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Commercial Plant Nurseries as Habitat for Wild Bees

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# Commercial Plant Nurseries as Habitat for Wild Bees

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

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in

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by

Jacob Mitchell Cecala

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The text of this dissertation, in part, is a reprint of the material as it appears in "Mark–recapture experiments reveal foraging behavior and plant fidelity of native bees in plant nurseries" (published in the journal *Ecology* in 2020; doi: https://doi.org/10.1002/ecy.3021). The co-author Erin E. Wilson Rankin listed in that publication directed and supervised the research which forms the basis for this dissertation.

# DEDICATION

I dedicate this dissertation to my family and friends for always reminding me of my capability, and for never letting me throw in the towel. Also, to my undergraduate and master's advisor Dr. Joan Leong and other professors in the Department of Biological Sciences at California State Polytechnic University, Pomona—thank you for helping lay the bedrock of my career in science.

Finally, to all the bees and plants immortalized in these pages: may your contributions to this work be used to one day secure a more verdant future for your kind.

# ABSTRACT OF THE DISSERTATION

## Commercial Plant Nurseries as Habitat for Wild Bees

by

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University of California, Riverside, June 2021
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California contains numerous horticultural nurseries: large lots encompassing patches of healthy containerized flowering plants year-round. While some ornamental plants attract pollinators, the ecological relationships between nurseries and wild bees remain uncharacterized. Management regimes such as systemic insecticide use may pose hazards to bees, while others, such as irrigation, may improve floral resources. My dissertation explored bee assemblages in nurseries, how individual bees forage on ornamental plants, and how plant management impacts bee reproduction.

In Chapters I and II, I documented bee assemblages in 13 nurseries during spring, summer, and autumn over two years and detected over 150 species visiting over 90 plant varieties. Greater cultivation of native plants influenced the abundance, richness, and composition of wild bee assemblages. A wide variety of bee species use plants inside nurseries across seasons, and nursery characteristics can influence the abundance and types of bees present.

In Chapter III, I used mark-recapture techniques to determine the fidelity of individual bees to nursery plants across days. I marked foraging sweat bees in nurseries and returned after 24 hours. I consistently rediscovered half of individuals across nurseries and seasons, with higher recapture rates on native plants. Nearly all recaptured individuals were found on the same plant species as the previous day, suggesting a high degree of plant fidelity. Wild bees thus regularly use nursery plants as resources over time.

In Chapter IV, I explored how ornamental plant management—irrigation level and insecticide application—affect bee foraging and reproduction. In flight cages, irrigation level influenced floral resources and pesticide concentrations in nectar, but did not affect reproduction of solitary bees. Neonicotinoid treatment below the label rate almost entirely halted bee nest initiation and brood cell construction. These results underscore dangers posed by irresponsible use of nursery insecticides.

This dissertation addressed the need for an understanding of bee community ecology in horticultural systems, foraging preferences between native and non-native ornamental plants, and impacts of nursery management practices on bee reproduction. This knowledge can be applied to inform practical management strategies that minimize exposure of wild bees to potential stressors, while simultaneously reflecting positively on environmentally minded nursery patrons.

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# LIST OF ABBREVIATIONS

| | |
|---|---|
| ALCB | alfalfa leafcutting bee, *Megachile rotundata* (Fabricius) |
| CI | confidence interval |
| FDis | functional dispersion |
| GLMM | generalized linear mixed (effects) model |
| HSD | honestly significant difference (Tukey's test) |
| HPLC/MS-MS | high performance liquid chromatography–mass spectrometry |
| LMM | linear mixed (effects) model |
| LR | label rate |
| SE(M), s.e. | standard error (of the mean) |
| VWC | volumetric water content |

# PREFACE

I was often told by my professors that good scientific writing tells a story. When I started my PhD, there were no stories about wild bees in plant nurseries, so I decided to write my own. In this story, I discover an astonishing diversity of these important insect pollinators in these overlooked agricultural areas (Chapters I and II), learn about how they live their day-to-day lives (III), and investigate the consequences of this lifestyle on their persistence (IV). This narrative is a culmination of my passions for botany, entomology, and their intersection with human society.

I hope that this research continues to change the way in which people view ornamental plants, in that they are more than simple aesthetic installations. They hold the potential to support biodiversity while they are still in the production system at nurseries, before they are even sold and planted in your neighborhood. The choice of plants that nurseries supply is ultimately a function of consumer demands. It is my wish that over time, varieties of plants that support biodiversity become increasingly prevalent in horticulture and accessible to all sectors of society. More generally, I hope that this work will encourage the horticulture industry as well as other agricultural sectors to be more mindful of how they may actively practice being stewards of pollinator populations, and to consider the economic benefits of doing so, beyond simply receiving pollination.

May 24, 2021

Jacob Cecala

# INTRODUCTION

A fundamental goal of ecology is to understand how changes in the environment impact communities (Sutherland et al. 2012). Human modified landscapes like agricultural and urban areas can influence the ecology of the organisms inhabiting them because the timing, availability, and quality of resources may differ fundamentally from those in undisturbed areas (Leong et al. 2015). The unique phenologies of artificially-constructed plant assemblages in these areas (Williams et al. 2011, Riedinger et al. 2013) contrast sharply with the vegetation in natural landscapes. This can affect local communities of animals, such as pollinators, which depend on these plants for resources (Leong and Roderick 2015), though different taxa of pollinators respond in different ways to land use change (Winfree et al. 2011). It is critical to understand the ecology of pollinators in these habitats to develop effective conservation and restoration strategies before these species are extirpated (Driscoll et al. 2013).

Bees (Hymenoptera: Anthophila) play a crucial ecological role by providing valuable pollination services in natural (Ollerton et al. 2011), agricultural (Winfree et al. 2008), and urban (Hennig and Ghazoul 2011) landscapes. Due to their benefits to humans, research on bees has surged (Pollinator Health Task Force 2015), paralleled with increases in public awareness around pollinator health (Larson et al. 2014). In the past decade, concerns over pollinator declines have erupted due to stressors like habitat loss, pathogens, pesticides, and other factors (Goulson et al. 2015). Declines in managed European honey bees, *Apis mellifera* (vanEngelsdorp et al. 2008, Lee et al. 2015), have prompted research on native non-*Apis* bee species as alternative pollinators. These wild insects are sensitive to agricultural disturbance, and much work has focused on how to optimize the process of restoring or ameliorating wild bee habitats (Menz et al. 2011, Kremen and M'Gonigle 2015, Williams et al. 2015, M'Gonigle et al. 2016). Accordingly, agricultural industries in various parts of the world have received criticism for exposing both managed and wild bees to additional stressors (Cressey 2013).

In particular, the horticulture industry has come under scrutiny by the public, government, and conservation agencies alike over bee health and conservation. In June 2013, application of a neonicotinoid pesticide to flowering linden trees in Oregon resulted in the largest mass die-off of bumble bees in the United States, eliciting public outcry and legislative action (Brown et al. 2014). While neonicotinoids are effective tools in the management of a variety of insect pests, these chemicals can contaminate pollen and nectar consumed by bees (Dyer et al. 2012, Stoner and Eitzer 2012), eliciting numerous detrimental sub-lethal effects (Alaux et al. 2010, Whitehorn et al. 2012, Pettis et al. 2013). While acreage covered by nurseries is far less than that of food crops (USDA NASS 2007), ornamental plants are often treated with pesticides at much higher levels, rendering the cosmetic use of these chemicals a more potent source of exposure for pollinators (Hopwood et al. 2012). Though many nurseries have pledged to reduce use of neonicotinoid pesticides, treated plants may still be widespread at many consumer retail outlets (Kegley et al. 2016)

In spite of these issues, large horticultural plant nurseries may serve as valuable resources for wild bees by acting as habitats providing a steady stream of floral resources across seasons (Leong et al. 2015) due to the year-round cultivation of well-watered, healthy flowering plants (Westrich 2006). In general, there is a positive association between the local abundance and diversity of flowering plants and these same metrics for bee assemblages (Ebeling et al. 2008, Kearns and Oliveras 2009, Matteson and Langellotto 2010, Nicholls and Altieri 2012, Carper et al. 2014). Furthermore, some nurseries specialize in regionally native ornamental plants, which can support more abundant (Fukase and Simons 2016), diverse, or compositionally distinct (McIntyre and Hostetler 2001, Pardee and Philpott 2014) bee faunas. Multiple studies suggest bees prefer to forage on native plants (Morandin and Kremen 2013, Chrobock et al. 2013, Aleixo et al. 2014), which are seeing an increase in horticultural cultivation in light of ongoing drought in California (Reid and Oki 2008, 2016). However, bees in disturbed areas still extensively use exotic plants (Williams et al. 2011) and exotic ornamentals may extend the seasonal availability of floral resources beyond that provided by native plants (Salisbury et al. 2015).

Despite numerous studies documenting wild bee assemblages in a diversity of urban and agricultural habitats (McFrederick and LeBuhn 2006, Tonietto et al. 2011, Pardee and Philpott 2014, Larson et al. 2014, Threlfall et al. 2015, Geslin et al. 2016), none have directly examined bees in nurseries through an ecological lens. In general, bee diversity in these "green" areas is lower compared to that in natural landscapes—with fewer soil-nesting species and fewer species that specialize on specific plant species (Hernandez et al. 2009)—but can be great nonetheless (Frankie et al. 2005). Since nursery growers rarely require ornamental plants to be pollinated, relatively little attention has been paid to wild bees in these areas. However, research has increasingly recognized the importance of ornamental plants as resources for bees and other beneficial insects when installed in urban landscapes (Wojcik 2011, Frankie et al. 2013, Pardee and Philpott 2014, Fukase and Simons 2016, Somme et al. 2016, Harris et al. 2016) but has overlooked their importance at their source, in nursery settings.

Though nurseries are undoubtedly intensively managed and complex agricultural systems (Parke and Grünwald 2012), they differ from other agricultural habitats in many ways. From an ecological standpoint, nurseries host diverse and dynamic assemblages of plant species that contrast sharply with the monocultural swaths that characterize many conventional food crop systems. Nurseries can contains hundreds of plant taxa at different stages of flowering in almost any given season (Parke and Grünwald 2012). This spatial heterogeneity is accompanied by extreme temporal heterogeneity as well, as plants are moved throughout their life from propagation houses to greenhouses to growing yards. As different plants require different methods of maintenance, this complexity is further accompanied by a diversity of irrigation regimes and pesticide application schedules (Parke and Grünwald 2012).

Furthermore, geographic areas in California that specialize in horticultural production overlap considerably with regions of high bee biodiversity. San Diego, Ventura, and Orange Counties have the highest horticultural sales revenue in the state (USDA NASS 2007). Globally, the highest abundance and diversity of wild bees occur in dry, warm, temperate areas like the Mediterranean basin and the Madrean floristic region of North America, which includes California (Michener 1979). The state harbors an estimated 1,985 species of bees (Moldenke 1976), representing roughly 40% of bee species in North America (Moissett and Buchmann 2011). Mediterranean climates are also considered to be highly sensitive to global change, and are expected to undergo the most severe relative declines in biodiversity (Sala et al. 2000). As an area critical to conservation biology, southern California is the ideal region in which to investigate nursery production areas as pollinator habitat.

The fundamental goals of this dissertation are to characterize and evaluate the role that nurseries play as habitats for wild pollinators. Using both observational and manipulative approaches, this work seeks to provide a holistic understanding of a previously unexplored ecological relationship between widespread and economically significant organisms and habitats. Specifically, this research will address the following objectives:

1. Characterize the abundance, richness, diversity, composition, and turnover of bee assemblages in nurseries in relation to local and landscape characteristics (Chapters I and II)
2. Investigate the day-to-day foraging behavior of individual generalist native bees on ornamental plants inside nurseries (Chapter III)
3. Determine the impact of nursery plant management practices on ornamental plant floral resources and solitary bee reproduction (Chapter IV)

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# CHAPTER I

## Diversity and turnover of wild bee and ornamental plant assemblages in commercial plant nurseries

## ABSTRACT

In human-modified landscapes like agricultural areas, understanding how habitat characteristics influence the diversity and composition of beneficial organisms is critical both to conservation efforts and ecosystem service modeling. Assessing turnover, or changes in species identity across sites or through time, is critical to fully understand how shifts in community composition relate to changes in ecosystem services. For pollinators like wild bees, factors affecting their abundance and richness have been well studied, but variables influencing temporal turnover, particularly across seasons within a year, remain relatively poorly understood. To investigate how local and landscape characteristics correlate with bee diversity and turnover across seasons, we recorded wild bee and flowering ornamental plant assemblages at several plant nurseries in southern California between spring and autumn over two years. Nurseries cultivate a broad diversity of flowering plant species that differ widely across sites and seasons, providing a field setting to test for correlations between turnover and diversity of plants and bees. As expected, we documented strong seasonal trends in wild bee diversity and composition. We found that local habitat factors, such as increased cultivation of native plants, were positively associated with bee diversity in sweep netting collections, whereas we detected

moderate influences of landscape level factors like proportion of surrounding natural area in passive trap collections. We also found a moderate positive correlation between overall gains in plant species and gains in bee species at nurseries across consecutive seasons. Our results have important considerations for the conservation of wild bees in horticultural operations and other landscapes dominated by ornamental plants, and highlight the utility of plant nurseries for investigating hypotheses related to diversity and turnover in plant-pollinator systems.

## INTRODUCTION

In human-modified habitats, it is crucial to understand the factors influencing the abundance and richness of beneficial species. Such metrics are important because they often serve as good proxies for ecosystem service delivery by these species (Kremen et al. 2002, Garibaldi et al. 2013). In addition to abundance and richness, quantifying species turnover—the number of replacements in species identity between locations or time periods (Leibold and Mikkelson 2002)—is important because ecosystem functioning depends, in part, on species-specific interactions and functional differences across taxa (Tilman et al. 2014). Discerning patterns in species turnover across space and time can teach us how species respond to changes in their environment (Beduschi et al. 2018) and inform models of ecosystem services at large scales (Winfree et al. 2018).

For insects like wild bees (Hymenoptera: Anthophila) that provide valuable pollination services (Klein et al. 2007), factors influencing the aforementioned community metrics have naturally received a great deal of attention in human-altered landscapes (Winfree et al. 2009, Shackelford et al. 2013). Generally, wild bee abundance, richness, and diversity are positively influenced by various local- and landscape-level factors (Winfree et al. 2009, Kennedy et al. 2013) which may interact with one another (Ayers and Rehan 2021). Both temporal and spatial components of bee species turnover have been quantified extensively (Quintero et al. 2010, Kehinde and Samways 2014, Beduschi et al. 2018) and constitute considerable proportions of bee gamma diversity in studies (Tylianakis et al. 2005, Rollin et al. 2015). However, factors determining the *magnitude* of temporal turnover, particularly across seasons within a year, are poorly understood relative to those influencing abundance, richness (Shackelford et al. 2013), and spatial turnover (Quintero et al. 2010, Beduschi et al. 2018). Increasing plant diversity can augment bee abundance and diversity over multiple years in agricultural landscapes by facilitating processes like colonization and persistence (Kremen and M'Gonigle 2015, M'Gonigle et al. 2015). However, how much intra-annual temporal turnover in bee assemblages is influenced by characteristics of their environment—beyond natural variation in species' phenological flight periods (Oertli et al. 2005, Michener 2007)—remains poorly characterized.

The rate of seasonal turnover in flowering plants varies widely across ecosystems, potentially allowing one to test if this metric correlates with that of resident bee assemblages (Fründ et al. 2010). Horticultural plant nurseries are an agricultural habitat displaying substantial variation in plant turnover across sites and seasons, but in which bee diversity and turnover have not yet been extensively examined (but see Egerer et al. 2020). These areas possess unique characteristics, which allow testing of unique hypotheses about bee assemblages through time and space. Nurseries are intensively managed agricultural areas that cultivate a wide diversity of ornamental plants, many of which are attractive to bees. There is striking variation in the types of plants grown across nurseries even within a given geographic region. In nurseries, turnover in flowering plant species is partly due to bloom phenology as in natural areas, but also the removal and addition of new species by humans, facilitated by their storage in portable containers. Research on plant-pollinator networks in natural areas suggest turnover in interactions themselves is highly variable, but can be largely driven by turnover in the plant community (Simanonok and Burkle 2014, Cirtwill et al. 2018, Schwarz et al. 2020). Thus, nurseries provide an experimental framework for testing if variation in artificial assemblages of plants across sites and between seasons correlate with that of local bee assemblages.

Using a dataset on wild bees collected in southern California nurseries over two years, we tested the hypothesis that bee diversity and turnover are driven by that of the local plant community. We expect to find positive correlations between metrics of diversity (abundance, richness, Shannon diversity, evenness, community composition, and turnover) of wild bees and those of ornamental plants in nurseries. California is, economically, the highest grossing state in the horticulture industry in the United States (USDA NASS 2019) and also a hotspot of bee biodiversity (Moldenke and Neff 1974), making it an ideal location to investigate this hypothesis.

## METHODS

### Study sites and bee collection

We collected wild bees at 13 wholesale or retail plant nurseries (each > 2 ha in area) in southern California, USA (Appendix A: Table A.1, Appendix A: Fig. A.1). We sampled each nursery from March 2016 – May 2018 once per season, except winter: once each in spring (March–May), summer (June–August), and autumn (September–November) (Appendix A: Table A.2). We used two methods to collect bees. First, we deployed blue vane traps (SpringStar, Woodinville, WA) suspended from 1.2-m hooks in established sampling plots (see below) at a density of roughly one plot per hectare of nursery property (2-12 plots per nursery). We collected vane traps 72 h after deployment. Second, a single observer used a sweep net to collect bees visiting flowering plants in nurseries for 30-minute periods on each day we deployed and collected vane traps, spending no longer than 5 minutes collecting from a given plant species. Non-native honey bees, *Apis mellifera*, were abundant on many plants at these nurseries and were intentionally not sweep netted, but were sometimes collected in the vane traps. We identified all wild bees to species (or morphotaxon, if they could not be confidently assigned to species) using keys (Michener 2007, Ascher and Pickering 2017), reference collections, and assistance from bee specialists at the University of California Riverside Entomology Research Museum.

## Local and landscape features

We surveyed flowering plants that were currently blooming, regardless of floral abundance, within a 15-m radius (~700 $m^2$) plot around each vane trap during each nursery visit. We designated each plant species as native or non-native to California using the CalFlora database (calflora.org). We further classified five nurseries as “native nurseries” because they (1) advertised themselves as cultivating mostly plants native to California, and (2) on average, over two-thirds of plant taxa documented in plots were California-native. We classified the eight other nurseries as “conventional nurseries”. We estimated floral cover as percent cover within plots by dividing the plot into quadrants and assigning a rank to each quadrant using an ordinal scale from 0 to 4: ‘0’ = no flowers of any species, ‘1’ = few flowers with sparse cover, ‘2’ = more than ‘1’ but covering less than 50% of quadrant, 3 = > 50% cover but including large patches with no flowers, and ‘4’ = near 100% cover, then averaging these values for the plot. Using QGIS (QGIS Development Team 2020) and the 2016 National Land Cover Database (mrlc.gov), we calculated the proportion of natural area inside a 1-km buffer around each nursery’s perimeter. We treated land cover classes 41-43, 52, 71, 90, and 95 as “natural” landscape, excluding classes denoting water and developed, agricultural, or barren land (11, 21-24, 31, 81, and 92) (Cecala and Wilson Rankin, in review). We also recorded from local weather stations the daily high temperature for each of the four calendar days that vane traps were deployed, which we then averaged.

### Statistical analyses

We conducted all statistical analyses in R version 3.3.3 (R Core Team 2021). All means are reported ± SEM. The dataset represented 58 sampling events for blue vane traps (of which 21 were at native nurseries) and 80 sampling events for sweep netting (32 at native nurseries). We excluded all *Apis mellifera* (633 specimens) from the vane trap dataset so as to focus on patterns in wild bee assemblages. Comparisons of analyses with the full dataset and the dataset excluding honey bees excluded revealed that their removal had minimal to no influence on the outcomes of our statistical models (Appendix A: Table A.3).

We performed individual-based rarefaction using *vegan* (Oksanen et al. 2018) and *iNEXT* (Hsieh et al. 2016) to examine sampling completeness of wild bees across sites, nursery types, and collection methods. For each sweep netting and vane trap sampling event, we calculated bee abundance, richness, Shannon diversity, and evenness. To account for differences in the number of vane traps deployed per nursery, we calculated bee abundance and richness per trap, then averaged across traps within a given sampling event. As Shannon diversity and evenness account for sample abundances, these metrics were calculated on the pooled capture of all blue vane traps in a sampling event. Vane trap abundance and richness were $\log_{10}(x+1)$-transformed before analysis.

For each survey plot, we calculated the richness of blooming plants and the proportion of richness represented by native plant species, then averaged across plots within a given sampling event. In statistical models, we substituted proportional native plant richness with the residuals of this variable obtained from a regression against nursery type, as these predictors were collinear (variance inflation factor > 3) (Graham 2003). The same was also done with average daily high temperature in blue vane trap models, which was collinear with season. We constructed eight separate linear mixed models (LMMs) using *lme4* (Bates et al. 2015) for each of the four bee metrics (abundance, richness, Shannon diversity, and evenness) and two collection methods. We included as fixed effects season and nursery type (and their interaction), blooming plant richness, proportional native plant richness, percent floral cover, daily high temperature, nursery area, and proportional surrounding natural area. Nursery, study year, and date of sampling served as random effects in LMMs. For LMMs, we confirmed lack of multicollinearity (VIF < 3) using 'vif' (*car*) (Fox and Weisberg 2011). Using the function 'emmeans' in the package *emmeans* (Lenth 2019), we conducted post-hoc Tukey's tests to compare treatment means for statistically significant factors and corrected for multiple comparisons.

We next examined variation in the composition of plant and wild bee assemblages in nurseries. For bees, we conducted these analyses only on vane trap samples, as sweep net samples were not large enough to sufficiently represent assemblage composition. We tested for differences in the multivariate centroids of samples using permutational multivariate analyses of variance (permANOVA) on dissimilarity matrices using 'adonis' (*vegan*). We included the aforementioned fixed effects and stratified permutations (10,000) by nursery. We also examined spatial turnover as an estimate of beta diversity by analyzing multivariate homogeneity in dispersion of plant and wild bee assemblages around their centroids using 'betadisper' (*vegan*) between nursery types, seasons, and years. We performed Mantel tests using ‘mantel’ (*vegan*) to explore correlations between dissimilarity matrices of plant and bee (vane trap samples) assemblages across nurseries separately in spring, summer, and autumn.

We used function ‘RAC_change’ in *codyn* (Hallett et al. 2016) to calculate relative changes in plant and bee richness through time (bees from both collection methods were pooled). Temporal species turnover can be partitioned into gains and losses (Faleiro et al. 2018). This function quantifies changes in richness between a pair of time periods as the number of species gained or lost divided by the total unique species present in both time periods. We calculated these changes for each nursery between consecutive seasons in which samplings occurred (spring to summer, summer to autumn, and autumn to the following spring, over two years), totaling six inter-season comparisons. To determine if turnover in bee species was related to that of plants, we constructed LMMs with changes in bee richness (as gains or losses) as dependent variables, and the corresponding plant turnover metric, nursery type, category of inter-season comparison, and their interaction as fixed effects.

Finally, to determine if any bee species in our sweep netting or vane trap collections were significantly associated with local or landscape factors, we conducted a multi-level pattern indicator species analysis using function ‘multipatt’ (*indicspecies*) (De Cáceres and Legendre 2009). This analysis identifies species whose occurrence is associated with groups of sites categorized by a factor. We conducted analyses for season, nursery type, proportional native plant richness (which we dichotomized as > or ≤ 50%

native), floral cover (> or ≤ the average percent cover of all plots), and proportional natural area within 1 km of the nursery (> or ≤ 50% natural area).

## RESULTS

We collected a total of 6,698 wild (non-*Apis*) bees belonging to 153 species, constituting roughly 64–69% of the total estimated species in our system (Chao estimate: 240 ± 28 species; Jack1 estimate: 220 ± 25 species). Individual-based rarefaction curves from native nurseries were generally positioned at or above those from conventional nurseries for both collection methods (Fig. 1.1, Appendix A: Fig. A.2). We generally detected more bee species from samples of fewer individuals at native nurseries.

### Bee abundance and richness

Bee abundance in both sweep net and vane trap samples differed across the three seasons. We collected twice as many individuals per sweep net sampling in summer than in autumn ($F_{2,28} = 3.33$, $P = 0.050$), but netting sample abundance was not related to daily high temperature ($F_{1,31} = 0.055$, $P = 0.82$). Vane trap samples exhibited similar seasonal patterns: we collected 3.9 times more individuals in summer samples than in spring or autumn samples ($F_{2,16} = 25.4$, $P < 0.0001$), but there was a slight positive correlation between the number of individuals trapped and average daily high temperatures ($F_{1,21} = 4.64$, $P = 0.043$). Nursery type was also moderately correlated with netted bee abundance: at native nurseries, we sweep netted 1.3 times more individuals ($F_{1,16} = 4.58$,

$P = 0.048$) than at conventional nurseries, although there was no effect of nursery type on abundance in vane trap samples ($F_{1,16} = 0.19$, $P = 0.67$). Moreover, proportional native richness of nursery plants and floral cover positively influenced the number of individuals sweep netted (proportional native richness: $F_{1,10} = 28.1$, $P = 0.00034$; floral cover: $F_{1,43} = 6.45$, $P = 0.015$). No other local or landscape variables influenced the number of individuals in sweep net samples (all $P > 0.05$). In vane trap collections, we found no effect of any local or landscape variables (all $P > 0.05$) on the number of individuals trapped.

Trends in bee richness resembled those in bee abundance for both sweep net and vane trap samples. We netted 1.6 times as many species in summer than in either spring or autumn ($F_{2,33} = 5.65$, $P = 0.0078$). In vane traps, we collected 2.2 times more species ($F_{2,17}$=25.9, $p$<0.0001) in summer samples than in spring or autumn samples. At native nurseries, we sweep netted 1.3 times more species ($F_{1,18} = 5.71$, $P = 0.028$) than at conventional nurseries. Similar to the vane trap abundance analysis, nursery type did not affect species richness of vane trap collections ($F_{1,17} = 0.60$, $P = 0.45$). Moreover, proportional native richness of nursery plants positively influenced the number of species ($F_{1,8} = 20.8$, $P = 0.0019$) sweep netted. Floral cover was also positively correlated with the number of species ($F_{1,48} = 4.66$, $P = 0.036$) in netting samples. No other local or landscape variables influenced the number of species in sweep net samples (all $P > 0.05$). In vane trap collections, we found no effect of any local or landscape variables (all $P >$ 0.05) on the number of species trapped.

### Bee Shannon diversity and evenness

Shannon diversity (*H'*) of sweep net samples was 78% higher in summer than in autumn ($F_{2,31} = 4.03$, $P = 0.028$). Interestingly, proportional native plant richness positively influenced *H'* of sweep net samples (Fig. 1.2a; $F_{1,9} = 14.3$, $P = 0.0045$; sample Pearson $r = 0.37$), but we found no effect of nursery type itself on *H'* ($F_{1,20} = 0.66$, $P = 0.43$). No other local or landscape variables influenced *H'* of sweep net samples (all $P > 0.05$). In vane trap samples, bee *H'* was 59% higher in spring and summer than in autumn ($F_{2,26} = 9.35$, $P = 0.00086$). While we detected no significant effect of nursery type ($F_{1,28} = 0.26$, $P$=0.61), there was a significant interaction between season and nursery type (Fig. 1.2b; $F_{2,30} = 3.96$, $P = 0.030$) such that, in spring only, *H'* was 34% higher at native nurseries than at conventional nurseries. *H'* of vane trap samples was not related to any other local or landscape variables (all $P > 0.05$) except for nursery area, with which it was slightly positively correlated ($F_{1,10} = 6.15$, $P = 0.032$).

Evenness of sweep net samples did not differ across seasons ($F_{2,32} = 0.97$, $P$=0.39) or between nursery types ($F_{1,15} = 0.15$, $P$=0.71). While evenness of sweep net samples was negatively correlated with nursery area ($F_{1,17} = 7.92$, $P$=0.012), it did not correlate with any other local or landscape variables (all $P > 0.05$). Evenness of blue vane trap samples was not related to any of our metrics (all $P > 0.05$).

### Bee and plant assemblage composition

We did not examine composition in sweep net samples due to the lower number of individuals and species collected per sampling event relative to vane traps (Fig. 1.1). Composition of vane trap samples (as Bray-Curtis dissimilarity) differed across seasons ($F_{2,57} = 7.24$, $P < 0.0001$) and between nursery types ($F_{1,57} = 2.39$, $P < 0.0001$). It was also influenced by the proportion of natural area surrounding the nursery ($F_{1,57} = 2.37$, $P = 0.0063$). It did not differ with year ($F_{1,57} = 1.41$, $P = 0.15$) or with any other local or landscape variables (all $P > 0.05$). Spatial turnover (beta diversity) in vane trap samples across nurseries was lower in summer than in spring ($F_{2,55} = 8.00$, $P = 0.00089$), but did not differ between nursery types ($F_{1,56} = 1.60$, $P = 0.21$).

Composition of plant assemblages (as Jaccard dissimilarity) varied across seasons ($F_{2,57} = 1.40$, $P < 0.0001$), nursery types ($F_{1,57} = 5.23$, $P < 0.0001$, and years ($F_{2,57} = 1.10$, $P = 0.0011$). Spatial turnover (beta diversity) in plant assemblages did not differ across seasons ($F_{2,55} = 0.12$, $P = 0.88$) but was higher at conventional nurseries than at native nurseries ($F_{1,56} = 7.30$, $P = 0.0091$). Bee and plant assemblages were not correlated across nurseries in spring (Mantel $r = 0.062$, $P = 0.30$) or summer ($r = 0.051$, $P = 0.34$), but were in autumn ($r = 0.51$, $P = 0.0079$).

### Temporal species turnover in bees and plants

For plants, changes in species richness did not differ across seasons ($F_{2,29} = 0.13$, $P = 0.88$), nursery types ($F_{1,8} = 0.16$, $P = 0.70$), or between years ($F_{1,33} = 0.068$, $P = 0.80$). In contrast, we observed the largest gains in bee species between spring and summer and between autumn and the following spring ($F_{2,28} = 17.6$, $P < 0.0001$), whereas most bee species were lost between summer and autumn ($F_{2,28} = 11.8$, $P = 0.00019$). This pattern was consistent between nursery types (for species gains: $F_{1,28} = 3.04$, $P = 0.092$; for species losses: $F_{1,27} = 1.56$, $P = 0.22$). There was a moderate positive correlation between gains in plant species and gains in bee species across seasons (Fig. 1.3; $F_{1,29} = 5.40$, $P = 0.027$; sample Pearson $r = 0.32$).

