

ORIGINAL ARTICLE

Pollen exploitation by non-native, feral honey bees: Potential consequences for interspecific competition

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Funding information

University of California : Multicampus Research Programs and Initiatives; Jeanne Marie Messier Memorial Endowed Fund; Sea and Sage Audubon Society; California Native Plant Society; University of California, San Diego : Frontiers of Innovation Scholar Fellowship; University of California, San Diego : McElroy Fellowship; Natural Reserve System, University of California : Institute for the Study of Ecological and Evolutionary Climate Impacts Graduate Fellowship; Natural Reserve System, University of California : Mildred E. Mathias Graduate Student Research Grant; National Science Foundation (NSF) Doctoral Dissertation Improvement Grant, Grant/Award Number: DEB-1501566

Editor: Alan John Stewart and Associate Editor: Bethanne Bruninga-Socular

Abstract

1. The globally distributed western honey bee (*Apis mellifera*) can reach high local abundances in both its native and introduced ranges. For instance, previous studies documented that honey bees outnumber the sum of all other floral visitors to native vegetation in Southern California.
2. To quantify potential resource competition exerted by honey bees, we used plant-pollinator network data to estimate the abundance and biomass of honey bees and native bees, and pollen removal experiments to estimate the amount of pollen removed by honey bees.
3. Honey bee biomass constituted 98% of total bee biomass across our study sites. Just two visits by honey bees resulted in the removal of more than 60% of available pollen produced by three common native plants (*Salvia mellifera*, *S. apiana* and *Phacelia distans*), and 80% of pollen was removed by the end of one day for each of the three species.
4. Based on documented relationships between pollen provision mass and bee body mass, we estimated that pollen removed by honey bees from these three plant species could produce many dozens to thousands of native bees of average size per hectare per day.
5. Our findings illustrate the potential for strong exploitative competition between honey bees and native bees, and underscore that resource consumption by honey bees should receive greater attention as a potential factor contributing to pollinator declines.

KEYWORDS

Apoidea, exploitative competition, floral visitation, intertegular distance, invasive species, plant-pollinator network, pollinator

INTRODUCTION

The western honey bee (*Apis mellifera* L.) is one of the world's most widespread species (Horn, 2006). In many regions, agricultural production depends on the management and transport of honey bees, a multi-million-dollar industry in the USA alone (Cilia, 2019; Costanza et al., 1997). Honey bee populations consist of managed colonies and,

in many locations, wild or feral populations. As super-generalist foragers, honey bees visit more plant species than any other species of pollinator (Crane, 1990; Hung et al., 2018), including many plant species in non-managed systems. A global study of pollination networks, for example, found that the western honey bee is the most common floral visitor to plants in non-managed habitats worldwide, accounting for 13% of all floral visitors (Hung et al., 2018).

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Despite the status of honey bees as a widespread and abundant introduced species (Hung et al., 2018; Russo, 2016), the ecological effects of honey bee introductions on native species remain unresolved (Beaurepaire et al., 2024; Iwasaki & Hogendoorn, 2022; Travis & Kohn, 2023). Public concern for honey bees often fails to consider their potential negative effects on native pollinators (Geldmann & González-Varo, 2018). Further, while managed honey bee colonies in some regions face increasing threats from diseases, pesticides and other anthropogenic environmental changes that reduce colony survival, numbers of managed honey bee colonies are nevertheless increasing worldwide (Halvorson et al., 2021; Osterman et al., 2021; Phiri et al., 2022). Meanwhile, at least some species of native bees are declining (Goulson et al., 2015; Sánchez-Bayo & Wyckhuys, 2019; Severns & Moldenke, 2010), although more data are needed globally to assess the spatial and taxonomic scopes of these declines (Cheshire et al., 2023).

Honey bees readily exploit high-quality resource patches (Hung, Kingston, et al., 2019) because of their large colonies and ability to recruit nestmates by communicating distance, direction and quality of floral resources (von Frisch, 1993). Cane and Tepedino (2017) demonstrated that across three summer months (June–August), a single managed honey bee colony can collect upwards of 10 kg of pollen, or enough to rear the progeny of 100,000 native bees the size of *Megachile rotundata* Fabricius, a solitary leafcutter bee whose mass, at about half that of the honey bee, is approximately average among native North American bee species (Bullock, 1999; Stubblefield et al., 1993). Using these metrics, a 40-hive apiary placed in a natural habitat could remove enough pollen each summer to provision four million *M. rotundata* offspring (Cane & Tepedino, 2017). Where honey bees reach high densities, pollen and nectar removal by honey bees seem likely to impact populations of other bees. Torné-Noguera et al. (2016), for example, showed that honey bees removed most of the pollen and nectar from two abundant scrubland plants in Garraf National Park (Spain). In addition, after accounting for variation in flower abundance, wild bee abundance declined in areas close to apiaries (Torné-Noguera et al., 2016). Experimentally elevated abundances of honey bees can reduce reproduction by native bees (Thomson, 2004), as well as reduce the abundance and alter the assemblage composition of bees visiting native plants in natural habitats (Magrach et al., 2017; Valido et al., 2019). Given that honey bees tend to focus their foraging on the most abundant floral resources (Hung, Kingston, et al., 2019), they may remove a large amount of the pollen and nectar that could otherwise be harvested by other bee species (Carneiro & Martins, 2012). While Cane and Tepedino (2017) used managed apiaries to calculate pollen consumption per hive and estimate the potential impact of honey bees on native bee populations, unmanaged feral honey bees may pose a more pervasive ecological challenge wherever they have become numerically dominant in natural and semi-natural landscapes, as has been documented in many areas around the world (e.g., Abe et al., 2011; Aguiar, 2003; Cunningham et al., 2022; Kato & Kawakita, 2004; Zárate et al., 2022). Unlike many managed apiaries, feral populations are present and active year-round, self-sustaining, and are extremely difficult to

remove once established (Oldroyd, 1998). Currently, resource consumption rates of feral honey bees in unmanaged systems represent a major knowledge gap in efforts to quantify the degree of exploitative competition between honey bees and native pollinators.

The present study leverages and builds upon a dataset of plant-pollinator interactions from unmanaged scrub ecosystems in San Diego County, California, USA, where honey bees made up 75% of all floral visitors observed visiting assemblages of predominantly native, blooming plant species (Hung et al., 2018). In this system, honey bees appear to be primarily feral (Kono & Kohn, 2015; Zárate et al., 2022) and have approximately 40% ancestry from the East African lowland honey bee subspecies (*A. mellifera scutellata* Lepeletier; Zárate et al., 2022). Conversely, the diverse native bee assemblages in this region are largely made up of solitary species (Moldenke & Neff, 1974), with females provisioning nest cells with pollen and nectar only for their own offspring. We ask two related questions: (i) what proportion of total bee biomass is currently represented by honey bees? And (ii) how much pollen do honey bees remove, and how many native bees might be produced by this quantity of pollen? We address the first question by combining published data on plant-pollinator interactions, measures of local-scale floral abundances and estimates of assemblage-level bee biomass derived from species-specific morphometric data. We address the second question by measuring daily pollen production of three locally abundant plant species and estimating the proportion of this pollen removed by honey bees. Pollen and microbes that feed on the pollen provision are essential resources for bee larval development (Keller et al., 2005; Steffan et al., 2019). The degrees to which factors such as food, weather, nesting sites, predators and pathogens limit native bee reproduction and population growth are poorly understood, but food limitation is believed to be generally important (Roulston & Goodell, 2011; Torné-Noguera et al., 2014). Combining empirical estimates of the relative biomass attained by free-living, feral honey bees with their contribution to pollen depletion in an unmanaged ecosystem is a key step in understanding the degree to which feral honey bees may be proliferating at the expense of native bees.

