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RESEARCH ARTICLE

Wild insects and honey bees are equally important to crop yields in a global analysis

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Abstract

Aim: Most of the world's food crops are dependent on pollinators. However, there is a great deal of uncertainty in the strength of this relationship, especially regarding the relative contributions of the honey bee (often a managed species) and wild insects to crop yields on a global scale. Previous data syntheses have likewise reached differing conclusions on whether pollinator species diversity, or only the number of pollinator visits to flowers, is important to crop yield. This study quantifies the current state of these relationships and links to a dynamic version of our analyses that updates automatically as studies become available.

Location: Global.

Time Period: Present.

Taxa studied: Insect pollinators of global crops.

Methods: Using a newly created database of 93 crop pollination studies across six continents that roughly triples the number of studies previously available, we analysed the relationship between insect visit rates, pollinator diversity, and crop yields in a series of mixed-effects models.

Results: We found that honey bees and wild insects contribute roughly equal amounts to crop yields worldwide, having similar average flower visitation rates and producing similar increases in yield per visit. We also found that pollinator species diversity was positively associated with increased crop yields even when total visits from all species are accounted for, though it was less explanatory than the total number of visits itself.

Main conclusions: Our analysis suggests a middle ground where honey bees are not responsible for the vast majority of crop pollination as has often been assumed in the agricultural literature, and likewise wild insects are not vastly more important than honey bees, as recent global analyses have reported. We also conclude that while pollinator diversity is less important than the number of pollinator visits, these typically involve many species, underscoring the importance of conserving a diversity of wild pollinators.

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KEYWORDS
abundance, biodiversity, crop yield, honey bee, pollination, wild insects

1 | INTRODUCTION

Over 75% of the world's food crops are dependent on pollinators to at least some degree (IPBES, 2017). In most crop systems, pollination is provided through a combination of managed honey bees and wild insects, which consist primarily of wild bees but also flies and other insects (Larson et al., 2001; Rader et al., 2016). Despite not being managed for crop pollination, wild insects often make up a significant fraction of total flower visits and can even be the dominant pollinators in cases where land conversion has been less extreme (Garibaldi et al., 2011; Kennedy et al., 2013; Kremen et al., 2002; Reilly et al., 2020; Ricketts et al., 2008).

There is emerging evidence that wild insect visits may increase crop yields per capita more strongly than honey bees (Blitzer et al., 2016; Garibaldi et al., 2013; Mallinger & Gratton, 2015; Winfree et al., 2007), and that honey bees alone can be insufficient for eliminating pollination limitation for many crops (Saez et al., 2022). The mechanism for this is not well understood but could be due to wild bees depositing higher amounts of pollen per visit (Eeraerts et al., 2019; Park et al., 2016; Winfree et al., 2007), or to differences in the behaviour of wild bees and the honey bee (Brittain et al., 2013; Greenleaf & Kremen, 2006). In fact, some recent synthetic analyses (Garibaldi et al., 2013; Rader et al., 2016) have found no significant effect of honey bee visits on crop yields whatsoever, which is a surprising and non-intuitive result given their accepted central role in agricultural pollination (e.g. Calderone, 2012; Delaplane & Mayer, 2000; Klein et al., 2007).

Given the potential for different pollinator groups to have different impacts on crop yields, there is a broader debate about whether it is simply the number of individual pollinator visits that matters for yield, or whether pollinator species diversity (generally measured as the number of pollinator species present, or species richness) is also important. In fact, this question is part of a major debate in ecology about whether the maintenance of ecosystem services (or functions) requires a diverse community of species, or whether most services result from the additive contributions of a few dominant species (Bommarco et al., 2013; Calderone, 2012). Within the pollination literature, diversity often has a positive effect on crop productivity (Dainese et al., 2019; Garibaldi et al., 2015; Garibaldi et al., 2016) but appears generally less important than pollinator abundance. A small number of dominant pollinator species tend to provide most of the pollination for a particular crop, but these species may not be dominant across different crops or within the same crop over time and space (Genung et al., 2020; Genung et al., 2022; Kleijn et al., 2015; Winfree et al., 2015; Winfree et al., 2018). The role of diversity is clearest when pollination needs to be provided across many sites or years (e.g. Lemanski et al., 2022; Klein et al., 2003; Senapathi et al., 2021; Winfree et al., 2018). Disentangling the effects of pollinator abundance and richness is challenging since these variables are frequently correlated (Chase et al., 2018; Roswell et al., 2021), and the answer to this question has been ambiguous even within analyses synthesizing the global pollination literature. For example, Garibaldi et al. (2013) found that pollinator richness was positively associated with fruit set, but that it did not provide any explanatory value to the model beyond pollinator visitation rate. However, Garibaldi et al. (2015) who used a slightly larger dataset (though not entirely overlapping), found that both pollinator abundance and pollinator richness had independent positive effects on fruit set. Given the many crop types and pollinator communities across different regions of the world, it is likely that the stability of these results has been limited by the number of available studies.

Here we use a recently published, global compilation of data on crop yield and flower visitation by wild and managed pollinators that roughly doubles the data available for previous analyses (the CropPol database; Allen-Perkins et al., 2022) to answer the following three questions:

1. What are the relative contributions of honey bees versus wild insects to crop yields worldwide?
2. Is the total number of flower visits by pollinators sufficient to predict crop yields, or is the diversity of pollinator species also important?
3. Are the relationships between pollinator visits, richness and yield stable with the number of studies currently available?

