



The impact of pollination requirements, pollinators, landscape and management practices on pollination in sweet and sour cherry: A systematic review

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ABSTRACT

Insect-mediated pollination is crucial for global production of multiple pollinator-dependent crops, including high-value crops like sweet and sour cherry. In the face of increasing agricultural demand and continued pollinator decline, it is essential to identify targeted management strategies to safeguard pollination services. Hence, we performed a systematic review on how cherry pollination is influenced by intrinsic and environmental requirements, flower-visiting insect communities, surrounding landscape and on-farm management practices. We found that most research was conducted in sweet cherry compared to sour cherry, and originated from North America and Europe, disregarding key global production areas. Cherry cultivars can be either self-compatible or self-incompatible, but insect pollination consistently benefits fruit set. Temperature has a strong effect on pollination success by mediating pollen germination, pollen tube growth and ovule longevity. Insect-mediated pollination is essential for adequate fruit set of both crops, whereas pollen limitation was detected for sweet, but not for sour cherry. A great diversity of insects visits cherry blossoms, with 185 species recorded, of which 142 were bees and 36 flies. With a mean relative abundance of 57 % across studies, honeybees were the dominant flower visitor. Little is known about the pollination performance of different taxa, with only one study comparing bees' single-visit efficiency, suggesting that mason bees and mining bees are more efficient pollinators compared to honeybees and bumblebees. This could explain why observational studies detect a positive relationship between wild pollinator visitation and cherry fruit set, which was not detected for honeybee visitation. Studies on managed pollinators focused on honeybees and mason bees, while bumblebee management was neglected. In sum, we conclude that pollination shortages can be improved by the promotion of wild pollinators, managed pollinators, or both, depending on the landscape context and pollination requirements of the cultivars. Wild bee visitation can be enhanced through conserving semi-natural habitats around orchards. Enhancing floral resources as an on-farm measurement has mixed results on pollinators, whereas other management practices such as polytunnels or pesticide effects on pollinators are understudied. Development of targeted guidelines for pollination management practices for farmers to enhance pollination services in cherry orchards should take into account multiple aspects, spanning from horticulture and agronomy (e.g., how to best manage flower strips) to applied entomology and landscape ecology (e.g., adding a landscape perspective to optimize honeybee management).

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1. Introduction

Animal-mediated pollination plays an essential role in fruit and seed production and in improving the quality in many pollinator-dependent crops (Klein et al., 2007; Gazzea et al., 2023; Siopa et al., 2024). Global agricultural production has become more reliant on animal pollination over time, increasing the importance of pollinators for food security (Aizen et al., 2019). In fact, recent studies frequently report pollen limitation in various pollinator-dependent crops (i.e., suboptimal yield due to insufficient levels of pollen deposition or pollinator visitation; Castro et al., 2021; Sáez et al., 2022; Eraerts et al., 2023a, 2024). Insects are the main pollinators of crops worldwide, including bees, wasps, flies and moths (Rader et al., 2016). To ensure and/or enhance pollination in crops, managed bees or flies are routinely used by farmers (Osterman et al., 2021a), particularly the western honeybee (*Apis mellifera*; Osterman et al., 2021b). In addition to managed pollinators, wild pollinators are also known to contribute to crop production (Garibaldi et al., 2013; Rader et al., 2016; Reilly et al., 2024). Managed and wild pollinator communities differ across regions and crops and are affected by farm management (Reilly et al., 2020; Dymond et al., 2021; Arachchige et al., 2023; Eraerts et al., 2023a). On-farm management, e.g., wildflower strips or honeybee hive deployment and landscape features, such as semi-natural habitats (SNH), can enhance visitation of both managed and wild pollinators to crop flowers (Osterman et al., 2023; Gaspar et al., 2022; Eraerts et al., 2023b; Mateos-Fierro et al., 2023).

Successful pollination of pollinator-dependent crops is also determined by crop reproductive traits, such as self-incompatibility, dioecy and floral development (Lech et al., 2008; Herrero et al., 2017). Self-incompatibility systems play an important role in determining the yield of many fruit and vegetable crops (e.g., Ramírez and Davenport, 2013; DeVetter et al., 2022), regardless of levels of pollinator dependence and pollinator activity. The lack of compatible pollen donors negatively impacts the contribution of pollinators in providing successful pollination in crops. Hence, orchard design needs to guarantee sufficient compatible pollen is available by including pollinizer cultivars (e.g., MacInnis and Forrest, 2020). Also, environmental factors like temperature impact floral development, including pollen viability,

stigma receptivity and ovule viability (Sebolt and Iezzoni, 2009; Walters and Isaacs, 2023). Self-incompatibility and the response to environmental factors vary among different crops and cultivars (Fotirić-Aksić et al., 2014), consequently affecting pollinator efficiency and crop yield (Sáez et al., 2022; Garratt et al., 2023).

Neglecting these traits may result in pollen limitation, which has been detected in some crops including sweet (*Prunus avium*) and sour (*P. cerasus*) cherry (Holzschuh et al., 2012; Reilly et al., 2020; Mateos-Fierro et al., 2023; Osterman et al., 2023). Both cherry species originated most likely from the area around the Caspian and Black seas (Blando and Oomah, 2019). To date, both crops are cultivated globally with major production areas in countries such as Turkey, U.S.A., Russia and Chile among others (Quero-García et al., 2017; FAOSTAT, 2023). Sweet and sour cherries are hermaphroditic and cultivars can be either self-incompatible or self-compatible (Lansari and Iezzoni, 1990; Cachi and Wünsch, 2014; Cachi et al., 2014; Radičević et al., 2021). Both cherry crops are highly dependent on insect pollination and flower early in the season, when weather conditions are likely inclement (Holzschuh et al., 2012; Fadón et al., 2015). Adverse weather conditions might limit the performance of insect pollinators which could further exacerbate pollen limitation and yield deficits (Vicens and Bosch, 2000; Hansted et al., 2015).

Cherry production continues to steadily increase with a global production in 2021 of 2.7 and 1.5 million tonnes for sweet and sour cherries, respectively (FAOSTAT, 2023). Hence, a global assessment of pollination requirements, insect communities pollinating these crops, the impact of landscape and management practices are therefore essential to identify geographical and thematic knowledge gaps to guide future research on cherry pollination (Fig. 1). Various topics of cherry production and management have been synthesized by Quero-García et al. (2017), yet this book does not cover aspects of insect-mediated pollination, or how landscape and farm-management mediate cherry pollination. Bridging the gap between disciplines such as ecology, entomology and horticulture is critical to develop sustainable crop pollination practices and management guidelines (Isaacs et al., 2017; DeVetter et al., 2022). Therefore, it is important to synthesize the knowledge on pollination of these different disciplines to identify

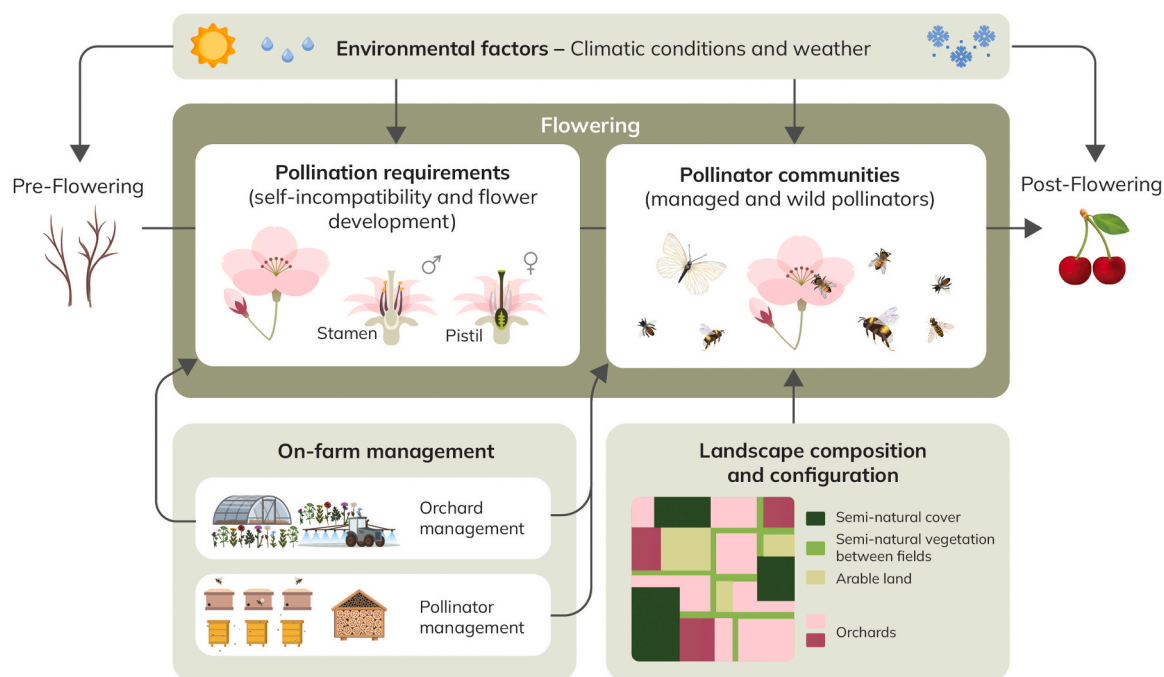


Fig. 1. Schematic overview of potential factors influencing cherry pollination from pre-flowering to flowering period. Environmental factors (climatic conditions and weather), landscape structure, orchard and pollinator management can influence pollination requirements and pollinator communities with consequences for fruit set.

synergies among them for managing crop production. Here, we present a systematic review of the following research questions:

1. What are the main geographical areas and research themes of cherry pollination studies?
2. What are the intrinsic pollination requirements of cherry and which extrinsic variables are affecting pollination success?
3. To what extent does cherry benefit from insect-mediated pollination and how often is pollen limitation reported?
4. Which insect species visit and pollinate cherry blossoms and how do these pollinators differ in their pollination contribution?
5. How does landscape structure influence pollinator communities and their pollination contribution?
6. Which effective management practices are studied to support cherry pollinator communities and the pollination services they provide?

