

POLLINATOR EFFECTIVENESS AND POLLINATION DEPENDENCY OF BILBERRY (*VACCINIUM MYRTILLUS*) IN SWEDISH HEMI-BOREAL FORESTS

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Abstract—Intensification of forest management to increase production of biomass has resulted in considerable habitat degradation with negative impacts on insect biodiversity, including beneficial insect groups such as pollinators. Yet, little is known about how reliant forest understory plants, such as bilberry (*Vaccinium myrtillus*), are on insect pollinators for reproduction. Here, we quantified the structure of the bilberry flower visitor community, compared the pollination effectiveness of the most common pollinators, and experimentally quantified bilberry pollination dependency. The bilberry pollinator community was comprised of several bee and hoverfly taxa. Bumblebees were the most important pollinators due to their high abundance and pollination effectiveness. Other bees, in particular, *Andrena* spp., and to a smaller extent, hoverflies, were also effective pollinators. Furthermore, bilberry was strongly pollen-limited, with only 40% of open-pollinated flowers setting fruit. Bilberry supports a diverse flower visitor community within hemi-boreal forests, for which it is highly dependent for reproduction. Given the ecological and cultural value of bilberry, the importance of insect pollinators for understory plants should be considered within forest management strategies.

Keywords—Bilberry, forest pollinators, pollination effectiveness, dwarf shrub

INTRODUCTION

Anthropogenic land-use changes leading to habitat loss and deterioration are key drivers of global biodiversity declines, which threaten to destabilise ecosystem functions related to animal pollination (Potts et al., 2010; Winfree, 2013). Given that the vast majority of all flowering plants and many important crops benefit from animal pollination, these declines could potentially negatively impact the diversity of wild plant communities as well as crop production worldwide (Klein et al. 2007; Potts et al. 2010; Ollerton et al. 2011). The world's largest terrestrial biome, the boreal forest, is home to an estimated 100 000 species across taxa, of which 20% have been identified (Ruckstuhl et al. 2008; Burton et al. 2010). In Sweden, most forest is boreal or hemi-boreal (Larsson et al. 2011), and covers 69% of the total land-area, of which 78% is under active management for timber production (Statistics Sweden 2019; Swedish NFI 2022). Over the last

century, Swedish forests have undergone similar rapid changes as many landscapes in Europe, with an intensification of management practices for production, introduction of monocultures and loss of natural habitats (Östlund 2004; Nilsson et al. 2021). This intensive management results on a homogenisation of forest stand age and an increase of stand density, decreasing forest structure heterogeneity and thus reducing the diversity of available habitats. This has had a massive impact on forest biodiversity with several species now in decline (Berg et al. 1995; Östlund 2004; SLU Artdatabanken 2020; Naturvårdsverket 2023), despite bird populations increasing in Swedish forests (Ram et al. 2017). In order to mitigate against biodiversity declines in boreal forests, conservation actions such as landscape restoration, maintaining old forest characteristics and the reintroduction of disturbance dynamics are now required (Hanski 2011; Angelstam et al. 2020; Berglund & Kuuluvainen 2021).

Insects form a significant component of boreal forest ecosystems, as pollinators, decomposers, and agents of large-scale disturbances (Ruckstuhl et al. 2008; Ulyshen 2016; Eckerter et al. 2019). Research on forest insect communities in Scandinavia has primarily focused on saproxylic beetles (Hyvärinen et al. 2009; Heikkala et al. 2016; Gustafsson et al. 2020). In contrast, little is known about the functioning of forest insect pollinator communities, as most studies on pollinators have been undertaken in agricultural systems (e.g. Öckinger & Smith 2006; Ekroos et al. 2013; Raderschall et al. 2021). Studies have demonstrated that pollinators benefit from semi-natural, floral rich habitats in agricultural landscapes (Persson et al. 2015; Söderman et al. 2016), but it is uncertain how these relationships translate to pollinators resident in forest ecosystems. To better understand these relationships, research is needed to assess how pollinator communities vary in space and time depending on forest characteristics and management types, and how these communities are linked to flowering plants (Rivers et al. 2018).

