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Restoration Potential of Soil Seed Banks for Coastal Heathlands and Calcareous Meadows in Western Norway

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Preface

With the completion of this thesis, I am concluding my journey toward the degree of Master of Science in Ecology at the Norwegian University of Life Sciences (NMBU) in Ås.

I would like to thank my supervisors, Jonathan E. Colman, Anders Gunnar Helle, and Line Rosef, for their support during the process of this thesis. I am grateful for all the comments and input I received that made it possible to get the best out of my thesis and improve my skills for the future. Special thanks also to Anders Gunnar Helle and Gaute Eiterjord, who have made the field work possible and been an incredible help during the field and lab work. I also want to thank Siri Lie Olsen for her expertise in statistics and Felix Hernandez Nohr for his help in identifying grasses.

Last but not least, I want to thank my family and friends in Germany, as well as my friends and roommates in Ås, for all the support during the writing process and also during the fun breaks in between.

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Abstract

Over the last centuries, traditional farming practices have created species-rich, semi-natural ecosystems that depend on human use to maintain the characteristic open vegetation. Recent land use changes, including abandonment and afforestation, decreased the extent and ecological condition of semi-natural ecosystems in Norway. Restoration efforts are now needed to counteract the loss of semi-natural ecosystems and their associated values. This thesis investigated whether the soil seed bank (SSB) of two semi-natural ecosystems in western Norway – coastal heathland and calcareous meadow – can support the restoration process after the deforestation of spruce plantations. One study area covered the two islands dominated by coastal heathland, Vågsøy and Silda, where soil samples were taken from intact coastal heathland sites, restoration sites, and Sitka spruce plantations. The other study area was a calcareous meadow located in Voss municipality, where soil samples were taken from an intact meadow and a restoration site that was a deforested Norwegian spruce plantation. Germination trials were conducted to compare seed density and species composition of the SSBs of the site types. The results showed a significantly higher seed density for the intact sites in both ecosystems and a significant difference in species composition between the site types, with more “target” species found in the intact sites. However, the results indicate differences in the restoration potential of the SSB of the two ecosystems. Seeds of target species germinated in the soil of about 50-year-old Sitka spruce plantations in the coastal heathland ecosystem, indicating that the SSB has the potential to support the restoration process. Future measures should include burning the restoration sites to enhance germination and grazing to increase seed input from intact sites. The results from the calcareous meadow ecosystem are rather ordinary and agree with other studies that spatial dispersal of seeds might be more relevant than the SSB for ecological restoration of meadows. Active input of seeds might be necessary, especially to prevent problem species from establishing in the restoration site.

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Introduction

Over the past centuries, people have applied traditional farming practices, such as grazing, mowing, and burning, and have created semi-natural ecosystems, which are nowadays associated with high cultural and biological values. The continuous and extensive use has led to the creation of open areas that support biodiversity as they are often rich in plant species and create habitats for rare species (Eriksson et al., 2002; Myklestad & Sætersdal, 2004). In Norway, they inhabit today the second-highest number of threatened species (Artsdatabanken, 2021). Two of these semi-natural ecosystems found in western Norway are coastal heathlands and calcareous meadows.

Coastal heathlands are characterized by low vegetation formed by the dominant common heather (*Calluna vulgaris*, following *Calluna*) and accompanied by various herbaceous plants, such as *Carex panicea*, *Empetrum nigrum*, and *Erica tetralix* (Artsdatabanken, n.d.-c), creating a tree-less, open ecosystem often in a mosaic with other ecosystems (Nilsen et al., 2009). Coastal Heathlands have a wide distribution range along the coasts of Western Europe, with one-third of this range located in Norway (Nilsen et al., 2009), which creates an international responsibility for Norway for the conservation of coastal heathlands. The distribution in the high latitudes of Norway is possible due to the influence of the oceanic climate along the coasts and the traditional practices of farmers in Norway (Artsdatabanken, n.d.-c; Haaland & Kaland, 2002). The farmers have created and maintained this ecosystem in Norway for around 5,000 thousand years: They used the areas for grazing and harvesting fodder and farmers used to burn old, woody heather to encourage regeneration and maintain a good fodder quality of the heather (Haaland & Kaland, 2002; Webb, 1998). A study by Vandvik et al. (2014) indicates that this process of human-induced burning has impacted this ecosystem type on an evolutionary level through adaptations of *Calluna* in the form of smoke-initiated germination of its seeds.

Due to their long history and traditional use, coastal heathlands in Norway have a great cultural value, but they also have ecological and recreational values (Gjedrem & Log, 2020; Haaland & Kaland, 2002). Burning coastal heathlands has increased the biodiversity, particularly the genetic diversity, of the areas (Øvstedal & Heegaard, 2001) and created a mosaic landscape, which is a habitat for many species depending on the unique environment. The vegetation of coastal heathlands contains endangered plant species, like *Erica cinerea*, that depend on this open landscape (Solstad et al., 2021b), as well as other organism groups. For example, a study by Schirmel and Fartmann (2014) showed that butterflies are abundant in coastal heathlands but decrease in number when larger shrubs and birch trees invade the area.

Calcareous meadows are usually formed over a long time through mowing or grazing by cattle or sheep, without plowing and (almost) no fertilizers. The meadow can be either open or wooded, and the soil of calcareous meadows is more or less rich in lime. Depending on the calcareousness of the soil and the farming intensity, calcareous meadows can be sorted into different types in ecosystem typologies (see Bratli et al., 2022, for details). Traditional management practices keep these meadows open and inhibit natural succession toward a closed-canopy forest ecosystem. Common species in calcareous meadows are grasses such as *Anthoxanthum odoratum*, *Festuca rubra*, and *Deschampsia cespitosa*, and herbaceous plants such as *Ranunculus acris, Rumex acetosa*, and *Trifolium repens* (Bratli et al., 2022). Semi-natural grasslands are often species-rich and can inhabit over 100 vascular plant species (Bär et al., 2021). Red-listed species found in western Norway, such as *Arnica montana* (Solstad et al., 2021c), and *Tractema verna* (Solstad et al., 2021a), depend on the openness and extensive use of meadows. The traditional management practices – mowing and grazing of the meadow – allow grassland plant species to persist in wooded meadows as the canopy is not dense. However, abandonment and the following natural succession or afforestation of the meadow cause the canopy to become more dense and light-demanding grassland species to be displaced, resulting in a lower species richness (Hansson & Fogelfors, 2000; Myklestad & Sætersdal, 2003; Oldén, 2016).

The recent changes in agricultural practices have led to the abandonment, intensification, or afforestation of semi-natural areas. As a result, the area of semi-natural ecosystems has decreased drastically (Hovstad et al., 2018), including the biodiversity and connectivity of these landscapes (Hooftman & Bullock, 2012). According to Miljødirektoratet (n.d.), over 80% of Norway's coastal heathland area has been lost since the 19th century. Almost half of the area that was semi-natural grassland in the 1960s was lost during the last decades in the 20th century and the beginning of the recent century, most of it due to conversion to arable land or forest (Aune et al., 2018). In Norway, many areas were afforested by forestry with Norwegian spruce (*Picea abies*), also outside of its natural occurrence, or the invasive Sitka spruce (*Picea sitchensis*) along the coast. This development is the main reason why many semi-natural ecosystems are today listed on the Norwegian "Red List for Ecosystem and Habitat Types", including coastal heathlands as endangered and semi-natural grasslands (meadow) as vulnerable (Hovstad et al., 2018).