2 | METHODS

2.1 | The CropPol database

The source of datasets for our analysis was the CropPol database (Allen-Perkins et al., 2022). CropPol is an open and dynamic (i.e. periodically updated) database of crop pollination studies that currently contains the data from 137 studies of 49 different crop species from around the world (version 2.0.0). The majority of these datasets provided data on both insect visitation rates and crop yields or related measurements and were used in the analyses conducted for this paper. Within each study, the most basic unit of observation at which pollinator visit frequency and the resulting yield can be paired was the site-year ("site" is typically a field or part of a field). Some sites were sampled for multiple years, but single-year sites were also common. In our analyses, we allowed multiple years of data to be part of the same study as long as the collection methods did not change. We only included studies with at least three site-years, resulting in a total of 93 studies of 35 crops (sensitivity of our results to the

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minimum number of site-years per study is explored in Appendix S1). Because some studies included multiple years, this dataset represents a total of 129 study-years, and a total of 2321 site-years. As expected, studies from Europe and North America were overrepresented in our sample, together totalling almost two thirds of the datasets. It is also likely that, even within regions, there are biases in the landscapes where studies were located and in which crops were selected. This limits our ability to infer patterns on a global scale, but currently represents the best available data.

A strength of the dynamic database is that it will allow continuous updates to our analysis as the number of available studies grows. We have posted a simplified dynamic version of this analysis that automatically draws from the CropPol database updating the models and storing past versions here: https://ibartomeus.github.io/CropPollinationModels/ (Bartomeus et al., 2023).

2.2 | Data processing

Across the 93 datasets, the number of insects visiting flowers was measured in two different ways: either by observing the number of insects visiting flowers per unit time (a true visit rate), or by netting insects visiting flowers and summing the number of specimens collected. In the context of crop pollination studies, the latter data type is commonly referred to as "net data" and might be more accurately described as visitor abundance on flowers than as a true visit rate. In this analysis, we used the two interchangeably as "number of visits". If both types of measurements were available for a given dataset, preference was given to true visit rates; any potential variation in mean or variance that might result from the different collection methods across studies should be mitigated because we converted all values to z-scores for the analysis. All datasets categorized visit rates or visitor abundances into the following insect groups: honey bee, bumble bees, other wild bees, non-bee Hymenoptera, Syrphids, Bombyliids, other flies, beetles, Lepidoptera and other insects, although not every study recorded every group. In this paper, we will refer to all insect visitors as "pollinators" even though it is possible that some taxa did not effectively provide pollen to flowers that they visited (e.g. King et al., 2013). For our main analysis, we chose to combine the visits by all pollinators other than the honey bee into a "wild insects" group. Thus, we compared two main groups, honey bee (HB) and wild insects (WI), consistent with previous analyses (Garibaldi et al., 2013). For an alternative analysis that breaks "wild insects" down into finer taxonomic groupings, see Appendix S1. We did not drop studies that found or reported only bees as visitors, on the assumption that researchers for the most part did not neglect sampling insect groups that were important for the pollination of their crop. We did however drop 10 studies that specifically focused on wild insect visitation and did not record honey bee visits at all, because these studies would misattribute to wild insects the yield due to honey bees. We did not need to do a similar filtering step for wild insects because wild insects were recorded in all 93 studies in the final set.

Crop yield is defined as the amount of agricultural production harvested per unit of harvested area. In our datasets, often this was simply kg per unit area, but sometimes was more specific to the crop, for example kg per plant, fruit per branch, fruit/seed set, and so forth. (Table S1). When more than one production variable was provided, we used the variable listed by the data providers as the primary value (i.e. "yield") in the online database as opposed to the secondary measure (i.e. "yield2"). We did not include any studies that only estimated pollen deposition (visits multiplied by pollen per visit) because this not a direct measurement of the effect of pollinator visitation. As above for insect visitation rates, we performed analyses on *z*-scores to mitigate differences in scale between metrics. The sensitivity of our results to the production variable provided is explored in Appendix S1.

2.3 | Relative contributions of honey bees versus wild insects to yield

We analysed the relative importance of the honey bee and wild insect visits to crop yields in two ways. First, we quantified the total number of visits provided by each pollinator group at each site-year combination and summarized the relative fraction of visits within each crop system. Although it is reasonable that the importance of pollinators to yield might follow directly from their relative visitation rates, potential differences in per-visit effectiveness could modify or even reverse the relative importance. Per-visit effectiveness estimates were not available for most crops and regions, therefore, as a second step, we used the number of insect visits by each group as predictors of crop yield in a set of general linear mixed-effects models, which we compared by AICc. This method has the advantage of being a direct measure of the effect of insect visits on yield that does not rely on the assumption that pollen deposition will be well-correlated with yield—which it may not be if, for example, crop yield is not limited by pollen deposition (Reilly et al., 2020). In total, we compared five models (model set 1) that varied in complexity. The full model included the effects of honey bee visits, wild insect visits and their interaction, whereas the simplest model included no predictors. All models included both random intercepts and slopes for study system. We chose to fit random slopes in addition to random intercepts because it is reasonable to assume that the slope of the relationship between visits and yield could vary across crop studies for any number of reasons that might differ across crops such as degree of pollinator dependence (Klein et al., 2007), bloom phenology, or management practices. However, to explore the sensitivity of our results to the choice of random effect structure, we also tested two other sets of models. First, for comparison with previous literature, we ran a parallel series of simpler models that estimated random intercepts only without random slopes (Table S2). Second, in order to evaluate whether crop species explained some of the variation across studies, we ran a more complex set of models that included random slopes and intercepts of crop species in addition

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to random slopes and intercepts of study nested within crop species (Table S3). Neither of these alternative analyses showed substantial support when compared with the main analysis by AICc.