MATERIALS AND METHODS

Estimating relative abundance and biomass of honey bees and native pollinators

To estimate the relative biomass of honey bees and native pollinating insects, we used data from Hung, Kingston, et al. (2019), in which we recorded the identities and frequencies of insect floral visitors to all blooming plant species across 11, 1-ha plots of natural vegetation found in both large scrub reserves (five plots, internal area $\gg$ 500 ha) and small scrub fragments (six plots, internal area $<$ 40 ha) in western San Diego County in the spring and summer of 2016. In each 1-ha plot, we conducted six pollinator surveys, once every 2–4 weeks on average, across the blooming season. Each survey consisted of 1-min observations of each blooming plant species during which time the

identity of every insect with body length > 2 mm that contacted flowers within each of 15 monitored patches was documented (see Supporting Information S1.1 for details). These surveys documented a total of 13,785 floral visitors: 10,012 honey bees and 3773 non-honey bee insects (pollinator identities are reported in Hung, Cen, et al., 2019). However, because monitoring effort was equal across all blooming plant species, these observations reflect rates of visitation by each pollinator taxon to the observed patches of each flowering plant species and do not account for interspecific variation in flower abundance. To correct for this, we used data on the number of open flowers of each plant species within each 1-ha plot (Hung, Kingston, et al., 2019). We multiplied per-plot counts of pollinator individuals by the ratio of plot-level and patch-level flower abundances for each plant species to obtain estimates of the scaled, plot-level abundance of each pollinator taxon (see Supporting Information S1.1 for details). We summed estimates of pollinator abundances across survey rounds within each 1-ha plot and then averaged these abundances across the 11 study plots to obtain overall estimates of the relative abundance of each pollinator taxon, with differences among plots providing an error estimate for the overall means.

We used plot-level measures of pollinator abundances to estimate (i) the biomass of honey bees relative to all native bees combined and (ii) the mass of an average native bee in our system. We focus on bees because they made up > 90% of all floral visitors (see Results) and were the only major pollinator group in our surveys that consumed pollen as a main larval food resource (see Supporting Information S1.2). We measured the intertegular distance ('ITD'; that is, the distance between the right and left tegulae on the thorax) of every bee species or morphospecies (hereafter collectively 'species') we collected in Hung, Cen, et al. (2019), as ITD strongly correlates with bee mass (Bullock, 1999; Cane, 1987; Hagen & Dupont, 2013). Measurements were made on three haphazardly selected females of each non-eusocial species or four haphazardly selected workers of each eusocial species, when possible, using a Nikon SMZ645 microscope with an eyepiece reticle. Individuals that could not be identified to species or morphospecies were assigned species-level averages for their respective genera (18 individuals) or for all native bees (two individuals). We used the *pollimetry* package (Kendall et al., 2019) in programme R version 4.3.2 (R Core Team, 2023) to estimate the dry mass of each bee species based on its ITD, continent of origin (all from North America except honey bees), sex (males were used for 2/114 species) and taxonomic family. For each plot, we multiplied the dry mass estimate for each bee species by its estimated plot-level abundance across all surveys and then summed these products across species to derive a total bee biomass estimate. We subtracted honey bee biomass from this total to derive the biomass of native bees on each plot and then divided the latter estimate by the estimated number of native bee individuals to determine the dry mass of the average native bee within each plot. Lastly, we averaged across the 11 plots to obtain mean and error estimates of (i) the proportion of bee biomass made up of honey bees and (ii) the dry mass of the average native bee in our system. Abundance distributions across mass categories are visualised using R package *ggplot2* (Wickham, 2016).

Honey bee visitation to and pollen removal from focal native plants

To document the amount of pollen removed by honey bees, we measured floral visitation, flower production, pollen production and pollen removal for three common native plant species: two species of perennial shrubs, *Salvia mellifera* Greene and *S. apiana* Jepson (Lamiaceae), and the annual herb, *Phacelia distans* Benth. (Boraginaceae). These plants produce large floral displays of several dozen to hundreds of protandrous, hermaphroditic flowers, which are attractive to both honey bees and native insects. In early spring of 2021, we established 1-ha study plots in scrub habitat at seven sites in western San Diego County with four plots for each *Salvia* species and two plots for *P. distans* (see Supporting Information S1.3). At each plot, the focal plant species was the most abundantly blooming plant at the time of surveys. For each focal plant species, we spent one day at each plot estimating the proportion of visitors represented by honey bees. Each hour from 7:30 to 19:00 on a survey day, we haphazardly selected 3–6 focal plant individuals for floral visitor observation (i.e., 12 rounds of observations per plant species per plot). Observations lasted 1 min for each plant individual, during which time we recorded the numbers and identities of all visitors that contacted a flower, as well as the number of flowers in bloom. We pooled observations across plants observed during the same hour and then averaged the proportion of observed floral visitors represented by honey bees across the 12 rounds of observations for each plant species at each plot.

We quantified daily pollen removal in 1-ha plots by haphazardly selecting 20 individual plants (30 for *P. distans*) and covering five inflorescences on each plant with fine chiffon bags to prevent pollinator visitation. On the day prior to pollen collection, we used acrylic paint to mark the calyces of bagged flowers that would be newly open the following day. The next morning, we returned before insect visitation began (7:00–7:30), unbagged flowers and exposed unvisited male-phase flowers to one of the following five experimental treatments: (i) Fresh anthers from unvisited flowers to determine the starting quantity of pollen ('fresh' treatment)—these anthers were collected at the time we unbagged the flowers, prior to their dehiscence, to ensure that no pollen grains were lost. (ii) Anthers from flowers exposed to a full day's visitation by pollinators and collected at ca. 17:00–18:00 ('open' treatment). (iii) Anthers from flowers that were left bagged and not exposed to pollinators for the entire day to determine how much pollen is lost via air movement ('excluded' treatment). (iv) Anthers from flowers that were exposed to one visit by a pollen-foraging honey bee, here defined as when a honey bee stopped its locomotion and made physical contact with the centre of the flower. (v) Anthers from flowers that were exposed to two consecutive visits by pollen-foraging honey bees. All anthers from each treatment flower were placed into a 1.5-mL centrifuge tube and brought back to the lab. To determine the number of pollen grains remaining in flowers from each treatment, we followed a protocol modified from Delesalle and Mazer (2009). We dried the collected anthers, sonicated them in an ethanol and detergent solution to dislodge and suspend the pollen, stained pollen with fuchsin to aid visualisation and then counted four subsamples of pollen grains using a

dissecting microscope with the aid of a haemocytometer (see Supporting Information S1.4 for additional details).

To assess differences in the number of pollen grains present across experimental groups, we constructed linear mixed-effects models for each plant species in programme R, using package *plyr* (Wickham, 2011) for data organisation and package *lme4* (Bates et al., 2015) for model fitting. In these models, the fixed effect was pollination treatment and random effects included individual plant and study plot identity. In the case of *Salvia apiana*, where the random effect of plant identity caused the model to fail to converge ($\chi^2_1 = 0$ as assessed by likelihood ratio test), it was removed from the model. To improve model assumptions of normality and homoscedasticity, we used a square root transformation for *S. mellifera* pollen grains, and a 2/3 power transformation for *P. distans* pollen grains. No transformation was necessary for *S. apiana*. Significance tests on the outputs of the linear mixed-effects models were performed using packages *lmerTest* (Kuznetsova et al., 2017), *multcomp* (Hothorn et al., 2008) and *lsmeans* (Lenth, 2016). When experimental groups differed from one another, we employed least squares means tests with Šidák-adjusted significance levels (Šidák, 1967) for five experimental groups ($\alpha = 0.05$).

