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Impacts of Managed Honey Bees on Plant-Pollinator Mutualisms

By

MAUREEN PAGE  
DISSERTATION

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DAVIS

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## **Abstract**

Globalization and industrial agriculture have led to a severe homogenization of ecological communities. European honey bees are now present on every continent except Antarctica and are rapidly replacing native bees as plant visitors. Maintaining global crop productivity requires that we support honey bees, but honey bees may be unsuitable replacements for native pollinators, and agricultural intensification should not come at the expense of plant and animal biodiversity. This dissertation examines how increasing honey bee abundance impacts native bees and their interactions with plants.

In Chapter 1, I investigate the impacts of increasing honey bee abundance on native bee visitation patterns, native bee pollen diets, and nectar and pollen resource availability in two California landscapes: wildflower plantings in the Central Valley and montane meadows in the Sierra. I find that, in both ecosystems, honey bee competition increases niche overlap between honey bees and native bees, leading to important shifts in the network of interactions between plants and pollinators. In the Sierra, native bees re-shuffle their interactions to escape competition, but honey bee abundance decreases pollen and nectar availability in both systems. This suggests that, although native bees can adapt to competition, increasing honey bee abundance may reduce native bee pollen and nectar collection with negative repercussions for native bee populations when floral resources are limiting.

Increasing honey bee abundance and associated shifts in plant-pollinator interaction patterns may also have important functional consequences for plants. However, assessing the overall impact of honey bee introductions on pollination is complicated because abundant honey bees can influence pollination directly, through their own floral visits, but also indirectly, by competitively influencing visits from other pollinators. In Chapter 2, I disentangle the direct and



indirect impacts of increasing honey bee abundance on the pollination of an ecologically important wildflower, *Camassia quamash*. I find compelling evidence that honey bee introductions indirectly decrease pollination by competitively excluding visits from more effective native bees, suggesting that hive introductions in sensitive ecosystems should be approached with extreme caution.

Although I focus on just one plant species in Chapter 2, I expect that replacing native bees with honey bees might decrease pollination for other plant species, particularly when honey bees are ineffective pollinators. In Chapter 3 (originally published in the *American Journal of Botany*), I assess the pollination effectiveness of honey bees compared to other floral visitors using a hierarchical meta-analysis and find that honey bees are less effective than the average bee and rarely the most effective pollinator of plants globally. As such, honey bees may be imperfect substitutes for the loss of wild pollinators.

Taken together, my dissertation demonstrates that increasing honey bee abundance may erode longstanding plant-pollinator mutualisms with negative consequences for plant reproduction and native bee floral resource collection. However, negative impacts for native bees will depend on whether their population growth is limited by floral resource availability and negative impacts for plant species will depend on the relative effectiveness of honey bees as pollinators. Improving our understanding of when, where, and how honey bee competition negatively impacts native bee and plant populations will be crucial for calibrating the balance between biodiversity conservation and agricultural production.

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# **Chapter 1: Evidence of exploitative competition between honey bees and native bees in two California landscapes**

Maureen L. Page and Neal M. Williams

## **Abstract**

Human-mediated species introductions provide real-time experiments in how communities respond to interspecific competition. For example, managed honey bees (*Apis mellifera*) have been widely introduced outside their native range and may compete with native bees for pollen and nectar. Indeed, multiple studies suggest that honey bees and native bees strongly overlap in their use of floral resources. Yet, for resource overlap to negatively impact resource collection by native bees, resource availability must also decline, and few studies investigate impacts of honey bee competition on native bee floral visits and floral resource availability simultaneously. In this study, we investigate impacts of increasing honey bee abundance on native bee visitation patterns, native bee pollen diets, and nectar and pollen resource availability in two Californian landscapes: wildflower plantings in the Central Valley and montane meadows in the Sierra. In both systems, honey bee competition increased niche overlap between honey bees and native bees and increased network-level complementary specialization (H2'). In the Sierra, native bees re-shuffled their interactions to escape competition, leading to a decrease in perceived apparent competition (PAC) when networks were compared against randomly re-assembled networks. However, increased honey bee abundance decreased pollen and nectar availability in both systems. Thus, although native bees can adapt to honey bee competition by shifting their floral visits, the coexistence of honey bees and native

bees is tenuous and will depend on floral resource availability. Preserving and augmenting floral resources is therefore essential in mitigating negative impacts of honey bee competition.

## **Introduction**

Competition occurs when species vie for a common but limited resource (Tilman 1982), leading to decreased population growth of species that fail to appropriately shift their resource use (Schoener et al. 1982). Ample evidence suggests that competition can alter the structure and function of ecological communities (Holway 1999; Gallardo et al., 2015; David et al. 2017), and ecological theory predicts that two perfectly similar species cannot coexist without one species competitively displacing the other (Gause 1934; Hardin 1960; MacArthur and Levins 1967). Yet, there remains considerable debate regarding the degree to which competition drives species evolution and extinctions (Schoener et al. 1982; Sax et al. 2007).

Understanding when and where overlapping resource use might eventually lead to competitive displacement is especially important in managing the impacts of exotic species. For example, hyper-generalist honey bees (*Apis mellifera*) have been introduced into many ecosystems outside of their native range (Crane 1999) and often overlap with other bees in their use of floral resources (Hung et al. 2019; Herrera 2020). However, shared use does not automatically indicate that competitive displacement is occurring. Nectar production and replenishment rates vary widely among and within plant species (Castellanos et al. 2002; Corbet and Delfosse 1984; Pyke 1980; Descamps et al. 2018; Descamps et al. 2021), as does pollen production (Hicks et al. 2016) and floral resources may not be limited if flowers are abundant or if rates of resource extraction equal rates of replenishment.

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

Many different studies have assessed competition using many different assessment tools (Malinger et al. 2017; Thomson and Page 2020). Field studies provide ample evidence that honey bee competition can alter wild bee visits to plants (Dupont et al. 2004) and restructure the community of interaction among plants and pollinators (Geslin et al. 2017; Magrach et al. 2017; Valido et al. 2019). At the level of individual foragers, competition among bumble bees can increase floral fidelity and conspecific pollen transport (Brosi and Briggs 2013). Although such questions have yet to be investigated in the context of honey bee competition, honey bee abundance can decrease niche breadth at the species-level (Magrach et al. 2017) and parallel changes may be occurring at the individual-level.

A few studies have measured the impact of honey bee abundance and apiary proximity on floral resource availability (Dupont et al. 2004) and floral resource collection by native bees

(Henry and Rodet 2018). These studies, in concert with field studies of floral visitation patterns, have considerably advanced our understanding of honey bee competition impacts. However, no studies investigate changes in resource availability and resource use shifts simultaneously. Exploitative competition occurs when resource collection by one species negatively impacts resource collection by another species (Hardin 1960; Tilman 1982). Thus, studying impacts of increased honey bee abundance on both resource availability and resource use would provide a more complete picture of whether exploitative competition is truly occurring. Perhaps more importantly, such information gets us much closer to understanding whether competition might have negative fitness consequences for displaced species. For example, if resource availability declines but visitation patterns remain static, there may be few pathways for native bees to behaviorally escape competition by using different resources. On the other hand, without evidence of declining resource availability, one cannot assume that exploitative competition is responsible for shifting interaction patterns.

Understanding when and where honey bees compete with wild bees for floral resources has important consequences for agricultural pollination, honey bee management, and conservation policy. Honey bees contribute billions of dollars to the U.S. economy as crop pollinators (Southwick and Southwick 1992) and wildflower honey is a highly valuable agricultural commodity. However, native bees are also important pollinators, particularly for crop species not efficiently pollinated by honey bees (Malingier and Gratton 2015; Page et al. 2021; Sáez et al. 2022) and the integration of managed and wild bees can additively and synergistically improve crop yields (Garibaldi et al. 2013; Brittain et al. 2013).

The most popular strategies for supporting honey bees and native bees include planting wildflowers in agricultural landscapes and preserving floral resources in natural landscapes.



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

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

network-level complementary specialization. We also assessed whether wild bee pollen fidelity, pollen diet diversity, and pollen diet composition responded to changes in honey bee abundance. Lastly, we asked whether honey bee abundance influenced pollen and nectar availability in key flowering species from each system.

## **Methods**

*Study sites and pollinator surveys* We conducted this work in the California Central Valley at 5 replicated wildflower plantings neighboring almond orchards which we sampled in 2017 and 2018. We also sampled 15 meadows in the Central Sierra in 2019. In both ecosystems, some variation in honey bee abundance was due to site proximity to commercial apiaries. In the Sierra, we also experimentally supplemented three meadows initially free of honey bees with 20 hives. A full description of honey bee treatments in the Sierra is described in Page and Williams 2022 (Chapter 2). For our Central Valley wildflower plantings, site selection and wildflower establishment methods are described in Rundlöf et al. (2022). Sites averaged 1.6 km to the nearest neighboring site in the Sierra and 11.3 km to the nearest neighboring site in the Central Valley. Within each ecosystem, sites were in consistent landscape contexts and drew from the same regional species pools of native pollinators.

In the Central Valley, we surveyed pollinators and their visits to flowering plants over four sample rounds from April – May. In the Sierra, we sampled sites from May – July. Most sites were sampled two to four times, but some sites were sampled up ten times if the blooms of *Camassia quamash* and *Penstemon rydbergii* lasted long enough. In the Central Valley, we netted insects actively visiting flowers during 10-minute walks of two 100 m<sup>2</sup> transects which were each sampled once in the morning and once in the afternoon (40 minutes total). In the

Sierra, we sampled one-hectare subplots that varied in floral species composition, netting active flower visitors while walking 100 m<sup>2</sup> transects for two 30-minute periods in the morning and the afternoon (60 minutes total). In both systems, we netted exclusively on sunny or partly cloudy days when average wind speeds were below 5 m/s and temperatures were above 13° C. Netted pollinators were collected individually in separate collection vials to minimize pollen contamination and euthanized using dry ice, except for bumble bee queens, which we identified on site and then released. In both systems, we collected up to twenty honey bees during netting transects and counted any additional honey bees. Native bee specimens were identified to morphospecies by expert taxonomists (Skyler Burrows, USDA Bee Lab, Logan, Utah, and Joel Gardner, University of Manitoba, Canada). For network analyses, we excluded bees not identified to morphospecies (~3% of all specimens). Because we were exclusively interested in documenting patterns of honey bee vs. native bee competition, we also excluded non-bee floral visitors from network analyses.

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

***Quantifying pollen resource depletion*** We measured the daily depletion of pollen and nectar resources from the most abundant and most consistently available plant species. In the

Central Valley, these species were *Eschscholzia californica*, *Collinsia heterophylla*, *Phacelia californica*, *Clarkia unguiculata*, and *Clarkia williamsonii*. In the Sierra, these species were *Camassia quamash*, *Bistorta bistortoides*, *Ranunculus occidentalis*, and *Trifolium longipes*. In both systems, at the end of each sampling day, we measured pollen and nectar availability in one to three flowers on 10-20 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  $\mu$ L capillary tubes.

**Network metrics** For each site and sample round in each year and system, we generated unique plant x pollinator visitation networks. In total, we generated 40 networks across two years of sampling for our Central Valley sites and 47 networks for our Sierra sites. For each network, we used the bipartite package (Dormann et al. 2009) and R (R Core Team, 2022) to calculate complementary specialization ( $H2'$ ) at the network level, perceived apparent competition (PAC) between honey bees and wild bees, and species-level specialization ( $d'$ ) at the pollinator-level. Perceived apparent competition estimates the degree of niche overlap between two species using Müller's index (Müller et al. 1999; Morris et al. 2005). For all pairwise comparisons of honey bees against other bee species we calculated Müller's index as:

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

Where  $\alpha_{ik}$  represents the number of interactions between pollinator  $i$  and plant  $k$ ,  $\alpha_{il}$  represents the number of interactions by pollinator  $i$  across all plants  $l$ ,  $\alpha_{jk}$  represents the number of interactions between pollinator  $j$  and plant  $k$ , and  $\alpha_{mk}$  represents visits to plant  $k$  from all pollinators  $m$ . Species-level specialization ( $d'$ ) measures partner diversity at the pollinator level using the Kullback-Leibler distance (Blüthgen et al. 2006). Complementary specialization varies

from 0 to 1 and measures the degree to which a network deviates from a perfectly exclusive network ( $H2' = 1$ ) in which no interactions are shared among multiple plants or pollinators. To assess whether network properties and interaction patterns were different than randomly assembled networks, we compared observed networks against null networks. To perform this comparison, we generated 500 randomized null networks using the `r2rtable` method, which resamples interactions but keeps row and column sums constant (Patefield 1981) and compared observed network metrics against null network metrics using Z-scores (Vázquez and Aizen 2003; Blüthgen et al. 2008; Dormann et al. 2009).

***Statistical analysis*** We assessed whether honey bee abundance in wildflower plantings, measured as the total number of honey bees visiting flowering plants during morning and afternoon netting transects, was associated with perceived apparent competition (PAC), wild bee specialization ( $d'$ ), and complementary specialization ( $H2'$ ) using separate generalized linear mixed effects models (GLMMs) for each network metric and each ecosystem. We constructed models with raw network values as the response variables and constructed models with Z-scores from observed vs. null comparisons as response variables. Each model included honey bee abundance as a fixed effect and site and sample round as separate random effects. For models of PAC and  $d'$ , which were measured at the pollinator species level, we also included native bee taxon as a fixed effect. For models predicting network metrics in the Central Valley, we included year as an additional fixed effect. We fit all models using the `lmer()` function in the `lme4` package (Bates et al., 2015) and tested for significance using likelihood ratio tests. All analyses were conducted in R (R Core Team, 2022).

We assessed whether honey bee abundance in wildflower plantings was associated with wild bee pollen fidelity and wild bee pollen diet diversity using separate GLMMs for each

response and ecosystem. Each model included honey bee abundance, bee taxon, and the plant taxon from which the specimen was caught as fixed effects and site and sample round as separate random effects. We fit models using the `lmer()` function in the `lme4` package (Bates et al., 2015) and tested for significance using likelihood ratio tests.

We assessed whether pollen species composition varied as honey bee abundance increased using permutational MANOVAs in R, using the `adonis` function in the `vegan` package (Oksanen et al., 2020; Anderson, 2001) with separate models for each ecosystem. We tested the effect of honey bee abundance, native bee taxon, and plant taxon visited. For bees caught in the Central Valley, we also tested the effect of year. Bee specimens were collected from different sites, and we accounted for nestedness using ‘`stata = site`’ in all models. Statistical results obtained from the `adonis()` function depend on the order in which variables are added so we ran multiple permutations and report the most conservative results (i.e., results from tests with predictors added in order of statistical significance).

We evaluated how pollen and nectar availability responded to honey bee introductions using separate GLMMs for each ecosystem and reward type. All models included as fixed effects: the abundance of honey bees, the plant species sampled, and, to control for baseline pollen and nectar resources, the mean pollen and nectar availability in unvisited bagged flowers. In the Central Valley, we also included year as an additional fixed effect. In the Sierra, nectar measurements varied by data collector, so we added data collector as a random effect. All models also included site and sample round as separate random effects. Pollen and nectar data were both zero-inflated. We modeled pollen availability as a binary response where successes were dehiscid anthers with visible pollen and failures were dehiscid anthers without visible

pollen. Nectar availability was also modeled as a binary response where successes were flowers with measurable nectar and failures were flowers with no measurable nectar.

## Results

Honey bee abundance in meadows, measured as the total number of honey bees visiting flowering plants during morning and afternoon netting transects, ranged from 9 – 2,363 bees per m<sup>2</sup> per hour in the Central Valley and 0 – 184 honey bees per m<sup>2</sup> per hour in the Sierra (Table 1.1). In the Central Valley, we recorded 1,082 native bees comprising 57 native bee morphospecies. In the Sierra, we recorded 2,329 native bees representing 116 native bee morphospecies.

Apparent competition between honey bees and native bees was higher at sites with more honey bees in both the Sierra and the Central Valley (Table 1.2). However, when comparing raw values from observed networks against null networks, there was no change in apparent competition in the Central Valley and apparent competition decreased with increasing honey bee abundance in the Sierra. Raw values for native bee specialization ( $d'$ ) decreased as honey bee abundance increased in the Central Valley, but there was no relationship between honey bee abundance and  $d'$  in the Sierra nor when comparing observed networks from either system against null networks. Raw values for complementary specialization ( $H2'$ ) decreased as honey bee abundance increased in the Central Valley but not the Sierra. However, when compared to null networks, increased honey bee abundance was associated with an increase in  $H2'$  relative to null expectations in both the Sierra and the Central Valley.

Neither the pollen fidelity of individual visitors nor the species richness of pollen carried on native bee bodies varied as honey bee abundance increased (Table 1.3). The species

composition of pollen was best explained by the plant taxon a bee had been visiting and bee taxonomic identity (Table 3). Honey bee abundance was not a significant predictor of pollen composition in the Central Valley. In the Sierra, honey bee abundance was associated with a subtle shift in pollen species composition but explained less than 1% of variation across bee specimen.

Pollen availability in flowers, measured as the proportion of dehisced anthers with visible pollen, declined as the number of honey bees visiting flowers increased in both the Sierra and the Central Valley (Table 1.4; Fig. 1.1). Likewise, the probability of observing measurable nectar in flowers declined sharply as honey bee abundance increased in both the Sierra and the Central Valley. Pollen and nectar availability also varied among plant species and in response to baseline pollen and nectar availability in both ecosystems.

## **Discussion**

Across two California ecosystems, increased honey bee abundance decreased floral resource availability, leading to shifts in native bee floral visitation patterns. Perceived apparent competition (PAC), a measure of niche-overlap, increased in both systems. However, when compared to randomly re-assembled null networks, honey bee abundance was associated with a decrease in apparent competition in the Sierra, suggesting native bees altered their interaction patterns to escape competition. These seemingly contradictory conclusions highlight the value of using null models to understand ecological data. For example, perceived apparent competition (PAC) increases when one of the competing species is disproportionately abundant. Our null models conserved total numbers of honey bee and native bee visits but randomly redistributed them to different plants. Thus, deviation from null networks suggests that species are non-



randomly shifting their visits to minimize niche overlap. Similarly, increasing abundance of generalist honey bees may decrease raw values of network-level complementary specialization as they account for an increasingly large share of all interactions. Again, null models help account for this bias to reveal shifts in interactions patterns across the full bee community.

Complementary specialization at the network level ( $H2'$ ) increased in both systems, suggesting plant-pollinator interactions became more specialized as honey bee abundance increased. In contrast, there was no change in specialization at the species level ( $d'$ ), however, this metric is sensitive to small samples sizes and thus it is not surprising that we detected significant changes at the network level but not the species level. These findings align with those from a similar study in Spain (Magrach et al. 2017) which also found that complementary specialization increased as honey bee abundance increased in natural habitat neighboring orange groves. Such changes in network structure may affect the robustness of communities to species loss (Thébault and Fontaine 2010) with potential implications for community functioning (Magrach et al. 2017; Valido et al. 2019). Observed changes in complementary specialization reveal that pollinators can adapt to minimize competition in the short term and such adaptive foraging may allow species and communities to persist (Valdovinos et al. 2013). On the other hand, specialized diets pose greater extinction risk for species (Vázquez et al. 2002) and the more specialized a network, the greater the extinction risk for interacting partners (Aizen et al. 2012). Thus, when there are diverse floral resources, native bees may be able to shift their visitation patterns to avoid competition with honey bees. However, in a world with decreasing floral abundance and diversity (Burkle et al. 2013), adaptive foraging may not always be possible and there could be delayed effects of competition on the ability of all plants and pollinators to persist across longer time scales.

Although we observed shifts in visitation patterns at the species level, the pollen fidelity of individual foraging bees, as well as the diversity and composition of pollen grains on their bodies were relatively unchanged by honey bee abundance. Furthermore, the absence of a significant relationship between honey bee abundance and pollen fidelity persisted even when we restricted data to single plant species (Appendix S1: Table S1.1). These results are, to our knowledge, the first test of whether honey bee competition might alter the composition of pollen carried by individual bees. Brosi and Briggs (2013) found that removal of a dominant bumble bee species led to a decrease in the pollen fidelity of bumble bees visiting *Delphinium barbeyi*, suggesting competition and high species diversity maintain high levels of niche segregation. In contrast, we find that honey bee competition is not a major driver of native bee pollen fidelity. Instead, most variation in pollen fidelity and pollen composition was explained by bee taxon and the plant species the bee had been visiting when it was captured. For example, in the Sierra, honey bee abundance was associated with a decrease in visits to *Camassia quamash* (Chi-sq = 58.171; d.f. = 1;  $p < 0.001$ ) with parallel declines in *C. quamash* pollen carriage (Appendix S1: Fig. S1.1). Although some plant species are over- or under-represented in the pollen data when compared to the visitation data (Appendix S1: Fig. S1.1), likely reflecting differences in pollen production among plant species and pollen vs. nectar collection by bees, shifting visitation patterns explain variation associated with changes in honey bee abundance. As such, while the pollen diets of wild bees were altered by honey bee competition, visitation data would have sufficiently documented this change.

By simultaneously documenting declines in floral resource availability and shifts in resource use we demonstrate that native bees are being competitively displaced by honey bees and are thus likely to collect fewer resources or collect different resources. Decreases in resource

availability could decrease native bee reproduction by limiting pollen collection and offspring provisioning (Thomson 2004; Hudewenz and Klein 2015). Indeed, although parasitism and nest site availability are sometimes more limiting than flowers (Steffan-Dewenter and Schiele 2008; Forrest and Chisholm 2017), floral resources almost universally increase bee reproduction (Goodell 2003; Williams and Kremen 2007; Carvell et al. 2017; Stuligross and Williams 2020) and flower availability is often a key limiting factor for population growth (Malfi et al. 2019; Crone and Williams 2016; Thomson and Page 2020). Collecting different resources may also decrease reproduction if resources are of lower nutritional quality (Vaudo et al. 2018) or otherwise unsuitable replacements for preferred host plants. For generalist feeders, having a large set of diet choices allows for maximum caloric and nutrition intake (Pulliam 1975), and pollen and nectar quality influence bee health and reproduction (Roulston & Cane 2002; Burkle and Irwin 2009; Alaux et al. 2010). As such, changes in native bee diets and floral resource availability are likely to have negative consequences for native bee populations.

