



Høgskulen
på Vestlandet

BACHELOROPPGAVE

Forvaltningseffekter på den funksjonelt viktige arten blåbær

Management effects on the functionally important species bilberry

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Preface

This bachelor's thesis represents the culmination of three years of study in Landscape Planning with Landscape Architecture (Landskapsplanlegging med landskapsarkitektur) at Western Norway University of Applied Sciences (Høgskulen på Vestlandet) – Campus Sogndal. Choosing this thesis topic was motivated by our keen interest in the subjects it encompasses, particularly its ecological focus, which we believe to be of great importance in the current times.

Throughout the course of our research, we have gained valuable insights into various aspects of this field, including the implementation of fieldwork, conducting statistical analyses, understanding ecological processes, and delving into the study of the bilberry plant itself. This journey has revealed to us how much we still have to learn and explore, serving as a motivation to pursue further studies at the master's level and aspire to build a career in a related field in the future. Expanding the understanding of the performance of important species like bilberry can contribute to a more holistic approach to forest management, and consequently have a positive effect on the nature crisis the world is currently facing.

We would like to express our gratitude to our supervisors, Professor Stein Joar Hegland and Associate Professor Mark Andrew Gillespie, for their encouragement, active involvement, and guidance throughout our work. This includes providing assistance in fieldwork, statistical analysis, and ecological knowledge; and generally valuable insights and ideas that helped shape the direction of our thesis.

Abstract

The way forests are managed, particularly through forestry, greatly impacts the abundance of functionally important species, which in turn affects ecosystem biodiversity. One such functionally important species commonly found in boreal forests is the European bilberry, *Vaccinium myrtillus*. Consequently, research into the performance of this plant can broaden our understanding of how human activities impact ecosystem functioning.

To investigate how bilberry is influenced by different types of forest environments, data was collected about light intensity, as well as cover percentage, size, and berry count of bilberry in semi-natural, managed monoculture pine and spruce forest stands in Kaupanger, Western Norway. We conducted quadrat samplings measuring 0.5 x 0.5 m over 5 plots at randomized locations within a total of 31 sites. 10 spruce and 10 pine sites were paired, controlling for age, productivity, maturity class and elevation, to investigate the effect of the dominant tree species on bilberry. 11 extra pine sites were chosen with a focus on variance of stand age in the samples to explore the relationship between bilberry and forest age.

Pine forests displayed significantly higher bilberry cover, larger size, and more berries than spruce, and this negative effect of spruce on bilberry performance was particularly high in our study area compared to previous research. Bilberry cover and size displayed a significant negative relationship with forest age, while berry count showed a non-significant tendency for a negative relationship. The differing levels of light availability between the dominant tree species, and between young and old forests are likely the primary driver of the observed differences. Available studies on the relationship between forest age and bilberry performance reveal conflicting results between more mixed stands, which typically display a positive relationship, and monocultures which show negative relationships similar to us. Overall, our findings indicate that in monocultures, younger forests, particularly those dominated by pine rather than spruce, are better for bilberry performance and consequently supports greater biodiversity in Kaupanger, Western Norway. Since younger forests are not ideal for forestry in a commercial context, encouraging more mixed stands or intensified thinning in older monocultures may represent a balanced solution for forest management in general.

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1. Introduction

The global environment is currently facing a severe biodiversity crisis, characterized by a rapid and alarming decline in biodiversity, largely attributed to human land management patterns (Diaz et al., 2019; Lindenmayer et al., 2023; Kong et al., 2021). Among the significant contributing factors to this crisis, land use changes play a critical role, as natural areas are continually being converted to anthropogenic land use types such as urban and industrial development, agriculture, forestry, and infrastructure (WWF, 2022). To prevent further losses, management needs to be more sustainable, and to enable that, we need more research into the impacts of management practices on biodiversity.

One sector that would benefit from sustainable management is forestry. It involves the science and practice of establishing, harvesting, and managing forests and trees (Hoen et al., 2023), and is recognized as one of the most prominent land use changes in the boreal zone. It has profound effects on landscapes, habitats, and individual species through transforming ecosystems by e.g., harvesting and establishing trees (Nickelsen, 2022), and is a central economic sector in Norway and the other Scandinavian countries (Miljødirektoratet, n.d.). Forests cover about 38% of Norway's land area, where 68.1% of this is productive forest area, meaning forests producing over 0.1 cubic meters of wood per decare every year, equivalent to approximately 82.8 million decare, is productive forest (SSB, 2022).

While Norwegian regulation on forestry aims to ensure the sustainable use of forests through active rejuvenation and healthy development (Forskrift om berekraftig skogbruk, 2006, § 1), earlier and current forestry practices, such as clearcutting and the establishment of even-aged, dense monocultures, have had negative impacts on forest structure, age distribution, and species diversity from the floor layer to the tree layer (Lindbladh, 1999; Nielsen et al., 2007; Ohlson et al., 1997). In Western Norway, Norway spruce (hereafter spruce; *Picea abies*) is predominantly introduced and planted for forestry purposes, whereas Scots pine (hereafter pine; *Pinus sylvestris*) occurs naturally and has been both planted and regenerated through natural reproduction (Øyen & Nygard, 2020). Planted spruce forests have been shown to have adverse effects on ecosystems compared to pine forests, primarily

due to their low canopy openness, which inhibits light-dependent species in the floor and shrub layers, resulting in less diverse forest floors dominated by moss and lichens (Pettersson, 2019; Apollon, 2018). Additionally, the lack of ecological competence among forest entrepreneurs who manage forests poses a problem, as forest management ideally should strive to benefit the ecology while safeguarding other interests (Eriksson et al., 2012).