To assess the mass of pollen removed from each focal plant species, we first estimated the number of pollen grains removed by all floral visitors from a single flower by subtracting the mean number of grains remaining in the 'open' treatment from that in the 'excluded' treatment on the same plant. We then used a modified protocol from Roulston et al. (2000) to estimate the dry mass of single pollen grains. Briefly, we suspended clean, dry pollen samples of known mass (seven samples for *P. distans*, six samples for each *Salvia* species) in 2 mL of 30% ethanol solution, used a haemocytometer to count the number of pollen grains in 10 replicate subsamples of the solution and then divided the mass of each sample by the estimated number of grains calculated using the average of the 10 subsamples (see Supporting Information S1.5 for additional details).

Lastly, we estimated the abundance of male-phase flowers per hectare by first counting the number of open male-phase flowers on 50 inflorescences, each from a different plant, and then the number of inflorescences per individual for another 50 plants. We also counted the total number of plants with floral displays in our plots. The product of these values estimated the total number of open male-phase flowers per day in each 1-ha plot when each species is blooming abundantly.

We applied Equation (1) to the empirical estimates described above to approximate the mass of pollen removed by honey bees, per hectare of each focal plant species each day:

This method assumes that a honey bee and the average non-honey bee pollinator remove pollen at the same rate. This is conservative given that (i) honey bees were much larger than the average native bee (see Results) and (ii) all observed honey bees were workers capable of collecting pollen, whereas non-honey bee visitors included non-bee insects and male native bees, neither of which collect pollen. However, since honey bee workers made up the vast majority of all visitors to these three plant species (see Results), this assumption is unlikely to alter our main conclusions.

To estimate the error associated with the product of Equation (1), we used a bootstrap resampling approach after Reynolds and Fenster (2008) and Rodríguez-Rodríguez et al. (2013). Briefly, we randomly sampled (with replacement) values from each component (or subcomponent) of Equation (1), with sample sizes equal to the number of empirical measures for each component; then calculated the mean of sampled values within each component; and lastly calculated the product of the means. Finally, we obtained the mean, standard deviation, and 95% confidence intervals of 10,000 resampling events (see Supporting Information S1.6 for details).

Converting pollen collected by honey bees into native bees

To estimate the number of native bees that could be produced with pollen removed by honey bees, we first estimated the mass of pollen contained in a community-weighted average single nest provision in our system. The mass of nest provisions increases with the mass of adult bees, but this relationship differs among bee families (Bosch & Vicens, 2002; Johnson, 1988; Klostermeyer et al., 1973; Neff, 2008). To account for these differences, we used conversion ratios (i.e., ratio of adult dry mass to provision dry mass) reported by Neff (2008). For species belonging to genera with conversion ratios reported by Neff (2008), we assigned the averaged conversion ratio across all reported members of their respective genus. For species belonging to genera with no reported conversion ratio, we assigned the average across all reported members of their respective taxonomic family. For the Colletidae (eight species in two genera in our dataset), no conversion ratio was available for any member of this family; we thus used the average of all conversion ratios reported by Neff (2008). We removed cleptoparasites from this analysis as they do not collect pollen provisions, but rather usurp those of their bee hosts. For each bee species, we multiplied its assigned conversion ratio by its dry mass to estimate the

mg of pollen removed by honey bees per hectare per day

$$= \frac{\text{\# of flowers}}{\text{hectare}} \times \frac{\text{\# of pollen grains removed by pollinators}}{\text{flower}} \times \frac{1 \text{ mg}}{\text{\# of grains}} \times \text{proportion of visitors that were honey bees.} \quad (1)$$

dry mass of its nest provision, which consists of both pollen and nectar sugar.

The proportion of a bee's nest provision consisting of pollen varies within and among species (Westrich, 1989), and limited data exist on the composition of provisions. In light of this data gap, we follow Cane and Tepedino (2017) in using *M. rotundata* as a stand-in for the 'average' native bee. *Megachile rotundata* nest provisions consist of 47% ($\pm 11\%$) nectar sugar, 33% ($\pm 5\%$) pollen and 20% ($\pm 3\%$) nectar water by mass (Cane et al., 2011; Cane & Tepedino, 2017; Klostermeyer et al., 1973), corresponding to 41% pollen in the dry mass of provisions (i.e., with water removed). Thus, we multiplied the dry mass estimates of nest provisions by 41% to determine the dry mass of pollen in the nest provision of each species. Finally, we scaled pollen provision dry mass estimates for each species to their estimated proportional abundance in each plot (see Honey bee visitation to and pollen removal from focal native plants) and then averaged these values across the 11 plots to approximate the dry mass of pollen in a nest provision of our community-weighted average native bee.

We calculated the number of community-weighted average native bee nest provisions that could be generated using Equation (2), below:

$$\# \text{ of native bees of average size produced per hectare per day} = \frac{\text{dry mass (mg) of pollen removed by honey bees per hectare per day (from Equation 1)}}{\text{dry mass (mg) of pollen required to rear 1 community-weighted average native bee}} \quad (2)$$

To estimate the error associated with the estimate from Equation (2), we use the same bootstrap resampling approach described for Equation (1), above. For each of the 10,000 resampling events, we divided the product of Equation (1) by the mean of a

random sample (with replacement) of 11 plot-level estimates of average nest provision pollen dry mass and calculated means, standard deviations and 95% confidence intervals as described for Equation (1) (see Supporting Information S1.6 for details).

RESULTS

Abundance and biomass of honey bees relative to native bees

When we converted the abundances we observed (Hung, Kingston, et al., 2019) from equal-timed observations of each plant species to estimated 1-ha plot-level abundances using the abundance of each plant species in each plot (see Supporting Information S1.1), 83.8% (SE = 1.8%) of all floral visitors were honey bees. Native bees represented 9.8% (SE = 1.5%) of all visitors, or 58.2% (SE = 4.5%) of all non-honey bee visitors (Supporting Information S1.2). Among only bees, honey bees made up 89.5% (SE = 1.6%) of all bees, with native bees making up the remaining 10.5%. Bee dry mass estimates were as

follows: honey bee = 33.31 mg and the average native bee = 7.40 mg (SE = 1.43 mg). Estimated individual honey bee dry mass exceeded that of 96 of the 110 native bee species and 97.5% of all bee individuals across all surveys at all study plots (Figure 1). The

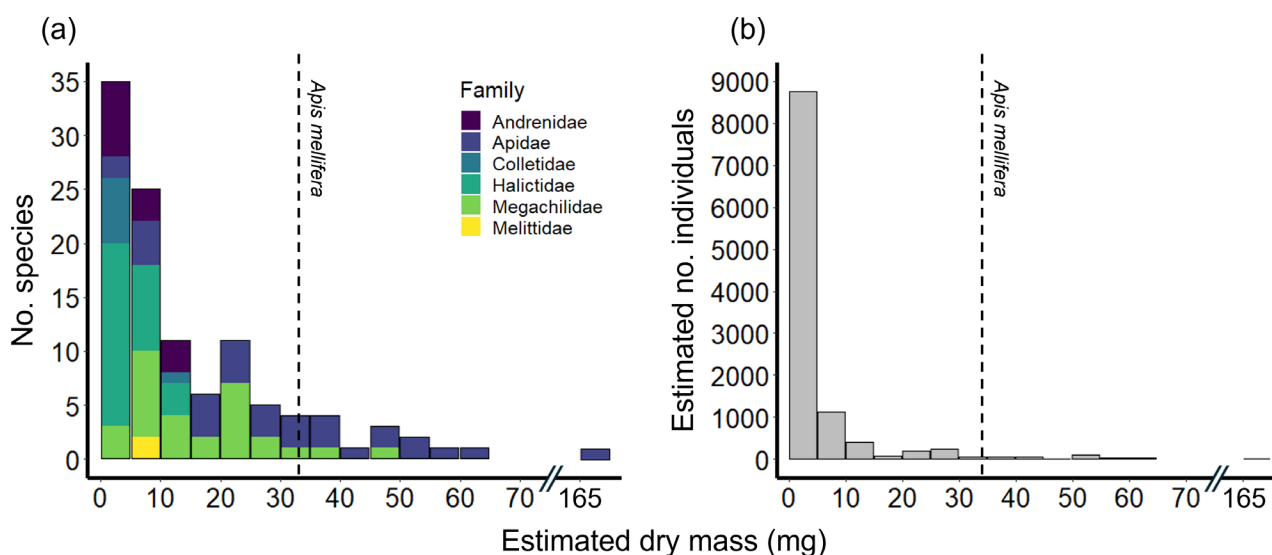


FIGURE 1 Frequency distributions of dry mass of native bees recorded in 2016. (a) Species; colours indicate taxonomic families. (b) Individuals, with estimated abundances summed across all surveys at all study plots. The dry mass of honey bees is indicated by the black dotted line on each panel.