In all models, visits by each insect group and the outcome variable (yield) were transformed to z-scores prior to running the model, so the slopes of the fixed effect estimates from the model were interpreted as effect sizes for comparison. We found that the variance of honey bee visits and wild insect visits were similar to each other within studies (Figure S1), which aided in interpretation. Across all five models, we also calculated relative importance values for wild insect and honey bee visits as predictors by summing the Akaike weights of the set of models in which each predictor appeared (Burnham & Anderson, 2002). Mixed-effects models were run using the lmer() function in the lme4 package (Bates et al., 2015) in R (R Core Team, 2021). Note that AICc model comparisons in lmer() were performed without restricted maximum likelihood (REML = F), while parameters were estimated with REML = T (Zuur et al., 2009). AICc values were calculated using the MuMIn package (Barton, 2020).

2.4 | Importance of pollinator richness versus abundance

To determine whether crop yields increased in the presence of more wild insect species or whether it was simply the total number of insect visits to flowers that was important, we analysed a new set of models that contained pollinator species richness in addition to flower visitation rate by honey bees and wild insects. As is common in observational studies, WI richness and abundance were indeed correlated (Pearson's $r = 0.54$), which means that some variance in crop yield explained by these variables will not be uniquely attributable to either. But, variance inflation factors were low—below 1.2—which suggests our models should be sufficient to assess the relative importance of abundance in WI richness. Note that there should be much less correlation between richness and HB visits because there was only one honey bee species in nearly all datasets ($r = 0.12$).

Including the interactions between the three main predictors resulted in 18 potential models. In addition, we tested models that used the sum of visits by all insects as a predictor instead of the individual effects of wild insects (WI) and honey bee (HB). Of particular interest were (1) comparisons between models with and without the richness effect, and (2) the relative importance values (sum of Akaike weights) of richness as a predictor compared to that of wild insect visits or all insect visits. Such comparisons allow us to assess the added value of richness while accounting for differences in abundance. For logical consistency, we did not allow "all insect" visits and visits by individual groups to be predictors within the same model, and we also did not calculate relative importance values or average across models that differed in how visits were summed. The studies included in this part of the analysis were further limited to those that provided richness measurements in addition to counts of honey bee and wild insect visits ($n = 63$ studies of 32 crops, representing 85 study-years and 1129 site-years).

2.5 | Sensitivity of results to the number of datasets used

To explore the sensitivity of our results to the number of datasets used for the analysis, we drew subsets of the full database, increasing the number of studies from two studies to the full number available. For each number of studies, we drew up to 1000 random subsets. There were a maximum of 93 available studies for our estimates of the slope of honey bee and wild insect visits, using the model described above that included both the fixed effects of wild insect visits and honey bee visits (the best model by AIC). For our estimates of richness, the maximum number of available studies was 63, this time using the model that included a fixed effect of species richness in addition to the sum of all insect visits (best model by AIC). To quantify how the uncertainty in our estimates decreased as the number of studies increased, we calculated empirical 95% confidence intervals based on the 0.025 and 0.975 quantiles of the subsampled datasets at each number of studies. These confidence intervals also allowed us to make comparisons to previous values from the published literature, which were calculated using fewer datasets than are now available.

We also repeated this same procedure on three specific crop systems to test model sensitivity to the number of datasets within crops. We chose oilseed (*Brassica napus*), blueberry (*Vaccinium corymbosum*) and apple (*Malus domestica*) because these were the three crops for which we had the largest number of studies ($n = 9$, 9, 16, respectively). For each crop, we specified a general linear mixed-effects model with the fixed effects of wild insect and honey bee visits, and a random intercept of study. We then generated all the unique possible combinations of studies at each number of studies from 1 to n within each crop, then ran the model for each subset of studies. This allowed us to understand how many studies per crop were needed to find reliable (i.e. stable) estimations of pollinator yield contribution.

3 | RESULTS

3.1 | What are the relative contributions of honey bees versus wild insects to crop yields worldwide?

The mean percent of visits provided by wild insects across all 93 studies we analysed was 47.8% (SE = 3.1%), that is nearly equal to that of the honey bee. However, this proportion varied widely among crops (Figure 1). Many studies showed dominance by either the honey bee or wild insects, and a few studies found one group exclusively. Studies showing high dominance by wild insects were more common: 12 studies had a median wild insect proportion of 1.0, compared with only two studies for the honey bee. Even for

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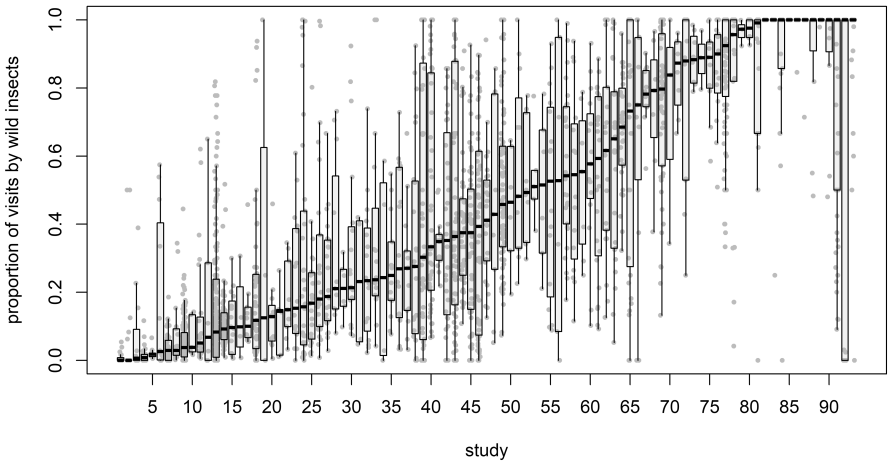