One approach to assess the functioning of managed forests for biodiversity purposes is to examine the occurrence of functionally important species. These species play essential roles in structuring habitats and are key contributors to various biotic interactions, making them relevant for understanding how human activities impact ecosystem functioning (Nybø et al., 2020). If functionally important species disappear or their distribution is reduced, it can lead to significant changes in the ecosystem composition and distribution of species. Bilberry (*Vaccinium myrtillus*), the most abundant floor shrub in the northern boreal zone (Sjörs, 1989), is considered one such functionally important species due to its high ecosystem importance. Bilberry exhibits large annual biomass production (Havas & Kubin, 1983), contributes to substantial humus accumulation, and significantly influences the establishment and growth of forest tree seedlings (Jaderlund et al., 1996). It also serves as a nutritional basis for numerous other species, such as herbivore and frugivore insects, birds, and mammals, as well as being highly attractive to pollinators (Lilleeng et al., 2021; Eldegard et al., 2019; Selås, 2001). Previous studies conducted in Sweden, Finland, and Eastern Norway have explored the response of bilberry plants to different boreal forest conditions. Many of these studies suggest a trend of declining bilberry abundance following the introduction of industrial forestry, potentially due to altered management practices, increased proportions of young and dense forests, and amplified spruce planting (Eldegard et al., 2019; Eckerter et al., 2019; Hedwall et al., 2013; Woziwoda et al., 2019; Parlane et al., 2006). Several of these studies have indicated that adequate light exposure to the forest floor is a crucial factor for bilberry, with thinning practices that reduce tree layer density, thereby favoring floor-level species in general (Hedwall et al., 2013). Moreover, they suggest that bilberry cover is best developed in intermediate tree stands, and greater canopy openness results in higher fruit and berry abundance, as well as better-quality berries (Eckerter et al., 2019).

In this bachelor's thesis, we have through fieldwork and statistical analysis investigated the performance of bilberry as a bioindicator species in managed spruce and pine monoculture forests near the village of Kaupanger, Western Norway. The study area primarily consisted of production forests, including various planted stands of spruce and pine (NIBIO, 2022). We sampled spruce and pine locations with different ages and productivity classes and collected data on bilberry cover, size, and berry production. The objective of this thesis is to examine how bilberry is influenced by different types of forest environments, thereby contributing to knowledge that can be applied in forest management to safeguard biodiversity. Most of the previously mentioned studies on bilberry have primarily focused on tree stand density and age as variables influencing bilberry response, with an emphasis on more natural and mixed forests comprising both deciduous and conifer forests that are less controlled. Consequently, there may exist knowledge gaps and limitations in these studies, and notably, no research on this topic has been conducted in Western Norway, where we might expect something different because Norway spruce rarely occurs naturally and has been introduced for forestry. It might benefit sustainable forestry management to expand our knowledge of bilberry responses into a broader range of bioclimates, along with addressing some of these knowledge gaps by focusing on managed, semi-natural monoculture forests, controlling for factors such as age, productivity classes, dominant tree species and elevation. The results from the aforementioned studies provide a robust foundation for the main hypotheses we intend to investigate:

1. We hypothesize that pine stands within the study area will exhibit more bilberry cover, larger bilberry size, and higher berry production compared to spruce stands.
2. We hypothesize that older pine stands within the study area will display more bilberry cover, larger bilberry size, and higher berry production compared to younger ones.

2. Method

2.1 Study area

The study area consisted of managed forests near Kaupanger in Sogndal municipality, Western Norway, a town situated along the northern shore of the Sognefjord (fig. 1). The hillsides around the settlements and cultivated areas are dominated by conifer forests, primarily of pine, with a few spruce-only stands and some mixed deciduous stands (NIBIO, 2022). During our field work we observed that lingonberry (*Vaccinium vitis-idaea*), bog bilberry (*Vaccinium uliginosum*), common heather (*Calluna vulgaris*) and European bilberry are common perennial shrubs in the area, in addition to several species of fungus, lichen and mosses (Pers. Obs. Gilhuus. J, Stensaker. M). The study area is located within landscape region 23, a landscape type characterized by a wide range of nature types, with fjords and steep mountains being the most visibly defining features (Puschmann, 2005).

The delimitation of the study area was based on forestry taxation maps obtained from the largest landowner in the region (Appendix 1, Kaupanger Hovedgård). The study area covers an approximate area of 16 km² and exhibits an elevation range of 200-600 meters above sea level. It primarily extends from Sogndal airport to Kaupanger valley, encompassing the slopes of Storehaugen and Haugmelen mountains (fig. 1). The study area is situated within both the south boreal and low alpine vegetation zones, as defined by the National Atlas of Norway (Moen, 1999). The geology of the area comprises anorthosite bedrock with varying thicknesses of sediment layers, ranging from thin to thick till (NGU, n.d.). The climate in the region is characterized by relatively mild winters and warm summers in the lowland areas (Moen, 1999). Based on data from the previous year, the average temperatures in January and July were recorded as -2.4 °C and 12 °C, respectively, and the annual precipitation ranged from 1261 mm to 2037 mm the last 5 years. (Norsk klimaservicesenter, n.d.).

