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FORTY YEARS OF CHANGE IN SOUTHWESTERN BEE ASSEMBLAGES

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by

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ABSTRACT

Changes in a regional bee assemblage were investigated by repeating a 1970s study from the U.S. Southwest of bees visiting native sunflower (*Helianthus annuus*). Results showed declines in abundance and species richness of native bees and increases in non-native *Apis mellifera*. Climate data indicate drought increased over the 40-year period, favoring introduced and generalist species. Experimental placement of *A. mellifera* in an area of low *A. mellifera* density in New Mexico reduced native bee visitation, but improved reproduction in *H. annuus* plants. Meta-analytic models comparing pollination effectiveness in specialist versus generalist, native versus non-native, and native pollinators versus introduced *A. mellifera* indicated no support for greater specialist effectiveness, but higher effectiveness of native bumble bees (*Bombus* spp.) compared to non-native pollinators, especially *A. mellifera*. Changes in pollinator species composition, particularly replacement of native pollinators by introduced *A. mellifera*, affect plant reproduction and may cascade to changes in plant community composition.

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CHAPTER 1

Declines in abundance and diversity of southwestern US sunflower pollinators resurveyed after 40 years

Abstract

Recent assessments of pollinator populations have revealed declines – a serious concern given the ecosystem services pollinators provide. Species-level datasets for tracking long-term changes in pollinator populations are therefore highly valuable. We investigated changes over the past 40 years in a regional bee assemblage by repeating a study conducted in the U.S. Southwest. Bees visiting sunflower (*Helianthus*) species were sampled from 1973–1977 by Hurd, LaBerge, and Linsley in Arizona, California, and New Mexico. We resampled the bee fauna at 11 of the original locations in 2015–2016. After accounting for sampling effort, we report significant declines in abundances of native bee species, and significant increases in introduced *Apis mellifera* abundance compared to the 1970s. Species richness decreased significantly at Arizona and New Mexico sites, driven mainly by declines in specialist bees, but richness at California sites did not differ from the 1970s. Overall, 83% of bee species collected in the 1970s were observed in 2015–2016. Generalist bee assemblage composition differed significantly from the 1970s at California sites, mostly due to changes in dominant species. Climatic data suggest drought conditions increased at all sites over the 40-year period, and further that bee population trends were not explained by chance sampling of years that were climatically extreme relative to decadal norms. We found significant correlations between six temperature/precipitation-related variables and changes in abundance in one or more of our bee categories (all bees, *Apis mellifera*, generalists, specialists). We conclude that sunflower bee abundance and diversity in the U.S. Southwest have decreased since the 1970s, and hypothesize that climate change has favored introduced and generalist species.

Introduction

Insect extinction rates have not been comprehensively monitored at the global scale, but there is recent evidence of dramatic regional-level declines across a broad range of taxa [Hallmann et al. 2017; Powney et al. 2019]. Among orders, Hymenoptera may be especially vulnerable to declines and extinctions, partly for genetic reasons: Haplodiploid sex determination results in the production of sterile males and reduces effective population size [Zayed & Packer 2005]. Their role as pollinators in agriculture and natural ecosystems accords the Hymenoptera considerable economic and ecological importance [Potts et al. 2010]. Bees, the largest contributors to pollination, have experienced population crashes and local extirpations [NRC 2007; Steffan-Dewenter et al. 2005]. Their status has become a key scientific and public policy concern [Potts et al. 2011; USDA-EPA 2015].

Extinction rates are not equally distributed across all species. A key question is whether specialist species, which have narrow habitat or dietary tolerances, are more vulnerable to declines than generalists with wider tolerances. (For convenience we use the dichotomous terms “specialist” and “generalist,” though their ecological manifestations are continuous). Evolutionary theory predicts that generalist adaptability should confer protection against long-term environmental variation [Richmond et al. 2005], as well as against frequent disturbance on shorter time scales [Kassen 2002], while theory and empirical evidence from multiple taxa puts specialists at greater risk of extinction. In vertebrates, habitat specialization has been linked with decreasing population trends and extirpations [Julliard et al. 2004; Powers & Jetz 2019]. A 25-year study of one butterfly family (Hesperiidae) also demonstrated that habitat specialists declined in all but the least-degraded areas [Swengel & Swengel 2015]. There is evidence that dietary-specialist pollinators are more susceptible to decline than generalists for both genetic and ecological reasons [Packer et al. 2005; Roberts et al. 2011]. A reexamination of a historical dataset of plant-pollinator interactions in Illinois indicated that specialist bees had declined more than generalists, even though their host plants were still present [Burkle et al. 2013]. Pollen specialization was also positively correlated with extinction risk for bumble bees in the northeastern U.S. [Bartomeus et al. 2013].

Other theoretical arguments and empirical evidence suggest that specialists should be buffered from extinction through close spatial and temporal synchronization with their resources and/or greater efficiency in resource collection [Javorek et al. 2002; Buechi & Vuilleumier 2014]. Among bees, pollen-specialist species provision their eggs with pollen taken from only one or a few closely related plant species, in contrast to generalists that utilize pollen from a variety of floral hosts. Some pollen specialists remain in diapause until conditions are optimal for their host plants, increasing the likelihood of both successful pollination and pollinator persistence [Minckley et al. 2013]. Selection for temporal alignment of adult bee emergence with host plant flowering should be strongest where rainfall/flowering is least predictable, as has been observed for specialist bees and their host plants in arid areas [Minckley 2000]. On the plant side, flowers adapted for specialist pollinators receive pollen more precisely and effectively [Wilcock & Neiland 2002]. Because specialization allows for finer niche partitioning, a plant community with high specialist-pollinator diversity should have better resilience and protection from extinction than a generalist-rich pollinator community [Clavel et al. 2011].

A pattern of declines and extinctions in local, rare specialists and their replacement with cosmopolitan, common generalists is known as biotic homogenization [McKinney & Lockwood 1999]. Homogenization is facilitated through one of the most ecologically transformative of human activities: the global redistribution of biota. Introduced species are a leading cause of biodiversity loss [Crowl et al. 2008; Vitousek 1997]. In the case of bees, potential negative impacts of introduced species include disruption of plant pollination, increased pollination of exotic plants, co-introduction of pathogens that can affect native bees, and competition for shared resources [Goulson 2003a]. Among introduced species, generalists have a higher probability of successful establishment — but since they are often redundant contributors to functional roles (such as pollination), a high generalist diversity does not necessarily bolster ecosystem stability [Clavel et al. 2011].

Long-term data on bee communities are rare; few studies have employed a temporal approach of resampling and comparing current bee faunas to historic datasets. We are aware of six attempts in North America and five in Europe, with studies spanning 10–100 years between samples. Kearns & Oliveras (2009) sampled the bee assemblage of Boulder, CO and found it yielded almost all (95%) of the species that had been recorded 100 years earlier, despite major changes to the landscape. Their results were comparable to Marlin & LaBerge (2001), who sampled bees in Carlinville, IL in 1970 and found no evidence of declines in bee species richness compared to samples from 75 years earlier, though again substantial land use changes had occurred. Two other studies (Banaszak 1992, Poland; Grixti & Packer 2006, Canada) documented similar persistence in bee species richness and/or community composition over a 40–50 year period. More recently, Hallmann, et al. (2017) reported steep declines across all insect groups over the past 27 years at sites in Germany. However, declines were measured in biomass rather than richness or relative abundance, which underscores the seriousness of the study findings but provides no insight on the status of particular taxa. Burkle et al. (2013) sampled sites from the Carlinville dataset in 2009–2010 and found all of the plant species, but less than half of the bee species observed in the 1800s. Numerous studies of bumble bee (*Bombus*) assemblages have also shown declines in species richness, abundances, and/or range extent compared to historical records [Bartomeus et al. 2013, U.S.; Cameron et al. 2011, U.S.; Colla & Packer 2008, U.S.; Dupont et al. 2011, Netherlands; Goulson 2003b, U.K.].

With the exception of the Boulder, CO study, the historical studies mentioned above were all conducted in mesic environments. However, global bee species richness is greatest in arid areas [Michener 2000]. The U.S. Southwest hosts highly diverse bee communities, with species richness largely driven by high numbers of pollen specialists: up to 50% of the bee species in the Southwest region are dietary specialists [Moldenke 1976; Neff et al. 1977]. Given this high diversity, it is perhaps surprising that one important historic record of bee assemblage composition that has not heretofore been reexamined is the study of bees visiting sunflower (*Helianthus* spp.), conducted by Paul Hurd, Jr., Wallace LaBerge, and E. Gorton Linsley (Hurd et al. 1980; hereafter, “HLL”). From 1972–1977, HLL carried out comprehensive field surveys at sites in California, Arizona, and New Mexico. Their primary objective was “to characterize the diurnal, seasonal, and geographical occurrence of the principal bees visiting *Helianthus*”. Survey data were combined with data extracted from museum specimens to achieve a secondary objective of determining which bees are specialists on *Helianthus* pollen. One advantage to following up on the HLL study is that sunflowers are highly attractive to bees, which are its principal pollinators [Free & Simpson 1964]. HLL recorded more than 400 species representing six of the seven families in the Anthophila (bee) clade visiting inflorescences for pollen, nectar or both. In addition, 30% of species observed collecting pollen from *Helianthus* are dietary specialists [Hurd et al. 1980]. Thus resampling sunflower visitors at HLL study locations can illuminate changes in *Helianthus* specialist bee status, as well as indicate wider changes in the regional pollinator community.

In the current study, we examine changes in bee abundances and species composition in the *Helianthus annuus* bee assemblage of the southwestern U.S. from the 1970s to the present. We revisited 11 of the original 12 study sites (omitting one site where the original sampling dates were not given and thus could not be matched) and sampled bees using methods comparable to those of HLL. We ask, 1) Has sunflower bee species richness and/or abundance changed over the past 40 years? 2) Are specialist bees less common than in the past? 3) Are generalists more common than in the past? 4) Are changes in climatic variables (precipitation, temperature) correlated with changes in bee abundances? Based on climatic shifts and human impacts in the Southwest, especially agricultural intensification at sites in California, we hypothesized that species richness would be lower in our study. We predicted declines in specialist bee species in particular, and persistence or increase among generalists.

Materials and methods

Study system & historic dataset

Helianthus annuus

Sunflower (*Helianthus annuus* Linnaeus) is a weedy, annual, self-incompatible forb that occurs throughout most of the United States, southern Canada, and northern Mexico. About 50 species of *Helianthus* are native to North and Central America; their historic range in the south-central U.S. is thought to have been greatly expanded via anthropogenic disturbance as well as transportation by indigenous people [Heiser et al. 1969]. In the southwestern U.S., *Helianthus annuus* plants begin growing in spring and usually reach peak flowering by late August, with some plants still flowering in late October in parts of the region. Plants can reach five meters in height (but are more typically 0.25 – 2m) and generally occur along roads, fences and fields, growing best in relatively moist soils. Inflorescences are composed of hundreds of individual florets, which produce nectar and pollen in large quantities [Simpson and Neff 1987].

From 1972–1977, HLL traveled the U.S. Southwest during the summer and early fall, collecting bees from sunflowers [Hurd et al. 1980]. Their collection sites were chosen to span the four major ecoregions of the Southwest: Chihuahuan Desert, Sonoran Desert, Mojave Desert, and cismontane California. Of the 412 sunflower bee species documented by HLL, they characterized 131 of the 284 pollen-collecting species (the remaining 128 species visited plants only for nectar) as either “primary” (collect pollen exclusively from plants in genus *Helianthus*) or “secondary” oligoleges (collect pollen exclusively from Asteraceae, mainly from *Helianthus*) [Hurd et al. 1980, Table 3, p. 23].

Study sites

The objective of the present study was to replicate the previous survey as closely as possible in terms of location, sampling date within the season, and sampling technique. Of 63 original survey sites, HLL selected 12 sites for detailed sampling (“primary surveys” [Hurd et al., Table 1, p. 5]). Sampling at these sites was conducted from mid-July through early October (Table 1).

Table 1. Locations and sampling dates of surveys of bees pollinating sunflower (*Helianthus annuus*, *H. petiolaris*) at 11 sites in the U.S. Southwest in the 1970s [Hurd, et al. 1980] and 2015–2016 (the present study). County names and coordinates in Table A3.

		1970s			**2015**	**2016**	**2015–2016**
state	**site name**	**sampling date(s)**	**sampling year**	**total person-hours***	**sampling dates**	**sampling dates**	**total person-hours†**
CA	Escalon	Jul 22	1977	50.0	Jul 19–20	Jul 25–26	32.0
CA	Madera 1	Jul 24	1977	44.0	Jul 21–22	Jul 27–29	32.0
CA	Bishop	Aug 27	1977	15.0	Aug 23–24	Aug 28–29	32.0
NM	Rodeo	Sep 2–4	1973	25.0	Sep 1, 5, 7	Sep 2–3	32.0
NM	Animas	Sep 4–5	1974	26.0	Sep 1–2††	Sep 4–5	32.0
NM	Silver City	Sep 11–12	1974	9.0	Sep 11–12	Sep 14–15	32.0
AZ	Benson	Sep 14	1974	11.0	Sep 8–9	Sep 11–12	32.0
CA	Indio	Sep 18	1977	14.0	Sep 29–30	Sep 8–9	32.0
CA	Merced	Oct 4	1975	15.0	Sep 24–25	Oct 10–11	32.0
CA	Madera 2	Oct 5	1975	42.0	Sep 22–23	Oct 12–13	32.0
CA	Corcoran	Oct 6	1975	28.0	Sep 26–28	Oct 7–8	32.0

† Total person hours = # collectors x # hours
†† Sampled in 2017 as the 2015 sampling date was cancelled due to rain.

HLL refer to their detailed samples at primary sites as time counts. We conducted time counts of bees at 11 of the 12 HLL primary survey locations (Figure 1). Our sampling included two sites in Madera, CA, which we sampled in July and October, respectively (vs. one Madera site sampled in July and September and another in October in the original HLL study). All sites were sampled within 10 days of the original sampling dates (Table 1). We did not sample in Double Adobe, AZ because no sampling dates were given in HLL.

Figure 1. Map of 11 study sites in the southwest United States of bees visiting sunflower (*Helianthus annuus, H. petiolaris*) in the 1970s and 2015–2016.

HLL’s sites were usually described in relation to the town center (e.g., “beyond the shoulder of a north-south highway 3 mi. west of the center of town”). We interpreted the town center as the location of the main post office, and attempted to locate sunflower populations in peak flowering either according to distances/directions given in HLL, or as near to the center of town as possible. In most cases, we were able to sample sunflower populations in the same county as HLL, but in three instances in 2016, the nearest sampling location was in a county adjacent to the original survey county (Table A4). Our precise sampling locations within a site differed in 2015 and 2016 for all sites other than

Bishop and Indio, where we found sunflowers growing in the same spot in both years.

With one exception (Rodeo), HLL did not provide information on sunflower patch sizes at their primary sites. We sought to sample the largest patch available (minimum 20 plants) within a 20-mi. distance of each town center. The plants tend to grow in disturbed areas where moisture is available, e.g., along irrigation and drainage ditches or road shoulders; thus, often the best and most accessible patches are in recently cultivated agricultural areas on the peripheries of small rural towns.

Though HLL did not report plant species identity from all sites, it appears they sampled primarily from *H. annuus* other than in Silver City, NM where they found a pure stand of *H. petiolaris* Nuttall. Based on their records it seems bees do not discriminate between *H. annuus* and *H. petiolaris*; the same bee species were observed visiting both plant species in pure and mixed stands with equal frequency [Hurd et al. 1980]. We did not find *H. petiolaris* at any of our sites and sampled exclusively from *H. annuus*.

Sampling protocol

We sampled *Helianthus*-visiting bees in the manner utilized by HLL, who in turn utilized the sampling procedure described in their prior study of *Larrea* bees [Hurd and Linsley 1975]. Bees were collected continuously from inflorescences, for half-hour periods, using standard aerial nets and cyanide killing jars. Specimens were transferred to cooled containers at the end of each sampling period and subsequently frozen until pinned.

No bee was taken until it actually alighted on an inflorescence. Though this method gives a good representation of overall visitor-species composition, HLL were of the opinion that it underestimates the abundance of oligolectic males, which briskly patrol flower patches (stopping only briefly for nectar or potential mates) and are likely undersampled due to their speed [Hurd et al. 1980]. No sampling was conducted in either the original or the current study during times of strong winds, heavily overcast periods, or rainy conditions. Bees sleeping on flower heads were not sampled.

The number of collectors and total sampling time varied in the original study (range, 2–4 collectors, 4.5–13 hours/day). In our surveys, sampling was conducted by a single collector (CLC). While HLL typically sampled a site on a single day in a given year, we sampled for two sequential days each year to compensate for the reduced number of collectors, aiming to achieve roughly the same number of person-hours per site per year. Sampling was conducted in two four-hour increments per day (0700–1100, 1300–1700). Sunflowers often grow in strips along roadsides, irrigation ditches and field margins; in such situations the collector began at one end of the strip and walked past all the plants in a circuit, netting continuously. For sunflowers growing in patches, we trampled a path through the patch on the day prior to sampling, attempting to pass by all plants at some point along the path, then followed the same continuous-circuit procedure as for strip formations. The sampling method was identical in both years. All sampling was conducted in 2015 and 2016 with the exception of Animas, where rain prevented sampling during 2015 and the site was instead sampled in 2016 and 2017. For ease of discussion we refer throughout to our sampling years as 2015–2016. Time periods were logged using local time. Air temperature was taken in the shade and recorded at the beginning of each sampling period using a digital thermometer.

Bee identifications

We used currently accepted taxonomic nomenclature for HLL's and our specimens, as published in the Integrated Taxonomic Information System (ITIS) database [retrieved 2015–2017; http://www.itis.gov] (Table A1). Voucher specimens for 2015-2016 collections are housed at the USDA-ARS Bee Biology & Systematics Laboratory in Logan, Utah and the University of New Mexico Museum of Southwest Biology in Albuquerque, New Mexico.

Species were designated as specialist, generalist, or nectar-visitors according to HLL's lists of bee taxa associated with *Helianthus* [Hurd et al. 1980, pp. 24–28] (Table A1). We characterized both "primary" and "secondary" oligoleges (as defined by HLL) as specialists. For the 2015-2016 samples, there were 15 unclassified species (i.e., specialist/generalist status unknown: three "sp.", 12 identified species; 169 total bees), resulting in 1.7% of bees excluded from specialist/generalist analyses. We lumped cleptoparasitic species with nectar visitors.

Molecular analysis

We determined whether *Apis mellifera* specimens from a subset of the sites (7 of 11 sites) belonged to Africanized lineages. Africanized and European *A. mellifera* are morphologically similar but genetically distinct, based on nuclear and mitochondrial

DNA markers. Bees were tested by Dr. Allen Szalanski, Department of Entomology, University of Arkansas using an assay that discriminates Africanized from European *A. mellifera* using a polymerase chain reaction method on a region of the mitochondrial DNA cytochrome b gene. This method produces a 485 base-pair amplicon for both Africanized and European honey bees, and a 385 base-pair amplicon that is specific for Africanized honey bees [Szalanski & McKern 2007]. We tested 15–20 *A. mellifera* specimens per site from 2015; where fewer 2015 specimens were available we analyzed 2016 specimens (Bishop) or amended with 2016 specimens to increase sample size (Rodeo).

Climate data

For each site (4km resolution), we downloaded monthly data from 1970-2016 (1970-2017 for the Animas site) from the PRISM database [PRISM Climate Group 2019]. We used the biovars() function in the R package ‘dismo’ [Hijmans et al. 2017] to estimate 19 climate variables from the PRISM data. We chose precipitation and temperature variables that are commonly used in ecological modeling and which we expected to be biologically meaningful for bees and their host plants, based on the “bioclim” variables BIO1–BIO19 as defined in WorldClim [Fick & Hijmans 2017]. In addition, we calculated monthly values of a drought index, the Standardized Precipitation Evapotranspiration Index (SPEI) [Vicente-Serrano et al. 2010]. We used the SPEI package in R [Beguería et al 2014] using the precipitation and potential evapotranspiration (calculated using the Thornthwaite equation) and averaged these across months to obtain yearly SPEI values.

Data analysis

Standardization

We standardized and constrained data prior to making interdecadal comparisons in four ways:

1) HLL reported bee abundances from half-hour sampling periods for all except what they termed “miscellaneous” species, for which abundances but no exact sampling periods were given. Miscellaneous species were typically rare (i.e., occurred in low numbers), but on average comprised about 40% of species recorded per sampling day. For analyses, we attributed an equal portion of each miscellaneous species count to each sampling period; e.g., if HLL reported that 16 individuals of miscellaneous species X were collected over an 8-hour sampling day at a given site, we assigned 1 individual of species X to each half-hour sampling period in the dataset to be analyzed. We reassigned observations of HLL-defined miscellaneous species in our data in a similar manner (e.g., if we observed 16 individuals of species X in our first half-hour sampling period and none thereafter in an 8-hour day, we reassigned the observations as 1 individual of species X per half-hour sampling period).

2) To initiate a sampling scheme that would allow inter-site comparisons and could also be easily repeated in future studies, we sampled all sites from 0700–1100 and 1300–1700. In contrast, HLL’s start times and sampling duration varied according to site: sampling usually began at 0600 and continued for a mean of 9 hours, often with a break in the middle of the day, but start times varied from 0600–0730 and total effort in a day ranged from 4.5–13 hours. To account for interdecadal differences in sampling effort and time-of-day, we constrained our analyses in this paper to only the overlapping sampling

periods from each site. For example, HLL sampled in Bishop, CA from 0600–1300. Therefore, for Bishop we compared only the bees we collected from 0700–1100 to bees HLL collected from 0700–1100 and ignored our bees collected from 1300-1700.

3) We corrected for the number of collectors (two to four per day in HLL; one per day in 2015–2016). Abundances are reported in "bees per person-hour" for all sites.

4) In the original study, collection vials and mounted specimens were labeled in 30-minute increments, but each period actually started on the half hour (0630, 0700, etc.) and ended 29 minutes later when vials and labels were changed (0629, 0659). We followed the same procedure as HLL but ended each sampling period at 25 minutes to allow time to change vials and labels, since in our case a single collector sampled without field assistants. When records (HLL's and ours) analyzed, we converted them to 30-minute periods; thus, "bees per person-hour" indicates a 60-minute hour for both the original and current study data.

Statistical procedures

Bee abundance, diversity, and composition

We analyzed Arizona and New Mexico sites separately from California sites, given the large geographic distance separating the two clusters of sites (Fig. 1) and because preliminary analyses indicated potentially different interdecadal patterns of change in the bee assemblages of the two areas. Such differences were expected *a priori*, given differences in climate patterns (the Mediterranean climate pattern in California is less conducive to late-summer annuals such as *H. annuus* than that of Arizona and New Mexico, where late summer rains are common), and in bee abundances and assemblage composition [Hurd et al. 1980].

To assess interdecadal differences in bee abundances, we conducted ANOVAs in R, version 3.3.2 [R Core Team 2016] running in RStudio, version 1.0.44 [Rstudio 2015] with year as the predictor and bees per hour as the response variable. We followed this with multiple comparisons using a Benjamini-Hochberg adjustment (controls false discovery/incorrectly rejected null hypothesis rate at alpha=0.05) to assess differences between years. In some cases, data were log-transformed to meet the normal distribution assumption. Where transformation was ineffective, we conducted non-parametric Kruskal-Wallis rank-based tests of differences between means, with post-hoc Dunn's tests of multiple comparisons using a Benjamini-Hochberg adjustment. In addition to assessing raw species richness and diversity, we also estimated the Chao1 index of species richness using EstimateS, version 9.1.0 [Colwell 2013]. This index accounts for the identities and relative abundances of species in a sample, including the probability of undetected species [Chao et al. 2005].

We analyzed interdecadal and interannual differences in bee assemblage composition using the R packages 'vegan' (version 2.4-2) and 'MASS' (version 7.3-50). We calculated Bray-Curtis dissimilarities of site-by-species matrices for each site-year combination and performed non-metric multidimensional scaling (nMDS) to visually assess compositional differences between assemblages. To test whether assemblages differed across site-years, we conducted permANOVAs of the effect of decade, followed by pairwise comparisons of the effect of year using a Benjamini-Hochberg adjustment [Bray & Curtis 1957; Martinez Arbizu 2017; Oksanen et al. 2017; Venables 2002].

Climatic representativeness of sampling years

With one historic sample (1970s) and two modern samples (2015, 2016) for each site, a concern is that the sampling years might be unrepresentative of their respective decades. For example, a sample taken during an extremely cool or extremely warm year could produce unrepresentative estimates of bee abundance and composition and skew the inferred direction or magnitude of long-term trends. We thus evaluated the climatic context of the sampling years. We chose the Standardized Precipitation Evapotranspiration Index [SPEI; Vicente-Serrano et al. 2010] as an integrative drought index that is highly relevant to plant growth, and thus should be related to production of floral resources available to sunflower bees [Phillips et al. 2018]. Highly negative SPEI values indicate dry, hot years while highly positive values indicate cool, wet years. Since drought has increased in many parts of the southwest U.S. over the past 40 years, we also investigated temporal trends in SPEI at our sites, to examine whether sampling-year SPEI deviated from the predicted SPEI given the temporal trend. To compare conditions from each sampling year to that of adjacent (e.g. same-decade) years, we focused on residual SPEI (observed minus predicted). We first standardized SPEI values to a mean of zero and standard deviation of one and constructed temporal trends in SPEI for each site using the lm() function in R. We then extracted the residuals from each site and plotted the mean residuals for each modeling year for the two regions (California and Arizona/New Mexico).

Correlates of changes in bee abundance

To investigate whether the changes we observed in native bee abundances were related to changes in abundance of introduced *A. mellifera*, we obtained the change in the number of bees sampled per person-hour at each site (Δ_{bee}, calculated as the difference of present minus past abundance, where present values were averages of 2015 and 2016 observations). We conducted regressions with change in *A. mellifera* abundance (Δ_{apis}) as the predictor and either change in generalist ($\Delta_{generalist}$) or specialist ($\Delta_{specialist}$) bee species abundances as the response.

Given that introduced *A. mellifera* did not seem to be a driver of native bee declines (see Results), we also investigated whether the temporal patterns we observed in bee abundances were related to climatic factors. We modeled site-specific relationships between bee abundances and climate variables using regressions of Δ_{bee} against change in environment (Δ_{envi}). For this analysis, we calculated Δ_{bee} as the difference between the number of bees per person-hour at each site for four groups: all bees, *A. mellifera*, generalists other than *A. mellifera*, and specialists. To estimate Δ_{envi}, we first standardized "bioclim" variables BIO1–BIO19 to a mean of zero and standard deviation of one and ran independent linear regressions of each climate variable through time (1970–2015 and 1970–2016) for each site. Taking the averaged slopes from these regressions as a measure of the change in climate at each site, we ran univariate regressions of standardized values for the four bee abundance changes against each of the 19 environmental variables for a total of 76 models. Given the large number of models, we treat this analysis as exploratory.

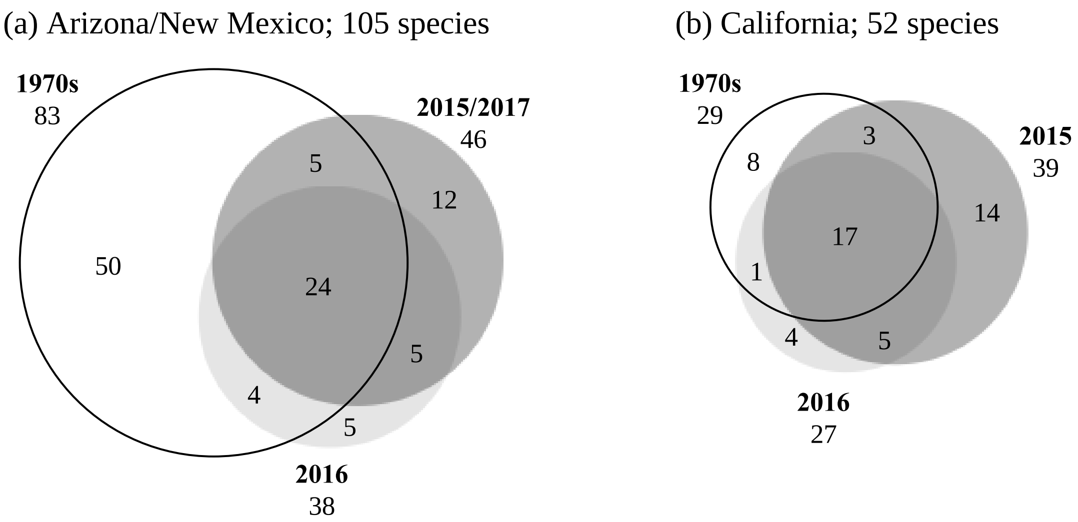
Values graphed are means ± 1 standard error. Alpha = 0.05 except where adjusted for multiple comparisons.

