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REVIEW

Global synthesis of apple pollination research highlights general pollen limitation and positive contributions of wild bees compared to honeybees

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Abstract

1. Apple is one of the most important pollinator-dependent fruit crops worldwide. To secure high-quality yields, it is crucial to know which, and to what extent, pollinating insects contribute to its pollination success as measured by fruit set, fruit weight and seed set.
2. We perform a meta-analysis of field studies conducted across multiple orchards on insect-mediated pollination in apple cultivation, using raw data from 29 studies,

Correction added on 30 August 2025, after first online publication: The ORCID for Paulo V. A. Borges has been corrected.

For affiliations refer to page 10.

totalling 532 orchard replicates. We assessed the extent of pollen limitation on different pollination outcomes and assessed the contribution of honeybees, wild bees and bee species richness to apple pollination.

3. Across all studies, we detected strong evidence of pollen limitation for fruit set and seed set, but not for fruit weight. Honeybees were the most abundant flower visitors (average relative visitation of 71.9%) compared to wild bees; but when correcting for their pollination efficiency, the relative pollination contribution of honeybees was lower compared to their relative visitation (vice versa for solitary bees).
4. We conclude that honeybee visitation rate did not influence fruit or seed set; yet increasing honeybee visitation had a small, negative effect on fruit weight. Fruit set was not influenced by wild bee visitation rate, whereas wild bee visitation had a small, but clear positive effect on fruit weight and seed set. Bee species richness had a small, positive effect on seed set; whereas it did not affect fruit set and fruit weight.
5. *Syntheses and applications*. Our study highlights that pollen limitation is common in this global crop. While managed honeybees are dominant pollinators, a diverse community of wild bees contributes significantly to apple pollination and high-quality yield. The positive effect of wild bees and species richness on fruit weight and seed set demonstrates that wild bee pollination results in better-quality fruit production (increased weight & seed set). Therefore, our synthesis highlights the importance of conserving pollinator diversity to maintain pollination services. The absence of a clear effect of honeybee visitation rate on fruit and seed set, coupled with its negative impact on fruit weight, suggests a need for further optimisation of honeybee management to improve the cost-efficiency of pollination management.

KEYWORDS
Apis mellifera, crop production, fruit set, *Malus* spp., meta-analysis, seed set, systematic review, wild pollinators

1 | INTRODUCTION

Most of the world's food crops depend on insect-mediated pollination to secure crop production (Eeraerts, Siopa, et al., 2025). Moreover, pollinating insects are essential for safeguarding nutritionally diverse human diets, as crops such as fruits, nuts and vegetables depend on insect-mediated pollination (Eilers et al., 2011; Gazzea et al., 2023). In crops, pollination is provided mainly by managed western honeybees (*Apis mellifera*) and wild insect pollinators (Rader et al., 2016; Reilly et al., 2024). Despite widespread research efforts on crop pollination management, many crops experience pollination deficits, whereby natural insect pollination does not meet the potential maximum. Recent analyses show that pollen limitation depends on the crop species (Holland et al., 2020; Osterman et al., 2024), the plant mating systems (Sáez et al., 2022), the cultivar (Eeraerts et al., 2024; Garratt et al., 2021), production region (Garratt et al., 2021; Olhnuud et al., 2022) and the pollination success parameter such as fruit set, fruit weight, seed set, among others (Chabert et al., 2022; Eeraerts et al., 2024).

Assessment of pollen limitation involves measuring the maximum pollination success of flowers supplemented with pollen by hand and comparing this with natural, insect-pollinated flowers. Including this hand-pollination treatment is essential since maximum pollination success varies from field to field due to variation of available (plant maternal) resources, cultivars and even conditions within a field (Chabert et al., 2022; Eeraerts et al., 2024; Garratt et al., 2021). Although comparing natural insect pollination with experimental hand pollination provides an assessment of the extent of suboptimal pollination, the pollen limitation assessment itself is difficult to translate into management when suboptimal pollination is detected. Here, insight into how pollination success varies along pollinator visitation gradients is needed to guide management to improve crop pollination (Chabert et al., 2022; Eeraerts, Siopa, et al., 2025; Reilly et al., 2024). Distinguishing honeybees and wild pollinators is relevant as both require different management approaches, with a focus on honeybee hives for honeybees and a focus on creating high-quality farms and landscapes for wild pollinators.

Global syntheses on the relation between flower visitation frequency, or flower visitation rates, by pollinating insects (hereafter referred to as 'pollinator visitation') and crop pollination show that both honeybees and wild pollinators contribute to crop production (Eeraerts, Siopa, et al., 2025; Garibaldi et al., 2013). Results from multi-crop syntheses that attempt to disentangle the importance of honeybee and wild pollinator visitation for crop pollination report high variability in the strength of the detected effects (Dainese et al., 2019; Eeraerts, Siopa, et al., 2025; Garibaldi et al., 2013; Rader et al., 2016; Reilly et al., 2024). Similarly to pollen limitation, the contributions of pollinating insects to crop pollination success are variable across crops (Pisman et al., 2022; Reilly et al., 2024), plant mating systems (Sáez et al., 2022), cultivars (Burns & Stanley, 2022; Eeraerts et al., 2024), region (Eeraerts et al., 2023; Gibbs et al., 2016) and landscape context (Dainese et al., 2019; Garibaldi et al., 2011). Pollination syntheses to date have often considered multiple crops simultaneously (Dainese et al., 2019; Eeraerts, Siopa, et al., 2025; Garibaldi et al., 2013; Rader et al., 2016; Reilly et al., 2024). As different crops have variable degrees of pollination dependency (Klein et al., 2007; Siopa et al., 2024), crop-focused syntheses may provide clearer insights into the observed patterns and hereby amend the high variability of the detected effects in multi-crop synthesis. For example, Woodcock et al. (2019) reported a positive impact of total visitation and pollinator species richness on oilseed rape pollination. However, Moreaux et al. (2022) did not detect any effect of pollinator species richness on coffee pollination. In blueberry, positive effects of both honeybee and wild bee visitation were concluded (Eeraerts et al., 2023).