If honey bee competition reduces resource availability, wildflower plantings may fail to benefit native bee populations, as has been shown in other systems (Angelella et al. 2020, Bommarco et al. 2021). However, in our Central Valley wildflower plantings, the benefit of augmenting floral availability seems to outweigh any negative effects of bee-bee competition. This is confirmed by work from a separate project, conducted at these same sites over the same time-period (Rundlöf et al. 2022) which showed that wildflower plantings enhanced *O. lignaria* and *B. vosnesenskii* reproduction when compared to un-enhanced control sites. As such, wildflower plantings remain a valuable conservation tool despite honey bee competition, in agreement with studies showing overall benefits of wildflower plantings for native bee populations (Williams et al. 2015; Boyle et al. 2020). Nonetheless, understanding how to

improve wildflower plant mix selection to minimize negative effects of honey bee competition remains a key conservation objective.

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

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

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## Tables and Figures

**Table 1.1.** Summary data for honey bee and native bee species richness and abundance across sampled sites in the California Central Valley and Sierra Nevada. Mean abundance measures the number of honey bees and native bee collected and counted per hour per m<sup>2</sup> during morning and afternoon netting transects (mean, maximum, and minimum numbers are multiplied by 3/2 in the Central Valley, where we counted bees in 40 minute transects rather than one hour transects). Total abundance measures the total number of native bees and honey bees counted or collected in both systems (not adjusted for variable sampling periods). Total richness is the species richness of specimens identified to species or morphospecies.

	<b>Total Richness</b>	<b>Total Abundance</b>	<b>Mean Abundance ± SD</b>	<b>Min.</b>	<b>Max.</b>
<b>Central Valley</b>					
Honey bees	1	13,605	510.2 ± 490.8	9	2,363
Native bees	57	1,082	40.7 ± 55.1	3	98
<b>Sierra Nevada</b>					
Honey bees	1	791	16.5 ± 36.1	0	184
Native bees	116	2,329	48.5 ± 36.7	10	260

**Table 1.2.** Effect of honey bee abundance and native bee taxon on perceived apparent competition (PAC), native bee specialization (d'), and complementary specialization (H2') for sites in the California Central Valley and the Sierra Nevada. For all network metrics, we present results from analyses investigating the effect of honey bee abundance on raw network metrics and analyses comparing observed networks against null networks using Z-scores.

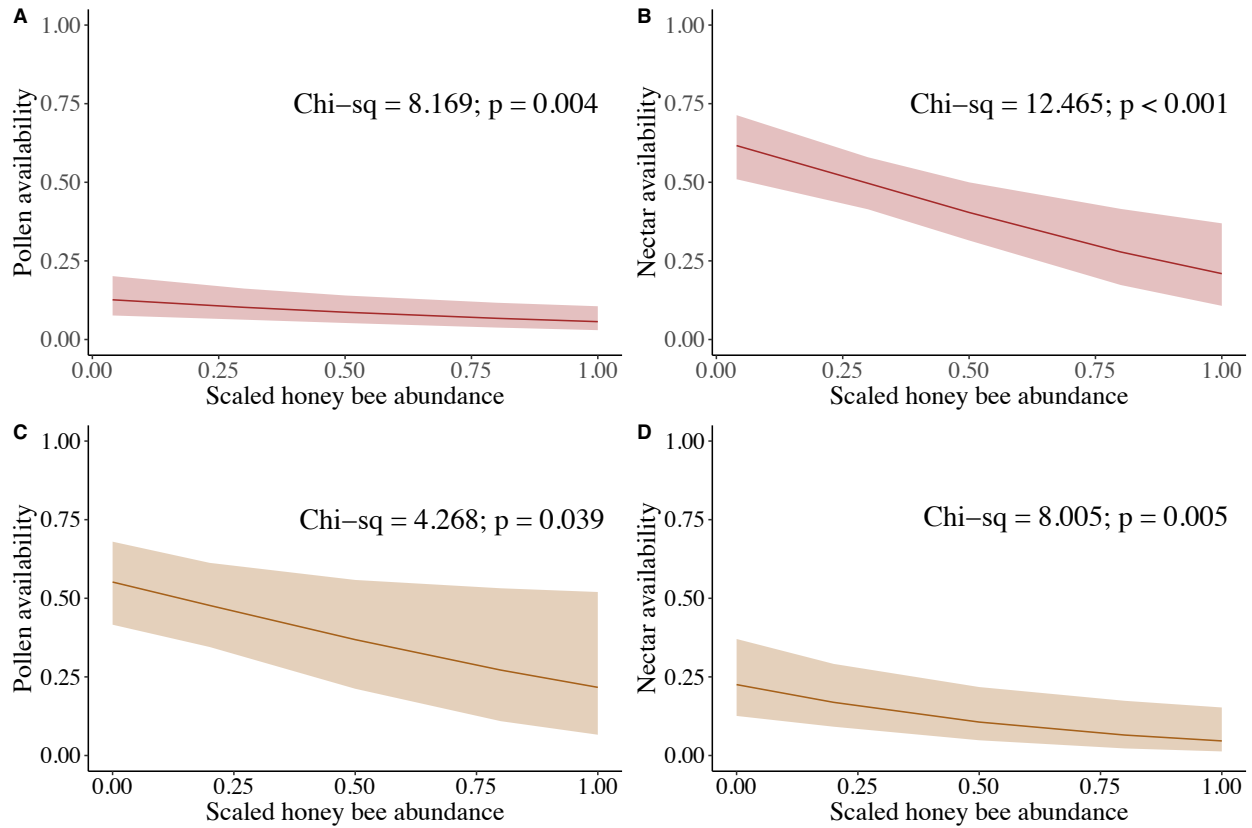
<b>Central Valley Wildflower Plantings</b>						
<b>Response</b>	<b>Predictor</b>	<b>Sign of effect</b>	<b>Chi-sq</b>	<b>df</b>	<b>p-value</b>	
PAC: raw	Honey bee abundance	positive	61.583	1	< 0.001	***
	Bee taxon	-	16.169	6	0.013	*
PAC: Z-score	Honey bee abundance	n.s.	0.025	1	0.874	
	Bee taxon	-	20.219	6	0.003	***
d': raw	Honey bee abundance	negative	12.796	1	<0.001	***
	Bee taxon	-	25.000	6	<0.001	***
d': Z-score	Honey bee abundance	n.s.	2.044	1	0.153	
	Bee taxon	-	32.461	6	<0.001	***
H2': raw	Honey bee abundance	negative	46.697	1	<0.001	***
H2': Z-score	Honey bee abundance	positive	6.374	1	0.012	**
<b>Sierra Nevada Montane Meadows</b>						
<b>Response</b>	<b>Predictor</b>	<b>Sign of effect</b>	<b>Chi-sq</b>	<b>df</b>	<b>p-value</b>	
PAC: raw	Honey bee abundance	positive	54.062	1	< 0.001	***
	Native bee taxon	-	10.842	7	0.146	
PAC: Z-score	Honey bee abundance	negative	11.096	1	< 0.001	***
	Native bee taxon	-	4.671	7	0.700	
d': raw	Honey bee abundance	n.s.	0.019	1	0.891	
	Native bee taxon	-	47.590	7	<0.001	***
d': Z-score	Honey bee abundance	n.s.	3.127	1	0.077	
	Native bee taxon	-	20.904	7	0.004	**
H2': raw	Honey bee abundance	n.s.	0.371	1	0.543	
H2': Z-score	Honey bee abundance	positive	28.391	1	<0.001	***

**Table 1.3.** Effect of honey bee abundance, native bee taxon, and plant species visited on native bee pollen fidelity, the diversity of pollen carried on native bee bodies, and pollen community composition for sites in the California Central Valley and the Sierra Nevada.

<b>Central Valley Wildflower Plantings</b>						
<b>Response</b>	<b>Predictor</b>		<b>Chi-sq</b>	<b>d.f.</b>	<b>p-value</b>	
Pollen fidelity	Honey bee abundance	-	0.002	1	0.969	
	Bee taxon	-	33.561	7	<0.001	***
	Plant taxon visited	-	82.534	6	<0.001	***
Diversity	Honey bee abundance	-	0.132	1	0.717	
	Bee taxon	-	83.489	7	<0.001	***
	Plant taxon visited	-	34.416	6	<0.001	***
<b>Response</b>	<b>Predictor</b>	<b>R2</b>	<b>F</b>	<b>d.f.</b>	<b>p-value</b>	
Composition	Honey bee abundance	0.002	3.230	1	0.952	
	Bee taxon	0.018	4.253	7	<0.001	***
	Plant taxon visited	0.356	98.597	6	<0.001	***
	Residual	0.624		1037		
<b>Sierra Nevada Montane Meadows</b>						
<b>Response</b>	<b>Predictor</b>		<b>Chi-sq</b>	<b>d.f.</b>	<b>p-value</b>	
Pollen fidelity	Honey bee abundance	-	0.727	1	0.394	
	Bee taxon	-	17.656	8	0.024	*
	Plant taxon visited	-	153.477	8	<0.001	***
Diversity	Honey bee abundance	-	0.040	1	0.842	
	Bee taxon	-	34.236	8	<0.001	***
	Plant taxon visited	-	72.884	8	<0.001	***
<b>Response</b>	<b>Predictor</b>	<b>R2</b>	<b>F</b>	<b>d.f.</b>	<b>p-value</b>	
Composition	Honey bee abundance	0.002	2.785	1	0.004	**
	Bee taxon	0.032	7.389	8	<0.001	***
	Plant taxon visited	0.264	61.254	8	<0.001	***
	Residual	0.703		1305		

**Table 1.4.** Summary results for models describing: (1) 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 (2) nectar availability in open-pollinated flowers, modeled as a binary response (measurable nectar or no measurable nectar). The model terms ‘Baseline pollen’ and ‘Baseline nectar’ are the average pollen and nectar availability in plants that were bagged at the beginning of each day to prevent insect visitation. See Methods section for detail on data collection and model structure.

<b>Central Valley Wildflower Plantings</b>						
<b>Response</b>	<b>Predictor</b>	<b><math>\beta</math> (S.E.)</b>	<b>Chi-sq</b>	<b>df</b>	<b>p-value</b>	
Pollen	Honey bee abundance	- 0.912 (0.319)	8.169	1	0.004	**
	Plant species sampled	-	485.342	4	<0.001	***
	Baseline pollen	3.828 (0.423)	81.839	1	<0.001	***
Nectar	Honey bee abundance	-1.879 (0.532)	12.465	1	<0.001	***
	Plant species sampled	-	28.050	3	<0.001	***
	Baseline nectar	0.125 (0.041)	9.306	1	0.002	**
<b>Sierra Nevada Montane Meadows</b>						
<b>Response</b>	<b>Predictor</b>	<b><math>\beta</math> (S.E.)</b>	<b>Chi-sq</b>	<b>df</b>	<b>p-value</b>	
Pollen	Honey bee abundance	-1.445 (0.699)	4.268	1	0.039	*
	Plant species sampled	-	58.036	5	<0.001	***
	Baseline pollen	4.946 (0.526)	88.415	1	<0.001	***
Nectar	Honey bee abundance	-1.786 (0.633)	8.005	1	0.005	**
	Plant species sampled	-	30.996	3	<0.001	***
	Baseline nectar	n.s.	0.889	1	0.346	



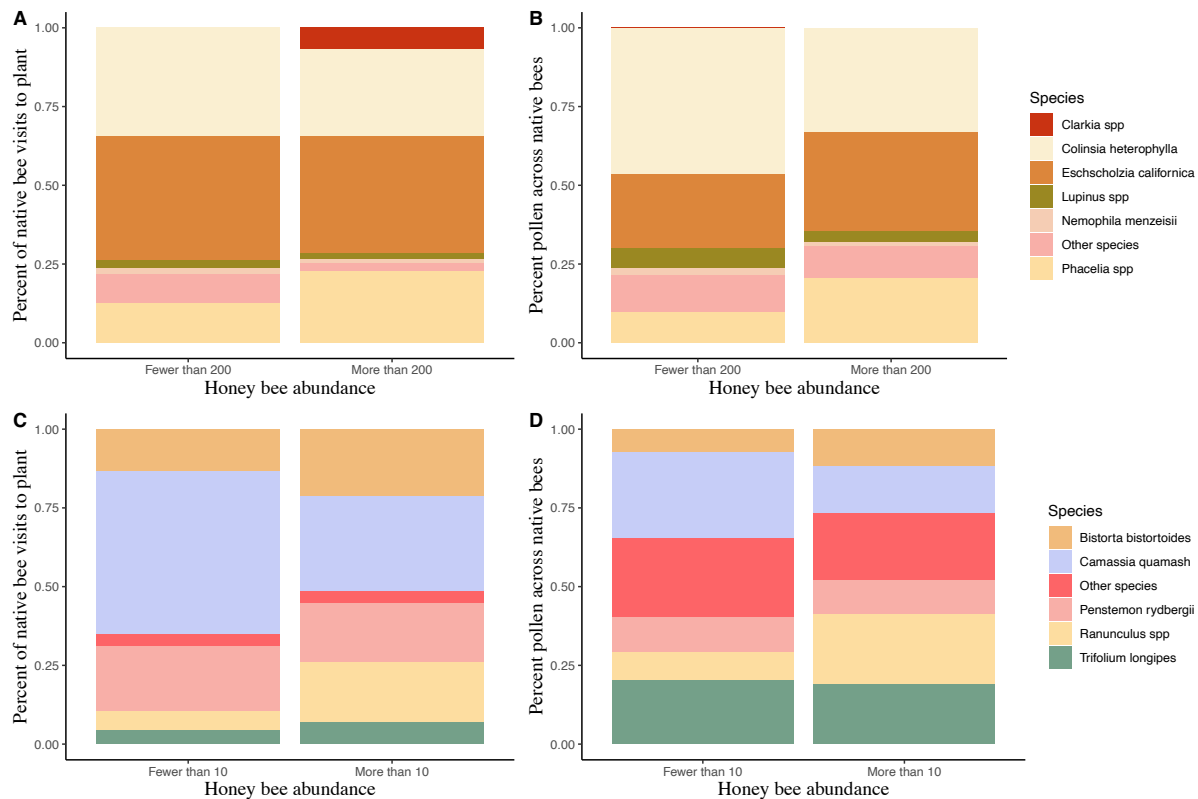
**Fig. 1.1.** Impact of honey bee abundance on the probability of detecting **A)** visible pollen and **B)** measurable nectar in wildflower plantings in the California Central Valley. Impact of honey bee abundance on the probability of detecting **C)** visible pollen and **D)** measurable nectar across montane meadows in the Sierra. The fitted lines plot predictions from models reported in Table 4 and the shading depicts error around point estimates.

## Appendix S1

**Table S1.1.** Effect of honey bee abundance and native bee taxon on native bee pollen fidelity for *Eschscholzia californica* and *Collinsia heterophylla* in the California Central Valley as well as *Camassia quamash* and *Penstemon rydbergii* in the Sierra Nevada. These plant species had the most bee visits (based on collected bee specimens) across all sites within their respective ecosystems.

<b>Central Valley Wildflower Plantings</b>					
<b>Response</b>	<b>Predictor</b>	<b>Chi-sq</b>	<b>d.f.</b>	<b>p-value</b>	
<i>E. californica</i>	Honey bee abundance	0.169	1	0.681	
	Bee taxon	41.550	6	<0.001	***
<i>C. heterophylla</i>	Honey bee abundance	0.043	1	0.837	
	Bee taxon	77.765	7	<0.001	***
<b>Sierra Nevada Montane Meadows</b>					
<b>Response</b>	<b>Predictor</b>	<b>Chi-sq</b>	<b>d.f.</b>	<b>p-value</b>	
<i>C. quamash</i>	Honey bee abundance	0.147	1	0.701	
	Bee taxon	17.702	8	0.024	*
<i>P. rydbergii</i>	Honey bee abundance	0.102	1	0.749	
	Bee taxon	34.998	5	<0.001	***





**Fig. S1.1.** Summary data on the percent of native bee visits to different plants and the species composition of pollen across all bee bodies at low and high levels of honey bee abundance in the Central Valley (A and B) and the Sierra (C and D). There were no major shifts in native bee visits and pollen diets in the Central Valley. However, in the Sierra, the proportion of *Camassia quamash* visits declined (Chi-sq = 58.171; d.f. = 1;  $p < 0.001$ ), while the proportion of visits to *Ranunculus* increased (Chi-sq = 52.513; d.f. = 1;  $p < 0.001$ ) as did visits to *Bistorta bistortoides* (Chi-sq = 14.189; d.f. = 1;  $p < 0.001$ ). Shifting visit patterns also led to parallel changes in the composition of pollen carried on insect bodies (B and D).

## **Chapter 2: Honey bee introductions displace native bees and decrease pollination of a native wildflower**

Maureen L. Page and Neal M. Williams

### **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*) are widely introduced outside their native range and 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, while 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 consequences of species introductions and more careful coordination of hive placements.

## **Introduction**

Introduced and invasive species are fundamentally altering the structure of ecological communities (Elton, 1958; Gallardo et al., 2015; 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 seemingly 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 (U.S. 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) Does increased honey bee abundance in meadows affect native bee visitation and indirectly influence *C. quamash* pollination?; (ii) What is the direct effect of increasing honey bee visits on pollination?; (iii) Does honey bee abundance affect pollen and nectar availability in *C. quamash* flowers?; and (iv) Do honey bees and native bees vary in their single-visit pollination effectiveness?

## **Methods**

**Field methods** – In 2019, we sampled 15 meadows in the Central Sierra Nevada (39°34'12" N, 120°20'60" W). All meadows were >500 m apart and varied in honey bee abundance across space and time because of experimental honey bee introductions and pre-existing apiary locations (Appendix S2: Fig. S2.1). We surveyed pollinator visitation patterns from May – 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. In three of the meadows, approximately halfway through the blooming period, we introduced 20 hives within 0.7 km of the site. There was also a commercial apiary with 100 hives located between 1 and 7 km from five sites where hives were not introduced as a part of our study.

At each site, we sampled one-hectare subplots that varied in floral species composition 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 the community of native bees visiting *C. quamash* and other flowers, we netted active flower visitors while walking 100 m transects for two 30-minute 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 potential changes in *C. quamash* visitation at a finer scale, we also conducted focal plant observations of 10-12 flowering *C. quamash* plants, noting all visitors during a 10-minute period. All focal plant observations occurred from 11:00-13:00, in-between morning and afternoon netting transects. At the end of each sampling day, we measured pollen and nectar availability in one to three flowers on 10-20 additional 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 twelve 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 8M NaOH at 35° C for 1 hour and stained pollen tubes by placing softened styles in a solution of 0.05% aniline blue in 0.1M KH<sub>2</sub>PO<sub>4</sub> for

24 hours. 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 and scored 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 zero and twenty) to freshly opened flowers and all other visitors were excluded. 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 S2: Table S2.1). 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: *Andrena* spp., *Apis mellifera*, *Bombus* spp., *Halictus* spp., *Osmia* spp., “Small dark bees”, and Syrphid flies. For both field experiments, we re-bagged plants to prevent further visitation after experimental visits had concluded, collected fruits two weeks later, and counted fertilized ovules.

***Data analysis*** – We lacked sufficient power to directly test the relationship between honey bee abundance and native bee abundance and instead used focal plant visits to understand



potential shifts in the community of *C. quamash* visitors. We evaluated how the number of honey bee visits responded to honey bee introductions by fitting a model which included honey bee abundance as a fixed effect and evaluated how native bee visits responded to honey bee introductions by fitting a model which included honey bee visits to focal plants and native bee abundance as fixed effects. Both models also included site and sample round as separate random effects. We fit this model using the `lmer()` function in the `lme4` package (Bates et al., 2015) and tested for significance of fixed effects using likelihood ratio tests. All analyses were conducted in R (R Core Team, 2022).

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 generalized linear mixed effects models (GLMMs). Each model 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. 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 as a random effect to account for non-independence of flowers on the same plant. For all models, we used the `glmmTMB` package (Brooks et al., 2015), and calculated p-values using likelihood ratio tests.

Using data from the controlled honey bee visit experiments described above, we assessed the direct relationship between increasing honey bee visits and *C. quamash* pollination by fitting a 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 that produced fertilized ovules and failures were flowers with no fertilized ovules. We tested for significance using likelihood ratio tests.

We evaluated how pollen and nectar availability responded to honey bee introductions by fitting two separate 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 dehiscid anthers with pollen) or the mean nectar availability in unvisited bagged flowers. Both models 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 a random effect in both models. Nectar and pollen data were zero-inflated, so we modeled nectar and pollen availability as presence/absence binary responses. We calculated p-values using likelihood ratio tests.

To assess whether native bees were more effective than honey bees as pollinators of *C. quamash* we first confirmed that pollinator taxon was an important predictor of effectiveness using generalized linear models. 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 S2: Table S2.1), 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. We tested for significance of predictors by stepwise model simplification and performed Chi-square tests to compare individual taxa.

## Results

During 96 half-hour netting periods along standard 100 m transects, we recorded 791 honey bees and 2,329 native bees visiting 14 plant species across 15 meadows in the Central Sierra Nevada in California, USA (Appendix S2: Table S2.2). Just over forty percent of floral visits were to *C. quamash*, which we chose as a focal species because of its consistent abundance, its cultural relevance, and its ecological importance. 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 – 184 bees per hour per 100 m transect while the abundance of native bees ranged from 10 – 260 bees. The abundance of honey bees visiting *C. quamash* ranged from 0 – 65 bees and native bees ranged from 0 – 63 bees.

