Honey bee introductions displace native bees and decrease pollination of a native wildflowe

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March 07, 2024

Received: 14 March 2022 | Revised: 6 October 2022 | Accepted: 13 October 2022

DOI: 10.1002/ecy.3939

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Honey bee introductions displace native bees and decrease pollination of a native wildflower

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Funding information
Division of Environmental Biology, Grant/Award Number: 1556885; U.S. Department of Defense, Grant/Award Number: NDSEG Fellowship

Handling Editor: Jessica R. K. Forrest

Abstract

Introduced species can have cascading effects on ecological communities, but indirect effects of species introductions are rarely the focus of ecological studies. For example, managed honey bees (*Apis mellifera*) have been widely introduced outside their native range and are increasingly dominant floral visitors. Multiple studies have documented how honey bees impact native bee communities through floral resource competition, but few have quantified how these competitive interactions indirectly affect pollination and plant reproduction. Such indirect effects are hard to detect because honey bees are themselves pollinators and may directly impact pollination through their own floral visits. The potentially huge but poorly understood impacts that non-native honey bees have on native plant populations combined with increased pressure from beekeepers to place hives in U.S. National Parks and Forests makes exploring impacts of honey bee introductions on native plant pollination of pressing concern. In this study, we used experimental hive additions, field observations, as well as single-visit and multiple-visit pollination effectiveness trials across multiple years to untangle the direct and indirect impacts of increasing honey bee abundance on the pollination of an ecologically important wildflower, *Camassia quamash*. We found compelling evidence that honey bee introductions indirectly decrease pollination by reducing nectar and pollen availability and competitively excluding visits from more effective native bees. In contrast, the direct impact of honey bee visits on pollination was negligible, and, if anything, negative. Honey bees were ineffective pollinators, and increasing visit quantity could not compensate for inferior visit quality. Indeed, although the effect was not statistically significant, increased honey bee visits had a marginally negative impact on seed production. Thus, honey bee introductions may erode longstanding plant-pollinator mutualisms, with negative consequences for plant reproduction. Our study calls for a more thorough understanding of the indirect effects of species introductions and more careful coordination of hive placements.

KEYWORDS
competition, conservation, honey bee, invasive species, mutualism, native bee, pollen deposition, pollination, single visit effectiveness, wild pollinators

INTRODUCTION

Introduced and invasive species are fundamentally altering the structure of ecological communities (Elton, 1958; Gallardo et al., 2016; O'Dowd et al., 2003), leading to increased species extinctions and biodiversity loss (Bellard et al., 2016; Capinha et al., 2015). In addition to shifting community composition, exotic species can impact ecosystem functioning by altering the growth and fitness of primary producers and become costly agricultural pests (Cameron et al., 2016; Paini et al., 2016). However, the impacts of exotic species may be more nuanced when they engage in keystone mutualisms like pollination. In these cases, there is potential for direct negative impacts through competition with native species for shared resources (Mallinger et al., 2017; Thomson & Page, 2020) but also potential to benefit other species through interactions that increase primary productivity (Vilà et al., 2011) and plant reproduction (Hanna et al., 2013). Indeed, recent meta-analyses of the invasive species literature largely ignore exotic mutualists (Mollot et al., 2017), and we are only beginning to understand the impacts of invasive species on mutualistic interactions (Geslin et al., 2017; Valdovinos et al., 2018).

The impacts of exotic species are even more contentious when the introduced species is actively managed for recognized benefits to humanity. For example, growing demand for agricultural pollination has led to steady increases in managed populations of the European honey bee (*Apis mellifera*) (Aizen & Harder, 2009), which has become a dominant floral visitor in many plant communities worldwide (Herrera, 2020; Hung et al., 2018). Despite mounting evidence that honey bees compete with wild bees for floral resources (Cane & Tepedino, 2016; Carneiro & Martins, 2012; Thomson & Page, 2020) with potential consequences for plant-pollinator interactions (Geslin et al., 2017; Valdovinos et al., 2018; Valido et al., 2019) and wild bee reproduction (Hudewenz & Klein, 2015; Thomson, 2004), the importance of honey bees as pollinators has led beekeeping to be promoted and even subsidized in some natural habitats (Geslin et al., 2017). However, the importance of honey bees does not automatically imply that honey bee introductions will benefit plant populations (Ollerton et al., 2012). Indeed, we currently lack robust studies investigating how honey bee introductions impact pollination and this knowledge gap limits our ability to inform conservation policies that safeguard plant and pollinator populations.

Assessing the overall impact of honey bee introductions on pollination is complicated because abundant honey bees can influence pollination directly, through their flower visits, but also indirectly, by competitively influencing visits from other pollinators. Pollination is expected to increase with increased floral visitation, and honey bees visit flowers frequently (Hung et al., 2018). However, a handful of studies have documented direct negative effects of high visitation rates by introduced pollinators, whereby increased visits increase pollen deposition but also damage stigmas (Sáez et al., 2014) or lead to clogging of styles with growing pollen tubes (Magrach et al., 2017), ultimately reducing successful reproduction. Honey bees can also damage flowers while nectar robbing, increasing floral abortion (Carbonari et al., 2009). In addition to visit numbers, the relative quality of visits (i.e., pollination effectiveness) also influences pollination (King et al., 2013), and honey bees can be ineffective at depositing the pollen they extract (Wilson & Thomson, 1991). Though their impacts might be less dramatic than direct floral damage, ineffective pollinators can indirectly decrease pollination by reducing pollen available for deposition by more effective visitors (Harder & Barrett, 1995; Harder & Thomson, 1989; Minnaar et al., 2019). Furthermore, regardless of their relative pollination effectiveness, honey bees can deplete floral rewards that attract pollinators (Carneiro & Martins, 2012; Paton, 1993), thus diminishing other pollinator visits (Hansen et al., 2002; Vaughton, 1996).

