



*“Here the ringing in my ear,  
The distant hum of doom,  
I know to avoid the stinging tail,  
Of the bumblebee buzz flying in to view.”*

- Bumblebee Buzz, Bumblebee Dear by Simon Clark, 2005

Master thesis

# **“What’s the buzz with bilberries?” – Bilberry pollinator community structure and function in relation to forest type and habitat structure**

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## Abstract

Over the last century, Swedish forests have undergone rapid land-use change due to intensification of management practices for timber production and the introduction of monocultures, which have resulted in considerable habitat loss and negative impacts to biodiversity. Insects form a significant component of forest biodiversity, yet forest-dwelling pollinators remain understudied, and little is known about how management strategies affect forest insect pollinator communities. The European bilberry (*Vaccinium myrtillus*), which forms a dominant component of Swedish forests' understory, is highly dependent on insect pollinators and is sensitive to habitat changes due to forest management. Here, I investigated how the structure and function of bilberry pollinator community differed between forest types (natural vs. managed forest) as well as in response to habitat structure variables (stand basal area, deadwood volume and floral density). Firstly, I recorded the abundance and diversity of the main bilberry floral visitors (nine bee species and four hoverfly morphospecies) in each forest type throughout the bilberry flowering period. Secondly, I conducted a pollination experiment to compare the pollinator effectiveness (*i.e.*, pollen deposition per single visit), of the most common floral visitor taxa, and quantify bilberry pollination dependency (*i.e.*, probability of fruit set with or without insect pollination).

I found that bumblebees were the most important pollinators in this system due to their high pollination effectiveness and abundance, but solitary bees, honeybees and hoverflies were also effective pollinators on a per visit basis. Deadwood availability and stem basal area were important determinants of bee community structure. The hoverfly community composition differed between forest types, which was likely driven by the higher floral densities in the managed forests. Furthermore, I found that bilberry was strongly pollen-limited; with only 40% of open-pollinated

flowers developing into fruit. This study demonstrates that natural and managed forests can host similar, diverse floral visitor communities, which contribute significantly to bilberry pollination, and therefore fruit development. Given the ecological and cultural importance of bilberry within boreal forests, forest management should consider the importance of mature forests as valuable habitats for insect pollinators, for example by keeping stands that differ in age and deadwood availability.

**Keywords:** Bilberry, biodiversity, conservation, ecosystem services, forest management, pollination.

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# 1 | Introduction

Anthropogenic land-use changes leading to habitat loss, landscape fragmentation and reduction of resource availability are key drivers of global biodiversity declines, which threatens to destabilise ecosystem functions related to animal pollination (Potts *et al.*, 2010; Winfree, 2013). Given that over 87% of all flowering plants are animal pollinated, these declines could potentially have catastrophic consequences for food production and negatively impact the diversity of wild plant communities worldwide (Potts *et al.*, 2010; Ollerton *et al.*, 2011). To counteract insect declines, strategies that decelerate landscape homogenization, such as ecological intensification and creation of semi-natural habitats in fragmented landscapes have been proposed (Potts *et al.*, 2016). Yet, how land management strategies can mitigate pollinator loss on larger scales and how stabilising mechanisms between different ecosystems interact, requires further attention (Winfree, 2013; Marini *et al.*, 2019).

The world's largest terrestrial biome, the boreal forest, is home to approximately 100 000 different species and stretches from Canada through northern Asia and Siberia to Scandinavia (Ruckstuhl *et al.*, 2008; Burton *et al.*, 2010). In Sweden, forest covers 69% of the total land-area, of which 78% is under active management for timber production (SCB, 2015; 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 (Krebs *et al.*, 1999; Östlund, 2004; Skogsdata, 2021; Stoate *et al.*, 2001). This intensive management has had a massive impact on forest biodiversity with several species now in decline (Berg *et al.*, 1995; Östlund, 2004; SLU artdatabanken, 2020). 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 and Kuuluvainen, 2021).

Insects form a significant component of boreal forest ecosystems, as pollinators, decomposers and agents of large-scale disturbances (Eckerter *et al.*, 2021; Ruckstuhl *et al.*, 2008; Ulyshen, 2016). Research on the effects of forest management on insect communities in Scandinavia has primarily focused on saproxylic beetles (Hyvärinen, Kouki and Martikainen, 2009; Heikkala *et al.*, 2016; Gustafsson *et al.*, 2020). However, little is known about how management strategies affect forest insect pollinator communities, as the majority of studies on pollinators have been undertaken in agricultural systems (Öckinger and Smith, 2007; Ekroos, Rundlöf and Smith, 2013; Raderschall *et al.*, 2021). Studies have demonstrated that pollinators benefit from semi-natural, floral rich habitats in agricultural landscapes and overall landscape complexity (Persson *et al.*, 2015; Söderman *et al.*, 2016) but it is uncertain how these relationships translate to pollinators resident in forest ecosystems, and with respect to forest management strategies. 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). Adding to this, measuring pollination rates and pollinator effectiveness further improves our understanding of flower visitor and plant interactions, making it possible to detect pollination deficiencies linked to pollinator declines (Ballantyne *et al.*, 2017; Thomson, 2001).

In Sweden, the European bilberry (*Vaccinium myrtillus*) is the dominant component of the forest understory (Skogsdata, 2021). It is a deciduous dwarf shrub widespread in spruce- and pine dominated heath forests in Europe and large parts of Asia and is a keystone food source for several ungulate, rodent, and bird species (Ericson, 1977; Nestby *et al.*, 2011; Boulanger-Lapointe *et al.*,

2017). Bilberry is also regarded as a crucial early-season floral resource for emergent bumblebee queens, as their nest searching coincides with the bilberry flowering period (Lundberg and Ranta, 1980). Further, diverse pollinator communities are related to bilberry with a large variety of bees (*Anthophila*) and hoverflies (*Diptera*) (Rodríguez and Kouki, 2015; Moquet *et al.*, 2018; Eckerter *et al.*, 2021).