Throughout boreal forests, the European bilberry (*Vaccinium myrtillus*) is the dominant component of the understory. This deciduous dwarf shrub is a keystone species widespread in spruce- and pine-dominated heath forests in Europe and large parts of Asia (Nestby et al. 2011; Boulanger-Lapointe et al. 2017). Bilberry is a crucial early-season floral resource for emergent bumblebee queens (Moquet et al. 2017b; Andresen 2019), and supports diverse pollinator communities, including numerous bee and hoverfly species (Rodríguez & Kouki 2015; Moquet et al. 2017a; Eckerter et al. 2021). Bilberry can be affected by forest management practices such as clear-cutting and plantation of young, dense conifer stands due to the extreme changes in light availability seen after these interventions (Hedwall et al. 2013; Rodríguez & Kouki 2015; Löhmus & Remm 2017). As a result, bilberry coverage has decreased by 22% in Sweden's managed forests from 1999 to 2015, while tree stem density has increased by more than 27% since 1985 (Jonsson et al. 2021; Swedish NFI 2022). Even though bilberry is capable of self-pollination, the *Vaccinium* genus is highly dependent on insect pollination (Nuortila et al. 2002; Jones et al. 2014). Considering its wide distribution throughout the northern hemisphere

and role as a keystone species in both managed and natural forests, bilberry is an ideal model plant species for monitoring forest structure effects on early-season pollinator communities (Jones et al. 2014).

In this study, we quantify the structure of bilberry pollinator community and assess their importance as bilberry pollinators. Specifically, we address the following questions:

1. What is the structure and composition of the bilberry flower visitor communities?
2. How dependent is bilberry on insect-pollination for reproduction?
3. How do bilberry pollinators differ in their pollination effectiveness?

MATERIALS AND METHODS

STUDY AREA AND DESIGN

This study was conducted during the spring of 2021 in the vicinity of SLU Asa Research Station located in SE Sweden, 37 kilometres north of Växjö (57°10'N, 14°47'E). This area is dominated by boreal forest and is situated at a high plateau with a mean elevation of 224 metres above sea level, with an annual rainfall of 827 mm per year and average temperature spanning from 16.8 °C in July and -1.9 °C in January (SMHI 2021). The study design included six sites with favourable stand densities for bilberry growth (20–40 m² per hectare) (Eldegard et al. 2019), in both managed and natural hemi-boreal forests. The sites were comprised of mature stands of Norway spruce (*Picea abies*) (57% for both managed and natural sites) and Scots pine (*Pinus sylvestris*) (38% vs. 25%, respectively) with an occasional mix of birch (*Betula pubescens*) and juniper (*Juniperus osteosperma*) (1%). The understory flora consisted primarily of bilberry and lingonberry (*V. vitis-idaea*) shrubs and a mossy ground layer. To ensure independence between pollinator communities at each site, sites were separated by at least 1 km in line with predictions of most bee foraging ranges being less than 1 km (Kendall et al. 2022), and more than 100 m from the forest edge to avoid edge effects (Bailey et al. 2014). At each site, we established five 3 x 3 m focal plots to observe bilberry pollinators.

FLOWER VISITOR SURVEYS

We recorded flower visitors to bilberries during 20-minute surveys in each of the 30 focal plots for the entirety of the bilberry bloom from May 14 to June 3. Observations were undertaken at two different time intervals (09.00-13.30 and 13.30-18.00, respectively) at each site on three days, resulting in a total of five hours of observation per site and one hour per plot within each site. Conditions for observation were met when temperatures exceeded 10 °C and wind speed was <2 m/s, and no precipitation. We quantified bilberry floral density by counting the number of open bilberry flowers in five quadrats located on the focal plot at the end of each observation. We classified hoverflies and solitary bees as groups and, when possible, determined bumblebees (*Bombus*) to species and caste. The four species *Bombus lucorum*, *B. terrestris*, *B. magnus*, and *B. cryptarum* are referred to as *B. lucorum* complex since they cannot be confidently identified by morphological characters in the field (Carolan et al. 2012). We also identified honeybees (*Apis mellifera*) to species in the field. Voucher specimens of both hoverflies and solitary bees were also collected for later identification to genus, or species level.

