinae) Sphecodes sp. E	R	R	R	U		U	U	U
338	Halictidae (Halictinae) Sphecodes sp. F	R	R						R
339	Halictidae (Halictinae) Sphecodes sp. I		R	R					R
340	Halictidae (Halictinae) Sphecodes sp. J		R						R
341	Halictidae (Halictinae) Sphecodes sp. K		R						
342	Halictidae (Halictinae) Sphecodes sp. L		R	R	U		R		
343	Halictidae (Halictinae) Sphecodes sp. M							R	
344	Halictidae (Rophitinae) Conanthalictus (Phaceliapis) bakeri		R	R	R		R		
345	Halictidae (Rophitinae) Conanthalictus (Phaceliapis) seminiger				R				
346	Halictidae (Rophitinae) Dufourea dentipes						R		
347	Halictidae (Rophitinae) Dufourea leachi	R	R	U	R		R	U	R
348	Halictidae (Rophitinae) Dufourea mulleri		R	R			R		

349	Halictidae (Rophitinae) Dufourea rhamni	R	R	R				R	U
350	Halictidae (Rophitinae) Dufourea sandhouseae		U	U			U	U	C
351	Halictidae (Rophitinae) Dufourea sparsipunctata	U	U	R	R		C	U	C
352	Halictidae (Rophitinae) Dufourea virgata	U	R	R	R		R	R	U
353	Halictidae (Rophitinae) Micralictoides altadenae		R				R		
354	Halictidae (Rophitinae) Micralictoides ruficaudus	R	R	R			U	R	U
355	Megachilidae (Megachilinae) Anthidiellum (Loyalanthidium) notatum						R		
356	Megachilidae (Megachilinae) Anthidiellum (Loyalanthidium) robertsoni		U	U					U
357	Megachilidae (Megachilinae) Anthidium (Anthidium) collectum	R	U	U	U		R	R	R
358	Megachilidae (Megachilinae) Anthidium (Anthidium) edwardsii							R	R
359	Megachilidae (Megachilinae) Anthidium (Anthidium) jocosum							R	
360	Megachilidae (Megachilinae) Anthidium (Anthidium) maculosum		R						

361	Megachilidae (Megachilinae) Anthidium (Anthidium) mormonum	R	R	R	R				
362	Megachilidae (Megachilinae) Anthidium (Anthidium) pallidiclypeum	R	R	R	R				
363	Megachilidae (Megachilinae) Anthidium (Anthidium) utahense	U	C	C	U		U	U	U
364	Megachilidae (Megachilinae) Anthidium (Callanthidium) illustre		U	R	R		R	R	R
365	Megachilidae (Megachilinae) Ashmeadiella sp.								R
366	Megachilidae (Megachilinae) Ashmeadiella aff. rufitarsis	R	R	R	R		R		U
367	Megachilidae (Megachilinae) Ashmeadiella (Arogochila) aff. salviae n.sp.						R		
368	Megachilidae (Megachilinae) Ashmeadiella (Arogochila) australis		R	R	R				R
369	Megachilidae (Megachilinae) Ashmeadiella (Arogochila) salviae	R	U	U	R		R	R	U
370	Megachilidae (Megachilinae) Ashmeadiella (Arogochila) timberlakei	U	C	U	U		R	R	U
371	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) aridula								R

372	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) bucconis		U	R				R	R
373	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) cactorum		R						
374	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) californica	R	U	U	U		R	R	
375	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) difugita		R	R			R		R
376	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) femorata		R		U				
377	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) foveata	R	U	U	U		R		
378	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) gillettei		R	R				R	U
379	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) meliloti		U	U				R	
380	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) pronitens		R						

381	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) rufitarsis							R	
382	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) sonora		R	R					U
383	Megachilidae (Megachilinae) Ashmeadiella (Ashmeadiella) titusi		U	R	R				
384	Megachilidae (Megachilinae) Atoposmia (Atoposmia) n. sp. 2	R	R	R			R		
385	Megachilidae (Megachilinae) Atoposmia (Atoposmia) pycnognatha		U	R	R				R
386	Megachilidae (Megachilinae) Atoposmia (Eremosmia) hemizoniae						R		
387	Megachilidae (Megachilinae) Atoposmia (Hexosmia) copelandica	R	U	R	R		R	R	R
388	Megachilidae (Megachilinae) Chelostoma sp.								R
389	Megachilidae (Megachilinae) Chelostoma (Chelostoma) aff. minutum n. sp.		R	R	R			R	R
390	Megachilidae (Megachilinae) Chelostoma (Chelostoma) californicum	U	C	U	U		U	R	R
391	Megachilidae (Megachilinae) Chelostoma (Chelostoma) cockerelli	U	U	U	C		U	U	R
392	Megachilidae (Megachilinae) Chelostoma (Chelostoma) incisulum	U	U	U	U		U	R	R

393	Megachilidae (Megachilinae) Chelostoma (Chelostoma) marginatum	U	U	U	R		U	R	R
394	Megachilidae (Megachilinae) Chelostoma (Chelostoma) n. sp.	R	U	U	R				
395	Megachilidae (Megachilinae) Chelostoma (Chelostoma) phaceliae	U	C	U	U		U	R	U
396	Megachilidae (Megachilinae) Chelostoma (Chelostoma) tetramerum						R	R	R
397	Megachilidae (Megachilinae) Coelioxys (Boreocoelioxys) octodentata		R	R			R		R
398	Megachilidae (Megachilinae) Coelioxys (Coelioxys) hirsutissima						R		R
399	Megachilidae (Megachilinae) Coelioxys (Coelioxys) serricaudata	R	R	R	R		R	R	R
400	Megachilidae (Megachilinae) Coelioxys (Cyrtocoelioxys) gilensis		R						
401	Megachilidae (Megachilinae) Coelioxys (Cyrtocoelioxys) gonaspis		R						
402	Megachilidae (Megachilinae) Dianthidium (Dianthidium) dubium		U	U	R		R	U	U
403	Megachilidae (Megachilinae) Dianthidium (Dianthidium) parvum						R	R	
404	Megachilidae (Megachilinae) Dianthidium (Dianthidium) pudicum	R	R	R	R		R	R	U

