



Høgskulen  
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# MASTER'S THESIS

The soil propagule bank along an  
elevation gradient - a key to  
understanding climate change dynamics

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I confirm that the work is self-prepared and that references/source references to all sources used in the work are provided, cf. Regulation relating to academic studies and examinations at the Western Norway University of Applied Sciences (HVL), § 12-1.

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## Abstract

Spanning Northern Europe, Asia, and North America, the boreal forest represents Earth's most expansive terrestrial vegetation zone, constituting approximately one-third of global forests and accounting for nearly 40% of Norway's land mass. This biome is currently under considerable threat from climate change, leading to a consequential necessity for forest species to either acclimate, adapt, or relocate to survive. One such adaptive strategy is 'bet-hedging,' which leverages dormant propagules in the soil to sustain species amidst environmental change. Despite its significance, our understanding of climate change's impact on boreal forests' propagule bank, including bryophytes and ferns, is limited. This study examines the species composition and richness of the propagule bank in a boreal pine forest compared to the standing vegetation. It investigates the influence of local environmental factors on the propagule bank's species composition and assess the role of the propagule bank as a bet-hedging strategy in response to environmental changes.

Results from this study show that the propagule bank held fewer species than the standing vegetation as the reproductive mechanisms of many boreal forest species seem to rely on clonal reproduction, which likely contributed to the lower species composition in the propagule bank. The propagule bank exhibited lower species richness compared to the standing vegetation, and a decline in species richness was observed along the elevation gradient.

Despite the recognized potential of propagule banks in buffering against environmental change by maintaining species richness and influencing community composition, this study shows that the boreal forest propagule bank may lack sufficient diversity to support current plant communities under evolving climatic conditions. With a likely dominance of few species not closely resembling the existing vegetation, the propagule bank's role in climate resilience could be undermined. Hence, rather than acting as a buffer or bet-hedging strategy, the propagule bank may instead indicate potential future vegetation structure and composition.

## Sammendrag

Den boreale skogen strekker seg over Nord-Europa, Asia og Nord-Amerika og representerer jordens mest vidstrakte terrestriske vegetasjonsregion, og utgjør omtrent en tredjedel av globale skoger og står for nesten 40% av Norges landareal. Dette biomet er for tiden under betydelig trussel fra klimaendringer, noe som fører til en følgelig nødvendighet for arter å enten akklimatisere, tilpasse seg eller flytte for å overleve. En slik adaptiv strategi er "innsatssikring", som utnytter propaguler i jorda for å opprettholde arter ved endringer i miljø. Til tross for dens betydning, er vår forståelse av klimaendringenes innvirkning på boreale skogers propagulebank, inkludert moser og bregner, begrenset. Denne studien undersøker artssammensetningen og artsrikdommen til propagulbanken i en boreal furuskog sammenlignet med den stående vegetasjonen. Den undersøker påvirkningen av lokale miljøfaktorer på propagulabankens artssammensetning og vurderer propagulabankens rolle som en sikringsstrategi som respons på miljøendringer.

Resultatene fra denne studien fant at propagulabanken hadde færre arter enn den stående vegetasjonen da reproduksjonsmekanismene til mange boreale skogarter er avhengige av klonal reproduksjon, noe som sannsynligvis bidro til den lavere artssammensetningen i propagulabanken. Propagulbanken viste lavere artsrikdom sammenlignet med den stående vegetasjonen, og det ble observert en nedgang i artsrikdom langs høydegradienten.

Til tross for det anerkjente potensialet til propagulebanker i å dempe miljøendringer ved å opprettholde artsrikdom og påvirke artssammensetning, antyder denne studien at den boreale propagulabanken kan mangle tilstrekkelig artsmangfold til å støtte nåværende plantesamfunn under utviklende klimatiske forhold. Med en sannsynlig dominans av få arter som ikke samsvarer med den stående vegetasjonen, kan propagulbankens rolle vedrørende klimamotstandsdyktighet bli undergravd. Derfor, i stedet for å fungere som en buffer eller sikringsstrategi, kan propagulbanken i stedet indikere potensiell fremtidig vegetasjonsstruktur og artssammensetning.

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## Introduction

The circumpolar boreal forest constitutes the Earth's most expansive terrestrial vegetation zone (Sanderson et al., 2012). Encompassing approximately 19 million km<sup>2</sup>, this biome extends throughout northern Europe, Asia, and North America. It is predominantly characterised by coniferous forest and accounts for almost one-third of forests globally (Gauthier et al., 2015). The boreal forest covers nearly 40% of Norway's land area (Framstad et al., 2017) and sustains a unique community of species, including shrubs, mosses, lichens and ferns (Kuuluvainen, 2002). The Nordic boreal forests feature a distinct layer of bryophytes (T. Økland, 1996), and with genera such as *Vaccinium* and *Empetrum* being commonly found in the field layer (Bryn et al., 2018). While these forests represent an intricate and vital component of our global ecosystem, their stability and persistence are under threat from the overarching challenge of climate change (Kellomäki et al., 2007; Price et al., 2013; Venäläinen et al., 2020).

Climate change is a significant driver of ecosystem change, with rising temperatures, altered precipitation patterns, and extreme weather events causing habitat loss, changes in species distributions, and increased stress on ecosystems (IPCC, 2023). The boreal forest, which has been shown to be highly sensitive towards environmental changes and particularly sensitive to warmer and drier environments (Keenan, 2015; Seidl et al., 2020), is undergoing unprecedented rates of warming, exceeding previous observations (Smith et al., 2015). Current evidence suggests that the boreal biome is expected to experience the greatest increase in temperature among all forest biomes in the 21<sup>st</sup> century (Chapin et al., 2005; IPCC, 2021), a consequence of Arctic amplification (IPCC, 2021; Parmesan & Yohe, 2003; Serreze & Barry, 2011). These changes are predicted to significantly affect the composition of Norway's boreal forests, potentially causing the majority of them to transition out of the prevailing boreal vegetation zone in the coming decades (VKM et al., 2022).

In order to respond to environmental changes, species need to acclimate, adapt or relocate, as failing to do so will result in extinction (Corlett & Westcott, 2013; Klanderud & Birks, 2003). As global temperatures rise, species move poleward or towards higher altitudes to track their optimal temperature niches, a phenomenon referred to as 'range-shift'

(Parmesan & Yohe, 2003), or adapt through phenotypic plasticity (Jump & Peñuelas, 2005). Prior studies have indicated that arctic and boreal mountain species are more likely to relocate than to adapt to environmental changes (MacDougall et al., 2021; Myers-Smith et al., 2011). However, the rate at which species are shifting their ranges frequently fails to keep pace with climate change (Corlett & Westcott, 2013; Rees et al., 2020).

Certain species leverage the adaptive strategy of bet-hedging to cope with diverse environmental changes, enabling them to persist even in unfavourable conditions (Cohen, 1966; Gremer & Venable, 2014). This strategy, also called temporal bet-hedging, involves the accumulation of transient and persistent propagules in the soil, such as seeds, spores, and other reproductive structures (Walck et al., 2005). Evidence shows that these propagules can remain dormant for an extended period until favourable conditions are met (Yashina et al., 2012). This strategy allows species to maintain their existence not just spatially, but across temporal scales as well (Childs et al., 2010; Vandvik et al., 2016; Wagner & Simons, 2009; Walck et al., 2005). In other words, the propagule bank serves as a genetic reservoir of plant communities (Simpson et al., 1989), and has an important function in community dynamics and regeneration, contributing to the future biodiversity of ecosystems (Faist et al., 2013).

Studies have shown that the composition and species richness of the propagule bank are affected by environmental factors such as pH, soil organic matter, temperature, and precipitation, which play an important role in seed germination and dormancy (Basto et al., 2015; Ooi et al., 2009). This implies that projected climatic changes will have an impact on the propagule bank in boreal forests (Walck et al., 2011), and, in turn, on the persistence of individual species and species communities (Ooi, 2012). As temperature decreases with elevation and precipitation increases with elevation throughout most of the world (Körner, 2007), using an elevation gradient can be a useful alternative to long-term studies for understanding how the propagule bank responds to climate change. This method, known as space-for-time substitution, allows for the use of an elevation gradient as a proxy to infer temporal patterns of change in response to environmental factors, such as climate change, by examining spatial patterns across elevation (Blois et al., 2013; Elmendorf et al., 2015). Space-for-time substitution studies have shed light on the relationship between the propagule bank and environmental change. Hegazy et al. (2009) and Sharma et al. (2009) have shown that species richness tends to decline with elevation, indicating that the



composition and richness of the propagule bank are influenced by environmental factors. These findings suggest that as environmental conditions change, the species composition within the propagule bank may also shift, potentially impacting ecosystem dynamics. Likewise, studies comparing the propagule bank and the standing vegetation have shown that the propagule bank have a species composition that differs from that of the standing vegetation (Birhanu et al., 2022; Rydgren & Hestmark, 1997), implying that not all species form propagule banks. Notably, the dissimilarity in standing vegetation and its corresponding propagule bank is highest within forest ecosystems, while it exhibits the highest similarity in grasslands (Hopfensperger, 2007).

As evident in the above-mentioned literature, the majority of studies examining the propagule bank have focused on plant species that produce seeds, disregarding the importance of seedless species such as bryophytes and ferns. The lack of comprehensive knowledge regarding the propagule bank in the boreal forest is a notable gap which not only hampers our comprehension of this ecosystem but also neglects to acknowledge the significance of ferns and bryophytes within it (T. Økland, 1996; Plue et al., 2017). To the best of my knowledge, there are no prior studies that have explored the propagule bank, specifically considering bryophytes and ferns, along an elevation gradient in a boreal forest, and compared this to the standing vegetation. This highlights a knowledge gap that needs to be explored.

By using a space-for-time approach, spanning an elevation gradient that ranges from 200 to 875 m a.s.l. in a boreal pine forest in Vestland county, western Norway, this study aims to answer the following questions: (1) How does the species composition and richness of the propagule bank in a boreal pine forest compare to the standing vegetation? (2) To what extent do local environmental factors influence the species composition of the propagule bank? (3) What can my findings reveal about the role of the propagule bank as a bet-hedging strategy in response to environmental changes, such as climate change? To answer these questions, I collected and germinated soil propagule bank samples in a growth room.

# Materials and methods

## Study site

The study site is located in Sogndal, Vestland county, Norway (61°13'N, 7°9'E; Figure 1) and is situated along a southwest-facing ridge of the mountain Hesteggi (907 m a.s.l.). Beginning in the residential area of Kjørnes, the 2.7 km long transect spans an elevation gradient from 200 to 875 m a.s.l. and is located in a weak oceanic, southern boreal vegetation zone which transitions to the low alpine zone towards the mountain's summit (Moen, 1998).

Characteristic of the boreal vegetation zone are cool summers and cold winters, accompanied by a moderate amount of precipitation ranging from 400 to 1000 mm per year. During winter, the ground is typically blanketed with snow, and the soil composition commonly comprises acidic podzol (Tomter & Larsson, 2023). The temperature and precipitation data interpolated across the study site's elevation indicate a decrease of approximately 4.7°C in temperature and an estimated increase of around 63 mm in precipitation from the foot to the top of the mountain (Appendix 1). In the lower region of the study site, the field layer consists of dwarf shrubs such as *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, and *Pinus sylvestris* being the dominant species in the canopy (Figure 2). The geological composition of the study site predominantly consists of Precambrian anorthosite and gneiss formations, which are intermittently covered by glacial deposits that exhibit a decrease in thickness as elevation increases (NGU, 2023).

