

## RESEARCH ARTICLE

# Evidence of exploitative competition between honey bees and native bees in two California landscapes

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U.S. Department of Defense Graduate Fellowship; Davis Botanical Society Grants; UC Davis Vansell Scholarship; National Science Foundation, Grant/Award Number: DEB1556885; UC Davis H. Laidlaw Endowment; The California Almond Board; Multiple USDA

**Handling Editor:** Ainhoa Magrach**Abstract**

1. Human-mediated species introductions provide real-time experiments in how communities respond to interspecific competition. For example, managed honey bees *Apis mellifera* (L.) have been widely introduced outside their native range and may compete with native bees for pollen and nectar. Indeed, multiple studies suggest that honey bees and native bees overlap in their use of floral resources. However, for resource overlap to negatively impact resource collection by native bees, resource availability must also decline, and few studies investigate impacts of honey bee competition on native bee floral visits and floral resource availability simultaneously.
2. In this study, we investigate impacts of increasing honey bee abundance on native bee visitation patterns, pollen diets, and nectar and pollen resource availability in two Californian landscapes: wildflower plantings in the Central Valley and montane meadows in the Sierra.
3. We collected data on bee visits to flowers, pollen and nectar availability, and pollen carried on bee bodies across multiple sites in the Sierra and Central Valley. We then constructed plant-pollinator visitation networks to assess how increasing honey bee abundance impacted perceived apparent competition (PAC), a measure of niche overlap, and pollinator specialization ( $d'$ ). We also compared PAC values against null expectations to address whether observed changes in niche overlap were greater or less than what we would expect given the relative abundances of interacting partners.
4. We find clear evidence of exploitative competition in both ecosystems based on the following results: (1) honey bee competition increased niche overlap between honey bees and native bees, (2) increased honey bee abundance led to decreased pollen and nectar availability in flowers, and (3) native bee communities responded to competition by shifting their floral visits, with some becoming more specialized and others becoming more generalized depending on the ecosystem and bee taxon considered.
5. Although native bees can adapt to honey bee competition by shifting their floral visits, the coexistence of honey bees and native bees is tenuous and will depend on floral resource availability. Preserving and augmenting floral resources is therefore essential in mitigating negative impacts of honey bee competition. In

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two California ecosystems, honey bee competition decreases pollen and nectar resource availability in flowers and alters native bee diets with potential implications for bee conservation and wildlands management.

#### KEYWORDS

competition, honey bee, native bee, nectar, niche overlap, plant-pollinator interactions, pollen, pollination network

## 1 | INTRODUCTION

Competition occurs when species vie for a common but limited resource (Tilman, 1982), leading to decreased population growth of species that fail to appropriately shift their resource use (Schoener, 1982). Ample evidence suggests that competition can alter the structure and function of ecological communities (David et al., 2017; Gallardo et al., 2016), and ecological theory predicts that two perfectly similar species cannot coexist without one species competitively displacing the other (Gause, 1934; Hardin, 1960; MacArthur & Levins, 1967). Understanding when and where overlapping resource use might eventually lead to competitive displacement is especially important in managing the impacts of abundant exotic species. For example, hyper-generalist honey bees *Apis mellifera* (L.) have been introduced into many ecosystems outside of their native range (Crane, 1999) and often overlap with other bees in their use of floral resources (Herrera, 2020; Hung et al., 2019). However, shared use does not automatically indicate that competitive displacement is occurring. Nectar production and replenishment rates vary widely among and within plant species (Castellanos et al., 2002; Descamps et al., 2018; Pyke, 1991), as does pollen production (Hicks et al., 2016) and resources may not be limited if flowers are abundant or if rates of resource extraction equal, or fall short of, rates of replenishment.

Assessing honey bee vs. wild bee competition is further complicated by the fact that bees may respond to competitive pressures by shifting floral visits to alternative floral resources (Valido et al., 2019; Walther-Hellwig et al., 2006) or by narrowing their diet breadth (niche partitioning; Inouye, 1978; Magrach et al., 2017; Pimm et al., 1985). As such, a snapshot of resource use may indicate that competitive displacement has occurred, but niche partitioning will not negatively affect the fitness of displaced species unless the quantity and quality of resources collected also declines. Thus, knowledge of niche overlap alone is insufficient to determine whether honey bee competition might have negative consequences for native bee populations (Thomson & Page, 2020). Indeed, although we know that honey bees collect massive amounts of pollen and nectar (Cane & Tepedino, 2016; Dupont et al., 2004; Torné-Noguera et al., 2016), whether such resource collection alters floral resource availability remains poorly tested.

Many studies have assessed competition using different assessment tools (Mallinger et al., 2017; Thomson & Page, 2020). Field studies provide ample evidence that honey bee competition can alter wild bee visits to plants (Dupont et al., 2004) and restructure interactions among plants and pollinators (Geslin et al., 2017;

Magrach et al., 2017; Valido et al., 2019). At the level of individual foragers, competition among bumble bees can increase floral fidelity and conspecific pollen transport (Brosi & Briggs, 2013). Although such questions have yet to be investigated in the context of honey bee competition, honey bee abundance can decrease niche breadth at the species-level (Magrach et al., 2017) and parallel changes may be occurring at the individual-level.

A few studies have measured the impact of honey bee abundance and apiary proximity on floral resource availability (Dupont et al., 2004) and floral resource collection by native bees (Henry & Rodet, 2018). These studies, in concert with field studies of floral visitation patterns, have considerably advanced our understanding of honey bee competition impacts. However, no studies investigate changes in resource availability and resource use shifts simultaneously. Exploitative competition occurs when resource collection by one species negatively impacts resource collection by another species (Hardin, 1960; Tilman, 1982). Thus, studying impacts of increased honey bee abundance on both resource availability and resource use would provide a more complete picture of whether exploitative competition is truly occurring. Such information also gets us much closer to understanding whether competition might have negative fitness consequences for displaced species. For example, if resource availability declines but visitation patterns remain static, there may be few pathways for native bees to escape competition by using different resources. On the other hand, without evidence of declining resource availability, one cannot assume that exploitative competition is responsible for shifting interaction patterns. For example, species turnover (CaraDonna et al., 2017), habitat loss (Lázaro & Gómez-Martínez, 2022), and a myriad of other factor can produce a re-shuffling of plant-pollinator interaction patterns in the absence of competition.

