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Nocturnal Pollination Services in Agroecosystems: A Case Study Examining Apple Horticulture in Norway

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Abstract

The role of day active pollinators in agroecosystems has been broadly studied over the last 50 years. However, much less is known about the contributions of night active pollinators to overall agricultural and horticultural production yields. Apples are the most grown fruit crop in Norway, accounting for over 80% of total fruit production by weight. Insect pollination services greatly enhance both apple quantity and quality and are therefore crucially important for high yields of profitable fruit.

I explored how nocturnal insect pollinators contribute to apple production in Norway on two commercial apple farms in eastern Norway during the flowering season of 2023. Light traps were used to assess the diversity of the night-active insect pollinator community and apple flower-visiting insects were recorded by field cameras within orchards. In addition, a pollinator exclusion experiment was implemented to compare the independent contributions of nocturnal and diurnal pollinators to apple quantity (fruit set) and quality (seed set).

I found that the nocturnal pollinator community within my sites was limited both in terms of species richness and abundance. Only sixteen moths were captured in the light traps during the flowering season and the absence of moths in the camera images implies that they are most likely not important pollinators for apples in these sites. The moth community in my study area may have been affected by site-specific conditions such as light pollution, agricultural intensification, or pesticides.

Lacewings (Neuroptera) were frequently observed visiting apple flowers during the night and may be contributing to nocturnal pollination services. However, little is known about the role of lacewings in apple pollination and future studies should aim to test this insect group as potential providers of pollination services at night.

Nocturnal pollinators do not appear to play a substantial role in apple pollination in Eastern Norway, likely because of the limited nocturnal pollinator community present in the study area. However, exclusion of night active insects did result in pollination deficits (lower seed set), which suggests that nocturnal pollinators do have positive effects on apple production. Further research across various geographical regions is needed to increase our understanding of the contribution of nocturnal pollinators to agricultural and horticultural systems.

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1. Introduction

Insects represent more than half of the world's biological diversity and are found in most habitats on Earth (Baillie et al., 2012; Gullan et al., 2014). However, during the last forty years, there has been a rapid decline of insects worldwide (Gaston & Fuller, 2007; Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019; van Klink et al., 2020; Wagner, 2020). In two-thirds of monitored populations assessed by IUCN (*Internation Union for Conservations of Nature*), the mean arthropod abundance (invertebrates, including insects) decreased by 45% (Dirzo et al., 2014). Furthermore, the results from a long-term study of flying insects in a German protected reserve, revealed that the total biomass was reduced by more than 75% during the 27 years of the study (Hallmann et al., 2017). One of the main drivers of the global insect decline is human induced land-use change, including urbanization and industrialized agriculture (Raven & Wagner, 2021; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020). As a consequence, the current insect biomass loss of 2.5% per year puts more than 40% of the world's insect species at risk of extinction in the coming decades (Sánchez-Bayo & Wyckhuys, 2019).

Similar decline trends have been reported for insect pollinators as a functional group (Potts et al., 2010; van der Sluijs & Vaage, 2016). Pollinators consume nectar and collect pollen for consumption. In doing so, pollinators also transport pollen grains from one flowering plant to another, which facilitates plant reproduction, increases outbreeding rates, and lead to species diversification (Potts et al., 2016; Wardhaugh, 2015). Most plants (87.5%) rely on pollinators for reproduction (Ollerton et al., 2011) and the most prominent groups/orders of pollinating insects are beetles (Coleoptera), flies (Diptera), moths and butterflies (Lepidoptera), and ants, wasps, and bees (Hymenoptera) (Wardhaugh, 2015). Among the taxa showing the highest rates of decline are the pollinating bees within the superfamily: Apoidea (Biesmeijer et al., 2006; Burkle et al., 2013; Kearns et al., 1998; Ollerton et al., 2014; Potts et al., 2010; Zattara & Aizen, 2021), where one in six species have already become regionally extinct (Sánchez-Bayo & Wyckhuys, 2019). Moths have also declined (Bell et al., 2020; Conrad et al., 2006; Fox, 2013; Fox et al., 2014; Franzén & Johannesson, 2007; Hallmann et al., 2020), with half of the Lepidopteran (including butterflies) species experiencing higher decline rates than the estimated annual average for all insects (Sánchez-Bayo & Wyckhuys, 2019). Pollinators and the services they provide, are under the same main threats as insects in general (Balmaki et al., 2024; Brown & Paxton, 2009; Potts et al., 2010; Vanbergen & Initiative, 2013), but the rapid expansion of agricultural land dominated by monocultural crops has resulted in lower pollinator diversity and reduced pollination (Aizen et al., 2022; Aizen et al., 2019). Furthermore, pollinators are vulnerable to the use of pesticides (Desneux et al., 2007; Gill et al., 2012), and specifically for moths, light pollution (artificial night lighting) has been identified as one of the potential drivers of their decline (Macgregor et al., 2015; Macgregor et al., 2017; van Langevelde et al., 2018).

Pollination is not only a vital ecosystem function, but also represents an important component of global food production, and thus is an ecosystem service that directly benefits humans (Potts et al., 2016). According to Klein *et al.* (2007), about 75% of the world's leading foods crops show increased production of fruit and/or seed set in the presence of pollinators (Klein et al., 2007). The total economic value of pollination services worldwide was estimated to be €153 billion in 2005, and pollinator dependent crops had an economic value that was more than five times higher than crops that did not depend on pollinators (Gallai et al., 2009). Pollinating bees (Apidae), both wild and managed, are considered the be the most important contributors to global food crop production (Aizen et al., 2009; Kearns et al., 1998; Khalifa et al., 2021; Klein et al., 2007; Potts et al., 2010). Managed honey bees, such as the Western honey bee (*Apis mellifera*), are used to ensure adequate crop pollination and to compensate for shortages of wild bees (Klein et al., 2007; Kremen et al., 2002). Although honey bees are both easily managed and a suitable economical option to ensure crop pollination (Klein et al., 2007), they should be used as a supplement, not a substitute for wild pollinators, because wild pollinators are more efficient pollinators and can increase fruit set twice as much as managed honey bees (Garibaldi et al., 2013). Honey bees are also eusocial and live in close colonies, making them vulnerable to diseases and pathogens in heavily managed conditions (e.g. parasitic mite or fungi attack) (Neov et al., 2019; Sammataro et al., 2000), thus making them less reliable than robust communities of native pollinators.

In addition to important environmental and economic consequences, pollinator decline can have serious implications for global food security (Potts et al., 2010; van der Sluijs & Vaage, 2016; Vanbergen & Initiative, 2013). The ongoing decline of wild bees coupled with the inherent limitations of managed honey bees, suggests that reliance on bees alone may not ensure optimal pollination. Non-bee insect pollinators (e.g. Lepidoptera) can be significant providers of pollination services in agricultural systems and may improve stability and resilience in agricultural pollination networks (Rader et al., 2016).

To date, most research on insect pollination has primarily been focused on day active (diurnal) pollinators, with an emphasis on bees. However, the global decline of pollinators has increased attention on less studied pollinator groups, such as those that forage at night (Macgregor & Scott-Brown, 2020). Insect activity is generally higher at night compared to day (Wong & Didham, 2024) and the most common night active (nocturnal) pollinators include beetles, bees (only in the tropics), flies and moths (Hahn & Bruhl, 2016; Hopkins et al., 2000; Knop et al., 2018; Macgregor & Scott-Brown, 2020). Although rarely mentioned, some lacewings (within the order Neuroptera) that feed on floral resources (Wardhaugh, 2015), have also been observed visiting flowers at night (Robertson et al., 2021a).

The majority of research focused on nocturnal pollination has been focused on moths. In a literature review examining interactions between moths and plants, Macgregor *et al.* (2015) identified 168 studies published between 1971 and 2013 that provided detailed examples of moths engaged in pollination (Macgregor et al., 2015). Since then, recent studies have shown moths to be pollen transport vectors in various natural ecosystems (Atwater, 2013; Banza et al., 2015; García et al., 2024; Hahn & Bruhl, 2016; He et al., 2022; Ribas-Marquès et al., 2022; Singh, N. et al., 2022), with the majority of species found within the families Geometridae (geometer moths), Sphingidae (hawk moths), Noctuidae (owlet moths) and the Erebidae family (tiger moths and underwings) (Devoto et al., 2011; Hahn & Bruhl, 2016; LeCroy et al., 2013; Macgregor et al., 2015; Van Zandt et al., 2020; Walton et al., 2020; Winfree et al., 2011). In general, moths involved in pollination are primarily nectivorous and visits flowers to feed on nectar, though a few species consume pollen as well (Atwater, 2013; Winfree et al., 2011). Results from a study of a sandhill ecosystem in the US, revealed that 66% of the nectar-feeding moths that were captured had pollen grains attached to them (Atwater, 2013). Similar results were found in a European biodiversity hotspot in the Mediterranean, where 76% of the collected moths carried pollen (Banza et al., 2015). Nocturnal pollinators have also been identified as an important part of native plant-pollinator networks within agroecosystems; a study from Britian found that 45.5% of captured moths transported wildflower pollen, despite being in an intensively managed agricultural landscape (Walton et al., 2020).

While there is a general understanding of the role of nocturnal pollinators in natural systems, there remains limited research on the contributions of nocturnal pollinators to agricultural crop production. More recently, researchers have sought to fill this knowledge gap (Buxton et al., 2022; Buxton et al., 2023; Cordeiro et al., 2021; Luo et al., 2011; Macgregor, C. J. et al., 2019; Macgregor & Scott-Brown, 2020; Requier et al., 2023; Robertson et al., 2021b). For example, a study of lowbush blueberry (*Vaccinium angustifolium*), an economically important crop in the US, found nocturnal pollinators (both flies and moths) significantly increased berry production

(Cutler et al., 2012). In addition, nocturnal pollinators improved fruit quality measures, such as weight and diameter, in strawberry production (*Fragaria x ananassa*), another popular and economically valuable commercial crop (Fijen et al., 2023).

Nocturnal pollinators have also been found to significantly contribute to apple (*Malus domestica*) production (Robertson et al., 2021a). This was revealed through a pollinator exclusion experiment and a comparison of the relative contributions from nocturnal and diurnal pollinators. Robertson *et al.* (2021a) found that nocturnal pollinators contributed with similar levels of pollination services to apple production as diurnal pollinators, and that these pollinator groups worked synergistically having an additive effective on each other's contribution. The most common nocturnal insects observed were from the orders Diptera, Neuroptera and Lepidoptera (moths), with moths within the family Noctuidae being the most common. To further explore the identity of the nocturnal pollinators, Robertson (2023) observed 15 moth species within the five families (from most to least) Noctuidae, Erebidae, Crambidae, Geometridae, and Sphingidae visiting apple flowers at night, which corresponded with abundance rankings within the orchards (Robertson, 2023).

Apples are considered one of the world's most important commercial food crops, with both a high production volume and great economic value on a global scale (Pardo & Borges, 2020), as well as providing human health benefits (Hyson, 2011). Most apple cultivars are partially self-incompatible and require cross-pollination from a genetically different cultivar type to ensure viable fruit set (Olhnuud et al., 2022; Ramírez & Davenport, 2013). Pollination improves both apple quantity (fruit set) (Olhnuud et al., 2022; Samnegård et al., 2019) and quality (seed set) (Buccheri & Di Vaio, 2005; Webber et al., 2020; Wu et al., 2021) and is therefore essential for high yields of profitable fruit (Garratt et al., 2014; Pardo & Borges, 2020). In Norway, 84% of the total fruit production by weight (23 997 ton) in 2023 originated from apple production, making apples the country's leading fruit crop (Statistisk sentralbyrå, 2024). The growing conditions in Norway are characterized by a cool climate, with risk of both early and late frost, leading to short, but intense growing seasons due to long daylight hours (Roitsch et al., 2022).

The Norwegian government has announced a desire to improve domestic production and self-sufficiency of agricultural goods, including increased fruit production in Norway, and acknowledge that an important prerequisite is facilitating and conserving pollinating insects (Meld. St. 11 (2023–2024)). Currently, 24.2% of all known pollinator species in Norway are on the «Norwegian Red list for Species», of which 13.8% of them have the status as threatened. (Artsdatabanken, 2021). For moths specifically, 30 years of data collection show that both species richness (-8.2% per decade) and diversity (-9.4% per decade) have decreased over the last three decades (Burner et al., 2021).

The documented decline of wild pollinators, together with importance of wild pollinators in agroecosystems, creates an urgent need for research focused on the contribution of nocturnal pollinator communities in agricultural and horticultural production. Thus, the goal of this study is to investigate how nocturnal pollinators contribute to apple production in Norway centered on the following questions:

1. *Which daytime and nighttime pollinating insects are present in apple orchards during the flowering season, and at what time of the day are they active?*

I predict that primarily bees (both wild and managed) will be most active in the daytime, and moths, especially within the families Noctuidae, Geometridae, Erebidae and Sphingidae at nighttime. This prediction is based on existing literature, stating that bees are the most important contributors to global crop production (Aizen et al., 2009; Kearns et al., 1998; Khalifa et al., 2021; Klein et al., 2007; Potts et al., 2010) and that moths, within these respective families, are identified as the most common nocturnal pollinators in apple horticulture (Robertson et al., 2021a; Robertson, 2023), and agroecosystems in general (Buxton et al., 2022; Walton et al., 2020).

2. *What is the fruit set (number of apple flowers that turn into mature fruit) from apple flowers on branches that have only been accessible to pollinators at night, compared to flowers only accessible during the day and not accessible to pollinators at all?*

I predict that fruit set will be higher for flowers accessible to pollinators only at night compared to flowers not accessible to pollinators at all, but not as high as from flowers accessible to pollinators only during the day. This prediction is supported by previous studies on apples (Robertson et al., 2021a) and other fruit crops (Cutler et al., 2012; Luo et al., 2011; Pelletier et al., 2001) in similar experiments.