405	Megachilidae (Megachilinae) Dianthidium (Dianthidium) singulare		R						
406	Megachilidae (Megachilinae) Dianthidium (Dianthidium) ulkei		R	R				R	R
407	Megachilidae (Megachilinae) Dioxys aurifusca		R						
408	Megachilidae (Megachilinae) Dioxys pacifica			R				R	
409	Megachilidae (Megachilinae) Dioxys pomonae	R	R	R	R		U	R	R
410	Megachilidae (Megachilinae) Dioxys producta	R	R	R	R		R	R	
411	Megachilidae (Megachilinae) Heriades (Heriades) sp.							R	
412	Megachilidae (Megachilinae) Heriades (Neotrypetes) occidentalis		C	U					R
413	Megachilidae (Megachilinae) Hoplitis sp.								R
414	Megachilidae (Megachilinae) Hoplitis (Acrosmia) aff. emarginata		U	R	R		R		
415	Megachilidae (Megachilinae) Hoplitis (Alcidamea) colei	R	U	R	U		U	U	U
416	Megachilidae (Megachilinae) Hoplitis (Alcidamea) grinnelli	R	U	R	R		R	R	
417	Megachilidae (Megachilinae) Hoplitis (Alcidamea) producta	U	U	U	U		U	R	R

418	Megachilidae (Megachilinae) Hoplitis (Alcidamea) sambuci	R	U	R	R				R
419	Megachilidae (Megachilinae) Hoplitis (Cyrtosmia) hypocrita	R	U	U	R		R	R	R
420	Megachilidae (Megachilinae) Hoplitis (Hoplitina) bunocephala	R		R					
421	Megachilidae (Megachilinae) Hoplitis (Hoplitina) howardi	U	C	U	U		R	R	R
422	Megachilidae (Megachilinae) Hoplitis (Monumetha) albifrons	U	C	U	U		U	U	C
423	Megachilidae (Megachilinae) Hoplitis (Monumetha) fulgida	U	U	U	U		U	R	U
424	Megachilidae (Megachilinae) Hoplitis (Penteriades) remotula	R	U	R			R	R	R
425	Megachilidae (Megachilinae) Hoplitis (Proteriades) cryptanthae	R	R						R
426	Megachilidae (Megachilinae) Hoplitis (Proteriades) jacintana	U	U	R	R		R		
427	Megachilidae (Megachilinae) Hoplitis (Proteriades) nanula	R	U	R	R		R		R
428	Megachilidae (Megachilinae) Hoplitis (Proteriades) seminigra	R	U	R	R		R		
429	Megachilidae (Megachilinae) Hoplitis (Proteriades) semirubra	R	R	R	R		R	R	R
430	Megachilidae (Megachilinae) Megachile (Argyropile) parallela		R						R

431	Megachilidae (Megachilinae) Megachile (Chelostomoides) angelarum		U	U			R	R	U
432	Megachilidae (Megachilinae) Megachile (Chelostomoides) davidsoni		U				R	R	
433	Megachilidae (Megachilinae) Megachile (Chelostomoides) exilis							R	R
434	Megachilidae (Megachilinae) Megachile (Chelostomoides) spinotulata		U	R					
435	Megachilidae (Megachilinae) Megachile (Eutricharaea) apicalis		U	R			R	U	U
436	Megachilidae (Megachilinae) Megachile (Litomegachile) brevis			R	R		R		
437	Megachilidae (Megachilinae) Megachile (Litomegachile) coquilletti	R	U	U			U	U	R
438	Megachilidae (Megachilinae) Megachile (Litomegachile) gentilis		R	R				R	R
439	Megachilidae (Megachilinae) Megachile (Litomegachile) lippiae							R	
440	Megachilidae (Megachilinae) Megachile (Litomegachile) onobrychidis						R	R	U
441	Megachilidae (Megachilinae) Megachile (Litomegachile) texana	R	R	R	R				

442	Megachilidae (Megachilinae) Megachile (Megachile) montivaga		R				R	R	R
443	Megachilidae (Megachilinae) Megachile (Megachiloides) gravita		R		U		U	U	U
444	Megachilidae (Megachilinae) Megachile (Megachiloides) aff. pascoensis								R
445	Megachilidae (Megachilinae) Megachile (Megachiloides) pascoensis	R	U	R	U		U	U	U
446	Megachilidae (Megachilinae) Megachile (Megachiloides) pseudonigra	R	R				R		R
447	Megachilidae (Megachilinae) Megachile (Megachiloides) aff. subnigra								R
448	Megachilidae (Megachilinae) Megachile (Megachiloides) subnigra			R			U	R	U
449	Megachilidae (Megachilinae) Megachile (Neoeutrichareae) rotundata								R
450	Megachilidae (Megachilinae) Megachile (Sayapis) fidelis		R	R				R	
451	Megachilidae (Megachilinae) Megachile (Sayapis) frugalis		C	U			R	R	R
452	Megachilidae (Megachilinae) Megachile (Sayapis) inimica		R						

453	Megachilidae (Megachilinae) Megachile (Sayapis) newberryae		R	R					
454	Megachilidae (Megachilinae) Osmia claremontensis	R	U	R	R		R		
455	Megachilidae (Megachilinae) Osmia sp.								R
456	Megachilidae (Megachilinae) Osmia (Acanthosmioides) integra								R
457	Megachilidae (Megachilinae) Osmia (Acanthosmioides) nigrifrons		R		R				
458	Megachilidae (Megachilinae) Osmia (Acanthosmioides) nigrobarbata	R	R	R	R		R	R	U
459	Megachilidae (Megachilinae) Osmia (Acanthosmioides) odontogaster	R	U	U	R		R	R	R
460	Megachilidae (Megachilinae) Osmia (Acanthosmioides) sedula						R		U
461	Megachilidae (Megachilinae) Osmia (Acanthosmioides) sp. A	R							
462	Megachilidae (Megachilinae) Osmia (Cephalosmia) californica	R	R	R	R		R	R	R
463	Megachilidae (Megachilinae) Osmia (Cephalosmia) montana	R	R	R	U	R	U	R	U
464	Megachilidae (Megachilinae) Osmia (Cephalosmia) subaustralis								R