14 species with individual dry mass exceeding that of honey bees include four bumble bee (*Bombus*) species, one carpenter bee (*Xylocopa*) species, seven digger bee (genera *Anthophora*, *Diadasia*, *Eucera*, *Habropoda* and *Xenoglossa* ('*Tetraloniella*')) species/species complexes and two leafcutter bee (*Megachile*) species. Due to their numerical dominance and relatively large body size, honey bees accounted for 97.8% (SE = 0.37%) of all bee biomass, with native bees accounting for the remaining 2.2%.

Honey bee visitation to and pollen removal from focal native plants

Honey bees were overwhelmingly the most common floral visitor to the three focal plant species (Table 1, Figure 2). Honey bees were especially abundant visitors to *Salvia*, comprising on average 93.2% (SE = 1.15%) of all visitors to *S. apiana* and 92.4% (SE = 3.80%) to *S.*

mellifera. Honey bees were less numerically dominant on *P. distans* but still made up, on average, 78.7% (SE = 1.59%) of all visitors. These high values of honey bee numerical dominance are consistent with previous pollinator surveys on these same *Salvia* species in other years (mean proportional representation by honey bees = 99% for *S. apiana* and 94% for *S. mellifera* across 2013, 2015, 2016; see Supporting Information S1.7).

Floral visitors removed the majority of pollen from the three focal species: comparing 'excluded' and 'open' pollination treatments, 77.8% (SE = 1.7%, *S. apiana*), 77.3% (SE = 1.5%, *S. mellifera*) and 81.2% (SE = 1.9%, *P. distans*) of pollen produced by male-phase flowers was removed by the end of one day (Figure 3). Relative to the amount of pollen found in the 'excluded' treatment, honey bees removed 25.6% (SE = 1.6%) of pollen from *S. apiana* flowers during the first visit, and 59.6% (SE = 1.5%) of pollen after two visits (Figure 3). Similarly, honey bees removed 28.9% (SE = 1.9%) of pollen from *S. mellifera* flowers during the first visit, and 67.3% (SE = 4.8%) of pollen after two visits. In

TABLE 1 Bootstrapped mean values for numbers of plants per hectare, male flowers per hectare, starting mass of pollen per flower, mass of pollen removed by honey bees—per flower, per plant and per hectare each day—and the number of average-sized native bees that could be produced with the pollen removed by honey bees per hectare each day.

Plant species	No. plants/ha	No. male flowers/ha	Starting mass (mg) of pollen/flower	Mass of pollen (mg) removed by honey bees/flower	Mass of pollen (g) removed by honey bees/plant/day	Mass of pollen (g) removed by honey bees/ha/day	No. average-sized native bees that can be produced with pollen removed by honey bees/ha/day
<i>Salvia apiana</i>	105 (11)	34,133 (3,70)	0.37 (0.06)	0.24 (0.009)	76.87 (4.57)	8.08 (0.98)	530 (135)
<i>Salvia mellifera</i>	208 (29)	387,568 (59,578)	0.28 (0.04)	0.19 (0.009)	380.16 (24.81)	73.96 (12.05)	4869 (1356)
<i>Phacelia distans</i>	500 (17)	6873 (575)	0.30 (0.07)	0.17 (0.007)	2.33 (0.20)	1.16 (0.11)	76 (18)

Note: Values are bootstrapped means for each plant species; standard deviations in parentheses.

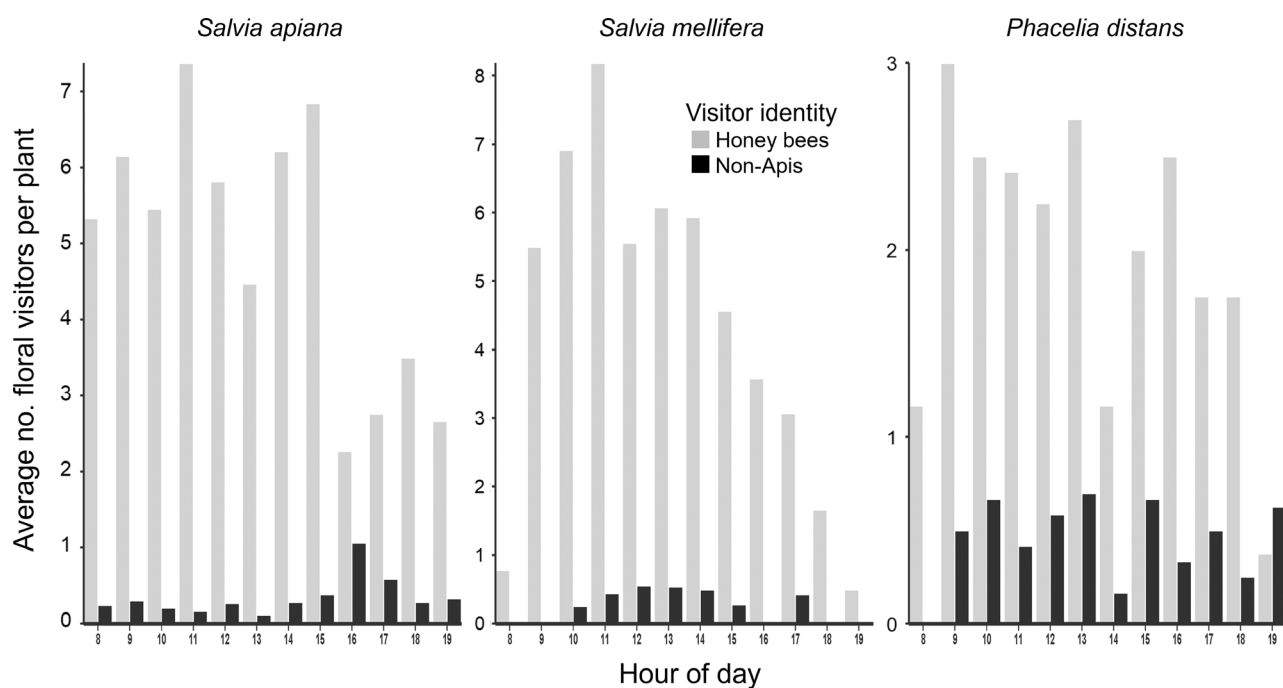


FIGURE 2 Floral visitation rates to three focal plant species in 2021. Bars for each hour of monitoring represent the mean number of foraging honey bees and native insects across all sites for each plant species.