SINGLE VISIT POLLEN DEPOSITION

To assess bees and hoverflies pollination effectiveness of bilberry, we measured single visit pollen deposition (SVD) rates of the most abundant species (Ne'eman et al. 2010). The method involves counting the pollen grains deposited on a stigma of a flower during a single visit of a pollinator. To determine single-visit pollen deposition rates, immature inflorescences (prior to anthesis) were randomly selected and covered with organza bags that exclude pollinators but are permeable to air. Upon anthesis, we randomly assigned covered inflorescence to three treatments: (i) *closed-pollination*: flowers bagged for the entire duration of flowering to prevent floral visitation; (ii) *open-pollination*: flowers were left exposed to flower visitors for the duration of flowering; (iii) *single visit treatment*. For the single visit treatment, we cut three to five inflorescences at the stem and tied them together to form a bouquet, which was then offered to flower visitors. Upon visitation, the pollinator was left undisturbed for the entire duration of the visit. We defined a legitimate visit as one where the insect

actively foraged for nectar or pollen from the bilberry flower by inserting their head or proboscis into the corolla opening. We recorded if the insect buzz-pollinated the flower or foraged without buzz-pollinating. If possible, flower visitors were caught in a net after visitation for identification. We separated the stigma from the flower using forceps and placed it onto a microscope slide with a cube of glycerine jelly mixed with basic fuchsin stain, which binds to protein within pollen grains, making them more visible (Brunel Microscopes Ltd., UK). The jelly was then heated, causing it to melt and sealed using a cover slip and clear nail polish. We used the same collection method for the open- and closed pollination treatments. All SVDs were done at a single site. Bilberry pollen can be identified from its tetrad shape, distinguishing them from other pollen. We counted the number of pollen grains by using traverse inspection under a x 10 magnification microscope.

POLLINATION EXPERIMENT

To evaluate pollination dependence of bilberry, we undertook a pollination experiment alongside each observation plot. We randomly selected 20 bilberry flowers prior to anthesis. All tagged flowers were assigned to two treatments: (i) *open-pollination*: flowers left exposed to flower visitors for the duration of the bilberry bloom; (ii) *closed-pollination*: flowers covered with organza bags to prevent floral visitation. One month after the end of the flowering period, we quantified fruit set as the proportion of tagged flowers that were developing into fruit.

STATISTICAL ANALYSIS

We carried out all data analyses in R v4.3.1 (R Core Team 2023).

Abundance and species richness

We used taxa accumulation curves to assess sampling coverage of the bilberry flower visitor community. We then assessed differences among flower visitor by quantifying the relative abundance of each flower visitor taxon. Species accumulation curves were constructed using the *vegan* package (Oksanen et al. 2022).

Single visit pollen deposition and foraging behaviour

All generalised linear (mixed) models (GL(M)Ms) were fitted using *glmmTMB* (v1.1.3; Brooks et al. 2017). All presented models passed

tests of normality and dispersion within the DHARMA package (v0.4.5; Hartig 2022).

To compare the pollination effectiveness of different flower visitor species and taxa, we analysed single visit pollen deposition (SVD) using a negative binomial GLMM. SVD was modelled as a function of species (bumblebees, honeybees) or taxa (*Andrena*, hoverflies, pollination treatments) (see Table S1). Species-level identification was not possible for *Andrena* and hoverflies within SVD experiments, so these were modelled at the genus and family level respectively. We analysed bumblebees and honeybees (*Apis mellifera*) as species, and solitary bees and hoverflies as groups. Given pollinator behaviour, and in particular buzz pollination in bumblebees is known to influence pollination effectiveness in bilberry (Moquet et al. 2017a), we also modelled single visit pollen deposition rates as a function of bumblebee behaviour (two levels: buzzing and non-buzzing individuals). SVD models were specified with negative binomial distributions, and we also allowed the dispersion parameter of the distribution to vary among taxon groups.

Pollination success

We specified a binomial GLMM to analyse the probability of fruit set as a function of treatment (two levels: open-pollination or closed-pollination). This model was a random effect of plot nested within site.