These direct and indirect effects can add to one another, or they can cancel each other out if effects are of opposite sign but similar magnitude (Strauss, 1991). Quantifying both direct and indirect impacts is needed to understand overall fitness consequences for plants, but few studies of honey bee introductions carefully partition direct and indirect effects. Indeed, across 29 studies of honey bee effects on pollination identified by Mallinger et al. (2017), all but four were purely correlative studies and none investigated both direct and indirect effects of honey bee abundance simultaneously. Studies that investigate both direct and indirect effects could shed light on how impacts vary across systems. For example, the generally positive direct effect of honey bee visits may be of greater importance in the absence of competition; in cases where native pollinators have become rare or locally extinct, honey bees often increase pollination (Hanna et al., 2013; Lomov et al., 2010) and can even "rescue" plant populations from reproductive failure in isolated habitat fragments (Dick, 2001). However, negative indirect effects may occur and even outweigh direct effects when honey bees competitively displace native pollinators, especially when honey bees are ineffective substitutes (Page et al., 2021).

In this study, we investigated whether honey bee introductions in montane meadows competitively displace native bees and impact pollination of *Camassia quamash* (Liliaceae), an herbaceous perennial plant which is an important floral resource for native bees

(Parachnowitsch & Elle, 2005) and culturally important within indigenous communities in North America (Carney et al., 2021; Turner & Kuhnlein, 1983). We sampled meadows in the Tahoe National Forest, an area where U.S. policy changes may soon allow for increased hive densities (United States Code of Federal Regulations, 2013). Using observational data of plant-pollinator interactions, experimental honey bee introductions, and a series of pollination experiments across multiple years we asked: (i) Do honey bees and native bees vary in their single-visit pollination effectiveness?; (ii) What is the direct effect of increasing honey bee visits on *C. quamash* pollination?; (iii) Does increasing honey bee abundance alter pollen and nectar availability and native bee visits to *C. quamash* flowers?; and (iv) What is the overall impact of increased honey bee abundance on *C. quamash* pollination?

METHODS

Study system

We studied the impact of honey bee introductions in montane meadows in the Central Sierra Nevada (39°34′12″ N, 120°20′60″ W). We chose this study system because it lacks feral honey bees. This allowed us to select meadows based on their proximity to seasonal apiaries, generating a gradient in honey bee abundance. We chose *C. quamash* (Liliaceae) as a focal study species because of its consistent abundance and its ecological and cultural importance. *C. quamash* is a long-lived perennial plant distributed across Western North America. Plants produce 8–16 flowers that open sequentially over multiple days. Each flower has one style and multiple ovules. Flowers are visited by a diverse community of insect pollinators (Parachnowitsch & Elle, 2005). Although *C. quamash* is self-compatible, plants receiving outcross pollen set considerably more seed (Gielens et al., 2014).

Field methods

In 2019, we selected 15 meadows, each >500 m apart, which varied in honey bee abundance across space and time due to their proximity to four seasonal apiaries (Appendix S1: Figure S1). For three of these apiaries, we worked with a local beekeeper to experimentally introduce 20 hives at three locations halfway through the blooming period of *C. quamash*. These apiaries were located between 0 and 8 km from meadows in the southern area of our study region. We also identified an additional apiary with approximately 100 hives located between 1 and 7 km from sites in the northern area of our study region, which was present throughout our sampling. Across these meadows, we surveyed pollinator visitation patterns from May to July. Most sites were sampled two to four times, but some were sampled up to seven times if the *C. quamash* bloom lasted long enough.

At each site, we sampled one-hectare subplots that varied in floral species composition but contained *C. quamash* and restricted sampling to only sunny or partly cloudy days when average wind speeds were below 5 m/s and temperatures were above 13°C. To assess the overall abundance of honey bees and native bees, we netted active flower visitors while walking 100 m transects for two 30-min periods (one between 8:00–12:00 and one between 12:00–16:00). All floral visitors were euthanized and returned to the lab for identification, except for *Bombus* queens which we identified in the field and released. To assess honey bee and native bee visitation to *C. quamash*, we conducted timed observations of 8–12 flowering *C. quamash* focal plants, noting all visitors in a 10-min period. All focal plant observations occurred from 11:00 to 13:00, in-between morning and afternoon netting transects. Before observing a plant, we used tape to mark which flowers were open on the inflorescence during observations. At the end of each sampling day, we measured pollen and nectar availability in one to three flowers on each of 10–20 open-pollinated *C. quamash* plants and 10–20 unvisited control plants which were bagged on site arrival. We measured pollen availability as the proportion of dehisced anthers with pollen visible to the naked eye and measured nectar availability using 1 μl capillary tubes.