Results

Overview of collections

HLL collected 8,649 bees in the 1970s from the 11 "primary sites" we revisited in our study. We collected 11,143 bees total: 5,241 in 2015 and 5,902 in 2016. When constrained to bees collected only during overlapping sampling periods from the three sampling years (see Methods), 6,174 bees were collected by HLL in the 1970s, compared to 8,883 bees in the 2010s, with 4,147 and 4,736 bees collected by us in 2015 and 2016, respectively. (Note that these are absolute numbers before differences in effort, e.g., number of collectors, are taken into account.)

HLL collected 97 species: 83 from Arizona and New Mexico sites, 29 from California sites, with 15 species common to both regions. We collected 81 species: 55 from Arizona and New Mexico, 44 from California; 18 common to both regions (Figure 2).


(a) Arizona/New Mexico; 105 species

(b) California; 52 species

Figure 2. Venn diagrams showing numbers of bee species visiting *Helianthus annuus* and *H. petiolaris* at (a) four sites in Arizona and New Mexico and (b) seven sites in California in the 1970s (white), 2015 (dark gray) and 2016 (light gray).

In several of our sampled sites, *Apis mellifera* likely represented Africanized strains (Table A2), which arrived in the south-central U.S. in the 1990s. In general, sites from southern New Mexico (Animas, Rodeo, Silver City) and southern and eastern California (Indio, Bishop) tested positive for Africanized mt-DNA, while sites from northern California (Merced, Madera 1) did not (Table A2).

Other than *A. mellifera*, no introduced bee species appeared in HLL's samples. We observed only one other introduced species (*Megachile apicalis*, Escalon, CA, n=6 individuals). "Native bees" in our summaries include all except these two species.

Patterns of change in bee abundance

Arizona and New Mexico

There was no interannual difference in the number of bees collected per person-hour (p=0.76, $F_{2,9}$=0.28). The number of native bees per person-hour was significantly higher in the 1970s (mean=42.21) than in 2015 (mean=14.16) and 2016 (mean=13.85, p=0.02, both comparisons). The number of *A. mellifera* per person-hour was significantly lower in the 1970s (mean=0.00; none were collected from any sites in AZ or NM) than in 2015 (mean=16.52, p=0.03) and 2016 (mean=18.83, p=0.02) (Figure 3).

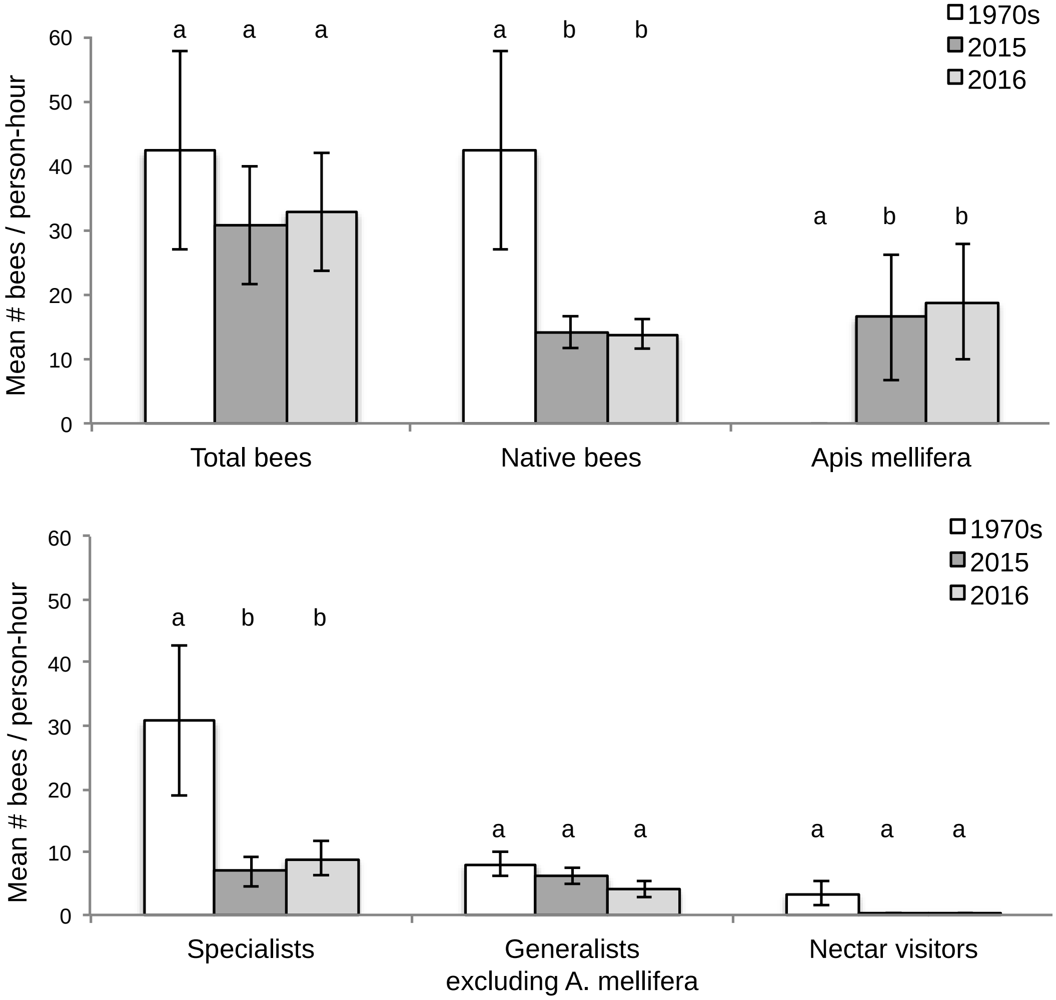


Figure 3. Abundances of bees visiting sunflower (*Helianthus annuus, H. petiolaris*) at four sites in Arizona and New Mexico in the 1970s. 2015, and 2016 (but Animas sampled in 2017 rather than 2015): total bees, native bees, *Apis mellifera*; pollen-specialist bees, pollen-generalist bees (excluding *A. mellifera*), nectar visitors. No *A. mellifera* were present in samples from the 1970s. Error bars are ±1 SE. Means that do not share a letter are significantly different.

The number of specialist bees per person-hour was significantly higher in the 1970s (mean=30.78) compared to 2015 (mean=6.94, p=0.01) and 2016 (mean=8.97, p=0.04 [significance level$_{adj}$=0.05]). There was no interdecadal difference in the number of generalists (excluding *A. mellifera*) (mean 1970s=8.07, 2015=6.12, 2016=4.05, p=0.24, $F_{2,9}$=1.68). The number of nectar visitors did not differ from the 1970s (mean=3.31) in 2015 or 2016 (2015 mean=0.27, 2016 mean=0.22, p=0.06) (Figure 3).

California

There was no interannual difference in the number of bees collected per person-hour (1970s mean=27.39, 2015=38.59, 2016=43.98, p=0.14, $F_{2,18}$=2.20). The number of native bees per person-hour was significantly higher in the 1970s (mean=26.73, $F_{2,18}$=8.50) than both 2015 (mean=14.53, p=0.004) and 2016 (mean=12.63, p=0.001). The number of *Apis mellifera* per person-hour was significantly higher in 2015 (mean=24.06, $F_{2,18}$=25.91) and 2016 (mean=31.36) than in the 1970s (mean=0.66, p<0.0001, both comparisons) (Fig. 4).

The number of specialist bees per person-hour was significantly higher in the 1970s (mean=24.28, $F_{2,18}$=8.95) compared to both 2015 (mean=10.96, p=0.003) and 2016 (mean=9.42, p=0.001). There was no interdannual difference in the number of generalists (excluding *A. mellifera*) (mean 1970s=2.17, 2015=2.15, 2016=0.72, p=0.22, $F_{2,18}$=1.64). The number of nectar visitors did not differ from the 1970s (mean=0.26) in either 2015 (mean=0.62) or 2016 (mean=2.15, p=0.16, chi squared=3.69, df=2) (Fig. 4).

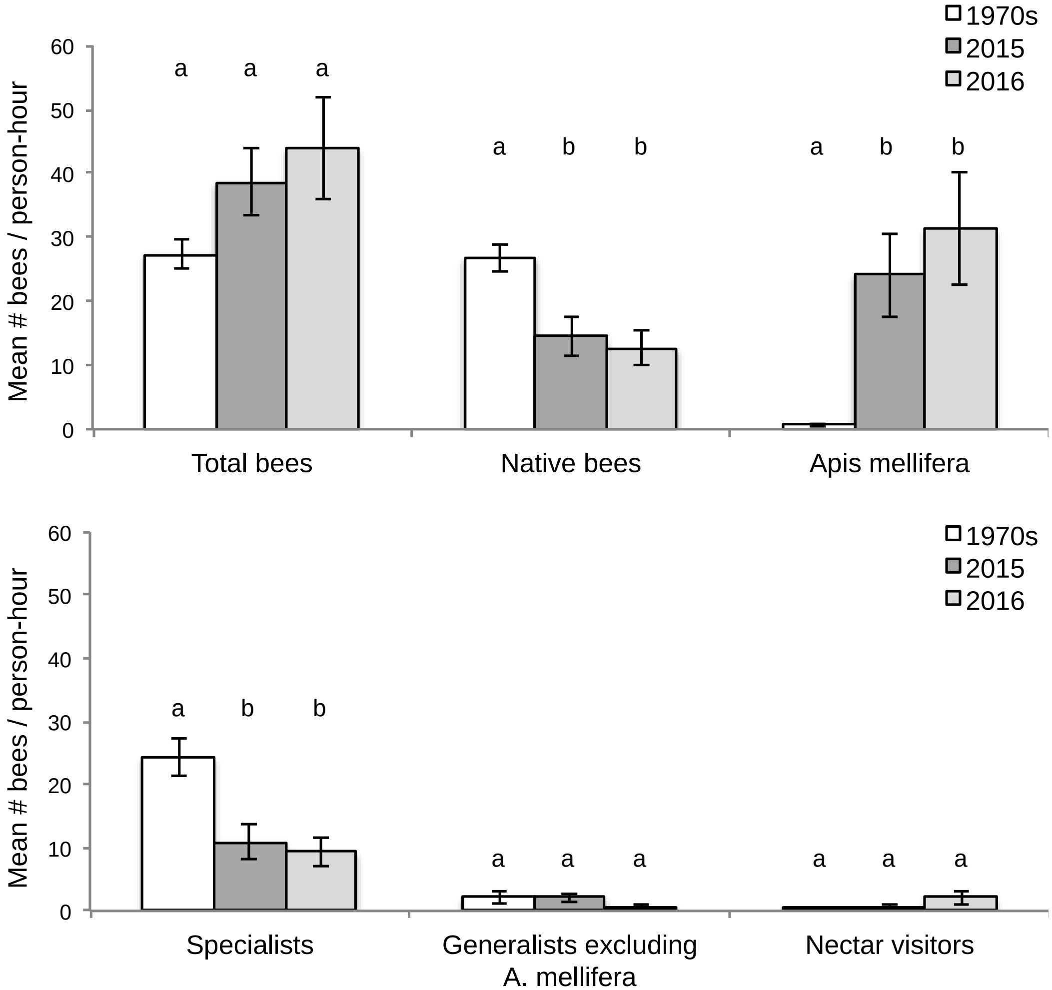


Figure 4. Abundances of bees visiting sunflower (*Helianthus annuus*, *H. petiolaris*) at seven sites in California in the 1970s, 2015, and 2016: total bees, native bees, *Apis mellifera*; pollen-specialist bees, pollen-generalist bees (excluding *A. mellifera*), nectar visitors. Error bars are ±1 SE. Means that do not share a letter are significantly different.

Both regions

There were no significant differences between 2015 and 2016 in any of the above comparisons of bee abundance.

Patterns of change in bee species richness

Arizona and New Mexico

There were fewer total species in 2015 (mean=18.75, p=0.03 [significance level$_{adj}$=0.05]) and 2016 (mean=17.25, p=0.02) compared to the 1970s (mean=35.75). There were significantly fewer specialist species in both recent years (1970s mean=15.75; 2015=8.00, 2016=8.25, $p \leq 0.01$, both comparisons). The estimated number of species (Chao1 estimator) did not differ between decades (1970s mean=35.26, 2015=24.91, 2016=20.36, p=0.17, $F_{2,9}$=2.15 (Figure 5).

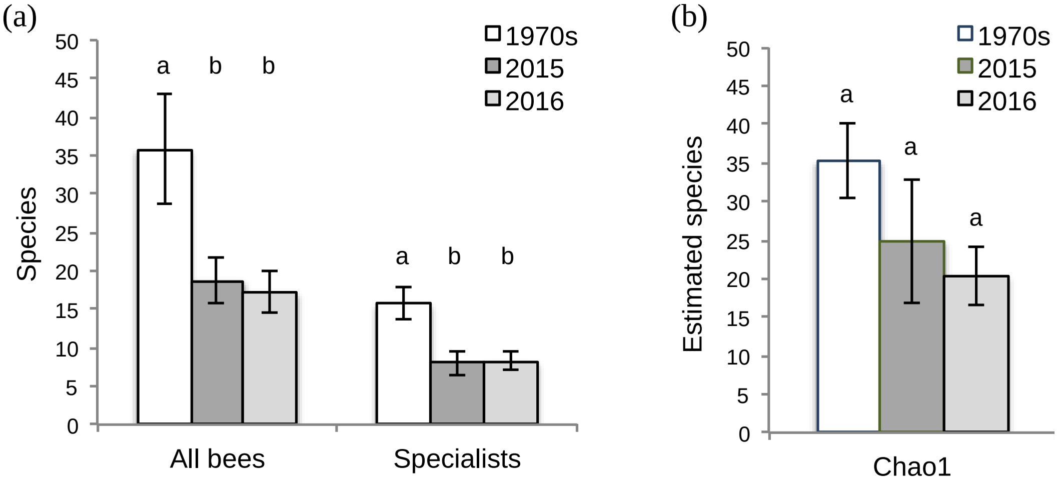


Figure 5. Arizona and New Mexico sites. Species richness of bees visiting sunflower (*Helianthus annuus*, *H. petiolaris*) at four sites in Arizona and New Mexico in the 1970s, 2015, and 2016 (but Animas sampled in 2017 rather than 2015): (a) total bee species richness, pollen-specialist bee species richness; (b) total estimated richness (Chao1). Error bars are ±1 SE. Means that do not share a letter are significantly different.

California

We found a total of 39 species in 2015 and 27 species in 2016, compared to 29 species from the same locations in the 1970s. This indicates an increase in regional species richness (total 2015–2016 richness = 44 species) compared to the past, yet there was no interannual difference in either the actual number of species (mean 1970s =10.71, 2015=12.28, 2016=10.14, p=0.49, $F_{2,18}$=0.74) or the estimated number of species per site (mean Chao1 1970s=14.89, 2015=14.38, 2016=11.63, p=0.83, $F_{2,18}$=0.19). There was no interannual difference in the number specialist species (mean 1970s=5.00, 2015=4.43, 2016=4.00, p=0.40, $F_{2,18}$=0.94) (Figure 6).

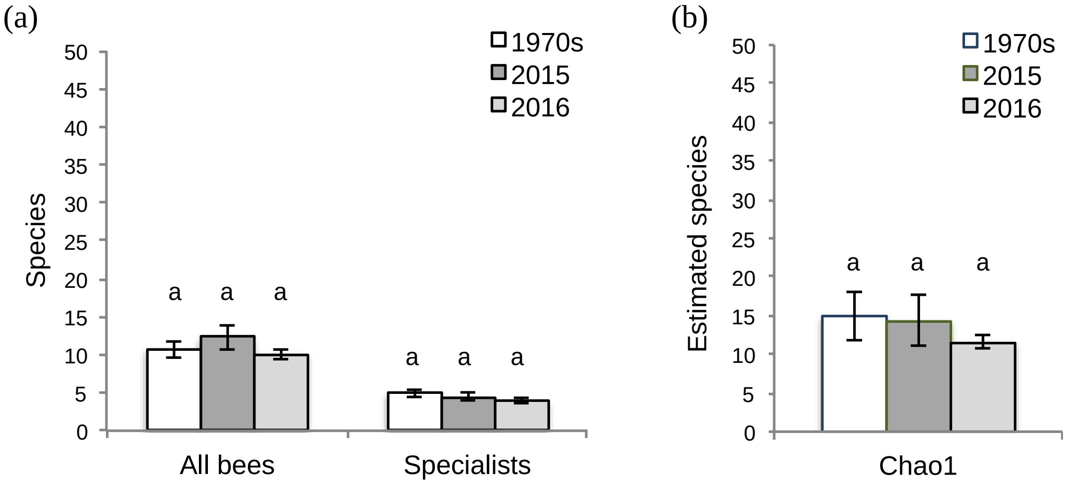


Figure 6. California sites. Species richness of bees visiting sunflower (*Helianthus annuus*, *H. petiolaris*) at seven sites in California in the 1970s, 2015, and 2016: (a) total bee species richness, pollen-specialist bee species richness; (b) total estimated richness (Chao1). Error bars are ±1 SE. Means that do not share a letter are significantly different.

Both regions

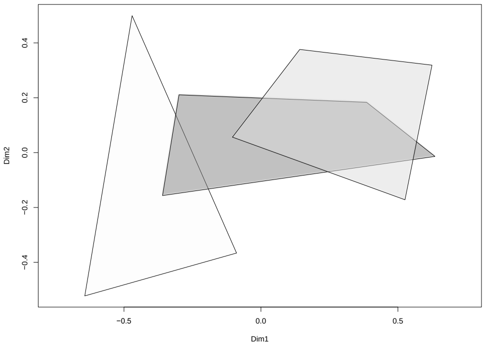
There were no significant differences between 2015 and 2016 in any of the above comparisons of bee species richness.

Patterns of change in bee assemblage composition

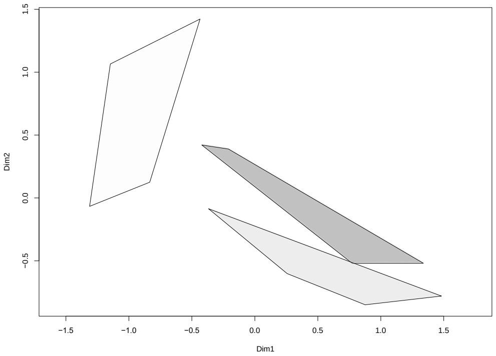
Arizona and New Mexico

There was no dissimilarity in overall assemblage composition between years (p=0.07, $F_{2,9}$=1.76). Among generalists and nectar visitors, assemblage composition did not differ significantly from the 1970s in 2015 (adj. p=0.09), but was weakly dissimilar from the 1970s in 2016 (adj. p=0.07). When *A. mellifera* was excluded, there was no dissimilarity between years in overall assemblage composition (p=0.07, $F_{2,9}$=1.59), generalist and nectar-visitor assemblage composition (p=0.04, $F_{2,9}$=1.93), or specialist assemblage composition (p=0.25, $F_{2,9}$=1.24) (Figure 7, Table A4).

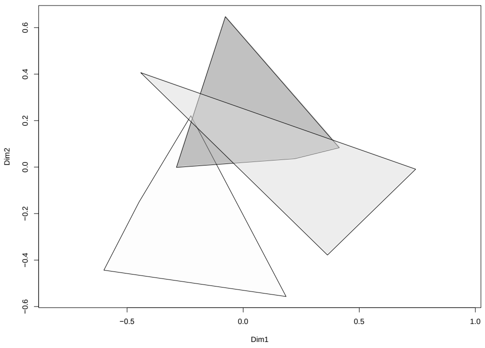
(a) With *Apis mellifera*.
All bees (stress=0.11)



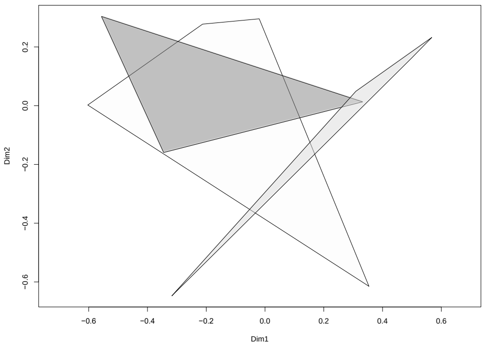
Generalists & nectar visitors (stress=0.11)



(b) Without *Apis mellifera*.
All bees (stress=0.11)



Generalists & nectar visitors (stress=0.13)



Specialists (stress=0.08)

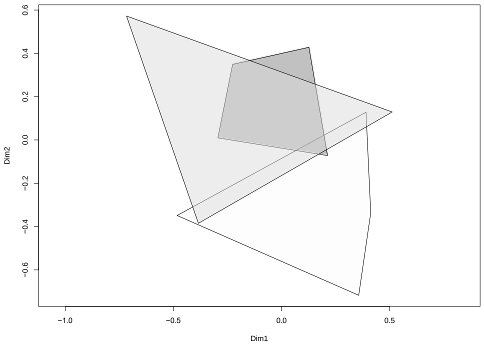
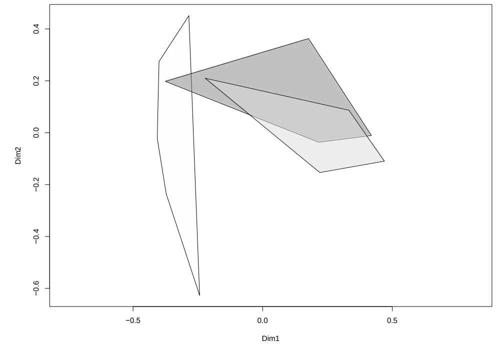
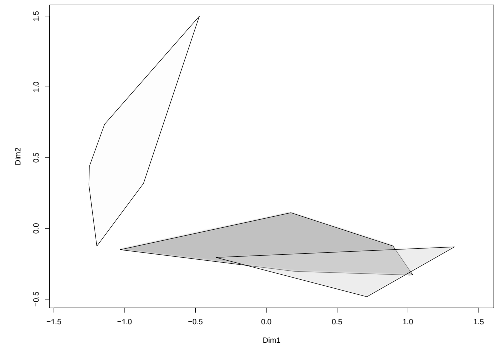


Figure 7. Arizona and New Mexico sites. Ordination plots (nMDS) of bee assemblage composition (a) with and (b) without *Apis mellifera*. Polygons surround four sites in Arizona and New Mexico sampled in the 1970s (white), 2015 (dark gray) and 2016 (light gray). Animas, NM was sampled in 2017 rather than 2015. Greater overlap between polygons indicates greater similarity in assemblage composition. Results from interannual comparisons are given in Table A5. All plots: k=2.

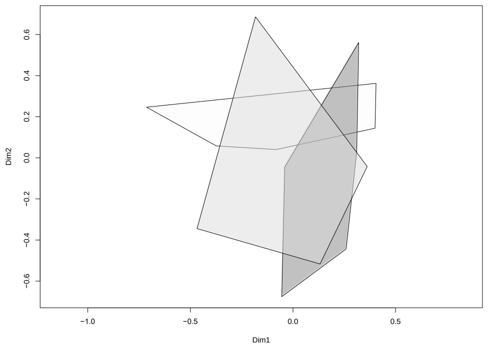
(a) With *Apis mellifera*.
All bees (stress=0.10)



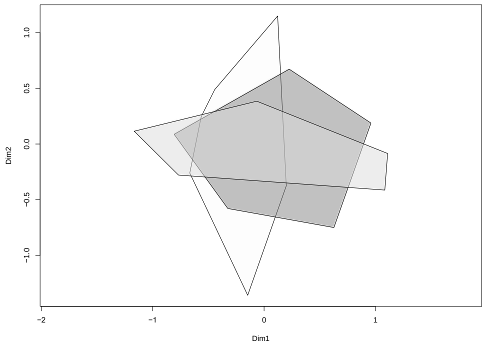
Generalists & nectar visitors (stress=0.05)



(b) Without *Apis mellifera*.
All bees (stress=0.16)



Generalists & nectar visitors (stress=0.21)



Specialists (stress=0.15)

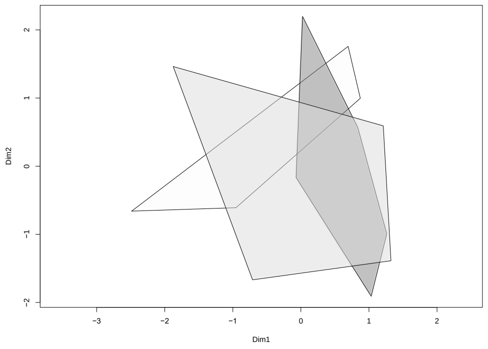


Figure 8. California sites. Ordination plots (nMDS) of bee assemblage composition (a) with and (b) without *Apis mellifera*. Polygons surround seven sites in California sampled in the 1970s (white), 2015 (dark gray) and 2016 (light gray). Greater overlap between polygons indicates greater similarity in assemblage composition. Results from interannual comparisons are given in Table A6 All plots: k=2.

California

Overall assemblage composition differed significantly from the 1970s in both 2015 (adj. p=0.006) and 2016 (adj. p=0.003). There was no significant difference between years when *A. mellifera* was excluded ($p=0.11$, $F_{2,18}=1.43$). Generalist and nectar-visitor assemblage composition differed from the 1970s in 2015 and 2016 (adj. $p=0.003$, both comparisons). When *A. mellifera* was excluded, generalist and nectar-visitor assemblages differed significantly from the 1970s ($p=0.04$, $F_{2,18}=1.58$) in 2015 (adj. $p=0.04$) but not in 2016 ($p=0.08$). There was no interannual difference in specialist assemblage composition ($p=0.17$, $F_{2,18}=1.36$) (Figure 8, Table A5).

Both regions

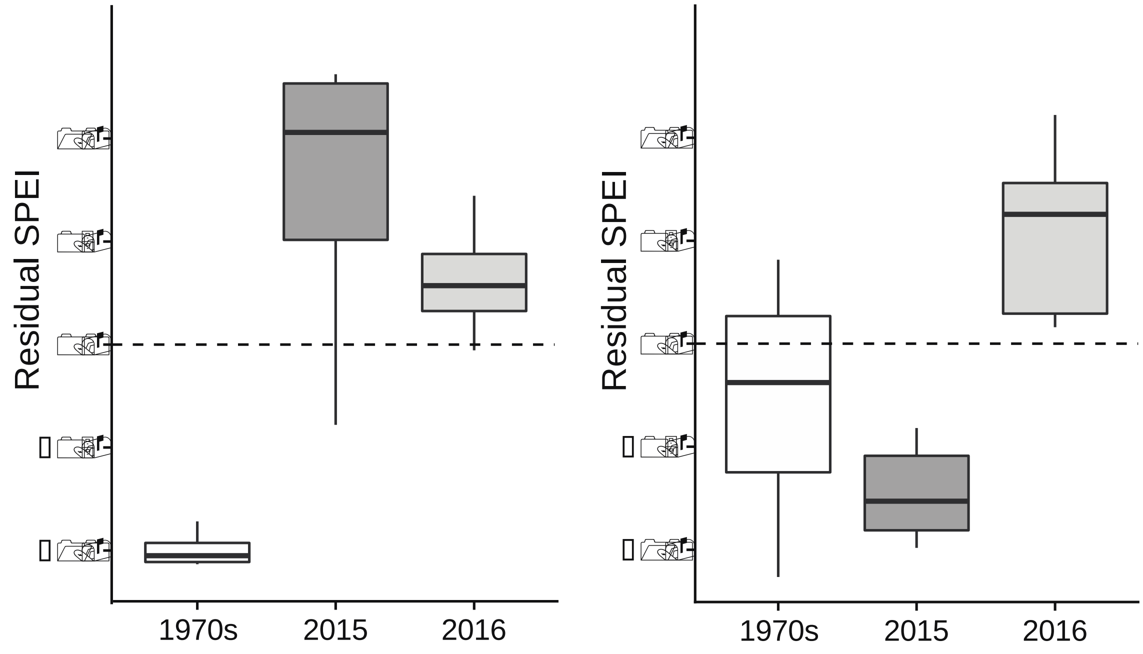
There were no significant differences between 2015 and 2016 in any of the above comparisons of bee assemblage composition.