**(i) Effect of honey bee abundance on *C. quamash* visitation and pollination** – Greater honey bee abundance in meadows led to increased honey bee visits to *Camassia quamash* focal plants (Appendix S2: Table S2.3;  $\chi^2 = 28.160$ ; d.f. = 1;  $p < 0.001$ ). As honey bee visits to *C. quamash* focal plants increased, native bee focal plant visits decreased (Appendix S2: Table S2.3;  $\chi^2 = 4.449$ ; d.f. = 1;  $p = 0.035$ ), such that 63% fewer native bees visited *C. quamash* when one or more honey bees visited focal plants. Changes in native bee and honey bee visitation led to changes in some but not all measures of pollination (Fig. 2.1). Neither native bee nor honey bee visitation predicted the number of conspecific pollen grains on *C. quamash* stigmas (Table 2.1), and flowers that were bagged to prevent visitation had similar quantities of conspecific pollen on stigmas compared to open-pollinated plants (Appendix S2: Fig. S2.2), suggesting an important component of self-deposition. In contrast, native bee visitation significantly increased both the number of pollen tubes growing to the base of *C. quamash* styles (Table 2.1;  $\chi^2 = 20.674$ , d.f. = 1,  $p < 0.001$ ) and the proportion of fertilized ovules in *C. quamash* fruits ( $\chi^2 =$

6.226, d.f. = 1,  $p = 0.013$ ), such that, when twenty or more native bees visited *C. quamash* during netting transects, ovule fertilization increased by 34%. Conversely, honey bee visitation had no effect on pollen tube numbers (Table 2.1;  $\chi^2 = 0.970$ , d.f. = 1,  $p > 0.05$ ) but significantly decreased the proportion of fertilized ovules in *C. quamash* fruits ( $\chi^2 = 15.346$ , d.f. = 1,  $p < 0.001$ ), such that, when ten or more honey bees visited *C. quamash* during netting transects, ovule fertilization decreased by 38%.

**(ii) 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 S2: Fig. S2.3;  $\chi^2 = 3.760$ , d.f. = 1,  $p = 0.053$ ). Likewise, unvisited flowers set as many seeds as those visited by honey bees (Appendix S2: Table S2.4).

**(iii) Effect of honey bee abundance on *C. quamash* pollen and nectar availability** – In meadows with higher honey bee abundance, the probability of observing visible pollen on dehisced anthers was reduced (Table 2.2;  $\chi^2 = 6.994$ , d.f. = 1,  $p = 0.008$ ). Likewise, the probability of detecting measurable nectar in flowers also declined sharply with increased honey bee abundance (Table 2.2;  $\chi^2 = 10.908$ , d.f. = 1,  $p < 0.001$ ), such that the percent of flowers with measurable nectar decreased by 78% when more than twenty honey bees visited flowers during netting transects. In contrast, native bee abundance did not predict pollen or nectar availability.

**(iv) Comparative single-visit effectiveness of honey bees and native bees** – During single-visit effectiveness trials, we observed 96 visits from 5 different pollinator taxa (Appendix S2: Table S2.5). Taxa differed in their single-visit effectiveness as pollinators and honey bees were among the least effective (Fig. 2.2). Specifically, *Bombus* spp. and *Osmia* spp. were both significantly more effective than honey bees and unvisited controls (Appendix S2: Table S2.5).

“Small dark bees”, which mostly comprised *Lasioglossum* and *Andrena*, were marginally more effective than honey bees, but were as effective as controls and when compared to other pollinator groups. Pollinators also varied in how often they contacted stigmas and other aspects of visit behavior (Appendix S2: Table S2.1). 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 S2: Fig. S2.4), whereas native bees did not rob nectar and often collected pollen.

## Discussion

***Honey bee abundance decreases native bee visitation and C. quamash pollination*** – In our natural meadow communities honey bees displaced native pollinators and reduced pollination. Abundant honey bees increased their own visits to *C. quamash* and decreased native bee visits. 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 (England et al., 2001; Dupont et al., 2004), 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.

***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). Indirect negative effects of honey bee visits may be severe when this behavior is frequent.

***Possible direct effects of honey bee abundance on pollination*** – If there is a direct negative effect of honey bee visits on *C. quamash* pollination, the mechanism is not obvious. 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, *C. quamash* does not refill nectar in the populations we studied and artificial nectar removal did not affect seed set for unvisited plants (Appendix S2: Table S2.6). 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 *C. quamash* pollination by reducing visits from more effective native bee pollinators. 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). Although resource competition seems a more likely explanation, other competition avoidance behaviors, including scent-cues (Stout & Goulson, 2001), could also reduce native bee visits in response to increased honey bee visits.

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 a natural element of bee communities 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 for which introducing honey bees or other highly abundant generalist pollinators may 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., 2018) 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 (U.S. 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.

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## Tables and Figures

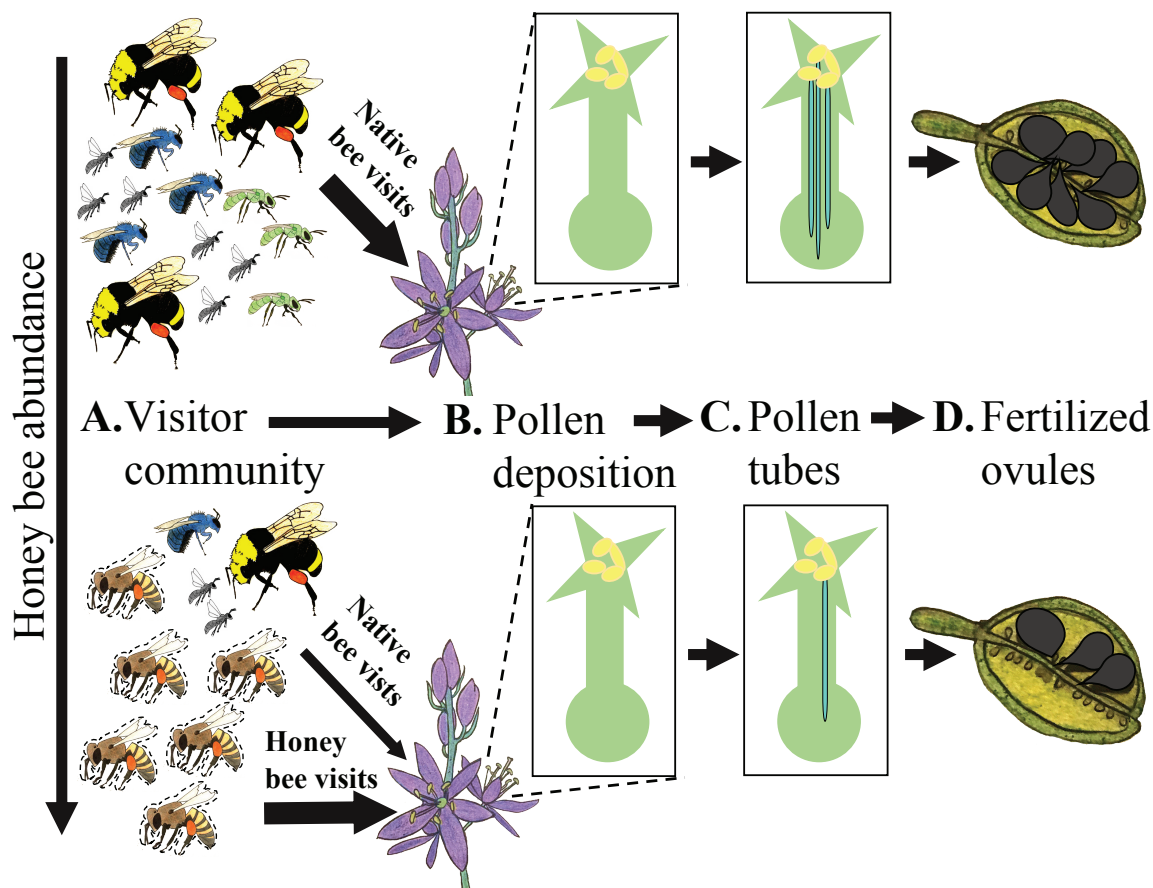
**Table 2.1.** Summary results for models describing the effect of honey bee and native bee visits on different measures of pollination success: conspecific pollen deposition on stigmas, the number of pollen tubes growing into styles, and the proportion of fertilized ovules in fruit. The p-values are from the Chi-square test of the null hypothesis that a model simplified by excluding the model term is not significantly different from a model that includes the model term.

<b>Pollen deposition</b>					
Model term	Coef. $\beta$	SE( $\beta$ )	Chi-sq	p-value	
Honey bee visits	0.001	0.003	0.043	0.836	
Native bee visits	0.005	0.004	1.363	0.243	
<b>Pollen tubes</b>					
Model term	Coef. $\beta$	SE( $\beta$ )	Chi-sq	p-value	
Honey bee visits	-0.004	0.004	0.970	0.325	
Native bee visits	0.027	0.006	20.674	< 0.001	***
<b>Fertilized ovules</b>					
Model term	Coef. $\beta$	SE( $\beta$ )	Chi-sq	p-value	
Honey bee visits	-0.023	0.006	15.346	< 0.001	***
Native bee visits	0.014	0.006	6.226	0.013	*

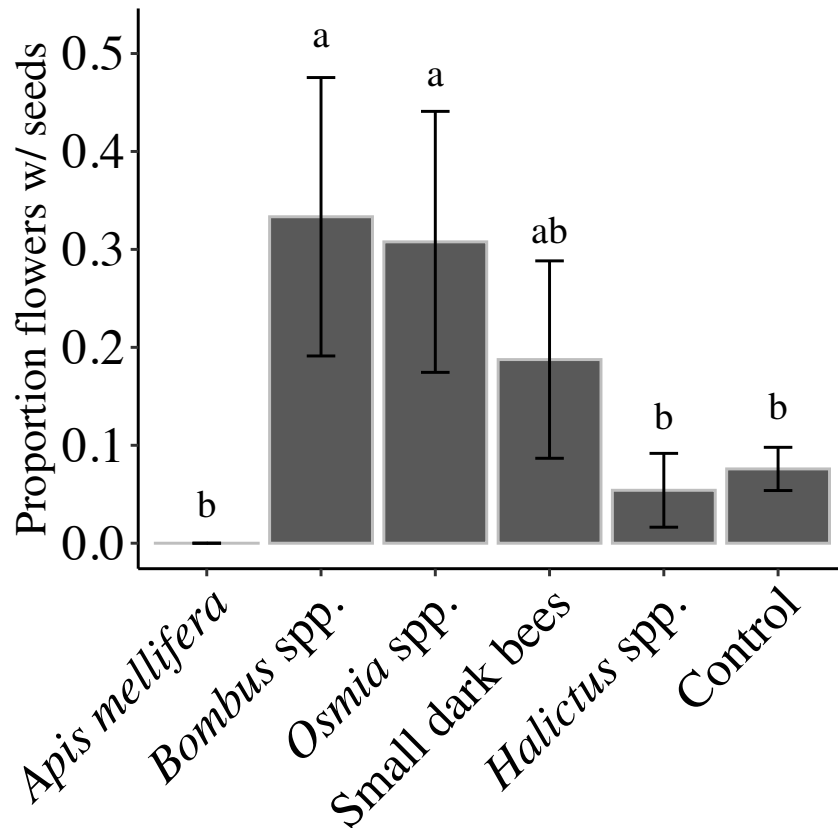
**Table 2.2.** Summary results for models describing: (1) pollen availability in open-pollinated flowers, modeled as a binary response (visible pollen on at least one dehisced anther or no visible pollen on any anthers), and (2) nectar availability in open-pollinated flowers, modeled as a binary response (measurable nectar or no measurable nectar). The model terms ‘Baseline pollen’ and ‘Baseline nectar’ are the average pollen and nectar availability in plants that were bagged at the beginning of each day to prevent insect visitation. See Methods section for detail on data collection and model structure.

<b>(1) <i>C. quamash</i> pollen availability</b>					
Model term	Coef. $\beta$	SE( $\beta$ )	Chi-sq	p-value	
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>(2) <i>C. quamash</i> nectar availability</b>					
Model term	Coef. $\beta$	SE( $\beta$ )	Chi-sq	p-value	
Honey bee abundance	-0.029	0.009	10.908	<0.001	***
Native bee abundance	0.008	0.010	0.614	0.433	
Baseline nectar	0.025	0.025	0.944	0.331	





**Fig. 2.1.** As honey bee abundance in meadows increased, *C. 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.



**Fig. 2.2.** Single-visit effectiveness, measured as the proportion of visits resulting in fertilized seeds, for different insects visiting *C. quamash*. Pollinator taxa were compared using Pearson's Chi-square 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 S2: Tables S2.4 and S2.5.

## Appendix S2

**Table S2.1.** Single-visit effectiveness and visit behavior data for the first flower visited on plants ‘1<sup>st</sup> visits’ and across all flowers visited during single-visit trials. All flowers were on bagged plants that had not previously been visited, but only the first flower visited by a given insect as it foraged on the plant was used in our single-visit analysis presented in Fig. 2. The proportion of visitors who contacted the stigmas, collected pollen, collected nectar, and robbed nectar (visiting from behind petals without touching reproductive structures) varied among taxa. The proportion of single visits leading to any seed production and the mean number of fertilized seeds produced per fruit also varied among taxa. For the single-visit effectiveness data, the denominator for ‘Prop. seed set all visits’ and ‘Prop. seed set 1<sup>st</sup> visits’ are the sample sizes for the mean number of fertilized seeds produced following single visits.

Pollinator taxon	Visit behavior (all visits)				Single-visit effectiveness			
	Stigma contact	Pollen collected	Nectar collected	Nectar robbed	Prop. seed set all visits	Prop. seed set 1 <sup>st</sup> visits	Seed set mean $\pm$ SE all visits	Seed set mean $\pm$ SE 1 <sup>st</sup> visits
<i>Andrena</i> spp.	8/9	9/9	3/9	0/9	0/9	0/2	0.0 <sup>+/-</sup> 0.0	0.0 <sup>+/-</sup> 0.0
<i>A. mellifera</i>	7/48	5/48	33/48	15/48	0/48	0/18	0.0 <sup>+/-</sup> 0.0	0.0 <sup>+/-</sup> 0.0
<i>Bombus</i> spp.	54/54	17/54	54/54	0/54	11/54	3/12	1.6 <sup>+/-</sup> 0.6	2.7 <sup>+/-</sup> 1.9
<i>Halictus</i> spp.	56/88	87/87	24/87	0/87	5/89	3/37	0.3 <sup>+/-</sup> 0.2	0.2 <sup>+/-</sup> 0.2
<i>Osmia</i> spp.	22/27	8/27	24/27	0/27	8/27	3/16	2.5 <sup>+/-</sup> 1.0	2.4 <sup>+/-</sup> 1.5
Sm dark bees	22/33	31/33	7/33	0/33	6/33	2/13	1.4 <sup>+/-</sup> 0.7	2.3 <sup>+/-</sup> 1.3
Syrphid flies	3/5	5/5	0/5	0/5	0/5	0/3	0.0 <sup>+/-</sup> 0.0	0.0 <sup>+/-</sup> 0.0

**Table S2.2.** Summary data from netting transects and focal plant observations across all meadows sampled. Across netting transects, 16 bee genera were observed visiting *C. quamash* (*Agapostemon*, *Andrena*, *Anthophora*, *Apis*, *Bombus*, *Colletes*, *Eucera*, *Habropoda*, *Halictus*, *Hoplitis*, *Lasioglossum*, *Megachile*, *Nomada*, *Osmia*, *Sphecodes*, and *Xylocopa*). Other plant species visited by insects during netting transects included: *Bistorta bistortoides*, *Ranunculus occidentalis*, *Trifolium longipes*, *Montia chamoissi*, *Delphinium nuttallianum*, *Taraxacum officinale*, *Potentilla gracilis*, *Ranunculus alimifolius*, *Epilobium ciliatum*, *Primula tetrandra*, *Plagiobothrys scouleri*, *Penstemon rydbergii*, and *Senecio scorzonella*. ‘Abundance’ describes the number of bees caught or counted during one-hour of netting flower visitors. ‘Abundance on *C. quamash*’ is the abundance of bees visiting exclusively *C. quamash*. ‘Visits to focal plants’ is the number of bees visiting focal *C. quamash* plants during 10-minute observation periods, which were conducted in-between morning and afternoon netting transects.

	<b>Total, across all samples</b>	<b>Mean ± SD</b>	<b>Min.</b>	<b>Max.</b>
<b>Abundance</b>				
Honey bees	791	16.5 ± 36.1	0	184
Native bees	2329	48.5 ± 36.7	10	260
<b>Abundance on <i>C. quamash</i></b>				
Honey bees	306	6.4 ± 13.6	0	65
Native bees	960	20.0 ± 15.6	0	63
<b>Visits to focal plants</b>				
Honey bees	68	0.22 ± 0.69	0	6
Native bees	254	0.82 ± 0.98	0	5

**Table S2.3.** Summary models describing (i) the effect of the abundance of honey bees during netting transects on honey bee visits to *C. quamash* focal plants (ii) the effect of the abundance of native bees during netting transects and honey bee visits to focal plants on native bee visits to *C. quamash* focal plants. For more details about the model structure please see the Methods section.

<b>Honey bee visits to <i>C. quamash</i> focal plants</b>					
Model term	Coef. $\beta$	SE( $\beta$ )	Chi-sq	p-value	
Honey bee abundance	0.006	0.001	28.160	<0.001	***
<b>Native bee visits to <i>C. quamash</i> focal plants</b>					
Model term	Coef. $\beta$	SE( $\beta$ )	Chi-sq	p-value	
Honey bee visits	-0.174	0.082	4.449	0.035	*
Native abundance	0.015	0.004	16.600	<0.001	***

**Table S2.4.** Single-visit pollination effectiveness Chi-square test comparisons. ‘Honey SVE’ is the single-visit effectiveness of honey bees, measured as the proportion of flowers that set at least one fertilized seed after receiving a single insect visit. ‘Native SVE’ is the single-visit effectiveness of native bee taxa and ‘Control’ plants are plants that were bagged and never visited by either native bees or honey bees. Data in 2019 were collected incidentally from a different experiment and were from a different meadow than the data collected in 2020.

<b>Bee group vs. unvisited control comparisons</b>						
Year	Prop. flowers setting seed (Native SVE)	Prop. flowers setting seed (Honey SVE)	Prop. flowers setting seed (Control)	Test df	Chi-sq	p-value
2019		7/11	18/37	1	0.763	0.382
2020		0/18	11/145	1	1.464	0.226
2020	13/78		11/145	1	4.354	0.037 *

**Table S2.5.** Single-visit pollination effectiveness model selection and pollinator taxa

comparisons. Deviance is the likelihood ratio test statistic. The p-values are from the Chi-square test of the null hypothesis that a model simplified by excluding the focal term is not significantly different from the model on the above line that includes the test term. The maximal model included three main effect terms of bee taxon observed ('taxon' with six levels: unvisited, *Bombus* spp., *Osmia* spp., *Halictus* spp., "Small dark bees", or *Apis mellifera*), whether the stigma was contacted during the visit ('stigma' with two levels), and the day of the visit ('day' with four levels). Models 3 and 4 were each compared to model 2 to test focal terms day and taxon, respectively. After model simplification, the minimal adequate model included only the main effect of taxon. After confirming that pollinator taxon was an important predictor of pollination effectiveness, we performed Chi-square tests comparing the proportion of single visits resulting in at least one fertilized seed for different pollinator taxa. 'Honey SVE' is the single-visit effectiveness of honey bees, measured as the proportion of single visits resulting in at least one fertilized seed. 'Native SVE' is the single-visit effectiveness of the indicated bee taxon.