FIGURE 1 Proportion of total visits provided by wild insects (vs. honey bee) for each pollination study ($n = 93$). In these boxplots, the bold centre line is the median, the hollow boxes cover the interquartile range (IQR), and the whiskers extend to the most extreme points within 1.5 × IQR from the median. If any points are more extreme than this, they are plotted as grey circles. Numbered Crop IDs on the *x* axis are listed in Table S1.

studies with a relatively even proportion of each group, there was high variability across individual sites and years (note the large boxes and whiskers in Figure 1). There was relatively little correlation between visits by wild insects and honey bees (Pearson's $r = 0.1$ when calculated across all site-years).

Although the average number of visits by wild insects and honey bees were similar, differences in per-visit effectiveness could still result in stronger effects on crop yield by one group or the other. However, in the mixed-effect models relating the effect of wild insect and honey bee visitation to yield, both the effects of WI and HB visits were retained by AIC selection and had similar values (Table 1). The best model (model 5: WI and HB) was substantially better than models including either WI or HB alone (ΔAICc = 32 and 13 respectively), or the null model (ΔAICc = 54), consistent with both wild insects and the honey bee being important to crop yields worldwide. No evidence was found for an interaction between wild insects and honey bee visits. The slopes for both WI and HB visits were positive, but relatively shallow (WI: slope = 0.061, HB: slope = 0.068), indicating that yields are expected to increase with increasing pollinator visits of either group within a system, albeit not very strongly. The effect size of HB was larger than that of WI, but only very slightly so. In the supplemental analysis that looked within wild insects, the largest effect sizes we found among the wild insect groups were those of bumblebees and non-bees (Table S7). Because the above slopes, that is effect sizes, are based on *z*-score data, their units are standard deviations (SD). Thus, an increase of 1 SD in the number of pollinator visits produced an increase approximately 1/15 SD in yields, regardless of type of pollinator. Given this, and since the variances of honey bee and wild insect visits were not different (Figure S1), the estimated increases in yield should also be similar on a per individual pollinator basis. We estimate that effect sizes of 0.061 and 0.068 would correspond to a 9.3% increase in yield per 1 SD increase in wild insects visits, and a 10.4% increase in yield per 1 SD increase in honey bee visits when averaged across all studies and fields. Due to high variation among studies, individual crops or fields within crops might see yield increases much higher or much lower than this amount.

TABLE 1 Model selection table with estimated coefficients for the 5 mixed-effects models (model set 1) we tested for the main comparison of the effects of wild insects (WI) and honey bee (HB) on crop yields.

Model	Intercept	WI	HB	WI × HB	AICc	ΔAICc
5	0.000	0.061	0.068		6444.1	0
9	0.008	0.065	0.073	0.005	6454.6	10.5
3	0.000		0.074		6456.9	12.8
2	0.000	0.064			6476.2	32.1
1	0.000				6497.8	53.7

Note: All models included both random intercepts and slopes by study ($n = 93$ studies). The best model by AICc is highlighted in yellow.

The relative importance values (sum of Akaike weights) we calculated for WI and HB were equivalent (both nearly equal to one, Table 2), consistent with the highly favourable AICc value of model 5. Estimates for the effects of wild insects and honey bees based on random slope estimates were highly variable across the individual crops, as high as 0.29 for wild insects on coffee in India, and 0.40 for honey bees on blueberry in the northeastern US. This means that, for example, blueberry yield increased by 0.4 SD when honey bee visitation increased by 1 SD (Figure 2).

3.2 | Is the total number of flower visits by pollinators sufficient to predict crop yields, or is the diversity of pollinator species also important?

We found that the best model by AICc was one including both the sum of "all insect" visits (wild insects + honey bees) and pollinator richness (model R8b, Table 3). In this model, the effect size of all insect visits was about three times the size of the effect size of richness (0.102 vs. 0.032). Consistent with this result, the next best model was nearly equivalent and included only the "all insect" visits predictor but not pollinator richness (R5b, ΔAICc = 0.5). In addition to these, there were three other models that were relatively close in AICc: Approximately equal support was found for model R7, which included HB and richness, but not WI (ΔAICc = 1.8) and model R5,

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which included both WI visits and HB visits separately but not richness (ΔAICc = 2.2). The support for model R5 (lacking a richness effect) is again consistent with visits being more important than richness. The support for model R7 is more surprising given that the HB and richness effects were similar in size. We believe that this is due to the relatively high correlation between WI visits and richness, and underscores the conclusion that HB visits alone are insufficient to explain crop yields. Model R8 retained the separate effects of WI and HB, in addition to the richness effect (ΔAICc = 4.4). Both visit effects were similar to each other and both larger than the richness effect (by about two times). Together, these five models had a cumulative weight of 0.955, that is the probability that the true best model is within this set. Consistent with these results, the effect size of richness was over five times smaller than the effect of "all insect" visits in the averaged model AVGb (0.02 vs. 0.11).