Sitka spruce is a coniferous tree that is native to northern America, where it grows along the western coast (Peterson & Martin, 1997). It was introduced and planted in Norway by the forestry sector during the late 19th century and the early 20th century, with most Sitka spruce planted during the 1960s and 1970s (Elven et al., 2018). Since 2007, Sitka spruce is listed as an invasive species in Norway (Gederaas et al., 2007), and since 2012 it is categorized as a severely high threat to Norwegian nature due to its high dispersal potential and negative interactions with native species and Norwegian ecosystems (Elven et al., 2018; Gederaas et al., 2012; Vandvik et al., 2023). Previously, the afforestation with Sitka spruce has been considered to have similar effects as native Norwegian spruce outside of its natural occurrence (Gederaas et al., 2012) but Saure et al. (2013) highlighted that plantations with invasive conifers have more severe negative effects, as Sitka creates a dense canopy suppressing light-demanding species. Sitka spruce nowadays covers a known area of about 6872 km^2 with a much higher estimate of total coverage (Vandvik et al., 2023), and it also has been recorded in coastal heathlands and semi-natural grasslands (Elven et al., 2018).

Invasive species and habitat loss due to land use change are considered the two most severe threats to nature and biodiversity worldwide (Bellard et al., 2016; IPBES, 2019; Pyšek et al., 2020). Consequently, there is a need for the removal of plantations on former semi-natural areas, especially Sitka spruce plantations, and the restoration of semi-natural ecosystems. The restoration of degraded ecosystems is currently a popular topic, which is apparent by the ongoing, large-scale initiatives, such as the UN decade on restoration (read more on www.decadeonrestoration.org) and the law to restore 20% of the land and the sea of the EU (European Parliament, 2024). The overall goal of ecological restoration can be described as "giving back" to nature, which aims with different measures to achieve good ecological condition of an area after human-induced degradation that interrupted natural processes. During the process of restoration, it is essential to apply methods that are efficient and appropriate for reaching the aimed results (Hobbs & Harris, 2001).

One method that recently gained interest is using soil seed banks (SSBs) for re-vegetation of degraded sites during the restoration process. The SSB are all the seeds found in a particular area that can germinate. More precisely, Nathan and Muller-Landau (2000, p. 279) define SSB as "the viable seeds present on or in the soil." Whether seeds germinate or not depends on the physiology of the seed and the environmental factors, which is why seeds can endure in the soil before they germinate for a specific time, depending on the species. Based on the longevity of the seeds, species are often divided into three simplified groups: transient species with seeds that are viable for less than one year, short-term persistent species with seeds that are viable for one to five years, and long-term persistent species with seeds that stay viable for more than five years (Bakker et al., 1996). Hence, SSBs often contain individuals in the form of seeds of the recent and past plant communities, which is why the SSB is also considered a "memory" of past plant communities (Bakker et al., 1996, p. 462). Some species that are present in the aboveground vegetation are not present in the SSB, as some species tend to reproduce more vegetatively. Consequently, the species composition of the SSB is often slightly different from the aboveground vegetation depending on the ecosystem type and vegetation history of the site (Bossuyt & Honnay, 2008).

Despite these differences, the idea is that this "memory" provided by the SSB can now be used for ecological restoration (follow the scheme shown in Fig. 1). In the initial, intact state of an observed area, the aboveground vegetation has created an SSB over a long time that is characteristic for the aboveground vegetation, even though species composition might slightly differ (Fig. 1, step 1). If then the aboveground vegetation of an observed area is altered, for example, by removing the vegetation and plantation of coniferous trees, the SSB remains in the beginning relatively unaffected in the soil of the area while the aboveground vegetation changes strongly (Fig. 1, step 2). In this example, the introduction of the tree creates a different ecosystem type and thus changes the environmental conditions of the area. These altered environmental conditions can hinder the germination of seeds of the initial vegetation and cause the seeds to become dormant in the soil. For example, Gimingham (1972) has shown that shadow can inhibit the germination of *Calluna* seeds. Over time, the species composition and seed density of the SSB will also change due to the change in the aboveground vegetation (Plue et al., 2021). This delayed response can be described as a time lag of the effect on the SSB compared to the aboveground vegetation, whereas the magnitude of this lag may differ from site to site (Chang et al., 2001; Ren et al., 2023). The idea of using SSBs for restoration is that when measures have been applied to a degraded area, here by removal of the introduced species, the seeds of the initial plant community that have remained viable in the SSB have now the potential to germinate as the environmental conditions are reversed again (Fig. 1, step 3). The goal is that the seeds of the initial vegetation recreate this vegetation to some degree.

Uncertainties remain about the efficiency of SSB for restoration, as differences in seed longevity change the seed composition over time (Fig. 1, a). An et al. (2022) showed that transient and persistent seeds responded differently to disturbance intensity. Therefore, it is important to investigate how similar the SSB is to the aboveground vegetation and how the SSB composition changes over time. Second, the input of seeds from other areas can also influence the restoration results positively and negatively (Fig. 1, b). Seed dispersal by wind or cattle from close areas into the restoration area can increase seed density and the number of target species (Bakker et al., 1996). Two studies also found that the spatial dispersal of seeds and propagules is more relevant in grassland restoration than the SSBs (Bisteau & Mahy, 2005; Dutoit & Alard, 1995). On the other side, the disturbance created by restoration could also create opportunities for (other) invasive or unwanted species to spread in the area.

