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Pollination deficits and their relation with insect pollinator visitation are cultivar-dependent in an entomophilous crop

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ABSTRACT

Insects contribute considerably to global crop pollination, with pollination deficits being documented for multiple entomophilous or pollinator-dependent crops. Different cultivars of crops are being cultivated within and across production regions, so it is essential to understand the cultivar variability of pollination deficits. Here, we used a dataset from 286 sites from multiple production regions to develop a synthesis on pollination deficits in two widely cultivated highbush blueberry cultivars, 'Bluecrop' and 'Duke'. Additionally, we determined if bee visitation or bee richness reduces pollination deficits in these cultivars. On average, neither cultivar showed pollination deficits regarding fruit set. However, for 'Bluecrop' we found pollination deficits for berry weight and seed set, which was not the case for 'Duke'. Increasing total bee visitation reduced pollination deficits of both berry weight and seed set for 'Bluecrop'. More specifically, a non-linear, negative exponential model best predicted this relation between bee visitation and pollination deficits. Our results highlight that pollination deficits and responses to pollinator visitation are variable between different cultivars of a single crop, which suggests opportunities to use certain cultivars that are less dependent on insect-mediated pollination in landscapes and regions where pollination services have been compromised. In addition, the non-linear response between bee visitation and pollination deficits suggests that optimal bee visitation rates need to be determined to improve pollination management and crop yield and to support accurate economic valuations of pollination services.

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1. Introduction

Safeguarding global food supplies requires an understanding of how biotic and abiotic variables mediate crop production (Tamburini et al., 2019, 2020). While foraging on flowers, multiple insect species contribute to pollination by transferring pollen from flower to flower. As such, both wild pollinators and managed bees provide considerable pollination services to crops (Garibaldi et al., 2013; Pisman et al., 2022; Eeraerts et al., 2023a). Recent analyses have shown that pollination success increases non-linearly with crop flower visitation by both honey bees and wild pollinators (Nicholson and Ricketts, 2019; Reilly et al., 2020; Chabert et al., 2022). This suggests that determining optimal flower visitation rates of key crop pollinators is necessary for cost-effective management of crops to ensure high levels of pollination and crop yield (see Garibaldi et al., 2020; Eeraerts, 2023).

Pollen limitation, or pollination deficit, is a lack of pollen quantity or quality deposited onto stigmas that restricts fruit and/or seed production below the potential maximum level (Ashman et al., 2004; Harder and Aizen, 2010). There is increasing evidence that pollination deficits limit crop yield in entomophilous crops, although the extent of these pollination deficits varies by crop and region (Reilly et al., 2020; Garratt et al., 2021; Olhnuud et al., 2022). The compatibility system, growth form (herbaceous vs woody), flower size, insect visitation, and ovule number per flower are among key traits determining the magnitude of pollination deficits and the extent to which insect-mediated pollination can reduce these deficits (Knight et al., 2005; Rodger and Ellis, 2016; Bennett et al., 2020; Rodger et al., 2021; Aizen et al., 2023). Additionally, multiple case studies have found that pollination deficits and the pollination service provided by insects are variable across cultivars of a single crop (Benjamin and Winfree, 2014; Button and Elle, 2014; Hudewenz et al., 2014; Bishop et al., 2020; Burns and Stanley, 2022). The latter suggests that different cultivars of a crop can also have variable pollination requirements. However, in recent syntheses this cultivar effect has often been confounded with study ID or region effects, prompting the need for further research to disentangle these components (Bishop and Nakagawa, 2021; Garratt et al., 2021; Olhnuud et al., 2022).