### Indicator species analysis

A total of 44 out of 153 bee species were identified as significantly associated with at least one of the examined categorical habitat characteristics (Table 1.1, Appendix A: Table A.2). The three categories with the highest number of associated indicator species were summer (17 species), sites with > 50% surrounding natural area (14 species) and sampling events where > 50% of blooming plant species in plots were native (12 species).

## DISCUSSION

We detected a considerable diversity of bee species in plant nurseries, with strong seasonal trends and bee species gains tracking plant species gains. As expected, bee assemblages were highly dynamic across seasons and sites. In spite of this variation, we found associations between local and landscape variables and bee abundance, richness, diversity, composition, and turnover. However, our two collection methods did not detect patterns equally. When combining collection methods, we detected roughly 90% the number of bee species found in another study in natural area fragments (Hung et al. 2021) near our study region that collected 65% more individuals than our study. Our results have important considerations for monitoring efforts and conservation of bees in horticultural production systems and other landscapes dominated by ornamental plants, like urban areas (Ayers and Rehan 2021).

Perhaps unsurprisingly, we detected more instances of local factors correlating with bee assemblage metrics in our sweep net dataset than in our vane trap dataset (as in Rhoades et al. 2017). We found higher proportional cultivation of native plant species was positively associated with abundance, richness, and diversity of bees sweep netted on flowers. More encouraging is that this effect of local native plant richness was significant even while controlling for differences in native and conventional nurseries. In vane trap samples, nursery type influenced bee assemblage composition and Shannon diversity in vane trap samples (though for diversity, only in spring), however we found no effect of the proportion of plants cultivated that were native. This latter result suggests that the differences in bee diversity and composition between nursery types may be due to site-level factors other than a nursery's choice of plant species cultivated, such as differences in attractiveness across plant species (Ricker et al. 2019).

Several studies have quantified temporal turnover in bee communities (Rollin et al. 2015) and sometimes that of bees and co-occurring plants (Kehinde and Samways 2014), but rarely do studies link the two. We found a positive association between proportional gains in bee and plant assemblages across seasons. Agricultural and urban areas can homogenize communities by causing losses in species sensitive to disturbance

(Beduschi et al. 2018, Ayers and Rehan 2021). Our findings demonstrate that richness gains in the local plant assemblage are moderately (sample Pearson $r = 0.32$) correlated with those of resident bees, mirroring longer-term results from other agricultural systems of how installation of floral resources increases bee diversity over multiple years (Ponisio et al. 2016). The factors underlying this relationship are likely very complex. Bee species exhibit differences in their seasonal activity periods, and bloom turnover in a plant community can exert different impacts across bee species that vary in their flight period (Fisogni et al. 2020) or their flexibility in the use of different flowering plant species (Ogilvie and Thomson 2016).

We observed relatively fewer influences of landscape-level factors on bee assemblages in nurseries compared to the aforementioned local variables. Studies often report a negative relationship between the proportion of surrounding developed land and local wild bee abundance and richness (Ahrné et al. 2009, Fortel et al. 2014, Geslin et al. 2016), but we found no such evidence in horticultural nurseries. In terms of area effects, we detected a moderate (sample Pearson $r = 0.34$) effect of nursery area on bee $H'$ in vane trap samples, while in netting samples, we identified a negative association (sample Pearson $r = –0.40$) with evenness. The effect of nursery area on $H'$ may have been driven by more vane traps deployed at larger sites, since our analysis revealed no corresponding relationship between area and bee richness (Phillips et al. 2018). While the negative relationship between bee evenness and nursery area was mainly driven by our largest nursery, Marini et al. (2014) also reported lower pollinator evenness in larger semi-natural habitat patches. In contrast, Hung et al. (2017) recorded lower bee evenness in smaller natural area fragments (< 120 ha) relative to larger reserves (>> 500 ha), though said fragments were over 19 times larger than the average nursery in our study (6.2 ± 2.0 ha). We found that surrounding natural area only influenced the composition of blue vane trap samples. In other ecosystems, landscape composition can alter bee community composition (Harrison and Winfree 2015) and spatial turnover (Beduschi et al. 2018) by differentially impacting species across different functional groups. In contrast, landscape factors do not appear to be the main driving forces shaping bee communities in horticultural nurseries. Rather, local factors like those related to the flowering plant assemblage appear to play more roles in shaping flower-visiting bee assemblages, as noted in other developed habitats (Wilson and Jamieson 2019).

Our results further highlight the very different conclusions resulting from different collection methods. In vane trap samples, we found no effect of local plant assemblage variables on bee abundance, richness, or evenness. The influence of native plant cultivation and floral cover were only apparent in netting samples of bees visiting flowering plants. While sweep netting collected far fewer individuals than vane traps (roughly 5.9% as many bees as the latter method), it discerned patterns due to local habitat characteristics (proportional plant native richness) whereas no such patterns were detected using vane traps. Vane traps may have attracted bees from greater distances (Rhoades et al. 2017), which is supported by the fact that the diversity and composition of vane trap samples were related to nursery area and surrounding natural area, respectively. As studies in other developed areas suggest (Prendergast et al. 2020), multiple methods are needed to build a comprehensive representation of bee assemblages in nurseries.

Overall, we found evidence that local management practices are tied to various metrics of bee diversity and turnover in nursery systems. Native plant cultivation was associated with the composition and diversity of the resident wild bee assemblage. However, the effect of this management practice was limited to certain seasons of the year, and partially influenced by surrounding landscape. Furthermore, we show that turnover in the plant assemblage, as gains in species between seasons, is positively correlated with that of native bees. Although plants at nurseries and garden centers rarely require pollination (Garbuzov et al. 2017), studying patterns in wild bee diversity and turnover in nurseries is useful for pollinator conservation in these habitats and other landscapes dominated by ornamental plants (Martins et al. 2017). Our study demonstrates that ornamental plant nurseries can serve as useful model systems to test how variation in plant assemblages might influence other aspects of wild bee assemblages, like foraging behaviors and fitness.

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**Table 1.1.** Results of indicator species analyses for bee species collected in plant nurseries. Numbers in the table represent the number of wild bee species (total = 153 species) that were significantly associated with various categorical habitat characteristics. Analyses were conducted separately for both bee collection methods. Names of species are given in Appendix A: Table A.4.

| categorical variable | category | vane trapping | sweep netting | both methods | total bee species |
|---|---|---|---|---|---|
| season | spring | 5 | 2 | 0 | 7 |
| | summer | 13 | 3 | 1 | 17 |
| | autumn | 0 | 3 | 0 | 3 |
| nursery type | native | 4 | 5 | 1 | 10 |
| | conventional | 1 | 2 | 0 | 3 |
| proportional native plant richness | > 50% | 6 | 5 | 1 | 12 |
| | ≤ 50% | 1 | 1 | 0 | 2 |
| floral cover | > average | 1 | 0 | 0 | 1 |
| | ≤ average | 1 | 2 | 0 | 3 |
| surrounding natural area at 1 km | > 50% | 12 | 0 | 2 | 14 |
| | ≤ 50% | 1 | 1 | 0 | 2 |
| nursery area | > median | 5 | 0 | 0 | 5 |
| | ≤ median | 0 | 1 | 0 | 1 |

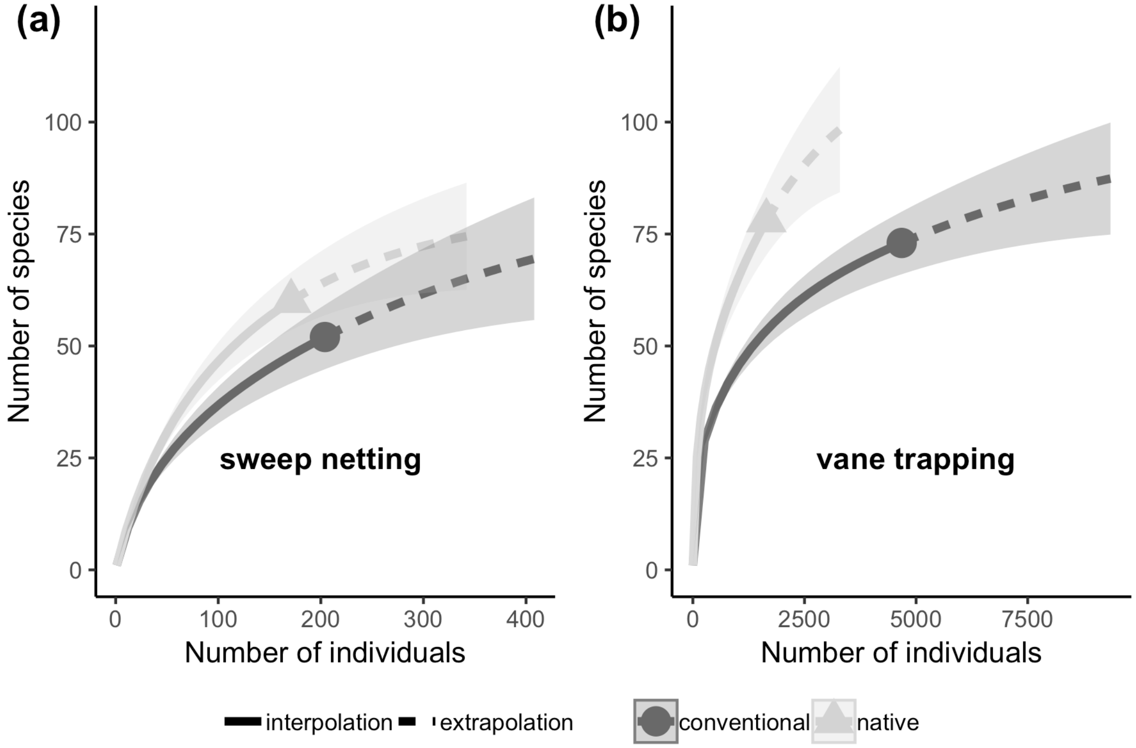

**Figure 1.1.** Individual-based species rarefaction curves for bee assemblages collected in native (light gray) and conventional (dark gray) plant nurseries via (a) sweep netting and (b) vane trapping. Plotted triangles/circles represent the observed numbers of species and individuals, while dotted lines indicate interpolated species richness estimates with shaded 95% confidence intervals from 1,000 bootstrap replications.

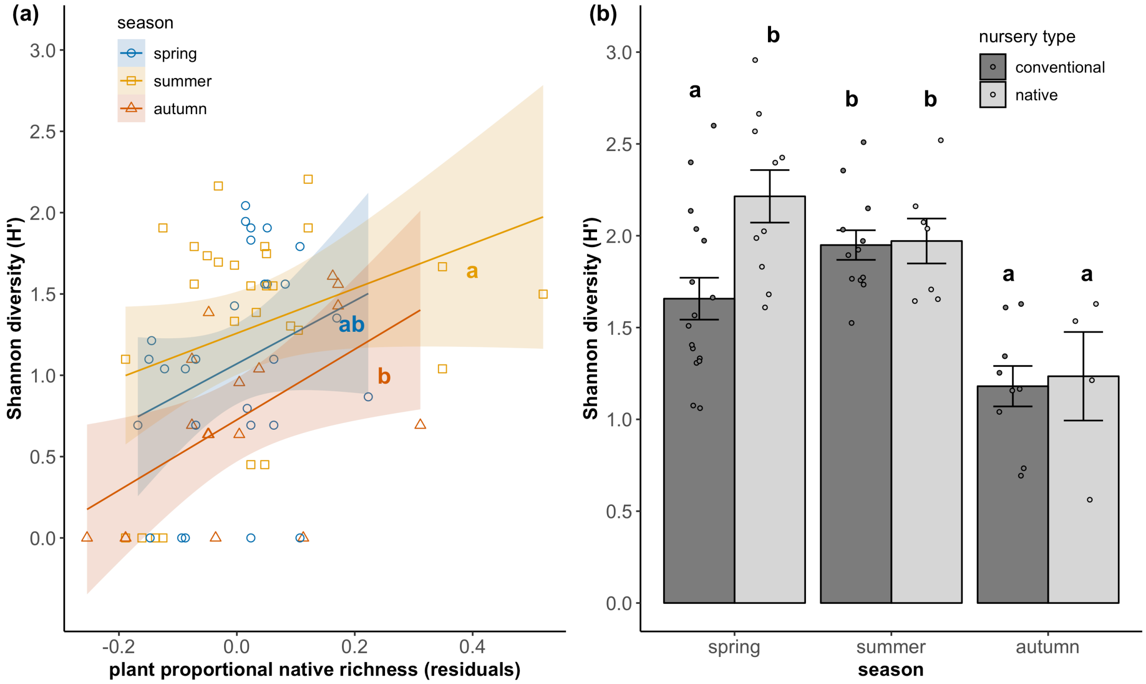

**Figure 1.2.** Shannon diversity of bee samples collected in plant nurseries across seasons. Each point represents a sample from one nursery in one season. (a) Shannon diversity of sweep netted bees in relation to proportional native plant richness (as residuals from a regression with nursery type, as these factors are correlated), and (b) Shannon diversity of vane trapped bees in relation to nursery type. Groups not connected by the same lowercase letter were significantly different in post-hoc Tukey's HSD tests.

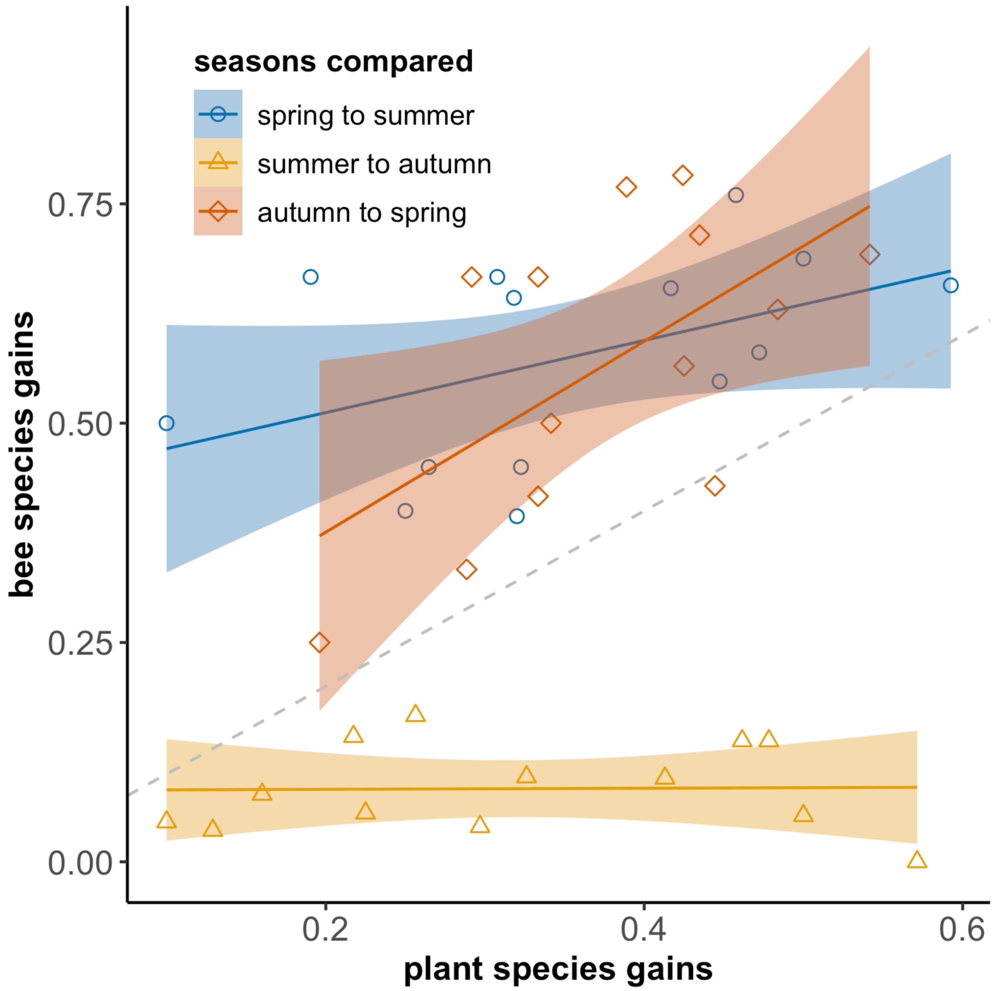

**Figure 1.3.** Turnover (as proportional gains in species) of wild bee and plant assemblages at nurseries. Each point represents a comparison of samples from two consecutive seasons at a nursery. Sweet net and vane trap samples were pooled. Each point represents a comparison between two consecutive (not counting winter) seasons at a single nursery. The gray dashed line represents a line crossing the origin with slope = 1. Seasons are plotted separately for clarity, but slopes did not differ significantly across seasons.

# CHAPTER II

## Wild bee functional diversity and plant associations in native and conventional plant nurseries

## ABSTRACT

An ongoing challenge in ecology is predicting how characteristics of communities correspond to habitat features. Examining variation in functional traits across species may reveal patterns not discernible from measures of mere abundance or richness. For beneficial insects like wild bees, functional trait-based approaches are often used to characterize communities in different agricultural habitats. However, no such approach has yet been applied in horticultural plant nurseries, which represent intensively managed artificial flowering plant assemblages. Certain nurseries mostly cultivate regionally native flowering plants, allowing one to test how differences between local plant assemblages may correlate with bee functional traits. We surveyed bee assemblages at native and conventional plant nurseries in southern California from spring through autumn over two years, while also documenting the native status of blooming plants in sampling plots. Bees were classified into different functional categories based on their diet breadth, nesting location, and social organization. At native plant nurseries, we detected proportionally more specialist bee species and fewer generalist species than at conventional nurseries, while nesting location and social organization did not differ between nursery types. Meanwhile, landscape-level features were not associated with any observed functional trait metrics of bee collections. Furthermore, network-level

specialization of bee-plant interactions was higher at conventional nurseries. Our results suggest that horticultural cultivation practices are quantifiably correlated with the functional distribution of resident bee assemblages. These results are important and encouraging to pollinator conservation efforts in nursery systems and other human-modified landscapes dominated by ornamental plants.

## INTRODUCTION

One of the goals of ecology is to understand how differences in the environment may impact community composition. Humans have altered natural ecosystems through processes such as urbanization and agricultural intensification, which subject resident species to novel pressures (Kremen et al. 2002). Nevertheless, human-modified landscapes may host appreciable biodiversity, though individual species are differentially impacted by environmental perturbations (Winfree et al. 2011). Studying functional traits, or measurable behavioral or physical features tied to a species' performance or fitness (Cadotte et al. 2011), may provide a more mechanistic understanding of how a given environment may affect each species' performance (Cadotte et al. 2015). Functional trait approaches offer insights not otherwise discernible from data on mere species abundance, richness, or taxonomic diversity (Mayfield et al. 2010).

The functional ecology of wild bees (Hymenoptera: Anthophila) in particular has received a great deal of recent attention (e.g., Forrest et al. 2015) because of the value of their functional trait complementarity to the pollination services they deliver (Fründ et al. 2013). Bees are functionally diverse, displaying substantial variation in life history characteristics, often used to organize them into tractable groups (Buchholz and Egerer 2020). Common groupings include those based on the breadth of their pollen diets, the locations in which they construct their nests, and their social organization, among others. These functional traits can mediate wild bees' responses to disturbances, such as agricultural intensification (Williams et al. 2010). Additionally, much research has focused on how bee species and their plant associations correlate to local and regional features of agricultural landscapes, such as management strategies, crop area, and landscape composition (e.g., Holzschuh et al. 2008).

Despite many studies on wild bee functional ecology in agricultural habitats (Williams et al. 2010), we know of none to date conducted in horticultural plant nurseries. Nurseries are intensively managed, compositionally complex agricultural areas (Parke and Grünwald 2012) representing the main source of cultivated plants for urban areas (Avolio et al. 2018). They host diverse, dynamic assemblages of containerized plants year-round (Pincetl et al. 2013), contrasting sharply with the monocultural swaths characterizing most food crops (Holzschuh et al. 2011). Flowering ornamentals are known to serve as foraging resources for wild bees in urban areas (Pardee and Philpott 2014, Baldock et al. 2019), but only recently are ecological interactions between ornamental plants and wild bees in nurseries garnering attention (Egerer et al. 2020, Cecala and Wilson Rankin 2020). One potential reason that nurseries have been overlooked by agroecologists is the small proportion of land they occupy relative to other types of agricultural areas. However, nurseries are important to study because flowering ornamentals are present in these areas year-round, not just seasonally (Avolio et al. 2020).

Furthermore, there is growing public interest in conserving pollinators using ornamental plants, in addition to escalating concerns over risks of exposure to systemic insecticides in treated ornamentals (Lentola et al. 2017).

Nurseries are particularly interesting from a functional trait perspective because of the astonishing diversity of plants they cultivate (Pincetl et al. 2013). While many ornamental plants in North America, for example, originate from other continents and are thus non-native, some nurseries specialize in cultivars of regionally native species (Avolio et al. 2020). This is a feature uncommon to other types of agricultural habitats, where crop plants tend to be non-native (Strickler and Cane 2003) and native plants may be specifically installed to benefit pollinators or natural enemies (Isaacs et al. 2009). There is evidence that plant native status can predict the functional traits of floral visitors and shape their visitation networks (Kuppler et al. 2017, Seitz et al. 2020). Recently, Erickson *et al.* (2019) found only generalist bees visiting annual ornamentals in semi-natural sites despite the presence of specialist bees in the environment. Developing a functional trait-based framework for how bees interact with nurseries would also allow us to test if ecological patterns discerned in other habitat types hold true in nursery systems, and would be valuable to pollinator conservation efforts in horticulture,

Nurseries thus provide a convenient venue for investigating whether variation in the native status of ornamental plant assemblages correlates with functional traits of local wild bees. In this study, we test the hypothesis that nursery type, specifically with regard to their cultivation of native or non-native plants, corresponds with the functional composition of resident bee assemblages. We predict that specialist bees will be more prevalent at nurseries cultivating native plants, though this effect may vary across seasons and with respect to other nursery characteristics. Moreover, we expect that network-level bee-plant visitation network metrics such as specialization and link density will vary between nurseries that mostly cultivate native plants versus those that mostly cultivate non-native plants. Since at least some native plants are cultivated at many nurseries (and likewise, some non-native plants at native plant nurseries), we also investigate differences in species-level network metrics between native and non-native plants as units. We expect relatively more generalization at conventional nurseries due to the lower availability or abundance of specialist bee host plants.

## METHODS

We conducted this study at 13 plant nurseries in southern California, USA (Appendix B: Table B.1). All nurseries were open-air yards with containerized flowering plants grown outside or under shade houses, thus being freely accessible to foraging bees (Appendix B: Fig. B.1). From March 2016 to May 2018, we sampled each nursery every three months, except in winter: once each in spring (March–May), summer (June–August), and autumn (September–November). Due to the number of nurseries and distance between them, it was not feasible to sample all nurseries simultaneously. Within each season, we sampled nurseries in a semi-randomized order within a period of about 6.5 weeks. We sampled each nursery at least twice, with the exception of one, resulting in 58 sampling events (Appendix B: Table B.2). We classified a nursery as a “native” nursery if it met two criteria: (1) it advertised itself as cultivating, mostly or exclusively, plants native to California, and (2) on average, greater than 2/3 of plant taxa documented in surveys (see below) were native to California. All five nurseries that met the second criterion also met the first. Eight nurseries not meeting both criteria were classified as “conventional”.

### Bee sampling in nurseries

In each sampling event (Appendix B: Table B.2), we used both blue vane traps (SpringStar, Woodinville, WA) and sweep nets to collect bees. Vane traps detect a wide diversity of bees (Rhoades et al. 2017) even near attractive floral resources. Moreover, conventional bowl traps for bees are vulnerable to flooding from overhead irrigation and disturbance from passerby. We deployed vane traps at a density of roughly one trap per hectare of nursery property (2–12 traps per site). Each vane trap was placed in the open, partially filled with soapy water, and suspended from a 1.2-m hook, then collected after 72 h. In every sampling event, we placed vane traps in roughly the same location at each nursery, which doubled as sampling plots for plant data collection (see below).

Each time we visited a nursery to deploy or collect vane traps (i.e., twice per sampling event), one observer sweep netted wild bees from flowering nursery stock for 30 minutes. Daily high temperatures on sweep netting days were at least 18 °C, wind velocities were low, and there was no precipitation. We recorded the associated plant species for each collected bee, and spent no more than 5 minutes collecting from any one plant species. Non-native honey bees, *Apis mellifera*, were not sweep netted due to their high prevalence on flowering plants at nurseries.

We identified all bees to species (or morphotaxon, if species-level identification was unfeasible) using published keys (Michener 2007, Ascher and Pickering 2017), reference collections, and consultation with bee specialists at the University of California, Riverside Entomology Research Museum. We categorized each species using published literature on the basis of three functional traits: pollen diet breadth, nesting location, and social organization (Appendix B: Table B.5). If these data were not available for a taxon, we assigned traits based on those of its congeners (as in Wilson and Jamieson 2019). For diet breadth, species were classified as generalists (collecting pollen of plants from many unrelated families to provision offspring, i.e., polylectic), specialists (oligolectic, mesolectic, or monolectic), or cleptoparasites that do not collect pollen (Cane and Sipes 2006). For nesting location, species were categorized as above-ground nesters (including cavity-renting and -excavating species nesting in stems or wood), below-ground nesters (soil excavators and burrow renters), or cleptoparasites that reproduce using host nests. For social organization, species were classified as eusocial (including primitively eusocial), solitary (including subsocial and communal), or cleptoparasites reliant on a host for reproduction (Buchholz and Egerer 2020).

## Local and landscape features of nurseries

In each sampling event, we surveyed blooming plants inside a 15-m radius around each vane trap (700 $m^2$ plot). We recorded all plant species, including weeds, currently blooming in each plot (as in Wilson and Jamieson 2019) regardless of floral abundance. We did not record graminoids, angiosperms not currently blooming, or non-angiosperms.

Using the online CalFlora database (calflora.org), we classified each species as native if any part of its native range fell within California state boundaries (as in Avolio et al. 2020). Hybrid cultivars were classified as native if all parent taxa were native.

Using QGIS (QGIS Development Team 2020), we calculated the proportion of natural area within a 1-km buffer around each nursery's perimeter. This distance encompasses the flight ranges of many wild bee species (Greenleaf et al. 2007). We used the 2016 National Land Cover Database (mrlc.gov, 30-m resolution) to classify land into cover types. We defined "natural" area as cover classes representing forests, shrubland, grassland, and wetlands (classes 41–43, 52, 71, 90, 95) and excluding classes representing water or land that is developed, managed for agriculture, or barren (11, 21–24, 31, 81, 92).

### Statistical analyses: bee functional traits

We conducted all statistical analyses in R version 3.3.3 (R Core Team 2021). All means are reported ± SEM. In 7 of 58 sampling events (Appendix B: Table B.2), no bees were collected via sweep netting, so these events were excluded from sweep netting analyses ($N = 51$). For each sampling event, we pooled captures from vane traps so as to render analyses comparable between sweep netting and vane trapping, as sweep netting was not conducted using plots. As honey bees were not sweep netted, we excluded from analyses the 633 specimens incidentally collected in vane traps. We re-analyzed the vane trap dataset *including* honey bees to detect whether their removal affected model results (Appendix B: Table B.4). For each collection method in each sampling event, we tallied the total number of bee species collected (richness) and the number of species in each category of the functional trait of interest (diet breadth, nesting location, or social organization). We converted these count data to proportions to account for differences in the numbers of species collected across samplings.

To examine variation in the proportions of species across functional trait categories, we constructed generalized linear mixed models in *lme4* (Bates et al. 2015) with binomial error distributions. We created six models, one for each functional trait and collection method. In models, the dependent variable was the proportion of bee species in each category of that functional trait; thus, each sampling event corresponded to three observations in a model.  We weighted each set of three proportions by the total number of species collected in that sampling event. We included as fixed effects the corresponding functional trait (factor, $k = 3$), season, and nursery type, and all interactions between these factors, and nursery area and proportional surrounding natural area. We included nursery and year as random factors. Similarly, we constructed six extra models using proportions of *individuals* collected in sampling events as dependent variables (Appendix B: Table B.4).

We also calculated functional dispersion (FDis) of bees collected in each sampling event using function ‘dbFD’ with a Cailliez correction (Forrest et al. 2015) in *FD* (Laliberte and Legendre 2010). FDis quantifies the functional trait diversity of a sample, is weighted by abundances, and is not influenced by richness. We constructed two linear mixed models, one for each collection method, with FDis as the dependent variable and included the same fixed and random effects as above.

We retained all non-significant ($P > 0.05$) interaction terms in models to facilitate comparisons across models. We confirmed the absence of multicollinearity (VIF < 3) among fixed effects using function 'vif' (*car*) (Fox and Weisberg 2011). Lastly, we conducted post-hoc Tukey's HSD tests using function 'emmeans' (*emmeans*) (Lenth 2019).

**Statistical analyses: bee-plant networks**

Using our sweep netting dataset, we subdivided our overall bee-plant interaction network matrix into sub-matrices representing each sampling event. We calculated the size of each sub-network as the product of the number of bee species collected and the number of plant species off which bees were netted (de Mendonça Santos et al. 2010). We examined variation in sub-network size by constructing a linear mixed model with the aforementioned fixed and random effects.

To examine generalization in bee-plant interactions in nurseries, we employed a null network approach using package *econullnetr* (Vaughan et al. 2017). We compared our observed bipartite bee-plant networks to null networks created using function 'generate_null_net'. Null networks were structured such that bees interact with plants in proportion to their relative abundances in observed networks, using seasons as subdivisions. Using function 'bipartite_stats', we compared observed values of network metrics to 95% confidence intervals from 1,000 iterations of null models; significantly different values fall outside this interval. Standard effect sizes for metrics were generated for comparisons between networks. To detect differences in generalization between networks from native and conventional nurseries, we divided our overall network into two sub-networks corresponding to nursery type, and compared their nestedness (NODF), specialization (H2), and linkages (connectance) to their respective null networks. To test for differences in generalization between native and non-native plant species and among bee diet breadth categories across nurseries, we used these groupings as factors in separate linear models to compare standardized effect sizes for centrality (closeness), specialization (d'), and linkages (effective partners).