Understanding when and where honey bees compete with wild bees for floral resources has important consequences for agricultural pollination, honey bee management, and conservation policy. Honey bees contribute billions of dollars to the U.S. economy as crop pollinators (Southwick & Southwick Jr., 1992) and wildflower honey is a highly valuable agricultural commodity. However, native bees are also important pollinators, particularly for crop species not efficiently pollinated by honey bees (Page et al., 2021; Sáez et al., 2022) and the integration of managed and wild bees can additively and synergistically improve crop yields (Brittain et al., 2013; Garibaldi et al., 2013).

The most popular strategies for supporting honey bees and wild bees include planting wildflowers in agricultural landscapes and

preserving floral resources in natural landscapes. Indeed, abundant and diverse floral resources may prevent summer colony losses (Seitz et al., 2015) and mitigate negative impacts of disease and pesticide exposure (Castle et al., 2022; Pasquale et al., 2013). Unfortunately, floral resources are rapidly disappearing from agricultural landscapes in the United States (Otto et al., 2016), increasing interest among beekeepers in pasturing hives in more verdant natural landscapes (Durant, 2019). However, scientists and conservation groups worry that non-native honey bees will compete with native bees for pollen and nectar resources (Cane & Tepedino, 2016; Mallinger et al., 2017; Thomson & Page, 2020), potentially endangering imperilled native bee species (Portman et al., 2018). In natural landscapes, and especially on public and protected lands in National Parks and Forests, co-managing for honey bees and native bees by planting sufficient flowers is not a management option. Instead, we must determine how, where and when honey bees compete with native bees to guide decisions around hive densities and apiary locations.

This study sought to assess whether honey bees compete with wild native bees for pollen and nectar resources using complementary measures of floral resource use and floral resource availability in two contrasting Californian landscapes: montane meadows in the Sierra and wildflower planting neighbouring almond orchards in the Central Valley. Both systems provide important floral resources to native bees but are also heavily used by managed honey bees. Wildflower plantings support honey bees immediately after almond pollination contracts and montane meadows provide abundant floral resources for summer honey production. As such, evaluating potential for competition is key to ensuring sustainable shared use of these landscapes. Using plant-pollinator visitation networks and data on the composition of pollen on native bee bodies, we asked whether increased honey bee abundance led to changes in apparent competition between honey bees and native bees and native bee specialization. We also assessed whether native bee pollen fidelity, pollen diet diversity, and pollen diet composition responded to changes in honey bee abundance. Lastly, we asked whether honey bee abundance influenced pollen and nectar availability in key flowering species from each system.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites and pollinator surveys

We conducted this work in the California Central Valley at 5 replicated wildflower plantings neighbouring almond orchards which we sampled in 2017 and 2018. We also sampled 15 montane meadows in the Central Sierra Nevada in 2019. In both ecosystems, sites varied in their proximity to commercial apiaries which generated considerable variation in honey bee abundance (Figure S1; Table S1). Central Valley wildflower plantings were established in 2015 and 2016 as 632–3612 m<sup>2</sup> plots using a consistent seeding mix of diverse plant species native to California. All plantings were

located within 0–30 m of semi-natural riparian habitat and directly adjacent to conventionally managed Almond orchards. For more details, please see Rundlöf et al. (2022). Sites averaged 1.6 km to the nearest neighbouring site in the Sierra and 11.3 km to the nearest neighbouring site in the Central Valley. Within each ecosystem, sites were in consistent landscape contexts and drew from the same regional species pools of native pollinators.

In the Central Valley, we surveyed pollinators and their visits to flowering plants over four sample rounds from April to May. In the Sierra, we sampled sites from May to July. Most sites were sampled two to four times, but some sites were sampled up to 10 times if the blooms of *Camassia quamash* (Pursh) and *Penstemon rydbergii* (Greene) lasted long enough. We targeted these two species to ensure that floral community composition remained relatively consistent across networks. In the Central Valley, we netted insects actively visiting flowers during 10-min walks of two 100 m<sup>2</sup> transects which were each sampled once in the morning and once in the afternoon (40 min total). In the Sierra, we sampled one-hectare subplots that varied in floral species composition, netting active flower visitors while walking 100 m<sup>2</sup> transects for two 30-min periods in the morning and the afternoon (60 min total). In both systems, we netted exclusively on sunny or partly cloudy days when average wind speeds were below 5 m/s and temperatures were above 13°C. Netted pollinators were collected individually in separate collection vials to minimize pollen contamination and euthanized using dry ice, except for bumble bee queens, which we identified on site and then released. In both systems, we collected up to 20 honey bees during netting transects and counted any additional honey bees. Native bee specimens were identified to morphospecies using identification guides (Roberts, 1973; Williams et al., 2014) and by expert taxonomists (Skyler Burrows, USDA Bee Lab, Logan, Utah, and Joel Gardner, University of Manitoba, Canada). For network analyses, we excluded bees not identified to morphospecies (~3% of all specimens). Because we were exclusively interested in documenting bee competition, we also excluded non-bee floral visitors from network analyses.

### 2.2 | Assessing pollen diet composition

In the lab, we swabbed specimens with fuchsin-tinted gelatin cubes (Kearns and Inouye, 1993) which we then melted onto microscope slides. We swabbed the entire body, focusing on scopal and corbicular pollen loads. We counted and identified pollen grains using a compound light microscope (Nikon Eclipse 80i, Nikon Instruments Inc.) and pollen reference collections. We calculated pollen fidelity as the number of pollen grains from the plant species from which the specimen was caught divided by the total number of pollen grains in the swabbed sample. Most pollen was identified to species, but we sometimes grouped pollen grains at the genus level. We calculated pollen diversity using the Shannon-Weiner diversity index (Shannon, 1948).

## 2.3 | Quantifying pollen resource depletion

We measured the daily depletion of pollen and nectar resources from the most abundant and most consistently available plant species. In the Central Valley, these species were *Clarkia unguiculata* (Lindl.), *Collinsia heterophylla* (Graham), *Eschscholzia californica* (Cham.), and *Phacelia californica* (Cham.). In the Sierra, these species were *Bistorta bistortoides* (Pursh), *Camassia quamash* (Pursh), *Penstemon rydbergii* (Greene), *Ranunculus occidentalis* (Nutt.) and *Trifolium longipes* (Nutt.). In both systems, at the end of each sampling day, we measured pollen and nectar availability in the field using one to three flowers on 10–20 “open-pollinated” plants and 10–20 unvisited control plants which were bagged on site arrival (between 6:30 and 7:30h) and prior to pollinator activity. We measured pollen availability as the proportion of dehisced anthers with pollen visible to the naked eye and measured nectar availability using 1  $\mu$ L capillary tubes.