2. Methodology

2.1. Literature review and data collection

Literature was sourced by means of a systematic literature search with ISI Web of Science Core Collection (all editions). The search terms were “cherry” OR “cherries” OR “*Prunus avium*” OR “*Prunus cerasi*” AND “bee” OR “bees” OR “pollinat*” for all fields. The search was performed on 29 January 2023 and yielded 418 potential peer reviewed publications. Each study was screened by reading the title and abstract according to the criteria listed below. In this selection stage, studies had to focus on i) pollinators and/or pollination and ii) sweet and/or sour cherry. This resulted in 122 suitable studies which were subject to full-text review. During the full-text screening, studies were selected if they conducted research relevant to this review’s key objectives (see research questions). During full-text screening, the reference list of each publication was checked, and we found 23 additional studies. From each suitable study, we extracted meta-data including geographical location, year of data collection, the research theme(s) (see below Section 2.2), pollinator survey method, pollinator taxa, level of pollinator species identification, cherry cultivars included, pollination metrics measured (e.g., fruit set), experimental pollination treatments conducted, number of sites and the main finding. The selection process is illustrated in a PRISMA diagram (Fig. S1), and the complete list of the studies is presented in Table S1.

In addition, we extracted information on sweet and sour cherry yield (tonnes) per country for 2021 from the Food and Agricultural Organization of the United Nations (FAOSTAT, 2023).

2.2. Literature processing and data analysis

To identify relevant literature for every study objective, we extracted information about the geographic coverage and every research theme(s) on which the study focused. We defined five research themes, and the studies were designated to one or more themes, 1) pollination requirements, 2) pollination service and pollen limitation, 3) cherry pollinators and their pollination contribution, 4) influence of the surrounding landscape and 5) on-farm management on pollination services.

2.2.1. Pollination requirements

Pollination requirements were divided into two subsections according to the nature of the factors affecting pollination 1) intrinsic factors (i.e., self-incompatibility and its impact in pollination) and 2) external factors (i.e., effects of rootstock and environmental factors on flower development).

For studies on intrinsic factors, we categorized studies into four groups: 1) self-incompatibility, i.e., pollination experiments to quantify self-fertility, 2) S-alleles, i.e., experiments to determine incompatibility between alleles, 3) crossability, i.e., experiments to assess compatibility

between cultivars and/or 4) pollinizers, i.e., experiments to identify best pollen donor cultivars. Additionally, the studies were also assigned to the crop (sweet and/or sour cherry), methodology used (pollination experiments and/or genetic approach, under field or semi *in vivo* conditions using branches maintained in controlled conditions) and response variables collected (i.e., pollen tube development, fruit set and/or other traits). The studies were designated to one (or more) categories according to the focus of the study.

For studies on biotic and abiotic external factors, we categorized the studies into two groups 1) effects of temperature and 2) effects of rootstock (as no other studies on biotic factors on pollination requirements were found). Effects of temperature on flower development included effects on i) flower female components (i.e., ovary development, ovule longevity and stigma receptivity), ii) flower male components (i.e., pollen germination and pollen tube growth) and iii) flowering phenology.

2.2.2. Pollination services and pollen limitation

Here, we selected studies that measured open fruit set (i.e., flowers exposed to field-realistic levels of pollinator visitation) in combination with one or two pollination treatments, namely pollinator exclusion (i.e., flowers excluded from pollinator visitation with a mesh-bag) and hand pollination (i.e., flowers pollinated by hand). Given the low number of studies we found, we could not perform a meta-analysis but opted to extract the raw data per study and conduct a synthesis analysis by means of linear-mixed effect models (LMER). Only data from observational field studies were included (i.e., no experimental greenhouse/laboratory studies as these settings do not allow the quantification of natural levels of pollinator visitation which are the basis to calculate pollination service and pollen limitation; (Eeraerts, 2023a; Garratt et al., 2021; Siopa et al., 2024). Within each study, fruit set data was extracted from the text, tables or figures with the software ImageJ. Fruit set data was extracted per pollination treatment, site, year and cultivar whenever data was available. In studies where self- (i.e., flowers hand pollinated with their own pollen), cross- (i.e., flowers hand pollinated with pollen from another cultivar) and supplement pollinations (i.e., flowers exposed to pollinators and supplemented with additional pollen by hand) were performed, we used the treatment with the highest fruit set as hand pollen supplementation treatment to avoid underestimations of pollen limitation.

With these fruit set data, the value of insect-mediated pollination can be determined (Garratt et al., 2023), i.e., pollination service, as:

$$\text{Pollination service} = 1 - \left[\left(\frac{\text{Pollinator exclusion}}{\text{Open pollination}} \right) \right] \times 100$$

In addition, pollen limitation can be determined (Garratt et al., 2023), which is interpreted as the amount of additional pollination required to achieve maximum pollination.

$$\text{Pollen limitation} = 1 - \left[\left(\frac{\text{Open pollination}}{\text{Hand pollination}} \right) \right] \times 100$$

LMERs were used to assess differences between sweet and sour cherry on open fruit set, pollination service and pollen limitation (lmer function, ‘lme4’ package; Bates et al., 2015). In these models, open fruit set, pollination service and pollen limitation were response variables, crop was specified as a fixed variable and study ID as a random variable. Additionally, for both pollination service and pollen limitation, a no-intercept LMER with crop as the fixed factor was used to infer whether the mean pollination service and mean pollen limitation of each crop were different from zero.

2.2.3. Cherry pollinators and their pollination contribution

Of the studies investigating cherry pollinators and their pollination performance, we aimed to extract data from those recording insect communities (Table S2). We distinguished relative abundance and

richness of cherry flower visitors, and relative abundance and richness of flying insects in cherry orchards (Table S2). All studies performing direct observations of cherry flower visiting insects (e.g., via transect walks or focal observations) were used for the relative abundance and/or richness of flower-visiting insects. To give a general overview of the relative abundance of flower visitors, we included only those studies which investigated flower visitors including honeybees. We then divided the flower-visiting insects into five morphological groups, honeybees, bumblebees (*Bombus* spp.), other wild bees, flies and other insects and reported their relative abundance (abundance/abundance of all insects). For those studies reporting abundance at the genus level for wild bees, we extracted the relative abundance for each genus. In addition, we extracted data on richness from studies reporting flower-visiting insects at species level. Studies using pan-traps or observations of non-cherry flower visitors (e.g., of wildflowers or in flower strips) were included in the relative abundance and richness of insects in cherry orchards.

For pollination efficiency and foraging behavior of different pollinator species or morphological groups, we summarized the main findings of the studies. In addition, we reviewed studies assessing the contribution of wild pollinators and honeybees (i.e., how pollinator visitation correlates with fruit set in observational, site-replicated studies). Here, no data summaries were performed due to the lack of uniformity of variables assessed across the studies.

2.2.4. Influence of the surrounding landscape

We reviewed studies assessing the effect of surrounding landscape structure on insect-mediated cherry pollination (i.e., how landscape structure influences pollinator communities and fruit set in observational, site-replicated studies). For this theme, no data summaries were performed due to the heterogeneous design among the identified studies.

2.2.5. On-farm management practices

We categorized on-farm management practices into two subsections 1) pollinator management (i.e., management practices directly involving pollinators (e.g., honeybee hive density)) and 2) orchard management (i.e., management practices at a farm level which do not directly involve pollinators). Orchard management included i) vegetation management (e.g., wildflower strips, alleyway mowing), ii) mechanical management (e.g., polytunnels), iii) attractant management (e.g., chemical lures to attract pollinators), iv) pesticide management (e.g., insecticide applications), and v) pollen management (e.g., pollen release by drones). We combined all these practices under orchard management due to the low number of studies exploring them individually.

Mean stocking densities (\pm SE) for managed honeybees and bumblebees were calculated based on the studies that provided this information. Mean stocking density was not calculated for nesting cavities (artificial trap nests) for managed solitary bees due to the lack of information in the respective studies.

