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A meta-analysis of single visit pollination effectiveness

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ABSTRACT

Premise – Many animals provide essential ecosystem services in the form of plant pollination. A rich literature documents considerable variation in the single visit pollination effectiveness of floral visitors, but this literature has yet to be comprehensively synthesized.

Methods – We conducted a hierarchical meta-analysis of 193 studies and extracted 1716 single visit effectiveness (SVE) comparisons for 252 plant species. We paired SVE data with visitation frequency data for 75 of these studies. Given the global dominance of honeybees in pollinator communities, we used these data to ask: 1) Do honeybees (*Apis mellifera*) and other floral visitors vary in their SVE?; 2) To what extent do plant and pollinator attributes predict the difference in SVE between honeybees and other visitors?; and 3) Is there a correlation between visitation frequency and SVE?

Key results – Honeybees were significantly less effective than the most effective non-honeybee pollinators and, although not significantly different, tended to be less effective than the mean community effectiveness. Honeybees were less effective as pollinators of crop plants and compared to birds and other bees. Visitation frequency and SVE were positively correlated, but this trend was largely driven by data from communities where honeybees were absent.

Conclusions – Although high visitation frequencies make honeybees important pollinators, they were slightly less effective than the average pollinator and rarely the most effective pollinator of the plants they visit. As such, honeybees may be imperfect substitutes for the loss of wild pollinators and safeguarding pollination will benefit from conservation of non-honeybee taxa.

KEY WORDS: *Apis mellifera*; bee; crop pollination; honeybee; pollen deposition; pollination efficiency; pollinator importance; visitation frequency; wild pollinator

INTRODUCTION

Over 70% of plants depend to some degree on animal pollinators to successfully reproduce (Ollerton et al. 2011). Among the diversity of pollinators, taxa vary in their contributions to pollination in multiple intricate dimensions, some quantitative (e.g., numbers of visits, numbers of pollen grains transferred: Herrera, 1987; King et al., 2013), others qualitative (e.g., proportion selfed versus outcrossed pollen, diversity of mates, spatial distances of mating: Valverde et al., 2019; Richardson et al., 2020). At its core, the functional contributions of different pollinator taxa can be measured by the quantity (frequency) and quality (effectiveness) of visits to plant reproductive success (Inouye et al., 1994; King et al., 2013). Quantitatively, although biodiverse pollinator assemblages increase pollination (Albrecht et al., 2012; Winfree et al., 2015; Winfree et al., 2018), a few dominant species often provide the majority of floral visits (Kleijn et al., 2015). For example, the numerical dominance of honeybees (*Apis mellifera*) as floral visitors has been hypothesized to drive their functional importance as pollinators (Hung et al., 2018). However, high visit frequencies can impair pollination in some contexts (Aizen et al., 2014) and we know little about whether strongly dominant visitors, such as honeybees, effectively pollinate the plants they visit.

Pollination effectiveness is defined as the per-visit contribution of floral visitors to pollination (Inouye et al. 1994). A long history of studies within the botanical and evolutionary

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

An extensive literature on pollinator importance – the product of per-visit effectiveness and relative visitation rates of different pollinators (King et al., 2013; Ballantyne et al., 2015) – has concluded that pollinators that visit more frequently are generally more important (Vásquez et al., 2012). This conclusion suggests that numerical dominance outweighs among-species variation in SVE, but it is also possible that pollination effectiveness and visitation frequencies are correlated. First, frequent pollinators could be inherently more effective because of deep phylogenetic signals. For example, Ballantyne et al. (2017) found a positive correlation between a pollinator's visit frequency and pollination effectiveness when comparing 23 plant species, likely because bees were both highly effective and highly frequent visitors compared to other floral visitors. Second, positive correlations between pollination effectiveness and visit frequency could occur if pollinators that visit frequently do so to the exclusion of other plant species. Such temporary fidelity (e.g., floral constancy: Free 1970) or long term fidelity would operate to minimize heterospecific pollen transfer, resulting in more effective pollination (Morales and Traveset, 2008). On the other hand, high visitation rates may be the result of many quick and

ineffective visits (Ohara et al., 1994) and have a negative or non-significant effect on reproductive success in many contexts (e.g., Sáez et al., 2014; reviewed in Willcox et al., 2017).