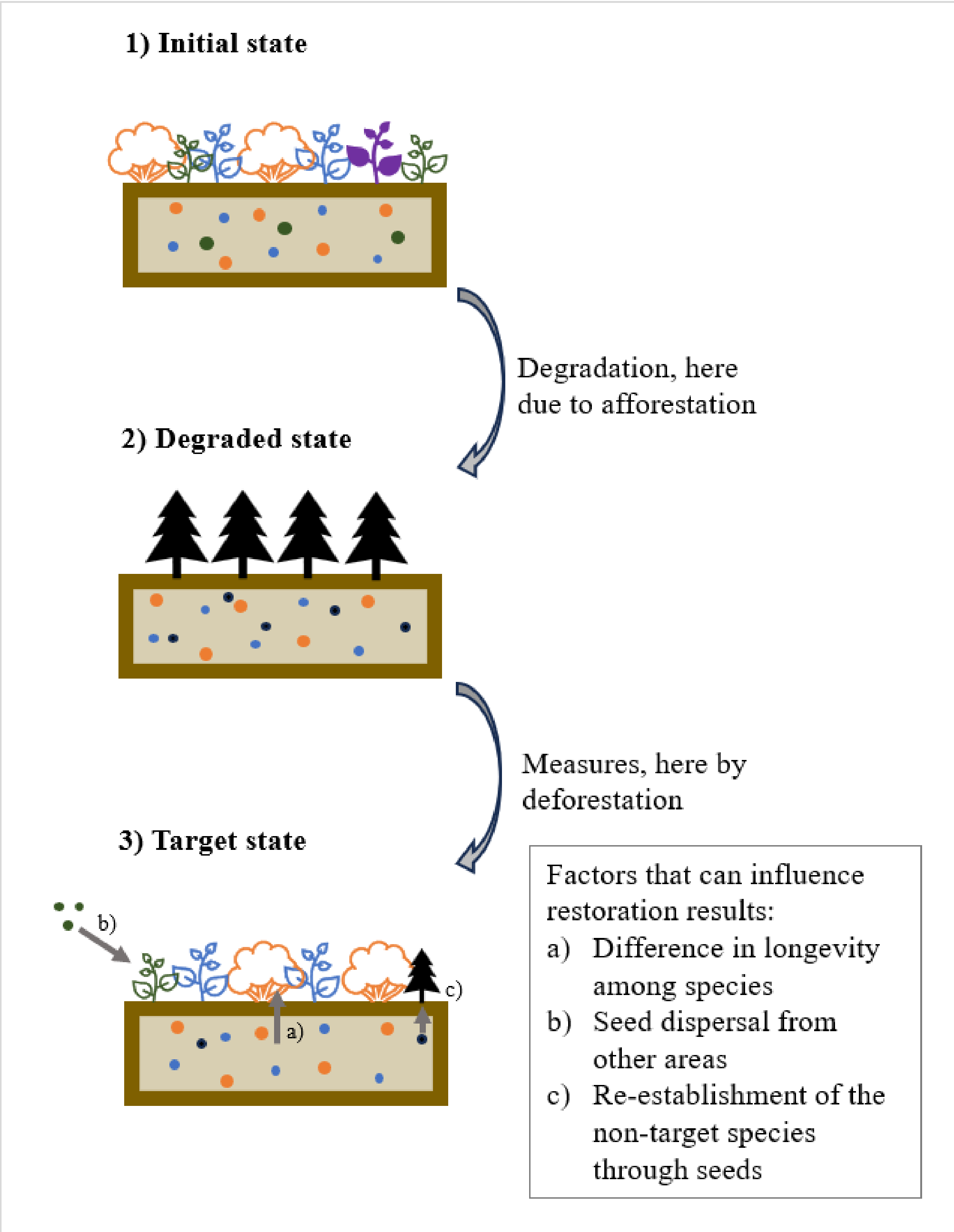

Figure 1: Schema of the process from initial, intact state (1), to degradation through afforestation (2) and finally restoration aiming for the target state (3) similar to the initial state. Additionally, factors that may influence restoration results are listed in the box.

According to Eriksson et al. (2006), species-rich grasslands in Scandinavia are particularly susceptible to invasive species as the fact that they are generally quickly colonized by new species – which makes these areas species-rich – also allows invasive species to invade easily. Lastly, for a long-lasting successful restoration, it is crucial that the source of degradation, in this example, the introduced coniferous tree species, is eliminated (Fig. 1, c). Vesterbukt (2019) and Vesterbukt (2018) found at two coastal heathland sites in Norway that Sitka spruce re-established after removal through seedlings in high numbers, especially during the first year after restoration.

Often, the factors mentioned earlier that can influence the SSB have to be viewed individually for each restoration project, as the same methods applied in comparable ecosystems can achieve different restoration results (see, for example, Saure et al., 2023), which is also the background for this thesis. Two areas in western Norway where spruce was planted during the 20th century are in the process of restoration. One area consists of two islands, Vågsøy and Silda, dominated by coastal heathland with several patches of Sitka spruce plantations in between (Helle, 2023). The other area is a calcareous meadow, and a large area to the north of the meadow where Norwegian spruce was planted on a former meadow in Voss municipality (Helle, n.d.). Both projects aim to restore a semi-natural ecosystem where spruce was afforested. The restoration process started in 2018 on Vågsøy and Silda, and in 2019 in Voss, by deforestation of several spruce stands. For both project areas, aboveground vegetation analyses of the intact and restoration sites were already conducted (for the calcareous meadow area by Helle et al., unpublished; for the coastal heathland area by Nielsen, 2023).

By collecting soil samples from restoration and intact sites from both areas for comparison of seed density and species composition in the SSB, this thesis supports these two restoration projects and contributes to filling the general knowledge gap about the extent to which SSBs can be used for restoration. More specifically, this thesis tries to answer the following questions:

(i) Does the seed density of the SSBs differ between the site types (intact sites, restoration sites, and Sitka plantations)?

(ii) Does the number of target species or the seed density of target species in the SSBs differ between the site types?

(iii) Does the species composition of the SSBs differ between the site types?

Overall, I expect to find significant differences in seed density with higher values for intact sites and that more seedlings of target species will be found in intact sites, and more pioneer species and invasive species, especially Sitka spruce, in the restoration sites. I expect to find different results for the coastal heathland ecosystem than the calcareous meadow ecosystem, as previous studies indicate a higher potential of the SSB for restoration in heathlands than in grasslands (Bossuyt & Honnay, 2008). To my knowledge, only very few studies have been specifically on the SSB of restoration sites of coastal heathland ecosystems. Studies that have been conducted on heathland ecosystems show that especially *Calluna* seeds have a recognizable longevity, which is crucial for restoration in general (Bossuyt & Hermy, 2003; Måren & Vandvik, 2009). Several studies on the aboveground vegetation of restoration areas of coastal heathland ecosystems have been conducted, showing different results for different sites (Nielsen, 2023; Saure et al., 2023; Vesterbukt, 2018, 2019). Most of these studies recorded a high number of Sitka spruce seedlings that emerged from seeds after clear-cutting of the plantation, which is why I expect a high number of Sitka spruce seedlings in the samples from restoration sites from the coastal heathland ecosystem.

Several studies on the SSB have already been conducted for semi-natural grasslands, and most of them negate the importance of the SSB in restoring grasslands due to low seed longevity (Bekker et al., 2000; Bossuyt & Hermy, 2003). However, Ludewig et al. (2021) found that the SSB of mountain meadows has the potential to restore sites after the invasion of non-native plant species and highlighted that results can differ from site to site. Hence, the study area of the calcareous meadow was still added to this thesis to investigate which measures should be focused on in the restoration project in Voss.

The results of this thesis should indicate whether the viability of the SSBs of the two ecosystems studied is sufficient for restoration or whether additional measures must be implemented. The aim of the thesis is to elaborate suggestions on how the restoration process of the sites on Vågsøy and Silda, and in Voss can be improved.

Material & Methods

Study Sites

The study area of the coastal heathland ecosystem was the two islands Vågsøy (about 58.7 km² large; Fig. 2) and Silda (about 1 km² large; Fig. 3) in the municipality of Kinn, western Norway. The climate of the area is strongly oceanic (Artsdatabanken, n.d.-b), typical for the western coast of Norway. While the study sites on Vågsøy were in the `sørboreal` (south-boreal) bioclimatic region, the study sites on Silda were in the `boreonemoral` bioclimatic region (Artsdatabanken, n.d.-b). The bedrock of both islands consists mainly of granitic gneiss (granittisk gneiss), with parts of Vågsøy consisting of mica slate (glimmerskifer) (Norges geologisk undersøkelse, n.d.). The mean annual temperature in Måløy, the largest town on Vågsøy, is 7°C with an annual precipitation of about 2,500 mm (Norsk Klimaservicesenter, 2022b). In 2022, the highest temperature measured on Vågsøy was 25.4°C in July and the lowest was -3.9°C in December, and the highest precipitation was recorded in January (272.2 mm) and the lowest in April (56.2 mm) (Norsk Klimaservicesenter, 2024). Both islands are dominated by heathlands with mainly *Calluna* and other species typical for heathlands, like *Vaccinium myrtillus* and *Empetrum nigrum*, as well as red-listed plants like *Erica cinerea* (Artsdatabanken, n.d.-a). Sitka spruce was planted in the area during the 1970s and early 1980s, resulting in several patches of dense Sitka spruce stands on both islands, some of which can be recognized as dark green patches in aerial images (Fig. 2 and 3). Several of these stands were deforested with logging machines and chain saws for ecological restoration. On Silda, several small patches were deforested in 2018, 2019, 2021, and 2022 (Fig. 3). On Vågsøy, one stand was deforested in 2021 (Fig. 2). To maintain the coastal heathland landscape, the area on Vagsøy is grazed by sheep throughout the year, and parts of the area are burnt, including some of the coastal heathland area on Vågsøy in April 2023.