Climatic representativeness of sampling years

Drought (as measured by more negative SPEI values) has significantly increased at all of our sampling sites over the past 40 years (Table 2, Figure A1). Residual SPEI during sampling years showed different patterns in our two regions. In Arizona/New Mexico, average conditions during the 1970s sampling were relatively hot and dry for the decade (residuals near -1.0; Figure 11a). Modern sampling (both 2015 and 2016) occurred during relatively cool and wet conditions relative to the decade's norm (residuals above zero; Figure 11a). In California, average SPEI during the 1970s sampling was near average for the decade (residuals near zero; Figure 11b). Modern sampling occurred during relatively hot and dry (2015; residuals below zero) and cool and wet (2016; residuals above zero) years relative to the decade's norm (Figure 11b), bracketing the 1970s relative conditions.

Table 2. Significant negative relationships between year and SPEI (Standardized Precipitation Evapotranspiration Index) at 11 sites in the U.S. Southwest in the 1970s [Hurd, et al. 1980] and 2015–2016 (the present study), indicating increases in drought over the 1970–2016 period. Plots shown in Figure A1.

Region	Site	Coefficient	p-value	Adjusted R^2
Arizona/New Mexico	Animas	-0.014	0.000	0.224
	Benson	-0.016	0.000	0.281
	Rodeo	-0.015	0.000	0.233
	Silver City	-0.008	0.041	0.070
California	Bishop	-0.015	0.000	0.271
	Corcoran	-0.011	0.003	0.163
	Escalon	-0.009	0.021	0.092
	Indio	-0.017	0.000	0.330
	Madera 1	-0.008	0.046	0.065
	Madera 2	-0.009	0.026	0.086
	Merced	-0.014	0.000	0.240

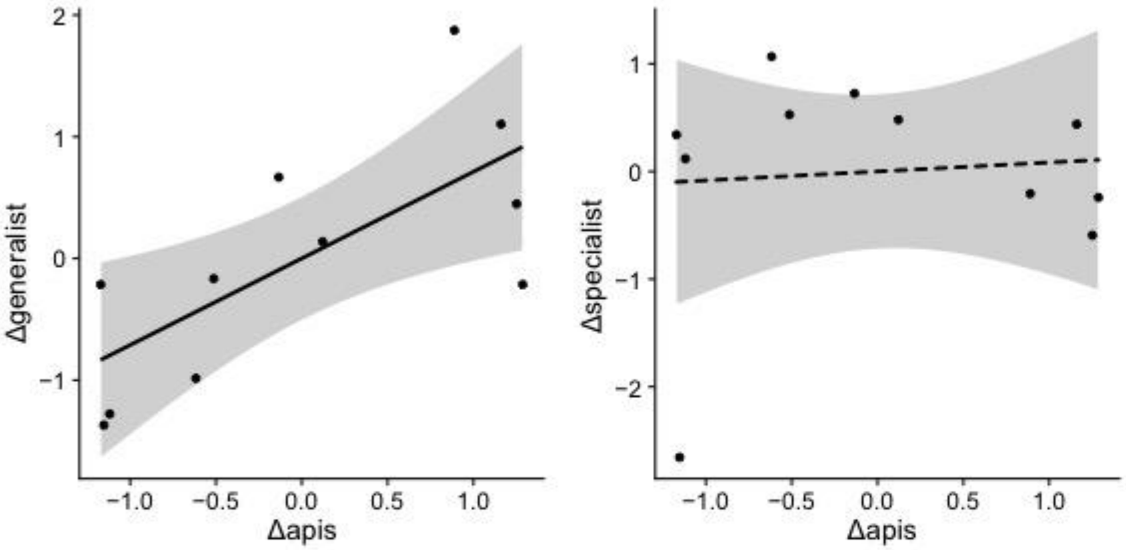

(a) Arizona/New Mexico sites (n=4)

(b) California sites (n=7)

Figure 11. Climatic contexts under which historic (1970s) versus modern (2015, 2016) bee sampling occurred. Boxplots depict the minimum, first quartile, median, third quartile, and maximum values of the residuals for the drought index SPEI for each region and time period, where residuals are calculated from the predicted SPEI shown as lines in Figure A1. Negative residuals indicate that conditions in the sampling year were hot and dry relative to those expected from adjacent years (i.e., years within the same decade); positive residuals indicate that conditions were relatively cool and wet.

Biotic and climatic correlates of changes in bee abundance

Sites where *A. mellifera* increased the most were generally those experiencing increases in native generalist bees ($R^2=0.45$; p=0.01; Figure 9a). Changes in *A. mellifera* abundance were not significantly correlated with changes in native specialist bee abundance ($R^2=-0.10$; p=0.81; Figure 9b).



(a) $\Delta_{generalist}$ vs. Δ_{apis} $R^2=0.45$; p=0.01

(b) $\Delta_{specialist}$ vs. Δ_{apis} $R^2=-0.10$; p=0.81

Figure 9. Models and model p-values of change (present minus past) in abundances of (a) generalist ($\Delta_{generalist}$) and (b) specialist bees ($\Delta_{specialist}$) visiting *Helianthus annuus* at 11 sites in Arizona, New Mexico and California, with change in *Apis mellifera* (Δ_{apis}) as the predictor.

Changes in several climatic variables were correlated with bee abundance changes (Fig. 10). Sites with the strongest increases in precipitation across the 40-year study period showed the largest increases in bee abundances, especially generalist bees including *Apis mellifera*. Sites with the strongest warming trends showed the largest declines in bee abundances. The direction and magnitude of these correlations were generally similar across the four categories of bees we examined (all bees, *Apis mellifera*, native generalists, and native specialists), although significance levels varied. For example, native specialist bees showed weak correlations with climate relative to other bee categories, only showing a significant (negative) correlation with changes in mean temperature in the driest quarter (Fig. 10).

Discussion

We found major changes in the sunflower bee assemblage of the U.S. Southwest over the past 40 years. Native bee abundance was significantly lower in 2015 and 2016 compared to the 1970s. Our results also support the expectation that specialist bees are more vulnerable to declines than generalists, despite their apparent resistance to changes in certain climatic conditions. Although we observed significant increases in introduced *A. mellifera* abundances in both regions, our data do not suggest *A. mellifera* increases are potential drivers of native bee declines, as [explain that A. mellifera abundances are + correl with generalist bee abundances, or more accurately, sites where Am increased the most also saw the biggest increases in generalists, suggesting competition was not in play]. Instead, climate change is implicated. Rising temperatures are associated with decreased abundances of all bees, and specialist bees in particular.

Changes in bee abundance

An overall pattern of declines in native, specialist bee abundances and increases in abundance of the introduced generalist *A. mellifera* was shown across both years and both regions of our study. We observed no statistically significant difference between 2015 and 2016 in any of our abundance measures — in fact in some cases we observed remarkable consistency between sampling years. We saw no significant declines in abundances of native generalist bees in either region, supporting the hypothesis that generalist species are more likely to persist in a context of environmental change. A study in Britain covering a comparable timespan (1980-2013) showed a similar trend of declines in overall bee species richness, but increases in crop-pollinating generalist species over the 33-year period [Powney et al. 2019]. The steeper declines in specialist compared to generalist bees shown in our and others' studies suggests that understanding the factors that contribute to specialist declines, and their interaction with environmental changes, should be a priority for future research. Further, do specialist and generalist bees contribute equally to the maintenance of ecosystem services, especially under variable environmental conditions? At least one mathematical model of ecosystem function (measured as community biomass, species richness over time, resilience and resistance to disturbance) has showed that ecosystem function in a species-poor community of generalists can be equal or greater than that of a species-rich community of specialists [Richmond et al. 2005], but whether this sceanrio actually plays out in real ecological communities is an open question.

Our observation of declines in bumble bee (*Bombus* spp.) abundances is consistent with other assessments [Burkle et al. 2013; Cameron et al. 2011; Colla & Packer 2008]. HLL encountered great numbers of *Bombus pensylvanicus* De Geer at some locations (e.g., 300+ individuals in a single sampling day in Rodeo, NM), reporting that huge numbers of *B. pensylvanicus* at sites in Arizona and California made it difficult or impossible to sample other species. In our surveys, *B. pensylvanicus* was absent, or present only in low numbers, at all except the highest-elevation site (Silver City, NM, 1,797m). It is possible that *B. pensylvanicus* has shifted to higher elevations/cooler temperatures, as has been reported for other *Bombus* species in connection with climate change [Biella et al. 2017, Ploquin et al. 2013]. Declines and range contractions in *Bombus* species could have especially severe and wide-ranging effects on pollination in natural and agricultural systems, owing to their very high efficiency in pollen transfer [Cameron et al. 2011].

Changes in species richness

Bee species richness at Arizona and New Mexico sites was significantly lower in 2015 and 2016 than the 1970s. We think this decline is unlikely to be related to human impacts such as development and/or fragmentation since the 1970s. The area is sparsely populated (e.g., Benson AZ; 2010 population=5,105 [U.S. Census 2010]), with vast acreages under low-impact agricultural use such as ranching. We know of no large-scale changes over the past 40 years that could have affected bee populations in the area. Our examination of climate variables indicates that although temperature increases are associated with reduced abundance of all bees, the relationship is strongest with specialist bees, particularly during the driest part of the year (mean temperature of driest quarter, figure 10). A possible explanation is that higher temperatures increase specialist bee mortality either directly (if species already living near the upper limit of their temperature tolerances are exposed to more frequent or intense heat) or indirectly (via effects on their host plants). For example, climate warming may induce earlier host plant emergence, which could potentially lead to phenological mismatches, since development and diapause in bees is regulated by a variety of environmental triggers [Sgolastra et al.

2010]. There is some indication that emergence from diapause is keeping pace with advances in host-plant flowering in certain generalist bee species [Bartomeus et al. 2011], but analogous studies of specialist species are needed.

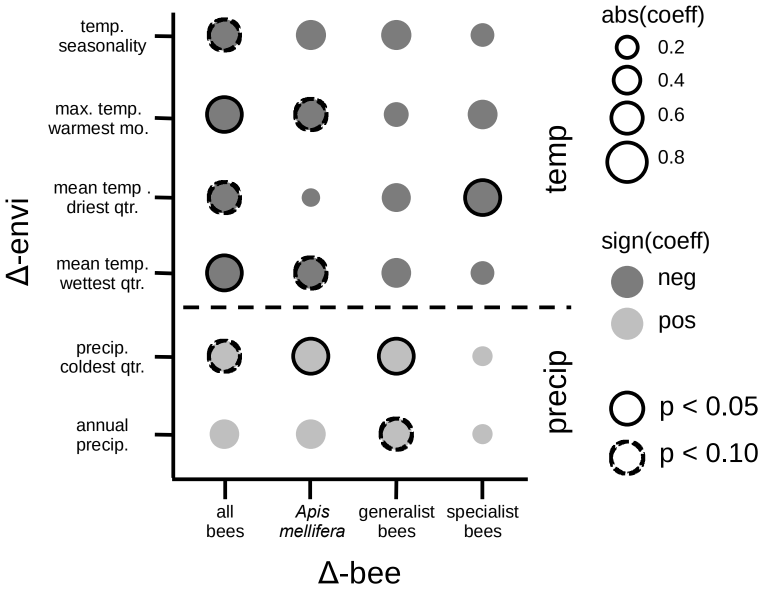


Figure 10. Changes (present minus past) in environmental variables (Δ_{envi}) significantly associated with changes in abundances of bees visiting *Helianthus annuus* (Δ_{bee}) at 11 sites in Arizona, New Mexico and California.
“all” = all bees, “am” = *Apis mellifera*, “gen” = generalists other than *A. mellifera*, “spec” = specialists, temperature seasonality=annual maximum–annual minimum

In California, we found an increase in regional species richness (all sites considered together) compared to the past, but no difference in either actual or estimated per-site species richness between years. We note, however, that generalist assemblage composition in 2015–2016 differed significantly from the 1970s at both California and Arizona-New Mexico sites, and that increased precipitation was strongly correlated with increases in generalist (but not specialist) abundance. This suggests high turnover in generalist bee species identity, yet overall generalist persistence. It is possible that interspecific competition affects species composition in generalist bees more than in specialists. In addition, unlike specialist species, generalist bee emergence is not closely synchronized with flowering in particular host plants; thus a certain number of generalist species are likely to be active and able to make use of periodic floral resources at any given point in the season.

It is important to bear in mind that bee assemblages generally vary greatly from year to year. For example, in a 10-year study of *Eucryphia cordifolia* Cav. Pollinators in Chile, only three out of 137 species were observed annually, with *Apis mellifera* dominant in some, but not all years [Smith-Ramírez et al. 2014]. Similarly, of 330 bee species recorded from bimonthly surveys in a 15-year study in New Mexico, about 300 species appear in <5% of samples [Karen Wright, unpublished data]. Others have reported similar variability in pollinator populations [Olesen et al. 2008; Williams et al. 2001]. Our data represent a two-year glimpse of sunflower bee status, and it is likely that some species were both present and undetected. But the high variability in assemblage composition shown in ours and others' studies heightens the importance of developing coordinated regional efforts to address the causes of bee declines. In agricultural settings, for example, greatly reduced diversity results in insufficient pollination service, while high diversity helps offset natural year-to-year variation [Kremen et al. 2002].

Bee dietary specialization

To improve the assessment of generalist vs. specialist extinction risk, we suggest that bee dietary specialization needs further clarification. Although HLL defined species as oligolectic or polylectic based on their preliminary observations, they also speculated that there are “few, if any, oligolectic bees associated solely with *Helianthus*, though there are many oligoleges of Compositae that visit sunflowers for pollen and nectar, and others that prefer sunflower pollen, when available, to that of other composites” [Hurd et al., p. 23]. Recent DNA analyses of pollen from museum specimens have indicated that some *Melissodes* species defined by HLL as primary oligoleges on *Helianthus* (e.g., *M. agilis* Cresson, *M. coreopsis* Robertson) are specialists on Asteraceae, but not solely on *Helianthus* [K. Wright, unpublished data]. A clearer understanding of bee dietary specialization would be helpful for making targeted conservation recommendations. If rare species are assumed to be specialists based on only a few observations from a limited number of resource or habitat types, this may result in an erroneous conflation between specialization and decline.

Increase in Apis mellifera abundance

In the HLL survey of the 1970s, *A. mellifera* was either present at low levels or absent, including at one site where “a large stand of *H. annuus* in excellent bloom and producing an abundance of pollen and nectar attracting other species of bees was growing within 50 yards of an apiary comprising approximately 25 [*A. mellifera*] colonies” [Hurd et al., p. 124]. Their assessment is consistent with a earlier study by Cockerell [1914], who reported that *A. mellifera* do not visit sunflower unless the supply of nectar from other plants runs short (for example, during drought conditions). This contrasts sharply with our observations. *Apis mellifera* was among the most commonly observed species at all sites, including all four sites in Arizona and New Mexico, where no *A. mellifera* were observed in the 1970s. In their discussion of *A. mellifera*, HLL report on an additional 16 survey sites [Hurd et al., p. 125] that we did not revisit in the current study; at these and their primary sites, HLL observed fewer than one *A. mellifera* per person-hour, compared to our average of more than 20 *A. mellifera* per person-hour.

We suggest that the increase in *A. mellifera* observed at California sites could be related to changes in agricultural practices since the 1970s. The number of acres in almond (*Prunus dulcis*) production in the state expanded from ~300,000 in 1980 to over 1,000,000 acres in 2015 [NASS 2016]. Almond production is dependent on pollination by *A. mellifera*, and commercial beekeepers transport 2–3 million colonies to California annually to meet demands for pollination services [Kulhanek et al., 2017; Sumner & Boriss 2006]. Although most commercial bees are relocated following the end of almond bloom in April, this huge annual influx of commercial colonies to California may have helped to maintain high levels of feral *A. mellifera* in the region, since at least some colonies will abandon their hives when disturbed and become feral. An increase in *A. mellifera* abundance in crop settings has not been shown to lead to decreases in native bees [Kremen et al. 2002; Williams et al. 2010], but there is evidence of negative effects on native bee visitation to wild plants [Henry & Rodet 2018]. We believe the question merits further investigation. Native pollinators have been demonstrated to be important contributors to crop productivity and stability of pollination service even when *A. mellifera* are abundant [Garibaldi et al. 2011]. This contribution may be even more important for the non-agricultural plants for which native bees are best adapted as pollinators and upon which they depend for their own reproduction.

Our results for *A. mellifera* suggest that the species needs to be monitored more closely in wildland settings. Despite considerable interest among melittologists in the potential for competition between *A. mellifera* and native bees (e.g., Beard 2015; Cane & Tepedino 2016; Geldmann & González-Varo 2018), *A. mellifera* is often excluded from sampling because it is a managed species. For example, Kearns & Oliveras (2009) reported *Apis* presence but not abundance in Boulder, CO, and *Apis* was purposefully not sampled in other historical comparisons (Bartomeus et al. 2013, Biesmeijer et al. 2006; Marlin & LaBerge 2001, Grixti & Packer 2006), so there is no information on possible changes in *Apis* abundance over time at these locations. Burkle et al. (2013) did not comment on *A. mellifera* specifically, but we noted that it was among a core group of generalists that persisted from the time of the original (1800s) Carlinville study to the present [Burkle et al. 2013, Supplementary Material, Fig. S9].

Our results also highlight the importance for researchers of including *A. mellifera* when documenting bee assemblages. We found no association between *A. mellifera* increases and native bee declines, but given that negative effects have been indicated in other studies [e.g., Badano 2011; Hudewenz 2015; Sugden & Pyke 1991], we emphasize the importance of tracking *A. mellifera* abundance and distribution as part of monitoring overall assemblage condition. *A. mellifera*'s status as a managed species does not cancel out its potential for competitive displacement of native bees, perhaps specialists in particular. In a review of the ecological impacts of *A. mellifera* introductions, Butz-Huryn (1997) argued that "invoking cause and effect from honey bee presence and native bee absence may ignore other factors that limit native populations" (e.g., habitat loss, climate change). However, we will be unable to make this distinction without documenting the shifting abundances of all bee species as anthropogenic impacts proceed.

Inferred bee abundance trends were not driven by climatically unrepresentative sampling years

Climate data from HLL's and our sampling years (Figure 11, Figure A1) suggest that our inferred bee population trends are not being driven by chance sampling of climatically extreme years that were unrepresentative of their respective decades. For Arizona/New Mexico sites, sharp declines in abundance and diversity of native bees (Figures 3a and 5a) occurred against a backdrop of poor conditions during 1970s sampling (hot and dry conditions relative to the 1970s decadal norm, with floral resources expected to be scarce) compared to good conditions during modern sampling (cool and wet conditions during both 2015 and 2016 relative to the 2010s decadal norm, with floral resources expected to be abundant). For California sites, declines in abundance of native bees (Figure 4a) coupled with stasis in species richness (Figure 6) were apparent regardless of whether the modern sampling year was hot and dry (2015) or cool and wet (2016) relative to the decadal norm.

Biotic and climatic correlates of changes in bee abundance

We found no evidence that introduced *A. mellifera* were drivers of declines in native bee species. Instead, it appears both *A. mellifera* and other generalist bees are responding similarly to changing environmental conditions, since sites where *A. mellifera* increased the most were generally those experiencing increases in native generalist bees as well.

Changes in *A. mellifera* abundance were not significantly correlated with changes in native specialist bee abundance.

Of the 19 environmental variables we examined in exploratory analyses, we found significant correlations between six of them (four related to temperature, two to precipitation) and abundance changes in at least one of our four bee groups (all bees, *A. mellifera*, generalists excluding *Apis*, and specialists). In general, sites where temperature increased the most over the past 40 years showed the biggest decreases in total bee abundance. This suggests a potential relationship with climate change, one that warrants further examination and hypothesis testing.

However, we note that no single environmental factor was strongly correlated with abundance changes in all four groups of bees. For example, temperature increase was associated with abundance decreases in different groups depending on time of year. Increases during the driest quarter were strongly correlated with decreases in specialist bee abundance but had no relationship with *A. mellifera* abundance, while increases during the wettest quarter were associated with a drop in total bee abundance (mainly driven by *Apis*) but the correlation with specialists was not significant. Similarly, increases in precipitation (especially during the coldest quarter) were strongly correlated with increases in *A. mellifera* and other generalist bees, but not specialists.

Taken together, these patterns suggest the potential for differential climatic effects on the host plants relevant to each group (e.g., different shifts in phenology or abundance). For example, increased precipitation during the coldest quarter could promote spring-flowering species that benefit generalist bees, but not necessarily the late-summer annuals that would most benefit the specialist bees in our region. We interpret the absence of a uniform relationship with climate variables across all bee groupings as indication that 1) climate variables may be poor proxies for host plant availability — an index of which would likely be more tightly associated with changes in the bee community, and 2) climatic shifts may affect specialist and generalist bees differently, perhaps in relation to effects on their host plants but possibly in connection with other factors, such as nesting conditions or cues affecting diapause. We emphasize that our climate analyses are exploratory and that the hypotheses generated need further independent testing.

Consequences for pollination services

Impacts of changes in native bee communities on native plant reproduction are poorly understood. If visitation frequency in *H. annuus* equates with pollination effectiveness — a reasonable assumption given its generalist floral morphology — then *A. mellifera* may be considered the principal pollinator of *H. annuus* in our study areas at present. Others have noted the possibility that *A. mellifera* dominance and high visitation frequency could promote fitness in introduced plants [Beard 2015, Kato et al. 1999]. Some native plants have shown signs of adapting to introduced pollinators [Medel et al. 2018]. Though we observed only 16 fewer bee species than HLL, it is important to remember that declines can lead to functional extinctions, wherein a species is so reduced in numbers that it can no longer perform its former role in ecosystem processes [Carlton et al. 1999]. In the case of native pollinator declines, this includes the possibility of changes in native plant communities resulting from changes in pollinator species composition.

The site conditions we encountered suggest possible changes in floral resources compared to the past. HLL reported no difficulty in locating suitable patches of *Helianthus* for sampling. This was not the case in the present study. HLL sampled at 52 locations in addition to primary sites (many sampled for multiple years), finding sunflowers along the edges of fields, orchards, ditch banks, fences, highway shoulders, on grazing land, even in vacant lots in Los Angeles, CA. This description of widespread occurrence contrasts markedly with our experience, where at almost all locations *Helianthus* was difficult to find in one or both years. For example, in 2016 in a thorough search along roadsides leading in every direction from Corcoran, CA we found only very small patches of sunflowers (<5 plants). The nearest viable sampling location was in Earlimart, 19.6 mi. south. Similarly, we found no sunflowers on the 135-mi. drive from Corcoran to Merced. HLL also recorded numerous sites with either *H. petiolaris* growing exclusively or in mixed stands with *H. annuus*. We did not observe *H. petiolaris* at any sites in either 2015 or 2016. Changes in *Helianthus* species composition, abundance, and/or range extent could be correlated with changes in bee assemblages.

Conclusion

Species richness at Arizona and New Mexico sites sharply decreased, whereas it appears stable at California sites. [Insert equivalent statement summarizing abundance changes]. Our results strongly suggest a greater susceptibility to decline for specialist bee species, which comprise a substantial portion of the bee biodiversity of the Southwest region.

Although we did not observe declines in total abundance of generalist bees in either region, we did find significant changes in generalist species composition, which suggests that some generalist species may emerge as “winners” and others as “losers” in a context of rapid anthropogenic change. Continued declines in native bee abundance and/or species richness could negatively impact pollination services and threaten both wild plant species and agricultural food plant production.

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CHAPTER 2

Introduced honey bees (*Apis mellifera*) alter native bee visitation and seed set in a native plant species

Abstract

Introduced species have been identified as primary drivers of global biodiversity loss. Destructive impacts have been brought about by a variety of taxonomic groups, including insects. The western honey bee (*Apis mellifera*) is among the world's most commonly introduced insects. Perhaps because the species is a highly valued agricultural pollinator, its potential for negative impacts has received minimal investigation. However, *A. mellifera*'s sociality and generalist adaptability suggests the species could exert a considerable influence on both native bee floral visitation and native plant reproduction in its introduced ranges, especially if it competes with native bees or has differential effectiveness as a pollinator. Using replicated experimental introductions of *A. mellifera* and controls in an area of low *A. mellifera* density in south-central New Mexico, USA, we asked whether *A. mellifera* influences native bee visitation to and reproduction in native plant populations. We measured native bee visitation to arrays of potted native plants, as well as seed set in one native plant, the common sunflower *Helianthus annuus*. We found a marginally significant negative effect of *A. mellifera* introduction on native bee visitation frequency, but significant positive effects on both seeds per inflorescence and whole-plant seed set in *H. annuus*. *Apis mellifera*'s dominance in its introduced ranges has led some researchers to speculate that high densities of *A. mellifera* should inevitably reduce native bee abundance and perhaps also native plant fitness. Results from this study suggest that introduced *A. mellifera* may decrease visitation frequency of native bees to their host plants, yet positively contribute to native plant reproduction.

Introduction

A primary driver of global biodiversity loss is the impact of introduced species [WWF 2014]. In North America, many introduced insects have been identified as invasive and having destructive impacts [USDA 2018]. The most commonly introduced insect worldwide is the western honey bee (*Apis mellifera*), usually introduced to improve agricultural pollination and therefore generally regarded as beneficial [Kearns et al. 1998]. Given the near-global success of feral *A. mellifera* colonies and the importance of pollination as a factor in plant reproduction [Hung et al. 2018; Klein et al. 2006; Traveset & Richardson 2006], the potential negative impacts of *A. mellifera* have received disproportionately minimal attention. But it is precisely its dominance and efficacy that give *A. mellifera* the potential to affect both pollinator and plant populations in places where it is introduced, and its influences warrant thorough investigation.

Effects of A. mellifera *on pollinators*

Prior studies on the impacts of *A. mellifera* on pollinators in its introduced ranges have revealed varying effects. Though some researchers maintain the evidence is inconclusive [Butz Huryn 1997; Paini 2004], there are cases of detrimental impacts of *A. mellifera* on native bees [e.g., Badano 2011; Hudewenz 2015; Sugden & Pyke 1991] leading others to assert that its effects are either negative [Beard 2015] or context-dependent [Aslan 2016]. For example, Badano (2011) reported a decrease in native bee diversity as *A. mellifera* abundance increased, and Hudewenz (2015) found decreased reproductive success in experimental native bee communities (caged 3 x 3-m plant arrays in the field) when *A. mellifera* was present. One reason for the lack of consensus on the ecological impact of

A. mellifera introduction is that, in most settings, both feral and managed *A. mellifera* colonies are widespread and control sites for comparison are hard to find. Some have suggested that the lack of definitive evidence primarily reflects the difficulty of carrying out field studies [Butz Huryn 1997; Goulson 2003]. The question has received renewed attention, however, in response to recent declines of both native bees and *A. mellifera* [Genersch 2010; Powney et al. 2019].