## 2.4 | Network metrics

For each site and sample round in each year and system, we generated unique plant  $\times$  pollinator visitation networks. In total, we generated 40 networks across 2 years of sampling for our Central Valley sites and 48 networks for our Sierra sites. For each network, we used the `BIPARTITE` package (Dormann et al., 2009) and R (R Core Team, 2022) to calculate pollinator specialization ( $d'$ ) and perceived apparent competition (PAC). Pollinator specialization ( $d'$ ) measures partner diversity at the pollinator level using the Kullback–Leibler distance (Blüthgen et al., 2006). Perceived apparent competition (PAC) estimates the degree of niche overlap between two species using Müller's index (Morris et al., 2005; Müller et al., 1999). For all pairwise comparisons of honey bees against other bees we calculated Müller's index as:

$$d_{ij} = \sum_k \left[ \frac{\alpha_{ik}}{\sum_l \alpha_{il}} \times \frac{\alpha_{jk}}{\sum_m \alpha_{mk}} \right],$$

where  $\alpha_{ik}$  represents the number of interactions between pollinator  $i$  and plant  $k$ ,  $\alpha_{il}$  represents the number of interactions by pollinator  $i$  across all plants  $l$ ,  $\alpha_{jk}$  represents the number of interactions between pollinator  $j$  and plant  $k$ , and  $\alpha_{mk}$  represents visits to plant  $k$  from all pollinators  $m$ . Because Müller's Index is sensitive to the relative abundance of competing species, we compared observed values of Müller's Index against indices calculated using null networks. To perform this comparison, we generated 500 randomized null networks using the `r2table` method, which resamples interactions but keeps row and column sums constant (Patefield, 1981) and compared observed metrics against null network metrics using Z-scores (Blüthgen et al., 2008; Dormann et al., 2009; Vázquez & Aizen, 2003). To complement calculations of PAC between honey bees and native bees, we also calculated the mean PAC value for all pairwise comparisons of native bees against other native bees.

## 2.5 | Statistical analysis

We assessed whether honey bee abundance, measured as the total number of honey bees visiting flowering plants during morning and afternoon netting transects, was associated with changes in native bee specialization ( $d'$ ) and perceived apparent competition (PAC) using separate linear mixed effects models for each network metric and each ecosystem. We also asked whether PAC was higher or lower than null expectations by fitting a model with the Z-score comparison of observed and null PAC values as the response variable. Finally, we assessed whether PAC among native bees varied with increasing honey bee abundance using the mean PAC values across all pairwise native bee vs. native bee comparisons as our response variable. Each model included native bee taxon (with five levels: *Andrena*, *Bombus*, Halictidae, Megachilidae, and “Other” bees), honey bee abundance, and their interaction as fixed effects and site and sample round as separate random effects. For models of PAC, we only considered networks where at least one honey bee was observed to keep our analysis conservative. For models predicting network metrics in in the Central Valley, we included year as an additional fixed effect. Where interaction effects were significant, we followed up with tests of the impact of honey bee abundance on network metrics for individual native bee taxa by fitting models with only honey bee abundance as a fixed effect and site and sample round as random effects. To correct for multiple testing, we applied a Bonferroni correction. We fit all statistical models using the `lmer()` function in the `LME4` package (Bates et al., 2014) in R (R Core Team, 2022) and tested for significance using likelihood ratio tests.

We assessed whether honey bee abundance was associated with changes in the composition of pollen carried on bee bodies via permutational MANOVAs using the `adonis` function in the `VEGAN` package (Anderson, 2001; Oksanen et al., 2020). Each model included honey bee abundance, bee taxon, and the plant taxon from which the specimen was caught as fixed effects. Specimens were collected from different sites, and we accounted for nestedness using ‘`stata = site`’ in all models. Statistical results obtained from the `adonis()` function depend on the order in which variables are added so we ran multiple permutations and report the most conservative results (i.e. results from tests with predictors added in order of statistical significance). We assessed whether honey bee abundance was associated with changes in native bee pollen fidelity and native bee pollen diet diversity using separate LMMs for each response and ecosystem. All models included honey bee abundance, native bee taxon, and the plant taxon from which the specimen was caught as fixed effects and site and sample round as separate random effects. All Central Valley models also included year as an additional fixed effect.

We evaluated how pollen and nectar availability responded to honey bee introductions using separate generalized linear mixed models (GLMMs) for each ecosystem and reward type. Each model included honey bee abundance, plant species sampled, and to control for baseline pollen and nectar resources, the mean pollen and nectar availability in unvisited bagged flowers as fixed effects as well as

site, sample round and plant as random effects. In the Sierra, nectar measurements varied by data collector, so we added data collector as a fixed effect. Pollen and nectar data were both zero-inflated. We modelled pollen availability as the proportion of dehisced anthers in a flower that had visible pollen using a beta-binomial error distribution. Nectar availability was modelled as a binary response where successes were flowers with measurable nectar and failures were flowers with no measurable nectar. We modelled GLMMs using the GLMMTMB package (Brooks et al., 2017) and tested for significance using likelihood ratio tests.

### 3 | RESULTS

Honey bee abundance in meadows, measured as the total number of honey bees visiting flowering plants during morning and afternoon netting transects, ranged from 9 to 2363 bees per m<sup>2</sup> per hour in the Central Valley and 0–184 honey bees per m<sup>2</sup> per hour in the Sierra (Table 1). In the Central Valley, we recorded 1048 native bees comprising 57 morphospecies. In the Sierra, we recorded 2329 native bees representing 116 morphospecies.