All visualization and analyses were performed using the software R (version R-4.2.3, R Core Team, 2023).

3. Results and discussion

3.1. Geographical coverage and research focus

In total, our search resulted in 99 published studies. Studies on cherry pollination and pollinators were primarily conducted in Europe (N = 45) and North America (N = 24; Fig. 2). The USA had the most studies per country (N = 20), followed by Belgium (N = 12), Spain (N = 10) and Turkey (N = 8). Surprisingly, we only detected one study from Chile, one from Uzbekistan and none from Russia, countries that have considerable cherry production (Fig. 2; Table S3). This mismatch between main production areas and research conducted has been reported in other crop-focused syntheses (Pardo and Borges, 2020; Dymond et al., 2021; Arachchige et al., 2023; Eeraerts et al., 2023a). Future studies should focus on these neglected key production regions to shed light on potential regional differences on the factors influencing insect-mediated pollination (Olhnuud et al., 2022; Eeraerts et al., 2023a). Indeed, factors such as pollinator communities, pollen limitation, weather conditions, and farm management practices including regional cultivar preferences, vary across production regions (Blando and Oomah, 2019; Reilly et al., 2020).

A total of 76 studies focused on sweet cherry, 17 studies on sour cherry and six studies investigated both crops. Some topics such as the pollination efficiency of different pollinator taxa and the effect of the surrounding landscape have not been studied at all in sour cherry. The fact that sour cherry is understudied compared to sweet cherry highlights a general trend in crop pollination ecology, as some crops are studied frequently (e.g., apple, oilseed rape) while others are under-represented (e.g., pear, pumpkin; Allen-Perkins et al., 2022). Only by studying pollination requirements in a broad range of crops and their cultivars, specifically in the main production regions, will we be able to understand and advise optimal management practices for farmers. See Fig. 3 for an overview of the cumulative number of publications per research theme. The focus of the studies varied across time, from early studies focusing on how pollination requirements affect pollination, to the effects of landscape and management practices, which were mainly

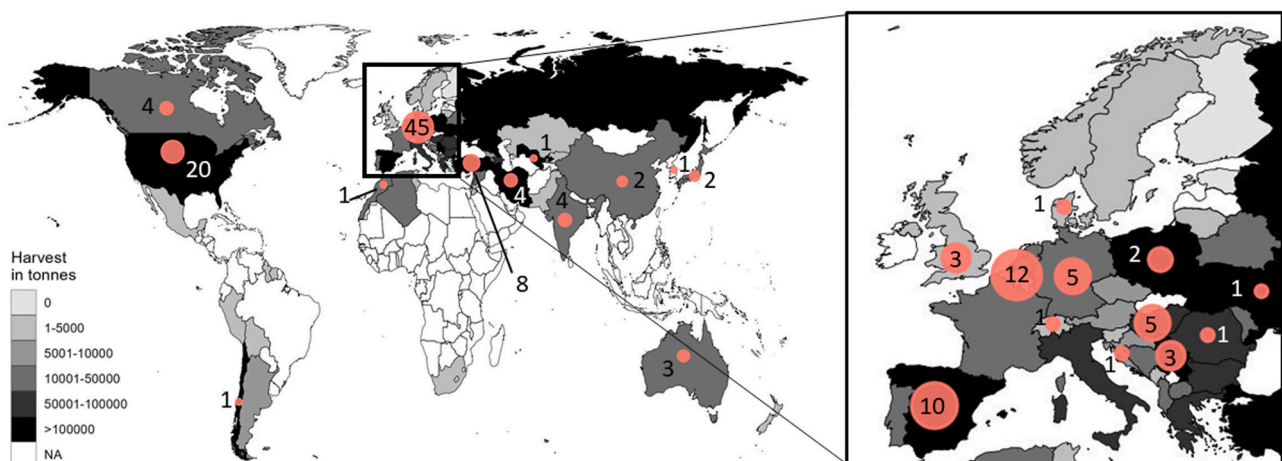


Fig. 2. World map with red circles indicating the number of studies on pollinators and pollination in sweet and sour cherry per country (total 99 studies). Three studies could not be assigned to a country, two were reviews and in one empirical study no country was mentioned. Summed sweet and sour cherry harvest in tonnes per country is illustrated in grey shades based on data from FAO (Table S3; FAOSTAT, 2023).

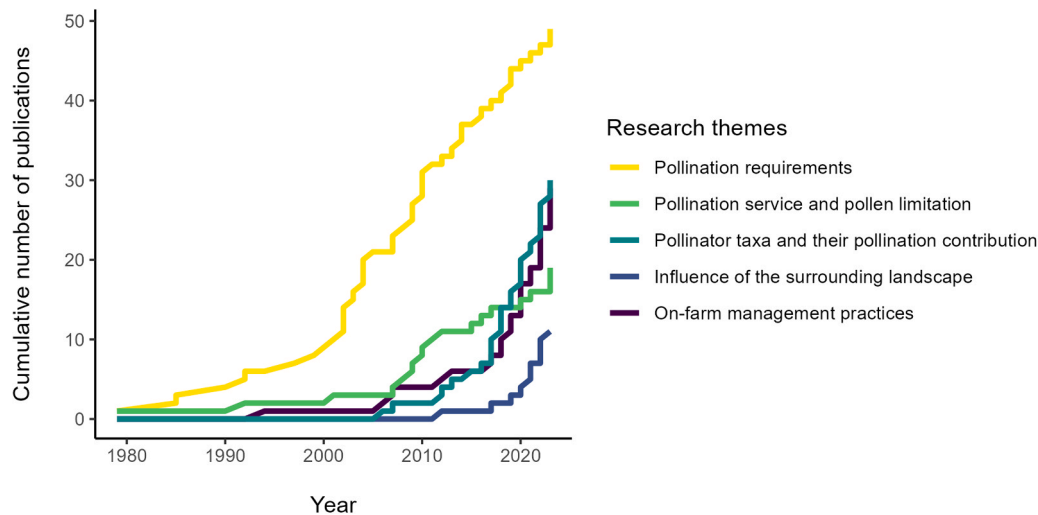


Fig. 3. Cumulative number of publications over time by research themes (pollination requirements (N = 49), pollination service and pollen limitation (N = 19), pollinator taxa and their pollination contribution (N = 30), influence of the surrounding landscape (N = 11) and on-farm management practices (N = 29).

explored in the last decade.

We recorded a total of 151 cultivars, 128 for sweet and 23 for sour cherry used in the studies (Table S4). Kordia (18 studies) and Regina (17 studies) were the most used cultivars for sweet cherry, while Montmorency (8 studies) was the most used for sour cherry. As with other crops, like apple and oilseed rape, studies mainly included one cultivar (Woodcock et al., 2019; Olhnuud et al., 2022; but see Eeraerts et al., 2024). Additionally, studies rarely included the same cultivar per study for a certain research theme, something that constrains performing qualitative syntheses to determine the true cultivar effect. To make robust inferences of cultivar variability across landscape or management factors, multiple cultivars need to be included in a single study (Eeraerts et al., 2024).

3.2. Pollination requirements

3.2.1. Intrinsic factors

Sweet and sour cherry exhibit a gametophytic self-incompatibility system controlled genetically by a multi-allelic S-locus carried by male gametophytes (i.e., pollen grains) that prevents self-fertilization (Crane and Lawrence, 1928; Lansari and Iezzoni, 1990; Yamane et al., 2003). More recently, genes not linked with the S-locus have also been found to determine self-compatibility in cherry (Kao and Tsukamoto, 2004; McClure et al., 2011). As a result, cross-pollination between compatible cultivars is essential for fruit set in many cultivars of sweet and sour cherry.

In this review, we retrieved 32 studies exploring the impact of pollen donors on sweet and sour cherry pollination (Table S1), which highlight the importance of plant-mating system in both crops. The scope varied from studies focusing on local cultivars (Nyéki et al., 1992, 2003; Beyhan and Karakaş, 2009; Ganji Moghadam et al., 2009), to studies aiming at increasing the global knowledge of cherry crops (Hauck et al., 2002; Granger, 2004; Hedhly et al., 2016). Research is clearly more advanced in sweet cherry (79 %; N = 25) than in sour cherry (27 %; N = 9) and main goals range from quantify self-incompatibility (70 %; N = 22) and identify S-alleles (36 %; N = 12) to assess cultivar compatibility (67 %; N = 21) and/or identify pollenizer cultivars (48 %; N = 15). Most studies were performed under field conditions (94 %; N = 30) and, thus, were impacted by other factors, while 25 % (N = 8) were conducted under semi *in vivo* conditions (using cut branches or flowers; Cerović and Ružić, 1992; Hormaza and Herrero, 1999) allowing only observation of pollen tube development. Interestingly, most molecular studies (85 %; N = 27) included controlled pollination experiments to validate results

and temporal variation was considered in 48 % (N = 15) of the studies. Fruit set was the most common response variable (76 %; N = 24), but many studies also explored pollen tube development (58 %; N = 19), with 36 % (N = 12) exploring both and only 9 % (N = 3) exploring other traits (e.g., fruit size and weight). However, because our search did not specifically target self-incompatibility, we provide an overview of the process from pollination to fertilization.