When competing for limiting resources, *A. mellifera* may be expected to impact native pollinators mainly through competitive exclusion. Active displacement at flowers is rare; instead, high densities of *A. mellifera* can be associated with decreased frequency of native bee floral visitation [Shavit et al. 2009] or altered foraging strategy in native bees [Thomson 2004]. Competitive exclusion should have the greatest impact on oligolectic bees whose host plants are favored by *A. mellifera*, since highly specialized foragers cannot switch to alternative plants when preferred resources are unavailable.

In response to pollinator declines, concern has arisen regarding the placement of *A. mellifera* colonies in natural habitats. Researchers emphasize the importance of setting stocking rates for managed *A. mellifera* such that adequate forage is still available for native bees [Beard 2015; Cane & Tepedino 2016; Geldmann & González-Varo 2018]. In the U.S., apicultural leases are issued to provide post-crop maintenance and honey production in managed *A. mellifera* colonies, which can result in huge numbers of *A. mellifera* concentrated in a single area. Particularly in the West, U.S. wildlands host diverse, robust native bee communities [Michener 2000]. “Safe” densities of managed bees in such environments, where wild pollinators are most abundant and which are important for pollinator conservation, will be different than in highly modified landscapes (e.g., crop monocultures). To determine what constitutes a reasonable stocking rate for *A. mellifera* in western wildlands, we need a clear understanding of how native bees and plants respond when *A. mellifera* are present, compared to when they are not.

Effects of A. mellifera *on plants*

The effects of *A. mellifera* on pollination of agricultural plants are usually (though not always) considered to be positive, i.e., *A. mellifera* generally increases crop yield and quality [McGregor 1976]. In contrast, the species' impact on wild plants has received less attention, despite awareness that *A. mellifera* readily and in some cases preferentially forages for pollen outside of the crops they are intended to pollinate [Gonzalez-Varo & Vila 2017; Requier et al. 2015]. In a recent review, Mallinger et al. (2017) concluded that the evidence for effects of *A. mellifera* on native plant reproduction is approximately equally divided between negative and positive outcomes [Mallinger 2017]. However, Mallinger et al. also noted that in the majority of studies examining effects of *A. mellifera* on native plants, *A. mellifera* density was not experimentally manipulated. As with studies of effects on native bees, others have pointed out that comparative studies with controls lacking *A. mellifera* are required in order to better understand how *A. mellifera* affects native plant reproduction [Dohzono & Yokoyama 2010].

Competitive exclusion of native bees by *A. mellifera* has greater potential to affect native plant populations if pollination effectiveness differs between the two bee groups. This can occur even if their per-visit pollination efficiency (seed set resulting from a single visit [Rader et al. 2009]) is equal. Pollination effectiveness can be calculated as a combination of efficiency and visitation frequency (i.e., overall visits of a pollinator relative to seed set [Motten et al. 1981]). Unlike most native bees, which are solitary, sociality in *A. mellifera* allows colony members to share information and forage cooperatively, which can result in the recruitment of large numbers of *A. mellifera* to a desirable resource. Thus *A. mellifera* can have high effectiveness regardless of efficiency, owing to high visitation frequency [Osorio-Beristain et al. 1997; Westerkamp 1991].

Floral resources are more likely to be intermittently scarce (and competition more fierce) in arid regions, which also contain the highest native bee diversity [Michener 2000]. The objective of this study was to investigate whether experimental supplementation of *A. mellifera* in an arid ecosystem elicits behavioral shifts in native pollinators, which in turn could alter native plant reproduction. Specifically, we assessed native bee visitation and fitness in the common sunflower *Helianthus annuus* in replicated supplemented vs. control sites in south-central New Mexico, USA. *A. mellifera* pollination improves domesticated sunflower seed set in agricultural settings [Oz et al. 2009], but does this effect hold when the species is foraging among native, specialist pollinators that coevolved with wild *H. annuus* as a host plant? If not, do these effects correspond to changes in native bee visitation? Effects should be positive if *A. mellifera* is an equal or more effective pollinator than native bees; but negative or neutral if *A. mellifera* is less effective. We hypothesized that *A. mellifera* would reduce native bee visitation due to competitive exclusion, and that this would result in decreased fitness in *H. annuus*.

Materials and methods

Study Sites and Experimental Design

This study was conducted in Chihuahuan basin-and-range territory in southwest New Mexico, Sierra County. Bee diversity in the southwest U.S., especially the northern Chihuahuan Desert, is among the highest in the world [Michener 2000; Minckley & Ascher 2013]. Specialist species surpass generalists in diversity, biomass and abundance [Minckley et al. 2000; Simpson & Neff 1987]. *Apis mellifera* colony establishment is constrained by low availability of water, lack of cavity-nesting sites, and *Varroa* mites [Ken Hays, personal communication; Loper 1995; Visscher et al. 1996]. As a result, feral colonies in the study area are scarce. For example, in three years of bee monitoring using funnel traps at Bosque del Apache Wildlife Refuge north of our study area (range, 11–60 miles from our sites), *A. mellifera* comprised < 0.5% of trapped specimens [Wright 2010].

In 2017 we selected 8 pairs of study sites from two sampling areas: northern (Armendaris Ranch; vicinity of San Marcial, NM) and southern (Elephant Butte Lake State Park, Caballo Lake State Park; vicinity of Truth or Consequences, NM). Sites occurred in two vegetation types: upland (dominated by creosote bush with desert grasses and cacti) and riparian (within 1 km of the Rio Grande; predominantly salt cedar with cottonwood and willow). We located two pairs of sites in each vegetation type in each of the two sampling areas (Figure 1).

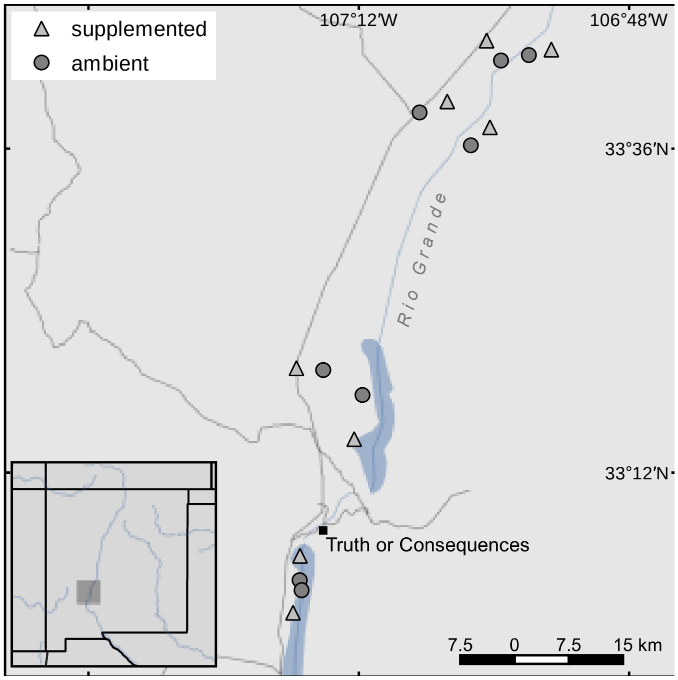

Figure 1. Map of 16 paired study sites (ambient=circles, *Apis mellifera*-supplemented= triangles) in the vicinity of Truth or Consequences, Sierra County, New Mexico USA.

Three weeks prior to the start of the experiment (July 28, 2017), we introduced *A. mellifera* hives at one randomly selected site per pair (“supplemented”), leaving the other without hives as a control (“ambient”). We used professionally-reared hives (Hays Honey and Apple Farm, Bosque Farms, New Mexico) of approximately equal size (15,000–25,000 bees) and initial condition. Supplemented sites received three hives each. *Apis mellifera* have been recorded foraging up to 14 km from their hives, but most foraging takes place within 2.5 km of the hive [Eickwort and Ginsberg 1980, Visscher & Seeley 1982]. To minimize the likelihood that supplemented *A. mellifera* would visit control sites, we located sites within a pair a minimum of 3.2 km apart (mean = 3.8 km). Neighboring pairs were at least 1.4 km apart; supplemented sites at least 6.9 km apart.

Hives were left in place for te duration of the experiment (12 weeks) and were checked weekly. Supplemental feedings (sugar solution) were given during the first two weeks in the field prior to the start of the experiment, as well as on one other occasion during the study period (September 15); otherwise, experimentally introduced bees foraged from plants in the study area. No commercial beehives other than those we introduced were in the vicinity during the sampling period.

Plant arrays

In the U.S. Southwest, many oligolectic bees rely on late-blooming annual plants (mostly in family Asteraceae) for pollen. For example, sunflowers (genus *Helianthus*) are visited by several hundred native bee species, about half of which are Asteraceae specialists [Hurd et al. 1980; Cumberland *et al.* in prep.]. *A. mellifera* also visit sunflowers, primarily for nectar (as opposed to native bees, which collect both nectar and pollen) [Free 1964; Neff & Simpson 1990].

We assessed bee visitation using four plant phytometers: *Helianthus annuus*, *Gaillardia pulchella*, *Verbesina encelioides*, and *Baileya multiradiata*. All are annual, native Chihuahuan Desert forbs in family Asteraceae that bloom during the North American monsoon season (mid-June to late September) and are visited by medium to high abundances and diversity of bees and other pollinators (wasps, flies, beetles) [USDA-NRCS 2013]. Our focal plants for reproductive-fitness measures were *H. annuus* and *G. pulchella*, since they are self-incompatible and thus had the potential to show strong responses to increased pollination via *A. mellifera* supplementation. *Verbesina* *encelioides* and *B. multiradiata* are self-compatible, but were included in arrays to mimic the structural and phenologic variation of a diverse native plant community, with the intention of attracting a greater number of pollinators to maximize cross-pollination in our focal plants.

Seeds from regionally-harvested seed stock (NM, CO, CA) were obtained from a native-plant nursery (Plants of the Southwest, Albuquerque, New Mexico). Beginning in spring 2017, we started seedlings bi-monthly at the University of New Mexico greenhouses and transplanted them to 1-gallon containers at bud stage. Placement in the field was timed to coincide with the earliest stages of bloom for all species.

There were three rounds of plant placement (August 19–27, September 17–24, and October 7–16, 2017); we refer to each as a "sampling period". Plants were randomly assigned to either *A. mellifera*-supplemented or ambient treatments. Plants were protected from herbivores in 1 x 1.25-m^2 enclosures constructed of 91.44-cm high chicken wire mesh attached to steel rebar supports. Enclosures at supplemented sites were placed ~15 meters from beehives. Each enclosure contained three polypropylene bus tubs (~ 50 x 40 x 20 cm) holding 15–20 L of water apiece. We set the plants in the bus tubs and added water as needed to ensure adequate hydration during the two-week sampling period. Three to six pots of flowering individuals of each species (one plant per pot) were placed at each site; the number of plants of a given species was equal between members of a (supplemented/ambient) pair. We recorded the number of open inflorescences (total for all plant species) in each enclosure at the beginning of each 20-minute pollinator observation period.

Environmental data

At the start of each 20-minute observation period, we recorded temperature and wind speed (maximum mph during the observation) with a hand-held anemometer (TACKlife DA02). Missing data for temperature and wind speed (6 and 10 records, respectively, of 131 total) were replaced with interpolated values, except that a missing value for the first or last observation on a given day was replaced with the nearest measurement. As a proxy for cloud cover, we recorded the probability of precipitation for each sampling day, as reported by the National Weather Service for each observation date (percent chance that rain would occur in the Truth or Consequences Municipal Airport forecast area).

Observations of pollinator visitation

We observed visitation 130 times during the three month study (ambient n = 64; supplemented n = 66). We observed insect foraging activity at each site at least two times during each sampling period, avoiding periods when weather was not conducive for pollinator activity. Observation periods were 20 minutes long and were divided equally between mornings (0800–1300) and afternoons (1300–1800). Observation time averaged 162.5 minutes per site for all three sampling periods combined (range, 150–180 minutes).

We watched all open inflorescences at each array and recorded the total number of native bee and *A. mellifera* visits made to open inflorescences during each observation as well as which plant species was visited. A visit was recorded as such only if a bee was observed obtaining pollen or nectar from an inflorescence. Activities such as perching and mate scouting were not counted as visits. We also recorded other visitors (wasps, flies, beetles, butterflies), and included these as covariates in initial data analysis to test for any influence on bee visitation, but found no significant effects.

We did not collect and voucher bees from this experiment because i) bees are repeat visitors, and thus collection could influence both visitation patterns and fitness outcomes, and ii) visitation was low throughout the experiment (mean = 6.5 visits per 20-minute observation), allowing time for visual identification. Where possible, we identified bees to genus or species by sight as they visited. Visual identifications were based on CC's prior experience of >300 hours collecting 87 species of bees visiting sunflowers across the southwestern U.S. (manuscript in preparation), as well as CC's reference collection of bees from a 2016 pilot study in the same vicinity as the present study.

Native plant fitness

We intended to assess seed set and fitness in both of the self-incompatible phytometer species, *H. annuus* and *G. pulchella*. Due to difficulties with greenhouse propagation and plant mortality caused by herbivores in the field, we were unable to obtain an adequate sample size of *G. pulchella* for fitness analyses (average of 1.12 inflorescences open per site during sampling periods). While *G. pulchella* was thus excluded from fitness analyses, it was present in experimental arrays and may have influenced visitation to *H. annuus* similarly to *V. encelioides* and *B. multiradiata*.

To compare seed set of *H. annuus* at the inflorescence and whole-plant levels at supplemented vs. ambient sites, we focused on inflorescences that opened during each two-week sampling period. A total of 701 *H. annuus* inflorescences were harvested from the experiment, 302 from ambient and 399 from supplemented sites. Prior to placement in the field, open inflorescences on plants were marked with paper tags to allow them to be distinguished from those opening in the field. At the end of each sampling period, inflorescences that had opened in the field were covered with polypropylene micro-mesh bags to prevent cross-pollination until senescence and retain seeds. Plants were transported back to the greenhouse and allowed to senesce, at which point total inflorescence number (focal inflorescences + all others produced before and after placement in the field) was counted for each plant. Mature, viable seeds were then removed from the bagged receptacles and counted. A seed was assumed to be viable if the pericarp did not collapse when firm pressure was applied with a pair of forceps. Mean inflorescence-level seed set was calculated for the bagged inflorescences. Whole-plant seed set was calculated as the product of mean inflorescence-level seed set × total inflorescence number; with the assumption that inflorescences opening before and after field placement of each plant would have been pollinated at the same rate as the focal inflorescences.

Statistical Analysis

To assess supplementation-treatment effects on bee visitation we used count models, which are better at detecting effects in pollination data than a frequency/visitation rate approach [Reitan & Nielsen 2016]. Visitation data of both native bees and *A. mellifera* did not meet the assumptions of normality or homogeneity of variance required for linear models and included a large number of zeros. We therefore modeled visitation using generalized count models, under the assumption of a negative binomial distribution to handle excess zeros in the data. We then performed model selection using the information-theoretic approach proposed by Anderson (2008), under which multiple candidate models are ranked according to how well they describe the relationship between a set of predictors and a response variable. The highest-ranked model (lowest AIC) is considered the best representation of reality, as defined by the data.

Our 32 candidate models for bee visitation contained six predictor variables: total inflorescence count (number of open inflorescences in array; total for all four plant species), precipitation (% chance), site, temperature (at start of observation), time (at start of observation), and treatment (supplemented/ambient). We ranked models based on all possible combinations of our predictors for each of the two response variables (*A. mellifera* visitation; native bee visitation). Visitation in models reflects visits per 20-minute observation period. We ranked the models according to QAIC, a modification of AIC developed for over-dispersed count data [Anderson 2008].

To assess supplementation-treatment effects on *H. annuus* seed set, we used linear models. Seed set data were square-root transformed to satisfy the normal distribution requirement. We then performed model selection from 16 candidate models containing five predictor variables: *H. annuus* inflorescence count (per-plant number of *H. annuus* inflorescences that opened during the two-week sampling period), site, month, vegetation type (riparian/upland), and treatment (supplemented/ambient). We ranked models based on all possible combinations of predictors for each of the two response variables (inflorescence-level seed set; whole-plant seed set). Models were ranked according to AICc, a correction of AIC for small sample sizes [Anderson 2008].

To assess supplementation-treatment effects on native bee community composition, we conducted a non-metric multidimensional scaling analysis (nMDS) of a Bray-Curtis distance matrix, and used PermANOVA to assess the effects of treatment and site [Bray & Curtis 1957; Clarke & Warwick 2005].

Statistical analyses were performed in R, version 3.3.2 [R Core Team 2016] running in RStudio, version 1.0.44 [RStudio 2015]. Model selection was performed using the R package MuMIn [Barton 2015]. Non-metric multidimensional scaling and PermANOVA were performed with Primer 6 [Clarke & Warwick 2005]. Parameter estimates (β's) reported are coefficients from the best model (lowest AICc). Values graphed are means ± 1 standard error.

Results

Bee visitation

Considering supplemented and ambient treatments together, we observed 103 *A. mellifera* visits to phytometer inflorescences, which were divided approximately evenly between morning (51%) and afternoon (49%) sampling periods. We observed 770 visits from native bees to phytometer inflorescences, with the majority (61%) occurring during morning sampling periods. Visitation in *A. mellifera* ranged from 0–87 visits per hour and increased over time, peaking in October. Visitation in native bees ranged from 0–201 visits per hour and peaked in September. There was no difference in visitation frequency for either native bees or *A. mellifera* at upland vs. desert sites (all p>0.30).

Experimental introduction of *A. mellifera* hives (supplementation) increased the frequency of *A. mellifera* visits at treatment sites compared to controls (Figure 2). Only 1% of observation periods at ambient sites included *A. mellifera* visitation, compared to 15% of observation periods at supplemented sites. Native bees visited ambient and supplemented sites with nearly equal frequency, though the mean number of visits per hour was lower at supplemented (19 visits/hr.) than at ambient sites (16 visits/hr.; Figure 2). Native bees visited more consistently than *A. mellifera* at all sites: we recorded native bee visitation in 70% of observation periods.

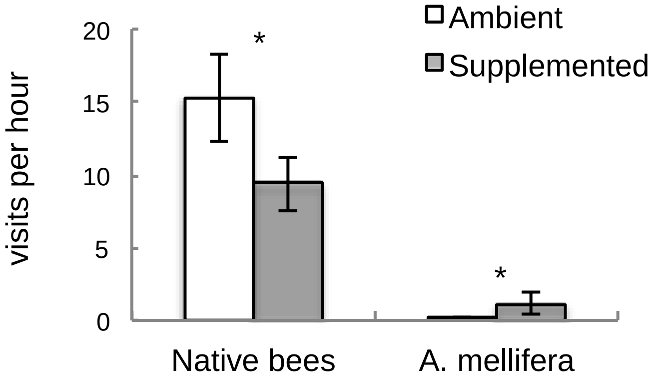

Figure 2. Effect of *Apis mellifera* supplementation on visitation in native bees and *Apis mellifera* to potted native plants in the field, after controlling for other factors. Asterisks indicate treatment (ambient vs. supplemented) was included in the best model in each case.

For *A. mellifera* visitation, model selection identified total inflorescence count, site, temperature, and treatment as predictors in the lowest-AICc model (Table 1), but this model was not statistically superior (i.e., ΔAICc < 2) to a second model that excluded temperature as a predictor. There was a positive effect of treatment (supplementation) on *A mellifera* visitation. Using coefficients from the best model, the expected number of *A. mellifera* visits at supplemented sites, with other variables held constant, is 9.81 times the number of visits per hour at ambient sites.

Table 1. Comparison of models explaining (a) *A. mellifera* visitation and (b) native bee visitation as a function of treatment and environmental conditions.

(a)

Model	df	logLik	AICc	ΔAICc	w_i
treat (+) + inflor (+) + site (-) + temp (-)	12	-59.61	143.22	0.00	0.39
treat (+) + inflor (+) + site (-)	11	-60.96	143.91	0.69	0.28
treat + site	10	-62.85	145.70	2.48	0.11

(b)

Model	df	logLik	AICc	ΔAICc	w_i
treat (-) + inflor (+) + precip (-) + temp (+) + time (-)	7	-325.02	586.54	0.00	0.42
treat + inflor + precip + temp + time + site	14	-318.50	589.11	2.56	0.12

Abbreviations: treat = treatment (*Apis* supplementation), inflor = inflorescences,
temp = temperature; (+) = positive coefficient, (-) = negative coefficient
w_i = Akaike model weight (probability that the given model produces the best representation of the data out of all candidate models).

For native bee visitation, model selection identified additional predictors: As with *A. mellifera*, the lowest-AICc model for native bee visitation included total inflorescence count, temperature, and treatment as predictors, but precipitation and time were also included while site was excluded (Table 2). All other candidate models had ΔAICc > 2. There was a negative effect of treatment (*A. mellifera* supplementation) on native bee visitation. Using coefficients from the best model, the expected number of native bee visits at supplemented sites, with other variables held constant, is 0.73 times the number of visits per hour at ambient sites.

Table 2. Comparison of models explaining (a) seeds per inflorescence and (b) whole-plant seed set (seeds per inflorescence × number of inflorescences) in potted *H. annuus* in the field.

(a)

Model	df	logLik	AICc	ΔAICc	w_i
treat (+) + mo (-) + veg (+)	6	-420.45	853.39	0.00	0.58
treat (+) + *H. annuus* inflor (+) + mo (+) + veg (+)	7	-420.45	855.55	2.16	0.20

(b)

Model	df	logLik	AICc	ΔAICc	w_i
treat + *H. annuus* inflor + mo + vegtype	7	-603.36	1221.37	0.00	0.59
treat + *H. annuus* inflor + mo	6	-605.26	1223.00	1.63	0.26
treat + mo + vegtype	6	-606.17	1224.82	3.45	0.11

Abbreviations: treat = treatment (*Apis* supplementation), *H. annuus* inflor = number of *H. annuus* inflorescences that opened during the sampling period, mo = month, veg = vegetation type (riparian)

w_i = Akaike model weight (probability that the given model produces the best representation of the data out of all candidate models).

Total inflorescence count had a positive effect on visitation in both bee groups, especially *A. mellifera*. There was no difference in total inflorescence count between treatments (p = 0.36). As temperature increased, *A. mellifera* visitation decreased but native bee visitation increased. Native bee visitation decreased as precipitation and time of day increased; these factors were not important predictors of *A. mellifera* visitation.

We recorded 11 native bee morphotypes (Table 3). Where possible, we identified visiting bees to genus; a large proportion (50%) of the native bees identified belonged to the genus *Melissodes*, with most others in genera *Lasioglossum*, *Diadasia* and *Halictus*; 1% were unidentified. NMDS analyses showed no significant effect of treatment (999 permutations; p=0.16), vegetation type, site, or interactions on native bee community composition (Figure 3).

Table 3. Counts of native bee genera/morphotypes visiting inflorescences at ambient vs. supplemented sampling sites, August–October 2017. (Note, counts ≠ visitors. Total number of bees visiting sites / visits per bee is unknown).

		count (visits to inflorescences)		
Genus	Species	Ambient	Supplemented	total
Agapostemon	*angelicus/melliventris*	7	8	15
Diadasia	spp.	25	75	100
Halictus	*ligatus/tripartitus*	26	43	69
Lasioglossum	spp.	80	38	118
Megachile	spp.	6	0	6
Melissodes	spp.	238	148	386
Svastra	spp.	29	39	68
Xylocopa	spp.	1	0	1
Unknown	sp. 1	4	0	4
Unknown	sp. 2	2	0	2
Unknown	sp. 3	0	1	1
		418	352	770

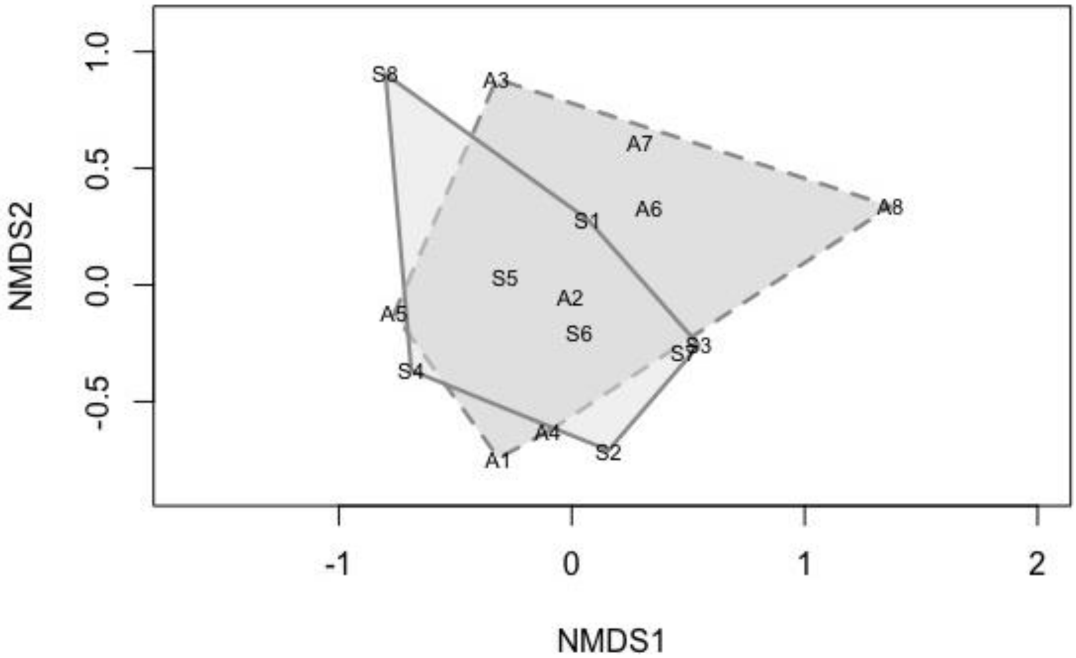

Figure 3. Ordination plot of native bee community data (k=2; stress=0.15). Polygons surround species (11 morphospecies; excludes *Apis mellifera*) observed at ambient (dashed lines) vs. supplemented (solid lines) sites. The large overlap indicates that native bee community structure at supplemented sites does not differ from ambient sites (p=0.16).

Helianthus annuus *Seed Set*

Inflorescence-level seed set

At the inflorescence level, model selection identified treatment, month, and vegetation type as predictors of seed set in the lowest-AICc model (Table 2). All other candidate models had ΔAICc > 2. The treatment effect was positive: Using coefficients from the best model, inflorescences from supplemented sites averaged 0.82 more seeds per inflorescence than those from ambient sites (95% CI=0.08–1.57). The effect of supplementation was small (Cohen’s D = 0.31). Plants from the August sampling period produced more seeds per inflorescence than September and October plants (Figure 4). There was also an effect of vegetation type, with more seeds per inflorescence produced from plants at riparian than at upland sites.

Whole-plant seed set

At the whole-plant level, model selection identified treatment, *H. annuus* inflorescence count, month, and vegetation type as predictors of seed set in the lowest-AICc model (Table 2). This model was statistically indistinguishable (ΔAICc < 2) from a second model that excluded vegetation type as a predictor. The treatment effect was positive: Plants from supplemented sites had higher whole-plant seed set than at ambient sites (mean increase, 2.65 seeds per plant, n = 92 plants; 95% CI=0.56–4.75). The effect of supplementation was moderate (Cohen’s D = 0.37). Plants from the August sampling period had higher whole-plant seed set, as did plants from riparian sites (Figure 4).