Finally, to assess if any bee species in our sweep netting dataset were significantly associated with either native or non-native ornamental plants, we conducted a multi-level pattern indicator species analysis using function 'multipatt' in package *indicspecies* (De Cáceres and Legendre 2009) with 10,000 iterations. This analysis identifies species whose occurrence is associated with groups of sites organized into categorical habitat types. Here, we treated plant species analogously to sites, categorizing them based on native status.

## RESULTS

### Blooming plant richness at nurseries

At native nurseries, 83.3 ± 2.4% of blooming plant species in survey plots were native to California, compared to 18.8 ± 2.6% of blooming plant species at conventional nurseries ($F_{1,10} = 42.2$, $P < 0.0001$). The proportion of blooming plant species that were native did not vary across seasons ($F_{2,40} = 1.86$, $P = 0.17$) and was not related to nursery area ($F_{1,9} = 0.0020$, $P = 0.97$) or proportional natural area surrounding the nursery ($F_{1,9} =$

0.023, $P = 0.88$). Native and conventional nurseries did not differ in the richness of blooming plant species (regardless of native status) in plots ($F_{1,10} = 0.71$, $P = 0.42$; 6.6 ± 0.5 species per plot) across seasons ($F_{2,41} = 0.13$, $P = 0.88$), and blooming plant richness was not related to nursery area ($F_{1,9} = 2.61$, $P = 0.14$) or proportional natural area surrounding the nursery ($F_{1,9} = 0.13$, $P = 0.73$).

### Functional traits of bee assemblages in nurseries

We collected a total of 6,687 wild (non-*Apis*) bees, representing 153 taxa (hereafter, "species") in 40 genera and 5 families. Of these, 76 species were identified as described species while 77 were identifiable only as morphotaxa, these accounting for 39.1% of all specimens. Sweep netting yielded 375 individuals from 92 species (29 ± 6 individuals in 14 ± 2 species per nursery), while vane trapping yielded 6,312 individuals from 102 species (486 ± 125 individuals in 28 ± 4 species per nursery) (Appendix B: Table B.1). Only 41 species (26.8% of all species detected) were detected by both methods (Appendix B: Table B.5).

The full results of all functional trait models are presented in Appendix B: Table B.4. Bee species representing each functional trait category we considered were collected, but some combinations of different functional traits were not represented (Appendix B: Table B.3). Nursery type (native versus conventional) corresponded to the proportion of bee *species* sweep netted in each diet breadth category ($\chi^2_1 = 5.99$, $P = 0.014$; Fig. 2.1a). We sweep netted proportionally fewer generalist species and more specialist species at native nurseries (80.4 ± 4.2% generalists vs. 16.4 ± 4.0% specialists) compared to conventional nurseries (96.3 ± 1.5% vs. 1.8 ± 1.3%). Cleptoparasites were sweep netted in low but equal proportions at both nursery types (diet breadth *x* nursery type interaction: $\chi^2_2 = 12.30$, $P = 0.002$; Fig. 2.1a). Similar patterns were observed for the proportions of *individuals* sweep netted in each diet breadth category (Appendix B: Table B.4, Appendix B: Fig. B.2). This pattern was not observed in vane trap collections (Fig. 2.1b). There was no effect of nursery type on the proportion of sweep netted bee *species* or *individuals* in nesting location (species: $\chi^2_1 = 0.034$, $P = 0.85$, Fig. 2.2a; individuals: $\chi^2_1 = 0.45$, $P = 0.50$, Appendix B: Fig. B.3a) or sociality categories (species: $\chi^2_1 = 0.18$, $P = 0.67$, Fig. 2.3a; individuals: $\chi^2_1 = 0.040$, $P = 0.84$, Appendix B: Fig. B.4a). Moreover, there was no effect of nursery type on the proportion of vane trapped species in nesting location ($\chi^2_1 = 3.70$, $P = 0.054$; Fig. 2.2b) or sociality categories ($\chi^2_1 = 0.84$, $P = 0.36$; Fig. 2.3b).

The proportions of *species* of in any functional trait categories did not vary across seasons in sweep net collections or in vane trap collections (all $P > 0.05$), with the sole exception that there were proportionally more generalist species and fewer specialist species in autumn (93.7 ± 2.6% generalists vs. 6.3 ± 2.6% specialists) than in either spring (77.1 ± 3.3% vs. 22.2 ± 3.2%) or summer (78.5 ± 1.9% vs. 21.0 ± 1.8%) (diet breadth *x* season interaction: $\chi^2_4 = 11.5$, $P = 0.021$). In terms of *individuals*, proportionally more solitary and fewer eusocial bees were sweep netted in spring than in either summer or autumn (season: $\chi^2_2 = 7.00$, $P = 0.030$; sociality *x* season interaction: $\chi^2_4 = 12.18$, $P = 0.016$; Appendix B: Fig. B.4). In terms of the proportions of individuals vane trapped, the three-way interaction among season, nursery type, and the functional trait of interest was significant for all three functional traits (three-way interaction terms for diet breadth: $\chi^2_4 = 187.9$, $P < 0.0001$; nesting: $\chi^2_4 = 15.8$, $P = 0.0034$; sociality: $\chi^2_4 = 40.5$, $P < 0.0001$; Appendix B: Fig. B.2, Appendix B: Fig. B.3, and Appendix B: Fig. B.4), indicating the effects of these variables on vane trap collections are interdependent.

Nursery area and proportional surrounding natural area were uncorrelated with the proportion of species collected in all functional trait category (all $P > 0.10$). We found no effect of season, nursery type, nursery area, or surrounding natural area on FDis of sweep netted bees (all $P > 0.05$; Fig. 2.4a). In vane trap collections, bee FDis was 69% higher at native nurseries than at conventional nurseries in spring, but did not differ between nursery types in summer or autumn (nursery type *x* season interaction: $F_{2,34} = 3.92$, $P = 0.029$). Bee FDis was constant across seasons at conventional nurseries, but at native nurseries was higher in spring and summer than in autumn (Fig. 2.4b).

### Wild bee and ornamental plant visitation networks

We collected 171 bees off 43 plant species at native nurseries, and 204 bees off 69 plant species at conventional nurseries. Both native and conventional nursery sub-networks displayed lower connectance (native: SES = –2.99, $P = 0.0027$; conventional: SES = –4.81, $P < 0.0001$) than respective null networks. Specialization (H2) was higher than null expectations in the conventional nurseries sub-network (SES = 3.65, $P = 0.00026$) but the native nurseries sub-network did not differ from null expectations (SES = –0.137, $P = 0.89$). Nestedness (NODF) for either sub-network did not differ from that of its respective null network (native: SES = 0.522, $P = 0.60$; conventional: SES = –0.483, $P = 0.63$).

Across nurseries, we collected 245 bees from 49 native plant species and 130 bees from 48 non-native plant species (Appendix B: Table B.6). At native nurseries, 95.3% of bees were collected from native plants compared to 40.2% of bees at conventional nurseries. Across nurseries, non-native plants had higher closeness ($F_{1,95} = 7.54$, $P = 0.0072$) than native plants, but plant native status was uncorrelated with specialization (d') ($F_{1,95} = 0.73$, $P = 0.40$) or effective partners ($F_{1,95} = 0.66$, $P = 0.42$). For bee species, none of the three network metrics were correlated with bee diet breadth categories (all $P > 0.05$).

Sub-network size was not correlated with nursery type ($F_{1,21} = 0.76$, $P = 0.39$), season ($F_{2,39} = 1.46$, $P = 0.24$), nursery area ($F_{1,9} = 1.42$, $P = 0.26$), or surrounding natural area ($F_{1,8} = 0.49$, $P = 0.50$). Indicator species analysis of our bee-plant network suggested that only the sweat bee *Halictus ligatus* was significantly associated with native plants (stat = 0.54, $P = 0.0076$), while no bee species were associated with non-native plants (all $P > 0.05$).

## DISCUSSION

Here, we document functionally diverse wild bee communities in horticultural plant nurseries. While most species and individuals detected were generalist, below ground-nesting, and solitary—as seems to be common in agricultural areas (Ahrenfeldt et al. 2019)—we also detected floral specialists, above-ground cavity nesters, and eusocial species. Moreover, we detected cleptoparasitic species, which serve as indicators of functionally diverse bee assemblages (Sheffield et al. 2013). Most importantly, we found an effect of the native status of plants cultivated on the functional distributions of wild bees present in nurseries, but no effect of landscape-level factors. Our findings have fundamental implications for pollinator conservation in nurseries and other landscapes dominated by ornamental plants.

We hypothesized that the type of nursery, with respect to its cultivation of mostly native or non-native plant species, was associated with the functional traits of wild bees found therein. While the functional dispersion of sweep netted bees did not differ between nursery types (though FDis of vane trap samples was higher at native nurseries in spring), we sweep netted proportionally more specialist species and individuals at native nurseries than at conventional nurseries. These results echo those of other studies, which find non-native plants tend to be visited by generalist pollinators (Seitz et al. 2020). We suspect this result is partly due to the presence of corresponding host plant species in native nurseries. Indeed, this was the case for certain specialist bee species in the genera *Diadasia*, *Micralictoides*, and *Ashmeadiella*, which we caught on ornamental plants belonging to their documented host families. More generally, it also may be that native plant cultivars tend to be less horticulturally modified relative to their natural counterparts than are exotic cultivars (Ricker et al. 2019) and are thus more attractive or accessible to specialist pollinators. Regardless, increased cultivation of regionally native plants may facilitate the presence of specialist bees, which is important given that this functional group is at higher risk from habitat disturbance (Burkle et al. 2013). The majority of specialist species detected were solitary ground-nesters, which suggests conservation strategies accommodating these groups of bees should be performed concurrently.

We did not detect any relationship between nursery type and bee nesting location or social organization. While these traits are good predictors of species' responses to environmental change in other agricultural systems (Williams et al. 2010), it is not entirely surprising we found no correlations with nursery type. A species' nesting biology is not inherently tied to floral specialization or social organization, though most eusocial species are generalists (Michener 2007). Furthermore, our analyses did not include data on local availability of nesting substrates like bare ground or wood. Nevertheless, it is surprising that most bee species we collected were ground nesters in light of the fact that the ground in nurseries was often impermeable due to weed barriers, gravel, or saturation from irrigation. The question remains as to where bees in this study were making their nests. Regardless, the proportions of species and individuals we observed in terms of nesting location and social organization might be homogeneous across nurseries, landscape types, or even across our study region.

Overall, we found very little evidence of variation across seasons in functional dispersion or the proportions of species detected in any given functional trait category. Our collection includes species of bees known to be seasonal with a limited flying period. However, purely from the standpoint of functional traits, the bee assemblages we observed were mostly consistent over our entire eight-month sampling timeframe

(Ramírez et al. 2015). Future work should examine how the taxonomic composition and phylogenetic diversity of bees in nurseries varies across time and between nursery types.

Surprisingly, we found no association between landscape-scale features (nursery size and proportional natural area surrounding the nursery) and functional dispersion or the proportions of species or individuals in any given functional trait category. FDis of bees has been found to decline with habitat size in natural areas (Hung et al. 2019), while pollinator FDis in orchards has also been shown to be positively associated with surrounding natural habitat (Martins et al. 2015, Geslin et al. 2016). One hypothesis is that bees in nurseries may not be subject to the same negative effects of surrounding land intensification as seen in other habitats (Winfree et al. 2011) because local factors like high floral abundance, diversity, and long bloom periods offset these effects (Wojcik and McBride 2011, Martins et al. 2017). While our analyses incorporated nursery size and surrounding natural area as covariates, our experimental design itself did not specifically control for them. Further research is necessary to tease apart any potential impact of these variables, as well as if they are correlated with other factors determining suitability of nurseries for different bee taxa, such as nesting substrate availability.

As more specialist bee species were detected at native nurseries, one would expect that bee-plant networks from native nurseries would be more specialized. However, this was not the case: networks from both native and conventional nurseries had lower connectance than null expectations, and only conventional nurseries displayed higher specialization (H2). The low connectance and high specialization of our networks may be due to several factors. First, the high numbers of bee and plant species in our dataset, compounded by the fact that most plants were not present at all nurseries, may have resulted in fewer realized links. Second, our collection method prohibited prolonged collection of bees from any one given plant species (Gibson et al. 2010). Previous studies have similarly found specialization of urban bee-plant networks is positively associated with plant richness (Baldock et al. 2015, Martins et al. 2017), but native and conventional nurseries did not differ in floral richness. One potential explanation for this is that networks at conventional nurseries were more specialized not because they hosted more specialist bees, but perhaps because non-native plants attracted only small, unique subsets of bee species, constraining certain bees to particular plant taxa (Carman and Jenkins 2016). More research on the attractiveness of native and non-native ornamental plants to specialist and generalist species in nurseries may shed light on such patterns (Sponsler et al. 2020).

The results of our sweep netting and vane trap collections highlight the differences between bee sampling methods, at least in nursery systems. Vane traps collected over 16 times as many individual bees as targeted sweep netting, but only 10% more species. Overlap in species recovered by the two methods was relatively low, further supporting the notion that multiple methods should be employed together to sample bee assemblages (Rhoades et al. 2017). While the proportions of species we collected in each functional trait category were similar between the two methods, use of multiple collection methods also safeguards against generalizations of functional trait metrics due to sampling biases.

There is broad interest among conservationists in the relationship between bee health and ornamental plants sold to the public (Lentola et al. 2017, Wignall et al. 2019). Despite this, little attention has been paid to actual horticultural production areas as pollinator habitats. Our study is valuable to efforts to support wild bees in nurseries as it is among the first to explore bees in these areas across space and time using a trait-based framework. Our results demonstrate that a management practice of nursery themselves—a majority cultivation of native plants—is associated with qualitative differences in their local bee assemblages. These effects were consistent regardless of landscape context. Further studies in nurseries that link functional traits to population dynamics, document bees in adjacent natural areas (e.g., Forrest et al. 2015), and employ manipulative approaches to establish causation, are needed before sweeping management recommendations can be made. However, our results are encouraging for future conservation efforts as they suggest a tractable management practice is quantifiably associated with resident bee assemblages.

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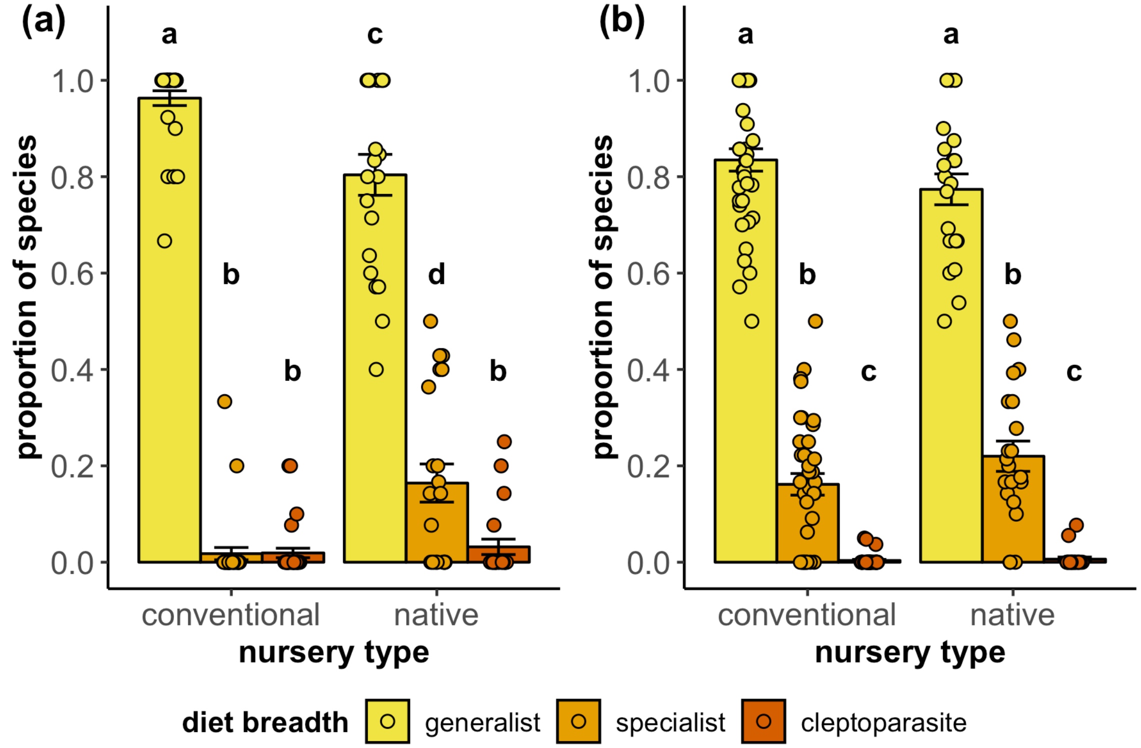

**Figure 2.1.** Diet breadth of collected bee species (a: sweep netting, b: vane trapping) at conventional and native plant nurseries. Bars and whiskers represent mean ± SEM. The vertical axis is the proportion of all species collected in a sampling event that fall into each of the three functional categories (adjacent bars). Proportions are averaged across seasons and years. Within each panel, bars not connected by the same letter are significantly different according to post-hoc tests.

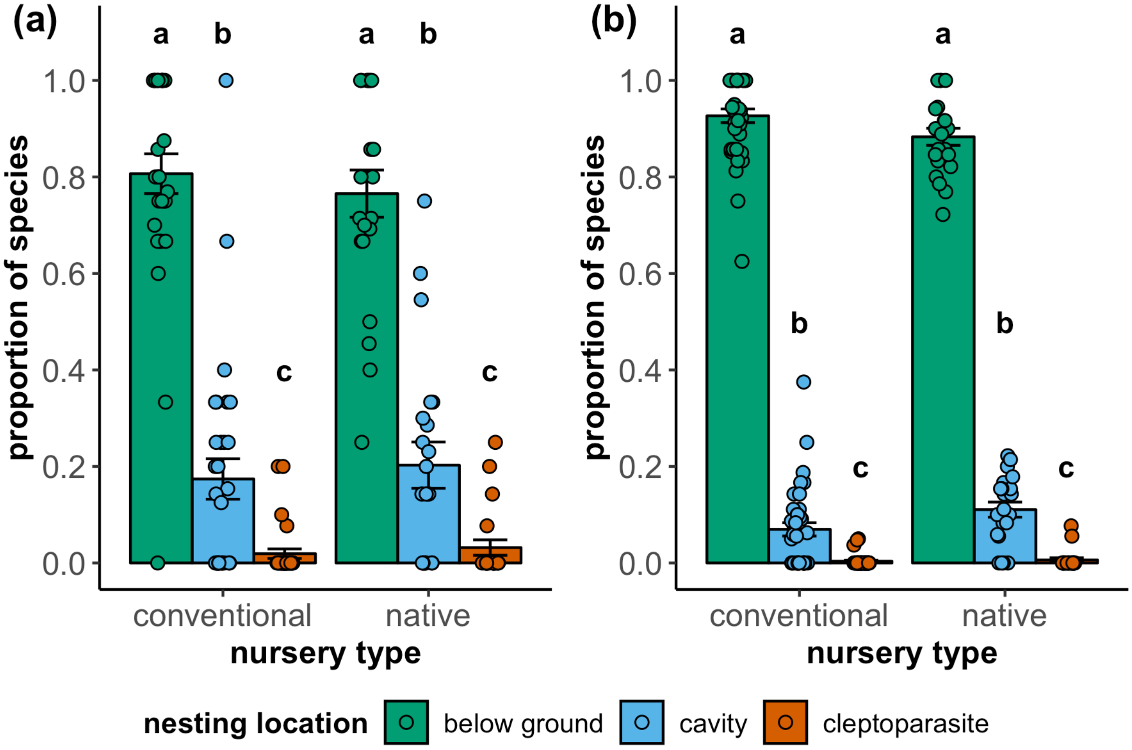

**Figure 2.2.** Nesting location of collected bee species (a: sweep netting; b: vane trapping) at conventional and native plant nurseries. See Fig. 2.1 legend for explanation of data.

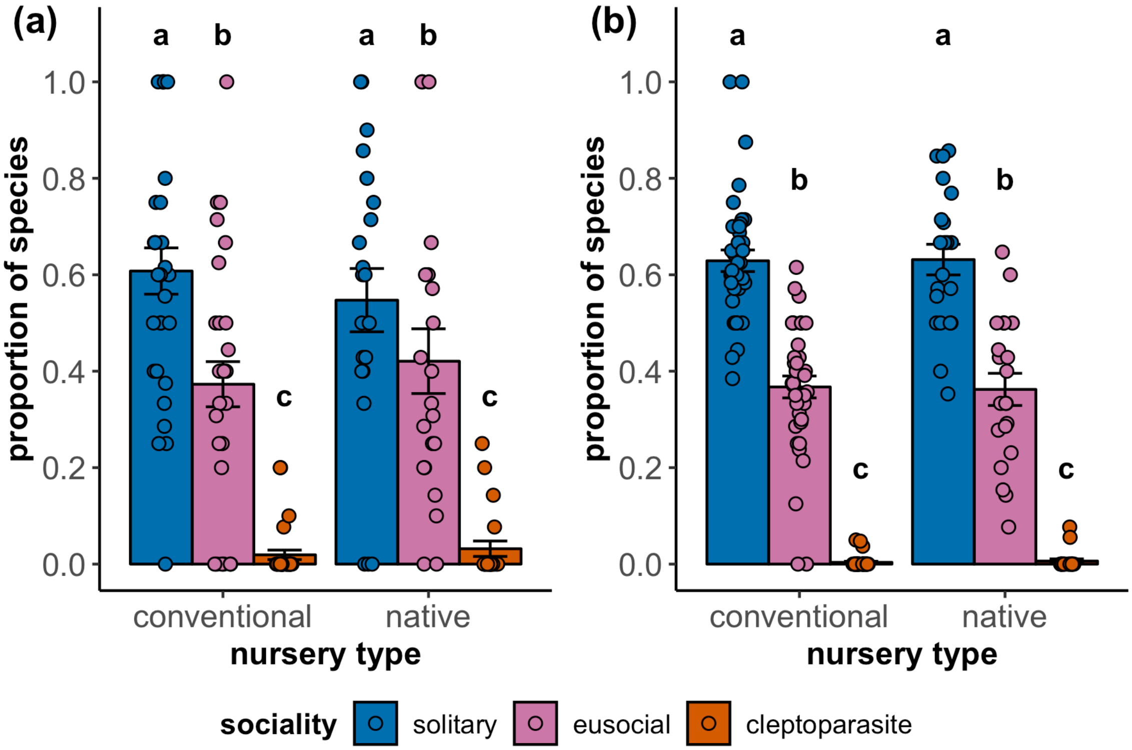

**Figure 2.3.** Social organization of collected bee species (a: sweep netting; b: vane trapping) at conventional and native plant nurseries. See Fig. 2.1 legend for explanation of data.

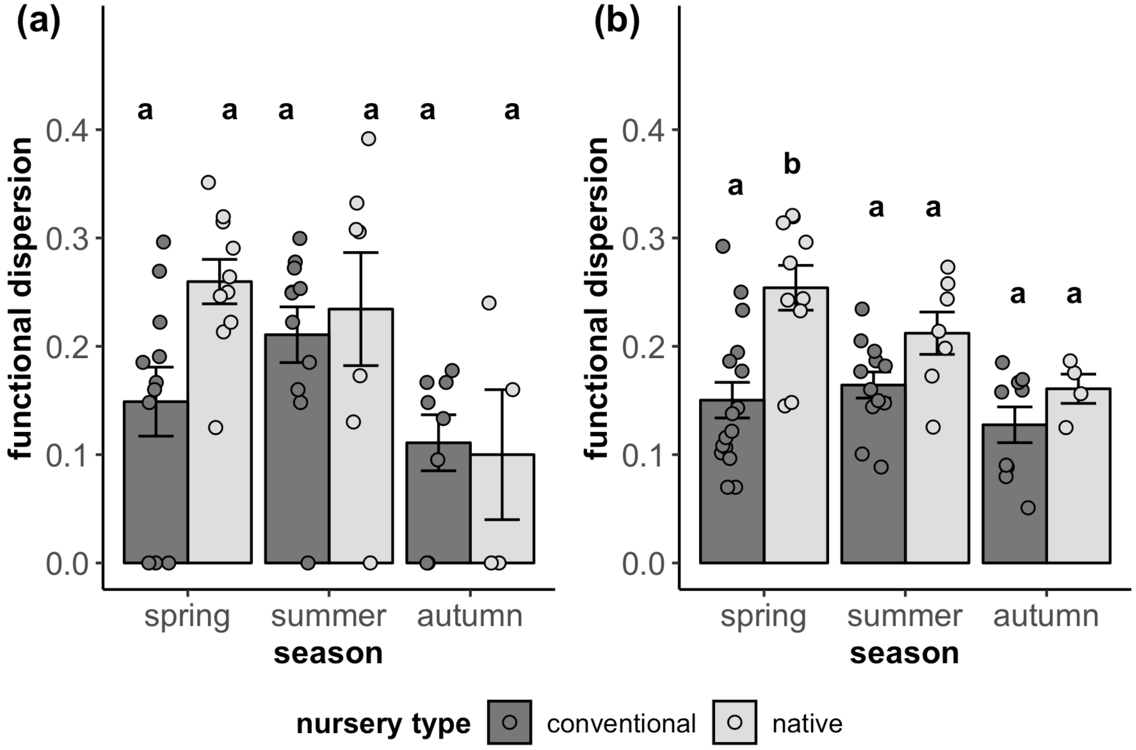

**Figure 2.4.** Functional dispersion (FDis) of collected bees (a: sweep netting; b: vane trapping) at native and conventional plant nurseries across seasons. Bars and whiskers represent mean ± SEM.

# CHAPTER III

## Mark-recapture experiments reveal foraging behavior and plant fidelity of native bees in plant nurseries

## INTRODUCTION

Understanding the spatial and temporal foraging patterns of pollinators is essential to conserving these organisms in human-modified landscapes, such as agroecosystems (Cranmer et al. 2011). Particularly, understanding foraging fidelity (i.e., returns to a particular plant species or area) is crucial for providing supportive habitats. Numerous approaches have been used to discern the movement and foraging of individual bees (reviewed by Mola & Williams 2019), ranging from highly technological to more traditional methods like mark-release-recapture experiments. While mark-recapture experiments are often hampered by low recapture rates, density dependence, and logistical constraints (Mola and Williams 2019), they can help us understand short-term local movement patterns (Dorchin et al. 2013) and fidelity (Ogilvie and Thomson 2016) of highly mobile organisms like bees.

Despite being the most common wild bees in temperate regions (Michener 2007), sweat bees (Halictidae) are greatly understudied in the mark-recapture literature. Although a few mark-recapture studies have examined a small number of other species (Appendix C: Table C.1), most of our knowledge on foraging fidelity is derived from studies on a handful of species (Bronstein et al. 2017), particularly bumble bees (*Bombus* spp.) (Mola and Williams 2019). It remains unknown if most native bee species return daily to specific habitats or plants and what factors may influence such fidelity, if it exists at all. In particular, our understanding of how plant fidelity varies across individuals within a population is limited. While a population of a generalist species will collectively visit a wide variety of plants, how flexible are an individual's day-to-day floral choices (Brosi 2016)?

To address this knowledge gap surrounding North America's most ubiquitous wild bees, we used a mark-recapture approach to track the day-to-day plant associations of sweat bees in large-scale commercial plant nurseries in southern California. Nurseries contain diverse and dynamic assemblages of containerized, healthy flowering plants that include blooming species in all seasons. By cultivating scores of different plant taxa in close proximity, nurseries offer a unique venue for studying foraging fidelity. We focused on the primitively eusocial sweat bee *Halictus ligatus* Say, which is commonly found in these nurseries. Though broadly recognized as a floral generalist, plant fidelity of individual sweat bees has not been investigated.

## METHODS

We conducted eight mark-release-recapture experiments (Appendix C: Detailed Methods and Statistical Analyses) at five large-scale commercial plant nurseries in southern California, USA surrounded by both suburban and natural landscapes. Experiments were conducted in summer and autumn 2018, between 11:00 and 14:00 on consecutive clear, sunny days. Three nurseries were sampled in both seasons, while one was sampled in summer only, and one in autumn only. A single observer hand-netted male and female *Halictus ligatus* on patches of blooming plants over areas up to 2 ha. If *H. ligatus* was not sufficiently abundant, we then focused on the few most abundant species of non-*Apis* bees, including solitary species. Captured bees were identified, marked on the thorax (Fig. 3.1) using non-toxic paint, then released. Paint color was used to indicate the plant species on which the bee was captured. The following day, we returned and netted marked and unmarked bees in the same and nearby patches where we marked bees the previous day. All individuals were retained in vials to ensure no individual was recaptured twice.

## RESULTS AND DISCUSSION

We documented remarkably high recapture rates and plant fidelity by individual bees, even though they collectively visited a diversity of plants (Appendix C: Fig. C.1). Across our eight replicate experiments, we captured and marked 205 bees on the first days of experiments, and captured 207 bees on the second days of experiments, 106 of which were marked. Thus, we recaptured 51.7% of all marked individuals (mean±SE per experiment 50.8±2.0%), almost all of which (102 or 96.2%) were foraging on the same plant species as the first day. Given the limitations of mark-recapture, the consistently high rates of recapture we documented across all eight experiments suggest that most individuals used the same plant species in the same area as resources day-to-day.

Our 205 marked bees included 12 species in 9 genera (Appendix C: Table C.2) with disparate natural histories; *Halictus ligatus* represented two-thirds (66.8%) of marked bees. Bee taxon had no effect on probability of recapture ($\chi^2_8$=9.03, $P$=0.34) in our study. Overall, marked bees were fairly evenly divided by sex (56.6% male), but interestingly, recapture rates did not vary by sex, despite the different proximate mechanisms underlying foraging behavior of males and females (Ne'eman et al. 2006).

While individual bees showed very high plant fidelity, as a community they visited 18 species of plants (Appendix C: Table C.3, Appendix C: Fig. C.1). These bees not only foraged in the same general location the next day, but of the 106 recaptured bees, 102 (96.2%) foraged on the same plant species as the previous day despite the broad diversity of plants flowering in nurseries. Although members of floral generalist species, individuals may act as short-term “serial specialists”, visiting only one plant species but switching to others later in their lifetime (Brosi 2016). Previous work has documented temporal preferences by *Halictus ligatus* for specific plants despite this species’ classification as a broad generalist (Ginsberg 1983). Our study builds on this work by providing a novel ecological view of individual-level foraging preferences for these common wild bees. Interestingly, four bees (3.8%) were recaptured on a different native plant species patch several meters from where each was marked the previous day. These limited observations suggest both site fidelity and plant fidelity are at play (Ogilvie and Thomson 2016).