Measuring pollination and seed set

At the end of each sampling day, we collected one style from a flower on 12 pre-marked *C. quamash* plants and mounted styles on fuchsin-tinted gelatin slides (Kearns & Inouye, 1993). We counted the number of conspecific and heterospecific pollen grains on stigmas using a compound light microscope (Nikon Eclipse 80i, Nikon Instruments Inc.). Seventy-two hours following pollinator observations and after the initiation of pollen tube growth, we collected a second style from these same pre-marked plants into 70% ethanol. In the lab, we softened styles with 8 M NaOH at 35°C for 1 h and stained pollen tubes by placing softened styles in a solution of 0.05% aniline blue in 0.1 M KH_2PO_4 for 24 h. We squashed styles beneath cover slips on microscope slides and counted pollen tubes near the base of styles using epifluorescence microscopy (Nikon Eclipse 80i, Nikon Instruments Inc.). Two weeks after conducting pollinator observations we collected fruits from these same plants and assessed seed set per fruit by scoring ovules as fertilized or unfertilized.

Single-visit effectiveness and controlled honey bee visit experiments

To assess the relative quality of honey bee visits and their direct contribution to *C. quamash* pollination, we performed two field experiments. In 2019, we conducted a controlled multiple-visit experiment to isolate the direct relationship between increasing honey bee visits and *C. quamash* pollination in one of the meadows where hives were introduced. In 2020, we returned to a different meadow, where honey bee abundance was more moderate, and assessed the single-visit pollination effectiveness of honey bees and other insect visitors. In both years, we bagged a selection of plants to prevent visitation and conducted observations from 7:00 until 16:00 across several days. For controlled honey bee visit experiments, we allowed a randomly assigned number of honey bee visits (between 0 and 20) to freshly opened flowers and all other visitors were excluded (i.e., swatted away). For single-visit effectiveness experiments, we allowed a single visit from different visitors, noting the pollinator identity and aspects of its visit behavior (described in Appendix S1: Table S1). Because we did not want to impact an insect's visit by capturing it, our identifications were done in the field. We grouped visitors into several broad categories: Large-bodied *Andrena* spp., *A. mellifera*, *Bombus* spp., *Halictus* spp., *Osmia* spp., "Small dark bees," and syrphid flies. The category "Small dark bees" comprised primarily *Lasioglossum* spp. and small-bodied *Andrena* spp. For both field experiments, we re-bagged plants to prevent further visitation after experimental visits had concluded, collected fruits 2 weeks later, and counted fertilized ovules.

Data analysis

First, to confirm that our study design impacted honey bee abundance as intended, we assessed whether distance to nearest apiary predicted honey bee abundance and visitation to *C. quamash*. Apiary distance was highly correlated with the number of honey bees observed during netting transects (Pearson's $r = -0.652$, $p < 0.001$, $N = 37$ site samples) and, according to a linear mixed effects model with apiary distance as a fixed effect and site and sample round as random effects, apiary distance was strongly associated with honey bee visits to *C. quamash* focal plants ($\chi^2 = 22.199$, df $= 1$, $p < 0.001$). We also checked whether honey bee and native bee visitation to *C. quamash* were spatially autocorrelated. We did not detect spatial autocorrelation in mean native bee visitation rates to *C. quamash* flowers (Moran's $I = -0.049$, $p = 0.852$). Mean honey bee visitation rates were positively spatially autocorrelated (Moran's $I = 0.190$, $p < 0.001$). However, this result is to be expected given the strong impact of distance to nearest apiary on honey bee visitation rates.

To assess whether bees varied in their effectiveness as pollinators of *C. quamash*, we first confirmed that pollinator taxon was an important predictor of effectiveness using a generalized linear model. We modeled seed set as a binomial response where successes were flowers that produced fertilized ovules and failures were flowers that produced no fertilized ovules. Flies and large-bodied *Andrena* spp. were infrequent visitors (Appendix S1: Table S1), so we removed their visits from the analysis. Our maximal model used three predictors: (i) the pollinator taxon observed, (ii) whether the stigma was contacted, and (iii) the day of the observation. Pollinator taxa varied in how often they contacted stigmas (Appendix S1: Table S1) and these two variables likely explain much of the same variation. Despite potential issues of collinearity, we included both variables in our initial maximal models because we wanted to understand which variables were better predictors of pollinator effectiveness. After constructing maximal models, we tested for significance of predictors by stepwise model simplification. To assess the relative effectiveness of different taxa we performed pairwise χ^2 tests comparing the proportions of visits resulting in fertilized seeds. All analyses were conducted in R (R Core Team, 2022).

Using data from the controlled multiple-visit experiment described above, we assessed the direct relationship between increasing honey bee visits and *C. quamash* pollination by fitting a generalized linear mixed effects model (GLMM), which included the number of honey bee visits as a fixed effect as well as date and plant ID as separate random effects to account for non-independence of flowers observed on the same plant and/or day. We modeled *C. quamash* pollination as a binomial response: successes were flowers with fertilized ovules and failures were flowers with no fertilized ovules.