Bilberry is sensitive to habitat changes due to forest management methods such as clear-cutting and plantation of young, dense conifer stands due to the extreme changes in light availability seen after these interventions (Eriksson, 2011; Hedwall *et al.*, 2013; Rodríguez and Kouki, 2015; Lõhmus and 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 (Swedish NFI, 2022). Even though bilberry is capable of self-pollination, the *Vaccinium* genus is highly dependent on insect pollination (Margariet *et al.*, 2000; Jones *et al.*, 2014). Pollen has two major functions, both as a reward for pollinators to visit flowers and as a carrier of genetic material. To ensure that sufficient pollen is not only consumed but also stored on the body of a floral visitor, approximately 9% of all flowering plants, including bilberry, release pollen when stimulated with vibration through a technique called "buzz pollination" (Buchmann, 1985; De Luca and Vallejo-Marín, 2013). Bees (*Anthophila*) and some hoverflies (*Syrphidae*) are important bilberry pollinators as they can generate sonic waves that effectively remove pollen from a flower's poricidal anthers (Buchmann, 1985; Vallejo-Marín and Vallejo, 2021; Moquet *et al.*, 2017). 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 management effects on early-season pollinator communities (Jones *et al.*, 2014).



In this study, I investigate bilberry pollinator community structure and function in relation to forest type and habitat structure, to determine how pollinators differ between natural and managed forests and assess their importance as bilberry pollinators. I specifically address the following questions:

- i) How does the structure of bilberry pollinator community composition differ between natural and managed forests?
- ii) Are differences among bilberry pollinator communities (abundance and species richness) mediated by forest structure and / or the availability of floral resources?
- iii) How do bilberry pollinators differ in their pollination effectiveness (single visit pollen deposition) and how does bilberry reproductive success vary between managed and natural forests?

## 2 | Methods

### 2.1 | Study area and design

I conducted my study 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) (fig. 1). 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 two different forest types: i) managed pine and spruce forests and ii) nature reserves consisting of natural forest. The managed sites were comprised of mature stands of Norway spruce (*Picea abies*) (57%) and Scots pine (*Pinus sylvestris*) (38%) in ages 48 – 155 years old (stem density 240 – 380 per hectare, basal area 26.4 m<sup>2</sup>ha<sup>-1</sup>) with an occasional mix of birch (*Betula pubescens*) (5%) and juniper (*Juniperus communis*)

(1%). The natural sites were dominated by Norway spruce (57%) interspersed with Scots pine (25%), birch (17%) and juniper (<1%) (stem density 470 - 580 per hectare, basal area 31.9 m<sup>2</sup>ha<sup>-1</sup>). The understory consisted mainly of bilberry and lingonberry (*V. vitis-idaea*) shrubs and a ground layer with a variety of mosses.

In order to conduct my study, I selected three sites with favourable stand densities for bilberry growth (20–40 m<sup>2</sup> ha<sup>-1</sup>) within each forest type (Eldegard *et al.*, 2019). To ensure independence between pollinator communities at each sites, I selected sites separated by at least 1 km (Kremen *et al.*, 2004) and more than 100 m from the forest edge to avoid edge effects (Bailey *et al.*, 2014). At each site, I established five 10 m x 10 m plots to measure forest structure. I then set up a 3 m x 3 m focal plot at the centre of each forest structure plot to observe bilberry pollinators (fig. 2).

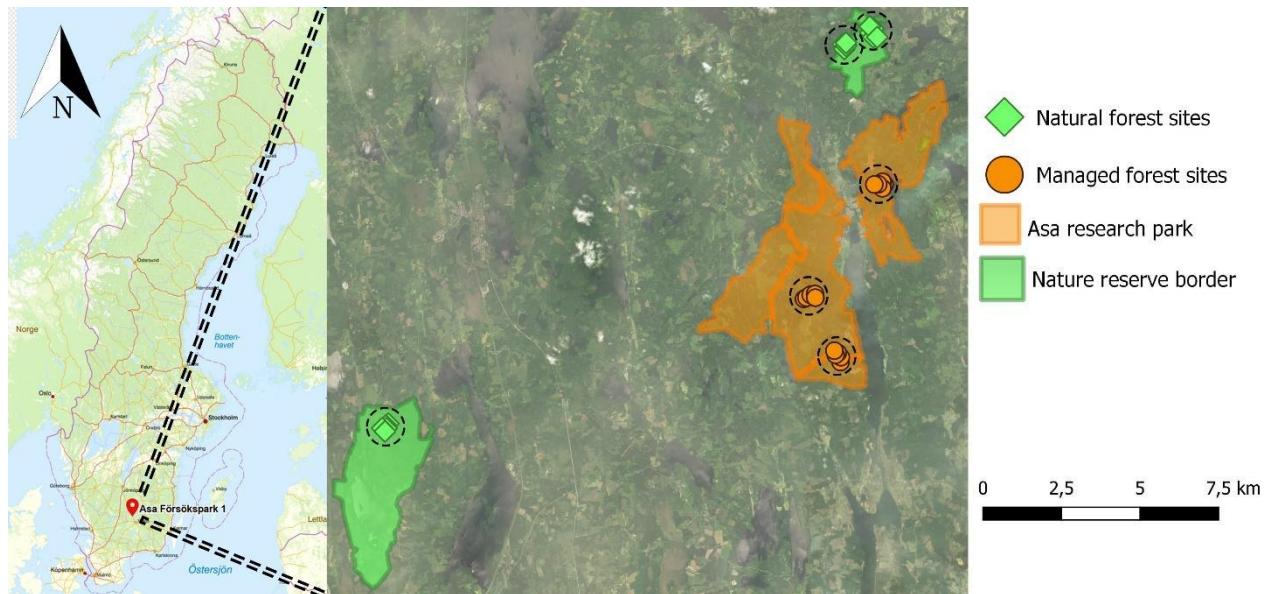


Figure 1. Location of study sites in Småland, Sweden.