In addition, we documented a 45% higher probability of recapture on California-native plants (Fig. 3.2) than on non-native plants ($\chi^2_1=16.09$, $P<0.0001$). Most marked bees (79.5%) were found on native plants initially, which may influence their subsequent foraging choices. After accounting for differences in floral abundance, we discovered that some native plant species were visited by either more or fewer bees than expected

(Appendix C: Table C.5, Appendix C: Table C.6). While more bees were recaptured on native plants overall, some bees still displayed relatively high rates of fidelity to non-native plants, though we found no preference for or against any non-native plant species. This corroborates previous findings evaluating the relative importance of native and non-native plants to bees, that while non-native plants are still visited (Williams et al. 2011, Salisbury et al. 2015), some native plants are preferred (Morandin and Kremen 2013).

Probability of recapture was 12% higher in summer than in autumn ($\chi^2_1$=22.93, *P*<0.0001), perhaps due to differences in weather or the taxa of plants in bloom at the time. Interestingly, the effect of plant native status was more pronounced in summer ($\chi^2_1$=12.23, *P*=0.00047, Fig. 3.2). This suggests that the level of fidelity by pollinators to floral resources could vary across seasons, perhaps depending on shifts in flowering phenology, resource availability in the surrounding landscape, floral nutrition, or reproductive behaviors of social species. Interestingly, while bees either preferred or avoided certain native plant species in summer, we found no evidence of this in autumn (Appendix C: Table C.5). Nurseries may serve as "control" sites for further study of these topics by allowing researchers to control for confounding variables such as patch size and within-patch floral diversity.

The recapture rates we documented are fairly high with respect to other mark-recapture studies on bees (Appendix C: Table C.1), even more so given our relatively modest search effort of three observer-hours per day. These high rates of recapture may indicate that nurseries represent high-density floral resource "islands" relative to lower levels of resources in the surrounding suburban and natural landscape (Steffan-Dewenter and Tscharntke 1999). Moreover, our observations would be wholly consistent with "traplining", in which organisms repeatedly visit persistent resources in a predictable order (Heinrich 1976, Thomson 1996), but this has not been well documented for sweat bees. It is unknown whether we would again retrieve 50% of marked individuals after two or more days, or if recapture rates would decrease by 50% each day. Longer-term data on day-to-day consistency of native bee foraging may shed light on this knowledge gap. While most mark-recapture studies of bees monitor a single cohort over longer time periods (Appendix C: Table C.1), they are rarely replicated across populations or seasons, and seldom track more than one or two plant species associations. A strength of our approach is its replication over multiple geographically separate habitats, populations of bees, and seasons, uncovering consistent patterns in recapture probability and individual plant fidelity in florally diverse environments.

Our findings also have relevance for the protection of pollinators in agricultural landscapes. The regular use of ornamental plants as a steady food resource does raise concerns over the potential for chronic exposure to agricultural toxicants via pollen and nectar. Insights into the consistency of these bee's day-to-day foraging patterns can be invaluable to implementing more effective conservation strategies. In addition, measures of site fidelity are useful for monitoring protocols that require detection probabilities derived from rapidly resampling habitats in succession (e.g., n-mixture models and occupancy modeling). Overall, our results underline the need for additional studies on movement patterns and foraging behavior by other bee taxa in human-modified landscapes.

## ACKNOWLEDGMENTS

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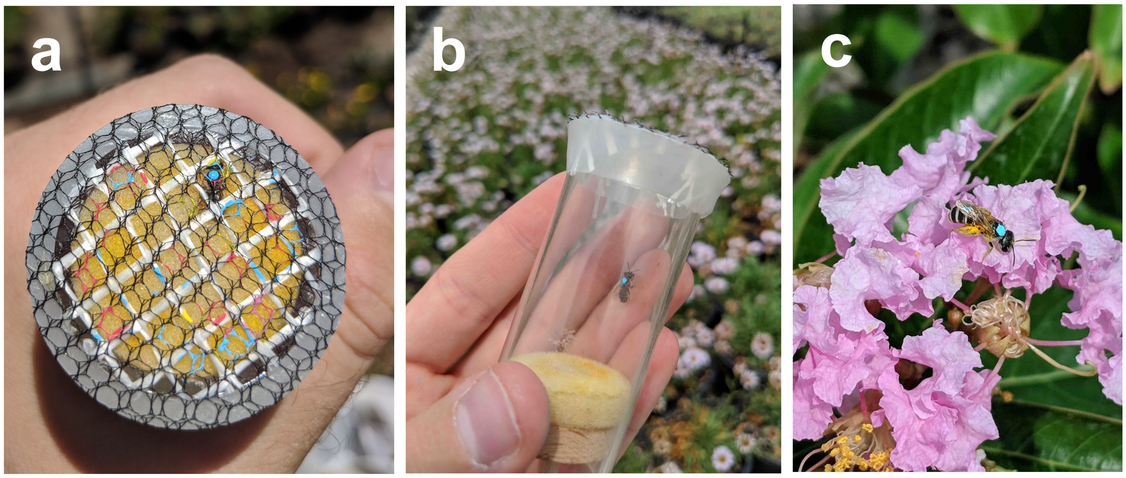

**Figure 3.1.** (a) Top view of modified honey bee queen marking plunger cage used to mark the thorax of native bees. Two layers of black tulle fabric (3.2-mm openings) were stretched over the original coarse white mesh to prevent small bees from escaping. The foam plunger was maneuvered so that the bee's scutum aligned with an opening in the tulle. (b) Foreground: A marked female *Halictus ligatus* inside the plunger cage. Background: A patch of containerized seaside fleabane, *Erigeron glaucus,* on which the bee was caught and marked at a nursery. (c) A female *Halictus ligatus* resting on petals of crepe myrtle, *Lagerstroemia indica*, shortly after being marked (blue spot on thorax).

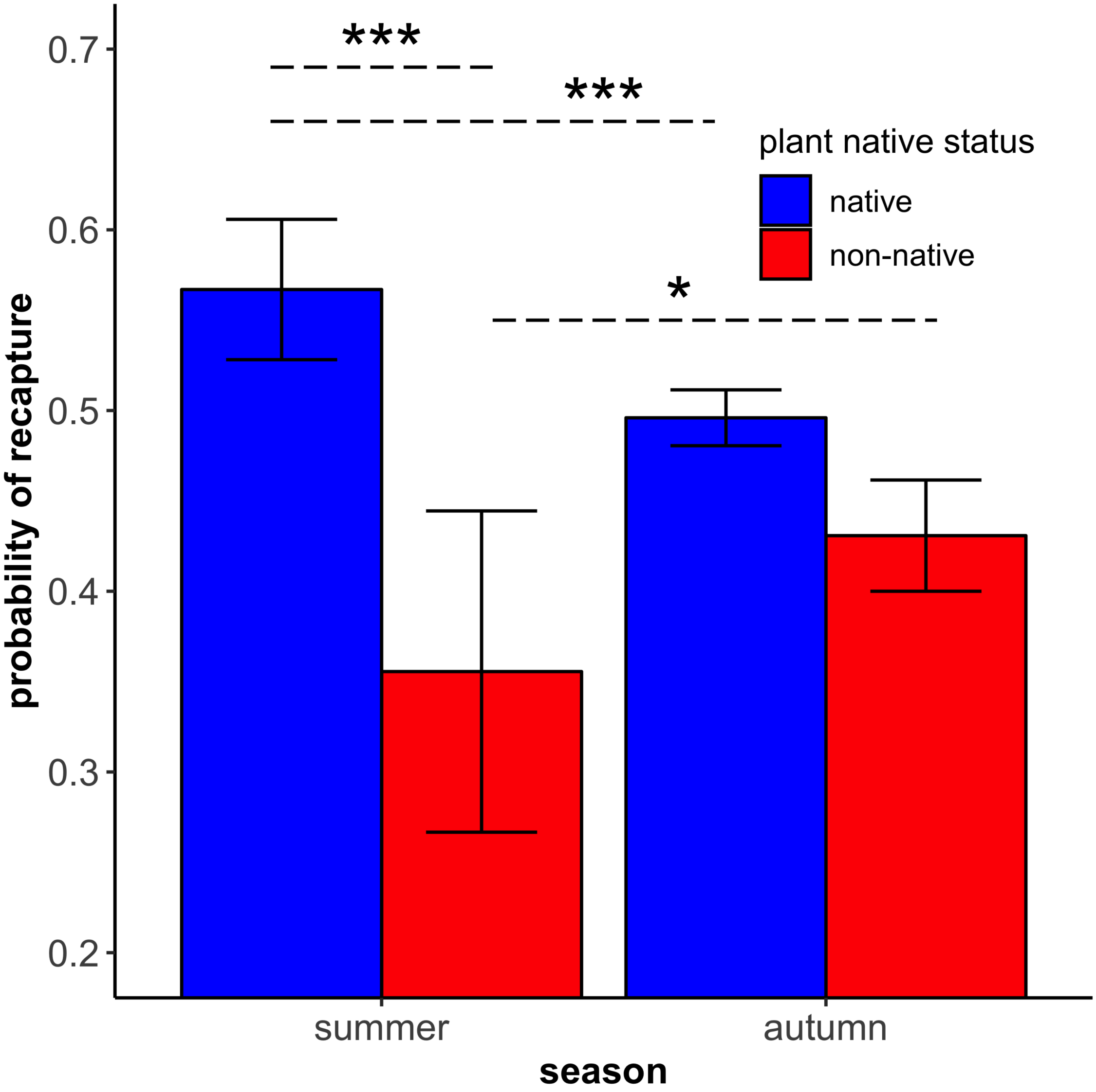

**Figure 3.2.** Mean (±SE) probability of recapture for native bees, categorized by season and native status of the plant on which each individual was captured. For this graph, the probability of recapture at each nursery in each season on each type of plant (native or non-native) is treated as a replicate (*N*=12). For the statistical model, see Appendix C: Table C.4. *: *P*<0.05; ***: *P*<0.001.

# CHAPTER IV

## Pollinators and plant nurseries: how irrigation and pesticide treatment of native ornamental plants impact solitary bees

## ABSTRACT

A key conservation goal in agroecosystems is to understand how management practices may affect beneficial species, such as pollinators. Currently, broad gaps exist in our knowledge as to how horticultural management practices, such as irrigation level, might influence bee reproduction, particularly for solitary bees. Despite the extensive use of ornamental plants by bees, especially little is known in general about how irrigation level may interact with insecticides, like water-soluble neonicotinoids, to influence floral rewards and bee reproduction. We designed a two-factor field cage experiment in which we reared *Megachile rotundata* on containerized ornamental plants grown under two different irrigation levels and imidacloprid treatments (30% label rate dosage of a nursery formulation or an untreated control). Lower irrigation was associated with modest decreases in nectar volume and floral abundance in untreated plants, whereas irrigation did not affect plants treated with imidacloprid. Furthermore, irrigation modulated the amount of imidacloprid entering nectar. Imidacloprid application strongly reduced bee foraging activity and reproduction, and higher irrigation did not offset any negative effects on bees. Our results link the effects of local management practices to flowering ornamental plants and solitary bee reproduction, while highlighting important considerations for the conservation of wild bees in nursery systems.

# INTRODUCTION

Ornamental plant nurseries represent a major agricultural sector that remains relatively unexplored with regard to its support of local insect communities. While ornamental plants and the urban greenspaces they occupy are well known to serve as foraging resources for pollinators (Baldock et al. 2019, Lowenstein et al. 2019), the role of horticultural nurseries as bee foraging habitat has just recently received attention (Stoner et al. 2019, Egerer et al. 2020, Sponsler et al. 2020, Cecala and Wilson Rankin 2020). However, we lack quantitative knowledge on how local management practices in horticulture may interact to affect resident wild bees, particularly solitary species. Relevant in-field management practices for bees in any agricultural area include those affecting vegetation quality, agrochemical input, and soil characteristics (Liere et al. 2017). Interactions between local management practices, such as whether one mitigates or exacerbates the effects of another, are only recently being investigated using manipulative experiments (Stuligross and Williams 2020, Klaus et al. 2021).

Pesticide use is a management practice influencing wild bee conservation in all agroecosystems. Throughout the past decade, concerns have arisen over systemic insecticide use in ornamental plants (Krischik et al. 2015, Kegley et al. 2016, Lentola et al. 2017). Neonicotinoid insecticides, for example, tend to be applied at higher levels in ornamental crops than in food crops (Hopwood et al. 2012, Krischik et al. 2015) due to differences in pest management goals, formulations, and application methods. Multiple factors influence the amount of these systemic insecticides entering pollen and nectar of ornamental plants (Stoner and Eitzer 2012, Cowles and Eitzer 2017), but we have a poor understanding of these factors and how they interact (Gierer et al. 2019). Recent studies revealed that increased local floral resource availability may buffer against some negative impacts of pesticide exposure in solitary bee populations (Stuligross and Williams 2020, Klaus et al. 2021). Provisioning hedgerows (Liere et al. 2017) for bees is unlikely to be financially incentivizing in nurseries, as most ornamental crops rarely require pollination services. Whether such a buffering effect would be observed in the context of higher pesticide concentrations potentially found in floral resources of ornamental plants remains unresolved (Cowles and Eitzer 2017).

Irrigation is another horticultural management practice potentially impacting bees, which is also tied to water conservation, pest management, and environmental runoff (Poudyal and Cregg 2019). Reduced water availability may negatively affect floral traits such as the quantity and quality of floral rewards (Waser and Price 2016, Burkle and Runyon 2017, Phillips et al. 2018, Wilson Rankin et al. 2020), and may cause cascading negative effects on pollinator visitation (Gallagher and Campbell 2017, Descamps et al. 2018) and crop yield (Gillespie et al. 2015, Raderschall et al. 2021). However, few experimental studies directly link water availability to pollinator fitness. Wilson Rankin et al. (2020) found that reduced water yielded lower quality pollen and nectar, which negatively impacted the fitness of eusocial bees that were fed nutritionally equivalent artificial diets. We know of no studies to date that investigate how plant irrigation level influences solitary bee reproduction and fitness under field conditions. Whether the benefits to bees from increased irrigation offset the detrimental effects of pesticide exposure remains unknown. Addressing potential interactions between irrigation and systemic pesticide use on bee fitness could specifically benefit nurseries by improving consumer perceptions of their pollinator stewardship efforts (Kegley et al. 2016).

To address these knowledge gaps, we reared alfalfa leafcutting bees ("ALCB", *Megachile rotundata*) on containerized ornamental plants from nurseries grown under different irrigation and neonicotinoid application regimes. ALCBs are a solitary, cavity-nesting species managed as a pollinator in North America, emerging as a model for studying solitary bee biology (Pitts-Singer and Cane 2011) and pesticide risk assessments (Frewin et al. 2019). We test the hypothesis that irrigation level of potted ornamental plants can modulate the effects of systemic pesticide application on bees. We predict that plants receiving higher irrigation levels will provide more abundant or higher quality resources for bees, which will offset some negative influences of neonicotinoid exposure on foraging and reproduction. Specifically, we expect that bees reared on higher irrigated plants will exhibit higher foraging activity and reproduction relative to those reared on plants irrigated at a lower level, both for bees reared on untreated and neonicotinoid-treated plants. Through manipulative experiments, we aim to improve our understanding of how interacting local management practices affect the population stability of this ecologically important pollinator.

## METHODS

We examined the effects of imidacloprid application and irrigation level on floral nectar and ALCB reproduction using a fully crossed randomized block design. From

March 2018 to July 2020, we maintained 20 field cages (5.8 $m^3$) in a 0.30-ha plot at University of California Riverside Agricultural Operations (33.965 °N, 117.341 °W). We used four cages for the nectar experiment and 16 for the ALCB reproduction experiment. Each cage served as a replicate mesocosm simulating conditions at a containerized nursery.

### Nectar experiment

We grew lacy phacelia (*Phacelia tanacetifolia*) in UC Soil Mix III (agops.ucr.edu/soil-mixing) in 2-L pots. We focused on containerized plants, as soil dynamics for plants in containers likely differ from those experienced by plants growing in the ground. We selected phacelia due to its attractiveness to bees, including ALCBs (Frewin et al. 2019), and its abundant floret production (Petanidou 2003). We assigned 180 plants to one of six treatments resulting from the crossing of irrigation level and imidacloprid treatment (Table 4.1), organized into two experimental blocks of two cages each (Appendix D: Fig. D.1a).

Inside cages, we inserted an individual high- or low-flow irrigation spike (Primerus Products, Encinitas, CA) into each pot. High-flow spikes emitted 2.6 times more water as low-flow spikes (Appendix D: Fig. D.2), resulting in 23% higher average midday volumetric water content (VWC; Appendix D: Fig. D.3a). Pots were automatically irrigated over the soil surface once per day at 0600 h for 60 s, increased to 120 s whenever plants visibly wilted due to heat. The ground inside each cage was lined with fabric barrier to prevent plants from rooting outside pots.

For imidacloprid treatments, we applied Marathon® 1% Granular (OHP, Bluffton, SC), a commercial nursery formulation, to pots on 28 January 2020. Formulated for use in greenhouses and nurseries, Marathon® consists of 1% imidacloprid and 99% inert ingredients by mass. Granular formulations allow the active ingredient to leach more slowly from potting soil than liquid drenches (Hinz et al. 2020). The label rate dosage for a 2-L pot equates to 1.4–2.0 g formulation. We used ~30% the label rate as our "high" dosage to be conservative, as near total ALCB mortality occurred when separate plants were treated at label rate (unpublished data).

Phacelia bloom began in early May 2020 and lasted six weeks. Six days during bloom, we measured floral nectar volume between 1030 and 1330 h (daily high temperatures between 22.2 to 36.1 °C) on five randomly selected flowers per treatment using microcapillary tubes (Drummond Scientific, Broomall, PA) and handheld calipers. We quantified total sugar concentration of each sample using a refractometer (Eclipse, Bellingham + Stanley). Eight days during bloom, we collected nectar during the same time of day, pooled samples within treatments within cages, and quantified imidacloprid residues in nectar via an ELISA. We used a QuantiPlate™ kit (EnviroLogix, Portland, ME) and microplate spectrophotometer (Thermo Fisher, Waltham, MA), which provides similar quality data to HPLC/MS-MS at less cost (Cowles and Eitzer 2017). Imidacloprid metabolites, also toxic to bees (Bonmatin et al. 2015), cross-react in the assay. Thus, assay results reflect the total concentration of the parent compound and its metabolites. Samples were diluted 10- to 100-fold before analysis as needed to complement the kit's quantification range.

### ALCB reproduction experiment

In the other 16 field cages, we placed the California-native ornamental plants *Erigeron glaucus*, *Sphaeralcea ambigua*, and *Baileya multiradiata* in 2-L pots (not previously treated with insecticides), purchased from a nursery in 2019 and 2020. We selected these species based on their drought tolerance to ensure bloom in low irrigation conditions, and from surveys of wild bees at nurseries (Cecala and Wilson Rankin, in review). We also included pots of lacy phacelia and alfalfa (*Medicago sativa*). The ratio of plant species in each cage varied slightly between years due to availability (Appendix D: Table D.1). We divided field cages into four experimental blocks, with one cage assigned to each of four treatments (Table 4.1, Appendix D: Fig. D.1b). The low dosage imidacloprid treatment was not included in the bee reproduction experiment.

We manipulated plant irrigation levels as in the phacelia nectar experiment. Although soil VWC varied across plant species, VWC in high irrigation pots was 44% higher than that of soil in low irrigation pots (Appendix D: Fig. D.3b). In imidacloprid treatment cages, we applied Marathon® four weeks before introducing bees to allow for translocation (as in Krischik et al. 2015). We applied Marathon® to each plant species *except* alfalfa, which we anticipated would serve as the principal leaf clipping source for nesting female ALCBs, to ensure bees were primarily exposed to imidacloprid through consumption of pollen and nectar, and not via leaf tissue.

In each cage, we provided one nest block constructed according to USDA-ARS specifications (USDA-ARS 2018) facing southeast. Each block contained 60 drilled tunnels into which we inserted paper straws (diameter 5 mm, length 12.7 cm). We allowed ALCB pre-pupae to develop into adults in an incubator at 30.3 ± 0.1 °C, 57.2 ± 0.4% relative humidity (mean ± s.e.) and a 12-hour light-dark cycle. Emergence occurred after 21 days. In mid-June 2019 and 2020, we introduced 30 male and 20 female ALCBs inside each cage to approximate sex ratios in commercial populations (Peterson and Roitberg 2006).

Over the following six weeks, two to three times per week, we recorded floral abundance (for each plant species and the entire cage) and ALCB foraging activity in each cage using ordinal indices. For floral abundance, we assigned: '0' if no flowers were present, '1' if a few flowers were present, '2' if flowers covered 10–50% the cage area, and '3' if flowers covered > 50% the cage area. For bee foraging activity, we visually monitored the inside of each cage for 10 seconds (similar to Frewin et al. 2019) and assigned: '0' if no foraging bees were visible, '1' if 1–3 bees were visible, '2' if 4–10 bees were visible, and '3' if > 10 bees were visible. We also recorded ambient temperature during observations.

After six weeks, we collected all straws and individually labeled and weighed each. After three weeks of storage at 22 °C, straws were kept at 5 °C over the winter. After at least four months, straws were incubated again. However, no bees emerged in either year, potentially due to the lack of a fluctuating temperature regime during cold storage (Rinehart et al. 2013). To assess reproduction, we dissected straws and quantified the cells per straw and the contents of each cell, noting incomplete or empty cells and the developmental stage of any brood.

## Statistical analysis

We conducted all analyses in R (version 3.3.3) (R Core Team 2021). All means are reported ± s.e. In all models, we checked for collinearity using function 'vif' (*car*) (Fox and Weisberg 2011). To assess how treatments impacted volume, sugar concentration, and imidacloprid concentration of phacelia nectar, we constructed linear mixed models (LMMs) using function 'lmer' (*lme4*) (Bates et al. 2015). We included as fixed effects irrigation level and imidacloprid treatment (and their interaction) and number of days elapsed since imidacloprid application. In the volume and sugar concentration models only, we included daily high temperature, known to influence nectar secretion in phacelia (Petanidou 2003). Cage nested within block served as random effects. Volume and imidacloprid concentration were $\log_{10}(x+1)$-transformed. In all models, we used function 'emmeans' (*emmeans*) (Lenth 2019) for post-hoc comparisons (Tukey's HSD tests) as appropriate.

To assess treatment effects on indices of cage-level floral abundance and ALCB foraging activity, we constructed additional LMMs. We included as fixed effects irrigation level, imidacloprid treatment, and year (and all interactions), and number of days elapsed since bees were added to cages. For the bee foraging activity model, we also included ambient temperature during the observation. We again included cage nested within block as random effects. To assess how treatments influenced nest initiation by ALCBs, we constructed a generalized linear mixed model (GLMM) using function 'glmer' (*lme4*) and a logit link. We treated each straw as a replicate, noting whether there was *any* evidence of nest construction or not. We included the same fixed and random effects as the bee foraging activity model. Furthermore, to determine if treatments influenced (per cage) the number of cells constructed, number of cells *containing brood*, or *proportion* of cells containing brood, we constructed LMMs with the aforementioned predictor variables. We square-root transformed the number of cells per cage and number of brood per cage. Finally, to determine if female ALCBs clipped plants *other* than alfalfa (which would further expose them to imidacloprid), we used Fisher's exact tests. We tested if the number of nest cells constructed with versus without alfalfa (never treated with imidacloprid) differed between imidacloprid or irrigation treatments.

## RESULTS

### Nectar experiment

Nectar volume was 19% higher in phacelia plants receiving high irrigation versus low irrigation (Fig. 4.1a; $F_{1,9} = 9.68$, $P = 0.0127$). Despite a significant effect of imidacloprid dosage, nectar volume differed by only 2.5% among imidacloprid treatments ($F_{2,302} = 3.38$, $P = 0.0352$). The effect of irrigation was mainly driven by an interaction with imidacloprid dosage (Fig. 4.1a; $F_{2,302} = 6.30$, $P = 0.00210$), specifically by plants in the control (54% higher volume in the high irrigation treatment) and low dosage (43% higher volume) treatments. In contrast, there was no irrigation effect on nectar volume for plants treated with the high imidacloprid dosage. Nectar volume declined with higher daily high temperatures ($F_{1,302} = 45.51$, $p < 0.0001$) and increasing time since imidacloprid application ($F_{1,302} = 80.37$, $p < 0.0001$).

Nectar sugar concentration was not correlated with any of our metrics. It was unaffected by irrigation (Fig. 4.1b; $F_{1,9} = 0.64$, $P = 0.443$) and imidacloprid dosage ($F_{2,84} = 3.02$, $P = 0.0540$; interaction: $F_{2,84} = 0.0819$, $P = 0.921$), although nectar from plants treated with a high dosage had 20% higher sugar concentration than nectar from the control treatment. Nectar sugar concentration did not vary with days since pesticide application ($F_{1,84} = 0.148$, $P = 0.702$), daily high temperature ($F_{1,84} = 0.0685$, $P = 0.794$), or nectar volume per flower ($F_{1,92} = 1.51$, $P = 0.223$).

As expected, imidacloprid dosage was positively correlated with imidacloprid concentrations in phacelia nectar (Fig. 4.1c; $F_{2,15} = 16.9$, $P = 0.000140$). Nectar from flowers in the high dosage contained the highest concentrations at 55 ± 22 ppb, while nectar from flowers in the low dosage contained 7.3 ± 1.9 ppb and did not differ in imidacloprid concentration from control nectar (3.2 ± 0.8 ppb; however, control nectar samples fell below the ELISA's lower quantification limit). There was no effect of irrigation alone on imidacloprid concentration in phacelia nectar ($F_{1,5} = 0.434$, $P = 0.541$). We did detect an interaction between irrigation and imidacloprid (Fig. 4.1c; $F_{2,15} = 5.28$, $P = 0.0183$) such that in the high dosage, nectar imidacloprid concentrations from low irrigation plants were 3.5 times higher than those from high irrigation plants. Imidacloprid concentration declined with days elapsed since application (slope: -0.0298; $F_{1,8} = 14.4$, $P = 0.00527$) during our sampling period (14.6–18.6 weeks post application). Excluding measurements from untreated control plants from the model yielded a similar result (slope: -0.0334; $F_{1,7} = 13.4$, $P = 0.00854$).

## ALCB foraging and reproduction experiment

We did not detect a significant effect of irrigation ($F_{1,60} = 0.379$, $P = 0.541$) or imidacloprid ($F_{1,60} = 1.51$, $P = 0.223$) on cage-level (across all plant species) floral abundance. However, there was an interaction between irrigation and imidacloprid (Fig. 4.2a; $F_{1,60} = 6.82$, $P = 0.0114$) such that, in control cages, cage-level floral abundance was higher in high irrigation cages (index: 1.91 ± 0.07) than in low irrigation cages (1.56 ± 0.06). For cages in the imidacloprid treatment, floral abundance did not differ between high irrigation (index: 1.96 ± 0.06) and low irrigation (2.09 ± 0.06) treatments, nor did cages in the imidacloprid treatment differ from the control, high-irrigation treatment. These patterns were observed in both study years (imidacloprid *x* irrigation *x* year interaction $F_{1,251} = 0.394$, $P = 0.531$), and floral abundance did not differ between years ($F_{1,251} = 0.777$, $P = 0.379$). Floral abundance declined slightly over time ($F_{1,251} = 5.00$, $P = 0.0263$) while bees were in cages.

ALCB foraging activity declined steeply over time ($F_{1,314} = 246.5$, $p < 0.0001$) and was lower in imidacloprid-treated cages than in control cages (Fig. 4.2b; $F_{1,14} = 24.7$, $P = 0.000224$). Bee foraging activity was slightly lower in 2020 ($F_{1,314} = 7.05$, $P = 0.00835$), and the negative effect of imidacloprid treatment was more pronounced in 2019 (imidacloprid *x* year interaction $F_{1,314} = 9.14$, $P = 0.00271$). Foraging activity was unaffected by irrigation treatment (Fig. 4.2b; $F_{1,13} = 1.94$, $P = 0.186$, irrigation *x* imidacloprid interaction $F_{1,13} = 0.242$, $P = 0.630$) and ambient temperature during observation periods ($F_{1,314} = 1.09$, $P = 0.297$).

ALCBs in imidacloprid-treated cages initiated on average only 4% the number of nests as in control cages, irrespective of nest contents (Fig. 4.3a; $\chi^2_1 = 6.93$, $P = 0.00849$). We observed no difference in nest initiation between irrigation treatments ($\chi^2_1 = 0.0254$, $P = 0.873$), and no interaction with imidacloprid treatment ($\chi^2_1 = 0.0226$, $P = 0.881$). Nest initiation in cages was not correlated with higher mean bee foraging activity ($\chi^2_1 = 3.52$, $P = 0.0606$) or mean cage-level floral abundance ($\chi^2_1 = 1.01$, $P = 0.315$), and did not differ between years ($\chi^2_1 = 0.340$, $P = 0.560$).

In control cages, nest mass (0.143 ± 0.009 g, *n* = 94) was unaffected by irrigation treatment ($F_{1,5} = 0.228$, $P = 0.653$), study year ($F_{1,63} = 0.215$, $P = 0.645$), mean floral abundance ($F_{1,14} = 2.41$, $P = 0.143$), or mean ALCB foraging activity ($F_{1,29} = 1.93$, $P = 0.176$). Only four nests (mass: 0.090 ± 0.021 g) were initiated across all imidacloprid-treated cages, so we could not statistically test for the effect of imidacloprid on nest mass. Mean nest mass per cage did not decline with the number of nests constructed per cage ($F_{1,5} = 0.432$, $P = 0.540$), suggesting floral and nesting resources within cages were not limiting for bees.

ALCBs in the imidacloprid treatment constructed only 5.3% as many total cells (including cells without brood) per cage as bees in the control treatment (Fig. 4.3b; $F_{1,21} = 13.31$, $P = 0.00154$), and constructed only 5.8% as many cells *containing brood*—as opposed to being empty or containing only pollen provisions—as bees in the control treatment (Fig. 4.3b; $F_{1,21} = 5.25$, $P = 0.0325$). However, the proportion of nest cells per cage that contained brood (0.14 ± 0.03, *n* = 32) did not vary with any treatment (Fig. 4.3b; imidacloprid: $F_{1,20} = 0.462$, $P = 0.504$; irrigation: $F_{1,20} = 1.02$, $P = 0.323$;

interaction: $F_{1,20} = 1.79$, $P = 0.195$). The proportion of nest cells constructed without alfalfa (using materials from the other plant species) was greater in the imidacloprid treatment (88.9%) than in the control (49.1%; odds ratio = 8.22, $P = 0.0346$; Appendix D: Fig. D.4), but was not correlated with irrigation treatment (odds ratio = 1.60, $P = 0.159$).