RESULTS

FLOWER VISITOR SURVEYS

In total, we counted 729 flower visitors to bilberry throughout 30 observation hours. The species accumulation curve showed that the flower visitor community was well-sampled (Fig. 1A). Hoverflies made up 77% of the recorded flower visitors, with bees making up the remaining 23% (bumblebees: 21% and other bees 2%) (Fig. 1B). The flower visitor community consisted of seven bumblebee species: *B. hypnorum*, *B. lucorum*, *B. hortorum*, *B. sylvestris*, *B. pascuorum*, *B. pratorum* and *B. soroeensis*, nine solitary bee species: *Andrena clarkella*, *A. fucata*, *A. fulva*, *A. haemorrhhoa*, *A. lapponica*, *A. nigriceps* and *A. nigroaenea*, *Lasioglossum* (one morphospecies), and *Osmia uncinata*, and species of nine syrphid genera (*Blera*, *Chrysotoxum*, *Epistrophe*, *Helophilus*, *Melangyna*, *Meliscaeva*, *Parasyrphus*, *Platycheirus* and *Syrphus*).

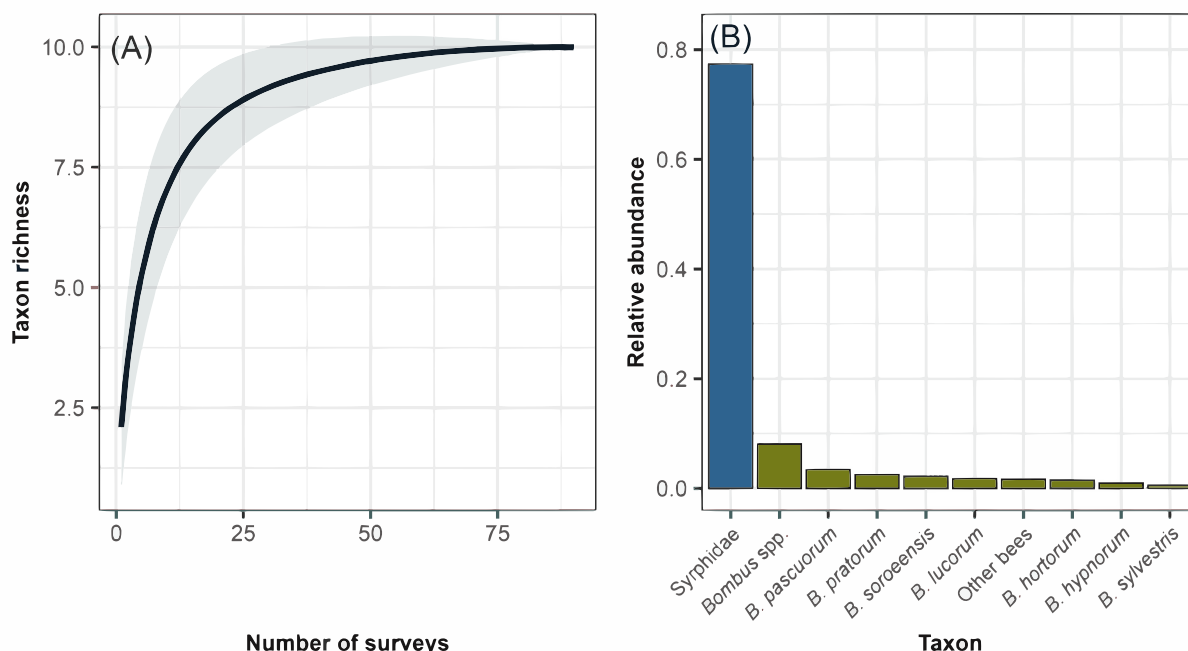


Figure 1. A) Taxon accumulation curve of bilberry flower visitor community, showing total number of species in relation to sampling effort. Shaded ribbon is the standard deviation of the richness estimate. B) Rank-abundance of observed flower visiting taxa.

