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Solitary bees reduce pollination and production deficits in apple cultivation

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ABSTRACT

Low pollinator richness and abundance is a primary driver of pollination deficits and may lead to reduced yields (production deficits). In response, domesticated honeybees are often used to increase pollination success, even though honeybees are less efficient pollinators than naturally occurring wild bees. Here, we explored whether Norwegian apple orchards experience pollination and production deficits, and if such deficits could be related to specific pollinator groups and activity. We conducted a supplemental pollination experiment and measured seed set and yield (fruit set x weight) for three cultivars, in six orchards, in two distinct apple growing regions in central Norway, for two years. In addition, we used cameras to record relative pollinator activity throughout the flowering period. Overall, we found a pollination and production deficit across all cultivars, although there were differences in pollination deficit among cultivars. Three orchards had a pollination deficit both years of the study, suggesting sub-optimal orchard structure and/or a lack of pollinators. However, we found that solitary bees significantly reduced both pollination and production deficit, suggesting that orchard management actions should focus on increasing wild bee diversity and abundance.

1. Introduction

As much as 75 % of the world’s crops are dependent on pollinators, making pollination by insects a crucial ecosystem service (Klein et al., 2007). For example, apple production increase between 40 % and 90 % when pollinators are present (Klein et al., 2007). Apples are a self-incompatible crop, requiring cross pollination from other apple cultivars and a pollinator vector for production to be sufficient for economic benefit (Garratt et al., 2023). Apples are the third most grown fruit worldwide, with a global crop of 6.9 million ha harvested in 2022 (FAO, 2023).

Bees and hoverflies are the main pollinators of apple (Garratt et al., 2016; Russo et al., 2017), although other insects such as flies, butterflies, moths and beetles may also contribute. Different pollinator species have different flower handling behaviors and relative abundance, which directly affects both pollination and fertilization rates (Blitzer et al., 2016). A high rate of fertilization, or seed set, is correlated with greater size and weight in apples (Webber et al., 2020), while partial fertilization can lead to economically less valuable misshapen fruits (Matsumoto et al., 2012). However, different cultivars respond to pollination in different ways, with some being more dependent on pollination for increased yield and quality than others (Garratt et al., 2021). Garratt et al. (2014) found that one apple cultivar had lower size and weight following supplementary pollination, compared to open pollination, highlighting the importance of considering cultivar specific responses when trying to understand pollinator effects on fruit production. In most cases, when apples have not been adequately pollinated, production deficits occur (Pardo and Borges, 2020). Deficits in yield, seed set, and fruit set have been found in multiple apple cultivars, countries and continents (Garratt et al., 2021; Olhnuud et al., 2022). Importantly, deficits can be mitigated with better pollination management (Blitzer et al., 2016; Garratt et al., 2016; Pardo and Borges, 2020).

High diversity of pollinators is important for increasing crop pollination (Senapathi et al., 2021), and a total of 57 native bee species have been proposed as pollinators of apple across Europe (19 are definite pollinators, 13 likely and 25 possible pollinators; Hutchinson et al.,

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2022). Despite this a few pollinator species tend to dominate crop flower visits (Kleijn et al., 2015). Bumblebees have a high flower visitation rate, frequently moving between rows of trees in the orchards, increasing the possibility of collecting compatible pollen (Campbell et al., 2017). Solitary bees on the other hand, are slower foragers, which increases the chance of stigma contact during a visit (Roquer-Beni et al., 2022). However, anthropogenic land-use change is putting significant pressure on wild pollinators, causing declines to local pollinator communities worldwide (Grab et al., 2019). Managed honeybees are therefore widely used to make up for the lack of wild pollinators. Honeybees can be introduced in large quantities, however they tend to deposit less pollen per visit, reducing their efficiency compared to other pollinators (Blitzer et al., 2016; Garratt et al., 2016). A greater honeybee abundance may not be enough to increase pollination in apples (Blitzer et al., 2016). A diverse pollinator community is therefore important to provide sufficient and resilient pollination of apples (Blitzer et al., 2016; Garratt et al., 2023), and reduce pollination deficits (Garratt et al., 2021).

In Norway, 25 % of pollinating insects are on the red list (Henriksen and Hilmo, 2015) primarily because of loss of habitat from land use change and agricultural intensification (Departementa, 2018). Further declines in pollinators may reduce overall pollination services and result in economic losses due to increased pollination deficits (Garratt et al., 2021, 2023). However, increased wild bee diversity is strongly correlated with the presence of herbaceous and uncultivated open areas within and surrounding apple orchards (Leclercq et al. (2023), suggesting that landscape management can contribute to overall pollinator community stability. The contribution of wild bees to Norwegian apple production, and whether pollination or production deficits exist, is not known. Thus, we sought to better understand the relationship between insect pollinators and potential deficits in Norwegian apple production to inform sustainable management of orchard pollination. We therefore ask the following questions: (1) Are there pollination and/or production deficit of apples in Norwegian orchards?; (2) To what extent do deficits vary in time, by orchard, region, or apple variety?; and (3) are deficits driven by variation in the activity of different pollinators?

2. Material and methods

2.1. Study design

This study was conducted in six locations across two of the main apple growing regions in Norway: Svelvik (east) and Ullensvang (west), over two years, 2022 and 2023. Locations were separated by at least 4 km to prevent overlap in the pollinating community (Zurbuchen et al., 2010). Each location had apple orchards containing the cultivars of Aroma, Discovery and Summerred, among the most widely grown cultivars in Norway (Kristiansen, 2022). In total, the study included 18 orchards (six locations, three orchards each).

2.2. Study locations

All orchards were conventionally managed but varied in size (230 m^2 to 27 000 m^2) and the spatial arrangement of compatible apple cultivars or 'pollinisers' within the orchard. Some orchards had rows of different cultivars planted in the vicinity of each other, while some had orchards of one cultivar, sometimes with individual polliniser trees planted within.

The orchards are situated in coastal regions, with the surrounding landscape mainly consisting of plantation spruce forest, or other fruit orchards. In the western site, there is a steep gradient from the sea to the orchards, followed by forest and mountains. In the east the terrain is relatively flat, however the fruit orchards tend to be bigger than in the west, and the surrounding area consists mainly of coniferous forest (pine and spruce; see Appendix B). In addition, all locations except Djønno have honeybee hives either inside the orchard or in close proximity to the orchards. In 2023 however there were a shortage of honeybee hives in Lofthus, and fewer hives were used compared to 2022.

2.3. Pollination treatments

In each of the 18 orchards ten trees were randomly selected each year ($n_{2022} = 172$ trees and $n_{2023} = 180$ trees). Data from fewer trees were collected in 2022 due to some markings on trees being lost between flowering and harvest. To ensure data was spatially representative of the orchard half of the trees were selected near the edge of the orchard and half towards the centre of the orchard. Three branches were randomly selected on each tree and given one of three treatments: (1) supplemental pollination treatment, receiving extra pollen in addition to being open for pollinators to visit, (2) open pollination treatment, where the branch received pollen through pollinator visits, (3) and an exclusion treatment, using fine mesh sleeves (Insect Rearing Sleeves, Megaview, Taiwan) to prevent pollinators from visiting the flowers (Fig. 1a). The treatments were assigned during bud formation prior to flowering, and all three treatment branches were on the same side of the tree to minimise variations in shade. For the supplemental pollination treatment, each flower was pollinated one to three times using pollen from cultivars located nearby (Appendix A). Stamens with pollen used for supplemental pollination were collected 24–48 hours prior to supplemental pollination and stored in petri dishes in room temperature (18–25°C) to speed up anther dehiscence (Fig. 1b). Pollen was then applied to the stigmas using a paint brush.

After all flowers had withered, the treatment branches were marked and mesh sleeves were removed. Apples on all treatment branches were thinned by the farmers, along with the rest of the orchard according to their usual management practice.

Ripe apples were harvested between one and seven days before commercial harvest, with the exception of Ullensvang, which was harvested two weeks before commercial harvest in 2022. Apples were kept at 4°C from one day to five weeks prior to measurements. For branches that had more than ten apples, ten apples were randomly selected for quality measurements, except in one case where apples were attacked by the fungus *Monilia fructigena*, in which case these were selectively removed.