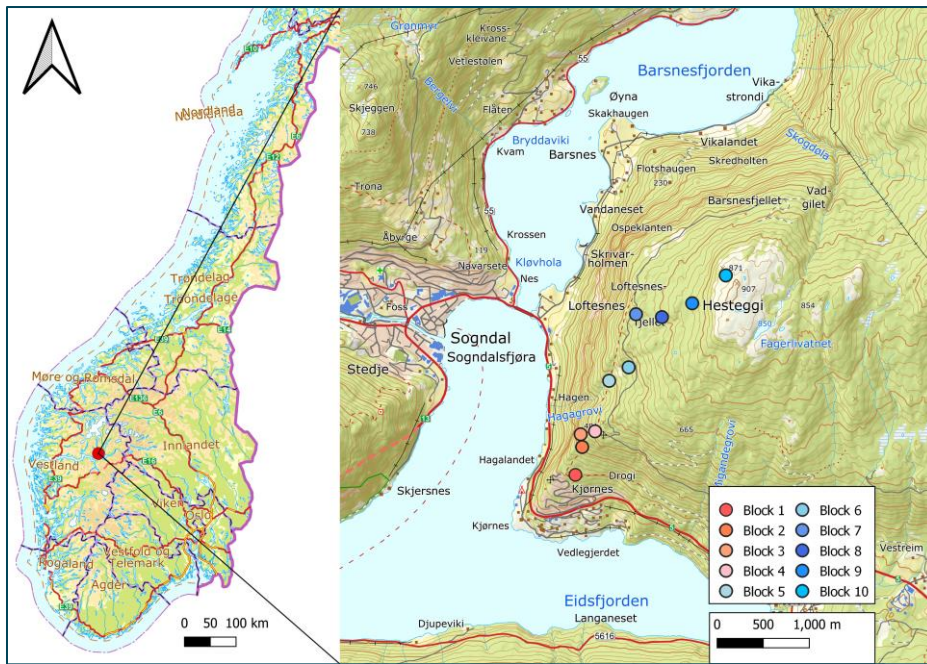


Figure 1. Map overview of the location of the study site in Sogndal municipality, Norway, with the location of the ten blocks from which soil samples were collected. © Kartverket

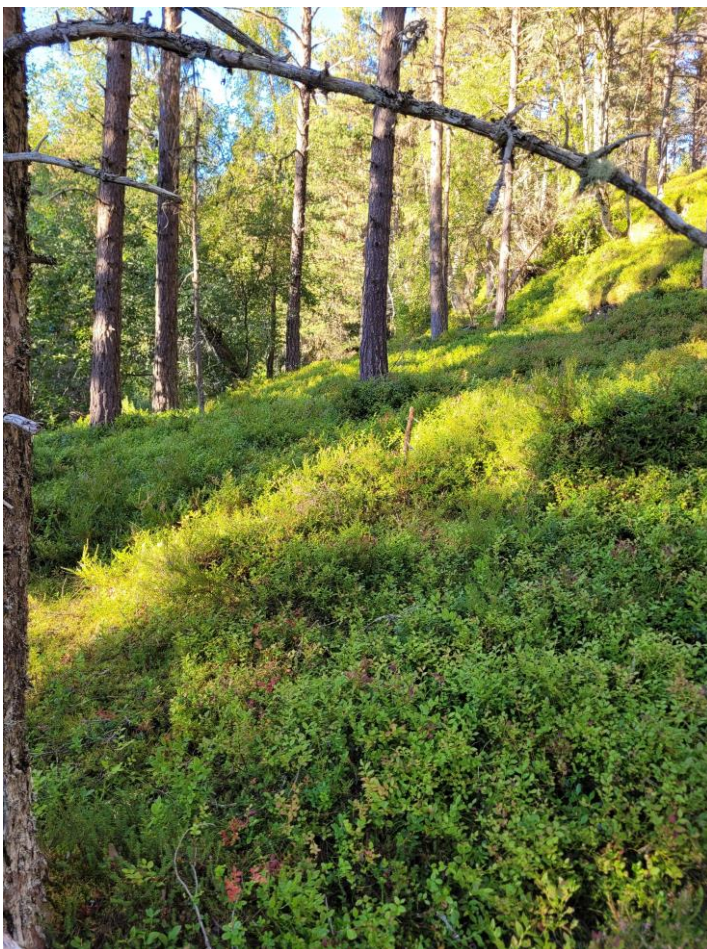


Figure 2. Vegetation in the lower region of the study site. Dominated by *Pinus sylvestris* and dwarf shrubs. Photo: Tor-Eirik Ness Sæther.

## Soil sampling

In September 2022, I collected soil propagule bank samples from ten blocks of 5 x 10 m along the elevation gradient (Figure 1). The ten blocks had been established subjectively in prior studies with the intention of spanning varying ecological conditions (Avdem & Lima, 2018; Berge, 2018). Each block consists of five 0.5 x 0.5 m plots with a minimum distance of one meter between each plot. Four samples were collected for each plot using a hand auger ( $\varnothing$  5 cm; 5 cm depth). These samples were taken from outside the plots, approximately 5 cm away from the outer edge, resulting in a total of 200 samples. The collected soil samples underwent vernalisation in cold storage at 4°C for an average of 6 weeks to break dormancy. The samples were collected from block 4-10 on September 11<sup>th</sup> and block 1-3 on September 14<sup>th</sup>.

## Lab processing

I processed the soil samples using a modified seedling emergence method based on the method of ter Heerdt et al. (1996) as well as the methods and recommendation in the ClimEX Handbook (Halbritter et al., 2020). The seedling emergence method by ter Heerdt et al. (1996) for processing soil samples involves sieving the samples with water to eliminate silt and soil particles, resulting in a reduced sample volume. However, in this study, which aimed to incorporate spores into the analyses, the application of water was omitted.

The soil samples were thoroughly shaken to loosen up and remove as much unwanted material as possible. Subsequently, the sieved soil samples were re-sifted to remove branches and larger debris, enabling visual inspection and manual removal of unwanted material. All residual material was discarded. The volume of the sieved soil sample was recorded, and samples were stored until all samples had been sifted. To reduce the chance of cross-contamination, the sieve and beakers were washed and dried before sieving another sample. An overview of the equipment used is shown in Figure 3 and the soil sifting process is shown in Figure 4.





Figure 3. Equipment used for sifting soil samples. 1: Bucket with discarded material. 2: Bucket used for transfer for second sifting. 3: Beakers used for volume registration. 4: 4 mm sieve with bottom pan and top lid.



Figure 4. A: The initial soil sample in its entirety prior to undergoing the sifting process. B: The fraction of the sample that remained after the first sifting. C: The residual material that was unable to pass through the sieve and was discarded.



Figure 5. Finished tray with pots filled with potting soil and soil propagule bank sample collected from the study site in Sogndal, Norway. Soil samples were spread on top of potting soil where each marker indicates the corresponding block and plot the soil sample came from. Two control pots per tray were used as indicated by the green outline.

Once samples were sieved, they were evenly spread on top of pots filled with potting soil. The mean volume of the soil samples from the plots was 420 ml. To maintain a thin layer of soil, soil samples from each plot were dispersed evenly over four separate pots, resulting in an average of 105 ml per pot (ca. 0.5 cm depth). The pots were labelled according to their block and plot number and were assigned a numerical identifier ranging from 1 to 4 (Figure 5). A comprehensive list of the nutrient content of the potting soil is provided in Appendix 2.

## Growth room

A total of eight trays, containing 200 experimental pots and 16 control pots (two control pots per tray to account for possible contamination), were subjected to a controlled-environment room, or growth room, as depicted in Appendix 3. A translucent fabric covered each tray as a means of preserving moisture and mitigating the potential for airborne contamination in early stages of the experiment. The fabric was removed once it seemed to inhibit vertical growth of the germinating plants.

Following recommendations in the ClimEx handbook to optimise germination, the temperature was set to 20°C during the day and 15°C during the night, with a light/dark cycle of 16/8 hours (Halbritter et al., 2020). Armatures used were Osram LUMILUX HE 14 W/830. The pots were watered weekly to maintain sufficient moisture levels and were bottom watered to avoid disrupting the soil sample layer. Species were registered and removed once they could be identified. The experiment was run for 25 weeks (October 24<sup>th</sup>/25<sup>th</sup>, 2022 to April 18<sup>th</sup>, 2023). Plants that had emerged but could not be identified to the species level before the end of the experiment were identified to the genus level. Nomenclature follows Norwegian Biodiversity Information Centre.

The rapid growth of bryophytes and ferns meant they could potentially inhibit the germination and growth of other species. At week 7 of the experiment, the cover of bryophytes and ferns was measured, and any pot with a cover of 50% or more had half the pot weeded (Appendix 4) The cover was determined using the "Color Recogniser" app (Secco, 2022), which calculates the percentage cover of a specific colour in an image (Appendix 5). Pictures were taken of each pot, with only the organic matter included in the image frame, and the green and yellow colours (yellow was included as it was a suitable proxy for plant material) were combined to determine the total percentage of plant cover. Samples from the weeded part of the pot were transplanted to new pots in case I needed them for identification if other species were accidentally weeded (Appendix 6).

Contamination was observed in all 16 control pots, predominantly by bryophytes, but also some ferns (*Athyrium filix-femina*, *Phegopteris connectilis* and *Gymnocarpium dryopteris*) and *Agrostis capillaris* (found in one control pot but in none of the experimental pots).

The decision to exclude species considered as contaminants from analyses was based on a quantitative criterion, i.e., species with a percentage cover or number of individuals smaller than the average percentage of number in control pots were considered contaminants. *Agrostis capillaris* was considered contamination as it was only found in the control pots. Similarly, *Bryum* sp. and *Marchantia polymorpha* were also excluded from analyses. The cover of ferns found in the control pots did not exceed the cover of ferns in the experiment pots and ferns were thus included in the analyses.

It should be mentioned that the air-conditioning system in the growth room malfunctioned on three separate occasions, whereby the temperature rose above the set temperature range (i.e., 15-20°C), along with a significant rise in humidity. For all three instances, it is estimated that the temperature stayed in the range of 28-34°C for roughly 12 to 24 hours at a time. Immediate steps were taken upon discovery whereby the door was kept open to lower the temperature until the air-conditioning system started working again.

### Statistical analysis

Registration of species was performed by counting the number of individuals that germinated from the pots, but ferns and bryophytes were registered in a binary format of presence/absence, as counting them individually was considered impractical. Prior to conducting statistical analyses, the data collected from this study was combined with the dataset from Avdem & Lima (2018), which includes information on the presence/absence of species in the standing vegetation, as well as environmental variables for each plot. As the datasets had different approaches for registering species presence/absence, the datasets were transformed through binarization, where continuous data is converted into binary (presence/absence) data (Hijmans & Graham, 2006). My data was binarized by assigning a value of 1 to species that were present in either of the four pots pertaining to a plot and a value of 0 to species that were absent. The dataset from Avdem & Lima (2018) was transformed by converting the 0-16 scaling used (where each plot was subdivided into 16 subplots), to the same present/absent (i.e., 1/0) scale as my data. For analyses performed on the angiosperms from the propagule bank, binarization was not needed, as the actual number of individuals were used. Figures provided in the results section are given in either



frequency or abundance when explaining various metrics. Frequency is given as a percentage of presence/absence in the 200 pots for the propagule bank and in the 16 subplots per plot in a block for the standing vegetation. Abundance refers to the number of individuals of a particular species from the 200 pots for the propagule bank or presence/absence in the 16 subplots per plot in a block for the standing vegetation.

To explore the underlying patterns and gradients in the species composition data, I performed ordination using detrended correspondence analysis (DCA; Hill & Gauch, 1980), implemented in the *vegan* package (Oksanen et al., 2022) using R version 4.2.3 (R Core Team, 2023). Detrended Correspondence Analysis (DCA) is a multivariate statistical technique commonly used in ecology and is a variation of Correspondence Analysis (CA) that accounts for the non-linear relationships and uneven variances that are often found in ecological data (Hill & Gauch, 1980).