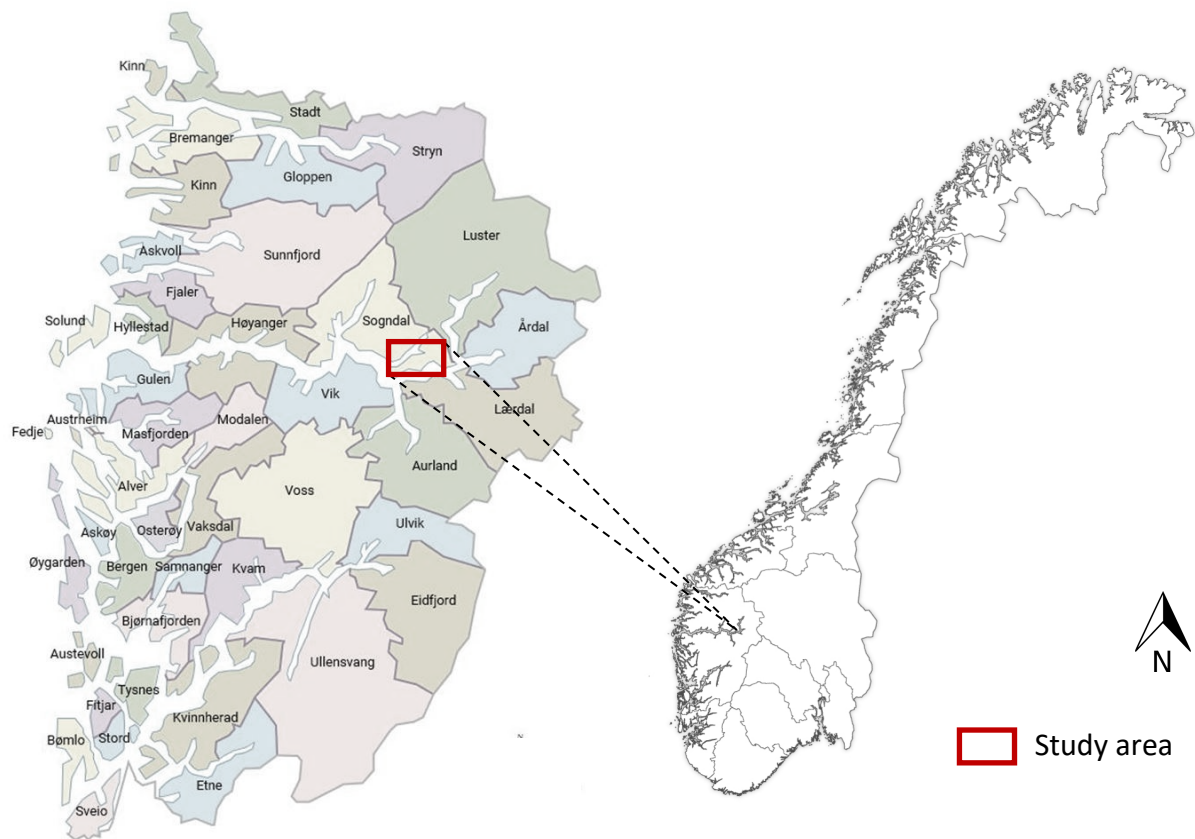


Figure 1: Location of study area with aerial photo of Kaupanger and surroundings with delimitation.

2.2 Study design

The study design was primarily based on the forestry information available in the forest taxation maps of the study area (appendix 1 & 2). These maps, along with the population overview (appendix 3) provided valuable insights into important forestry variables such as stand age, productivity, maturity classes, and dominant tree species, which were visually represented by stands of varying sizes on the maps (appendix 1 & 2).

To ensure a standardized comparison between spruce and pine forests, we selected 10 pairs of sites from the taxation maps. Each pair consisted of one spruce site and one pine site, with similar values in terms of age, productivity, maturity class and height above sea level. These paired sites had been previously established for a master's thesis conducted in the same area (fig. 2; Olsson, 2022).

In addition to the comparison between pine and spruce, we aimed to examine the relationship between bilberry and forest age in greater detail. Since the study area exhibited a significantly higher abundance of bilberry in pine stands (fig. 3) compared to spruce stands (fig. 4), and because spruce stands had a low age variance, we decided to focus solely on pine for this analysis. We selected an additional 11 pine sites from the taxation maps based on criteria of more varied stand ages, particularly we aimed for more mature stands above 80 years as they were lacking in the paired ones. This approach allowed us to obtain a comprehensive dataset comprising 21 pine sites ranging from 20 to 130 years old, and 10 spruce sites, totaling 31 sites for analysis.