3. *What is the seed set (number of fully developed seeds per apple) from apples harvested from flowers that have only been accessible to pollinators at night, compared to flowers only accessible during the day?*

I predict that the seed set from apples developed from flowers accessible to pollinators only at night will be similar to the seed set from the apples developed from flowers accessible to pollinators only during the day. This prediction is based on results from the study by Robertson *et al*. (2021a), where seed set was similar among apples developed from flowers that had only been accessible to pollinators at night and apples developed from flowers that had only been accessible to pollinators during the day (Robertson et al., 2021a).

2. Material and Methods

2.1. Study Site

Experiments were conducted during the apple flowering season in spring 2023 (May 16 - June 2), at the two separate commercial apple production farms Berle (59°36'3.5028" N, 10°23'49.4412" E) and Høyen (59°33'54.8748" N, 10°23'44.988" E) in Svelvik, Eastern Norway (Figure 1). The distance between these farms was approximately 4.7 km and each site consisted of three orchards with the apple cultivars Aroma, Discovery, and Summerred. I selected ten trees of each cultivar per orchard (30 trees per site) for this study (Figure 2; Figure 3). The orchards varied in size from 389,25 m² to 1602,57 m² at Berle and 13411,09 m² to 26 987,28 m² at Høyen (Table 1). Adjacent areas at both sites were primarily dominated by fruit crop production, while the surrounding habitat mainly consisted of residential infrastructure.

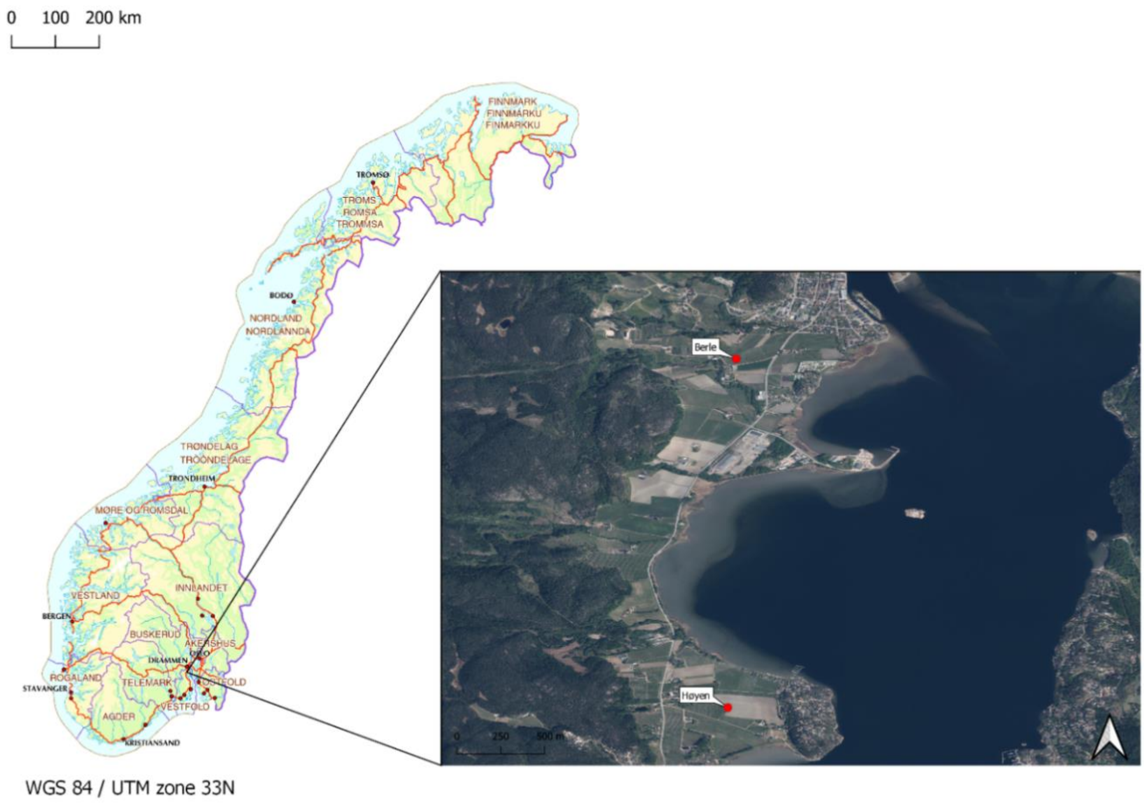

Figure 1. Location of the sites Berle and Høyen in Svelvik, Norway. Orthophoto: Geonorge (n.d.). *Norge i bilder WMS-Ortofoto*. Available at: geonorge.no (accessed: 04.02.2024).

Figure 2. Location of the apple orchards at the Berle site. Dots represents each individual study tree of the cultivars Aroma (yellow), Discovery (orange) and Summerred (red). Geonorge (n.d.). *Norge i bilder WMS-Ortofoto*. Available at: geonorge.no (accessed: 04.02.2024).

Figure 3. Location of apple orchards at the Høyen site. Dots represents each individual study tree of the cultivars Aroma (yellow), Discovery (orange) and Summerred (red). Geonorge (n.d.). *Norge i bilder WMS-Ortofoto*. Available at: geonorge.no (accessed: 04.02.2024).

Table 1. Total size of sites and orchards (cultivars) in square meters (m²).

	Berle (m²)	Høyen (m²)
Aroma	1110,51 m²	13 411,09 m²
Discovery	1602,57 m²	15 266,27 m²
Summerred	389,25 m²	26 987,28 m²
Total	**3102,33** m²	**55 664,64** m²

At the larger Høyen site, pollinizer trees of a different apple cultivar were evenly distributed in the orchards by the farmer to ensure cross-pollination, and at Berle the cultivars were planted alternately. To ensure applicable research results in terms of agriculture, farmers continued with their regular practices throughout the whole study. For instance, farmers deliberately thin the apple trees by removing fruitlets (early-stage fruit), either chemically or mechanically, after the flowering season. This is done to improve the size and quality (market value) of the remaining fruit and reduce the chance of branch breakage and biennial bearing (Jackson, 2003; Meland, 2009).

2.2. Study Species

Domestic orchard apples (*Malus domestica)* are deciduous trees, belonging to the Rosaceae family (Sheffield et al., 2005). Most apple cultivars are self-incompatible and rely on cross-pollination from a genetically different cultivar to ensure fruit set (Olhnuud et al., 2022; Ramírez & Davenport, 2013). However, the level of self-incompatability varies between cultivars, which means self-pollination may occur in some cultivars (De Witte et al., 1996; Garratt et al., 2014; Ramírez & Davenport, 2013). Still, cross-pollination leads to a higher fruit set (Pardo & Borges, 2020; Samnegård et al., 2019) and is thus a factor influencing the number of apples a tree will produce (Olhnuud et al., 2022).

The gynoecium of the apple fruit consists of five carpels arranged in a pentagram, where each carpel has two ovules that produce two seeds, and though there are differences among cultivars, a full seed set for apples generally consists of ten seeds per fruit (Sheffield et al., 2005). Pollination increases apple seed set (Garratt et al., 2014; Olhnuud et al., 2022; Samnegård et al., 2019; Webber et al., 2020). A low seed set with unbalanced seed distribution can cause the apple to grow unevenly, leading to deformed apples with a lower economic value (Jackson, 2003).

In addition to lowering the proportion of unevenly shaped apples (Webber et al., 2020; Wu et al., 2021), a greater seed set positively influences other fruit quality measures such as size and mineral content (Buccheri & Di Vaio, 2005; Samnegård et al., 2019), which increases the economic value of the fruit (Garratt et al., 2014). As seed set affects both fruit quality and yield (in terms of marketable fruit) it is considered to be a measurement of the levels of pollination (or potential pollination deficit) in an orchard (Webber et al., 2020).

2.3. Experimental Design

2.3.1. Species Richness and Abundance of Moths

Figure 4. Light trap in the orchard during morning collection.

To find out which and how many moths were present during flowering season, a light trap (LepiLED UV-LED 1.5. Maxi) attached with a white vane trap for highest trapping efficiency (Brehm, 2017; Brehm et al., 2021; Singh, R. P. et al., 2022), was connected with a 30 000 mAh powerbank (Sandberg Survivor Powerbank 30000 PD45W) and placed at each site (Figure 4) and operated over eight consecutive nights between May 24 – June 1. Specimens were collected each morning. Collected specimens were placed in the freezer for euthanization and storage. Specimens were later pinned and identified to species level or to the lowest taxonomic rank possible without genitalia dissection. Moths were identified using the field guide "*Norges sommerfugler: håndbok over Norges dagsommerfugler og nattsvermere*" (Aarvik et al., 2009), and the web resources "*Vilken art? – Artbestämning av fjärilar i Sverige*" (Lemurell, n.d.) and "*Artsorakel*" (Artsdatabanken, n.d.). Bees were identified using the *"Field Guide to the Bees of Great Britain and Ireland"* (Falk & Lewington, 2018).

2.3.2. Pollinator Observation Study

To register which daytime and nighttime pollinating insects were visiting flowers and at what time of the day they were active, field-cameras were installed in the orchards. In total, 16 timelapse cameras (Wingscapes® Moultrie WCT-00126 Timelapse-Cam Pro) with automatic LED-flash were placed in the orchards as the cultivars started to bloom; six in Summered, six in Discovery, and four in Aroma (Figure A1). As the Summerred flowers started to wither, two cameras were moved to the Aroma cultivar. The cameras were programmed to take high-quality images (6080 x 3420p) of one or multiple flower clusters every five minutes (May 15 – May 23) and later (May 23 – June 1) to take pictures every minute to improve data capture probability. Cameras were either mounted on an iron bar hammered into the ground or on a wood post in the apple rows (Figure 5). Depending on the focus and distance of the camera, the number of flower clusters present in the picture frame varied between cameras.

Figure 5. Left: field-camera mounted on a wood-post in the orchard. Right: field-camera focused on apple flowers.

The VGG Image Annotator (VIA) software (Dutta et al., 2019) was used to manually quantify, and sort all insects present in the pictures to taxonomic ranks (similar approach as in (Lunde et al., 2023) (Figure 6; Figure 7). The taxonomic ranks were selected based on what could provide useful information about insect activity, together with what was realistically manageable to distinguish in the pictures.

The taxonomic groups included in this study were Lepidoptera (butterflies and moths), Apis (honey bees), solitary bees, Bombus (Bumblebees), Syrphidae (Hoverflies), non-Syrphid Diptera (primarily flies and mosquitos) and Neuroptera (lacewings). With each registration, insect identity, date, time, site and apple cultivar were noted. Pictures taken between 22:00 – 04:59 were classified as "night" and pictures taken between 05:00 – 21:59 were classified as "day". When an insect was present in several photos in a row without visiting any new flowers, the individual was only registered once to avoid overrepresentation. When insects were too difficult to identify due to various factors such as variable image quality (blurriness), distance between flower and camera, and sun position, these insects were categorized as "unknown" and excluded from the analysis. Especially for the nighttime pictures, the camera flash caused overexposure (reflection) of the white flowers, making it more difficult to distinguish insects from the general flower structure.

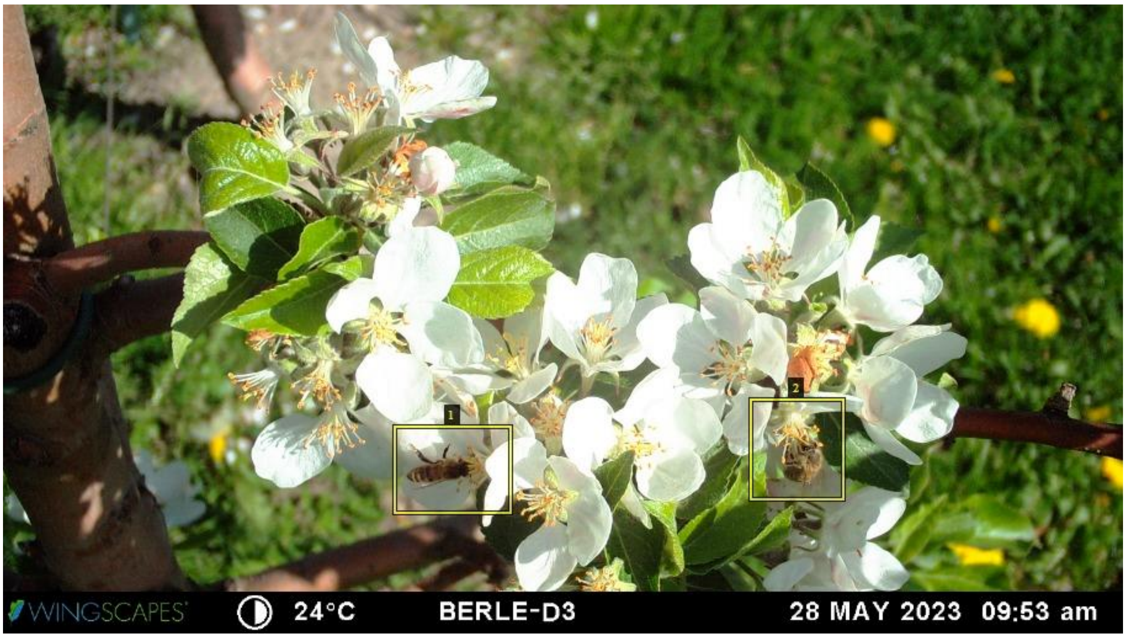

Figure 6. Daytime camera image annotated with the VGG Image Annotator (VIA) software with observations of two honey bees (Apis).

Figure 7. Nighttime camera image annotated with the VGG Image Annotator (VIA) software with observations of a lacewing (Neuroptera).