Apple (*Malus domestica*) is a globally important crop with high economic and nutritional value, with 95.83 million tonnes produced globally from 4.83 million ha of orchards (FAOSTAT, 2025). As this crop is cultivated globally, apples are cultivated in a diverse set of landscape contexts, ranging from small orchards in diverse landscapes (Dorji et al., 2021; Zanini et al., 2024) to large fields in homogeneous landscapes (Geslin et al., 2017; Osterman, Theodorou, et al., 2021), as well as intermediate contexts (Leclercq et al., 2023; Nunes-Silva et al., 2020; Pisman et al., 2022). Apple relies on insect pollination to produce fruits of marketable value (Ramírez & Davenport, 2013). Apple is generally self-sterile through the gametophytic self-incompatibility mechanism, which implies that cross-pollination from a compatible polliniser cultivar is required to set fruits with seeds and produce economically viable yields (i.e. cross-pollination; Ramírez & Davenport, 2013; Chabert et al., 2024). Furthermore, apple quality, expressed as fruit size, symmetry and shelf-life, benefits from insect-mediated pollination (Matsumoto et al., 2012; Samnegård et al., 2019). Apple flowers are visited by a great diversity of insects, including bees, hoverflies, other flies, wasps and moths (Pardo & Borges, 2020; Roquer-Beni et al., 2021), yet flower visits by honeybees and wild bees are the most frequent and often considered the most efficient (Bernauer et al., 2022; Thomson & Goodell, 2001). Among bee species, most often certain bumble bee species and solitary bee species are more efficient than the honeybee (Park et al., 2016; Roquer-Beni et al., 2022; Vicens & Bosch, 2000). To ensure pollinator visitation to facilitate apple orchards, they are stocked with honeybee hives, yet densities per area of orchards vary within and across production regions (Mallinger & Gratton, 2015; Geslin et al., 2017; Osterman, Theodorou, et al., 2021; Wu, Dai, et al., 2021; Wu, Tscharntke, et al., 2021; Dorji et al., 2021; Zanini et al., 2024). In apple, the number of seeds is regarded as a key driver and proxy for fruit quality, as increasing seed number improves fruit weight, fruit symmetry and shelf-life (Buccheri & Di Vaio, 2004; Garratt et al., 2021; Pisman et al., 2022). However, the link between seeds and apple quality also depends on the cultivar, crop load and farm management (Buccheri & Di Vaio, 2004; Garratt et al., 2021; Naschitz & Naor, 2005; Siopa et al., 2024). Recent syntheses summarised the extent of pollen limitation in apple, concluding that pollen limitation is variable across its cultivars and production regions (Garratt et al., 2021; Olhnuud et al., 2022; Siopa et al., 2024). Additionally, apple is one of the most studied crops in terms of pollination (Siopa et al., 2024), allowing for a comprehensive synthesis on the role of insect-mediated pollination in apple production.

Synthesis of the available data can reveal patterns that inform how a global crop like apple is pollinated and how honeybees and wild bees contribute to this critical component of crop production. This may also identify patterns that will guide future research and the application of optimal pollination strategies. Therefore, in this study, we used an extensive dataset of pollination research in apple to explore the following research objectives:

1. Establish the prevalence of pollen limitation on different pollination outcomes in this crop (by comparing insect pollination with experimental hand pollination).
2. Determine the relative flower visitation rates of honeybees and wild bees in apple cultivation, and how their relative visitation differs from the relative pollination contribution for each bee taxon.
3. Quantify the extent to which honeybee visitation, wild bee visitation and bee species richness correlate with apple pollination success measured as fruit quantity (i.e. fruit set) and quality (i.e. fruit weight and seed set).

2 | MATERIALS AND METHODS

2.1 | Review of the literature

We conducted a systematic review by searching the ISI Web of Science Core Collection (Science Citation Expanded) as a primary database with the search terms ('apple' OR '*Malus domestica*') AND ('bee' OR 'bees' OR 'pollin*'; methods see Eeraerts et al., 2023). The search was completed on 12 January 2023 and produced 843 potential studies. Each study was screened by reading the title and abstract. During this initial screening, we excluded studies that had not been conducted in apple orchards or that did not deal with insect pollinators or insect-mediated pollination.

Next, the full text of the remaining studies was reviewed for potential inclusion in the quantitative syntheses. For objective 1, we selected studies that measured apple pollination using different pollination treatments (both insect- and hand pollination; see below). We included studies that: (1) measured pollination in commercial apple orchards (i.e. fruit set, fruit weight and/or seed set), (2) included measurements of experimental hand-pollination treatment in addition to insect pollination, (3) were conducted under outdoor, open-field conditions, (4) included a minimum of five independent orchards (i.e. studies that conducted observations in multiple, independent orchard sites) and (5) reported original data (i.e. no meta-analyses or modelling studies that used empirical data from other studies that were already published). For objectives 2 and 3, we selected studies that investigated the relationship between honeybee and wild bee visitation and insect pollination. We focused on honeybees and wild bees as they are the most common pollinators in apple pollination research (Blitzer et al., 2016; Leclercq et al., 2023; Mallinger & Gratton, 2015; Pardo & Borges, 2020; Pisman et al., 2022), since they have been included in all studies we identified. Here, we included studies that: (1) conducted pollinator surveys in commercial apple orchards (distinguishing honeybees and wild bees), and selection criteria 1, 3, 4 and 5 of objective 1 were also applied. If a study did not include data on all pollination metrics, it was still included for analysis of the relevant pollination metrics. The selection process is illustrated in a PRISMA flow diagram (Figure S1).

2.2 | Data collection

We collected the raw data from the suitable studies identified by the systematic literature review by contacting the authors of the studies (for methods see Eeraerts et al., 2023). Here, a success rate of 91.7% was achieved (22 of 24 studies). Furthermore, raw data were collected from seven unpublished studies within the network of the authors (Tables S1–S3), resulting in data obtained from a total of 29 studies (totalling 532 orchard replicates). Data on apple pollination and visitation by bees to apple flowers were gathered from these studies as average values per orchard per region/year/cultivar. In some studies, data were collected for more than one cultivar, in more than one region or over multiple years. For the meta-analyses, we calculated the effect sizes and analysed the data separately per cultivar (as long as the minimum number of orchards for each cultivar was 5), region, or year as separate study records (Eeraerts et al., 2023; Reilly et al., 2024). Hence, the 29 studies yielded data from 43 study records, hereafter referred to as Study_ID (Table S2).