Several studies described the occurrence of self-incompatible and self-compatible cultivars in both sweet cherry (Lane, 1979; Godini et al., 1998; Choi et al., 2002; Wünsch and Hormaza, 2004; Cachi and Wünsch, 2014; Cachi et al., 2014) and sour cherry (Lansari and Iezzoni, 1990; Hauck et al., 2002; Nyéki et al., 2003; Ansari et al., 2010; Radičević et al., 2021). In self-incompatible cultivars, studies consistently reported an initial similar rate of pollen tube growth as cross-pollen, but reduced growth as time went on. Specifically, self-pollen tubes start to branch, burst or grow in reverse and eventually stop about halfway down the styles, never reaching the ovary (sweet cherry: Lech et al., 2008; Radičević et al., 2013, 2016; Cachi and Wünsch, 2014; sour cherry: Lansari and Iezzoni, 1990; Cerović and Ružić, 1992; Hauck et al., 2002; Radičević et al., 2021). Yet, evidence of self-incompatibility was also observed in the upper third of the style in some sour cherry cultivars (Cerović and Ružić, 1992). In self-compatible cultivars, self-pollen successfully reached the end of the style in sour cherry (Lansari and Iezzoni, 1990; Hauck et al., 2002) and the ovary in sweet cherry (Cerović and Ružić, 1992; Radičević et al., 2013; Cachi and Wünsch, 2014; Piri et al., 2022). Self-compatibility in sour cherry emerges from natural mutations accumulation resulting in at least two non-functional S-haplotypes within an individual (Hauck et al., 2006).

The advantages of self-compatible cultivars are linked with on-farm orchard management. Indeed, self-compatible cultivars do not require compatible pollen donors, therefore single cultivar orchards can be designed as solid blocks instead of multiple cultivar orchards (Lane, 1979; Godini et al., 1998; Piri et al., 2022). In addition, self-compatible cultivars can be used as ‘universal pollen donors’ (Lane, 1979). Fully self-compatible sweet cherry cultivars can produce similar yields with self- and cross-pollination (Choi and Andersen, 2001; Piri et al., 2022), and the presence of other pollen donors might not be required. However, other studies have also shown that self- and cross-pollen may yield higher fruit set and/or quality (e.g., weight) in self-compatible cultivars (Beyhan and Karakaş, 2009; Sebolt and Iezzoni, 2009; Ansari et al., 2010). In some self-compatible cultivars, pollen tubes from self-pollen grew slower than cross-pollen, and very few self-pollen tubes reached the last third of the style in both sweet cherry (Cachi et al., 2014) and

sour cherry (Lansari and Iezzoni, 1990; Radićević et al., 2021). This mating strategy allows self-fertilization in the absence of compatible cross-pollen but favors cross-pollination. Gene flow assessment of self-compatible sweet cherry cultivars supports this strategy showing no evidence of self-fertilization (Granger, 2004).

Consequently, it is important to determine S-locus genotypes to identify cross-compatibility groups (Choi et al., 2002; Hauck et al., 2002; Cachi and Wünsch, 2014). The latest review recognized 72 cross-compatibility groups among 1700 sweet cherry cultivars based on the identification of S genotypes (Schuster and Schröpfer, 2023). However, the lack of systematization of S-allele combinations in sour cherry to identify cross-compatibility groups certainly indicates that future research should aim at finding compatible groups for this crop (Sebolt and Iezzoni, 2009; Radićević et al., 2021). The list of cross-incompatible groups of cultivars (Schuster and Schröpfer, 2023), along with cultivar flowering phenologies (Nyéki et al., 2003; Ganji Moghadam et al., 2009; Radunić et al., 2017; Eraerts, 2022) are useful to identify compatible cultivars when building an orchard or when exploring pollination shortages in established orchards.

3.2.2. External factors

Beyond the compatibility system, we argue that successful pollination is also affected by 1) the overlap between the availability of compatible pollen and stigma receptivity, 2) the successful transfer of compatible pollen to stigmas, 3) pollen adherence and germination to stigmas, 4) pollen tube growth and fertilization, and 5) ovary development and ovule longevity (Fig. 1). Regarding these external factors, we found a total of 22 studies, with 13 studies addressing the effect of temperature on sweet and sour cherry flower's female and/or male components (Table 1). Studies consistently showed that high temperature decreased ovule longevity (Postweiler et al., 1985; Beppu et al., 1997; Hedhly et al., 2007; Zhang et al., 2018), decreased the effective period of stigma receptivity (Hedhly et al., 2003; Zhang et al., 2018), and negatively affected ovary development (Beppu et al., 1997). High temperatures also consistently accelerated pollen tube growth (Cerović and Ružić, 1992; Pirlak et al., 2002; Hedhly et al., 2004, 2007; Zhang et al., 2018). Overall, temperature impacts the effective pollination

period because while high temperatures increase pollen tube growth, it also shortened both stigma and ovule receptivity decreasing the window for the pollen tube to reach the ovule while it is viable.

While the effects of high temperature on the female components and on pollen tube growth are consistent across studies, the effect reported for pollen germination are mixed with some studies reporting a decrease in germination rate (Hedhly et al., 2003, 2004, 2005; highest temperature 30°C) and others an increase (Pirlak, 2002, highest temperature 20°C; Zhang et al., 2018, highest temperature 24°C). Interestingly, many studies report an interaction between temperature and cultivar (e.g., Guerrero-Prieto et al., 1985; Postweiler et al., 1985; Hedhly et al., 2004, 2005; Radićević et al., 2016; Radićević et al., 2021), which may provide valuable information for the selection of cultivars that are best adapted to a given orchard location.

Ten of the reviewed studies investigated the relationship between phenology and temperature, the main conclusions being that higher temperatures lead to earlier flowering and that there is a cultivar dependent response of flowering to temperature (Table 1). Indeed, higher temperatures were associated with earlier flowering, reduced flower size (Beppu et al., 1997; Zhang and Whiting, 2012), shorter flowering period (Li et al., 2010; Xu et al., 2023), and greater flower injury due to late frosts (Beppu et al., 1997; Choi et al., 2002; Beyhan and Karakaş, 2009; Paltineanu and Chitu, 2020; Xu et al., 2023). Particularly, the study by Paltineanu and Chitu (2020), which analyzed temperature and sweet cherry phenology data from 1970 to 2018, showed an increase in air temperature during January through May, significant in March and April, and found a relationship between the rise in air temperature and advance in earlier phenological stages. Considering these findings and the predicted climate change scenarios (IPCC, 2021), there is a risk that cherries advance their phenological stages becoming more exposed to increased risk of damage due to late frosts (Beppu et al., 1997; Choi et al., 2002; Beyhan and Karakaş, 2009; Paltineanu and Chitu, 2020; Xu et al., 2023) and increasing the risk of mismatches between cherry and key pollinators (Eraerts, 2022).

Application of growth regulators and rootstock cultivar (i.e., cultivar on which the scion is grafted) can also influence flower development, yet only two studies explored this. Here, Xu et al. (2023) found that growth regulators did not affect pollen abundance on the stigma, number of pollen tubes, and pistil browning. Rootstock identity was found to affect the start of flowering and flower size (Dziedzic et al., 2019). This sheds light on the potential of rootstock to postpone cherry flowering in years with mild winters and warm springs and lower the potential mismatch with pollinator emergence and the risk for overnight frost.

3.3. Pollination services and pollen limitation

A total of 19 studies provided pollination data measured as fruit set. Fruit set from open pollinated flowers was significantly different between sour and sweet cherry (LMER estimate = 13.28 ± 6.13 , $t = 2.17$, $p = 0.048$; Fig. 4A). Sour cherry ranged from 2 % to 49 %, while sweet cherry fruit set ranged from 2 % to 71 % (Table S5).

Pollination service by insects was significantly different between cherry crops (LMER estimate = 29.82 ± 5.34 , $t = 5.59$, $p < 0.01$; Fig. 4B; Table S6). Both crops are highly dependent on insect pollination, as pollination service was significantly greater than zero for sour and sweet cherry (Table 2; Fig. 4B). Pollination service is found to vary across regions for other crops (Olhnuud et al., 2022; Eraerts et al., 2023a), which highlights the need for further research to better understand regional variation, particularly because key production regions of cherry are severely understudied.

Pollen limitation values did not differ between sweet and sour cherry (LMER estimate = 18.15 ± 11.28 , $t = 1.61$, $p = 0.17$; Fig. 4C; Table S7). For sour cherry, we did not detect significant pollen limitation, whereas pollen limitation for sweet cherry was on average greater than zero (Table 2; Fig. 4C). This crop-dependent pollen limitation is in line with research in other crops (Reilly et al., 2020; Siopa et al., 2024). Therefore,

Table 1
Summary of main effects of flowering phenology and flower development to increased temperatures (arrow down = negative relationship, arrow up = positive relationship, n.s. = no significant relationship found).