2.3.3. Pollinator Exclusion Experiment

To compare the contribution of nocturnal and diurnal pollinators on apple quantity (fruit set) and quality (seed set), a pollinator exclusion experiment was implemented. Sites were set-up and prepared for the exclusion experiment before start of flowering season (May 5). Individual trees were selected at random, evenly spread throughout the orchard rows. Branches attached with treatment sleeves (Figure 8) were selected based on the criteria of choosing branches that had flower clusters and being able to access the treatments (max height 150 cm). With a total of thirty replicates of each treatment/control per site, each tree had two treatments and two controls (in total 120 treatment branches per site, and 240 branches overall receiving treatments). Flower clusters were either accessible only during the day (sunrise to sunset), accessible only at night (sunset to sunrise), not accessible to pollinators at all (closed control) or always accessible to pollinators (open control). Treatments and controls were randomly assigned to branches by using a randomizing online tool (https://www.random.org/) and marked with colored ribbons. Treatments and closed control were covered by a L40 x W20 cm Insect Rearing sleeves (BugDorm) made of fine nylon netting covering a branch with a section of flower clusters (Figure 8). As certain branches were crooked and more difficult to cover, some branches were covered by a larger sleeve (L70 x W30 cm) to be able to cover a branch with minimum two clusters.

Figure 8. Left: tree with treatment branches covered with net sleeves. Right: tree with "Day" treatment set in closed position (green ribbon) and "Night" treatment in open position (red ribbon).

Apple flowers are in bloom for approximately 10 days. The flowering period differs between the cultivars with Summerred blooming earliest, followed by Discovery, and lastly Aroma. An apple flower was considered to be "in bloom" once the bud had burst and before the flower petals began to whither and fall. As the apple flowers started to bloom, nets on selected treatment branches were opened and closed (Figure 8) accordingly twice per day at sunrise and sunset, while the controls were locked in a permanent position. The exclusion nets for the two control treatments "open" and "closed" were held open and closed respectively during the entire flowering season. The "day" treatments had their exclusion nets opened at sunrise and then closed at sunset, allowing pollinators access to the flowers only during the daytime. Conversely, the "night" treatments had their exclusion nets opened at sunset and then closed at sunrise, only allowing pollinators to access the flowers during the night. In May, sunrise in Svelvik was during the period 04:15 - 04:45 and sunset during the period 21:50 - 22:15. Because it would take some time to attach or reattach the exclusion nets, the order in which the orchards were visited for net position switch were alternated, to ensure that treatments at different locations had similar pollinator exposure times. Once the flower petals fell off and started to wither, nets were permanently closed consecutively during time of switch.

Due to chemical spraying of the orchards and associated safety precautions, about two days of data collection were disrupted during flowering season. In this period, all nets were closed at the night switch and kept permanently closed for approximately 48 hours. Once the flowering season was over, all nets were removed and the number of flower clusters per branch was counted. In addition, individual flowers on 30 random, non-treatment trees were counted for each cultivar, which were later used in the analysis to make predictions for mean number of flowers per cluster. To be able to detect the study trees later for apple harvesting, tree trunk and treatment branches were marked with string and labels.

Apples from the study trees were harvested on three separate occasions in the fall, about 1–7 days before the farmers harvested their crops, with Discovery first (August 18), followed by Summerred (August 25) and Aroma (September 18). The collected apples were stored in a cold storage room until they were processed in the lab, where seed set (number of fully developed seeds) was counted for each individual apple.

2.4. Statistical Analysis

Statistical analyses were performed with R Statistical Software version 4.3.1 (R Core Team, 2023), and RStudio (Posit team, 2024). The packages “readxl” (Wickham & Bryan, 2023), “dplyr” (Wickham et al., 2023) was used to load and organize data, while the “knitr” package (Xie, 2023) was used to combine tables. Figures and graphs were visualized using the plot functions from the “ggplot2” package (Wickham, 2016).

2.4.1. Pollinator Observation Plot

To visualize and explore the activity window of the different insect groups (per site and cultivar) present in the orchards, graphs based on the registered observational data from the cameras was generated. The function “dmy_hms” from the “lubridate” package (Grolemund & Wickham, 2011) was used to parse dates from the data set and the function “round_date” was used to round the registered time up to the nearest hour. To account for the fact that some cameras were on for a longer time than others, and consequently had a higher number of pictures, data was adjusted by calculating the proportion of pictures with insect observations per hour, site, cultivar and insect taxonomic group. This was used to generate a graph visualizing the activity time of the different taxonomic groups with proportions of observations (y-axis) by the hour of the day (x-axis) for the different cultivars (grid) and sites (lines) (Figure 9). To separate the night (22:00 – 04:59) from the day (05:00 – 21:59) treatment in the graph, the night treatment was included as a shaded area in the plot.

2.4.2. Comparative Analysis of Fruit Set

To find the proportion of apple flowers that bear fruit (fruit set) from branches applied with the different treatments (Night, Day, Open, Closed) for the different cultivars (Aroma, Discovery, and Summerred) and sites (Berle and Høyen) in the pollinator exclusion experiment, a comparative analysis of fruit set was performed. Fruit set is calculated by the number of developed apples divided by the number of flowers for each treatment branch. To improve time-efficiency, only flower clusters were counted for each treatment branch in this experiment. To estimate the number of flowers per cluster for each apple cultivar, individual flowers from 30 random clusters per cultivar were counted on each site. Hereafter, data on the number of flowers taken from the 30 random clusters from each cultivar are referred to as the 'FPC' (flowers per cluster) data set, and the data on the number of apples counted from a known number of clusters as the 'AKC' (apples from a known number of clusters) data set.

The Poisson regression model with the log-link function is the most common generalized linear model (GLM) applied for count data (Fox, 2016). The Poisson model has a discrete distribution that only models the probability of nonnegative integers, which makes it a good fit for modelling count data (with 0 or greater values) (Coxe et al., 2009). By applying the Poisson regression model, with the expected number of fruit at the i^{th} data point denoted here by $\mathbb{E}\ (A_i)$, the modelling framework in this experiment follows the following formula:

$$\mathbb{E}\ (A_i) = c_i y_i z_i$$

where c_i represents the number of clusters, y_i is the average number of flowers per cluster and z_i is the probability of a flower becoming a fruit (for data point i). This formulation is based on the assumption that the total number of flowers (F_i) at the ith data point follows a Poisson distribution:

$$F_i \sim Poisson\ (c_i y_i)$$

and the number of fruit borne from these flowers, A_i, is the result of a binomial thinning process (see "On Binomial thinning and mixing" by (Kella & Löpker, 2023), where:

$$A_i \sim Binomial\ (F_i z_i)$$

which corresponds to:

$$A_i \sim Poisson\ (c_i y_i z_i)$$

When applied to the model formulation above, the Poisson regression model with the log link function, this formulates a linear model for the log of expectation, such that:

$$\log\,[\mathrm{E}(F_i)] = \log(c_i) + \log(y_i)$$

$$\log[\mathrm{E}(A_i)] = \log(c_i) + \log(y_i) + \log(z_i)$$

Then, when relating a set of predictor variables to the average number of flowers per cluster (y_i) and the probability of a flower becoming a fruit (z_i), this results in the following two models:

Expected number of flowers:	$\log(c_i) + \log(y_i) = \log(c_i) + \beta_1 x_{1i} + \beta_2 x_{2i} + \dots + \beta_k x_{ki}$
Probability of a flower bearing fruit:	$\log(z_i) = \gamma_1 h_{1i} + \gamma_2 h_{2i} + \cdots + \gamma_\ell h_{\ell i}$

where x_{ti} is the value of the t^{th} predictor variable (of a total of k predictor variables) for the total number of flowers at the i^{th} data point, and β_t is the regression coefficient associated with that predictor variable (fitted by the model function). Correspondingly, h_{ti} is the value of the t^{th} predictor variable (of a total of ℓ predictor variables) for the probability that a flower becomes a fruit at the ith data point and the γ_t is the regression coefficient associated with that predictor variable.

This model formulation allows a model to be fit to both the FPC and the AKC data set simultaneously and allows for the accurate treatment of covariance between the likelihood surface across the regression coefficients within and between the two sub-models and the accurate representation of the uncertainty arising from this covariance in any model predictions. For this application, this was performed by merging the data from the FPC and AKC data set through the following steps:

1. Creation of a new response variable (hereafter defined as “item count”) which contains the number of flowers counted in a cluster for those data rows that are taken from the FPC data set and contains the number of apples for those data rows that are taken from the AKC data set.
2. Creation of an offset variable which is the number of clusters present at each data point. For the data rows that correspond to data taken from the FPC data set, this value is always set to ‘1’ by definition of the experiment.

For the data rows that correspond to data taken from the AKC data set, this value is just set to the known number of clusters at that data point.

3. Creation of two sets of covariates to be used as predictor variables in the two sub-models. For covariates that belong to the sub-model defining the expected number of apples then they are set to the values that were recorded for these covariates for those data rows that correspond to data taken from the AKC data set and set to ‘0’ for those data rows that correspond to data taken from the FPC data set. For covariates that belong to the sub-model defining the expected number of flowers then they are set to the values that were recorded for these covariates in the corresponding constituent data set.
4. Creation of covariates corresponding to intercept terms for the two sub-models. For the sub-model defining the expected number of flowers, this was achieved by simply adding a covariate that had the value ‘1’ for all data rows. For the sub-model defining the expected number of apples then this was achieved by creating a covariate that had the value ‘1’ for all data rows that correspond to the AKC data set and the value ‘0’ for all data rows that correspond to the FPC data set.

The merged FPC/AKC data set was analyzed using a Poisson regression model fit with the “glm” function. As flowers per cluster may vary depending on the different cultivars, the cultivar predictor variable was included in the FPC sub-model (table 2). And based on the assumption that the effects of treatments on fruit set might vary depending on both cultivar and site, interactions between treatment and cultivar, plus treatment and site was included in the AKC sub-model (table 2).

Table 2. Covariates present in the “Flower per cluster” (FPC) sub-model and “apples from a known number of clusters” (AKC) sub-model.

FPC sub-model	flowerFormula <− nflowers ~ cultivar + offset(log(nclusters))
AKC sub-model	fruitFormula <− napples ~ cultivar ∗ treatment + site ∗ treatment

The combined model was then used to create two predictions: one to predict the number of flowers per cluster and one to predict the fruit set for each combination of the predictor variables. The predictions with the estimated number of flowers per cluster for each cultivar was visualized in a histogram (Figure 10) displaying the confidence interval and predicted means. This estimated number of flowers per cluster, stored in the combined model, was used when making the fruit set predictions.

The predicted number of fruits per cluster was visualized in a plot displaying the observed data as jittered points with overlaying predicted means and confidence intervals as tiles, separated in different facets for each combination of "cultivar" and "treatment" for the different sites (Figure C1). Following the same set-up, the predicted probability of getting a fruit from a flower was visualized in a plot showing the proportion of flowers that bear fruit for each treatment, cultivar and site (Figure 11). Since the fruit set predictions were based on the flower predictions (estimated number of flowers per cultivar), the jittered data points in this plot (showing the individual (mean) estimate of fruit set) included error bars to display the variance/uncertainty range of these estimates.

To inspect the level comparisons of the different factors, a "Tukey's Honest Significant Difference" (HSD) post-hoc test was conducted after performing an "Analysis of Variance" test (ANOVA) on the fruit set model. While controlling for the family-wise error rate, the HSD-test performed a pairwise comparison between group means and identified which means differed significantly from each other for both marginal and interactive effects. To provide a visual summary of the post-hoc test results, results were generated in the form of plots to highlight the significant differences between the levels of each factor (Figure C2; Figure C3).

2.4.3. Comparative Analysis of Seed Set

To investigate the seed set (number of fully developed seeds per apple) from apples harvested from the different treatments, cultivars, and sites in the pollinator exclusion experiment, a comparative analysis of the seed set data was performed. To find the appropriate regression model fit for the seed set response variable, data was assessed for overdispersion. To inspect the data for overdispersion, a common occurrence for count data (Fox, 2016), mean, and variance was calculated. This revealed that the variance was greater than the mean, indicating that the data was over-dispersed. In this scenario, a negative binomial regression model is a better option to analyze this kind of data (Coxe et al., 2009; Fox, 2016; Lawless, 1987; Venables & Ripley, 2002). The negative binomial model adds an additional parameter (theta) to adjust for the overdispersion and connects the mean of the count data to the predictor variables trough a log link function (Fox, 2016; Venables & Ripley, 2002).

The function “glm.nb” from the package “MASS” (Venables & Ripley, 2002) was used to fit the negative binomial regression model. Similar as with the fruit set, the interactions between the predictor variables (treatment * cultivar + treatment * site) included in the final model were chosen based on the assumption that the effects of treatments on seed development might vary depending on both cultivar and site. Both statistical testing in the form of a Likelihood Ratio Test (LRT) Chi-square test and model complexity vs. interpretability were considered when choosing the interactive terms in the model. Despite the treatment * site interaction not reaching statistical significance, it was kept in the model to enhance the comprehensive understanding of how treatments impact seed development across different environmental conditions. After fitting the final model, the “check model” function from the “performance” (Lüdecke et al., 2021) package was used to assess the model for various assumptions. This test revealed that the model met the assumptions regarding normality of residuals, passed the posterior predictive check, showed no influential observations, and indicated homogeneity of variance.

The fitted negative binomial regression model was used to produce a prediction for the seed set (number of developed seeds per apple) expected under each combination of predictor variables. Predictions were visualized in a plot displaying the observed data as jittered points with overlaying predicted means and confidence intervals as tiles, separated in different facets for each combination of “cultivar” and “treatment” for the different sites (Figure 12).

Following the same approach as with the fruit set, results from the ANOVA and HSD post-hoc test on level comparisons of the different factors affecting seed set (both marginal and interactive effects) were visualized in plots (Figure D1; Figure D2).

