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POLLINATION SUCCESS IN APPLES IS DEPENDENT UPON WILD BEES AND ORCHARD DESIGN

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Abstract—Insect pollinators are important drivers of fruit quality and yield in horticultural systems. The global reduction in wild bee populations has increased the demand for managed honeybees, despite honeybees relatively low pollination efficiency. Here, we assessed how bee communities, bee behaviour, and orchard design in Norwegian apple orchards affects apple pollination success, an important determinant of apple quality. We placed pan and vane traps in 18 apple orchards, in six distinct locations, within the two main apple growing regions in Norway. We also tracked individual bees (honeybees, bumblebees, and solitary bees) throughout the apple flowering season, and recorded their flower handling time, number of flower visits, stigma contact, and movement between apple flowers. Finally, we calculated the seed set rate (ovules developed into seeds / total number of ovules) from 908 harvested apples to estimate pollination success. Our key finding is that pollination success was driven by the abundance of wild bees and overall orchard planting design. We found lower pollination success in block design orchards where a single cultivar is planted continuously over a large area, compared to orchards with an integrated design where compatible cultivars are planted within the orchard. We also found that stigma contact decreased as apple flowering progressed, and that solitary bees visited fewer flowers per foraging event but were potentially more thorough foragers. Our results highlight the importance of promoting wild bees in apple orchards while also ensuring there is compatible pollen in the orchards for optimal pollination.

Keywords—Seed set, solitary bees, behaviour, pollen limitation, fruit production, bumblebees

INTRODUCTION

Agricultural intensification and human-induced land use change has resulted in a global decline of wild pollinating bees, with consequences for pollinator dependent food crops (Potts et al. 2010; Garratt et al. 2021). Apples are the third most grown fruit crop worldwide (FAO 2023) and are dependent upon pollinators for increased quality and yield (Garratt et al. 2014). The loss of pollinators can lead to pollination and production deficits, resulting in reduced apple quality and quantity (Vassvik et al. 2025). This, in turn, has broader implications for food security and economic value (Klein et al. 2007; Lautenbach et al. 2012). As a consequence, there is increased demand for managed pollinators, such as honeybees, to ensure successful pollination (Santibañez et al. 2022). However, fruit set in apple orchards with managed honeybees is not significantly different from orchards without managed honeybees (Mallinger & Gratton 2015), therefore honeybees are unlikely to overcome the loss of wild pollinators (Russo et al. 2017). In contrast, pollination by wild bees increases fruit set and provides greater economic returns for apple growers than pollination by honeybees (Garratt et al. 2016). High species richness of bees increases the likelihood of effective species being present in the apple orchards, where different pollinators can have complementary traits, such as time of emergence, and foraging behaviours that enhance pollination services (Blitzer et al. 2016). In addition, a higher wild bee abundance increases flower visitation and results in more pollen deposited on the stigma (Park et al. 2016; Eeraerts et al. 2025).

Knowledge about the foraging behaviour of different pollinators is important when considering their pollination performance within an orchard (Pardo & Borges 2020). Bumblebees have been found to forage five times faster than solitary bees, enabling them to visit more apple flowers in a day (Campbell et al. 2017; Eeraerts et al. 2020b). However, solitary bees deposit more pollen to apple flowers due to their slow foraging behaviour, which allows them to have more frequent stigma contact (Roquer-Beni et al. 2022; Pirttiletho 2023). Honeybees are thought to have high flower constancy, but Roquer-Beni et al. (2022) and Pirttiletho (2023) found that honeybees have a lower pollen deposition per visit, making them less effective pollinators of apple compared to wild bees (Eeraerts et al. 2025). This may be because honeybees often collect either pollen or nectar when visiting apple flowers. When honeybees collect nectar, they tend to visit the flower from the side where they can reach the nectar but avoid stigma contact (Pardo & Borges 2020). Thus, stigma contact is thought to be the most important pollinator behaviour affecting pollination success (Roquer-Beni et al. 2022).

Effective pollinators also need to transport compatible pollen to the apple cultivar being pollinated (Kron et al. 2001b). Apple orchards in Norway either have a block design, with one cultivar planted over a larger area, or an integrated design, with rows of different cultivars planted close together (*pers. obs. L. Vassvik*). To ensure sufficient pollination, it is important to have two or more compatible cultivars present (Kron et al. 2001b). In block design orchards, pollinators have to travel relatively long distances to successfully pollinate flowers using a compatible pollen source. Flight distances as little as 10-30 meters between compatible apple cultivars can result in pollen limitation (Matsumoto et al. 2008; Carisio et al. 2020). The flight distance of bees is dependent upon species, colony size, and body size (Kendall et al. 2022). Solitary bees often travel between 150 to 600 meters, with smaller bees traveling shorter distances (Gathmann & Tscharntke 2002). Social bees on the other hand travel three times further than solitary bees, mainly because of increased resource competition between colony members close to the nest (Grüter & Hayes 2022). Within orchards, bees have been found to fly across four rows of trees on average, and bees that move across rows have a higher chance of collecting pollen from compatible cultivars than bees that fly within rows (Kron et al. 2001a). Therefore, an integrated orchard design where compatible cultivars are in adjacent rows greatly increases pollinator success, while block orchard designs limit the distribution of compatible pollen and result in reduced pollinator effectiveness (Kron et al. 2001a).

Pollination and production deficits resulting in reduced apple yield have been found in apple growing regions all over the world (Garratt et al. 2021; Olhnuud et al. 2022), including Norway (Vassvik et al. 2025). Studies have shown that increased wild bee richness has positive effects on apple quality (Blitzer et al. 2016; Sapir et al. 2017), and Vassvik et al. (2025) found that increased solitary bee activity can decrease both pollination and production deficits in Norwegian apple orchards, highlighting the importance of solitary bees as effective pollinators. Therefore, it is important to better understand the contributions of different pollinating bee groups, particularly in temperate regions, such as Norway, that experience large fluctuations in temperature and precipitation during the short period of apple flowering (Karbassioon et al. 2023) and have varying orchard designs. Here, we sought to answer the following research questions: (i) what is the species richness and abundance of bees in Norwegian apple orchards, and does it vary among locations? (ii) how do bees behave when they pollinate apple flowers? and (iii) how does bee diversity (species richness and abundance) and the availability of compatible pollen within an orchard affect pollination success?