We calculated a relative importance value (sum of Akaike weights across all models) for richness of 0.59, approximately equal to the value of 0.52 for WI visits (Table 2), but less than that of HB visits (0.998). In the "all insects" models, the relative importance of richness was also less than that of "all insects" (0.57 vs. 0.99). In general, the results for relative importance values suggest a similar conclusion to that of relative effect sizes: that the effects of wild insect visits and richness on crop yields were similar to the extent that they could be separated, but that the effect of total visits by all insects were somewhat more important than the effect of pollinator richness.

TABLE 2 Relative variable importance values for predictors tested in each set of mixed-effects models, calculated by summing the Akaike weights for each of the models in which it is present.

Predictor	Model set 1	Model set 2a	Model set 2b
WI	0.998	0.523	
HB	1.000	0.976	
AI			0.990
RICH		0.593	0.569

Note: Model set 1 did not include any richness effects and was based on a larger dataset ($n = 93$ studies) than model sets 2a or 2b (63 studies). Model set 2a did not contain any models testing "all insects" and model set 2b did not include any models that separated the effects of WI an HB.

3.3 | Are the relationships between pollinator visits, richness and yield stable with the number of studies currently available?

As the number of studies included in the analysis was increased, we found that the estimated slopes (i.e. the effect size of pollinators on yield) of wild insect visits, honey bee visits, all insect visits, and pollinator richness converged quickly toward their final mean estimates for approximately the first 10 studies, but then slowed drastically (Figure 3). A surprisingly large number of studies were required before the lower bound of the empirical 95% CI did not overlap zero for all four predictors (62, 43, 28, and 48 studies for WI, HB, AI, and richness respectively). This is presumably due to the large variation among studies, which made it difficult to predict the true mean effect from even a fairly large sample of studies. Funnel plots show that some previous results from the literature were still markedly outside the range of what we estimated. In particular, Garibaldi et al., 2013 found much higher effects of wild insect visits (points 3 and 4 on Figure 3) and Garibaldi et al. (2015) found much higher effects for all insect visits (point 9) than would be expected based on rarefaction of the CropPol datasets. These estimates were outside the 95% CIs that we estimated for the number of studies, suggesting that the distribution of crops in those datasets may differ from that of the crops analysed here. On the other hand, most or all of the other literature estimates were fairly consistent with our values, given the differences in sample size. For instance, the at-first surprisingly low (slightly negative) effect size for honey bee visits in Rader et al., 2016 (point 5 on Figure 3) is well within the range of values we found for subsamples with a similar number of studies ($n = 19$). Likewise, so was the estimated effect size for Dainese et al., 2019, the largest ($n = 42$ studies, point 8 on Figure 3) and most recent of the meta-analyses. On the one hand, these results suggest that the current number of studies is sufficient to reach stable estimates, but on the other hand this stable estimate may not be globally representative. Future work should focus on under-represented crops and study regions.

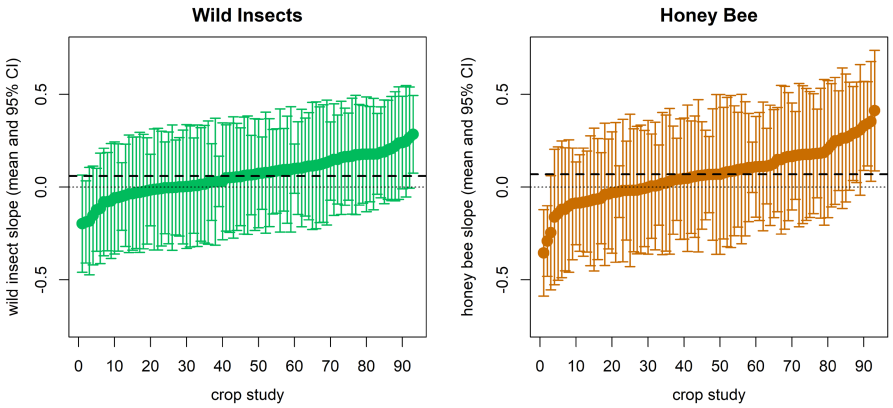

FIGURE 2 Estimated means and 95% CIs for the effect of wild insects and the honey bee on crop yield for each pollination study ($n = 93$). Dashed black line is the overall mean across all studies. Means were calculated using the random effect estimates from Model 5.

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TABLE 3 Model selection table with estimated coefficients for the mixed-effects models we tested to evaluate the effect of pollinator species richness on crop yields (using the richness dataset, $n = 63$ studies).

Model	Intercept	WI	HB	AI	RICH	WI × HB	WI × RICH	HB × RICH	AI × RICH	AICc	ΔAICc
R8b	−0.019			0.102	0.032					3109.9	0.0*
R5b	−0.021			0.122						3110.4	0.5*
R7	−0.022		0.075		0.071					3111.7	1.8*
R5	−0.017	0.084	0.087							3112.1	2.2*
R8	−0.016	0.060	0.077		0.036					3114.3	4.4*
R9	−0.007	0.091	0.095			−0.021				3116.6	6.7
R15b	−0.013			0.108	0.032				−0.020	3117.3	7.4
R3	−0.022		0.088							3117.8	7.9
R4	−0.023				0.075					3117.9	8.0
R12	−0.011	0.069	0.088		0.031	−0.023				3120.0	10.1
R11	−0.019		0.077		0.070			−0.013		3120.2	10.3
R13	0.003	0.075	0.080		0.032		−0.038			3120.5	10.6
R6	−0.019	0.048			0.046					3121.6	11.7
R14	−0.013	0.062	0.079		0.035			−0.019		3121.9	12.0
R2	−0.017	0.082								3122.2	12.3
R17	0.008	0.083	0.088		0.028	−0.018	−0.035			3125.7	15.8
R16	−0.013	0.069	0.088		0.031	−0.022		−0.002		3127.2	17.3
R10	−0.001	0.064			0.041		−0.036			3128.0	18.1
R15	0.004	0.077	0.081		0.030		−0.037	−0.019		3128.4	18.5
R1	−0.023									3130.6	20.7
R18	0.009	0.083	0.089		0.027	−0.016	−0.035	−0.004		3135.0	25.1
AVGa	−0.019	0.041	0.079		0.038	−0.001	0.000	0.000			
AVGb	−0.019			0.110	0.019				0.000		