Highbush blueberry cultivation includes northern (*Vaccinium corymbosum*) and southern (*V. corymbosum* interspecific hybrids) highbush blueberry cultivars (hereafter "blueberry"). Blueberry is an important crop with production expanding in many parts of the world, including North and South America, Asia, Australia, and Europe (Eeraerts et al., 2023a). Flower visitation by honey bees and wild bees is vital for adequate pollen transfer, effective pollination and consequent fruit production (DeVetter et al., 2022; Eeraerts et al., 2023a). Blueberry is self-compatible, meaning ovules can be fertilized by both self-pollen and cross-pollen. Yet, blueberry is partly self-sterile, meaning some of the embryos fertilized by self-pollen may abort at a higher rate than cross-pollen, and this degree of self-sterility is variable across cultivars due to an early-acting inbreeding depression (DeVetter et al., 2022). Blueberry pollination research has focused on a relatively small number of cultivars across the world (Eeraerts et al., 2023a). Hence, compiling the data of pollination research of the main cultivars provides an opportunity to use blueberry as a model system for separating cultivar-effects of pollination deficits and pollination services from other study- or region-specific effects.

As the cultivated area of pollinator-dependent crops, and blueberry in particular, is increasing globally (Aizen et al., 2019; Eeraerts et al., 2023a), it is essential to understand if pollination deficits are variable among different cultivars of a single crop and, if so, whether different cultivars need differentiated pollinator management to mitigate these pollination deficits. In this study, we used an extensive dataset of blueberry pollination studies to explore the following research questions:

1. To what extent are two common blueberry cultivars pollen limited?
2. Does bee visitation or bee richness reduce pollination deficits of these two cultivars?

2. Materials and methods

2.1. Literature review

A systematic literature search was conducted with Web of Science Core Collection as the primary database with the search terms ("blueberry" OR "Vaccinium") AND ("bee" OR "bees" OR "pollin*"). The search was finalized on 14 April 2023 and yielded 517 potential studies. Each study was screened by reading the title and abstract. For our study, we were interested in all studies on pollinators and pollination in two northern highbush blueberry cultivars, Bluecrop and Duke. A review of blueberry pollination research found that both cultivars have been most widely studied in site-replicated studies relevant for our study question (Eeraerts et al., 2023a) and both cultivars are widely planted and of commercial importance across multiple blueberry production regions. During the initial screening, studies not performed in blueberry, or not referring to insect pollinators or insect-mediated pollination were excluded.

Next, the full texts of the remaining studies were reviewed for potential inclusion in the analyses. Here, we applied the following study selection criteria: 1) studies had to conduct a pollinator survey in commercial blueberry fields under open-field conditions (i.e., no experimental greenhouse/tunnel studies), 2) measurements were made of blueberry pollination (i.e., fruit set, fruit weight and/or seed number), 3) pollination-related variables had to be measured under open-field conditions, and with the inclusion of a supplementary hand pollination treatment, 4) pollination and pollinator measurements had to be conducted on the cultivars Bluecrop and/or Duke, and, 5) a minimum of 5 blueberry fields had to be included per study. Additionally, during full text review, the reference list of each publication was checked to find additional studies. This selection process is illustrated in the PRISMA flow diagram (Fig. S1).

2.2. Data collection

Data from 8 published studies were requested through contacting the data-holders and requesting the raw data. A success rate of 87.5% was achieved with these data requests, with data collected from another 4 additional unpublished studies identified by Eeraerts et al. (2023a) (Tables S1, S2). Raw data on blueberry pollination and bee visitation were collected from these studies as average values per field per year per cultivar (cfr. Eeraerts et al., 2023a). Bee visitation data were grouped into honey bee visitation and wild bee visitation. In these studies, bee visitation was measured using insect nets or scan sampling (Tables S1, S2). We focused on honey bees and wild bees as they are the main pollinators of blueberry (DeVetter et al., 2022; Eeraerts et al., 2023a). In addition, most studies identified bee specimens to species, genus or morphospecies (Table S1), which enabled us to extract bee richness values per field.