Perceived apparent competition (PAC) between honey bees and native bees was higher at sites with more honey bees in both the Central Valley and the Sierra (Table 2). In the Sierra, there was also a significant interaction, such that the magnitude of increase in PAC values varied by native bee taxon (Figure 1d). Comparing predicted effects at minimum and maximum values of honey bee abundance, PAC increased by 104% in the Central Valley and by 417% in the Sierra. Perceived apparent competition (PAC) among native bees was low overall but was nonetheless subtly influenced by increasing honey bee abundance in both systems. Comparing predicted effects at minimum and maximum values of honey bee abundance, competition among native bees increased by 14.4% in the Sierra (going from 0.081 to 0.096). In the Central Valley, mean PAC scores dropped from 0.067 to 0.000, indicating there was virtually no competition among native bees when honey bees were at peak abundance.

When comparing observed and null values of PAC between honey bees and native bees using Z-scores, the impact of honey bee abundance varied among native bee taxa and across systems

(Table 2). In the Sierra, Z-scores decreased with increasing honey bee abundance, indicating that PAC was lower than null expectations at higher levels of honey bee abundance. Comparing predicted effects at minimum and maximum values of honey bee abundance, Z-scores decreased from -0.219 to -3.482. The magnitude of decrease in Z-scores also varied by taxa (Figure 1e; Table S2). In the Central Valley, the impact of honey bee abundance depended on the native bee taxon considered (Table 2). However, there was no consistent overall effect and, although slope estimates varied by taxa (Figure 1b), no trends proved statistically significant (Table S2).

Native bee specialization (d') varied as honey bee abundance increased but the direction and magnitude of this impact varied among native bee taxa and across systems (Table 2). Comparing predicted effects at minimum and maximum values of honey bee abundance, d' decreased by 58% in the Central Valley. The magnitude of decrease in generalization also varied by taxa (Figure 1c). In the Sierra, there was no overall impact of honey bee abundance on d'. Instead, the impact of honey bee abundance depended on the native bee taxon considered (Figure 1f); *Bombus* spp. became more specialized as honey bee abundance increased (Chi-sq: 14.217; Bonferroni-corrected  $p < 0.001$ ) but there was no significant change for other taxa (Table S2).

Neither the pollen fidelity of individual visitors nor the species richness of pollen carried on bee bodies changed as honey bee abundance increased (Table 3). In both systems, the species composition of pollen was best explained by bee taxonomic identity and the plant taxon it was visiting (Table 3). Honey bee abundance was not a significant predictor of pollen composition in the Central Valley. In the Sierra, honey bee abundance was associated with a subtle shift in pollen species composition but explained less than 1% of variation among individuals.

Nectar availability, measured as the probability of detecting measurable nectar in flowers, strongly declined as honey bee abundance increased in both the Central Valley and the Sierra (Figure 2a,c). Comparing predicted effects at minimum and maximum values of honey bee abundance, nectar availability declined by 67% in the Central Valley and by 91% in the Sierra. Pollen availability, measured as the proportion of anthers with pollen, declined by 74% in the Sierra (Figure 2d), but there was no impact of honey bee abundance

**TABLE 1** Summary data for honey bee and native bee species richness and abundance across sampled sites in the California Central Valley and Sierra Nevada. Total richness is the species richness of specimens identified to species or morphospecies across all site samples. Abundance is measured as the number of bees collected or counted per hour per m<sup>2</sup> across morning and afternoon netting transects for a given site sample.

	Total richness	Total abundance	Mean abundance $\pm$ SD	Minimum	Maximum
Central Valley					
Honey bees	1	13,605	510.2 $\pm$ 490.8	9	2363
Native bees	57	1048	39.3 $\pm$ 28.2	3	92
Sierra Nevada					
Honey bees	1	791	16.5 $\pm$ 36.1	0	184
Native bees	116	2329	48.5 $\pm$ 36.7	10	260

**TABLE 2** Effect of honey bee abundance, native bee taxon, and their interaction on perceived apparent competition between honey bees and native bees (PAC: *Apis*), among native bees (PAC: Native), observed vs. null values of PAC (PAC: Z-score), and native bee specialization ( $d'$ ) for sites in the Central Valley and the Sierra Nevada.

Response	Predictor	Chi-sq	df	p-value
<b>Central Valley wildflower plantings</b>				
PAC: <i>Apis</i>	Honey bee abundance	72.512	1	<0.001
	Native bee taxon	19.497	4	<0.001
	Interaction	5.783	4	0.216
PAC: Native	Honey bee abundance	29.300	1	<0.001
	Native bee taxon	3.366	4	0.499
	Interaction	4.815	4	0.307
PAC: Z-score	Honey bee abundance	0.766	1	0.381
	Native bee taxon	16.199	4	0.003
	Interaction	10.863	4	0.028
$d'$	Honey bee abundance	13.143	1	<0.001
	Native bee taxon	30.126	4	<0.001
	Interaction	14.738	4	0.005
<b>Sierra Nevada montane meadows</b>				
PAC: <i>Apis</i>	Honey bee abundance	57.262	1	<0.001
	Native bee taxon	5.735	4	0.220
	Interaction	22.270	4	<0.001
PAC: Native	Honey bee abundance	5.998	1	0.014
	Native bee taxon	9.132	4	0.058
	Interaction	4.360	4	0.359
PAC: Z-score	Honey bee abundance	7.182	1	0.007
	Native bee taxon	1.147	4	0.887
	Interaction	16.373	4	0.003
$d'$	Honey bee abundance	0.142	1	0.706
	Native bee taxon	38.532	4	<0.001
	Interaction	17.949	4	0.001

in the Central Valley, where pollen availability was consistently low (Figure 2b). Pollen and nectar availability also varied among plant species and in response to baseline resource availability (Table S3).