MATERIALS AND METHODS

STUDY LOCATION AND DESIGN

This study was conducted in 2023 in 18 orchards, in six locations (Berle, Høyen, Sando, Lofthus, Urheim and Djønno), across two of the main apple-growing regions in Norway: Svelvik, in the east, and Ullensvang, in the west (Fig. 1). In Svelvik (Berle, Høyen, and Sando), the terrain is flat, going from the sea to the orchards and then coniferous forest. In Ullensvang (Lofthus, Urheim, and Djønno), the surrounding landscape is a steep terrain from the sea to the mountains with orchards restricted to the lowest elevation close to the sea, and a belt of deciduous and planted coniferous forest above the orchards. Each location consisted of three closely associated orchards of cultivars Summerred, Discovery, and Aroma. The flowering season in Norway starts in mid-May and lasts until the end of May/early June. Summerred is the first cultivar in our study to flower, closely followed by Discovery, and then Aroma. Within one region the locations are separated by at least 4 km, to prevent overlap in their pollinator communities (Zurbuchen et al. 2010). All locations, except Djønno, also have honeybee hives either inside the orchard or in close proximity. In 2023, however, there was a shortage of honeybee hives in Lofthus, and fewer hives were used than normal (*pers. comm. BA Hatteland*).

All orchards were conventionally managed but varied in size (from 430 m^2 to 28 000 m^2). Eleven orchards had rows of different cultivars within the same orchard (integrated design), while seven orchards were dominated by one cultivar (block design), sometimes with polliniser trees planted within.

In early May, before apple flowering, one branch on ten different trees in every orchard was randomly selected and marked. Apples were later harvested from these branches between mid-

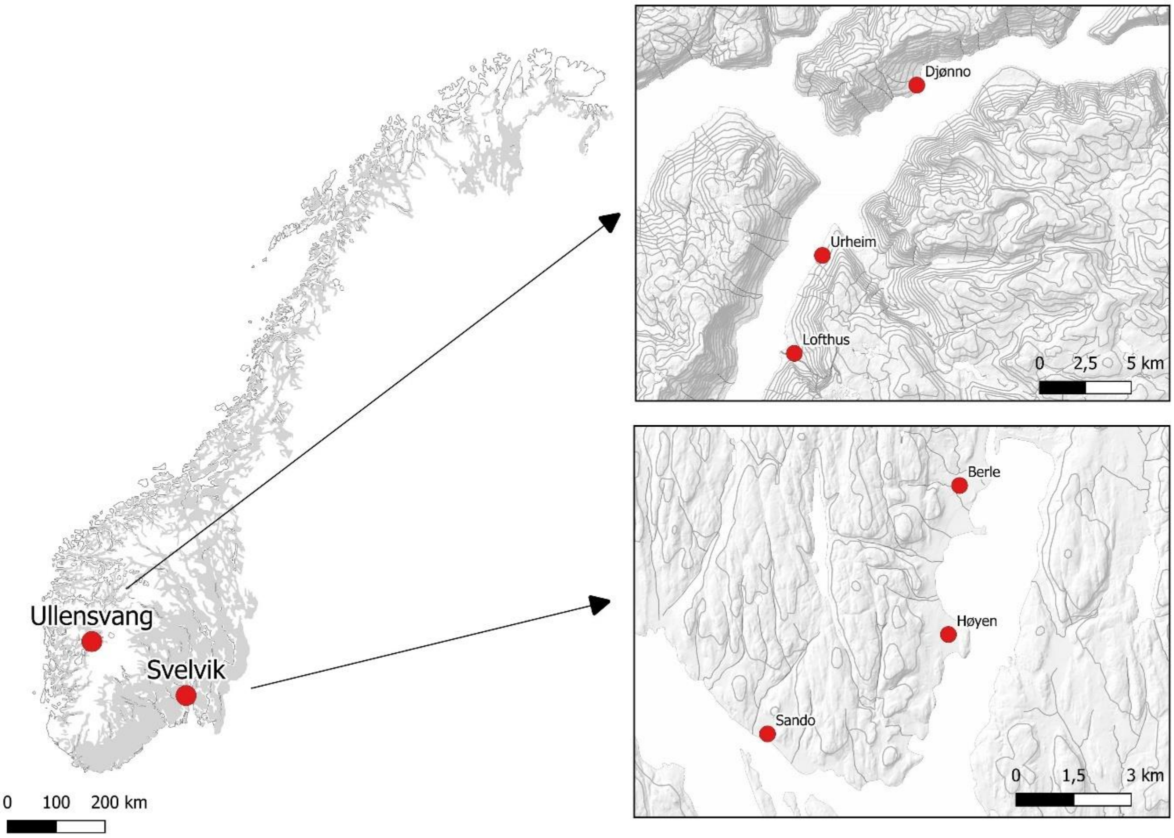

Figure 1. Map of Norway with the three locations in Ullensvang (west): Djønno, Urheim, and Lofthus, and the three locations in Svelvik (east): Berle, Høyen, and Sando. All locations have three orchards, one per cultivar (Summerred, Discovery, and Aroma).

August and late-September depending on the cultivar and region. To estimate the effect tree position within an orchard has on pollination success, five trees were selected close to the edge, and five trees closer to the centre of the orchard. However, in some cases this was not possible: two orchards had trees with frost damage at the edge, while four orchards were very small or narrow, with most trees located close to an edge. In total, from all 180 trees, 86 trees were located near the edge of the orchard, and 94 trees were located close to the centre of the orchard (Appendix A).

INSECT TRAPS AND TAXONOMIC IDENTIFICATION

Bees were collected from 36 sets of traps in all 18 orchards using pan trap triplets and vane traps. Two different types of traps were used since previous studies have stressed the importance of combining methods due to trapping biases (Bell et al. 2023; Graham et al. 2023). Each pan trap triplet consisted of a blue, yellow, and white bowl, whereas all vane traps had a blue top and a yellow collector (Appendix B). A pan trap triplet and a vane trap were placed together as different colours and trap types collect different species of bees (Joshi et al. 2015; Acharya et al. 2022). Pan traps were placed 0.5 m above the ground and vane traps were hung between 0.5 – 1.5 m above the ground. One set of traps was placed inside the orchard, and one set of traps was placed at the edge of the orchard. Depending on the landscape, the edge of the orchard was either a forest, a road, agricultural field, or apple trees of a different cultivar (Appendix A). All traps were filled with water and clear, scentless, soap to break the surface tension. Traps were in the orchards continuously during apple flowering and emptied every three days. Abundance, the absolute abundance of all species caught in the traps, was used to compare bee abundance among all six locations.