The environmental variables from Avdem & Lima (2018) were chosen based on which environmental variables were shown to be significant in their split-plot GLM analysis. The variables include m a.s.l., slope, light, soil moisture content, soil organic matter and pH. I fitted the variables as contour lines with the function 'ordisurf' from the *vegan* package (Oksanen et al., 2022). I tested the environmental variables against the DCA axis scores using Kendall's rank correlation test (Kendall, 1938). It is important to acknowledge that significance tests from the correlation analyses have not been given much weight, as spatial autocorrelation was not accounted for in the analysis. The results derived from Kendall's rank correlation tests should be interpreted with caution, serving primarily as an indication of potential trends. This is because samples that are located closer to each other tend to be more similar than more distant samples, resulting in a type I error (Legendre, 1993). Any reference to significance in subsequent sections of the thesis is merely intended to report the numerical values, rather than implying actual statistical significance.

Species richness was calculated by counting the number of different species present within each plot in both the standing vegetation and the propagule bank. I performed a Wilcoxon rank-sum test to test for significance between the two (Mann & Whitney, 1947). Similar caution in interpreting the results from this test applies, as spatial autocorrelation was not accounted for. In examining the species richness of both the standing vegetation and the soil

propagule bank, lichens identified in the standing vegetation were excluded from the analysis. This exclusion was justified by their low probability of germination from the soil propagule bank as their growth is slow and can take years to establish (McMullin & Rapai, 2020). With the standing vegetation dataset containing 12 lichen species (predominantly lichens in the genus *Cladonia*), their inclusion would have introduced outliers and distorted the comparison of species richness.

# Results

## Species frequency, abundance, and richness

### *Propagule bank*

In total, 19 species germinated from the 50 sampled plots. Among them, 13 were vascular plants, including 3 species of ferns, and 3 were bryophytes (Figure 6), where ferns and bryophytes were found to be particularly prevalent. The five most frequent species in the propagule bank occurred in 50% or more of the plots (Figure 6). Of these, the bryophyte *Pohlia nutans* occurred in all 50 plots, followed by the ferns *Phegopteris connectilis* (96%), *Gymnocarpium dryopteris* (92%) and *Athyrium filix-femina* (76%). Of the other vascular plants, *Empetrum nigrum* and *Vaccinium myrtillus* were the most abundant (Figure 8) with an abundance of 482 and 136, respectively, followed by *Luzula Pilosa* ( $n = 38$ ), *Betula pubescens* ( $n = 18$ ), *Carex pilulifera* ( $n = 14$ ), *Vaccinium uliginosum* ( $n = 8$ ) and *Urtica dioica* ( $n = 4$ ).

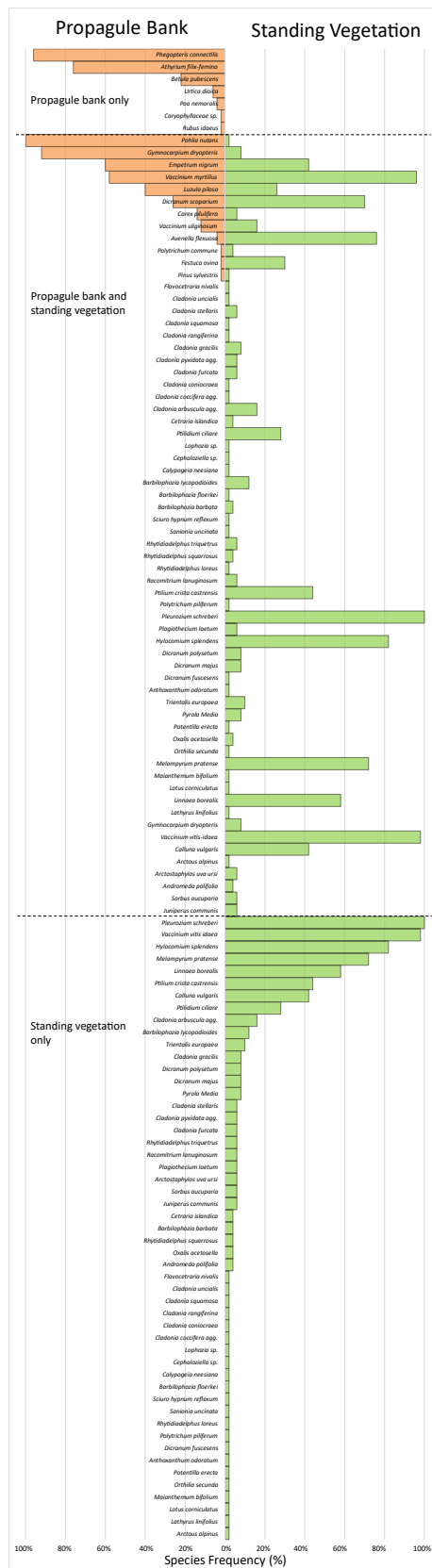


Figure 6. Species frequency distribution (%) from the 50 plots between the standing vegetation and the propagule bank. The standing vegetation is colour-coded in green (right) and the propagule bank in orange (left). Top section shows species that were only found in the propagule bank. The mid section shows species that were found in both the standing vegetation and the propagule bank, and the bottom section shows species that were only found in the standing vegetation.

Species richness was higher in the standing vegetation compared to the propagule bank across the entire elevation gradient. Wilcoxon rank sum test showed a statistically significant difference in species richness between the standing vegetation and the propagule bank ( $z = -6.924, p < 0.001$ ) (Figure 7). Across the elevation gradient, species richness in the propagule bank declined from its peak at 345 m a.s.l., whereas the species richness in the standing vegetation appeared to remain relatively stable across the elevation gradient except at the highest elevation (Figure 7).

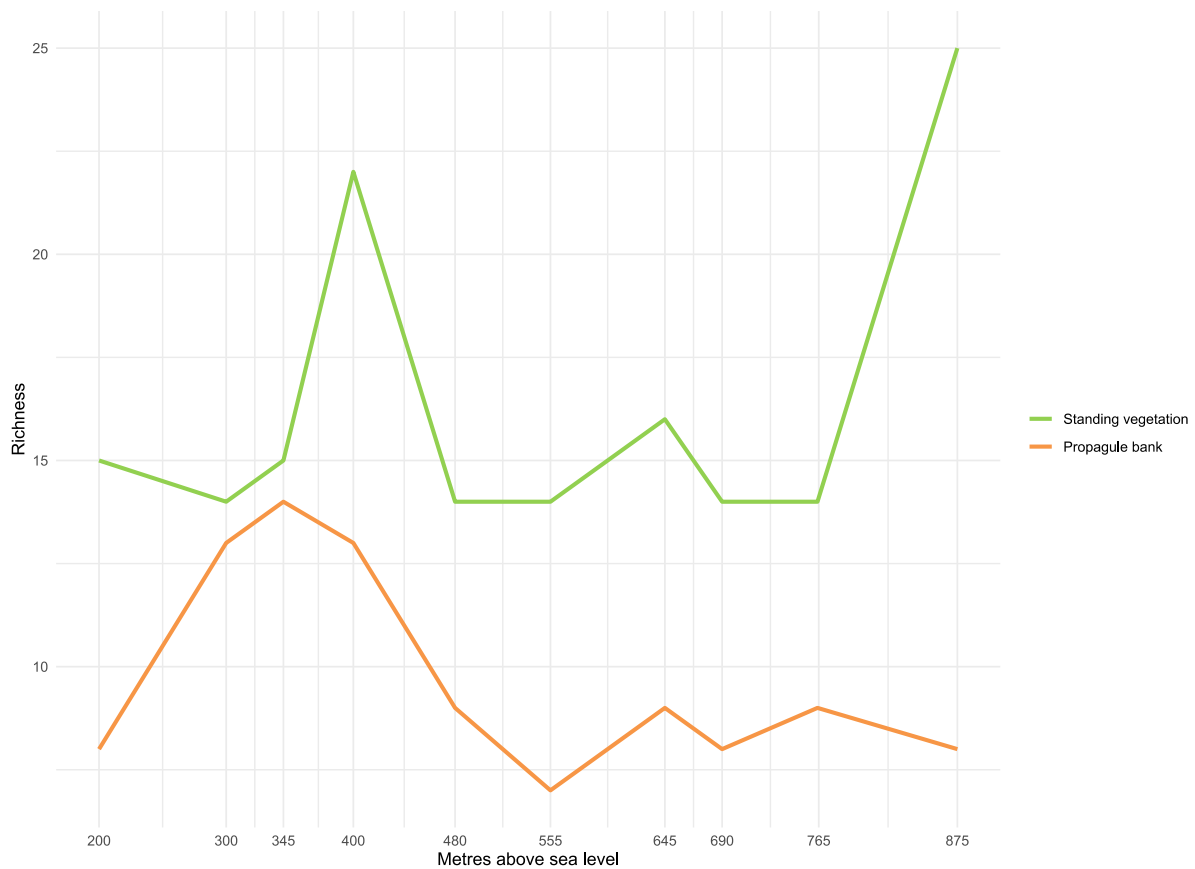


Figure 7. Species richness of the standing vegetation and the propagule bank along the elevation gradient. Species richness was statistically significantly higher ( $p < 0.001$ ) in the standing vegetation compared to the propagule bank.

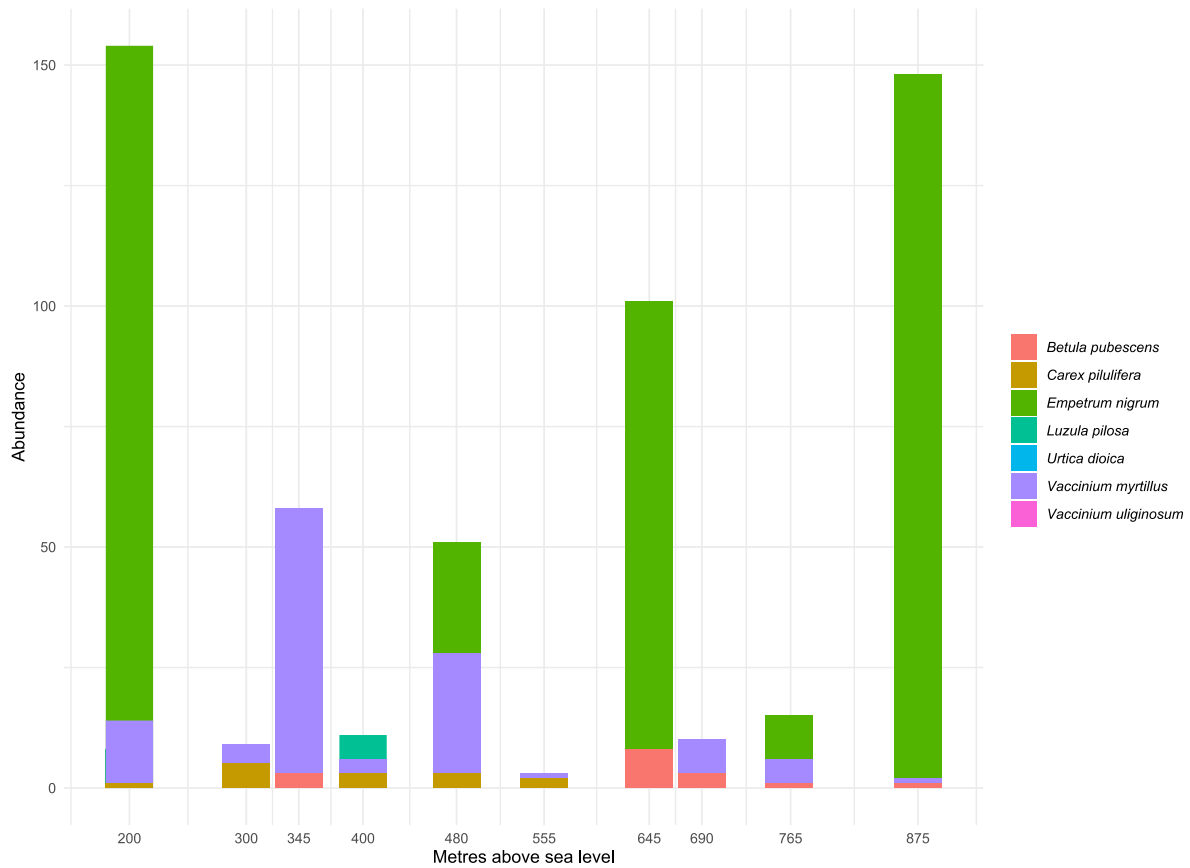


Figure 8. Cumulative species abundance of selected angiosperms that germinated from the propagule bank along the elevation gradient for the 200 total pots. Species were selected based on a minimum abundance of 4 or greater in all pots. *Empetrum nigrum* had the highest abundance ( $n = 482$ ), followed by *Vaccinium myrtillus* ( $n = 136$ ), *Luzula pilosa* ( $n = 38$ ), *Betula pubescens* ( $n = 18$ ), *Carex pilulifera* ( $n = 14$ ), *Vaccinium uliginosum* ( $n = 8$ ) and *Urtica dioica* ( $n = 4$ ). Due to the high abundance of *Empetrum nigrum* and *Vaccinium myrtillus*, both *Vaccinium uliginosum* and *Urtica dioica* are not visible in the figure.