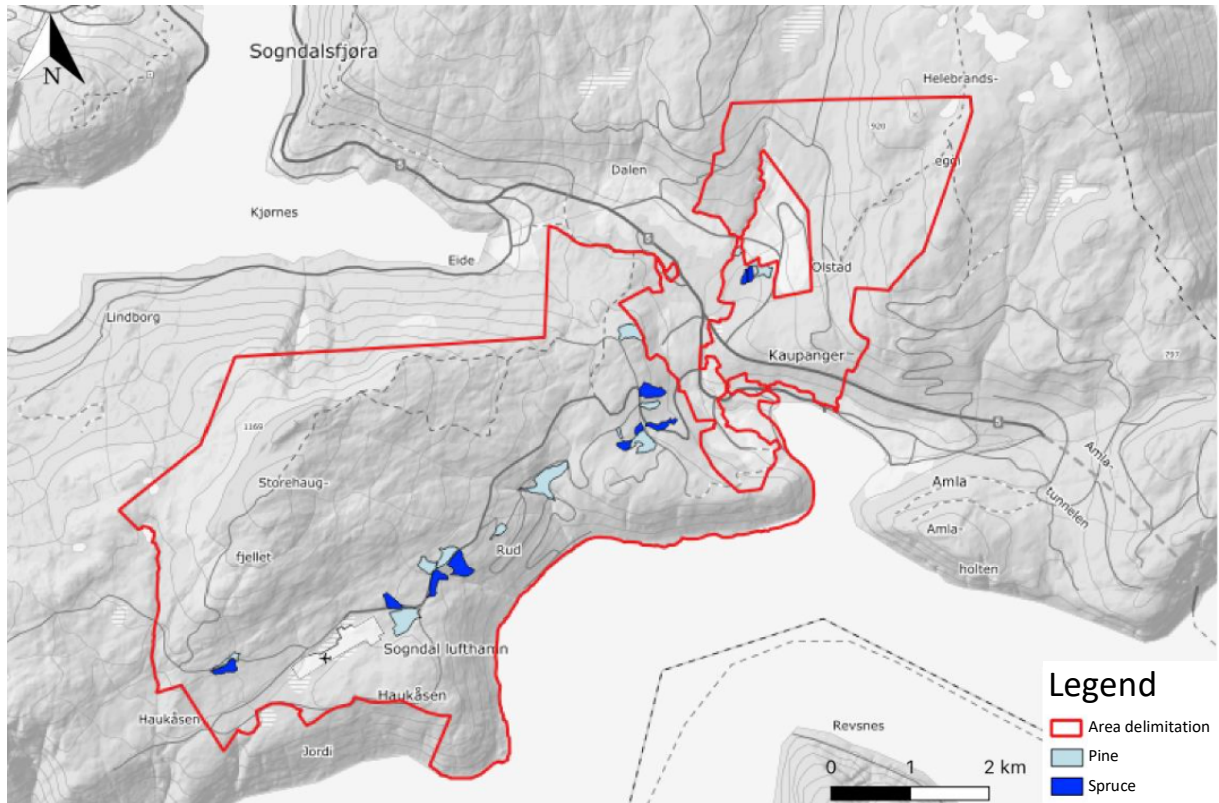


Figure 2: Sampling locations for paired pine and spruce sites in Kaupanger. The extra pine sites are not shown (Olsson, 2022).



Figure 3: Example of one of the pine-bilberry sites in Kaupanger. This stand was classified as 130 years old, productivity class 11, and maturity class 51.



Figure 4: Example of one of the spruce-bilberry sites in Kaupanger. This stand was classified as 75 years old, productivity class 20, and maturity class 41.

2.3 Data collection

Data collection took place over a three-week period in August 2022, a period coinciding with peak abundance of berries. To minimize bias and reduce measurement errors, a standardized approach was employed to our field work strategy. The site-level explanatory variables, forest age and dominant tree species, were obtained from the aforementioned forest taxation maps (appendix 1 & 2).

For each site, a block measuring 20 x 20 meters was established within the forest stand. Once a stand was located, we entered the forest and established a block at least 5 meters away from the forest edge to avoid edge effects such as variations in light conditions. Within this block, five sub-plots were established with quadrats measuring 0.5 x 0.5 meters. The locations of these sub-plots were determined by splitting the block into a grid of 1 x 1 m and numbering the coordinates of the grid as 0 to 20, from south to north, and west to east, then generating a number between 0 and 20 with a random number generator, revealing the coordinates of the chosen grid square. For practical purposes, the locations of the grid squares were measured using walking steps (fig. 5), and the same person performed the step measurements for all site plots. If the plots happened to land on a spot with hindrances such as large rocks or other debris, we always placed it to the left of the original location by 1-meter increments until the obstacle was avoided. We measured light intensity by holding a lux meter (Votcraft LX-10) towards south at 0.5 m height (fig. 6) as a proxy for light availability for photosynthesis. The lux measurements are likely influenced by error, as we did not control for the weather and time of day.

Furthermore, data were collected on the cover percentage, size, and berry production of bilberry within each plot, which constituted our response variables. First, we placed a 0.5 x 0.5 m quadrat over the plot. The quadrat featured strings dividing the plot into 16 grid squares serving as a reference for estimating the cover percentage (fig. 7). We measured what percentage of the plot square was covered by bilberry as seen from above, using an approximate estimation. The total number of berries occurring at the plot was then counted. Lastly, individual plant measurements were taken by systematically selecting four plants closest to the same four corners of the smaller string-squares within the plot square. Sticks

were inserted into the ground at these corners to facilitate the identification of the closest plant (fig. 7). If no plants were found inside the quadrat, this would give a 0 for number of plants, thus the number of individual plants measured per plot ranged from 0 to 4.

Measurements included the height of the plant when stretched out, stem diameter at the base, and the number of shoots on the plant. Defining the exact starting point of the plant base or ground level could be challenging due to the intricate tangle of plant stems, roots, and litter, which likely contributed to some measurement error, however we consistently pulled the stem with adequate force so it would be straight without ripping the roots out of the ground. The point where ground (usually moss) touched the stem, would be the plant base we measured height from.

The individual plant size response variables were combined to create a response variable of the plant's estimated total dry mass (size). The formula used to compute the total dry mass was based on a multiple regression model from a study by Hegland et al. (2010):

$$\log_2(\text{DM}) = 1.41700 \times \log_2(\text{DS}) + 0.97104 \times \log_2(\text{H}) + 0.44153 \times \log_2(\text{AS} + 1) - 7.52070$$

where DM represents the dry mass, DS is the stem diameter, H is the height, and AS is the number of annual shoots. The $\log_2(\text{DM})$ value obtained from this equation was then transformed back into gram units by raising 2 to the power of the $\log_2(\text{DM})$ value.