All bees collected from the traps were placed in plastic bags, sorted by trap type, colour, and collection date, and stored in a -18 °C freezer until identification. Bees were morphologically identified to species, with some exceptions. *Bombus lucorum, Bombus terrestris, Bombus cryptarum, Bombus sporadicus* and *Bombus magnus* were grouped together as *Bombus sensu stricto* due to the difficulty of separating these morphologically (Murray et al. 2008). For the same reason, some species in the *Lasioglossum* genus were grouped together: *Lasioglossum calceatum* and *Lasioglossum albipes, Lasioglossum fulvicorne* and *Lasioglossum fratellum,* and *Lasioglossum morio* and *Lasioglossum leucopus*.

BEE BEHAVIOUR

Bee behaviour was recorded in all orchards during apple flowering using the android based mobile app BORIS (Behavioural Observation Research Interactive Software; Friard & Gamba 2016). BORIS is an open-source software that allows customisation for recording the specific behavioural traits of interest. Individual bees were tracked opportunistically within the apple orchards, tracking bees as they were encountered. Efforts were made to find bumblebees and solitary bees due to their lower abundance in the orchards compared to honeybees. We recorded the bees' handling time on the apple flowers, number of flower visits per individual bee, if the bee had stigma contact while foraging, and the bee's movement between flower visits. Bee movement was measured using three categories: 1. Flying to a new apple flower on the same tree, 2. Flying to an apple flower on a different tree in the same row or, 3. Flying to an apple flower on a tree in a new row or further. For the behavioural study, each bee was identified to one of three functional groups: honeybees, bumblebees, and solitary bees. Bees were identified into broader groups due to the difficulty of identifying species in the field. Behaviour recordings were conducted when there was little wind and no rain and ended if the bee stopped to groom for a long time, if we lost track of the bee, or if we had recorded the bee's activity for an extensive period (> 3 minutes). Following individual bees over long distances was not possible in our study orchards because the rows of apple trees constrained how far we are able to move. We were therefore not able to follow bees for their full foraging trip, and this might affect the data we were able to collect on movement between rows.

APPLE HARVEST AND POLLINATION SUCCESS (SEED SET RATE)

Up to ten apples were harvested from each pre-marked branch between mid-August and late September, just prior to commercial apple harvest. For branches that had more than ten apples, ten apples were randomly selected, except in the case where apples were attacked by the fungus *Monilia fructigena*; these apples were selectively removed.

Seeds from all harvested apples were counted in the lab and separated into three categories: fully developed seeds, partially developed seeds, and not developed seeds, to assess pollination success (seed set rate). Because partially developed seeds likely reflect poor or no pollination and are likely to be nonviable, partially developed seeds were classed as not developed seeds for the analysis.

STATISTICAL ANALYSIS

Statistical analyses were conducted using five generalised linear models (models 1-5 and 7), one generalised linear mixed effect model (model 8; Table 1) from the glmmTMB package (Brooks et al. 2017), and one multinomial model (model 6; Table 1) from the nnet package (Venables & Ripley 2002) in R version 4.4.1 (R Core Team 2024). Models vary depending on the nature and structure of the data. Overdispersion, model selection and model fit was assessed using the performance package (models 1-5 and 7-9; Lüdecke et al. 2021) or AIC (model 6). Emmeans package (Lenth 2024) was used for Post-hoc Tukey tests. A summary over the statistical models can be found in Table 1.

Models 1 and 2 – Research question 1

In these two models we assessed if species richness and abundance varied among locations. Species richness and abundance records for a particular trap type at an orchard (location + apple cultivar) on a particular date were pooled. Response variable is count data and a Poisson error distribution was used.

Models 3 to 6 – Research question 2

In these models we wanted to test if bee behaviour on apple flowers: flower handling time (s), number of flower visits, stigma contact across day of the year (days after January 1st; DOY), and bee movement, varied among the three groups of pollinating bees: honeybees, bumblebees and solitary bees. Flower handling time (s) was calculated per flower visit and log transformed. We counted number of flower visits for each individual bee. Proportion of stigma contact was analysed as proportion of visits with stigma contact and number of visits without stigma contact. Lastly, bee movement was analysed as proportion of movement among the three categories: 1. Moved to a new apple flower on the same tree, 2. Moved to a new apple flower on a new tree in the same row, 3. Moved to a new apple flower on a tree in a new row or flew further. All models had bee group as fixed effect. In model 5, both bee group and DOY was included because we wanted to test if stigma contact varied throughout apple flowering season. Interaction between bee group and DOY was not included because of high multicollinearity (Appendix E). Gaussian error distribution was added to model 3 because homoscedasticity was achieved after log transforming the response variable, models 4 had a negative binomial error distribution, model 5 had betabinomial error distribution due to overdispersion, and model 6 had no error distribution since to the response variable was categorical.

Models 7 and 8 – Research question 3

Two models were used to study the effects on pollination success of location (model 7) and of bee species richness and abundance, as well as the spatial arrangement of compatible pollen within apple orchards (model 8). Spatial arrangement included orchard structure and tree placement. Pollination success was estimated using seed set as the response variable, calculated as the number of ovules that developed into seeds (fully developed seeds) and the number of ovules that did not develop into seeds (partially developed seeds + not developed seeds). Fixed effects were location in model 7, and abundance of honeybees, wild bee species richness, wild bee abundance, orchard structure (block design or integrated design) and its interaction with tree placement (central in the orchard or at the edge of the orchard), and apple cultivar (to account for variations in cultivar) in model 8. Species richness and abundance records for all traps at an orchard (location + apple cultivar) were pooled to allow for comparison with pollination success (seed set rate). In model 8 we separated the trap collections between wild bees (bumblebees and solitary bees) and managed honeybees, because we wanted to assess the separate effect wild- and managed bees had on pollination success. Location was added as random effect for model 8. Interaction between species richness and wild bee abundance was not included because of high multicollinearity (Appendix E). For all models we used a betabinomial error distribution due to overdispersion.