To quantify pollination success, we collected data on the following pollination metrics: fruit set, fruit weight (g per fruit) and number of seeds per apple (hereafter 'seed set'). For fruit set, some studies provided either early fruit set (i.e. fruit set measured 3–4 weeks after bloom), final fruit set (fruit set measured right before harvest) or both (see the data analyses section for how we dealt with this). From all studies, pollination data were collected as insect-pollination data, meaning that flowers were exposed to pollinator visitation during bloom (i.e. required for objectives 2 and 3). In addition to insect-pollination data, we collected pollination data from studies that included the hand-pollination treatment (i.e. flowers exposed to insect pollinators and with additional pollen supplied manually). With the data from the hand-pollination treatment, we can determine the amount of additional pollination needed to reach maximum pollination by comparing the hand pollination with the insect-pollination data for a specific pollination metric (i.e. pollen limitation) (i.e. required for objective 2; Garratt et al., 2021; Eeraerts et al., 2023).

The bee visitation data were used from studies that conducted a bee survey in each apple orchard in which pollination was measured. Bees were actively surveyed either by net catches or direct observations. Data from surveys using pan traps were not included, as this sampling method catches different bee communities compared to active sampling methods and may not reflect bee activity on crop flowers (Eeraerts & Meeus, 2025; O'Connor et al., 2019). Bees were grouped into honeybees and wild bees. In most studies, wild bees were identified at the species level, allowing us to extract bee species richness per orchard and to group the most common bee genera in fruit tree crops such as apple (i.e. *Andrena* spp., *Bombus* spp., *Lasioglossum* spp., *Osmia* spp.; Pardo & Borges, 2020; Osterman et al., 2024).

See Tables S1 and S2 for an overview of which studies we could collect data on the various pollination metrics, pollination treatments and pollinator variables.

2.3 | Objective 1: Pollen limitation meta-analyses

Meta-analysis is a statistical approach to integrate results from independent studies that test a common hypothesis (Borenstein et al., 2009; Koricheva et al., 2013). We calculated the effect sizes to address objective 1 using the collected data. For assessing pollen limitation, the mean, standard deviation and number of replicates were determined for both insect- and hand-pollination treatments per Study_ID. Next, we determined the unbiased standardised mean difference (Hedges' *g*) as effect size with the following formula (measure '*SMD*', function *escalc*, R package *metafor*; Viechtbauer, 2010; Koricheva et al., 2013):

$$g = \frac{X_1 - X_2}{\sqrt{\frac{(n_1 - 1)S_1^2 + (n_2 - 1)S_2^2}{n_1 + n_2 - 2}}} * \left(1 - \frac{3}{(4 * \mathrm{df} - 1)}\right)$$

With X_1 and X_2 the sample means of each treatment group (i.e. insect- and hand pollination), n_1 and n_2 the sample sizes of each treatment group, S_1 and S_2 the standard deviation of each sample group and df the degrees of freedom. Effect sizes were calculated separately for the three different pollination metrics that we considered (fruit set, fruit weight and seed set). We provide Cohen's benchmarks for Hedges' g to interpret effect sizes: $g<0.2$—very small effect, $0.2 \le g < 0.5$—small effect, $0.5 \le g < 0.8$—moderate effect and $g \ge 0.8$—large effect (Cohen, 1988).

For objective 1, we tested the extent of pollen limitation for each pollination metric (i.e. fruit set, fruit weight and seed set) by performing mixed-effects categorical meta-analyses using the pollination metric as a moderator variable (function *rma.mv*, R package *metafor*; for methods see Eeraerts et al., 2023). Separate models were run for honeybee visitation rate, wild bee visitation rate and bee species richness.

2.4 | Objective 2: Relative visitation and pollination contribution

For every study-record, the relative visitation rates of honeybees, bumblebees and solitary bees were extracted from the pollinator data (i.e. the proportion of visitation attributed to each taxa). We also calculated the relative visitation of the most common solitary bee genera, *Andrena* spp., *Lasioglossum* spp. and *Osmia* spp. Next, based on data from the available studies on the pollination efficiency of bees in apple, the average pollination efficiency of different bee genera was calculated (Table S4). Pollination efficiency studies are those in which the single-visit pollination efficiency is measured for certain bee species or genera, measured as the percentage of fruits set or the number of pollen grains deposited after a single flower visit (e.g. Vicens & Bosch, 2000; Thomson & Goodell, 2001; Table S4). The average pollination efficiency for each genus of bee was expressed relative to that of the honeybee, and the average for bumblebees and solitary bees was calculated in the included studies (Table S4). Next, the relative pollination contribution of the three different bee taxons, honeybees, bumblebees and solitary bees, was calculated using the following formula (for methods see Eeraerts et al., 2023):

$$\mathrm{RP}_{\mathrm{bee}} = \frac{\mathrm{RV}_{\mathrm{bee}} * \mathrm{AP}_{\mathrm{bee}}}{\sum \left(\mathrm{AP}_{\mathrm{bee}} * \mathrm{AP}_{\mathrm{bee}}\right)}$$

$\mathrm{RP}_{\mathrm{bee}}$ is the relative pollination contribution of each bee taxon, $\mathrm{RV}_{\mathrm{bee}}$ is the relative visitation of each bee taxon, and $\mathrm{AP}_{\mathrm{bee}}$ is the average pollination efficiency of each bee taxon. For each bee taxon, a linear mixed-effects model (LMM) was used to determine if $\mathrm{RV}_{\mathrm{bee}}$ and $\mathrm{RP}_{\mathrm{bee}}$ were different (function *lmer*, R package *lme4*; Bates et al., 2015). Here, a fixed categorical variable (i.e. $\mathrm{RV}_{\mathrm{bee}}$ vs. $\mathrm{RP}_{\mathrm{bee}}$) was included, with Study_ID as a random variable.