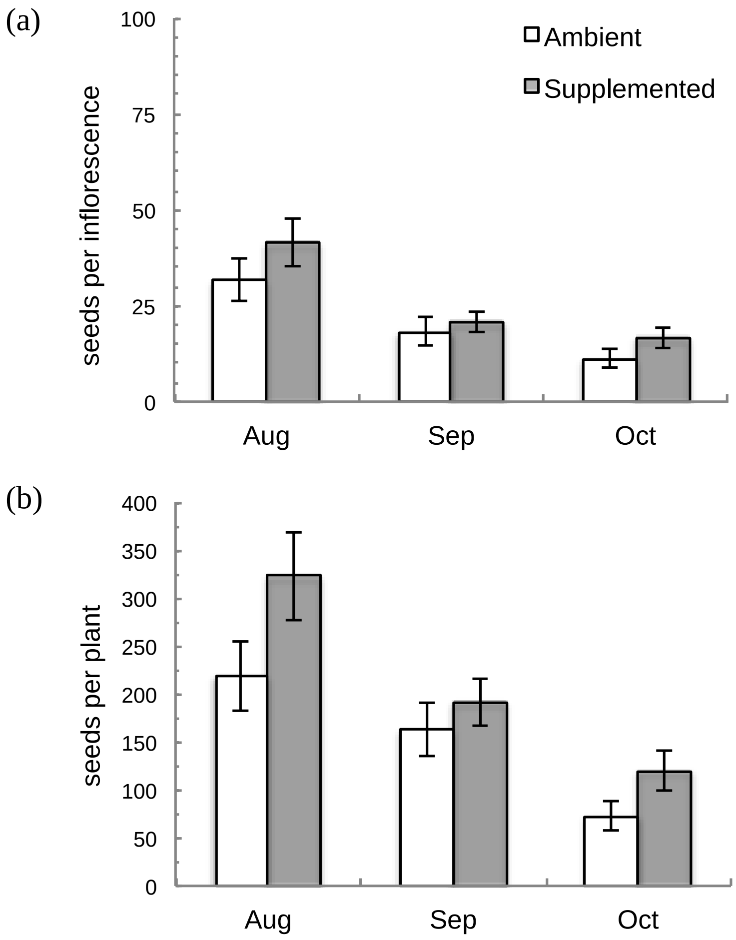

Figure 4. Effects per month of *Apis mellifera* supplementation and other covariates on (a) seeds per inflorescence and (b) whole-plant seed set (seeds per inflorescence × number of inflorescences) in potted *Helianthus annuus* in the field.

Discussion

Effects of A. mellifera *on native bee visitation*

We found lower native bee visitation at supplemented than at ambient sites. This is consistent with other research demonstrating negative effects of *A. mellifera* on native bee foraging activity [Goulson 2002; Gross 2001; Kato 1999; Osorio-Berestain 1997]. In some cases *A. mellifera* have been observed actively displacing native pollinators from foraging [Gross & Mackay 1998; Shavit et al. 2009]; we did not observe this in the present study but we note that even passive displacement (exploitation competition) has been shown to reduce resource availability for native bees [Wilms & Wiekers 1997]. Our results conform to a general pattern of negative outcomes of *A. mellifera* introductions for native bees, as indicated in a recent systematic review [Mallinger et al. 2017].

Given the dual outcome of increased seed set in *H. annuus* and increased *A. mellifera* visitation at supplemented sites, our data suggest that if exploitation competition occurred between *A. mellifera* and native bees in our study system, it was more likely for *H. annuus* nectar than *H. annuus* pollen. Other investigations have found evidence that nectar competition between *A. mellifera* and native bees can lead to reduced reproductive potential in native bees; for example, pollen storage in tropical *Melipona* species peaked only during periods of bloom in Apis-preferred plants, when interspecific competition for nectar was at its lowest [Wilms & Wiechers 1997]. Similarly, Thomson (2004) observed increases in foraging trips for nectar relative to pollen by native bumble bees (*Bombus occidentalis*) in response to *A. mellifera* introductions, suggesting reduced nectar availability with *A. mellifera* present. A significant negative correlation between reproductive success in *B. occidentalis* and a higher ratio of nectar foraging trips indicated a fitness cost of nectar scarcity [Thomson 2004].

Other studies have shown no effect of *A. mellifera* on native pollinator resource collection, including cases where the native pollinators in question were pollen-specialist bees potentially competing with *A. mellifera* for access to their host plants. In a review of the evidence, Butz-Huryn (1997) concluded that although changes in foraging behavior of some native pollinators were observed in response to *A. mellifera* introduction, detrimental impacts on native bee populations had not been conclusively demonstrated. In another survey of visitation in native bees and *A. mellifera* in Brazilian *cerrado* habitat, de Menezes Pedro & De Camargo (1991) found minimal resource overlap between *A. mellifera* and native bees, and no evidence of reduced native bee abundance during peaks in *A. mellifera* abundance. Roubik et al. (1983) also observed no change in native bee foraging activity resulting from *A. mellifera* introductions in forests of French Guiana, hypothesizing that the greater foraging range of *A. mellifera* relative to native bees obviated competition for resources (though a later study in lowland forest of Panama showed declines in resource harvest for native bees when *A. mellifera* also foraged [Roubik et al. 1986]). In our case, native bee visitation was reduced where *A. mellifera* hives were present, but was still higher than *A. mellifera* visitation at both site types. We also found no evidence that native bee community composition was affected by *A. mellifera* introductions; the same native bee species that appeared at ambient sites also visited supplemented sites.

We note that decreased visitation of native bees to their host plants following *A. mellifera* introduction does not demonstrate that native bees are negatively affected at the population scale. Reduced visitation or resource harvesting indicates a potential for negative impacts, but as others have observed, only reduced reproductive success of native bees resulting from *A. mellifera* introduction would be conclusive [Paini 2004]. The logistical difficulty of obtaining quantitative measures of fitness in native bees has resulted in scant and conflicting empirical evidence thus far [e.g., Paini 2004; Paini &

Roberts 2005; Thomson 2004]. However, given that resource overlap and suppressed visitation in native bees following *A. mellifera* introduction have been demonstrated in a number of study systems including our own, we maintain that the subject calls for further examination.

Effects of A. mellifera *on* H. annuus *fitness*

Introduction of *A. mellifera* colonies improved seed set in *H. annuus* at both the inflorescence and whole-plant level. This result supports a hypothesis proposed by others: Generalist bees and nectar visitors ("secondary" pollen foragers; *sensu* Westerkamp 1991) may be more effective pollinators of some plants than pollen specialists ("primary" foragers) because they become dusted with pollen while visiting yet may not deliberately collect it. In contrast, "primary" foragers visit flowers specifically for the purpose of taking pollen away, and specialists are more efficient at it than generalists [cf. Minckley et al. 1994]. This could result in more pollen being removed than deposited by a specialist visitor to its host plant. If *A. mellifera* is visiting sunflower plants primarily for nectar and acting as a "secondary" forager, it may ultimately be highly effective because pollen adhering to nectaring visitors (in the case of *Apis*, not packed into corbiculae) remains available for stigmatic deposition [Westerkamp 1991]. In addition, in our study *A. mellifera* reduced but did not eliminate native bee visitation to study plants; thus the potential remained for improvement of seed set via interactions between *A. mellifera* and native bees (e.g., by increasing the frequency of *A. mellifera* pollen transfer between sunflower plants and distributing pollen more evenly, as has been observed elsewhere [Greenleaf & Kremen 2006]).

Our result both contradicts our expectations and differs from impacts observed on some other native plant species. For example, native *Cistus* shrubs in Spain receiving high *A. mellifera* visitation were visited by fewer species of native pollinators and produced fewer seeds per fruit than shrubs with low *A. mellifera* visitation, while native pollinators were shifted toward less abundant resources [Magrach et al. 2017]. Seed set was also negatively correlated with *A. mellifera* visitation to flowers of Brazilian *Clusia arrudae* trees, despite no evidence of change in native pollinator visitation [Mendes do Carmo & Francesschinelli 2004]. In contrast, native bees visiting the Australian shrub *Melastoma affine* were frequently displaced from foraging by *A. mellifera*, which deposited less pollen on *Melastoma* stigmas compared to native bees, resulting in decreased seed set [Gross & Mackay 1998]. Notably, *A. mellifera* were observed collecting pollen from plants in these studies, not just nectar — in other words, acting as primary foragers. Also, unlike most native bees whether specialist or generalist, *A. mellifera* forages collectively and thus exerts colony-level impacts on preferred floral resources, in some cases removing >90% of available pollen from native plants before native bees arrive [Carneiro & Martins 2011; Mendes do Carmo & Francesschinelli 2004]).

Other study results are consistent with ours. In observational studies of native *Echium* populations, Dupont et al. (2004) observed similar seed set and viability in plants with and without *A. mellifera* visitation. Nectar was the primary resource harvested; heavy *A. mellifera* foraging depleted the standing crop to near-zero levels [Dupont 2004]. In other situations, increased seed set resulting from *A. mellifera* pollination has been associated with reproductive success in weedy plants. For example on islands in the northwest Pacific, *A. mellifera* strongly depends on introduced nectariferous plants especially during periods when native melittophilous plants are not in bloom; introduced plant densities are higher (and native bee abundances lower) on islands where *Apis* is present [Kato et al. 1999].

Numerous prior studies have been conducted of *A. mellifera*'s effectiveness as a sunflower pollinator [Chambó et al. 2011; du Toit 1990; Oz 2009], with at least one study showing results contradicting our own [Parker 1981]. Agricultural trials can be highly artificial, and *Apis* effectiveness is often evaluated in comparison to pollination by insects that, like *A. mellifera*, did not coevolve with sunflower (e.g., *Astylus atromaculatus*; du Toit 1990). The aim of our study was to assess the effects of *A. mellifera* on fitness in non-commercial sunflower plants grown from wild-collected seed, in a context where both the plants and other insect visitors are native to the surrounding ecosystem. Despite these contextual and procedural differences, our results are consistent with the majority of other sunflower pollination studies: Seed set and whole-plant fitness were higher where *A. mellifera* was present (but see Parker 1981). In a separate study, we evaluated the effectiveness of various types of pollinators and found polylectic generalists such as *A. mellifera* are significantly more effective at pollinating *H. annuus* than specialists [Cumberland et al. in prep]. We caution, however, that *H. annuus* may be highly unrepresentative of other native plant species with regard *A. mellifera* pollination effectiveness. As a late-summer-blooming annual, *H. annuus* is characteristic of other native plants in our study system. However, our results cannot be assumed to portray the typical impacts of *A. mellifera* introduction.

Finally, there was an unexpected effect of vegetation type on seed set, likely owing to environmental factors. Riparian vegetation was a predictor for increased seed set. We noted that plants more often appeared heat- and/or wind-stressed at upland sites than at riparian sites, and we recorded more plant mortalities at upland sites. We also observed a great number of *A. mellifera* visiting plant containers at some upland sites for water; we did not observe this at riparian sites. This suggests harsher conditions at upland sites may have reduced sunflower pollination success. Wind speed and temperature did not differ significantly between upland and riparian sites (p=0.18 and 0.12, respectively), but higher vegetation density at riparian sites was likely associated with increased site-level relative humidity. Low relative humidity has been demonstrated to shorten the duration of stigma receptivity, reduce pollen germination, and inhibit pollen tube growth in sunflowers [Degrandi-Hoffman & Chambers. 2006]. Since neither native bee nor *A. mellifera* visitation differed between riparian and upland sites (all p>0.30), we attribute the effect of vegetation type on seed set to relative humidity or other abiotic factors.

Introduced *A. mellifera* has been found to be the most effective pollinator of some native plants, e.g., Brazilian *Jatropha* and Californian *Triteleia* species [Chamberlain and Schlising 2008; Neves and Viana 2011), as well as introduced weeds [Goulson 2010; Jarvis et al. 2006]. It has particularly been implicated in the spread of introduced plants from its native host range, with which it potentially coevolved (e.g., yellow starthistle, *Centaurea solstitialis*) [Barthell et al. 2001]. In the systematic review of effects of *A. mellifera* mentioned earlier, Mallinger et al. found equal proportions of positive and negative outcomes (36% each) of impacts of *A. mellifera* on native plants [Mallinger 2017]. Our results for *H. annuus* add to the "positive" total, but we caution that there could be indirect negative effects. For example, if *Apis* enhances reproduction in some native plants, those species could expand in range and/or abundance at the expense of other species. The potential also exists for *Apis* pollination to lead to long-term changes in genetic structure in native plants, as observed in a Chilean population of native *Erythranthe* (Andean monkeyflower), which shows signs of adaptation to its most effective pollinator, the introduced bumble bee *Bombus terrestris* [Medel et al. 2018].

Conclusion

The ecosystem-scale effects of *A. mellifera* introduction have been little investigated. Our evidence suggests *A. mellifera* can increase plant seed set despite reducing native bee visitation. This could occur in either wildland or agricultural settings, but effects on wild plants may have broader consequences, since they generally coexist with a greater diversity of plant and animal taxa than agricultural crops, and their reproduction and distribution is not human-controlled. Due to its rapid growth rate and phenotypic plasticity, *H. annuus* is usually characterized as a "weedy native" [Whitney et al. 2006]. Thus the positive effect of *A. mellifera* that we observed on *H. annuus* can be viewed simply as a mutually beneficial relationship between two disturbance-tolerant generalists. If *A. mellifera* promotes reproductive success in other weedy plants (whether native or introduced), this could ultimately reduce overall plant diversity and evenness [cf. Beard 2015].

Current evidence of the effects of *A. mellifera* introduction is inconclusive, but the species' sociality, ubiquity, and safeguarded status as a domesticated pollinator increase its potential to influence on native bee and plant populations, which justifies continued investigation. Care should be taken to assess floral resources prior to issuing apicultural leases in wildland areas, especially where rare or endemic plants are present. Native bees and *A. mellifera* can partition resources and coexist where resources are abundant, but differential reproductive success of *A. mellifera*-pollinated wild plants could have ecosystem-level repercussions.

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CHAPTER 3

Are specialist and native pollinators more effective than generalists and non-natives?

A meta-analysis

Abstract

Recent reports of pollinator declines raise the question of how changes in pollinator species composition may affect reproduction in wild and agricultural plants, resulting from between-pollinator differences in the quality of pollination service provided. Dietary-specialist pollinators have stronger fidelity to their host plants than generalists, and may be more likely to arrive at flowers bearing conspecific pollen and be effective contributors to plant reproduction. Similarly, native pollinators' shared evolutionary history with native plants increases the likelihood of adaptations to their hosts and could increase their pollination effectiveness. Neither of these ideas has previously been tested in a meta-analysis framework. We conducted a quantitative review of pollination effectiveness in specialist versus generalist and native versus non-native pollinators, including a separate evaluation of effectiveness in native pollinators versus non-native honey bees (*Apis mellifera*), comparing phylogenetic and non-phylogenetic meta-analytic models. Our analysis of 157 effect sizes (20 studies) of specialist versus generalist effectiveness indicated no support for greater specialist effectiveness. Our analysis of 97 effect sizes (42 studies) of native versus non-native effectiveness suggests generalizations cannot be made on native effectiveness as a whole, but indicates higher effectiveness of native bumble bees (*Bombus* spp.) compared to non-native pollinators. Our analysis of 79 effect sizes (36 studies) comparing *A. mellifera* to native pollinators showed lower *A. mellifera* effectiveness, again driven by high effectiveness by native *Bombus* spp. Our results indicate that anthropogenic changes in pollinator species composition, particularly replacement of native pollinators by introduced *Apis mellifera*, has measurable effects on plant reproduction that may cascade to changes in plant community composition.

Introduction

Reports of pollinator declines have received increasing attention in both the scientific and popular media [Schwartz 2016; Powney et al. 2019] and have catalyzed a host of public awareness campaigns and pollinator conservation initiatives [EU Environment Commission 2018; NCSL 2018; USDA 2015]. Since declines are not equally distributed across pollinator taxa [Biesmeijer et al. 2006], an important subject to address is whether all pollinators are equally important contributors to pollination services. The question is usually raised in a context of human food security, since about 75% of agricultural plant species are animal-pollinated [Ollerton et al. 2011], and insect pollen-deposition has been demonstrated to improve quality and production even in some wind-pollinated crops [Brauman & Daily 2008]. But crop plants represent <2% of global flowering plant diversity [Khoshbakht & Hammer 2008], and thus only a fraction of potential plant-pollinator interactions at the global scale. In contrast, 87% of wild flowering plants are insect pollinated [Ollerton et al. 2011]. An evaluation of the relative importance of different types or taxa of pollinators for wild plant reproduction would be useful in making targeted conservation recommendations, and would provide insight into the possible ecosystem-scale consequences of declines in highly effective pollinators, the implications of which have scarcely been explored [Buchmann & Nabhan 1996].

The ability of a pollinator to contribute to reproductive success in a plant is referred to as its pollination effectiveness. Proxies for pollination effectiveness range from the amount of pollen transferred by a pollinator to seed set following a pollinator visit [Ne’eman et al. 2010;see discussion in Methods, below]. Research interest in comparative pollinator effectiveness arose out of studies of floral evolution, following on the early observations of Darwin (1862) that pollinators and their host plants appear to exert mutual selective pressure on each other, in some cases leading to tightly coevolved relationships. The theory of trait selection in plants by pollinators is summed up in the “most effective pollinator principle,” defined by Stebbins (1970): “The characteristics of a flower will be molded by those pollinators that visit it most frequently and effectively in the region where it is evolving.” In turn, pollinators that contribute the most to plant fitness are expected to favor the evolution of floral traits that attract and maintain the effectiveness of those pollinators, in a process of mutually adaptive specialization.

Pollinators are usually classified as specialized or generalized according to their diet breadth: Specialists collect pollen from only a limited number of plant species or genera; generalists collect from a variety of plant genera or families [Michener 2000]. For ease of comparison, diet breadth is treated as dichotomous, though the reality is often a dynamic continuum [Cane & Sipes 2006; Fishbein & Venable 1996]. Behavioral adaptations of dietary specialists include floral fidelity (visiting only flowers of particular species) and higher-than-average foraging efficiency (more pollen collected per visit) [Minckley & Roulston 2006]. Some specialist bees will remain in diapause until conditions are optimal for flowering of their host plants, increasing the likelihood of both pollinator persistence and successful host plant pollination [Minckley et al. 2013]. Since their fidelity makes them likely to arrive at a flower bearing conspecific pollen, dietary specialists are hypothesized to be highly effective pollinators of their host plants, but the empirical evidence is mixed. Some studies have shown greater specialist than generalist pollination effectiveness for particular plant species (e.g. Larsson 2005; Rymer et al. 2005), but others have found no difference (Tepedino 1981; Motten et al. 1981) or even the opposite (Maldonado et al. 2013; Moeller & Geber 2005).

In contrast, the non-specific foraging behavior of generalist pollinators could make them less effective pollinators than specialists for any particular plant species. For example, the negative correlation between generalist floral visitation and seed set in urban *Centaurea solstitialis* plants suggests that generalists provide poorer-quality pollination services than a mixed community of specialist and generalists, presumably due to higher rates of heterospecific pollen deposition [Leong et al. 2014]. There is evidence that generalist adaptability makes them better able to persist in disturbed environments, and that specialist pollinators are declining more rapidly than generalists [Biesmeijer et al. 2006]. A shift from mixed communities to one consisting mostly of generalists (which tend to dominate in human-altered environments) could lead to alterations in plant communities and reduced overall plant and pollinator biodiversity.

A corollary to the question of whether specialist pollinators are more effective than generalists is whether native pollinator species are superior at pollinating native plants. Since native pollinators share a longer coevolutionary history with their host plants than introduced, non-native pollinators, following Stebbins' hypothesis they might perform more effectively. This question has special relevance in settings where introduced pollinators have become common, e.g. *Apis mellifera* in Australia, North America, and South America [Beard 2015; Goulson 2003; Roubik 1983] and *Megachile sculpturalis* in

North America [Roulston & Malfi 2012]. Non-native pollinators may also decrease reproductive success in native plants through competitive displacement of more effective native pollinators [see Madjidian et al. 2008]. For example, *Apis mellifera* has been introduced nearly worldwide but has not been found to be a significant pollinator of wild plant populations in most regions [Ollerton et al. 2011], which suggests their presence could influence native plant community composition by favoring reproduction in either non-native plant species (e.g. Barthell et al. 2001, Kato et al. 1999) or in native plant species for which they happen to be effective pollinators, or both [see Sun et al. 2013]. Decreases in native plant diversity could follow. As well as these community-level consequences, non-native pollinators could also influence the evolutionary trajectories of plant species for which they are highly effective [Medel et al. 2018].

Meta-analysis is a quantitative review of research aimed at clarifying whether a predictor has an effect on an outcome of interest, and if so, the magnitude of the effect and the factors influencing the effect. In ecological meta-analyses, it is also important to account for non-independence of effect sizes introduced by phylogenetic relationships among the study taxa [Chamberlain et al. 2012]. We used phylogenetic meta-analyses to quantify pollinator effectiveness across multiple pollinator taxa (bees, wasps, butterflies/moths, flies, beetles, bats, birds). We asked: i) Does dietary specialization predict pollinator effectiveness? i.e., are specialist pollinators more effective than generalists?, and ii) Does pollinator origin predict effectiveness?, i.e., are native species more effective pollinators of native plants than non-native species? In addition we assessed whether effectiveness is associated with factors such as pollinator taxonomic group (e.g. bee, fly, wasp, butterfly) and flower shape. Finally, since the honey bee *Apis mellifera* is among the world's most important crop pollinators and at the same time among the most widely introduced non-native insect species, we separately analyzed whether pollinator origin predicts effectiveness on native plants in the specific case where the non-native pollinator in question is *A. mellifera*.

Materials and methods

Literature search

We followed the PRISMA protocol [Moher et al. 2009] to locate and curate studies from the Web of Science and ScienceDirect databases for each of our analyses. We conducted our initial search in 2014 (January–July) and updated it in January 2019. For studies that addressed the influence of pollinator diet breadth on effectiveness we searched these terms in the topic field: "pollinat* effective* generalist OR specialist", "pollinat* effective* polyle* OR oligole*", "pollinat* efficiency generalist OR specialist", "pollinat* efficiency polyle* OR oligole*", "single visit pollinat*", "pollinat* efficiency]". We located 1,073 articles in this initial search, reviewed the abstracts and downloaded 268 articles for closer examination. We also evaluated a dataset of pollination in 417 plant species, obtained from 216 studies compiled for a meta-analysis of pollination syndromes [Rosas-Guerrero et al. 2014]. We screened the articles from both sources using the criteria described below. This resulted in 20 studies retained in our pollinator dietary-specialization analysis.

For our analysis addressing the influence of native versus non-native origin on pollinator effectiveness, we started with the same set of 20 studies from our dietary specialization analysis, excluding 11 in which all of the pollinators in the study were native (we did not obtain any studies where all were non-native). We then augmented this dataset by conducting a new database search using similar terms as in our diet breadth analysis, but substituting the search terms "native"/"non-native" in place of "polyle*"/"oligole*" and "generalist"/"specialist". We located an additional 89 studies for closer examination, which we screened using the criteria for inclusion described below. This resulted in 42 studies total for our native versus non-native analysis.

Many studies involved the globally introduced *Apis mellifera*, therefore we also analyzed *A. mellifera* effectiveness separately. We conducted this analysis on a subset of the origin study set, consisting only of studies where native pollinators were compared to *A. mellifera* (36 studies). This subset comprised the majority (78/97) of comparisons ("pairs") from our native versus non-native dataset.

Criteria for inclusion

Pollinator effectiveness has been evaluated using various methods, some of which are more precise than others at characterizing the actual contribution made by a pollinator to plant reproduction. The strengths and weaknesses of different measures of effectiveness have been investigated and debated among pollination researchers [e.g., King et al. 2013; Ne'eman et al. 2010; Olsen 1997; Padyšáková et al. 2013]. We only included studies that reported at least one of the following measures, ranked in order of decreasing precision:

1) seed set following a visit, 2) fruit set following a visit, 3) pollination (% of flowers forming pollen tubes or % of styles retracting following a visit), 4) single-visit deposition (amount of pollen deposited on a stigma in one pollinator visit), 5) pollen load (mean number of pollen grains carried or removed). If two or more effectiveness measures were reported in a study, we analyzed the highest-ranking measure reported.

Studies were included only if they reported sample size, mean and standard deviation (or a measure of variance from which we could calculate standard deviation) and also included replication (multiple measurements on each pollinator species). We rejected studies with only one pollinator species observed, studies that did not provide pollination effectiveness measures at the level of individual pollinator species (e.g., “nocturnal” vs. “diurnal” pollinators, hymenoptera vs. lepidoptera, *A. mellifera* vs. “other visitors”, “control” vs. “open” pollination), studies where reproductive outcomes were not provided for all pollinators, and studies where all pollinators were either generalist or native. We obtained the parameters from each study from the text or figures; if exact values were not reported, we extracted values from graphs using ImageJ/Fiji 2.0.0 [Schindelin et al. 2012].

We designated each pollinator to a taxonomic category. Since a majority of our studies evaluated pollination performance in honey bees (*Apis mellifera*) and bumble bees (*Bombus* species), these each received their own category. Other categories were beetles, flies, wasps, bats, birds, ants, and “other” bees (non-*Apis*, non-*Bombus*). We also determined a focal category for each analysis: specialists in the dietary specialization analysis and native species in the origin analysis. We designated *Apis mellifera* as non-focal in our native versus *Apis mellifera* analysis, because our pollinator phylogeny corresponded to species in the native (focal) group (see below). We defined a pollinator as native if it came from the same geographical area as the plant species in the study (Eurasia, North America, Australia, etc.). For crop plants, we defined the pollinator as native if it came from the same geographical area as the ancestral plant. There were three cases where the "native" pollinator was not native to the region where the test was conducted: *A. mellifera* pollinating Old World apples (*Malus domestica*) and almonds (*Prunus dulcis*); European *Hoplitis anthocopoides* pollinating European *Echium vulgare*; all tested in the United States.

Statistical Analysis

We paired each focal pollinator species in a study to each non-focal species to calculate effect sizes. For example, if a study reported seed set from one (focal) specialist and two (non-focal) generalist pollinators, we calculated two separate effect sizes: mean seed set for the specialist compared to mean seed set for each generalist. We accounted for this hierarchical data structure by including "study" as a random variable in our analyses, nesting "pair" within it. Effect sizes were calculated for all possible pairwise comparisons within a study except in two cases where data was not provided: Artz 2010 compared three native species to non-native 1 and one native to non-native 2; Aizen 2001 compared one specialist species to generalists 1–4, a second specialist to generalist 5, and a third specialist to generalists 5–6.

For all analyses, we followed the model selection methodology outlined in Nakagawa & Santos (2012), which uses maximum likelihood tests and Akaike Information Criteria scores to compare the quality of statistical models for a given data set. We constructed our models starting with only the random effects of study and pair (nested within study). We then added additional random effects individually to the base model, testing for improvement of model fit using likelihood ratio tests. We used the best-fitting random effects model to evaluate moderators (see below for description).

We checked our data for outliers using the base R 'influence' function, and assessed heterogeneity and phylogenetic signal in our models by calculating I^2, which estimates the amount of variance due to heterogeneity (i.e., variance in the true effect) relative to the total variance [Higgins & Thompson 2002]. We used an equation for computing I^2 that can be applied to mixed models to evaluate how much variance is unaccounted for by study-level moderators [Nakagawa & Santos 2012]. An I^2 of 0% indicates that all variability in effect size estimates is due to sampling variance within studies and none is due to variation between studies.

Traditional and phylogenetic meta-analyses

To compare pollination effectiveness between the focal and nonfocal category in each analysis, we calculated the standardized mean difference (Hedges' d) between members of each pair i within a given study [Hedges 1981]:

$$d_i = \frac{\overline{\mathrm{X}}_F - \overline{\mathrm{X}}_N}{s_p} J_i$$

where d_i is the estimate of the true effect size of focal species F compared to nonfocal species N, $\overline{\mathrm{X}}_F$ is the mean effectiveness (e.g., seed set) for the focal species within a study, $\overline{\mathrm{X}}_N$ is the mean effectiveness for a given nonfocal species within the same study, and s_p is the pooled standard deviation for the pair. The formula for the pooled standard deviation is

$$s_p = \sqrt{\frac{(n_F-1)s_F^2+(n_N-1)s_N^2}{(n_F-1)+(n_N-1)}}$$

with s_F and n_F denoting the standard deviation and number of observations for the focal species of the *i*th pairing, and s_N and n_N denoting the standard deviation and number of observations for the nonfocal species. The correction J for small sample size bias in the *i*th pairing is

$$J_i = \left(1 - \frac{3}{4(n_F + n_N - 2) - 1}\right)$$

Positive Hedges' d values indicate greater effectiveness of the focal group (specialists in the dietary specialization analysis, natives in the origin and *Apis* analyses). We obtained an overall Hedges' d (mean of d_i's) for the focal category in each analysis. The overall effect is considered significant if the 95% confidence interval of the effect size does not include zero.