<b>Model selection</b>					
Model	Resid. df		Test df	Deviance	p-value
1	231				
2	232	stigma	1	0.050	0.820
3	235	day	3	5.540	0.140
4	237	taxon	5	14.580	0.010 *

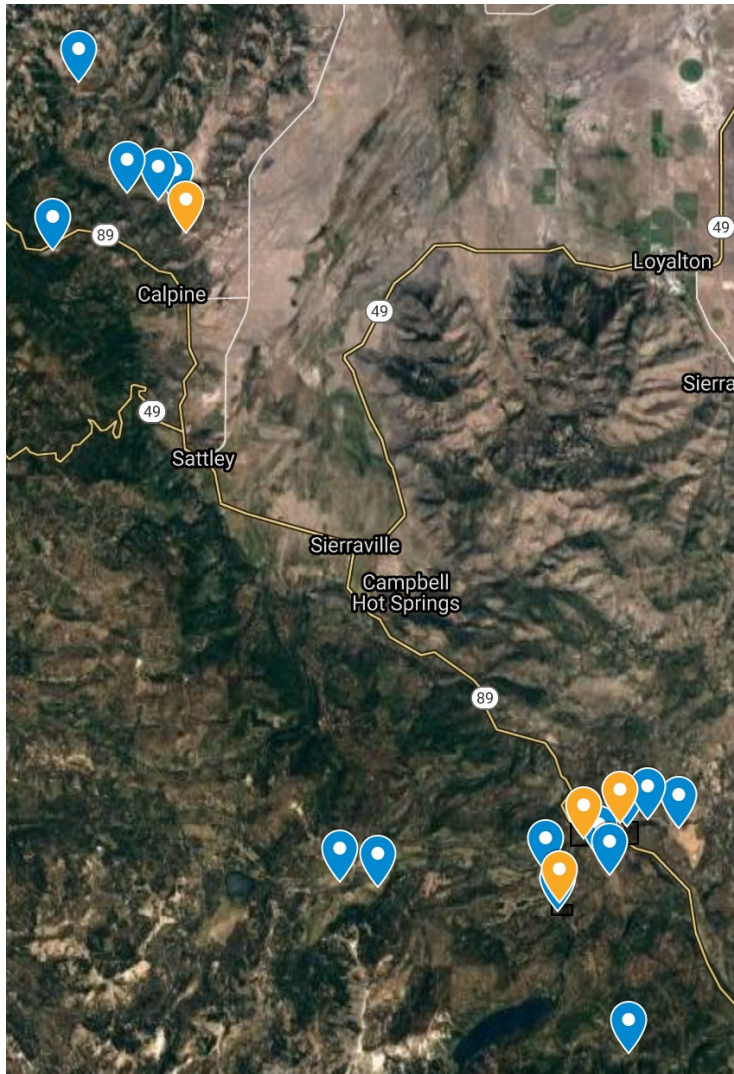
  

<b>Honey bee vs. native bee taxa comparisons</b>					
Native bee taxon	Honey SVE	Native SVE	Test df	Chi-sq	p-value
<i>Bombus</i> spp.	0/18	4/12	1	6.923	0.009 **
<i>Osmia</i> spp.	0/18	4/13	1	6.359	0.012 *
"Small dark bees"	0/18	3/16	1	3.702	0.054
<i>Halictus</i> spp.	0/18	2/37	1	1.001	0.315

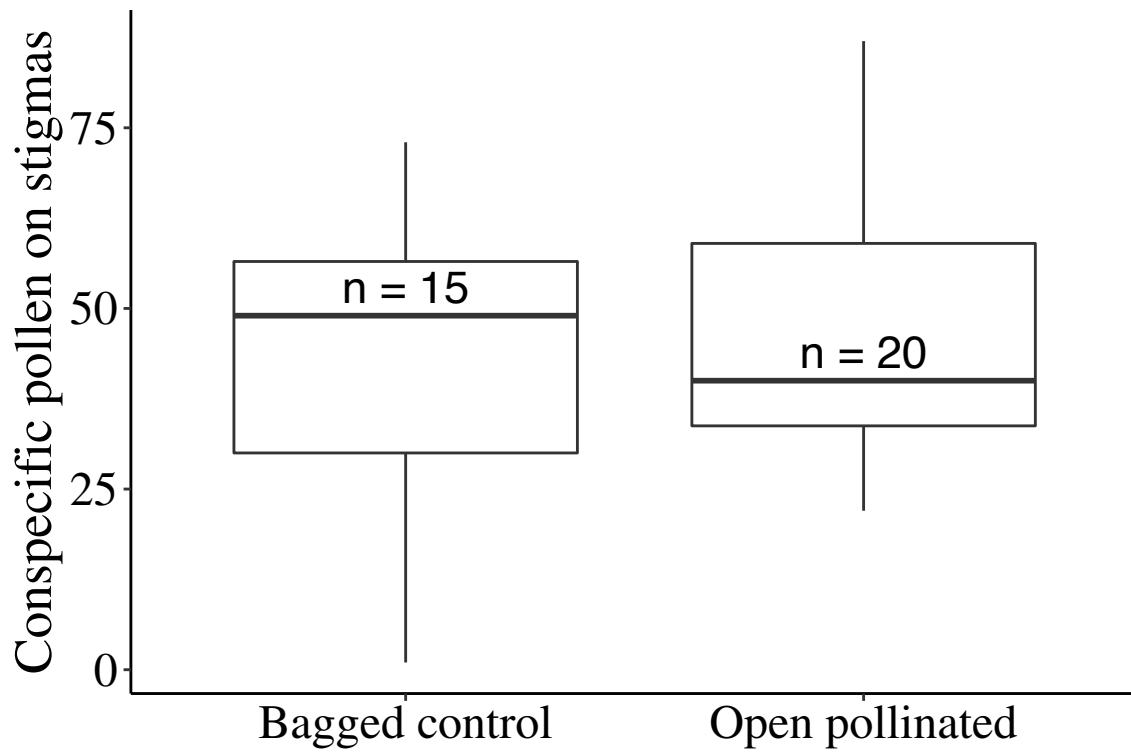
**Table S2.6.** Summary of nectar removal data. In 2021, we returned to one the meadows we had studied in 2019 and 2020 to assess whether *C. quamash* replenished nectar within 3 hours after nectar was artificially drained with microcapillary tubes. We also compared the proportion of flowers that set seed for flowers that had nectar removed and unmanipulated flowers. We removed nectar from one flower on a previously bagged, unvisited plant and used a second flower on that same plant as a control. Nectar refill was uncommon and very little nectar refilled overall, suggesting that flowers produce a set amount of nectar and do not respond to removal by producing more nectar. Seed set was low overall but there is no evidence to suggest that nectar removal affects pollination for self-pollinated plants.

<b>Nectar removal treatment</b>	<b>Prop. fruit set</b>	<b>Prop. flowers that replenished any nectar</b>	<b>Percent of removed nectar that was replenished (N = 24)</b>
Control	1/17		
Removed	1/16	3/24	4.95%

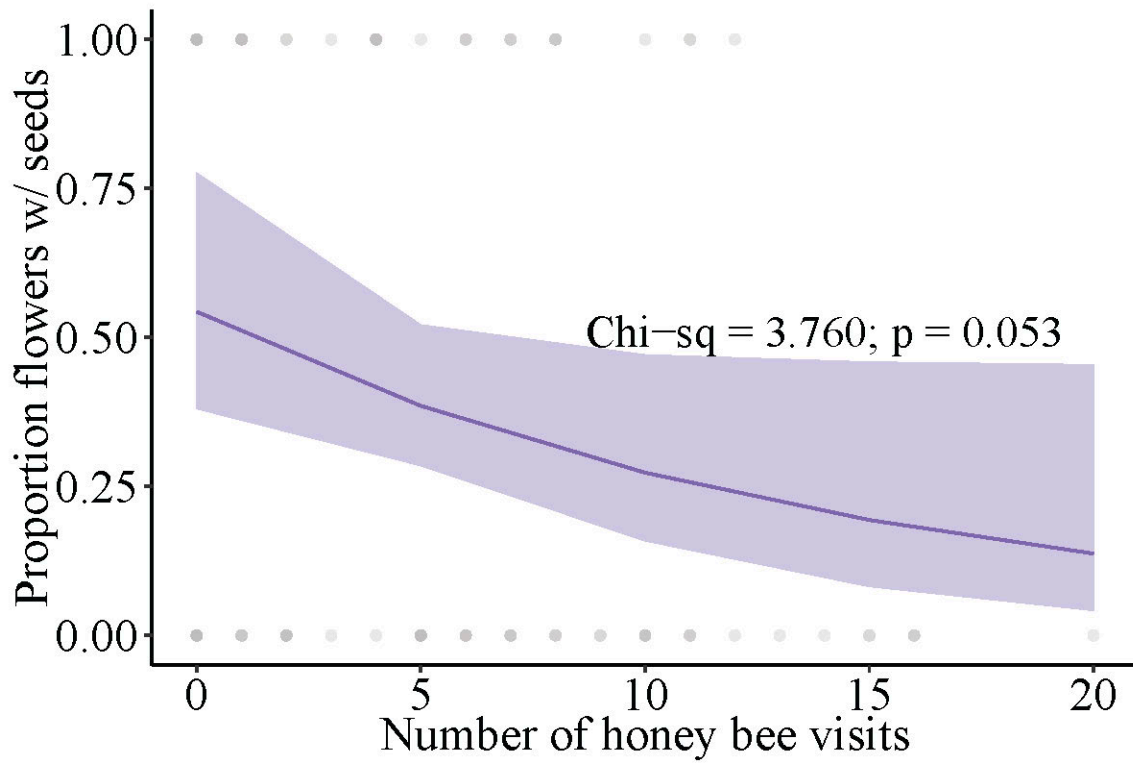




**Fig. S2.1.** Sites and apiary locations. Blue markers are sampled meadows and yellow markers are where apiaries are located. All sites are separated by at least 500 m and are between 5300 ft and 7000 ft in elevation. Apiaries are all located on private property neighboring Tahoe National Forest land. The three apiaries in the south were experimentally introduced halfway through the *C. quamash* bloom period to generate additional variance in honey bee abundance and each apiary consisted of 20 hives. The apiary in the north is a commercial apiary of approximately 100 hives.



**Fig. S2.2.** Conspecific pollen deposition on stigmas of control plants, which were bagged at the beginning of the day to prevent insect visitation, and open-pollinated plants from two of the sites sampled. Black bars are the median and box hinges correspond to the first and third quartiles (the 25th and 75th percentiles).



**Fig. S2.3.** Direct effect of increasing honey bee visits on pollination of *C. quamash*. The purple line plots the probability that flowers will set seed after receiving different numbers of honey bee visits. Grey points are the raw data, and the purple shading depicts the confidence range. Predictions are from a generalized linear mixed model which includes number of honey bee visits as a fixed effect and date and plant ID as random effects.



**Fig. S2.4.** Honey bee “robbing” nectar from a *C. quamash* plant by visiting from behind petals.

### **Chapter 3: A meta-analysis of single visit pollination effectiveness comparing honey bees and other floral visitors\***

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#### **Abstract**

Many animals provide ecosystem services in the form of pollination, including honeybees which have become globally dominant floral visitors. A rich literature documents considerable variation in single visit pollination effectiveness, but this literature has yet to be extensively synthesized to address whether honeybees are effective pollinators. We conducted a hierarchical meta-analysis of 168 studies and extracted 1564 single visit effectiveness (SVE) measures for 240 plant species. We paired SVE data with visitation frequency data for 69 of these studies. We used these data to ask: 1) Do honeybees (*Apis mellifera*) and other floral visitors differ in their SVE?; 2) To what extent do plant and pollinator attributes predict differences in SVE between honeybees and other visitors?; and 3) Is there a correlation between visitation frequency and SVE? Honeybees were significantly less effective than the most effective non-honeybee pollinators but as effective as the average pollinator. The type of pollinator moderated these effects. Honeybees were less effective compared to the most effective and average bird and bee pollinators but were as effective as other taxa. Visitation frequency and SVE were positively

correlated, but this trend was largely driven by data from communities where honeybees were absent. Although high visitation frequencies make honeybees important pollinators, they were less effective than the average bee and rarely the most effective pollinator of the plants they visit. As such, honeybees may be imperfect substitutes for the loss of wild pollinators and safeguarding pollination will benefit from conservation of non-honeybee taxa.

## **Introduction**

Over 70% of plants depend to some degree on animal pollinators to successfully reproduce (Ollerton et al., 2011). Among the diversity of pollinators, taxa vary in their contributions to pollination in multiple intricate dimensions, some quantitative (e.g., numbers of visits, numbers of pollen grains transferred: Herrera, 1987; King et al., 2013), others qualitative (e.g., proportion selfed versus outcrossed pollen, diversity of mates, spatial distances of mating: Valverde et al., 2019; Richardson et al., 2021). At its core, the functional contributions of different pollinator taxa can be measured by the quantity (frequency) and quality (effectiveness) of visits to plant reproductive success (Inouye et al., 1994; King et al., 2013). From a quantitative perspective, although biodiverse pollinator assemblages increase pollination (Albrecht et al., 2012; Winfree et al., 2015; Winfree et al., 2018), a few dominant species often provide the majority of floral visits (Kleijn et al., 2015). For example, the numerical dominance of honeybees (*Apis mellifera*) as floral visitors has been hypothesized to drive their functional importance as pollinators (Hung et al., 2018). However, high visit frequencies can impair pollination in some contexts (Aizen et al., 2014) and we know little about whether strongly dominant visitors, such as honeybees, effectively pollinate the plants they visit.

Pollination effectiveness is defined as the per-visit contribution of floral visitors to pollination (Inouye et al., 1994). A long history of studies within the botanical and evolutionary ecology literature documents variation in single visit effectiveness (SVE) among plant visitors (e.g., Herrera, 1987; King et al., 2013; Page et al., 2019). To some extent, variation in pollination effectiveness reflects the wide range of methods used to measure it (Ne'eman et al., 2010), such as single visit pollen deposition (King et al., 2013), the number of developed pollen tubes within styles (Zhang et al., 2015), and/or fruit or seed set (Vicens and Bosch, 2000). Regardless, evidence for variation in SVE comes from numerous individual studies and this literature has yet to be synthesized in a way that would address whether and why particular taxa are more effective than others and whether dominant visitors are more effective pollinators of the plants they visit. Meta-analysis is a particularly valuable way to investigate such questions.

An extensive literature on pollinator importance – the product of per-visit effectiveness and relative visitation rates of different pollinators (King et al., 2013; Ballantyne et al., 2015) – has concluded that pollinators that visit more frequently are generally more important (Vázquez et al., 2012). This conclusion suggests that numerical dominance outweighs among-species variation in SVE, but it is also possible that pollination effectiveness and visitation frequencies are correlated. First, frequent pollinators could be inherently more effective because of deep phylogenetic signals. For example, Ballantyne et al. (2017) found a positive correlation between a pollinator's visit frequency and pollination effectiveness when comparing 23 plant species, likely because bees were both highly effective and highly frequent visitors compared to other floral visitors. Second, positive correlations between pollination effectiveness and visit frequency could occur if pollinators that visit frequently do so to the exclusion of other plant species. Such temporary fidelity (e.g., floral constancy: Free, 1970) or long-term fidelity would operate to

minimize heterospecific pollen transfer, resulting in more effective pollination (Morales and Traveset, 2008). On the other hand, high visitation rates may be the result of many quick and ineffective visits (Ohara et al., 1994) and have a negative or non-significant effect on reproductive success in many contexts (e.g., Sáez et al., 2014; reviewed in Willcox et al., 2017).

Despite their high visitation frequencies, the effectiveness of honeybees relative to other pollinators remains unclear. Bees are often the most effective pollinators of flowers (Ballantyne et al., 2017) and *Apis mellifera* is the most common flower-visiting bee species. However, there are several reasons to suspect that honeybees might be less effective than other bees. First, outside of their native range, honeybees lack the evolutionary history with endemic plants that could have selected for increased pollinator effectiveness (Javorek et al., 2002). Furthermore, honeybees are floral generalists that visit a high proportion of available plants in ecosystems across the globe (Hung et al., 2018), and thus may not be particularly effective at pollinating specific flowering species. Second, honeybees sometimes ‘rob’ plants (Irwin et al., 2010) and efficiently extract and groom pollen from plants without depositing the pollen they extract (Westerkamp, 1991; Koch et al., 2017) or collect nectar without contacting reproductive structures (Vicens and Bosch, 2000; Thomson and Goodell, 2001). On the other hand, honeybees can be highly effective pollinators, even for plants with which they have no shared evolutionary history (e.g., Wist and Davis, 2013), suggesting that honeybees are highly adaptable and capable pollinators.

Understanding pollinator effectiveness has important practical implications for safeguarding the production of pollinator-dependent crops. Highly effective non-honeybee pollinators are important for ensuring crop pollination in the face of global change (Rader et al., 2013) and functionally diverse pollinator communities can increase crop pollination (Woodcock



et al., 2019). Furthermore, pollination may differ in cultivated settings because interspecific plant competition, the spatial arrangement of flowers, and the pollinator taxa that provide pollination may vary between agricultural and natural landscapes (Harrison et al., 2018).

We used a meta-analysis of the pollination effectiveness literature to address three key questions. First, how does the SVE of honeybees compare to that of other floral visitors? We hypothesized that honeybees would exhibit lower SVE relative to other pollinators because honeybees are broad generalists and might efficiently extract nectar and pollen without effectively pollinating plants. Second, to what extent do plant and pollinator attributes predict the comparative SVE of honeybees? Specifically, we evaluated whether pollinator taxonomic groups (e.g., bees, birds, etc.), crop status (crop vs. non-crop plant species), and if plant species exist within the native range of honeybees predict differences in comparative SVE. We hypothesized that the SVE of honeybees would be lower compared to other bees, in crop systems, and for plant species outside the native range of honeybees because previous studies have suggested such trends (Ballantyne et al., 2017; Hung et al., 2018). Third, is there a correlation between floral visitation frequency and SVE? We evaluated this question separately for communities where honeybees were present or absent. We expected to find a positive correlation between visitation frequency and SVE that would be reduced when honeybees were present because honeybees are often highly frequent visitors and might be less consistently effective. Although previous studies have synthesized subsets of the pollination effectiveness literature (notably, Hung et al., 2018; Földesi et al., 2020), this paper is, at present, the most extensive meta-analysis to synthesize published results concerning single visit effectiveness.

## Methods

**Study screening** – We performed a Web of Science (WoS) search using a multiterm query (Appendix S3: Fig. S3.1) designed to capture the highly variable terminology describing pollination effectiveness detailed in Ne'eman et al. (2010). In May 2020, this search yielded 1,036 results. One of us (MP) screened the abstracts found by WoS to determine whether they potentially contained single visit effectiveness (SVE) data. This yielded 388 papers. We also performed a Google Scholar search of the literature using a similar multi-term query (Appendix S3: Fig. S3.1), which yielded 116 additional papers. We found 62 papers from the reference sections of previously included papers. After removing duplicates and reading abstracts, we identified 468 papers which seemed appropriate for a more thorough screening.

We followed the PRISMA protocol for collecting and screening data from the literature (Appendix S3: Fig. S3.1; Moher et al., 2009). To be included in our analysis, the paper had to contain empirical data on the per-visit contribution of at least one free-foraging visitor to plant reproduction. We considered pollen deposition, percent fruit set, fruit weight, and/or seed set as measures of SVE. Most studies were conducted with intact flowers, but we also included data from experiments that used the “interview stick” method (in which a cut flower was presented to potential visitors). We did not include estimates of SVE based on equations or model outputs nor did we include data from trials that manipulated dead bees to deposit pollen. We extracted means, sample sizes, and measures of error (e.g., standard deviation, standard error) directly from the text of the paper or from graphs using WebPlotDigitizer (v. 4.4, Rohatgi, 2020). When lower and upper error estimates were not symmetrical, we used the upper error estimate. When possible, we converted measures of error to standard deviation. When a paper did not report sample sizes, error, or other important information, we contacted the study authors. If we were

unable to retrieve or estimate information on mean effectiveness and error, we excluded the paper from our analysis. We also excluded papers if we couldn't convert other measures of error to standard deviation (e.g., when studies did not report sample sizes). After screening papers, 168 studies remained in our analytical dataset. We also extracted data on study year and location, plant species, plant family, whether the plant species was a crop-plant, pollinator taxon, pollinator group (e.g., bird, fly, bee), and the native range of pollinator and plant species. We determined range status to biogeographical realms by looking up the nativity of each taxon in the scientific literature and using occurrence records on the Global Biodiversity Information Facility (GBIF) website. If papers reported SVE outcomes from multiple sites or years, we extracted these data as separate outcomes and dealt with their non-independence statistically (see below).

We collected information on the visitation rates of pollinators if it was reported for the same plant species for which pollinator effectiveness data were reported. This rate could be reported as the number of visits to a focal flower or patch of flowers per unit time or the number of flowers visited per unit time and/or per unit area. We did not include data on the relative abundance of different visitors unless data were collected in a homogeneous landscape (like an orchard) in which most visitors would have been visiting the focal plant species. If a study reported visitation data, we matched those data to the corresponding SVE data from the same study and plant species. Perfect matches required that pollinator taxa were reported to the same taxonomic resolution and that data were collected in the same year and location. When more than one measure of visit frequency was reported we preferentially used data on the number of visits to a focal flower per unit time. When more than one measure of SVE was reported, we preferentially chose whichever measure was better represented in our data, such that pollen deposition data were chosen over seed set data and seed set data were chosen over fruit set data.

Ultimately, our dataset contained 1564 SVE records (i.e., average effectiveness values for pollinators visiting plants) drawn from 168 peer-reviewed and published studies (Appendix S3: Table S3.1). Research was conducted on every ice-free continent, with most work occurring in the Nearctic (N = 52) or West Palearctic (N = 39) over a period of 39 years, from 1981 to 2020 (Fig. 3.1). Many studies (30) investigated pollination of more than one plant species (range: 2-23), with a total of 240 plant species assessed belonging to 67 families. Among the 168 studies which reported SVE values, 69 also included data on the visitation dates of different pollinators. Of the plant species included in our analysis of the comparative effectiveness of honeybees (Appendix S3: Table S3.2), only 13/95 were studied more than once.

**Meta-analysis** – To address questions about the single visit effectiveness of honeybees and non-honeybees, we defined the effect size as the standardized mean difference (SMD, i.e., Hedges' *g* (Hedges, 1981)) of SVE values between honeybees and non-honeybees for each unique study, plant, site, and year combination. We chose to use Hedges' *g* over other effect sizes because it is commonly used in the ecology literature for comparing two means (Nakagawa and Santos, 2012), and it includes a correction for small sample sizes, which occurred with our data. Following Hung et al. (2018), we calculated effect sizes for two separate comparisons: (1) the difference between honeybees versus the most effective non-honeybee taxon and (2) the average difference between honeybees and non-honeybee taxa (hence, 'average effectiveness'). The SMD value is  $> 0$  when other pollinators are more effective than honeybees and  $< 0$  if the opposite occurs. We calculated each effect size in *R* (R Core Development Team, 2020) using the *escalc* function in the '*metafor*' package (v. 2.1-0, Viechtbauer, 2010).

We fit meta-analytic and meta-regression multilevel linear mixed-effects models, using the *rma.mv* function in the '*metafor*' package (v. 2.1-0, Viechtbauer, 2010). We used three

random effects to control for non-independence of effect sizes collected from the same study or plant species: study ID, plant species, and an observation-level ID for individual SVE measures. We used phylogenetic comparative methods (Cornwell and Nakagawa, 2017) to account for non-independence that may arise due to shared evolutionary history of focal plants by including a phylogenetic covariance matrix. The phylogeny and branch lengths (Appendix S3: Fig. S3.2) used to compute a phylogenetic covariance matrix came from a recently published, dated megaphylogeny contained in the package '*V.Phylomaker*' (Jin and Qian, 2019), which combines the seed plant phylogeny from Smith and Brown (2018) with the pteridophyte phylogeny from Zanne et al. (2014). Despite slightly higher AIC values and larger P values (Appendix S3: Fig. S3.3), we present results from models including phylogenetic controls to fully account for non-independence due to shared ancestry (Chamberlain et al., 2012). Both analyses produced qualitatively similar results and neither the magnitude nor the sign of SMD estimates changed when phylogenetic controls were included (Appendix S3: Fig. S3.3 and Table S3.3). However, uncertainty around SMD estimates was consistently smaller in models without phylogenetic controls, such that marginally significant effects became significant when phylogenetic controls were removed. Thus, inclusion of phylogenetic controls renders our analysis more conservative.

With this mixed-effects structure, we specified four models, which include an intercept only model (i.e., overall meta-analytic model), and three meta-regression models for different fixed effects/moderators: (1) pollinator taxonomic group, (2) whether the plant was a crop plant (crop status), and (3) for native plants, whether it was in the honeybee's native range (range status). We follow Hung et al. (2018) and define the West Palearctic as the honeybee's native range (Ruttner, 1988). For the analysis comparing honeybee comparative effectiveness inside and outside of the honeybee's native range, we excluded non-native plants from the analysis.