The study area of the calcareous meadow was located in Voss municipality in western Norway (Fig. 4). The area is also influenced by the oceanic climate of the western coast (Artsdatabanken, n.d.-b) and is located in the 'sørboreal` (south-boreal) bioclimatic zone (Artsdatabanken, n.d.-b). The bedrock of the study area consists of phyllite (Norges geologisk undersøkelse, n.d.). The annual mean temperature of Vossevangen, which is a part of Voss municipality, is 5.8°C and the annual precipitation is around 1,330 mm (Norsk Klimaservicesenter, 2022a), and the study area was on the south side of a mountain. In 2022, the highest temperature measured in Vossevangen was 30.5°C in June and the lowest -17.5°C in December, and the highest precipitation was recorded in October (202.8 mm) and the lowest in April (18.3 mm) (Norsk Klimaservicesenter, 2024). The meadow is wooded and characterized by calcareous soil with a diverse grassland-species-community. To the north of the meadow, Norwegian spruce was planted during the 1970s and early 1980s. One large area was deforested in 2019 and 2020 for ecological restoration aimed at recreating a semi-natural meadow. Afterwards, excavators were used to remove logging debris, and the area was manually cleared. The intact meadow and the restoration site were grazed by sheep in early spring and late autumn with free movement between the sites (Helle, n.d.).

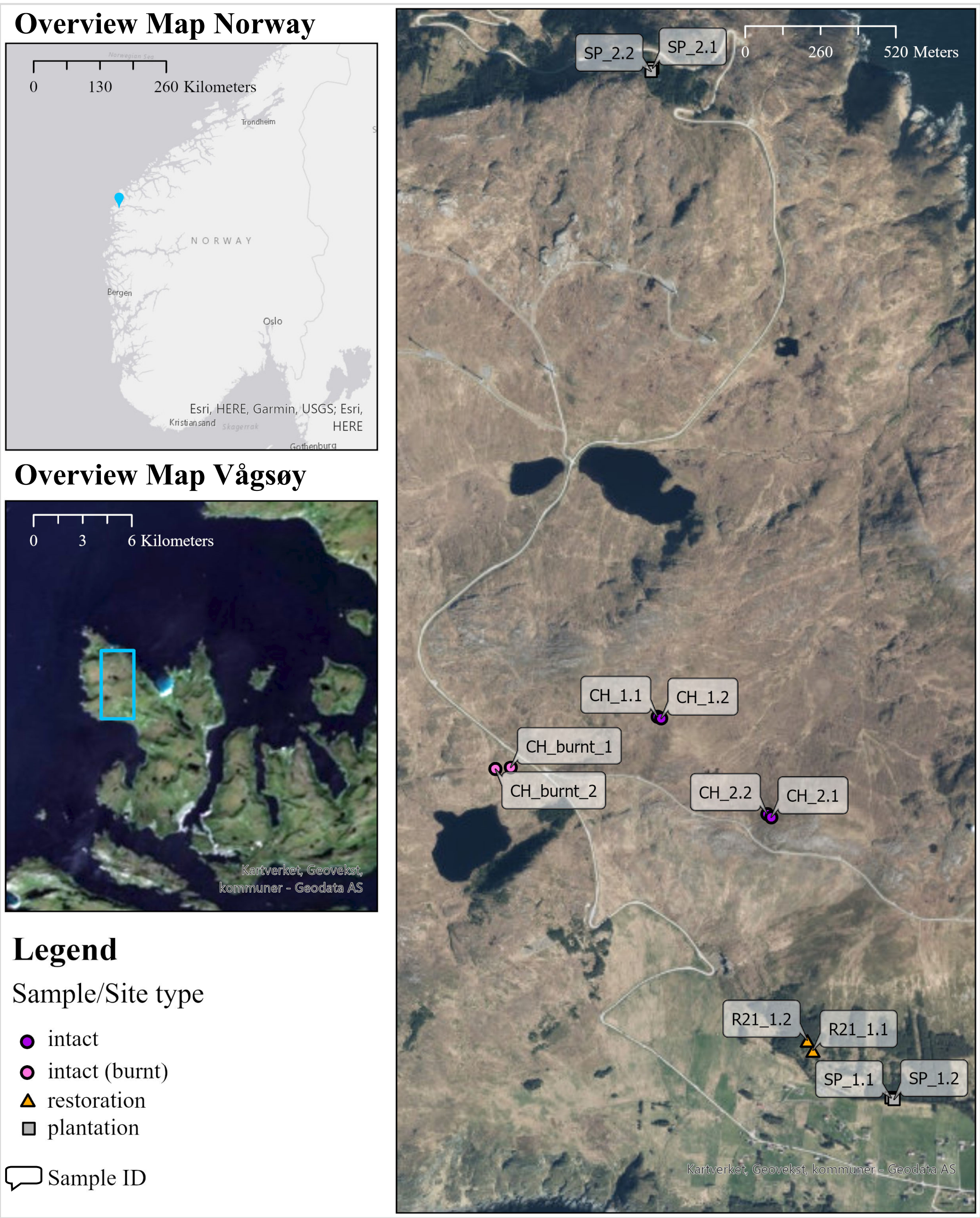

Figure 2: Location of Vågsøy in Norway (two left maps) and overview of the sampling sites on Vågsøy (right map). The sampling sites are shown according to site type and labeled with the sample ID.