2.5 | Objective 3: Bee visitation meta-analyses

For objective 3 we calculated the effect sizes for each pollination metric and Study_ID to address how bee visitation relates to apple pollination. Linear models (LM, function *lm*, R package *stats*) were used to determine the slopes and standard deviations of the pollination contribution of honeybees and wild bees on each pollination metric. Pollination metrics from the insect-pollinated treatment were used as the response variable, and honeybee and wild bee visitation were fixed variables (additive model without their interaction). To allow direct comparisons across studies, honeybee and wild bee visitation were scaled and centred to a mean of 0 and a standard deviation of 1. Collinearity between explanatory variables was checked before analyses using variance inflation factor (VIF) analyses. Model residuals were evaluated visually (residuals versus fitted values plot, QQ-plot) and with the Lilliefors test. When there was evidence of multicollinearity between honeybee and wild bee visitation (VIF >2), we did not include data from these specific studies in further analysis (see Table S5 for an overview of the number of effect sizes per objective and pollination metric). As some studies also provided data on bee species richness, we ran LMs for each pollination metric with bee species richness as a fixed variable. From these data and the model statistics, we calculated Pearson's correlation coefficient (r) as the effect size per Study_ID (Koricheva et al., 2013):

$$r = \beta * \frac{\mathrm{SD}_x}{\mathrm{SD}_y} \quad \text{if} \quad y = \alpha + \beta x$$

With y the pollination metric, x either honeybee visitation, wild bee visitation or bee species richness, SD the standard deviation, α the intercept and β the slope. For performing the meta-analysis models, Pearson's r values were transformed to Fisher's z and its variance (Borenstein et al., 2009; Koricheva et al., 2013). Fisher's z was re-transformed to Pearson's r for visualisation, and based on Pearson's r, we calculated R^2 for interpretation ($R^2 = r * r * 100$), which expresses the percentage of explained variance (Koricheva et al., 2013). Cohen's benchmarks for Pearson's r and its percentage of explained variance are provided for interpretation of the obtained effect sizes: $r<0.1$ (R^2 of <1%)—very small effect, $0.1 \le r < 0.3$ (1%–9%)—small effect, $0.3 \le r < 0.5$ (9%–25%) moderate effect and $r \ge 0.5$ (>25%)—large effect (Cohen, 1988).

For objective 3, we tested the effect of visitation of honeybees, wild bees and bee species richness on each pollination metric by performing mixed-effects categorical meta-analyses using the pollination metric as a moderator variable (separate meta-analyses model for honyebees, wild bees and bee species richness). Similarly to objective 1, study_ID was used as a random factor; we also conducted a separate analysis in which early and late fruit sets were considered separate pollination metrics.

2.6 | Publication bias

To test if publication bias influenced the results of our meta-analyses of objectives 1 and 3, we used funnel plots and the multi-level meta-regression test (i.e. Egger's regression; Nakagawa et al., 2022). All analyses were performed using R version 4.2.0 (R Development Core Team, 2020).

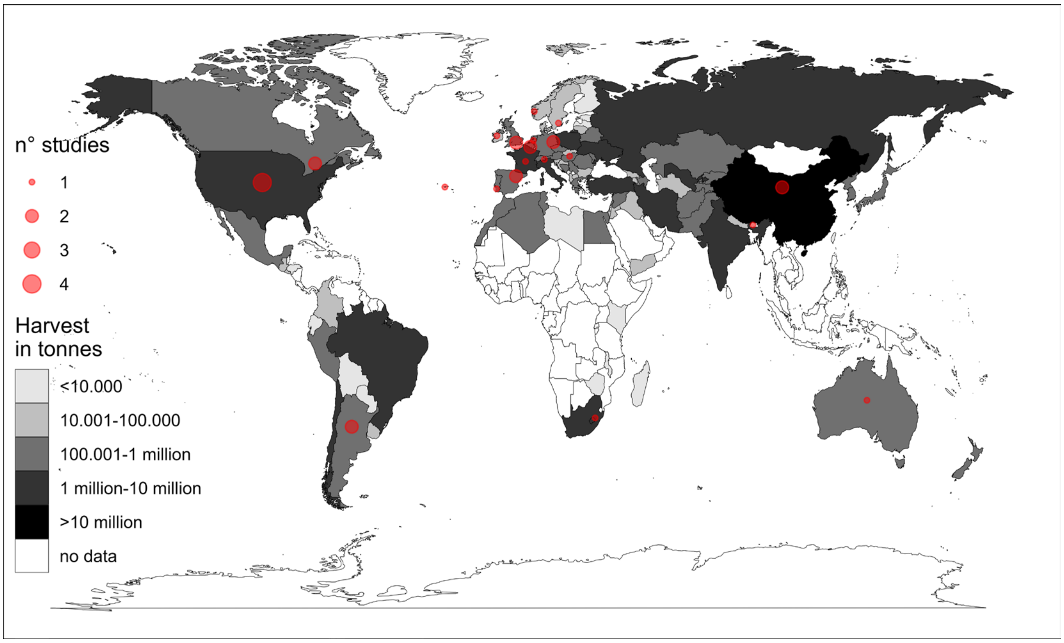

FIGURE 1 World map providing an overview of the number of studies on insect pollination in apple in each country. Apple harvest in 2023 in tonnes per country is illustrated in grey shades based on FAOSTAT data (FAOSTAT, 2025).

3 | RESULTS

3.1 | General

Of the 29 studies included in our synthesis, 16 originated from Europe (Figure 1; Table S1). Additionally, four studies originated from the USA, two from Argentina, two from Canada, two from China, one from Australia, one from Bhutan and one from South Africa. The cultivars included in the studies were highly variable, with multiple studies conducted in orchards with mixed cultivars (Table S1). Only six cultivars were included in more than one study: Gala (included in six studies), Fuji (three studies), Jonagold (three studies), McIntosh (two studies), Red Delicious (two studies) and Rennet (two studies).