## DISCUSSION

Here, we demonstrate that application of a nursery formulation of imidacloprid to potted ornamental plants strongly affects the foraging activity and reproduction of a solitary bee. Plant irrigation level, in contrast, did not influence bee foraging or reproduction, but did affect the plants themselves. Lower irrigation resulted in higher imidacloprid concentrations in nectar of treated phacelia, and caused slight decreases in nectar volume and overall floral abundance in control cages. However, imidacloprid application seemingly negated the effects of irrigation on these floral metrics that we observed in untreated control plants. Despite affecting the plants directly, higher irrigation did not buffer bee foraging activity or reproduction against the negative impacts of imidacloprid application. Our study is, to our knowledge, the first to examine the consequences of a nursery neonicotinoid formulation on solitary bee reproduction. Our results have important implications for wild bee conservation in horticulture and other agroecosystems.

Applying a granular nursery formulation of imidacloprid at only 30% label rate reduced brood production by 90%. In general, granular formulations are understudied relative to seed and foliar applications (Lundin et al. 2015). Furthermore, field studies on neonicotinoids and ALCBs are surprisingly uncommon relative to laboratory exposure trials (Abbott et al. 2008, Anderson and Harmon-Threatt 2019, Hayward et al. 2019, Cecala et al. 2020). Field enclosure experiments with closely related solitary bees (*Osmia*) and neonicotinoid-treated crops, albeit using different application methods, found varying effects on bee reproduction (Rundlöf et al. 2015, Ruddle et al. 2018). Findings range from no observable effect in seed-treated *Brassica* (Ruddle et al. 2018, Dietzsch et al. 2019) to a 50% decline in brood production with drench applications to wildflowers (Stuligross and Williams 2020). Open-field experiments on seed-treated *Brassica* yield even more disparate results, ranging from no effects (Peters et al. 2016, Woodcock et al. 2017, Strobl et al. 2021) to a complete lack of nesting (Rundlöf et al. 2015).

A potential reason for the stark reduction in reproduction we observed is the leaf-clipping behavior of nest building female ALCBs. Cutting leaves can result in contact exposure to systemic insecticides that would not be experienced by *Osmia* or eusocial bees (Kopit and Pitts-Singer 2018, Boyle and Pitts-Singer 2019, Sgolastra et al. 2019). We did not treat alfalfa in anticipation of it serving as the main nest building resource, yet 51.2% of all cells in our study contained no alfalfa. Instead, these cells comprised clippings of petals from *Baileya* and *Sphaeralcea* and leaves of the latter. While sample size was low, 8/9 cells collected from imidacloprid-treated cages were constructed exclusively with *Baileya* petals (Appendix D: Fig. D.4). While we did not analyze plant tissues for imidacloprid, studies report leaves containing higher neonicotinoid concentrations than nectar in treated plants (Dively and Kamel 2012, Kegley et al. 2016, Lentola et al. 2017) and high concentrations in whole-flower samples after label-rate Marathon® application (Krischik et al. 2015). Thus, there are additional pathways by which ALCBs may encounter pesticides besides nectar and pollen consumption.

Exposure routes aside, we attribute the greater reductions in bee reproduction in our study relative to others in part to the insecticide's application method (Giorio et al. 2018) and resulting concentrations in floral resources. Undoubtedly, this stems from pest management paradigms for nursery plants, where tolerance for aesthetic damage from pests is much lower than in field row crops (Cloyd et al. 2011). In experiments with *Osmia*, neonicotinoid concentrations in seed-treated *Brassica* nectar are generally < 15 ppb (Rundlöf et al. 2015, Peters et al. 2016, Ruddle et al. 2018, Strobl et al. 2021). Based on phacelia nectar in our study, ALCBs encountered mean imidacloprid concentrations of at least 55 ppb, above the "field realistic" range for seed-treated crop nectar (generally Goulson 2013, Wood and Goulson 2017) and rivaling "maximum" concentrations for nectar in reviews (Sánchez-Bayo and Goka 2014, Bonmatin et al. 2015, Giorio et al. 2018). Soil applications tend to result in higher neonicotinoid concentrations in floral resources compared to seed treatments, but the levels we documented exceed even the range of values reported for soil-treated crops (Goulson 2013). Perhaps because plants in our study were confined to containers, imidacloprid did not leach as much from plants' root zones as it would in the ground. Our results emphasize the importance of formulation and dosage when assessing pesticide exposure risks to bees across crops and agricultural habitats.

We suspect the mechanism underlying the imidacloprid-associated reductions in ALCB reproduction was premature mortality in adults, rather than decreased nesting. This is supported by our occasional observations of dead bees on flowers only in imidacloprid cages. While oral $LD_{50}$ and $LC_{50}$ values of imidacloprid for ALCBs are not well established (but see Scott-Dupree et al. 2009, Lewis and Tzilivakis 2019, Zioga et al. 2020), Cecala et al. (2020) documented 29% and 68% reductions in adult ALCB longevity from ingesting 30 and 200 ppb sucrose syrups. Although comparing effects between laboratory and field studies is difficult (Stark et al. 1995), other laboratory experiments (Scott-Dupree et al. 2009, Hayward et al. 2019) suggest imidacloprid is more toxic to ALCBs than to *Osmia*, and more detrimental than other compounds like insect growth regulators (Scott-Dupree et al. 2009) (Pitts-Singer and Barbour 2016). Furthermore, we suspect ALCBs were exposed to imidacloprid concentrations in nectar higher than those recorded in our accompanying phacelia nectar experiment. Samples from the nectar experiment were collected 15–18 weeks post application (due to delays in onset of phacelia flowering), while ALCBs foraged on plants only 4–10 weeks post application. Generally, neonicotinoid residues in plants decline over time, though this depends on numerous factors (Cowles and Eitzer 2017). In 2019, six nectar samples taken from phacelia 5–8 weeks post treatment with a “high” dosage ranged from 63–219 ppb (low irrigation:162 ± 28 ppb; high irrigation: 85 ± 1.6 ppb), but there were too few samples to permit analysis. Applying a nursery formulation of imidacloprid, even at a reduced dosage well before bloom, may result in lethal concentrations in floral resources (Cowles and Eitzer 2017). Our results support concerns about high concentrations and extended persistence of nursery formulations of neonicotinoids in plants (Hopwood et al. 2012, Krischik et al. 2015, Kegley et al. 2016, Lentola et al. 2017).

Plant irrigation level did not affect ALCB reproduction. Even in untreated plants, we observed no benefits to bees from increased irrigation. Thus, we found no evidence of additive or synergistic effects between reduced irrigation and imidacloprid exposure. The lack of effect of irrigation could be due to our choice of native, drought-tolerant plants, though we had to ensure sufficient flowering in our low irrigation treatment. Regardless, our low irrigation treatment is likely not as stressing as drought (Wilson Rankin et al. 2020) or resource-limiting treatments in similar studies (Peterson and Roitberg 2006, Pitts-Singer and Bosch 2010, Stuligross and Williams 2020). Rather, our low irrigation treatment mimicked a reduced watering regime, such as that which would be employed in a nursery, that avoids excessively water stressing plants. For example, Stuligross and Williams (2020) found that imidacloprid exposure and resource limitation additively affected *Osmia*, though we are unable to compare pesticide exposure levels between studies as the authors reported no pesticide analyses of nectar or soil samples. Our results support the notion that reduced irrigation of potted ornamental plants, in the absence of pesticides, does not directly hinder solitary bee reproduction.

While we found no interactive effects between our imidacloprid and irrigation treatments on bees, we did detect interactions for containerized plants. Most interestingly, irrigation level mediated the effects of imidacloprid application in phacelia by affecting the amount of imidacloprid resulting in nectar, with higher concentrations in low irrigation plants. This pattern could be due to soil moisture and/or leaching rates (Pietrzak et al. 2020). First, low soil moisture causes plants to transpire more and increases xylem tension, resulting in higher water mobility and increased movement of water-soluble neonicotinoids (Tapparo et al. 2011, Stamm et al. 2015). Second, higher irrigation may lead to greater rates of imidacloprid leaching from potting soil (Bonmatin et al. 2015, Gierer et al. 2019). While reduced irrigation may not diminish bee foraging or reproduction, it could result in elevated nectar concentrations of imidacloprid, which could indirectly harm bees. It remains to be seen if increased irrigation offsets the risks of neonicotinoid exposure at concentrations lower than those in this study. While neonicotinoid mobility in soil and plants in response to environmental conditions has received extensive study (Bonmatin et al. 2015), we know of no research linking differing irrigation rates and soil moistures to neonicotinoid concentrations in floral resources. This topic deserves further investigation, particularly in bee-attractive plants (Gierer et al. 2019).

Furthermore, application of our high imidacloprid dosage appeared to alter the effects of increased irrigation on floral resources that we observed in untreated plants. In untreated phacelia, higher irrigation positively influenced nectar volume. However, in phacelia treated with the high imidacloprid dosage, nectar volume did not differ with irrigation. We observed a similar trend for cage-level floral abundance in the ALCB reproduction experiment. High irrigation increased floral abundance, but only in untreated cages. In imidacloprid treated cages, floral abundance did not differ with irrigation level. This pattern, in which imidacloprid alters the effects of reduced water on plants, could stem from the “stress shield” phenomenon, whereby neonicotinoids purportedly offer plants resistance to abiotic stress by activating salicylate-associated defense pathways (Thielert 2007, Ford et al. 2010). However, our results emphasize that any potential improvements to floral resources from neonicotinoid application do not compensate for the corresponding reproductive costs imposed on bees.

The effects of imidacloprid we document in this study may exceed those in a comparable field scenario. As in other field enclosure studies, bees were limited exclusively to flowering plants in cages, each of which (other than alfalfa) were treated with imidacloprid. In the field, a bee's foraging range might encompass plants both with and without pesticides. Available alternative forage can diminish the impacts of neonicotinoids on solitary bees (Klaus et al. 2021). However, previous work on wild bee foraging in nurseries suggests high day-to-day fidelity to floral patches (Cecala and Wilson Rankin 2020). The composition of wild *Megachile* pollen provisions also suggest a narrow use of available flowering species (Killewald et al. 2019). Therefore, it is reasonable that even patchily distributed pesticide-treated plants could result in chronic exposure for solitary bees. Field experiments explicitly examining solitary bee nesting in nurseries in relation to management practices are needed.

This study quantifies the impact of a commercial nursery formulation of a neonicotinoid on the foraging behavior and reproduction of a solitary bee. We demonstrate that differing irrigation levels, such as those that employed by a nursery, do not directly affect bees. However, we highlight interesting interactions between irrigation level and neonicotinoid application in plants themselves. Our results provide a broader understanding of solitary bee reproduction and how it can be impacted by local management practices in ecologically overlooked agricultural settings like nurseries.

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**Table 4.1.** Treatments and sample sizes, as numbers of plants, resulting from the crossing of irrigation and imidacloprid treatments in the phacelia (*P*) nectar and solitary bee (*B*) reproduction experiments. In the latter, the low imidacloprid dosage treatment was excluded. Also noted is the imidacloprid mass added to each pot, where 0.1 g Marathon® = 1 mg imidacloprid, and the proportional label rate (LR).

| | | **irrigation** | |
|---|---|---|---|
| | | **low** | **high** |
| **imidacloprid** | **control**<br>0 mg imidacloprid = 0% LR | *P*: 30<br>*B*: 120 x 2 yrs | *P*: 30<br>*B*: 120 x 2 yrs |
| | **low dosage**<br>0.5 mg imidacloprid = 3% LR | *P*: 30<br>*B*: excluded | *P*: 30<br>*B*: excluded |
| | **high dosage**<br>5.0 mg imidacloprid = 30% LR | *P*: 30<br>*B*: 120 x 2 yrs | *P*: 30<br>*B*: 120 x 2 yrs |

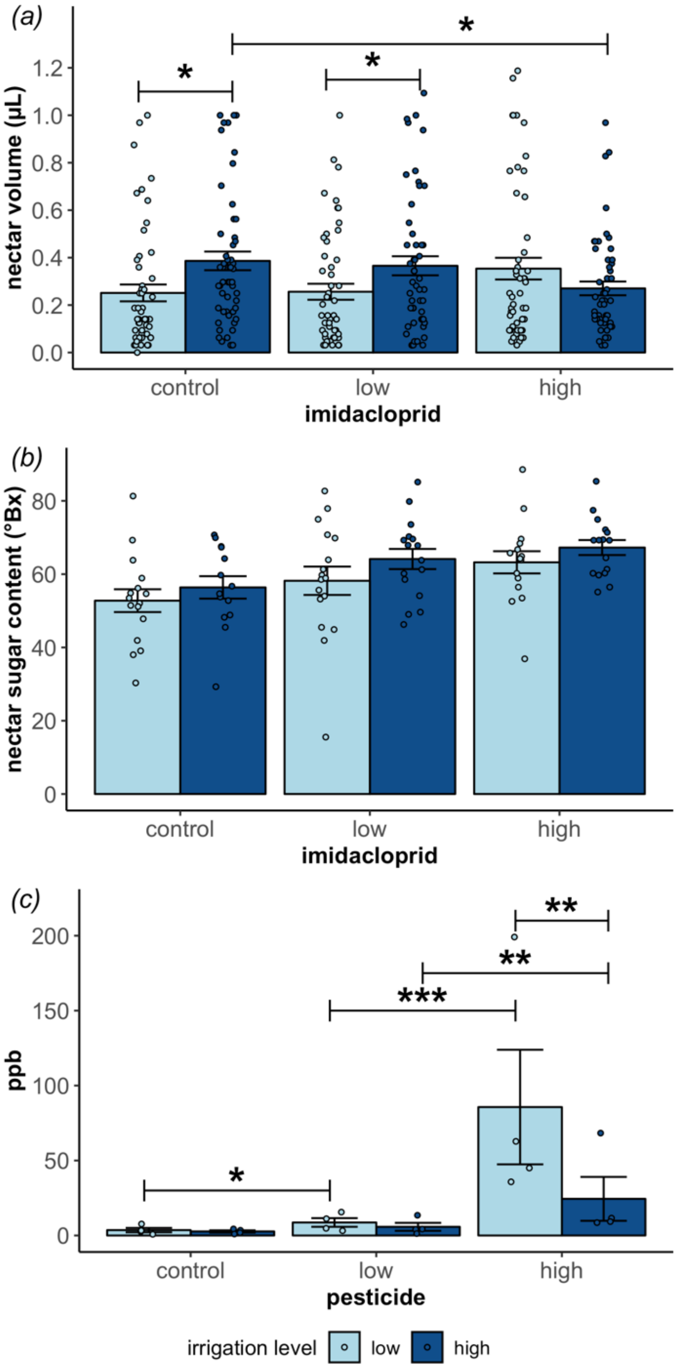

**Figure 4.1.** Phacelia floral nectar characteristics in response to irrigation and imidacloprid treatments: (a) nectar volume, (b) nectar sugar concentration, and (c) imidacloprid concentration. Points represent raw data, while bars and whiskers show mean ± s.e. Lines indicate significant comparisons from post-hoc Tukey's HSD tests (*: $0.01 < p < 0.05$; **: $0.001 < p < 0.01$; ***: $p < 0.001$).

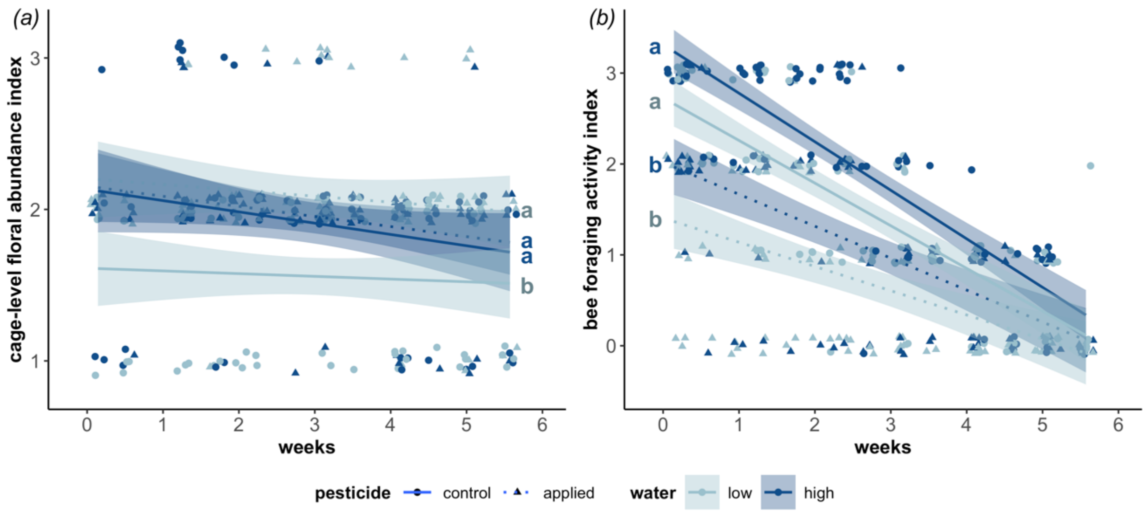

**Figure 4.2.** Irrigation and imidacloprid effects on (a) cage-level floral abundance and (b) ALCB foraging activity, both years combined. Points are jittered to improve visibility. Week "0" represents the day bees were added into cages. Bands around each fitted line represent 95% CIs. Fitted lines not connected by the same lowercase letter were significantly different ($p < 0.05$) in post-hoc Tukey's HSD tests.

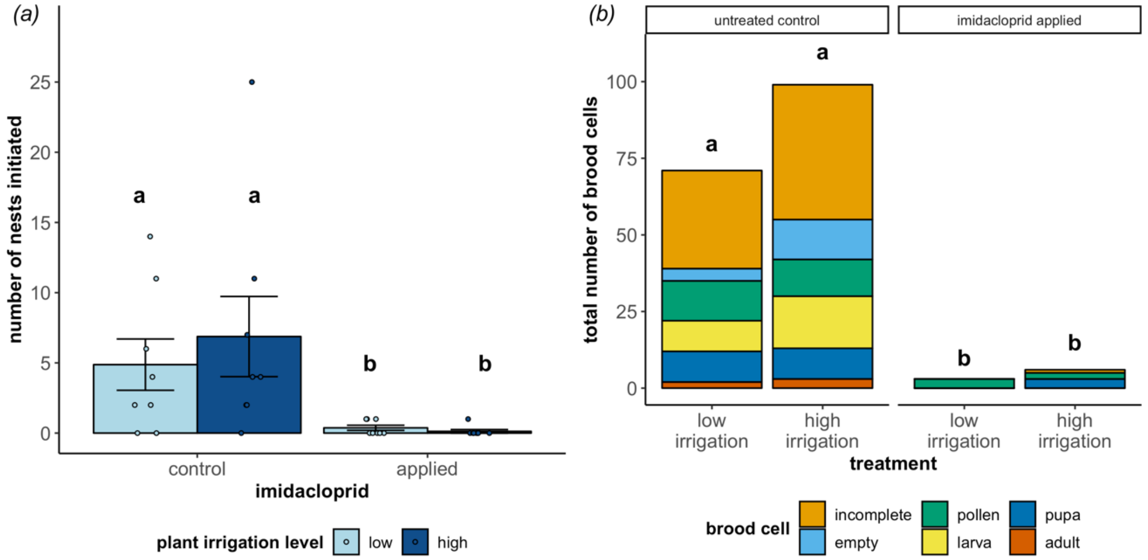

**Figure 4.3.** ALCB nesting responses to irrigation and imidacloprid treatments. (a) Nests initiated per cage. Each point represents one cage per study year ($N = 32$). (b) Cumulative number of cells constructed by treatment summed across cages and years. Bars not connected by the same lowercase letter were significantly different ($p < 0.05$) in post-hoc Tukey's HSD tests.

# CONCLUSION

In Chapters I and II, I found that nurseries, despite their highly artificial and dynamic design, host diverse assemblages of wild bees—over 150 species were detected visiting over 90 varieties of ornamental plants. Local factors such as the cultivation of native plants were associated with bee abundance, richness, diversity, and assemblage composition. Furthermore, there was a positive relationship between gains in plants species and gains in bee species in nurseries across seasons within a year. More specialist bee species were found at native nurseries, likely due to the availability of native host plants. Surprisingly, landscape-level features were not correlated with bee functional trait distributions, suggesting the above patterns are widely applicable to different nurseries. I also detected cleptoparasitic bee species, which serve as further indicators of diverse bee communities. Plant-bee networks were overall low in connectance, and more specialized at conventional nurseries, indicating selective use of resources. These findings are significant in that they offer a mechanistic understanding of patterns in bee assemblages in nurseries—and by extension, other ornamental landscapes—at an ecosystem scale. Such insights are critical to designing efficient bee management strategies in nursery systems, which are important given bees may encounter a variety of stressors (e.g., systemic insecticides) in these areas.

In Chapter III, I found that wild bees (mostly *Halictus ligatus*) display considerable fidelity to flowering ornamentals inside nurseries. In eight sperate experiments, half of all foraging bees marked were consistently captured on the subsequent day. With very few exceptions, each recaptured bee was found foraging on the same species of plant as the previous day. When examined separately, recapture rates of bees were higher on California-native plants than on plants exotic to California. These findings are some of the first of their kind for these non-model system bees. This work broadens our understanding of the foraging biology of understudied species by identifying important environmental factors associated with behavior. Importantly, this research opens up new lines of inquiry into wild bee foraging biology and how their fidelity to plants may vary through time and space.

In Chapter IV, I found that increased irrigation of potted plants elevated floral nectar volume and floral abundance, but this effect was altered by neonicotinoid application. In neonicotinoid treated plants, there was no effect of irrigation on these floral metrics. Interestingly, nectar neonicotinoid concentrations were higher in low irrigation plants. Also surprising was that increased irrigation of potted plants did not translate into any benefits to the bees themselves. At 30% label rate application, a nursery formulation of imidacloprid reduced bee reproduction by over 90% relative to the control. This study is among the first to link the interacting effects of plant irrigation level and neonicotinoid application to floral resources and solitary bee reproduction. This work opens up several lines of research and identifies gaps in our knowledge surrounding interactions between local agricultural management practices (e.g., soil moisture and type of pesticide formulation) and pollinator conservation. More narrowly, results from this work help us understand how management practices in nurseries directly affect the health of wild bee populations.

From a basic scientific perspective, this dissertation has addressed the ongoing need for an increased understanding of bee community ecology in agricultural areas, bee foraging preferences between exotic and native plants in disturbed landscapes (Jha et al. 2013), and impacts of ornamental plants and pesticides on non-*Apis* bee health (Brittain and Potts 2011). This research is also consistent with the goals of the 2015 White House Pollinator Research Action Plan, aligning with the call for surveys of bee communities in ecosystems to assess the status of and trends in wild pollinator populations and to develop strategies to enhance landscapes that sustain pollinators. The report calls for "broad-scale assessments of pollinator distribution" in different commercial agriculture management regimes, and for research that links composition of the landscape surrounding habitats to pollinator demography (Pollinator Health Task Force 2015).

From an applied perspective, this dissertation addresses major interests of the California nursery industry. First, it provides quantitative data on bee communities in nurseries across seasons that can be used to shape management strategies that mitigate the exposure of pollinators to stressors like pesticides without major expense to growers. This issue is escalating in importance as the acreage used for production of nursery stock grew between 2014 and 2019 (open area by 10%, and area under natural shade by 25%) (USDA NASS 2020) For example, growers can use spatial and temporal data on bee communities, plant flowering phenology, and bee-plant interaction networks to make decisions regarding when and how pesticides can be applied to which plants. In addition to simply altering the schedule and targets of pesticide application, this information can also lay the groundwork for future approaches combining monitoring of pollinator health with pest management practices (Biddinger and Rajotte 2015). Second, this project establishes a standardized methodology for assessing pollinator abundance and diversity in commercial nurseries and highlights the strengths and weaknesses of active and passive collection methods. Monitoring efforts would allow growers to gauge how large an impact a particular nursery has on local bee populations by estimating the degree to which a nursery could support different wild bee species.

Furthermore, this dissertation highlights the ways in which large-scale nurseries may serve as important resources for pollinators. There is growing public interest in conserving pollinators using ornamental plants (Lentola et al. 2017). A 2016 poll (Kegley et al. 2016) found that two-thirds of Americans felt positively about retail garden centers' commitments to eliminate pesticide-treated plants from their stores. Half of respondents said they are more likely to shop at a retailer due to such a commitment, while almost 40% said they would view retailers who had not made this pledge negatively. There is economic incentive (Campbell et al. 2017, Campbell and Steele 2020) for growers to demonstrate awareness of beneficial insects interacting with their stock , as consumers will perceive this positively (Rihn and Khachatryan 2016). California serves as a leader in eco-conscious legislation and technology, and is the top state in the nation in terms of horticultural revenue—$2.9 billion in 2014 (21% of national industry revenue) (USDA NASS 2014) and $2.6 billion in 2019 (USDA NASS 2020). This research represents one of various avenues by which the California nursery industry may benefit from pollinator conservation efforts.

Overall, this dissertation demonstrates that nurseries do likely serve as foraging habitat for bees, and represents a quantitative investigation into their specific contributions to regional bee faunas. A broad diversity of wild bees consistently forage on numerous taxa of flowering plants found in nurseries throughout the year across southern California. Given the use of bee-harmful chemicals in nurseries, this and further critical investigations are necessary to determine the potential threats they pose to bees alongside their apparent benefits. Knowledge regarding the ecology of such economically critical insects in these widespread agricultural areas has both basic and applied implications for horticulture and other agricultural sectors, as well as restoration efforts using ornamental plants.

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# APPENDIX A

**Table A.1.** Characteristics of the 13 plant nurseries sampled and the total numbers of individuals and species of wild bees collected at each via sweep netting and vane trapping (summed across seasons and years).

| **nursery** | **nursery type** | **nursery area (ha)** | **number of plots** | **proportional surrounding natural area (1 km)** | **sweep netting** | | **vane trapping** | |
|---|---|---|---|---|---|---|---|---|
| | | | | | **bees** | **species** | **bees** | **species** |
| **11** | native | 3.10 | 3 | 0.301 | 52 | 29 | 185 | 29 |
| **08** | | 7.30 | 7 | 0.793 | 42 | 23 | 751 | 53 |
| **06** | | 0.50 | 2 | 0.711 | 5 | 4 | 5 | 5 |
| **07** | | 4.83 | 4 | 0.915 | 50 | 23 | 386 | 37 |
| **12** | | 7.21 | 7 | 0.300 | 22 | 12 | 319 | 22 |
| **09** | conventional | 4.58 | 4 | 0.106 | 44 | 21 | 1,004 | 37 |
| **10** | | 4.29 | 4 | 0.151 | 10 | 8 | 147 | 20 |
| **01** | | 4.00 | 4 | 0.257 | 61 | 19 | 1,437 | 28 |
| **02** | | 2.90 | 3 | 0.210 | 44 | 18 | 524 | 26 |
| **03** | | 3.89 | 4 | 0.289 | 7 | 5 | 245 | 22 |
| **04** | | 3.80 | 4 | 0.081 | 0 | 0 | 17 | 8 |
| **05** | | 30.00 | 12 | 0.562 | 21 | 10 | 1,098 | 41 |
| **13** | | 3.86 | 4 | 0.614 | 17 | 12 | 194 | 30 |
| | | | | **TOTALS:** | **375** | **92** | **6,312** | **102** |

**Table A.2.** Schedule of the 58 sampling events (gray cells) at the 13 plant nurseries in the study from March 2016 to May 2018. A gray cell indicates that nursery was sampled in that season and year, while a white cell indicates the nursery was not sampled in that season and year (largely due to logistical reasons). Black cells indicate seasons when sampling was not permitted due to nursery closure.

| Nursery | 2016 | | | 2017 | | | 2018 |
|---|---|---|---|---|---|---|---|
| | spring | summer | autumn | spring | summer | autumn | spring |
| 01 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 02 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 03 | ▨ | ▨ | ■ | ■ | ■ | ■ | ■ |
| 04 | ▨ | □ | □ | ▨ | ■ | ■ | ■ |
| 05 | ▨ | ▨ | ▨ | ▨ | ▨ | □ | □ |
| 06 | ▨ | ■ | ■ | ■ | ■ | ■ | ■ |
| 07 | ▨ | ▨ | ▨ | ▨ | ▨ | □ | ▨ |
| 08 | □ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 09 | ■ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 10 | □ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 11 | □ | ▨ | ▨ | ▨ | ▨ | □ | ▨ |
| 12 | □ | □ | □ | ▨ | ▨ | □ | ▨ |
| 13 | □ | □ | □ | □ | ▨ | □ | ▨ |

**Table A.3.** Results of significance tests for fixed effects from linear mixed models with nursery, year, and date of collection as random effects. Symbols in cells indicate the results of that hypothesis test: ***: $P \leq 0.001$; **: $P \leq 0.01$; *: $P \leq 0.05$; ns: $P > 0.05$. Parentheses around a symbol indicate that, in the identical model with *Apis mellifera* included, the $P$-value for that hypothesis differed (i.e., if the effect was statistically significant in that model without *Apis mellifera*, it was not statistically significant when *Apis mellifera* was included).

| **collection method** | **fixed effect** | **univariate models** | | | | **multivariate models** | |
|---|---|---|---|---|---|---|---|
| | | **abundance** | **richness** | **Shannon (*H'*)** | **evenness (*J'*)** | **composition (permANOVA)** | **beta diversity (PERMDISP2)** |
| sweep netting | season | . | ** | * | ns | *** | ** |
| | nursery type | * | * | ns | ns | * | ns |
| | plant richness | ns | ns | . | ns | . | |
| | plant proportional native richness | *** | ** | ** | ns | ns | |
| | floral abundance | * | * | ns | ns | ns | |
| | temperature | ns | ns | ns | ns | * | |
| | nursery area | ns | ns | ns | * | ns | |
| | proportion natural area | ns | ns | ns | ns | . | |
| | season *x* nursery type | ns | ns | ns | . | ** | |
| vane trapping | season | *** | *** | *** | ns | *** | *** |
| | nursery type | ns | ns | ns | ns | *** | ns |
| | plant richness | ns | ns | ns | ns | ns | |
| | plant proportional native richness | ns | ns | ns | ns | ns | |
| | floral abundance | ns | ns | ns | ns | ns | |
| | temperature | (*) | . | ns | ns | ns | |
| | nursery area | ns | ns | (*) | ns | . | |
| | proportion natural area | ns | ns | ns | ns | ** | |
| | season *x* nursery type | ns | ns | * | ns | ns | |