3. Results

3.1. Light traps

A total of 22 specimens were caught in the light traps during the flowering season of 2023 (Table 3), from eight nights of trapping. This included sixteen moths, two honey bees, one solitary bee, one bumblebee, one species within the superfamily Ichneumonoidea, and one species within the suborder Nematocera. The two sites differed in number of caught specimens, with a higher number of specimens (n = 15) caught at the Berle site (68%) compared to the number of specimens (n = 7) caught at the Høyen site (32%).

The most frequently caught moth families in the light traps were Erebidae (n = 6), followed by Noctuidae (n = 4), Geometridae (n = 3) and Tortricidae (n = 1).

In total, the moths comprised nine different species (eleven, including two damaged specimens). *Diaphora mendica* was the most common (31.3%) followed by *Xanthorhoe quadrifasiata* (12.5%), which were the only species caught at both sites. *Agrotis exclamationis* (6.3%), *Anarta trifolii* (6.3%), *Cabera exanthemata* (6.3%), *Cochylis nana* (6.3%), and one species within the genus Diarsia (6.3%) were only caught at the Berle site, while *Lithophane socia* (6.3%) and *Spilosoma lubricipeda* (6.3%) were only caught at the Høyen site.

Bee species caught only at the Berle site included the honey bees *Apis mellifera* (40%), the bumblebee species *Bombus platorum* (20%) and a wasp species within the superfamily Ichneumonoidea (20%), while the solitary bee *Andrena barbilabris* (20%) was the only bee species caught at the Høyen site. The only fly caught in the light traps was a species within the suborder Nematocera caught at the Høyen site.

Table 3. List of insects caught in light traps identified to taxonomic rank.

Order	Family/suborder/genus/species (lat.)	Site	
Lepidoptera		Høyen	Berle
	Agrotis exclamationis (Noctuidae)		1
	Anarta trifolii (Noctuidae)		1
	Cabera exanthemata (Geometroidae)		1
	Cochylis nana (Tortricidae)		1
	Diaphora mendica (Erebidae)	1	4
	Diarsia spp. (Noctuidae)		1
	Lithophane socia (Noctuidae)	1	
	Spilosoma lubricipeda (Erebidae)	1	
	Xanthorhoe quadrifasiata (Geometridae)	1	1
	Unknown macromoth (damaged)		1
	Unknown micromoth (damaged)	1	
Hymenoptera			
	Andrena barbilabris	1	
	Apis mellifera		2
	Ichneumonoidea spp.		1
	Bombus platorum		1
Diptera			
	Nematocera spp.	1	
Total		**7**	**15**

3.2. Pollinator Observations

In total, 177,329 photos were taken during the flowering season, with 94,159 photos taken at Berle and 83,170 photos taken at the Høyen site. The total observations of insects in photos for both sites was 2144 recorded visits with 1892 (88.25%) of the observations recorded during the day (05:00–21:59) and 252 (11.75%) recorded during the night (22:00 and 04:59).

Adjusted by the total pictures taken by each camera, calculating the proportion of pictures with observations, the Berle site had about 2.7 times more daily visits and 9.4 times more visits at night compared to Høyen (Figure 9; Table B1). The Discovery cultivar had the highest proportion of visits both during the day and the night, followed by Aroma and Summerred (except during the night) (Figure 9; Table B1).

All taxonomic groups were observed during the day, with different frequencies depending on site and cultivars, with Apis (honey bees) and Non-Syrphid Diptera being the most common at both sites and across the different cultivars (Figure 9). At night, only Neuroptera and non-Syrphid Diptera were observed, with peak activity of Neuroptera between 00:00 – 03:00, while non-Syrphid Diptera were in general more active throughout the day. Only a few Lepidoptera were observed during the day between 10:00 – 15:00 in the Aroma and Discovery orchards.

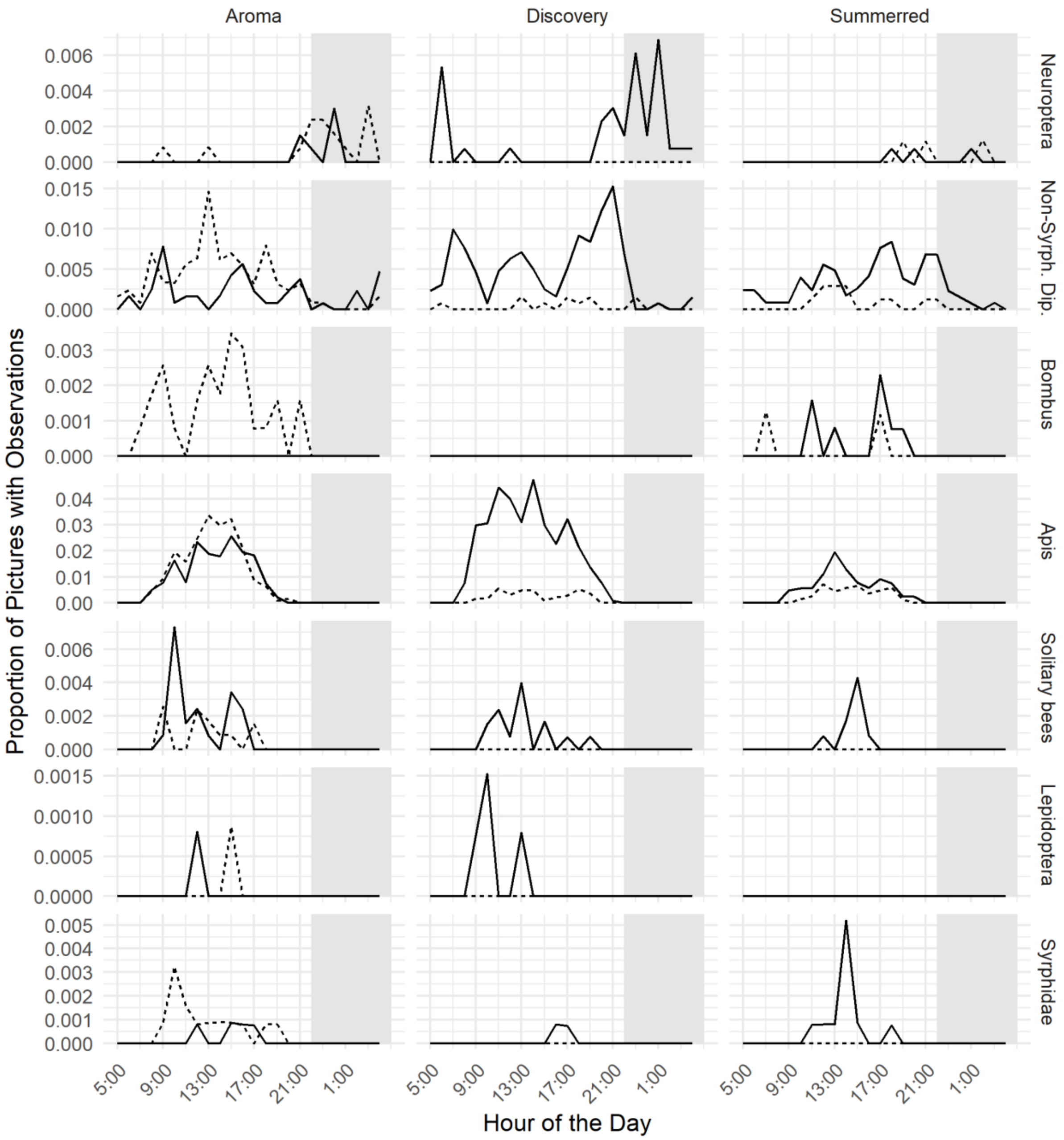

Figure 9. Proportion of pictures with observations (y-axis) of the taxonomic groups Neuroptera, Non-Syrph. Dip. (Non-Syrphid Dipterans), Bombus, Apis, Solitary bees, Lepidoptera and Syrphidae during the hours of the day (x-axis). Sites separated with Berle = solid line and Høyen = dotted line. Day (treatment) between 05:00 – 21:59 and night (treatment) between 22:00 – 04:59 (shaded area).

3.3. Pollinator Exclusion Experiment

3.3.1. Fruit Set Model

A total of 1700 clusters and 491 developed apples were counted on the treatment branches (Table C1). In addition, 970 individual flowers were counted from 30 clusters per site and cultivar (Table C3). The predicted mean number of flowers per cluster per cultivar was estimated to be 5.08 for Aroma, 5.79 for Discovery and 5.28 for Summerred (Figure 10).

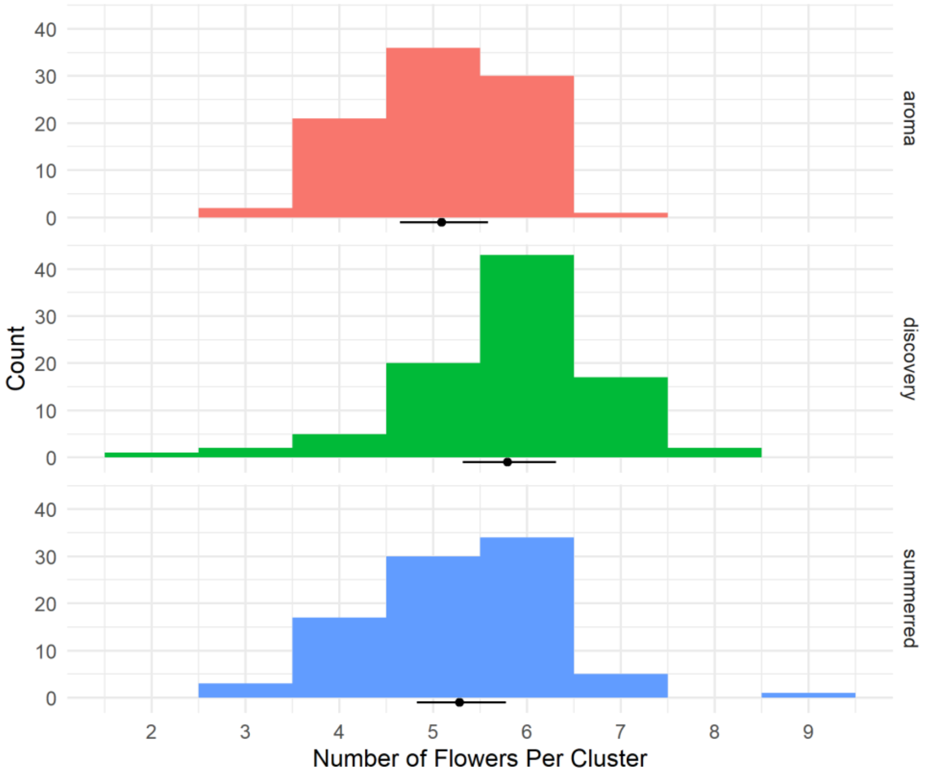

Figure 10. Histogram with the predicted number of flowers per cluster for each cultivar used in the fruit set model. The black lines represent the 95% confidence interval predicted by the model and the black dots is the mean prediction of flowers per cluster.

Predictions based on the Poisson regression model and the Tukey HDS post-hoc comparisons of means on the fruit set response variable revealed that the night treatment had a significantly lower proportion of flowers that bear fruit (fruit set) compared to the day treatment (Figure 11; Table C4). For marginal effects, the night treatment was not significantly different compared to the closed control ($p = 0.999$) (Figure 11; Table C4) and the day treatment was not significantly different than the open control ($p = 0.876$) (Figure 11; Table 4).

For interactive effects, the fruit set for the day treatment at Høyen was significantly lower compared to the open control at Berle (Figure 11; Table 4).

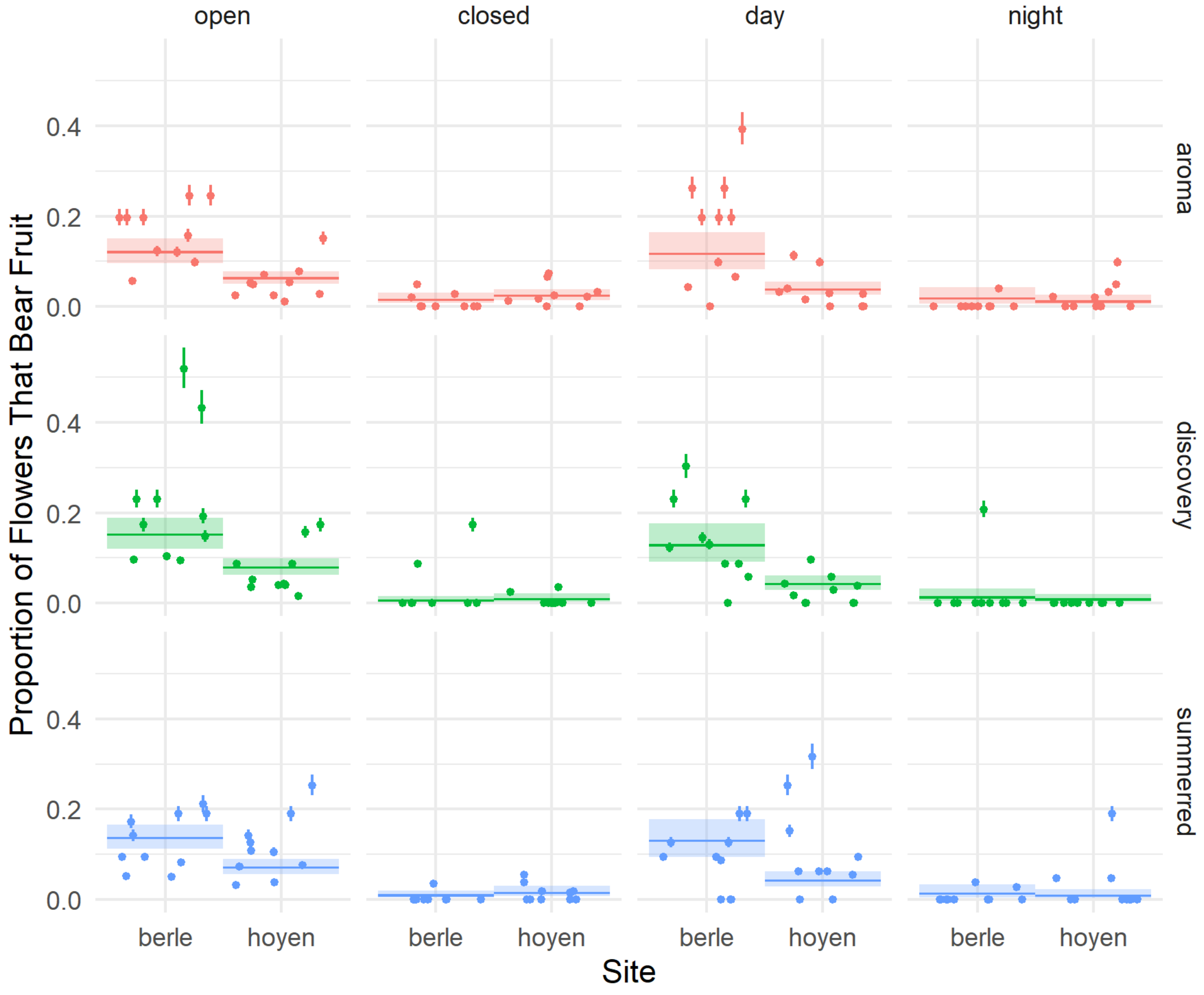

Figure 11. Generalized linear (glm) Poisson regression model with the predicted proportion of flowers that bear fruit. The dots represent the proportion of flowers that bear fruit assuming that each cluster has the expected number of flowers per cluster as predicted by the flower density model, including the respective 95 % confidence interval predicted in this model. The shaded region represents the 95 % confidence interval predicted by the fruit set model. The bold middle line represents the mean prediction made by the model.