465	Megachilidae (Megachilinae) Osmia (Euthosmia) glauca	R	U	U	U		U	U	U
466	Megachilidae (Megachilinae) Osmia (Helicosmia) coloradensis		U	U	R		R	R	U
467	Megachilidae (Megachilinae) Osmia (Helicosmia) texana		U	R	R		R	R	R
468	Megachilidae (Megachilinae) Osmia (Melanosmia) aff. hesperos						R		
469	Megachilidae (Megachilinae) Osmia (Melanosmia) aglaia	R	C	U	U		U	C	C
470	Megachilidae (Megachilinae) Osmia (Melanosmia) atrocyanea	R	U	U	U		U	U	U
471	Megachilidae (Megachilinae) Osmia (Melanosmia) austromaritima								R
472	Megachilidae (Megachilinae) Osmia (Melanosmia) bakeri	U	U	U	U		U	R	
473	Megachilidae (Megachilinae) Osmia (Melanosmia) brevis	U	C	U	U	R	C	U	C
474	Megachilidae (Megachilinae) Osmia (Melanosmia) calla	R	U	U	U		U	U	U
475	Megachilidae (Megachilinae) Osmia (Melanosmia) cara	U	U	U	U		U	U	U
476	Megachilidae (Megachilinae) Osmia (Melanosmia) clarescens	R	U	U	R		R	R	U
477	Megachilidae (Megachilinae) Osmia (Melanosmia) cyanella	U	U	U	U		U	U	U

478	Megachilidae (Megachilinae) Osmia (Melanosmia) aff. cyanopoda								R
479	Megachilidae (Megachilinae) Osmia (Melanosmia) cyanopoda	R	U	R	R			R	
480	Megachilidae (Megachilinae) Osmia (Melanosmia) dakotensis								R
481	Megachilidae (Megachilinae) Osmia (Melanosmia) densa	U	U	U	R		U	U	U
482	Megachilidae (Megachilinae) Osmia (Melanosmia) aff. gabrielis								R
483	Megachilidae (Megachilinae) Osmia (Melanosmia) gabrielis	U	U	U	U		U	U	U
484	Megachilidae (Megachilinae) Osmia (Melanosmia) gaudiosa						U	R	R
485	Megachilidae (Megachilinae) Osmia (Melanosmia) granulosa	R	U	U	U		U	U	R
486	Megachilidae (Megachilinae) Osmia (Melanosmia) inurbana			R			U	U	C
487	Megachilidae (Megachilinae) Osmia (Melanosmia) kincaidii	U	U	U	U		U	U	R
488	Megachilidae (Megachilinae) Osmia (Melanosmia) laeta	R	U	U	R		U	U	U
489	Megachilidae (Megachilinae) Osmia (Melanosmia) malina			R					
490	Megachilidae (Megachilinae) Osmia (Melanosmia) melanopleura								U

491	Megachilidae (Megachilinae) Osmia (Melanosmia) pusilla	R	U		R		R	R	R
492	Megachilidae (Megachilinae) Osmia (Melanosmia) raritatis	R	R	R	R		R	R	R
493	Megachilidae (Megachilinae) Osmia (Melanosmia) regulina	R	U	U	U		C	C	C
494	Megachilidae (Megachilinae) Osmia (Melanosmia) rostrata				R				
495	Megachilidae (Megachilinae) Osmia (Melanosmia) trevoris			R	R		U	U	
496	Megachilidae (Megachilinae) Osmia (Melanosmia) tristella		R	R	R				
497	Megachilidae (Megachilinae) Osmia (Melanosmia) vandykei		R	R	R				
498	Megachilidae (Megachilinae) Osmia (Melanosmia) visenda	U	U	U	R		U	U	U
499	Megachilidae (Megachilinae) Osmia (Mystacosmia) nemoris		R	U	C	C	C	C	C
500	Megachilidae (Megachilinae) Osmia (Osmia) lignaria	R	U	C	R	R	U	U	R
501	Megachilidae (Megachilinae) Osmia (Osmia) ribifloris		R	R					R
502	Megachilidae (Megachilinae) Osmia (Pyrosmia) nigricollis						R	R	

503	Megachilidae (Megachilinae) Osmia (Trichinosmia) latisulcata		R	R	R		U		U
504	Megachilidae (Megachilinae) Protosmia (Chelostomopsis) rubifloris	U	C	C	U		C	U	C
505	Megachilidae (Megachilinae) Stelis frohlichi								R
506	Megachilidae (Megachilinae) Stelis n. sp. 2								R
507	Megachilidae (Megachilinae) Stelis (Protostelis) anthidioides	R		R			R		R
508	Megachilidae (Megachilinae) Stelis (Protostelis) hurdi		R	R	R		R		
509	Megachilidae (Megachilinae) Stelis (Stelis) aff. foederalis		R		R		R		
510	Megachilidae (Megachilinae) Stelis (Stelis) ashmeadiellae		R	R	R		R	R	R
511	Megachilidae (Megachilinae) Stelis (Stelis) calliphorina		R						
512	Megachilidae (Megachilinae) Stelis (Stelis) chemsaki							R	
513	Megachilidae (Megachilinae) Stelis (Stelis) cockerelli				R		R	R	
514	Megachilidae (Megachilinae) Stelis (Stelis) interrupta				R			R	R

515	Megachilidae (Megachilinae) Stelis (Stelis) lateralis		R	R	R		R		R
516	Megachilidae (Megachilinae) Stelis (Stelis) micheneri	R	R		R		R		R
517	Megachilidae (Megachilinae) Stelis (Stelis) montana	R	R	R	R		R	R	R
518	Megachilidae (Megachilinae) Stelis (Stelis) nigriventris		R	R					
519	Megachilidae (Megachilinae) Stelis (Stelis) occidentalis	R	R					R	
520	Megachilidae (Megachilinae) Stelis (Stelis) subcaerulea								R
521	Megachilidae (Megachilinae) Stelis (Stelis) subemarginata	R	R	R	R		R		R
522	Megachilidae (Megachilinae) Trachusa (Heteranthidium) timberlakei		R	U	U		R	R	R
523	Megachilidae (Megachilinae) Trachusa (Trachusomimus) perdita		U	C	U	U	C	R	U
524	Melittidae (Dasypodinae) Hesperapis (Amblyapis) ilicifoliae	U	C	C	C	R	U	U	U
525	Melittidae (Dasypodinae) Hesperapis (Panurgomia) regularis	U	C	C	C	C	C	C	C

Note. Groups are marked as Rare, ‘R’, if N ≤ 10, Uncommon, ‘U’, if 10 < N < 100, and Common,‘C’, if N ≥ 100. Bold lines separate each survey. Species highlighted in yellow were not found in 2020, but had been observed in the park previously. Species highlighted in green were found in 2020, but had not been seen since 2002 or earlier. Species highlighted in blue are new to the inventory as of 2020. Bees highlighted in orange were unable to be identified in 2020, which may affect the species list, particularly within *Andrena* and *Nomada* species.