We evaluated the association between increasing honey bee abundance and pollen and nectar availability in *C. quamash* flowers by fitting two GLMMs, which included as fixed effects (i) the abundance of honey bees in meadows, (ii) the abundance of native bees in meadows, and (iii) to control for baseline pollen and nectar resources, either the mean pollen availability (measured as the proportion of dehisced anthers with pollen) or the mean nectar availability in unvisited bagged flowers. Both models also included site and sample round as separate random effects. Data collectors varied in their ability to extract nectar from flowers, so we also included data collector as an additional fixed effect in our model of nectar availability. Nectar and pollen data were zero-inflated, so we modeled nectar and pollen availability as presence/absence binary responses.

We assessed the impact of honey bee introductions on honey bee and native bee visitation rates to *C. quamash* focal plants by fitting separate linear mixed effects models, which each included honey bee abundance as a fixed effect and site and sample round as separate random effects. We fit models using the lmer() function in the lme4 package (Bates et al., 2015). For all models, we tested for significance using likelihood ratio tests.

We determined the association between native bee and honey bee *C. quamash* visitation and three measures of pollination: pollen deposition, pollen tubes, and seed set. Because these measures were taken from the same plants, but not necessarily the same flowers, we performed separate analyses using GLMMs. We considered two measures of *C. quamash* visitation: visitation rates to focal plants and the abundance of *C. quamash* visits summed across morning and afternoon netting transects. We chose to use the latter variable because it offered a more complete picture of the visitor community across a full day of pollination. As such, each model of pollination included as fixed effects (i) the abundance of honey bees visiting *C. quamash* and (ii) and the abundance of native bees visiting *C. quamash*. We also included random intercepts for site and sample round. Native bee abundance and honey bee abundance were strongly negatively correlated and likely explain much of the same variation. Removing either variable increases the statistical significance of the remaining predictor, but we chose to retain both variables in our models of pollination to keep our analysis conservative. Pollen deposition and pollen tube data were over-dispersed, so we modeled responses using negative binomial distributions. We modeled seed set as a binary response where fertilized ovules were successes and unfertilized ovules were failures and included plant and flower nested within plant as random effects to account for non-independence of flowers on the same plant and ovules within the same flower. For all models, we used the glmmTMB package (Brooks et al., 2017), and calculated *p*-values using likelihood ratio tests.

RESULTS

During 96 half-hour netting periods along standard 100 m transects, we recorded 791 honey bees and 2329 native bees (comprising 116 species) visiting 14 plant species across 15 meadows in the Central Sierra Nevada in California, USA (Appendix S1: Table S2). We use the term "native" to describe all non-*Apis* bees. To our knowledge, all 116 species are indeed native to our study region. Honey bee abundance in meadows, measured as the total number of honey bees visiting flowering plants during morning and afternoon netting transects, ranged from 0 to 184 bees per hour per 100 m transect while the abundance of native bees ranged from 10 to 260 bees. The abundance of honey bees visiting *C. quamash* ranged from 0 to 65 bees and native bees ranged from 0 to 63 bees. Visitation to *C. quamash* focal plants ranged from 0 to 6 bees per 10-min observation period.

Comparative single-visit effectiveness of honey bees and native bees

During single-visit effectiveness trials, we observed 96 visits from five different pollinator taxa (Appendix S1: Table S3). Taxa differed in their single-visit effectiveness as pollinators and honey bees were among the least effective (Figure 1). Specifically, *Bombus* spp. and *Osmia* spp. were both significantly more effective than honey bees and unvisited controls (Appendix S1: Table S3). "Small dark bees," which mostly comprised *Lasioglossum* and

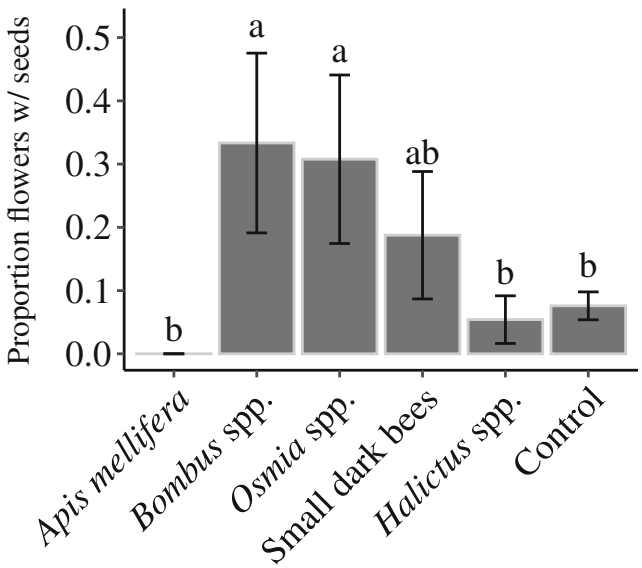

FIGURE 1 Single-visit effectiveness, measured as the proportion of visits resulting in fertilized seeds, for different insects visiting *Camassia quamash*. Pollinator taxa were compared using Pearson's χ^2 tests. *Bombus* spp. and *Osmia* spp. were more effective than *Apis mellifera* (*Bombus* spp. $\chi^2 = 6.923$, df = 1, $p = 0.009$; *Osmia* spp. $\chi^2 = 6.359$, df = 1, $p = 0.012$), *Halictus* spp. (*Bombus* spp. $\chi^2 = 6.577$, df = 1, $p = 0.010$; *Osmia* spp. $\chi^2 = 5.861$, df = 1, $p = 0.015$), and unvisited controls (*Bombus* spp. $\chi^2 = 8.502$, df = 1, $p = 0.004$; *Osmia* spp. $\chi^2 = 7.462$, df = 1, $p = 0.006$), but were as effective as "Small dark bees." "Small dark bees" were marginally more effective than honey bees ($\chi^2 = 3.702$, df = 1, $p = 0.054$). No other comparisons were statistically significant. Letters above bars indicate significance for pairwise comparisons at $p < 0.05$. Error bars show standard error. For sample sizes, see Appendix S1: Table S1.