For the blueberry pollination measurements, we collected data from studies comparing different pollination treatments: 1) open pollination (i.e., flowers exposed to insect pollinators), and 2) hand pollination (i.e., flowers exposed to insect pollinators and pollen-supplemented by hand). For the hand pollination treatment, self-pollen was used in most studies, but some studies used cross-pollen from a different cultivar or used a mix of self- and cross-pollen (Table S1). For pollination measurements, berry data were collected just before commercial harvest. The pollination metrics considered were percentage fruit set, berry weight and number of viable seeds per berry (hereafter "seed set"). With these data, the pollination deficit of each pollination metric was determined as the difference between the open and the hand pollination treatment, and this difference was interpreted as the amount of pollen tetrads missing on stigmas to reach the maximum values of pollination metrics (Garratt et al., 2021; Eeraerts et al., 2023a).

2.3. Data analyses

Because different research teams used different methods in the studies from which we collected raw data, it was necessary to standardize the data to allow comparisons among studies. Accordingly, pollination data of both the open and hand pollination treatments were standardized between 0 and 1 per yield metric and per study ($y = (x - x_{min})/(x_{max}-x_{min})$) (i.e., x_{min} is the smallest value for both pollination treatments per study). Hence, the fixed effect estimates from the model could be interpreted as effect sizes for comparison. Afterwards, the pollination deficit per field was determined as the difference between hand and open pollination treatments. Here, a positive value indicates a pollination deficit, and a zero or negative value indicates no pollination deficit. The extent of the pollination deficit was assessed with a linear mixed-effects model (LME; function *lme*, package *nlme*).

First, for each pollination metric we tested if the pollination deficit was different between the two cultivars. Here, cultivar was specified as a fixed variable and site ID nested within study ID were included as random factors. Second, for each pollination metric, we also tested a no-intercept model with cultivar as the fixed factor to infer if the mean pollination deficit of a cultivar was different from zero. Site ID nested within study ID were both added to the model as random factors.

Both honey bee and wild bee visitation data were also standardized between 0 and 1 per study. To account for variable pollination contributions of both wild bees and honey bees (Benjamin and Winfree, 2014; Eeraerts et al., 2020, 2023a), total bee visitation per field was determined as the sum of the standardized wild bee visitation and the standardized honey bee visitation (hence, the theoretical maximum value of total bee visitation is 2). Both honey bees and wild bees contribute considerably to blueberry pollination (Gibbs et al., 2016; Eeraerts et al., 2023a). Hence, for this self-compatible crop, we were interested in testing and comparing linear and non-linear models of total visitation as this has relevant management applications (see Reilly et al., (2020); Beyer et al., (2022); Mateos-Fierro et al. (2023) for similar approaches). The relation between total bee visitation and pollination deficit was examined by comparing three different models: i) a null model, ii) a linear model (LME; $y = a\text{-}b^*x$) and iii) a negative exponential model ($y = a^*e\hat{}(\text{-}b^*x)$). Site ID nested within study ID were added as random factors in all three models. We tested the three different models for each pollination metric and for each cultivar separately and ranked them based on their AIC_C. For each pollination metric and each cultivar, the best model with the lowest AIC_C was reported ($\Delta AIC_C > 2$). Similarly, the relation between bee richness and pollination deficit was examined by comparing the above-mentioned three models for each pollination metric and each cultivar. Bee richness was determined as the number of bee species or morphospecies per site, and richness was standardized between 0 and 1 per study before analyses.

Using cross-pollen from another cultivar for the hand pollination treatment might exacerbate pollination deficits compared to using self-pollen (i.e., cross-pollination vs self-pollination; see DeVetter et al., 2022). Hence, analyses were conducted with or without data using cross-pollen for hand pollination (Table S1). Model fit was evaluated visually by checking the normality of the model residuals (quantile--quantile plot, plot of the residuals versus the fitted values and Lilliefors test). All analyses were performed with R, version 4.2.0 R Development Core Team, 2022).

3. Results

Data were collected from a total of 286 sites, amounting to 256, 286 and 133 sites for pollination deficit analyses for fruit set, berry weight and seed set analyses, respectively (Table S1). A total of 179 sites with 'Bluecrop', and 107 sites with 'Duke'. Most studies were conducted in the USA (176 sites), followed by Canada (55 sites), Spain (40), and the Netherlands (15). Within the USA, Michigan provided data from 82 sites, Oregon 28 sites, Washington 26 sites, New Jersey 23 sites, and Vermont 17 sites (see Table S1 for a complete overview).