3.2 | Objective 1: Pollen limitation meta-analyses

Pollen limitation was detected for the fruit set and seed set, meaning that compared to insect pollination, hand pollination strongly increased fruit set and seed set (Hedges'$g > 0.8$, large effect; Figure 2; Table 1). Pollen limitation was not detected for fruit weight (Figure 2; Table 1). Considering early and late fruit sets as separate pollination metrics did not change the outcome of the analyses (Table S6).

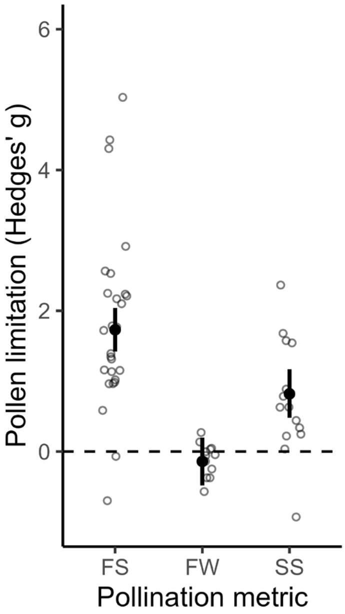

FIGURE 2 Effect sizes (Hedges' *g*) of pollen limitation for apple pollination expressed as fruit set (FS), fruit weight (FW) and seed set (SS). The open points indicate study-level effect sizes, and the black points indicate the mean effect sizes and their 95% confidence interval. The overall effects represent significant ($p < 0.05$) effects if their 95% confidence interval does not overlap zero.

3.3 | Objective 2: Relative visitation and pollination contribution

The relative visitation rate of honeybees to apple flowers was 71.9±4.1% across all studies, while for bumblebees and solitary bees, this was 10.9±2.12% and 19.2±3.4%, respectively (Figure 3). For the most common genera of solitary bees, the relative visitation rates were 10.1±10.0% for *Andrena* spp., 2.9±5.0% for *Lasioglossum* spp. and 1.5±1.6% for *Osmia* spp. (Figure S2). For honeybees, the relative pollination contribution was 11.4% lower compared to the relative visitation rate, whereas for bumble bees and solitary bees, this was 1.6% and 10.4% higher, respectively (Figure 3). This difference between the

TABLE 1 Results of the set of random-effects categorical meta-analyses using pollination metric as a moderator variable (FS = fruit set, FW = fruit weight and SS = seed set) for each objective (PL = pollen limitation, HB = honeybee visitation, WB = wild bee visitation, SR = bee species richness).

Objective	ES type	Moderator	Estimate	LCI	UCI	*p*	Q_{res}	p_{res}	Q_{mod}	p_{mod}
Obj. 2: PL	Hedges' *g*	**FS**	**1.73**	**1.42**	**2.04**	**<0.001**	273.46	<0.001	190.10	<0.001
		FW	−0.14	−0.48	0.20	0.42				
		SS	**0.82**	**0.48**	**1.17**	**<0.001**				
Obj. 3: HB	Pearson's *r*	FS	−0.04	−0.17	0.09	0.52	337.55	<0.001	11.39	0.01
		FW	**−0.14**	**−0.29**	**−0.01**	**0.049**				
		SS	0.08	−0.06	0.22	0.27				
Obj. 3: WB	Pearson's *r*	FS	0.01	−0.09	0.10	0.89	168.83	<0.001	12.96	<0.01
		FW	**0.12**	**0.01**	**0.23**	**0.028**				
		SS	**0.16**	**0.06**	**0.26**	**<0.01**				
Obj. 3: SR	Pearson's *r*	FS	0.05	−0.11	0.20	0.57	278.41	<0.001	8.04	0.045
		FW	0.08	−0.08	0.24	0.34				
		SS	**0.19**	**0.04**	**0.34**	**0.012**				

Note: Effect size type (ES) is given per objective and model statistics reported that are the model estimate, lower 95% confidence interval (LCI), upper 95% confidence interval (UCI) and *p*-value. Significant moderator effects are indicated in bold ($p < 0.05$). The residual heterogeneity of the different meta-analyses models is also given (Q_{res} and *p*-value [p_{res}]), as well as the moderator heterogeneity of each model (Q_{mod} and *p*-value [p_{mod}]).

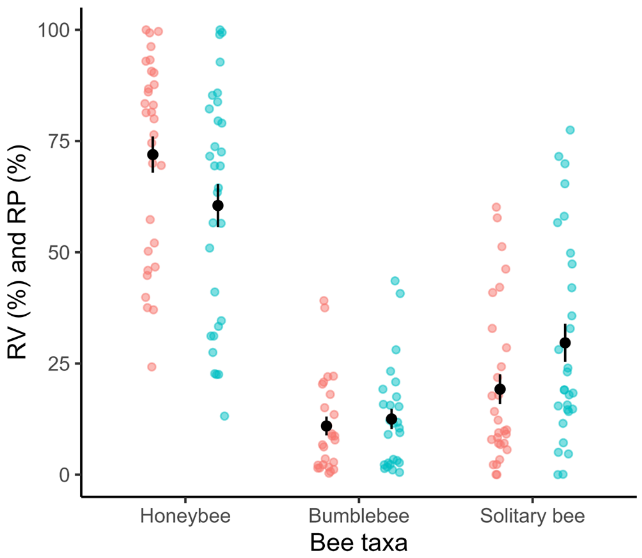

FIGURE 3 The relative visitation (RV, red dots) of the different bee taxa and their relative pollination contribution (RP, blue dots) in apple studies across the world. The coloured dots indicate the data points, and the black dots indicate the mean and the standard error of the mean.

relative visitation rate and the relative pollination contribution was significant for both honeybees (LMM test: $t = -4.18$, $p < 0.001$) and solitary bees ($t = 5.05$, $p < 0.001$), but not for bumblebees ($t = 1.03$, $p = 0.31$).

3.4 | Objective 3: Bee visitation meta-analyses

The meta-analyses with pollination metric as moderator variable showed that honeybee visitation rate did not influence fruit set or seed set; yet we detected a negative effect for honeybee visitation rate on fruit weight (fruit weight R^2: 2.0%, small effect; Figure 4a; Table 1). Fruit set was not affected by wild bee visitation rate, whereas fruit weight and seed set increased with increasing visitation of wild bees (fruit weight R^2: 1.4%; seed set R^2: 2.6%, small effects) (Figure 4b; Table 1). Bee species richness did not show an effect on fruit set and fruit weight; yet seed set increased with increasing bee species richness (R^2: 3.6%, small effect; Figure 4c; Table 1). Also, here, considering early and late fruit sets as separate pollination metrics did not change the outcome of the analyses (Table S6).