To test whether there was a relationship between a pollinator taxon's single visit effectiveness and visit frequency, we calculated Pearson's correlation coefficients ( $r$ ) for the relationship between visit frequency and pollinator effectiveness for each unique study, plant, site, and year combination in which there were at least five pollinator taxa represented. We filtered data because sample variances cannot be confidently estimated when fewer than five observations are used to calculate correlation coefficients. In total, 26 studies of 50 plant species had visit frequency and effectiveness data for at least five taxa, and 62% of studies were fully excluded. After calculating correlation coefficients, we used the *escalc* function in the *metafor* package to calculate Fisher's r-to-Z transformed correlation coefficients and corresponding sampling variances. Using the same multilevel linear mixed-effects model structure and phylogenetic controls as described above we generated three models. The first model was an intercept-only model to test for the overall relationship between a pollinator's visit frequency and single visit effectiveness. The second model compared three categories against one another: studies where honeybees were present, studies where honeybees were absent, and studies where we artificially removed all points corresponding to honeybees (re-calculating effect sizes as detailed above). We generated this third category to determine whether the patterns we observed were solely driven by honeybees themselves or whether there might also be indirect effects of honeybee presence on the relationship between visit frequency and single visit effectiveness. The third model tested whether there was an interaction between crop status and honeybee presence.

***Tests for publication bias*** – Publication bias was assessed by visual inspection of funnel plots for each model (Appendix S3: Fig. S3.4 and Fig. S3.5) and via a modified Egger's test (Egger et al., 1997; Sterne and Egger, 2005) on meta-analytic residuals in which effect size precision ( $\sqrt{1/\text{variance}}$ ) is included as a moderator (Nakagawa and Santos, 2012). A

significant slope for precision would indicate statistically significant funnel asymmetry after controlling for all other variables in the model. We considered analyses to be biased if the intercept differed from zero at  $P = 0.10$  (as in Egger et al., 1997).

## Results

Across plant species and studies, relative effectiveness values were normally distributed, but most pollinators (54%) were less effective than the mean effectiveness of all visitors, compared to 43% which were more effective than the mean and 3% which were as effective as the mean (Appendix S3: Fig. S3.6). For studies that reported visit frequency data ( $N = 69$ ), the distribution of relative visit frequency values was skewed to the right (Appendix S3: Fig. S3.6), such that only 27% of visitors visited more frequently than the mean visit frequency. Within studies that reported paired effectiveness and visit frequency data for at least five taxa ( $N = 26$ ), honeybees were the most frequent visitor 23% of the time but the most effective pollinator only 9% of the time.

*How does the SVE of honeybees compare with other floral visitors?* – A total of 72 studies reported comparisons between *A. mellifera* and at least one other taxon. These studies focused on 95 plant species and include crops ( $N = 32$ ) and non-native plant species ( $N = 22$ ) (Appendix S3: Table S3.1). From these comparative studies, 577 individual effect sizes were obtained and summarized for each combination of plant and pollinator group within a study. This yielded 185 effect sizes comparing the most effective non-honeybee pollinator and honeybees (Most Effective Pollinator (MEP) comparisons) and 185 effect sizes comparing the average effectiveness of all non-honeybee pollinators and honeybees (Average Effective Pollinator (AEP) comparisons). When comparing overall study-level effect sizes, we found that non-

honeybee pollinators were more effective than honeybees. This outcome was statistically significant for Most Effective Pollinator (MEP) comparisons (Appendix S3: Table S3.3; overall standardized mean difference (SMD): 0.512, [0.233, 0.792 95% CI];  $P < 0.001$ ). For Average Effective Pollinator (AEP) comparisons, honeybees were less effective than the average pollinator at the 10% significance level but were equally effective at the 5% significance level (SMD: 0.241, [-0.013, 0.495];  $P = 0.063$ ). The data showed little evidence of publication bias in terms of funnel plot asymmetry of meta-analytic residuals as revealed by plot inspection (Appendix S3: Fig. S3.4). Results from Egger's tests suggested little to no degree of asymmetry for our overall meta-analytic model (MEP:  $P > 0.10$ ; AEP:  $P > 0.10$ ).

***To what extent do plant and pollinator attributes predict the comparative SVE of honeybees?*** – Computing effects separately for each pollinator group revealed that the type of pollinator moderated the comparative SVE of honeybees (Fig. 3.2). The most effective bees and birds were significantly more effective than honeybees (Fig. 3.2a; bee SMD: 0.663, [0.442, 0.885];  $P < 0.001$  & bird SMD: 2.275, [1.461, 3.089];  $P < 0.001$ ). For average effectiveness comparisons, only other bees and birds were significantly more effective than honeybees (Fig. 3.2b; bee SMD: 0.316, [0.094, 0.538];  $P = 0.005$ ; bird SMD: 1.313, [0.675, 1.952];  $P < 0.001$ ). Honeybees were as effective as the most effective and average pollinators from all other groups (Appendix S3: Table S3.3;  $P > 0.05$ ). At the study level, 61% of effect sizes compared other bees and honeybees; we therefore focus subsequent analyses on bees.

The most-effective bees were more effective pollinators of crops than honeybees (Fig. 3.3a; SMD: 0.870, [0.534, 1.205];  $P < 0.001$ ); this was true for average effectiveness comparisons as well (Fig. 3.3b; SMD: 0.606, [0.352, 0.861];  $P < 0.001$ ). For non-crop plants, honeybees were less effective than the most effective other bees (Fig. 3.3a; SMD: 0.465, [0.145,



0.786];  $P = 0.004$ ), but were not significantly different than the average bee pollinator. The most-effective bees were better pollinators of native plants than honeybees (Fig. 3.4a); this was true for plants occurring within (SMD: 0.644, [0.196, 1.093];  $P = 0.005$ ) and outside (SMD: 0.758, [0.331, 1.186];  $P < 0.001$ ) *Apis mellifera*'s native region (West Palearctic). Honeybees were comparable to the average SVE of bees (Fig. 3.4b), inside their native range ( $P = 0.117$ ) and were less effective at the 10% significance level but equally effective at the 5% significance level outside their native range ( $P = 0.067$ ).

*Is there a correlation between floral visitation frequency and SVE?* – Overall, there is a positive relationship between visit frequency and single visit effectiveness (Estimate: 0.407 [0.149, 0.665 95% CI];  $P = 0.002$ ). However, data from systems in which honeybees are absent drive this positive result. When honeybees are present, there is no relationship between visit frequency and effectiveness (Fig. 3.5; Estimate: 0.309 [-0.085, 0.703];  $P > 0.05$ ) and this lack of a significant relationship persisted when we artificially removed data corresponding to honeybee visits. We observed a positive association between visit frequency and SVE only when *Apis mellifera* was actually absent (Fig. 3.5; Estimate: 0.627 [0.210, 1.044];  $P = 0.003$ ). There was also a slight interaction between honeybee presence and crop status, such that the positive relationship between visit frequency and effectiveness was statistically significant only in non-crop systems where honeybees were absent (Appendix S3: Fig. S3.7; Estimate: 0.576 [0.074, 1.079];  $P = 0.025$ ). In crop-systems where honeybees were absent there was a significant relationship at the 10% significance level but not at the 5% significance level (Estimate: 0.629 [-0.042, 1.299];  $P = 0.066$ ). For both crop and non-crop systems where honeybees were present there was no relationship. An Egger's test suggested there was minimal publication bias ( $P > 0.10$ ). Although there was one obvious outlier to the right of funnel plots (Appendix S3: Fig.

S3.5), removing this outlier did not change our findings.

## **Discussion**

Our meta-analysis supports the hypothesis that honeybees are frequently not the most effective pollinator of plants globally. Across six continents and hundreds of plant species, honeybees showed significantly lower single visit effectiveness than the most effective pollinator (Fig. 3.2). This general pattern is likely driven by comparison of honeybees against birds and other bees. The most effective bird and bee pollinators were significantly more effective than honeybees, as were the average bird and bee pollinators. The finding that birds are more effective than honeybees is based on only six studies that were likely focused on flowers frequently pollinated by birds. Nevertheless, it supports the idea that plants adapted to bird pollination have traits that enhance pollination by birds at the expense of pollination by bees (Castellanos et al., 2006). Although data for non-bee taxa were relatively sparse, honeybees were as effective as the average and most effective ant, beetle, butterfly, fly, moth, and wasp pollinators, confirming that non-bee insects can be important pollinators (Orford et al., 2015; Rader et al., 2020). Our results bolster initial work summarizing honeybee pollination effectiveness (Hung et al., 2018) and demonstrate that honeybees are less effective than many other visitors and at best average.

Analysis of crop plants also revealed important differences between honeybees and non-*Apis* pollinators. Despite their abundance in commercial cropping systems, honeybees are less effective crop pollinators than the most effective bee pollinators and the average non-honeybee bees (Fig. 3.3). This finding supports the idea that the importance of honeybees as crop pollinators derives largely from their numerical dominance as crop visitors (Hung et al., 2018).

Our analysis adds robust evidence to a growing consensus that wild bees have the potential to contribute greatly to agricultural pollination. Indeed, wild bee species richness, functional diversity, and visit rates increase crop yield (Blitzer et al., 2016; Woodcock et al., 2019), and the use of managed honeybee hives might not compensate for losses in wild bee species richness and abundance (Mallinger and Gratton, 2015; Pérez-Méndez et al., 2020). For example, increases in honeybee visitation only occasionally increase crop pollination whereas wild insect visitation universally increases fruit set (Garibaldi et al., 2013). As such, managed honeybees alone may be insufficient to meet the increased pollination demands of global agricultural production (Aizen and Harder, 2009) and our results validate the importance of actions to promote resilient native bee communities within agricultural lands (Isaacs et al., 2017).

Honeybees were equally effective as pollinators of plants inside and outside of their native range and were less effective compared to the most effective other bees in both regions (Fig. 3.4). This result is not entirely surprising based on what we know about the co-evolution of plants and pollinators. The non-honeybee bee community may contain specialists sympatric with their host plants. Meanwhile, if honeybees are broad generalists, selective pressure might be less consistent, even within the native range of honeybees. Furthermore, if the morphological features relevant to pollination are relatively consistent across plants within the same genus or family, insects may be capable of pollinating novel plant species. For example, *Prunus* spp. occur in Europe and North America and *Osmia* spp. are highly effective pollinators of *Prunus* tree crops in both regions (Vicens and Bosch, 2000; Bosch et al., 2006), despite the fact that North American *Osmia* spp. do not have shared evolutionary history with the *Prunus* species introduced as tree crops.

We found an overall positive relationship between visit frequency and single visit pollinator effectiveness, but this relationship was largely driven by data from systems in which honeybees were absent (Fig. 3.5). The overall positive correlation suggests that more frequent visitors are also more effective, but this result should not be interpreted to indicate that visitation frequency is an adequate proxy for overall pollination importance (Vázquez et al., 2012; Ballantyne et al., 2017). This positive correlation may suggest that pollinators which visit frequently do so to the exclusion of other plant species, such that they display high floral constancy. High floral constancy may indicate that visitors gather and transport more conspecific pollen (Brosi and Briggs, 2013). Although the pollen loads of visitors do not always adequately predict effective pollination (Adler and Irwin, 2006), high conspecific pollen transport likely predisposes visitors to higher pollination effectiveness on average. Another possible explanation is that, for pollen-collecting visitors, more frequent visitors could be more efficient at extracting large quantities of pollen (e.g., Parker et al., 2016) and might therefore transfer more pollen depending on how well pollen is groomed. Addressing whether more frequent visitors transport more conspecific pollen or deliver fewer heterospecific pollen grains are ripe questions for further study.

The finding that honeybees erode this otherwise positive correlation suggests that this hyper-generalist species is often a numerically dominant visitor with modest effectiveness and may modify the pollination context for plant communities. Interestingly, when comparing systems with and without honeybees, visit frequency and pollination effectiveness do not positively correlate even when we artificially remove the data on honeybees and re-calculate correlation coefficients. This result suggests that honeybee presence may indirectly influence the relationship between visitation frequency and pollination effectiveness by altering the visitation

patterns and effectiveness of other plant visitors. High honeybee visitation frequencies may indicate that honeybees efficiently extract nectar and pollen without also efficiently depositing the pollen they extract (Westerkamp, 1991; Wilson and Thomson, 1991; Goodell and Thomson, 1997). If honeybees deplete floral nectar, this could make plants less attractive to other common visitors (Hansen et al., 2002) and alter their visit behavior and effectiveness (Thomson, 1986). If they extract large amounts of pollen (Cane and Tepedino, 2017), this could reduce the amount available for collection and deposition by other pollinators (Harder and Barrett, 1995). Indeed, honeybees can outcompete and reduce visits from other pollinators, reducing wild pollinator abundance and the diversity of plant species visited by non-*Apis* species (Valido et al., 2019). Honeybee competition can also decrease interaction diversity by causing pollinators to become more specialized (Magrath et al., 2017). Such changes in plant-pollinator interaction patterns can ultimately reduce the reproductive success of plants species frequently visited by honeybees and change the pollination context for other species.

There are several potential limitations of our study and possibilities for future work. First, we only included measures of female reproductive success in assessing pollination effectiveness (e.g., pollen deposition, seed set). The proportion of extracted pollen that is successfully transferred to stigmas may be a better assessment of the overall reproductive contribution of different taxa (Parker et al., 2016), because pollen that is removed but not successfully transferred represents a loss to male fitness (Harder and Thomson, 1989; Minnaar et al., 2019). Unfortunately, data on such transfer dynamics are much rarer in the literature. Second, there are likely other factors about plant and pollinator taxa that moderate the effects we observe but which we do not test in this study, for example, functional traits such as plant and pollinator specialization. We hope our study will motivate other researchers to pair our data with trait

databases and information on single visit pollen removal to further investigate the factors that influence effective pollination.

## **Conclusions**

As honeybees become increasingly dominant globally, the abundance and species richness of other pollinators visiting plants is expected to decrease (Valido et al., 2019). If honeybees replace visits from other pollinators, whether through competitive displacement or otherwise (Herrera, 2020), these changes in community composition may have cascading effects on plant pollination, reproduction, and persistence (Gómez et al., 2010). Species loss and fluctuations in the abundance of important pollinators can imperil ecosystem service delivery (Cardinale et al., 2012; Winfree et al., 2015). Even rare species are important to ecosystem functioning (Winfree et al., 2018) and functionally diverse pollinator assemblages enhance plant community diversity (Fontaine et al., 2005). If honeybees are not particularly effective, it will be crucial to understand whether and how honeybees influence the visitation frequencies and effectiveness of other pollinators. Another key question is how consistently honeybees can compensate for the inferior quality of their visits with increased visit frequency, which can occur (Sun et al., 2013). Ultimately, some plants will thrive as their visitor community becomes increasingly dominated by honeybees, while others may experience declines. Given increasing honeybee dominance, it will be important to identify and protect diverse and effective pollinator communities especially when confronted with ineffective substitutes.

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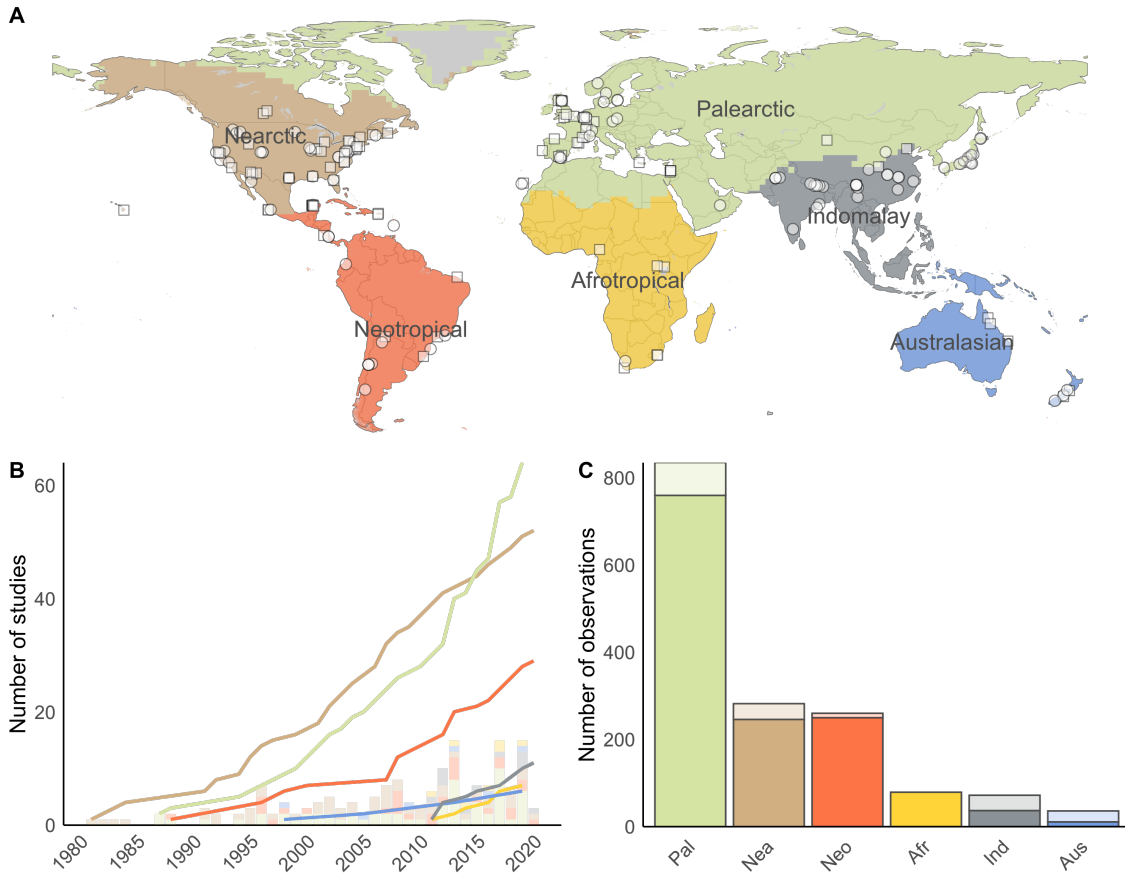
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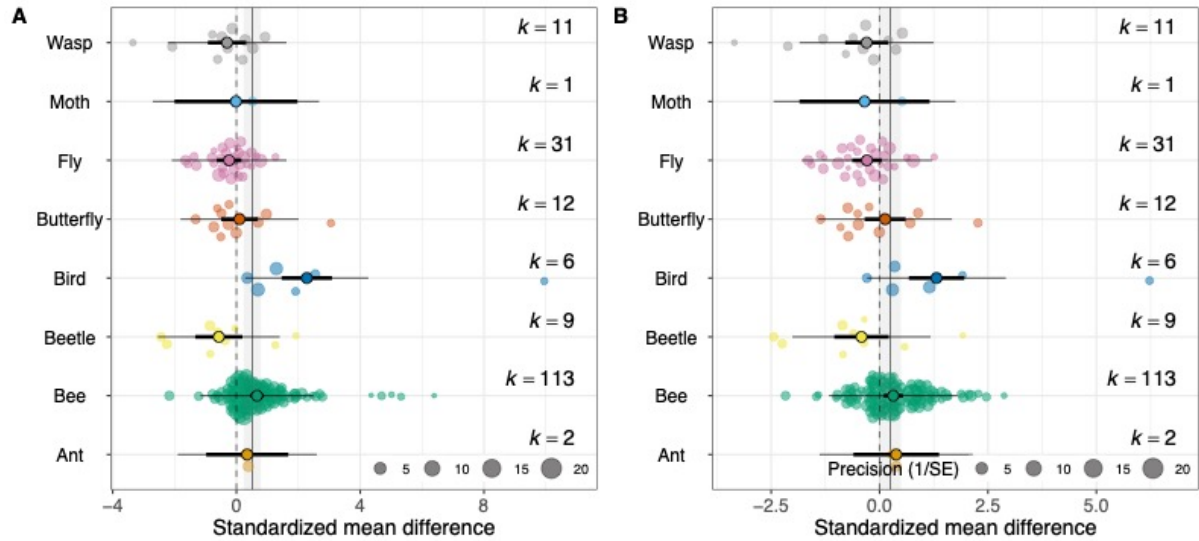
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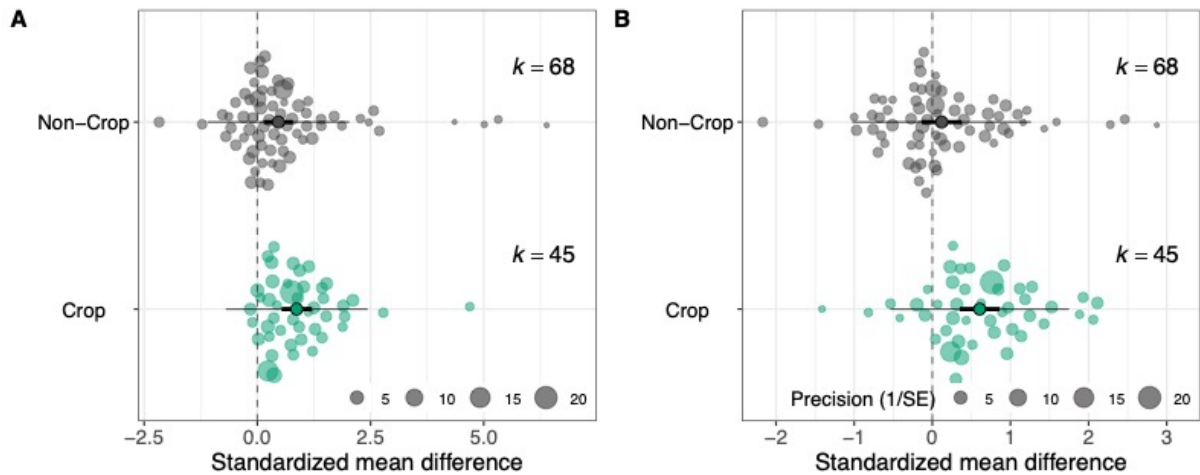
## Tables and Figures



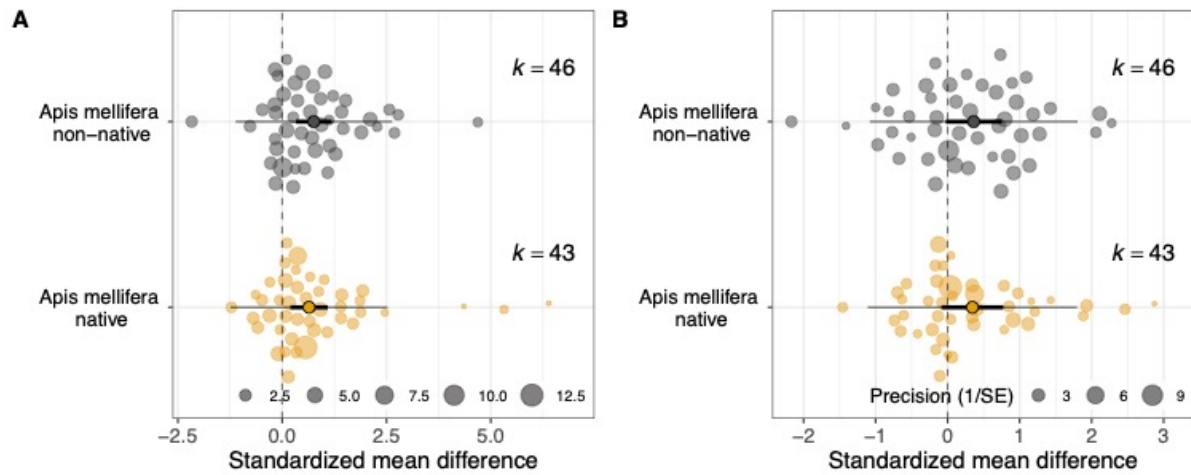
**Fig. 3.1.** The research into single visit effectiveness (SVE) is geographically widespread and has progressed consistently over time. (A) Map of study locations depicting whether research recorded SVE measures for honeybees and other taxa (squares) or if honeybees were the sole taxon or absent (circles). (B) Trends in SVE research show the cumulative number of studies per region (lines) and the annual number of studies (rug). (C) Some studies have more than one SVE observation (e.g., multiple pollinators visiting multiple plants); observation totals varied across regions and based on whether plants were native (dark colors) or non-native (lighter colors).