Despite their high visitation frequencies, the effectiveness of honeybees relative to other pollinators remains unclear. Outside of their native range, honeybees lack the evolutionary history with endemic plants that could have selected for increased pollinator effectiveness (Javorek et al., 2002). Because honeybees are floral generalists that visit a high proportion of available plants in ecosystems across the globe (Hung et al., 2018), they may not be particularly effective at pollinating specific flowering species. Furthermore, honeybees sometimes 'rob' plants (Irwin et al., 2010) and efficiently extract and groom pollen from plants without depositing the pollen they extract (Westerkamp, 1991) or collect nectar without contacting reproductive structures (Vicens and Bosch, 2000; Thomson and Goodell, 2001). However, honeybees can be highly effective pollinators even for plants with which they have no shared evolutionary history (Wist and Davis, 2013), suggesting that shared evolutionary history is not a prerequisite to effective pollination.

Understanding pollinator effectiveness has important practical implications for safeguarding the production of pollinator-dependent crops. Highly effective non-honeybee pollinators are important for ensuring crop pollination in the face of global change (Rader et al., 2013) and functionally diverse pollinator communities can increase crop pollination (Woodcock et al., 2019). Furthermore, pollination may differ in cultivated settings because interspecific plant competition, the spatial arrangement of flowers, and the pollinator taxa that provide pollination may vary between agricultural and natural landscapes (Harrison et al., 2018).

We used a meta-analysis of the pollination effectiveness literature to address three key questions. First, how does the SVE of honeybees compare to that of other floral visitors? We

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

MATERIALS AND METHODS

Study Screening – We performed a Web of Science (WoS) search using a multiterm query (Appendix S1; see Supplemental Data with this article) designed to capture the highly variable terminology describing pollination effectiveness detailed in Ne'eman et al. (2010). In May 2020, this search yielded 1,036 results. One of us (MP) screened the abstracts found by

WoS to determine whether they potentially contained single visit effectiveness (SVE) data. This yielded 388 papers. We also performed a Google Scholar search of the literature using a similar multi-term query (Appendix S1), which yielded 116 additional papers. We found 62 papers from the reference sections of previously included papers. After removing duplicates and reading abstracts, we identified 468 papers which seemed appropriate for a more thorough screening.

We followed the PRISMA protocol for collecting and screening data from the literature (Appendix S1; Moher, 2009). To be included in our analysis, the paper had to contain empirical data on the per-visit contribution of at least one free-foraging visitor to plant reproduction. We considered pollen deposition, percent fruit set, fruit weight, and/or seed set as measures of SVE. Most studies were conducted with intact flowers, but we also included data from experiments that used the "interview stick" method (in which a cut flower was presented to potential visitors). We did not include estimates of SVE based on equations or model outputs nor did we include data from trials that manipulated dead bees to deposit pollen. We extracted means, sample sizes, and measures of error (e.g., standard deviation, standard error) directly from the text of the paper or from graphs using WebPlotDigitizer (v. 4.4, Rohatgi, 2020). When lower and upper error estimates were not symmetrical, we used the upper error estimate. When possible, we converted measures of error to standard deviation. When a paper did not report sample sizes, error, or other important information, we contacted the study authors. If we were unable to retrieve or estimate information on mean effectiveness and error, we excluded the paper from our analysis. After screening papers, 193 studies remained in our analytical dataset. We also extracted data on study year and location, plant species, plant family, whether the plant species was a crop-plant, pollinator taxon, pollinator group (e.g., bird, fly, bee), and the native range of pollinator and plant species. We determined range status to biogeographical realms by looking up the nativity of each

