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# Global meta-analysis shows an indispensable role of pollinator diversity in promoting fruit quality

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ABSTRACT

Global pollinator decline threatens pollination services, biodiversity, and food security. However, large knowledge gaps remain regarding how pollinator diversity influences agricultural productivity, particularly in relation to multiple fruit quality traits. Here, we conducted a comprehensive global assessment of 79 studies with 451 effect sizes to investigate whether and how pollination services affect various fruit quality traits including organoleptic traits (e.g., size, shape, firmness) and nutritional traits (e.g., carbohydrates, macronutrients, micronutrients). Our analysis confirmed that animal pollination significantly enhances fruit quality by more than 30 %, a finding that is consistently observed across different ecological and agricultural systems, although such effects vary across different quality traits. For instance, organoleptic quality traits are highly dependent on the existence of animal pollination but are insensitive to high-quality pollination. Meanwhile, nutritional quality traits are promoted by increases in both pollinator species richness and visitation rate, although they are less affected by the presence or absence of animal pollination, suggesting a need for high-quality pollination. Interestingly, further analyses revealed that pollinator species richness promotes fruit micronutrients, while visitation rate enhances fruit macronutrients, indicating a complementary role of wild and managed pollinators in boosting fruit quality. Our results highlight the exclusive role of pollinator diversity in sustainable agriculture and therefore reinforce the rationale for wild pollinator conservation in the face of global pollinator decline.

## 1. Introduction

Approximately 90 % of flowering plants (Ollerton et al., 2011; Tong et al., 2023) and 35 % of global food crops (Klein et al., 2007) depend on animal pollination for successful fertilisation. Globally, pollinators are rapidly declining in both abundance and species richness in the Anthropocene due to threats such as pesticide use, habitat loss and climate change (Potts et al., 2010, 2016). Such biodiversity loss impairs plant-pollinator interactions and subsequent pollination services (Hooper et al., 2005; Albrecht et al., 2012), which are critical not only for global food supply but also for human nutrition (Klein et al., 2007; Eilers et al., 2011; Turo et al., 2024). Surveys in the United States and the United Kingdom evidenced that fruit and vegetable nutrient composition had been declining in the last decades (Davis, 2009). However, the influence of pollination on crop yield quality (e.g., nutritional and organoleptic fruit traits), remains underexplored compared to its effects on yield quantity (Klein et al., 2007; Aizen et al., 2009; Garibaldi et al., 2014; but see Gazzea et al., 2023). A recent global analysis showed that optimised animal pollination increases the quality of food crops, although the biological basis is not well understood (Gazzea et al., 2023). Pollination services contribute to the production of fruits with superior nutritional value, including essential micro- and macronutrients rich in vitamins, minerals, and antioxidants, which are essential for disease prevention, cognitive development and human growth (Free, 1993; Eilers et al., 2011; Garratt et al., 2014; Smith et al., 2015; Garibaldi et al., 2022). Pollination also affects organoleptic traits

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such as size, shape, texture, and commercial grade, which are important for consumer preference and marketability (Garratt et al., 2014; Wietzke et al., 2018; Gazzea et al., 2023). Well-pollinated fruits generally have better shelf life and appearance, reducing food waste by minimising the discarding of malformed or substandard fruits (Klatt et al., 2014a, 2014b). However, the multiple components of quality traits may respond differently to pollination services, which remains unclear (Gazzea et al., 2023). Disentangling the role of animal pollination in determining different fruit quality traits should be useful for not only orchard management, but also for agriculture in general to improve fruit marketability and overall production value. The well-established and quantifiable quality traits of popular pollinator-dependent fruits provide an ideal study system to detect the influence of pollination services on different components of fruit quality traits.

Pollination outcomes are highly dependent on ecological and agricultural systems due to variation in pollinator diversity, which in turn directly influences agricultural productivity (Tamburini et al., 2019; Dicks et al., 2021). A comprehensive analysis, integrating multiple moderators, is required to gain a global understanding of the potentially different influences of pollination services on fruit quality traits. In addition, the phenotypic constraints that shape pollination interactions may necessitate a specific pollination environment for a given plant species (Phillips et al., 2020). Consequently, flowers exhibiting such constraints may experience heightened pollen limitation for fruit crops within agricultural ecosystems. Furthermore, fruit quality traits may exhibit differential dependence on the quality of pollination services. High-quality pollination services can be quantified by enhancement of visitation rate and/or species richness of pollinators. To illustrate, a quality trait may have a low demand for high-quality pollination if pollination merely initiates the developmental pathway, although it is an essential prerequisite (Godoy et al., 2021). Conversely, other quality traits may require a high-quality pollination for well development if a heavy pollen load from diverse sources can facilitate the pathway (Zhang et al., 2019; Deng et al., 2022). Nevertheless, all the aforementioned arguments remain to be investigated.

In this study, we conducted a systematic literature search across the globe, and employed multivariate meta-analyses to investigate the following specific questions: 1) Are the effects of pollination services on fruit quality traits contingent on moderators such as the fruit quality attributes (organoleptic and nutritional), biomes, pollinator guilds (e.g., Diptera and Hymenoptera), and the distinction between wild and managed pollinators, the experimental scale (flower, branch, whole plant), and greenhouse versus field conditions? 2) Do fruit crops with different flower architectures (floral structures influencing pollinator access) vary in their dependence on pollination services in terms of fruit quality? 3) Do various fruit quality traits differentially respond to an enhancement of visitation rate and species richness of pollinators?

## 2. Methods

### 2.1. Literature search and inclusion criteria

To determine the effect of pollination on fruit crop quality, we conducted a literature search in the ISI Web of Science following the Population Intervention Comparator Outcome (PICO) framework on May 25th, 2024, with time restriction of 1985 to the search date. The fruit crops were selected based on their dependence on animal pollinators (Klein et al., 2007). The following search terms were used: fruit* OR *berry OR *cherry OR *melon OR apple OR cantaloupe OR plums OR peach OR pears OR avocado OR fig* OR mango OR apricot OR banana OR papaya OR kiwi OR passion OR citrus OR tangelo OR oranges OR mandarins OR grapes OR *currant OR lulo OR rambutan OR loquat OR lychee AND pollinat* OR *bee OR *bees OR hover fly OR hover flies OR fly OR flies OR butterfly OR butterflies OR *moth OR *moths OR beetle OR beetles OR bat OR bats OR chiropteran OR lorikeets OR wasp OR wasps OR avian OR flowerpecker OR flowerpeckers OR hummingbird OR hummingbirds OR bird OR birds AND qualit* (Gazzea et al., 2023). These search terms resulted to 18,024 studies.