Fruit quality was assessed by counting number of seeds and measuring fresh fruit weight in grams using a balance. Fruit set was calculated using flowers present on the treatment branches during flowering and apples left on the same branch at harvest. Only fully developed seeds were counted as a seed.

2.4. Fruit set

On all study branches, the number of flower clusters were counted towards the end of the flowering season, prior to commercial thinning. Number of flowers per cluster was then estimated by counting the flowers in 270 clusters (90 cluster per cultivar) in all three locations in Eastern Norway in 2023. Average number of flowers per cluster (Summerred = 5.3 ± 0.10, Discovery = 5.8 ± 0.10, Aroma = 5.10 ± 0.09) was then multiplied by the number of clusters to estimate total number of flowers per branch. All harvested apples from all study branches were counted and divided by the estimated total number of flowers on the branch to give an estimate of percentage fruit set.

A total of 4251 apples were collected over the two years ($n_{2022} = 2107$, $n_{2023} = 2144$), where 2067 apples were hand pollinated, 1959 apples were open pollinated, and 225 apples were produced when pollinators were excluded.

2.5. Pollination and production calculations

Pollination and production, in relation to pollination, calculations were done according to (Garratt et al., 2023):

Fig. 1. (a) Branch with mesh to prevent pollinator visits (b) hand pollination with collected anthers and paintbrush.

$$Deficit = \frac{OSupp - OOpen}{OSupp}$$

Where OSupp is output from supplemental pollination and OOpen is output from open pollination. In cases where the output for open pollination was larger than for supplementary pollination the surplus was calculated as:

$$Surplus = \frac{OSupp - OOpen}{OOpen}$$

Pollination deficit and surplus pollination was calculated by averaging seed set per apple by branch, and production deficit and surplus production was calculated as fruit set x average fresh apple weight (g) per branch.

2.6. Pollinator surveys

To assess pollinator activity in the orchards we conducted pollinator surveys using timelapse cameras (Wingscapes, USA; Fig. 2) in 2023 in the three eastern locations: Berle, Høyen and Sando. Cameras were placed approximately 1.5 m above ground on a metal pole, and they took a photo every minute, 24hrs a day during the entire flowering period. For two of the locations (Berle and Høyen), three cameras were randomly placed within each apple cultivar, and for the last location (Sando) one camera was placed in the Discovery and Summerred orchard, and two cameras were used in the Aroma orchard. All images showing a bee visiting a flower were annotated using the VGG Image Annotator (VIA) software (Dutta et al., 2019). Bees were classified as honeybees, bumblebees or solitary bees. Not all flowers in each photo were perfectly angled toward the lens which made identifying visiting bees difficult and resulting in a fourth classification: unknown bees.

The field of view of each camera contained a different number of flowers and due to the flowers facing different directions, counting the total number of flowers per photo was not possible. In addition, each camera took different number of total pictures, as the flowering period varied between trees, cultivars, and locations. This method limits the ability to calculate absolute visitation rates (e.g. visits per flower per minute), but we are able to compare relative pollinator activity on the apple flowers between location and time points.

Fig. 2. Wingscapes cameras taking photos of apple flowers every minute to record relative pollinator activity.

2.7. Statistical analysis

To investigate if pollination- and production differed between the different variables, linear mixed effect models, using the nlme package (Pinheiro and Bates 2022), were used. Apple cultivar, region and year were set as fixed effects, and tree nested within location was used as a random effect (Table 1a). The pollination and production data were normally distributed. The 95 % confidence interval was calculated and when the confidence interval did not cross the 0 line, indicating optimal pollination (supplementary pollination = open pollination), the orchard was considered to have a significant deficit or surplus pollination.

To assess the effect the individual pollinator groups had on both pollination- and production, linear mixed effect models were used. The pollinator groups, honeybees, bumblebees and solitary bees and apple cultivar was included as fixed effects. The pollination and production data were normally distributed. One model was created for each pollinator group as we were interested in their individual effect (Table 1b). In addition, we performed ANOVA analysis to test for a significant interaction between the pollinator group and the three cultivars. No interaction was found, so the interaction term was removed from the models. To test for a difference in ovules produced in the three different apple cultivars we performed an ANOVA and a Tukey test. And to test for differences in relative pollinator activity between locations we performed a negative binomial linear mixed effect model, due to overdispersion in the data, and a Tukey test. All analyses were carried out in R version 4.4.1 (R Core Team, 2024) and all data and code are available on GitHub: https://github.com/linnvassvik/Prod_Poll_Def

3. Results

Average seed set for hand pollinated apples was 65.1 ± 0.6 %, for open pollinated treatments was 55.5 ± 0.7 % and exclusion treatment was 9.8 ± 1.3 %. Average fruit set for hand pollination treatments was 12.2 ± 0.4 %, for open pollinated treatments was 10.6 ± 0.4 % and exclusion treatment was 1.9 ± 0.2 %. For data on the different cultivars see Appendix C. The different cultivars also produced different number of seeds, Aroma produced significantly more seeds ($p = 0.005$), with a maximum of 15 seeds, compared to both Discovery and Summerred, that produced a maximum of 10 and 12 seeds respectively.

3.1. Pollination deficit across cultivars, regions, year, and location

Overall, in Norway we found pollination deficits. The pollination deficit did not differ significantly between regions or year, but there was a significant difference between cultivars, with Aroma having a higher

Table 1
Pollination and production deficit models, split between (a) three variables: apple cultivar (Aroma, Discovery and Summerred), region (Eastern- and Western Norway) and year (2022 and 2023), and between (b) different pollinator groups (solitary bees, bumblebees and honeybees) and accounting for apple cultivar. Tree nested within location was added as random effects for models 1 and 2, analysing pollination and production deficits between apple cultivar, region and year. Location was added as random effect for models 3–8, analysing pollination and production deficits between the different pollinator groups. Pollination and production deficit had a normal distribution.

(a) Pollination and production between apple cultivar, region and year				
Model number	Response variable	Fixed effect	Random effect	Distribution
1	Pollination	Apple cultivar (Aroma, Discovery and Summerred) + Region (East and West) + Year (2022 and 2023)	Tree/ Location	Normal
2	Production in relation to pollination	Apple cultivar (Aroma, Discovery and Summerred) + Region (East and West) + Year (2022 and 2023)	Tree/ Location	Normal
(b) Pollination and production between different pollinator groups				
Model number	Response variable	Fixed effect	Random effect	Distribution
3	Pollination	Apple cultivar + Solitary bee	Location	Normal
4	Pollination	Apple cultivar + Bumblebee	Location	Normal
5	Pollination	Apple cultivar + Honeybee	Location	Normal
6	Production in relation to pollination	Apple cultivar + Solitary bee	Location	Normal
7	Production in relation to pollination	Apple cultivar + Bumblebee	Location	Normal
8	Production in relation to pollination	Apple cultivar + Honeybee	Location	Normal

deficit compared to both Discovery, and Summerred (Fig. 3; Table 2).

To better understand the large variation in the data we analysed cultivar and year for each location separately (see Appendix D for figure). Aroma was the cultivar with the greatest variation, three locations (Sando, Høyen and Djønno) had a pollination deficit both years of the study, and two locations (Urheim and Berle) had a pollination deficit in one of the years. For Discovery, two locations (Høyen and Lofthus) had a pollination deficit both years, and two locations (Sando and Djønno) only in 2023. Summerred had the fewest locations with pollination deficits; only one location (Djønno) had a pollination deficit both years of the study, while two locations (Urheim and Høyen) a pollination deficit in one of the years.

3.2. Production deficit across cultivars, regions, year and location

Across all sites, cultivars, and years, we found a significant production deficit, meaning that the overall yield (fruit set x weight) was lower in open pollinated apples compared to when pollen was supplemented. However, production deficit did not significantly differ between cultivars, regions or year (Fig. 4; Table 3).