**Table A.4.** Results of indicator species analyses for bee species collected in plant nurseries.

| **bee species** | **season** | | | **nurs. type** | | **% n. pl. rich.** | | **fl. cov.** | | **nat. area** | | **nurs. area** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | spring | summer | autumn | conv. | native | >50% | ≤50% | > average | ≤ average | >50% | ≤50% | >median | ≤ median |
| *Lasioglossum (Evylaeus) sp. 2* | | | | | 🟩 | 🟩 | | | 🟨 | 🟩 | | 🟦 | |
| *Ashmeadiella bucconis* | | 🟨 | | | 🟨 | 🟨 | | | | | | | |
| *Augochlorella pomoniella* | | 🟦 | 🟨 | | | 🟦 | | | | | | | |
| *Calliopsis rhodophila* | | | | | 🟦 | 🟦 | | | | 🟦 | | | |
| *Ceratina nanula* | | 🟦 | | | 🟦 | 🟦 | | | | | | | |
| *Lasioglossum sisymbrii* | 🟦 | | | | 🟨 | 🟨 | | | | | | | |
| *Panurginus sp. A* | | | | | 🟦 | 🟦 | | | | 🟦 | | | |
| *Perdita interrupta* | 🟨 | | | | 🟨 | 🟨 | | | | | | | |
| *Lasioglossum (Dialictus) sp. B* | | 🟦 | | | | | | | | 🟦 | | 🟦 | |
| *Lasioglossum (Evylaeus) sp. 1* | | | | | | | | 🟦 | | 🟦 | | 🟦 | |
| *Lasioglossum (Evylaeus) sp. 3* | 🟦 | | | | | | | | 🟦 | 🟦 | | | |
| *Agapostemon melliventris* | | | | 🟦 | | | 🟦 | | | | 🟦 | | |
| *Agapostemon texanus* | | | | 🟨 | | | | | | | 🟨 | | 🟨 |
| *Bombus californicus* | | 🟦 | | | | | | | | 🟦 | | | |
| *Diadasia nitidifrons* | | | | | 🟨 | 🟨 | | | | | | | |
| *Dufourea sp. 2* | | | | | 🟦 | 🟦 | | | | | | | |
| *Lasioglossum (Dialictus) sp. 3* | | | | | 🟨 | 🟨 | | | | | | | |
| *Melissodes sp. D* | | 🟦 | | | | | | | | 🟩 | | | |
| *Anthophora urbana* | | | 🟨 | | | | | | | | | 🟦 | |
| *Ceratina acantha* | | | | | | 🟦 | | | 🟨 | | | | |
| *Xylocopa varipuncta* | | | | | | | | | | 🟦 | | 🟦 | |
| *Halictus ligatus* | | | | | | | | | | 🟦 | | | |
| *Anthophora californica* | 🟨 | | | | | | | | | | | | |
| *Bombus sonorus* | | 🟦 | | | | | | | | | | | |
| *Bombus vosnesenskii* | | | | | | | | | | 🟦 | | | |
| *Colletes sp. B* | | | 🟨 | | | | | | | | | | |
| *Diadasia australis* | 🟦 | | | | | | | | | | | | |
| *Diadasia bituberculata* | 🟦 | | | | | | | | | | | | |
| *Diadasia laticauda* | | 🟦 | | | | | | | | | | | |
| *Diadasia rinconis* | | 🟦 | | | | | | | | | | | |
| *Dufourea cf. trochantera* | 🟦 | | | | | | | | | | | | |
| *Eucera (Peponapis) pruinosa* | | 🟦 | | | | | | | | | | | |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Hylaeus mesillae* | | | | | | | 🟨 | | | | | | |
| *Habropoda tristissima* | | | | | | | | | | 🟦 | | | |
| *Halictus farinosus* | | | | | | | | | | 🟦 | | | |
| *Halictus tripartitus* | | 🟨 | | | | | | | | | | | |
| *Lasioglossum (Dialictus) sp. 2* | | 🟨 | | | | | | | | | | | |
| *Lasioglossum (Dialictus) sp. A* | | | | 🟨 | | | | | | | | | |
| *Lasioglossum (Dialictus) sp. D* | | | | | | | | | | 🟦 | | | |
| *Lasioglossum (Dialictus) sp. E* | | 🟦 | | | | | | | | | | | |
| *Melissodes sp. A* | | 🟩 | | | | | | | | | | | |
| *Melissodes sp. B* | | 🟦 | | | | | | | | | | | |
| *Melissodes sp. C* | | 🟦 | | | | | | | | | | | |
| *Xenoglossa strenua* | | 🟦 | | | | | | | | | | | |

**Figure A.1.** Containerized flowering plants at a conventional plant nursery in Riverside County, California in June 2017.

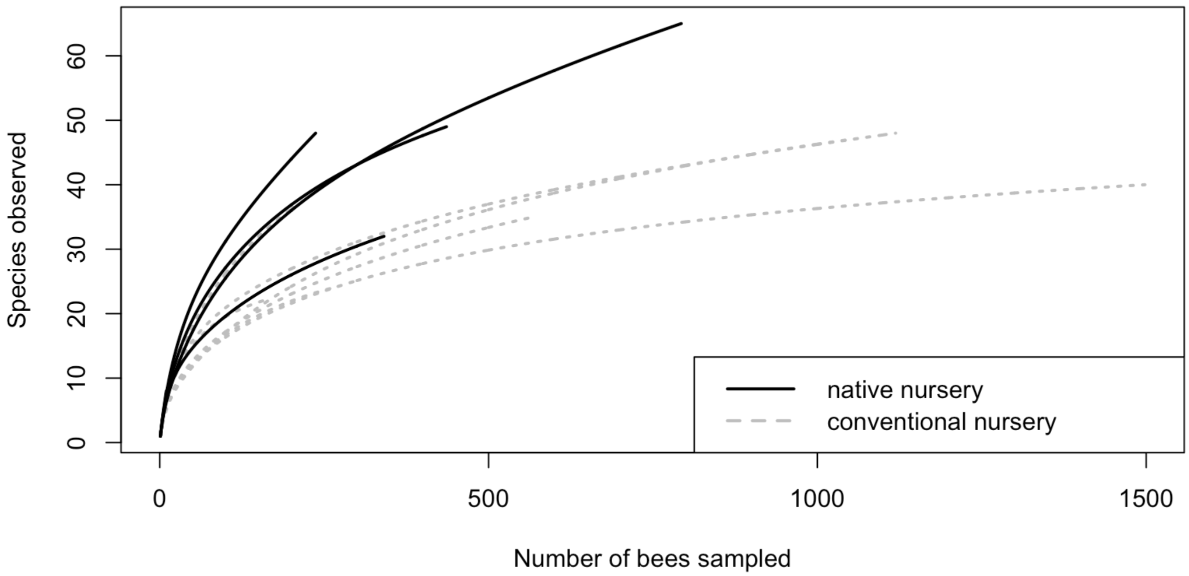

**Figure A.2.** Individual-based species rarefaction curves for bee assemblages collected at each of the five native nurseries (solid black lines) and eight conventional nurseries (dashed gray lines) in the study. Both sweep net and vane trap collections are combined within sites. Lines terminate at the observed number of species and individuals for a site. Interpolations and confidence intervals are omitted for clarity.

# APPENDIX B

**Table B.1.** The 13 plant nurseries sampled and their physical characteristics. Also included are the total numbers of individuals and species of bees collected by sweep netting and vane trapping, respectively, at each nursery.

| **Nursery** | **Type** | **County (California, USA)** | **Area (ha)** | **Number of plots** | **Proportion natural area (1-km buffer)** | **Elevation (m)** | **Sweep netted bees** | **Vane trapped bees** |
|---|---|---|---|---|---|---|---|---|
| **01** | conventional | Riverside | 4.00 | 4 | 0.257 | 316 | 61 bees in 19 spp. | 1,437 bees in 28 spp. |
| **02** | conventional | Riverside | 2.90 | 3 | 0.210 | 303 | 44 bees in 18 spp. | 524 bees in 26 spp. |
| **03** | conventional | Riverside | 3.89 | 4 | 0.289 | 580 | 7 bees in 5 spp. | 245 bees in 22 spp. |
| **04** | conventional | Riverside | 3.80 | 4 | 0.081 | 523 | 0 bees | 17 bees in 8 spp. |
| **05** | conventional | Riverside | 30.00 | 12 | 0.562 | 471 | 21 bees in 10 spp. | 1,098 bees in 41 spp. |
| **06** | native | San Diego | 0.50 | 2 | 0.711 | 105 | 5 bees in 4 spp. | 5 bees in 5 spp. |
| **07** | native | San Diego | 4.83 | 4 | 0.915 | 471 | 50 bees in 23 spp. | 386 bees in 37 spp. |
| **08** | native | Orange | 7.30 | 7 | 0.793 | 114 | 42 bees in 23 spp. | 751 bees in 53 spp. |
| **09** | conventional | Los Angeles | 4.58 | 4 | 0.106 | 151 | 44 bees in 21 spp. | 1,004 bees in 37 spp. |
| **10** | conventional | Los Angeles | 4.29 | 4 | 0.151 | 104 | 10 bees in 8 spp. | 147 bees in 20 spp. |
| **11** | native | Los Angeles | 3.10 | 3 | 0.301 | 303 | 52 bees in 29 spp. | 185 bees in 29 spp. |
| **12** | native | San Diego | 7.21 | 7 | 0.300 | 12 | 22 bees in 12 spp. | 319 bees in 22 spp. |
| **13** | conventional | Riverside | 3.86 | 4 | 0.614 | 775 | 17 bees in 12 spp. | 194 bees in 30 spp. |
| | | | | | | **TOTAL** | 375 bees in 92 spp. | 6,312 bees in 102 spp. |

**Table B.2.** Sampling schedule for the 13 nurseries in the study from March 2016 to May 2018. A “1” indicates that nursery was sampled, while a “0” indicates it was not sampled due to logistical reasons. Blacked-out cells indicate seasons when sampling was not possible due to closure of nursery property. Columns sums (bottom row) indicate the total number of nurseries sampled in that season, while row sums (rightmost column) indicate the total number of times that nursery was sampled in the study.

| **Nursery** | **2016** | | | **2017** | | | **2018** | **samplings per nursery** |
|---|---|---|---|---|---|---|---|---|
| | **Spring** | **Summer** | **Autumn** | **Spring** | **Summer** | **Autumn** | **Spring** | |
| **01** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 7 |
| **02** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 7 |
| **03** | 1 | 1 | ■ | ■ | ■ | ■ | ■ | 2 |
| **04** | 1 | 0 | 0 | 1 | ■ | ■ | ■ | 2 |
| **05** | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 5 |
| **06** | 1 | ■ | ■ | ■ | ■ | ■ | ■ | 1 |
| **07** | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 6 |
| **08** | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 6 |
| **09** | ■ | 1 | 1 | 1 | 1 | 1 | 1 | 6 |
| **10** | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 6 |
| **11** | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 5 |
| **12** | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 3 |
| **13** | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 |
| **nurseries sampled** | 7 | 9 | 8 | 10 | 10 | 5 | 9 | 58 |

**Table B.3.** Numbers of bee species detected via sweep netting and vane trapping, categorized by three functional traits of interest: diet breadth, nesting location, and social organization. Cleptoparasites are tallied separately.

| **Sweep netting (92 spp.)** | | eusocial | solitary |
|---|---|---|---|
| generalist | below ground | 26 | 22 |
| | cavity | 0 | 25 |
| specialist | below ground | 0 | 14 |
| | cavity | 0 | 1 |
| cleptoparasites: 4 | | | |
| **Vane trapping (102 spp.)** | | eusocial | solitary |
| generalist | below ground | 22 | 22 |
| | cavity | 0 | 20 |
| specialist | below ground | 0 | 31 |
| | cavity | 0 | 2 |
| cleptoparasites: 5 | | | |

**Table B.4.** Results of significance tests for fixed effects, including interaction terms, from mixed models with nursery and year as random effects. Symbols in cells indicate the results of that hypothesis test: ***: $P \leq 0.001$; **: $P \leq 0.01$; *: $P \leq 0.05$; ns: $P > 0.05$. Parentheses around "ns" indicate that, in the identical model with *Apis mellifera* included, the *P*-value for that hypothesis test was $\leq 0.05$. Functional dispersion (FDis) accounts for multiple functional traits, so the two models for this variable lacked a functional trait effect and associated interactions ("N/A").

| **bee collection method** | **independent variable** | numerator degrees of freedom | proportions of **individuals** | | | proportions of **species** | | | functional dispersion (FDis) |
|---|---|---|---|---|---|---|---|---|---|
| | | | diet breadth | nesting location | social organization | diet breadth | nesting location | social organization | |
| sweep netting | functional trait | 2 | *** | ** | *** | *** | ** | * | N/A |
| | season | 2 | ns | * | * | ns | ns | ns | ns |
| | nursery type | 1 | ** | ns | ns | * | ns | ns | ns |
| | prop. natural area at 1 km | 1 | ns | ns | ns | ns | ns | ns | ns |
| | nursery area | 1 | ns | ns | ns | ns | ns | ns | ns |
| | trait *x* season | 4 | ns | ** | * | ns | ns | ns | N/A |
| | trait *x* nursery type | 2 | *** | ns | ns | ** | ns | ns | N/A |
| | season *x* nursery type | 2 | ns | ns | ns | ns | ns | ns | ns |
| | trait *x* season *x* nursery type | 4 | ns | ns | ns | ns | ns | ns | N/A |
| vane trapping | functional trait | 2 | *** | *** | *** | *** | *** | *** | N/A |
| | season | 2 | *** | (ns) | *** | ns | ns | ns | ns |
| | nursery type | 1 | ns | *** | *** | ns | ns | ns | ns |
| | prop. natural area at 1 km | 1 | ns | ns | ns | ns | ns | ns | ns |
| | nursery area | 1 | ns | ns | ns | ns | ns | ns | ns |
| | trait *x* season | 4 | *** | (ns) | *** | * | ns | ns | N/A |
| | trait *x* nursery type | 2 | (ns) | *** | *** | * | * | ns | N/A |
| | season *x* nursery type | 2 | *** | * | *** | ns | ns | ns | * |
| | trait *x* season *x* nursery type | 4 | *** | ** | *** | ns | ns | ns | N/A |

**Table B.5.** List of bee species and morphotaxa, ordered by family and genus, collected in this study via sweep netting and blue vane traps. Morphotaxa are indicated by a species epithet consisting of "sp." followed by a unique identifier. Each species' diet breadth, nesting location, and social organization is designated along with the corresponding literature reference as a bracketed number. Species-level information on functional traits was not available for all species in the study, or, of course, for morphotaxa. In such cases, functional traits were assigned based on inference from their taxonomy at the genus level (e.g., Michener (2007) notes that "all *Andrena* species nest in the ground"). Instances where functional traits were assigned in this manner are indicated by table cells merged across species within the column designating the trait. Lastly, the numbers of individual bees (by sex and collection method) collected in the study are listed at the right. In the "subgenus" column: [unk] = taxon was not identifiable to a described subgenus; [NA] = subgenera are not currently broadly established for this genus.

| Taxonomy | | | | Functional traits | | | sweep netting | | vane trapping | |
|---|---|---|---|---|---|---|---|---|---|---|
| **family** | **genus** | **subgenus** | **species** | **diet breadth** | **nesting location** | **social organization** | **F** | **M** | **F** | **M** |
| Andrenidae | *Andrena* | *Plastandrena* | *Andrena prunorum* | generalist[1] | below ground[2] | solitary[2] | 0 | 1 | 0 | 5 |
| | | *Simandrena* | *Andrena angustitarsata* | generalist[3] | | | 1 | 0 | 1 | 0 |
| | | [unk] | *Andrena* sp. 2c-A | specialist[4] | | | 0 | 0 | 5 | 1 |
| | | [unk] | *Andrena* sp. 2c-B | | | | 0 | 0 | 2 | 0 |
| | | [unk] | *Andrena* sp. 3c-B | | | | 0 | 0 | 2 | 0 |
| | | [unk] | *Andrena* sp. 3c-C | | | | 0 | 0 | 1 | 2 |
| | | [unk] | *Andrena* sp. 3c-D | | | | 0 | 10 | 0 | 2 |
| | *Calliopsis* | *Calliopsis* | *Calliopsis rhodophila* | generalist[5] | below ground[2] | solitary[6] | 4 | 1 | 11 | 1 |
| | | *Nomadopsis* | *Calliopsis scutellaris* | generalist[3] | | | 2 | 1 | 0 | 0 |
| | *Panurginus* | [NA] | *Panurginus bilobatus* | specialist[3] | below ground[2] | solitary[6] | 2 | 1 | 5 | 3 |
| | | | *Panurginus* sp. B | | | | 0 | 0 | 1 | 0 |
| | *Perdita* | *Perdita* | *Perdita rhois* | generalist[3] | below ground[2] | solitary[6] | 1 | 5 | 0 | 0 |
| | | *Pygoperdita* | *Perdita interrupta* | specialist[3] | | | 1 | 4 | 0 | 0 |
| | | *Pygoperdita* | *Perdita micheneri* | specialist[2] | | | 3 | 1 | 1 | 2 |
| | | *Pygoperdita* | *Perdita mojavensis* | specialist[3] | | | 0 | 0 | 1 | 1 |
| | | [unk] | *Perdita* sp. B | specialist[2] | | | 0 | 0 | 2 | 3 |
| | | [unk] | *Perdita* sp. D | | | | 0 | 0 | 4 | 0 |

|  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  | [unk] | *Perdita* sp. E |  |  |  | 0 | 0 | 2 | 0 |
|  |  | [unk] | *Perdita* sp. F |  |  |  | 2 | 0 | 5 | 3 |
| Apidae | *Anthophora* | *Anthophoroides* | *Anthophora californica* | generalist [7] | below ground[7] | solitary[2] | 9 | 7 | 4 | 7 |
|  |  | *Micranthophora* | *Anthophora curta* | generalist[3] | below ground[2] | solitary[2] | 1 | 0 | 0 | 0 |
|  |  | *Mystacanthophora* | *Anthophora urbana* | generalist[3] |  |  | 6 | 0 | 126 | 10 |
|  |  | [unk] | *Anthophora* sp. A | generalist[3] |  |  | 1 | 0 | 0 | 0 |
|  | *Anthophorula* | *Anthophorisca* | *Anthophorula nitens* | generalist[8] | below ground[8] | solitary[8] | 0 | 0 | 0 | 1 |
|  |  | *Anthophorula* | *Anthophorula albicans* | generalist[3] | below ground[2] | solitary[2] | 0 | 0 | 1 | 0 |
|  |  | *Anthophorula* | *Anthophorula cerei* | generalist[3] |  |  | 0 | 0 | 1 | 0 |
|  |  | *Anthophorula* | *Anthophorula torticornis* | generalist[3] |  |  | 0 | 0 | 1 | 1 |
|  | *Apis* | *Apis* | *Apis mellifera* | generalist[2] | cavity[2] | eusocial[6] | 10 | 0 | 633 | 0 |
|  | *Bombus* | *Bombias* | *Bombus nevadensis* | generalist[3] | below ground[3] | eusocial[3] | 0 | 1 | 0 | 0 |
|  |  | *Cullumanobombus* | *Bombus crotchii* |  |  |  | 0 | 0 | 3 | 0 |
|  |  | *Pyrobombus* | *Bombus melanopygus* |  |  |  | 2 | 0 | 1 | 0 |
|  |  | *Pyrobombus* | *Bombus vandykei* |  |  |  | 0 | 0 | 1 | 0 |
|  |  | *Pyrobombus* | *Bombus vosnesenskii* |  |  |  | 1 | 0 | 10 | 1 |
|  |  | *Thoracobombus* | *Bombus californicus* |  |  |  | 1 | 3 | 4 | 4 |
|  |  | *Thoracobombus* | *Bombus sonorus* |  |  |  | 2 | 0 | 12 | 1 |
|  | *Ceratina* | *Ceratinula* | *Ceratina arizonensis* | generalist[3] | cavity[2] | solitary[2] | 0 | 0 | 2 | 1 |
|  |  | *Zadontomerus* | *Ceratina acantha* | generalist[3] |  |  | 9 | 3 | 40 | 0 |
|  |  | *Zadontomerus* | *Ceratina micheneri* | generalist[3] |  |  | 0 | 0 | 1 | 0 |

|  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  | *Zadontomerus* | *Ceratina nanula* | generalist[3] |  |  | 1 | 0 | 9 | 0 |
|  |  | *Zadontomerus* | *Ceratina sequoiae* | specialist[3] |  |  | 0 | 0 | 1 | 0 |
|  | *Diadasia* | *Coquillettapis* | *Diadasia angusticeps* | specialist[9] | below ground[2] | solitary[9] | 0 | 0 | 1 | 0 |
|  |  | *Coquillettapis* | *Diadasia australis* |  |  |  | 1 | 1 | 20 | 26 |
|  |  | *Coquillettapis* | *Diadasia bituberculata* |  |  |  | 1 | 0 | 9 | 6 |
|  |  | *Coquillettapis* | *Diadasia diminuta* |  |  |  | 0 | 5 | 3 | 3 |
|  |  | *Coquillettapis* | *Diadasia laticauda* |  |  |  | 0 | 0 | 13 | 4 |
|  |  | *Coquillettapis* | *Diadasia lutzi* |  |  |  | 0 | 0 | 1 | 0 |
|  |  | *Coquillettapis* | *Diadasia nitidifrons* |  |  |  | 0 | 4 | 8 | 2 |
|  |  | *Coquillettapis* | *Diadasia rinconis* |  |  |  | 0 | 0 | 125 | 42 |
|  |  | *Coquillettapis* | *Diadasia vallicola* |  |  |  | 2 | 0 | 0 | 0 |
|  |  | *Dasiapis* | *Diadasia ochracea* |  |  |  | 1 | 0 | 22 | 0 |
|  |  | *Diadasia* | *Diadasia enavata* |  |  |  | 0 | 0 | 2 | 0 |
|  | *Eucera* | *Synhalonia* | *Eucera cordleyi* | generalist[3] | below ground[2] | solitary[2] | 0 | 0 | 1 | 3 |
|  |  | *Synhalonia* | *Eucera dorsata* | generalist[3] |  |  | 0 | 0 | 1 | 0 |
|  |  | *Synhalonia* | *Eucera lunata* | generalist[3] |  |  | 0 | 0 | 1 | 0 |
|  | *Habropoda* | [NA] | *Habropoda depressa* | generalist[10] | below ground[10] | solitary[10] | 2 | 0 | 0 | 0 |
|  |  |  | *Habropoda tristissima* | generalist[10] | below ground[10] | solitary[10] | 0 | 0 | 8 | 0 |
|  | *Melecta* | *Melecta* | *Melecta pacifica* | cleptoparasitic[2] | cleptoparasitic[2] | cleptoparasitic[2] | 0 | 0 | 1 | 0 |
|  | *Melissodes* | [unk] | *Melissodes* sp. 4 | generalist[2] | below ground[2] | solitary[11] | 0 | 0 | 1 | 0 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | [unk] | *Melissodes* sp. A | | | | 3 | 12 | 202 | 133 |
| | | [unk] | *Melissodes* sp. B | | | | 1 | 3 | 103 | 17 |
| | | [unk] | *Melissodes* sp. C | | | | 1 | 4 | 78 | 107 |
| | | [unk] | *Melissodes* sp. D | | | | 4 | 4 | 31 | 62 |
| | *Nomada* | [NA] | *Nomada* sp. A | cleptoparasitic[2] | cleptoparasitic[2] | cleptoparasitic[2] | 1 | 1 | 0 | 0 |
| | *Oreopasites* | [unk] | *Oreopasites* sp. 1 | cleptoparasitic[2] | cleptoparasitic[2] | cleptoparasitic[2] | 0 | 0 | 0 | 1 |
| | | [unk] | *Oreopasites* sp. A | | | | 0 | 0 | 3 | 0 |
| | *Peponapis** | *Peponapis* | *Peponapis pruinosa* | specialist[2] | below ground[7] | solitary[12] | 0 | 0 | 53 | 116 |
| | *Svastra* | *Epimelissodes* | *Svastra sabinensis* | generalist[13] | below ground[14] | solitary[13] | 0 | 2 | 0 | 0 |
| | *Triepeolus* | [NA] | *Triepeolus concavus* | cleptoparasitic[2] | cleptoparasitic[2] | cleptoparasitic[2] | 0 | 1 | 0 | 0 |
| | | | *Triepeolus* sp. B | | | | 2 | 1 | 0 | 0 |
| | *Xenoglossa* | *Eoxenoglossa* | *Xenoglossa strenua* | specialist[2] | below ground[2] | solitary[2] | 0 | 0 | 72 | 103 |
| | | *Xenoglossa* | *Xenoglossa patricia* | | | | 0 | 0 | 1 | 3 |
| | *Xeromelecta* | *Melectomorpha* | *Xeromelecta californica* | cleptoparasitic[2] | cleptoparasitic[2] | cleptoparasitic[2] | 0 | 0 | 0 | 1 |
| | *Xylocopa* | *Neoxylocopa* | *Xylocopa varipuncta* | generalist[15] | cavity[2] | solitary[2] | 2 | 0 | 75 | 2 |
| | | *Notoxylocopa* | *Xylocopa tabaniformis* | generalist[15] | | | 0 | 4 | 0 | 0 |
| Colletidae | *Colletes* | [NA] | *Colletes* sp. A1 | generalist[3] | below ground[2] | solitary[2] | 1 | 0 | 0 | 0 |
| | | | *Colletes* sp. A2 | | | | 1 | 0 | 0 | 0 |
| | | | *Colletes* sp. B | | | | 3 | 0 | 0 | 0 |
| | *Hylaeus* | *Hylaeus* | *Hylaeus mesillae* | generalist[2] | cavity[2] | solitary[2] | 2 | 12 | 2 | 1 |
| Halictidae | *Agapostemon* | *Agapostemon* | *Agapostemon femoratus* | generalist[16] | below ground[2] | solitary[17] | 0 | 0 | 28 | 1 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *Agapostemon* | *Agapostemon melliventris* | generalist[16] | | solitary[17] | 1 | 1 | 274 | 16 |
| | | *Agapostemon* | *Agapostemon texanus* | generalist[16] | | solitary[18] | 12 | 17 | 1692 | 112 |
| | *Augochlorella* | *Augochlorella* | *Augochlorella pomoniella* | generalist[19] | below ground[20] | eusocial[21] | 1 | 2 | 22 | 3 |
| | *Conanthalictus* | *Phaceliapis* | *Conanthalictus cockerelli* | specialist[2] | below ground[22] | solitary[23] | 0 | 0 | 0 | 1 |
| | *Dieunomia* | *Epinomia* | *Dieunomia nevadensis* | generalist[24] | below ground[24] | solitary[24] | 1 | 1 | 0 | 0 |
| | *Dufourea* | [NA] | *Dufourea* sp. 2 | specialist[25] | below ground[23] | solitary[23] | 1 | 0 | 8 | 2 |
| | | | *Dufourea trochantera* | | | | 0 | 1 | 308 | 39 |
| | *Halictus* | *Nealictus* | *Halictus farinosus* | generalist[26] | below ground[26] | eusocial[27] | 0 | 0 | 36 | 3 |
| | | *Odontalictus* | *Halictus ligatus* | generalist[28] | below ground[28] | eusocial[28] | 40 | 15 | 40 | 2 |
| | | *Seladonia* | *Halictus tripartitus* | generalist[29] | below ground[30] | eusocial[30] | 9 | 0 | 198 | 0 |
| | *Lasioglossum* | *Dialictus* | *Lasioglossum* sp. dia1 | generalist[2] | below ground[2] | eusocial[2] | 1 | 0 | 0 | 0 |
| | | | *Lasioglossum* sp. dia10 | | | | 1 | 0 | 0 | 0 |
| | | | *Lasioglossum* sp. dia11 | | | | 1 | 0 | 0 | 0 |
| | | | *Lasioglossum* sp. dia12 | | | | 1 | 0 | 0 | 0 |
| | | | *Lasioglossum* sp. dia2 | | | | 11 | 0 | 0 | 0 |
| | | | *Lasioglossum* sp. dia3 | | | | 0 | 4 | 0 | 0 |
| | | | *Lasioglossum* sp. dia4 | | | | 4 | 0 | 0 | 0 |
| | | | *Lasioglossum* sp. dia5 | | | | 1 | 0 | 0 | 0 |
| | | | *Lasioglossum* sp. dia6 | | | | 1 | 0 | 0 | 0 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Lasioglossum* sp. dia7 | | | | 2 | 1 | 0 | 0 |
| | | | *Lasioglossum* sp. dia8 | | | | 5 | 1 | 0 | 0 |
| | | | *Lasioglossum* sp. dia9 | | | | 1 | 0 | 0 | 0 |
| | | | *Lasioglossum* sp. diaA | | | | 0 | 8 | 0 | 0 |
| | | | *Lasioglossum* sp. diaD | | | | 0 | 1 | 0 | 0 |
| | | | *Lasioglossum* sp. diaE | | | | 0 | 1 | 0 | 0 |
| | | | *Lasioglossum* sp. disA | | | | 0 | 0 | 980 | 10 |
| | | | *Lasioglossum* sp. disB | | | | 0 | 0 | 66 | 0 |
| | | | *Lasioglossum* sp. disD | | | | 0 | 0 | 5 | 0 |
| | | | *Lasioglossum* sp. disE | | | | 0 | 0 | 333 | 0 |
| | | *Evylaeus* | *Lasioglossum* sp. EV01 | generalist[2] | below ground[2] | eusocial[2] | 0 | 0 | 208 | 3 |
| | | | *Lasioglossum* sp. EV02 | | | | 5 | 0 | 19 | 0 |
| | | | *Lasioglossum* sp. EV03 | | | | 1 | 0 | 42 | 1 |
| | | | *Lasioglossum* sp. EV04 | | | | 0 | 0 | 3 | 0 |
| | | | *Lasioglossum* sp. EV05 | | | | 0 | 0 | 1 | 0 |
| | | | *Lasioglossum* sp. EV06 | | | | 1 | 0 | 3 | 0 |
| | | | *Lasioglossum* sp. EV07 | | | | 0 | 0 | 2 | 0 |
| | | *Lasioglossum* | *Lasioglossum* sp. LA02 | generalist[2] | below ground[2] | eusocial[2] | 0 | 0 | 3 | 0 |
| | | | *Lasioglossum sisymbrii* | generalist[31] | below ground[32] | solitary[33] | 4 | 0 | 49 | 0 |
| | *Micralictoides* | [NA] | *Micralictoides ruficaudus* | specialist[34] | below ground[35] | solitary[35] | 4 | 1 | 4 | 1 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Sphecodes* | [NA] | *Sphecodes* sp. A | cleptoparasitic[2] | cleptoparasitic[2] | cleptoparasitic[2] | 1 | 1 | 0 | 1 |
| Megachilidae | *Anthidium* | *Anthidium* | *Anthidium placitum* | specialist[36] | below ground[36] | solitary[36] | 0 | 0 | 1 | 0 |
| | *Ashmeadiella* | *Ashmeadiella* | *Ashmeadiella bucconis* | generalist[37] | cavity[37] | solitary[6] | 9 | 2 | 0 | 0 |
| | | *Ashmeadiella* | *Ashmeadiella cubiceps* | generalist[3] | | | 1 | 0 | 0 | 0 |
| | | *Ashmeadiella* | *Ashmeadiella difugita* | generalist[3] | | | 2 | 0 | 0 | 0 |
| | | *Ashmeadiella* | *Ashmeadiella meliloti* | generalist[3] | | | 1 | 0 | 0 | 0 |
| | | *Ashmeadiella* | *Ashmeadiella* sp. 1 | generalist[3] | | | 0 | 0 | 0 | 1 |
| | | *Cubitognatha* | *Ashmeadiella salviae* | specialist[37] | | | 2 | 0 | 0 | 0 |
| | *Atoposmia* | *Eremosmia* | *Atoposmia* sp. A | specialist[3] | cavity[3] | solitary[6] | 0 | 0 | 1 | 0 |
| | *Dianthidium* | *Dianthidium* | *Dianthidium parvum* | generalist[3] | cavity[3] | solitary[6] | 0 | 0 | 1 | 0 |
| | | *Dianthidium* | *Dianthidium pudicum* | generalist[3] | cavity[3] | | 1 | 0 | 1 | 0 |
| | *Hoplitis* | [unk] | *Hoplitis* sp. 1 | generalist[3] | cavity[2] | solitary[6] | 0 | 0 | 1 | 0 |
| | | [unk] | *Hoplitis* sp. 2 | | | | 0 | 0 | 4 | 2 |
| | *Megachile* | *Litomegachile* | *Megachile brevis* | generalist[38] | cavity[38] | solitary[38] | 1 | 0 | 0 | 0 |
| | | *Sayapis* | *Megachile inimca* | generalist[3] | cavity[2] | solitary[2] | 2 | 0 | 0 | 0 |
| | | [unk] | *Megachile* sp. 2 | generalist[3] | cavity[2] | solitary[2] | 0 | 1 | 0 | 0 |
| | | [unk] | *Megachile* sp. 3a | | | | 0 | 1 | 0 | 0 |
| | | [unk] | *Megachile* sp. 3b | | | | 0 | 1 | 0 | 0 |
| | | [unk] | *Megachile* sp. 4 | | | | 0 | 0 | 0 | 1 |
| | | [unk] | *Megachile* sp. 5 | | | | 0 | 0 | 0 | 1 |
| | | [unk] | *Megachile* sp. D | | | | 1 | 0 | 0 | 0 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | [unk] | *Megachile* sp. E | | | | 1 | 0 | 2 | 0 |
| | | [unk] | *Megachile* sp. F | | | | 1 | 0 | 0 | 0 |
| | | [unk] | *Megachile* sp. G | | | | 0 | 0 | 2 | 0 |
| | | [unk] | *Megachile* sp. H | | | | 0 | 0 | 3 | 0 |
| | | [unk] | *Megachile* sp. I | | | | 0 | 0 | 1 | 0 |
| | | [unk] | *Megachile* sp. J | | | | 0 | 0 | 1 | 0 |
| | | [unk] | *Megachile* sp. X | | | | 1 | 4 | 0 | 0 |
| | *Osmia* | [unk] | *Osmia* sp. 1 | generalist[3] | cavity[2] | solitary[2] | 0 | 1 | 0 | 0 |
| | | [unk] | *Osmia* sp. A | | | | 3 | 0 | 0 | 0 |
| | | [unk] | *Osmia* sp. C | | | | 1 | 0 | 0 | 0 |
| | | [unk] | *Osmia* sp. D | | | | 1 | 0 | 0 | 0 |
| | | [unk] | *Osmia* sp. E | | | | 1 | 0 | 0 | 0 |
| | | [unk] | *Osmia* sp. F | | | | 2 | 0 | 0 | 0 |
| | | [unk] | *Osmia* sp. G | | | | 0 | 0 | 2 | 0 |
| | | [unk] | *Osmia* sp. H | | | | 0 | 0 | 1 | 0 |