**Fig. 3.2.** Results for the meta-regression comparing single visit effectiveness differences (A) between honeybees and the most effective non-honeybee taxon within each group and (B) between the average effectiveness across all non-honeybee taxa within each group for a given plant-study. We used standardized mean differences (SMD) to calculate effect sizes. Meta-analytic means are represented as point estimates with their 95% CI (thick lines) and prediction intervals (thin lines). Point estimates from meta-regressions are depicted with their 95% CI (thick lines) and prediction intervals (thin lines). Individual effect sizes are scaled by their precision (1/SE). Positive SMD values (points to the right of zero) indicate that other pollinators were more effective than honeybees.

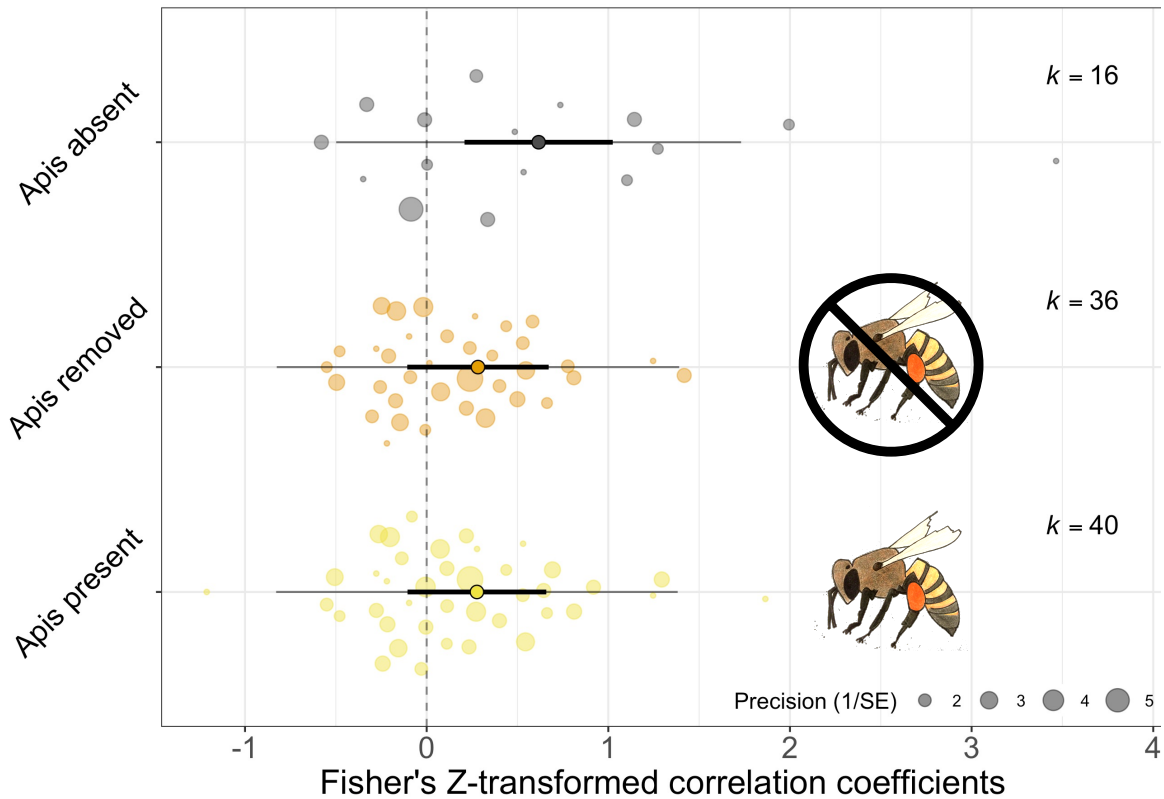


**Fig. 3.3.** Results for the meta-regression comparing crop single visit effectiveness differences (A) between honeybees and the most effective non-honeybee bee and (B) between the average effectiveness across all non-honeybee bees for a given plant-study. Effect sizes (standardized mean difference: SMD) were compared for non-crop (gray circles) and crop species (green circles). Meta-analytic means are represented as point estimates with their 95% CI (thick lines) and prediction intervals (thin lines). Individual effect sizes are scaled by their precision (1/SE). Positive SMD values (points to the right of zero) indicate that other bees were more effective than honeybees.



**Fig. 3.4.** Results for the meta-regression comparing native plant single visit effectiveness differences (A) between honeybees and the most effective non-honeybee bee and (B) between the average effectiveness across all non-honeybee bees for a given plant-study. Effect sizes (standardized mean difference: SMD) were compared outside (gray circles) and inside (orange circles) the honeybee native range. Meta-analytic means are represented as point estimates with their 95% CI (thick lines) and prediction intervals (thin lines). Individual effect sizes are scaled by their precision (1/SE). Positive SMD values (points to the right of zero) indicate that other bees were more effective than honeybees.





**Fig. 3.5.** Results for the meta-regression assessing the relationship between a pollinator’s visit frequency and single visit effectiveness for studies with and without honeybees present. Effect sizes (Fisher’s Z-transformed correlation coefficients) were compared for systems where honeybees were absent (gray circles), systems where honeybees were present (yellow circles, also indicated by honeybee icons), and systems where honeybees were present when data were collected, but we artificially removed data corresponding to their visits and re-calculated correlation coefficients (orange circles, also indicated by crossed-out honeybee icons). Estimates are shown with their 95% CI (thick lines) and prediction intervals (thin lines). Effect sizes are scaled by their precision (1/SE).

## Appendix S3

**Table S3.1.** Studies included in the meta-analysis.

Citation	Plant species	Crop or Non-Crop	Apis present?
Adler and Irwin (2006)	<i>Gelsemium sempervirens</i>	Non-Crop	yes
Akram et al. (2019)	<i>Grewia asiatica</i>	Crop	no
Albano et al. (2009)	<i>Fragaria x ananassa</i>	Crop	yes
Ali et al. (2011)	<i>Brassica napus</i>	Crop	no
Ali et al. (2014)	<i>Cucurbita pepo</i>	Crop	no
Arizmendi et al. (1996)	<i>Salvia mexicana</i>	Non-Crop	no
Arizmendi et al. (1996)	<i>Fuchsia microphylla</i>	Non-Crop	no
Artz and Nault (2011)	<i>Cucurbita pepo</i>	Crop	no
Ashman and Stanton (1991)	<i>Sidalcea oregana</i>	Non-Crop	yes
Ballantyne et al. (2015)	<i>Calluna vulgaris</i>	Non-Crop	no
Ballantyne et al. (2015)	<i>Erica cinerea</i>	Non-Crop	yes
Ballantyne et al. (2015)	<i>Erica tetralix</i>	Non-Crop	yes
Ballantyne et al. (2015)	<i>Ulex europaeus</i>	Non-Crop	yes
Ballantyne et al. (2015)	<i>Ulex minor</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Allium trifoliatum</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Asphodelus aestivus</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Bellevalia flexuosa</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Centaurea cyanoides</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Cistus creticus</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Cistus salvifolius</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Convolvulus coelestiacus</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Cynoglossum creticum</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Echium judaeum</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Hirschfeldia incana</i>	Non-Crop	yes

Ballantyne et al. (2017)	<i>Linum pubescens</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Lomelosia prolifera</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Moraea sisyrinchium</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Nonea obtusifolia</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Ochthodium aegyptiacum</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Ornithogalum narbonense</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Phlomis viscosa</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Prasium majus</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Ruta chalepensis</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Salvia fruticosa</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Scandix verna</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Stachys neurocalycina</i>	Non-Crop	yes
Ballantyne et al. (2017)	<i>Tordylium carmeli</i>	Non-Crop	yes
Bertin (1982)	<i>Campsis radicans</i>	Non-Crop	yes
Bischoff et al. (2013)	<i>Ourisia glandulosa</i>	Non-Crop	yes
Bischoff et al. (2013)	<i>Wahlenbergia albomarginata</i>	Non-Crop	no
Bloch et al. (2006)	<i>Dianthus carthusianorum</i>	Non-Crop	no
Bruckman and Campbell (2014)	<i>Phacelia parryi</i>	Non-Crop	no
Campbell et al. (2018)	<i>Citrullus lanatus</i>	Crop	yes
Cane and Schiffhauer (2001)	<i>Vaccinium macrocarpon</i>	Crop	yes
Cane and Schiffhauer (2003)	<i>Vaccinium macrocarpon</i>	Crop	yes
Cane et al. (2011)	<i>Cucurbita pepo</i>	Crop	no
Canto-Aguilar and Parra-Tabla (2000)	<i>Cucurbita moschata</i>	Crop	no
Caro et al. (2017)	<i>Bixa orellana</i>	Crop	yes
Castro et al. (2013)	<i>Polygala vayredae</i>	Non-Crop	yes
Chacoff et al. (2008)	<i>Citrus paradisi</i>	Crop	yes
Chatterjee et al. (2020)	<i>Brassica rapa</i>	Crop	yes
Chatterjee et al. (2020)	<i>Solanum melongena</i>	Crop	no
Connelly et al. (2015)	<i>Fragaria x ananassa</i>	Crop	no

Conner et al. (1995)	<i>Raphanus raphanistrum</i>	Non-Crop	no
Cordeiro et al. (2017)	<i>Campomanesia phaea</i>	Crop	no
Cuautle and Thompson (2010)	<i>Lithophragma heterophyllum</i>	Non-Crop	yes
Cuautle and Thompson (2010)	<i>Lithophragma parviflorum</i>	Non-Crop	yes
Cunnold (2018)	<i>Buddleja davidii</i>	Non-Crop	no
Cunnold (2018)	<i>Calendula officinalis</i>	Non-Crop	no
Cunnold (2018)	<i>Calystegia silvatica</i>	Non-Crop	yes
Cunnold (2018)	<i>Campanula persicifolia</i>	Non-Crop	yes
Cunnold (2018)	<i>Cistus salviifolius</i>	Non-Crop	yes
Cunnold (2018)	<i>Cotoneaster horizontalis</i>	Non-Crop	yes
Cunnold (2018)	<i>Crataegus monogyna</i>	Non-Crop	yes
Cunnold (2018)	<i>Deutzia x hybrida</i>	Non-Crop	yes
Cunnold (2018)	<i>Digitalis purpurea</i>	Non-Crop	yes
Cunnold (2018)	<i>Echinops ritro</i>	Non-Crop	yes
Cunnold (2018)	<i>Echium vulgare</i>	Non-Crop	yes
Cunnold (2018)	<i>Eupatorium cannabinum</i>	Non-Crop	yes
Cunnold (2018)	<i>Geranium x johnsonii</i>	Non-Crop	yes
Cunnold (2018)	<i>Leucanthemum x superbum</i>	Non-Crop	yes
Cunnold (2018)	<i>Nepeta cataria</i>	Non-Crop	yes
Cunnold (2018)	<i>Pentaglottis sempervirens</i>	Non-Crop	yes
Cunnold (2018)	<i>Phacelia tanacetifolia</i>	Non-Crop	yes
Cunnold (2018)	<i>Philadelphus coronarius</i>	Non-Crop	yes
Cunnold (2018)	<i>Polygonatum hybridum</i>	Non-Crop	yes
Cunnold (2018)	<i>Pulmonaria officinalis</i>	Non-Crop	yes
Cunnold (2018)	<i>Rosa xanthina</i>	Non-Crop	yes
Cunnold (2018)	<i>Rubus fruticosus</i>	Crop	yes
Cunnold (2018)	<i>Salvia nemorosa</i>	Non-Crop	yes
de Castro et al. (2017)	<i>Navaea phoenicea</i>	Non-Crop	yes
de Jager et al. (2011)	<i>Oxalis pes-caprae</i>	Non-Crop	yes

de Santiago-Hernandez et al. (2019)	<i>Ipomoea alba</i>	Non-Crop	yes
de Santiago-Hernandez et al. (2019)	<i>Ipomoea ampullacea</i>	Non-Crop	yes
de Santiago-Hernandez et al. (2019)	<i>Ipomoea bracteata</i>	Non-Crop	no
de Santiago-Hernandez et al. (2019)	<i>Ipomoea chamelana</i>	Non-Crop	yes
de Santiago-Hernandez et al. (2019)	<i>Ipomoea coccinea</i>	Non-Crop	yes
de Santiago-Hernandez et al. (2019)	<i>Ipomoea hederifolia</i>	Non-Crop	yes
de Santiago-Hernandez et al. (2019)	<i>Ipomoea meyeri</i>	Non-Crop	yes
de Santiago-Hernandez et al. (2019)	<i>Ipomoea neei</i>	Non-Crop	yes
de Santiago-Hernandez et al. (2019)	<i>Ipomoea quamoclit</i>	Non-Crop	yes
de Santiago-Hernandez et al. (2019)	<i>Ipomoea trifida</i>	Non-Crop	yes
Despres (2003)	<i>Trollius europaeus</i>	Non-Crop	no
Dieringer (1992)	<i>Agalinis strictifolia</i>	Non-Crop	yes
Dieringer and Cabrera (2002)	<i>Penstemon digitalis</i>	Non-Crop	yes
Diller et al. (2019)	<i>Aloe ferox</i>	Non-Crop	yes
Dohzono et al. (2004)	<i>Clematis stans</i>	Non-Crop	yes
Eckhart et al. (2006)	<i>Clarkia xantiana</i>	Non-Crop	no
Esterio et al. (2013)	<i>Mimulus luteus</i>	Non-Crop	yes
Fagua and Ackerman (2011)	<i>Melocactus intortus</i>	Non-Crop	no
Fan et al. (2015)	<i>Zingiber densissimum</i>	Non-Crop	no
Fishbein and Venable (1996)	<i>Asclepias tuberosa</i>	Non-Crop	no
Fleming and Etcheverry (2017)	<i>Crotalaria pumila</i>	Crop	no
Fleming and Etcheverry (2017)	<i>Crotalaria stipularia</i>	Crop	no
Fleming and Etcheverry (2017)	<i>Desmodium incanum</i>	Crop	yes
Fleming and Etcheverry (2017)	<i>Desmodium subsericeum</i>	Crop	no
Freitas and Paxton (1998)	<i>Anacardium occidentale</i>	Crop	no
Frier et al. (2016)	<i>Lonicera caerulea</i>	Crop	no
Fumero-Cabán and Meléndez-Ackerman (2007)	<i>Pitcairnia angustifolia</i>	Non-Crop	no
Gallagher and Campbell (2020)	<i>Mertensia ciliata</i>	Non-Crop	yes
Garantonakis et al. (2016)	<i>Citrullus lanatus</i>	Crop	no

Gomez and Zamora (1999)	<i>Hormathophylla spinosa</i>	Non-Crop	no
Goodell and Thomson (2007)	<i>Brassica rapa</i>	Crop	no
Goodell and Thomson (2007)	<i>Cucumis melo</i>	Crop	no
Greenleaf and Kremen (2006)	<i>Helianthus annuus</i>	Crop	yes
Gross and Mackay (1998)	<i>Melastoma affine</i>	Non-Crop	no
Gyan and Woodell (1987)	<i>Prunus spinosa</i>	Non-Crop	yes
Gyan and Woodell (1987)	<i>Rosa canina</i>	Non-Crop	yes
Gyan and Woodell (1987)	<i>Rubus fruticosus</i>	Crop	yes
Henselek et al. (2018)	<i>Prunus dulcis</i>	Crop	yes
Herrera (1987)	<i>Lavandula latifolia</i>	Non-Crop	yes
Hiei and Suzuki (2001)	<i>Melampyrum roseum</i>	Non-Crop	yes
Hollens et al. (2017)	<i>Diascia cardiosepala</i>	Non-Crop	yes
Hollens et al. (2017)	<i>Diascia floribunda</i>	Non-Crop	yes
Howlett et al. (2017)	<i>Allium cepa</i>	Crop	yes
Ida and Kudo (2010)	<i>Weigela middendorffiana</i>	Non-Crop	no
Ivey et al. (2003)	<i>Asclepias incarnata</i>	Non-Crop	no
Jacquemart et al. (2006)	<i>Pyrus communis</i>	Crop	no
Janeckova et al. (2019)	<i>Gentianella praecox</i>	Non-Crop	yes
Javorek et al. (2002)	<i>Vaccinium angustifolium</i>	Crop	no
Jennersten et al. (1988)	<i>Silene viscaria</i>	Non-Crop	yes
Jin et al. (2017)	<i>Mazus miquelii</i>	Non-Crop	yes
Junker et al. (2010)	<i>Metrosideros polymorpha</i>	Non-Crop	no
Kamke et al. (2011)	<i>Aechmea caudata</i>	Non-Crop	no
Kandori (2002)	<i>Geranium thunbergii</i>	Non-Crop	no
Kawai and Kudo (2009)	<i>Pedicularis chamissonis</i>	Non-Crop	yes
Kearns and Inouye (1994)	<i>Linum lewisii</i>	Non-Crop	no
Keys et al. (1995)	<i>Prosopis velutina</i>	Non-Crop	no
King et al. (2013)	<i>Agrimonia eupatoria</i>	Non-Crop	no
King et al. (2013)	<i>Byrsonima crassifolia</i>	Non-Crop	no

King et al. (2013)	<i>Centaurea nigra</i>	Non-Crop	yes
King et al. (2013)	<i>Cirsium arvense</i>	Non-Crop	yes
King et al. (2013)	<i>Digitalis purpurea</i>	Non-Crop	yes
King et al. (2013)	<i>Geranium pratense</i>	Non-Crop	yes
King et al. (2013)	<i>Helicteres guazumifolia</i>	Non-Crop	yes
King et al. (2013)	<i>Heracleum sphondylium</i>	Non-Crop	yes
King et al. (2013)	<i>Ipomoea trifida</i>	Non-Crop	yes
King et al. (2013)	<i>Knautia arvensis</i>	Non-Crop	yes
King et al. (2013)	<i>Malvaviscus arboreus</i>	Non-Crop	yes
King et al. (2013)	<i>Rubus fruticosus</i>	Crop	yes
King et al. (2013)	<i>Trifolium pratense</i>	Crop	yes
Kishore et al. (2012)	<i>Amomum subulatum</i>	Crop	yes
Kishore et al. (2012)	<i>Annona squamosa</i>	Crop	yes
Koski et al. (2018)	<i>Campanula americana</i>	Non-Crop	yes
Larsson (2005)	<i>Knautia arvensis</i>	Non-Crop	no
Lefebvre et al. (2019)	<i>Geranium sylvaticum</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Erithalis fruticosa</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Gonzalagunia hirsuta</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Guettarda crispiflora</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Manettia dominicensis</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Palicourea crocea</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Psychotria guadalupsis</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Psychotria uliginosa</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Psychotria urbaniana</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Schradera exotica</i>	Non-Crop	no
Lehmann et al. (2019)	<i>Spermacoce assurgens</i>	Non-Crop	no
Li et al. (2014)	<i>Epimedium mikinorii</i>	Non-Crop	no
Liu and Huang (2013)	<i>Adenophora khasiana</i>	Non-Crop	no
Liu and Huang (2013)	<i>Adenophora jasionifolia</i>	Non-Crop	no