Pollination deficit for fruit set was not different between the two cultivars ($F = 4.24$, $p = 0.06$). No significant pollination deficits were observed for fruit set over the average of all locations and studies for both 'Bluecrop' and 'Duke', yet for 'Bluecrop' this was only marginally non-significant (Table 1; Fig. 1A). Pollination deficits for berry weight and seed set were different between the two cultivars (berry weight: $F = 21.28$, $p < 0.001$; seed set: $F = 12.93$, $p = 0.011$). For 'Bluecrop', significant pollination deficits were detected over the average of all locations and studies for both berry weight and seed set, whereas for 'Duke' these deficits were not significantly different from zero (Table 1; Figs. 1B, C).

Total bee visitation did not affect the pollination deficit for fruit set as the null model was the best model for both cultivars (Table 2, **S3**). For 'Bluecrop', the negative exponential model best explained the relation between total bee visitation and both the berry weight and seed set deficits (Fig. 2; Table 2, **S3**). In contrast, for 'Duke', no clear relation was detected as no model outperformed the null model (Table 2, **S3**). For both cultivars, bee species richness did not show any relation with any of the pollination metrics (Table S4).

Analyses excluding data using cross-pollen for the hand pollination treatment gave the same results (Tables S5, S6, S7, S8).

4. Discussion

By analyzing data from studies conducted across various locations, we conclude that pollination deficits vary between cultivars, a result that is in line with case studies and crop-specific syntheses (Benjamin and Winfree, 2014; Hudewenz et al., 2014; Bishop et al., 2020; Bishop and Nakagawa, 2021; Garratt et al., 2021; Burns and Stanley, 2022; Olhnuud et al., 2022). More specifically, Button and Elle (2014) reported that pollination deficits are also greater for 'Bluecrop' compared to 'Duke'. Experimental studies that compare no, self- and cross-pollination for different blueberry cultivars also conclude variable qualitative pollination requirements between cultivars (DeVetter et al., 2022 and references therein). As observational studies on this topic are scarce, the number of studies in 'Bluecrop' and 'Duke' provide the opportunity to synthesize this variability across multiple studies, without the cultivar effect being confounded with study ID or study region (Bishop and Nakagawa, 2021; Olhnuud et al., 2022). As such, our synthesis provides robust evidence that insect-mediated pollination limits crop yield depending on the cultivar grown. However, we advise that more studies include multiple cultivars in order to facilitate additional broader and robust cultivar comparisons in the future.

As in other studies (e.g., Garratt et al., 2021), we found evidence of cultivar variability in pollination deficits. Blueberry is self-compatible, and so it is possible that all flowers set fruits with self-pollination and pollination deficits are low (Gibbs et al., 2016; Eeraerts et al., 2023b). However, low or no pollination deficits of fruit set can nevertheless cascade into decreased fruit weight, as very high fruit set or fruit number per plant might reduce the amount of resources the plant can partition to individual fruits and consequently reduce fruit weight (see Strik et al.,

Table 1
Model assessing blueberry pollination deficits for fruit set, berry weight and seed set of 'Bluecrop' and 'Duke'. Reported are the model estimates, standard error (SE), *t*-statistics and *P*-values.