The meta-analytic method accounts for methodological differences between studies. Differences in measures taken, sampling procedures or other characteristics will cause between-study variation (heterogeneity) among the true effect sizes, treated as random in our models. We conducted two meta-analyses for each of our questions based on how we modeled heterogeneity. Our “traditional” model for each meta-analysis was the best-fitting random effects model; this was our base model. For “phylogenetic” meta-analytic models we added the random effect of plant phylogenetic relatedness to the base model (see below for phylogeny construction). We also tried models including plant species as an additional random effect (separate from phylogenetic effect; some plant species appeared in more than one study) as recommended by Nakagawa and Santos (2012). Since we did not obtain a significant improvement to model fit from the addition of plant species in any of our models we do not discuss it further. Similarly, we tested phylogenetic relatedness of the focal pollinators (see below) in each analysis. Each additional random effect was tested singly using a log-likelihood ratio test, with retention of only those significantly improving model fit.

Moderators

In the meta-analytic context, study-level predictor variables are referred to as moderators. After finding the best-fitting random effects model, we tested the effect of adding moderators. Testing additional moderators was planned *a priori*, as we expected that effect size could vary in association with: focal pollinator type (bee, bumble bee, wasp, ant, moth, fly, beetle, bat, bird); plant family; flower shape (actinomorphic, zygomorphic, or mixed [family Asteraceae, where an inflorescence is composed of both actinomorphic and zygomorphic flowers that together function as a single “flower”]), and pollination effectiveness measure (as described in ‘Criteria for inclusion’). We retained moderators unless they increased model AIC >2 units relative to the base model. We assessed the effect size at each level of the moderator using meta-regressions and by conducting Q_m-

tests. The null assumption is of no difference in mean effect size between levels of a moderator; we report only results showing significant differences for at least one level ($p<0.05$).

Plant phylogeny

We pruned the 31,383-species Qian and Jin (2016) plant phylogeny (a revised and corrected version of the Zanne et al. 2014 phylogeny) to include focal plant taxa. Of our total 42 focal plant taxa, one genus (*Melocactus*) was not present in the Qian and Jin phylogeny, so we temporarily replaced it with the contribal genus *Cereus*. We attempted to match our 42 species with those in the Qian and Jin (2016) phylogeny, either using their original names or names standardized to The Plant List v. 1.1 (http://www.theplantlist.org/) using the function TPL in the R package Taxonstand [Cayuela et al. 2012]. We then merged the remaining unmatched taxa with the phylogeny using the function congeneric.merge in package pez [Pearse & Purvis 2013], which replaces the target genus topology with a polytomy containing the original species as well as any new addition(s). We then pruned the phylogeny of all taxa not on our original 42-species list, and finally extracted smaller phylogenies from it to match species lists for each of our analyses (Table 1).

Table 1. Number of pollinator species and effect sizes in meta-analyses of pollination effectiveness, organized by plant species.
ES = total number of effect sizes calculated for a plant species in each meta-analysis.

		SvG[1]			NvNN[2]			NvA[3]
Plant family	Plant species	spec	gen	ES	nat	non	ES	nat
Alstroemeriaceae	*Alstroemeria aurea*				4	2	4	3
Anacardiaceae	*Anacardium occidentale*				1	1	1	1
Apocynaceae	*Asclepias incarnata*				4	1	4	4
	Asclepias sp.				6	1	6	6
	Asclepias tuberosa				1	3	3	3
Arecaceae	*Neodypsis decaryi*				1	1	1	1
Asteraceae	*Echinacea angustifolia*				1	4	4	4
	Helianthus annuus	6	3	18	2	1	2	2
	Heterotheca subaxillaris	1	8	8				
Balsaminaceae	*Impatiens capensis*				2	1	2	2
Bignoniaceae	*Campsis radicans*				4	1	4	4
	Chilopsis linearis				3	1	3	3
Boraginaceae	*Echium vulgare*	1	4	4	1	3	3	
Bromeliaceae	*Pitcairnia angustifolia*				3	1	3	3
Cactaceae	*Melocactus intortus*				1	2	2	1
	Opuntia brunneogemmia	3	6	18				
	Opuntia viridirubra	3	4	12				
	Pachycereus pecten-aboriginum				1	1	1	1
Cucurbitaceae	*Cucurbita moschata*	2	1	2	2	1	2	2
	Cucurbita pepo	1	3	3	2	1	2	2
Dipsacaceae	*Knautia arvensis*	1		5				
Ericaceae	*Vaccinium angustifolium*				3	2	6	3
	Vaccinium ashei	2	1	2	2	1	2	2
	Vaccinium corymbosum	1	5	5	1	1	1	1
	Vaccinium macrocarpon				2	2	4	2
Euphorbiaceae	*Jatropha curcas*				1	1	1	1
Fabaceae	*Cajanus cajan*	1	6	6				
	Hedysarum scoparium				6	1	6	6
	Prosopis velutina	2	3	6	2	1	2	2
Lamiaceae	*Satureja thymbra*				4	1	4	
Loganiaceae	*Gelsemium sempervirens*				4	1	4	4
Malvaceae	*Sidalcea oregana*	1	4	4				
Melastomataceae	*Melastoma affine*				4	1	4	4
Myrtaceae	*Metrosideros polymorpha*				1	1	1	1
Onagraceae	*Clarkia xantiana*	8	5	40				
	Oenothera cespitosa	3	6	7				
Orobanchaceae	*Pedicularis densispica*				2	1	2	2
Papaveraceae	*Corydalis ambigua*				2	1	2	
Ranunculaceae	*Aconitum septentrionale*	3	1	3				

Table 1, continued.

Rosaceae	*Malus domestica*				1	2	2	
	Prunus dulcis				1	1	1	1
	Prunus persica				1	1	1	1
Saxifragaceae	*Lithophragma parviflorum*	1	6	6				
Scrophulariaceae	*Agalinis strictifolia*				1	1	1	1
	Penstemon penlandii	2	4	8				
Solanaceae	*Capsicum chinense*				2	1	2	2
	Goetzea elegans				1	1	1	1
	Solanum lycopersicon				2	1	2	2
Zygophyllaceae	*Kallstroemia grandiflora*				1	1	1	
				157			97	78

[1] SvG = specialist versus generalist effectiveness (n=20 studies). spec = number of specialist pollinator species; gen = number of generalists.

[2] NvNN = native versus non-native effectiveness (n=42 studies). nat = number of native pollinator species; non = number of non-native.

[3] NvA = native versus non-native *Apis mellifera* (n=36 studies). nat = number of native pollinator species; all non-native = 1 (*Apis mellifera*).

[†] Four native: three compared to non-native 1, one compared to non-native 2.

[††] Three specialists: one compared to generalists 1–4, one compared to compared to generalist 5, one compared to compared to generalists 5 & 6.

Focal pollinator phylogeny

Across our datasets, we identified 104 focal pollinator species. We started with a genus-level phylogeny of bees, obtained from Hedtke et al. 2013; this was the second of the 10 trees given in their Electronic Supplementary Material, Additional File 3 (chosen because it contained the largest number of genera). Of the total 34 bee genera in our dataset, 32 were present in the Hedtke et al. phylogeny. Two missing genera (*Chalepogenus*, tribe Tapinotaspidini; and *Chalicodoma*, tribe Megachilini) were added to the tree based on their tribal affiliations (the first in place of genus *Tapinotaspoides*, the second as sister to genus *Megachile*). The tree was then pruned to these 34 genera. We added bee species to the tree by hand, as polytomies within each genus. The remaining non-bee focal pollinator species (birds, lepidoptera, flies, wasps, one beetle, and one bat) were also added to the tree by hand, following phylogenetic relationships represented in the Tree of Life Project (http://tolweb.org/tree/, accessed March 23, 2019). Resolution within these groups was added based on family affiliations, plus McGuire et al. 2014 (for hummingbirds) and Wiegmann et al. 2011 (for flies). We then pruned the phylogeny of all taxa not on our original 104-species list, and finally extracted smaller phylogenies from it to match species lists for each of our analyses (Table 2).

Diagnostics

We checked for publication bias (underrepresentation of studies with non-significant outcomes) in our analyses using Egger's regression test ($p<0.10$ indicates significant asymmetry in the dataset), analyses of model residuals, and funnel plots (Figure 7). We did not apply formal tests of publication bias (e.g., the "trim and fill" method) due to high heterogeneity in the dataset, which presents a challenge for such approaches [Peters et al. 2007].

All phylogenetic tree editing was performed in Mesquite 3.51 [Maddison & Maddison 2018]. Statistical analyses were performed in RStudio 1.0.44 using the package 'metafor' 2.0-0 [Viechtbauer 2010].

Table 2. Number of effect sizes in meta-analyses of pollination effectiveness, organized by focal pollinator species.

			SvG[1]	NvNN[2]	NvA[3]
Family	Species	type	gen	non	nat
Andrenidae	*Andrena anograe*	bee	2		
	Andrena hattorfiana	bee	5		
	Andrena helianthi	bee	3	1	1
	Andrena lewisorum	bee	5		
	Andrena sp.	bee		2	1
	Perdita sp.	bee	3	1	1
	Pseudopanurgus rugosus	bee	3		
Apidae	*Amegilla anomala*	bee		1	1
	Amegilla sp.	bee		1	1
	Anthophora sp.	bee		1	1
	Apis mellifera	honey bee		4	
	Bombus affinis	bumble bee		2	1
	Bombus ardens	bumble bee		1	
	Bombus atrocinctus	bumble bee		2	2
	Bombus bimaculatus	bumble bee		1	1
	Bombus consobrinus	bumble bee	3		
	Bombus dahlbomii	bumble bee		2	1
	Bombus hypocrita	bumble bee		1	
	Bombus impatiens	bumble bee		1	1
	Bombus patagiatus	bumble bee		1	1
	Bombus pensylvanicus	bumble bee		1	1
	Bombus sonorus	bumble bee		2	2
	Bombus sp.	bumble bee		5	4
	Bombus ternarius	bumble bee		1	1
	Bombus vosnesenskii	bumble bee	5		
	Centris tarsata	bee		1	1
	Ceratina sequoiae	bee	5		
	Chalepogenus caeruleus	bee		1	1
	Diadasia angusticeps	bee	5		
	Diadasia nigrifrons	bee	4		
	Eucera helvola	bee		1	
	Eucera venusta	bee	5		
	Exomalopsis sp.	bee		2	2
	Frieseomelitta nigra	bee		1	1
	Habropoda laboriosa	bee	6	3	3
	Melissodes agilis	bee	3	1	1
	Peponapis limitaris	bee	1	1	1
	Peponapis pruinosa	bee	3	2	2
	Peponapis sp.	bee	1	1	1
	Ptilothrix fructifera	bee	10		
	Svastra obliqua	bee	3		
	Trigona nigra	bee		1	1

Table 2, continued.

	Xylocopa bombylans	bee		1	1
	Xylocopa californica	bee		1	1
	Xylocopa cf.gressitti	bee		1	1
	Xylocopa nasalis	bee		1	1
	Xylocopa virginica	bee		3	3
Bombyliidae	*Systoechus vulgaris*	fly		1	1
Coerebidae	*Coereba flaveola*	bird		2	2
Colettidae	*Hylaeus sp.*	bee		1	1
Colletidae	*Cephalocolletes rugata*	bee	10		
	Colletes mandibularis	bee	8		
	Colletes sp.	bee	3	1	1
Crabronidae	*Tachytes crassus*	wasp		1	1
Halictidae	*Augochloropsis sp.*	bee		2	2
	Halictus sp.	bee		5	4
	Lasioglossum lusorium	bee	5		
	Lasioglossum pullilabre	bee	5		
	Lasioglossum sp.	bee		1	1
	Nomia sp.	bee		1	1
Hesperiidae	*Epargyreus clarus*	butterfly		1	1
Megachilidae	*Chalicodoma sp.*	bee		1	
	Hoplitis anthocopoides	bee	4	3	
	Lithurgus rufiventris	bee	10		
	Megachile addenda	bee		2	1
	Megachile fortis	bee	3		
	Megachile gravita.pascoensis	bee	5		
	Megachile lanata	bee	6		
	Megachile parallela	bee	3		
	Megachile pugnata	bee		1	1
	Megachile sp.	bee		2	2
	Megachile spissula	bee		1	1
	Osmia brevis	bee	4		
	Osmia lignaria	bee		1	1
	Osmia ribifloris	bee	1	1	1
	Osmia sp.	bee		1	
Mellitidae	*Hesperapis regularis*	bee	5		
Meloidae	*Epicauta ferruginea*	beetle		1	1
Nemestrinidae	*Trichophthalma sp.*	fly		1	1
Phyllostomidae	*Chiroptera sp.*	bat		1	1
Prodoxidae	*Greya politella*	moth	6		
Sphecidae	*Sphex ichneumoneus*	wasp		1	1
	Sphex pennsylvanicus	wasp		1	1
Syrpidae	*Syrphus vitripennis*	fly		1	1
Thynnidae	*Myzinum carolinianum*	wasp		1	1
	Myzinum sp.	wasp		2	2

Table 2, continued.

Trochilidae	*Anthracothorax dominicus*	bird		2	1
	Anthracothorax viridis	bird		1	1
	Archilochus colubris	bird		1	1
	Chlorostilbon maugaeus	bird		1	1
Vespidae	*Pseudomasaris vespoides*	wasp	4		
	Ropalidia sp.	wasp		1	1
			157	97	78

[1] SvG = specialist versus generalist effectiveness (n=20 studies)
gen = number of generalist pollinator species compared to focal specialist.

[2] NvNN = native versus non-native effectiveness (n=42 studies)
non = number of non-native pollinator species compared to focal native.

[3] NvA = native versus non-native *Apis mellifera* (n=36 studies)
nat = number of native pollinator comparisons to *Apis mellifera*.

Results

Data sets

Specialists versus generalists

Our set of 20 studies provided 157 specialist versus generalist pair comparisons (Table 1). The majority of specialist pollinators were non-*Bombus* bee species (n=139), followed by bumble bees (*Bombus* spp.; n=8), moths (n=6) and wasps (n=4). Most generalists were non-*Bombus* bee species (n=106); others were bumble bees (*Bombus* spp.; n=24), honey bees (*Apis mellifera*; n=11), flies (n=7), moths (n=5), butterflies (n=3) and 1 beetle (Table 2). There were 18 plant species in the study set (Table 3). The majority were herbaceous perennials (n=9), followed by herbaceous annuals (n=5), woody perennials (n=3) and 1 herbaceous biennial. Six plant species were agricultural while 12 were non-agricultural.

Table 3. Study location, species name, agricultural status, and life-form of plant species in meta-analyses of pollination effectiveness.
crop=agricultural species

Study location	Plant species	crop	life-form	
Norway	*Aconitum septentrionale*		herbaceous	perennial
USA	*Agalinis strictifolia*		herbaceous	annual
Argentina	*Alstroemeria aurea*		herbaceous	perennial
Brazil	*Anacardium occidentale*	x	woody	perennial
USA	*Asclepias incarnata*		herbaceous	perennial
USA	*Asclepias tuberosa*		herbaceous	perennial
USA	*Asclepias sp.*		herbaceous	perennial
India	*Cajanus cajan*	x	herbaceous	perennial
USA	*Campsis radicans*		herbaceous	perennial
México	*Capsicum chinense*	x	herbaceous	perennial
USA	*Chilopsis linearis*		woody	perennial
USA	*Clarkia xantiana*		herbaceous	annual
Japan	*Corydalis ambigua*		herbaceous	perennial
México	*Cucurbita moschata*	x	herbaceous	annual
USA	*Cucurbita pepo*	x	herbaceous	annual
Canada	*Echinacea angustifolia*		herbaceous	perennial
USA	*Echium vulgare*		herbaceous	biennial
USA	*Gelsemium sempervirens*		woody	perennial
Puerto Rico	*Goetzea elegans*		woody	perennial
China	*Hedysarum scoparium*		herbaceous	perennial
USA	*Helianthus annuus*	x	herbaceous	annual
USA	*Heterotheca subaxillaris*		herbaceous	annual
USA	*Impatiens capensis*		herbaceous	annual
México	*Jatropha curcas*	x	woody	perennial
México	*Kallstroemia grandiflora*		herbaceous	annual
Sweden	*Knautia arvensis*		herbaceous	perennial
USA	*Lithophragma parviflorum*		herbaceous	perennial
USA	*Malus domestica*	x	woody	perennial
Australia	*Melastoma affine*		woody	perennial
Puerto Rico	*Melocactus intortus*		woody	perennial
USA	*Metrosideros polymorpha*		woody	perennial
Madagascar	*Neodypsis decaryi*		woody	perennial
USA	*Oenothera cespitosa*		herbaceous	perennial
Brazil	*Opuntia brunneogemmia*		herbaceous	perennial
Brazil	*Opuntia viridirubra*		herbaceous	perennial
México	*Pachycereus pecten-aboriginum*		woody	perennial
China	*Pedicularis densispica*		herbaceous	annual
USA	*Penstemon penlandii*		herbaceous	perennial

Table 3, continued.

Puerto Rico	*Pitcairnia angustifolia*		herbaceous	perennial
USA	*Prosopis velutina*		woody	perennial
USA	*Prunus dulcis*	x	woody	perennial
China	*Prunus persica*	x	woody	perennial
Israel	*Satureja thymbra*		herbaceous	perennial
USA	*Sidalcea oregana*		herbaceous	perennial
México	*Solanum lycopersicon*	x	herbaceous	perennial
Canada	*Vaccinium angustifolium*	x	woody	perennial
USA	*Vaccinium ashei*	x	woody	perennial
USA	*Vaccinium corymbosum*	x	woody	perennial
USA	*Vaccinium macrocarpon*	x	woody	perennial

Native versus non-native

Our set of 42 studies provided a total of 97 native versus non-native pair comparisons (Table 1). Most native pollinators were non-*Bombus* bee species (n=53) and bumble bees (*Bombus* spp.; n=20); others were wasps (n=7), birds, (n=7), honey bees (*Apis mellifera*; n=4), flies (n=3) and 1 bat, 1 beetle, 1 butterfly. Almost all non-native species were honey bees (*Apis mellifera*; (n=78); others were non-*Bombus* native bees (n=9), bumble bees (n=9), and 1 ant species (Table 2). There were 38 plant species in the study set (Table 3). The majority were woody perennials (n=18), followed by herbaceous perennials (n=12), herbaceous annuals (n=7), and 1 herbaceous biennial. There were 14 agricultural and 24 non-agricultural plant species in the study set.

Native versus introduced *Apis mellifera*

Our set of 36 studies provided a total of 78 native versus *Apis mellifera* pair comparisons (Table 1). For this analysis, honey bees were the only non-native species considered (n=78). Native species were mostly non-*Bombus* native bees (n=44), followed by bumble bees (*Bombus* spp.; n=15), wasps (n=7), birds (n=6), flies (n=3) and 1 bat, 1 beetle, 1 butterfly (Table 2). There were 33 plant species in the study set (Table 3). The majority were woody perennials (n=16), followed by herbaceous perennials (n=10) and herbaceous annuals (n=7). There were 12 agricultural and 21 non-agricultural plant species in the study set.

The geographic distribution of studies is given in Table 3. Not all plants were native to the study area in any of our analyses.

Effect of dietary specialization on pollination effectiveness

Meta-analysis

Our base model contained only the random effects of study and pair (nested within study). We found no improvement to model fit of adding plant phylogeny (Δ log-likelihood=0.30; p=0.44); or pollinator phylogeny (Δ log-likelihood=-0.33; p=0.25) to the base model.

Using our final model, while the effect size was positive (specialist effectiveness > generalist) it was not significantly distinguishable from zero (p=0.18) (Figure 1). Heterogeneity across our dataset was high (I^2 = 99.3%), with about a third of that variability due to study (I^2_s=30.6%) and the remainder due to pair nested within study (I^2_p=68.7). Egger's regression results indicated the potential for publication bias (p=0.0001), with fewer than expected effect sizes >0 (Figure B1-a).

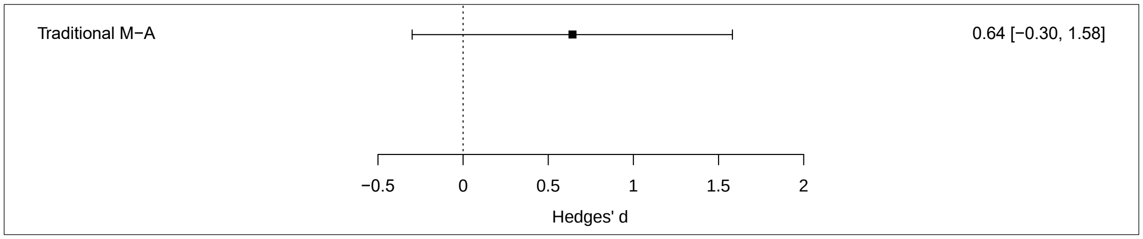


Figure 1. Overall effect size from non-phylogenetic meta-analysis of the effect of dietary specialization on pollination effectiveness (n=157 effect sizes from 20 studies). Plot shows Hedges' *d* (difference in mean effectiveness expressed in units of pooled standard deviation) and 95% confidence intervals. Dotted line marks Hedges' *d* of zero; dot shows mean effect size. A positive *d* value means that specialists have greater pollination effectiveness than generalists. Horizontal bars represent 95% confidence intervals. Bars overlapping the dotted line indicate the effect size is not significantly different from zero.

Moderator analyses

We found two moderators that explained significant amounts of heterogeneity: plant family (Q_m=37.10, p=0.0002) and effectiveness measure (Q_m=11.12, p=0.049). Specialist effectiveness was higher than generalist effectiveness when pollination was the effectiveness measure used (effect size significantly >0; p=0.002) and for the plant family Cactaceae (p<0.0001) (Figure 2).

a) Effect of pollination effectiveness measure.

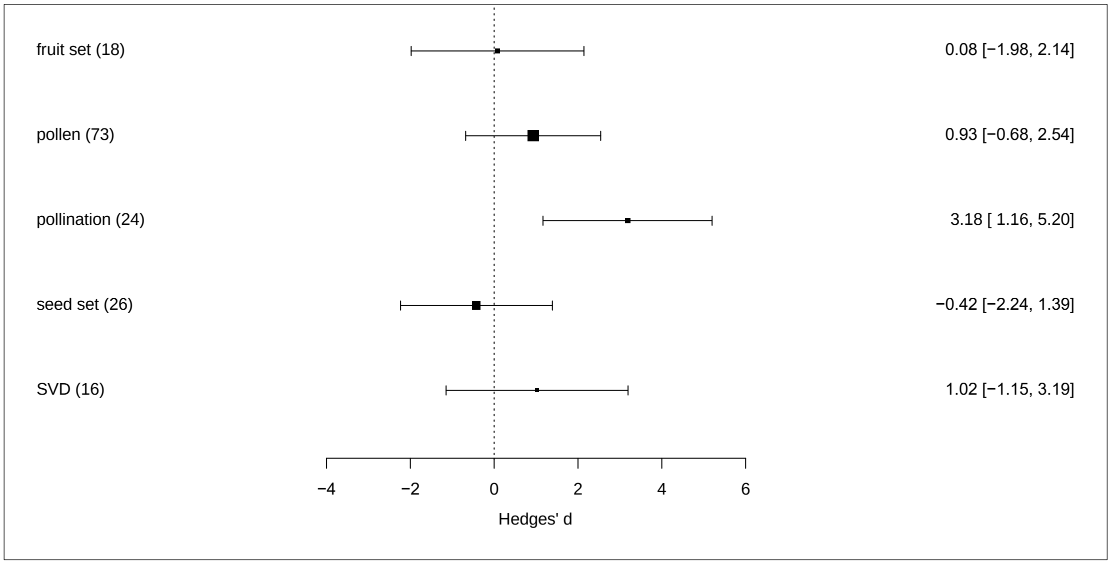


Figure 2.

Figure 2, continued.

b) Effect of plant family.

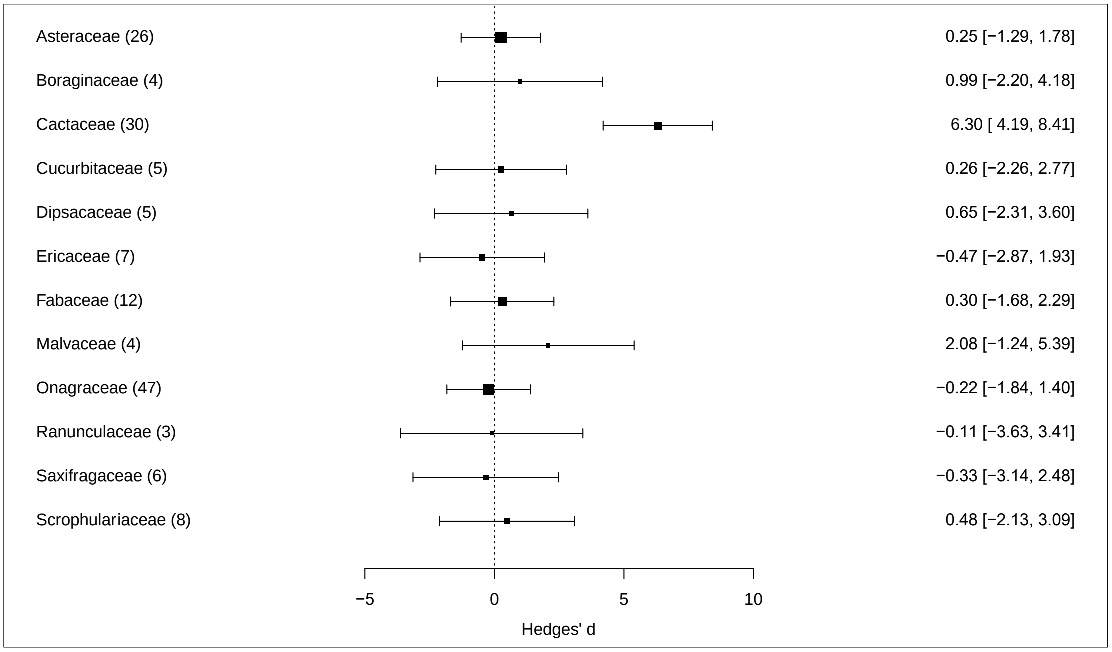


Figure 2. Results from meta-regressions testing the effects of moderators on mean specialist pollinator effect size, using the traditional (non-phylogenetic) meta-analysis as a base model (n=20 studies). Plots show show Hedges' *d* (difference in mean effectiveness expressed in units of pooled standard deviation) and 95% confidence intervals. Dotted line marks Hedges' *d* of zero. Dots show mean effect size; the size of the dot is proportional to sample size. A positive *d* value means that specialists have greater pollination effectiveness than generalists. Horizontal bars represent 95% confidence intervals. Bars overlapping the dotted line indicate the effect size is not significantly different from zero. Sample sizes for each category are in parentheses. Note different scales.

Effect of pollinator origin on pollination effectiveness

Meta-analyses

Our base model contained only the random effects of study and pair (nested within study). We obtained no improvement to fit of adding plant phylogeny (Δ log-likelihood=0; p=1.00). Adding pollinator phylogeny significantly improved model fit compared to the base model (Δ log-likelihood=3.00; p=0.01).

Using our base model, the overall estimate of the effect of pollinator origin on pollination effectiveness was positive (native effectiveness > non-native) and significantly different from zero ($p=0.03$). Using our final (pollinator-phylogenetic) model, while the effect size was positive, it was not significantly distinguishable from zero ($p=0.51$) (Figure 3). Heterogeneity was very high ($I^2=99.9\%$), with most of that variability due to study ($I^2_s=49.1\%$) and pair nested within study ($I^2_p=38.8\%$) and a small amount due to phylogenetic relationships among native pollinator species (12.2%). Egger's regression analysis indicated asymmetry in our dataset and the potential for publication bias ($p<0.0001$), with fewer than expected effect sizes >0 (Figure B1-b).