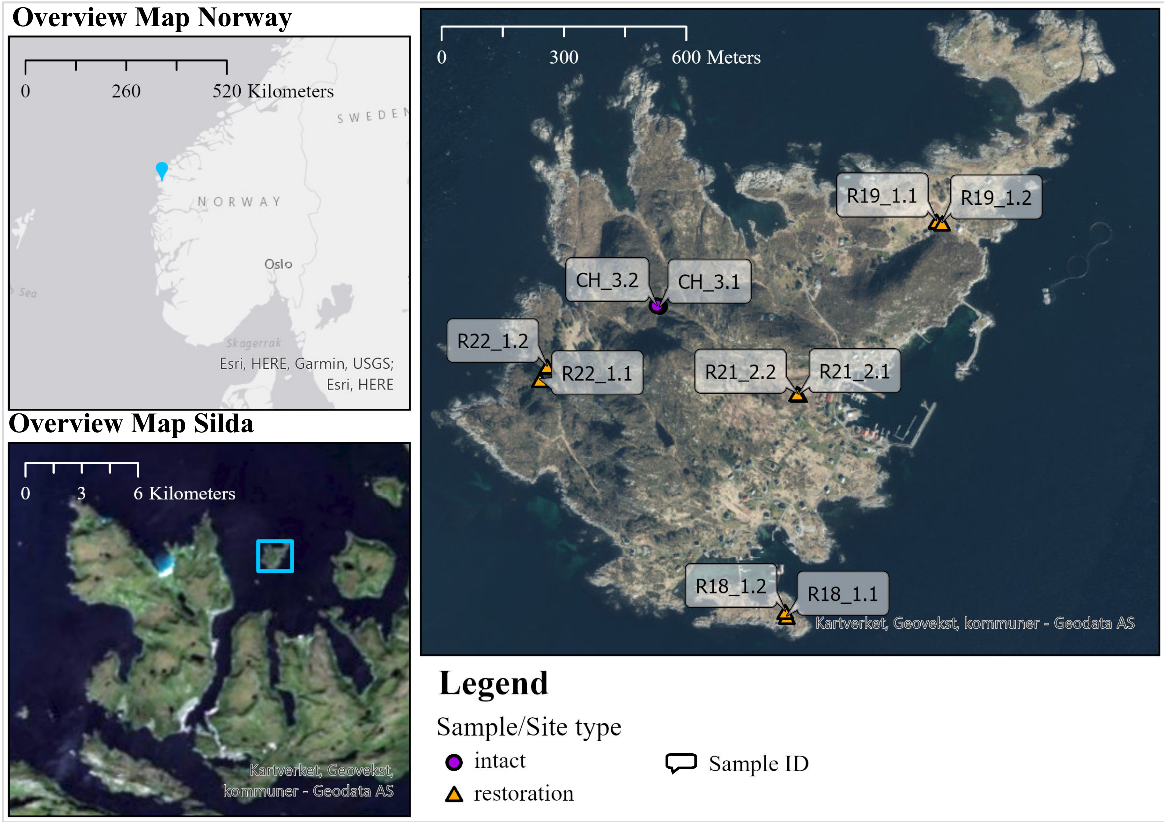

Figure 3: Location of Silda in Norway (two left maps) and overview of the sampling sites on Silda (right map). The sampling sites are shown according to site type and labeled with the sample ID.

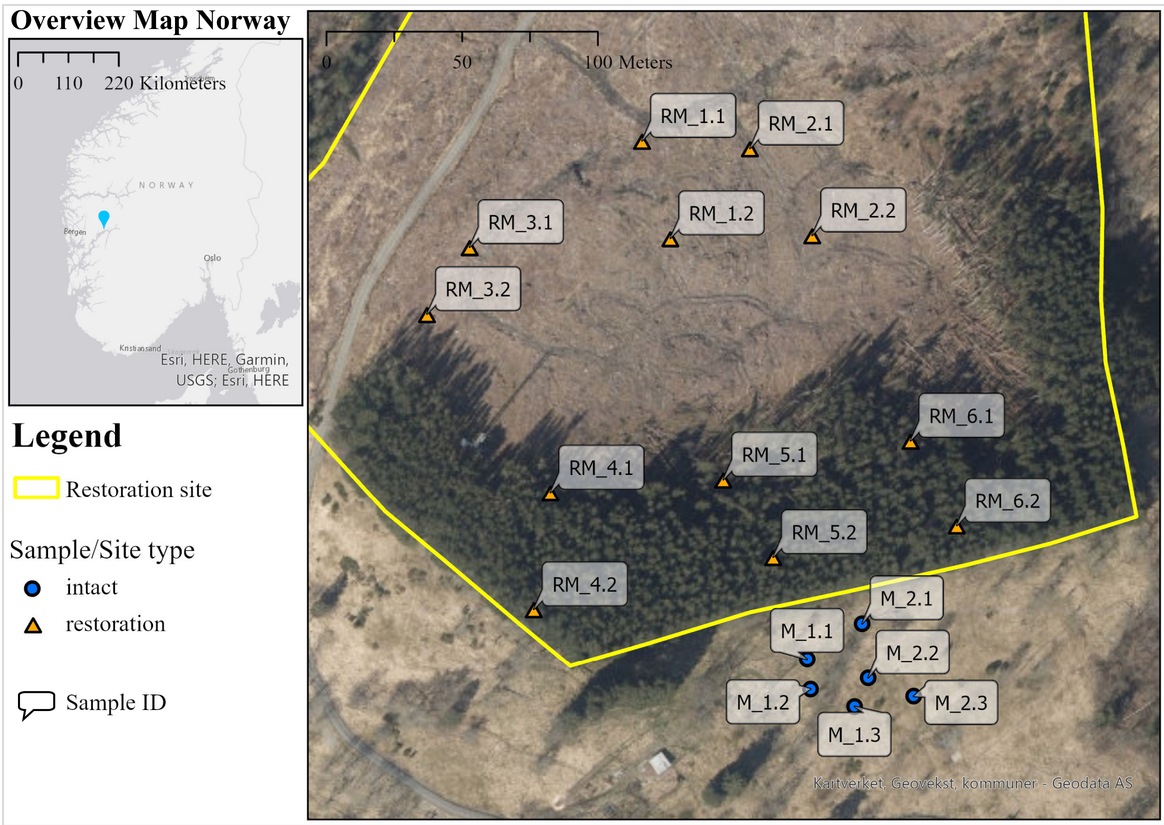

Figure 4: Location of Voss in Norway (left map) and overview of the sampling sites (right map). The sampling sites are shown according to site type and labeled with the sample ID.

Data Collection

Sampling

Soil samples from Vågsøy and Silda (in the following called CH-samples) were collected on the 15th of April 2023 at eleven different sites (Fig. 2 and 3). The temperature measured on Vågsøy during the last four weeks before sampling was between -1.7°C and 14.1°C (Norsk Klimaservicesenter, 2024). Samples from three sites with coastal heathland where Sitka spruce was never planted – remained intact – were collected, one on Silda and two on Vågsøy. Additionally, samples were taken from one site of intact coastal heathland that was burnt one week before sampling for maintenance of the coastal heathland vegetation. Two sites where Sitka spruce plantations on Vågsøy were still present were sampled. One site each was sampled for the areas where Sitka spruce was deforested in connection with restoration in 2018, 2019, and 2022 on Silda. For 2021, two sites were sampled, with one site located on Vågsøy and one on Silda. The samples were sorted into one of the three site types: intact (all

Table 1: Overview of the samples from Vågsøy and Silda, including the sample ID, site type, and description of the sample location.

Sample ID	**Site Type**	**Description of the location**
CH_1.1	intact	Area with typical coastal heathland vegetation, where Sitka spruce was never planted; on Vågsøy.
CH_1.2	intact	
CH_2.1	intact	
CH_2.2	intact	
CH_3.1	intact	Area with typical coastal heathland vegetation, where Sitka spruce was never planted; on Silda.
CH_3.2	intact	
CH_burnt_1	intact	Area with typical coastal heathland vegetation, where Sitka spruce was never planted; the area was burnt one week before sampling; on Vågsøy.
CH_burnt_2	intact	
R18_1.1	restoration	Area with previous Sitka spruce stand that was deforested in 2018; on Silda.
R18_1.2	restoration	
R19_1.1	restoration	Area with previous Sitka spruce stand that was deforested in 2019; on Silda.
R19_1.2	restoration	
R21_1.1	restoration	Area with previous Sitka spruce stand that was deforested in 2021; on Vågsøy.
R21_1.2	restoration	
R21_2.1	restoration	Area with previous Sitka spruce stand that was deforested in 2021; on Silda.
R21_2.2	restoration	
R22_1.1	restoration	Area with previous Sitka spruce stand that was deforested in 2022; on Silda.
R22_1.2	restoration	
SP_1.1	plantation	Sitka spruce plantation established around 50 years ago.
SP_1.2	plantation	
SP_2.1	plantation	
SP_2.2	plantation	

samples from intact coastal heathland), plantation (samples from Sitka spruce plantations), and restoration (samples from restoration sites) (Table 1).