Table 4. Coefficient table on effects of treatment, cultivar and site on the proportion of flowers that bear fruit (fruit set). Tested in a Poisson regression model.

	Effect ± SE	z	P
Cultivar (Aroma)	- 2.12 ± 0.13	- 16.73	**< 2e^{-16} *****
Cultivar (Discovery)	0.23 ± 0.15	1.47	0.142
Cultivar (Summerred)	0.12 ± 0.15	0.81	0.42
Treatment (Closed)	- 2.07 ± 0.38	- 5.43	**5.70e^{-08} *****
Treatment (Day)	- 0.03 ± 0.21	- 0.16	0.876
Treatment (Night)	- 1.92 ± 0.47	- 4,05	**5.07e^{-05} *****
Site (Høyen)	- 0.65 ± 0.12	- 5.67	**1.46e^{-08} *****
Cultivar (Discovery), treatment (Closed)	- 1.22 ± 0.52	- 2.35	**0.019 ***
Cultivar (Summered), treatment (Closed)	- 0.62 ± 0.43	- 1.43	0.154
Cultivar (Discovery), treatment (Day)	- 0.13 ± 0.26	- 0.51	0.608
Cultivar (Summerred), treatment (Day)	- 0.02 ± 0.26	- 0.07	0.947
Cultivar (Discovery), treatment (Night)	- 0.57 ± 0.57	- 0.99	0.322
Cultivar (Summerred), treatment (Night)	- 0.44 ± 0.61	- 0.72	0.470
Treatment (Closed), Site (Høyen)	1.11 ± 0.40	2.78	**0.005 ****
Treatment (Day), Site (Høyen)	- 0.47 ± 0.22	- 2.14	**0.032 ***
Treatment (Night), Site (Høyen)	0.19 ± 0.49	0.39	0.700

Bold text indicates significant values P < 0.05

3.3.2. Seed Set Model

The apple quality assessment revealed that the mean number of fully developed seeds per apple was 2.44 for the night treatment, 4.82 for the day treatment, 6.05 for open control and 2.09 for closed control (Table D1).

Predictions based on the negative binomial regression model and the Tukey HSD post-hoc comparison of means on the seed set response variable revealed that the night treatment had significantly fewer fully developed seeds compared to the day treatment (Figure 12; Table D2). For marginal effects, the open treatment had significantly more fully developed seeds compared to the day treatment (Figure 12; Table D2) and the night treatment was not significantly different compared to the closed control (p = 0.278) (Figure 12; Table 5). For interactive effects, the open treatment had a significantly higher number of seeds than the day treatment at both Berle and Høyen (Figure 12; Table D3).

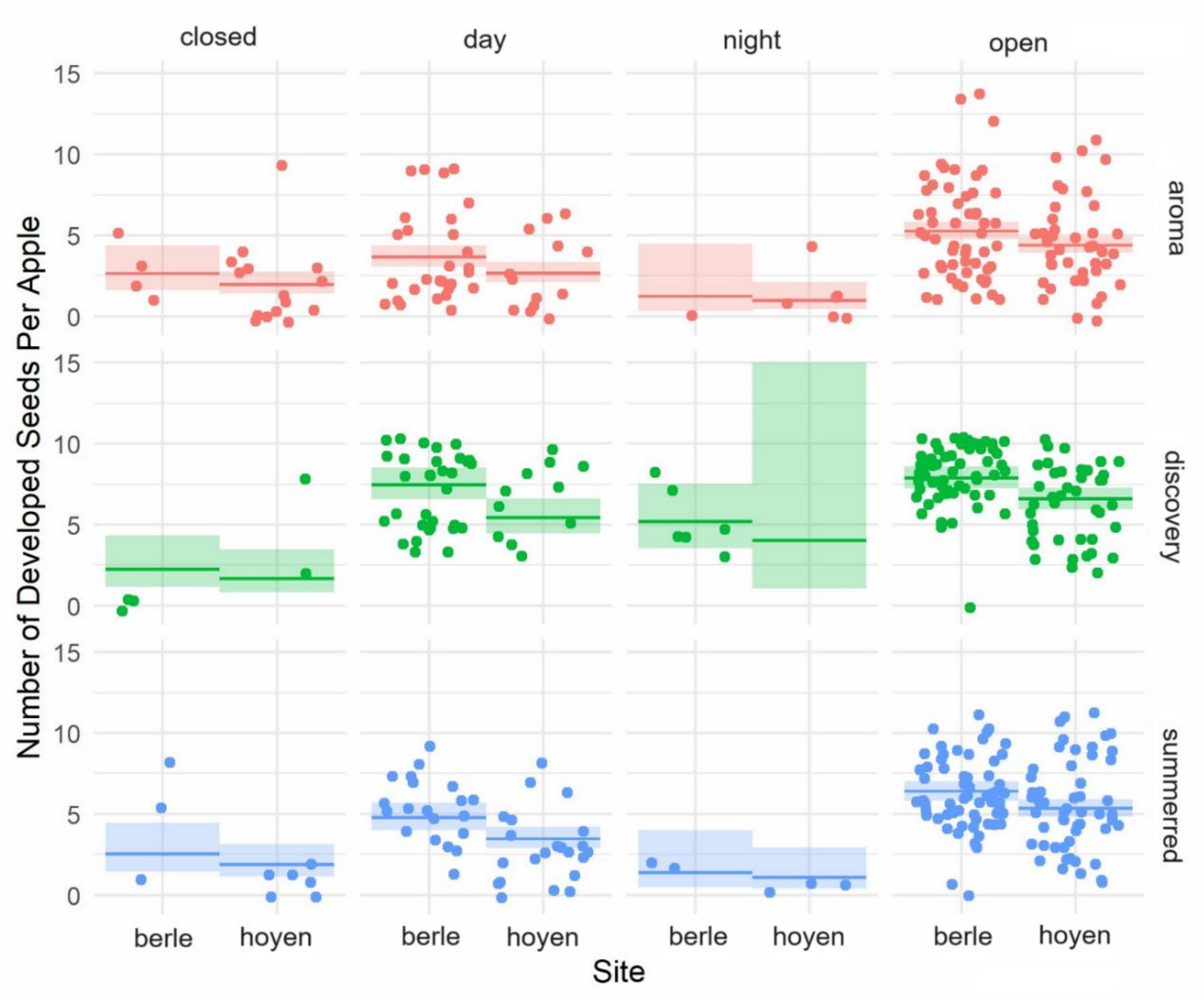

Figure 12. Negative binomial regression model with the predicted number of fully developed seeds per apple. Data point as jitter, and the shaded region represents the 95% confidence interval predicted by the model. The bold middle line represents the mean prediction made by the model.

Table 5. Coefficient table on effects of treatment, cultivar and site on number of fully developed seeds (seed set) in harvested apples. Tested in a negative binomial regression model.

	Effect ± SE	z	P
Cultivar (Aroma)	0.97 ± 0.26	3.77	**0.000** ***
Cultivar (Discovery)	- 0.16 ± 0.38	- 0.42	0.885
Cultivar (Summerred)	- 0.04 ± 0.29	- 0.15	0.885
Treatment (Day)	0.32 ± 0.27	1.18	0.236
Treatment (Night)	- 0.76 ± 0.70	- 1.08	0.278
Treatment (Open)	0.69 ± 0.26	2.61	**0.009** **
Site (Høyen)	- 0.30 ± 0.27	- 1.11	0.269
Cultivar (Discovery), treatment (Day)	0.87 ± 0.39	2.22	**0.027** *
Cultivar (Summerred), treatment (Day)	0.31 ± 0.31	0.98	0.328
Cultivar (Discovery), treatment (Night)	1.59 ± 0.78	2.04	**0.041** *
Cultivar (Summerred), treatment (Night)	0.15 ± 0.66	0.23	0.816
Cultivar (Discovery), treatment (Open)	0.57 ± 0.38	1.48	0.140
Cultivar (Summerred), treatment (Open)	0.24 ± 0.30	0.81	0.420
Treatment (Day), Site (Høyen)	- 0.02 ± 0.29	- 0.07	0.942
Treatment (Night), Site (Høyen)	0.05 ± 0.70	0.07	0.942
Treatment (Open), Site (Høyen)	0.12 ± 0.28	0.43	0.668

Bold text indicates significant values $P < 0.05$

4. Discussion

This study presents the first data on the pollination services provided by night active insects in Norwegian apple horticulture.

The pollinator observation study showed that honey bees (Apis) were the most abundant taxonomic groups during the day. These findings upholds the prediction that primarily bees would be the most active insects in the daytime, based on the recognition of bees as the most important contributors to global crop production (Aizen et al., 2009; Kearns et al., 1998; Khalifa et al., 2021; Klein et al., 2007; Potts et al., 2010). However, as non-Syrphid Dipterans were the second most abundant insect group during the day, this reject the prediction that wild bees would be among the most abundant day active pollinators.

In total, only sixteen moths were captured in the light traps and not a single moth was observed in the pollinator observation study during the flowering season.

Furthermore, the only active insect groups observed during the night were lacewings (Neuroptera) and non-Syrphid Dipterans. These findings reject the prediction that moths would be the most abundant insect group active during the night, based on the nocturnal pollinator communities found previously in apple orchards (Robertson et al., 2021a; Robertson, 2023) and other agroecosystems (Buxton et al., 2022; Walton et al., 2020).

According to the results from the pollinator exclusion experiment, flowers that had only been accessible to pollinators during the night produced significantly less fruit than flowers only accessible at day. These findings are in line with the predictions based on what has been found in similar experiments for other fruit crops (Cutler et al., 2012; Luo et al., 2011; Pelletier et al., 2001), but not for apples specifically (Robertson et al., 2021a). Moreover, flowers only accessible to pollinators during the night resulted in a similar number of fruits as flowers not accessible to pollinators at all. These results differs from what has been found previously for apples, where flowers only accessible during the night resulted in a fruit set that was greater than the closed control (Robertson et al., 2021a).

Seed set in apples from flowers only accessible to pollinators at night was significantly lower compared to the seed set in apples from flowers only accessible during the day. These results reject the prediction based on what was been found previously for apples, with apples pollinated only during the night having a similar seed set as apples pollinated only during the day (Robertson et al., 2021a).

4.1. The pollinator community

4.1.1. The absence of moths

Among nocturnal pollinators, moths have been recognized as the main providers of pollination services at night (Buxton et al., 2022; Macgregor et al., 2015; Macgregor, C. J. et al., 2019). However, in my study only a few moths were caught in the light traps during the flowering season, and not a single moth was observed in the pollinator observation study. The only Lepidopterans that were registered were day-active butterflies. According to SLU Artdatabanken, all the moth species that were caught in the light traps are categorized within the ecological group of herbivores, feeding on living plant parts such as leaves and needles (SLU Artdatabanken., 2024). Furthermore, three of the moth species of the family Noctuidae; *Agrotis exclamationis*, *Anarta trifoii* and *Lithophane socia*, all associated with agricultural landscapes, are known to feed on nectar and pollen as well (SLU Artdatabanken., 2024).

While the few moths that were caught in the light traps confirms that there are moths present in the area, even species known to exploit floral resources, their absence in the camera images implies that they most likely do not visit the apple flowers at these sites.

My results contradict other studies examining moth communities in apple orchards. For example, Robertson (2023) found a rich moth community within apple orchards during the flowering season (Robertson, 2023). While most of the captured moth species in the study did not visit flowers (68 species from 12 families), the moth species that were observed visiting flowers (15 species from 5 families) were the most abundant overall. Comparison of the moths captured in my study to the list of confirmed floral visitors in Roberston's study (2023) showed no overlap. Furthermore, during the three-year study, Robertson (2023) captured a total of 1087 moths with eight nights of trapping per year, averaging 362 captured moths annually. In comparison, only 16 moths were captured over the same trapping duration in my study. This disparity raises the question: why are there so few moths at the Norwegian sites? While only speculative, several possible explanations for the low moth abundance and diversity in these areas can be considered.