Andrena, were marginally more effective than honey bees, but were as effective as controls and other pollinator groups. Pollinators also varied in how often they contacted stigmas and other aspects of visit behavior (Appendix S1: Table S1). 76.7% of native bees contacted stigmas during single-visit trials compared to only 14.6% of honey bees. Honey bees almost exclusively collected nectar, sometimes "robbing" plants by visiting from behind petals (Appendix S1: Figure S2), whereas native bees did not rob nectar and often collected pollen.

Direct effect of increased honey bee visits on *C. quamash* pollination

During multiple-visit trials, we observed honey bee visits to 83 flowers, and 37 flowers were used as unvisited controls. Flowers receiving more honey bee visits were marginally less likely to set seed (Appendix S1: Figure S3; $\chi^2 = 3.760$, df = 1, $p = 0.053$). Likewise, unvisited flowers set as many seeds as those visited by honey bees (Appendix S1: Table S4).

Effect of honey bee abundance on *C. quamash* pollen and nectar availability and native bee visitation

In meadows with higher honey bee abundance, the probability of observing visible pollen on dehisced anthers was reduced (Table 1; $\chi^2 = 6.994$, df = 1, $p = 0.008$). Likewise, the probability of detecting measurable nectar in flowers also declined sharply with increased honey bee abundance (Table 1; $\chi^2 = 11.042$, df = 1, $p < 0.001$), such that the likelihood of detecting measurable nectar decreased by 2.9% for every additional honey bee visiting flowers during netting transects. Native bee abundance was associated with a marginally significant decrease in pollen availability (Table 1; $\chi^2 = 3.069$, df = 1, $p = 0.080$), but had no effect on nectar availability. Greater honey bee abundance in meadows was associated with increased honey bee visitation to *C. quamash* focal plants (Appendix S1: Table S5; $\chi^2 = 28.160$, df = 1, $p < 0.001$), and decreased native bee visitation (Figure 2; $\chi^2 = 8.590$, df = 1, $p = 0.003$), such that there were 0.030 fewer native bee visits per hour and 0.036 more honey bee visits per hour for every additional honey bee observed visiting flowers during netting transects.

Overall effect of honey bee introductions on *C. quamash* pollination

Changes in native bee and honey bee visitation led to changes in some but not all measures of pollination (Figure 3). Neither native bee nor honey bee visitation predicted the number of conspecific pollen grains on *C. quamash* stigmas (Table 2), and flowers that were bagged to prevent visitation had similar quantities of conspecific pollen on stigmas compared to open-pollinated plants (Appendix S1: Figure S4), suggesting considerable autogamous pollen deposition. In contrast, native bee visitation was associated with a significant increase in the number of pollen tubes growing to the base of *C. quamash* styles (Table 2; $\chi^2 = 20.674$, df = 1, $p < 0.001$) and the proportion of fertilized ovules in *C. quamash* fruits

TABLE 1 Summary results for models describing: (a) pollen availability in open-pollinated flowers, modeled as a binary response (visible pollen on at least one dehisced anther or no visible pollen on any anthers), and (b) nectar availability in open-pollinated flowers, modeled as a binary response (measurable nectar or no measurable nectar).

Model term	Estimate	SE	χ^2	*p* value
(a) *Camassia quamash* pollen availability				
(Intercept)	−2.929	0.618		
Honey bee abundance	−0.010	0.004	6.994	0.008
Native bee abundance	−0.015	0.008	3.069	0.080
Baseline pollen	5.092	0.577	77.900	<0.001
(b) *C. quamash* nectar availability				
(Intercept)	−2.473	0.600		
Honey bee abundance	−0.029	0.009	11.042	<0.001
Native bee abundance	0.007	0.010	0.505	0.477
Baseline nectar	0.026	0.025	1.067	0.302

Note: The model terms "baseline pollen" and "baseline nectar" are the mean pollen and nectar availability in flowers that were bagged to prevent insect visitation and account for variability not related to visits.