At each site, two soil samples were taken, in total 22 samples of 2 L from the upper 5 cm soil layer were collected, which is recommended and applied by previous studies (see for example, Csontos, 2007). The soil was collected with a hand shovel and stored in a plastic box with a 2 L capacity. When the soil was covered with vegetation, the vegetation was carefully removed before sampling (Appendix Fig. A1-A). Additionally, notes on the vascular plant species that were close (<2 m) to the sampling spot were taken to aid later identification in the lab. All samples where vegetation plot markers by Nielsen (2023) were present were taken 1 m to the northern direction of the plot markers to compare the results of the aboveground vegetation analysis with the results of this thesis. All CH-samples were stored in a refrigerator at 4.6 °C with no light until the start of the germination trial on the 22nd to the 24th of May 2023.

The samples from Voss (in the following called M-samples) were taken on the 1st of May 2023 using the same method as above. The temperature measured in Vossevangen during the last four weeks before sampling was between -3.9°C and 18.9°C (Norsk Klimaservicesenter, 2024), and due to the late sampling, many seedlings were observed in the field (Appendix Fig. A1-B). The samples from the restoration site were taken close to previous plots for vegetation analysis by Helle et al. (unpublished), which was conducted along six transects, each with six plots. For this thesis, two samples were taken in each transect about 1.5 m away from the plot marker, resulting in twelve samples for the restoration site in Voss. As no previous vegetation analysis was done for the intact calcareous meadow, two transects were established, each with three plots at least 20 m apart, resulting in six samples for the intact meadow. In total, 18 samples were taken from the calcareous meadow area (Table 2). The samples were also stored in a refrigerator at 4.6°C with no light until the start of the germination trial. However, there was only space for half of the samples, and thus, the germination trial was initiated for only 9 of the 18 samples on the 25th of May 2023. The other samples (RM_1.2, RM_2.2, RM_3.2, RM_4.2, RM_5.2, RM_6.2, M_1.2, M_2.2, and M_2.3) were stored from the 25th of May 2023 to the 14th of September 2023 in a freezer at -22°C, and the germination trial was initiated on the 15th of September 2023 after defrosting the samples for 24 hours at room temperature.

Table 2: Overview of the samples from Voss, including the sample ID, site type, and description of the sample location.

Sample ID	Site Type	Description of the location
M_1.1	intact	Semi-natural, calcareous wooded meadow, where Norwegian spruce was not planted
M_1.2	intact	
M_1.3	intact	
M_2.1	intact	
M_2.2	intact	
M_2.3	intact	
RM_1.1	restoration	Area north to the intact meadow with previous Norwegian spruce stand that was deforested in 2019 and 2020.
RM_1.2	restoration	
RM_2.1	restoration	
RM_2.2	restoration	
RM_3.1	restoration	
RM_3.2	restoration	
RM_4.1	restoration	
RM_4.2	restoration	
RM_5.1	restoration	
RM_5.2	restoration	
RM_6.1	restoration	
RM_6.2	restoration	

Environmental variables

The pH value of the soil was measured in the lab for each subsample using pH-test paper strips (Appendix Fig. A1-C). The elevation in meters above sea level, slope in degree, and slope orientation for each sample site were determined using their coordinates and the terrain data from Kartverket (2017). The distance of restoration sites and plantations to intact coastal heathland on Vågsøy and Silda was measured in ArcGIS Pro using aerial images. The distance was not measured for the samples in Voss, as the elevation can be used representative for the distance because of the continuously increasing slope from south to north (see Fig. 4 and Appendix Table A2).

Germination trial

For the germination trial, a plant tray (inner size: 21.5 cm width, 36 cm length, and 5.5 cm depth) was prepared for each sample. Peat-free planting soil was heated to 80°C in a microwave (brand: KENWOOD; Model nr.: K20MSS10E; Rated voltage: 230V~ 50 Hz; Power input (microwave): 1270W; Frequency: 2450MHz; Power output (microwave): 800W) to avoid contamination that could influence the results, spread out as a 2 cm thick soil layer in each tray, watered, and left until it cooled down to room temperature. One liter of each soil sample was then prepared for the germination trial. The preparation involved (1) the removal of larger roots (Appendix Fig. A1-D), (2) collecting seedlings that had already germinated (Appendix Fig. A2-A) to grow them in separate, smaller pots, and finally, (3) weighing the soil. After the preparation, the soil samples were each evenly spread in a tray on top of the planting soil.

The CH-samples were placed indoors on a bench (Appendix Fig. A2-C) with two growing lamps, each with one 400W light bulb 1 m above the bench, kept on the entire time to ensure stable conditions. The air conditioner was turned on to the highest setting, aiming for a temperature around 20°C on the bench. However, the temperature was slightly higher, around 22.8°C (measured with a Temperature/Relative Humidity Smart Sensor connected to a HOBO Micro Station Data Logger (Onset, Bourne, MA, USA) every five minutes between the 6th June 2023 and the 16th August 2023). The trays were rotated twice a week so that all trays received the same exposure to the growing lights. The soil was kept moist by watering it when needed and checking it daily during the germination trial. The trays were covered with plastic foil with holes to reduce evaporation while allowing air circulation at the same time.

The M-samples were kept in an environmental test chamber (brand: SANYO; model: MLR-351; fluorescent lamps: 800W) with a temperature set to 20°C and three light bulbs (one in the front and one on each side) turned on (Appendix Fig. A2-B). Again, the trays were rotated twice a week to ensure equal light exposure.

After around five weeks, the approximate cover of moss that established in the trays was noted for each tray. As a control for seed contamination, one tray with only planting soil was placed with the CH-samples on the bench, and one in the chamber with the M-samples. No seeds germinated from the control trays.

Identification and counting

For the identification, appropriate literature was used (Elven et al., 2022; Lye, unpublished; Mossberg et al., 2018), and aboveground vegetation analysis provided guidance (for the CH-samples Nielsen (2023); for the M-samples Helle et al. (unpublished)). To avoid competition among seedlings, the seedlings that could not be identified at an early stage and became too large or too abundant were removed and planted in separate pots until they became identifiable. As only a part of the *Carex* species could be determined, all specimens of the *Carex* genus were included in *Carex* spp. When identification was possible, the seedlings were removed from the tray and counted according to species. At the beginning of the germination trial, some plants grew from roots that were too small to remove from the soil. These individuals were easily distinguished from seedlings as the roots were visibly older and, therefore, were removed from the sample without being counted. Seedlings that could not be identified were counted as "indeterminate" so that the total seed densities could be determined. Seed density refers to the total number of germinated seeds per 1 liter of soil.