Table 1. Structure of the eleven models used in the analysis, models response variable, fixed effects, random effects, their error distribution, and the research questions each model answer.

Model	Response variable	Fixed effect	Random effect	Error distribution	Research question
1	Species richness	Location	-	Poisson	1
2	Abundance	Location	-	Poisson	1
3	log(Flower handling time) (s)	Bee group	-	Gaussian	2
4	Number of flower visits	Bee group	-	Negative binomial	2
5	Stigma contact	Bee group + day of the year (DOY)	-	Betabinomial	2
6	Bee movement category	Bee group	-	-	2
7	Seed set	Location	Location/Tree	Betabinomial	3
8	Seed set	Species richness of wild bees + wild bee abundance + honeybee abundance + (Orchard structure * tree placement) + Apple cultivar	Location/Tree	Betabinomial	3

Information about statistical models and results comparing effects of trap colour (three colours of pan traps and vane traps) and trap placement (centre or edge of orchard) on species richness and abundance can be found in Appendix B.

Data and code are available on GitHub: https://github.com/linnvassvik/Applepollination_behavior

RESULTS

BEE SPECIES RICHNESS AND ABUNDANCE VARY AMONG LOCATIONS

In all orchards combined we collected 2331 bees, excluding non-pollinating bees (see: Hutchinson et al. 2021), representing 37 species (Appendix C). The most abundant genus was *Lasioglossum* (41.5%), followed by *Bombus* (37.9%), *Apis* (13.6%) and *Andrena* (6.2%), *Osmia*, *Halictus*, *Hylaeus* and *Hoplitis* (all < 1%; Fig. 2).

Species richness and abundance varied among locations (*P*-value < 0.001 for both). Djønno had a higher species richness and overall higher abundance compared to all other locations. Abundance at Urheim was higher than at Berle, Høyen, and Sando, and in addition, Lofthus had a higher abundance than Sando (model output and post-hoc tests in Appendix D).

BEE BEHAVIOUR

Behaviour was recorded for 489 individual bees, where 262 (54%) were honeybees, 181 (37%) were bumblebees, and 46 (9%) were solitary bees. Flower handling time varied among the three groups of bees (*P*-value < 0.001 for all; model output and post-hoc tests in Appendix D). Bumblebees had the shortest flower handling time, average of 3.2 ± 0.1 seconds, followed by honeybees, average of 6.6 ± 0.1 seconds, and solitary bees had the longest flower handling time, average of 11.7 ± 1.2 seconds (all numbers are mean ± SE; Fig. 3a). The number of flower visits recorded per foraging individual differed among all bee groups (*P*-value < 0.001 between bumblebees and honeybees, and bumblebees and solitary bees, and *P*-value = 0.001 between honeybees and solitary bees), and was on average 14.9 ± 1.1 for bumblebees, 8.0 ± 0.5 for honeybees, and 4.9 ± 0.9 for solitary bees (Fig. 3b). Stigma contact varied across day of the year (DOY; *P*-value = 0.016), and was higher earlier in the flowering season, compared to later (Fig. 3c). Honeybees also had lower stigma contact compared to bumblebees (*P*-value < 0.001), but no difference in stigma contact was found between bumblebees and solitary bees, and solitary bees and honeybees. All groups of bees moved most frequently between flowers on the same tree, followed by new tree, and least often to a new row or further (Table 2). No difference in