Appendix C

Species list for plants that bees visited at Pinnacles National Park in 2020 and associated historic collections

	Plant Name	**1996**	**1997**	**1998**	**1999**	**2002**	**2011**	**2012**	**2020**
1	Adoxaceae Sambucus nigra ssp.caerulea						R	U	R
2	Alliaceae Allium crispum								R
3	Alliaceae Allium fimbriatum						R		
4	Alliaceae Allium lacunosum		U	U	R				
5	Alliaceae Allium lacunosum var.micranthum							R	R
6	Alliaceae Allium sp.	U	U	R					
7	Anacardiaceae Toxicodendron diversilobum						R		R
8	Apiaceae Anthriscus caucalis						R		
9	Apiaceae Apiaceae sp.		R	U					
10	Apiaceae Apiaceae sp. (yellow)			R			R		
11	Apiaceae Lomatium dasycarpum							R	
12	Apiaceae Lomatium sp.		U	R				R	

13	Apiaceae Lomatium utriculatum			R			U	R	U
14	Apiaceae Perideridia californica			R					
15	Apiaceae Sanicula bipinnata								U
16	Apiaceae Sanicula bipinnatifida								R
17	Apiaceae Sanicula crassicaulis						R		
18	Apiaceae Sanicula sp.		R						
19	Apiaceae Sanicula tuberosa						R	R	
20	Asclepiadaceae Asclepias sp.			U					
21	Asparagaceae Bloomeria crocea		U	U			U		U
22	Asparagaceae Dichelostemma capitatum spp.capitatum		U				R	U	R
23	Asteraceae Achillea millefolium		R				R	R	U
24	Asteraceae Agoseris grandiflora						R		
25	Asteraceae Agoseris sp.		R						R
26	Asteraceae Anaphalis margaritacea		R						
27	Asteraceae Asteraceae sp.		R	U					U

28	Asteraceae Asteraceae sp. (yellow)			R					R
29	Asteraceae Baccharis pilularis		U	U					R
30	Asteraceae Baccharis salicifolia	U	R		U		U	U	
31	Asteraceae Carduus pycnocephalus								R
32	Asteraceae Carduus tenuiflorus		U						
33	Asteraceae Centaurea melitensis						R	R	
34	Asteraceae Centaurea solstitialis		U	U		R		R	R
35	Asteraceae Chaenactis glabriuscula		R				C	U	U
36	Asteraceae Cirsium occidentale		R	U	R		R	R	R
37	Asteraceae Cirsium sp.		U	R					
38	Asteraceae Cirsium vulgare		R	R					
39	Asteraceae Erigeron foliosus		U						R
40	Asteraceae Erigeron foliosus var.foliosus							R	R
41	Asteraceae Erigeron petrophilus		U						
42	Asteraceae Eriophyllum confertiflorum		U	U	U		R	R	R
43	Asteraceae Eriophyllum lanatum			R					

44	Asteraceae Eriophyllum multicaule							R	
45	Asteraceae Eriophyllum sp.		U						
46	Asteraceae Euthamia occidentalis		R						
47	Asteraceae Gnaphalium bicolor						R		
48	Asteraceae Gnaphalium californicum						R	R	
49	Asteraceae Hemizonia lobbii		U						R
50	Asteraceae Heterotheca sessiliflora		U						
51	Asteraceae Hypochaeris glabra						R		
52	Asteraceae Hypochaeris radicata						U	R	
53	Asteraceae Lasthenia californica	R	U	C			U	U	U
54	Asteraceae Layia hieracioides		R						
55	Asteraceae Lessingia tenuis				U				
56	Asteraceae Madia sp.		R						
57	Asteraceae Malacothrix californica						R		
58	Asteraceae Microseris douglasii						R		
59	Asteraceae Packera breweri						R		

60	Asteraceae Pectis papposa		R						
61	Asteraceae Senecio flaccidus		R						R
62	Asteraceae Senecio sp.		U						
63	Asteraceae Stephanomeria virgata			R					R
64	Asteraceae Wyethia helenioides	R					U	U	R
65	Asteraceae Wyethia sp.				R				
66	Boraginaceae Amsinckia menziesii	U			R	R	U	U	U
67	Boraginaceae Amsinckia menziesii var.menziesii		U	U	R		R		
68	Boraginaceae Amsinckia sp.					U			
69	Boraginaceae Cryptantha sp.	U	C	U	R			R	R
70	Boraginaceae Emmenanthe penduliflora			R	U				
71	Boraginaceae Eriodictyon sp.			R					
72	Boraginaceae Eriodictyon tomentosum	U	C	U	C		U	U	U
73	Boraginaceae Heliotropium curassavicum		U				U	U	U
74	Boraginaceae Nemophila menziesii var.integrifolia		U	U					
75	Boraginaceae Nemophila menziesii var.menziesii						R	R	

76	Boraginaceae Phacelia brachyloba		U						
77	Boraginaceae Phacelia californica		U						
78	Boraginaceae Phacelia distans		U	U				R	R
79	Boraginaceae Phacelia imbricata		U	U	U		R		U
80	Boraginaceae Phacelia malvifolia			R	U				
81	Boraginaceae Phacelia ramosissima		U	U	R		R		U
82	Boraginaceae Phacelia sp.	U	C	U	U			R	R
83	Boraginaceae Phacelia sp. (white)	U							
84	Boraginaceae Pholistoma auritum	U	C	C	R			R	
85	Boraginaceae Pholistoma auritum var.auritum						U	R	U
86	Boraginaceae Pholistoma membranaceum			U			R	R	
87	Boraginaceae Plagiobothrys canescens						U		
88	Boraginaceae Plagiobothrys nothofulvus			C					
89	Boraginaceae Plagiobothrys sp.		R	U		U		R	R
90	Brassicaceae Brassica nigra		C	U	U				
91	Brassicaceae Brassicaceae sp.					R			