158 taxon in the scientific literature and using occurrence records on GBIF. If papers reported SVE
159 outcomes from multiple sites or years, we extracted these data as separate outcomes and dealt
160 with their non-independence statistically (see below).
161 We collected information on the visitation rates of pollinators if it was reported for the
162 same plant species for which pollinator effectiveness data were reported. This rate could be
163 reported as the number of visits to a focal flower or patch of flowers per unit time or the number
164 of flowers visited per unit time and/or per unit area. We did not include data on the relative
165 abundance of different visitors, unless data were collected in a homogeneous landscape (like an
166 orchard) in which most visitors would have been visiting the focal plant species. If a study
167 reported visitation data, we matched that data to the corresponding SVE data from the same
168 study and plant species. Perfect matches required that pollinator taxa were reported to the same
169 taxonomic resolution and that data were collected in the same year and location. When more than
170 one measure of visit frequency was reported we preferentially used data on the number of visits
171 to a focal flower per unit time. When more than one measure of SVE was reported, we
172 preferentially chose whichever measure was better represented in our data, such that pollen
173 deposition data were chosen over seed set data and seed set data were chosen over fruit set data.
174 ***Meta-analysis*** – To address questions about the single visit effectiveness of honeybees
175 and non-honeybees, we defined the effect size as the standardized mean difference (SMD, i.e.,
176 Hedges *g* (Hedges, 1981)) of SVE values between honeybee and non-honeybees for each unique
177 study, plant, site, and year combination. We chose to use Hedge's g over other effect sizes
178 because it is commonly used in the ecology literature for comparing two means (Nakagawa and
179 Santos, 2012), and it includes a correction for small sample sizes, which occurred with our data.

Following Hung et al. (2018), we calculated effect sizes for two separate comparisons: (1) the difference between honeybees versus the most effective non-honeybee taxon and (2) the average difference between honeybees and non-honeybee taxa (hence, 'average effectiveness'). The SMD value is > 0 when other pollinators are more effective than honeybees and < 0 if the opposite occurs. We calculated each effect size in *R* (R Core Development Team, 2020) using the *escalc* function in the '*metafor'* package (v. 2.1-0, Viechtbauer, 2010).

We fit meta-analytic and meta-regression multilevel linear mixed-effects models, using the *rma.mv* function in the '*metafor'* package (v. 2.1-0, Viechtbauer, 2010). We used three random effects to control for non-independence of effect sizes collected from the same study or plant species: study ID, plant species, and an observation level ID. We used phylogenetic comparative methods (Cornwell and Nakagawa, 2017) to account for non-independence that may arise due to shared evolutionary history of focal plants by including a phylogenetic covariance matrix. The phylogeny used to compute a phylogenetic covariance matrix (Zanne et al., 2014) was constructed using the package '*brrranching'* (v. 0.6.0, Chamberlain, 2020), and branch lengths were set following Grafen's method (Grafen, 1989) using the *R* package '*ape'* (v. 5.1, Paradis and Schliep, 2019)). Despite slightly higher AIC values and larger P values (Appendix S2), we present results from models including phylogenetic controls to fully account for non-independence due to shared ancestry (Chamberlain et al., 2012). With this mixed-effects structure, we specified four models, which include an intercept only model (i.e., overall meta-analytic model), and three meta-regression models for different fixed effects/moderators: (1) pollinator taxonomic group, (2) whether the plant was a crop plant (crop status), and (3) for native plants, whether it was in the honeybee's native range (range status). We follow Hung et al. (2018) and define the West Palearctic as the honeybees' native range (Ruttner, 1988).

To test whether there was a relationship between a pollinator taxon's single visit effectiveness and visit frequency, we calculated Pearson's correlation coefficients (r) for the relationship between visit frequency and pollinator effectiveness for each unique study, plant, site, and year combination in which there were at least five pollinator taxa represented. After calculating correlation coefficients, we used the *escalc* function in the *metafor* package to calculate Fisher's r-to-Z transformed correlations and corresponding sampling variances. Using the same multilevel linear mixed-effects model structure and phylogenetic controls as described above we generated three models. The first model was an intercept-only model to test for the overall relationship between a pollinator's visit frequency and single visit effectiveness. The second model compared three categories against one another: studies where honeybees were present, studies where honeybees were absent, and studies where we artificially removed all points corresponding to honeybees (re-calculating effect sizes as detailed above). We generated this third category to determine whether the patterns we observed were solely driven by honeybees themselves or whether there might also be indirect effects of honeybee presence on the relationship between visit frequency and single visit effectiveness. The third model tested whether there was an interaction between crop status and honeybee presence.