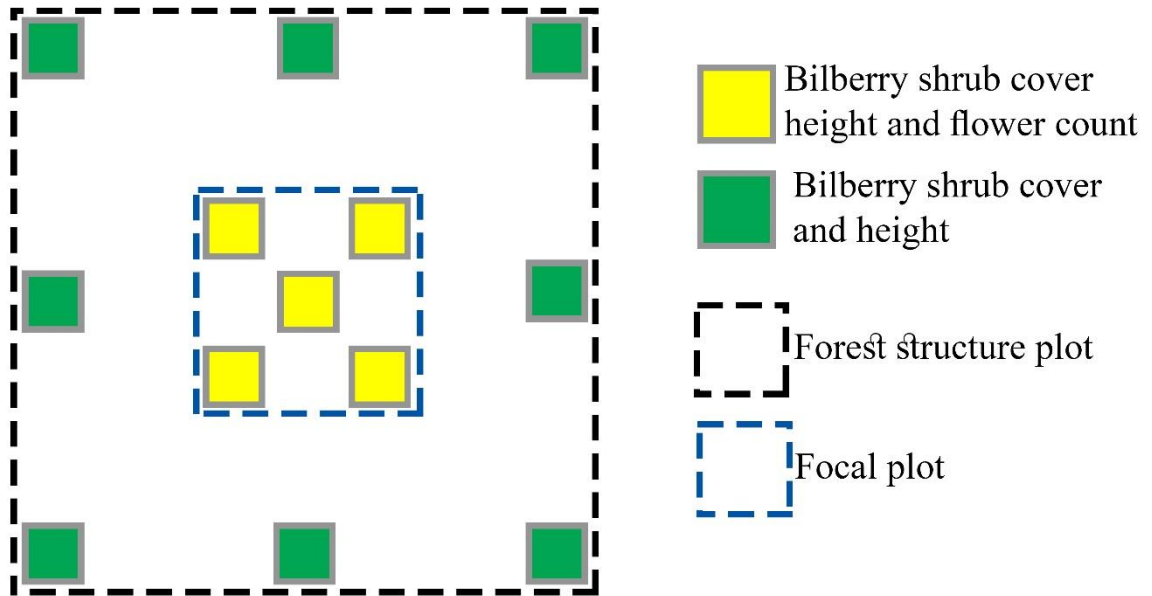


Figure 2: 10 x 10 m forest structure plot which including a 3 x 3 m focal plot. Deadwood was measured along the sides of the forest structure plot (black, dotted line) and trees were measured and counted inside both forest structure and focal plot.

## 2.2 | *Measuring forest structure*

In order to quantify variation in forest structure, I measured habitat variables at each plot. I estimated bilberry shrub cover within five 0.25 m<sup>2</sup> quadrats placed in the corners and centre of each focal plot and at eight quadrats along the sides and corners of the larger structure plot (fig. 2). I counted the number of open bilberry flowers (open corolla and not senescent) in each of the five quadrats of the focal plot at the end of each observation. To standardise measurements, floral

densities were calculated by multiplying the average of shrub coverage with the average number of flowers for each plot. Bilberry shrub cover was estimated as percentage from 0% to 100%.

Stand basal area is a common way of quantifying stand densities and can be described as the average area of trees at breast height per hectare (McElhinny *et al.*, 2005). It is strongly related to leaf area index which is a proxy for the amount of sunlight reaching the forest understory, which is known to affect the growth of bilberries (Yan *et al.*, 2019; Goude, Nilsson and Holmström, 2019; Mensah *et al.*, 2020; Miina, Hotanen and Salo, 2009; Kardell and Eriksson, 2011). I counted and identified to species all canopy tree species inside the structure plot and calculated stand basal area by measuring their diameter at breast height and calculating the average area per hectare.

I quantified coarse woody debris (deadwood) in each site to account for the differences in structural heterogeneity and availability to nesting sites between the forest types (Rodríguez and Kouki, 2015). To calculate the volume of deadwood, I measured the circumference at the longitudinal midpoint and length of all horizontal dead trees, branches and stumps with >5 cm in diameter intersecting the sides of the structure plot. Standing dead trees were measured at breast height. Deadwood volume was derived using Huber's formula  $V = LA_m$  where L is length and  $A_m$  is the cross-sectional area at the longitudinal midpoint of the deadwood (Fraver *et al.*, 2007).

### 2.3 | *Floral visitor surveys*

I recorded floral visitors to bilberries during 20-minutes observations in each of the 30 focal plots for the entirety of the bilberry bloom from mid-May to early June. Observations were undertaken at two different time intervals (between 09.00-13.30 and 13.30-18.00) at each site on three days, resulting in a total of five hours of observation per site. Conditions for observation were met when

temperatures exceeded 10°C and wind speed was <2 m per second, and no precipitation. At the start and end of each survey, I measured air temperature and humidity.