To better understand the large variation in the data we analysed cultivar and year for each location separately (see Appendix D for figure). Aroma was the cultivar with the largest variation, where one location (Høyen) had a production deficit both years of the study, and two locations (Sando and Berle) had a production deficit in one of the

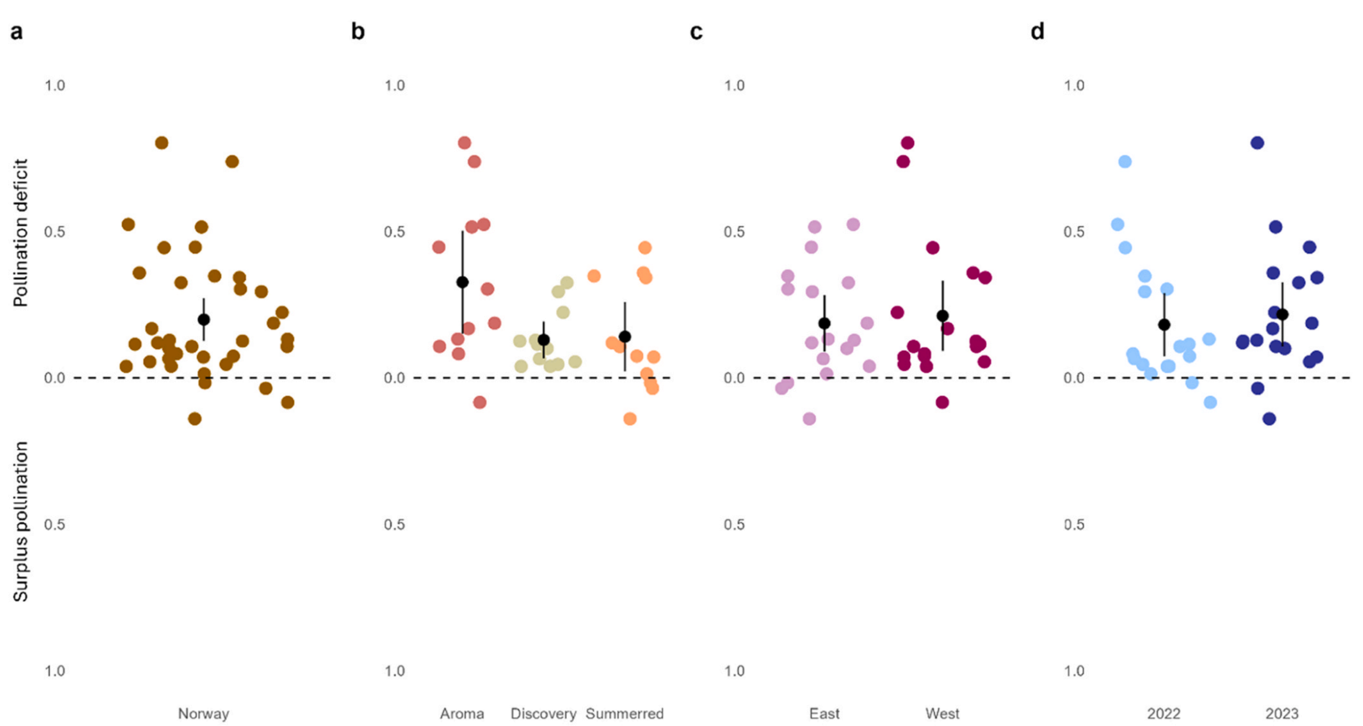

Fig. 3. Comparing pollination deficit and surplus pollination between (a) all orchards in Norway across two years, (b) apple varieties, (c) regions and (d) years, 2022 and 2023. Pollination is measured as seed set per treatment branch, comparing open pollinated apples with supplementally pollinated apples. Each orchard is represented with two datapoints as the study was conducted over two years, and average and 95 % confidence interval is marked out in black.

Table 2
Analysis of how pollination deficit and surplus pollination is affected by different spatial scales using linear mixed effect models. Difference in spatial scale on deficit was measured as difference between the three apple cultivars, Aroma, Discovery and Summerred, the two regions (East and West) and the two years of the study (2022 and 2023). Significant values ($p < 0.05$) are indicated in bold.

Pollination				
	Value ± SE	DF	t	p
Intercept	−63.82 ± 63.42	245	−1.01	0.315
Discovery	**−0.19 ± 0.04**	**245**	**−4.89**	**< 0.001**
Summerred	**−0.19 ± 0.04**	**245**	**−5.01**	**< 0.001**
West	0.02 ± 0.05	49	0.43	0.667
Year	0.03 ± 0.03	245	1.01	0.313

years. For Discovery none of the locations had a production deficit in ether year of the study, but three (Djønno, Berle and Lofthus) had a production deficit in 2023. For Summerred there were no production deficit in any of the locations during this study. Two locations also had surplus production (Urheim 2022 and Sando 2023), both in Aroma, indicating that production decreased with supplementary pollination.

3.3. *Bee activity related to pollination- and production deficits in eastern Norway*

The cameras in the three eastern locations in 2023 took a total of 206 420 photos, evenly distributed between the three cultivars (Aroma = 68132, Discovery = 70559, Summerred = 67729). From all photos 2076 of them contained a bee visiting an apple flower. Out of these 87.7 % of the visits were from honeybees, 8.5 % of the visits from solitary bees, and 3.8 % of the visits were from bumblebees. Discovery had the highest number of visits (43.5 %), followed by Aroma (38.6 %), and Summerred (17.9 %). In addition, there were 583 bees visiting a flower that could not be identified to a pollinator group.

Relative solitary bee activity differed significantly between locations, with Høyen having a significantly lower relative activity than both Berle and Sando ($p = 0.044$ and $p = 0.005$ respectively; Table 4). No difference in relative activity was found between locations for honeybees or bumblebees.

Relative honeybee- and bumblebee activity did not significantly decrease pollination deficit (Appendix E), but solitary bee activity had a significant negative relationship between proportion of visits and pollination deficit (Fig. 5a; Table 5a). For production deficit the same results were found, with no significant relationship between production deficit and honeybee- and bumblebee activity, but a decrease in production deficit with increased solitary bee activity (Fig. 5b; Table 5b). A significant effect for cultivar on size of both pollination and production deficit was also found (Table 5).

4. Discussion

4.1. *Variations in pollination and production deficits in Norwegian apple orchards*

We found both pollination (seed set) and production (yield) deficits in Norwegian apple orchards, however the degree of deficit varied.

Table 3
Analysis of how production deficit and surplus production is affected by different spatial scales using linear mixed effect models. Difference in spatial scale on deficit was measured as different between the three apple cultivars, Aroma, Discovery and Summerred, the two regions (East and West) and the two study years (2022 and 2023). Significant values ($p < 0.05$) are indicated in bold.

Production				
	Value ± SE	DF	t	p
Intercept	−24.92 ± 110.36	251	−0.23	0.822
Discovery	−0.06 ± 0.07	251	−0.83	0.410
Summerred	−0.11 ± 0.07	251	−1.72	0.087
West	−0.07 ± 0.05	49	−1.27	0.211
Year	0.01 ± 0.05	251	0.23	0.820