Among the ferns that germinated, *Athyrium filix-femina* demonstrated the most notable increase in frequency with elevation (Figure 9). It was found in only 20% of the pots at 200 m a.s.l., whereas it reached 65% at 645 to 690 m a.s.l. *Phegopteris connectilis* had the highest frequency and remained fairly even throughout the elevation gradient. *Gymnocarpium dryopteris* presented a more diffuse pattern of frequency but increased notably from 45% at 555 m a.s.l. to 90% at 645 m a.s.l.

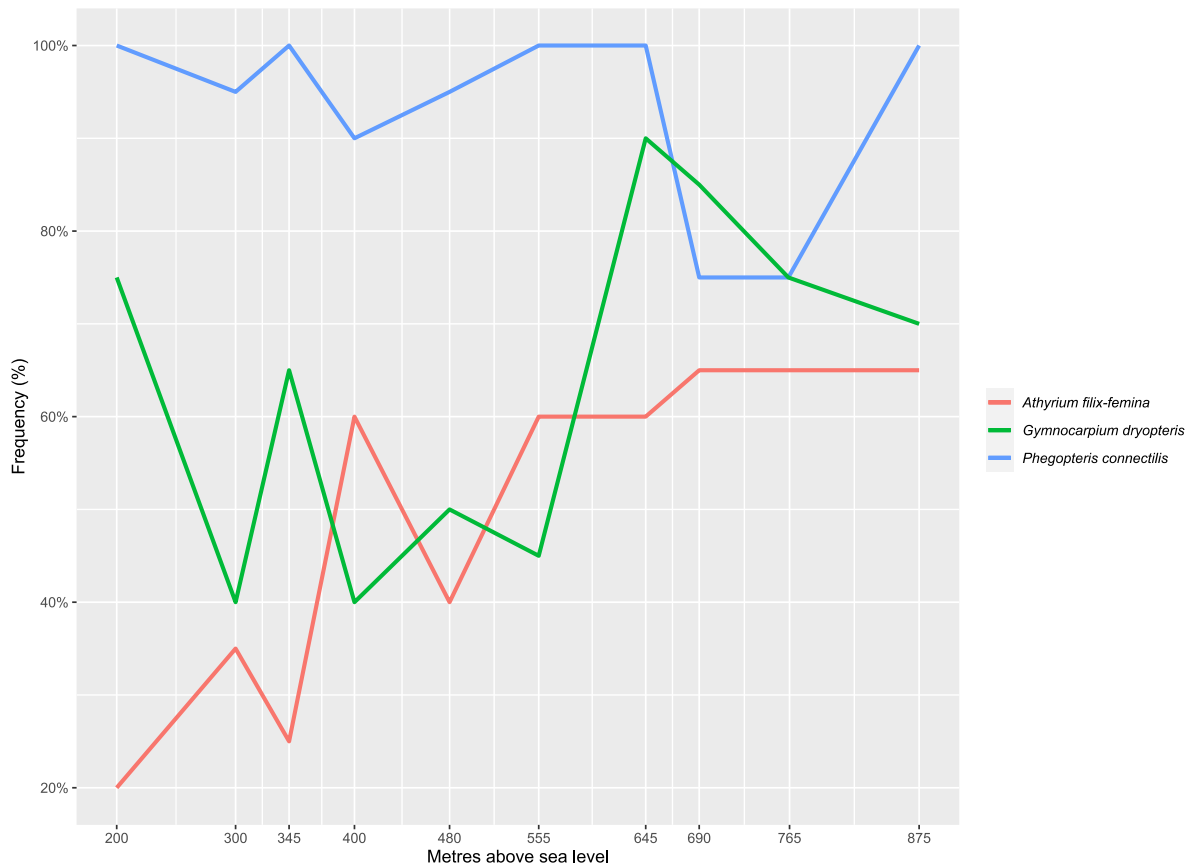


Figure 9. Species frequency of the three fern species that germinated from the propagule bank along the elevation gradient. Frequency was calculated based on the presence/absence within each of the 200 pots, i.e., a frequency of 50% at 200 m a.s.l. means that it occurred in 50% of all pots for block 1.

### *Propagule bank and standing vegetation*

Twelve species germinated from the propagule bank that were also present in the standing vegetation (Figure 6). The frequency of *Pohlia nutans* and *Gymnocarpium dryopteris* were found to be distinctly higher in the propagule bank compared to the standing vegetation (Figure 6). In contrast, *Pleurozium schreberi* and *Vaccinium vitis-idaea* were not found in the propagule bank, but had a high frequency in the standing vegetation of 100% and 98%, respectively. *Pinus sylvestris* was the only species with an equal frequency in the standing vegetation and the propagule bank (2%). Only 19% of the species from the standing vegetation were found in the propagule bank (Figure 6). However, this percentage increased to 24% when lichens in the standing vegetation were not taken into consideration.

A total of seven species were only found in the propagule bank, i.e., *Phegopteris connectilis*, *Athyrium filix-femina*, *Betula pubescens* ( $n = 18$ ), *Poa nemoralis* ( $n = 6$ ), *Urtica dioica* ( $n = 4$ ), *Caryophyllaceae sp.* ( $n = 1$ ) and *Rubus idaeus* ( $n = 1$ ). The abundance of *Empetrum nigrum* in the propagule bank were highest at both 200 and 875 m a.s.l., whereas *Vaccinium myrtillus* appeared to decline in abundance with increasing elevation (Figure 10a). In the standing vegetation, *Empetrum nigrum* showed a fairly even abundance from 200 to 765 m a.s.l., which is in contrast to *Vaccinium myrtillus*, which showed an increase in abundance with elevation from 555 m. a.s.l. (Figure 10b).



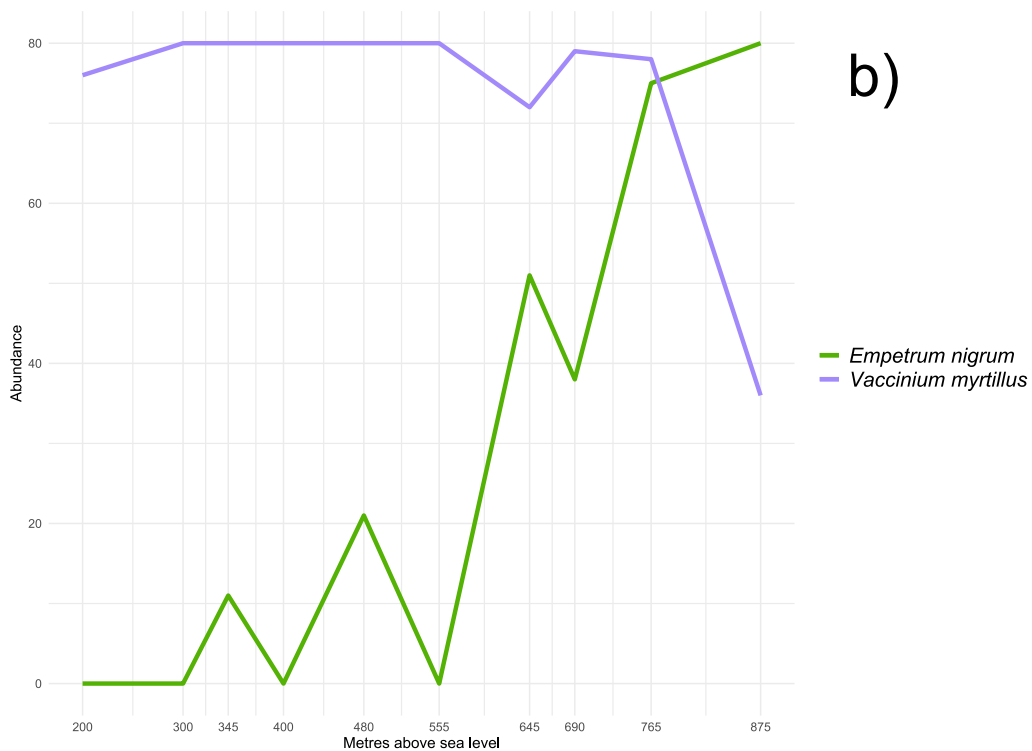
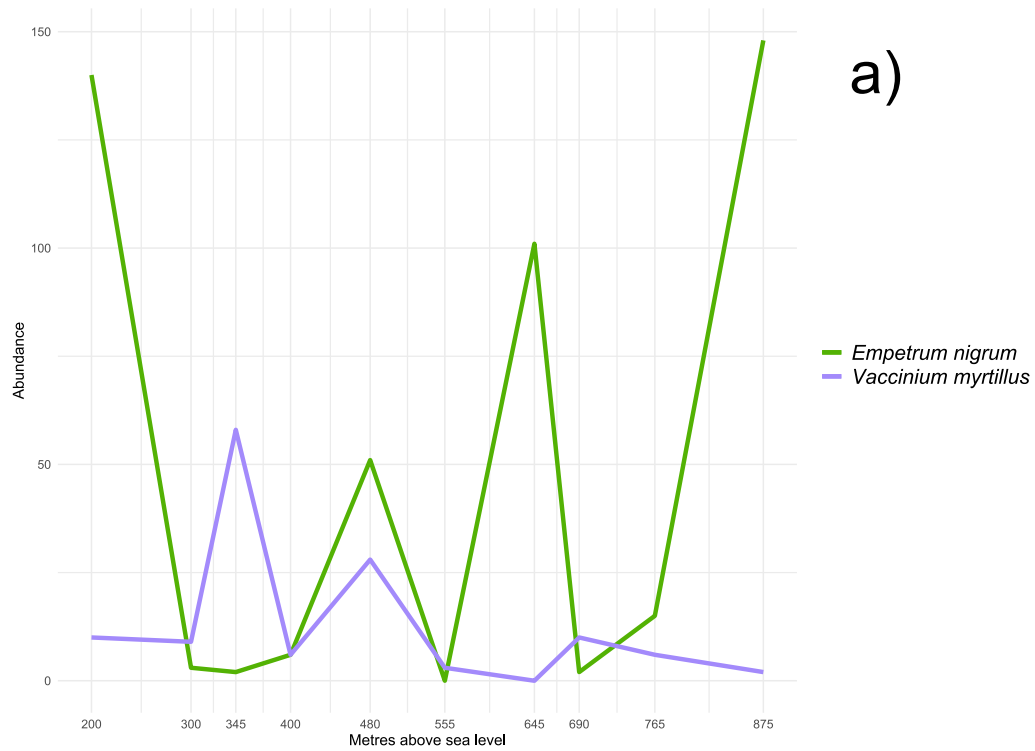


Figure 10. Abundance of *Empetrum nigrum* and *Vaccinium myrtillus* for the propagule bank a) and the standing vegetation b) along the elevation gradient. The abundance in the propagule bank is registered in count of the total number of occurrences, whereas the standing vegetation was measured as the sum of subplot occurrences.