On May 26th, 2024, we conducted a Google Scholar search using the term "pollination fruit quality", and this resulted to 199,000 studies. We sorted these results by relevance and manually reviewed the abstracts and titles of the first 700 studies for eligibility. This review included research articles and theses, and considered non-English literature with English abstracts to avoid linguistic bias. Specifically, seven non-English studies were included in our analysis, published in four languages: Spanish (n = 3), Chinese (n = 2), Korean (n = 1), and German (n = 1). After removing the duplicates from the two databases, we manually filtered the studies by screening the titles and abstracts and kept those that were relevant to our topic of study. After the initial screening, 336 studies were retained. The full texts of the retained studies were read and the studies that did not meet the following inclusion criteria were excluded: 1) presented primary data derived from manipulative experiments, allowing for the extraction of relevant information; 2) reported at least one measure of fruit quality (Table S1 for quality traits) in the presence and absence of pollinators; 3) mentioned specific pollinators and fruit species used in the experiment. Data was extracted from the 56 studies that met this inclusion criteria. Additional data was extracted from 23 studies reported from previously published review articles. To avoid pseudo-replication, we cross-checked these articles against our primary database and removed any duplicates. This resulted in a total of 79 studies (including the seven non-English articles) ($N_p$; Appendix A) reporting 451 paired observations ($N_o$; fruit quality in presence and absence of pollinators) from almost all continents and biomes (Fig. 1). We used Web of Science and Google Scholar to provide broad and overlapping search coverage. Although we did not use Scopus directly due to lack of full access, we included 23 studies from review articles that had used Scopus. Our final dataset of 79 studies, compiled from diverse sources, provides a robust foundation for this meta-analysis. To ensure reproducibility, we presented the data from the literature search and outcomes in a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) statement (Fig. S1).

### 2.2. Data extraction

The pollination service was defined as the difference between the open pollination treatment, where pollinators were present, and the pollinator exclusion (closed treatment), where pollinators were excluded, but wind pollination was allowed. From each study that met our inclusion criteria we extracted the mean, standard deviation, and sample size for each quality trait in the presence and absence of pollinators. These data were extracted from texts, tables, data or other data repositories. Where data was only available in figures, we used WebPlotDigitizer 4.8 (Rohatgi, 2021) to extract the mean and standard deviation from the figures. A number of studies presented standard errors and confidence intervals instead of standard deviations and in such cases, Revman calculator (https://training.cochrane.org/resource/revman-calculator) was used to get the standard deviation estimates.

Fruit quality is not uniformly defined across species and may sometimes include seed traits such as number or size. However, for many animal-pollinated fruits, such as citrus, grapes, and watermelon or pomegranate, seed traits are not primary indicators of quality. Therefore, we focused on broader quality metrics applicable across fruit types. In this study, fruit quality traits were classified into two broad categories termed quality broad, i.e., organoleptic and nutritional (Gazzea et al., 2023; Table S1). Among them, the organoleptic category are the sensory-based traits including size, shape, and commercial grade while the nutritional category are macronutrients like carbohydrates and micronutrients like vitamins. Consequently, the traits were further grouped into seven amassed quality aggregates: shape, size, sensory (taste and appearance), firmness, commercial grade, macronutrients, and micronutrients (Table S1).

In addition, from each study, we also extracted the latitude and

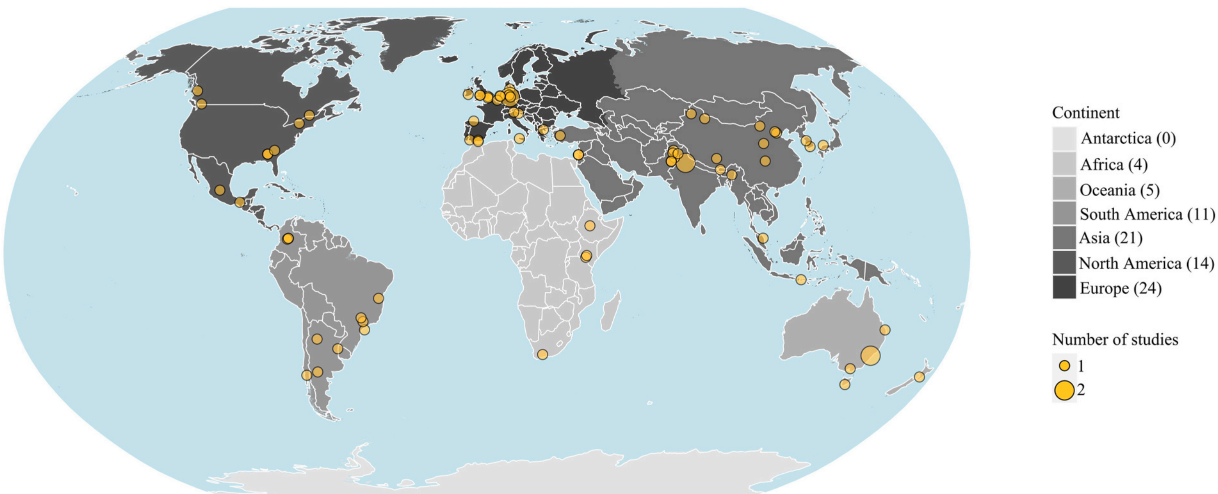


**Fig. 1.** Geographical distribution of studies used in the meta-analysis (N = 79). Countries were categorized into three climatic zones based on their latitude namely: tropical (0–23$^0$), sub-tropical (23–33$^0$), and temperate (>33$^0$).

longitude of the experimental sites, pollinator guilds, fruit plant, quality traits, experimental scale, managed vs. wild pollinators, and fruit environment (greenhouse vs. field) as well as pollinator species richness and visitation rate. Cultivar identity was excluded as a variable in this analysis, as it was not consistently reported across the reviewed studies. The pollinator guild analysis focused solely on Diptera and Hymenoptera, as these groups were identified as the most abundant and effective pollinators across the studies. Although other groups may be important pollinators for some fruit plants, we lacked adequate data for inclusion. The experimental sites were categorised into three climatic zones based on their latitude: tropical (0–23°), subtropical (23–33°), and temperate (>33°) (Gazzea et al., 2023). Based on the level of manipulation for pollination treatment (experimental scale) in each study, we categorized the data into either whole plant, branch, or flower. The flower scale was for pollinator exclusion experiments at the individual flower level; the branch scale was when the experiment was conducted on the part of the plant, and the plant scale was when an experiment was carried out on the whole plant. The pollinators mentioned in the studies were categorised as wild or managed depending on whether cages or hives were present or absent in the field or greenhouse experiment sites (Gazzea et al., 2023). This classification may not fully reflect the diversity of pollinator management strategies. For example, some managed species, such as solitary bees (e.g., *Osmia* spp.), do not reside in hives, and cage use does not necessarily imply active management. Nonetheless, this approach was adopted to ensure consistency with previous studies and comparability across experimental contexts. Pollinator species richness was defined as the total number of pollinator species visiting the fruit crops. Visitation rates referred to the number of visits by pollinators on a fruit crop per unit of time.