Response	Cultivar	estimate	SE	*t*	*P*
Fruit set deficit	Bluecrop	0.062	0.028	2.21	0.06
	Duke	0.056	0.030	1.90	0.09
Berry weight deficit	Bluecrop	0.11	0.022	4.81	< 0.001
	Duke	0.035	0.024	1.45	0.15
Seed set deficit	Bluecrop	0.15	0.031	4.74	< 0.01
	Duke	0.071	0.038	1.84	0.12

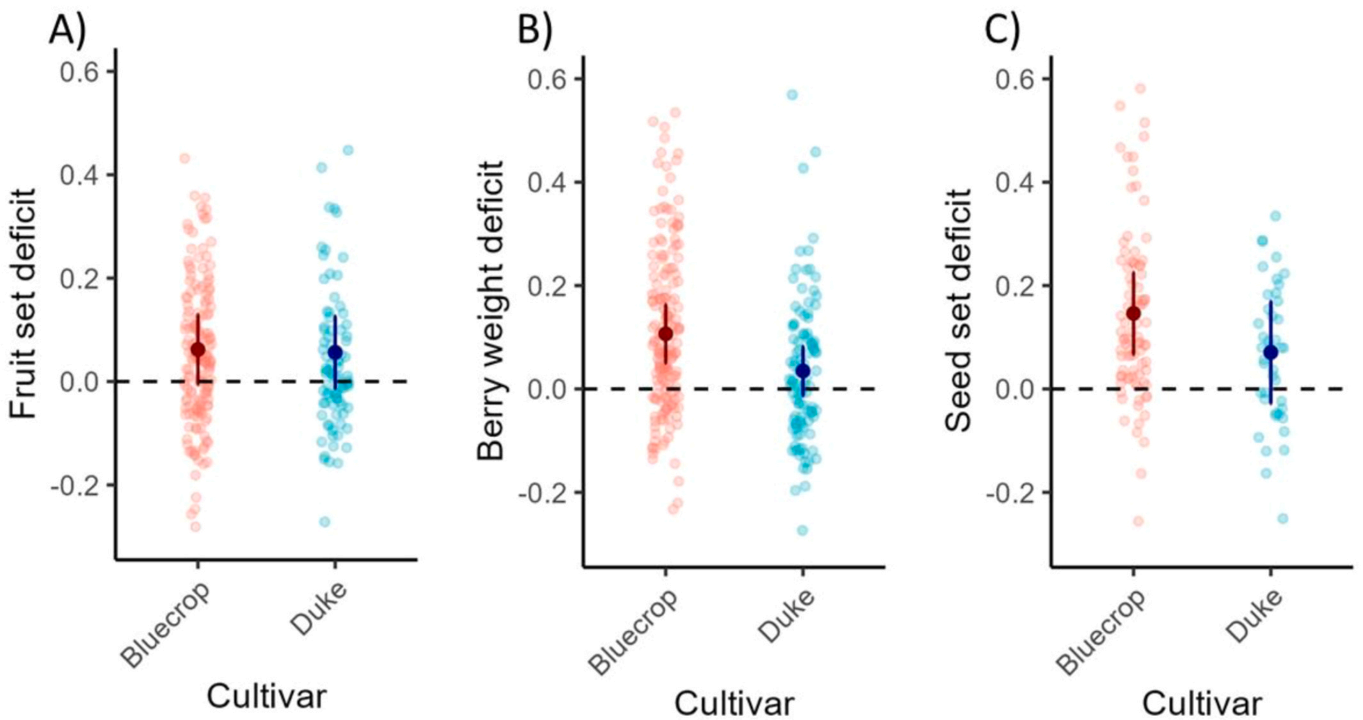

Fig. 1. Pollination deficits for A) fruit set, B) berry weight and C) seed set of 'Bluecrop' and 'Duke' in red and blue, respectively. The shaded points indicate the raw data, the bold dots and bold lines indicate the means and 95% confidence intervals.

Table 2
Linear mixed-effect models assessing the effect of total bee visitation (bees) on highbush blueberry pollination deficits for fruit set, berry weight and seed set. For each response, a null model, a linear model and a negative exponential model was tested per cultivar. Only the best models are reported with their model estimates, standard errors (SE), *t*-statistics, *P*-values and ΔAIC_c are given. ΔAIC_c is the difference between the AIC_c of the model with the lowest AIC_c and the AIC_c of the model with the second lowest AIC_c.