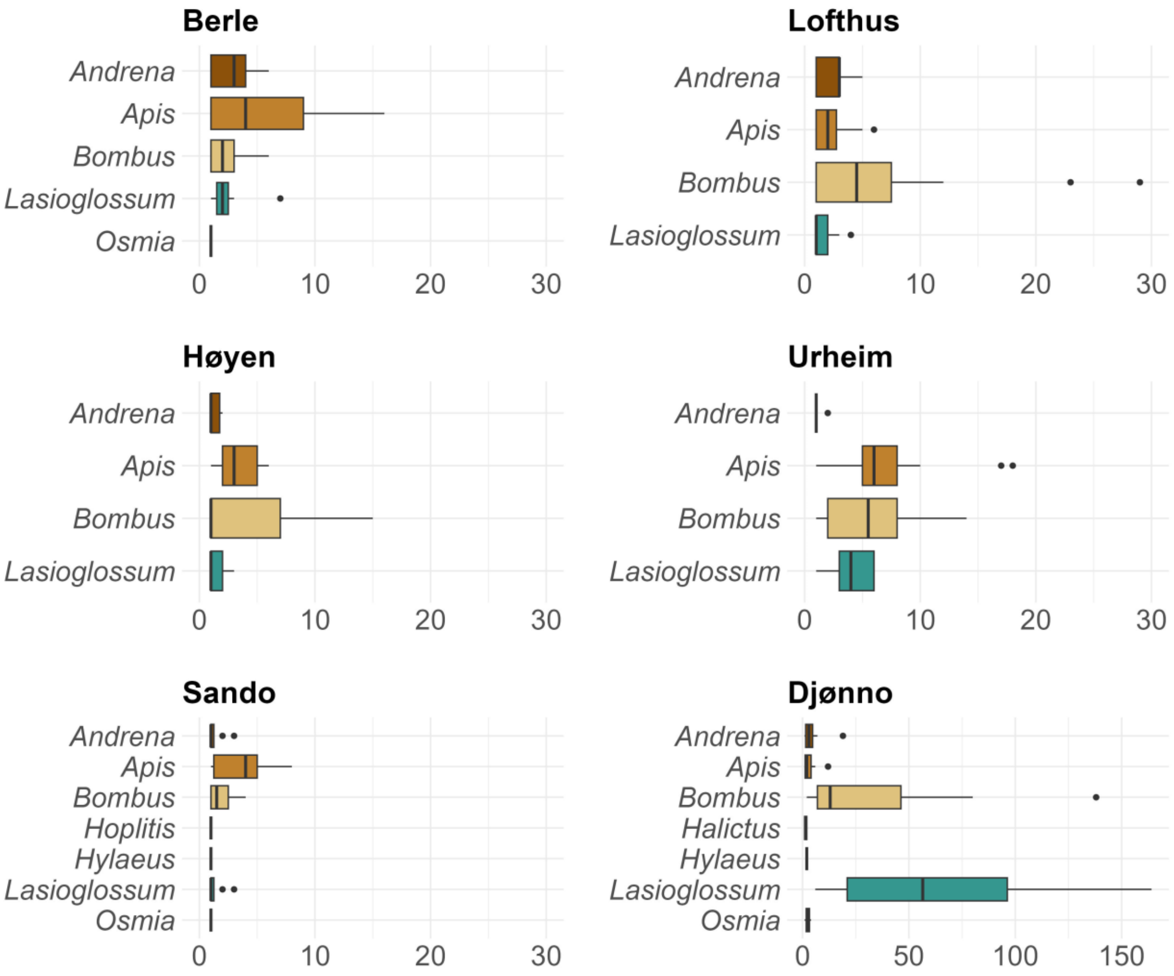

Figure 2. Bee genera and total number of individuals caught in pan- and vane traps per sampling (every three days during apple flowering) in six different locations: Berle, Høyen, Sando, Lofthus, Urheim, and Djønno. Locations in Svelvik (east) on the left, and Ullensvang (west) on the right. Number of individuals on x-axis are the same for all locations except Djønno. Each bar is colour coded by genus. Box width is the interquartile range, line is the median, and whiskers are the range of data excluding outliers (marked with dots).

Table 2: Percentage bee movement (mean ± SE) within each bee group (bumblebee, honeybee and solitary bee) among three movement categories: visits to a new flower on the same tree, to a new flower on a new tree within the same row, or to a new flower on a tree in a new row/further away. Significance (P-value < 0.05) is indicated in bold.

Bee group	New flower same tree (mean ± SE)	New tree (mean ± SE)	New row/further (mean ± SE)
Bumblebee	89.2 ± 0.6 %	8.2 ± 0.5 %	2.6 ± 0.3 %
Honeybee	86.6 ± 0.8 %	9.8 ± 0.7 %	3.6 ± 0.4 %
Solitary bee	90.4 ± 2.2 %	5.7 ± 1.7 %	4.0 ± 1.5 %

movement within each category was found among honeybees, bumblebees and solitary bees (Fig. 3d; model output and post-hoc tests for all behaviour results in Appendix D).

POLLINATORS AND POLLEN AVAILABILITY IN RELATION TO POLLINATION SUCCESS (SEED SET RATE)

Pollination success varied among locations (*P*-value = 0.001; model output and post-hoc tests in Appendix D). Sando had higher pollination success compared to Høyen and Djønno. Berle had

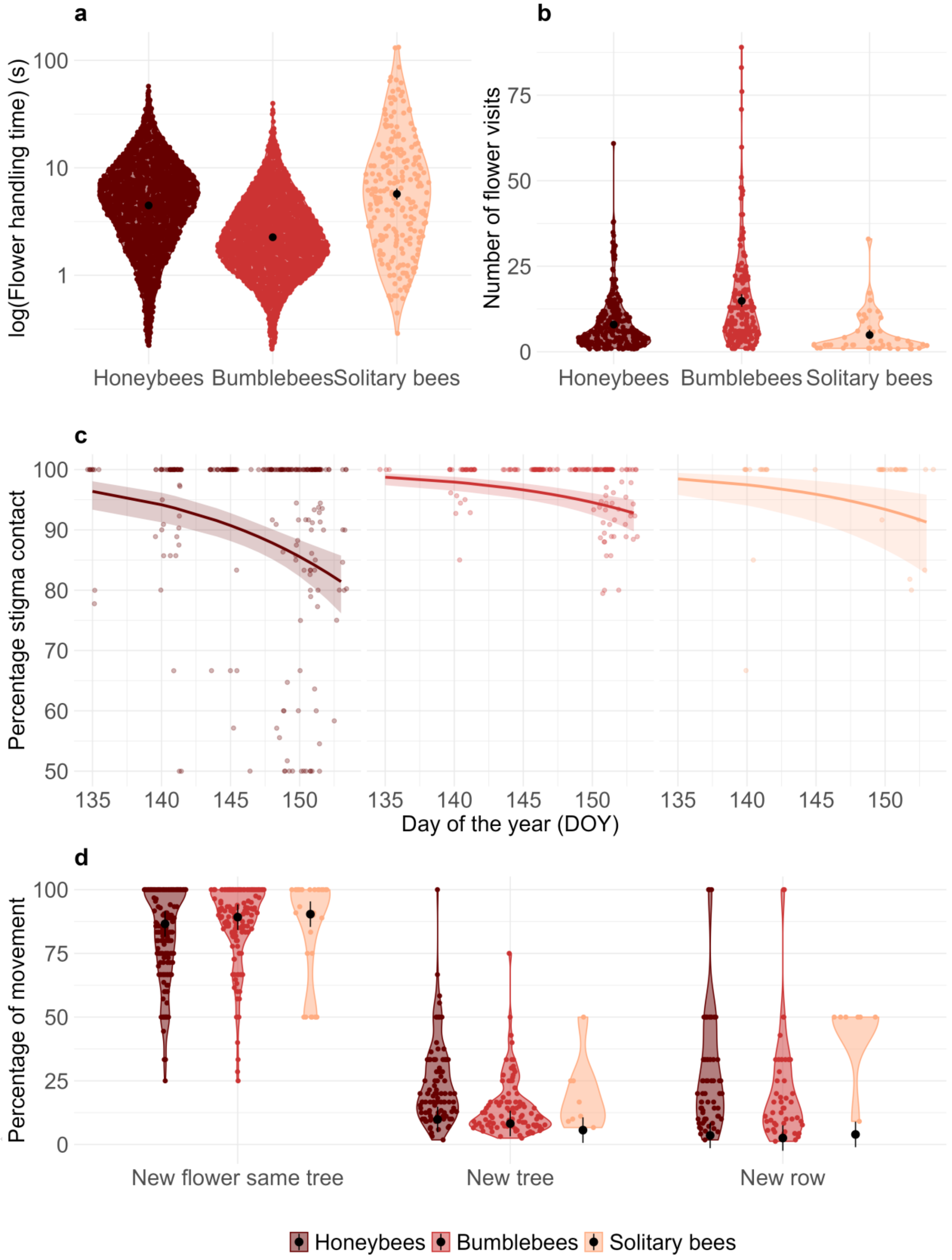

Figure 3. Bee behaviour for the three groups: Honeybees, bumblebees, and solitary bees, with (a) flower handling time (s) per flower visit, (b) number of flower visits per individual bee, (c) percentage of visits with stigma contact per observed foraging event across day of the year (DOY) during apple flowering, and (d) proportion of bee movement among each observed foraging event split into three categories: New flower on the same tree, new tree, or new row/further. Mean predicted value and confidence interval is shown in black. Raw data are shown with dots. Colours indicate the different groups of bees: honeybee (dark red), bumblebee (red), and solitary bee (orange).