In addition to the identification, species were categorized into "target" species associated with coastal heathlands or calcareous meadows. Target species for the CH-samples were all species listed for the different types of coastal heathlands (kystlynghei) in Natur i Norge (NiN version 2.3: Bratli et al., 2022): *Agrostis sp*., *Avenella flexuosa*, *Calluna vulgaris*, *Empetrum nigrum*, *Galium saxatile*, *Potentilla erecta*, *Trichophorum cespitosum*, *Vaccinium myrtillus*, and *Vaccinium vitis-idaea.* For the M-samples, all species mentioned for the categories T32-8 (slightly calcareous meadow with fertilizer influence), T32-7 (slightly calcareous meadow with clear signs of cultivation), and T32-10 (strongly calcareous meadow with extensive cultivation) in Natur i Norge (NiN version 2.3: Bratli et al., 2022) were categorised as target species: *Achillea millefolium, Agrostis capillaris, Anthoxanthum odoratum, Campanula rotundifolia, Cerastium fontanum* subsp. *vulgare, Deschampsia cespitosa, Festuca rubra, Hypericum maculatum, Pimpinella saxifraga, Plantago lanceolata, Poa annua, Potentilla erecta, Ranunculus acris, Rumex acetosa, Scorzoneroides autumnalis, Silene dioica, Stellaria graminea, Trifolium pratense, Trifolium repens, Urtica dioica*, and *Veronica officinalis.*

<u>Statistical Analysis</u>

All statistical analyses was conducted in R version 4.3.1 (R Core Team, 2023). Graphs were created using the package *ggplot2* (Wickham, 2016). And all analyses were performed for both CH- and M-samples in the same way unless otherwise described.

For the differences in seed densities and number of species between the site types (intact, restoration, and plantation), the Kruskal-Wallis rank sum test was applied. All tests were used for the total number of seedlings and species, as well as for the target species only. Linear models were created to analyze the relationship between moss cover and the number of seedlings germinated in the tray.

For the analysis of the species composition, Permutational Multivariate Analysis of Variance (PerMANOVA), Non-Metric Multidimensional Scaling (NMDS), and, for comparison to the NMDS, Detrended Correspondence Analysis (DCA) using the *vegan* package version 2.6-4 (Oksanen et al., 2022) were conducted. The PerMANOVAs were used to analyze differences between the site types and were conducted with 1,000 permutations and the "Bray-Curtis"-method for intact sites and restoration sites for the CH-samples and the M-samples, and also for intact sites and plantations, and restoration sites and plantations for the CH-samples. For the NMDS, the *metaMDS()*-function was used with four dimensions to calculate and visualize the similarities of the species composition between the different sites and to visualize the associated species. The DCA using the *decorana()*-function was conducted to compare the ordination to the NMDS. The correlations between the axes of the NMDS and DCA were calculated using the Kendall rank correlation coefficient.

To analyze the influence of environmental variables on the species composition, a Redundancy Analysis (RDA), again using the *vegan* package version 2.6-4 (Oksanen et al., 2022), was conducted. For the RDA, the data was standardized using the *decostand()*-function with the Hellinger-method for the species composition variables and the log-method for the environmental variables. The environmental variables used in the RDA were slope (in degrees), pH value, distance to the closest intact area (in meters), and elevation (in meters above sea level). Additionally, the seed densities of the target species of the M-samples were plotted against the elevation (meters above sea level) for the M-samples, and a linear model was created.

Results

Coastal Heathland Samples

Seed density

A total number of 2,933 seedlings from the 22 CH-samples germinated during the trial. Most seedlings germinated in the samples from intact sites, resulting in a mean seed density of 252.63±163.72 seedlings that germinated per liter soil (following seeds/L) (Table 3). The two samples with the highest seed density were CH_burnt_1 with 503 seeds/L, followed by CH_burnt_2 with 445 seeds/L (Fig. 5). Both samples were from the same intact coastal heathland site, that was burnt one week before sampling.

The Kruskal-Wallis rank sum test showed a significant difference in seed density between the three site types ($H(2) = 13.85$; $p < 0.001$). The seed density of the intact sites was significantly higher than the seed density of the restoration sites ($p = 0.016$; $r = -0.66$) and the seed density of the plantations ($p = 0.002$; $r = -0.99$). Even when excluding the two burnt samples from the intact sites, that had a higher seed density than the other samples form intact sites, the Kruskal-Wallis rank sum test showed a significant difference in seed density ($H(2) = 11.40$; $p = 0.003$; intact-restoration: $p = 0.048$; $r = -0.60$; intact-plantation: $p = 0.003$; $r = -1.03$). The restoration sites had a mean seed density of 80.60±70.42 seeds/L with an outstanding high number of seedlings in R21_2.2 (256 seeds/L) which were mainly seedlings of non-target species (see Fig. 5 and Fig. 6-A). The samples from Sitka plantations had overall the lowest seed density with a mean of 26.50±23.70 seeds/L. The maximum seed density of the Sitka plantation samples was 58 seeds/L and the lowest 5 seeds/L, being the overall lowest seed density.

The same pattern was visible for the seed density of target species only with a significant difference in seed density between the site types ($H(2) = 14.14$; $p <0.001$). For the intact sites most seedlings were target species, especially *Calluna* (compare Fig. 5). The mean seed density of target species from intact sites was 210.13±155.45 seeds/L. Restoration sites and plantations showed a significant lower seed density than intact sites, with 25.50±25.39 seeds/L ($p = 0.002$; $r = -0.81$) and 21±23.82 seeds/L ($p = 0.013$; $r = -0.83$), respectively (Fig. 6-B).

The number of germinated seedlings was significantly lower when the estimated moss cover of the trays was higher after about five weeks since the start of the germination trial ($F(1,20) = 14.46$; $p = 0.001$; Appendix Fig. A4).

Table 3: Mean seed density and standard deviation of the samples from the coastal heathland ecosystem in number of seeds per liter and converted for comparison with other studies in number of seeds per m² for each site type (intact sites, restoration sites, and plantations) for all species and target species only.

	Intact sites	**Restoration sites**	**Plantations**
All species			
Mean no. of seeds/L	252.63±163.72	80.60±70.42	26.50±23.70
Mean no. of seeds/m²	12,632	4,030	1,325
Target species			
Mean no. of seeds/L	210.13±155.45	25.50±25.39	21±23.82
Mean no. of seeds/m²	10,507	1,275	1,050