Flowers of fruit plants with different architectures may be effectively pollinated by pollinators with different traits (Phillips et al., 2020). We therefore tested the effects of different pollinators on a given fruit crop with applicable dataset. The information on pollinator identity was also extracted from the studies while the pollinator traits were extracted from external sources such as pollinator databases, books, and previous studies focused on these traits (Appendix B). Pollinators were classified into different categories based on three traits, namely, sociality (social/eusocial and solitary), body size, and tongue length (Fontaine et al., 2006; Garibaldi et al., 2015). Additionally, in our dataset, bees, dipterans, and bumblebees were identified as the frequently effective pollinators with clear information on these functional traits and thus formed the focus of our analysis.

We determined the body size of bees and bumblebees based on their intertegular distance (ITD). The categorisation of body sizes was as follows: Small bees had body sizes ranging from < 1.5–2.0 mm, medium-sized bees was from 2.0 to 3.3 mm, and large bees referred those longer than 3 mm (Greenleaf et al., 2007). We similarly classified dipterans to maintain consistency. The length of the tongue/proboscis or mouthpart of bees was categorised as small (< 3 mm), medium (3–8 mm), or long (> 8 mm; Stang et al., 2006). For bumble bees, the tongue length was categorised as short (5–6 mm), medium (7–8 mm), long (9–10 mm), and very long (> 10 mm) as bumble bees' tongue lengths have a higher variation compared to other bee taxa (Balfour et al., 2013; Arbetman et al., 2017). However, data on pollinator traits extracted from the publications were unequal between pollinator groups and flowers of different crops.

### 2.3. Statistical analysis

Log response ratio (ln(RR)) was used to estimate the effect size. The ln(RR) was calculated using the "*escalc*" function from the R package "*metafor*" (Viechtbauer, 2010). It was chosen due to the ability to mitigate bias, even when the denominator has a large-standardized mean and its relatively normal distribution (Hedges et al., 1999). The lnRR was calculated by computing the ratio between the treatment group (open pollination with pollinators) and the control group (pollinator exclusion) to assess the effect of pollination on fruit quality. The following equation was used:

$$\ln(RR) = \ln\frac{X_1}{X_2}$$

where $X_1$ represents the open pollination treatment and $X_2$ represents the pollinator exclusion treatment. The values above one indicate that pollinators presence increases fruit quality while values below one show that pollinators presence decreases fruit quality. The variance for the ln (RR) was calculated using the equation below:

$$Var(\ln(RR)) = \frac{(SD)_{1i}^2}{n_{1i}\overline{X}_{1i}^2} + \frac{(SD)_{2i}^2}{n_{2i}\overline{X}_{2i}^2}$$

where $n_{1i}$ represents the sample size for the treatment (open pollination) and $n_{2i}$ represents the sample size of the control (pollinator exclusion). $(SD)_{1i}^2$ represents the standard deviation of the treatment (open pollination), $(SD)_{2i}^2$ represents the standard deviation for the control (pollinator exclusion). $\overline{X}_{1i}^2$ represents the reproductive success of the treatment while $\overline{X}_{2i}^2$ represents the mean for the control. We back transformed the ln(RR) values using exp() function from base R to get the percentage values of pollination effect on fruit quality. The following equation was used:

$$Percent\ change = \left(e^{\ln(RR)} - 1\right) \times 100$$

Many of the references provided more than one effect size in a study, which may result in pseudo-replications. We therefore fitted a hierarchical random effect model by nesting effects within studies (Tuck et al., 2014), in which a publication-level random effect was added to incorporate the non-independency. We first carried out a random effects meta-analysis by "*rma.mv*" function in R package "*metafor*" to calculate the overall mean effect size of pollination on broad and aggregate fruit quality traits separately. Effect sizes were considered statistically significant if their 95 % bias-corrected bootstrap confidence intervals (CI) did not overlap with zero (Borenstein et al., 2021). Secondly, we incorporated moderators, including the biome, experimental scale, wild vs. managed pollinators, pollinator guild, quality broad, quality aggregate, and fruit environment as fixed effects to evaluate their influence on the effect of pollination on fruit quality in the random-effects models. We calculated the *P*-value of the $Q_t$ statistics. When they were statistically significant ($p < 0.05$), the influence of moderators was examined with $Q_m$.

We selected four widely studied pollinator-dependent fruit crops (apple, kiwi, blueberry and strawberry) with at least 20 case observations ($N_o \geq 20$) from five or more independent publications ($N_p \geq 5$), that met the recommended threshold for statistical robustness in ecological meta-analyses (Koricheva et al., 2013). This dataset allowed us to examine how pollinator traits influence the overall effect size of fruit quality (Table S2). We fitted random effects models to evaluate the overall effect sizes based on specific pollinator traits, in which pollinators were categorized by body size (large, medium, small), tongue length (short, medium, long), and sociality (social, solitary).

Our dataset also provided opportunities to examine the potential influences of pollinator visitation rate ($N_p = 21$, $N_o = 125$) and species richness ($N_p = 30$, $N_o = 181$) on multiple fruit quality traits. The visitation rate was determined by tallying the number of pollinator visits to flowers during each observation period or by capturing the insects visiting the flowers using sweep nets and summing the total number of insects collected (Turo et al., 2024). To address the variation in measurement methods across studies, visitation rate analyses were conducted using z-scores (Turo et al., 2024). We log-transformed the species richness data before analysis to stabilize its variance. Maximum likelihood meta-regression models (Filazzola et al., 2020) were applied in this analysis. The Knapp and Hartung adjustment method was used to account for uncertainty in the variance between studies (Knapp and Hartung, 2003).