Figure 5: Walking steps being performed for determining a plot location in one of the pine sites.



Figure 6: Various plot locations and lux-measurements being taken (left)



Figure 7: Bilberry measurements being taken at plot.

2.4 Data analysis

All the statistical analysis for this thesis was conducted using the software R (R Core Team, 2021). To investigate the influence of tree species and forest age on bilberry performance we used the following response variables for bilberry:

- Cover as the average percent cover of the five study plots per site.
- Size as the average dry mass of individual plants
- Berry production as the average number of berries in the five study plots per site

We also measured light intensity (lux) to estimate relevant differences in light availability in forest stands dependent on the dominant tree species and stand age. However, upon exploring the data, we observed no clear significance or discernible patterns or relationships other than between dominant tree species, which we suspect may be attributed to measurement error. Nonetheless, we retained the lux data for descriptive statistics and to test if the light penetration was different between pine and spruce. The lux data was not normally distributed, but this was fixed with a log transformation, so we chose to run a paired t-test on the 10 paired sites.

To investigate the effect of tree species on bilberry cover and berry production, we conducted statistical tests to determine if there were significant differences in cover and berries between the paired sites. To address the non-normal distribution of the data, which was not improved by transformations, we employed Wilcoxon paired tests. All 10 paired sites were included in this analysis.

When examining bilberry dry mass, the objective was to assess differences in size where bilberry actually occurred. Since 5 of the spruce sites did not contain any bilberry plants, those pairs had to be removed from this analysis. The dry mass variable exhibited non-normal distribution; however, a log transformation resolved this issue. Therefore, we performed a paired t-test on the transformed data.

To investigate the impact of forest age on cover, size, and berry production, we specifically focused our tests on pine sites. This decision was based on the regular occurrence of bilberry in pine sites in contrast to the almost nonexistent presence in spruce sites, as well as lower variance in forest age in spruce sites. Using the data from 21 pine-site samples, we conducted linear regressions to examine the relationships between the three response variables and the age of the forests. To address non-normal distributions, the dry mass variable was log-transformed, and the berries variable was square-root transformed. The cover appeared to follow a normal distribution and did not require any adjustments. Furthermore, to ensure adherence to the assumptions of linear regression, we conducted a thorough assessment in R, examining the linearity, normality, equal variance, and independence of residuals, all of which were deemed appropriate for the test.

3. Results

3.1 Descriptive statistics

With a maximum number of 20 plants to be measured at each site, we measured a total of 404 plants in the 21 pine sites (average 19.2 / 20, per site) and 75 plants in the 10 spruce sites (average 7.5 / 20, per site). In pine plots, there were ramets to measure at every site, whereas in spruce we found no ramets in 5 of the sites. Bilberry size, as dry mass, was in pine on average at ~ 0.73 grams, and ~ 0.32 grams in spruce sites where bilberry existed. We found a total of 772 berries in the 21 pine stands, and 5 berries in the 10 spruce stands. There was also a significant difference in light intensity (lux) between the two tree species ($p = 0.012$, $t = 3.1$). Spruce forests (median = 1168 lux) were much darker in general than pine (median = 6241 lux), which exhibited a 434% higher median lux value across all sites, although there were a few outliers.

3.2 Effects of tree species on bilberry

The bilberry cover differed greatly between stands dominated by spruce or pine ($p = 0.002$), with very low abundance spruce sites (median = 0.8%) and high abundance in pine sites (median = 53%) (fig. 8). Plant sizes varied between the tree species where bilberry was found, however, the observed difference in size was only marginally significant ($p = 0.076$, $t = 2.4$). Specifically, bilberry plants in pine sites exhibited a larger size compared to spruce (mean dry mass in pine sites = -0.49 grams on a logarithmic scale, mean dry mass of spruce = -1.25 grams on a logarithmic scale [median dry mass of pine = 0.59 grams, median dry mass of spruce = 0.23 grams, indicating a 153% difference]). Berry count was also significantly higher in pine forests ($p = 0.009$), with spruce forests containing berries in only one out of a total of 50 examined plots (median = 0 berries), while pine had berries across all sites and almost every plot as well (median = 8.5 berries) (fig. 8).