Response	Cultivar	Best model	ΔAIC_c	Fixed factor	estimate	SE	*t*	*P*
Fruit set deficit	Bluecrop	Null	2.95					
	Duke	Null	4.49					
Berry weight deficit	Bluecrop	Exponential	5.95	exp(-bees)	0.32	0.061	5.24	< 0.001
	Duke	Null	2.15					
Seed set deficit	Bluecrop	Exponential	1.88	exp(-bees)	0.28	0.09	3.15	< 0.01
	Duke	Null	1.43					

2003; Spornberger et al. 2011; Samnegård et al., 2019). Future assessment of pollination deficits should encompass further method standardization and consider possible interactions with horticultural management to study resource limitation (Tamburini et al., 2019; Garratt et al., 2021).

The observed variability of pollination deficits between two cultivars can be understood through three mechanisms, 1) the 'pollination demand', 2) the 'ability to be pollinated', and 3) the 'flowers:plant resources ratio'. Cultivars can have variable pollination demands, i.e. one cultivar can need the deposition of more pollen onto the stigma to fertilize all the ovules, compared to another for several reasons: (i) the cultivar has a lower degree of parthenocarpy (Knapp et al., 2017; Strik and Vance, 2019; DeVetter et al., 2022), (ii) there are fewer ovules per flower to fertilize (Moore et al., 1972; Knight et al., 2005; Burns et al., 2019; Strik and Vance, 2019), (iii) the period of pistil receptivity is shorter (Sanzol and Herrero, 2001; Chabert et al., 2018), (iv) pollen has lower viability, germination rate, and/or the pollen tubes have a lesser ability to reach the ovary (e.g., Walters and Isaacs, 2023), or (v) self-pollination can result in higher ovule abortion due to early-acting inbreeding depression if the species, such as blueberry, is self-compatible but more self-sterile (Aizen and Harder, 2007; Gibbs, 2014; DeVetter et al., 2022; Krebs and Hancock, 1990). On the other hand, one cultivar can experience a lower ability to be pollinated by autonomous self-pollination, wind or pollinator visitation compared to another one, due to: (i) a lower pollen production per flower (Santiago et al., 2021) that can affect the number of pollen grains deposited on the stigma by autonomous self-pollination, (ii) flower morphology being less favorable for autonomous self-pollination (e.g., if stigma is further from anthers), wind pollination (e.g., if stigma protrudes from the corolla), or for attracting pollinators through harder access to the nectar and pollen resources (Courcelles et al., 2013; Sampson et al., 2013; Prasifka et al., 2018), (iii) a lower production of floral rewards leading to a lower attractiveness to pollinators (Prasifka et al., 2018), or (iv) less favorable bloom phenology that is asynchronous with the phenology of the pollinator community (Button and Elle, 2014; Eeraerts, 2022). Finally, a cultivar can have variable flowers:plant resources ratios. It is a relatively common among angiosperms that plants are able to produce many more flowers than they have resources to set them into fruits (Knight et al., 2005), especially in self-compatible species that experience embryo abortion due to genetic load through early-acting inbreeding depression such as blueberry (Porcher and Lande, 2005; Harder and Johnson, 2023).

In the specific case of 'Bluecrop' and 'Duke', the difference could possibly be attributed to the differences in flower dimensions. Compared