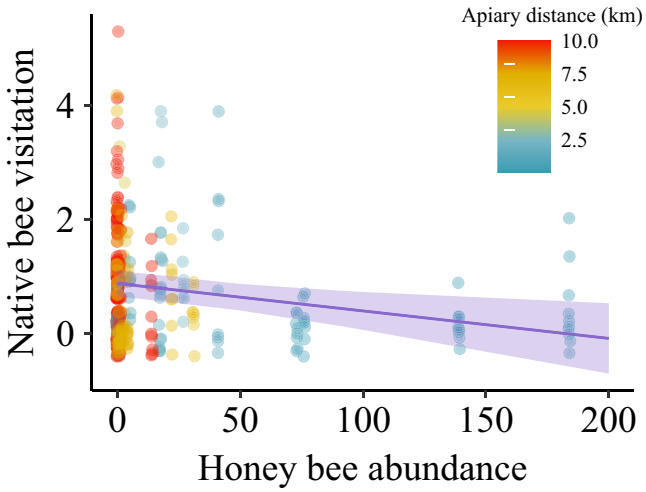

FIGURE 2 Relationship between honey bee abundance (bees per hour per m^2) and native bee visitation rates to *Camassia quamash* focal plants (bees per plant per 10 min). Points are the raw data, colored by distance to nearest apiary, and purple lines and shading show model estimates and error. Higher honey bee abundance was associated with decreased native bee visitation ($\chi^2 = 8.590$, df = 1, $p = 0.003$). See *Methods* for more information about model structure.

($\chi^2 = 5.677$, df = 1, $p = 0.017$), such that ovule fertilization increased by 1.6% for every additional native bee visiting *C. quamash* during netting transects. Conversely, honey bee visitation had no effect on pollen tube numbers (Table 2; $\chi^2 = 0.970$, df = 1, $p = 0.325$) but was associated with a significant decrease in *C. quamash* ovule fertilization ($\chi^2 = 15.458$, df = 1, $p < 0.001$), such that ovule fertilization decreased by 2.8% for every additional honey bee visiting *C. quamash* during netting transects.

DISCUSSION

Honey bees are ineffective pollinators of *C. quamash*

Although honey bees visit *C. quamash* frequently, they are ineffective pollinators compared to native bees and extract pollen and nectar without pollinating *C. quamash* flowers. Both visit frequency and visit quality (i.e., pollination effectiveness) determine the relative importance of different floral visitors as pollinators (King et al., 2013). In some other systems, frequent honey bee visits increase pollination, even when honey bees are less effective than other visitors on a per-visit basis (Sun et al., 2013). However, in our system, increased visit quantity by honey bees does not compensate for poor visit quality. As such, the direct contribution of honey bees to pollination in this system is negligible, and, if anything, negative.

We suspect that honey bees are ineffective pollinators because of their behavior at flowers. Native bees contacted stigmas nearly six times more often than honey bees, who frequently removed nectar from behind petals without contacting reproductive structures. Such "robbing" is common for honey bees and results in low stigma contact compared to other pollinators (Goodell & Thomson, 1997; Rammell et al., 2019; Vicens & Bosch, 2000; Westerkamp, 1991). Negative effects of increasing honey bee abundance may be severe when this behavior is frequent. Nectar collectors can, however, be effective pollinators of *C. quamash* when they visit "legitimately." Indeed, *Bombus* spp. and *Osmia* spp. were the most effective pollinators of *C. quamash* and often exclusively collected nectar.

Honey bee introductions decrease native bee visitation and *C. quamash* pollination

In our natural meadow communities honey bees displaced native pollinators and reduced pollination. Plants at sites closer to introduced apiaries received more visits from honey bees and fewer visits from native bees. The abundance of native bees visiting *C. quamash* positively predicted compatible pollen deposition and ovule fertilization. In contrast, flowers that received more honey bee visits produced fewer fertilized ovules. Thus, as honey bee visits increased and native bee visits decreased, pollination declined.

Relative differences in the quality of conspecific pollen transferred appear especially important in determining successful pollination in this system. Although the total number of conspecific pollen grains on stigmas was not affected by honey bee or native bee visitation, honey bees, which often move within inflorescences and thus promote geitonogamy and inbreeding (Dupont et al., 2004; England et al., 2001), decreased ovule fertilization in *C. quamash*. Cross-pollination increases seed set compared to self-pollination in most self-compatible species (Husband & Schemske, 1996) including *C. quamash* (Gielens et al., 2014) and self-pollen can even interfere with cross-pollination (Kawagoe & Suzuki, 2005). Our data strongly suggest that increasing honey bee dominance results in decreased outcrossing and reduced pollen quality.

Possible direct effects of honey bee visits on pollination

If there is a direct negative effect of honey bee visits on *C. quamash* pollination, the mechanism is not obvious.