Tests for publication bias – Publication bias was assessed based on visual inspection of funnel plots for each model (Appendix S3; Appendix S4) and via a modified Egger's test (Egger et al., 1997; Sterne and Egger, 2005) on meta-analytic residuals in which effect size precision (sqrt(1/variance)) is included as a moderator (Nakagawa and Santos, 2012). A significant slope for precision would indicate statistically significant funnel asymmetry after controlling for all

other variables in the model. We considered analyses to be biased if the intercept differed from zero at P = 0.10 (as in Egger et al., 1997).

RESULTS

We built a dataset of 1716 SVE records (i.e., average effectiveness values for pollinators visiting plants) drawn from 193 peer-reviewed and published studies (Appendix S5). Research was conducted on every ice-free continent, with most work occurring in the Nearctic (N = 68) or West Palearctic (N = 42) over a period of 39 years, from 1981 to 2020 (Fig. 1). Many studies (34) investigated pollination of more than one plant species (range: 2-23), with a total of 252 plant species assessed belonging to 67 families. Across plants and studies, relative effectiveness values were normally distributed (Appendix S6), but most pollinators (53%) were less effective than the mean effectiveness of all visitors, compared to 44% who were more effective than the mean. For studies that reported visit frequency data (N = 75), the distribution of relative visit frequency values was skewed to the right (Appendix S6), such that only 27% of visitors visited more frequently than the mean visit frequency. Within studies that reported paired effectiveness and visit frequency data, honeybees were the most frequent visitor 28% of the time but the most effective pollinator only 9% of the time.

How does the SVE of honeybees compare with other floral visitors? – A total of 84 studies reported comparisons between *A. mellifera* and at least one other taxon. These studies focused on 96 plant species and include crops (N = 32) and non-native plant species (N = 22) (Appendix S7). From these comparative studies, 621 individual effect sizes were obtained and

summarized for each combination of plant and pollinator group within a study. This yielded 186 effect sizes comparing the most effective non-honeybee pollinator and honeybees (Most Effective Pollinator (MEP) comparisons) and 186 effect sizes comparing the average effectiveness of all non-honeybee pollinators and honeybees (Average Effective Pollinator (AEP) comparisons). When comparing overall study-level effect sizes, we found that non-honeybee pollinators were more effective than honeybees. This outcome was statistically significant for Most Effective Pollinator comparisons (Appendix S2; overall standardized mean difference (SMD): 0.497, [0.211, 0.783 95% CI]; P = 0.001), but not Average Effective Pollinator comparisons (SMD: 0.207, [-0.094, 0.508]; P = 0.177). The data showed little evidence of publication bias in terms of funnel plot asymmetry of meta-analytical residuals as revealed by plot inspection (Appendix S3). Results from Egger's tests suggested little to no degree of asymmetry for our overall meta-analytic model (MEP: P = 0.06; AEP: P > 0.10).

To what extent do plant and pollinator attributes predict the comparative SVE of honeybees? – Computing effects separately for each pollinator group revealed that the type of pollinator moderated the comparative SVE of honeybees (Fig. 2). The most effective bees and birds were significantly more effective than honeybees (Fig. 2a; bee SMD: 0.665, [0.463, 0.868]; P < 0.001 & bird SMD: 2.269, [1.457, 3.082]; P < 0.001). For average effectiveness comparisons, only birds were significantly more effective than honeybees (Fig. 2b; SMD: 1.344, [0.667, 2.020]; P < 0.001). Although the average non-*Apis* bee tended to be more effective than honeybees, this difference was not statistically significant (SMD: 0.247, [-0.094, 0.588]; P = 0.156). However, significant differences were detected in models without phylogenetic controls

(Appendix S2; SMD: 0.322, [0.137, 0.506]; P = 0.001), suggesting that additional data might confirm this trend. At the study level, 61% of effect sizes compared other bees and honeybees; we therefore focus subsequent analyses on bees.