92	Brassicaceae Cardamine californica			U					
93	Brassicaceae Cardamine californica var.californica			U			R		R
94	Brassicaceae Erysimum capitatum var.capitatum						R		
95	Brassicaceae Erysimum sp.		R						
96	Brassicaceae Hirschfeldia incana						C	C	U
97	Brassicaceae Rorippa nasturtium-aquaticum		U		R				
98	Brassicaceae Thysanocarpus curvipes			C					
99	Brassicaceae Thysanocarpus laciniatus							R	
100	Brassicaceae Tropidocarpum gracile								R
101	Caprifoliaceae Lonicera hispidula			U					
102	Caprifoliaceae Lonicera sp.			U				R	
103	Caprifoliaceae Lonicera subspicata var.denudata						R		R
104	Caprifoliaceae Plectritis ciliosa							R	U
105	Caprifoliaceae Plectritis macrocera			U			U		R
106	Chenopodiaceae Chenopodium californicum						R		
107	Convolvulaceae Calystegia collina						R	U	

108	Convolvulaceae Calystegia collina ssp.venusta						R		R
109	Convolvulaceae Calystegia purpurata							R	R
110	Convolvulaceae Calystegia sp.			R					
111	Convolvulaceae Calystegia subacaulis	R	U						
112	Convolvulaceae Convolvulus arvensis						R		
113	Crassulaceae Dudleya cymosa		R	R	R				
114	Crassulaceae Dudleya sp.		R						
115	Crassulaceae Sedum spathulifolium		R						
116	Cucurbitaceae Marah fabaceus								R
117	Cupressaceae Juniperus californica								U
118	Cuscutaceae Cuscuta californica		R						
119	Ericaceae Arctostaphylos pungens			C			U		
120	Ericaceae Arctostaphylos sp.			R		U			
121	Euphorbiaceae Euphorbia sp.			R					
122	Fabaceae Glycyrrhiza lepidota		R						
123	Fabaceae Acmispon americanus var.americanus								U

124	Fabaceae Acmispon glaber var.glaber						C	U	U
125	Fabaceae Lotus humistratus/wragelianus						R		R
126	Fabaceae Lotus micranthus						R		
127	Fabaceae Lotus purshianus		U				R		
128	Fabaceae Lotus scoparius	U	C	C					
129	Fabaceae Lotus sp.		U	U	R				
130	Fabaceae Lotus wrangelianus			U					
131	Fabaceae Lupinus albifrons	R	U	U			R	U	
132	Fabaceae Lupinus albifrons var.albifrons						U	U	U
133	Fabaceae Lupinus bicolor		R						R
134	Fabaceae Lupinus concinnus						R		
135	Fabaceae Lupinus microcarpus var.densiflorus						R		
136	Fabaceae Lupinus sp.	R	R	R					
137	Fabaceae Melilotus indicus		R				U	R	
138	Fabaceae Trifolium albopurpureum						R		
139	Fabaceae Trifolium depauperatum						R		

140	Fabaceae Trifolium gracilentum var.gracilentum						R		
141	Fabaceae Trifolium microcephalum		R					R	
142	Fabaceae Trifolium sp.	U	U	R					R
143	Fabaceae Trifolium willdenovii			U			R	R	
144	Fabaceae Vicia sp.			R					
145	Fabaceae Vicia villosa		U	R			U	U	U
146	Fagaceae Quercus agrifolia						R	R	R
147	Fagaceae Quercus agrifolia var.agrifolia						U	U	
148	Fagaceae Quercus douglasii						R	R	R
149	Fagaceae Quercus lobata						R		
150	Fagaceae Quercus sp.	U	R	R			R	R	U
151	Fumariaceae Dicentra chrysantha		U	R	U			R	
152	Fumariaceae Dicentra sp.			U					
153	Geraniaceae Erodium botrys						R	R	
154	Geraniaceae Erodium brachycarpum						U	U	R
155	Geraniaceae Erodium cicutarium			R			U	U	R

156	Geraniaceae Erodium sp.		R						
157	Hippocastanaceae Aesculus californica		R	R			R		
158	Lamiaceae Lamium amplexicaule							R	
159	Lamiaceae Lepechinia calycina		U	U	R		R	U	R
160	Lamiaceae Marrubium vulgare						U	U	U
161	Lamiaceae Mentha spicata		U						
162	Lamiaceae Mentha suaveolens		U						
163	Lamiaceae Monardella lanceolata		R						
164	Lamiaceae Monardella sp.			R					
165	Lamiaceae Monardella villosa		R				R	R	U
166	Lamiaceae Salvia columbariae						R		
167	Lamiaceae Salvia mellifera	R	U	U	U		U	R	R
168	Lamiaceae Stachys albens								R
169	Lamiaceae Stachys bullata		U	R	U		R	U	R
170	Lamiaceae Trichostema lanatum	R	U	U	R		R	R	R
171	Lamiaceae Trichostema lanceolatum	R	U					R	R

172	Liliaceae Brodiaea sp.		R						
173	Liliaceae Brodiaea terrestris		R	U			R	R	
174	Liliaceae Calochortus splendens								R
175	Liliaceae Calochortus venustus		U	U	U		U	U	R
176	Liliaceae Triteleia hyacinthina		R						
177	Liliaceae Triteleia lugens		R	U				U	
178	Liliaceae Zigadenus fremontii		R	R					
179	Liliaceae Zigadenus venenosus							R	
180	Linaceae Hesperolinon micranthum								U
181	Malvaceae Eremalche parryi				U				
182	Malvaceae Malacothamnus aboriginum		U	U			U	U	R
183	Montiaceae Claytonia perfoliata spp.perfoliata		R	U			U	R	U
184	Oleaceae Fraxinus dipetala		R				R		
185	Onagraceae Camissonia sp.	R	U	R	R			R	
186	Onagraceae Clarkia affinis		R				R		
187	Onagraceae Clarkia cylindrica		R	R				R	R

188	Onagraceae Clarkia modesta		R	R	R		R		
189	Onagraceae Clarkia purpurea	R	U	U	U		C	U	C
190	Onagraceae Clarkia similis		R						
191	Onagraceae Clarkia sp.	U	U	U	U				
192	Onagraceae Clarkia speciosa						R	R	R
193	Onagraceae Clarkia unguiculata		C	C	U		C	C	C
194	Onagraceae Epilobium canum			R					
195	Onagraceae Epilobium densiflorum								R
196	Orobanchaceae Castilleja affinis			R			R		
197	Orobanchaceae Castilleja exserta		R	R			R		R
198	Orobanchaceae Castilleja foliolosa								R
199	Orobanchaceae Castilleja sp.		R	R					
200	Orobanchaceae Pedicularis densiflora						R		
201	Orobanchaceae Pedicularis sp.			R					
202	Orobanchaceae Triphysaria pusilla						R		
203	Papaveraceae Dendromecon rigida		U	R	R		R		R