The dataset used for statistical analyses are presented in Figshare (https://doi.org/10.6084/m9.figshare.28078808) upon publication, and currently through this private link (https://figshare.com/s/af5fabe87e4cf9d9740e). All analyses were performed in R statistical software version 4.4.1 (R Core Team, 2023) using the *metafor* package (Viechtbauer, 2010).

### 2.4. Publication bias

Contour funnel plot was used to visually assess publication bias (Palmer et al., 2008). Following this, we computed Rosenberg's fail-safe number to determine the robustness of our meta-analysis data (Rosenberg, 2005), which represents the minimum number of unpublished, insignificant studies needed to change a significant outcome to non-significant. A fail-safe number is considered robust when it is larger than 5k + 10, where k is the number of observations in our study (Rosenthal, 1986).

## 3. Results

In total, 79 articles were retained generating 451 effect sizes (Fig. 1; Table S2; Appendix A). The geographical distribution of the studies was biased (Fig. 1), with 30.37 % of publications carried out in Europe ($N_p = 24$), followed by Asia 26.58 % ($N_p = 21$), North America 17.72 % ($N_p = 14$), South America 13.9 % ($N_p = 11$), Oceania 6.32 % ($N_p = 5$), and Africa 5.06 % ($N_p = 4$). When classified by biomes, the temperate region hosted 63.29 % ($N_p = 50$), while the subtropical and tropical regions accounted for 20.25 % ($N_p = 16$) and 16.45 % ($N_p = 13$) of the studies, respectively. A total of 20 popular pollinator-dependent fruit crops was included with at least one observation (Table S2).

### 3.1. Overall effect of pollination on fruit quality

The hierarchical random effect model showed that pollination increases fruit quality by more than 30 % (*estimate* = 0.3367, CI = [0.17, 0.50], $p < 0.0001$; Fig. 2A; Table S3). This positive effect of pollination on fruit quality varied across observations ($Q = 82785.85$, df = 450, $p < 0.0001$).

### 3.2. Effect of pollination on broad and aggregate fruit quality

The increment of fruit quality by pollination services varied with broad quality traits (Table S4) and the magnitude was higher for organoleptic traits than the nutritional traits (Fig. 2A; Table S3). The effect of pollination on fruit quality varied with the quality aggregate traits (Table S4). Shape, size, commercial grades and firmness were significantly improved by pollination, while such effects were less noticeable on micronutrients, macronutrients and sensory traits (Fig. 2B; Table S3).

### 3.3. The association of the effect of pollination on fruit quality and moderators

Globally, the positive effect of pollination on fruit quality persisted across biomes (Fig. 3A; Table S5), but there were no significant variations between temperate, tropical and sub-tropical regions (Table S4). Similarly, pollination increased fruit quality regardless of experimental scale (Fig. 3B; Table S5), however, there were no significant differences on pollination effect between flower, branch and whole plant (Table S4). Both wild and managed pollinators significantly enhanced fruit quality (Fig. 3C; Table S5), but there was no significant variation between their effects (Table S4). Although the effects of pollination on fruit quality was positive for both different pollinator guild (Hymenoptera vs. Diptera; Fig. 3D; Table S5) and the fruit environment (greenhouse vs. open field; Fig. 3E; Table S5), such effects were not dependent on the two moderators (Table S4).

### 3.4. The effects of pollinator traits on fruit quality for plants with different flower architectures

Pollinator traits demonstrated varying effects on fruit quality across the popular pollinator-dependent fruits (Table S6). For strawberries, all pollinator traits except solitary, small body and medium tongue increased fruit quality. Among these traits, large-bodied and short-tongued pollinators had the most pronounced effects (Fig. 4A). Only large body pollinators increased the fruit quality of kiwi (Fig. 4B). For blueberries, all the pollinator traits had a significant effect on fruit quality (Fig. 4C). In contrast, none of the pollinator traits tested had a significant effect on apple fruit quality (Fig. 4D).

### 3.5. The influence of pollinator species richness and visitation rate on multiple fruit quality traits

Our results did not report a role of pollinator species richness on the

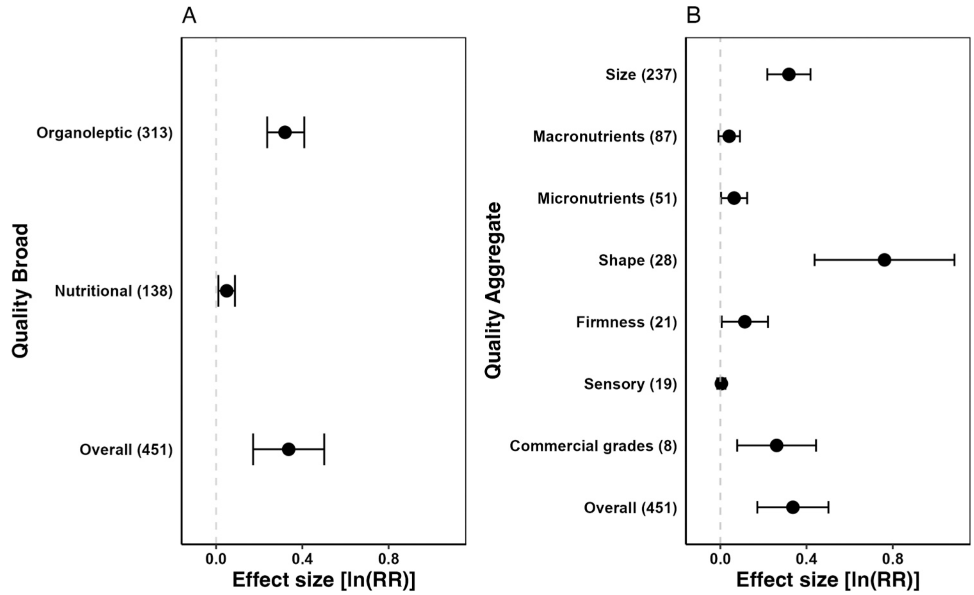


**Fig. 2.** Forest plot of the effect of pollination on different quality traits. The effect of pollination on broad fruit quality traits (A) and quality aggregate (B). The effect size is not statistically different from zero when the error bar overlaps with the vertically dashed line. Number of observations are in parentheses.