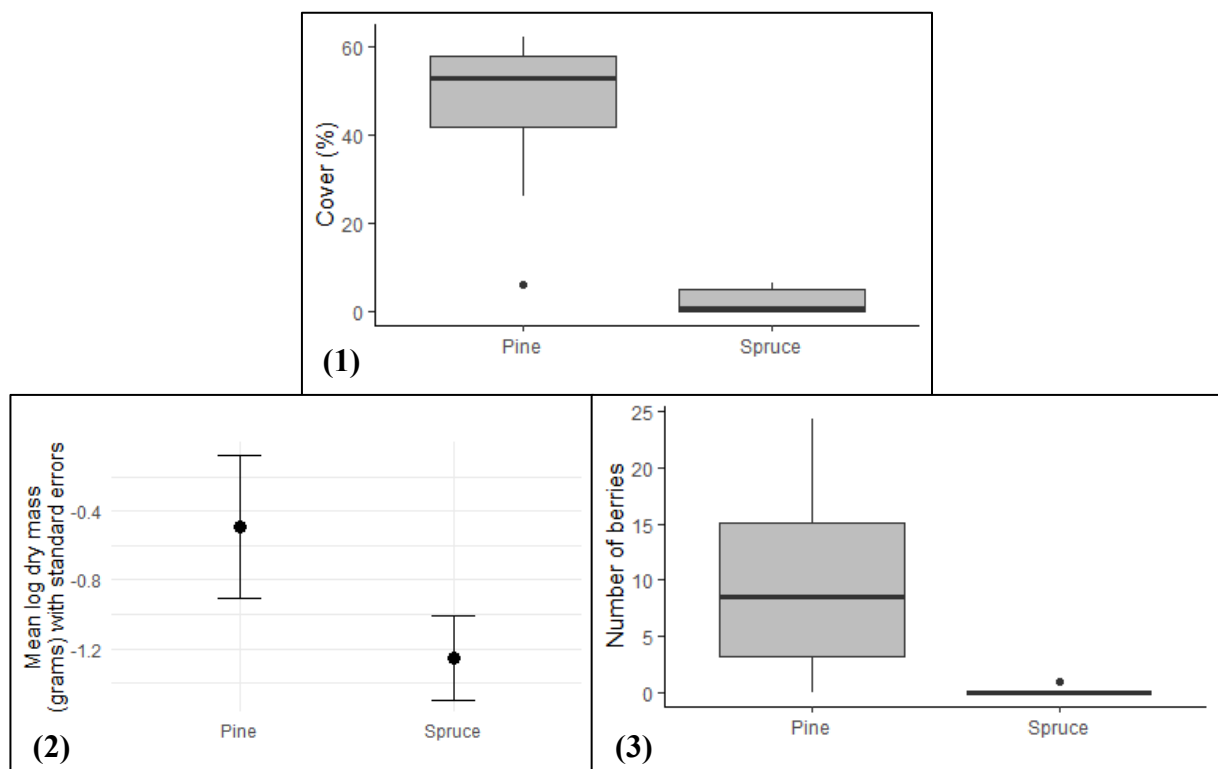


Figure 6: (1) Significantly higher percentual bilberry cover in pine over spruce forests. (2) Significantly higher mean log dry mass in pine over spruce forests. (3) Significantly more berries in pine over spruce forests.

3.3 Effects of pine stand age on bilberry

The results showed that bilberry cover and dry mass decreased linearly with forest age (fig. 8) The regression reveals a significant negative relationship for both cover (adjusted R-squared = 0.401, slope = -0.391, $p = 0.001$) and dry mass (adjusted R-squared = 0.231, slope = -0.012, $p = 0.016$), although there was much variability, and the explanatory value was quite low. There was a tendency toward a negative relationship also between age and berry count, but it was not significant ($p = 0.177$).

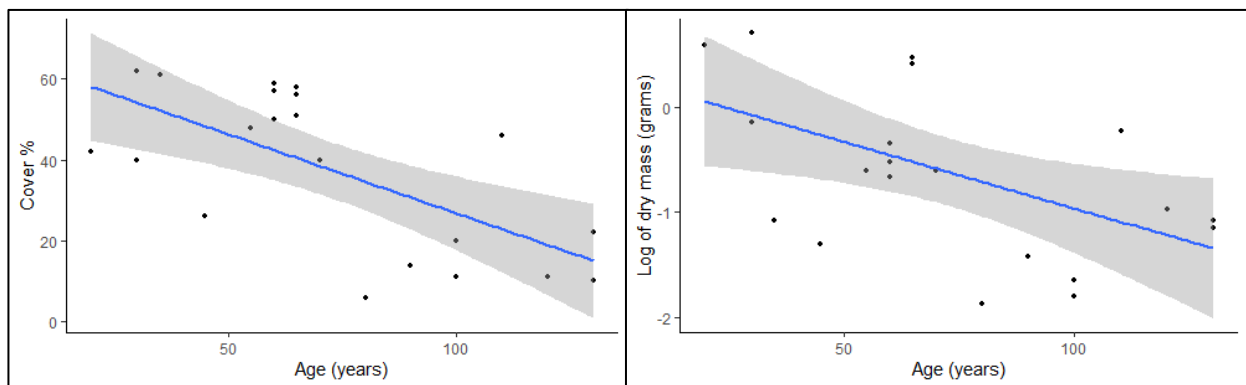


Figure 7: The significant negative relationship between: (1) percent bilberry cover and age. (2) log of dry mass and age. The blue lines are lines of best fit and grey areas are 95% confidence bands.

4. Discussion

4.1 Effects of tree species on bilberry

To test our first hypothesis, we compared bilberry responses between paired pine and spruce forest-stands within the study area. The findings agreed with our hypothesis, which revealed that the sampled pine forests exhibited higher bilberry cover, larger bilberry size and greater berry production compared to spruce forests, independent of stand productivity, age, and height above sea level. The negative effects of spruce on bilberry cover and berry production were surprisingly large compared to previous research. For example, Miina et al. (2009) found that in pine, the coverage of bilberry was only 1.13 times higher, and berry count twice as high as in spruce, much less significant than our samples. Nielsen et al. (2007) also observed a comparatively higher bilberry cover (mean = 31%) and berry count (mean = 0.22) in spruce stands than us.