To start with, there are general environmental differences between Fayetteville (Arkansas, US), where the study by Robertson *et al.* (2021a) was conducted, compared to my study in Svelvik (Norway). With Fayetteville located at latitude 36.01 and Svelvik at 59.61, the studies took place in different geographical zones. Highly influenced by latitude, The "Köppen climate classification" is based on temperature and precipitation patterns, both major drivers of species distribution (Beck et al., 2023). According to this system, Arkansas has a "humid subtropical" climate (Cfa), while south-eastern Norway has a "hemiboreal" climate (Dfb). As per the *National Weather Service* in the US, the average temperature in Fayetteville in May during the study years 2017 and 2018 was 17.7 °C and 15.6 °C (https://www.weather.gov) while in Svelvik the mean temperature in May 2023 according to the Norwegian Meteorological Institute was 11.2 °C (https://www.yr.no/). Studies have shown that moth activity increases with temperature (Knop et al., 2018; Yela & Holyoak, 1997), with greater species richness and abundance captured in light traps on warmer nights (Botham et al., 2015; Jonason et al., 2014). Hence, the lower mean temperature in Norway compared to Arkansas might partly account for the overall differences in the total number of moths captured in the light traps.

Precipitation is another environmental factor affecting insect flight activity (Dickerson et al., 2014; Lawson & Rands, 2019) and therefore the weather conditions during the nights of light trap sampling could affect trap success rates. However, rainfall was only recorded on one of the dates when the light traps were on (max 0.8 mm), which means that it most likely did not affect how many moths were captured in my study.

The low moth abundance and high variation between the sites (11 moths at Berle compared to 5 moths at Høyen) suggests that site-specific conditions may affect their capacity to support viable moth populations. Both of my sites are located in a rural residential area close to a road with streetlights. Artificial light pollution is an increasing anthropogenic threat affecting ecological communities (Sanders & Gaston, 2018) and is hypothesized to be one of the main drivers behind negative moth population trends (Macgregor et al., 2015; Macgregor & Scott-Brown, 2020; van Langevelde et al., 2018). A recent study by Battles *et al.* (2024) revealed that light traps have become less effective at attracting moths over the past 25 years, likely due to the increase in light pollution (Battles et al., 2024). Artificial light has also been shown to disrupt nocturnal pollination networks. Knop *et al.* (2017) found flower visitation in areas illuminated by artificial light was reduced by 62%, which resulted in the fruit set being reduced by 13% (Knop et al., 2017). Additionally, Macgregor *et al.* (2016) demonstrated that street lighting led to an overall reduction in nocturnal pollen transport by moths, with illuminated sites showing a 50% lower moth abundance and over 25% lower species richness (Macgregor et al., 2017). The long-term impacts of artificial light pollution on moths in urban areas may result in reduced flight-to-light behavior (Altermatt & Ebert, 2016). While this evolutionary behavioral change appears to be an adaptive strategy for increased survival, it can potentially lead to overall reduced flight mobility and consequently lower flower-visitation rates and pollination (Altermatt & Ebert, 2016). Altogether, these studies suggest that light pollution may have disrupted the local moth populations in my study area and may explain the low capture rates in my light traps. To assess if the low abundance and diversity of moths in these areas are affected by light pollution, alternative methods to the light traps should be considered. For example, transects are a common method used to estimate and monitor Lepidoptera populations (Pollard, 1977; van Swaay et al., 2008). Future studies should implement timed walks of defined transects within the study areas to systematically observe and count active moths during the night. Sweep netting of insects along the transects could allow for later identification, if necessary (Montgomery et al., 2021).

The sites used in my study are part of a large, commercial apple horticulture farm landscape where the agricultural land is intensively managed. Agricultural intensification is identified as one of the main drivers of moth decline (Fox, 2013; Fox et al., 2014) and has been found to reduce moth species diversity with increasing levels of agricultural intensity (Ekroos et al., 2010). In a global meta-analysis on the effect of anthropogenic disturbances, Dirzo *et al*. (2014) found that Lepidoptera species richness and abundance was substantially lower in disturbed areas compared to undisturbed areas (Dirzo et al., 2014). As these commercial farms sites have a high level of human disturbance, this may explain the overall low abundance and species richness of moths in the area. Notably, the larger and more intensively managed site at Høyen is predominantly surrounded by monocultures of fruit crop trees. Extensive monocultures are associated with lower pollinator diversity and reduced pollination (Aizen et al., 2022; Aizen et al., 2019). Another factor that may have affected the flower visitation rate (especially linked to the monocultures at Høyen) is distance to natural areas. According to Ricketts *et al.* (2008), both species richness and flower-visitation rates declines with increasing distance to natural habitat (Ricketts et al., 2008). Garibaldi *et al*. (2011) also found that pollinator species richness, flower visitation rate, and fruit set all declined with increasing levels of isolation (distance) from natural areas (Garibaldi et al., 2011).

Insecticides are often used in apple orchards to reduce the populations of apple pest moths, particularly the codling moth *Cydia pomonella* and the apple fruit moth *Argyresthia conjugella*, which are known to cause considerable damage to apple crops worldwide (Franck et al., 2007; Kadoić Balaško et al., 2020; Satake et al., 2004). However, pesticides can also have detrimental effects on pollinators (Desneux et al., 2007; Gill et al., 2012; Goulson et al., 2015; Potts et al., 2010) and have been found to reduce the pollination services provided by adult moths (Hahn et al., 2015). Furthermore, some moths (especially within the Noctuidae family) may act as pollinators as adults, but cause damaging effects at the larvae stage (Van Zandt et al., 2020). Robertson (2023) found that some of the moths originally known as pests were also found visiting the apple flowers. This illustrates the tension between the need to manage apple pest moths and the need to conserve nocturnal pollinators. Future studies should consider the trade-offs between pest management and improved fruit production from nocturnal pollinators.

Insect populations may in general experience annual variation (Hallmann et al., 2017; Wagner, 2020) (thought to be driven by complex weather conditions (Müller et al., 2024)) and several studies have shown high between-year variability and periodicity in moth populations (Devoto et al., 2011; Macgregor, J. et al., 2019; Robertson, 2023). This emphasizes the importance of long-term studies, and why this study should be repeated to identify clear entomological trends and draw more concluding remarks. With additional resources, it would also be interesting to count pollen grains (if any) on captured moths and use DNA metabarcoding (see (Macgregor, C. J. et al., 2019)) to identify which plants the moths (potentially) visited.

4.1.2. Neuroptera as potential pollinators

The only night active insects found in camera images were lacewings within the order Neuroptera and non-Syrphid Dipterans like flies and mosquitos. While the non-Syrphid Dipterans were often observed in the same spot for several pictures (and hours), the lacewings were frequently observed moving around from flower to flower and may therefore be contributing to nocturnal pollination of apples.

At present, Neuroptera is not recognized as a pollinator contributing to apple production (Pardo & Borges, 2020; Ramírez & Davenport, 2013). Furthermore, lacewings are not included in the Buxton *et al.* (2022) review on the contribution of nocturnal pollinators to agriculture (Buxton et al., 2022). This omission could be because Neuroptera are not strictly nocturnal but can instead be active during the day as well. However, a study on the diel activity patterns of Neuroptera by Vas *et al.* (1999) found that most lacewings were predominantly active during the night (Vas et al., 1999). This aligns with my findings, as lacewings were observed both during the day and night, but with peak activity during the darkest hours of the night (between 00:00 and 03:00). Robertson *et al.* (2021a) found Neuroptera were among the more common insects visiting apple flowers at night where they were regularly observed visiting the anthers of apple flowers and feeding on pollen from a single flower for long durations (Robertson et al., 2021a). Although lacewings observed in my study spent several minutes on a single flower, they were regularly seen moving around from flower to flower during the night.

From an evolutionary perspective, lacewings with elongated mouthparts have been described as early pollinators of gymnosperms who, with the ecological rise of angiosperms, were later replaced by pollinators better adapted to access the nectar of flowering plants (Labandeira et al., 2016). Today, about 5 % of 5868 described species within the Neuroptera order are thought to be regular flower-visiting species (Wardhaugh, 2015). The Neuroptera in my study appeared to be green lacewings, which makes it likely that they are in the Chrysopidae family. Some species within the Chrysopidae family have a combined diet, feeding on floral resources such as nectar and pollen and phytophagous insects (Devetak & Klokočovnik, 2016). As species within the Chrysopidae family feeds on insect pests, they are regularly used as biological pest control in agricultural systems (Stelzl & Devetak, 1999). The most common species within the Chrysopdiae family in Norway is *Chrysoperla carnea,* which is used as a pest control in Norwegian agriculture (Artsdatabanken., 2016b). While the larvae feeds on insects, adults mainly feed on honey dew and nectar (Artsdatabanken., 2016a). In the spring, *C. carnea* is also known to feed on pollen on early flowering trees (e.g. maple) (Artsdatabanken., 2016b). In France, this species has been found to consume pollen from 28 different plant families (Villenave-Chasset et al., 2005). Thus, as Chrysopidae may act as both pest control and as pollinators, they can prove to be particularly useful in agroecosystems. Furthermore, as the proportion of flower-visiting lacewings calculated in the review by Wardhaugh (2015) is only an estimate, much is still unknown and further research is needed to uncover the full pollination potential of lacewings (Wardhaugh, 2015).

4.2. Indications of nocturnal pollination activity

In general, both the quantity and quality of apples from flowers only accessible to pollinators at night was lower than expected, particularly in the context of previous studies (Robertson et al., 2021a). The nocturnal pollinator communities in my sites were limited both in terms of abundance and species richness, and while there were some Neuroptera observed visiting the flowers, the total proportion of visits at night during the whole study period was relatively low. Generally, a diverse pollinator community has been linked to higher levels of pollination (Albrecht et al., 2012; Blüthgen & Klein, 2011) and to promote greater crop pollination (Garibaldi et al., 2013; Rader et al., 2016). Based on this knowledge, it is altogether reasonable that this likely affected both the fruit and seed set in apples developed from flowers only accessible to pollinators at night, resulting in an overall lower outcome in my study. Together with results indicating nocturnal pollination activity, additional factors that may have influenced the results will be examined more closely in the subsequent sections.

4.2.1. Apple quantity (fruit set)

In my study, flowers that had only been accessible to pollinators during the night resulted in a significantly lower fruit set than flowers only accessible during day. These results differ from previous findings by Robertson *et al*. (2021a), where fruit set from the flowers only accessible to nighttime pollinators was similar to the fruit set from flowers only accessible to daytime pollinators. These differences might be explained by the studies being conducted in different geographical zones (at different latitudes), which also affects the timing of sunrise and sunset.

In Arkansas, sunrise was at 07:00 in the morning, while sunset at 20:00 in the evening (Robertson et al., 2021a). Consequently, the day treatment in Robertson *et al.* study was open for about 13 hours, while the night treatment was open for 11 hours each night. In Norway, which is located at a higher latitude, sunset was around 22:00 in the evening and sunrise about 05:00 in the morning during the flowering season, which means the day treatment in my study was open for about 17 hours, and the night treatment was open for about 7 hours. Hence, the nocturnal pollinators in Robertson *et al.* (2021a) study had approximate 60% more time per night to pollinate apple flowers than in my experiment. The substantial difference in time between the studies may explain why the contribution from nighttime pollinators resulted in a lower fruit set in my study.

Another possible explanation is that the distinction between day and night may be arbitrary or more gradual, making it difficult to define the exact cutoff point of where the day ends and night begins. Insects may interpret night and day differently than exactly at sunset and sunrise, and there may be a zone of overlap between the diurnal and nocturnal insects that the exclusion experiment did not account for. Furthermore, moths have been found to be most active during the first two hours after sunset (Robertson, 2023). Since the net position switch was done during this time period, it could potentially have caused disturbance at a critical moment for the night active insects, which may have influenced the overall visitation rate and affected fruit set.

However, exclusion of nocturnal pollinators (day treatment) at Høyen resulted in significantly lower fruit set compared to the permanently open treatment at Berle. This may indicate that some level of nocturnal pollination activity occurs within the landscape. If there was no nocturnal pollination activity, we would expect that exclusion of nighttime pollinators (day treatment) would yield similar results as no pollinator exclusion (permanently open treatment) across all sites and cultivars. Høyen, in general, had fewer night-active pollinators than Berle, which may explain the difference in fruit set across treatments and sites. None-the-less, the subtle, positive effect of nocturnal pollinators between my sites suggests that future studies should include more sites across a broad geographic area to better understand how variation in pollinator communities affects apple production.

4.2.2. Apple quality (seed set)

Several studies have shown that insect pollinators increase the seed set in apples (Garratt et al., 2014; Olhnuud et al., 2022; Samnegård et al., 2019), and a low seed set is considered to be an indication of insufficient levels of pollination and potential pollination deficits in orchards (Webber et al., 2020). In my study, the seed set in the apples harvested from the night treatment had a significantly lower number of seeds compared to the day treatment. This indicates that the pollination services provided by nocturnal pollinators is substantially lower than what is provided by daytime pollinators in my study area. Additionally, exclusion of day active pollinators (night treatment) and all pollinators (permanently closed control) in my study resulted in apples with a similar seed set. These results contradict previous findings by Robertson *et al.* (2021a), where seed set was similar among apples from the night and day treatment, suggesting that comparable levels of pollination services were provided by diurnal and nocturnal pollinators. The underlying cause of the disparity between my results and the findings by Robertson *et al.* (2021a) might be explained by the limited nocturnal pollinator community within my study sites.

However, apples harvested from flowers permanently accessible to pollinators (open treatment) had a significantly higher number of seeds than apples from flowers inaccessible to nighttime pollinators (day treatment). Given that the exclusion of nocturnal pollinators (day treatment) lead to pollination deficits (lower seed set), this suggests that nocturnal pollination activity may be occurring within my study sites.