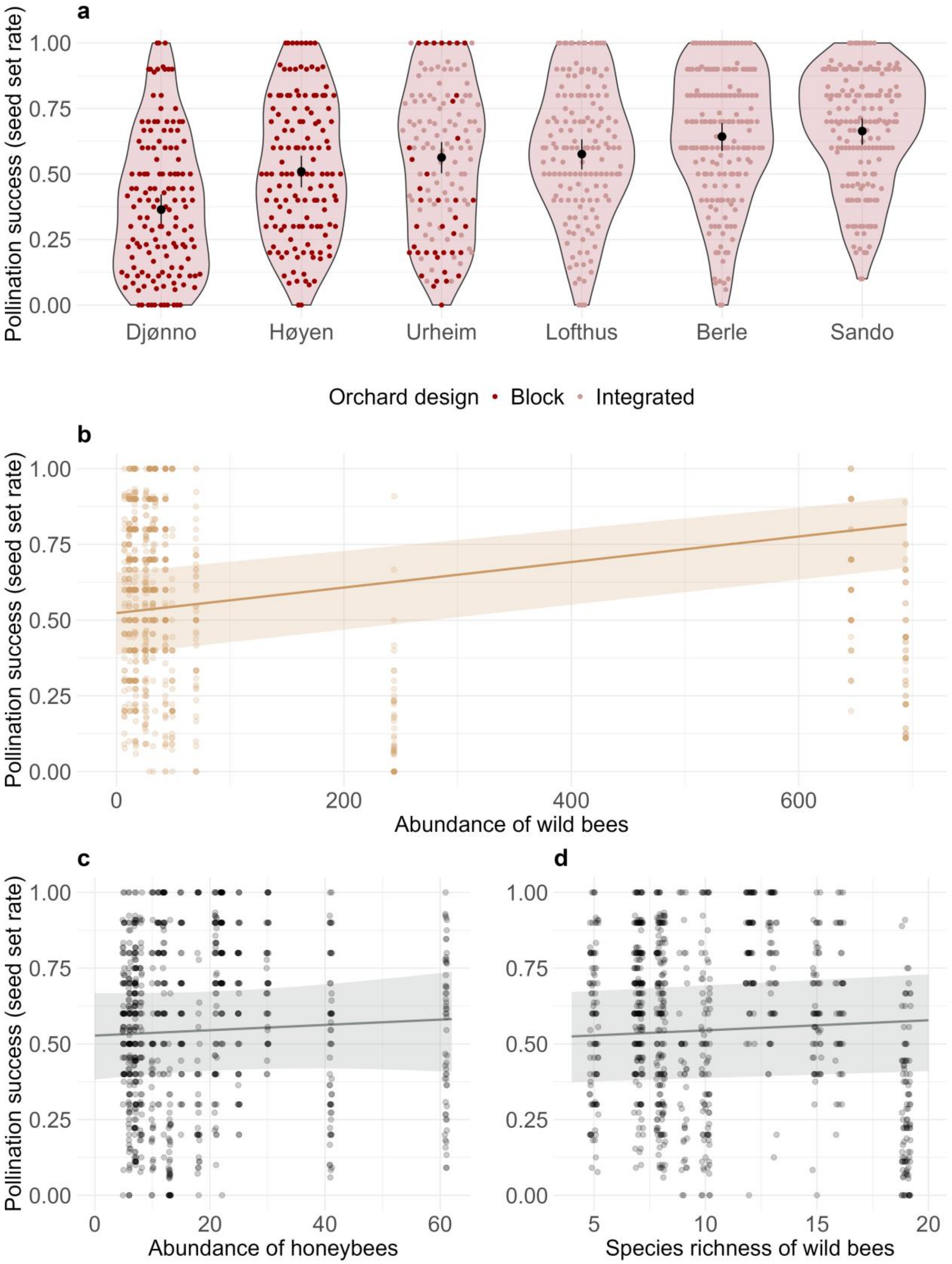

Figure 4: (a) Violin plot showing pollination success (seed set rate) per location: Djønno, Høyen, Urheim, Lofthus, Berle, and Sando. Each dot represents one apple, with predicted mean pollination success (seed set rate) and confidence interval shown with a black dot. Width of violin plot represents the density of the data at the different values. Pollination success (seed set rate) for (b) wild bee abundance, (c) honeybee abundance, and (d) species richness of wild bees. Line represents predicted mean and confidence interval. Pollination success (seed set rate) is calculated as number of developed seeds/(number of developed seeds + number of not developed seeds). Colour in plot b-d indicate if results are significant (yellow) or not significant (grey).