The most-effective bees were more effective pollinators of crops than honeybees (Fig. 3a; SMD: 0.786, [0.328, 1.244]; P = 0.001); this was true for average effectiveness comparisons as well (Fig. 3b; SMD: 0.511, [0.137, 0.886]; P = 0.007). For non-crop plants, honeybees were marginally less effective than the most effective other bees (Fig. 3a; SMD: 0.413, [-0.033, 0.859]; P = 0.069), but were not significantly different than the average bee pollinator. The most-effective bees were better pollinators of native plants than honeybees (Fig. 4a); this was true for plants occurring within (SMD: 0.608, [0.021, 1.195]; P = 0.042) and outside (SMD: 0.683, [0.105, 1.261]; P = 0.021) *Apis mellifera*'s native region (West Palearctic). Honeybees were comparable to the average SVE of bees (Fig. 4b), inside and outside their native range.

Is there a correlation between floral visitation frequency and SVE? – Overall, there is a positive relationship between visit frequency and single visit effectiveness (Estimate: 0.600 [0.127, 1.074 95% CI]; P = 0.013). However, data from systems in which honeybees are absent drive this positive result. When honeybees are present, there is no relationship between visit frequency and effectiveness (Fig. 5; Estimate: 0.390 [-0.131, 0.911]; P > 0.05) and this lack of a significant relationship persisted when we artificially removed data corresponding to honeybee visits. We observed a positive association between visit frequency and SVE only when *Apis mellifera* was actually absent (Fig. 5; Estimate: 0.758 [0.242, 1.273]; P = 0.004). There was no interaction between honeybee presence and crop status (Appendix S8). An Egger's test

confirmed minimal publication bias ($P > 0.10$). There were a few outliers to the right of funnel plots (Appendix S4). Removing these data did not influence our findings.

DISCUSSION

Our meta-analysis supports the hypothesis that honeybees are frequently not the most effective pollinator of plants globally. Across six continents and hundreds of plant species, honeybees showed significantly lower single visit effectiveness than the most effective pollinator in a community (Fig. 2). Although not statistically different, honeybees also tended to be less effective than the community mean. This general pattern is likely driven by comparison of honeybees against birds and other bees. The most effective bird and bee pollinators were significantly more effective than honeybees, as were the average bird pollinators. Although not statistically different, honeybees were also less effective than the average non-*Apis* bee. The finding that birds are more effective than honeybees is based on only six studies that were likely focused on flowers frequently pollinated by birds. Nevertheless, it supports the idea that plants adapted to bird pollination have traits that enhance pollination by birds at the expense of pollination by bees (Castellanos et al., 2006). Although data for non-bee taxa were relatively sparce, honeybees were equally as effective as the average and most effective ant, beetle, butterfly, fly, moth, and wasp pollinators, confirming that non-bee insects can be important pollinators (Orford et al., 2015; Rader et al., 2020). Our results bolster initial work summarizing honeybee pollination effectiveness (Hung et al., 2018) and demonstrate that honeybees are less effective than many other visitors and at best average.

Analysis of crop plants also revealed important differences between honeybees and non-*Apis* pollinators. Despite their abundance in commercial cropping systems, honeybees are less

313 effective crop pollinators than the most effective bee pollinators and the average non-honeybee
314 bees (Fig. 3). This finding supports the idea that the importance of honeybees as crop pollinators
315 derives largely from their numerical dominance as crop visitors (Hung et al., 2018). Our analysis
316 adds robust evidence to a growing consensus that wild bees have the potential to contribute
317 greatly to agricultural pollination. Indeed, wild bee species richness, functional diversity, and
318 visit rates increase crop yield (Blitzer et al., 2016; Woodcock et al., 2019), and the use of
319 managed honeybee hives might not compensate for losses in wild bee species richness and
320 abundance (Mallinger and Gratton, 2015; Pérez-Méndez et al., 2020). As such, managed
321 honeybees alone may be insufficient to meet the increased pollination demands of global
322 agricultural production (Aizen and Harder, 2009) and our results validate the importance of
323 actions to promote resilient native bee communities within agricultural lands (Isaacs et al., 2017).
324 Honeybees were consistently less effective compared to other bees when pollinating
325 native plants both inside and outside the honeybee's native range (Fig. 4). This result is not
326 entirely surprising based on what we know about the co-evolution of plants and pollinators. The
327 non-honeybee bee community may contain specialists sympatric with their host plants.
328 Meanwhile, if honeybees are broad generalists, selective pressure might be less consistent, even
329 within the native range of honeybees. Furthermore, if the morphological features relevant to
330 pollination are relatively consistent across plants within the same genus or family, insects may be
331 capable of pollinating novel plant species. For example, *Prunus* spp. occur in Europe and North
332 America and *Osmia* spp. are highly effective pollinators of *Prunus* tree crops in both regions
333 (Vicens and Bosch, 2000; Bosch et al., 2006), despite the fact that North American *Osmia* spp.
334 do not have shared evolutionary history with the *Prunus* species introduced as tree crops.