## 4 | DISCUSSION

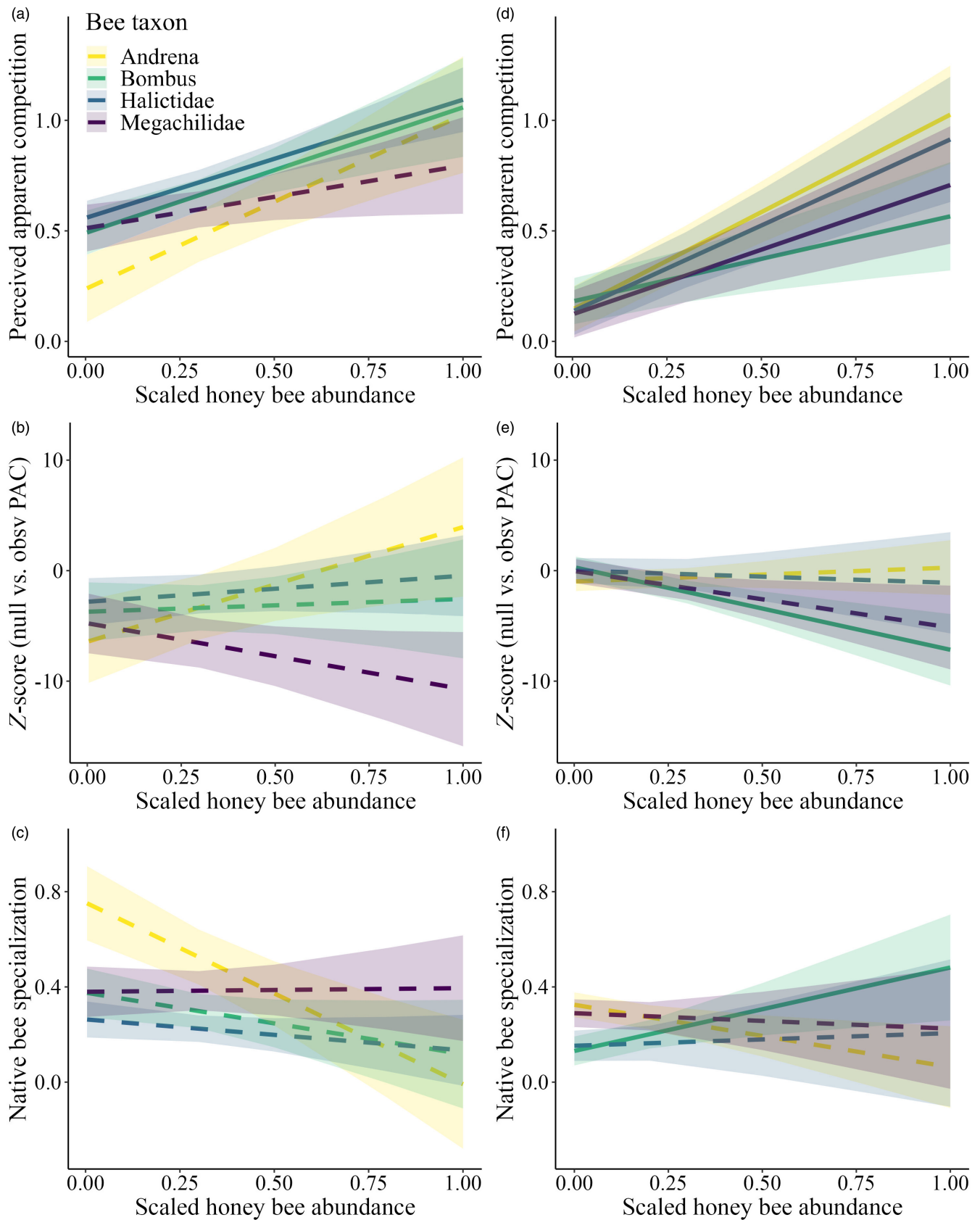
Across two California ecosystems, increasing honey bee abundance was associated with decreased floral resource availability, leading to shifts in native bee floral visitation patterns. Perceived apparent competition (PAC), a measure of niche-overlap, increased in both systems. However, when compared to randomly re-assembled null networks, honey bee abundance was associated with a decrease in perceived apparent competition in the Sierra. These seemingly contradictory conclusions highlight the value of using null models to understand ecological data. Our null models conserved total numbers of honey bee and native bee visits but randomly

redistributed them to different plants. Thus, deviation from null networks reveals that species are non-randomly shifting their visits, potentially to minimize niche overlap. Such a response conforms with ecological theory, which predicts that species respond to interspecific competition by partitioning niches, either through increased specialization (Inouye, 1978; Pimm et al., 1985) or switching to alternate hosts (Walther-Hellwig et al., 2006). Indeed, although there was no overall impact of honey bee abundance on native bee specialization ( $d'$ ) in the Sierra, *Bombus* spp. responded to increased honey bee abundance by becoming more specialized, in accordance with ecological theory.

The response by the community of native bees in the Central Valley contrasted with that of the bees in the Sierra. In the Central Valley, species-level pollinator specialization ( $d'$ ) decreased as honey bee abundance increased. These findings parallel those from a similar study in agricultural landscapes in Spain (Magrach et al., 2017) which found that complementary specialization ( $H2'$ ) decreased as honey bee abundance increased in natural habitat neighbouring orange groves. In our study,  $H2'$  also tended to decrease as honey bee abundance increased, but this trend was not statistically significant (Table S4). Decreasing values of  $d'$  and  $H2'$  indicate that native bees are visiting a greater proportion of available plant species and share more interactions with other native bees. The contrasting results in the Sierra and Central Valley imply that competition can both increase and decrease specialization depending on the ecological context and species considered. Although increasing specialization is considered a more "classic" response to competition (Heinrich, 1979), generalist bees sometimes respond by becoming more generalized (Fontaine et al., 2008). Furthermore, bees with wider diet breadths often persist better in disturbed habitats (Biesmeijer et al., 2006), and generalist foraging could confer a selective advantage where resources are scarce (Kunin & Iwasa, 1996).

Another important difference between these two ecosystems is that honey bees were much more abundant in the Central Valley, whereas honey bees were entirely absent from Sierra Nevada meadows before they were experimentally introduced. As such, honey bees actively disturbed plant-pollinator interactions in the Sierra, prompting niche partitioning as expected by ecological theory (MacArthur & Levins, 1967). In contrast, native bees in the Central Valley were already partitioning niche space with honey bees at moderate levels of honey bee abundance, and there was likely little room for improvement as honey bee abundance increased. Ultimately, although the exact responses vary, shifting interaction patterns in both systems reveal that pollinators can modify their use of flowering resources to minimize competition in the short term and such adaptive foraging may allow species and communities to persist (Valdovinos et al., 2013). However, in a world with decreasing floral abundance and diversity (Burkle et al., 2013), adaptive foraging may not always be possible and there could be delayed effects of competition on the ability of all plants and pollinators to persist across longer time scales.