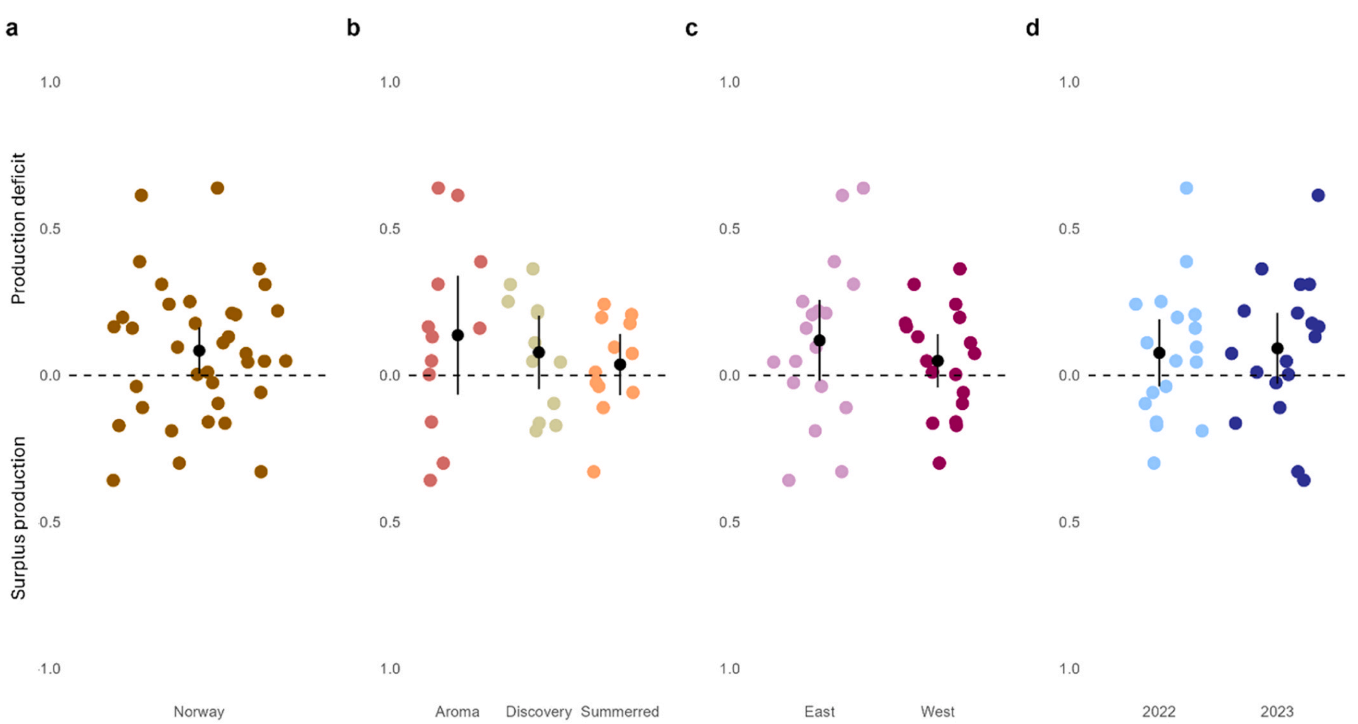

Fig. 4. Comparing production deficit and surplus production between (a) all orchards in Norway across two years, (b) apple varieties, (c) regions and (d) two years, 2022 and 2023. Production is measured as fruit set × weight per treatment branch, comparing open pollinated apples with supplementally pollinated apples. Each orchard is represented with two datapoints as the study was conducted over two years, and average and 95 % confidence interval is marked out in black.

Table 4
Analysis on difference in relative bee activity between locations, for (a) the linear mixed effect model and (b) Tukey test. Relative bee activity is measured as total number of bees recorded per camera for each location. The three different groups of bees, honeybee, bumblebee and solitary bee, and the tree locations, Berle, Høyen and Sando, are the predictor. Significant values ($p < 0.05$) are indicated in bold.

(a) Pollinator activity				
	Estimate ± SE		z	p
Intercept	4.19 ± 0.29		14.40	< 0.001
Bumblebee	**−3.44 ± 0.47**		**−7.33**	**< 0.001**
Solitary bee	**−2.47 ± 0.43**		**−5.71**	**< 0.001**
Høyen	−0.58 ± 0.41		−1.42	0.157
Sando	−0.60 ± 0.41		−1.13	0.258
Bumblebee - Høyen	0.58 ± 0.53		0.88	0.379
Solitary bee - Høyen	−1.13 ± 0.68		−1.65	0.098
Bumblebee - Sando	0.54 ± 0.85		0.64	0.525
Solitary bee - Sando	1.28 ± 0.77		1.67	0.096
(b) Pollinator activity between locations				
	Estimate ± SE	**DF**	**z**	**p**
Honeybee Berle - Honeybee Høyen	3.44 ± 0.47	Inf	7.33	< 0.001
Honeybee Berle - Honeybee Sando	0.60 ± 0.53	Inf	1.13	0.100
Honeybee Høyen - Honeybee Sando	0.011 ± 0.53	Inf	0.02	1.000
Bumblebee Berle – Bumblebee Høyen	0.01 ± 0.52	Inf	0.01	1.000
Bumblebee Berle – Bumblebee Sando	0.05 ± 0.67	Inf	0.08	1.000
Bumblebee Høyen – Bumblebee Sando	0.05 ± 0.67	Inf	0.08	1.000
Solitary bee Berle – Solitary bee Høyen	**1.71 ± 0.56**	**Inf**	**3.15**	**0.044**
Solitary bee Berle – Solitary bee Sando	−0.68 ± 0.56	Inf	−1.22	0.952
Solitary bee Høyen – Solitary bee Sando	**−2.40 ± 0.64**	**Inf**	**−3.78**	**0.005**

Variation in deficits in apple has previously been found in multiple countries (Garratt et al., 2021) and suggests opportunities exist for improved pollination management. Deficits can occur due to low pollinator diversity and abundance in orchards (Blitzer et al., 2016), sub-optimal orchard management (e.g. fruit thinning; Verma et al., 2023), or lack of compatible pollen from a different cultivar in the near vicinity (Carisio et al., 2020).

We found no overall difference in pollination or production deficit between Eastern and Western Norway, or between years, suggesting that deficits are site specific. However, there were differences in pollination deficit between the three apple cultivars in our study; Aroma had higher pollination deficits compared to both Discovery and Summerred. Such differences in deficits between cultivars has been found previously in apples (Garratt et al., 2021) and blueberries (Eeraerts et al., 2024) and may occur for different reasons. Firstly, cultivars may have different abilities to attract pollinators (Garratt et al., 2016) through nectar concentration and/or floral scent (Rachersberger et al., 2019). Apple cultivars emit different volatile organic compounds (VOC) to produce scent. Aroma seems to emit less VOC than the other two cultivars (Hanna Thostemann et al., unpublished data), potentially making it less attractive to pollinators. Secondly, pollinator dependence can vary between cultivars. For example, cultivars have different numbers of ovules, resulting in variable pollination requirements to reach the threshold needed for fruit production (Strik and Vance, 2019). We found that Aroma produced more seeds than the other two cultivars and could indicate that Aroma needs more pollinator visits per flower, or visits from more efficient pollinators, to fertilise the higher number of seeds. Finally, Aroma flowers later than both Discovery and Summerred, which are some of the first flowering apple cultivars (Gasi et al., 2023) which means that Aroma overlaps more in flowering period with both early and late flowering apple cultivars, in addition to other flowering plants in the surroundings, potentially increasing competition for pollinators. Competition for pollinators between cultivars of the same crop has not, to our knowledge, been studied before, however competition for pollinators between different mass-flowering crops has been shown between apples and strawberries (Grab et al., 2017), and apples and *Brassica rapa*

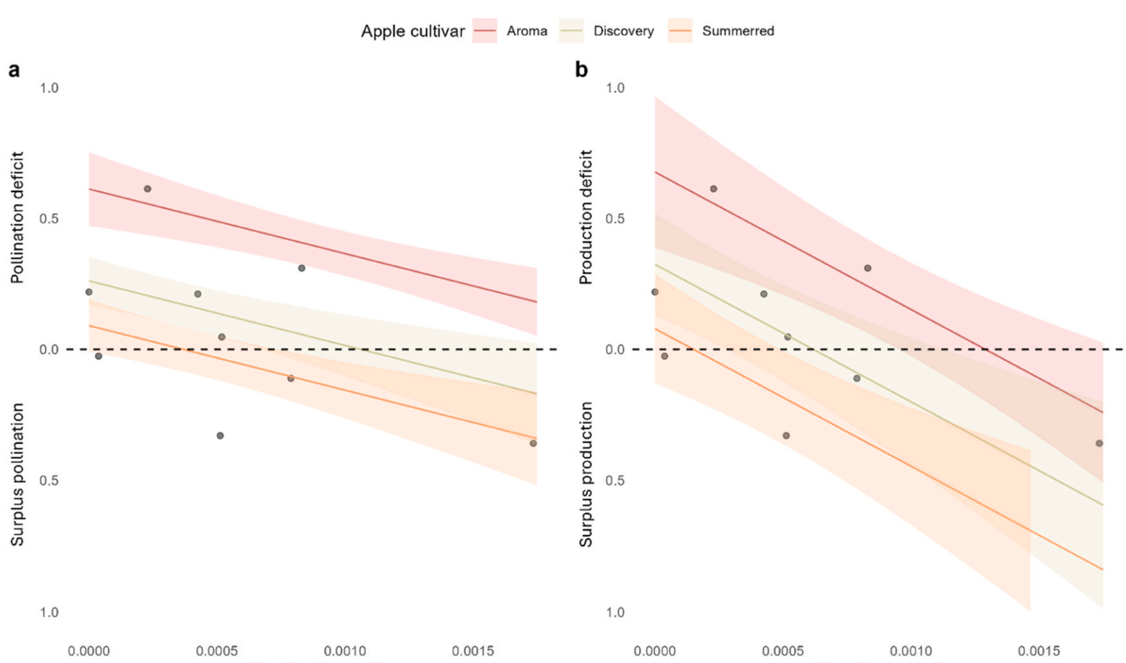

Fig. 5. Relative bee activity from camera recordings for solitary bees and their relation to (a) pollination, and (b) production. Pollination is measured as seed set per treatment branch, comparing open pollinated apples with supplementally pollinated apples, and production is measured as fruit set × weight per treatment branch, comparing open pollinated apples with supplementally pollinated apples. The points show the raw data while the line is the model prediction with confidence intervals. Colours indicate the three different apple cultivars: Aroma (red), Discovery (green) and Summerred (orange).