Note: All models included both random intercepts and slopes by study. The best model by AICc is highlighted in yellow. The coefficients of a model created by averaging model set 2a (R1-R18, not including the "all insects" models) are listed at the bottom as AVGa. The coefficients created by averaging model set 2b (the "all insects" models R5b, R8b, R15b and other relevant models R1, R4) are listed as AVGb. *The starred models together had a cumulative weight of 0.955.

Within the three crops having a sufficient number of studies to test how model certainty increased with sample size (oilseed, blueberry and apple), we found three different patterns. For oilseed, mixed models using only a few datasets varied widely, but converged to an effect size of 0.01 for wild insect visits and 0.06 for honey bees (Figure 4), indicating fairly weak correlations between visits and yield. In oilseed, neither effect was significantly greater than zero ($p > 0.5$), consistent with high variation across the nine oilseed studies. For blueberry, the datasets converged on a mean effect for wild insect visits of −0.06 (but not significantly different from zero, $p = 0.17$), and a mean effect for honey bee of 0.14 ($p = 0.001$). Previous studies of blueberry have found pollination limitation in at least some areas (e.g. Benjamin & Winfree, 2014; Isaacs & Kirk, 2010; Reilly et al., 2020). Our results are consistent with an interpretation that these pollination effects are largely driven by honey bees. For apple, we estimated positive effects for both wild insect visits (0.07) and honey bee visits (0.05), but neither was significant ($p > 0.2$). The estimates of WI and HB effects for all three crops were consistent with those of the alternative analysis that estimated a random effect of study nested within crop (Figure S2), suggesting that they are robust at these sample sizes. In general, these results underscore the high variability observed among single studies even within the same crop, showing that extreme results could be obtained using some combinations of two or three studies. Such variability might be partly due to the inclusion of studies with a relatively low number of sites, or to studies being based on different yield metrics, but it is difficult to evaluate this with the available data for single crop systems. In any case, such extremes become much less likely above four studies, with the overall pattern becoming clear. In the case of blueberry, the effect of honey bee visits was clearly above zero even at two or three studies. Despite this, many of the crops in our database are represented by only one or two studies, highlighting the need for more data collection.

4 | DISCUSSION

We found that in 93 studies of crop pollination from around the world, wild insects accounted for roughly half the pollinator visits to crop flowers, with the other half provided by honey bees, in most

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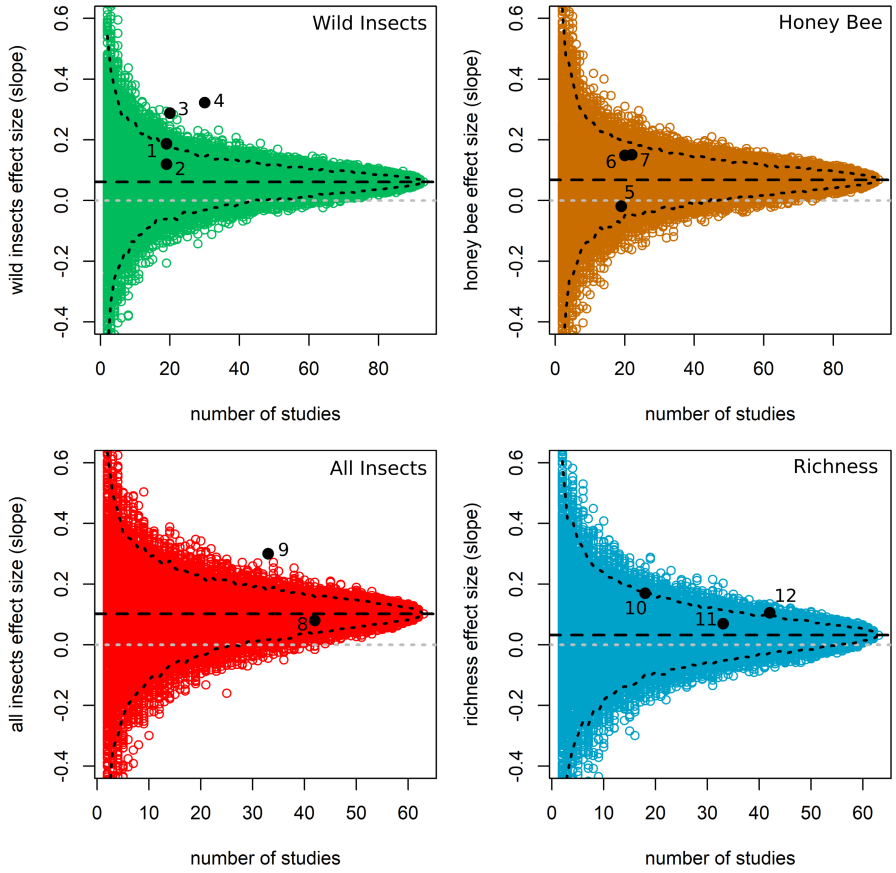