Although we observed shifts in visitation patterns at the species level, the pollen fidelity of individual foraging bees, as well as the



**FIGURE 1** Impact of honey bee abundance on (a) perceived apparent competition (PAC) between honey bees and native bees, (b) Z-score comparisons of null vs. observed PAC values, and (c) native bee specialization (d') for different native bee taxa in the Central Valley. Impact of honey bee abundance on (d) perceived apparent competition, (e) Z-score comparisons and (f) native bee specialization in the Sierra. Lines and shading show model predictions and confidence intervals for different taxa. Dashed lines indicate non-significant trends. For more details see [Table S2](#).

**TABLE 3** Effect of honey bee abundance, native bee taxon, and plant taxon visited on native bee pollen fidelity, the diversity of pollen carried on native bee bodies, and pollen community composition for sites in the California Central Valley and the Sierra Nevada.

Central Valley wildflower plantings					
Response	Predictor		Chi-sq	df	p-value
Pollen fidelity	Honey bee abundance	—	0.075	1	0.784
	Native bee taxon	—	27.561	4	<0.001
	Plant taxon visited	—	83.212	6	<0.001
Diversity	Honey bee abundance	—	0.007	1	0.933
	Native bee taxon	—	57.978	4	<0.001
	Plant taxon visited	—	35.130	6	<0.001
Response	Predictor	R <sup>2</sup>	F	df	p-value
Composition	Honey bee abundance	0.001	2.202	1	1.000
	Native bee taxon	0.014	5.710	4	<0.001
	Plant taxon visited	0.356	98.932	6	<0.001
	Residual	0.622		1038	
Sierra Nevada montane meadows					
Response	Predictor		Chi-sq	df	p-value
Pollen fidelity	Honey bee abundance	—	0.223	1	0.637
	Native bee taxon	—	10.046	4	0.040
	Plant taxon visited	—	134.555	5	<0.001
Diversity	Honey bee abundance	—	0.222	1	0.637
	Native bee taxon	—	26.723	4	<0.001
	Plant taxon visited	—	67.973	5	<0.001
Response	Predictor	R <sup>2</sup>	F	df	p-value
Composition	Honey bee abundance	0.002	3.139	1	<0.001
	Native bee taxon	0.026	11.894	4	<0.001
	Plant taxon visited	0.254	92.976	5	<0.001
	Residual	0.718		1312	

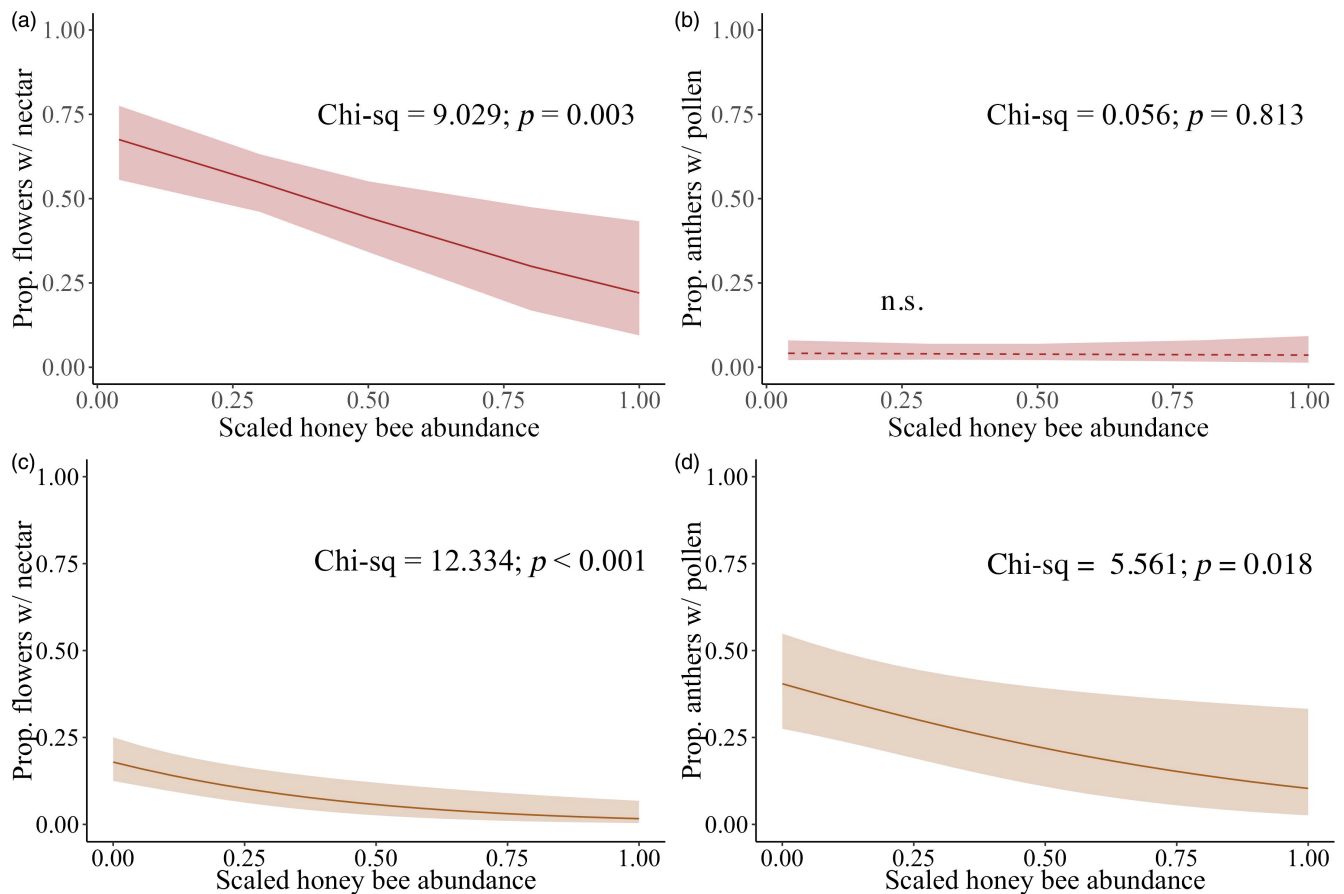
diversity and composition of pollen grains on bee bodies were relatively unchanged by honey bee abundance. Indeed, the absence of a significant relationship between honey bee abundance and pollen fidelity persisted even when we restricted data to single plant species (Table S5). Brosi and Briggs (2013) found that removal of a dominant bumble bee species led to a decrease in the pollen fidelity of bumble bees visiting *Delphinium barbeyi*, suggesting competition and high species diversity maintain high levels of niche segregation. Although our data are not a perfect comparison given that we focus on all bees rather than exclusively *Bombus* spp, we nonetheless find contrasting results: honey bee competition is not a major driver of native bee pollen fidelity, suggesting the impact of competition on pollen fidelity is highly context dependent. Instead, most variation in pollen fidelity and pollen composition was explained by the plant species a bee had been visiting when captured. For example, in the Sierra, honey bee abundance was associated with a decrease in the proportion of native bees visiting *Camassia quamash* (Chi-sq=58.171;  $df=1$ ;  $p<0.001$ ) with parallel declines in *C. quamash* pollen carriage (Figure S2). Although some plant species are over- or under-