Response variable	Effects	References
Flowering period	Earlier	Beppu et al. (1997); Zhang and Whiting, (2012); Paltineanu and Chitu, (2020);
Flower size	Shorter	Li et al. (2010); Xu et al. (2023)
Stigma receptivity		Beppu et al. (1997); Zhang and Whiting, (2012)
Ovule longevity		Hedhly et al. (2003); Zhang et al. (2018)
Ovary development	Reduced	Postweiler et al. (1985); Beppu et al. (1997); Hedhly et al. (2007); Zhang et al. (2018)
Pollen germination		Beppu et al. (1997)
Pollen tube growth		Hedhly et al. (2003), (2004), (2005)
Effect of cultivar	Significant	Pirlak, (2002), highest temperature 20°C; Zhang et al. (2018)
		Cerović and Ružić, (1992); Pirlak (2002), Hedhly et al. (2004), (2007); Zhang et al. (2018)
		Guerrero-Prieto et al. (1985); Postweiler et al. (1985); Pirlak (2002); Hedhly et al. (2004), (2005); Radićević et al. (2016); Zhang et al. (2018); Radićević et al. (2021)



Fig. 4. A) Fruit set of open pollinated flowers for sweet ($N = 86$ data points across 19 studies) and sour cherry ($N = 24$ data points across 5 studies) after natural pollination levels. B) Pollination service for sweet ($N = 48$ data points across 4 studies) and sour cherry ($N = 8$ data points across 2 studies). C) Pollen limitation for sweet ($N = 45$ data point across 7 studies) and sour cherry ($N = 20$ data points across 4 studies). The colored dots indicate data points per orchard for both crops (dark red: sweet cherry, orange: sour cherry), the black dots represent the means and the error lines the standard error.

Table 2
No-intercept models assessing open pollination, pollination service and pollen limitation for fruit set, of both sour cherry and sweet. The model estimates, standard error (SE), t -statistics and P -values are reported.

Response	Crop	estimate	SE	t	P
Open fruit set	Sour cherry	16.45	5.18	3.18	< 0.01
	Sweet cherry	29.73	3.28	9.07	< 0.001
Fruit set pollination service	Sour cherry	65.10	4.59	14.19	< 0.001
	Sweet cherry	94.92	2.73	38.83	< 0.001
Fruit set pollen limitation	Sour cherry	1.60	9.19	0.17	0.87
	Sweet cherry	19.75	6.53	3.02	0.049

factors driving pollen limitation need to be better understood through studies involving open and hand pollination. Management practices could reduce pollen limitation (e.g., wildflower strips) by enhancing pollinators but the connection between these themes is clearly under-represented in cherry with studies showing contradictory results (Holzschuh et al., 2012; Mateos-Fierro et al., 2023).

3.4. Cherry pollinators and their pollination contribution

3.4.1. Abundance and species richness

The relative abundance of flower-visiting insects was extracted from 12 studies (Fig. 5; Table S8). Honeybees were the most abundant cherry flower visitor across all studies except for one (Ryder et al., 2020; Fig. 5A), ranging from 9 % to 81 % (mean \pm SE, 57 ± 5 %). Wild bees (other than bumblebees, mostly solitary bees) were the second most abundant flower visitors (15 ± 4 %; range 1 % - 49 %), followed by bumblebees (13 ± 5 %; range 1 % - 44 %) and flies (13 ± 5 %; range 0 % - 62 %). Other insects (e.g., wasps, ants, beetles) were only mentioned by five studies with a mean of 8 % (8 ± 4 %; range 1 % - 24 %). Additionally, 14 studies looked specifically at wild bees, recording a total of 21 wild bee genera from six families (Fig. S2, Table S9). Mining bees (*Andrena* spp.) were the most abundant genus of the wild bees (43 ± 9 %, range 12 % - 94 %), followed by bumblebees

(31 ± 8 %, range 0 % - 96 %), mason bees (*Osmia* spp.; 15 ± 7 %, range 0 % - 65 %) and sweat bees (*Lasioglossum* spp.; 10 ± 6 %, range 0 % - 65 %; Fig. 5B). All other bee genera were less common (mean below 5 %; Fig. S2).

Data on cherry visitor species richness was extracted from ten studies, conducted in either Belgium, UK, USA or India (Table S10). Cherry flower visitors are a diverse group (see Fig. 6). In total, 185 different insect species were recorded visiting cherry flowers of which 142 were bees, two Formicidae, two Vespidae, 36 Diptera, two Lepidoptera, one Hemiptera and one Odonata (Fig. S3). Mining bees (Andrenidae) were the most diverse bee family, with 50 different species recorded (of which all were from the genus *Andrena*), followed by sweat bees (Halictidae) with 48 species (Fig. S3). Species richness per study ranged from six (Sharma et al., 2016) to 79 (Wood et al., 2018). Within flies (Diptera), hoverflies (Syrphidae) were the most diverse family with 28 different species recorded. Relative abundance of insects caught by pan traps or on wildflowers within the orchard and their richness are recorded in Table S11 and Table S12.

Overall, our study demonstrates that a diverse set of insects visit cherry flowers, mostly bees and flies. Honeybees are the most abundant visitors in commercial orchards, a pattern also found in other crops (Pardo and Borges, 2020; Reilly et al., 2020; Dymond et al., 2021; Eeraerts et al., 2023a). Within wild bees, bumblebees and mining bees were the most abundant and diverse genera, which is also in line with some other spring-flowering crops (Pardo and Borges, 2020; Eeraerts et al., 2023a). Most fly species recorded belong to hoverflies (Syrphidae), yet this might be due to biases in the recording (some studies only recorded species belonging to Syrphidae). Wasps, butterflies and beetles were seldom included in flower-visitor assessments and when recorded, their visitation was rather low (Eeraerts et al., 2019; Osterman et al., 2023). This might be because both cherry crops flower early in spring, limiting the number of species present (Balfour et al., 2018), or that non-bees are neglected in pollinator surveys, particularly in North America and Europe, where most studies were done.

3.4.2. Pollination efficiency and foraging behavior

We found nine studies that investigated pollination efficiency and/or foraging behavior of cherry pollinators (Table S1). To date, only one study measured fruit set of cherry after a single flower visit, concluding

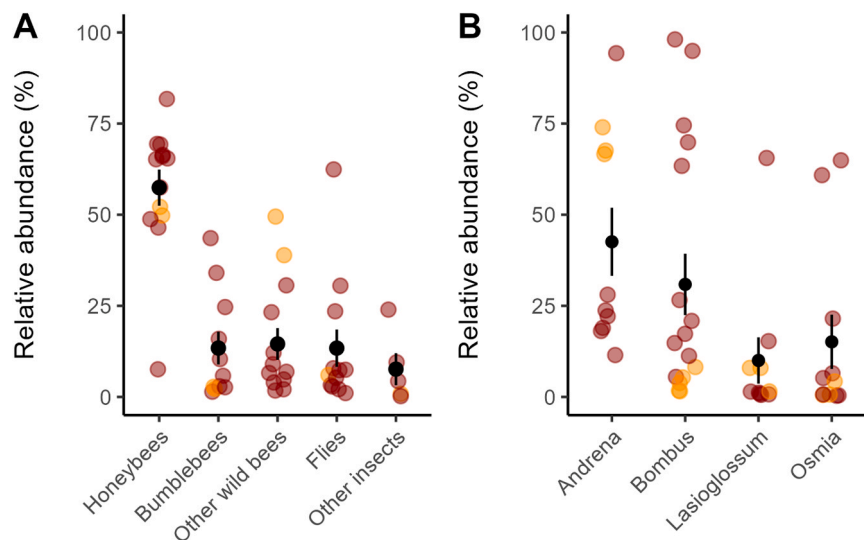


Fig. 5. A) Mean relative abundance of flower-visiting insects and B) the most common bee genera per study in sweet (A: N = 11 studies; B: N = 12 studies; dark red) and sour cherry (A: N = 2 studies; B: N = 3 studies; orange). The colored dots indicate data points per study, region, survey method, crop and insect group. The black dots represent the mean and the error line the standard error. The category “other insects” was only recorded by five studies and included, for instance, butterflies, ants and beetles. In some studies, *Bombus* and *Osmia* were managed to some extent.