3.5 | Objectives 1 and 3: Publication bias

Based on the multi-level regression test, we concluded that publication bias did not influence our results (Table S7), but some of the funnel plots showed signs of asymmetry (Figures S3 and S4). In this case, we applied the trim-and-fill method as a form of sensitivity analysis (Jennions et al., 2013), which did not change the outcome of our meta-analyses (Tables S8 and S9; Figures S5 and S6).

4 | DISCUSSION

4.1 | General

Using the available global data, we detected pollen limitation for both fruit set and seed set, which emphasises the potential to improve pollination management in this crop. We conclude that honeybees are the dominant flower visitors in this crop, and that bumblebees and solitary bees can be abundant depending on the study. Increasing wild bee visitation rates and bee species richness clearly enhanced fruit weight and seed set of apple, which are

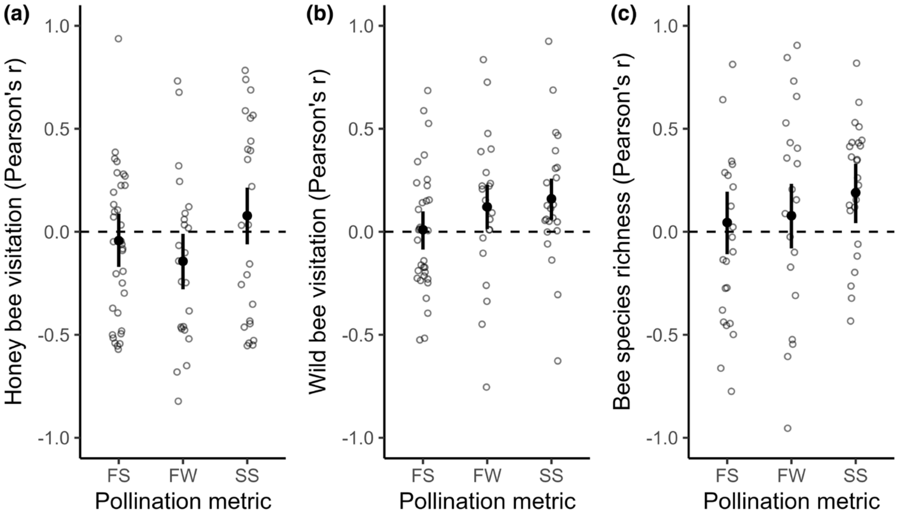

FIGURE 4 Effect sizes (Pearson's *r*) for the visitation rate of honeybees (a), the visitation rate wild bees (b) and bee species richness (c) in apple pollination expressed as fruit set (FS), fruit weight (FW) and seed set (SS). The open points indicate study-level effect sizes, and the black points indicate the mean effect sizes and their 95% confidence interval. The overall effects represent significant ($p < 0.05$) effects if their 95% confidence interval does not overlap zero.

proxies for apple quality. In contrast, increasing honeybee visitation rates did not improve fruit set and seed set; yet we detected a negative effect on fruit weight.

4.2 | Pollen limitation meta-analyses

Our meta-analyses showed evidence of pollen limitation in apple, as fruit set and seed set were clearly pollen-limited, similar to recent pollen limitation syntheses in apple (Garratt et al., 2021; Olhnuud et al., 2022) and other crops (Eeraerts et al., 2023, 2024; Sáez et al., 2022). Our pollen limitation assessment advanced the recent syntheses of Garratt et al. (2021) and Olhnuud et al. (2022) as we focused on field studies with a minimum of five orchard replicates and as we considered pollen limitation for different pollination metrics separately. More efforts are encouraged to combine pollen limitation data from multiple studies and additional crops to improve our understanding of how to mitigate suboptimal pollination and thereby increase crop production.

In contrast to fruit set and seed set, we did not find pollen limitation for fruit weight, a result that highlights the importance of considering different pollination metrics separately. Fruit weight is often influenced by fruit set or seed set (Eeraerts, Kogan, et al., 2025; Matsumoto et al., 2012; Pisman et al., 2022; Samnegård et al., 2019). Therefore, compared to the insect pollination treatment, additional fruits with more seeds in the hand pollination treatment can serve additional fertilisation and water so that they can increase their fruit weight to the same extent, as the resources for fruit growth have to be distributed to all fruits of the tree (Klein et al., 2015). Additionally, the relationship between fruit weight and fruit set or seed set is also dependent on the cultivar and other factors such as fertilisation, irrigation and thinning (Buccheri & Di Vaio, 2004; Garratt et al., 2021; Naschitz & Naor, 2005). Hence, future studies should focus on the interaction between pollen limitation and farm management, and how this affects fruit quality and yield (Eeraerts, Kogan, et al., 2025; Tamburini et al., 2019).

4.3 | Relative visitation and pollination contribution

Honeybees were found to be the dominant flower visitor across all apple studies, similar to the results of a global sampling in apple orchards (Leclercq et al., 2023) and the results of syntheses in other crops (Dymond et al., 2021; Eeraerts et al., 2023; Osterman et al., 2024). Additionally, multiple genera of wild bees were abundant (*Bombus* spp. and *Andrena* spp.) or occurred commonly (*Lasioglossum* spp. and *Osmia* spp.) in many of the studies. When correcting for the relative pollination efficiency, the relative pollination contribution of solitary bees was higher compared to their relative visitation (vice versa for honeybees). In general, the honeybee has a relatively moderate pollination efficiency, but for each crop, there are always different solitary bees or bumblebees that are much more efficient than the honeybee (Hung et al., 2018). Indeed, this higher pollination efficiency of solitary bees corresponds with studies in other tree fruit crops like almond and cherry (Brittain et al., 2013; Osterman et al., 2024) as well as for annual crops like oilseed rape and watermelon (Jauker et al., 2012; Pisanty et al., 2016) This further confirms that wild bees are important for crop production despite their low abundance compared to the honeybee (Garibaldi et al., 2013; Reilly et al., 2024). This finding also suggests that visitation rates can be used as an indicator of bumblebee contribution, whereas for honeybees and solitary bees analyses are needed that include information on their pollination efficiency.