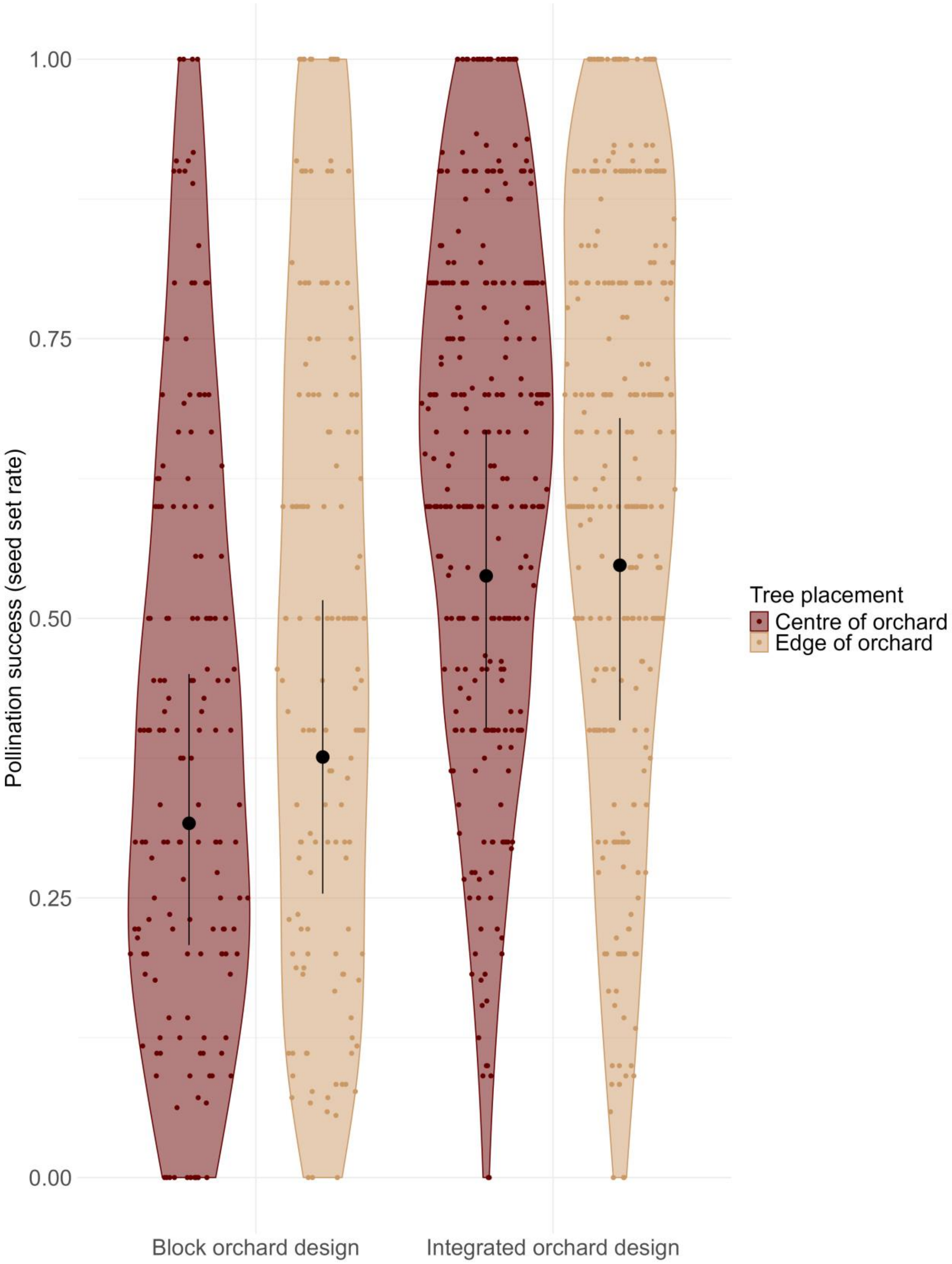

Figure 5: Violin plot showing pollination success (seed set rate) per orchard design: block or integrated, and tree placement: centre of the orchard or edge of the orchard. Each dot represents one apple, with predicted mean pollination success (seed set rate) and confidence interval shown with a black dot. Width of violin plot represents the density of the data at the different values. Colours indicate the two different tree placements, centre of the orchard (dark red) and edge of the orchard (light brown).

higher pollination success compared to Høyen and Djønno. Lofthus had higher pollination success compared to Djønno. Urheim had higher pollination success compared to Djønno. Høyen had higher pollination success compared to Djønno (Fig. 4a).

Pollination success was dependent upon abundance of wild bees (Fig. 4b; P-value < 0.001; model output in Appendix D). Pollination success was not dependent upon abundance of honeybees (Fig. 4c; P-value = 0.528) or species richness of wild bees (P-value = 0.554; Fig. 4d).

The individual effects of orchard design and tree placement affected pollination success. In orchards with block design, pollination success was lower compared to integrated design (P-value < 0.001), and trees in the centre of the orchard had lower pollination success compared to the edge of the orchard (P-value = 0.043). The interaction between orchard design and tree placement was not significant (P-value = 0.179; Fig. 5). In addition, pollination success varied between apple cultivars (model output in Appendix D).

DISCUSSION

We found that the effects of bee species richness, abundance, and behaviour on apple pollination success (seed set rate) are complex and context dependent. For example, we found that a higher abundance of wild bees increased pollination success, while increased abundance of honeybees had no effect. In addition, we found that when multiple cultivars are planted within an orchard pollination success is higher, likely because the bees in our study sites did not fly far between flowers. Therefore, effective pollen transfer depends not only on the abundance of wild bees and bee behaviour, but also on the spatial proximity of compatible apple cultivars. These findings highlight the importance of managing for increased bee diversity through increased floral and nesting resources, but also optimising orchard design, to ensure cross-pollination.

BEE SPECIES RICHNESS AND ABUNDANCE VARY AMONG LOCATIONS

Across all orchards, we collected a total of 37 different species of bees. We found large overlap in genera with what has been previously found in apple orchards across Europe, such as *Andrena* spp., *Bombus* spp., *Lasioglossum* spp., and *Osmia* spp. (Hutchinson et al. 2021; Leclercq et al. 2023). We also found a high degree of variation in species richness among locations in our study (Appendix B), which may be explained by factors operating at the landscape scale outside the orchards.

We found that the four trap types (vane trap and three colours of pan traps) collected both an overlap in species, but also unique species. This highlights the importance of combining trapping methods when studying bee species richness and abundance in apple orchards (Joshi et al. 2015), since different trap types attract and trap bees at different rates (Graham et al. 2023). We also found that abundance varied depending on trap placement, with a higher abundance caught at the edge of the orchard compared to the centre. This is likely because the edge of orchards offer more suitable habitat for bees and foraging distances may be limited by the abundance of flowers during apple bloom. It is important to note that the abundance of bees caught in our traps might not reflect the actual abundance of the bees in the orchard, and that some bees caught in the traps may not contribute to pollination services (Hutchinson et al. 2021). Bee abundance in our traps may be influenced by sampling biases, but since all traps were out at the same time within the same study system, differences in abundance among apple orchards are comparable (O'Connor et al. 2019).