Liu and Huang (2013)	<i>Adenophora khasiana</i>	Non-Crop	no
Ma et al. (2019)	<i>Incarvillea sinensis</i>	Non-Crop	no
Macias-Macias et al. (2009)	<i>Capsicum chinense</i>	Crop	no
Macias-Macias et al. (2009)	<i>Solanum lycopersicum</i>	Crop	yes
Madjidian et al. (2008)	<i>Alstroemeria aurea</i>	Non-Crop	no
Maldonado et al. (2013)	<i>Opuntia sulphurea</i>	Non-Crop	no
Mallinger et al. (2019)	<i>Helianthus annuus</i>	Crop	no
Mayfield et al. (2001)	<i>Ipomopsis aggregata</i>	Non-Crop	no
Mazzeo et al. (2020)	<i>Erythranthe lutea</i>	Non-Crop	no
Medel et al. (2018)	<i>Erythranthe lutea</i>	Non-Crop	no
Minarro and Twizell (2015)	<i>Actinidia deliciosa</i>	Crop	no
Missagia and Alves (2018)	<i>Costus spiralis</i>	Non-Crop	no
Miyake and Yahara (1998)	<i>Lonicera japonica</i>	Non-Crop	no
Monzon et al. (2004)	<i>Pyrus communis</i>	Crop	no
Moquet et al. (2017)	<i>Calluna vulgaris</i>	Non-Crop	yes
Moquet et al. (2017)	<i>Erica tetralix</i>	Non-Crop	no
Moquet et al. (2017)	<i>Vaccinium myrtillus</i>	Crop	no
Moquet et al. (2017)	<i>Vaccinium vitis-idaea</i>	Crop	yes
Motten (1983)	<i>Erythronium umbilicatum</i>	Non-Crop	yes
Munyuli (2014)	<i>Coffea canephora</i>	Crop	yes
Natalis and Wesselingh (2012)	<i>Rhinanthus angustifolius</i>	Non-Crop	yes
Natalis and Wesselingh (2012)	<i>Rhinanthus minor</i>	Non-Crop	yes
Navarro et al. (2008)	<i>Disterigma stereophyllum</i>	Non-Crop	yes
Olsen (1996)	<i>Heterotheca subaxillaris</i>	Non-Crop	yes
Ono et al. (2008)	<i>Rhododendron semibarbatum</i>	Non-Crop	no
Osorio-Beristain et al. (1997)	<i>Kallstroemia grandiflora</i>	Non-Crop	no
Padyšáková et al. (2013)	<i>Hypoestes aristata</i>	Non-Crop	no
Page et al. (2019)	<i>Echinacea angustifolia</i>	Non-Crop	no
Palma et al. (2008)	<i>Capsicum chinense</i>	Crop	no



Parker et al. (2016)	<i>Claytonia virginica</i>	Non-Crop	yes
Patchett et al. (2017)	<i>Brassica rapa</i>	Crop	yes
Paudel et al. (2015)	<i>Roscoea purpurea</i>	Non-Crop	no
Paudel et al. (2017)	<i>Roscoea alpina</i>	Non-Crop	no
Paudel et al. (2019)	<i>Roscoea auriculata</i>	Non-Crop	no
Paudel et al. (2019)	<i>Roscoea capitata</i>	Non-Crop	no
Paudel et al. (2019)	<i>Roscoea tumjensis</i>	Non-Crop	no
Perez-Balam et al. (2012)	<i>Persea americana</i>	Crop	no
Pettersson (1991)	<i>Silene vulgaris</i>	Non-Crop	no
Pfister et al. (2017)	<i>Cucurbita maxima</i>	Crop	no
Philipp and Hansen (2000)	<i>Geranium sanguineum</i>	Non-Crop	no
Potts et al. (2001)	<i>Satureja thymbra</i>	Non-Crop	no
Quinet and Jacquemart (2017)	<i>Pyrus communis</i>	Crop	no
Rader et al. (2009)	<i>Brassica rapa</i>	Crop	no
Rafferty and Ives (2012)	<i>Asclepias incarnata</i>	Non-Crop	yes
Rafferty and Ives (2012)	<i>Tradescantia ohiensis</i>	Non-Crop	no
Revanasidda and Belavadi (2019)	<i>Cucumis melo</i>	Crop	yes
Reynolds et al. (2009)	<i>Silene caroliniana</i>	Non-Crop	no
Reynolds et al. (2009)	<i>Silene stellata</i>	Non-Crop	no
Reynolds et al. (2009)	<i>Silene virginica</i>	Non-Crop	no
Reynolds and Fenster (2008)	<i>Silene caroliniana</i>	Non-Crop	no
Richardson (2004)	<i>Chilopsis linearis</i>	Non-Crop	yes
Robertson et al. (2005)	<i>Peraxilla colensoi</i>	Non-Crop	yes
Robertson et al. (2005)	<i>Peraxilla tetrapetala</i>	Non-Crop	yes
Rodet et al. (1998)	<i>Trifolium repens</i>	Crop	yes
Rodriguez-Rodriguez et al. (2013)	<i>Isoplexis canariensis</i>	Non-Crop	yes
Romero and Quezada-Euán (2013)	<i>Jatropha curcas</i>	Crop	no
Saeed et al. (2012)	<i>Momordica charantia</i>	Crop	yes
Sahli and Conner (2007)	<i>Raphanus raphanistrum</i>	Non-Crop	no

Sakamoto and Morinaga (2013)	<i>Clerodendrum trichotomum</i>	Non-Crop	no
Sampson et al. (2004)	<i>Vaccinium ashei</i>	Crop	no
Sánchez-Lafuente et al. (2012)	<i>Linaria lilacina</i>	Non-Crop	no
Spears (1983)	<i>Ipomoea trichocarpa</i>	Non-Crop	no
Stanghellini et al. (2002)	<i>Citrullus lanatus</i>	Crop	yes
Stanghellini et al. (2002)	<i>Cucumis sativus</i>	Crop	no
Stanley et al. (2016)	<i>Desmodium setigerum</i>	Non-Crop	yes
Stoepler et al. (2012)	<i>Asclepias exaltata</i>	Non-Crop	no
Stoepler et al. (2012)	<i>Asclepias syriaca</i>	Non-Crop	yes
Stoepler et al. (2012)	<i>Asclepias syriaca x exaltata</i>	Non-Crop	yes
Stone (1996)	<i>Psychotria suerrensis</i>	Non-Crop	no
Stubbs and Drummond (1996)	<i>Vaccinium angustifolium</i>	Crop	yes
Stubbs and Drummond (1996)	<i>Vaccinium corymbosum</i>	Crop	yes
Stubbs and Drummond (1996)	<i>Vaccinium macrocarpon</i>	Crop	yes
Stubbs and Drummond (1999)	<i>Vaccinium angustifolium</i>	Crop	yes
Sun et al. (2013)	<i>Pedicularis densispica</i>	Non-Crop	yes
Suzuki et al. (2002)	<i>Hosta sieboldiana</i>	Non-Crop	yes
Suzuki et al. (2007)	<i>Isodon umbrosus</i>	Non-Crop	no
Tang et al. (2019)	<i>Epimedium pubescens</i>	Non-Crop	yes
Tepedino (1981)	<i>Cucurbita pepo</i>	Crop	yes
Theiss et al. (2007)	<i>Asclepias incarnata</i>	Non-Crop	yes
Theiss et al. (2007)	<i>Asclepias syriaca</i>	Non-Crop	no
Theiss et al. (2007)	<i>Asclepias verticillata</i>	Non-Crop	yes
Thompson and Merg (2008)	<i>Heuchera grossulariifolia</i>	Non-Crop	no
Thompson and Pellmyr (1992)	<i>Lithophragma parviflorum</i>	Non-Crop	no
Thostesen and Olesen (1996)	<i>Aconitum septentrionale</i>	Non-Crop	no
Vaissiere et al. (1996)	<i>Actinidia deliciosa</i>	Crop	yes
Vicens and Bosch (2000)	<i>Malus domestica</i>	Crop	yes
Wang et al. (2017)	<i>Cyananthus delavayi</i>	Non-Crop	yes

Wang et al. (2019)	<i>Dipsacus asper</i>	Non-Crop	yes
Wang et al. (2019)	<i>Dipsacus chinensis</i>	Non-Crop	no
Watts et al. (2013)	<i>Iris atropurpurea</i>	Non-Crop	no
Wester and Johnson (2017)	<i>Syncolostemon densiflorus</i>	Non-Crop	no
Willcox et al. (2019)	<i>Macadamia integrifolia</i>	Crop	yes
Willcox et al. (2019)	<i>Mangifera indica</i>	Crop	yes
Willcox et al. (2019)	<i>Persea americana</i>	Crop	no
Willmer and Finlayson (2014)	<i>Echium vulgare</i>	Non-Crop	no
Willmer and Finlayson (2014)	<i>Geranium sanguineum</i>	Non-Crop	no
Willmer et al. (1994)	<i>Rubus idaeus</i>	Crop	no
Willmott and Burquez (1996)	<i>Merremia palmeri</i>	Non-Crop	no
Wilson (1995)	<i>Impatiens capensis</i>	Non-Crop	no
Wilson (1995)	<i>Impatiens pallida</i>	Non-Crop	yes
Wilson and Thomson (1991)	<i>Impatiens capensis</i>	Non-Crop	yes
Wist and Davis (2013)	<i>Echinacea angustifolia</i>	Non-Crop	yes
Witter et al. (2015)	<i>Brassica napus</i>	Crop	yes
Wolin et al. (1984)	<i>Oenothera speciosa</i>	Non-Crop	yes
Xiao et al. (2016)	<i>Eomecon chionantha</i>	Non-Crop	yes
Xiao et al. (2017)	<i>Parnassia wightiana</i>	Non-Crop	yes
Yang et al. (2017)	<i>Schima superba</i>	Non-Crop	no
Young (1988)	<i>Dieffenbachia longispatha</i>	Non-Crop	no
Young et al. (2007)	<i>Impatiens capensis</i>	Non-Crop	yes
Yu et al. (2012)	<i>Pedicularis lachnoglossa</i>	Non-Crop	yes
Zhang et al. (2007)	<i>Glechoma longituba</i>	Non-Crop	yes
Zhang et al. (2015)	<i>Prunus persica</i>	Crop	no
Zych et al. (2013)	<i>Fritillaria meleagris</i>	Non-Crop	no

**Table S3.2.** Summary information about plant species for *Apis mellifera* single visit effectiveness comparison studies. Updated species names (used in the phylogeny), the original species names used in studies, number of studies of each plant species, and the total number of pollinator taxa for which single visit pollination effectiveness data was collected across all studies of that species.

Species name in phylogeny	Species name in studies	Number of studies	Number of visitor taxa
<i>Actinidia chinensis</i>	<i>Actinidia deliciosa</i>	1	2
<i>Agalinis strictifolia</i>	<i>Agalinis strictifolia</i>	1	2
<i>Allium cepa</i>	<i>Allium cepa</i>	1	3
<i>Aloe ferox</i>	<i>Aloe ferox</i>	1	2
<i>Anacardium occidentale</i>	<i>Anacardium occidentale</i>	1	2
<i>Asclepias incarnata</i>	<i>Asclepias incarnata</i>	3	7
<i>Asclepias syriaca</i>	<i>Asclepias syriaca</i>	2	5
<i>Asclepias tuberosa</i>	<i>Asclepias tuberosa</i>	1	3
<i>Asclepias verticillata</i>	<i>Asclepias verticillata</i>	1	4
<i>Asphodelus aestivus</i>	<i>Asphodelus aestivus</i>	1	3
<i>Bellevalia flexuosa</i>	<i>Bellevalia flexuosa</i>	1	3
<i>Brassica napus</i>	<i>Brassica napus</i>	1	3
<i>Brassica rapa</i>	<i>Brassica rapa</i>	2	4
<i>Buddleja davidii</i>	<i>Buddleja davidii</i>	1	4
<i>Calluna vulgaris</i>	<i>Calluna vulgaris</i>	2	4
<i>Calystegia silvatica</i>	<i>Calystegia silvatica</i>	1	4
<i>Campanula persicifolia</i>	<i>Campanula persicifolia</i>	1	3
<i>Campomanesia phaea</i>	<i>Campomanesia phaea</i>	1	2
<i>Campsis radicans</i>	<i>Campsis radicans</i>	1	3
<i>Capsicum chinense</i>	<i>Capsicum chinense</i>	1	2
<i>Centaurea cyanooides</i>	<i>Centaurea cyanooides</i>	1	4

<i>Chilopsis linearis</i>	<i>Chilopsis linearis</i>	1	2
<i>Cistus creticus</i>	<i>Cistus creticus</i>	1	3
<i>Cistus salviifolius</i>	<i>Cistus salviifolius</i>	1	3
<i>Citrullus lanatus</i>	<i>Citrullus lanatus</i>	3	3
<i>Cotoneaster horizontalis</i>	<i>Cotoneaster horizontalis</i>	1	2
<i>Crataegus monogyna</i>	<i>Crataegus monogyna</i>	1	2
<i>Cucumis melo</i>	<i>Cucumis melo</i>	1	2
<i>Cucumis sativus</i>	<i>Cucumis sativus</i>	1	2
<i>Cucurbita maxima</i>	<i>Cucurbita maxima</i>	1	2
<i>Cucurbita moschata</i>	<i>Cucurbita moschata</i>	1	2
<i>Cucurbita pepo</i>	<i>Cucurbita pepo</i>	2	3
<i>Echinacea angustifolia</i>	<i>Echinacea angustifolia</i>	1	4
<i>Echinops ritro</i>	<i>Echinops ritro</i>	1	2
<i>Echium vulgare</i>	<i>Echium vulgare</i>	1	3
<i>Erica cinerea</i>	<i>Erica cinerea</i>	1	3
<i>Erica tetralix</i>	<i>Erica tetralix</i>	1	3
<i>Eupatorium cannabinum</i>	<i>Eupatorium cannabinum</i>	1	3
<i>Fragaria ananassa</i>	<i>Fragaria x ananassa</i>	2	3
<i>Gelsemium sempervirens</i>	<i>Gelsemium sempervirens</i>	1	2
<i>Geranium johnsonii</i>	<i>Geranium x johnsonii</i>	1	2
<i>Geranium sanguineum</i>	<i>Geranium sanguineum</i>	1	2
<i>Grona setigera</i>	<i>Desmodium setigerum</i>	1	2
<i>Helianthus annuus</i>	<i>Helianthus annuus</i>	1	2
<i>Hirschfeldia incana</i>	<i>Hirschfeldia incana</i>	1	3
<i>Hypoestes aristata</i>	<i>Hypoestes aristata</i>	1	2
<i>Impatiens capensis</i>	<i>Impatiens capensis</i>	2	3
<i>Ipomoea meyeri</i>	<i>Ipomoea meyeri</i>	1	4
<i>Ipomoea trifida</i>	<i>Ipomoea trifida</i>	1	4
<i>Jatropha curcas</i>	<i>Jatropha curcas</i>	1	2

<i>Kallstroemia grandiflora</i>	<i>Kallstroemia grandiflora</i>	1	2
<i>Lavandula latifolia</i>	<i>Lavandula latifolia</i>	1	5
<i>Linaria verticillata</i>	<i>Linaria lilacina</i>	1	2
<i>Lomelosia prolifera</i>	<i>Lomelosia prolifera</i>	1	3
<i>Lonicera caerulea</i>	<i>Lonicera caerulea</i>	1	2
<i>Macadamia integrifolia</i>	<i>Macadamia integrifolia</i>	1	2
<i>Malus pumila</i>	<i>Malus domestica</i>	1	2
<i>Malva phoenicea</i>	<i>Navaea phoenicea</i>	1	5
<i>Mangifera indica</i>	<i>Mangifera indica</i>	1	3
<i>Melastoma malabathricum</i>	<i>Melastoma affine</i>	1	2
<i>Melocactus intortus</i>	<i>Melocactus intortus</i>	1	3
<i>Metrosideros polymorpha</i>	<i>Metrosideros polymorpha</i>	1	2
<i>Nepeta cataria</i>	<i>Nepeta cataria</i>	1	3
<i>Parnassia wightiana</i>	<i>Parnassia wightiana</i>	1	2
<i>Pedicularis densispica</i>	<i>Pedicularis densispica</i>	1	2
<i>Persea americana</i>	<i>Persea americana</i>	2	5
<i>Phacelia parryi</i>	<i>Phacelia parryi</i>	1	2
<i>Phacelia tanacetifolia</i>	<i>Phacelia tanacetifolia</i>	1	3
<i>Philadelphus coronarius</i>	<i>Philadelphus coronarius</i>	1	3
<i>Phlomis viscosa</i>	<i>Phlomis viscosa</i>	1	2
<i>Pitcairnia angustifolia</i>	<i>Pitcairnia angustifolia</i>	1	2
<i>Polygaloides vayredae</i>	<i>Polygala vayredae</i>	1	3
<i>Prasium majus</i>	<i>Prasium majus</i>	1	2
<i>Prosopis velutina</i>	<i>Prosopis velutina</i>	1	3
<i>Prunus dulcis</i>	<i>Prunus dulcis</i>	1	2
<i>Prunus persica</i>	<i>Prunus persica</i>	1	2
<i>Pyrus communis</i>	<i>Pyrus communis</i>	3	4
<i>Raphanus raphanistrum</i>	<i>Raphanus raphanistrum</i>	1	4
<i>Rosa xanthina</i>	<i>Rosa xanthina</i>	1	2

<i>Rubus fruticosus</i>	<i>Rubus fruticosus</i>	3	9
<i>Rubus idaeus</i>	<i>Rubus idaeus</i>	1	2
<i>Ruta chalepensis</i>	<i>Ruta chalepensis</i>	1	2
<i>Salvia fruticosa</i>	<i>Salvia fruticosa</i>	1	2
<i>Salvia nemorosa</i>	<i>Salvia nemorosa</i>	1	2
<i>Satureja thymbra</i>	<i>Satureja thymbra</i>	1	3
<i>Scandix verna</i>	<i>Scandix verna</i>	1	2
<i>Solanum lycopersicum</i>	<i>Solanum lycopersicum</i>	1	2
<i>Stachys neurocalycina</i>	<i>Stachys neurocalycina</i>	1	3
<i>Syncolostemon densiflorus</i>	<i>Syncolostemon densiflorus</i>	1	7
<i>Ulex europaeus</i>	<i>Ulex europaeus</i>	1	2
<i>Vaccinium angustifolium</i>	<i>Vaccinium angustifolium</i>	2	3
<i>Vaccinium corymbosum</i>	<i>Vaccinium corymbosum</i>	1	2
<i>Vaccinium macrocarpum</i>	<i>Vaccinium macrocarpon</i>	2	3
<i>Vaccinium virgatum</i>	<i>Vaccinium ashei</i>	1	2
<i>Vaccinium vitis-idaea</i>	<i>Vaccinium vitis-idaea</i>	1	2

**Table S3.3.** Model outputs for most effective (MEP) and average effectiveness (AEP) effect size calculations graphed in Fig. 3.2, 3.3, and 3.4. When phylogenetic covariance applied is ‘1’ this indicates that models included phylogenetic covariance matrices as random effects. When phylogenetic covariance applied is ‘0’ no such control was not included. All models had study ID, site, year, and plant species as random effects. Despite slightly higher AIC values and larger P values we present results from models including phylogenetic controls to fully account for non-independence due to shared ancestry.

	Effectiveness calculation group	Phylogenetic covariance applied	Modifier	SMD	CI low	CI high	P	AIC
<i>Overall meta-analytic models</i>								
	MEP							
		0		0.504	0.299	0.710	< 0.001	617.441
		1		0.512	0.233	0.792	< 0.001	617.356
	AEP							
		0		0.255	0.069	0.441	0.007	495.639
		1		0.241	-0.013	0.495	0.063	496.162
<i>Pollinator group models</i>								
	MEP							
		0	ant	0.279	-1.037	1.595	0.678	568.730
		0	bee	0.660	0.462	0.858	< 0.001	568.730
		0	beetle	-0.615	-1.348	0.119	0.101	568.730
		0	bird	2.252	1.452	3.052	< 0.001	568.730
		0	butterfly	0.162	-0.412	0.737	0.580	568.730
		0	fly	-0.226	-0.601	0.149	0.237	568.730



0	moth	-0.228	-2.162	1.705	0.817	568.730
0	wasp	-0.367	-0.973	0.239	0.235	568.730
1	ant	0.348	-0.979	1.675	0.607	570.740
1	bee	0.663	0.442	0.885	< 0.001	570.740
1	beetle	-0.570	-1.332	0.193	0.143	570.740
1	bird	2.275	1.461	3.089	< 0.001	570.740
1	butterfly	0.099	-0.495	0.693	0.744	570.740
1	fly	-0.238	-0.633	0.158	0.239	570.740
1	moth	-0.017	-2.004	1.970	0.987	570.740
1	wasp	-0.303	-0.923	0.316	0.337	570.740

AEP

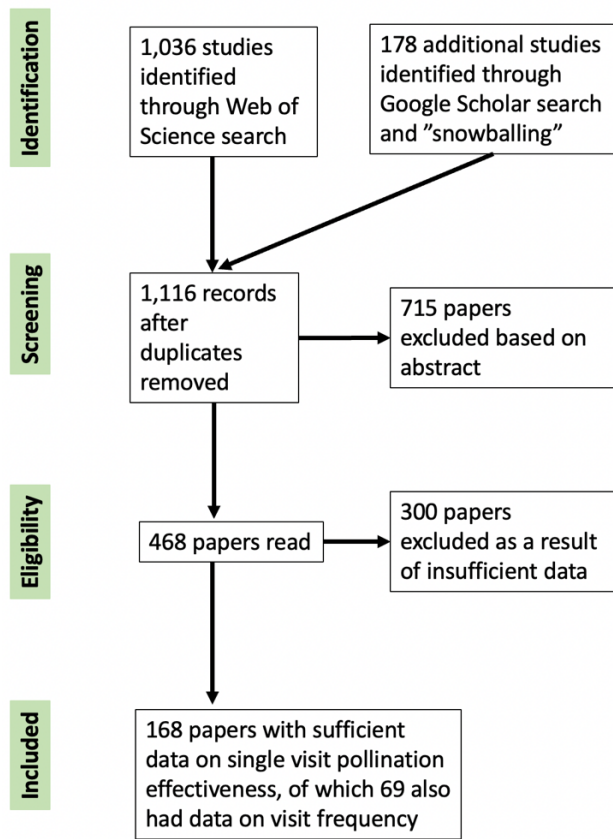
0	ant	0.298	-0.661	1.257	0.543	465.572
0	bee	0.322	0.137	0.506	< 0.001	465.572
0	beetle	-0.438	-1.034	0.158	0.150	465.572
0	bird	1.306	0.695	1.918	< 0.001	465.572
0	butterfly	0.189	-0.251	0.628	0.400	465.572
0	fly	-0.262	-0.575	0.051	0.101	465.572
0	moth	-0.412	-1.819	0.996	0.567	465.572
0	wasp	-0.311	-0.773	0.150	0.186	465.572
1	ant	0.384	-0.604	1.372	0.446	467.898
1	bee	0.316	0.094	0.538	0.005	467.898
1	beetle	-0.417	-1.045	0.211	0.193	467.898
1	bird	1.313	0.675	1.952	< 0.001	467.898
1	butterfly	0.129	-0.346	0.603	0.595	467.898
1	fly	-0.291	-0.633	0.0502	0.095	467.898
1	moth	-0.347	-1.847	1.153	0.650	467.898
1	wasp	-0.298	-0.795	0.198	0.239	467.898