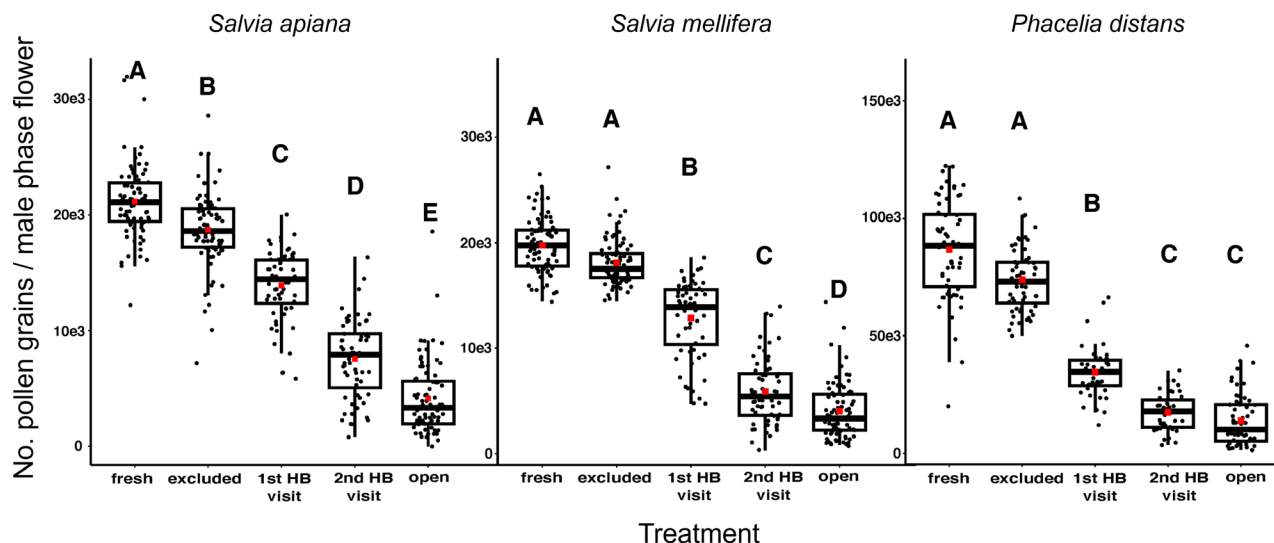


FIGURE 3 The number of pollen grains remaining within each male-phase flower following pollination treatments. Boxplots: Horizontal lines show medians; red squares show means; boxes and the whiskers represent interquartile ranges; dots represent the mean number of pollen grains per subsample for one plant. Letters indicate statistically significant differences ($\alpha = 0.05$) between treatments. Treatment groups: Fresh—beginning of the day, no visitation. Excluded—end of the day, no visitation. 1st HB Visit—remaining pollen after 1 honey bee visit. 2nd HB Visit—remaining pollen after 2 honey bee visits. Open—end of the day, after visitation.

both cases, two visits by honey bees removed significantly less pollen than the amount removed in the ‘open’ treatment. Honey bees visiting *P. distans* flowers removed 53.3% (SE = 0.6%) of pollen during the first visit and 76.3% (SE = 0.25%) after two visits; the latter value was not significantly different from the amount of pollen removed in the ‘open’ treatment. Pollinator exclusion treatments were effective: for both *S. mellifera* and *P. distans*, the average amount of pollen remaining in the ‘excluded’ treatment at the end of the day was not significantly different from that in the ‘fresh’ treatment collected at the beginning of the day. For *S. apiana*, there was a small but significant decrease (11.5%, SE = 2.4%), presumably because its long stamens, which protrude well outside of the corolla, caused pollen to rub onto the pollinator exclusion bags.

Estimated amounts of pollen removed per hectare per day by honey bees were 8.08 g for *S. apiana* (SD = 0.98 g, 95% CI = 6.14–10.00 g); 73.96 g for *S. mellifera* (SD = 12.05 g, 95% CI = 48.56–95.64 g); and 1.16 g for *P. distans* (SD = 0.11 g, 95% CI = 0.96–1.39 g) (Table 1).

Converting pollen collected by honey bees into native bees

The dry mass of pollen in a single nest provision of the community-weighted average native bee across our 1-ha study plots was 15.91 mg (SE = 3.44 mg). Using our estimates of the dry mass of pollen in nest provisions, the pollen removed by honey bees from 1-ha plots containing *S. apiana*, *S. mellifera* and *P. distans*, based on observed plant densities on our plots, could provision approximately 530 (SD = 135, 95% CI = 323–846), 4869 (SD = 1356, 95%

CI = 2709–7946), and 76 (SD = 18, 95% CI = 48–120) native bee progeny respectively, each day when these plant species are blooming abundantly (Table 1).

DISCUSSION

We estimate that western honey bees constitute an astonishing 90% of the abundance and 98% of the biomass of bees visiting flowers in native scrub habitats of San Diego County, a global bee diversity hotspot (Moldenke & Neff, 1974). Since all bees in our system require pollen and nectar for reproduction, one might extrapolate a nearly 50-fold increase in native bee biomass, and therefore abundance, if floral resources used to make non-native honey bees were instead used by native bees for reproduction. Our observation of consistently high honey bee abundances across multiple study years (Supporting Information S1.7) motivated us to estimate the amount of pollen honey bees remove from high-reward resource plants. The combination of high visitation frequency (Figure 2) and high efficiency at removing pollen (Figure 3) results in the majority of pollen from our three focal plant species being removed by honey bees. We calculate that many dozens to thousands of native bees of average size could be produced per hectare each day during the period when these plants are blooming at the densities observed at our study sites. In our experience, abundant blooming of our focal species lasts ca. 30 days in a typical year. Thus, in areas with large populations of *S. apiana*, *S. mellifera* and *P. distans*, we would expect that the pollen removed by honey bees from these species could rear approximately 15,914, 145,785 and 2290 native bee progeny per hectare, respectively, over the period of abundant bloom. Thus, the relative biomass of honey

bees and the pollen removal estimates both point to potentially large negative impacts of honey bees on native bee populations.

Although our study system experiences one of the highest abundances of honey bees in unmanaged ecosystems reported in a recent global meta-analysis (Hung et al., 2018), this situation is hardly unique. Feral honey bee colonies are thought to outnumber managed colonies globally (Visick & Ratnieks, 2023), and numerical domination of floral resources by feral honey bees is known from a diverse set of ecosystems worldwide (e.g., Abe et al., 2011; Aguiar, 2003; Kato & Kawakita, 2004). Alarming, feral honey bees may in fact be increasing in abundance in some parts of the world. In the southwestern United States, for example, recent resurvey studies suggest that feral *Apis mellifera scutellata*-hybrid honey bees have been replacing native bees at flowers of both widespread, abundant plants (Cumberland, 2019) and rare, patchily distributed ones (Portman et al., 2018).

As far as we are aware, this study is the first to estimate the biomass of honey bees (managed or feral) relative to other bees in any system of plants and their pollinators. The relative biomass of honey bees, rather than their relative abundance, might better predict honey bee impact on native bees because honey bees exceed the majority of bee species in mass and would thus be expected to require more floral resources per individual. In our system, the mass of a honey bee is > 4 times that of the average native bee when the latter is calculated based on the mass and relative frequency of each species. We note that Cane and Tepedino (2017) did not take relative abundances into consideration when designating *M. rotundata* as their average native bee. One reason for the large discrepancy in average body size is that the ca. 13% of bee species with body sizes larger than honey bees were quite rare in our system, accounting for only 2.5% of the total bee abundance (Figure 1). For example, bumble bees, which are widespread and numerically important floral visitors in many other temperate ecosystems (Hung et al., 2018), made up only 0.1% of all floral visitors in our 1-ha plots.

The observed rarity of large-bodied native bees may in part be driven by exploitative competition from honey bees. Thomson (2004, 2016, 2021) demonstrated that when honey bee hives were placed in close proximity to bumble bee colonies, bumble bees produced smaller workers and fewer reproductive individuals. In the U.K., honey bees and bumble bees also appear to compete (Elbgami et al., 2014; Goulson & Sparrow, 2009). If resource depletion by honey bees disproportionately affects larger bees (see also Torné-Noguera et al., 2016), there may be downstream impacts on pollination rendered by the floral visitor community, as larger-bodied species, in general, deposit more pollen per visit on stigmas (Földesi et al., 2021). In our system, large native bees are considered the best pollinators for *S. mellifera* (Grant & Grant, 1964). The unusual flowers of *S. apiana*, with long filaments (> 2 cm) protruding well outside of corollas, appear adapted for pollination by large carpenter bees (*Xylocopa* spp.) and perhaps bumble bees (Grant & Grant, 1964; Ott et al., 2016). Another effect of honey bees in this system is that, while honey bees are responsible for the vast majority of visitation to the three species studied here, their visits result in plant offspring with low fitness

compared to those produced by native insect pollination (Travis & Kohn, 2023). This fitness reduction appears to result from honey bees' penchant to visit more flowers on the same plant before moving to another, resulting in higher rates of self-fertilisation and inbreeding depression.