I determined hoverflies and solitary bees to morphospecies in the field, and, where possible, bumblebees (*Bombus*) to species and caste. The four species *Bombus lucorum*, *Bombus terrestris*, *Bombus magnus*, and *Bombus cryptarum* are referred to as *B. lucorum* complex since they cannot be confidently identified by morphological characters in the field (Carolan *et al.*, 2012). I assigned hoverflies into four morphospecies categories (small, big-tigered, big-dark and *Rhingia* spp.) according to size, colour, and shape. I collected and preserved voucher specimens of each morphospecies and identified these in the laboratory after the end of the field season. Taxonomy and nomenclature of the specimens follow Dyntaxa (2022). Since the observations were done in two distinct time periods with unfavourable weather in between, I divided the dates of survey in the analysis into the two groups: early (14<sup>th</sup> to 22<sup>nd</sup> May) and late (29<sup>th</sup> May to 3<sup>rd</sup> of June).

## 2.4 | *Single visit pollen deposition*

To assess bees and hoverflies pollination effectiveness of bilberry, I measured the single visit pollen deposition rates of the most abundant species. Several studies have shown that single visit pollen deposition (SVD) is an appropriate method to use for quantifying pollinator efficiency (Ne'eman *et al.*, 2009; Benjamin, Reilly and Winfree, 2014; Rader *et al.*, 2016; Ballantyne *et al.*, 2017). 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 (transparent 13 x 18 cm). Upon anthesis, I randomly assigned covered inflorescence to two

treatments: closed-pollination (negative control) or single visit treatment. The negative control was bagged for the entire duration of flowering to prevent floral visitation. I also set up an open-pollination treatment (positive control), where flowers were left exposed to floral visitors for the duration of flowering. For the single visit treatment, I cut three to five inflorescences by the stem and tied them together forming a bouquet, which I offered to visiting pollinators. Upon visitation, the pollinator was left undisturbed for the entire duration of the visit. I 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. I recorded if the insect buzz-pollinated the flower or foraged without buzz-pollinating. If needed, the pollinator was caught in a net after visitation for identification. I 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 tracks protein and makes pollen grains visible (Brunel Microscopes Ltd., UK). The jelly was then heated, causing it to melt and sealed using a cover slip and clear nail polish. I used the same collection method for the open- and closed treatments. All SVDs were done at the same managed forest site.

Bilberry pollen can be identified from its tetrad shape, distinguishing them from other pollen. I counted the number of pollen grains by using traverse inspection under a x10 magnification microscope.

## *2.5 / Pollination experiment*

To evaluate pollination dependence of bilberry and pollination success between the two forest types, I undertook a pollination experiment. Adjacent to each observation plot, I randomly selected 20 flowers of immature bilberry flowers prior to anthesis. Flowers were assigned to two treatments:

open-pollination or closed-pollination. I tagged all flowers and left the open-pollination flowers exposed to floral visitors for the duration of the bilberry bloom. Closed-pollination flowers were covered with organza bags to prevent floral visitation. I then quantified the proportion of fruit set by counting the number of tagged flowers from both treatment that were developing into fruit one month after the end of the flowering period.

## 2.6 / *Data analysis*

I carried out all data analyses in R v4.1.1 (R Core Team, 2021).

### 2.6.1 / *Variable correlations*

I assessed the relationship between habitat variables using Spearman rank-correlation tests since the data was not normally distributed. Except temperature and air humidity ( $|r| = 0.78$ ), none of the variables were correlated. Since temperature is known to influence pollinator activity (McCall and Primack, 1992; Sanderson, Goffe and Leifert, 2015) and collinearity can affect model predictions (Dormann *et al.*, 2013), thus, I excluded air humidity from all subsequent analyses.

All GLMMS were fitted using *glmmTMB* (v1.1.3; Magnusson *et al.*, 2021). All presented models passed tests of normality and under- and overdispersion within the DHARMA package (v0.4.5; Hartig, 2022).

## 2.6.2 / *Differences between forest types*

I tested for differences in habitat variables between the forest types using GLMMs. I modelled each variable as a function of forest type. Site was included in each model as a random effect because each habitat variable was measured at the plot-level (*i.e.*, one measurement per plot). Temperature was modelled with a Gamma distribution. Deadwood volume and floral densities were modelled with hurdle Gamma distributions and stem basal area was modelled with a negative binomial distribution due to significant overdispersion.

## 2.6.3 / *Community composition*

- i) How does the structure of bilberry pollinator community composition differ between natural and managed forests?

To test if the composition of the bilberry pollinator community (bees, hoverflies, or combined measured as floral visitors) differed between forest types, I first calculated the pairwise Bray-Curtis dissimilarity between plots using the *vegan* package (v.2.3-5, Oksanen *et al.*, 2021). Then, permutational analysis of variances (PERMANOVA) (Anderson, 2001) were used to test for differences in species composition as a function of forest type (natural, managed), time period (early, late) and forest structure characteristics (deadwood volume, stem basal area, flower densities and temperature). Differences in species composition between sites were visualised using non-metric multidimensional scaling (NMDS) ordination (fig 3).

- ii) Are differences among bilberry pollinator communities (abundance and species richness) mediated by forest structure and / or the availability of floral resources?



To assess the relationship between bilberry pollinator abundance and species richness and forest structure, I first calculated the abundance and species richness of a) the entire community, b) bees and c) hoverflies. I then used generalised linear mixed models (GLMMs), to test for differences in abundance and species richness between forest type and time period. Each community was modelled separately. Abundance and species richness was modelled as a function of forest type (natural, managed) in interaction with time period (early, late). Each model was specified with a random effect of *plot* nested within *site* to account for dependencies among samples arising for the same or different plots within a site. The species richness of the entire community was modelled with *Poisson* distributions whereas bee and hoverfly species richness were modelled with Conway-Maxwell-Poisson distributions as these datasets were significantly under-dispersed. Across the overall and hoverfly community, abundance was modelled with negative binomial distributions due to significant overdispersion and bee abundances with a *Poisson* distribution.