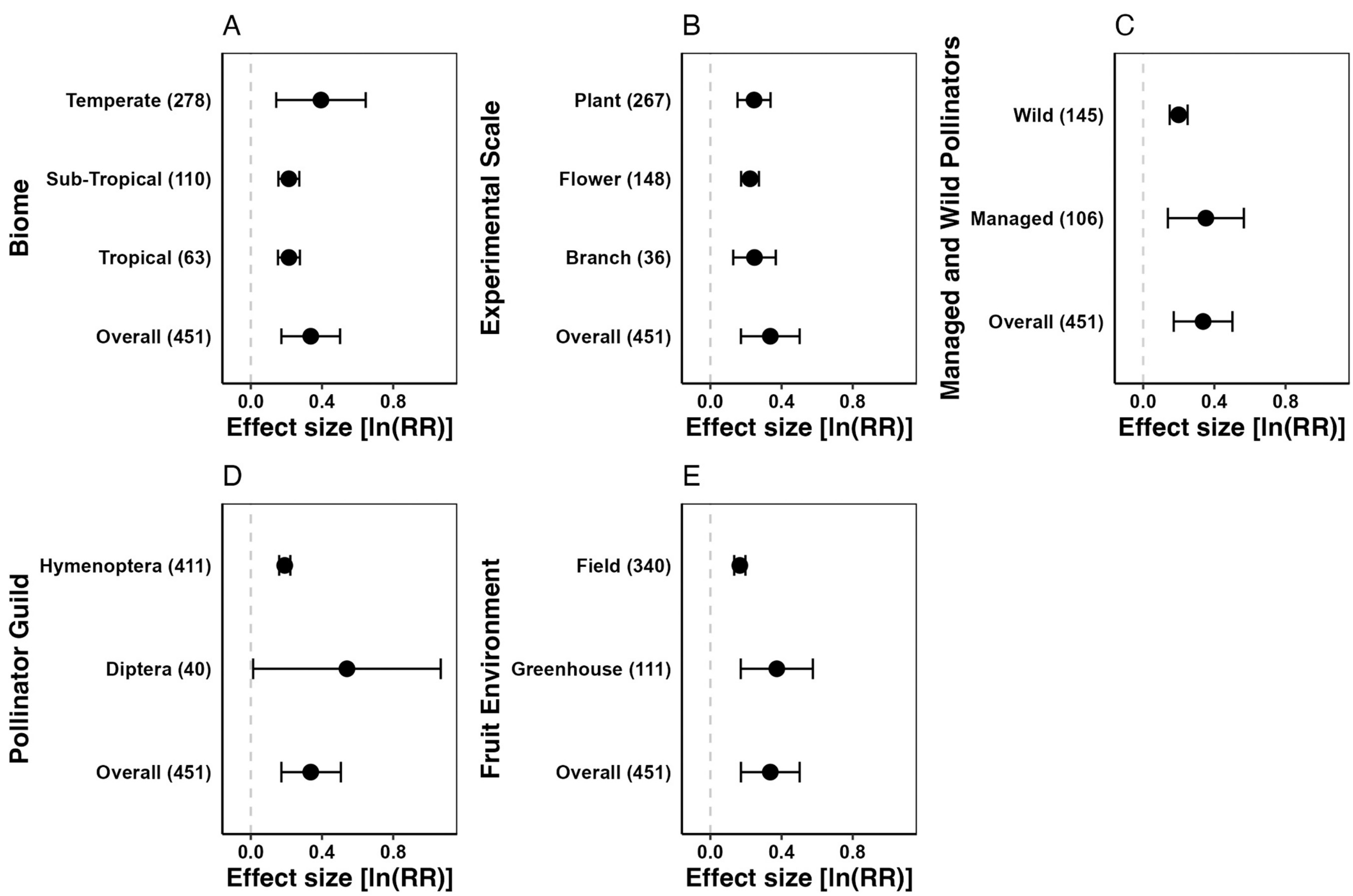


**Fig. 3.** Forest plot of the effect of pollination on fruit quality as influenced by various moderators A) biome, B) experimental scale, C) managed vs wild pollinators, D) pollinator guild showing by the insect order, and E) fruit environment. The effect size is not statistically different from zero when the error bar overlaps with the vertically dashed line. Number of observations are in parentheses.

effect of pollination on fruit quality in terms of the two broad quality traits (organoleptic and nutritional traits, Fig S2A, B). However, the importance of pollinator species richness was observed when those broad quality traits were subdivided into several aggregate quality traits. Pollinators species richness displayed a marginally negative correlation with fruit firmness (Fig S2C), although it did not determine the effect of pollination on commercial grade, macronutrients, fruit shape, and fruit size (Fig S2D-G). More importantly, pollinator species richness