SINGLE VISIT POLLEN DEPOSITION

Single visit pollen deposition (SVD) was measured for 60 individual pollinators, including five species of bumblebees (37 individuals), seven individuals of solitary bees (all *Andrena* spp.), four individuals of honeybees and 12 hoverfly individuals (mixed genera, Fig. 2). All groups of flower visitors deposited pollen grains (i.e. pollen deposition was higher than the closed pollination treatment), but SVD varied considerably between taxa (Table S1). *Bombus soroensis* and *Andrena* spp. deposited, on average, the most pollen grains per visit (163 and 160 respectively) and *B. hypnorum*, *B. lucorum*, *B. pascuorum*, *B. pratorum* and honeybees deposited similar amounts at one visit as the open pollination treatment. Hoverflies, in general, deposited less pollen grains than bees, although still significantly more than the closed pollination treatment. Buzz-pollinating bumblebee foragers deposited more pollen grains than non-buzzing foragers ($Z = 2.429$, $P = 0.015$).

POLLINATION SUCCESS

We found that open pollination led to statistically greater fruit set than closed-pollinated flowers ($Z = 7.56$, $P < 0.0001$). Open pollination led to significantly greater fruit set, 40.33% [29.71 – 51.94%, C.I.], than closed pollination: 0.58% [0.16 – 2.05% C.I.].

DISCUSSION

This study shows that bilberry within hemi-boreal forests supports a diverse flower visitor community. Bees were the most effective bilberry pollinators, with most species depositing large amounts of pollen grains per single visit, and significantly contributing to pollen deposition compared to flowers without insect visitation (i.e., closed pollination). In contrast, hoverflies were less effective as pollinators than bees on a per visit basis, however they likely contribute to pollination success due to their high relative abundance (Rader et al. 2009; Bernauer et al. 2022). Furthermore, we found strong evidence of pollen limitation in bilberry. These results demonstrate the importance of insect pollinators within forest ecosystems and highlight the importance of these habitats during the early summer for insect pollinator communities.