Sampling sites also differed in forest structure, both between and within forest types (see section 2.6.5). Therefore, to further evaluate how forest structure affected bilberry pollinator abundance and species richness, I modelled abundance and species richness for all groups as a function of deadwood volume, stem basal area and flower densities at each site.

#### 2.6.4 | *Single visit pollen deposition and foraging behaviour*

iii) How do bilberry pollinators differ in their pollination effectiveness (single visit pollen deposition) and how does bilberry reproductive success vary between manage and natural forests?

To compare the pollination effectiveness of different floral visitor species and taxa, I analysed single visit pollen deposition rates as a function of species or taxa (see Table 1 for species and taxon groups). Taxon groups also included open-pollinated and closed-pollinated stigmas for comparison as positive and negative controls. I analysed bumblebees and honeybees (*Apis mellifera*) as species, and solitary bees as a group. I divided hoverflies into two categories depending on size (big or small). Given pollinator behaviour, and in particular buzz pollination in bumblebees is known to influence pollination efficiency in bilberry (Moquet *et al.*, 2017), I also modelled single visit pollen deposition rates as a function of bumblebee behaviour (two levels: buzzing and non-buzzing individuals). These models were specified with negative binomial distributions as these data were significantly overdispersed. I also allowed the dispersion parameter of the distribution to vary among taxa groups.

### 2.6.5 / *Pollination success*

To assess pollination success between forest types, I specified a GLMM to analyse the probability of fruit set (binary: 0,1) as a function of forest type and treatment (Two levels: open-pollination or closed-pollination). This model was parametrised with a binomial distribution and a nested random effect of plots within site.

## 3 | Results

### 3.1 | Forest structure

The natural forests had higher volumes of deadwood and higher temperature than the managed forests ( $F = -2.697, p = 0.007$  and  $F = -2.47, p = 0.0134$ ) but flower densities were higher in the managed forests ( $F = 2.463, p = 0.0138$ ) (fig. 6). There was no difference in stem basal area between the forests, but there was a higher variety in the natural forest. Wind or air humidity did not differ between the forests. I could not find any other floral resources inside or between the forest structure plots.

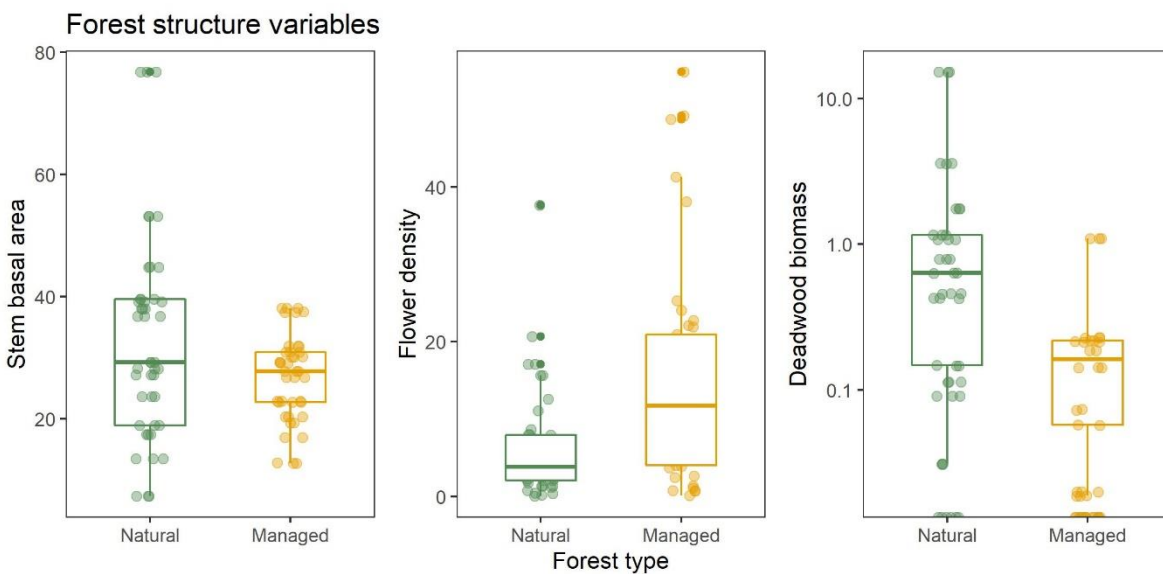


Figure 5: Box-plots showing differences in stem basal area ( $\text{m}^2\text{ha}^{-1}$ ), flower densities and deadwood volume between natural and managed forests structure plots. The median is indicated by a line across the box and the box ranges from the first (25%) to the third (75%) interquartile range.

### 3.2 | *Floral visitor surveys*

In total, I counted 729 floral visitors to bilberries during 30h of observation. Hoverflies made up 77% of the total number of floral visitors recorded, bumblebees 21% and solitary bees <2%. I observed seven different species of bumblebees, of which 61% of the observed individuals could be identified to species level. The majority of specimens recorded belonged to the small hoverfly category (60%).

Hoverfly community composition differed significantly between the forest types ( $F = 2.8759$ ,  $p = 0.032$ ) as suggested by their separation in the multivariate analysis (fig. 3), whilst bee or the overall community did not ( $F = 1.9242$ ,  $p = 0.082$  and  $F = 0.9844$ ,  $p = 0.423$ ). The overall and hoverfly community were related to floral densities ( $F = 3.8577$ ,  $p = 0.003$  and  $F = 5.8919$ ,  $p = 0.001$ ) while the bee community were associated with stem basal area and deadwood volume ( $F = 2.2919$ ,  $p = 0.033$  and  $F = 2.4008$ ,  $p = 0.031$ ). The overall community was also related to time period ( $F = 2.1395$ ,  $p = 0.041$ ). I found no effect of temperature on floral visitor community composition ( $F = 0.8988$ ,  $p = 0.05$ ).