A number of studies have shown that a low seed set is associated with lower apple quality (Webber et al., 2020) both in terms of shape (Wu et al., 2021) and size (Buccheri & Di Vaio, 2005; Samnegård et al., 2019), which affects the economic value of the fruit (Garratt et al., 2014; Jackson, 2003). Thus, it is likely that the apples harvested from the night and control treatment have a lower quality (and lower market value) compared to apples harvested from the day and open treatment. Apples have been described as having imperfect syncarpy (syncarpous), meaning that the way the transported pollen grains are allocated among the five receptive stigmas affects the seed set distribution (Sheffield et al., 2005). Consequently, if some of the seeds in the carpels do not develop properly (due to the level of pollination), this can cause the apple to grow unevenly, leading to deformed apples and lower market value (Jackson, 2003). However, in a study by Sheffield *et al.* (2005) the apple cultivar "Summerland McIntosh" was found to have perfect syncarpy (Sheffield et al., 2005).

This means that the distribution of pollen among the carpels does not necessarily need to be uniform and as long as at least one of the stigmas receives adequate levels of pollination, a complete seed set can still develop (Sheffield et al., 2005). This may have implications for how seed set is interpreted in relation to apple quality and pollination success. And although multiple studies have linked apple seed set to fruit quality (Garratt et al., 2014; Jackson, 2003; Webber et al., 2020; Wu et al., 2021), the study by Sheffield *et al.* (2005) demonstrates that we may not always be able to automatically assume that a low seed set implies low quality for all apple cultivars. To confirm if the harvested apples from the night and closed treatment truly had lower fruit quality than apples from the day and open treatment in my study, comparisons of additional quality measures, such as size, shape symmetry, and sugar content should be considered.

Lastly, I found that some flowers not accessible to pollinators (closed treatment) developed into some matured apples. Apple cultivars are considered self-incompatible and rely on pollinators to ensure fruit set (Olhnuud et al., 2022; Ramírez & Davenport, 2013), however, the level of self-compatibility varies between cultivars (De Witte et al., 1996; Garratt et al., 2014; Ramírez & Davenport, 2013). This may explain why some apples matured from the closed control treatment, even when pollinators were permanently excluded. Another possibility is that pollen contamination may have occurred; either during the removal and/or reinstallation of the nets or via wind dispersed pollen grains entering through the mesh fabric of the exclosures.

4.3. Conclusion

This case-study provides novel data on the nocturnal pollination services provided by night-active insects in agroecosystems in Norway. Overall, nocturnal pollinators do not seem to play a substantial role in apple pollination in eastern Norway. However, exclusion of night active insects did indicate pollination deficits (lower seed set). As such, the effect of nocturnal pollinators on apple production appears to be nuanced and further studies are needed to better understand where and when nocturnal pollinators are important contributors to agroecological systems.

While the few moths caught in light traps within my study area confirms that moths are present, their absence in camera images suggests they do not visit apple flowers in my study orchards. Since moth populations may experience high between-year variability (Devoto et al., 2011; Macgregor, J. et al., 2019; Robertson, 2023), repeated, long-term studies are needed to gain a complete understanding of the factors affecting moth abundance.

Lacewings (Neuroptera) were the insects observed visiting apple flowers the most during the night in my study and could potentially be contributing to nocturnal pollination of apples. Future studies should aim to test lacewings (Neuroptera) as potential providers of pollination services at night.

Global food crop production is highly reliant upon pollination services by insects (Aizen et al., 2009; Klein et al., 2007). Therefore, the worldwide decline of insects can have serious implications for food production and security (Potts et al., 2010; van der Sluijs & Vaage, 2016). The ongoing decline of diurnal wild bees (Biesmeijer et al., 2006; Burkle et al., 2013; Kearns et al., 1998; Ollerton et al., 2014; Potts et al., 2010; Sánchez-Bayo & Wyckhuys, 2019; Zattara & Aizen, 2021) and the inherent limitations of managed honey bees (Garibaldi et al., 2013; Neov et al., 2019; Sammataro et al., 2000), emphasizes the urgent need to further expand our knowledge on other non-bee, nocturnal pollinators. Preservation of diverse pollinator communities, both diurnal and nocturnal, is fundamental for stabile and resilient global food production.

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Appendix A. Location of field cameras in the orchards

Figure A1. Location of the initial camera locations at the Berle (top) and Høyen (bottom) site.

Appendix B. Pollinator observations: additional tables

Table B1. Camera observations per site and cultivar during the day and night.

	Total visits		Proportion of visits (adjusted)	
	Day	Night	Day	Night
Site				
Berle	1316	87	24.012375	0.46962582
Høyen	712	29	9.405031	0.05188555
Cultivar				
Aroma	677	39	10.179944	0.1236024
Discovery	908	54	19.466377	0.2552266
Summerred	443	23	3.771086	0.1426824

Table B2. Camera observations of the taxonomic groups per site and treatment

Site	**Taxonomic group**	**Total visits**		**Proportion of visits (adjusted)**	
		Day	Night	Day	Night
Berle					
	Neuroptera	24	41	7.339604e-02	0.22048871
	Non-syrphid Diptera	371	46	3.277625e+00	0.24913711
	Bombus	23	0	3.692132e-02	0.00000000
	Apis	810	0	2.036698e+01	0.00000000
	Solitary bees	61	0	2.019745e-01	0.00000000
	Lepidoptera	6	0	7.722571e-03	0.00000000
	Syrphidae	21	0	4.775287e-02	0.00000000
Høyen					
	Neuroptera	7	20	6.341335e-03	0.04139844
	Non-syrphid Diptera	159	9	8.679277e-01	0.01057711
	Bombus	33	0	6.133569e-02	0.00000000
	Apis	471	0	8.401803e+00	0.00000000
	Solitary bees	19	0	3.493139e-02	0.00000000
	Lepidoptera	1	0	8.710801e-04	0.00000000
	Syrphidae	22	0	3.182063e-02	0.00000000

Appendix C. Fruit set: additional tables and figures

Table C1. Number of clusters and apples counted per treatment.

	Number of clusters	Number of apples
Open	621	313
Closed	437	33
Day	338	127
Night	304	18
Total	**1700**	**491**

Table C2. Number of apples counted per treatment, cultivar and site.

		Open	Day	Night	Closed
	Berle				
	Aroma	56	28	1	4
	Discovery	60	32	6	3
	Summerred	61	20	2	3
Total		**177**	**80**	**9**	**10**
	Høyen				
	Aroma	42	13	6	15
	Discovery	41	11	0	2
	Summerred	53	23	3	6
Total		**136**	**47**	**9**	**23**

Table C3. Total number of individual flowers counted per site and cultivar

	Number of flowers		
	Aroma	Discovery	Summerred
Berle	168	170	158
Høyen	145	174	155
Per cultivar	**313**	**344**	**313**
Total		**970**	

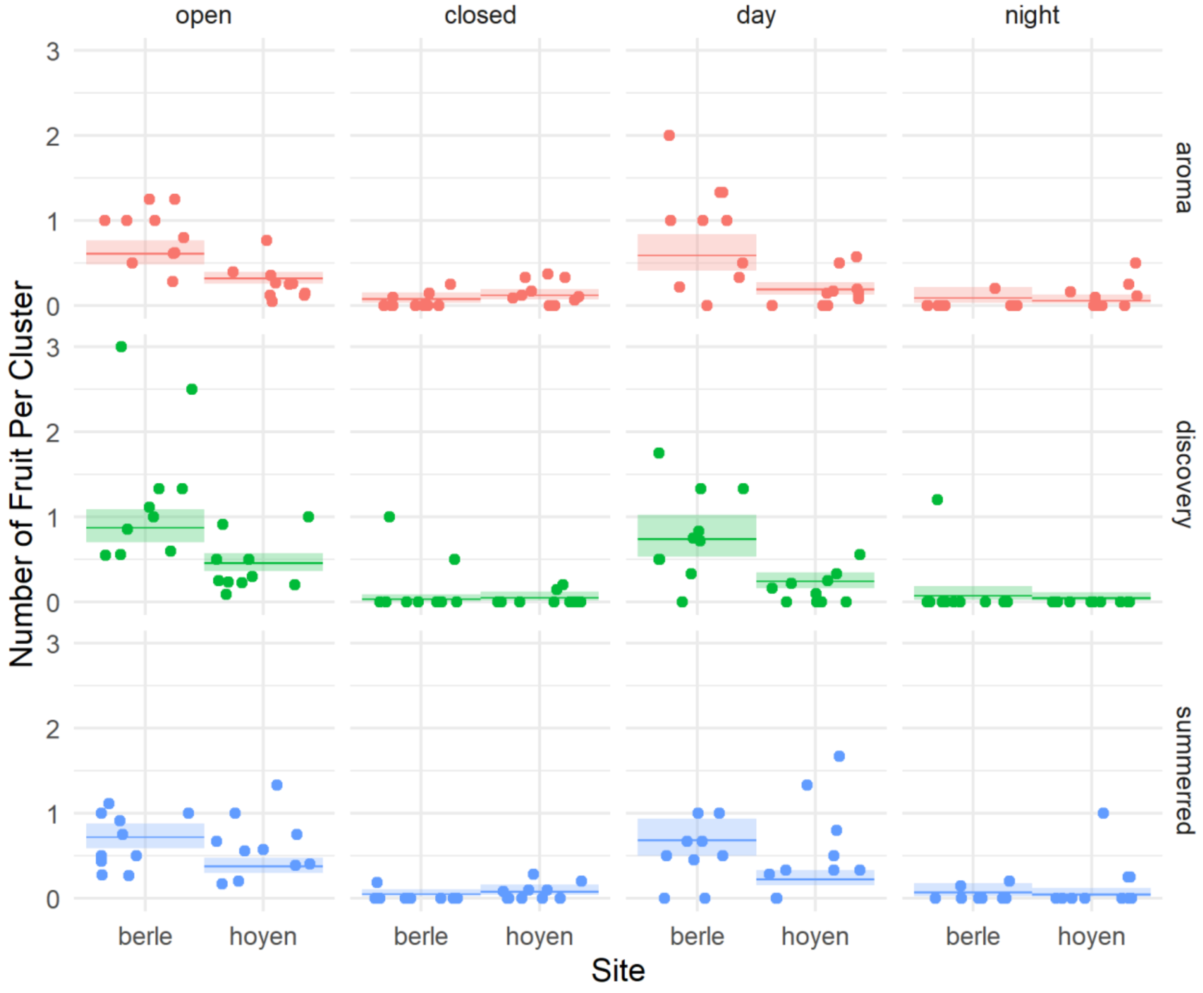

Figure C1. Generalized linear (glm) poisson regression model with predicted number of fruit per cluster. Dots represent the values of the number of fruits per cluster and shaded region represents the 95 % confidence interval predicted by the model. The bold middle line represents the mean prediction made by the model.

Table C4. Tukey multiple comparisons of means with 95 % family-wise confidence interval (post-hoc test) on marginal effects in fruitSet model.

	diff	lwr	upr	P adj
Cultivar				
Discovery – Aroma	0.0036076286	- 0.02099527	0.02821053	0.9361696
Summerred – Aroma	- 0.0000190257	- 0.02454444	0.02450639	0.9999982
Summerred – Discovery	- 0.0036266543	- 0.02822955	0.02097625	0.9355172
Treatment				
Closed – Open	- 0.110262279	- 0.14146217	- 0.0790623917	**0.0000000**
Day – Open	- 0.030603078	- 0.06167160	0.0004654402	0.0552437
Night – Open	- 0.112097258	- 0.14316578	- 0.0810287389	**0.0000000**
Day – Closed	0.079659200	0.04845931	0.1108590876	**0.0000000**
Night – Closed	- 0.001834979	- 0.03303487	0.0293649085	0.9987396
Night – Day	- 0.081494179	- 0.11256270	- 0.0504256605	**0.0000000**
Site				
Høyen – Berle	- 0.03958672	- 0.05634687	- 0.02282656	**5.6e^{-06}**

Bold text indicates significant values P < 0.05

Table C5. Tukey multiple comparisons of means with 95 % family-wise confidence interval (post-hoc test) on interactive effects in fruitSet model.