represented in the pollen data when compared to the visitation data (Figure S2), likely reflecting differences in pollen production among plant species and pollen vs. nectar collection by bees, shifting visitation patterns explain most of the variation associated with changes in honey bee abundance. As such, although the pollen diets of native bees were altered by honey bee competition, visitation data would have sufficiently documented this change.

An important caveat to this study is that shifting plant composition also influences bee foraging. Indeed, for nearly all plant species, proportional floral abundance was a good predictor of proportional visitation to that species by native bees (Table S6). However, increasing honey bee abundance was also associated with statistically significant shifts in the proportion of native bees visiting different plant species. Thus, we cannot conclude that all observed shifts are due to competitive displacement, but our data nonetheless suggest that competition is at least one factor influencing bee foraging decisions.

By simultaneously documenting declines in floral resource availability and shifts in resource use we demonstrate that native bees are likely to collect fewer resources, or collect different resources, when honey bees are abundant. Decreases in resource availability could decrease native bee reproduction by constraining pollen collection and





**FIGURE 2** Impact of honey bee abundance on (a) nectar availability (the probability of detecting measurable nectar) and (b) pollen availability (the proportion of dehiscid anthers with pollen) in the Central Valley. Impact of honey bee abundance on (c) nectar availability and (d) pollen availability in the Sierra Nevada. Fitted lines and shading plot predictions and confidence intervals from models reported in Table S3. Dashed lines indicate non-significant trends.

offspring provisioning (Hudewenz & Klein, 2015; Thomson, 2004). Indeed, although parasitism and nest site availability are sometimes more limiting than flowers (Forrest & Chisholm, 2017; Steffan-Dewenter & Schiele, 2008), floral resources almost universally increase bee reproduction (Carvell et al., 2017; Goodell, 2003; Williams & Kremen, 2007) and flower availability is often a key limiting factor for population growth (Crone & Williams, 2016; Malfi et al., 2019; Thomson & Page, 2020). Collecting different resources may also decrease reproduction if resources are of lower nutritional quality (Vaudo et al., 2018) or otherwise unsuitable replacements for preferred host plants. For generalist feeders, having a large set of diet choices allows for maximum caloric and nutrition intake (Pulliam, 1975), and pollen and nectar quality influence bee health and reproduction (Burkle & Irwin, 2009; Roulston & Cane, 2002). Indeed, in the Central Valley, competition-mediated shifts in floral visitation resulted in bees collecting less-nutritious pollen (in terms of Protein, M. Page: unpubli. data). As such, changes in native bee diets and floral resource availability are likely to have negative consequences for native bee populations.

In the Sierra, increasing honey bee abundance led to a pronounced decrease in end-of-day nectar availability, which was already low across sites before honey bees were introduced. In the Central Valley, where honey bees were more abundant, increasing honey

bee abundance had a more moderate effect on nectar availability, which tended to be high across all site samples. A few differences between these systems could explain these contrasting results. First, we did not augment floral resources in the Sierra whereas wildflower plantings were added to otherwise resource-poor landscapes in the Central Valley with plant species selected for their attractiveness to bees. Furthermore, all dominant plant species in Central Valley wildflower plantings refill nectar (M. Page; unpubli. data), and, although we lack complete data in the Sierra, one of the most dominant species, *Camassia quamash*, does not refill nectar (Page & Williams, 2023a). When plants refill nectar, this should theoretically increase end-of-day nectar availability, even across a backdrop of nectar competition. As such, context-specific factors such as plant species composition may be important in understanding where and when honey bees are more likely to deplete nectar and pollen resources to levels that could negatively impact collection by native bee communities.

If honey bee competition reduces resource availability in wildflower plantings, these habitat enhancements may fail to benefit native bee populations, as has been shown in other systems (Angelella et al., 2021; Bommarco et al., 2021). However, in our Central Valley sites, the benefit of augmenting floral availability seems to outweigh any negative effects of bee-bee competition. This is confirmed by

work from a separate project, conducted at these same sites over the same time-period (Rundlöf et al., 2022) which showed that wildflower plantings enhanced *O. lignaria* and *B. vosnesenskii* reproduction when compared to un-enhanced control sites. As such, wildflower plantings remain a valuable conservation tool despite honey bee competition, in agreement with studies showing overall benefits of wildflower plantings for native bee populations (Boyle et al., 2020; Williams et al., 2015). Nonetheless, clearer guidance on selection of species for wildflower plant mixes to minimize negative effects of honey bee competition warrants additional exploration.

Our findings also have important implications for honey bee management in natural landscapes. In the Sierra, honey bee abundance was more than 20 times lower than it was in the Central Valley and native bees were able to shift resource use to minimize niche overlap. Nonetheless, pollen and nectar resource availability declined in both systems and the observed increases in native bee specialization may make the Sierra bee community more susceptible to species extinction (Aizen et al., 2012). Thus, even moderately abundant honey bees may disturb ecosystems locally and future hive placements in sensitive habitat should be approached with extreme caution.

More generally, this study contributes to our ecological understanding of competition. We document compelling evidence that honey bee competition increases niche overlap among species, alters native bee resource use and decreases floral resource availability, broadly meeting the definition of exploitative competition (Schoener, 1982; Tilman, 1982). Yet, the age-old question of whether such competition might drive future extinctions remains unresolved. Honey bees have been implicated in the extirpation of native bee species (Portman et al., 2018), but there are also cases where honey bees and native bees coexist without one species fully displacing the other (Roubik & Villanueva-Gutiérrez, 2009). Our findings suggest that native species can adapt to honey bee competition by shifting floral visitation patterns but declines in resource availability imply there is a limit to coexistence. Understanding what that limit is and how to sustainably manage honey bees in a way that reduces risk of native bee extinctions remains a key ecological and ethical question for wildlands management.