Overall floral visitor abundance and hoverfly abundance were both related to floral density when including the effects of floral densities, deadwood volume and stem basal area ( $F = 3.917$ ,  $p = <0.001$  and  $F = 3.295$ ,  $p = <0.001$ ). Bee abundance was higher in the managed forests later in the season ( $F = 5.162$ ,  $p = <0.001$ ) as well as the species richness of all floral visitors groups in both forest types (all:  $F = 3.706$ ,  $p = <0.001$ , bees:  $F = 3.381$ ,  $p = <0.001$  and hoverflies:  $F = 2.918$ ,  $p = <0.001$ ). Species richness and floral visitor abundance were not related to stem basal area nor deadwood volume.

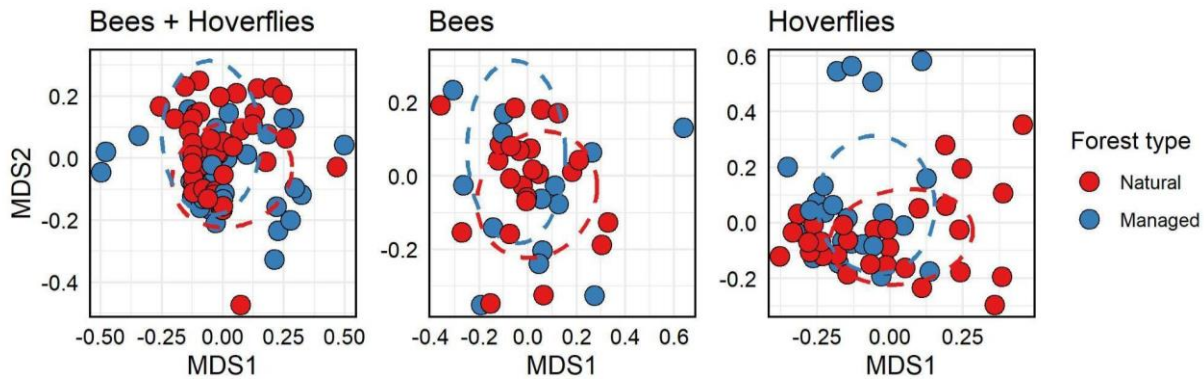


Figure 3: Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity calculation to plot community composition of bilberry floral visitors.

### 3.3 / *Pollination success*

Out of the 600 flowers tagged for the pollination experiment, 123 of the open-pollinated flowers (41%) and only three of the close-pollinated flowers (0,01%) developed into fruit. There was a statistically significant difference in the probability of flowers developing into fruit between the open-pollinated flowers and close-pollinated treatments ( $F = 4.984, p < 0.001$ ).

### 3.4 / *Single visit pollen deposition and foraging behaviour*

Single visit deposition was measured for 60 individuals in total, including five species of bumblebees (37 individuals), seven individuals of solitary bees, four individuals of honeybees and six individuals of big and small hoverflies (fig. 4). Differences in SVD between taxa and individuals of the same species varied remarkably and all groups except small hoverflies deposited significantly more pollen grains than found without visitation (closed pollinated stigmas). Individuals of *B. soroeensis* and solitary bees 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 as the open control. *B. soroeensis* deposited more pollen grains than *B. pascuorum* ( $F = 3.49$ ,  $p = 0.016$ ) but similar to other bumblebees and, together with solitary bees ( $F = 2.91$ ,  $p = 0.014$ ), more than big hoverflies ( $F = 3.14$ ,  $p = 0.050$ ). Buzz pollinating individuals deposited more pollen grains than non-buzzing ( $F = 22.314$ ,  $p < 0.001$ ) (fig. 4).

Table 1: Mean, minimum and maximum pollen grains deposited during a single visit to Bilberry by individuals of each taxonomic group and compared to negative control.

Species group	N (no. of single-visit experiments)	Pollen grains deposited per visit (average)	Standard error	Min /max deposited	Compared to negative control z-value / p-value
Solitary bees	7	159.9	47.3	(14 – 352)	8.406 / <0.001
<i>Apis mellifera</i>	4	94.5	42.9	(20 – 196)	6.837 / <0.001
<i>Bombus hypnorum</i>	3	84.7	22.1	(41 – 112)	8.216 / <0.001
<i>Bombus lucorum</i>	11	65.0	25.1	(0 – 215)	6.272 / <0.001
<i>Bombus pascuorum</i>	7	78.4	20.4	(26 – 158)	8.034 / <0.001
<i>Bombus pratorum</i>	9	82.2	35.5	(2 – 326)	6.799 / <0.001
<i>Bombus soroensis</i>	7	162.7	25.7	(110 – 304)	10.337 / <0.001
Small hoverflies	6	3.6	1.73	(0 – 9)	1.229 / 0.338
Big hoverflies	6	21.5	14.6	(0 – 94)	3.780 / 0.001
Closed-pollinated	10	1.3	0.539	(0 – 5)	0
Open-pollinated	16	83.5	21.6	(0 – 244)	7.146 / <0.001