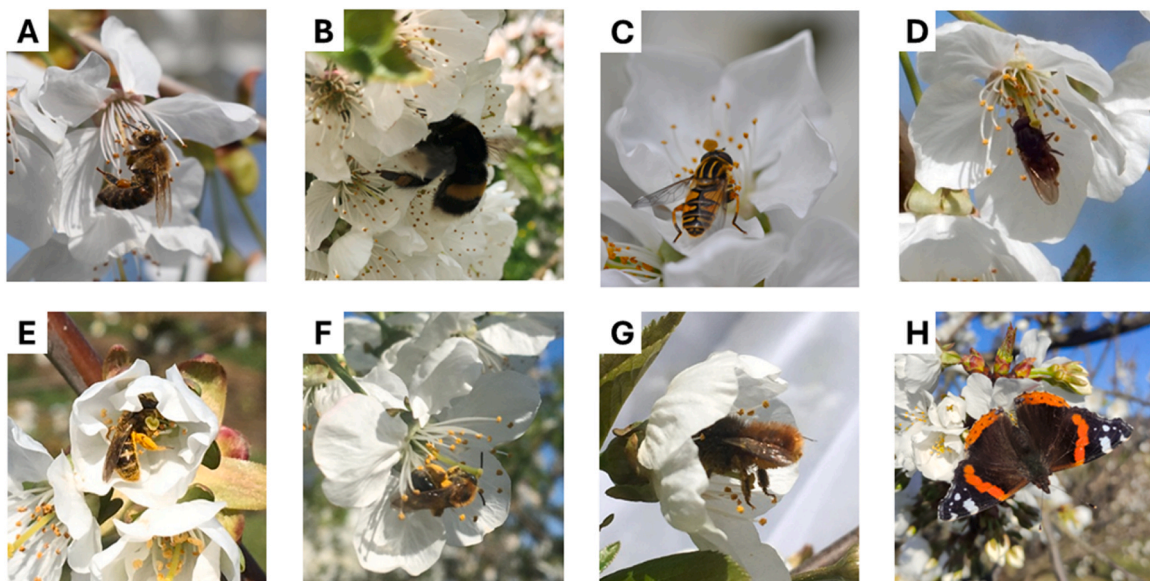


Fig. 6. Different pollinators on sweet cherry flowers: A) the western honeybee (*Apis mellifera*), B) a bumblebee (*Bombus terrestris* agg.), C), the hoverfly *Helophilus pendulus*, D) the hoverfly *Rhingia campestris*, E) a sweat bee (*Lasioglossum* spp.), F) the mining bee *Andrena haemorrhoa* and G) the mason bee *Osmia cornuta* and H) the butterfly *Vanessa atalanta* (photo credit A: R. Vanderhaegen, B: J. Osterman, C: Z. Mateos-Fierro, D-G: M. Eeraerts and H: C. Siopa).

that the European orchard bee (*O. cornuta*) and mining bees are more efficient than honeybees and bumblebees (Eeraerts et al., 2020a). Different parameters were measured in several studies to characterize the foraging behavior, including visitation rate (i.e., flowers visited per minute) and the rate whereby pollinators changed trees within and across tree rows (i.e., a prerequisite for possible cross-pollination, see below). A consistent result across studies was the lower visitation rate of honeybees compared to that of bumblebees (Eeraerts et al., 2020a, 2020b; Mateos-Fierro et al., 2022). The visitation rate of *O. cornuta* is higher than that of honeybees, whereas the visitation rate of mining bees is lower than that of honeybees and bumblebees (Eeraerts et al., 2020a; Mateos-Fierro et al., 2022). Additionally, Bakshi et al. (2018) concluded that honeybees visit more flowers per minute than hoverflies.

The relative contribution of flower visitors to pollination can be calculated based on the visitor abundance, their visitation rate and their

pollination efficiency (Reilly et al., 2020; Eeraerts et al., 2023a). However, in cherry, pollination efficiency of flower visitors is highly understudied, especially the contribution of non-bee flower visitors needs more research (Eeraerts et al., 2020a; Mateos-Fierro et al., 2022). Additionally, more studies investigating single-visit deposition are needed (e.g., Eeraerts et al., 2020a). The only study investigating single-visit deposition showed that solitary bees (mason bees and mining bees) were more efficient than honeybees and bumblebees (Eeraerts et al., 2020a). This may have important implications for farmers when adopting pollinator strategies and they may benefit from investing in habitat creation measures to enhance these pollinators rather than renting honeybee hives or purchasing bumblebee boxes (Blaauw and Isaacs, 2014; Mateos-Fierro et al., 2023). However, pollinator contributions could vary greatly, depending on the dominating pollinator species.

For cultivars requiring cross-pollination, compatible pollinizer cultivars are planted interspersed in the same or different rows next to the commercial cultivar. Hence, to transfer compatible pollen, insects need to move between trees or from one row of trees to another. Solitary bees and bumblebees changed rows more often compared to honeybees, whereas changes within the same row varied when comparing different pollinator taxa (Eeraerts et al., 2020a, 2020b; Mateos-Fierro et al., 2022). Additionally, certain pollinators might also influence the pollination performance of other pollinators. Here, Eeraerts et al. (2020b) found that the visitation rate and the rate of row changes of honeybees increased with bumblebee abundance and diversity. This effect of wild bees on honeybees has also been observed in other crops (Brittain et al., 2013), and could explain the synergistic effect of wild bees and honeybees on fruit set detected by Osterman et al. (2023).

Other less common parameters have also been used to describe the pollination performance such as time spent on a flower, stigma contact, pollen grains carried on the body and pollen and nectar collection (Table S1). Pollinator abundance and therefore their contribution are also affected by weather conditions, which are often suboptimal as cherry flowers early in spring. Across studies, non-*Apis* bees seem to be less affected by time of the day and temperature compared to honeybees and might consequently act as insurance for inclement weather conditions (Mateos-Fierro et al., 2022; Vicens and Bosch, 2000). However, we need a better understanding of the functional complementarity of different pollinator taxa and how this explains their contribution to cherry pollination (Blüthgen and Klein, 2011).

3.4.3. Importance of pollinator visitation

We found eight studies that modeled pollinator visitation and its relationship with cherry pollination (Table S1). Sweet cherry fruit set increased with increasing wild bee visitation (Holzschuh et al., 2012; Eeraerts et al., 2017, 2019; Pisman et al., 2022) and increasing richness of pollinator visitation (Eeraerts et al., 2017, 2019). Again, this is in line with most of the research on other crops (Garibaldi et al., 2013; Rader et al., 2016). Indeed, wild bees are excellent at cross-pollination (Travis and Koh, 2023), which could be the reason for their higher single-visit efficiency to many plants compared to honeybees (Page et al., 2021). However, Mateos-Fierro et al. (2023) did not conclude a positive relationship between fruit set and pollinator richness, but only between fruit set and total pollinator visitation (i.e., the sum of wild and managed pollinators). Additionally, in both sweet and sour cherry in the USA, the relationship between total bee visitation and fruit set was non-linear, indicating an asymptotic relationship (Reilly et al., 2020).

Of the studies distinguishing honeybees and wild pollinator visitation, none concluded a positive effect of honeybees on fruit set (Holzschuh et al., 2012; Eeraerts et al., 2017, 2019; Pisman et al., 2022), which is also in line with research on other crops (Garibaldi et al., 2013; Rader et al., 2016). Osterman et al. (2023) concluded that fruit set was enhanced by increasing honeybee visitation, but only when mason bees were highly abundant, which further emphasizes the contribution of wild bees. In general, the lack of a linear relation with honeybees alone can be explained by the fact that honeybee visitation is often high in these studies, and might have reached a saturation threshold (Reilly et al., 2020; Eeraerts et al., 2024). Indeed, farmers stock the orchards with honeybee hives and consequently, studies lack fields with low to medium honeybee visitation in their experimental designs. On the contrary, wild pollinator visitation often encompasses maximal gradients, spanning from very low to very high visitation across fields. Hence, detecting the effects of honeybees is less straightforward compared to detecting the effects of wild pollinators. To this end, non-linear models could be useful, as they would enable the detection of an asymptotic relationship between pollinator visitation and pollination (Reilly et al., 2020; Eeraerts et al., 2024). This would enable us to determine the required (honey)bee visitation rate for optimal cherry pollination, which could lead to clear guidelines for farmers and beekeepers.

Only one of these observational, site-replicated study looked at

cherry fruit mass, yet this was not affected by pollinator visitation (Mateos-Fierro et al., 2023). Fruit quality can be affected by animal pollination (Gazzea et al., 2023) and directly impacts marketability (Kappel et al., 1996). Size, firmness, color and nutritional value are important market traits for sweet and sour cherry (Blando and Oomah, 2019). Additionally, fruit set might impact fruit weight (Spornberger et al., 2014), a relationship that also requires further research as the fresh market value is determined by fruit size (i.e., bigger cherries are preferred and of higher value; Wermund et al., 2001). Indeed, in crops like apple and blueberry, it has been shown that high levels of fruit set can lead to decreased fruit weight, as very high fruit set might reduce the amount of resources the plant can invest to individual fruits, possibly reducing fruit weight (Strik et al., 2003; Samnegård et al., 2019).