The relatively large body size of honey bees may in part contribute to the proficiency with which they remove pollen. In just two visits, honey bees remove the majority of the pollen from flowers of our three focal plant species—in particular, for *P. distans*, no significant further removal of pollen occurred after two honey bee visits. Approximately 20% of pollen remained in anthers at the end of the day for all three focal species; this level of pollen removal is about average compared to the 32 species reviewed by Johnson and Harder (2023) that distribute their pollen as individual grains. Bees may forgo collecting the remaining pollen grains if these grains prove difficult or unprofitable to extract, since the extended time necessary to collect these pollen grains might result in reduced time for nest defence (Goodell, 2003) and increased exposure to predators (Romero et al., 2011) and pathogens (Adler et al., 2018; Pritchard et al., 2021). At our study plots, honey bees and other larger-bodied bees seldom foraged for pollen from our focal plant species beyond the morning, instead seeming to almost exclusively extract nectar (authors' personal observation). This shift in foraging behaviour appears to support the notion that the leftover pollen is not profitable from the perspective of these bees.

Although our findings suggest strong resource competition exerted on native bees by honey bees, we lack several pieces of evidence that would bolster such a conclusion. First, there are no baseline data from our study area on native pollinator abundances prior to either the introduction of honey bees to California in 1853 (Watkins, 1969) or the arrival of *Apis mellifera scutellata*-hybrid feral bees into San Diego County in 1994 (Visscher et al., 1997). Second, we have no data on pollen removal by native bees in the absence of honey bees. Finally, we lack data directly demonstrating that there would be more native pollinators in the absence of honey bees. Nevertheless, it is difficult to imagine a scenario in which the population sizes of native species that rely on pollen for reproduction remain unaffected when 80% of this essential resource is removed by a non-native species that attains 98% of the assemblage's biomass.

Pollen is regarded as the primary resource that limits bee populations (Roulston & Goodell, 2011). Pollen requirements for many bee species are high (Müller et al., 2006; Neff, 2008), and the availability of floral resources predicts variation in bee abundances better than does nest site availability (Torné-Noguera et al., 2014). In areas without honey bees, pollinators often remove the majority of available pollen each day, typically within a few hours (Carvalho & Schlindwein, 2011; Larsson & Franzén, 2007; Müller et al., 2006). Therefore, it seems likely that, in the absence of honey bees in our area, the majority of pollen produced by native plants would be removed by native bees. Lastly, several studies have shown that native bees cease foraging on their preferred (and usually most abundant) pollen resource when honey bee numbers increase (Dupont et al., 2004; Magrach et al., 2017; Page & Williams, 2023a), and conversely, at least one study demonstrated an increase in native bee

visitation to a native plant species when introduced honey bees were experimentally prevented from accessing pollen for just a few hours (Carneiro & Martins, 2012).

Non-native honey bees are increasingly scrutinised for the types of negative impacts often associated with either invasive species or domesticated livestock (Cane, 2024; Carneiro & Martins, 2012; Page & Williams, 2023a, 2023b; Portman et al., 2018; Quinlan et al., 2024; Thomson, 2004, 2016, 2021). Our estimates of the relative biomass of feral honey bees, together with the estimates both here and those in Cane and Tepedino (2017) on the potential impact of pollen collection by honey bees on native bee populations, should motivate continued research into competitive interactions between honey bees and native pollinators, especially as mounting evidence suggests downstream impacts on pollination (Dupont et al., 2004; Page & Williams, 2023a; Travis & Kohn, 2023; Wang et al., 2024). Although large-scale eradication of feral honey bees may be economically and logistically challenging (Oldroyd, 1998) and possibly controversial (Beaurepaire et al., 2024), managers of sensitive habitats harbouring threatened plant-pollinator interactions (e.g., Portman et al., 2018) may increasingly need to consider methods to control feral honey bee populations as they now do for other invasive species. Our findings also contribute to ongoing discussions by policymakers and land managers regarding the appropriateness of using public land as forage for managed honey bee colonies—indeed, a recent synthesis has identified resource availability and resource requirement parameters as key data gaps in efforts to reconcile the needs of managed versus wild bees (Beaurepaire et al., 2024). In parts of the world where native pollinators are in decline, unchecked introductions of honey bees may work, in concert with other threats, to further jeopardise native bees and the crucial functions they provide.

AUTHOR CONTRIBUTIONS

Dillon J. Travis: Conceptualization; methodology; data curation; investigation; validation; formal analysis; supervision; funding acquisition; visualization; project administration; writing – original draft; writing – review and editing. **Joshua R. Kohn:** Conceptualization; methodology; investigation; validation; formal analysis; supervision; funding acquisition; project administration; writing – original draft; writing – review and editing; resources. **David A. Holway:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; writing – review and editing; formal analysis; project administration; supervision; resources. **Keng-Lou James Hung:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; supervision.

ACKNOWLEDGEMENTS

D.J.T. was supported by a research grant from the Sea and Sage Audubon Society, the Jeanne Marie Messier Memorial Endowed Fund, and a University of California Multicampus Research Programs and Initiatives grant to J.R.K. K.-L.J.H. was supported by NSF Doctoral Dissertation Improvement Grant DEB-1501566 to D.A.H. & K.-L.J.H., a Mildred E. Mathias Graduate Student Research Grant and an

Institute for the Study of Ecological and Evolutionary Climate Impacts Graduate Fellowship from the University of California Natural Reserve System, a Frontiers of Innovation Scholar Fellowship and a McElroy Fellowship from UC San Diego, and research grants from the Sea and Sage Audubon Society and the California Native Plant Society. We thank V. Apaldetti, P. Arroyo Jr., D. Barros, H. Cen, J. Davids, L. Hansen, J. Kingston, A. Lee, Y. Wang, V. Epps, J. Kesler, K. Wilson, A. Robles, D. Shrader, M. O'Connor and S. Blaker for their assistance in data collection. This work was performed in part at the University of California's Elliott Chaparral and Dawson Los Monos Canyon Reserves. Permission to collect insect and plant specimens for our study was obtained from the following entities: University of California Natural Reserve System; Open Space Parks departments in the cities of Chula Vista, La Mesa and San Diego; and the Otay-Sweetwater Unit of the San Diego National Wildlife Refuge.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw data used in this study are made available through the Open Science Framework: <https://osf.io/3cmht/>.