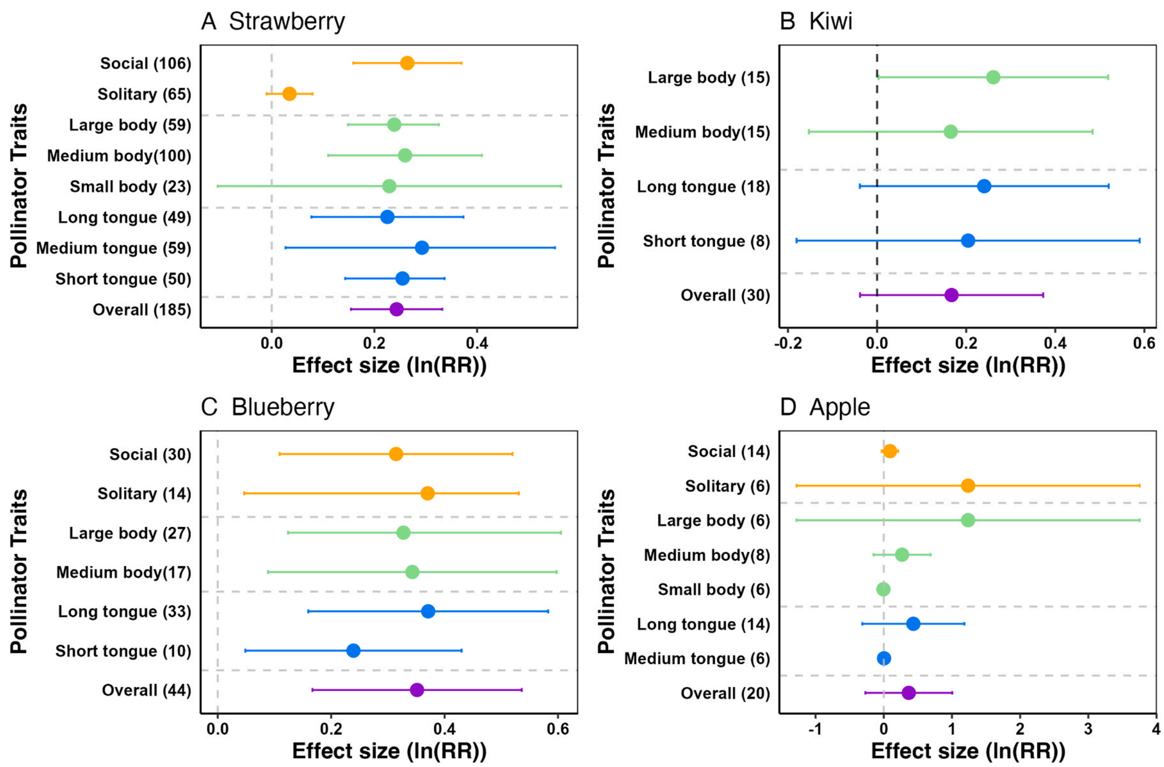


**Fig. 4.** Forest plot of the effect of different pollinator traits on overall fruit quality in four popular pollinator-dependent fruit crops. The effect size is not statistically different from zero when the error bar overlaps with the vertically dashed line. Number of observations are in parentheses.

significantly enhanced micronutrients of fruits (Fig. 5A; Table S7). For broad quality traits, visitation rate was not correlated with the effect of pollination on fruit quality for organoleptic traits (Fig S3A) but displayed a marginally positive influence on nutritional traits and a negative effect on fruit firmness (Fig S3B, C). In addition, our results indicated that visitation rate did not affect micronutrients and fruit size (Fig S3D, E; Table S8). Moreover, our analysis revealed that pollinator visitation rate enhanced macronutrients although it was a marginally significant level (Fig. 5B; Table S8); indicating that pollinator species richness and visitation rate had complementary roles in promoting fruit nutritional quality traits.

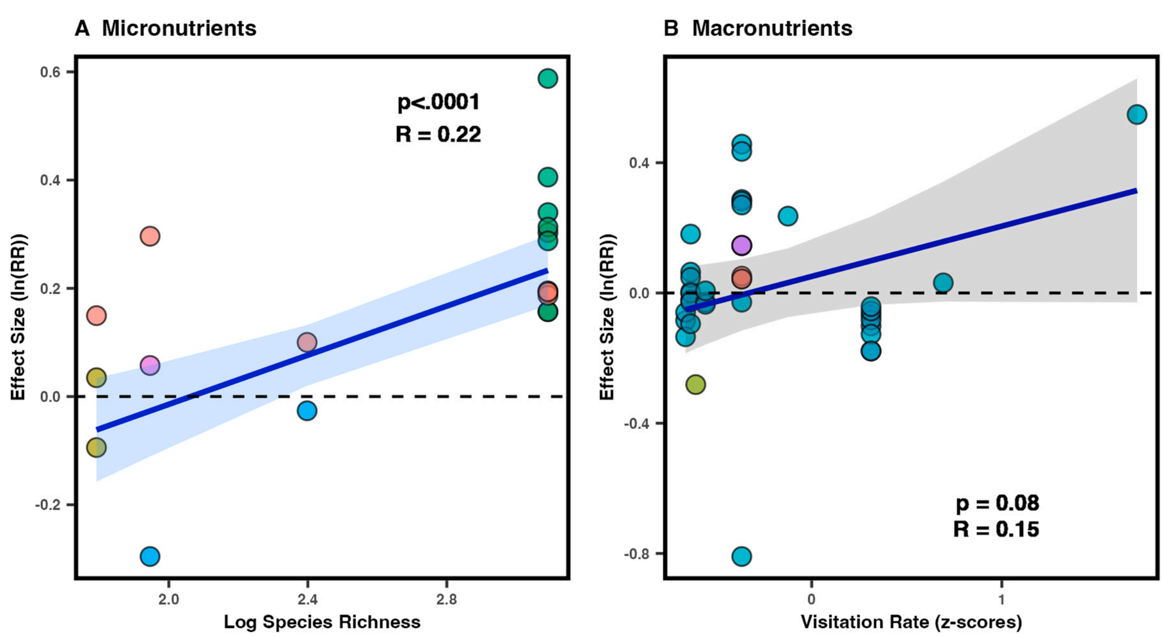


**Fig. 5.** The relationship between pollinator species richness (log transformed) and effect size of micronutrients (A), and the relationship between visitation rate (z-score) and effect size of macronutrients (B). The predicted relationship is shown by the solid black lines and the shaded areas indicate the 95 % confidence intervals. The circles represent cases that investigated visitation rate and fruit quality metrics, circle sizes are weighted by their variances (1/sqrt(vi)), and different colours represent the different quality metrics measured.

### 3.6. Publication bias

The contour funnel plot between standard error and the effect size visually checking publication bias was asymmetrical and skewed to the right (Fig. S4), meaning more studies reported the positive effect of pollination on fruit quality and the negative effects of pollination on fruit quality are often not reported. Our Rosenberg fail-safe number (N = 1015721) was higher than the observations in our study (N = 2265). Therefore, we can be confident in the validity and reliability of our findings.

## 4. Discussion

### 4.1. Overall effect of pollination on fruit quality

The findings of our meta-analysis align with the prevailing perspective that pollination services exert a beneficial impact on fruit quality (Klatt et al., 2014b; Garratt et al., 2014; Bishop et al., 2021; Gazzea et al., 2023). The observed improvement exceeded 30 % on average, although the magnitude of the effect varied considerably across observations and fruit crops. The overall effect of pollination on organoleptic quality traits, including fruit size, shape and commercial grade, lends support to the previous findings that pollination is essential to ensure successful ovule fertilisation, thereby facilitating uniform fruit development, consistent shape and size, and desirable attributes such as colour, taste, fewer malformations, increased shelf life and commercial value (Klatt et al., 2014a; Garratt et al., 2014; Wietzke et al., 2018). An increased visitation rate and species richness of pollinators did not result in enhanced organoleptic quality traits. Pollination is a requisite trigger to initiate the development of the organoleptic traits, however, they might have a low demand for high-quality pollination.