BEE BEHAVIOUR VARIES AMONG DIFFERENT GROUPS OF BEES IN APPLE ORCHARDS

Flower handling time and number of flower visits varied among bee groups, with bumblebees spending the shortest time per flower and therefore the greatest number of flowers visited per observation. Similar results have also been found in other studies (Martins et al. 2015; Campbell et al. 2017). On the other hand, we found that solitary bees spent the longest time foraging, which could increase their likelihood to come in contact with the stigma multiple times, and potentially explain why other studies find solitary bees to have higher rates of pollen deposition, compared to bumblebees and honeybees (Roquer-Beni et al. 2022). Honeybees had less stigma contact than bumblebees, which could be because bumblebees are large and hairy, which increases stigma contact (Földesi et al. 2021). We did however find that stigma contact decreased as apple flowering progresses for all three groups of bees. This may be because social bees tend to collect pollen early in the season to feed the larva and nectar later to feed the workers (Pereboom 2000; Stabler et al. 2015). Mateos-Fierro et al. (2022) showed that when bees only forage for nectar they often miss contact with the stigma compared to when foraging both nectar and pollen.

Aroma is the last cultivar in our study to flower and Vassvik et al. (2025) found Aroma had higher pollination deficits compared to Discovery and Summerred in Norwegian apple orchards. Lower stigma contact later in the season could therefore be related to Aroma being less preferred for pollen collection by honeybees and bumblebees. Variation in pollen and nectar collecting behaviour can vary dramatically among apple cultivars. Vicens & Bosch (2000) found that only 3 % of visiting honeybees collected pollen from `Red Delicious' apples, while 55 % collected pollen from other cultivars. Therefore, cultivar specific traits that drive pollinator behaviours should be further studied to better understand the relationship between flower attractiveness and pollination success.

All three groups of bees in our study mainly flew between flowers on the same tree or moved to a neighbouring tree and continued foraging on flowers. This is in line with optimal foraging theory, where densely blooming apple trees offer high reward, and bees do not need to fly far between visits to maximise their foraging efficiency (Pyke 1984). However, higher abundance and diversity of bees have been found to increase movement in orchards because of increased resource competition (Sapir et al. 2017; Eeraerts et al. 2020a), and bees that move across rows have a higher chance of depositing compatible pollen, increasing pollination success (Kron et al. 2001a). Therefore, managing for greater bee diversity and abundance could increase cross-pollination in apple orchards.

WILD BEES AND THE AVAILABILITY OF POLLEN IS IMPORTANT FOR POLLINATION SUCCESS OF APPLE

In our study, higher abundance of wild bees increased pollination success, but higher species richness of wild bees had no effect on pollination success. Pollination success is dependent on the amount of compatible pollen that is transferred to the stigma, which is a function of pollinator morphology and behaviour (Roquer-Beni et al. 2022), as well as pollen availability. Many different species of wild bees are capable of pollinating apple flowers, largely because of a high degree of similarity in ecological and behavioural traits (Leclercq et al. 2023); this could explain why species richness was not significant in our study. High diversity of bees is however important because it can buffer year-to-year variations in pollinator communities, which will increase resilience of pollination services over time (Senapathi et al. 2021)

Interestingly, we found no effect of increased abundance of honeybees on pollination success. In a recent review by Eeraerts et al. (2025) honeybees were found to have low relative pollination contribution, despite being the most abundant flower visitor. In the UK, solitary bees and bumblebees together contribute nearly three times more to the economic value of apple pollination (£70.0M) than honeybees (£21.4M; Garratt et al. 2016), underscoring the importance of wild bees in pollinator-dependent crops.

Pollination success in our study was also highly dependent on the structure of the orchards. Integrated design orchards, where multiple compatible cultivars are planted close together, had higher pollination success compared to a block design orchard, where cultivars are planted separately and often with large distances in between. In addition, we found that pollination success was higher for individual trees located near the edge of the orchard compared to trees located near the centre of the orchard. The direct effect orchard design and tree placement has on pollination success has, to our knowledge, not been studied empirically before (but see: Hung et al. 2023; Chabert et al. 2024), and brings important knowledge to the design of orchards. Lower pollination success in block design orchards is most likely because of the large distances bees must cross between compatible cultivars (Matsumoto et al. 2008; Carisio et al. 2020). Kron et al. (2001a) suggest that one cultivar should only be planted across a maximum of three successive rows or include polliniser trees positioned for every three fruit bearing trees. Norwegian apple growers often use polliniser trees, however some of our study orchards did not contain polliniser trees, while in others, polliniser trees were infrequent or did not co-flower with the commercial cultivar (*pers obs. L. Vassvik*). Our results suggest that orchard design may be just as important as managing for increased wild bee abundance to increase pollination success of apple.

Planting more compatible apple cultivars or polliniser trees in the orchards might not be possible as an immediate solution but could be done over multiple years as trees are replaced. However, increasing wild bee species richness and abundance could be implemented immediately. For example, since apple flowers only provide bees with resources for a limited period, additional floral resources could be added to increase bumblebee and solitary bee abundance across the season and avoid a temporal mismatch in floral resource supply and bee abundance (Wright et al. 2015; Bishop et al. 2024).

Overall, apple growers need to balance managing orchards for efficient harvesting of apples (block design orchards) and supporting pollination services to increase overall productivity (integrated design). This is a challenge that extends to other self-incompatible crops in the face of ongoing pollinator decline (Potts et al. 2010). For apples, establishing flower rich habitats by reducing intensive mowing in and around orchards could provide the floral resources necessary to support more diverse pollinator communities (Saunders et al. 2013; Campbell et al. 2017). Future research efforts should focus on better understanding how wild bee populations respond to increased floral resources in orchards, and the subsequent effects on apple productivity.

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AUTHOR CONTRIBUTION

Concept and design: LV, ETA, AN, MPDG, BAH & JDC. Data collection: LV, SMMH & JJ. Data analysis: LV, ETA, AN, MPDG & JDC. Writing - original draft preparation: LV. Writing – review, editing, and approval for publication: LV, ETA, AN, MPDG, BAH, JDC, SMHH & JJ.

DISCLOSURE STATEMENT

Authors have no competing financial or personal relationships to declare.

GENERATIVE AI DISCLOSURE STATEMENT

The authors declare that no generative AI tools were used in the writing, analysis, or preparation of this manuscript.

DATA AVAILABILITY STATEMENT

Data and code are available at GitHub: https://github.com/linnvassvik/Applepollination_behavior

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix A. Orchard design and tree placement.

Appendix B. Statistical analysis and results from data collected from pan- and vane traps.

Appendix C. Bee species richness, abundance and diversity indices.

Appendix D. Model output and post-hoc Tukey tests.

Appendix E. Multicollinearity analysis.

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