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**Table B.6.** List of flowering plant species off which bees were collected, organized by their native status ($N = 375$ bees). Shown are the numbers of bees collected off each plant species at native and at conventional plant nurseries, respectively (note that a "0" does *not* necessarily imply that plant species was present at that type of nursery).

| **plant species name** | **California native status** | **native nurseries** | **conventional nurseries** |
|---|---|---|---|
| *Salvia clevelandii* | native | 5 | 25 |
| *Encelia californica* | native | 12 | 8 |
| *Baileya multiradiata* | native | 14 | 0 |
| *Erigeron glaucus* | native | 10 | 3 |
| *Eschscholzia californica* | native | 13 | 0 |
| *Abutilon palmeri* | native | 10 | 1 |
| *Eriophyllum confertiflorum* | native | 2 | 7 |
| *Salvia mellifera* | native | 8 | 1 |
| *Ceanothus* sp. | native | 8 | 0 |
| *Grindelia camporum* | native | 8 | 0 |
| *Penstemon heterophyllus* | native | 1 | 6 |
| *Baccharis pilularis* | native | 0 | 6 |
| *Corethrogyne filaginifolia* | native | 5 | 1 |
| *Dendromecon harfordii* | native | 6 | 0 |
| *Eriogonum fasciculatum* | native | 3 | 3 |
| *Penstemon spectabilis* | native | 4 | 2 |
| *Trichostema lanatum* | native | 6 | 0 |
| *Malosma laurina* | native | 5 | 0 |
| *Sphaeralcea ambigua* | native | 5 | 0 |
| *Baccharis salicifolia* | native | 3 | 1 |
| *Rosa californica* | native | 3 | 1 |
| *Encelia farinosa* | native | 0 | 3 |
| *Epilobium canum* | native | 3 | 0 |
| *Eriogonum parvifolium* | native | 3 | 0 |
| *Fallugia paradoxa* | native | 3 | 0 |
| *Helianthus annuus* | native | 3 | 0 |
| *Isocoma menziesii* | native | 1 | 2 |
| *Achillea millefolium* | native | 0 | 2 |
| *Astragalus trichopodus* | native | 2 | 0 |
| *Chilopsis linearis* | native | 0 | 2 |
| *Clarkia unguiculata* | native | 2 | 0 |
| *Frangula californica* | native | 0 | 2 |
| *Grindelia stricta* | native | 2 | 0 |
| *Phyla nodiflora* | native | 0 | 2 |
| *Sidalcea malviflora* | native | 2 | 0 |
| *Tetraneuris acaulis* | native | 2 | 0 |
| *Bahiopsis laciniata* | native | 1 | 0 |
| *Calystegia macrostegia* | native | 1 | 0 |
| *Dichelostemma capitatum* | native | 1 | 0 |
| *Eriogonum grande* | native | 1 | 0 |
| *Helianthus californicus* | native | 1 | 0 |
| *Malacothamnus clementinus* | native | 1 | 0 |

| | | | |
|---|---|---|---|
| *Malacothamnus fasciculatus* | native | 1 | 0 |
| *Monardella odoratissima* | native | 1 | 0 |
| *Monardella villosa* | native | 1 | 0 |
| *Romneya coulteri* | native | 0 | 1 |
| *Salvia leucophylla* | native | 0 | 1 |
| *Salvia pachyphylla* | native | 0 | 1 |
| *Sambucus mexicana* | native | 0 | 1 |
| *Salvia greggii* | non-native | 0 | 9 |
| *Gaillardia grandiflora* | non-native | 0 | 8 |
| *Lagerstroemia indica* | non-native | 0 | 8 |
| *Eremophila hygrophana* | non-native | 0 | 6 |
| *Salvia chamaedryoides* | non-native | 0 | 6 |
| *Caryopteris clandonensis* | non-native | 0 | 5 |
| *Melampodium leucanthum* | non-native | 1 | 4 |
| *Vitex agnus-castus* | non-native | 0 | 5 |
| *Bulbine frutescens* | non-native | 0 | 4 |
| *Ligustrum lucidum* | non-native | 0 | 4 |
| *Oenothera cf. biennis* | non-native | 0 | 4 |
| *Rosmarinus officinalis* | non-native | 0 | 4 |
| *Berlandiera lyrata* | non-native | 3 | 0 |
| *Cistus salviifolius* | non-native | 0 | 3 |
| *Lamium amplexicaule* | non-native | 3 | 0 |
| *Oenothera speciosa* | non-native | 0 | 3 |
| *Pelargonium sidoides* | non-native | 0 | 3 |
| *Salvia microphylla* | non-native | 1 | 2 |
| *Salvia uliginosa* | non-native | 0 | 3 |
| *Tecoma capensis* | non-native | 0 | 3 |
| *Verbesina encelioides* | non-native | 0 | 3 |
| *Calandrinia spectabilis* | non-native | 0 | 2 |
| *Coreopsis grandiflora* | non-native | 0 | 2 |
| *Duranta erecta* | non-native | 0 | 2 |
| *Lavandula dentata* | non-native | 0 | 2 |
| *Lavandula stoechas* | non-native | 0 | 2 |
| *Leptospermum scoparium* | non-native | 0 | 2 |
| *Leucophyllum frutescens* | non-native | 0 | 2 |
| *Perovskia atriplicifolia* | non-native | 0 | 2 |
| *Ageratina adenophora* | non-native | 0 | 1 |
| *Buddleja davidii* | non-native | 0 | 1 |
| *Callistemon viminalis* | non-native | 0 | 1 |
| *Ceratostigma plumbaginoides* | non-native | 0 | 1 |
| *Cercidium* sp. | non-native | 0 | 1 |
| *Cistus purpureus* | non-native | 0 | 1 |
| *Convolvulus sabatius* | non-native | 0 | 1 |
| *Cosmos bipinnatus* | non-native | 0 | 1 |
| *Felicia amelloides* | non-native | 0 | 1 |
| *Gaura lindheimeri* | non-native | 0 | 1 |
| Gnaphalieae sp. | non-native | 0 | 1 |
| *Lavandula ginginsii* | non-native | 0 | 1 |
| *Monarda* sp. | non-native | 0 | 1 |
| *Nerium oleander* | non-native | 0 | 1 |

|  |  |  |  |
|---|---|---|---|
| *Pallenis maritima* | non-native | 0 | 1 |
| *Penstemon* cf. *cobaea* | non-native | 0 | 1 |
| *Sagina subulata* | non-native | 0 | 1 |
| *Salvia farinacea* | non-native | 0 | 1 |
| *Vitex trifolia* | non-native | 0 | 1 |

**Figure B.1.** View of a sampling plot with blue vane trap deployed at a conventional plant nursery in Riverside County, California, on 21 June 2016.

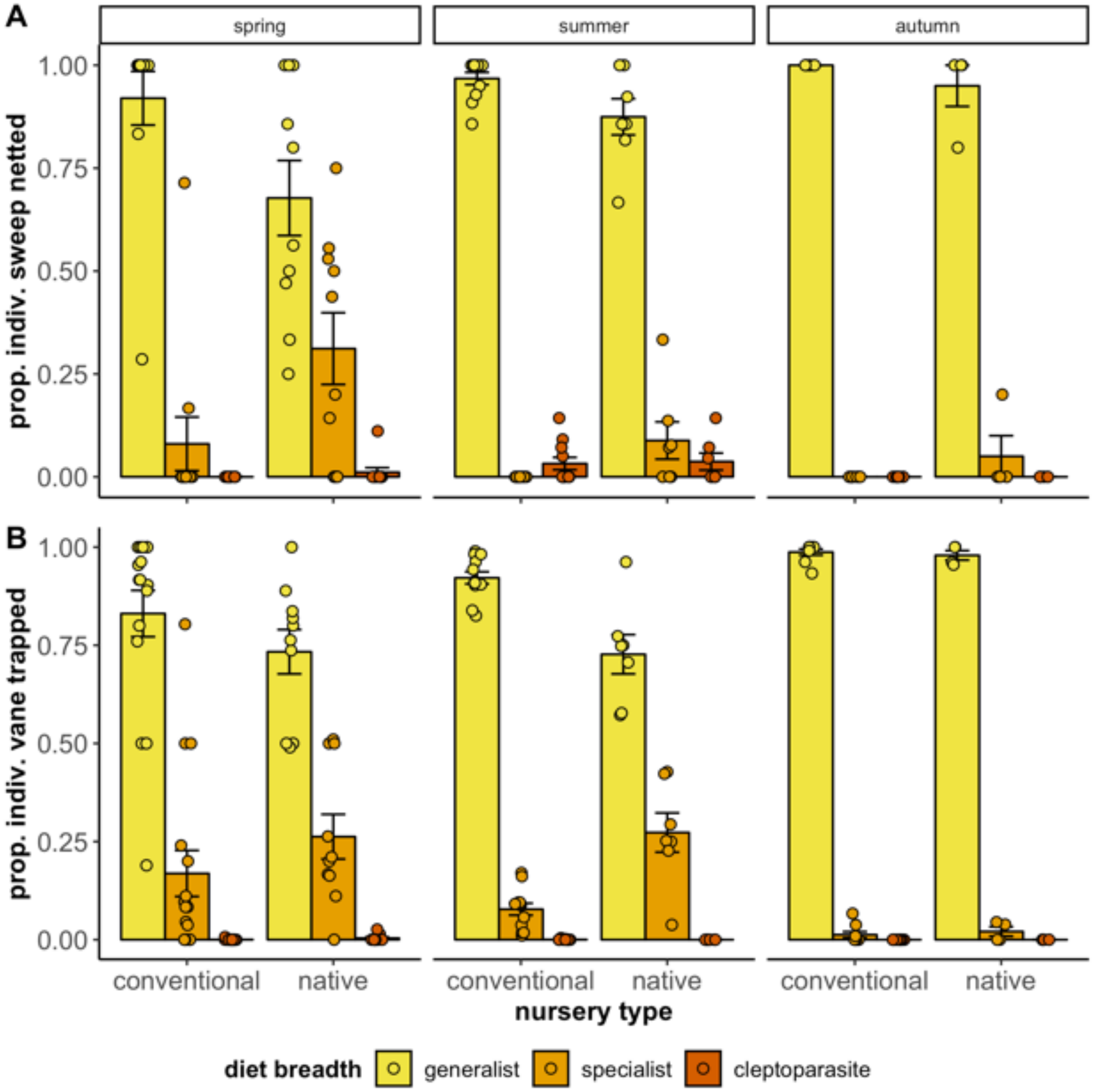


**Figure B.2.** Diet breadth of bee individuals collected by (A) sweep netting and (B) vane trapping. Proportions represent the fraction of individual bees detected a given sampling that fall into each of three functional categories—generalist, specialist, or cleptoparasite—out of all individuals collected in that given sampling. Bars and whiskers represent mean±SE. Samplings are arranged by season and type of nursery. For sweep netting (A), the two-way interaction between diet breadth and nursery type was statistically significant. For vane trapping (B), the three-way interaction between diet breadth, season, and nursery type was statistically significant (Table S4).

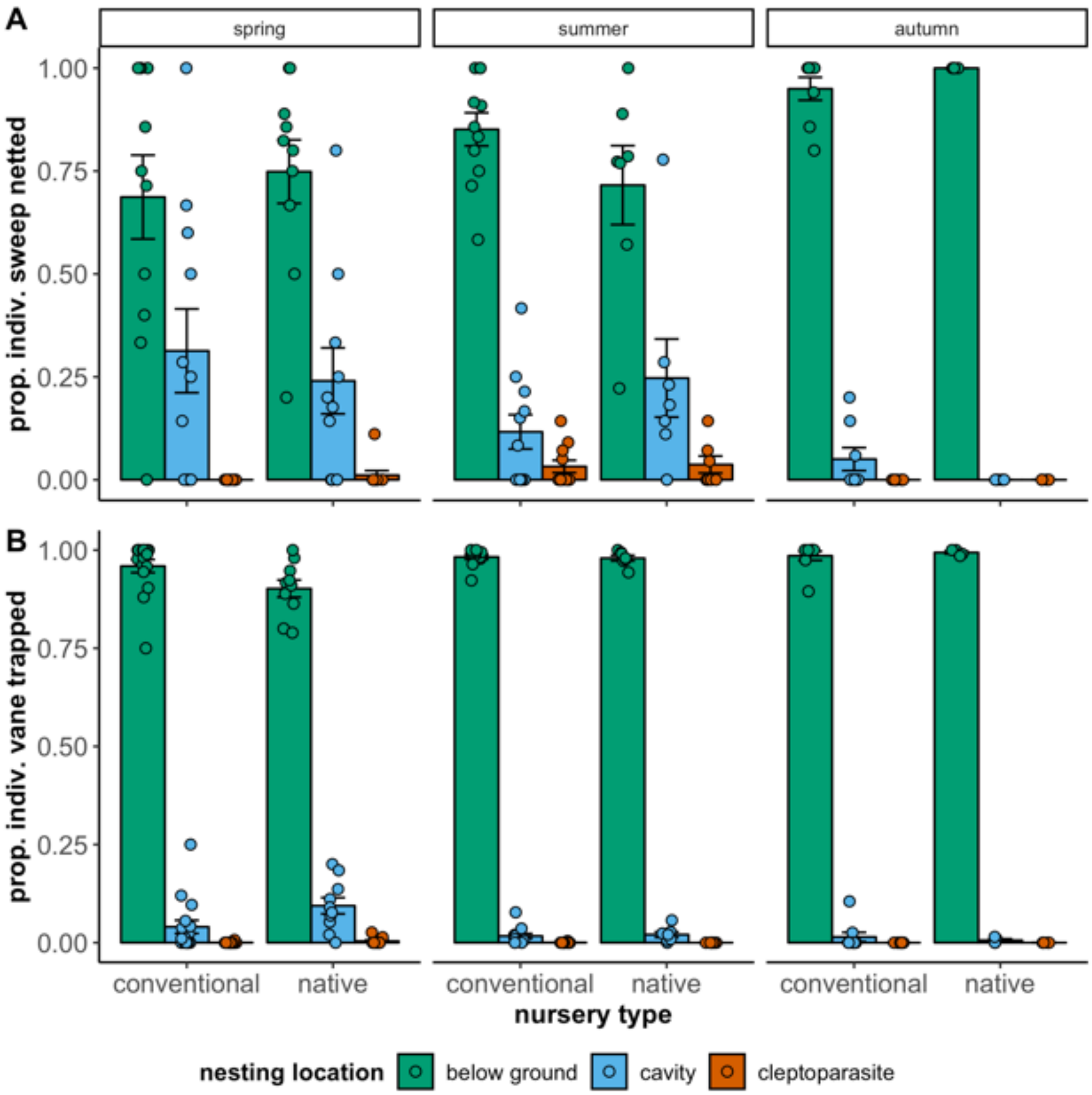


**Figure B.3.** Nesting location of bee individuals collected by (A) sweep netting and (B) vane trapping. Proportions represent the fraction of individual bees detected a given sampling that fall into each of three functional categories— below ground, cavity, or cleptoparasite—out of all individuals collected in that given sampling. Bars and whiskers represent mean±SE. Samplings are arranged by season and type of nursery. For sweep netting (A), the two-way interaction between nesting location and season was statistically significant. For vane trapping (B), the three-way interaction between diet breadth, season, and nursery type was statistically significant (Table S4).

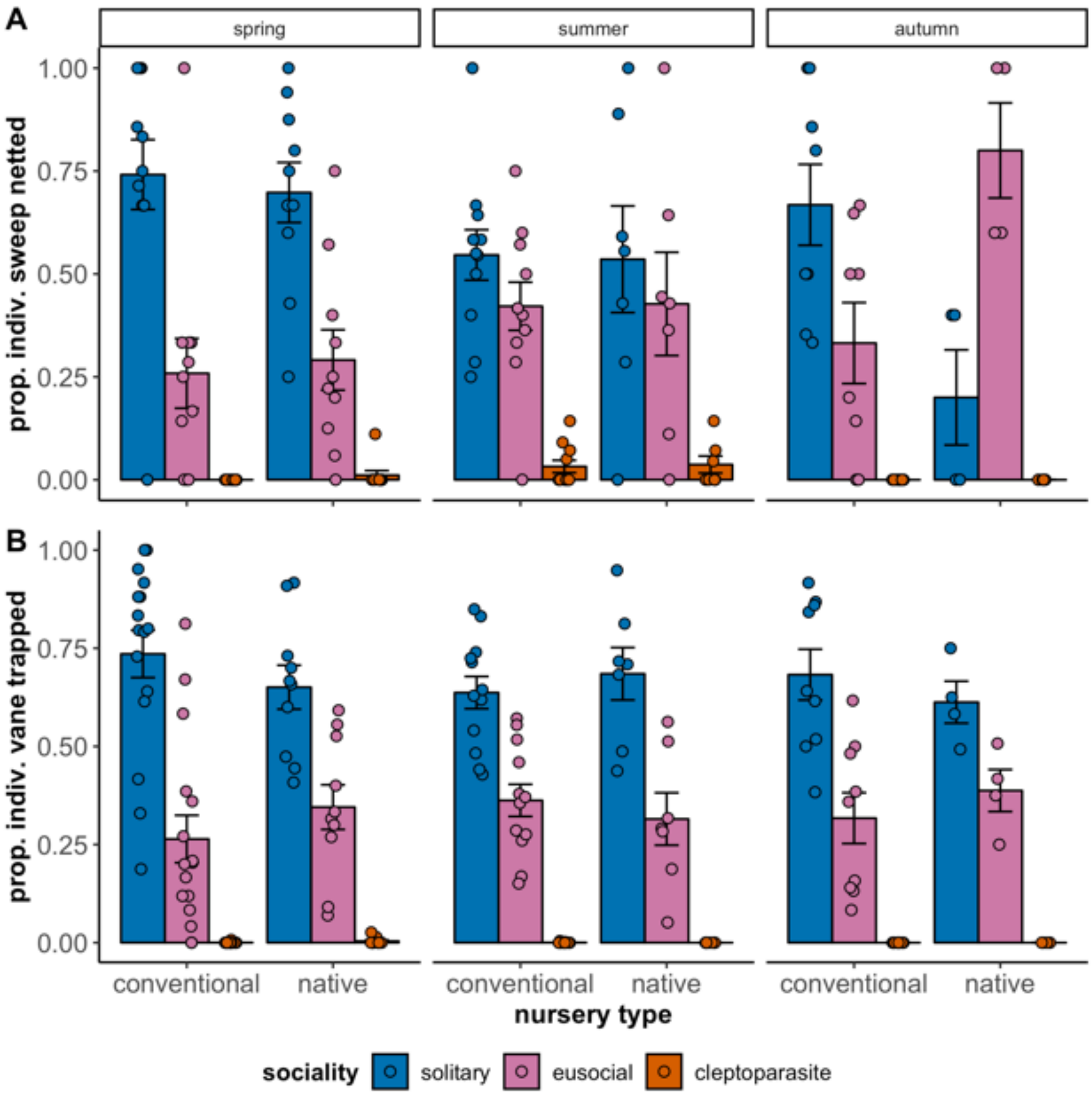


**Figure B.4.** Social organization of bee individuals collected by (A) sweep netting and (B) vane trapping. Proportions represent the fraction of individual bees detected a given sampling that fall into each of three functional categories— solitary, eusocial, or cleptoparasite —out of all individuals collected in that given sampling. Bars and whiskers represent mean±SE. Samplings are arranged by season and type of nursery. For sweep netting (A), the two-way interaction between sociality and season was statistically significant. For vane trapping (B), the three-way interaction between diet breadth, season, and nursery type was statistically significant (Table S4).

# APPENDIX C

## Detailed Methods and Statistical Analyses

We conducted mark-release-recapture experiments between 25 July – 16 August (summer) and 10 October – 9 November (autumn) 2018 at five commercial plant nurseries in southern California, USA ranging in area from 3 to 7 hectares. Each nursery was surrounded by varying degrees of suburban and natural landscapes. Experiments were conducted on sunny, clear days, with daily high temperatures ranging from 21 to 37 °C. The experiment was replicated eight times across the five nurseries: of the five, three were sampled in both seasons, one only in summer, and one only in autumn. Each mark-recapture experiment occurred over two consecutive days. On the first day, between 11:00 and 14:00, we searched for males and females of the primitively eusocial halictid bee *Halictus ligatus* Say on patches of blooming plants over areas up to 2 ha. The size, spatial configuration, and floral density of patches varied greatly across nurseries and seasons, but consisted of discrete blocks of containers of a single species of plant. If *H. ligatus* was not abundant enough, we focused on the few most abundant species of medium- to large-sized non-*Apis* bees.

Foraging bees were hand netted off flowers, transferred to a modified honey bee queen marking plunger cage (Brushy Mountain Bee Farm, Moravian Falls, NC) and marked on the thorax using non-toxic paint pens (Mitsubishi Pencil Co. Ltd., Tokyo, Japan). The color of the mark indicated the species of plant off which the bee was captured. For each bee, we recorded its sex, species, associated plant species, and mark color. After marking, each bee was released in the immediate vicinity of capture. We continued marking bees in a patch until two or more marked individuals were spotted within 30 seconds of one another, then we moved to another patch. On the following day, we hand netted bees in same patches where we marked bees the previous day, as well as in adjacent patches. All individuals, marked and unmarked, were collected and retained in tubes until the end of the period, to ensure an individual was not recaptured twice. Again, for each captured bee, we recorded its sex, species, associated plant, and presence and color of marking.

Statistical analysis: All analyses were conducted in R 3.3.3 (R Core Team 2019). In the package *lme4* (Bates et al. 2015), we used a generalized linear mixed model with a binomial error structure to determine which factors influenced our dependent variable—whether each marked bee was recaptured or not. In the model, each replicate (marked bee) was weighted according to the number of individuals marked by bee species, bee sex, and mark color at each nursery and season, to ensure recapture rates calculated from larger numbers of individuals had a larger influence in the analysis. We checked predictor variables for collinearity (variance inflation factor >2) using the function 'vif' in the *car* package (Fox and Weisberg 2011), and used function 'dredge' in the package *MuMIn* (Barton 2018) to select the optimal model on the basis of Akaike information criterion (AICc) values ($\Delta$AICc>2 indicating statistical significance). We included the species of plant off which a bee was captured and the nursery as random factors. We used function 'Anova' (*car* package) to determine the statistical significance of independent variables in our optimal model using type III sums of squares, and function 'emmeans' in the *emmeans* package (Lenth 2019) for all post-hoc comparisons. The residuals from our generalized linear mixed model were checked graphically using function ‘binnedplot’ in the *arm* package (Gelman and Su 2019). We used the *ggplot2* package (Wickham 2016) to create figures.