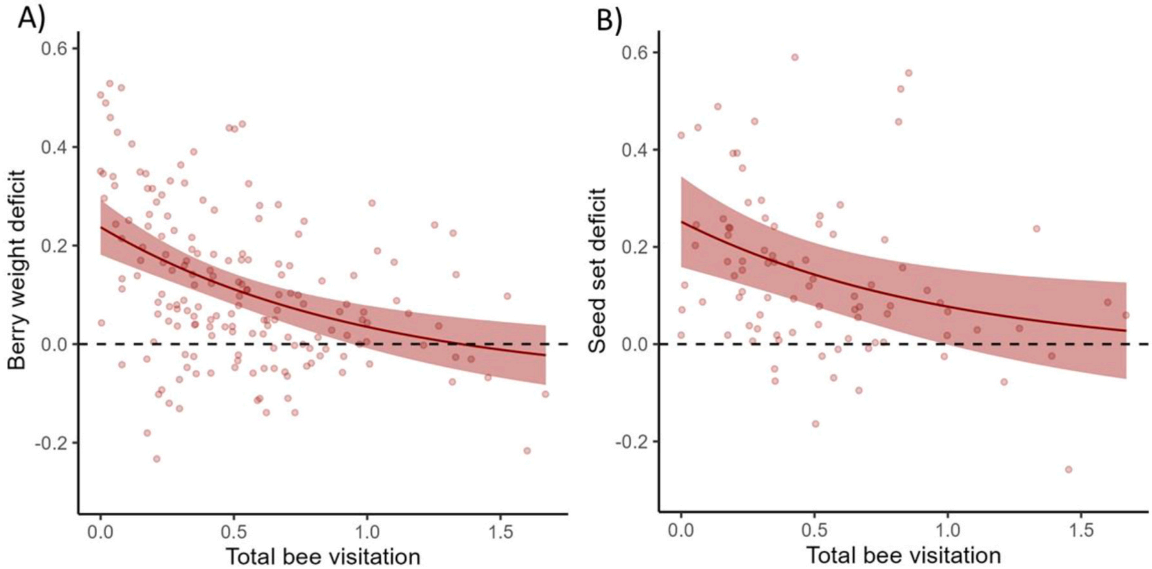

Fig. 2. Relation between total bee visitation and A) berry weight deficit and B) seed set deficit for the highbush blueberry cultivar 'Bluecrop', as modeled by a negative exponential relation. The solid line shows the significant relation, the grey shaded area shows the 95% confidence interval and the dots show the raw data.

to 'Bluecrop', 'Duke' bears flowers with a larger corolla aperture diameter (i.e., variable pollination ability; Courcelles et al., 2013; Castro et al., 2023), and 'Duke' is probably more readily visited by honey bees and less subject to nectar-robbing. In addition, 'Duke' is also more sensitive to early-acting inbreeding depression following self-pollination than 'Bluecrop' (i.e., variable pollination ability; Chabert S. unpublished data), meaning that pollination deficits may have been more underestimated for 'Duke' compared to 'Bluecrop' when hand pollinations treatments with self-pollen are applied. Variable pollination demand and flowers-plant ratio might also be relevant, yet currently we lack data on these mechanisms in blueberry.

This is the first synthesis that models the relation between pollination deficits and pollinator visitation across different cultivars of a single crop across multiple studies. The cultivar-dependent relation that we found between berry weight and seed set deficits and bee visitation is similar to case studies in blueberry (Button and Elle, 2014) and in other crops as well (Hudewenz et al., 2014; Bishop et al., 2020). Button and Elle (2014) found that wild bee visitation decreased berry weight deficits of 'Bluecrop', but not for 'Duke'. These findings, together with our results, emphasize the need for more studies to include multiple cultivars to better match pollinator management to the pollination requirements of different cultivars of a single crop. For 'Duke' and fruit set of 'Bluecrop', we did not detect a clear relation between pollination deficit and bee visitation. Yet, in such cases, when no average pollination deficits are detected, further improving crop yield might require management measures beyond pollinator management (e.g., fertilization, irrigation; Marini et al., 2015; Tamburini et al., 2019). For both cultivars, bee richness did not appear to be related to any pollination metric. Indeed, the pollination services provided of wild pollinators are often driven by the contributions of more abundant and more common species compared to less abundant and rarer species (Kleijn et al., 2015). Yet, the latter often make up most of the richness in a field, but they do not always contribute considerably to pollination. Indeed, the more common and abundant wild pollinators still have a very important role to play as they contribute considerably to crop production (Kleijn et al., 2015). On the other hand, the lack of a richness effect may also be explained by the fact that some studies identified wild bees only to genus or morphospecies level, so the gradient of bee richness was less pronounced in some studies, making it more difficult to detect a significant effect.