Table 5
Analysis from relative bee activity for (a) pollination deficit and (b) production deficit using linear mixed effect models. Pollination deficit is measured as seed set per treatment branch, and production deficit is measured as fruit set × weight per treatment branch, comparing open pollinated apples with supplementally pollinated apples. The three different apple cultivars, Aroma, Discovery and Summerred, and the pollinator group (visits/recording) are the predictors. Significant values ($p < 0.05$) are indicated in bold.

(a) Pollination				
Solitary bees	Value ± SE	DF	t	p
Intercept	0.61 ± 0.07	3	8.56	0.003
Discovery	**−0.35 ± 0.07**	**3**	**−5.00**	**0.015**
Summerred	**−0.52 ± 0.07**	**3**	**−7.88**	**0.004**
Solitary bees	**−246.6 ± 61.42**	**3**	**−4.01**	**0.028**
Bumble bees				
Intercept	0.42 ± 0.11	3	3.82	0.032
Discovery	−0.23 ± 0.10	3	−2.33	0.102
Summerred	**−0.42 ± 0.09**	**3**	**−4.75**	**0.018**
Bumble bees	−80.72 ± 139.75	3	−0.58	0.604
Honeybees				
Intercept	0.43 ± 0.14	3	3.10	0.054
Discovery	−0.19 ± 0.09	3	−2.19	0.116
Summerred	**−0.42 ± 0.10**	**3**	**−4.09**	**0.027**
Honeybees	−7.22 ± 18.16	3	−0.40	0.718
(b) Production				
Solitary bees	**Value ± SE**	**DF**	**t**	**p**
Intercept	0.68 ± 0.15	3	4.59	0.019
Discovery	−0.35 ± 0.15	3	−2.36	0.100
Summerred	**−0.60 ± 0.14**	**3**	**−4.21**	**0.024**
Solitary bees	**−524.95 ± 124.69**	**3**	**−4.21**	**0.025**
Bumble bees				
Intercept	0.05 ± 0.26	3	0.18	0.868
Discovery	0.09 ± 0.30	3	0.30	0.781
Summerred	−0.27 ± 0.28	3	−0.97	0.404
Bumble bees	310.85 ± 408.71	3	0.76	0.502
Honeybees				
Intercept	−0.02 ± 0.33	3	−0.06	0.959
Discovery	−0.05 ± 0.24	3	−0.20	0.855
Summerred	−0.24 ± 0.27	3	−0.88	0.445
Honeybees	35.16 ± 46.12	3	0.76	0.501

(oilseed rape; Osterman et al., 2021). Summered was the only cultivar that had no orchards with production deficit, potentially because it is more attractive to pollinators or flowers at a more optimal time. In order to decrease pollination deficits in Aroma, more studies should focus on flower visits and what attracts different species of pollinators into the orchard and also how to best improve management of key pollinators (e.g. solitary bees) increasing their activity in orchards (Fountain et al., 2023; Garratt et al., 2023; O'Reilly and Stanley, 2023).

4.2. Variation in pollination and production deficits of the same cultivars between locations

We found variations in the extent of deficits between orchards of the same cultivar between locations and years. Aroma had pollination deficits in both years of the study at Høyen, Sando and Djønno, only for one year at Berle and Urheim, and no pollination deficits in any of the years at Lofthus. Pollination deficit at Høyen also translated into a production deficit. Seed set is related to pollination and can further affect both fruit set and apple quality (Webber et al., 2020). Orchards with pollination deficits could suffer from a lack of pollinators, however it could also be explained by the orchard structure. The orchards at Djønno and Høyen have a block design, with one cultivar planted within a continuous area, versus a mixed design where rows of different apple cultivars are planted close together. The block design could constrain the amount of viable pollen that pollinators are able to collect and deliver, even if pollinator visitation rates are sufficient. This is particularly important for solitary bees as they have a shorter flight range than both bumblebees and honeybees. The foraging range for solitary bees has been found to be about 150 – 600 m and correlates with body size, with larger bees travelling further (Gathmann and Tscharntke, 2002). Social bees, such as bumble bees and honeybees, travel much further due to their high foraging activity in the vicinity of the nest, increasing resource competition among colony members and the need to travel further to forage (Grüter and Hayes, 2022; Kendall et al., 2022). A mixed orchard design, planting two or more cultivars in the same area, has been shown to result in better pollination (Chabert et al., 2024). Carisio et al. (2020) found that apple trees more than 30 m away from a compatible pollen source had a higher risk of pollen limitation, suggesting that the group of pollinator and the spatial arrangement of cultivars is an important driver of pollination success.

Aroma and Discovery are often considered good polliniser trees, both for each other, but also for other cultivars, such as Summerred (Gasi et al., 2023). At Høyen and Djønno, the Aroma and Discovery orchards are planted 250 and 200 m apart, while all other locations have these cultivars planted within 50 m or less from each other. In addition, Aroma at Høyen is mainly surrounded by the triploid apple cultivar Gravenstein, which is an incompatible pollen source for all of our diploid study cultivars (Gasi et al., 2023). Despite the high pollination deficit for Aroma at Djønno, this does not translate into a high production deficit. This may be because orchard fruit management actions (e.g. manual thinning) allow the tree to allocate resources towards apples with lower seed set, potentially buffering the lack of viable pollen transferred to the flower (Webber et al., 2020). Sando also had pollination deficits, however this orchard has a mixed design with Aroma and Discovery planted close together, therefore compatible pollen should be accessible for the pollinators. The deficits here may therefore be explained by the specific pollinator community present in the orchard (Mallinger and Gratton, 2015), although this requires further exploration.

We also found pollination deficit for Discovery at Høyen and Summerred at Djønno in both years. Both of these cultivars are grown in a block design, which likely constrains optimal pollinator services. Also, for Summerred at Djønno, Aroma is the nearest compatible cultivar, however these two cultivars have low overlap in flowering. Interestingly, none of these pollination deficits resulted in production deficits, probably due to orchard fruit management actions.

Some orchards in this study, across all cultivars, have a deficit (pollination and/or production) during only one year of the study. Variation in deficits from one year to another could be explained by the fluctuations in the pollinator community (Garratt et al., 2023), weather conditions during the flowering period and fruit development up until harvest (Li et al., 2018), or variation in management needs from year to year (Verma et al., 2023). Inconsistent deficits year to year might not translate into long-term average deficits, however year to year variation could have large economic impacts for farmers (Garratt et al., 2023), and therefore understanding what causes deficits is important.

Overall, we speculate that pollination and production deficits are primarily affected by the orchard structure, highlighting the importance of having a mixed orchard design with compatible pollen sources nearby to exploit pollination services from all pollinators (Gasi et al., 2023). In addition, management actions may be able to buffer the effects of pollination and/or production deficits, however it is unclear whether management actions are sufficient to reliably overcome losses in production because of poor pollination.