We found an overall positive relationship between visit frequency and single visit pollinator effectiveness, but this relationship was largely driven by data from systems in which honeybees were absent (Fig. 5). The overall positive correlation suggests that more frequent visitors are also more effective, but this result should not be interpreted to indicate that visitation frequency is an adequate proxy for overall pollination importance (Vásquez et al., 2012; Ballantyne et al., 2017). This positive correlation may suggest that pollinators which visit frequently do so to the exclusion of other plant species, such that they display high floral constancy. High floral constancy may indicate that visitors gather and transport more conspecific pollen (Brosi and Briggs, 2013). Although the pollen loads of visitors do not always adequately predict effective pollination (Adler and Irwin, 2006), high conspecific pollen transport likely predisposes visitors to higher pollination effectiveness on average.

The finding that honeybees erode this otherwise positive correlation suggests that this hyper-generalist species is often a numerically dominant visitor with modest effectiveness and may modify the pollination context for plant communities. Interestingly, when comparing systems with and without honeybees, visit frequency and pollination effectiveness do not positively correlate even when we artificially remove the data on honeybees and re-calculate correlation coefficients. This result suggests that honeybee presence may indirectly influence the relationship between visitation frequency and pollination effectiveness by altering the visitation patterns and effectiveness of other plant visitors. High honeybee visitation frequencies may indicate that honeybees efficiently extract nectar and pollen without also efficiently depositing the pollen they extract (Westerkamp, 1991; Wilson and Thomson, 1991; Goodell and Thomson, 1997). If honeybees deplete floral nectar, this could make plants less attractive to other common visitors (Hansen et al., 2002) and alter their visit behavior and effectiveness (Thomson, 1986). If

they extract large amounts of pollen (Cane and Tepedino, 2017), this could reduce the amount available for collection and deposition by other pollinators (Harder and Barrett, 1995).

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

CONCLUSIONS

As honeybees become increasingly dominant globally, the abundance and species richness of other pollinators visiting plants is expected to decrease (Valido et al., 2019). If honeybees replace visits from other pollinators, whether through competitive displacement or otherwise (Herrera, 2020), these changes in community composition may have cascading effects on plant pollination, reproduction, and persistence (Gómez et al., 2010). Species loss and fluctuations in the abundance of important pollinators can imperil ecosystem service delivery (Cardinale et al., 2012; Winfree et al., 2015). Even rare species are important to ecosystem

functioning (Winfree et al., 2018) and functionally diverse pollinator assemblages enhance plant community diversity (Fontaine et al., 2005). If honeybees are not particularly effective, it will be crucial to understand whether and how honeybees influence the visitation frequencies and effectiveness of other pollinators. Another key question is whether honeybees can compensate for the inferior quality of their visits with increased visit frequency, which can occur (Sun et al., 2013). Ultimately, some plants will thrive as their visitor community becomes increasingly dominated by honeybees, while others may experience declines. Given increasing honeybee dominance, it will be important to identify and protect diverse and effective pollinator communities especially when confronted with ineffective substitutes.

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AUTHOR CONTRIBUTIONS

MLP and CCN are joint first authors. All authors contributed to data collection, idea generation, and manuscript revisions. MLP and CCN wrote the manuscript and analyzed the data.