## Species composition

### *Species composition between the standing vegetation and the propagule bank*

There was a clear separation between the standing vegetation and the propagule bank in terms of species composition (eigenvalue = 0.69, axis length = 4.12 S.D. units). These two formed clusters at different ends of DCA axis 1 (Figure 11).

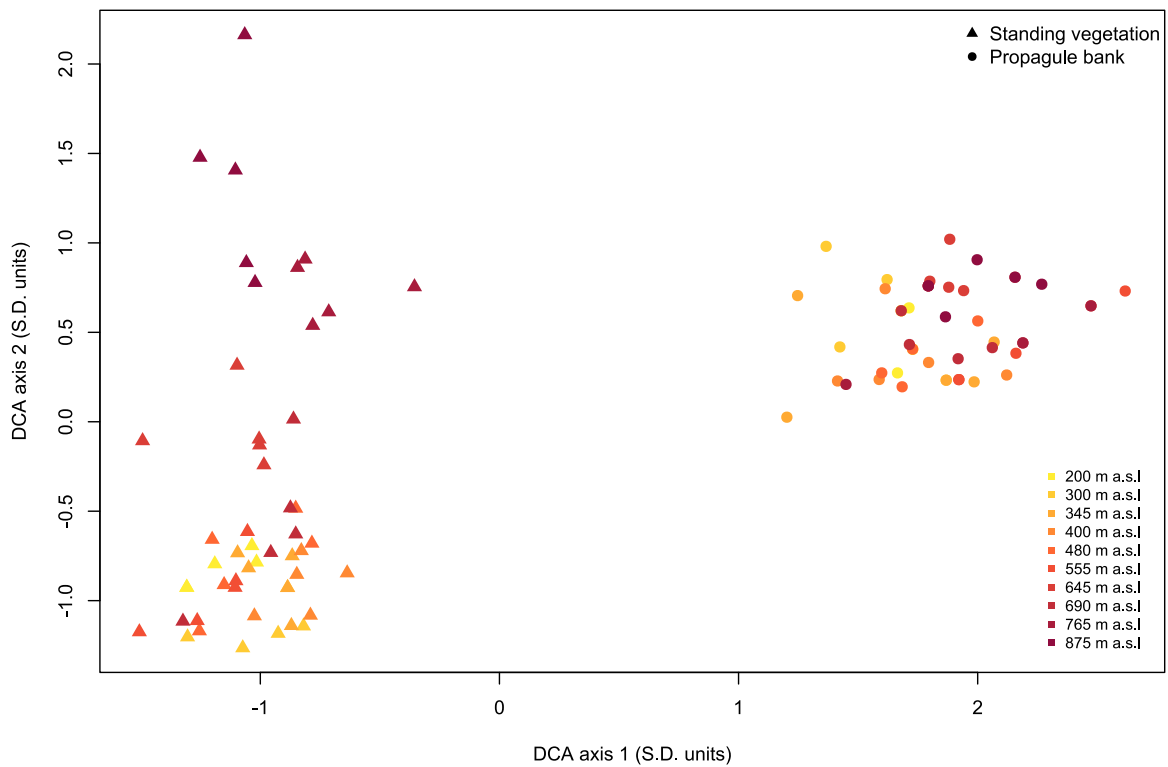


Figure 11. Detrended Correspondence Analysis (DCA) of axes 1 and 2 of the standing vegetation (triangle;  $n = 50$ ) and the propagule bank (circle;  $n = 50$ ). m a.s.l is colour-coded ranging from light yellow at 200 m a.s.l. to dark purplish-red at 875 m a.s.l.

## *Propagule bank*

The species composition of the propagule bank varied the most along the first axis (eigenvalue = 0.15, axis length = 2.37 S.D. units). However, the difference between the two axes were small in terms of explaining the variation in species composition (axis 2: eigenvalue = 0.12, axis length = 2.11 S.D. units) (Figure 12).

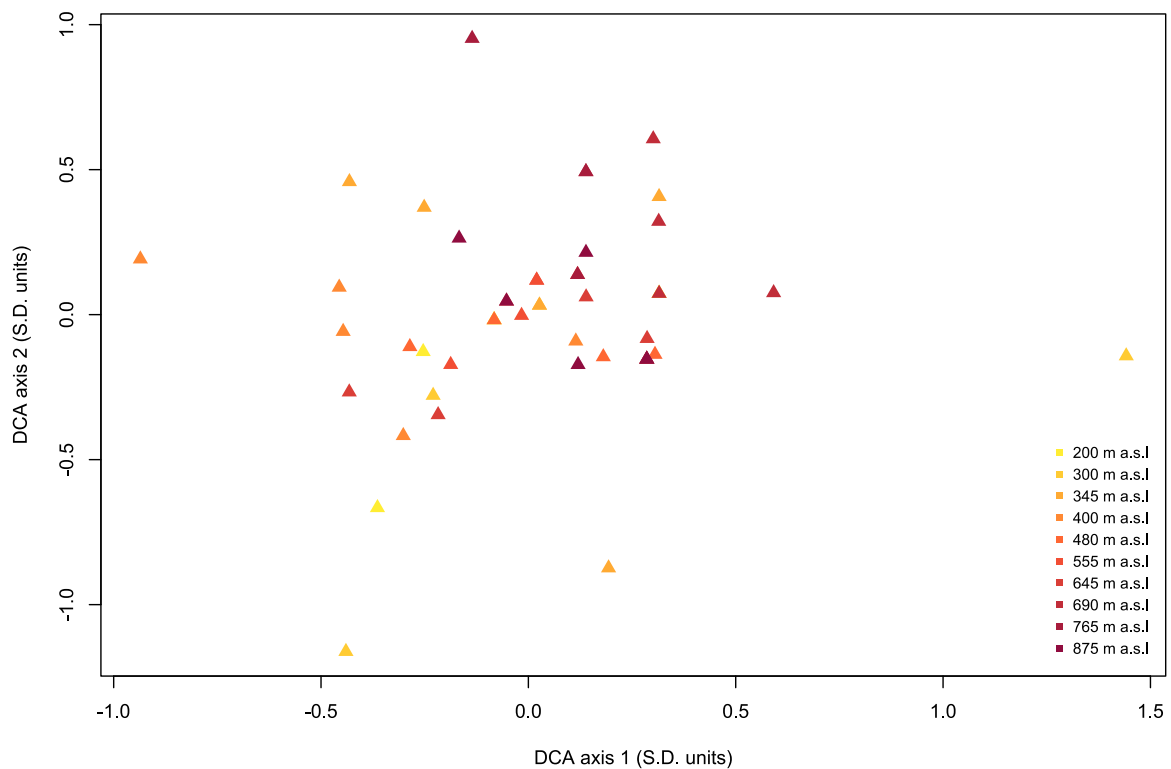


Figure 12. Detrended Correspondence Analysis (DCA) of axis 1 and 2 of species composition of the propagule bank from the 50 sample plots. m a.s.l is colour-coded ranging from light yellow at 200 m a.s.l. to dark purplish-red at 875 m a.s.l.

### Standing vegetation

The species composition of the standing vegetation varied the most along the first axis (eigenvalue = 0.47, axis length = 3.77) compared to the second axis (eigenvalue = 0.20, axis length = 2.19 S.D. units) (Figure 13). At lower elevations, the species composition exhibited the lowest degree of variation, while at the highest elevation, it displayed the highest degree of variation.

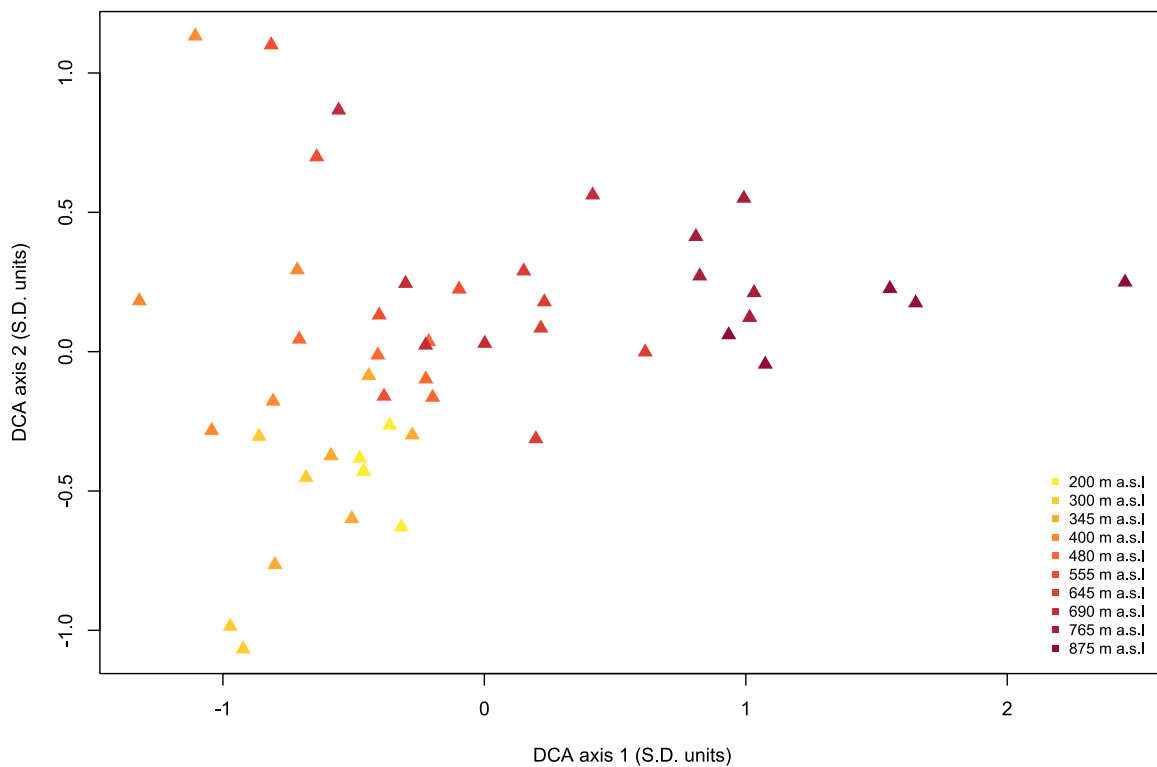


Figure 13. Detrended Correspondence Analysis (DCA) of axis 1 and 2 of species composition of the standing vegetation from the 50 sample plots. m a.s.l. is colour-coded ranging from light yellow at 200 m a.s.l. to dark purplish-red at 875 m a.s.l.

## Species composition of propagule bank with environmental variables

Of the environmental variables, the two that exhibited statistically significant correlation with variation in species composition of the propagule bank along the first DCA axis were pH ( $p = 0.01$ ) (Figure 14c) and soil organic matter ( $p = 0.02$ ) (Figure 14b) (Table 1). pH had a moderate negative correlation ( $\tau = -0.24$ ), whereas soil organic matter had a moderate positive correlation ( $\tau = 0.22$ ). m a.s.l. ( $p = 0.08$ ) (Figure 14a), although not statistically significant, was the environmental variable that correlated the most with the second DCA axis ( $\tau = 0.16$ ), but only marginally when compared to the first axis ( $\tau = 0.16$ ,  $p = 0.08$ ). Soil moisture (Figure 14d) was similar to m a.s.l. in explaining the variance along the first DCA axis ( $\tau = 0.17$ ,  $p = 0.08$ ). However, the influence of soil moisture was relatively weaker in explaining the variance along the second DCA axis ( $\tau = 0.08$ ,  $p = 0.38$ ).