4.3. Interactions between pollination and management

Different groups of pollinators contribute to apple pollination to varying extents (Blitzer et al., 2016). High pollination deficits are expected to result in high production deficits, but we found that Aroma in Urheim in 2022 and Sando in 2023 had surplus production, which is unexpected. Surplus production occurs when the yield (fruit set x weight) is higher for open pollinated apples compared to supplementally pollinated apples. This could be due to resource limitation, meaning that there is a fixed amount of resources for the tree to spend on producing apples. Therefore, with more pollinated apples left on the tree fewer resources are allocated to each apple and they get smaller. Fruit thinning is a normal practice to prevent resource limitation during fruit formation and alternate year fruit bearing for the apple trees (Verma et al., 2023). However, different management regimes are practiced in Norway for Aroma because Aroma apples can get too big if there are too few fruits produced by the tree, making them unsuitable to sell for direct consumption. Manual thinning removes the under pollinated fruits (i.e. small and asymmetrical), leaving only the high-quality apples. Thinning apples generates a more optimal load and higher quality fruit (Webber et al., 2020). However manually thinning apples is very labour demanding. Both Høyen and Djønno had pollination deficits in Aroma both years of our study. Aroma at Høyen is not thinned, while at Djønno the fruits are manually thinned. The management regime at Høyen could result in the production of many small apples due to resource limitation and result in an overall production deficit, whereas at Djønno, optimal fruit load is managed through thinning and thus no production deficit is observed. In addition, surplus pollination (i.e. over pollination) could occur due to too much pollinator activity, resulting in stigma damage (Sáez et al., 2014) or stigma clogging (Brown and Mitchell, 2001), however none of the orchards in this study had a significant surplus pollination. Surplus production does not necessarily imply a need for reduced pollinator activity but may instead indicate that management of the fruit load needs to be adjusted accordingly.

4.4. *Managing pollination services in orchards*

We found that increased activity of solitary bees decreased both pollination and production deficits, likely by increasing seed set, fruit number and fruit weight. This could be related to the behavior of solitary bees, which have high rates of stigma contact and pollen deposition during flower visits (Roquer-Beni et al., 2022). Solitary bee richness and abundance is also higher when orchards are near natural areas because of nesting preferences. Therefore, a diverse landscape in close proximity to the apple orchards are important to exploit the pollination services provided by solitary bees (Joshi et al., 2016). In contrast, we found no effect of bumble bee activity on pollination or production deficit, even though bumble bees are generally thought to provide good pollination services (Sapir et al., 2017). Finally, honeybee activity had no effect on pollination or production deficit, despite the fact that most of our study orchards had managed honeybee colonies either inside or in close proximity to the orchards to improve pollination. The reason we do not see any effect of honeybees and bumblebees is likely because their relative activity did not differ between locations.

Different apple cultivars rely on pollinators to a varying degree (Garratt et al., 2021), where we found that Aroma is more pollinator dependent than both Discovery and Summerred, with Summerred having the overall lowest pollinator dependency. This is further supported by our finding that fewer visits from solitary bees are required for optimal pollination of Summerred compared to both Aroma and Discovery. For Summerred that means that fewer management actions are needed to increase bee activity in the orchards, however, to avoid surplus pollination (i.e. over pollination) it is important to manage fruit loads. For Aroma, management should focus on increasing bee activity in the orchards to avoid pollination and production deficits.

The relationship between pollinators and pollination deficit is poorly understood. Garratt et al. (2013) did not detect any relationship between pollinator group and fruit or seed set for the Cox apple cultivar in the Kent region in the UK. However, bumblebees reduced the seed number deficit and solitary bees reduced apple size deficits for the Gala cultivar in the same region (Garratt et al., 2023). Both studies calculated bee activity on apple flowers using manual observations, however in our study we estimated relative bee activity using time lapse cameras. Cameras are less labour intensive and more efficient than manual observations, providing data that are non-invasive to the pollinators and continuous throughout the day and growing season (Besson et al., 2022). Cameras have the potential to collect more data than manual observations (Naqvi et al., 2022), providing us with a greater understanding of pollinator activity, which is especially important for apples that have a short and intensive flowering period. We were not able to separate the individual solitary bees in our photos into a lower taxonomical identification due to flower and pollinator orientation. We do however know from a study across 33 countries, and six continents, that solitary bees associated with apple orchards have high taxonomical diversity (Leclercq et al., 2023). Apple pollinating bees also vary when they are active, their body size and their flower handling behaviour (Danforth et al., 2019; Høydal, 2024; Roquer-Beni et al., 2022). Recent recordings of declines in solitary bee abundance (Powney et al., 2019) highlight the importance of managing for pollinators, which can be done through surrounding landscapes. This can provide the bees with floral- and nesting resources throughout the flight season, which is crucial for survival, enhancing solitary bee diversity, in addition to increasing apple production (Eeraerts et al., 2021).

5. Conclusion

Here, we found that pollination and production deficits occur in three commonly grown apple cultivars in the two largest apple growing regions in Norway. However, the degree of pollination deficit varied between cultivars, likely due to orchard structure and variation in pollinator diversity. One cultivar, Aroma, displayed greater variation in both pollination and production deficits compared to the Summerred and Discovery cultivars during our study. This suggests that the Aroma cultivar may present greater risk to apple growers because of uncertainty in yield across years. Understanding pollination and production deficits within pollinator dependent crops, such as apples, can help growers enact appropriate management actions to improve yield and mitigate financial risk by identifying cultivars that have stable production over time. We also found that solitary bees generally improved apple pollination success and production. However further research on pollinator behavior, foraging time, pollen deposition, and stigma contact, is required to better understand the complex relationship between pollinator communities and apple production.

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CRediT authorship contribution statement

Vassvik Linn: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Aschehoug Erik Trond:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Hatteland Bjørn Arild:** Writing – review & editing, Methodology, Conceptualization. **Chipperfield Joseph:** Writing – review & editing, Conceptualization. **Nielsen Anders:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Garratt Michael P. D.:** Writing – review & editing, Methodology, Formal analysis, 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.

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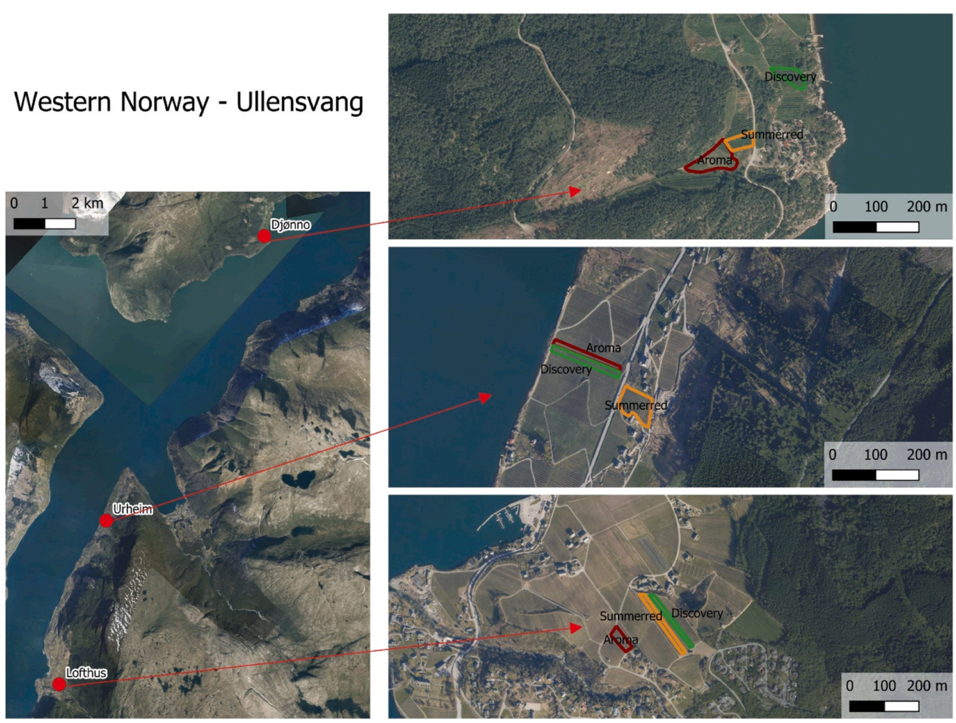
Appendix A. – Polliniser cultivars

Overview of cultivars used to pollinize the different cultivars in the supplemental pollination study. Flowering apple cultivars growing the near vicinity of study orchards was used.