The differences we observed in bilberry performance between dominant tree species are likely to be primarily attributed to the distinct light conditions created by the canopies of pine and spruce trees. Spruce trees, with their dense canopies and high shade-casting ability, have a strong influence on light conditions, while pine trees typically create semi-light conditions with a less dense canopy (Johansson, 1987; Vandekerkhove & Hermy, 2004). This aligns with our fieldwork observations, where we saw visually obvious variations in light conditions between the paired sites (Pers. Obs. Gilhuus. J, Stensaker. M). In studies from Scotland and Sweden, it was found that semi-light or partial shading conditions, like those produced by pine trees, are optimal for bilberry cover, particularly due to competition with other field-layer species like heathers that benefit more from increased sun exposure (Parlane et al., 2006; Bergstedt & Milberg, 2001). The ability of bilberry to thrive in intermediate light intensity conditions can be attributed to its superior shade-tolerance compared to competing species. Previous research by Hester et al. (1991a); Hester et al., (1991b) on the succession from heather moorland to birch woodland, demonstrated that *Calluna vulgaris*, a heather species that typically dominates the early stages of succession, experienced a significant reduction in cover as tree canopies developed and shade levels increased. They observed that increased shading also had a negative effect on bilberry

performance; however, this reduction was considerably lower compared to the other plants they examined. As a result, bilberry can outcompete other species and establish dominance under more intermediately shaded conditions. Anecdotally, our own fieldwork observations confirmed the prevalence of *Calluna vulgaris* in sunnier and drier locations throughout the study area (Pers. Obs. Stensaker. M, Jakob. G). Conversely, the optimal light intensity for berry production may be higher due to increased pollinator activity (Eckerter et al., 2019). In support of this, the only sampled spruce site where we found any berries had higher lux measurements than the median.

Bilberry cover is known to peak at a higher tree density in relation to basal area in pine forests (up to 40 m² ha⁻¹) compared to spruce forests (up to 20 m² ha⁻¹), but spruce dominant forests can still provide a favorable habitat if the tree density is sufficiently open (Eldegard et al., 2019). Furthermore, Miina et al., (2009) observed that thinning (i.e., removal of some tree biomass by forest managers to improve timber quality) of spruce during mid-ages (43 and 58 years) caused a significant, temporary increase in bilberry cover, indicating that our sampled spruce stands are too dense or not being thinned enough for bilberry to thrive. Because of our paired study design that considers forest productivity, age, and height above sea level it seems likely that the shading effect of the dominant tree species is the most important factor affecting bilberry in our samples. Adding to this, a related study (Olsson, 2022) using the same sites, observed little difference in soil carbon among them, further underlining that light availability is a crucial factor.

The average size of individual plants varied less between the dominant tree species than cover and berry count, being only marginally significant. There appears to be fewer studies conducted on the effect of dominant tree species on the size distribution of bilberry. Agreeing with our results, Parlane et al. (2006) found that bilberry height was greater in open pine forests compared to more shaded areas like thickets, further underlining that light conditions play a major role in the observed differences. Our data indicates that bilberry recruitment is less likely to occur within spruce forests. Endozoochory, which refers to the dispersal of seeds through animal ingestion, increases the likelihood for germination of bilberry seeds, and seedling growth is also more likely to occur on decaying wood, although it's far more common for bilberry to reproduce vegetatively once it's established in a

location (Eriksson & Fröberg, 1996; Steyaert et al., 2019). Endozoochory by browsing deer or other animals may be responsible for some of the limited bilberry recruitment occurring in spruce, though the lack of decaying wood due to the forest stands being managed, coupled with low light levels, make it unlikely for seedlings to establish. For vegetative reproduction, or bilberry growth in general, browsing may also be an important limiting factor in spruce stands, as Weisberg et al. (2005) discovered that below a certain level of light availability, bilberry exhibits a considerably reduced ability to recover after browsing. We surmise that the few bilberry individuals that do sprout within spruce stands may have a decent chance of growing relatively large without producing berries or successfully reproducing vegetatively, by allocating more resources to growth/survival, and because pollinators are less likely to enter dark forests (Eckerter et al., 2019). This may partly explain why the observed differences in size were less significant compared to cover and berry count, although the smaller sample size used in that analysis probably also influenced the results.

It's also noteworthy that bilberry cover and berry count distributions in sampled pine plots, in addition to performing better, displayed a lot more variance than spruce. The exception to this is again in the estimated size of bilberry where the spread observed in our data is more equal between the dominant tree species. It's challenging to determine the exact reasons behind this. However, apart from the probable influence of sample size differences, one possible explanation could be that the light factor is so overruling in spruce stands. In contrast, pine stands, which offer greater light availability, may be more influenced by other factors, thereby contributing to this variation.

4.2 Effects of pine stand age on bilberry

Our second hypothesis, that increased forest age would influence bilberry performance positively, was examined within a larger sample of pine forests. Disagreeing with our hypothesis, we found that the older pine stands displayed lower bilberry cover and smaller bilberry size compared to younger ones, while there was a non-significant tendency for a negative relationship regarding berry production, suggesting that younger forests are better for bilberry performance. These results should be viewed with caution, displaying a large variation around the line of best fit. The R values showed that approximately 40% of the

variation in cover, but only 23% of the variation in dry mass can be attributed to the age of the forest, meaning a substantial amount of the variation are caused by other factors.

Like the differences between pine and spruce forests, we propose that structural changes occurring as the forest matures, such as tree density and canopy development, leading to alterations in light conditions, may be a primary driver of the observed relationship.