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REFERENCES

- Abe, T., Wada, K., Kato, Y., Makino, S. & Okochi, I. (2011) Alien pollinator promotes invasive mutualism in an insular pollination system. *Biological Invasions*, 13, 957–967.
- Adler, L.S., Michaud, K.M., Ellner, S.P., McArt, S.H., Stevenson, P.C. & Irwin, R.E. (2018) Disease where you dine: plant species and floral traits associated with pathogen transmission in bumble bees. *Ecology*, 99, 2535–2545.
- Aguiar, C.M.L. (2003) The use of floral resources by bees (Hymenoptera, Apoidea) in an area of Caatinga (Itatim, Bahia, Brazil). *Revista Brasileira de Zoologia*, 20, 457–467.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software*, 67, 1–48.
- Beaurepaire, A.L., Hogendoorn, K., Kleijn, D., Otis, G.W., Potts, S.G., Singer, T.L. et al. (2024) Avenues towards reconciling wild and managed bee proponents. *Trends in Ecology & Evolution*, 40, 7–10. Available from: <https://doi.org/10.1016/j.tree.2024.11.009>
- Bosch, J. & Vicens, N. (2002) Body size as an estimator of production costs in a solitary bee. *Ecological Entomology*, 27, 129–137.
- Bullock, S.H. (1999) Relationships among body size, wing size and mass in bees from a tropical dry Forest in México. *Journal of the Kansas Entomological Society*, 72, 426–439.
- Cane, J.H. (1987) Estimation of bee size using intertegular span (Apoidea). *Journal of the Kansas Entomological Society*, 60, 145–147.
- Cane, J.H. (2024) Honeybees prevail at native wildflowers distant from wildland apiaries. *Biological Conservation*, 296, 110732.
- Cane, J.H., Gardner, D.R. & Harrison, P.A. (2011) Nectar and pollen sugars constituting larval provisions of the alfalfa leaf-cutting bee (*Megachile rotundata*) (Hymenoptera: Apiformes: Megachilidae). *Apidologie*, 42, 401–408.
- Cane, J.H. & Tepedino, V.J. (2017) Gauging the effect of honey bee pollen collection on native bee communities. *Conservation Letters*, 10, 205–210.

- Carneiro, L.T. & Martins, C.F. (2012) Africanized honey bees pollinate and preempt the pollen of *Spondias mombin* (Anacardiaceae) flowers. *Apidologie*, 43, 474–486.
- Carvalho, A.T. & Schlindwein, C. (2011) Obligate association of an oligolectic bee and a seasonal aquatic herb in semiarid northeastern Brazil. *Biological Journal of the Linnean Society*, 102, 355–368.
- Cheshire, P.R., Fischer, E.E., Dowdy, N.J., Griswold, T.L., Hughes, A.C., Orr, M.C. et al. (2023) Completeness analysis for over 3000 United States bee species identifies persistent data gap. *Ecography*, 2023, e06584.
- Cilia, L. (2019) The plight of the honeybee: a socioecological analysis of large-scale beekeeping in the United States. *Sociologia Ruralis*, 59, 831–849.
- Costanza, R., Arge, R.D., De Groot, R., Farber, S., Grasso, M., Hannon, B. et al. (1997) The value of the world's ecosystem services and natural capital. *Nature*, 387, 253–260.
- Crane, E. (1990) *Bees and beekeeping: science, practice, and world resources*. Ithaca, NY: Comstock Pub. Associates.
- Cumberland, C. (2019) *Forty years of change in southwestern bee assemblages* (PhD). The University of New Mexico, NM, USA.
- Cunningham, S.A., Crane, M.J., Evans, M.J., Hingee, K.L. & Lindenmayer, D.B. (2022) Density of invasive western honey bee (*Apis mellifera*) colonies in fragmented woodlands indicates potential for large impacts on native species. *Scientific Reports*, 12, 3603.
- Delesalle, V.A. & Mazer, S.J. (2009) Size-dependent pollen:ovule ratios and the allometry of floral sex allocation in *Clarkia* (Onagraceae) taxa with contrasting mating systems. *American Journal of Botany*, 96, 968–978.
- Dupont, Y.L., Hansen, D.M., Valido, A. & Olesen, J.M. (2004) Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biological Conservation*, 118, 301–311.
- Elbgami, T., Kunin, W.E., Hughes, W.O.H. & Biesmeijer, J.C. (2014) The effect of proximity to a honeybee apiary on bumblebee colony fitness, development, and performance. *Apidologie*, 45, 504–513.
- Földesi, R., Howlett, B.G., Grass, I. & Batáry, P. (2021) Larger pollinators deposit more pollen on stigmas across multiple plant species—a meta-analysis. *Journal of Applied Ecology*, 58, 699–707.
- Geldmann, J. & González-Varo, J.P. (2018) Conserving honey bees does not help wildlife. *Science*, 359, 392–393.
- Goodell, K. (2003) Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia*, 134, 518–527.
- Goulson, D., Nicholls, E., Botias, C. & Rotheray, E.L. (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, 347, 1255957.
- Goulson, D. & Sparrow, K.R. (2009) Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *Journal of Insect Conservation*, 13, 177–181.
- Grant, K.A. & Grant, V. (1964) Mechanical isolation of *Salvia apiana* and *Salvia mellifera* (Labiatae). *Evolution*, 18, 196–212.
- Hagen, M. & Dupont, Y.L. (2013) Inter-tegular span and head width as estimators of fresh and dry body mass in bumblebees (*Bombus* spp.). *Insectes Sociaux*, 60, 251–257.
- Halvorson, K., Baumung, R., Leroy, G., Chen, C. & Boettcher, P. (2021) Protection of honeybees and other pollinators: one global study. *Apidologie*, 52, 535–547.
- Horn, T. (2006) *Bees in America: how the honey bee shaped a nation*. Pbk. ed. Lexington, KY: University Press of Kentucky.
- Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363.
- Hung, K.-L.J., Cen, H.J., Lee, A. & Holway, D.A. (2019) *Plant-pollinator interaction networks in coastal sage scrub reserves and fragments in San Diego*. La Jolla, CA: UC San Diego Library Digital Collections.
- Hung, K.-L.J., Kingston, J.M., Albrecht, M., Holway, D.A. & Kohn, J.R. (2018) The worldwide importance of honey bees as pollinators in natural habitats. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20172140.
- Hung, K.-L.J., Kingston, J.M., Lee, A., Holway, D.A. & Kohn, J.R. (2019) Non-native honey bees disproportionately dominate the most abundant floral resources in a biodiversity hotspot. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182901.
- Iwasaki, J.M. & Hogendoorn, K. (2022) Mounting evidence that managed and introduced bees have negative impacts on wild bees: an updated review. *Current Research in Insect Science*, 2, 100043.
- Johnson, M.D. (1988) The relationship of provision weight to adult weight and sex ratio in the solitary bee, *Ceratina calcarata*. *Ecological Entomology*, 13, 165–170.
- Johnson, S.D. & Harder, L.D. (2023) The economy of pollen dispersal in flowering plants. *Proceedings of the Royal Society B: Biological Sciences*, 290, 20231148.
- Kato, M. & Kawakita, A. (2004) Plant-pollinator interactions in New Caledonia influenced by introduced honey bees. *American Journal of Botany*, 91, 1814–1827.
- Keller, I., Fluri, P. & Imdorf, A. (2005) Pollen nutrition and colony development in honey bees: part 1. *Bee World*, 86, 3–10.
- Kendall, L.K., Rader, R., Gagic, V., Cariveau, D.P., Albrecht, M., Baldock, K.C.R. et al. (2019) Pollinator size and its consequences: robust estimates of body size in pollinating insects. *Ecology and Evolution*, 9, 1702–1714.
- Klostermeyer, E.C., Mech, S.J. & Rasmussen, W.B. (1973) Sex and weight of *Megachile rotundata* (Hymenoptera: Megachilidae) progeny associated with provision weights. *Journal of the Kansas Entomological Society*, 46, 536–548.
- Kono, Y. & Kohn, J.R. (2015) Range and frequency of Africanized honey bees in California (USA). *PLoS One*, 10, e0137407.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2017) lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26.
- Larsson, M. & Franzén, M. (2007) Critical resource levels of pollen for the declining bee *Andrena hattorfiana* (Hymenoptera, Andrenidae). *Biological Conservation*, 134, 405–414.
- Lenth, R.V. (2016) Least-squares means: the R package lsmeans. *Journal of Statistical Software*, 69, 1–33.
- Magrach, A., González-Varo, J.P., Boiffier, M., Vilà, M. & Bartomeus, I. (2017) Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nature Ecology & Evolution*, 1, 1299–1307.
- Moldenke, A.R. & Neff, J.L. (1974) The bees of California, a catalogue with special reference to pollination and ecological research. In: *Origin and structure of ecosystems, technical reports*. Santa Cruz, CA: University of California Press.
- Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C. & Dorn, S. (2006) Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee–flower relationships. *Biological Conservation*, 130, 604–615.
- Neff, J.L. (2008) Components of nest provisioning behavior in solitary bees (Hymenoptera: Apoidea). *Apidologie*, 39, 30–45.
- Oldroyd, B.P. (1998) Controlling feral honey bee, *Apis mellifera* L. (Hymenoptera: Apidae), populations in Australia: methodologies and costs. *Australian Journal of Entomology*, 37, 97–100.
- Osterman, J., Aizen, M.A., Biesmeijer, J.C., Bosch, J., Howlett, B.G., Inouye, D.W. et al. (2021) Global trends in the number and diversity of managed pollinator species. *Agriculture, Ecosystems & Environment*, 322, 107653.
- Ott, D., Hühn, P. & Claßen-Bockhoff, R. (2016) *Salvia apiana*—a carpenter bee flower? *Flora*, 221, 82–91.
- Page, M.L. & Williams, N.M. (2023a) Honey bee introductions displace native bees and decrease pollination of a native wildflower. *Ecology*, 104, e3939.
- Page, M.L. & Williams, N.M. (2023b) Evidence of exploitative competition between honey bees and native bees in two California landscapes. *Journal of Animal Ecology*, 92, 1802–1814.