*Crop  
status  
models*

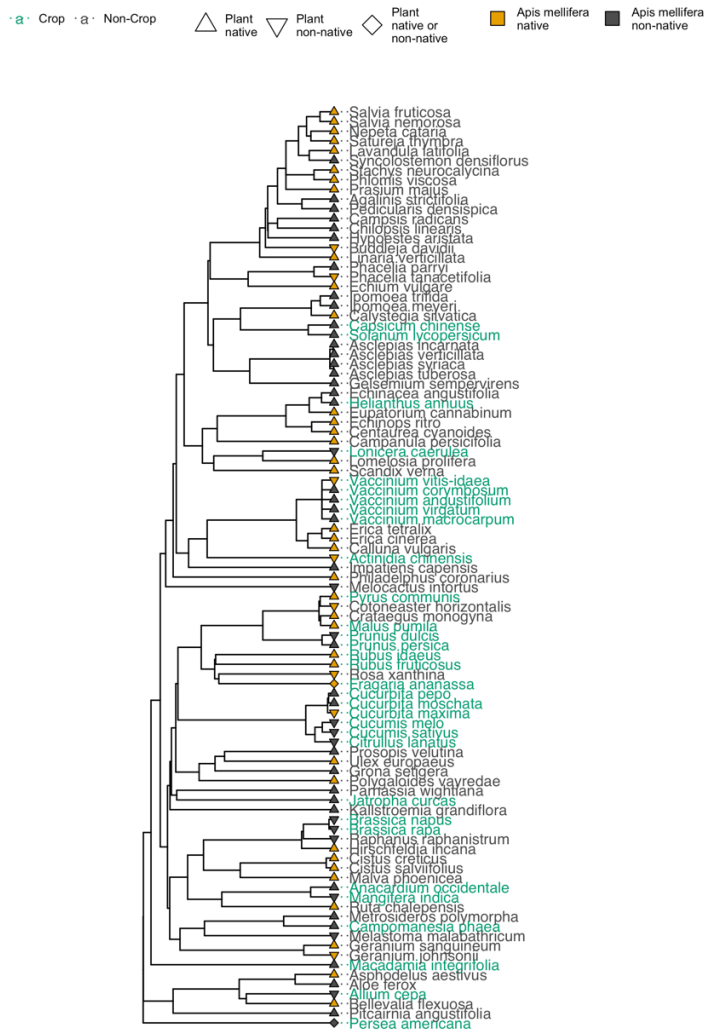
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MEP

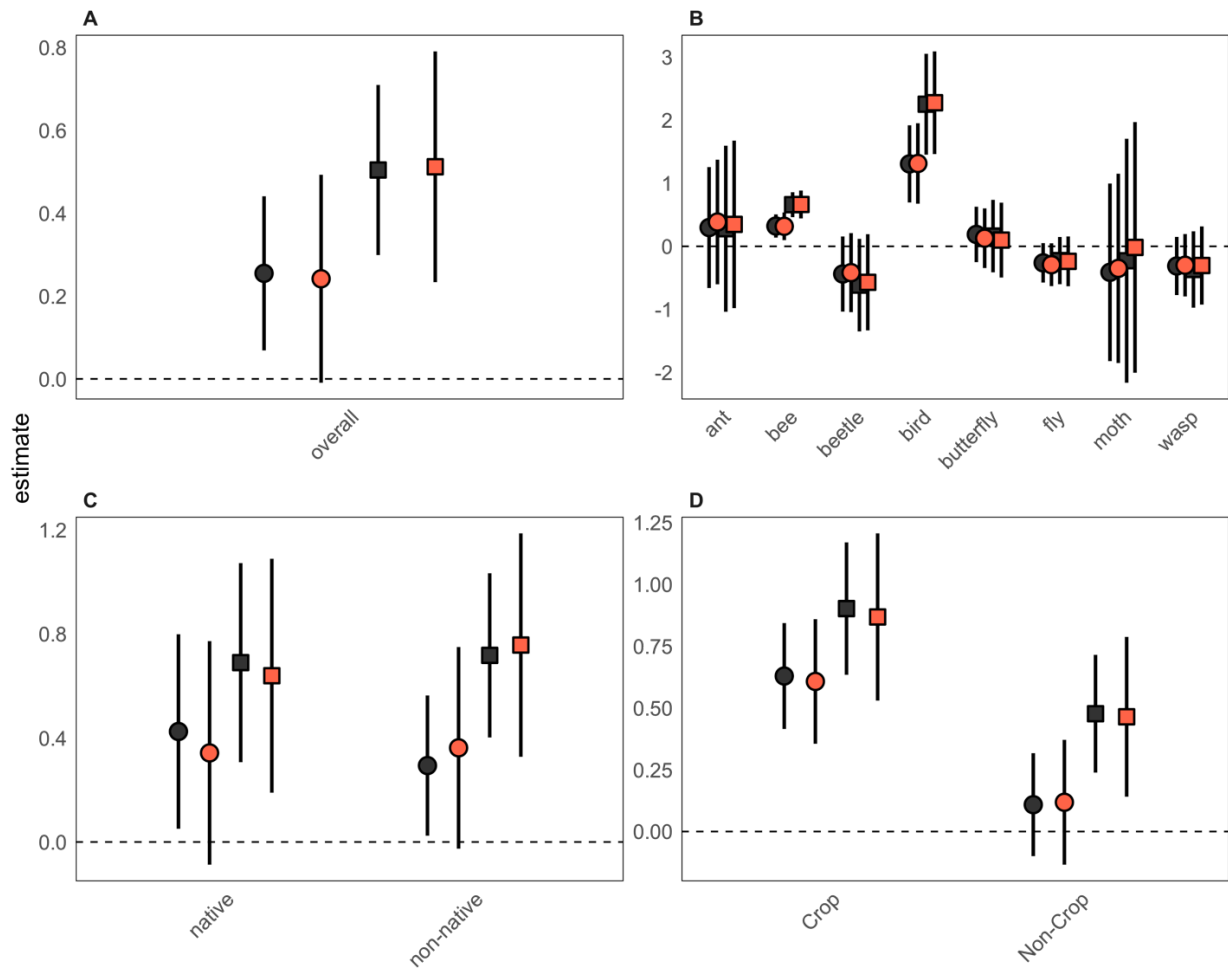
	0	crop	0.902	0.634	1.170	< 0.001	328.658
	0	non-crop	0.477	0.238	0.715	< 0.001	328.658
	1	crop	0.870	0.534	1.205	< 0.001	328.412
	1	non-crop	0.465	0.145	0.786	0.004	328.412
AEP							
	0	crop	0.629	0.415	0.843	< 0.001	252.348
	0	non-crop	0.109	-0.100	0.317	0.306	252.348
	1	crop	0.606	0.352	0.861	< 0.001	252.395
	1	non-crop	0.119	-0.136	0.374	0.360	252.395
<i>Range status models</i>							
MEP							
	0	native	0.690	0.307	1.073	< 0.001	277.914
	0	non-native	0.718	0.402	1.034	< 0.001	277.914
	1	native	0.644	0.196	1.093	0.005	277.137
	1	non-native	0.758	0.331	1.186	< 0.001	277.137
AEP							
	0	native	0.425	0.051	0.799	0.026	221.240
	0	non-native	0.294	0.024	0.564	0.033	221.240
	1	native	0.344	-0.086	0.773	0.117	220.416
	1	non-native	0.362	-0.025	0.750	0.067	220.416



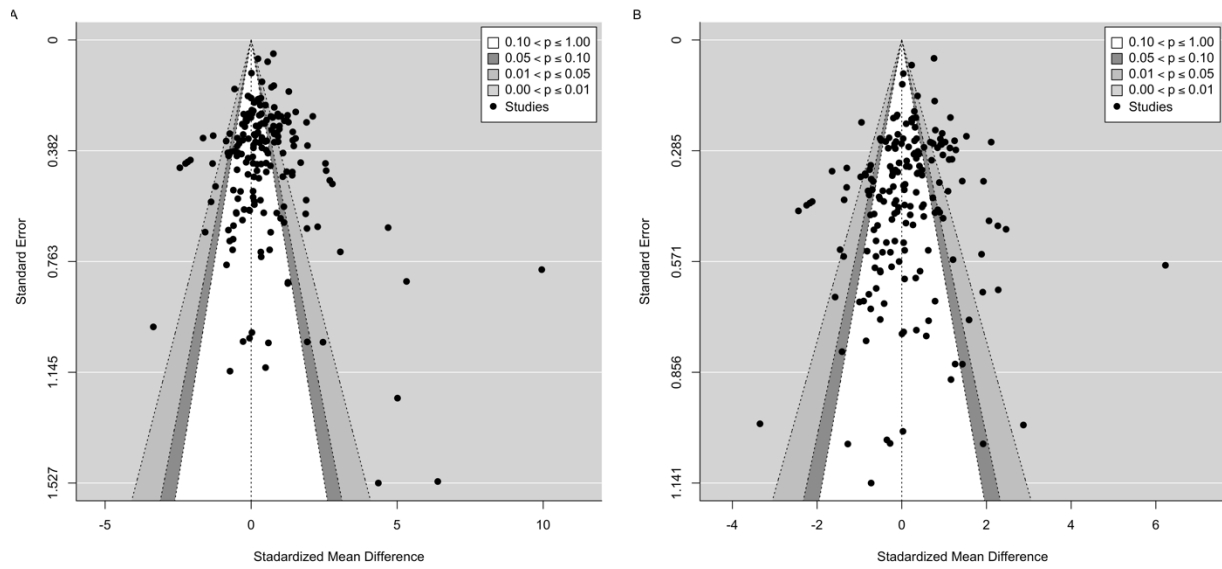
**Fig. S3.1.** PRISMA diagram demonstrating the path through which papers were filtered for inclusion in the meta-analysis. We performed a Web of Science (WoS) search using the query: ["pollinat\* effectiveness" OR "pollinat\* efficacy" OR "pollinat\* effectiveness" OR "pollinat\* intensity" OR "pollinat\* importance" OR "pollinat\* level" OR "stigmatic fertilization success" "pollen transfer effect\*" OR ("per visit" AND poll\*) OR ("per-visit" AND poll\*) OR ("per visit" AND seed) OR ("per-visit" AND seed) OR ("per visit" AND fruit) OR ("per-visit" AND fruit) OR ("single visit" AND fruit) OR ("single visit" AND seed) OR ("single visit" AND poll\*)]. We performed a Google Scholar search using the keywords: (“single visit deposition”), (“per-visit” AND pollen), (pollinat\* AND SVD), and (“pollen receipt” AND “per-visit”).



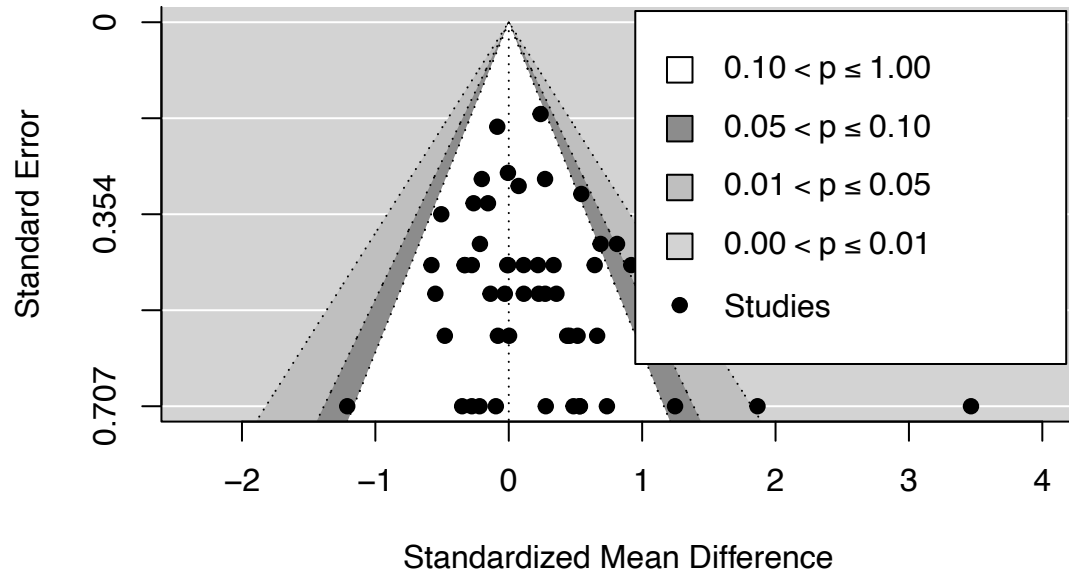
**Fig. S3.2.** Phylogeny of plant species included in the meta-analysis. Studies with honeybee visitors explored single visit effectiveness in 95 plant species. Both crops (green text) and non-crops (black text) were examined outside (gray fill) and inside (orange fill) honeybees' native range. These plant species were both native (triangles) and non-native (inverted triangles) to the regions in which they were studied. A few plant species were also investigated both inside and outside of their native range (diamonds). We included a phylogenetic covariance matrix based on this phylogeny as a random effect in all models.



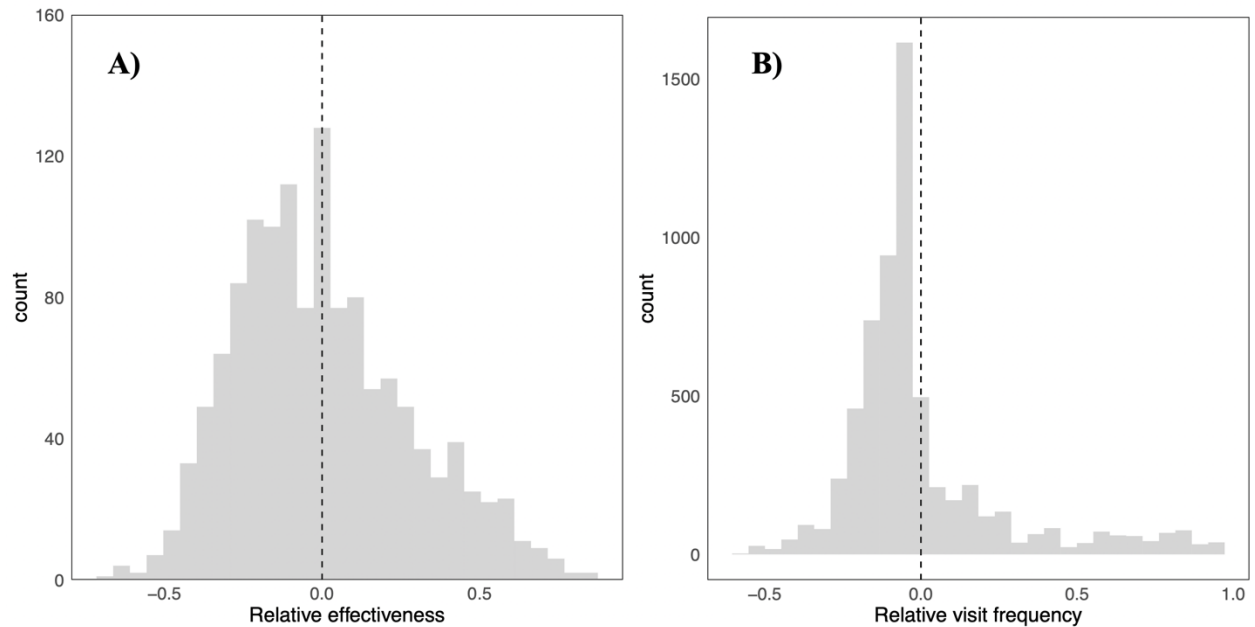
**Fig. S3.3.** Results with and without phylogenetic controls. Comparisons of meta-analysis results when phylogenetic corrections are included in the meta-analytic models (red points) and in the absence of corrections (black points) between results for average (circles) and most-effective (squares) pollinator comparisons. Panels correspond to main findings in the manuscript text: Fig. 3.2 results are compared in panels A and B, Fig. 3.3 in panel C, and Fig. 3.4 in D. Using phylogenetic controls produces more conservative but otherwise not substantially different results. One analysis which changes slightly is the analysis comparing honeybee effectiveness inside and outside of the honeybee's native range. In this case, different species occur in different regions and thus including phylogenetic controls is of particular importance.



**Fig. S3.4.** Funnel plots A) with most effective (MEP) values and B) with average effectiveness (AEP) values.

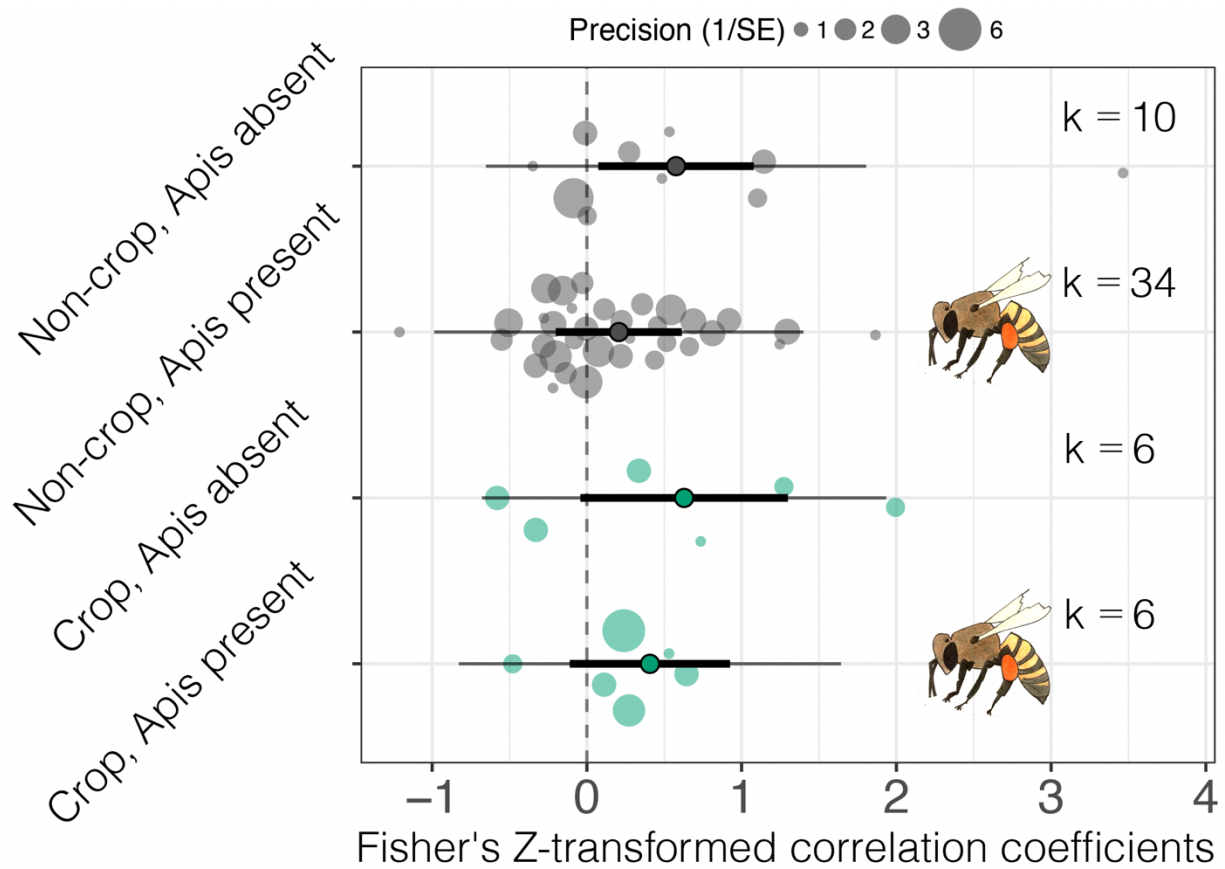


**Fig. S3.5.** Funnel plot for the meta-regression comparing pollinator’s visit frequencies and single visit effectiveness.



**Fig. S3.6.** Histograms of **A)** relative effectiveness values for all pollinators included in our meta-analysis and **B)** the relative visit frequencies for all pollinators included in the subset of studies that reported paired data on visit frequencies and single visit effectiveness values. The relative effectiveness value is calculated as:  $(\text{effectiveness value} - \text{mean effectiveness for unique study and plant}) / \text{maximum effectiveness for unique study and plant}$  such that positive values represent pollinators who were more effective than average and negative values represent pollinators who are less effective than average. Similarly, relative visit frequencies are calculated as:  $(\text{visit value} - \text{visit value mean for unique study and plant}) / \text{maximum visit value for unique study and plant}$  such that positive values represent pollinators who visit more frequently than average and negative values represent pollinators who visit less frequently than average. Dividing by the maximum values for each unique study and plant ensures that the relativized effectiveness and visitation values are between -1 and 1 despite highly variable measures of visit frequency and effectiveness between studies.





**Fig. S3.7.** Results for the meta-regression assessing the relationship between a pollinator’s visit frequency and single visit effectiveness for crop and non-crop plants in studies with and without honeybees present. Effect sizes (Fisher’s Z-transformed correlation coefficients) were compared for non-crop (gray circles) and crop species (green circles) in studies where honeybees were present (as indicated by the honeybee icons) and systems where they were absent. Meta-analytic means are represented as point estimates with their 95% CI (thick lines) and prediction intervals (thin lines). Individual effect sizes are scaled by their precision (1/SE).