The overall low impact of pollination on fruit nutritional traits (e.g. macro- and micronutrients) indicates that factors other than pollination may also exert a significant influence on fruit quality. Such factors may include crop management practices that affect soil health and nutrient availability (Marini et al., 2015), in conjunction with environmental influences (Dumas et al., 2003). Nevertheless, further analysis indicated that the nutritional quality traits could be enhanced by an increase in visitation rate and species richness of pollinators. This suggests that high-quality pollination may be a crucial factor in promoting nutritional quality traits, although it may not be the primary determinant of such traits.

The enhancement of pollination on fruit quality may be attributed to several biological mechanisms, including enhanced pollination efficiency, which facilitates more effective pollen transfer, leading to better fertilisation and higher quality fruit set (Klatt et al., 2014a; Garratt et al., 2014; Gazzea et al., 2023; Turo et al., 2024). In addition, increased pollinator activity facilitates cross-pollination, which in turn leads to greater genetic diversity and more resilient fruit crops (Winfree et al., 2007; Garibaldi et al., 2013). Furthermore, pollination has been demonstrated to induce hormonal changes in plants, which can enhance fruit development and quality (Aizen et al., 2009; Roussos et al., 2009; Schurr et al., 2022). The findings of our study highlight the necessity for the conservation of pollinators in the context of the alarming decline of global pollinators. The implementation of practices that facilitate the construction of pollinator-friendly agricultural ecosystems has the potential to enhance fruit marketability, address human nutritional requirements and bolster food security.

### 4.2. The association of the effect of pollination on fruit quality and moderators

Our analysis demonstrated that the impact of pollination services on fruit quality remained consistent across diverse biomes, experimental scales, pollinator sources (wild and managed) and orders (hymenopteran and dipteran), and cultivation environments (field and greenhouse). This finding underscores the pervasive and pivotal role of pollination services in determining fruit quality (Gazzea et al., 2023). Hymenopterans, particularly bees, are renowned for their efficient pollination behaviour, which results in higher fruit set and improved fruit quality due to their ability to transfer pollen effectively (Brittain et al., 2013). Our results also revealed that Dipterans play a crucial role in promoting fruit quality, underscoring the significance of dipterans in the attainment of optimal fruit quality. As pollinators of many plants, flies can be just as effective or even more effective than bees, depending on the crop and environmental context (Rader et al., 2009; McCabe and Cobb, 2021). In addition, wild pollinators typically provide more effective pollination services than their managed counterparts, largely due to their behavioral diversity in resource exploitation strategies and the functional complementarity exhibited across taxa under unpredictable environments (Garibaldi et al., 2013). Managed pollinators, such as honeybees, are indispensable in contemporary global agricultural systems (Kleijn et al., 2015). With regard to fruit quality, our findings emphasise the significance of both wild and managed pollinators. This highlights the necessity of conserving wild pollinator habitats in conjunction with the utilisation of managed pollinators to guarantee optimal pollination services. Field environments typically exhibit greater diversity and/or abundance of pollinators when compared to greenhouse settings (Garibaldi et al., 2013). Consequently, greenhouse environments may rely on pollination services to a considerable extent. However, no significant difference existed between cultivating environments, which could be offset by managed pollinators such as bumblebees or honeybees. Our findings revealed no significant difference in the impact of pollination services on fruit quality across biomes although the diversity of bees, the primary pollinators globally, is unevenly distributed across geographic regions (Orr et al., 2021). Pollinators might be an indicator of high biodiversity linked to management of pest suppression (Gurr et al., 2017) and therefore, collectively contribute to promoting fruit quality. Even though our study did not directly evaluate the influence of pest dynamics on fruit quality, the positive effects of pollination on fruit quality may be also partially mediated by interactions between pollinators and pest control services. Diverse pollinator communities have been associated with improved pest regulation in agroecosystems, as they can support natural enemies of pests and contribute to plant health beyond pollination alone (Tamburini et al., 2020; Katumo et al., 2022). This suggests that pollinator diversity may play a dual role, enhancing both pollination and biological control, which could further amplify benefits to fruit quality. Our results underscore the universal significance of pollinators in diverse ecological and agricultural contexts. The substantial benefits of pollination on fruit quality highlight the necessity for conservation and management strategies to safeguard pollinator diversity.

### 4.3. Influence of pollinator traits on fruit quality for plants with different flower architectures

The results demonstrated that the impact of diverse pollinator traits on the overall effect size of fruit quality varied considerably across the four fruits with distinct flower architectures. The influence of pollinators on fruit quality was generally contingent upon the overall impact of pollination on the quality of a given fruit crop. Any pollinators would be beneficial when pollination is a determinant of fruit quality. Strawberry is a fruit that develops from a whole inflorescence, comprising numerous flowers that bloom asynchronously. For optimal fruit development, pollinators must make continuous visits to the plant. Except for solitary bees and small-bodied insects, a range of pollinators have been demonstrated to enhance its fruit quality (Klatt et al., 2014a). Despite the capacity of kiwi flowers to be pollinated by a range of insects, our results based on limited observations did not report a significant overall effect size of pollination on fruit quality. However, we evidenced that large-bodied pollinators exerted a significant positive influence on fruit quality. For flowers of this dioecious fruit crop, insects with large body size have been identified as effective pollinators (Broussard et al., 2022) and may therefore be essential in determining the fruit quality. Our analysis indicated that pollination had a positive overall effect on the fruit quality of the blueberry, which was enhanced by all observed pollinators. Blueberries have bell-shaped flowers with poricidal anthers, and the success of pollen transfer always requires specific pollinators through buzz pollination. Therefore, the blueberries might have a high possibility to experience pollen limitation, given their specific pollination requirements. However, this may be offset by the presence of pollinators capable of handling the flowers (Cortés-Rivas et al., 2023). While the impact of pollination on apple fruit quality was not observed, the results may be subject to challenge due to the relatively limited sample size. However, the radial bisexual flowers with exposed floral rewards may attract and allow diverse pollinators to visit the plants, thereby facilitating effective pollen transfer. The presence of a limited number of ovules per flower serves to mitigate the risk of pollen limitation. It is possible that sporadic instances of pollen transfer may prove sufficient to fulfil the requirement for fertilisation. This may account for the lack of significance in the effects of specific pollinators and overall pollination on fruit quality. The findings confirm that flowers with different architectures vary their pollination system, which may be an evolutionary consequence of plant-pollinator interactions. It is possible that constraints are imposed by the complementarity in interactions between the phenotypes and phenologies of flowers of certain fruits and their pollinators (Santamaría and Rodríguez-Gironés, 2007). In such cases, it would be advisable to consider recruiting the correspondingly specific pollinators in the cultivating environments of fruit crops with special flower architectures to relieve the constraints. Here, the limitation is that each type of floral architecture was represented by a single species, which may confound the effects of flower type with species-specific traits. While this restricts the generalizability of our conclusions, our results nonetheless highlight key differences in how floral architecture can influence pollination dynamics. Future field-based studies incorporating multiple species per floral type are necessary to more precisely disentangle the effects of flower morphology from other biological or ecological factors.