FIGURE 3 Funnel plots for the effect sizes of wild insect visits, honey bee visits, all insect visits, and richness as the number of studies increases. Each point represents an estimate generated by using a random subsample of the crop studies available in the full dataset. Dotted black lines represent empirical 95% CIs based on quantiles of the 1000 subsampled datasets at each number of studies. The dashed black line is the estimate based on the full subset of crops ($n = 93, 93, 63, 63$). Model 5 was used for WI and HB, and model R8b was used for all insects and richness. The numbered dots correspond to values reported in the literature (Table S4). Because all effect sizes were based on regressions using *z*-scored data, it is reasonable to compare them on the same plot.

cases a domesticated species (*Apis mellifera*, or in some cases *A. cerana*) managed for crop pollination. These results are largely confirmatory as they are similar to findings of previous studies (Garibaldi et al., 2013, Rader et al., 2016, Reilly et al., 2020, others), albeit with a larger sample size. Obviously our results also depend on farmers' decisions around honey bee stocking levels. However, this is not a problem--it means that *given current management practices*, which are not decided on arbitrarily, honey bees still provide only half of global pollination services. Although the number of flower visits from wild insects and honey bees were remarkably similar on average, different types of crops varied widely in the extent to which they are visited by wild insects (Figure 1, Table S1), and in the types of wild insects involved (Figure S3). For example, several tropical trees (e.g. soursop, acerola, achiote, sugar apple) and a number of other crops including okra, cucumber, calabash and cotton were visited almost exclusively by wild insects, whereas a few crops including almond, blueberry, sunflower and apple obtained >95% of their flower visits from honey bees, at least in some regions. Interestingly, some crops that show clear patterns of dominance by honey bees in certain parts of the world (e.g. blueberry in North America, Reilly et al., 2020) appear to be supported by a much more even mix of honey bee and wild insects on a global scale.

Likewise, our analysis showed that flower visits by wild insects and honey bees had similar effects on increasing crop yield. That is, for a given number of pollinator visits to crop flowers, the increase in crop yield is similar whether the pollinator was a wild insect or a honey bee. If anything, and in contrast to previous conclusions, the importance of wild insect visits was slightly less than that of honey bee visits overall, although the difference was not statistically significant (Table 2). Our findings contrast with some recent studies suggesting that honey bees are less important than wild insects, or even unimportant, as drivers of global crop yields (Garibaldi et al., 2013; Rader et al., 2016). They also contrast with the perception, possibly more prevalent in agricultural than in academic contexts, that the managed honey bee is the primary agricultural pollinator (e.g. Delaplane & Mayer, 2000; Klein et al., 2007).

In any case, the relatively shallow slopes of the relationship between visitation and yield that we found indicate less than a 1/10 unit increase in yield per 1 unit increase in pollinator visits, continuing to highlight the large amount of variation in global yields that is probably not attributable to pollination deficits (Garibaldi et al., 2016). On the other hand, this seemingly small effect might have real importance for farmers. If increases of one standard deviation of pollinator visitation are ecologically achievable (e.g. through managing for wild bees or the addition of honey bee colonies), we predict that this could result in average yield increases of around 10%.

We found that simply the number of visits crop flowers receive from insect pollinators is the best predictor of crop yield, with the number of species visiting the flowers being of secondary importance. While abundance and richness were positively correlated, which can make it difficult to perfectly separate their effects (Roswell et al., 2021), variance inflation factors were low, making this dataset sufficient to gauge these variables' relative importance. And indeed, both methods we used to compare these effects (effect

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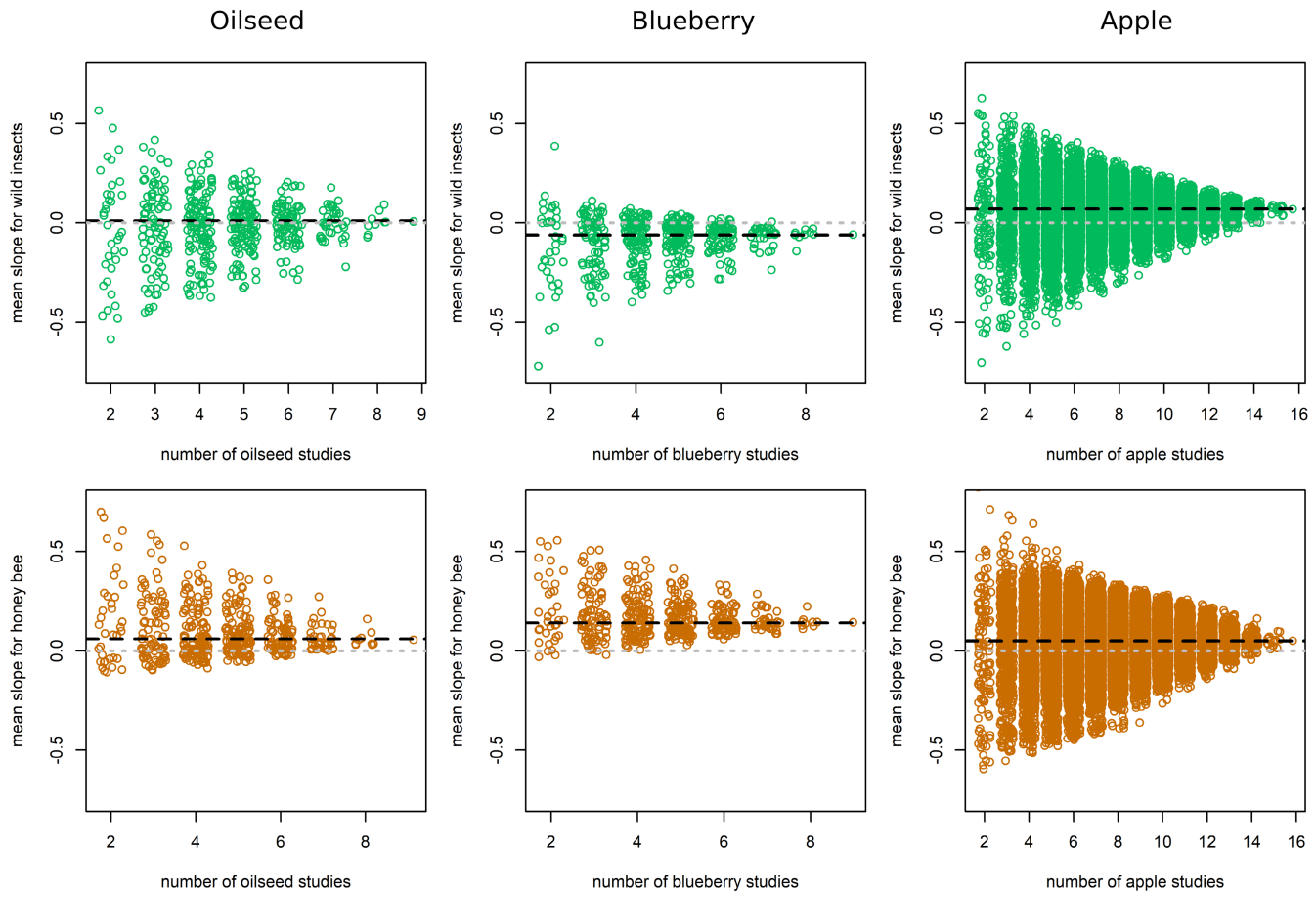