Furthermore, the dominant disturbance regime of the forest, e.g., regular clearcutting, is likely an important factor in determining whether forest age has a positive or negative effect on bilberry performance (Eldegard et al., 2019). According to them, forest density is linked to the impact of forest age on bilberry performance, with optimal tree density for bilberry cover being lower in very young forests than in older ones, due to less light being transmitted through the canopy of a stand with many small trees compared to fewer big trees given the same basal area.

Previous studies have yielded conflicting conclusions regarding the forest age-bilberry relationship, adding further complexity to the interpretation of our results. For example, Hedwall et al. (2013) found that an increase in forest age might favor bilberry due to it being adversely affected by disturbances such as clearcutting, which drastically increases light intensity, thereby favoring early- succession competing species like *A. flexuosa* and *Calluna Vulgaris* (Bergstedt & Milberg, 2001; Parlane et al., 2006). In support of this, research has shown that bilberry has recovery periods, i.e., the time it takes for bilberry abundance to return to optimum levels, between 60-100 years (Löhmus & Remm, 2017; Kardell, 1980) following clearcutting. However, the study by Hedwall et al. (2013) was conducted in mixed boreal and temperate forests in Sweden. Similarly, Eldegard et al. (2019) found that bilberry cover increased with forest age, but this study was performed in mixed boreal stands, in Norway. These studies didn't specify how their sampled forests were managed, but their mixed stands ensure additional ecological factors that could influence the observed patterns such as more varying tree densities and canopies, as well as having a potential productivity advantage over monocultures (Kelty, 1992). Research by Nielsen et al. (2007), however, was conducted in intensely managed forest stands in Norway, more comparable to ours, albeit mainly comprising spruce monocultures and with an extra selection criterion of two other plant species being present in addition to bilberry. In line with our findings, they observed a

decrease in bilberry performance (including cover, height, biomass, and number of berries) with increasing forest maturity. Nybakken et al. (2012) also found that bilberry can benefit from shorter rotations (the time between planting new trees and cutting) in spruce monocultures, observing positive effects on bilberry growth quickly following clearcutting. Nielsen et al. (2007) argue that the contrasting results between theirs and other research may partly be explained by the size of the clear-cuts in their study landscape being relatively small, reducing the levels of stress and damage from erosion and elevated light intensity due to shorter distances to surrounding forest stands. It's possible that similar conditions apply to our study area, and we also surmise that the interspecific competition of mixed stands could create more light gaps than intraspecific competition in monocultures. Regardless of the exact mechanisms driving it, managed spruce and pine monoculture stands appear to reach optimal light conditions for bilberry relatively quickly after clearcutting, compared to mixed stands which undergo a more gradual transition towards such optimal conditions.

The contrasting results among these studies highlight the complexity of the relationship between bilberry and forest age, which may vary depending on the specific forest composition and management practices. Overall, the discrepancies in findings emphasize the need for further investigation into the relationship, considering the specific forest types and management contexts. Our findings suggest that for managed monocultures, younger, lighter forests are better for bilberry, likely due to them growing too dark over time, compared to mixed stands which benefit more from being left to grow old. Most of the aforementioned studies were not conducted in pine or spruce monocultures but in more mixed forests. Our study design, with paired sites controlling for age, productivity, maturity class and height above sea level and tree species may have contributed to more robust results regarding bilberry productivity in these forest types, particularly within this region of Norway.

4.3 Implications for forest management

The ongoing shift from Scots pine to Norway spruce is associated with negative outcomes for biodiversity and various ecosystem services on a landscape scale (Pettersson, 2019), highlighting the need for further research on the potential ecological benefits of spruce

forests as well. The spruce stands in Kaupanger, as observed during our field work, exhibited distinct environmental and vegetation characteristics compared to pine forests (Pers. Obs. Gilhuus. J, Stensaker. M), providing a unique niche and habitat for species that thrive in such conditions like fungi, lichens, and bryophytes (Petersson et al., 2019). Our study displays particularly dramatic negative effects of spruce stands on bilberry cover and berry count compared to pine. This agreed with our hypothesis, but the observed differences are large compared to previous research (Nielsen et al., 2007; Miina et al., 2009), likely due to excessive stand densities and insufficient thinning practices (Miina et al., 2009). In general, our results suggest that in monoculture stands in Kaupanger, forest managers should focus on pine to enhance biodiversity. Regarding the promotion of bilberry cover in spruce stands, reducing tree density compared to pine stands can achieve a similar level of bilberry presence (Eldegard et al., 2019). However, this approach may lead to decreased profits due to reduced wood production per unit area. Therefore, to strike a balance between satisfactory wood production and the promotion of bilberry, prioritizing pine over spruce in monocultures is preferable. Where spruce is used, lower stand densities, more thinning, or switching to mixed stands should be encouraged (Felton et al., 2010; Miina et al., 2009).

Disagreeing with the second hypothesis, the results showed a decline in bilberry cover and size with forest age, suggesting that younger, lighter forests and shorter rotations might benefit bilberry and, consequently, biodiversity in managed monoculture-stands. However, younger, smaller forests are not commercially ideal for timber production (Bergseng et al., 2018). In contrast, bilberry performance in mixed stands appear to benefit from longer recovery periods between severe disturbances, e.g., clear-cutting (Eldegard et al., 2019; Hedwall et al., 2013). Thinning must be adapted to a forests particular stand density to avoid adverse effects on bilberry performance (Miina et al., 2009). In sum, we reason that in a broader forest management context, considering both ecological and commercial interests, it may be beneficial to encourage mixed stands if they are going to be left to grow old, and if they are not, then more regular thinning adapted to stand densities in older pine monocultures is preferable.

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