# Single visit pollen deposition

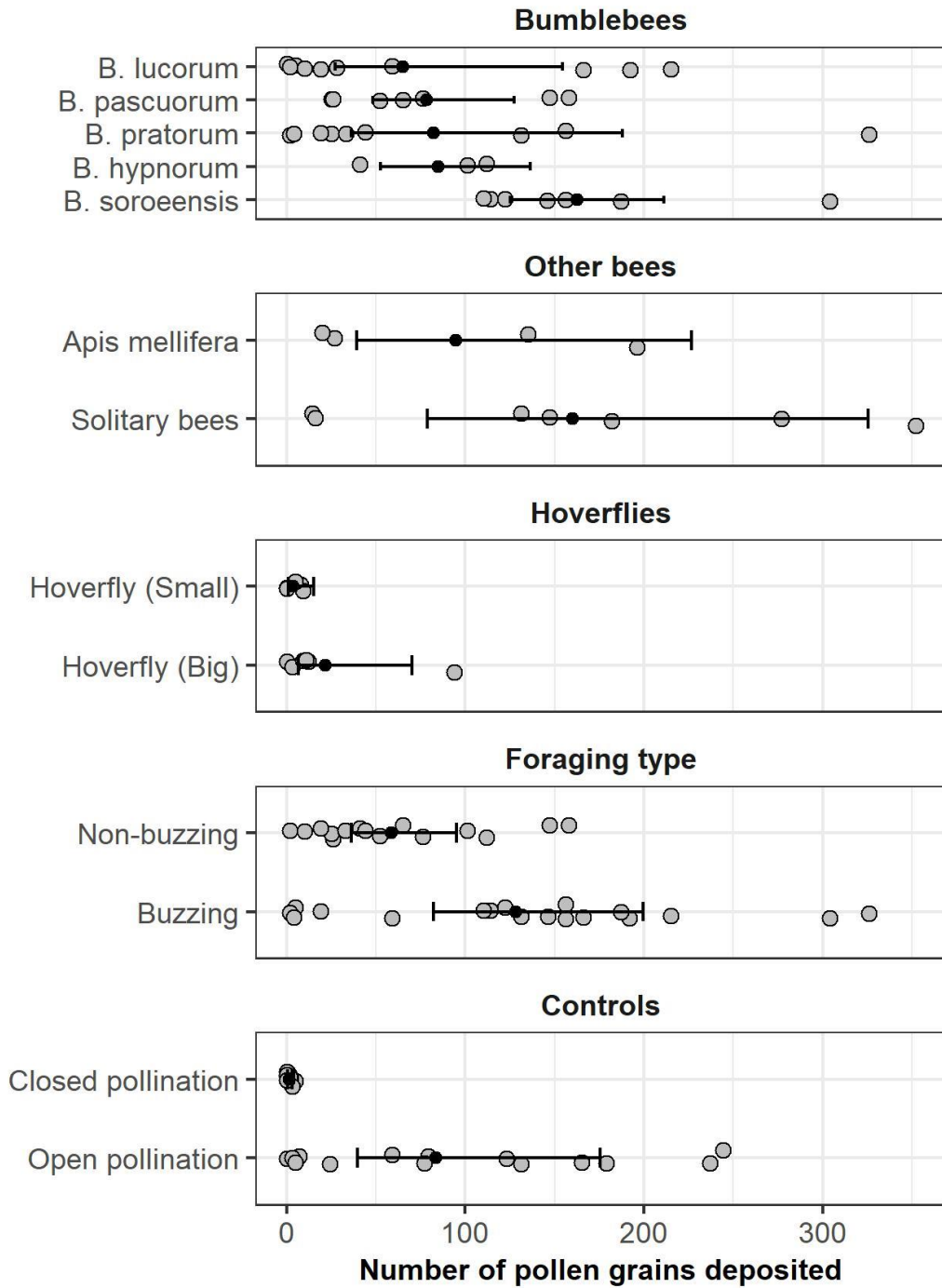


Figure 4. Single visit pollen deposition by species of each taxon group. Data are shown as mean  $\pm$  95% confidence intervals.



## 4 | Discussion

This study shows that bilberry supports a diverse pollinator community (*i.e.*, floral visitors), within boreal forests. Key aspects of the community differed due to forest management and structure. Differences in the composition of the overall and the hoverfly community were related to floral availability while the differences in the bee community were related to deadwood availability and stem basal area. Overall floral visitor and hoverfly abundances were associated with bilberry floral densities, and bee abundance and overall species richness increased later in the bilberry flowering period.

Bees were the most effective bilberry pollinators, with all but one species depositing similar amounts of pollen grains per single visit. Interestingly, big hoverflies also deposited similar amounts of pollen grains as the majority of the bees. However, I found evidence of strong pollen deficits in both forest types, which shows that there are insufficient pollinators occurring on a local scale in the systems. These results demonstrate the importance of bilberry as an early-season resource for both bees and hoverflies and show that both mature managed and natural forests are valuable habitats for insect pollinator communities.

### *4.1 | Community trends and forest structure*

Deadwood availability and stem basal area were important determinants of bee community structure. In coniferous forests, deadwood benefits bumblebees and other solitary bees by providing nesting sites and enhancing habitat structural complexity (Rodríguez and Kouki, 2015; Eckerter *et al.*, 2021). Swedish managed forests have generally less than 10 % deadwood volume compared to

natural forests (Bengtsson *et al.*, 2000; Jonsson *et al.*, 2016). In line with this, the managed forests of this study had lower volumes of deadwood (<9%) than the natural forests. There was no difference in stem basal area between the forests but the variation in stem basal area was higher in the natural forests, indicating that they are more structural heterogeneous. Further, stem basal area can be negatively correlated with pollinator species richness and abundance (Fye, 1972; Hanula, Horn and O'Brien, 2015; Rhoades *et al.*, 2018). In contrast, my results could not relate abundance nor species richness to neither deadwood availability nor stem basal area. This suggests that compositional differences reflect species-specific combinations of pollinators that benefit from or prefer habitat with greater volumes of deadwood, such as natural forests.