#### AUTHOR CONTRIBUTIONS

Maureen L. Page and Neal M. Williams conceived and planned the study. Maureen L. Page collected and analysed the data and led the writing of the manuscript. Both authors read and approved the final manuscript.

#### ACKNOWLEDGEMENTS

We thank Andrew Buder, Staci Cibotti, Deanna Deterding, Lindsey Hack, Heather Spaulding and Annie Zell for their assistance with field work. Skyler Burrows of the USDA Bee Lab in Logan, Utah, and Joel Gardner of the University of Manitoba, Canada helped us identify bees to species. We are also grateful to Randy and Eric Oliver who helped supplement sites in the Sierra with honey bees as well as landowners who allowed us to place hives on their land. We acknowledge that research took place on indigenous lands

of the Washoe and Patwin people and we are grateful for their stewardship. Early manuscript drafts benefited from feedback from Rachel Vannette and Louie Yang. Research support was provided by a U.S. Department of Defense Graduate Fellowship, Davis Botanical Society Grants, and a UC Davis Vansell Scholarship awarded to Maureen L. Page. Additional support was provided by National Science Foundation grant DEB1556885, the UC Davis H. Laidlaw Endowment, The California Almond Board, and multiple USDA grants awarded to Neal M. Williams.

#### CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to disclose.

#### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.25338/B80S8F> (Page & Williams, 2023b).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1.** Summary information about site proximity to apiaries, number of times a site was sampled, and the mean and total richness of bee species included in networks for each site. We were not always able to locate hives, nor could we consistently communicate with beekeepers. Some information was provided by private landowners who gave their best estimates of apiary density and arrival dates.

**Table S2.** Effect of honey bee abundance on perceived apparent competition between honey bees and native bees (PAC: Apis), native bee specialization (d'), and observed vs. null values of PAC (PAC: Z-score) for different native bee taxa in the Central Valley and the Sierra Nevada. All reported *p*-values include Bonferroni corrections for multiple testing. Note that we excluded the “other bee” single taxon analysis in the Sierra due to low sample size ( $N \leq 30$ ).

**Table S3.** Summary results for models describing: (1) pollen availability in open-pollinated flowers, modeled as a binary response (where successes are dehiscid anthers with visible pollen and failures are dehiscid anthers without visible pollen), and (2) nectar availability in open-pollinated flowers, also modeled as a binary response (measurable nectar or no measurable nectar). The model terms ‘Baseline pollen’ and ‘Baseline nectar’ are the average pollen and nectar availability in plants that were bagged at the beginning of each day to prevent insect visitation. See Methods section for detail on data collection and model structure.

**Table S4.** Effect of honey bee abundance on network level complementary specialization ( $H2'$ ), for sites in the Central Valley and the Sierra Nevada. Models of  $H2'$  included honey bee abundance as a fixed effect and site and sample round as separate random effects. To eliminate the direct impact of honey bee interactions on  $H2'$ , we removed honey bees from networks before calculating  $H2'$ . After removing honey bees, a few networks become too small to calculate  $H2'$ ; these networks were removed from analyses.

**Table S5.** Effect of honey bee abundance and native bee taxon on native bee pollen fidelity (the proportion of conspecific pollen on bodies of bee visitors) for *Eschscholzia californica* and *Collinsia heterophylla* in the California Central Valley as well as *Camassia*

and *Penstemon rydbergii* in the Sierra Nevada. These plant species had the most bee visits (based on collected bee specimens) across all sites within their respective ecosystems.

**Table S6.** Effect of honey bee abundance (measured as a categorical variable: ‘high’ vs. ‘low’) and proportional floral abundance on the proportion of visits native bees made to different plant species in the Central Valley and the Sierra Nevada. Proportional native bee visitation rates are summarized at the level of the site sample. Floral abundance surveys were taken on the same day that bees were collected by counting and identifying all flowers in 10 equally spaced 1 m<sup>2</sup> quadrats that were placed along the length of netting transects. For each analysis, we rarefied the data to only include cases where the indicated flowering species was present. We fit models using lmer() with random effects for site and sample round and we tested for significance of predictors using likelihood ratio tests. Relative to its floral abundance, native bees visited *Collinsia heterophylla* more and *Phacelia* spp. less when honey bees were abundant. Likewise, relative to its floral abundance, native bees visited *Ranunculus* spp. more and *Camassia quamash* less when honey bees were more abundant.

**Figure S1.** Sites and apiary locations in (A) the Central Valley and (B) the Sierra Nevada. Blue stars are sampled sites and orange markers are where apiaries are located. In the Central Valley, we sampled wildflower plantings neighboring almond orchards. These sites exist in a consistent landscape context (agricultural land with nearby riparian habitat) and draw from the same regional species pool of native pollinators. There are likely many other apiaries in this landscape; our search only includes apiaries within 500m of plantings. In the Sierra, apiaries are all located on private property neighboring Tahoe National Forest land and are between 5300 ft and 7000 ft in elevation. The three apiaries in the south were experimentally introduced halfway through the *C. quamash* bloom period to generate additional variance in honey bee abundance and each apiary consisted of 20 hives. The apiary in the north consisted of approximately 100 hives.

**Figure S2.** Summary data on the proportional abundance of different plant species in sampled transects (based on #florets), the proportion of native bee visits to these plants, and the species composition of pollen across all native bee bodies at low and high levels of honey bee abundance in the Central Valley (A, B, & C) and the Sierra (D, E, & F). Proportional floral abundance and honey bee abundance were both good predictors of proportional visitation rates (see Table S6 for more details). Shifting visit patterns also led to parallel changes in the composition of pollen carried on insect bodies in the Sierra.

**How to cite this article:** Page, M. L., & Williams, N. M. (2023). Evidence of exploitative competition between honey bees and native bees in two California landscapes. *Journal of Animal Ecology*, 92, 1802–1814. <https://doi.org/10.1111/1365-2656.13973>