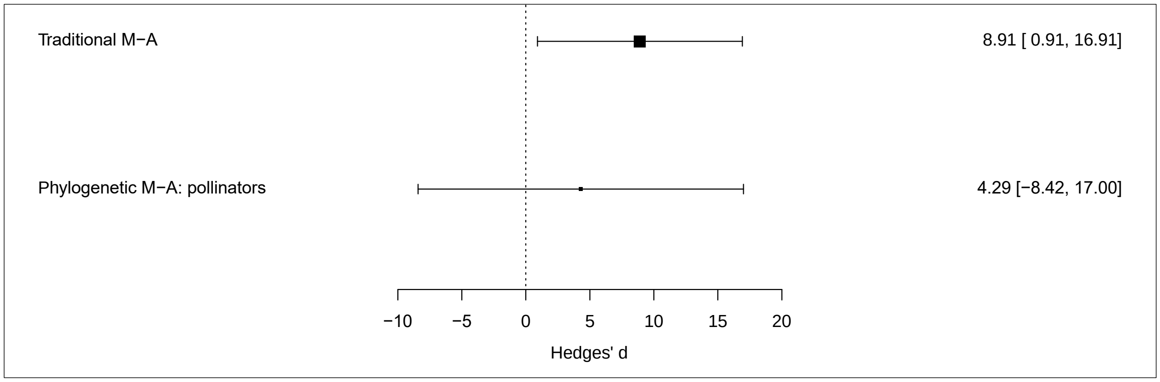


Figure 3. Overall effect sizes from meta-analyses of the effect of pollinator origin (native vs. nonnative) on pollination effectiveness (n=97 effect sizes from 42 studies), showing Hedges' *d* (difference in mean effectiveness expressed in units of pooled standard deviation) and 95% confidence intervals. Dotted line marks Hedges' *d* of zero; dot shows mean effect size. A positive *d* value means that native species have greater pollination effectiveness than non-native species. Horizontal bars represent 95% confidence intervals. Bars overlapping the dotted line indicate the effect size is not significantly different from zero.
Traditional M-A = non-phylogenetic meta-analysis.
Phylogenetic M-A = phylogenetic meta-analysis using native pollinator phylogeny

Moderator analyses

We found three moderators that explained marginally significant or significant amounts of heterogeneity: effectiveness measure (Q_m=10.16, p=0.0707), flower shape (Q_m=7.54, p=0.0565), and native pollinator type (Q_m=20.62, p=0.0144). Native pollinator effectiveness was significantly higher than non-native pollinator effectiveness when fruit set was the effectiveness measure used (effect size significantly >0; p=0.02) and when the native pollinators were bumble bees (*Bombus* spp.; p<0.0001). Native pollinator effectiveness was significantly lower than non-native pollinator effectiveness (effect size significantly <0) when the flower shape was mixed (flowers in family Asteraceae; p=0.04) (Figure 4).

a) Effect of pollination effectiveness measure.

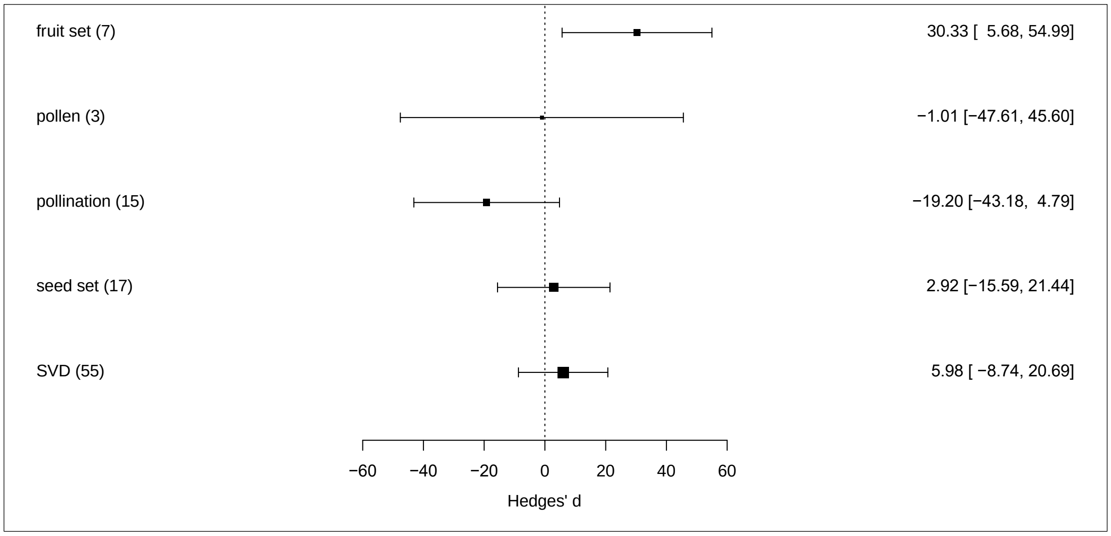
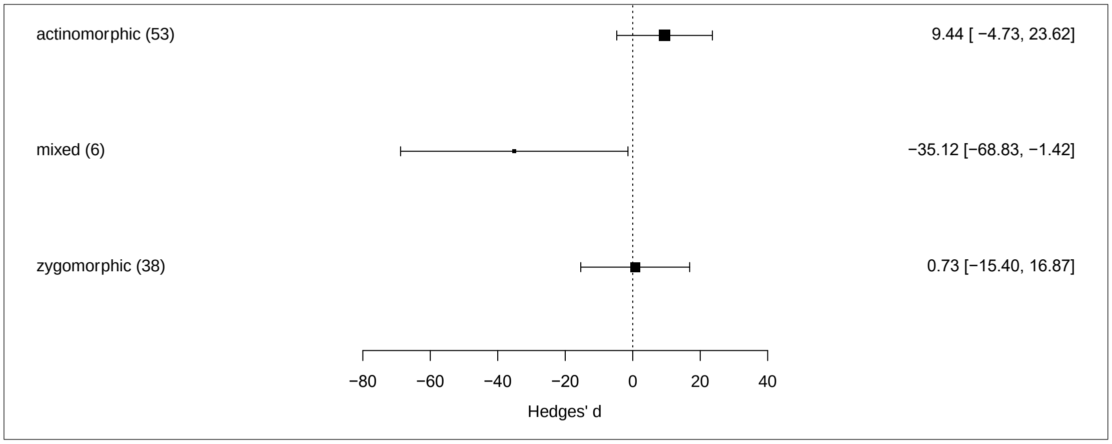


Figure 4.

Figure 4 (continued).

b) Effect of flower shape.



c) Effect of native pollinator type.

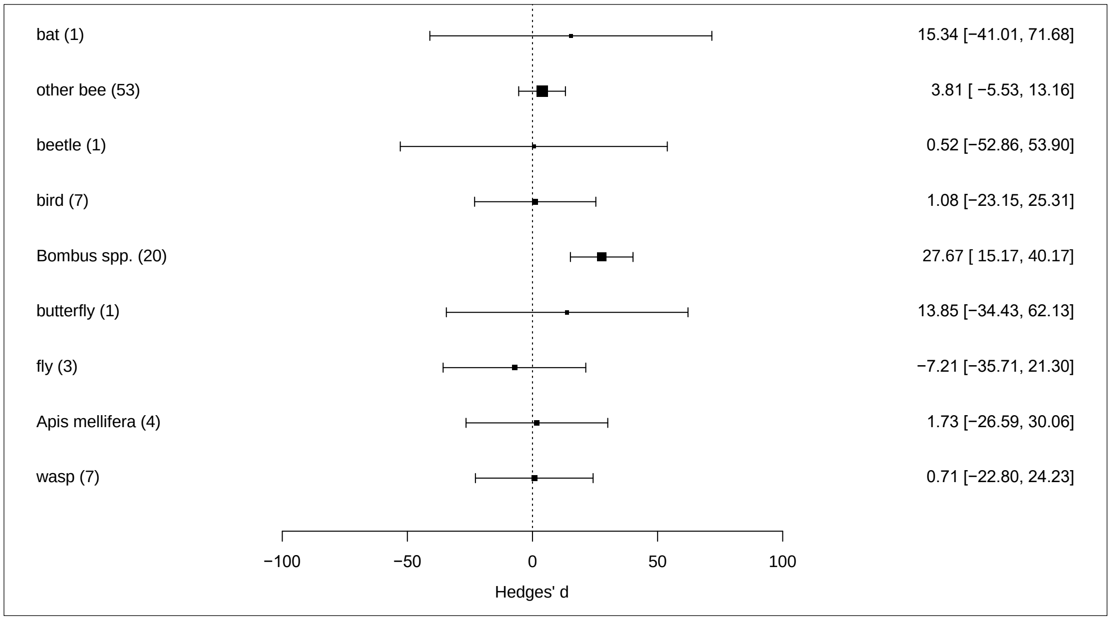


Figure 4. Results from meta-regressions testing the effects of moderators on mean native pollinator effect size, using the phylogenetic meta-analysis (with pollinator phylogeny) as a base model (n=97 effect sizes from 42 studies). Plots show Hedges' *d* (difference in mean effectiveness expressed in units of pooled standard deviation) and 95% confidence intervals. Dotted line marks Hedges' *d* of zero. Dots represent mean effect size; the size of the dot is proportional to sample size. A positive *d* value means that native species have greater pollination effectiveness than non-native species. Horizontal bars represent 95% confidence intervals; bars overlapping the dotted line indicate the effect size is not significantly different from zero. Sample sizes for each category are in parentheses. Note different scales.
mixed = actinomorphic + zygomorphic florets in the same inflorescence (Asteraceae)

Effect of pollinator origin with Apis mellifera *as non-native*

Meta-analyses

Our base model contained only the random effects of study and pair (nested within study). We obtained no improvement to fit of adding plant phylogeny (Δ log-likelihood=0.09; p=0.68) or pollinator phylogeny (Δ log-likelihood=1.47; p=0.09).

Using our final model, the effect size was positive (native effectiveness > *Apis mellifera*) and marginally different from zero (p=0.05) (Figure 5). Heterogeneity was very high (I^2=99.9%), due to both study (I^2_s=67.8%) and pair nested within study (I^2_p=32.2%). Egger's regression analysis indicated significant asymmetry (p<0.001), with fewer than expected effect sizes >0 (Figure B1-c).

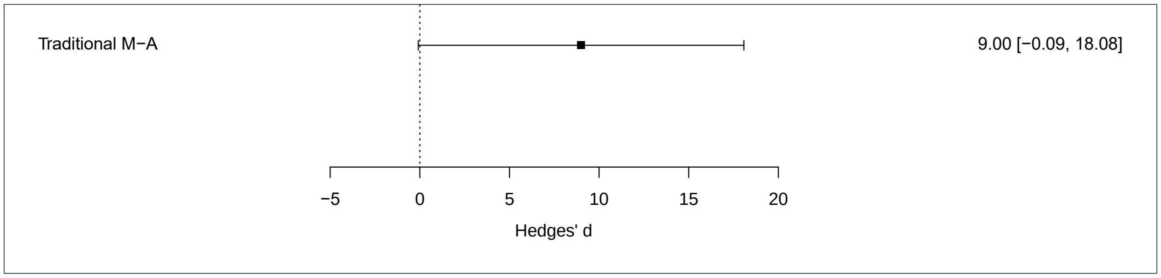


Figure 5. Overall effect size from meta-analysis of the effect of pollinator origin (native vs. nonnative) on pollination effectiveness when the non-native is *Apis mellifera* (n=78 effect sizes from 36 studies). Plots show Hedges' *d* (difference in mean effectiveness expressed in units of pooled standard deviation) and 95% confidence intervals. Dotted line marks Hedges' *d* of zero; dot shows mean effect size. A positive *d* value means that native species have greater pollination effectiveness than *Apis mellifera*. Horizontal bars represent 95% confidence intervals. Bars overlapping the dotted line indicate the effect size is not significantly different from zero.
Traditional M-A = non-phylogenetic meta-analysis.

Moderator analyses

We found four moderators that explained significant or marginally significant amounts of heterogeneity: native pollinator type (Q_m=14.52, p=0.0691), effectiveness measure

(Q_m=14.825, p<0.001), flower shape (Q_m=9.99, p=0.019), and plant family (Q_m=52.44, p=0.0002). Native pollinator effectiveness was higher than *Apis mellifera* effectiveness (effect size significantly >0) when the native pollinator type was bumble bee (*Bombus* spp.; p=0.0003), when the measure was fruit set or single visit deposition (p=0.004, p=0.04, respectively), when the flower shape was actinomorphic (p=0.01) (Figure 6), and for plant families Euphorbiaceae (p=0.0001) and Rosaceae (p<0.0001). In contrast, native pollinator effectiveness was significantly lower (native effectiveness < *Apis mellifera*) for plant family Asteraceae (p=0.04). (Figure B2).

a) Effect of native pollinator type.

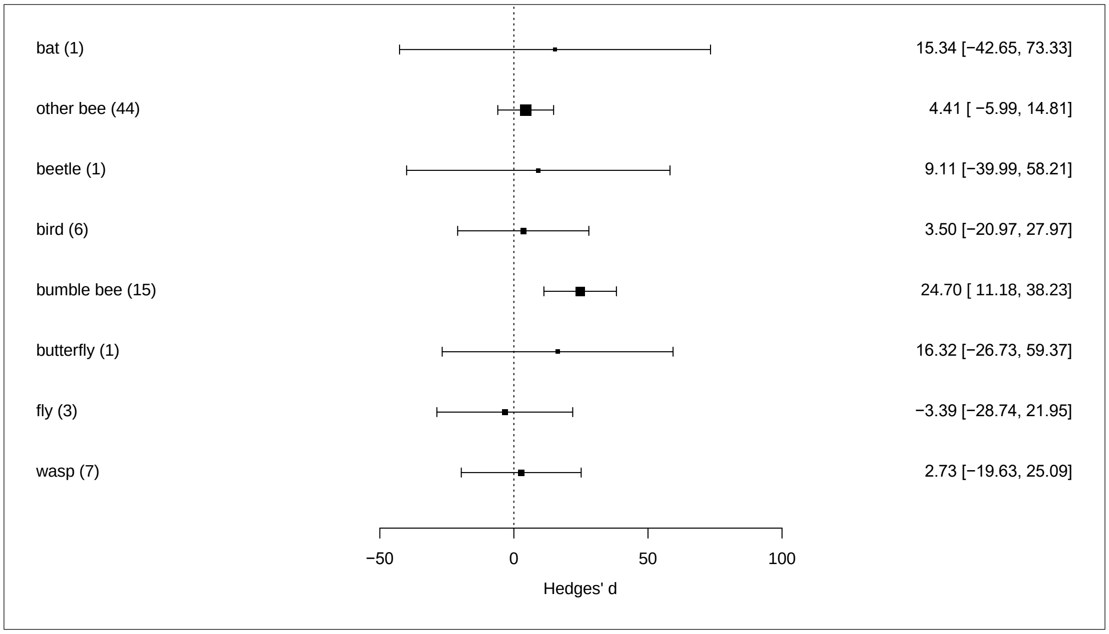
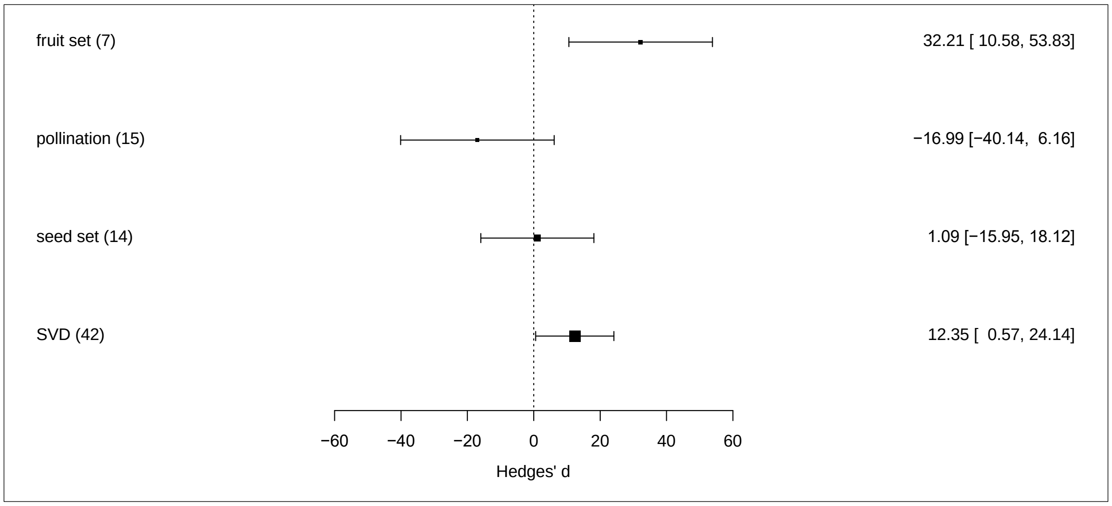


Figure 6.

Figure 6 (continued).

b) Effect of pollination effectiveness measure.



c) Effect of flower shape.

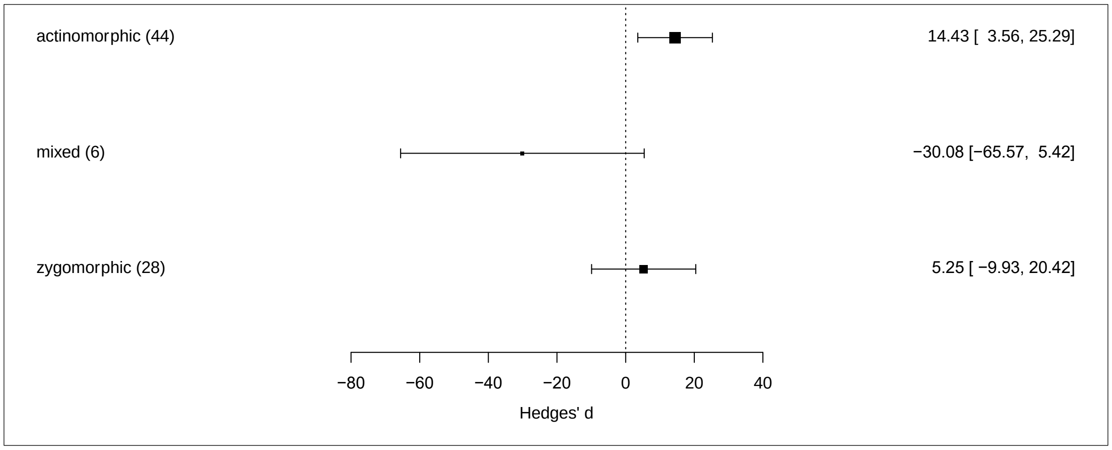


Figure 6. Results from meta-regressions testing the effects of moderators on mean native pollinator effect size when the non-native pollinator is *Apis mellifera* (n=78 effect sizes from 36 studies), using the traditional (non-phylogenetic) model as a base model. Plots show Hedges' *d* (difference in mean effectiveness expressed in units of pooled standard deviation) and 95% confidence intervals. Dotted line marks Hedges' *d* of zero. Dots represent mean effect size; the size of the dot is proportional to sample size. A positive *d* value means that native species have greater pollination effectiveness than *Apis mellifera*. Horizontal bars represent 95% confidence intervals; bars overlapping the dotted line indicate the effect size is not significantly different from zero. Sample sizes for each category are in parentheses. Note different scales.
mixed = actinomorphic + zygomorphic florets in the same inflorescence (Asteraceae)

Discussion

The overall effect sizes were in the expected directions for all three of our analyses, but often did not reach statistical significance. First, a positive effect size of dietary specialization indicated a trend towards greater specialist effectiveness compared to generalists; but (perhaps because of substantial variability across studies/systems) the effect size in this case was not significantly different from zero. Second, for native compared to non-native pollinators, mean effect size indicated significantly greater native effectiveness in a traditional meta-analytic model; however, the effect was not significant after accounting for pollinator phylogeny, suggesting that pollinator effectiveness varies phylogenetically, with bumble bees accounting for the most effective group in our dataset. Lastly, we found significantly greater native pollinator effectiveness in our native versus *Apis mellifera* meta-analysis, which helps to justify continued investigations aimed at reconciling *A. mellifera*'s value as an effective crop pollinator with its potentially detrimental impacts as an introduced species.

Effect of dietary specialization on pollination effectiveness

We found minimal support for the hypothesis of greater specialist than generalist effectiveness. The outcome of our moderator analysis validates this conclusion: the effect size for ten out of twelve plant families in our study set were less than one unit from zero (Figure 2b). Specialists were more effective than generalist pollinators only for the plant family Cactaceae, which in our dataset represents two species in the genus *Opuntia*. The floral morphology of *Opuntia* favors dietary-specialist bees, which unlike generalist bees stimulate the movement of stamens toward the center of the flower, allowing access to the nectar furrow below [Schlindwein & Wittmann 1997]. Other researchers have also reported greater specialist than generalist pollination effectiveness on *Opuntia* and other cactus species [McFarland et al. 1989, McIntosh 2002], so the overall effect suggested by our result appears to be highly influenced by a single plant genus.

It is certainly possible for a specialist pollinator to be an entirely ineffective floral visitor, for example when collecting nectar without contacting anthers/stigma. Some dietary specialist bees have been documented visiting their host plants and making infrequent or no stigma contact [Epps et al. 2015; Moeller & Geber 2005]. In addition, the strong floral fidelity of specialist pollinators may diminish their effectiveness if it increases inbreeding and reduces genetic diversity (through higher rates of self-pollination). We also caution that our acceptance of the "specialist" and "generalist" classifications provided by authors in our study set does not adequately capture the range of pollination behaviors observed in the real world, where diet breadth is continuous, not categorical. The term "specialist" should perhaps be reserved for pollinators at the extreme narrow end of the dietary breadth spectrum, in which case we expect that far fewer species would qualify for the "specialist" designation. For example, in summarizing their results from a study in Greece, Petanidou et al. (2008) concluded that "no species recorded in all four years was truly a specialist." This led Petanidou et al. to speculate that reported levels of specialization in the pollination literature are overestimates.

Neff and Simpson (1990) also found no difference between specialists and generalists in their analysis of pollination effectiveness in bees visiting *Helianthus annuus*. Instead they noted that pollination effectiveness in their study system corresponded with bee body size: large bees were more effective than small bees. Depending on the flower, small-sized bees can often access nectar by passing between stigma and anthers, neither accumulating pollen nor transferring it to stigmas (thus making an “illegitimate” floral visit). Our results for bumble bees lend support to the idea that high pollination effectiveness may be related to body size, a hypothesis that has been both supported [Tepedino et al. 2011; Willmer & Finlayson 2014] and rejected [Zych 2007] in empirical studies. However, is also worth noting that bumble bee body size can vary as much as ten-fold within a colony as well as within a season [Alford 1975], so perhaps bumble bee pollination effectiveness is related to factors other than size (e.g., sonication or other behaviors, such as the “car park” maneuver of bumble bee floral approach).

We emphasize that though the positive effect size we obtained for Cactaceae was calculated from 30 species-pair comparisons, all 30 come from a single study; thus the significant effect cannot be taken as strong evidence of greater specialist effectiveness at the family level. However, combined with our overall result, we do interpret this to indicate that while specialists are likely not more effective pollinators of all plants, they are likely highly effective pollinators of particular plant species or genera.

Effect of pollinator origin on pollination effectiveness

For native compared to non-native pollinators visiting native plants, mean effect size was positive and significant in a traditional meta-analytic model, and positive but not significant when the effect of pollinator phylogeny was accounted for. [Insert here the summary of what the native vs. apis result was]. Given that 1) our origin study set—and the pollination effectiveness literature in general—is dominated by two dominant pollinator taxa (*Bombus* species and *Apis mellifera*); 2) we found indications of differential pollination effectiveness between these two taxa; and 3) the two taxa are closely related, we have some reservations when interpreting the phylogenetic meta-analytic effect size.

Effectiveness of introduced Apis mellifera *compared to native pollinators*

Our results suggest that *Apis mellifera*, is perhaps not always the most effective pollinator of plants with which it shares no coevolutionary history. Low effectiveness of *A. mellifera* has been demonstrated in several agricultural cultivars with New World ancestors (e.g., pumpkin, sunflower, tomato) and is also suggested by the agricultural practice of "saturating" fields of New World cultivars with *Apis mellifera* in order to obtain adequate pollination [Westerkamp 1991].

Other researchers have proposed that *Apis* pollination effectiveness is diminished by their behavior of grooming pollen from their bodies, moistening it, and packing it into their corbiculae, thus rendering it unavailable for pollination [Park et al. 2016]. While this could reduce *Apis* pollination effectiveness in some situations (especially if the particular pollen species in question is highly valued for provisioning larvae), it does not suffice to explain their low effectiveness in comparison to *Bombus* species, which also possess corbiculae. Instead, we attribute the overall effect of more effective natives vs non-natives to a non-random pattern of study, with one highly effective genus attracting more research effort.

An important caveat to our result showing superior *Bombus* than *Apis* pollination performance is the potential effect of abundance. *Bombus* may deliver more pollen grains per visit, but *Apis* may ultimately emerge as an equally or more effective pollinator if it is more abundant than *Bombus* in a given year or location [Fishbein & Venable 1996; Maldonado et al. 2013]. The studies in our meta-analysis are focused on effectiveness at the individual pollinator visit scale, and thus do not account for population-level differences in abundance and thus visitation. High visitation frequency despite low per-visit efficiency (number of pollen grains deposited per visit) can ultimately result in higher pollinator effectiveness, including in situations where the “high-frequency/low-efficiency” and “low-frequency/high-efficiency” pollinators are both *Bombus* species [Madjidian et al. 2008]. In addition, large interannual variation in the effectiveness of various pollinator species (primarily related to changes in abundance/visitation rate) observed by Fishbein & Venable (1996) led them to conclude that estimates of the effectiveness of various pollinators, even if based on precise measurements taken in a single season, may not represent long-term mean patterns. Indeed, bumble bee pollination effectiveness can even vary depending on life stage: *Bombus* queens (which begin foraging earlier in the season than worker bees) have been shown to be more efficient pollinators of some plants than workers [Kudo et al. 2011].

Measures of pollination effectiveness

We expected that different measures of pollination effectiveness might give different results because some measures more completely capture all the important aspects of pollination. For example, if nonnative generalists (like *Apis mellifera*) deliver an abundance of pollen (but heterospecific pollen), then we would expect to see greater native than non-native effectiveness when measured by fruit set, but not necessarily by pollen load. This is in fact what we did observe in our native versus non-native effectiveness analysis.

We also expected that different results could arise if only because the measurements were taken from different pollinators and plants in each study. As with plant species, we are hindered from making inference by small sample size (in terms of number of studies representing different combinations of our moderators). For example, pollination emerged as an important modifier of effect size in our specialist versus generalist analysis. Since pollination was the measure used to measure effectiveness in family Cactaceae, which also emerged as significant, we take this result as evidence of multicollinearity rather than an indication of greater effectiveness of specialists when pollination is the measurement used.

The single visit deposition method (SVD) was the most commonly used measure in our study set (41/94 studies). The technique (described in Ne'eman et al. 2010) has been the most extensively adopted effectiveness-assessment methodology. However, SVD gives the researcher a measure of potential positive effects, but provides no measure of possible negative effects (e.g., pollen tube inhibition resulting from heterospecific pollen deposition) [Padyšáková et al. 2013]. More important, it does not measure a fitness outcome, instead assuming a positive correlation between pollen deposition and reproduction, which is not always the case [Wang et al. 2017]. Of the single-visit studies in our initial set, only 58% reported whether the pollen deposited had been verified as conspecific to the plant. If seed set measurements are not possible, we suggest that SVD studies at a minimum should report some measure of pollen conspecificity. We note that in our native versus non-native analysis, fruit set emerged as a significant indicator of greater native pollinator effectiveness, while SVD did not. A similar result was obtained in our native versus *Apis mellifera* moderator analysis, where, despite a much smaller sample size for fruit set (7) compared to SVD (42), the effect size for fruit set was nearly three times that of the effect size for SVD. We suggest these are indications that pollen deposition is not a reliable proxy for reproductive success.