The overall abundance of floral visitors, as well as hoverfly abundances, were positively related to bilberry floral density. My results are consistent with other studies, which demonstrate that hoverflies exploit floral resources where these are most abundant (Branquart and Hemptinne, 2000; Meyer, Jauker and Steffan-Dewenter, 2009; Moquet *et al.*, 2018). Given that hoverfly community composition also differed between the forest types, this suggests that the two forest types may differ in the habitats they provide, as hoverfly larvae are phytophagous and different species dietary preferences can be bound to specific habitats (Moquet *et al.*, 2018). This adds to previous findings that maintaining connectedness between suitable adult and larval habitats is important for conserving diverse and abundant hoverfly communities not only in agricultural landscapes but also in boreal forests (Meyer, Jauker and Steffan-Dewenter, 2009; Herrault *et al.*, 2016; Moquet *et al.*, 2018).

## 4.2 / *Species pollination effectiveness & pollen limitation*

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.*, 2017; Eckerter *et al.*, 2019). Also in congruence with other studies done on the *Vaccinium* genus, both solitary bees, and honeybees were highly effective bilberry pollinators (Benjamin, Reilly and Winfree, 2014; Moquet *et al.*, 2017). Yet, despite most bee species being equally effective, buzz pollinating foragers deposited more pollen grains than non-buzzing individuals. These results highlight that even though buzz pollination allows bees to deposit and collect more pollen grains, non-buzzing species and behaviour 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, Reilly and Winfree, 2014).

In contrast to previous studies, I found that large hoverflies might be equally effective pollinators as many bee species (Moquet *et al.*, 2017). It was recently discovered that hoverflies are able to produce thoracic vibrations that release pollen from buzz-pollinated flowers, which emphasizes their potential importance as a *Vaccinium* pollinator taxon (Vallejo-Marín and Vallejo, 2021, De Luca and Vallejo-Marín, 2013). However, this result is possibly driven by an outlier, as one individual deposited 94 pollen grains in a single visit, despite all other individuals depositing less than 12. As such, further research, with greater replication, is now required to assess the pollination effectiveness of hoverflies to bilberry.

These results have key implications of ecosystem functioning and service provision. Hoverflies contribute to different 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). As such, they represent an integral component of terrestrial ecosystems. However, their importance as pollinators in boreal forests remains understudied (Lucas *et al.*, 2018; Doyle *et al.*, 2020). This study demonstrates that not only are boreal forests important habitats for hoverflies, but also that they are essential pollinators of bilberry, and likely contribute to other ecosystem functioning in forests.

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. In a bilberry pollination experiment in Finland, Nuortila *et al.*, (2006) showed that the maximal pollination achieved was 80% compared to the 41% in my study. This low probability of fruit set in the open-pollinated flowers is indicative of pollen limitation (*i.e.*, a deficit of actual pollination vs. maximal pollination) which suggests that there is an insufficient number of pollinators occurring in my system. However, bilberries are known to have cyclic years of fruit production with years of high floral availability (Swedish NFI, 2022) and mass-flowering can dilute populations of floral visitors throughout the landscape, leading to reduced pollination (Holzschuh *et al.*, 2011). In combination with periods of unfavourable weather during flowering, these factors may have resulted in low pollination rates in my study. However, it is surprising that I observed no difference in fruit set between the two forest types, despite differing floral densities yet having similar floral visitor abundance. This may suggest that floral densities did not differ enough between forest types to affect landscape-level dilution effects. Undertaking hand-pollination experiments in comparison with open-pollination, repeated during several consecutive years would be required to confirm these hypotheses. This would enable a greater understanding of vulnerability of bilberry systems to pollination deficits, and aid in identifying forest management practises vulnerable to reduced pollination rates.

### 4.3 / *Conclusions and implications for forest management*

My results show that mature, managed forests can host similar early-season floral visitor communities as natural forest and not only act as reservoirs for floral visitor communities, but that abundant communities of floral visitors contribute to pollination, and therefore fruit development of bilberry. This gives incentive to maintain mature, managed forests as conservation elements of pollinators in the boreal landscape. Moreover, considering the cultural and recreational values of picking bilberries; conserving healthy, high-yielding forests is also important for anthropological concerns (Kangas and Markkanen, 2001). Therefore, attempting conservation efforts targeting forest-dwelling pollinators, such as maintaining rich floral resources throughout seasons, creating suitable nesting habitats and maintaining connectedness between these habitats, might be of high value in the boreal landscape.

It takes approximately 55 years after clearcutting for bilberry shrub to return to pre-cutting levels and stands between 10 and 60 years are not big producers of bilberries (Kardell, and Eriksson, 2011). Considering this, it is alarming that between 2004 and 2017 the average age for harvesting stands in Sweden decreased from 120 to 100 years (Swedish NFI, 2022). This means that the age gap for managed forests to host potentially floral rich bilberry habitats for pollinators, has decreased by one third, a trend which could have negative effects on ecosystem function and services associated with bilberry.

This study adds to the growing body of evidence that mature, managed forests can act as important habitats in maintaining biodiversity for a large range of taxa (Eckerter *et al.*, 2021; Savilaakso *et al.*, 2021). Also, it provides evidence that patterns of habitat complexity and floral resources are

key determinants of pollinator community structure in the boreal landscape. To confirm the results, the study should be expanded to northern and southern latitudes with increased replication that separates stands in different ages. To benefit bilberry and their pollinators, management should aim for keeping a patchwork of mature forests with mixed deadwood availability of different ages.

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