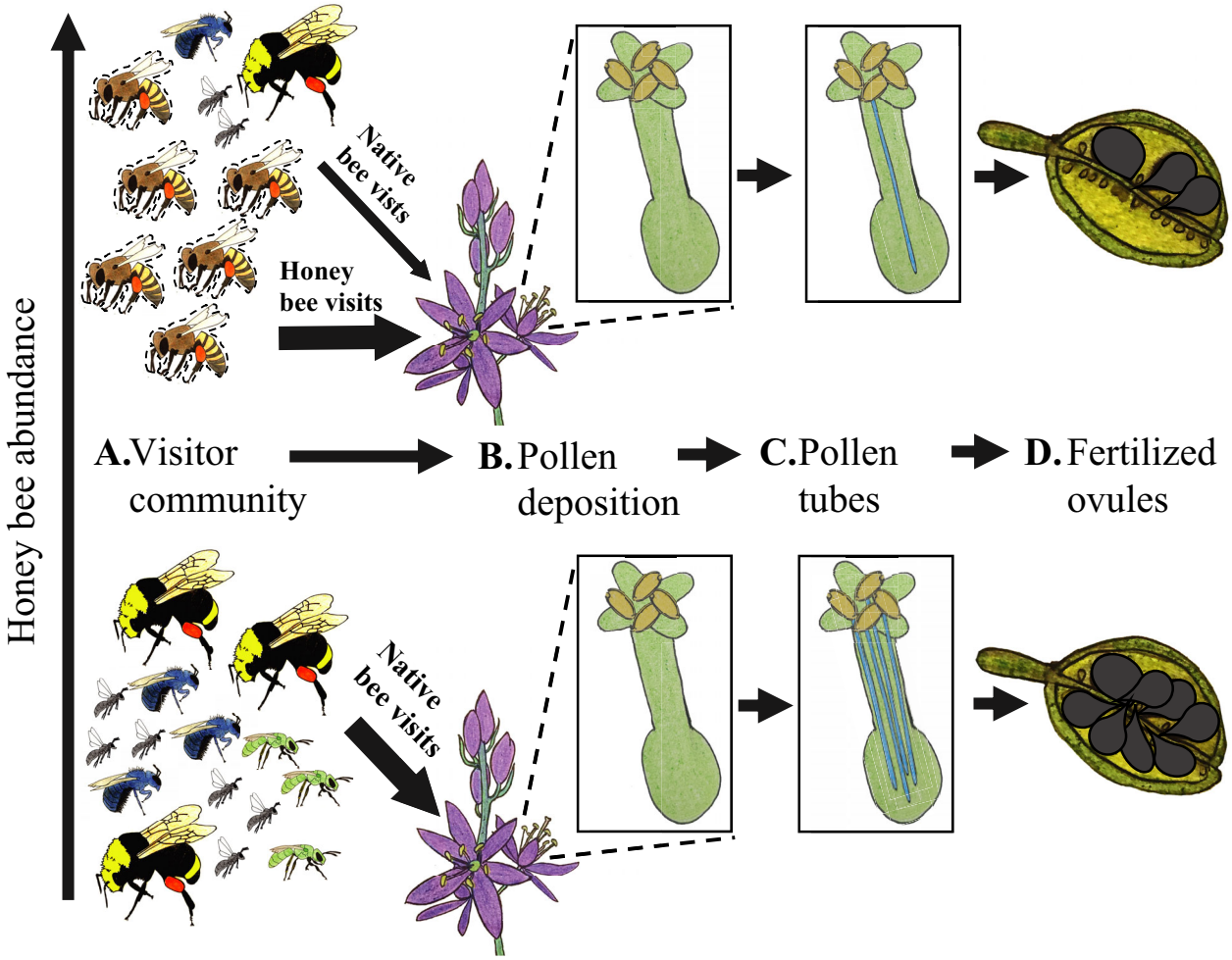

FIGURE 3 As honey bee abundance in meadows increased, *Camassia quamash* received more visits from honey bees (outlined in dotted black) and fewer visits from native bees. Increased honey bee visitation and decreased native bee visitation (A) did not influence the number of conspecific pollen grains on stigmas (B) but led to fewer pollen tubes growing in styles (C) and reduced ovule fertilization (D). These results suggest that pollen quality declines when honey bees replace native bees as *C. quamash* visitors, leading to reduced plant reproduction. Illustrations by Maureen L. Page.

We did not observe signs of stigma damage and, although excessive pollen receipt can lead to pollen tube competition (Aizen et al., 2014), increased honey bee visits were not associated with changes in pollen deposition. Visitors that remove nectar without pollinating can directly reduce fitness by forcing plants to allocate resources to refilling nectar instead of fertilizing ovules (Pyke, 1991). However, we observed little nectar replenishment in flowers from which nectar was experimentally removed (Appendix S1: Table S6). Other possible direct negative effects of visitation include fungal infections (Antonovics, 2005), ovary damage by nectar-foragers (Traveset et al., 1998), and floral abortion induced by nectar robbing (Carbonari et al., 2009), but these mechanisms are rarely documented. Thus, there might be direct negative effects of honey bee visitation, but indirect effects mediated by changes in the visitor community are more convincing.

Clear indirect effects of honey bee abundance on pollination

Honey bee abundance indirectly decreased pollination by reducing native bee *C. quamash* visitation. These reductions are likely the result of exploitative competition, because both pollen and nectar availability declined with increased honey bee abundance, as has been shown in other systems (Carneiro & Martins, 2012; Paton, 1993), and resource competition can lead native bees to shift visits to different meadows or plant species (Herbertsson et al., 2016; Valido et al., 2019). A direct response to resource depletion seems the most likely explanation for reductions in native bee visits with increased honey bee visits; however, deterrence by scent cues (Stout & Goulson, 2001) or other indicators of honey bee presence could also be involved.

TABLE 2 Summary results for models describing the effect of honey bee and native bee visits on different measures of pollination success: conspecific pollen deposition on stigmas, the number of pollen tubes growing into styles, and the proportion of fertilized ovules in fruit.