204	Papaveraceae Eschscholzia caespitosa								C
205	Papaveraceae Eschscholzia californica	U	C	U	C	R	C	C	C
206	Papaveraceae Eschscholzia sp.					R			
207	Papaveraceae Meconella linearis		R						
208	Papaveraceae Platystemon californicus								R
209	Papaveraceae Platystemon sp.			R					
210	Phyrmaceae Diplacus aurantiacus	R	C	R	C		U	R	R
211	Phyrmaceae Diplacus linearis								R
212	Phyrmaceae Mimetanthe pilosa								R
213	Phyrmaceae Mimulus guttatus				R		U	R	
214	Phyrmaceae Mimulus pilosus		U						
215	Phyrmaceae Mimulus sp.		R	R					U
216	Pinaceae Pinus sabiniana						R	R	U
217	Plantaginaceae Antirrhinum multiflorum		U	R					R
218	Plantaginaceae Antirrhinum sp.			R	R				
219	Plantaginaceae Collinsia heterophylla	U	C	C	U		R	U	U

220	Plantaginaceae Collinsia parviflora		U						
221	Plantaginaceae Keckiella breviflora		U	U					U
222	Plantaginaceae Penstemon centranthifolius		U	R			U	U	R
223	Plantaginaceae Penstemon heterophyllus		R	U			U	U	U
224	Plantaginaceae Plantago erecta						R		R
225	Plantaginaceae Veronica anagallis-aquatica		U				R		R
226	Polemoniaceae Eriastrum densifolium								U
227	Polemoniaceae Gilia achilleifolia			U					
228	Polemoniaceae Gilia angelensis		U						
229	Polemoniaceae Gilia capitata	R	R				R		R
230	Polemoniaceae Gilia sp.		R	U					
231	Polemoniaceae Linanthus parviflorus						R		
232	Polemoniaceae Linanthus sp.		R	R				R	
233	Polemoniaceae Navarretia hamata							U	
234	Polemoniaceae Navarretia sp.			R					
235	Polygonaceae Chorizanthe douglasii	R	U		C		U	U	R

236	Polygonaceae Eriogonum elongatum		U						
237	Polygonaceae Eriogonum fasciculatum	U	C	C	U		R		C
238	Polygonaceae Eriogonum fasciculatum var.foliolosum						C	C	
239	Polygonaceae Eriogonum gracile		R						
240	Polygonaceae Eriogonum nortonii		R				R		
241	Polygonaceae Eriogonum saxatile								R
242	Polygonaceae Eriogonum sp.			U					R
243	Polygonaceae Eriogonum vimineum		U						
244	Polygonaceae Polygonum punctatum		R						
245	Polygonaceae Polygonum sp.				U				
246	Portulacaceae Montia fontana		R						
247	Primulaceae Anagallis arvensis			R				R	
248	Primulaceae Primula clevelandii							R	
249	Primulaceae Primula clevelandii ssp.patulum						R		R
250	Primulaceae Dodecatheon sp.		R						

251	Ranunculaceae Clematis lasiantha		R				R	R	
252	Ranunculaceae Clematis sp.		R						
253	Ranunculaceae Delphinium hesperium							R	
254	Ranunculaceae Delphinium hesperium ssp.pallescens						R		
255	Ranunculaceae Delphinium parryi						R	R	R
256	Ranunculaceae Delphinium parryi/patens						R		
257	Ranunculaceae Delphinium sp.		U	R	R				
258	Ranunculaceae Ranunculus californicus		R	U			C	U	U
259	Rhamnaceae Ceanothus cuneatus		R	C	U		U		
260	Rhamnaceae Ceanothus cuneatus var.cuneatus						U	U	U
261	Rhamnaceae Ceanothus sp.			R		R			
262	Rhamnaceae Rhamnus ilicifolia		R	U	C		R	R	U
263	Rhamnaceae Rhamnus sp.						R		
264	Rosaceae Adenostoma fasciculatum	U	U	C	R		C	C	C
265	Rosaceae Cercocarpus betuloides		R				R	R	

266	Rosaceae Drymocallis glandulosa							R	
267	Rosaceae Heteromeles arbutifolia		U				R		
268	Rosaceae Prunus ilicifolia		U	R	C		R		
269	Rosaceae Rosa californica		R				U	R	R
270	Rosaceae Rubus parviflorus				R				
271	Rosaceae Rubus sp.		R						
272	Rosaceae Rubus ursinus		U						U
273	Rubiaceae Galium sp.		R						
274	Salicaceae Salix exigua						U	U	C
275	Salicaceae Salix laevigata						U	R	
276	Salicaceae Salix lasiolepis						U	U	
277	Salicaceae Salix sp.		U	C					U
278	Sapindaceae Aesculus californica								R
279	Saxifragaceae Lithophragma affine			R					
280	Saxifragaceae Saxifraga californica			U					
281	Scrophulariaceae Scrophularia californica		R		R				

282	Solanaceae Solanaceae sp.					R			
283	Solanaceae Solanum umbelliferum		U	R			U	U	R
284	Valerianaceae Plectritis sp.		R	U					
285	Verbenaceae Verbena lasiostachys var.scabrida						R	R	
286	Verbenaceae Verbena sp.							R	
287	Violaceae Viola pedunculata		R	U			U	U	U
	Count of floral taxa sampled on:	**30**	**142**	**115**	**49**	**11**	**128**	**102**	**113**

Note. Groups are marked as Rare, ‘R’, if N ≤ 10, Uncommon, ‘U’, if 10 < N < 100, and Common,‘C’, if N ≥ 100. Bold lines separate each survey. Species highlighted in yellow were not collected on in 2020, but had been observed in the park previously. Species highlighted in blue were collected on for the first time as of 2020.