### *4.4. Differences in the effects of pollinator species richness and visitation rate on fruit quality*

The analysis revealed that fruit firmness was negatively influenced by both pollinator visitation rate and species richness. Although our dataset was limited due to the few numbers of studies that have explicitly examined how pollination services affect fruit firmness, the effect of pollinator species richness was slightly weaker than that of visitation rate. While we did not directly measure pollen deposition, previous studies suggest that enhanced pollen loads on stigmas may increase metabolic activity and accelerate fruit development, potentially resulting in softer fruits (González et al., 2006; Zhang et al., 2010). This aligns with findings in raspberries, where high bee visitation reduced drupelet set despite increased pollen deposition (Sáez et al., 2014). Similarly, elevated honeybee visitation has been linked to lower fruit weight and size in mandarins (Monasterolo et al., 2022). Our findings are consistent with the possibility that frequent visits may lead to intense pollen deposition over a short period. In contrast, staggered visitation by diverse pollinators may buffer against such negative effects on fruit quality, promoting balanced pollen delivery and improved fruit development (Rollin and Garibaldi, 2019).

Furthermore, our findings indicated that pollinator species richness and visitation rate exerted distinct influences on the various components of nutritional quality traits. Pollinator species richness was found to significantly enhance fruit micronutrients, while visitation rate promoted macronutrients, although the effect was at a marginal significance level. Fruit micro-nutritional traits are primarily composed of secondary metabolites, including acids, vitamins, and other organic compounds. In contrast, macro-nutritional traits are mainly associated with photosynthetic products, such as carbohydrates and water content. The impact of pollination services on fruit quality may be mediated by hormonal processes initiated by pollen load on the stigma and/or by defensive responses against the overexploitation of flowers by insects (Roussos et al., 2009; Schurr et al., 2022). The visitation rate of pollinators may directly correlate with an increase in the size of the stigmatic pollen load. The presence of diverse pollinators may contribute to the complexity of the stigmatic pollen load, as different pollinator species exhibit varying foraging behaviours and engage in competitive interactions for floral resources. This could result in a diverse source for the pollen load (Adler and Irwin, 2006; Cusser et al., 2016, 2021; Katumo et al., 2022). Overall, our results emphasise the significance of pollinator diversity in fruit quality, which not only enhances the marketability and value of fruits but also benefits food security and public health (Garibaldi et al., 2013; Chaplin-Kramer et al., 2014).

## 5. Conclusion

Our comprehensive hierarchical/multivariate meta-analysis confirms the essential roles of pollination services on fruit quality although the effects vary across fruit quality traits and fruit crops with different flower architectures. Organoleptic quality traits have a low demand for high-quality pollination service although pollination is essential to initiate their development. While nutritional quality traits can be promoted by high-quality pollination service although they appear to be less affected by the existence of pollination. Moreover, pollinator species richness and visitation rate exert differential effects on nutritional quality traits and complementarily boost fruit quality. The findings highlight the pivotal role of pollinator species richness, which could not be substituted by the enhancement of pollination through managed pollinators (Kleijn et al., 2015). Additionally, our findings indicated a detrimental effect of elevated visitation rates on fruit firmness, which may be particularly prevalent in ecosystems with managed pollinators. A diversified and dispersed pollination strategy, facilitated by diverse pollinators, could potentially offset this negative impact. Nevertheless, further comprehensive investigations, encompassing a broader range of fruits under diverse cultivation conditions, are essential to elucidate the nuanced influence of pollination on diverse fruit attributes.

## Implications and recommendations

Although the analysis is based on limited available studies, our findings have considerable implications for agricultural practices and the understanding of the merits of pollinator diversity. To achieve the greatest possible quality in crops, it is vital to promote species richness through the implementation of effective habitat management and conservation strategies. This can be achieved by preserving natural habitats, planting diverse flowering plants, and reducing pesticide use in agricultural systems and surrounding ecosystems, since these factors exert a significant influence on pollinator diversity. Furthermore, enhancing species richness rather than merely increasing visitation rates through managed pollinators can increase fruit quality more effectively, which may lead to an improvement in marketability and value of fruits due to the additional benefit of micro-nutritional quality traits. Moreover, fruit firmness and commercial grade, which are key organoleptic traits in regards to marketability and consumer preference, have been insufficiently studied in relation to pollination services. Future field research targeting these traits would provide a more comprehensive understanding of how pollinators influence both the sensory and nutritional dimensions of fruit quality across crop systems.

## CRediT authorship contribution statement

**Xiao-Li Shao:** Writing – review & editing, Methodology. **Denis Mburu Njoroge:** Writing – review & editing, Visualization, Software, Formal analysis. **Qing-Feng Wang:** Writing – review & editing, Validation, Supervision. **Robert Wahiti Gituru:** Writing – review & editing, Validation, Supervision, Project administration. **Anne Christine Ochola:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Chun-Feng Yang:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

## Data and Code Avail ability

The dataset and R scripts we used in our meta-analysis have been deposited at Figshare and will be publicly available at (https://doi.org/10.6084/m9.figshare.28078808) as of the date of publication. The dataset can be assessed through (https://figshare.com/s/af5fabe87e4cf9d9740e).

## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Chun-Feng Yang reports financial support was provided by Department of Science and Technology of Hubei Province. Chun-Feng Yang reports financial support was provided by National Natural Science Foundation of China. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109829.

## Data availability

We have shared the link of our data and code deposited in figshare. The link is available at the resresearch data attach file section.

Global meta-analysis shows an indispensable role of pollinator diversity in promoting fruit quality. Data and codes_Ochola et al. (Figshare)

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