	diff	lwr	upr	P adj
Cultivar:Treatment				
Summered:Night – Summerred:Open	-0.1035858421	-0.172255267	-0.034916417	**0.0000792**
Summerred:Night – Summerred:Day	-0.0808174983	-0.149486923	-0.012148073	**0.0072723**
Summerred:Night – Summerred:Closed	0.0087349949	-0.059934430	0.077404420	0.9999996
Summerred:Day – Summerred:Open	-0.0227683438	-0.091437769	0.045901081	0.9946432
Summerred:Day – Summerred:Closed	0.0895524932	0.020883068	0.158221918	**0.0014570**
Summerred:Closed – Summerred:Open	-0.1123208370	-0.180990262	-0.043651412	**0.0000108**
Discovery:Night – Discovery:Open	-0.1368783328	-0.205547758	-0.068208908	**0.0000000**
Discovery:Night - Discovery:Day	-0.0732040033	-0.141873428	-0.004534578	**0.0254801**
Discovery:Night – Discovery:Closed	-0.0070937267	-0.076660829	0.062473376	1.0000000
Discovery:Day – Discovery:Open	-0.0636743295	-0.132343754	0.004995095	0.0980662
Discovery:Day – Discovery:Closed	0.0661102766	-0.003456826	0.135677379	0.0798670
Discovery:Closed – Discovery:Open	-0.1297846061	-0.199351709	-0.060217503	**0.0000002**
Aroma:Night – Aroma:Open	-0.0958275978	-0.164497023	-0.027158173	**0.0004153**
Aroma:Night – Aroma:Day	-0.0904610358	-0.159130461	-0.021791611	**0.0012209**
Aroma:Night – Aroma:Closed	-0.0071172346	-0.075786660	0.061552190	1.0000000
Aroma:Day – Aroma:Open	-0.0053665620	-0.074035987	0.063302863	1.0000000
Aroma:Day – Aroma:Closed	0.0833438012	0.014674376	0.152013226	**0.0046495**
Aroma:Closed – Aroma:Open	-0.0887103632	-0.157379788	-0.020040938	**0.0017137**
Treatment:Site				
Night:Høyen – Open:Høyen	-0.0635450553	-0.115484811	-0.011605300	**0.0055741**
Night:Høyen – Day:Høyen	-0.0396734064	-0.091613162	0.012266349	0.2782642
Night:Høyen – Closed:Høyen	-0.0004131341	-0.052352889	0.051526621	1.0000000
Night:Berle – Open:Berle	-0.1606494598	-0.212589215	-0.108709704	**0.0000000**
Night:Berle – Day:Berle	-0.1233149518	-0.175254707	-0.071375197	**0.0000000**
Night:Berle – Closed:Berle	-0.0031942496	-0.055579848	0.049191349	0.9999996
Day:Høyen – Open:Høyen	-0.0238716489	-0.075811404	0.028068106	0.8536274
Day:Høyen – Closed:Høyen	0.0392602724	-0.012679483	0.091200028	0.2912295
Day:Berle – Open:Berle	-0.0373345079	-0.089274263	0.014605247	0.3560581
Day:Berle – Closed:Berle	0.1201207022	0.067735104	0.172506301	**0.0000000**
Closed:Høyen – Open:Høyen	-0.0631319213	-0.115071677	-0.011192166	**0.0060773**
Closed:Berle – Open:Berle	-0.1574552102	-0.209840808	-0.105069612	**0.0000000**

Bold text indicates significant values P < 0.05

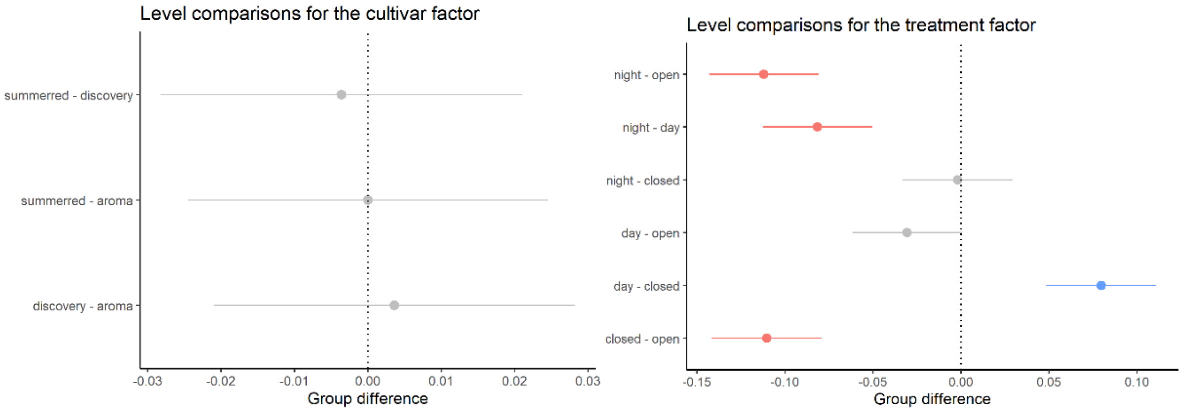

Figure C2. Tukey HSD post-hoc test illustrating the level comparisons for marginal effects on the cultivar (left) and treatment (right) predictor variable on fruitSet model.

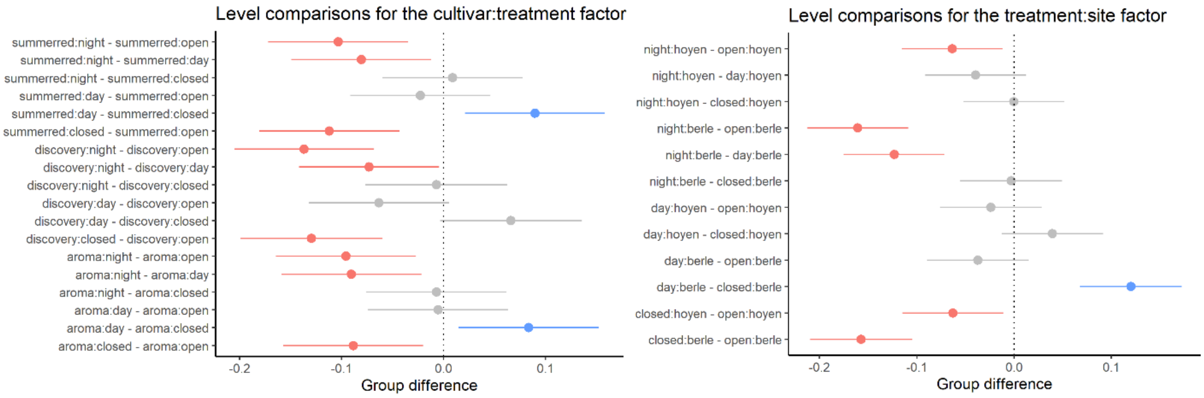

Figure C3. Tukey HSD post-hoc test illustrating the level comparisons on interactive effects on the cultivar:treatment (left) and treatment:site (right) pairwise comparison on fruitSet model.

Appendix D. Seed set: additional tables and figures

Table D1. Mean number of fully developed seeds per apple.

	Mean number of seeds
Open	6.05
Closed	2.09
Day	4.82
Night	2.44

Table D2. Tukey multiple comparisons of means with 95 % family-wise confidence interval (post-hoc test) on marginal effects in seedSet model.

	diff	lwr	upr	P adj
Cultivar				
Summerred – Discovery	-1.862998	-2.5112299	-1.214766	**0.0000000**
Summerred – Aroma	1.105526	0.4676518	1.743400	**0.0001594**
Discovery – Aroma	2.968524	2.3156248	3.621423	**0.0000000**
Treatment				
Open – Night	3.5427264	1.9913221	5.0941306	**0.0000000**
Open – Day	1.2546883	0.5793922	1.9299844	**0.0000133**
Open – Closed	3.3509466	2.1794843	4.5224089	**0.0000000**
Night – Day	-2.2880381	-3.9008329	-0.6752432	**0.0016081**
Night – Closed	-0.1917797	-2.0672547	1.6836952	0.9935784
Day - Closed	2.0962583	0.8446290	3.3478876	**0.0001127**
Site				
Høyen – Berle	-1.084409	-1.528737	-0.6400816	**2.2e-06**

Bold text indicates significant values P < 0.05

Table D3. Tukey multiple comparisons of means with 95 % family-wise confidence interval (post-hoc test) on interactive effects in seedSet model.

	diff	lwr	upr	P adj
Cultivar:Treatment				
Summerred:Open – Summerred:Night	4.6310228	0.905254102	8.3567915	**0.0030205**
Summerred:Open – Summerred:Day	1.6672662	0.195411066	3.1391213	**0.0118479**
Summered:Open – Summerred:Closed	3.8487698	1.025458831	6.6720808	**0.0005793**
Summerred:Night – Summerred:Day	-2.9637566	-6.821373745	0.8938605	0.3278580
Summerred:Night – Summerred:Closed	-0.7822530	-5.330432568	3.7659265	0.9999911
Summerred:Day – Summerred:Closed	2.1815036	-0.813649513	5.1766567	0.4133404
Discovery:Open – Discovery:Night	2.7269915	-0.699387617	6.1533706	0.2747084
Discovery:Open – Discovery:Day	0.5207568	-0.964037113	2.0055507	0.9920265
Discovery:Open – Discovery:Closed	5.6468683	1.911038534	9.3826981	**0.0000612**
Discovery:Night – Discovery:Day	-2.2062347	-5.759830528	1.3473610	0.6662428
Discovery:Night – Discovery:Closed	2.9198768	-2.017719196	7.8574729	0.7318665
Discovery:Day – Discovery:Closed	5.1261116	1.273269314	8.9789538	**0.0009225**
Aroma:Open – Aroma:Night	3.4743254	0.284165684	6.6644852	**0.0195327**
Aroma:Open – Aroma:Day	1.5871093	0.070470091	3.1037485	**0.0310433**
Aroma:Open – Aroma:Closed	2.6493093	0.605299693	4.6933189	**0.0014845**
Aroma:Night – Aroma:Day	-1.8872162	-5.221937194	1.4475049	0.7839653
Aroma:Night – Aroma:Closed	-0.8250161	-4.430310195	2.7802779	0.9998413
Aroma:Day – Aroma:Closed	1.0622000	-1.200811351	3.3252114	0.9281474
Treatment:Site				
Open:Høyen – Night:Høyen	3.1943057	0.59282659	5.79578474	**0.0050852**
Open:Høyen – Day:Høyen	1.5189918	0.22980944	2.80817425	**0.0087638**
Open:Høyen – Closed:Høyen	2.9277232	1.22363430	4.63181200	**0.0000070**
Open:Berle – Night:Berle	3.7493639	1.16665395	6.33207377	**0.0003257**
Open:Berle – Day:Berle	1.2210682	0.20280044	2.23933590	**0.0069892**
Open:Berle – Closed:Berle	3.3868624	0.93011100	5.84361383	**0.0008409**
Night:Høyen – Day:Høyen	-1.6753138	-4.43022892	1.07960128	0.5851171
Night:Høyen – Closed:Høyen	-0.2665825	-3.23836392	2.70519890	0.9999944
Night:Berle – Day:Berle	-2.5282957	-5.18568877	0.12909739	0.0755361
Night:Berle – Closed:Berle	-0.3625014	-3.83532398	3.11032108	0.9999841
Day:Høyen – Closed:Høyen	1.4087313	-0.52149734	3.33895995	0.3403861
Day:Berle – Closed:Berle	2.1657942	-0.36935368	4.70094217	0.1580803

Bold text indicates significant values P < 0.05

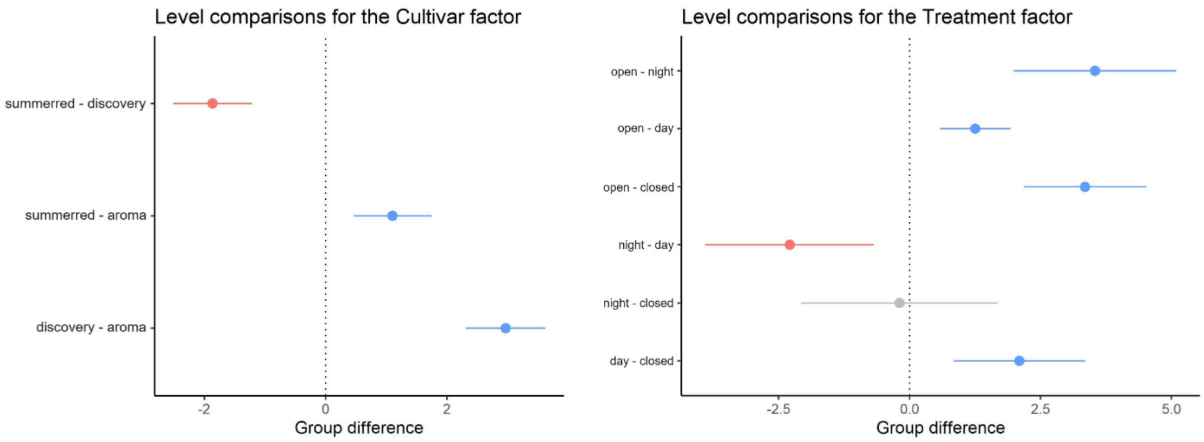

Figure D1. Tukey HSD post-hoc test illustrating the level comparisons on marginal effects on the cultivar (left) and treatment (right) predictor variable on the seed set response variable.

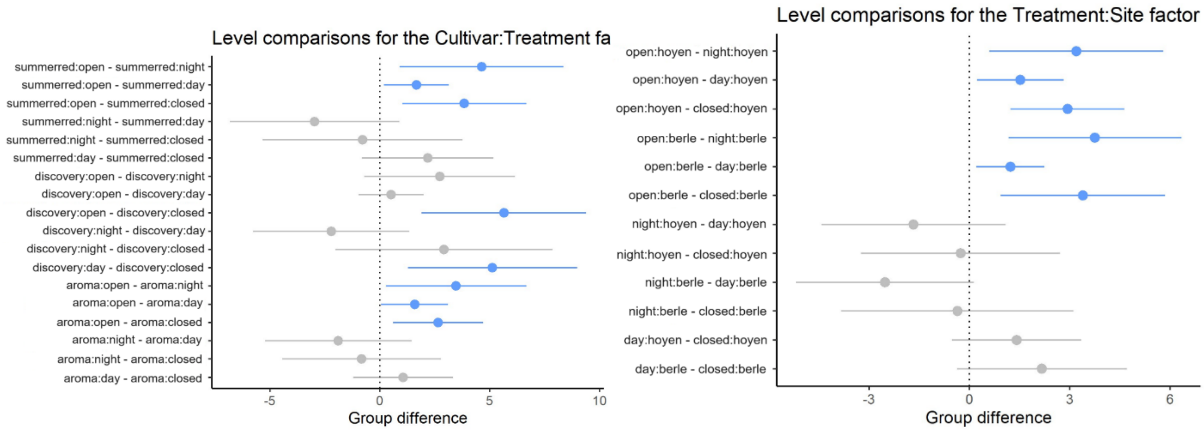

Figure D2. Tukey HSD post-hoc test illustrating the level comparisons on interactive effects on the cultivar:treatment (left) and treatment:site (right) pairwise comparison on the seed set response variable.

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