- Phiri, B.J., Fèvre, D. & Hidano, A. (2022) Uptrend in global managed honey bee colonies and production based on a six-decade viewpoint, 1961–2017. *Scientific Reports*, 12, 21298.
- Portman, Z.M., Tepedino, V.J., Tripodi, A.D., Szalanski, A.L. & Durham, S.L. (2018) Local extinction of a rare plant pollinator in southern Utah (USA) associated with invasion by Africanized honey bees. *Biological Invasions*, 20, 593–606.
- Pritchard, Z.A., Hendriksma, H.P., St Clair, A.L., Stein, D.S., Dolezal, A.G., O'Neal, M.E. et al. (2021) Do viruses from managed honey bees (Hymenoptera: Apidae) endanger wild bees in native prairies? *Environmental Entomology*, 50, 455–466.
- Quinlan, G.M., Doser, J.W., Kammerer, M.A. & Grozinger, C.M. (2024) Estimating genus-specific effects of non-native honey bees and urbanization on wild bee communities: a case study in Maryland, United States. *Science of the Total Environment*, 953, 175783.
- R Core Team. (2023) R: a language and environment for statistical computing.
- Reynolds, R.J. & Fenster, C.B. (2008) Point and interval estimation of pollinator importance: a study using pollination data of *Silene caroliniana*. *Oecologia*, 156, 325–332.
- Rodríguez-Rodríguez, M.C., Jordano, P. & Valido, A. (2013) Quantity and quality components of effectiveness in insular pollinator assemblages. *Oecologia*, 173, 179–190.
- Romero, G.Q., Antiqueira, P.A.P. & Koricheva, J. (2011) A meta-analysis of predation risk effects on pollinator behaviour. *PLoS One*, 6, e20689.
- Roulston, T.H., Cane, J.H. & Buchmann, S.L. (2000) What governs protein content of pollen: pollinator preferences, pollen–pistil interactions, or phylogeny? *Ecological Monographs*, 70, 617–643.
- Roulston, T.H. & Goodell, K. (2011) The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, 56, 293–312.
- Russo, L. (2016) Positive and negative impacts of non-native bee species around the world. *Insects*, 7, 69.
- Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: a review of its drivers. *Biological Conservation*, 232, 8–27.
- Severns, P.M. & Moldenke, A.R. (2010) Management tradeoffs between focal species and biodiversity: endemic plant conservation and solitary bee extinction. *Biodiversity and Conservation*, 19, 3605–3609.
- Šidák, Z. (1967) Rectangular confidence regions for the means of multivariate normal distributions. *Journal of the American Statistical Association*, 62, 626–633.
- Steffan, S.A., Dharampal, P.S., Danforth, B.N., Gaines-Day, H.R., Takizawa, Y. & Chikaraishi, Y. (2019) Omnivory in bees: elevated trophic positions among all major bee families. *The American Naturalist*, 194, 414–421.
- Stubblefield, J.W., Seger, J., Wenzel, J.W. & Heisler, M.M. (1993) Temporal, spatial, sex-ratio and body-size heterogeneity of prey species taken by the beewolf *Philanthus sanbornii* (Hymenoptera: Sphecidae). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 339, 397–423.
- Thomson, D. (2004) Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology*, 85, 458–470.
- Thomson, D.M. (2016) Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters*, 19, 1247–1255.
- Thomson, D.M. (2021) Novel data support model linking floral resources and honey bee competition with bumble bee abundances in coastal scrub. *Journal of Pollination Ecology*, 27, 47–56.
- Torné-Noguera, A., Rodrigo, A., Arnan, X., Osorio, S., Barril-Graells, H., Da Rocha-Filho, L.C. et al. (2014) Determinants of spatial distribution in a bee community: nesting resources, flower resources, and body size. *PLoS One*, 9, e97255.
- Torné-Noguera, A., Rodrigo, A., Osorio, S. & Bosch, J. (2016) Collateral effects of beekeeping: impacts on pollen–nectar resources and wild bee communities. *Basic and Applied Ecology*, 17, 199–209.
- Travis, D.J. & Kohn, J.R. (2023) Honeybees (*Apis mellifera*) decrease the fitness of plants they pollinate. *Proceedings of the Royal Society B: Biological Sciences*, 290, 20230967.
- Valido, A., Rodríguez-Rodríguez, M.C. & Jordano, P. (2019) Honeybees disrupt the structure and functionality of plant–pollinator networks. *Scientific Reports*, 9, 4711.
- Visick, O.D. & Ratnieks, F.L.W. (2023) Density of wild honey bee, *Apis mellifera*, colonies worldwide. *Ecology and Evolution*, 13, e10609.
- Visscher, P.K., Vetter, R.S. & Baptista, F.C. (1997) Africanized bees, 1990–1995: initial rapid invasion has slowed in the U.S. *California Agriculture*, 51, 22–24.
- von Frisch, K. (1993) *The dance language and orientation of bees*. 1st Harvard University Press pbk. ed. Harvard University Press, Cambridge, MA.
- Wang, L.-L., Huang, Z.Y., Dai, W.-F., Yang, Y.-P. & Duan, Y.-W. (2024) Mixed effects of honey bees on pollination function in the Tibetan alpine grasslands. *Nature Communications*, 15, 8164.
- Watkins, L.H. (1969) John S. Harbison: California's first modern beekeeper. *Agricultural History*, 43, 239–248.
- Westrich, P. (1989) *Die Wildbienen Baden-Württembergs*. Stuttgart: E. Ulmer.
- Wickham, H. (2011) The Split-apply-combine strategy for data analysis. *Journal of Statistical Software*, 40, 1–29.
- Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.
- Zárate, D., Lima, T.G., Poole, J.D., Calfee, E., Burton, R.S. & Kohn, J.R. (2022) Admixture in Africanized honey bees (*Apis mellifera*) from Panamá to San Diego, California (U.S.A.). *Ecology and Evolution*, 12, e8580.

SUPPORTING INFORMATION

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

Data S1. Supplemental methods and auxiliary data.

How to cite this article: Travis, D.J., Kohn, J.R., Holway, D.A. & Hung, K.-L.J. (2025) Pollen exploitation by non-native, feral honey bees: Potential consequences for interspecific competition. *Insect Conservation and Diversity*, 18(6), 1109–1119. Available from: <https://doi.org/10.1111/icad.12858>