The non-linear relation between bee visitation and pollination deficits for 'Bluecrop' detected in this study is in line with recent studies using non-linear models to infer this relation in crops (e.g., Nicholson and Ricketts, 2019; Reilly et al., 2020; Chabert et al., 2022; Eeraerts, 2023). Based on our synthesis, maximal pollination success is achieved in these observational studies for 'Duke', while for 'Bluecrop' pollination success can be further improved with increasing bee visitation rates up to a certain threshold. Determining these optimal bee visitation thresholds should be subject of future studies, as determining a threshold with standardized data of different studies like this study is useful, but merely conceptual (but see Chabert et al., 2022; Eeraerts, 2023). In any case, this non-linear relation suggests that there is an optimal visitation rate beyond which additional visitation does not further minimize pollination deficits. Determining this optimum visitation rate for commercially important crops and cultivars is needed to improve cost-effective pollination management and crop yield. Depending on the region-specific-context bee visitation can be achieved with wild bees, managed (honey) bees or both for blueberry (Gibbs et al., 2016; Mallinger et al., 2021; Eeraerts et al., 2023b) or other crops (Reilly et al., 2020; Eeraerts et al., 2022; Pisman et al., 2022). Here, landscape and habitat management benefits pollination services, but they can also contribute to wild pollinator conservation (Hass et al., 2018; Eeraerts, 2023; Mateos-Fierro et al. 2023). For pollinator-dependent crops like fruit or vegetable crops it is a common practice to combine different cultivars into a single field, farm, or landscape. Given the extent of sites with pollination deficits, our results suggest there are opportunities to use certain cultivars that are less dependent on insects for pollination in landscapes where pollination services have been compromised. In contrast, cultivars that have a higher pollination dependency may be used in landscapes with diverse and abundant pollinator communities.

5. Conclusion

With this synthesis we conclude that pollination deficits are variable across different cultivars of a single crop, and, for specific cultivars experiencing high deficits, enhancing pollinator visitation to crop flowers has the potential to mitigate these deficits. Despite the global importance of insect-mediated pollination for optimal crop yield, and the widespread cultivation of different cultivars within and across production regions, few studies have synthesized this cultivar-variability of pollination deficits and its link with pollinator visitation. We have used two self-compatible blueberry cultivars as a model system, but we suggest that this approach needs to be applied to other insect-pollinated crops, including cultivars and crops that are self-incompatible and have greater pollination requirements.

CRediT authorship contribution statement

Maxime Eeraerts: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Stan Chabert:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Lisa W. DeVetter:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Péter Batáry:** Writing – review & editing, Methodology, Conceptualization. **John Ternest:** Writing – review & editing, Methodology, Data curation. **Kris Verheyen:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Kyle Bobiwash:** Writing – review & editing, Data curation. **Kayla Brouwer:** Writing – review & editing, Data curation. **Daniel Garcia:** Writing – review & editing, Data curation. **G. Arjen de Groot:** Writing – review & editing, Data curation. **Jason Gibbs:** Writing – review & editing, Data curation. **Lauren Goldstein:** Writing – review & editing, Data curation. **David Kleijn:** Writing – review & editing, Data curation. **Andony Melathopoulos:** Writing – review & editing, Data curation. **Sharron Z. Miller:** Writing – review & editing, Data curation. **Marcos Miñarro:** Writing – review & editing, Data curation. **Ana Montero-Castaño:** Writing – review & editing, Data curation. **Charlie Nicholson:** Writing – review & editing, Data curation. **Jacquelyn A. Perkins:** Writing – review & editing, Data curation. **Nigel E. Raine:** Writing – review & editing, Data curation. **Sujaya Rao:** Writing – review & editing, Data curation. **James R. Reilly:** Writing – review & editing, Data curation. **Taylor H. Ricketts:** Writing – review & editing. **Emma Rogers:** Writing – review & editing, Data curation. **Rufus Isaacs:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, 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

Data will be made available on request.

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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.2024.109036.

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