Model term	Estimate	SE	χ^2	*p*-value
Pollen deposition				
(Intercept)	4.189	0.132		
Honey bee visits	0.001	0.003	0.043	0.836
Native bee visits	0.005	0.004	1.363	0.243
Pollen tubes				
(Intercept)	3.632	0.176		
Honey bee visits	−0.004	0.004	0.970	0.325
Native bee visits	0.027	0.006	20.674	<0.001
Fertilized ovules				
(Intercept)	−0.337	0.260		
Honey bee visits	−0.028	0.007	15.458	<0.001
Native bee visits	0.016	0.007	5.677	0.017

Past studies have demonstrated that honey bees compete with wild bees for floral resources, but our study is unique in that we clearly document mechanistic evidence of floral resource depletion. Furthermore, this study is among the first to partition direct and indirect pathways through which introduced honey bees influence pollination. By isolating the minimally negative direct effect of honey bee visits, we can confidently conclude that indirect effects drive the magnitude of the negative association between honey bee abundance and pollination.

Generalizability of findings

Honey bees were absent in most meadows before we experimentally introduced hives and the native bee community was abundant and diverse. In systems where honey bees are native or naturalized or when other pollinator populations are diminished (e.g., in disturbed or agricultural systems), the negative effects we observed might be lessened or even reversed. For example, when native pollinator populations have been reduced due to habitat fragmentation or other stressors, honey bees can "rescue" plants from reproductive failure (Dick, 2001), and, after honey bees have become naturalized, removing them may disrupt pollination of plants they would otherwise visit (Nabors et al., 2018).

However, regardless of whether honey bees are native or naturalized, dramatic increases of any species could disrupt species interactions and ecological processes (Geslin et al., 2017), particularly when floral resources are limited. For example, in France, where honey bees are native, highly abundant managed honey bees can over-exploit limited floral resources, reducing pollen and nectar collection by wild bees (Henry & Rodet, 2018). Indeed, although we studied only one plant species in a specific context, there are likely many systems where introducing honey bees or other highly abundant generalist pollinators could indirectly reduce pollination by competitively displacing other pollinators. Several recent meta-analyses have revealed that honey bees are less effective than other bees (Földesi et al., 2021; Page et al., 2021). Furthermore, honey bees have been implicated in the extirpation of native bee species (Portman et al., 2019) and frequently compete with other pollinators for limited pollen and nectar resources (Cane & Tepedino, 2016; Hudewenz & Klein, 2015; Thomson, 2016). Hive density is negatively correlated with wild bee abundance and diversity in many ecosystems (Angelella et al., 2021; Valido et al., 2019), and honey bees are replacing wild bees as floral visitors in some areas (Herrera, 2020). Plant pollination declines when ineffective pollinators are over-represented in plant visitor communities (Hansen et al., 2002; Vaughton, 1996). Thus, indirect negative effects of honey bee introductions may be common where wild pollinator communities already effectively pollinate native plants.

Conclusions

Our findings bear on ongoing discussion about permitting of honey bee hives on public lands. Historically, the placement of managed hives in U.S. National Forests and Parks has been restricted and tightly regulated. However, beekeepers have successfully lobbied to have honey bees considered a "non-consumptive" use of U.S. National Forest land (United States Code of Federal Regulations, 2013). If adopted widely, such changes will likely lead to a massive increase in the number of managed honey bees in natural areas. Although honey bees are important pollinators in other systems, we show that indirect negative effects of competition can lead to overall negative effects of honey bee introductions on pollination. As such, introducing hives to sensitive ecosystems should be approached with extreme caution.

More fundamentally, we show that introduced pollinators can disrupt plant-pollinator mutualisms and impair ecosystem functioning. These mutualists, although infrequently studied in the invasive species literature, broadly meet the definition of an "invasive" species (IUCN, 2018) despite their economic benefits to human society. Untangling direct and indirect effects allowed us to mechanistically understand the functional consequences of honey bee introductions. We recommend that future

studies carefully consider indirect impacts of introduced species as biodiversity continues to decline and ecological communities become increasingly homogenous.

ACKNOWLEDGMENTS

Maureen Page and Neal Williams conceived and planned the study. Maureen Page collected and analyzed the data and led the writing of the manuscript. Both authors read and approved the final manuscript. Pollen tube staining methods were adapted for *C. quamash* by Jenny Van Wyk in communication with Susan Kephart. Deanna Deterding, Annie Zell, Kathleen Page, and Skyler Bennis assisted with field and lab work. We are grateful to Randy and Eric Oliver who helped supplement sites with honey bees as well as landowners who allowed us to place hives on their land. We would like to acknowledge that research took place on indigenous lands of the Washoe people (Wašišiw), and we are grateful for their stewardship. Manuscript drafts benefited from feedback from Rachel Vannette, Louie Yang, Charlie Nicholson, Clara Stuligross, Jake Francis, and two anonymous reviewers. 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 Page. Additional support was provided by NSF grant DEB1556885 awarded to Neal Williams and the UC Davis H. Laidlaw Endowment.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Page & Williams, 2022) are available in Dryad at https://doi.org/10.25338/B8393N.

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SUPPORTING INFORMATION

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

How to cite this article: Page, Maureen L., and Neal M. Williams. 2023. "Honey Bee Introductions Displace Native Bees and Decrease Pollination of a Native Wildflower." *Ecology* 104(2): e3939. https://doi.org/10.1002/ecy.3939