Appendix D

Statistical results of ANOVAs for each combination of collection method and Hill-diversity metric in plots at Pinnacles National Park

Hill-diversity	Fixed effect	Collection method	Pr(>F)	F	Df	Df.res
N0	Year	Combined	0.126	2.4	2	16
		Aerial Net	0.535	0.6	2	16
		Pan Trap	0.731	0.4	3	19
	Habitat	Combined	0.813	0.3	3	5
		Aerial Net	0.757	0.4	3	5
		Pan Trap	0.488	1.0	4	6.3
N1	Year	Combined	0.095	2.7	2	16
		Aerial Net	0.019	5.1	2	16
		Pan Trap	0.037	3.5	3	19
	Habitat	Combined	0.55	0.8	3	5
		Aerial Net	0.568	0.7	3	5
		Pan Trap	0.529	0.9	4	6.3
N2	Year	Combined	0.158	2.1	2	16
		Aerial Net	0.019	5.1	2	16
		Pan Trap	0.106	2.3	3	19
	Habitat	Combined	0.689	0.5	3	5
		Aerial Net	0.435	1.1	3	5
		Pan Trap	0.621	0.7	4	6.5

Appendix E

Geologic units of sampled plots at Pinnacles National Park

Plot	Geologic unit	Area (m^2)
High Peaks	Dacite member	9626
Lower McCabe	Alluvium	10226
Needlegrass BOW	Alluvium; unit is compiled from Rosenberg (2010) and Wagner, et al. (2002)	1640
Needlegrass BOW	Unnamed Miocene sedimentary rocks; unit is compiled from Rosenberg (2010) and Wagner, et al. (2002)	7880
Needlegrass LOW	Alluvium; unit is compiled from Rosenberg (2010) and Wagner, et al. (2002)	8219
Needlegrass LOW	Unnamed Miocene sedimentary rocks; unit is compiled from Rosenberg (2010) and Wagner, et al. (2002)	3340
Peaks View	Alluvium; unit is compiled from Rosenberg (2010) and Wagner, et al. (2002)	10592
South Wilderness	Alluvium; unit is compiled from Rosenberg (2010) and Wagner, et al. (2002)	2695
South Wilderness	Quartz monzonite of Bickmore Canyon	7315
Upper McCabe	Alluvium	10661
W. North Wilderness	Pinnacles Volcanic Formation, Breccia Member—white, aphanitic rhyolite flows	315
W. North Wilderness	Alluvial deposits, undifferentiated	8129

W. North Wilderness	Pinnacles Volcanic Formation, Breccia Member—white, aphanitic rhyolite flows	1766
West Gate	Quartz diorite-granodiorite of Johnson Canyon	8180

Note. Data was obtained from the NPS Geologic Resources Inventory Program.

Appendix F

Flow of the Habitat Suitability Modeler in ArcGIS Pro using Ceratina sequoiae as an example

Note. The goal is to model suitable habitat for *C. sequoiae* using the base criteria of *Clarkia* locations, *Sambucus* location, elevation, water, geologic unit, and vegetation type. From the base criteria more data can be derived such as the distance to these habitat features, aspect, or slope. The data are then transformed to calculate suitability values, weighted, and combined to produce the habitat suitability model.

Appendix G

Suitability values categorically assigned to topographic factors in the Habitat Suitability Modeler

Topographic Factor	Description	Suitability Value (SV)
Elevation	218-299 m	10
	299-377 m	9
	377-456 m	8
	456-535 m	7
	535-614 m	6
	614-693 m	5
	693-772 m	4
	772-851 m	3
	851-930 m	2
	930-1009 m	1
Aspect	North	1
	NE	2
	East	5
	SE	9
	South	10
	SW	9
	West	5
	NW	2
Slope	0.005 -1º	10
	1-2º	9
	2-3º	8

	3-4º	7
	4-5º	6
	5+º	1
Distance to	0-100 m	10
	100-200 m	9
	200-300 m	8
	300-400 m	7
	400-500 m	6
	500+ m	1

Note. ‘Distance to’ represents variables that use distance to that landscape feature to determine suitability (*Clarkia*, *Sambucus*, water, vegetation type, and geologic unit).

CURRICULUM VITAE

Abigail Lehner

EDUCATION

MSc Utah State University, Logan, UT

- **Degree:** Master of Science, Biology emphasis in Entomology, *Aug 2022*
- **Committee:** Edward W. Evans (PhD), Terry L. Griswold (PhD), and Shannon W. Belmont (MS)
- **Thesis:** *Biodiversity and foraging preferences of bee communities at Pinnacles National Park over time*
- **GPA:** 4.0
- **Relevant Coursework:** Insect Systematics and Evolution, GIS for Natural Resource Applications, Advanced GIS for Natural Resource Applications, Geospatial Analysis for Natural Resource Management, and Design and Analysis of Ecological Research Using R

BSc Union College, Schenectady, NY

- **Degree:** Bachelor of Science, Biology, June 2018
- **Minors:** Chemistry and Theater
- **Advisor:** Steven K. Rice (PhD)
- **Thesis:** *Bee communities in native and restored habitats in the Albany Pine Bush Preserve*
- **GPA:** 3.2
- **Relevant Coursework:** Entomology, Ecology, Conservation Biology, Plant Biology, Herpetology, Developmental Biology, Calculus 1 and 2, Statistics, Survey of Biochemistry, Organic Chemistry 1 and 2, and Environmental Chemistry

AWARDS AND HONORS

Vlogbrothers Sponsorship, Complexly, $4,500 (Dec 2021)
Joseph E. Greaves Endowed Scholarship, Utah State University, $3,000 (Oct 2021)
Sigma Xi Research Honor Society, Nominated and inducted at Union College (May 2018)
Dean's List, Union College (2017/18)
Student Research Grant, Union College, $400 (Oct 2017)

RESEARCH EXPERIENCE

***Research Assistant*, Utah State University Biology Department,**
Logan, UT (Feb 2020-Jan 2022)

- Inventoried bee communities at Pinnacles National Park by collecting samples from 11 sites using pan trapping and aerial netting methods
- Sampled additional areas of interest in the park and trail segments when possible
- Mentored a field technician with their first bee collection experience over two field seasons
- Pinned, labeled, and identified the specimens collected to prepare for quantitative community analysis
- Pressed, labeled, and identified plant specimens

***Laboratory Technician*, Bee Identification Solutions,**
Logan, UT (Aug 2020-Feb 2021)

- Utilized a Keyence VHX5000 to image exotic bee specimens
- Photoshopped images to create presentable fact sheet and key photos for a website and online key to genera
- Entered specimen identification data into a database and labeled specimens appropriately