FIGURE 4 Within-crop funnel plots for the slopes (effect sizes) of the relationship between crop yields and wild insect visits (top row) or honey bee visits (bottom row), as the number of studies increases. Each point represents an estimate generated by using a unique combination of the studies available for each crop (oilseed, blueberry, and apple), from two up to all available studies. The dashed black line is the estimate using all available studies ($n = 9, 9, 16$). All models contained the fixed effects of WI visits and HB visits and a random intercept of study.

sizes and relative importance values) agreed, suggesting that the number of pollinator visits was up to five times more important than pollinator richness. The larger effect of pollinator abundance found here could be due to the influence of a few numerically dominant species such as honey bees or bumblebees that deposit most of the pollen (Kleijn et al., 2015; Winfree et al., 2015). In the case of the honey bee, numerical dominance may be high enough to overcome mediocre effectiveness on a per-visit basis (Hung et al., 2018). In this respect, pollinator communities are like the vast majority of other taxa communities, in that they are numerically dominated by a small number of species (McGill et al., 2007). Although some studies of the pollination of a single crop have found that different pollinator species are complementary, leading to non-additively increased yield when more pollinator species are present (Bluthgen & Klein, 2011; Chagnon et al., 1993; Fründ et al., 2013; Hoehn et al., 2008), biologically we might expect most complementarity to occur *across* crop plants. This is because different crops are pollinated by different pollinator faunas, likely due to differences in bloom morphology and reward, as well as the geographic region and habitat where the crop is grown, and the time of year the crop blooms (Ahrenfeldt et al., 2015; Lemanski et al., 2022; Simpson, 2022; Willcox et al., 2019; Winfree et al., 2018). Thus, relatively few pollinator species might account for most of the pollination of a single crop, but the identity of these key species might differ across crops, leading to a greater role for species diversity when analysed at that larger scale (Simpson, 2022). Furthermore, although honey bees were dominant in many crop systems, honey bee visits were not sufficient to predict yields in the best models—at least some aspect of wild insects was required, either their visitation rate or species richness. We also found evidence that non-bee visits may be as important as or even more important than bee visits in many crop systems (Table S7), consistent with studies highlighting the importance of non-bees for pollination services (Rader et al., 2016).

At last, our analysis, which was based on 93 studies of crop pollination from 31 countries, offers a useful perspective on the results obtained by earlier synthetic analyses asking similar questions. Most notably, we found wild insects and honey bees to be similarly abundant as crop pollinators overall, and also similar in their effectiveness at increasing yield, whereas earlier syntheses based on fewer studies concluded that wild insects are more important than

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honey bees. Our current results do not support this on average at the global scale, although it is certainly true for many crop systems. Some of the variability across crop systems and regions is likely attributable to variation in the effectiveness of honey bees in different contexts and among the many taxa of wild insects. One area where improvement could be made is in incorporating estimates of pollinator efficiency into the relationship between visitation rates and yields. Those data do not currently exist for many of crops and regions around the world, but they should be a valuable explanatory variable as more of those data are published. We must also keep in mind that the patterns that define the current state of pollination are dependent on many complex variables that overviews such as ours are unable to measure, such as the size of wild insect populations near crop fields and the decisions growers make about honey bee stocking levels, and thus must be monitored closely as future conditions change. By creating a pipeline which automatically updates the main results as more data are added to the database under version control (Kim et al., 2022), we give the first step to obtain robust iterative conclusions on the long term.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the CropPol database at https://github.com/ibartomeus/OBservData with DOI: 10.5281/zenodo.4311291. A simplified dynamic version of the analysis can be found at https://ibartomeus.github.io/CropPollinationModels/ with DOI: 10.5281/zenodo.7481551.

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SUPPORTING INFORMATION

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