4.4 | Bee visitation meta-analyses

Our analyses also show that increasing wild bee visitation rate had no effect on fruit set, but had a positive effect on both apple fruit weight and seed set, highlighting the importance of wild bees for fruit quality. This positive effect of wild bees on fruit weight and seed set is in line with previous pollination research in apple (Blitzer et al., 2016; Pisman et al., 2022) and other crops (Dainese et al., 2019; Eeraerts et al., 2023; Reilly et al., 2024). For bee species richness, we detected a positive effect on apple seed set, an effect which has been found in multiple crops (Eeraerts et al., 2023; Reilly et al., 2024), including apple (Blitzer et al., 2016). The positive effects of wild bees can be explained by the fact that they are more efficient pollinators compared to honeybees (cfr. Objective 2), and because wild bees are known to improve the pollination efficiency of honeybees in tree fruit crops (Brittain et al., 2013). Wild bees can be promoted by on-farm measures like wildflower strips, hedgerows or bee nesting aids (Eeraerts et al., 2022; von Königslöw et al., 2022) and pesticide reduction (Devetter et al., 2022) or off-farm measures like habitat creation and conservation (Eeraerts, 2023; Tscharntke et al., 2021). We also found a low visitation rate of mason bees (*Osmia* spp.) across all studies, which again aligns with a global sampling in apple orchards (Leclercq et al., 2023) and with results from syntheses of other fruit crops (Eeraerts et al., 2023; Osterman et al., 2024). The remarkably low relative visitation of mason bees is in contrast with the ease of management and their high pollination performance for apple and other tree fruit crops (Brittain et al., 2013; Osterman et al., 2024; Roquer-Beni et al., 2022; Vicens & Bosch, 2000). Through semi-structured interviews, Eeraerts, Borremans, et al. (2020) found that the implementation of nest sites for solitary bees by fruit growers is low, mainly due to a lack of practical guidelines. Increasing efforts to better inform farmers on how to improve local populations of mason bees on farms could be an easy way to increase pollination in regions where these species occur (Eeraerts et al., 2022; Osterman, Aizen, et al., 2021).

We conclude that there is no effect of honeybee visitation rate on fruit set or seed set, whereas increasing honeybee visitation rate had a negative effect on fruit weight. Previous studies have also concluded no effect of honeybee visitation rate on crop pollination in multiple crop synthesis (Dainese et al., 2019; Garibaldi et al., 2013), as well as case studies in apple (Blitzer et al., 2016; Pisman et al., 2022). In fact, this is the first crop pollination synthesis that detects such a negative effect of honeybee visitation on crop pollination. The negative relation between honeybee visitation rate and pollination has been detected in other crops, but requires more research in order to fully understand the mechanism behind this pattern (Eeraerts, Siopa, et al., 2025; Miñarro et al., 2023; Sáez et al., 2014). The negative effect of honeybees could be explained by the fact that high honeybee densities may displace wild bees, resulting in apples with fewer seeds and thus indirectly leading to lighter, smaller apples (Buccheri & Di Vaio, 2004; Mallinger et al., 2017). Alternatively, the lower pollination efficiency of honeybees compared to wild bees could result in slower fertilisation, slower fruit ripening and, hence, smaller apples at harvest. This mechanism whereby enhanced pollination affects ripening time has been studied in sweet cherry and blueberry, but remains unexplored in apple (Cachi et al., 2014; Nicholson & Ricketts, 2019; Ryder et al., 2020). More research is needed to reveal the mechanism driving this honeybee effect. As beekeepers stock the orchards with honeybee colonies during apple flowering, orchards are often saturated with honeybees. To optimise honeybee pollination management, it may be useful to determine the threshold of honeybees or bee hives that is useful, beyond which adding more honeybees does not further improve apple quantity and quality (Eeraerts, Siopa, et al., 2025).

Important to note is that we conclude small effect sizes for the detected effects of honeybee and wild bee visitation ($R^2 < 0.1$). This result is similar to the conclusion of the multi-crop synthesis by Reilly et al. (2024), who also found small effects on crop pollination in a global dataset (see also Eeraerts, Siopa, et al., 2025). These small effects are also linked to the nature of the data, as it is unlikely to expect large R^2 in observational, field-realistic studies in agriculture and ecology, in which representative gradients of pollinators are better represented (Reilly et al., 2024). Nevertheless, small effects may still be relevant to farmers because they can translate into valuable pollination gains as long as increases in wild bee visitation are ecologically and agronomically feasible. Additionally, while Reilly et al. (2024) found an overall positive effect of both honeybee and wild bee visitation on crop pollination in multiple crops, their subset analyses for apple data alone concluded no significant effect of honeybee and wild bee visitation rate on apple pollination. The 16 apple studies in their dataset use different response variables, ranging from fruit set and seed set to tonnes per ha and kg per tree. Compared to previous pollination syntheses (Dainese et al., 2019; Eeraerts, Siopa, et al., 2025; Garibaldi et al., 2013; Rader et al., 2016; Reilly et al., 2024), we conclude that bee visitation responses vary by specific pollination metrics; as such, our study highlights the importance of analysing these relationships separately for each metric in order to obtain clear relationships.

4.5 | Limitations and future directions

We were unable to assess the effect of bee visitation on pollen limitation in our analyses. Indeed, pollination measured from the insect-pollinated treatment in our objective 3 approach should ideally be compared with pollen limitation measured as the difference between hand-pollinated and insect-pollination treatments to assess the degree of suboptimal pollination in all fields and studies (Chabert et al., 2022; Eeraerts et al., 2024). Due to a lack of available studies that collected bee survey data in combination with hand pollination data, this was not possible. Future projects are encouraged to include these hand pollination treatments to further fine-tune our understanding and guide pollination management in agriculture.