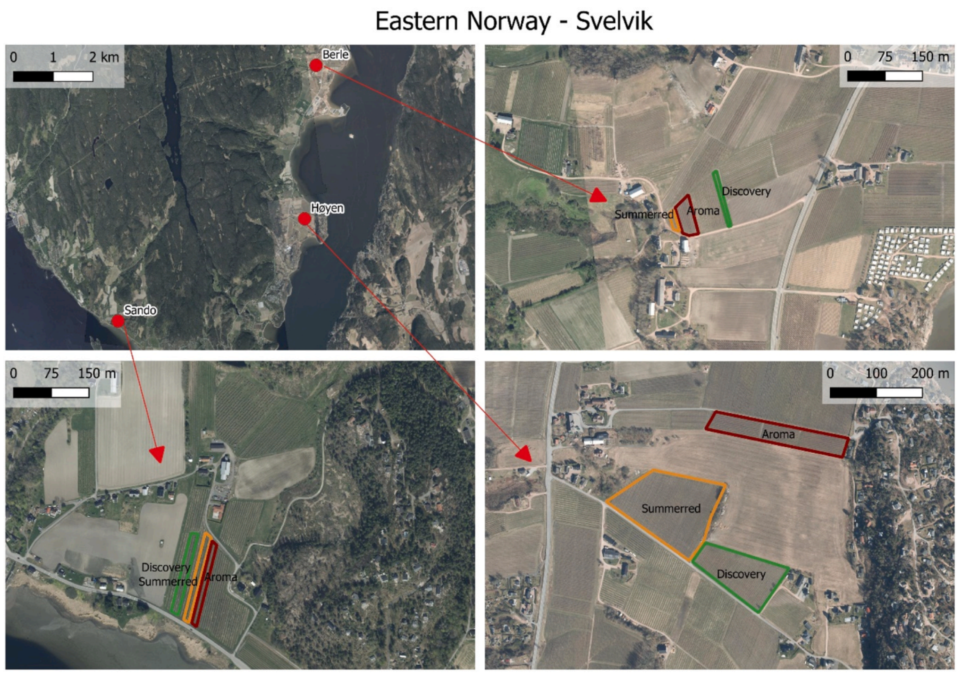
Region	Location	Apple cultivar	Polliniser cultivar
Svelvik	Berle	Summerred	Discovery, Aroma, July Red, Dr Springer, Asfari and July Red
		Discovery	Aroma, Katja and Red Cobenza
		Aroma	Discovery, July Red and Zari
	Høyen	Summerred	Discovery and crab apple
		Discovery	Summerred and crab apple
		Aroma	Karin Schneider
	Sando	Summerred	Discovery, Aroma and July Red
		Discovery	Summerred, Aroma and July Red
		Aroma	Elstar, July Red and Discovery
Ullensvang	Lofthus	Summerred	Vista Bella, Aroma and Discovery
		Discovery	Aroma, Vista Bella and Summerred
		Aroma	Discovery
	Urheim	Summerred	Aroma, crab apple and Discovery
		Discovery	Aroma, Summerred and crab apple
		Aroma	Discovery
	Djønno	Summerred	Discovery and Aroma
		Discovery	Aroma and Summerred
		Aroma	Discovery

Appendix B. – Map of locations

Map of locations and orchards in Western Norway.



Map of locations and orchards in Eastern Norway.