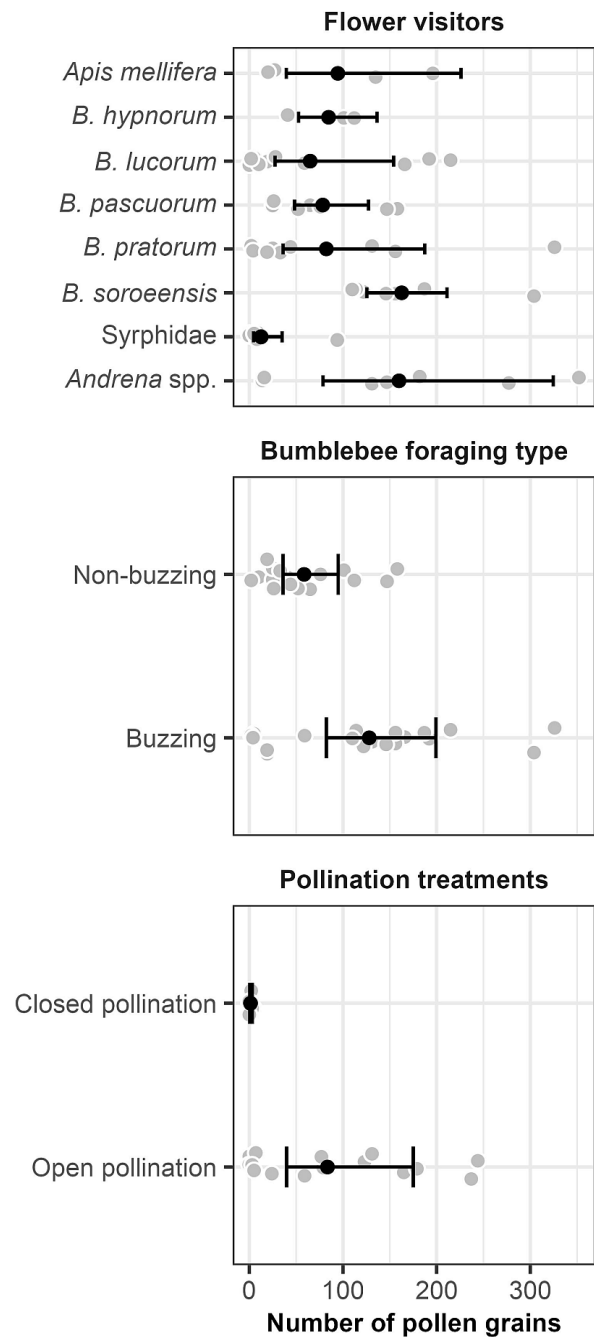


Figure 2. Single visit pollen deposition by species of each taxon group (top), foraging type in bumblebees (middle), or between pollination treatments (bottom). Black dots and error bars are mean \pm 95% confidence intervals and background grey points are actual data.

Consistent with other studies, bumblebees were the most important pollinators in this system due to both their high pollination effectiveness and abundance (Jacquemart 1993; Moquet et al. 2017a; Eckert et al. 2019; Bartholomée et al. 2023). Also, in congruence with other studies done on the *Vaccinium* genus, solitary *Andrena* bees, and honeybees were highly effective bilberry

pollinators (Benjamin et al. 2014; Moquet et al. 2017a). Buzz-pollinating foragers deposited more pollen grains than non-buzzing individuals. Even though buzz pollination allows bees to deposit and collect more pollen grains, non-buzzing foraging bees also result in high rates of pollen deposition, as has been observed in the closely related highbush blueberry (*Vaccinium corymbosum*) (Courcelles et al. 2013; Benjamin et al. 2014). We also suggest that hoverflies might be important bilberry pollinators despite their low effectiveness, given their high relative abundance. It was recently discovered that hoverflies can produce thoracic vibrations that release pollen from buzz-pollinated flowers, which emphasizes their potential role as a *Vaccinium* pollinator (De Luca & Vallejo-Marín 2013; Vallejo-Marín & Vallejo 2021). As such, further research is now required to examine the pollination effectiveness of hoverflies to bilberry, reinforcing their role in providing ecosystem services, depending on their life stage: biological control of pests and recycling of organic material as larvae, as well as pollination and long-distance pollen transfer as adults (Moquet et al. 2018; Doyle et al. 2020).

Insect pollination is highly important for bilberry fruit development, as demonstrated by the large deficit in fruit set resulting from closed-pollinated flowers relative to open-pollinated flowers. The maximal fruit set of this study – 41% – is much lower than the 80% reached in a Finnish bilberry pollination experiment (Nuortila et al. 2006) and is indicative of strong pollen limitation, suggesting an insufficient number of pollinators occurring in our system. However, bilberries are known to have cyclic years of fruit production with years of high floral availability (Swedish NFI 2022), and mass-flowering events, such as those that occur in bilberry stands, may dilute populations of flower visitors throughout the landscape, leading to reduced pollination (Holzschuh et al. 2011). Undertaking hand-pollination experiments, which can quantify maximal pollination rates, in the absence of pollen limitation, in comparison with open-pollination, would be required to confirm these hypotheses. This would enable a greater understanding of the vulnerability of bilberry to pollination deficits, and aid in identifying forest management practises that improve pollination rates.

In conclusion, we show that hemi-boreal forests play host to a diverse flower visitor community that contributes to bilberry pollination. This provides incentive to incorporate pollinator conservation into forest management practices. Moreover, considering the cultural and recreational values of picking bilberries, conserving healthy, high-yielding forests is also important for anthropological concerns (Kangas & Markkanen 2001). Therefore, conservation efforts that benefit forest-dwelling pollinators, such as the promotion and maintenance of a flowering understory, creation of nesting habitats, and/or maintaining connectivity among forest habitat patches, might be of high value in these environments.

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AUTHOR CONTRIBUTION

Concept and design DS & EC, data collection EC, data analysis DS, writing DS, edits and approval for publication DS & EC." to "Concept and design OB, JB, & LK, data collection OB, JB, & LK, data analysis JB & LK, writing JB, edits and approval for publication OB, JB, LK & HS.

DISCLOSURE STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data are available upon request.

APPENDICES

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

Appendix I. Details of the single visit pollen depositions

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