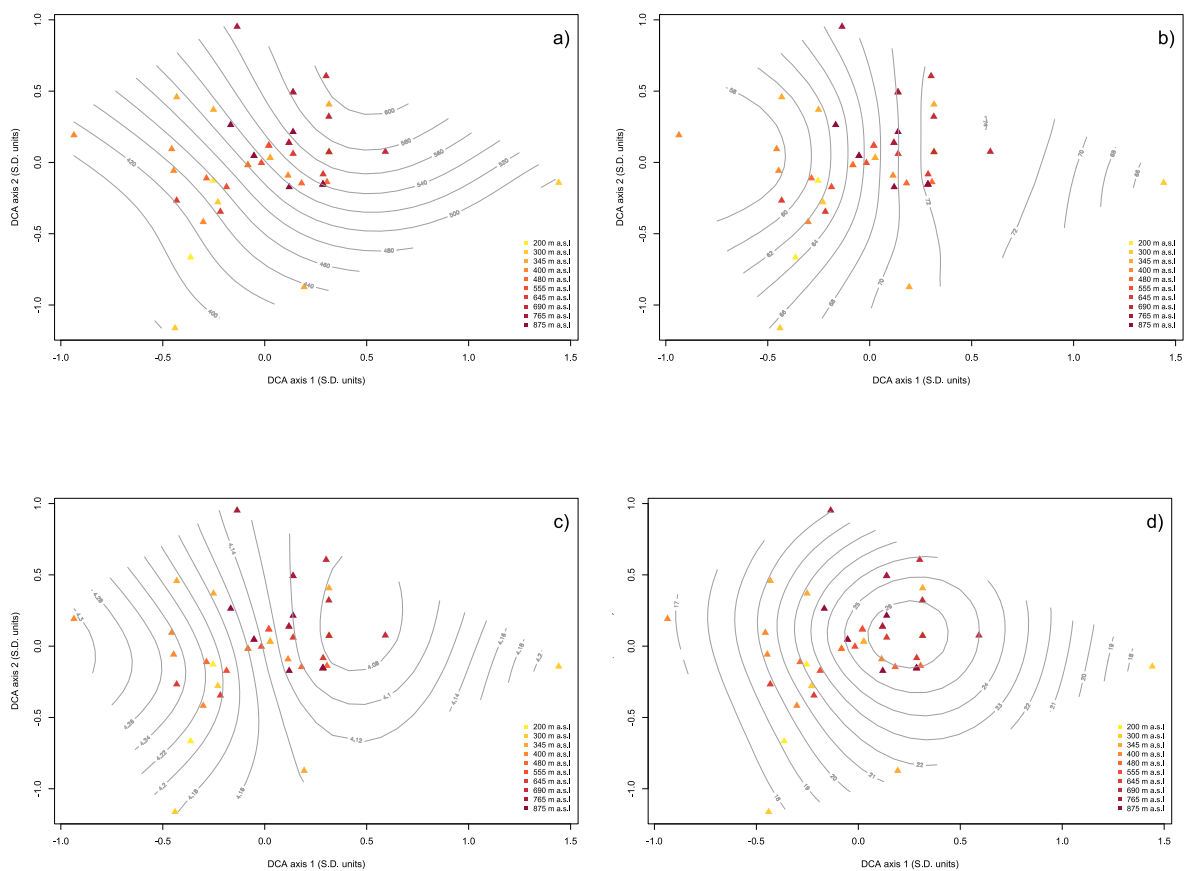


Figure 14. Detrended Correspondence Analysis (DCA) of axis 1 and 2 of species composition of the propagule bank from the 50 sample plots with a) fitted with m a.s.l. and b) with soil organic matter, c) with pH and d) with soil moisture as contour lines. m a.s.l. is colour-coded ranging from light yellow at 200 m a.s.l. to dark purplish-red at 875 m a.s.l.

Table 1. Kendall's rank correlation test on DCA axis 1 and 2 for the five environmental variables. Significant  $p$ -values ( $p < 0.05$ ) outlined in bold.

Variables	DCA Axis 1			DCA Axis 2		
	$\tau$	$p$		$\tau$	$p$	
m a.s.l.	0.16	0.09	-	0.16	0.08	-
Slope	-0.06	0.52	-	-0.01	0.88	-
Light	0.00	1.00	-	-0.01	0.85	-
Soil moisture	0.17	0.09	-	0.08	0.37	-
Soil organic matter	0.22	<b>0.02</b>	*	0.12	0.21	-
pH	-0.24	<b>0.01</b>	*	-0.12	0.19	-

## Discussion

This study aimed to answer the following questions: (1) How does the species composition and richness of the propagule bank in a boreal pine forest compare to the standing vegetation? (2) To what extent do local environmental factors influence the species composition of the propagule bank? (3) What can my findings reveal about the role of the propagule bank as a bet-hedging strategy in response to environmental changes, such as climate change?

### Species composition

The results of this study revealed that the propagule bank held fewer species than the standing vegetation, with only 19% of the species found in the standing vegetation also being present in the propagule bank. When lichens were excluded from the results, the compositional similarity in species between the propagule bank and standing vegetation increased to 24%. Based on studies conducted by Plue et al. (2021) and Hopfensperger (2007) dissimilarities in species composition between the propagule bank and the standing vegetation were observed across several ecosystems, with forests displaying the least resemblance between the standing vegetation and the propagule bank. However, the findings of Plue et al. (2021), which revealed greater species diversity in the propagule bank than in the standing vegetation in forests, my study yielded contrasting results. But, the studies by Plue et al. (2021) and Hopfensperger (2007) did not distinguish between the specific types of forest ecosystems which makes it challenging to correlate or extrapolate their results directly to the findings of my study. One potential reason why the species composition was lower in the propagule bank compared to the standing vegetation in my study may be due to the reproductive mechanisms of the many species found in boreal forests. Many of the vascular plant species in the understory of boreal forests rely on clonal reproduction (Eriksson, 1989), indicating that this method serves as a better means of ensuring survival in frigid regions and areas where the production of seeds is limited due to a shorter period for growth. This likely accounts for the absence of *Vaccinium vitis-idaea* in the propagule bank, which relies on clonal reproduction (Persson & Gustavsson, 2001). Similar

observations have been made by Vieno et al. (1993), where *Vaccinium vitis-idaea* showed low abundance. Clonal reproduction is also common for species such as *Vaccinium myrtillus* and *Empetrum nigrum* (Albert et al., 2003; Bell & Tallis, 1973). Interestingly, although *Vaccinium myrtillus* showed a decrease in abundance along the elevation gradient in the propagule bank, *Empetrum nigrum* was abundant at both ends of the elevation gradient. This could mean that while *Vaccinium myrtillus* relies more on clonal reproduction as a method of reproduction, *Empetrum nigrum* may additionally depend on a propagule bank. The notion that *Empetrum nigrum*, while mainly relying on clonal reproduction, have been shown to have high seed production as well as reported by Vieno et al. (1993) and Boudreau et al. (2010). Further evidence reinforces the concept that many species may only rely on clonal reproduction instead of relying on a propagule bank as is evident from the notable absence of species such as *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis* in the propagule bank, despite their high frequency in the standing vegetation. Similar findings have been reported by Rydgren and Hestmark (1997).

The fern species *Athyrium filix-femina* and *Phegopteris connectilis* were notably abundant but also exclusively found in the propagule bank. It is possible that their absence from the standing vegetation can be attributed to unfavourable conditions, as the growth room provided more optimal climatic conditions that were better suited for their germination compared to in-situ conditions. They also germinated from samples from all elevations in the growth room, including *Gymnocarpium dryopteris*. Fern spores are effective dispersal agents contributing to long-distance dispersal (Sundberg, 2013) which might imply that *Athyrium filix-femina* and *Phegopteris connectilis* have been wind-dispersed and subsequently remained dormant in the propagule bank and have yet to germinate due to unfavourable conditions.



## Species richness

The observed species richness in the propagule bank was found to be lower than that in the standing vegetation. Additionally, a decrease in species richness was observed along the elevation gradient. I found no previous research that examined the species richness of the propagule bank across an elevation gradient in a boreal forest, making comparisons challenging. Nonetheless, a study conducted by Luo et al. (2017) investigated the propagule bank along elevational gradients in tropical, subtropical, and subalpine forests located in Yunnan Province, southwest China. Their results, similar to mine, demonstrated a decline in species richness with increasing elevation across all ecosystems. A comparable pattern was also observed in a study by Sharma et al. (2009) in a temperate forest in the Himalayas, where a decrease in species richness was noted as elevation increased.

Interestingly, species richness in the standing vegetation remained fairly even across the elevation gradient and even showed a spike in species richness at the highest elevations. As reported by Odland and Birks (1999), species richness in the standing vegetation tend to decline with elevation, but this might only apply to vascular plants. However, lichens, which are non-vascular plants, were excluded from analysis in examining species richness in the standing vegetation. This implies that a decrease in species richness is expected, but that was not observed. A possible reason for this might be that greater solar radiation and significant daily temperature fluctuations near or above the tree line may account for an increased species richness. These specific temperature conditions are particularly conducive to the growth of dwarf plant species, including species from the family Ericaceae (Germino et al., 2002; Körner, 2003).

## Environmental influence on propagule bank species composition

It is well known that species composition in the standing vegetation in forests changes with elevation as elevation correlates with changes in abiotic factors such as light, temperature, precipitation, pH and soil organic matter (Grell et al., 2005; Keller et al., 2000; R. H. Økland & Eilertsen, 1993). My results indicated that the main vegetation variation in the propagule bank related positively with soil organic matter and negatively with pH along the first DCA axis. Soil pH has been shown to decrease with elevation, likely due to a slower rate of decomposition of organic matter (Smith et al., 2002). The slower rate of decomposition of organic matter at higher elevation reduces the input of organic matter into the soil (Sheikh et al., 2009). Similarly, the increase in soil moisture levels observed on the first DCA axis supports established research indicating a positive relationship between precipitation and elevation (Körner, 2007; Sevruk, 1997). Higher elevations generally experience more precipitation, resulting in higher soil moisture content. The fact that pH decreases, soil organic matter increases, and soil moisture increases along the first DCA axis is potentially indicative of an indirect elevation gradient. The weak correlation of elevation with species composition is, however, in contrast with previous research, where elevation was shown to have the largest impact in determining species composition of the propagule bank (Wani et al., 2023; Yang et al., 2021).

However, it is important to approach the interpretation of my findings with caution due to the presence of outliers observed in the ordination analysis. Specifically the occurrence of *Rubus idaeus* and *Pinus sylvestris* near the right end of the first DCA axis (Figure 12). The similarity between both axes in explaining the variation in species composition within the propagule bank may suggest that the outliers could potentially have distorted the results and could thus have underestimated the relationship between the fitted environmental variables and species composition. Excluding the outliers could potentially result in different results, thereby potentially emphasizing the effect of elevation or other environmental factors on the species composition of the propagule bank to a greater extent.

## Propagule bank bet-hedging potential

While species have demonstrated a propensity for range-shifts in response to climate change (MacDougall et al., 2021; Myers-Smith et al., 2011), the pace at which these shifts occur often fails to keep up with the rate of environmental change (Corlett & Westcott, 2013; Rees et al., 2020). Recognizing the limitations of such range shifts, the propagule bank has been discussed to potentially buffer against environmental change, both through its capacity to sustain species richness and through effects on community composition (Chesson, 2000; Plue & Cousins, 2018; Royo & Ristau, 2013). My findings suggest that the propagule bank in the boreal forest may not possess the diversity to ensure the continuation of the present plant community under different future climatic conditions. If the propagule bank is indeed dominated by a limited number of species with low resemblance to the standing vegetation, its ability to foster resilience against climate change may be compromised. As a result, the propagule bank might not serve as a buffer or as a bet-hedging strategy, but rather as an indication of the likely composition and structure of future vegetation (Fisher et al., 2009).