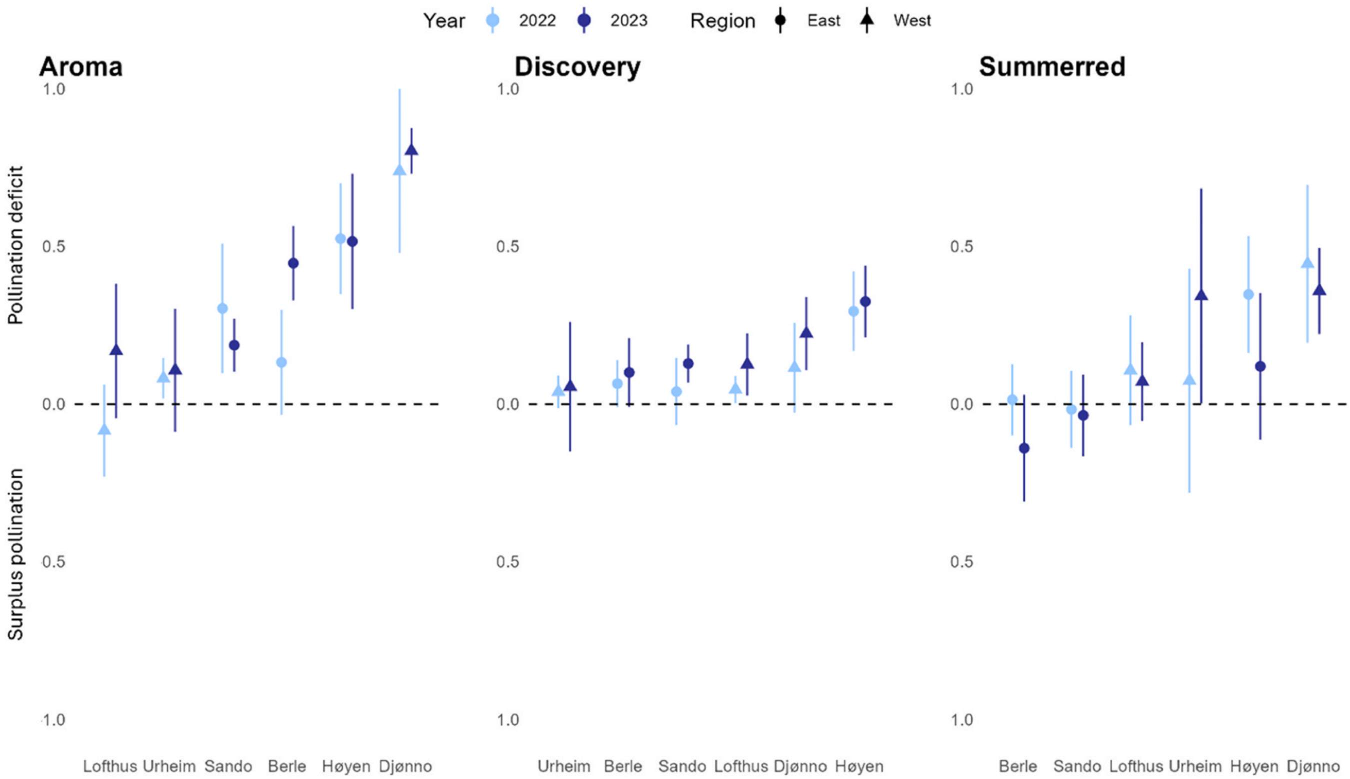


Appendix C. – Seed set and fruit set per treatment and cultivar

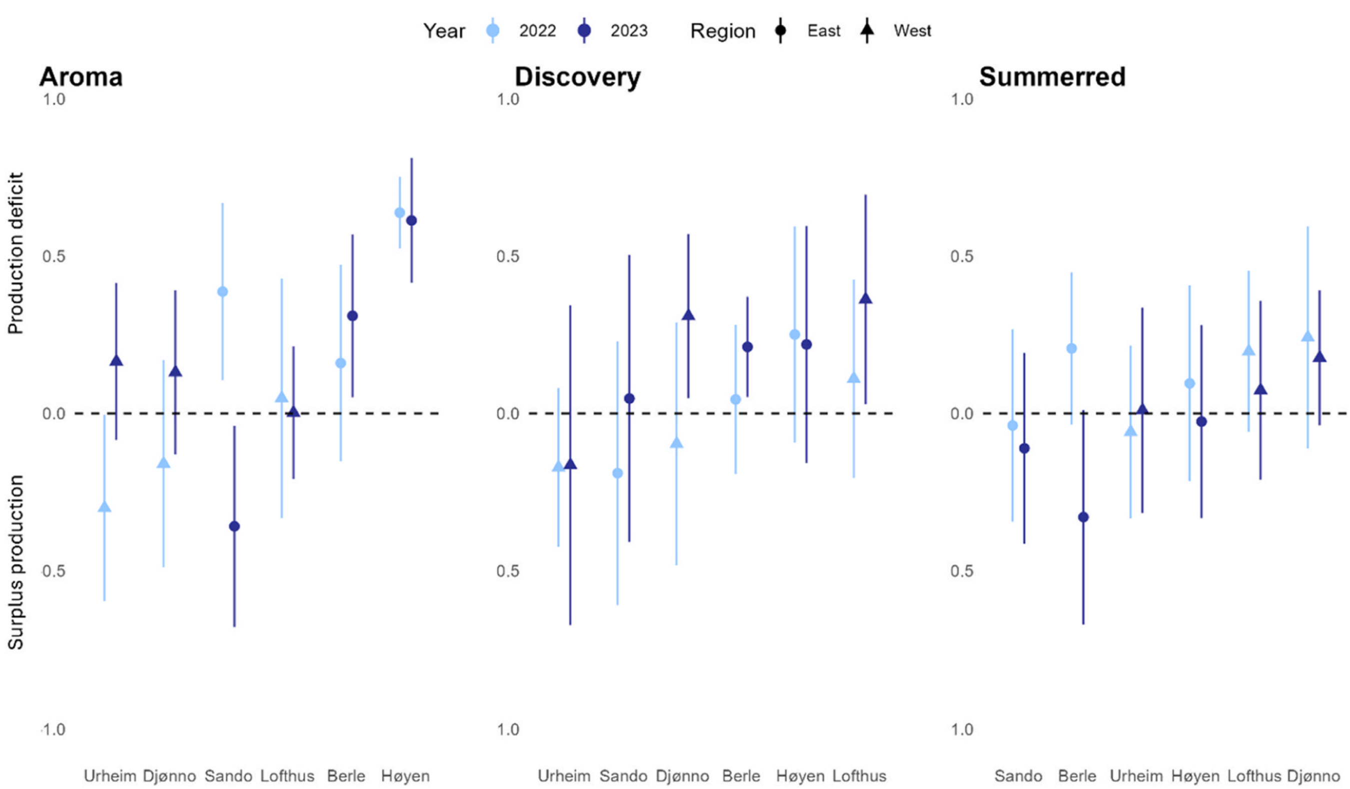
Data from the three different pollination treatments, exclusion of pollinators, supplementary pollination and open pollination, and how seed set (%) and fruit set (%) vary between the treatments

Treatment	Cultivar	Average seed set (%) ± SE	Average fruit set (%) ± SE
Exclusion of pollinators	Aroma	7.9 ± 1.5	2.9 ± 0.4
Exclusion of pollinators	Discovery	29.0 ± 6.5	1.0 ± 0.3
Exclusion of pollinators	Summerred	7.2 ± 2.0	1.7 ± 0.3
Supplementary pollination	Aroma	66.3 ± 1.0	13.4 ± 0.7
Supplementary pollination	Discovery	83.0 ± 0.7	11.7 ± 0.8
Supplementary pollination	Summerred	49.3 ± 0.9	11.4 ± 0.6
Open pollination	Aroma	49.6 ± 1.3	9.7 ± 0.6
Open pollination	Discovery	73.0 ± 0.9	10.9 ± 0.8
Open pollination	Summerred	46.6 ± 1.0	11.0 ± 0.6

Appendix D. – Pollination and production between locations



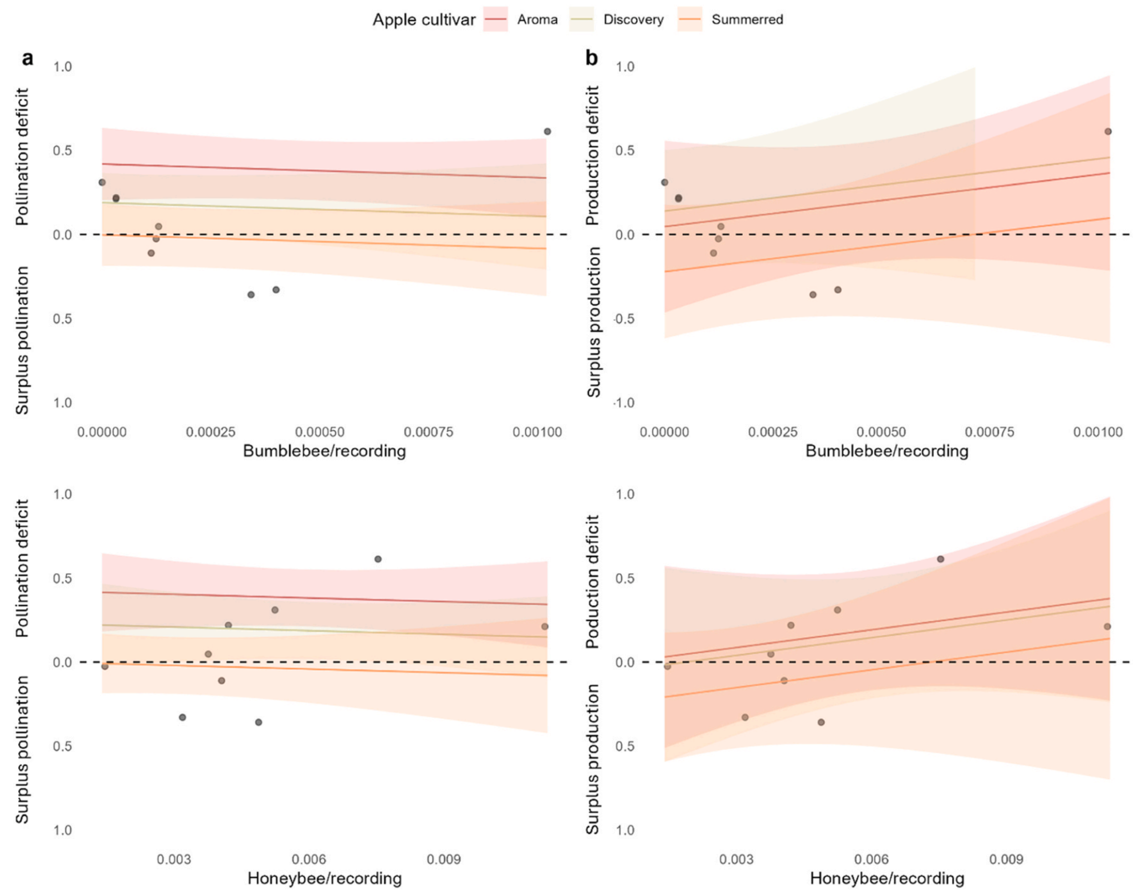
Comparing pollination deficit and surplus pollination between the six locations split by the apple cultivars (a) Aroma, (b) Discovery and (c) Summerred, over two years, 2022 (light blue) and 2023 (dark blue). Eastern orchards are marked with a circle and Western orchards are marked with a triangle. Pollination is measured as seed set per treatment branch, comparing open pollinated apples with supplementally pollinated apples. Points show the average deficit per orchard per year with lines representing the 95 % confidence interval. X axis is arranged from location with lowest mean deficit (both years combined) to highest mean deficit.



Comparing production deficit and surplus production between the six locations split by the apple cultivars (a) Aroma, (b) Discovery and (c) Summerred, over two years, 2022 (light blue) and 2023 (dark blue). Eastern orchards are marked with a circle and Western orchards are marked with a triangle. Production is measured as fruitset × weight per treatment branch, comparing open pollinated apples with supplementally pollinated apples. Points show the average deficit per orchard per year with lines representing the 95 % confidence interval. X axis is arranged from location with lowest mean deficit (both years combined) to highest mean deficit.

Appendix E. – Bumblebees and honeybees' effect on pollination and production deficit

Bumblebees and honeybees did not significantly decrease pollination deficit (increase seed set) or production deficit (increase fruit set and fruit weight).



Pollinator visits from camera recordings for bumblebees and honeybees and their relation to (a) pollination, and (b) production. Pollination is measured as seed set per treatment branch, comparing open pollinated apples with supplementally pollinated apples, and production is measured as fruitset × weight per treatment branch, comparing open pollinated apples with supplementally pollinated apples. The points show the raw data while the line is the model prediction with confidence intervals. Colours indicate the three different apple cultivars: Aroma (red), Discovery (green) and Summerred (orange).

Data availability

I have shared the link to my data in the paper, both under Material and Methods, and under "Data availability" before acknowledgement

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