**Table C.1.** Mark-recapture studies with wild bees where individuals were marked and recaptured while foraging on flowers. Excluded are studies: (1) examining fidelity of bees to nests or male aggregation sites (Alcock 1993, Bischoff 2003); (2) estimating foraging distances (Zurbuchen et al. 2010); (3) that experimentally manipulated floral rewards (Cartar 2004); and (4) that did not explicitly report proportions of marked bees that were reobserved (Heinrich 1976). It should be noted that experimental designs varied considerably among studies (particularly the spatial layout, observer-hours, and temporal frequency of resampling for marked individuals), which somewhat hinders their direct comparison.

| type of bee | species | bees marked | % reobserved | sites | total study area (ha) | study duration (days) | plant sp. associations tracked | seasons | years | location | habitat | study |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bombus* spp. | *pratorum, jonellus, pascuorum* | 144 | 53.6 to 60 | 1 | unclear; plots < 330 m long | 7 | yes; 3 spp. | 1 | 2 | Netherlands | natural (meadows) | Kwak et al. 1991 |
| | 7; mostly *lucorum, pascuorum, pratorum* | 182 | 80 | 2 | 0.4875 | 7 | unclear | 1 | 1 | Norway | agricultural (farmland) | Saville et al. 1997 |
| | *hortorum, ruderatus, pascuorum* | 35 | 77 | 1 | 0.08 | 11 | yes; mostly 1 sp. | 1 | 1 | Italy | natural (national park) | Comba 1999 |
| | *lapidarius* | 1104 | 22 to 28 | 1 | 2.34 | ~7 | unclear; mostly 1 sp. | 1 | 2 | United Kingdom | natural-agricultural matrix | Osborne and Williams 2001 |
| | *impatiens, affinis*; included *Xylocopa* spp. | 367 | 31 | 1 | 0.1852 | subsequent days | yes; 2 spp. | 1 | 3 | USA: Massachusetts | conservation area | Bhattacharya et al. 2003 |
| | 10; mostly *lucorum, terrestris, pascuorum* | 901 | 12 to 14 | 11 | unclear | 5-10 hours after marking and following days | yes; 33 spp. | 1 | 1 | Poland | natural (alder and beech forests) | Pawlikowski et al. 2007 |
| | *impatiens* | 229 | 45 | 6 | ~0.546 | 2 to 3 | none | 1 | 1 | USA: New York | urban (community gardens) | Matteson and Langellotto 2009 |
| | 6; mostly *bifarius, moderatus, flavifrons* | 2439 | 5.7 | 1 | unclear; within an 1100-ha area | subsequent days | yes; 12 spp. | 1 | 2 | Canada | natural (subalpine forest) | Foster and Cartar 2011 |

## Table C.1 (continued)

| type of bee | species | bees marked | % reobserved | sites | total study area (ha) | study duration (days) | plant sp. associations tracked | seasons | years | location | habitat | study |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| non-*Bombus* apids | 70; mostly unspecified apids and megachilids | 1605 | < 35 | 1 | unclear; transect-based | 2 | yes; mostly on 1 sp. | 1 | 1 | Costa Rica | natural (lowland dry forest) | Frankie et al. 1976 |
| | *Exaerate smaragdina* | 7 | 57 | 1 | not stated | 13 | yes; 2 spp. | 1 | 1 | Panama | natural (tropical forest) | Ackerman et al. 1982 |
| | *Euglossa imperalis* | 15 | 40 | | | | | | | | | |
| | *Euglossa cordata* | 649 | 33 | 12 | 12 sites of unspecified size | 121 to 212 | yes; 1 sp. | 2 | 2 | Brazil | urban (street sidewalks) | Lopez-Uribe et al. 2008 |
| | *Eulaema nigrita* | 221 | 25 | | | | | | | | | |
| | mostly *Eucera, Anthophora* | ~1460 | 36 | 2 | 3.96 | recorded simultaneously | yes | 1 | 1 | Israel | natural-agricultural matrix | Dorchin et al. 2013 |
| | *Xylocopa frontalis* | 241 | 28.6 | 1 | 0.5 | 4 to 6 | no | 1 | 3 | Brazil | agricultural (orchard) | Yamamoto et al. 2014 |
| | *Xylocopa suspecta* | 252 | 9.9 | | | | | | | | | |
| | *Xylcopa grisescens* | 25 | 28 | | | | | | | | | |
| | *Xylocopa hirsutissima* | 4 | 25 | | | | | | | | | |
| non-apid bees | *Anthidium porterae* males | 54 | 70 | 1 | 0.105 | ~30 | no | 1 | 1 | USA: Arizona | natural (desert grassland) | Villalobos and Shelly 1991 |
| | *Anthidium palliventre* males | 38 | 58 | | | | | | | | | |
| | *Colletes cunicularius* males | 577 | 17 | 1 | 0.08 | subsequent days | unclear; focused on 1 sp. | 1 | 1 | Switzerland | natural (hilltop) | Peakall and Schiestl 2004 |
| | *Andrena hattorfiana* females | 841 | 75.3 | 10 | unclear; transect-based | 37 | yes; 1 sp. | 1 | 3 | Sweden | natural-agricultural matrix | Larsson and Franzén 2008 |
| | *Andrena hattorfiana* females | 720 | 37.5 | 2 | unclear; transect-based | ~30 | yes; 1 sp. | 1 | 3 | Sweden | natural-agricultural matrix | Franzén et al. 2009 |
| | 12; mostly *Halictus ligatus, Agapostemon texanus* | 205 | 51 | 5 | 21.88 | 2 | yes; 18 spp. | 2 | 1 | USA: California | agricultural (plant nursery) | this study |

**Table C.2.** The 12 native bee taxa captured and marked in this study.

| **bee taxon** | **bee family** | **bee social organization** | **number of bees recaptured / number of bees marked** | **% bees recaptured** |
|---|---|---|---|---|
| *Halictus ligatus* | Halictidae | primitively eusocial | 73/137 | 53.3 |
| *Agapostemon texanus* | Halictidae | solitary | 11/29 | 37.9 |
| *Anthophora urbana* | Apidae | solitary | 5/12 | 41.7 |
| *Ashmeadiella* spp. | Megachilidae | solitary | 10/12 | 83.3 |
| *Anthophora curta* | Apidae | solitary | 3/3 | 100 |
| *Megachile* spp. | Megachilidae | solitary | 2/3 | 66.7 |
| *Ceratina* spp. | Apidae | mostly solitary | 1/2 | 50 |
| *Melissodes* spp. | Apidae | solitary | 1/2 | 50 |
| *Xylocopa varipuncta* | Apidae | solitary | 0/2 | 0 |
| *Agapostemon melliventris* | Halictidae | solitary | 0/1 | 0 |
| *Anthidium* sp. | Megachilidae | solitary | 0/1 | 0 |
| *Xylocopa californica* | Apidae | solitary | 0/1 | 0 |
| **Total** | | | **106/205** | **51.7** |
| **Total, excluding bee taxa with n<10** | | | **99/190** | **52.1** |

**Table C.3.** The 18 plant species off which bees were captured and marked in this study. Not all plant species were present at all nurseries.

| **plant species** | **plant family** | **California native status** | **number of bees recaptured / number of bees marked** | **% bees recaptured** |
|---|---|---|---|---|
| *Encelia californica* | Asteraceae | native | 25/44 | 56.8 |
| *Achillea millefolium* | Asteraceae | native | 16/34 | 47.1 |
| *Erigeron glaucus* | Asteraceae | native | 15/27 | 55.6 |
| *Grindelia camporum* | Asteraceae | native | 14/20 | 70.0 |
| *Chrysactinia mexicana* | Asteraceae | non-native (SW U.S., Mexico) | 6/19 | 31.6 |
| *Tetraneuris acaulis* | Asteraceae | native | 8/14 | 57.1 |
| *Salvia chamaedryoides* | Lamiaceae | non-native (Mexico) | 6/13 | 46.2 |
| *Melampodium leucanthum* | Asteraceae | non-native (SW U.S.) | 4/9 | 44.4 |
| *Corethrogyne filaginifolia* | Asteraceae | native | 5/6 | 83.3 |
| *Helianthus annuus* | Asteraceae | native | 1/6 | 16.6 |
| *Solidago californica* | Asteraceae | native | 2/3 | 66.7 |
| *Bahiopsis lacinata* | Asteraceae | native | 1/2 | 50 |
| *Chilopsis linearis* | Bignoniaceae | native | 0/2 | 0 |
| *Isocoma menziesii* | Asteraceae | native | 2/2 | 100 |
| *Baileya multiradiata* | Asteraceae | native | 1/1 | 100 |
| *Melilotus indica* | Fabaceae | non-native (Old World) | 0/1 | 0 |
| *Trichostema lanatum* | Lamiaceae | native | 0/1 | 0 |
| *Bahiopsis parishii* | Asteraceae | native | 0/1 | 0 |
| **Total** | | | **106/205** | **51.7** |
| **Total, excluding plant taxa with n<10** | | | **90/171** | **52.6** |

**Table C.4.** ANOVA table for optimal binomial generalized linear mixed model ($R^2$=0.498, model weight=0.420, ΔAICc=2.04).

| **Term** | **df** | **Wald $\chi^2$** | ***P*** |
|---|---|---|---|
| bee genus | 8 | 9.03 | 0.34 |
| season | 1 | 22.93 | <0.0001 |
| plant native status | 1 | 16.09 | <0.0001 |
| plant native status x season | 1 | 12.23 | 0.00047 |
| error | 193 | | |
| total | 204 | | |

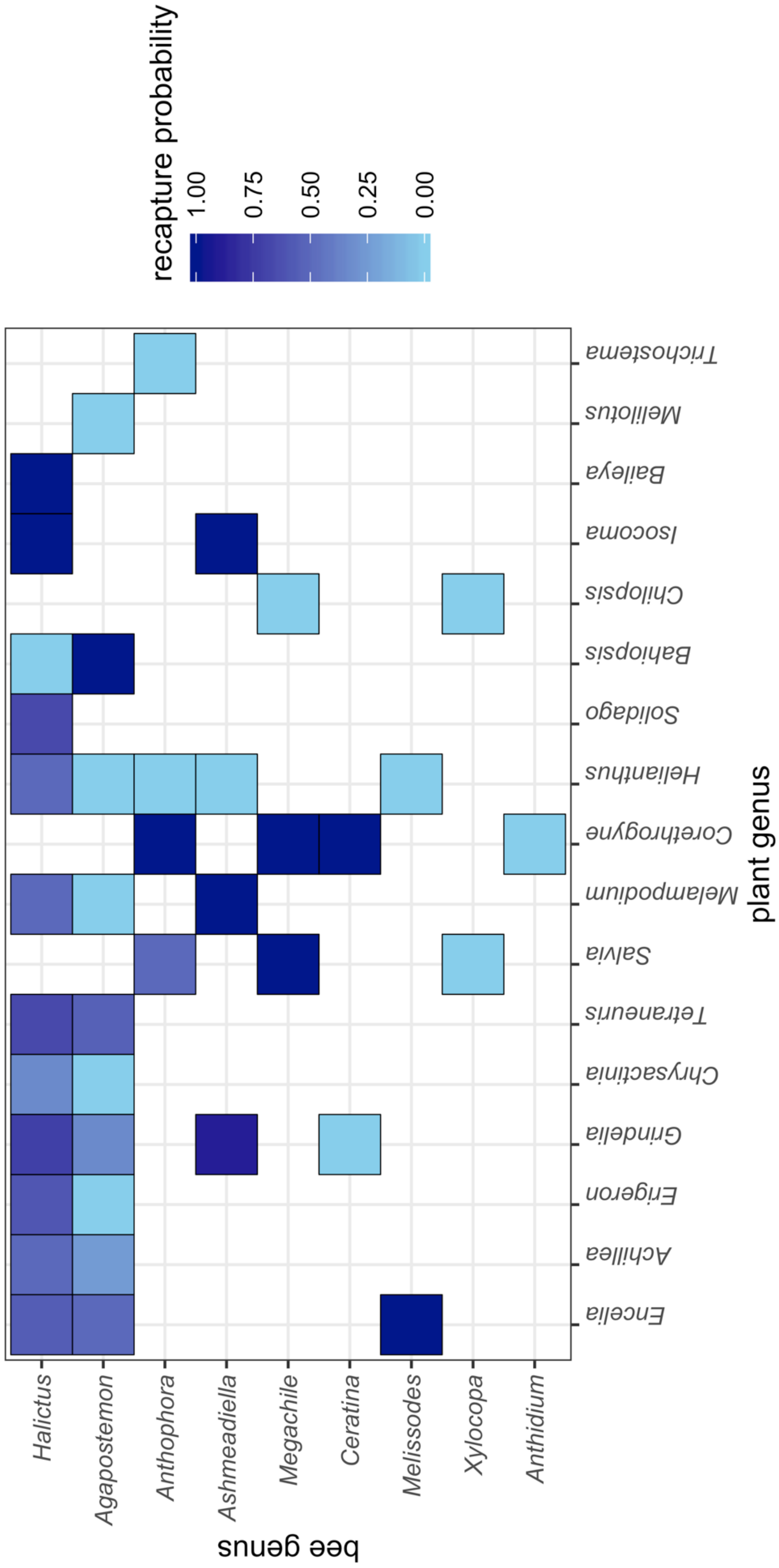
**Table C.5.** Temporal differences in site-specific electivities ($E_{ij}$) by marked bees (N=205) for the different plant species in this study. Electivity (Jacobs 1974) describes foraging organisms' preferences for or against different types of resources (here, species of plants) while controlling for underlying differences in the availabilities (here, patch area) of these resources in the environment. A positive index implies more bees were marked on that plant species than expected given the area of the patch of that plant species. A negative index implies fewer bees were marked. Electivity is calculated using six variables, which we directly adapted to our dataset from Jenkins (1979) as outlined in Table S6. Significance of each index is tested against a chi-squared distribution (df=1). No asterisk: $P>0.05$; *: $0.05<P<0.01$; **: $0.01<P<0.001$; ***: $P<0.001$. Each number represents an index from one site in one season.

| **California native status** | **plant species** | **electivity index, $E_{ij}$** | |
|---|---|---|---|
| | | **summer** | **autumn** |
| native | *Encelia californica* | +0.02 | +1.04<br>+0.14 |
| | *Achillea millefolium* | -2.59***<br>-0.35 | -0.77 |
| | *Erigeron glaucus* | +2.59*** | |
| | *Grindelia camporum* | +1.20**<br>+1.06* | -0.98 |
| | *Tetraneuris acaulis* | | +0.77 |
| | *Corethrogyne filaginifolia* | +0.67 | |
| | *Helianthus annuus* | +1.21<br>+0.49 | |
| | *Solidago californica* | -0.50 | -1.02 |
| | *Bahiopsis lacinata* | -0.35 | |
| | *Chilopsis linearis* | -1.95* | |
| | *Isocoma menziesii* | -0.71 | |
| | *Baileya multiradiata* | -2.02 | |
| | *Trichostema lanatum* | | +0.09 |
| | *Bahiopsis parishii* | -1.50 | |
| non-native | *Chrysactinia mexicana* | +0.50 | -0.36 |
| | *Salvia chamaedryoides* | | +0.62 |
| | *Melampodium leucanthum* | +0.47 | |
| | *Melilotus indica* | | +1.16 |

**Table C.6.** Description of variables used by Jenkins (1979) to test electivity ($E_{ij}$) of beavers (*Castor canadensis*) for different genera of trees, and the corresponding variables used in this study.

| variable | Jenkins 1979 | This study |
|---|---|---|
| $r_{ij}$ | the **proportion** of trees cut at time *j* which belonged to genus *i* | the **proportion** of bees collected in season *j* visiting plant species *i* |
| $p_{ij}$ | the **proportion** of trees available at time *j* which belonged to genus *i* | the **proportion** of area occupied by bee-attractive flowering plants in season *j* which belonged to species *i* |
| $x_{ij}$ | **number** of trees of genus *i* cut at time *j* | **number** of bees collected in season *j* visiting plant species *i* |
| $y_{ij}$ | **number** of trees of genus *i* available at time *j* | **area** ($m^2$) occupied by bee-attractive flowering plants of species *i* in season *j* |
| $m_j$ | **total number** of trees cut at time *j* | **total number** of bees collected in season *j* |
| $n_j$ | **total number** of trees available at time *j* | **total area** ($m^2$) occupied by bee-attractive flowering plants in season *j* |

**Figure C.1.** Heatmap showing the genera of bees (*y*-axis) and genera of plants (*x*-axis) in this study. The presence of a box at the intersection of a bee and plant indicates that at least one bee was marked while visiting that plant species on the first day of experiments. The absence of a box indicates that bee-plant interaction was not observed in our study. The color of a box, ranging from light blue (0.00) to dark blue (1.00), indicates the probability of recapture, i.e. the proportion of marked bees in that category that were recaptured on the second days of experiments. For sample sizes of marked bees, see Tables S2 (bees) and S3 (plants).


recapture probability
1.00
0.75
0.50
0.25
0.00
bee genus
Halictus
Agapostemon
Anthophora
Ashmeadiella
Megachile
Ceratina
Melissodes
Xylocopa
Anthidium
plant genus
Encelia
Achillea
Erigeron
Grindelia
Chrysactinia
Tetraneuris
Salvia
Melampodium
Corethrogyne
Helianthus
Solidago
Bahiopsis
Chilopsis
Isocoma
Baileya
Melilotus
Trichostema

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# APPENDIX D

**Table D.1.** Ornamental plant species supplied to alfalfa leafcutting bees (*Megachile rotundata*) inside field cages. Numbers in columns represent the number of 2-L pots of each plant inside each cage in that study year (total = 30 pots per cage). Ratios differed between years due to nursery stock availability; red numbers are those that differed between the two study years. These plant species, other than alfalfa (*Medicago sativa*), were chosen because they are widely cultivated in nurseries, produce abundant floral resources (pollen and/or nectar), have long bloom periods in cultivation, and are attractive to alfalfa leafcutting bees and other bee species.

| **Plant family** | **Plant species name** | **Plant common name*** | **2019** | **2020** |
|---|---|---|---|---|
| Asteraceae | *Erigeron glaucus* | seaside daisy, seaside fleabane | **16** | **10** |
| Malvaceae | *Sphaeralcea ambigua* | desert globemallow, apricot mallow | **2** | **5** |
| Asteraceae | *Baileya multiradiata* | desert marigold | **2** | **5** |
| Boraginaceae | *Phacelia tanacetifolia* | lacy phacelia, tansy leafed phacelia | **5** | **5** |
| Fabaceae | *Medicago sativa* | alfalfa, lucerne | **5** | **5** |
| | | **Total number of pots per cage:** | **30** | **30** |

*According to the Calflora database. https://www.calflora.org/. Accessed February 2021.

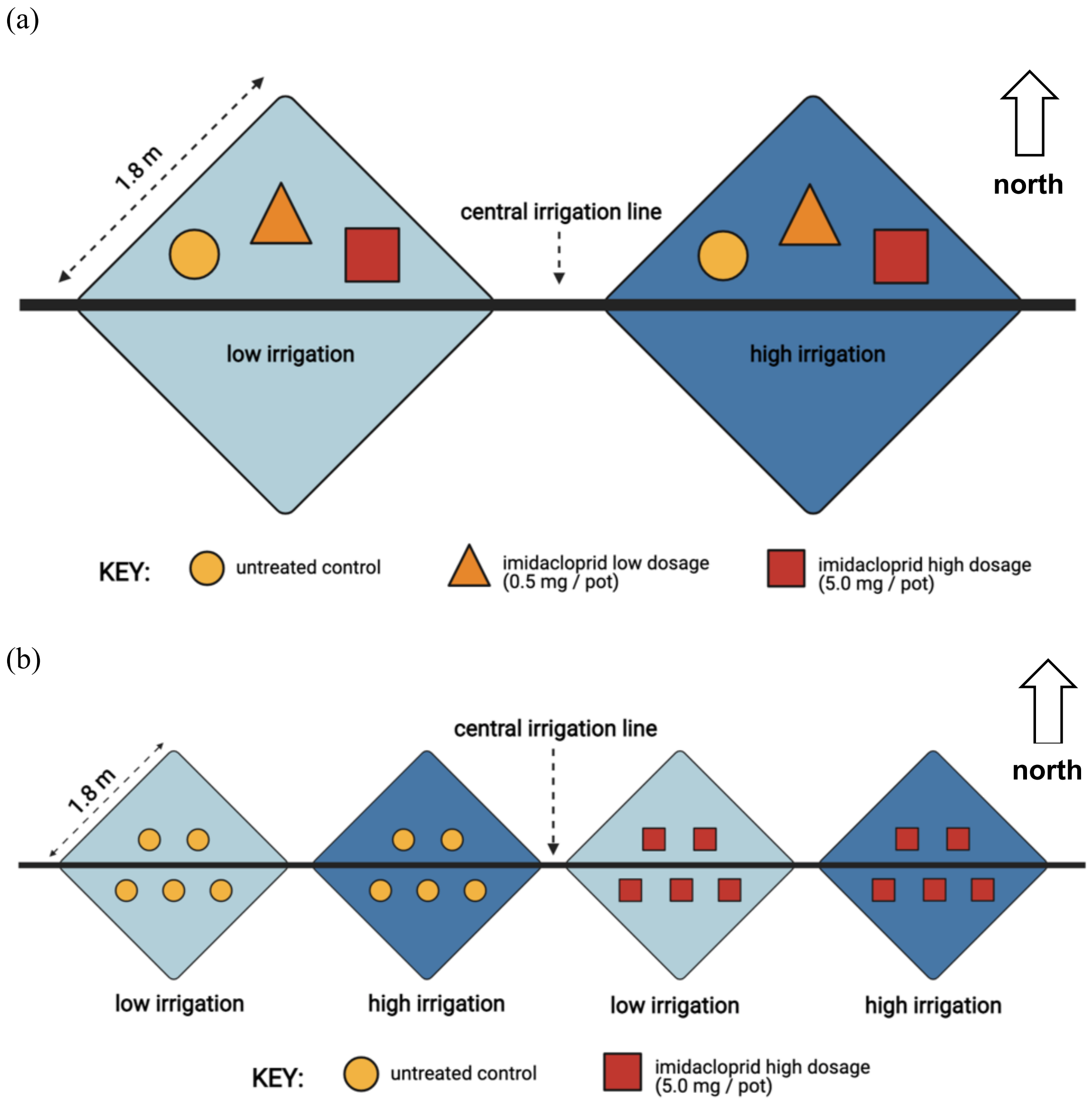

**Figure D.1.** Schematic overhead view of an individual experimental block in the (*a*) phacelia nectar experiment (2 blocks) and (*b*) alfalfa leafcutting bee reproduction experiment (4 blocks). Each blue diamond represents a field cage. We systematically varied the linear order of cages within blocks so that a treatment was not always, e.g., east or west of other treatments, and so that any pressure differences along the irrigation line were uncorrelated with treatment. In (*a*), one symbol represents 15 lacy phacelia plants. In (*b*), symbols represent the five plant species used as resources for alfalfa leafcutting bees. See table S1 for numbers of pots inside cages. Figure created with BioRender (biorender.com).

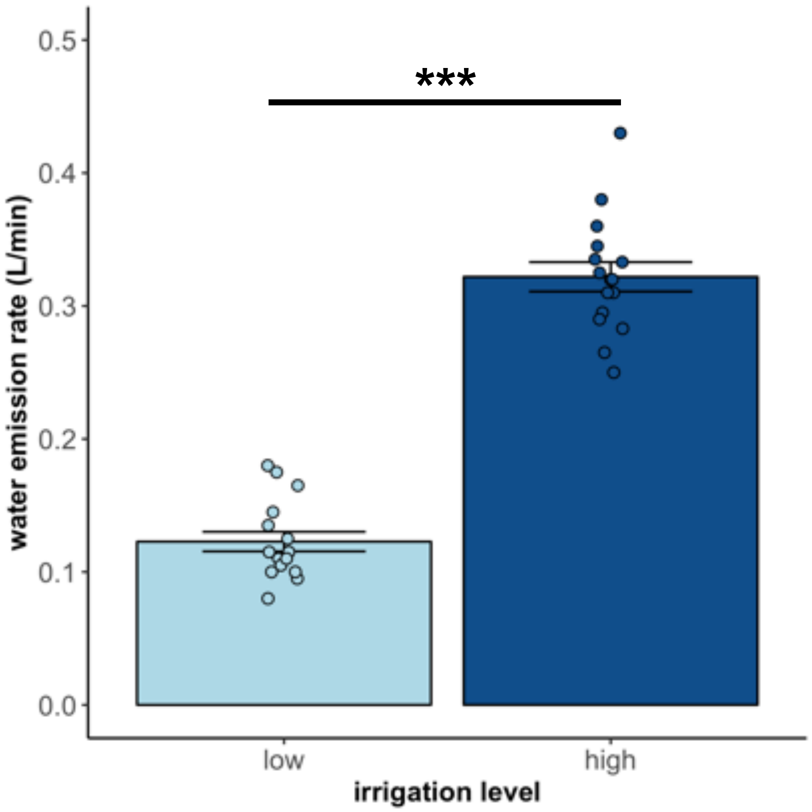

**Figure D.2.** Rates of water emission (in liters of water emitted per 60 s) for high- and low-flow irrigation spikes (SPOT-SPITTER™, Primerus Products, Encinitas, CA). These spikes characterized the low and high irrigation treatments. There was a difference in water emission rate between the two types of spikes as measured using graduated cylinders ($N = 32$; linear mixed model $F_{1,9} = 91.96$, $p < 0.0001$). Bars and whiskers represent mean ± s.e.

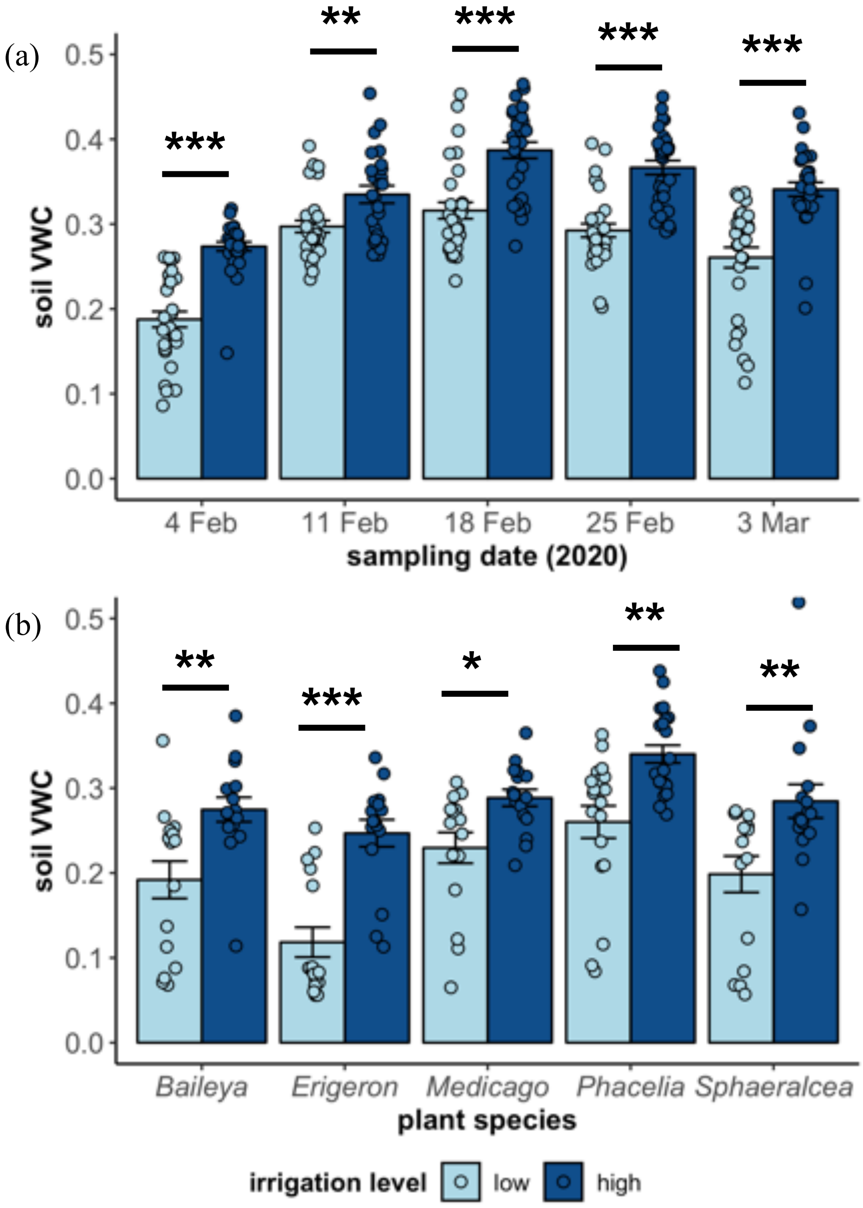

**Figure D.3.** Soil moisture, as volumetric water content (VWC, $m^3$ $m^{-3}$), of low- and high-irrigation pots inside cages, measured near mid-day (1200 h) using a GS3 soil moisture sensor (Decagon Devices, Pullman, WA). Soil moisture varied by (a) date of sampling in the 2020 tansy leafed phacelia (*Phacelia tanacetifolia*) nectar experiment, and (*b*) across plant species used in the bee reproduction experiment. In (b), a linear mixed model ($N = 160$) indicated an effect of irrigation level on soil VWC across plant species (irrigation $F_{1,90} = 10.10$, $p = 0.00203$, irrigation *x* plant species interaction $F_{4,136} = 1.05$, $p = 0.386$), but plant species differed in VWC ($F_{4,136} = 3.87$, $p = 0.00523$), with *Erigeron glaucus* exhibiting the lowest VWC. Bars and whiskers represent mean ± s.e.

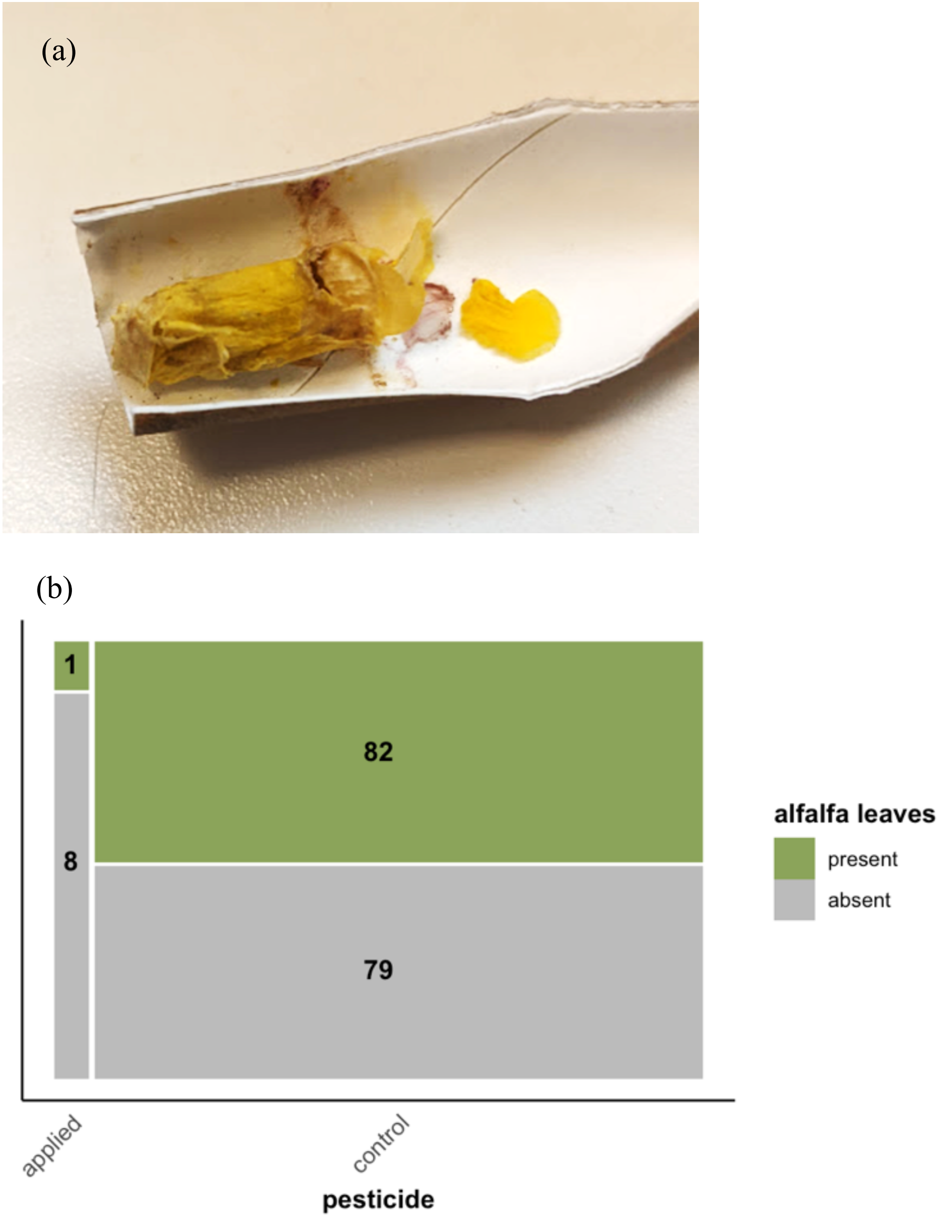

**Figure D.4.** (a) An alfalfa leafcutting bee nest cell inside a dissected paper nesting straw (diameter 5 mm). This cell is constructed entirely out of desert marigold (*Baileya multiradiata*) petals. (b) Mosaic plot of the proportions of nest cells containing alfalfa leaves, grouped by imidacloprid treatment and summed across irrigation treatments and study years. Column height is scaled to be identical, while width is proportional to the sample size for that treatment. Sample sizes, as numbers of nest cells, are shown for each of the four categories ($N = 170$ cells).