3.5. Influence of the surrounding landscape

The influence of landscape composition on pollinators and pollination in cherry orchards was investigated by 11 studies (Table 3 and Table S1). The amount of SNH was positively correlated with pollinator richness and wild pollinator abundance in cherry orchards (Holzschuh et al., 2012; Eeraerts et al., 2019; Eeraerts, 2023), as well as with cherry pollination (Holzschuh et al., 2012). SNH in these studies mainly consists of forests, semi-natural grassland, shrubland, hedgerows and field margins. Additionally, solitary bee and bumblebee abundance increased with increasing amounts of SNH (Pisman et al., 2022; Eeraerts, 2023). This positive effect of SNH is consistent with landscape ecological research in general (Martin et al., 2019). As wild pollinators enhance cherry pollination, the spill-over effect of SNH implies that farmers and stakeholders should try to conserve and create SNH around cherry orchards.

Another common measure to characterize landscape composition is

Table 3
Summary of main responses of pollinator visitation, pollinator richness, cherry fruit set and wild pollinator reproduction detected in studies of the two main studied landscape variables, semi-natural habitat (SNH) and intensive fruit cultivation (IFC; arrow down = negative relationship, arrow up = positive relationship, n.s. = no significant relationship found).

Landscape variable	Response variable	Effect	Reference
SNH	Wild pollinator visitation	↗	Holzschuh et al. (2012); Eeraerts et al. (2017), (2019); Gilpin et al. (2022b); Pisman et al. (2022); Eeraerts, (2023)
	Wild pollinator richness	↗	Eeraerts et al. (2017), (2019); Gilpin et al. (2022b); Eeraerts, (2023)
	Honeybee visitation	n.s.	Holzschuh et al. (2012); Eeraerts et al. (2017), (2019); Pisman et al. (2022)
	Fruit set	↗	Holzschuh et al. (2012)
	Wild pollinator reproduction	↗	Eeraerts et al. (2022)
IFC	Wild pollinator visitation	↘	Eeraerts et al. (2017)
	Wild pollinator richness	↘	Eeraerts et al. (2017)
	Honeybee visitation	↗	Eeraerts et al. (2017)
	Fruit set	↘	Eeraerts et al. (2017)
	Wild pollinator reproduction	↘	Eeraerts et al. (2021b)

the amount of intensive agriculture. Here, landscapes dominated by intensive fruit orchards negatively affected pollinator richness, wild pollinator abundance and cherry pollination but had a positive effect on honeybee visitation (Eeraerts et al., 2017). This negative effect of intensive agriculture on pollinators and pollination highlights agricultural landscapes should contain sufficient resources throughout the year. Variable amounts of intensive fruit orchards in the landscape did not affect the reproductive output of two mason bee species relevant to cherry pollination during flowering (Eeraerts et al., 2021b). However, after the flowering period, the reproductive output of both mason bee species decreased with increasing orchard cover (Eeraerts et al., 2021b). Additionally, increasing SNH around the orchards enhanced bee reproduction by increasing the proportion of females in the offspring of *O. cornuta* (Eeraerts et al., 2022). The positive effects of SNH on the reproduction of wild bees that are key cherry pollinators further underscores the importance of SNH.

The positive effect of SNH on pollinator visitation, reproduction and pollination was positively correlated with the supply of abundant and diverse floral resources, both before and after cherry flowering (Eeraerts et al., 2021a; Gilpin et al., 2022b). Additionally, SNH in the surrounding landscape provided diverse nesting resources for wild bees (Eeraerts et al., 2021a), of which the presence increased wild bee cherry visitation (Kay et al., 2020; Ariza et al., 2022). To provide farmers and stakeholders with quantitative guidelines for habitat creation, Eeraerts (2023) determined a required minimum of 15 % SNH to ensure adequate wild pollinator visitation. However, the benefits of landscape on pollinators and, ultimately, on yield need also to be quantified in less-studied regions, as current studies mainly originate from central Europe.

While the effect of landscape composition on cherry pollinators and pollination is well studied (Table 3; Holzschuh et al., 2012; Eeraerts et al., 2017, 2019), we have a poor understanding of the role of landscape configuration in these crops (but see Pisman et al., 2022). Given the importance of landscape configuration parameters in other crops, like field size and connectivity on ecosystem delivery (Martin et al., 2019; Pisman et al., 2022), we argue this should be subject of future studies as this can lead to valuable evidence for both biodiversity conservation and pollination management.

3.6. On-farm management practices

3.6.1. Pollinator management

In total, 29 studies explored management practices (Table S1), of which 11 (37.9 %) explored direct pollinator management and 19 (65.5 %) orchard management, with one study exploring both management types. Directly managing pollinators can be the most straightforward practice to increase flower visitation. Among the managed pollinators, honeybees were the main pollinator used by farmers (Eeraerts et al., 2020c; Osterman et al., 2023; Table S13). Across studies, honeybee hive stocking densities ranged from 2.4 to 6.0 hives per ha (mean \pm SE, 3.60 ± 0.56 ; Fig. 7; Table S13), with honeybee visitation to cherry flowers increasing with hive density (Osterman et al., 2023). Despite their frequent use, there is no consensus on the optimal honeybee hive density to optimize pollination in cherry or other crops (Osterman et al., 2021b; Eeraerts et al., 2023b). Some studies conducted in commercial orchards provided the observed honeybee hive densities (e.g., Eeraerts et al., 2019; Osterman et al., 2023), but for many studies, it was not possible to extract hive densities per hectare. However, field-level stocking densities might not be directly linked to honeybee contributions to cherry pollination, which further hinders general guidelines on commercial hive densities (Eeraerts et al., 2023b; Gaines-Day and Gratton, 2016). Indeed, given their large foraging range, the interplay between floral resources and honeybee hives in the surrounding landscape also affects the pollination contribution of honeybees (Eeraerts et al., 2023b; Gaines-Day and Gratton, 2016). Hence, both hive management and landscape context need to be considered

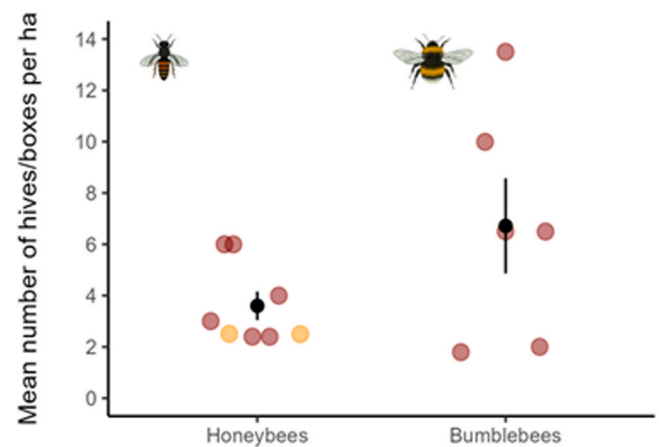


Fig. 7. Mean number of honeybee hives and bumblebee boxes per ha. The colored dots indicate data points per study, crop (red: sweet cherry; orange: sour cherry) and managed bee. The black dots represent the mean across studies and the error line the standard error of the mean. Bee icons were designed by Jose Luis Ordóñez and Ignasi Bartomeus.

simultaneously to develop evidence-based guidelines for pollination management.

No management study focused on bumblebees, but when used, stocking densities varied from 1.8 to 13.5 boxes per ha (6.72 ± 1.86 ; Fig. 7; Table S13). However, due to the price of the boxes and the uncertain contribution of bumblebees to cherry pollination (Eeraerts et al., 2020a, 2020c), it is important to investigate the best practices such as spatial placement (Evans et al., 2021) and colony longevity in poly-tunnels (Kendall et al., 2021).

All studies investigating alternative pollinator management (compared to honeybee management) focused on mason bees. Artificial trap nests can increase mason bee visitation in cherry orchards (Hamroud et al., 2023; Osterman et al., 2023), and adequate nesting cavities was estimated at 1000–1500 per ha (Osterman et al., 2023). To effectively manage mason bees, adequate nesting material can improve nesting success and reduce parasite infestation (Eeraerts et al., 2022). Moreover, an even distribution of trap nests throughout orchards can enhance mason bee propagation in highly intensified landscapes (Biddinger et al., 2013; Boyle and Pitts-Singer, 2017). However, some studies reported that most of the insects that used trap nests do not visit cherry flowers (Gilpin et al., 2022a), and vice versa, as most wild bee species that visit cherry flowers do not use artificial nests (see 3.4.1).

The effect of mason bee management on cherry pollination is unclear. Using mason bees in combination with honeybees was found to increase pollination of sweet cherry (Osterman et al., 2023), but not that of sour cherry (Boyle and Pitts-Singer, 2019). Using mason bees alone, without honeybees, improved pollination success of both sweet (2.2 times yield increase reported by Bosch et al., 2006) and sour cherry (Biddinger et al., 2013). Drawing overall conclusions on best management practices is difficult due to different mason bee species were used in these studies, which, in turn, were performed in different contexts. In addition, a lack of reported study details (e.g., orchard size, cultivar identity, pollinizer planting scheme) inhibited calculating the required density (Bosch et al., 2006; Boyle and Pitts-Singer, 2019).