DATA ACCESSIBILITY STATEMENT

Data will be permanently archived on Figshare when our paper is accepted. Until then, we are happy to share data upon request.

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SUPPORTING INFORMATION: Additional Supporting Information may be found online in the supporting information section at the end of the article.

APPENDIX S1. PRISMA diagram demonstrating the path through which papers were filtered for inclusion in the meta-analysis.

APPENDIX S2. Model outputs for most effective (MEP) and average effectiveness (AEP) effect size calculations graphed in Fig. 2, 3, and 4.

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

APPENDIX S4. Funnel plot for the meta-regression comparing pollinator's visit frequencies and single visit effectiveness.

APPENDIX S5. Studies included in the meta-analysis.

APPENDIX S6. Histograms of A) relative effectiveness values for all pollinators included in our meta-analysis and B) the relative visit frequencies for all pollinators included in the subset of studies that reported paired data on visit frequencies and single visit effectiveness values.

APPENDIX S7. Phylogeny of plant species included in the meta-analysis.

APPENDIX S8. Meta-regression results for the relationship between a pollinator's visit frequency and single visit effectiveness for crop and non-crop plants in studies with and without honeybees present.

FIGURE LEGENDS

Fig. 1. The research into single visit effectiveness (SVE) is geographically widespread and has progressed consistently over time. (A) Map of study locations depicting whether research recorded SVE measures for honeybees and other taxa (squares) or if honeybees were the sole taxon or absent (circles). (B) Trends in SVE research show the cumulative number of studies per region (lines) and the annual number of studies (rug). (C) Some studies have more than one SVE observation (e.g., multiple pollinators visiting multiple plants); observation totals varied across regions and based on whether plants were native (dark colors) or non-native (lighter colors).

Fig. 2. Meta-regression results for single visit effectiveness differences (A) between honeybees and the most effective non-honeybee taxon within each group and (B) between the average effectiveness across all non-honeybee taxa within each group for a given plant-study. We used standardized mean differences (SMD) to calculate effect sizes. Meta-analytic means are represented as point estimates with their 95% CI (thick lines) and prediction intervals (thin lines). Point estimates from meta-regressions are depicted with their 95% CI (thick lines) and prediction intervals (thin lines). Individual effect sizes are scaled by their precision (1/SE). Positive SMD values (points to the right of zero) indicate that other pollinators were more effective than honeybees.

Fig. 3. Meta-regression results for crop single visit effectiveness differences (A) between honeybees and the most effective non-honeybee bee and (B) between the average effectiveness across all non-honeybee bees for a given plant-study. Effect sizes (standardized mean difference: SMD) were compared for non-crop (gray circles) and crop species (green circles). Meta-analytic means are represented as point estimates with their 95% CI (thick lines) and prediction intervals (thin lines). Individual effect sizes are scaled by their precision (1/SE). Positive SMD values (points to the right of zero) indicate that other bees were more effective than honeybees.

Fig. 4. Meta-regression results for native plant single visit effectiveness differences (A) between honeybees and the most effective non-honeybee bee and (B) between the average effectiveness across all non-honeybee bees for a given plant-study. Effect sizes (standardized mean difference: SMD) were compared outside (gray circles) and inside (orange circles) the honeybee native

667 range. Meta-analytic means are represented as point estimates with their 95% CI (thick lines) and
668 prediction intervals (thin lines). Individual effect sizes are scaled by their precision (1/SE).
669 Positive SMD values (points to the right of zero) indicate that other bees were more effective
670 than honeybees.
671
672 **Fig. 5.** Meta-regression results for the relationship between a pollinator's visit frequency and
673 single visit effectiveness for studies with and without honeybees present. Effect sizes (Fisher's Z-
674 transformed correlation coefficients) were compared for systems where honeybees were absent
675 (gray circles), systems where honeybees were present (yellow circles, also indicated by honeybee
676 icons), and systems where honeybees were present when data were collected, but we artificially
677 removed data corresponding to their visits and re-calculated correlation coefficients (orange
678 circles, also indicated by crossed-out honeybee icons). Estimates are shown with their 95% CI
679 (thick lines) and prediction intervals (thin lines). Effect sizes are scaled by their precision (1/SE).