Conclusion

Even after decades of research, the pollination biology of most non-crop flowering plants is unknown, simply due to the vast number of species available for study. Our meta-analyses have provided information on general patterns of the performance of different pollinator groups, but our results require verification from a broader range of plant and pollinator taxa. Our literature search suggested that empirical tests of Stebbins' "most effective pollinator principle" peaked in the 1960s–1970s and the subject has received diminished research attention since the 1990s (with a few notable exceptions). We are hopeful that recent reports of pollinator declines will reinvigorate research on the question of pollinator effectiveness and help identify general organizing principles underlying differential effectiveness of pollinators across an array of study systems.

Predicting the impacts of pollinator declines requires an understanding of whether different pollinator groups have differential effectiveness. Our meta-analyses provide some evidence that they do, and that strong differences may exist even between closely related species. The large confidence intervals we obtained for our effect size estimates suggest that further sampling is needed in order to resolve the question of whether specialist vs. generalist, and native vs. non-native pollinators are equally effective. Continued assessments of the importance of different pollinator types under various types and intensities of anthropogenic disturbance will be important to help plan for potential changes in pollination services that could arise in our changing environment.

Acknowledgments

Funding was provided by the University of New Mexico Department of Biology (to CLC), and NSF DEB 1257965 (to KDW).

Appendix A

Table A1. Species identifications and dietary specialization of bees visiting sunflower (*Helianthus annuus*) at 11 sites in the U.S. Southwest in the 1970s [Hurd, et al. 1980] and 2015–2016. Name changes reflect taxonomic updates since the 1970s. ITIS = Integrated Taxonomic Information System; BBSL = USDA Bee Biology and Systematics Lab; G, N, S = generalist, nectar feeder, specialist; unk = dietary specialization unknown

Name (ITIS/BBSL)	name changes	Diet breadth (HLL)	G, N, S
Agapostemon angelicus/texanus	BBSL: *A. angelicus* + *A. texanus*	casual polylege	G
Agapostemon femoratus		casual polylege	G
Agapostemon melliventris		casual polylege	G
Agapostemon obliquus	formerly *A. cockerelli*	casual polylege	G
Agapostemon tyleri		casual polylege	G
Anthophora curta		casual polylege	G
Anthophora montana	formerly *A. montana* + *A. smithii*	casual polylege	G
Apis mellifera		casual polylege	G
Bombus morrisoni		regular polylege	G
Bombus pensylvanicus/sonorus	BBSL: *B. pensylvanicus* + *B. sonorus*	regular polylege	G
Colletes fulgidus		casual polylege	G
Exomalopsis solani		casual polylege	G
Exomalopsis solidaginis		casual polylege	G
Halictus confusus		casual polylege	G
Halictus ligatus		regular polylege	G
Halictus tripartitus		casual polylege	G
Lasioglossum kincaidii		casual polylege	G
Lasioglossum pectoraloides	formerly *Evylaeus pectoraloides*	casual polylege	G
Lasioglossum semicaeruleum	formerly *Dialictus pruinosiformis*	casual polylege	G
Megachile agustini		casual polylege	G
Megachile angelarum	formerly *Chalicodoma angelarum*	casual polylege	G
Megachile brevis		regular polylege	G
Megachile frugalis		casual polylege	G
Megachile montivaga		regular polylege	G
Megachile policaris		regular polylege	G
Megachile texana		casual polylege	G
Melissodes paroselae		casual polylege	G
Melissodes sonorensis		regular polylege	G
Melissodes tepidus	formerly *tepida*	casual polylege	G
Melissodes thelypodii		casual polylege	G
Melissodes tristis		casual polylege	G
Anthidiellum robertsoni			G?
Anthophora californica			G?
Calliopsis helianthi			G?
Anthidium maculosum		nectar visitor	N
Anthidium porterae		nectar visitor	N
Anthophora urbana		nectar visitor	N
Centris atripes		nectar visitor	N
Centris caesalpiniae		nectar visitor	N
Ceratina dallatorreana		nectar visitor	N

Table A1 (continued).

Coelioxys apacheorum		cleptoparasite	N
Coelioxys edita		cleptoparasite	N
Coelioxys menthae		cleptoparasite	N
Coelioxys texana		cleptoparasite	N
Colletes louisae		nectar visitor	N
Colletes wootoni		nectar visitor	N
Diadasia diminuta		nectar visitor	N
Diadasia ochracea		nectar visitor	N
Dieunomia nevadensis	formerly *Nomia nevadensis angelesia*	nectar visitor	N
Lasioglossum amicum	formerly *Evylaeus amicus*	nectar visitor	N
Lasioglossum clematisellum	formerly *Dialictus clematisellus*	nectar visitor	N
Lasioglossum microlepoides	formerly *Dialictus microlepoides*	nectar visitor	N
Lasioglossum semibrunneum	formerly *Dialictus oleosus*	nectar visitor	N
Megachile occidentalis	formerly *Chalicodoma occidentalis*	nectar visitor	N
Megachile sidalceae		nectar visitor	N
Melissodes verbesinarum		nectar visitor	N
Nomada formula			N
Nomada sp.		cleptoparasite	N
Paranomada velutina		cleptoparasite	N
Peponapis pruinosa		nectar visitor	N
Sphecodes sp.		cleptoparasite	N
Svastra sabinensis		nectar visitor	N
Svastra sila		nectar visitor	N
Tetraloniella eriocarpi	*formerly Xenoglossodes eriocarpi*	nectar visitor	N
Tetraloniella sp.	*Formerly Xenoglossodes*	nectar visitor	N
Triepeolus concavus		cleptoparasite	N
Triepeolus helianthi	formerly *T. helianthi* + *T. lineatulus*	cleptoparasite	N
Triepeolus norae		cleptoparasite	N
Triepeolus robustus		cleptoparasite	N
Triepeolus sp.		cleptoparasite	N
Triepeolus subalpinus	formerly *T. lestes*	cleptoparasite	N
Triepeolus trichopygus		cleptoparasite	N
Xeromelecta californica		cleptoparasite	N
Xeromelecta interrupta		cleptoparasite	N
Xylocopa californica	formerly *californica arizonensis*	nectar visitor	N
Xylocopa varipuncta			N?
Andrena accepta		primary oligolege	S
Andrena helianthi		primary oligolege	S
Andrena pecosana		secondary oligolege	S
Colletes rufocinctus		secondary oligolege	S
Diadasia enavata		primary oligolege	S
Dieunomia heteropoda	formerly *Nomia*	primary oligolege	S
Dieunomia micheneri	formerly *Nomia*	primary oligolege	S
Dieunomia triangulifera		primary oligolege	S
Dufourea marginata		primary oligolege	S
Megachile aff. parallela		primary oligolege?	S
Megachile inimica/inimica sayi	BBSL: *inimica* + *inimica sayi*	secondary oligolege	S

Table A1 (continued).

Megachile manifesta		secondary oligolege	S
Megachile parallela		primary oligolege	S
Melissodes agilis		primary oligolege	S
Melissodes appressus	formerly *appressa*	secondary oligolege	S
Melissodes brevipyga		secondary oligolege	S
Melissodes compositus	formerly *composita*	secondary oligolege	S
Melissodes confusus	formerly *confusa*	secondary oligolege	S
Melissodes coreopsis		primary oligolege	S
Melissodes humilior		secondary oligolege	S
Melissodes limbus		secondary oligolege	S
Melissodes lupinus	formerly *lupina*	secondary oligolege	S
Melissodes lustrus	formerly *lustra*	secondary oligolege	S
Melissodes menuachus		secondary oligolege	S
Melissodes montanus	formerly *montana*	secondary oligolege	S
Melissodes perlusus	formerly *perlusa*	primary oligolege	S
Melissodes robustior		primary oligolege	S
Melissodes subagilis		secondary oligolege	S
Melissodes submenuachus	formerly *submenuacha*	secondary oligolege	S
Paranthidium jugatorium		secondary oligolege	S
Perdita lingualis		primary oligolege	S
Perdita verbesinae		secondary oligolege	S
Pseudopanurgus aethiops		primary oligolege	S
Pseudopanurgus helianthi	formerly *Pterosarus helianthi*	primary oligolege	S
Svastra helianthelli		primary oligolege	S
Svastra machaerantherae		primary oligolege	S
Svastra obliqua		primary oligolege	S
Svastra petulca	formerly *petulca suffusa*	secondary oligolege	S
Svastra texana	formerly *texana eluta*	secondary oligolege	S
Syntrichalonia exquisita		secondary oligolege	S
Trachusa cordaticeps	formerly *Heteranthidium cordaticeps*	primary oligolege	S
Trachusa occidentalis		primary oligolege	S
Anthophorula sp.			unk
Dialictus sp.			unk
Lasioglossum sp.			unk
Megachile apicalis			unk
Megachile comata			unk
Megachile lippiae			unk
Megachile onobrychidis			unk
Megachile perihirta			unk
Megachile prosopidis			unk
Megachile rossi			unk
Melissodes communis			unk
Melissodes comptoides			unk
Melissodes sphaeralceae			unk
Protandrena illustris			unk
Tetraloniella perconcinna			unk

Table A2. Results of mtDNA analysis of *Apis mellifera* to determine whether specimens belonged to Africanized lineages [Alan Szalanski, personal communication].
Africanized = Africanized *A. mellifera* mtDNA, European = European *A. mellifera* mtDNA, PCR failure = amplification unsuccessful

Year/State	Site	mtDNA type			
2015		Africanized	European	PCR failure	total Apis analyzed
NM	Animas	12	0	8	20
	Silver City	5	0	15	20
CA	Indio	12	2	1	15
	Madera 1	0	11	8	19
	Merced	0	13	6	19
2015+2016					
NM	Rodeo	7	0	8	15
2016					
CA	Bishop	2	5	13	20

Table A3. Coordinates of surveys of bees pollinating sunflower (*Helianthus annuus, H. petiolaris*) at 11 sites in the U.S. Southwest in the 1970s [Hurd, et al. 1980] and during 2015–2016 (the present study).

state	**HLL site name**	**HLL county**	**2015 county**	**Latitude-Longitude**	**2016 county**	**Latitude-Longitude**
CA	Escalon	San Joaquin	San Joaquin	37.786, -120.992	San Joaquin	37.798, -120.999
CA	Madera (site 1, Jul.)	Madera	Madera	37.020, -120.121	Madera	37.048, -120.111
CA	Bishop	Inyo	Inyo	37.361, -118.361	Inyo	37.361, -118.361
NM	Rodeo	Hidalgo	Hidalgo	31.819, -109.043	Cochise (AZ)[1]	31.490, -109.341
NM	Animas	Hidalgo	Hidalgo	31.964, -108.815[†]	Hidalgo	31.524, -108.978
NM	Silver City	Grant	Grant	32.762, -108.303	Grant	32.787, -108.274
AZ	Benson	Cochise	Cochise	31.905, -110.230	Cochise	31.906, -110.251
CA	Indio	Riverside	Riverside	33.670, -116.233	Riverside	33.670, -116.233
CA	Merced	Merced	Merced	37.357, -120.637	Stanislaus[2]	37.467, -120.827
CA	Madera (site 2, Sep.)	Madera	Madera	36.926, -120.056	Madera	37.040, -120.214
CA	Corcoran	Kings	Kings	36.083, -119.577	Tulare[3]	35.872, -119.391

[†] Sampled in 2017 (2015 sampling cancelled due to rain).

[1] 22 mi S. of Rodeo, NM.

[2] 23 mi N. of Merced, CA.

[3] 20 mi S. of Corcoran, CA.

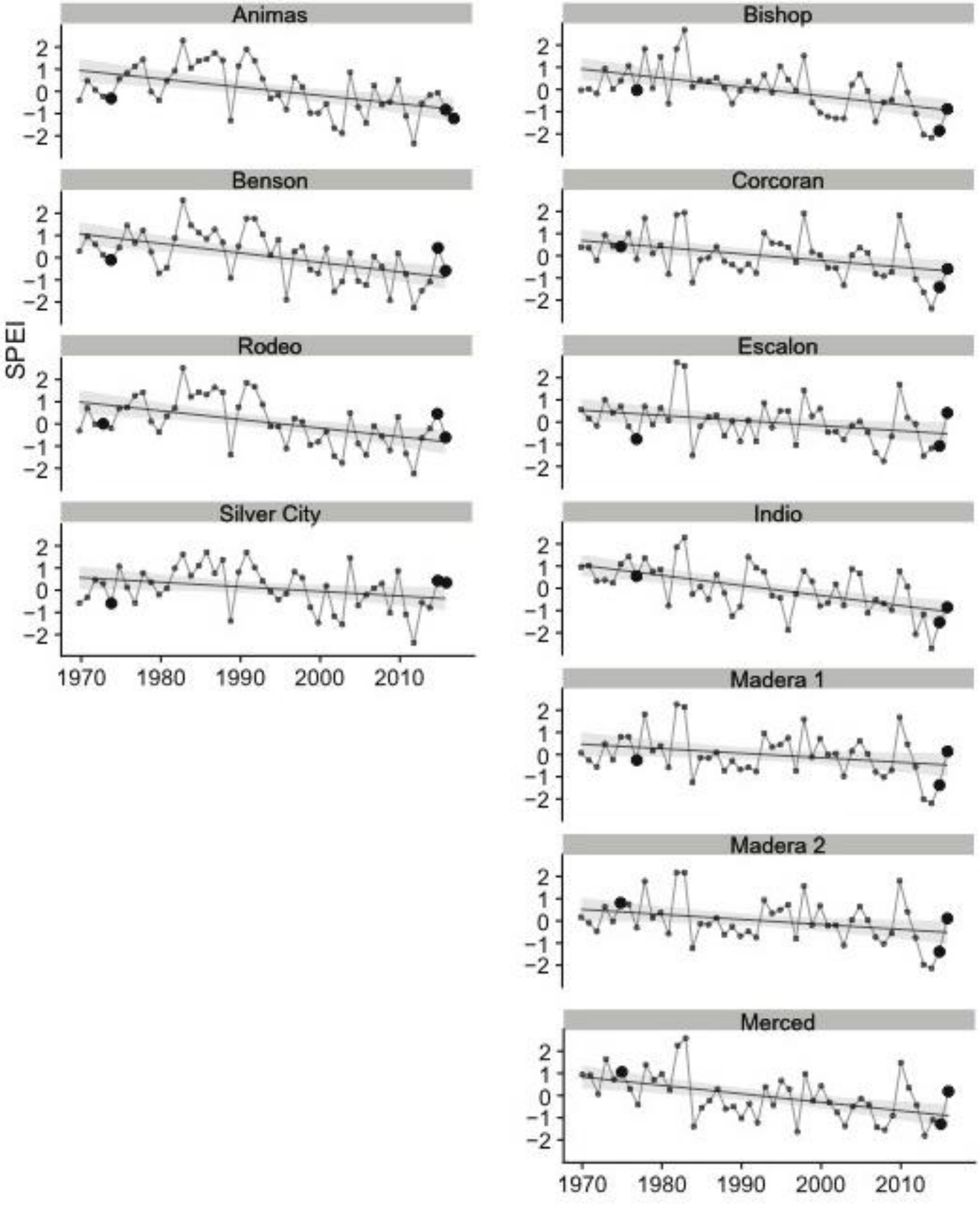
Table A4. PermANOVA tests and pairwise comparisons of nMDS ordinations of differences in community composition for bees pollinating sunflower (*Helianthus annuus*, *H. petiolaris*) at four sites in Arizona/New Mexico in the 1970s and 2015–2016 (except Animas, NM, sampled in 2016–2017).

		PermANOVA					Pairwise comparisons				
Region			Df	F.model	R2	Pr(>F)	pair	F.model	R2	unadjusted p	adjusted p
Arizona & New Mexico	All, with *Apis mellifera*	Decade	2	1.759	0.281	0.074	1970s - 2015	1.873	0.238	0.078	0.117
		Residuals	9		0.719		1970s - 2016	2.735	0.313	0.059	0.117
		Total	11				2015 - 2016	0.664	0.100	0.561	0.561
	Generalists and nectar visitors, with *Apis mellifera*	Decade	2	2.028	0.311	0.047	1970s - 2015	1.834	0.234	0.063	0.095
		Residuals	9		0.689		1970s - 2016	3.348	0.358	0.025	0.075
		Total	11				2015 - 2016	0.880	0.128	0.398	0.398
	All, without *Apis mellifera*	Decade	2	1.586	0.261	0.069	1970s - 2015	1.598	0.210	0.100	0.179
		Residuals	9		0.739		1970s - 2016	1.871	0.238	0.119	0.179
		Total	11				2015 - 2016	1.275	0.175	0.210	0.210
	Generalists and nectar visitors, without *Apis mellifera*	Decade	2	1.929	0.300	0.044	1970s - 2015	1.365	0.185	0.253	0.253
		Residuals	9		0.700		1970s - 2016	2.391	0.285	0.085	0.249
		Total	11				2015 - 2016	2.053	0.255	0.166	0.249
	Specialists	Decade	2	1.245	0.217	0.253	1970s - 2015	1.889	0.239	0.086	0.258
		Residuals	9		0.783		1970s - 2016	1.259	0.173	0.256	0.384
		Total	11				2015 - 2016	0.667	0.100	0.764	0.764

Table A5. PermANOVA tests and pairwise comparisons of nMDS ordinations of differences in community composition for bees pollinating sunflower (*Helianthus annuus*, *H. petiolaris*) at seven sites in California in the 1970s and 2015–2016.

			PermANOVA				Pairwise comparisons					
Region			Df	F.model	R2	Pr(>F)	pair	F.model	R2	unadjusted p	adjusted p	
California	All, with *Apis mellifera*	Decade	2	4.273	0.322	0.003	1970s - 2015	5.042	0.296	0.004	0.006	*
		Residuals	18		0.678		1970s - 2016	6.591	0.355	0.001	0.003	*
		Total	20				2015 - 2016	0.623	0.049	0.653	0.653	
	Generalists and nectar visitors, with *Apis mellifera*	Decade	2	7.703	0.461	0.001	1970s - 2015	8.892	0.426	0.001	0.003	*
		Residuals	18		0.539		1970s - 2016	13.912	0.537	0.002	0.003	*
		Total	20				2015 - 2016	0.434	0.035	0.746	0.746	
	All, without *Apis mellifera*	Decade	2	1.433	0.137	0.114	1970s - 2015	2.084	0.148	0.027	0.081	
		Residuals	18		0.863		1970s - 2016	1.462	0.109	0.142	0.213	
		Total	20				2015 - 2016	0.820	0.064	0.631	0.631	
	Generalists and nectar visitors, without *Apis mellifera*	Decade	2	1.581	0.149	0.045	1970s - 2015	1.975	0.141	0.045	0.117	
		Residuals	18		0.851		1970s - 2016	1.697	0.124	0.078	0.117	
		Total	20				2015 - 2016	1.084	0.083	0.398	0.398	
	Specialists	Decade	2	1.360	0.131	0.169	1970s - 2015	2.200	0.155	0.038	0.114	
		Residuals	18		0.869		1970s - 2016	1.316	0.099	0.245	0.368	
		Total	20				2015 - 2016	0.651	0.051	0.748	0.748	

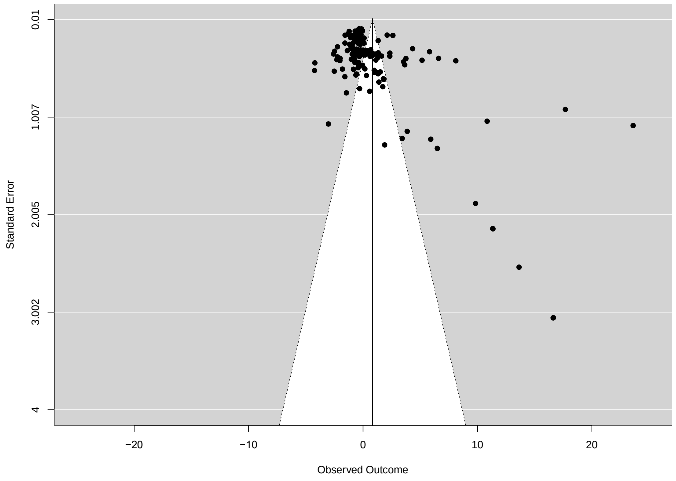
Figure A1. Trends in the SPEI drought index across time at each sampling site. Negative values of SPEI indicate relatively hot, dry years; positive values indicate relatively cool, wet years. Years in which bee assemblages were sampled are indicated with large points; unsampled years are shown with small points. Correlation coefficients and statistical significances shown in Table 2.



(a) Arizona/New Mexico sites (b) California sites

Appendix B

(a) Specialist versus generalist (n=20 studies; plot excludes three points with large SE).



(b) Native versus non-native (n=42 studies; plot excludes two points with large SE).

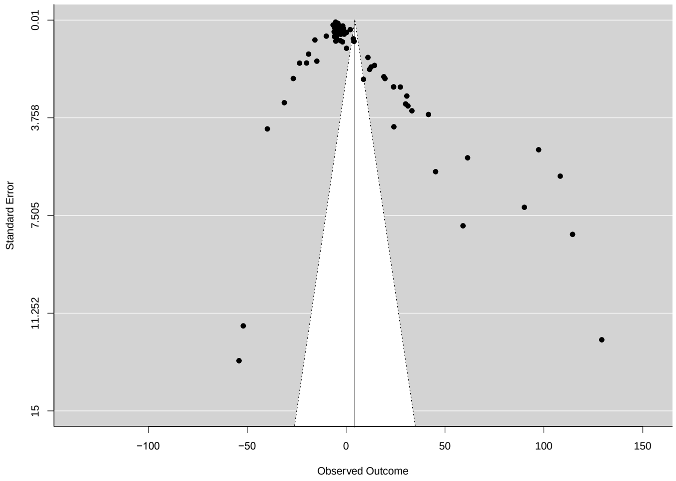


Figure B1.

Figure B1, continued.

(c) Native versus *Apis mellifera* (n=36 studies; plot excludes two points with large SE).

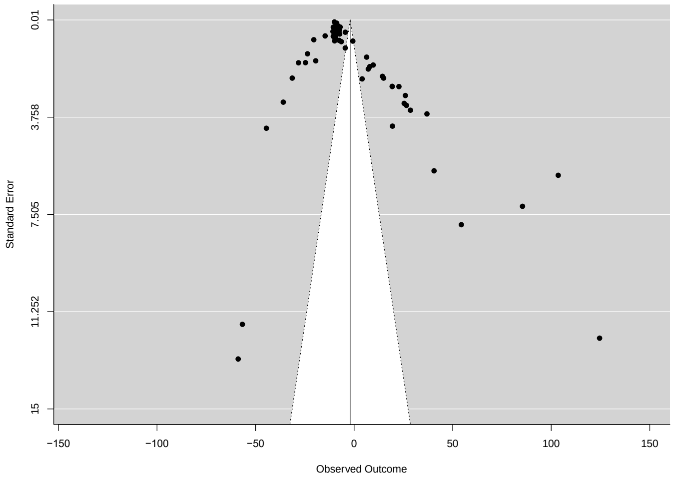


Figure B1. Diagnostic (funnel) plots of studies used in meta-analyses of pollination effectiveness. (a) Specialist versus generalist (n=20 studies; plot excludes three points with large SE); (b) Native versus non-native (n=42 studies; plot excludes two points with large SE); (c) Native versus *Apis mellifera* (n=36 studies; plot excludes two points with large SE).

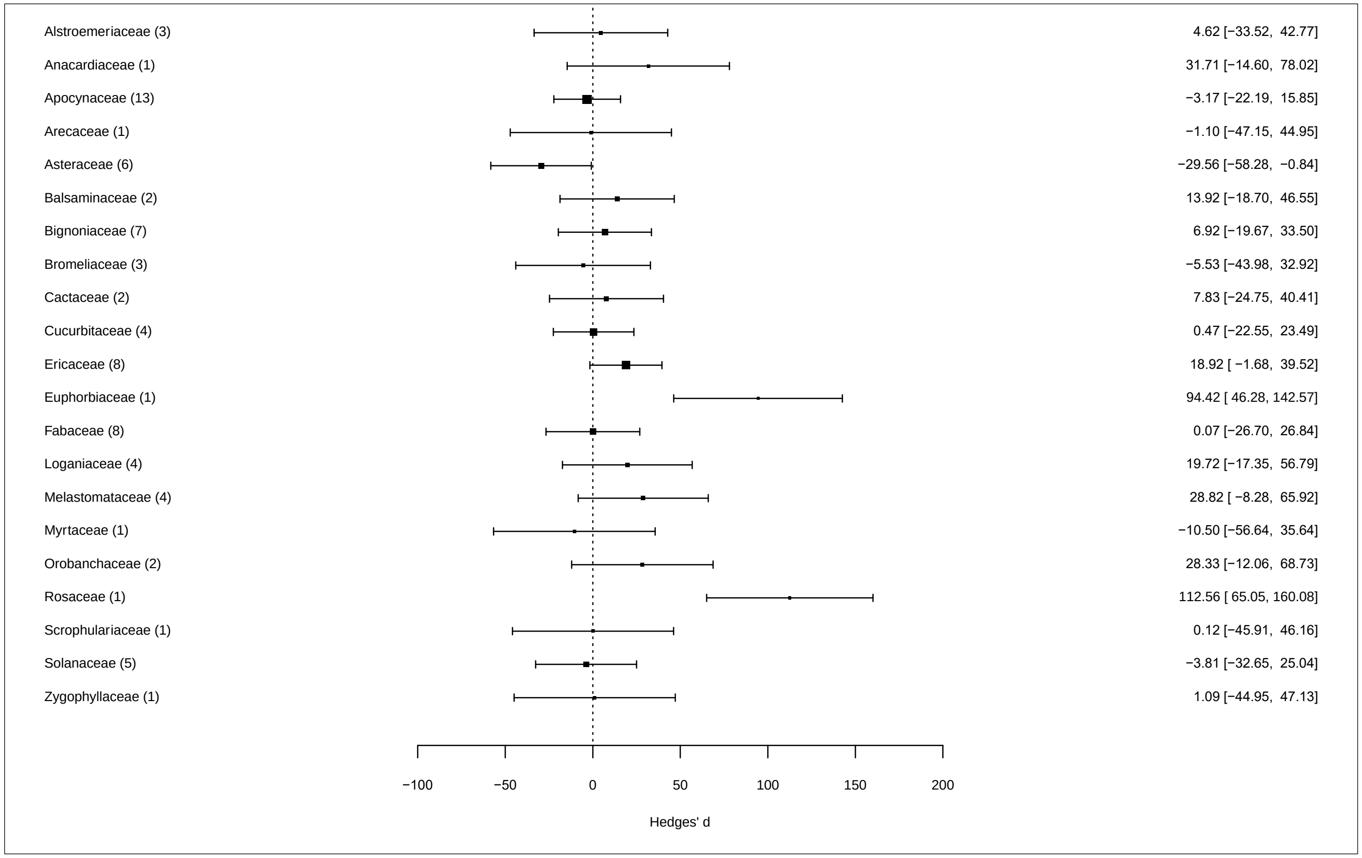


Figure B2. Effect sizes from meta-regression testing the effects of plant family on mean native pollinator effectiveness when the non-native pollinator is *Apis mellifera*, using the non-phylogenetic model as a base model and showing Hedges' *d* and 95% confidence intervals. Dotted line marks Hedges' *d* of zero; dots mark mean effect size; the size of the dot is proportional to sample size. A positive *d* value indicates that native species have greater pollination effectiveness than *Apis mellifera*. Horizontal bars represent 95% confidence intervals; bars overlapping the dotted line indicate the effect size is not significantly different from zero. Sample sizes for each category are in parentheses.

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