Interestingly, studies regarding pollinator management so far are neglecting mining bees, the most abundant and diverse wild bee genus in cherry orchards (Holzschuh et al., 2012; Eeraerts et al., 2019). Yet, mining bees are clearly very efficient cherry pollinators (Eeraerts et al., 2020a). Recent research focused on ground-nesting bees and their nesting habitats (e.g., Eeraerts et al., 2021b; Ariza et al., 2022), which increases the potential for gaining an understanding of how to manage nesting sites for mining bees in and around orchards (Tsiolis et al., 2022; Fountain et al., 2023). Nonetheless, since most of the studies deeming

mining bees as the most abundant and diverse bee genus were conducted in Europe and North America, practices to enhance mining bees may be only relevant to these regions. Studies conducted elsewhere, such as India and Turkey, showed that sweat bees were dominant and, therefore, future studies on pollinator management should target those species.

3.6.2. Orchard management

In addition to direct pollinator management, several other management practices to enhance pollination were studied. Naturally occurring vegetation can be preserved or wildflower strips can be established to provide additional floral resources and boost pollinator populations (Eeraerts et al., 2020c, 2021a; Mateos-Fierro et al., 2023). Some studies found that either flower strips or spontaneous flowering, herbaceous vegetation in the alleyways between the trees in the orchard, had a positive effect on wild and managed pollinator visits to cherry flowers (Christmann et al., 2017; Eeraerts et al., 2019; Gilpin et al., 2022b; Mateos-Fierro et al., 2023). Trap-nesting bee reproduction was also enhanced by flower strips (Graham et al., 2020). However, this positive effect of flower strip or naturally occurring vegetation on cherry flower visitors was not always confirmed (Holzschuh et al., 2012; Wood et al., 2018). Wildflower strips enhanced fruit set in some cases (Christmann et al., 2017) but not in others (Mateos-Fierro et al., 2023). Although Mateos-Fierro et al. (2023) found that wildflower strips did not lead to increases in fruit set, pollen limitation (i.e., difference between hand and open fruit set) was still greater in alleyways without established wildflowers. Wildflower strips can also be actively managed, reducing the height to minimize inconvenience to farmers without affecting pollinator diversity and abundance (Mateos-Fierro et al., 2023).

Given the variable results across studies, the potential of wildflowers and naturally occurring vegetation needs to be further investigated to confirm its effect. Here, landscape structure is found to mediate the effect of these measures (Scheper et al., 2013), whereby it is required to include this landscape perspective in future studies on this topic. Furthermore, the lack of increasing pollinator visitation could have been because summer-wildflowers were sown rather than wildflowers flowering in spring (see Wood et al., 2018). The positive outcome in visits to cherry flowers in studies investigating naturally occurring vegetation co-flowering with cherry in orchards suggests that using spring-wildflowers may increase pollinator visitation and yields (Gilpin et al., 2022b). A major concern for farmers is the potential competition between cherry flowers and wildflowers but none of the studies reported pollinators being drawn away from visiting cherry flowers (Holzschuh et al., 2012; Eeraerts et al., 2019; Gilpin et al., 2022b; Mateos-Fierro et al., 2023). Thus, a simple measure farmers can take is to mow alleyways less frequently. This enables wildflowers to thrive and provide extra resources for pollinators, which can then boost pollinator densities in the orchard and, consequently, may increase visits to cherry blossoms (Eeraerts et al., 2021a). Farmers could also benefit from farmer stewardships that are offered by some governments (e.g., Countryside Stewardship in the UK or the Conservation Reserve Program in the USA). Farmer stewardships aim to protect and improve the environment in cropped areas by establishing plant species such as wildflower strips. These types of initiatives can boost farmers' willingness to adopt these practices to improve pollination services in cherry and other pollinator-dependent crops (Osterman et al., 2021b). However, this option is far from possible in many countries where governments would not provide economic support to farmers.

Other suggested approaches to enhance cherry pollination have been less studied. Under polytunnels, honeybees can be used, trees flower earlier, fruits ripe earlier, harvest is advanced and fewer insecticide applications are required (Dekova and Blanke, 2007; Hamm et al., 2007; Blanco et al., 2019). Other possible benefits are buffering of low temperatures (e.g., frost). Additionally, postponed irrigation during anthesis can improve fruit set (Salvadores and Bastías, 2023; Xu et al., 2023). The use of polytunnels is increasing in some countries (personal observation

J. Osterman and M. Eeraerts), and more information on how to safeguard pollination in polytunnel covered cherry orchards is needed. Another suggested approach to enhance cherry pollination is using attractants applied to cherry flowers, yet so far none of the tested compounds influenced pollinator visitation, fruit set or fruit size (Naumann et al., 1994; Williamson et al., 2018). Mechanical pollination has also been tested to improve cherry pollination using electrostatic and airblast pollen sprayers or drones, but this is limited to application to recently open flowers (2–3 days after anthesis) on days free of wind and rain (Eyles et al., 2022). In general, the effects of polytunnels, attractants and mechanical pollination are popular solutions but understudied and trials with paired designs and robust replications are needed to resolve their effect.

Pesticide management was only investigated by three studies. In conventional orchards, pesticide exposure to cherry pollinators has only been tested for fungicides (Kuivila et al., 2021; Perkins et al., 2023), yet fungicide residues clearly accumulated in nectar, pollen and bees. Comparing conventional and organic cherry orchards, Rosas-Ramos et al. (2020) found that organic management had a positive effect on pollinator diversity and visitation. Cherry is a preferred nectar and pollen source for some bee species, e.g., *O. cornuta* (Eeraerts et al., 2021a, 2021b). When orchards are treated with pesticides, this preference could exacerbate exposure and consequently the risk for pollinators foraging on cherry blossoms (Knapp et al., 2023). In addition, cherry is an early flowering crop, with many bumblebee queens visiting its flowers, which could be exposed in a critical phase in their lifecycle (nest-founding; Eeraerts et al., 2021a). That could explain why organic cherry orchards increased pollinator abundance and richness compared to conventional orchards (Rosas-Ramos et al., 2020).

Surprisingly, no studies investigated orchard design in terms of cultivar density and cultivar placement on the transfer of compatible pollen through pollinators, which is essential for pollination, especially in self-incompatible cultivars (MacInnis and Forrest, 2020). The finding that different cherry cultivars are visited by different pollinator communities (Eeraerts, 2022), underscores the importance of studying orchard design and how this interacts with the pollinator community and their pollination contribution.

4. Conclusions

We conclude that pollination research in cherry is biased regionally and towards sweet cherry, with sour cherry being particularly understudied. There are substantial contributions of insect pollinators to fruit set in both sweet and sour cherry, and we detect pollen limitation for sweet cherry. As both managed bees and wild pollinating insects forage on cherry blossoms, management strategies to enhance cherry pollination could focus on honeybee hive deployment, using alternative managed bees (e.g., mason bees), supporting wild pollinators, or a combination of the aforementioned pollinators. As both self-compatible and self-incompatible cultivars are available for both crops, on-farm management strategies might be tailored to specific cultivars to guarantee sufficient availability of high-quality compatible pollen and ensure wild bees are promoted to facilitate cross-pollination. Indeed, future research should focus on understudied regions and/or both sweet and sour cherry, pollination and pollinators in sour cherry, the effect of pollinators and pollination on cherry quality and the effects of orchard design. This all together can further inform the development of more targeted evidence-based guidelines for pollinator management.

5. Future research

In the different sections we have highlighted certain knowledge gaps and outstanding questions for future research. Certain topics that are currently understudied require more research, and studies on how different aspects interact to shape pollinators and pollination in this crop are required as well. Here we provide a brief list of example questions for

future research, yet this list is not intended to be exhaustive.

- How does research in sour cherry and in various understudied production regions align with our current understanding of the current knowledge on pollination?
- What insights can be gained from studies incorporating multiple cultivars to infer true cultivar effects, such as pollen limitation, required densities of honeybees and mason bees?
- How do weather variables, beyond temperature, and climate change proxies such as extreme heat impact cherry pollinators and pollination?
- To what extent do floral rewards and traits interact with biotic factors (e.g., cultivar ID) and abiotic factors (e.g., temperature) to influence pollinator visitation and pollination success?
- What is the pollination efficiency of different species of wild bees and flies compared to bumblebees and honeybees? How would this pollination efficiency vary in both crops and different cultivars?
- How does landscape configuration influence pollinators and pollination in cherry?
- How do required densities of honeybees and other managed bees interact with the surrounding landscape and other orchard management measures (e.g., flower strips, polytunnels) to optimize pollination success in cherry?

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CRediT authorship contribution statement

Julia Osterman: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Zeus Mateos-Fierro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Catarina Siopa:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Helena Castro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Data curation. **Silvia Castro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation. **Maxime Eraerts:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The Authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All code and data used in the manuscript can be found in the supplementary files and on GitHub: https://github.com/JuliaOsterman/Cherryreview_Osterman_MateosFierro

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2024.109163](https://doi.org/10.1016/j.agee.2024.109163).

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