From our literature review, we found only a limited number of studies with a site-replicated field design that measured fruit quality with measures beyond fruit weight (e.g. aspects like fruit firmness, shape, sugar content; Burns & Stanley, 2022). As we found clear effects of honeybees and wild bees on seed set and fruit weight, and given the importance of obtaining high-quality yields in agriculture, it is recommended to include more quality parameters in future apple pollination research. This will allow us to better understand how bees influence crop quantity and quality.

Furthermore, we conclude that site-replicated field studies on pollination in apple cultivation are geographically biased towards Europe. As such, important production regions are underrepresented in the USA or China, or are omitted, like Brazil, Chile and India. This geographical bias is not limited to apple but is found in crop pollination research in general (Eeraerts et al., 2023; Osterman et al., 2024). Within these understudied regions, we need more research on other high-value fruit tree crops that rely on insect-mediated pollination to produce marketable seeds and fruit, such as macadamia, avocado, mango, citrus, etc. (Dymond et al., 2021; Siopa et al., 2024; Trueman et al., 2022). We also conclude that considerable heterogeneity exists, which was not explained by our moderator variables. This variation is probably due to region-specific aspects such as cultivar identity, orchard design and pollination management, landscape context and wild bee composition, and specific conditions like weather that may affect pollination (Chabert et al., 2024; Devetter et al., 2022; Eeraerts et al., 2023; Gibbs et al., 2016; Garratt et al., 2021; Olhnuud et al., 2022). Most of the studies we identified were conducted in different cultivars, whereby cultivar is confounded with study, and cultivar effects could not be studied (see Eeraerts et al., 2024; Olhnuud et al., 2022). This further emphasises the need to expand research in global crops like apple to cover the main production regions, allowing the development of region-specific guidelines for crop pollination management tailored to specific landscape and agronomic contexts.

5 | CONCLUSIONS

Our study underscores the presence of pollen limitation in apple fruit and seed set, which can be mitigated by improved wild bee management. Indeed, increasing wild bee visitation enhanced apple fruit weight and seed set, while increasing honeybee visitation reduced fruit weight, possibly due to reduced visitation by wild bees with high honeybee densities (Mallinger et al., 2017). To promote crop pollination, our synthesis suggests supporting wild bees in agricultural landscapes, optimising honeybee management or both. Future research should aim to address geographic biases by incorporating a broader range of locations, assessing pollen limitation and accounting for farm management practices and landscape variables to unravel the mechanisms behind the effect of bee visitation on crop pollination.

AUTHOR CONTRIBUTIONS

Maxime Eeraerts, Julia Osterman, Péter Batáry, Alexandra-Maria Klein and Kris Verheyen conceived the study idea. Maxime Eeraerts and Péter Batáry conducted the literature review. Maxime Eeraerts requested the raw data. Maxime Eeraerts, Julia Osterman, Alexandra-Maria Klein, Matthias Albrecht, Georg K. S. Andersson, András Báldi, Olivia M. Bernauer, Leah Blechschmidt, Eleanor J. Blitzer, Paulo A. V. Borges, Jordi Bosch, Katherine L. W. Burns, Alistair J. Campbell, Sílvia Castro, James M. Cook, Robin Daelemans, Bryan N. Danforth, Arjen G. de Groot, Kinley Dorji, Rita Földesi, Hannah R. Gaines Day, Daniel García, Lucas A. Garibaldi, Michael P. D. Garratt, Andrew Gonzalez, Heather Grab, Claudio Gratton, Maren Kristine Halvorsen, Peter A. Hambäck, Bjørn Arild Hatteland, Olivier Honnay, Eva Hulsmans, Sandra Kaasen Vestheim, David Kleijn, Anikó Kovács-Hostyánszki, Martin J. Lechowicz, Nicolas Leclercq, Yunhui Liu, João Loureiro, Rachel E. Mallinger, Leon Marshall, Ivan Meeus, Marcos Miñarro, Diego N. Nabaes Jodar, Adara Pardo, Mia G. Park, Robert J. Paxton, Néstor Pérez-Méndez, Rafael A. Pincante De Carvalho, Paavo Pirttilehto, Matti Pisman, Simon G. Potts, Nigel E. Raine, James R. Reilly, Laura Roquer-Beni, Ulrika Samnegård, Dara A. Stanley, Louis Sutter, Kyle Teixeira-Martins, Simon M. Tierney, Ruan Veldtman, Nicolas J. Vereecken, Felix Wäckers, Timothy Weekers, Julliana K. Wilson and Panlong Wu collected and delivered data. Maxime Eeraerts analysed the data. Maxime Eeraerts led the writing and editing of the manuscript with help from Julia Osterman, Péter Batáry, Alexandra-Maria Klein and Kris Verheyen. All authors contributed critically to manuscript drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare. Péter Batáry is an Associate Editor of *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data was used from 29 studies (see Data Sources, Tables S1 and S3) and the raw data used in the study is available via Figshare, https://doi.org/10.6084/m9.figshare.29900609.v1 (Eeraerts, 2025).

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SUPPORTING INFORMATION

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

Table S1. Overview of the studies identified through a systematic literature review, with study metadata, pollinator and pollination data.

Table S2. Overview of the studies and their inclusion in the different objectives.

Table S3. Methods of unpublished studies.

Table S4. Average pollination efficiency values.

Table S5. Number of effect sizes for each objective.

Table S6. Model statistics of the categorical meta-analyses for each objective, considering early and final fruit set as separate pollination metrics.

Table S7. Multi-level meta-regression test.

Table S8. Model statistics of the categorical meta-analyses for each objective after trim-and-fill.

Table S9. Multi-level meta-regression test after trim-and-fill.

Figure S1. PRISMA flow diagram.

Figure S2. Relative visitation of honeybees and the most common wild bee genera.

Figure S3. Funnel plots.

Figure S4. Funnel plots showing the relationship between effect size and standard error for the pollination contribution of honeybees (A), wild bees (B) and bee species richness (C).

Figure S5. Funnel plots after trim-and-fill.

Figure S6. Funnel plots showing the relationship between effect size and standard error for the pollination contribution of honeybees (A), wild bees (B) and bee species richness (C).

Data S2.

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