***Researcher*, AgriProtein,**
Ontario, CA (Sep 2019-Jan 2020)

- Assisted in the establishment and management a black soldier fly colony and designed experiments to determine what factors best increase bioconversion in larvae
- Ran larval feeding trials, ensured all data was recorded correctly, and advised junior staff in experimental work, data analysis, and report writing
- Adapted protocols to increase efficiency, analyzed data and wrote reports, and ordered products for the laboratory

***Volunteer Research Assistant*, Perrotis College,**
Thessaloniki, Greece (Feb 2019-Apr 2019)

- Worked with agro-environmental systems professor, Christos Vasilikiotis, to examine the effectiveness of various cover crops
- Sampled the nitrogen content of various species of cover crops to determine how successful the cover crop is

***Thesis Student,* Union College Biology Department,**
Schenectady, NY (Jun 2017-Jun 2018)

- Worked with advisor and Albany Pine Bush Entomologist, Amanda Dillon, to monitor bee populations at the Albany Pine Bush
- Collected samples in native plant species sites and sites restored from black locust invasion using pan trapping and aerial netting methods

- Pinned, labeled, and identified the specimens collected to prepare for quantitative community analysis
- Analyzed by comparing species abundances and diversity indices and evaluate community composition using non-metric multidimensional scaling to determine how restoration has affected bee communities

Work Study Student, **Union College Biology Department,**
Schenectady, NY (Oct 2016-Jun 2017)

- Worked with biology professor, Steven Rice, to prepare *Sphagnum* samples and perform carbon and oxygen stable isotope analysis
- Performing stable isotope analyses on *Sphagnum* allow us to look at the climatic response of moss all over the world

Work Study Student, **Union College Biology Department,**
Schenectady, NY (Apr 2015-Oct 2016)

- Assisted biology professor, Roman Yukilevich, to study evolution and adaptation in *Drosophila sp.*
- Performed multiple-choice mating experiments between *Drosophila athabasca* (derived) and *Drosophila affinis* (ancestral) to study the sexual isolation between sister species of flies
- Examined flies under the microscope in order to identify species, sex, and count flies
- Multiple-choice mating tests were conducted in both bottles and cages for approximately 30 minutes, copulating pairs would be aspirated out, identified, and recorded

PROFESSIONAL EXPERIENCE

Teaching Assistant**, Utah State University Biology Department,**
Logan, UT (Jan 2022-May 2022)

- Teach laboratory sections of BIOL 4500 Applied Entomology
- Lecture on insect orders, common families, and insect damage symptoms
- Prepare and display specimens for use in lab activities
- Write, administer, and grade exams, weekly lab quizzes, worksheets, and other assignments

Elementary English Language Fellow, **American Farm School,**
Thessaloniki, Greece (Aug 2018-Jun 2019)

- Assisted during English classes by encouraging K-6 students to interact in English and create a fun and safe learning environment

- Worked with English teachers to develop lesson plans and suggest targeted exercises
- Helped students accomplish oral and written tasks both in class and during study hours
- Developed, demonstrated, and lead appropriate language building games and class activities to help students further their knowledge of the English language and American culture and traditions
- Prepared Forensics students at the elementary and high school levels for competition by leading various activities to enhance public speaking skills
- Co-directed two fourth grade plays in English, choreographed dances, designed set pieces and costumes, edited scripts, selected music, and held daily rehearsals

Senior Admissions Intern, **Union College Admissions,**
Schenectady, NY (Aug 2017-Jun 2018)

- Conducted interviews with prospective students on campus or over Skype and wrote a report following interviews
- Delivered information sessions to prospective students and their families
- Assisted admissions deans with open house duties

PRESENTATIONS, AND GUEST LECTURES

Invited Guest Lecturer**, BIO-322 Conservation Biology Union College,**
Schenectady, NY (Apr 2021)

- Gave a guest lecture on the economic and ecological value of native bees, the importance of science communication, and how conservation biologists work with the public and the government

Oral Presentation**, Union College Steinmetz Symposium,**
Schenectady, NY (May 2018)

- On: *Bee communities in native and restored habitats in the Albany Pine Bush Preserve*

Poster Presentation**, Northeast Natural History Conference,**
Burlington, VT (Apr 2018)

- On: *Bee communities in native and restored habitats in the Albany Pine Bush Preserve*

Poster Presentation**, Union College Admitted Students Day,**
Schenectady, NY (Apr 2018)

- On: *Bee communities in native and restored habitats in the Albany Pine Bush Preserve*

CITIZENSHIP AND OUTREACH

***Social Media Science Educator*, TikTok (41k) and Instagram (3k),** (Mar 2020-present)

- Film and edit educational videos covering topics in entomology, ecology, conservation, life as a graduate student, and being a woman in STEM
- Answer the public's questions on these topics in an easily accessible and understandable way
- Create infographic posts for social media
- Partner with relevant companies to promote products. Past partnerships include Murphy's Naturals, KIND Snacks, and Pela.
- Hosted virtual insect trivia nights to spur public interest in entomology (Jul 2020-Aug 2020)

***Invited Guest Speaker,* Varsity Tutors Star Course,**
Virtual (Jun 2022 and *Aug 2022*)

- Prepare and execute two 45 minute courses for K-12 students on pollinators and conservation in partnership with the Varsity Tutors Star Courses

***Invited Guest Speaker,* The University of Texas Rio Grande Valley,**
Edinburg, TX (Apr 2022)

- Nominated by the Women in STEM Programs organization to give a talk on my experience as an entomologist and woman in STEM

***Invited Guest Speaker,* Ericson Elementary Transitional Kindergarten,**
Fresno, CA (Mar 2022)

- Speak with kindergarten students about what an entomologist is, the importance of insects, and show the diversity of bees

EXTRACURRICULAR ACTIVITIES

***Native Bee Monitoring Workshops*, National Native Bee Monitoring RCN** (Oct 2021-present)

- Participate in a series of workshops designed to gather ideas and perspectives from the professional bee monitoring community on strategies for national native bee monitoring practices
- Discussions and presentations from these workshops will be synthesized into a national native bee monitoring plan

***Greek Lessons,* Greek Language Experts,** (May 2021-present)

- Attend weekly lessons on Greek language

Biological Illustration Workshop**, Idaho State University,** Pocatello, ID (Aug 2020)

- Participated in a three day workshop on creating biological art
- Received instruction on a variety of illustration techniques that can be implemented in the field
- Learned how to incorporate art into science research
- Sketched and painted live animals, fossils, bones, plants, and animal specimens