## Limitations and future recommendations

### *Limitations*

The removal of the plants through weeding was necessary to prevent their interference with the germination and development of other species. However, the weeding procedure led to the unintended loss of propagule soil samples, primarily due to their adherence to the weeded plants. It is plausible that certain seeds and/or spores may have been inadvertently discarded. Furthermore, the malfunction of the air-condition system led to increased stress on the plants, whereby the high temperature might have been fatal for some species. While no germinated species were found to have died from the incidents, it is plausible that species that had yet to germinate may have failed to survive the high temperatures. Additionally, in a study conducted by Vandvik et al. (2016) revealed that a higher resemblance in species composition exists between the propagule bank and standing vegetation when both are sampled at equivalent spatial resolutions. In contrast, the sampling resolution in my experiment only had four samples taken from the outer edges of the plot. This particular approach may serve as a rationale for the discrepancy observed in my study regarding the species composition between the standing vegetation and the propagule bank. Moreover, the two datasets that were used in this study were obtained several years apart. The dataset containing information on standing vegetation and the ecological variables was obtained in 2017, whereas my dataset was obtained in 2022, representing a five-year difference. It is possible that this difference could potentially introduce inaccuracies when comparing the two.

### *Future recommendations*

This preliminary study, being the first of its kind, examines the propagule bank with the inclusion of bryophytes and ferns in a boreal forest along an elevation gradient and compares it to the standing vegetation. Further research is needed to expand on these findings, given the lack of previous studies in this area. Furthermore, it would be of interest to investigate in-situ disturbance and its impact on germination from the propagule bank, as growth rooms may not adequately represent the complex interactions found in nature that determines the response of species to environmental change.

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## Appendix

### Appendix 1. Interpolated temperature (Sogndal airport) and precipitation (Selseng) for the study site

Based on data provided for Sogndal Airport weather station (MET, 2021), which is situated ca. 7 km south of the study site at 497 m a.s.l, its average monthly temperature was used to interpolate the temperature gradient which spans the study site (200-875 m (rounded to 900)) assuming a 0.65°C lapse rate per 100 m (Arnold et al., 2006). Similar was done for precipitation assuming a 9 mm lapse rate per 100 m (Førland, 1979) using the Selseng weather station (17 km distance, 421 m a.s.l) (MET, 2021).

Station	Station nr	Elevation (m)	mm/yr	lapse rate (mm/100m)		
Selseng	55730	421	1662	9		
	January	February	March	April	May	June
	195	146	132	59	78	83
	July	August	September	October	November	December
	94	118	163	185	180	194

#### Interpolated precipitation

Masl	January	February	March	April	May	June
200	175	126	112	39	58	63
300	184	135	121	48	67	72
400	193	144	130	57	76	81
500	202	153	139	66	85	90
600	211	162	148	75	94	99
700	220	171	157	84	103	108
800	229	180	166	93	112	117
900	238	189	175	102	121	126
	July	August	September	October	November	December
200	74	98	143	165	160	174
300	83	107	152	174	169	183
400	92	116	161	183	178	192
500	101	125	170	192	187	201
600	110	134	179	201	196	210
700	119	143	188	210	205	219
800	128	152	197	219	214	228
900	137	161	206	228	223	237

Station	Station nr	Elevation (m)	Avg. ann. Temp	lapse rate (°C/100m)		
Sogndal airport	55700	497	4.3	0.65		
	January	February	March	April	May	June
	-2.8	-2.1	0	3.5	7.3	11
	July	August	September	October	November	December
	13.6	12.8	9.4	4.7	1.3	-1.4

#### Interpolated temperature

Masl	January	February	March	April	May	June
200	-0.9	-1.1	0.9	4.8	8.9	12.9
300	-1.5	-1.7	0.3	4.2	8.3	12.3
400	-2.2	-2.4	-0.4	3.5	7.6	11.6
500	-2.8	-3.0	-1.0	2.9	7.0	11.0
600	-3.5	-3.7	-1.7	2.2	6.3	10.3
700	-4.1	-4.3	-2.3	1.6	5.7	9.7
800	-4.8	-5.0	-3.0	0.9	5.0	9.0
900	-5.4	-5.6	-3.6	0.3	4.4	8.4
	July	August	September	October	November	December
200	16.0	14.4	10.7	5.6	2.4	-0.4
300	15.4	13.8	10.1	5.0	1.8	-1.0
400	14.7	13.1	9.4	4.3	1.1	-1.7
500	14.1	12.5	8.8	3.7	0.5	-2.3
600	13.4	11.8	8.1	3.0	-0.2	-3.0
700	12.8	11.2	7.5	2.4	-0.8	-3.6
800	12.1	10.5	6.8	1.7	-1.5	-4.3
900	11.5	9.9	6.2	1.1	-2.1	-4.9

Appendix 2. Potting soil nutrient information.

<b>Potting soil nutrient information</b>	
pH	6
Dry matter	150 g/L
Organic matter	>80% of dry matter
Density	390 kg/m <sup>3</sup>
Total nitrogen (EN 13654-1)	1500 mg/l
Composition	Light & dark sphagnum peat, sand, lime, fertilizer

<b>Additions per m<sup>3</sup></b>	
Limestone flour	3 kg
Dolomite flour	2 kg
NPK 11-5-18	1 kg

<b>Nutrients CAT mg/L</b>	
N/NO <sub>3</sub> -N+NH <sub>4</sub> -N	110
B	0.3
Cu	0.5
P	45
Fe	40
K	210
Mn	19
Ca	200
Mo	0.2
Mg	230
Zn	3.5
S	150

Appendix 3. Overview of the growth room showing the eight trays with pots. Trays were covered with fabric to ensure sufficient moisture levels and to reduce potential cross-contamination.

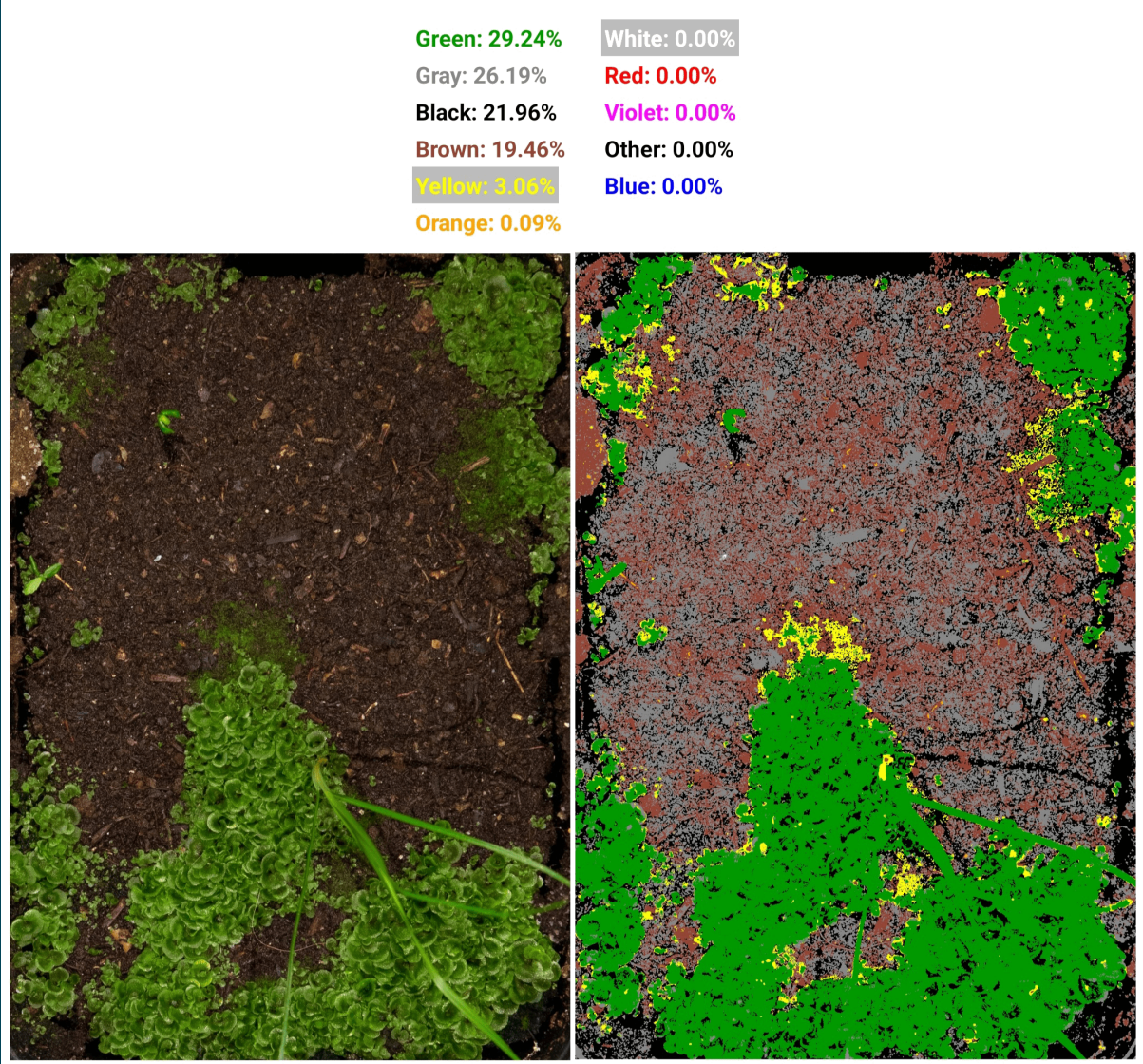


Appendix 4. Overview of pots which had been weeded. Half the area of the pots which were determined to be weeded were removed and had samples taken which were transplanted. Weeding was done to ensure germination of species which might have been inhibited due to excessive gametophyte cover.





Appendix 5. Color Recogniser was used to determine percentage cover for weeding due to rapid growth of bryophytes and ferns. Yellow and green colours were used to determine percentage cover.



Appendix 6. Overview of transplanted samples from pots that were weeded.





## Appendix 8. Propagule bank dataset of bryophytes.

Block	Plot	Subplot	Polisia_nidulans	Dicranum_scaparium	Stryum_sp.	Polystichum_complanatum	Marchantia_polymorpha
1	46	1	1	0	0	0	0
1	46	1	2	0	0	0	0
1	46	1	3	1	0	0	0
1	46	1	4	1	0	0	0
1	200	2	1	0	0	0	0
1	200	2	2	1	0	0	0
1	200	2	3	1	0	0	0
1	200	2	4	1	0	0	0
1	204	3	1	0	0	0	0
1	204	3	2	1	0	0	0
1	204	3	3	1	0	0	0
1	204	3	4	1	0	0	0
1	217	4	1	1	0	0	0
1	217	4	2	1	0	0	0
1	217	4	3	1	0	0	0
1	217	4	4	1	0	0	0
1	281	5	1	1	0	0	0
1	281	5	2	1	0	0	0
1	281	5	3	1	0	0	0
1	281	5	4	1	0	0	0
2	2	6	1	1	0	0	0
2	2	6	2	1	0	0	0
2	2	6	3	1	0	0	0
2	2	6	4	1	0	0	0
2	18	7	1	1	0	0	0
2	18	7	2	1	0	0	0
2	18	7	3	1	0	0	0
2	18	7	4	1	1	0	0
2	19	8	1	1	0	0	0
2	19	8	2	1	1	0	0
2	19	8	3	1	0	0	0
2	19	8	4	1	1	0	0
2	71	9	1	1	0	0	0
2	71	9	2	1	0	0	0
2	71	9	3	1	0	0	0
2	71	9	4	1	0	0	0
2	111	10	1	1	0	0	0
2	111	10	2	1	0	0	0
2	111	10	3	1	0	0	0
2	111	10	4	1	0	0	0
3	19	11	1	1	0	0	0
3	19	11	2	1	0	0	0
3	19	11	3	1	0	0	0
3	19	11	4	1	0	0	0
3	92	12	1	1	0	0	0
3	92	12	2	1	0	0	0
3	92	12	3	1	0	0	0
3	92	12	4	1	0	0	0
3	99	13	1	1	0	0	0
3	99	13	2	1	0	0	0
3	99	13	3	1	0	0	0
3	99	13	4	1	1	0	0
3	130	14	1	1	0	0	0
3	130	14	2	1	0	0	0
3	130	14	3	1	0	0	0
3	130	14	4	1	0	0	0
3	130	14	5	1	0	0	0
3	130	14	6	1	0	0	0
3	130	14	7	1	0	0	0
3	130	14	8	1	0	0	0
3	130	14	9	1	0	0	0
3	130	14	10	1	0	0	0
3	130	14	11	1	0	0	0
3	130	14	12	1	0	0	0
3	130	14	13	1	0	0	0
3	130	14	14	1	0	0	0
3	130	14	15	1	0	0	0
3	130	14	16	1	0	0	0
3	130	14	17	1	0	0	0
3	130	14	18	1	0	0	0
3	130	14	19	1	0	0	0
3	130	14	20	1	0	0	0
3	130	14	21	1	0	0	0
3	130	14	22	1	0	0	0
3	130	14	23	1	0	0	0
3	130	14	24	1	0	0	0
3	130	14	25	1	0	0	0
3	130	14	26	1	0	0	0
3	130	14	27	1	0	0	0
3	130	14	28	1	0	0	0
3	130	14	29	1	0	0	0
3	130	14	30	1	0	0	0
3	130	14	31	1	0	0	0
3	130	14	32	1	0	0	0
3	130	14	33	1	0	0	0
3	130	14	34	1	0	0	0
3	130	14	35	1	0	0	0
3	130	14	36	1	0	0	0
3	130	14	37	1	0	0	0
3	130	14	38	1	0	0	0
3	130	14	39	1	0	0	0
3	130	14	40	1	0	0	0
3	130	14	41	1	0	0	0
3	130	14	42	1	0	0	0
3	130	14	43	1	0	0	0
3	130	14	44	1	0	0	0
3	130	14	45	1	0	0	0
3	130	14	46	1	0	0	0
3	130	14	47	1	0	0	0
3	130	14	48	1	0	0	0
3	130	14	49	1	0	0	0
3	130	14	50	1	0	0	0
3	130	14	51	1	0	0	0
3	130	14	52	1	0	0	0
3	130	14	53	1	0	0	0
3	130	14	54	1	0	0	0
3	130	14	55	1	0	0	0
3	130	14	56	1	0	0	0
3	130	14	57	1	0	0	0
3	130	14	58	1	0	0	0
3	130	14	59	1	0	0	0
3	130	14	60	1	0	0	0
3	130	14	61	1	0	0	0
3	130	14	62	1	0	0	0
3	130	14	63	1	0	0	0
3	130	14	64	1	0	0	0
3	130	14	65	1	0	0	0
3	130	14	66	1	0	0	0
3	130	14	67	1	0	0	0
3	130	14	68	1	0	0	0
3	130	14	69	1	0	0	0
3	130	14	70	1	0	0	0
3	130	14	71	1	0	0	0
3	130	14	72	1	0	0	0
3	130	14	73	1	0	0	0
3	130	14	74	1	0	0	0
3	130	14	75	1	0	0	0
3	130	14	76	1	0	0	0
3	130	14	77	1	0	0	0
3	130	14	78	1	0	0	0
3	130	14	79	1	0	0	0
3	130	14	80	1	0	0	0
3	130	14	81	1	0	0	0
3	130	14	82	1	0	0	0
3	130	14	83	1	0	0	0
3	130	14	84	1	0	0	0
3	130	14	85	1	0	0	0
3	130	14	86	1	0	0	0
3	130	14	87	1	0	0	0
3	130	14	88	1	0	0	0
3	130	14	89	1	0	0	0
3	130	14	90	1	0	0	0
3	130	14	91	1	0	0	0
3	130	14	92	1	0	0	0
3	130	14	93	1	0	0	0
3	130	14	94	1	0	0	0
3	130	14	95	1	0	0	0
3	130	14	96	1	0	0	0
3	130	14	97	1	0	0	0
3	130	14	98	1	0	0	0
3	130	14	99	1	0	0	0
3	130	14	100	1	0	0	0
3	130	14	101	1	0	0	0
3	130	14	102	1	0	0	0
3	130	14	103	1	0	0	0
3	130	14	104	1	0	0	0
3	130	14	105	1	0	0	0
3	130	14	106	1	0	0	0
3	130	14	107	1	0	0	0
3	130	14	108	1	0	0	0
3	130	14	109	1	0	0	0
3	130	14	110	1	0	0	0
3	130	14	111	1	0	0	0
3	130	14	112	1	0	0	0
3	130	14	113	1	0	0	0
3	130	14	114	1	0	0	0
3	130	14	115	1	0	0	0
3	130	14	116	1	0	0	0
3	130	14	117	1	0	0	0
3	130	14	118	1	0	0	0
3	130	14	119	1	0	0	0
3	130	14	120	1	0	0	0
3	130	14	121	1	0	0	0
3	130	14	122	1	0	0	0
3	130	14	123	1	0	0	0
3	130	14	124	1	0	0	0
3	130	14	125	1	0	0	0
3	130	14	126	1	0	0	0
3	130	14	127	1	0	0	0
3	130	14	128	1	0	0	0
3	130	14	129	1	0	0	0
3	130	14	130	1	0	0	0
3	130	14	131	1	0	0	0
3	130	14	132	1	0	0	0
3	130	14	133	1	0	0	0
3	130	14	134	1	0	0	0
3	130	14	135	1	0	0	0
3	130	14	136	1	0	0	0
3	130	14	137	1	0	0	0
3	130	14	138	1	0	0	0
3	130	14	139	1	0	0	0
3	130	14	140	1	0	0	0
3	130	14	141	1	0	0	0
3	130	14	142	1	0	0	0
3	130	14	143	1	0	0	0
3	130	14	144	1	0	0	0
3	130	14	145	1	0	0	0
3	130	14	146	1	0	0	0
3	130	14	147	1	0	0	0
3	130	14	148	1	0	0	0
3	130	14	149	1	0	0	0
3	130	14	150	1	0	0	0
3	130	14	151	1	0	0	0
3	130	14	152	1	0	0	0
3	130	14	153	1	0	0	0
3	130	14	154	1	0	0	0
3	130	14	155	1	0	0	0
3	130	14	156	1	0	0	0
3	130	14	157	1	0	0	0
3	130	14	158	1	0	0	0
3	130	14	159	1	0	0	0
3	130	14	160	1	0	0	0
3	130	14	161	1	0	0	0
3	130	14	162	1	0	0	0
3	130	14	163	1	0	0	0
3							

## Appendix 9. Propagule bank dataset of ferns.

Block	Plot	Subplot	<i>Phagopteris_cornedilla</i>	<i>Athyrium_fils-femina</i>	<i>Gymnocarpium_dryopteris</i>
1	46	1	1	0	0
1	46	1	2	0	0
1	46	1	3	0	0
1	46	1	4	0	0
1	200	2	1	0	1
1	200	2	2	0	0
1	200	2	3	1	1
1	200	2	4	1	1
1	200	3	1	1	1
1	200	3	2	1	1
1	200	3	3	1	1
1	200	3	4	1	1
1	200	4	1	0	1
1	200	4	2	0	1
1	200	4	3	0	1
1	200	4	4	0	1
1	200	5	1	0	1
1	200	5	2	0	1
1	200	5	3	0	1
1	200	5	4	0	1
1	200	6	1	0	1
1	200	6	2	0	1
1	200	6	3	0	1
1	200	6	4	0	1
1	200	7	1	0	1
1	200	7	2	0	1
1	200	7	3	0	1
1	200	7	4	0	1
1	200	8	1	0	1
1	200	8	2	0	1
1	200	8	3	0	1
1	200	8	4	0	1
1	200	9	1	0	1
1	200	9	2	0	1
1	200	9	3	0	1
1	200	9	4	0	1
1	200	10	1	0	1
1	200	10	2	0	1
1	200	10	3	0	1
1	200	10	4	0	1
1	200	11	1	0	1
1	200	11	2	0	1
1	200	11	3	0	1
1	200	11	4	0	1
1	200	12	1	0	1
1	200	12	2	0	1
1	200	12	3	0	1
1	200	12	4	0	1
1	200	13	1	0	1
1	200	13	2	0	1
1	200	13	3	0	1
1	200	13	4	0	1
1	200	14	1	0	1
1	200	14	2	0	1
1	200	14	3	0	1
1	200	14	4	0	1
1	200	15	1	0	1
1	200	15	2	0	1
1	200	15	3	0	1
1	200	15	4	0	1
1	200	16	1	0	1
1	200	16	2	0	1
1	200	16	3	0	1
1	200	16	4	0	1
1	200	17	1	0	1
1	200	17	2	0	1
1	200	17	3	0	1
1	200	17	4	0	1
1	200	18	1	0	1
1	200	18	2	0	1
1	200	18	3	0	1
1	200	18	4	0	1
1	200	19	1	0	1
1	200	19	2	0	1
1	200	19	3	0	1
1	200	19	4	0	1
1	200	20	1	0	1
1	200	20	2	0	1
1	200	20	3	0	1
1	200	20	4	0	1
1	200	21	1	0	1
1	200	21	2	0	1
1	200	21	3	0	1
1	200	21	4	0	1
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1	200	22	2	0	1
1	200	22	3	0	1
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1	200	24	2	0	1
1	200	24	3	0	1
1	200	24	4	0	1
1	200	25	1	0	1
1	200	25	2	0	1
1	200	25	3	0	1
1	200	25	4	0	1
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1	200	26	2	0	1
1	200	26	3	0	1
1	200	26	4	0	1
1	200	27	1	0	1
1	200	27	2	0	1
1	200	27	3	0	1
1	200	27	4	0	1
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1	200	28	2	0	1
1	200	28	3	0	1
1	200	28	4	0	1
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1	200	29	2	0	1
1	200	29	3	0	1
1	200	29	4	0	1
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1	200	31	4	0	1
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1	200	32	3	0	1
1	200	32	4	0	1
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1	200	33	4	0	1
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1	200	34	3	0	1
1	200	34	4	0	1
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1	200	35	4	0	1
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1	200	36	4	0	1
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1	200	37	3	0	1
1	200	37	4	0	1
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1	200	38	2	0	1
1	200	38	3	0	1
1	200	38	4	0	1
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1	200	39	2	0	1
1	200	39	3	0	1
1	200	39	4	0	1
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1	200	40	2	0	1
1	200	40	3	0	1
1	200	40	4	0	1
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1	200	41	3	0	1
1	200	41	4	0	1
1	200	42	1	0	1
1	200	42	2	0	1
1	200	42	3	0	1
1	200	42	4	0	1
1	200	43	1	0	1
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1	200	43	3	0	1
1	200	43	4	0	1
1	200	44	1	0	1
1	200	44	2	0	1
1	200	44	3	0	1
1	200	44	4	0	1
1	200	45	1	0	1
1	200	45	2	0	1
1	200	45	3	0	1
1	200	45	4	0	1
1	200	46	1	0	1
1	200	46	2	0	1
1	200	46	3	0	1
1	200	46	4	0	1
1	200	47	1	0	1
1	200	47	2	0	1
1	200	47	3	0	1
1	200	47	4	0	1
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1	200	48	2	0	1
1	200	48	3	0	1
1	200	48	4	0	1
1	200	49	1	0	1
1	200	49	2	0	1
1	200	49	3	0	1
1	200	49	4	0	1
1	200	50	1	0	1
1	200	50	2	0	1
1	200	50	3	0	1
1	200	50	4	0	1