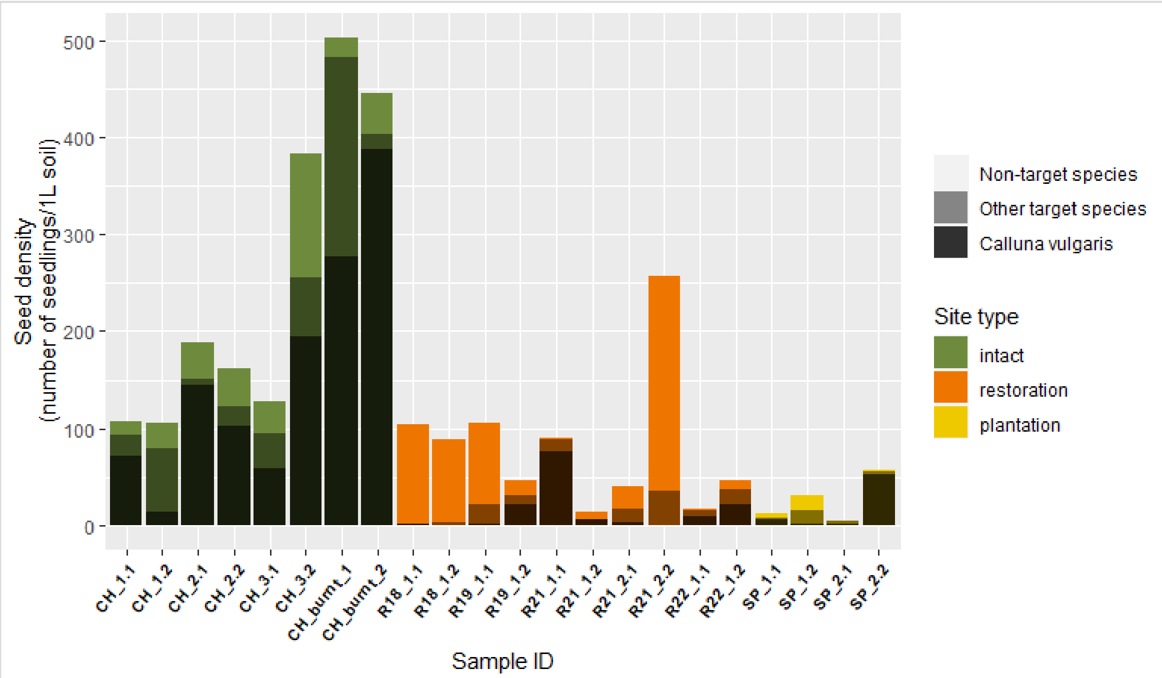

Figure 5: Seed density (number of germinated seedlings per 1 liter of soil) for each sample. Each bar shows the part of *Calluna*-seedlings (dark-grey cover), the part of other target species (light-grey cover), and the part of non-target species (no cover) that add to the total seed density.

Number of species and abundance

The restoration sites had the highest mean number of species (8.8±3.79), followed by the plantations with a mean of 6.75±6.29 species and last the intact sites with a mean of 5.75±1.49 species. The highest number of species in one sample was 16 species, which were found in sample SP_1.2. The Kruskal-Wallis rank sum test showed no significant difference in number of species between the site types ($H(2) = 3.48$; $p = 0.176$; Fig. 7-A). Looking at the target species only (Fig. 7-B), the intact sites had the highest number of species with a mean of 4.38±1.06 target species, followed by similar means for the restoration sites (3±1.56) and the plantations (3±1.41). For the number of target species only, the Kruskal-Wallis rank sum test also showed no significant difference between the site types ($H(2) = 4.46$; $p = 0.108$).

The most abundant species was *Calluna* with 1,456 seedlings that germinated during the trial. Most of the *Calluna* seedlings germinated in samples from intact sites (1,252 seedlings, see Fig. 8 and Appendix Table A3). Following in descending order, *Trichophorum cespitosum* (172 seedlings), *Rumex longifolius* (165 seedlings), *Galium saxatile* (154 seedlings), *Carex* sp. (140 seedlings), *Potentilla erecta* (94 seedlings), *Epilobium ciliatum* (86 seedlings), *Juncus effusus* (70 seedlings), and *Agrostis* sp. (56 seedlings) had the highest abundances. Most of the seedlings of *T. cespitosum*, *G. saxatile*, *Carex* sp., and *P. erecta* germinated in samples from intact sites, while seedlings of *R. longifolius*, *E. ciliatum*, *J. effusus*, and *Agrostis* sp. only germinated in samples from restoration sites or plantations (see Fig. 8 and Appendix Table A3).

Species composition

The NMDS showed a clear grouping of the intact sites, while the restoration sites and plantations were further spread (Fig. 9-A). This indicates that the species compositions of the intact sites were relatively similar to each other, while the species compositions of the restoration sites and the plantations differed between the samples, respectively. The results of the PerMANOVAs showed a significant difference in species composition between the intact sites and the restoration sites ($F(1,16) = 4.14$; $p = 0.002$), and between the intact sites and the plantations ($F(1,10) = 3.14$; $p = 0.014$), but the species composition between restoration sites and plantations did not differ significantly ($F(1,12) = 0.87$; $p = 0.511$). Many species associated with coastal heathlands were placed close to the samples from the intact sites in the NMDS (such as Cal_vul: *Calluna vulgaris*, Tri_ces: *Trichophorum cespitosum*, Vac_vit: *Vaccinium vitis-idea*, and Emp_nig: *Empetrum nigrum*; Fig. 9-B).

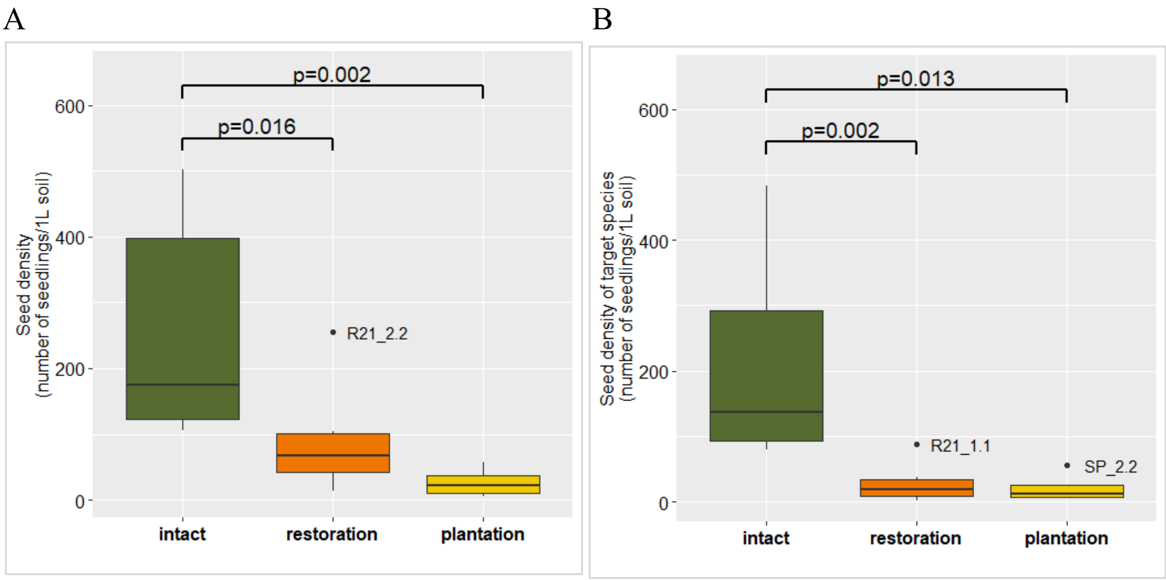

Figure 6: Seed densities (number of germinated seedlings per 1 liter of soil) of the site types intact (green), restoration (orange), and plantation (yellow). Graph A shows the seed densities for all germinated seedlings and graph B for the seedlings of target species only. The boxplots show the median (vertical line inside the box), the first quartile (lower end of the box), the third quartile (upper end of the box), the minimum and maximum seed density (lower and upper end of the whiskers, respectively), except outliers that are shown individually (dots labeled with the sample ID). The *p*-values from the Kruskal-Wallis rank sum test for the site types that differ significantly in seed density are shown above the boxplots.

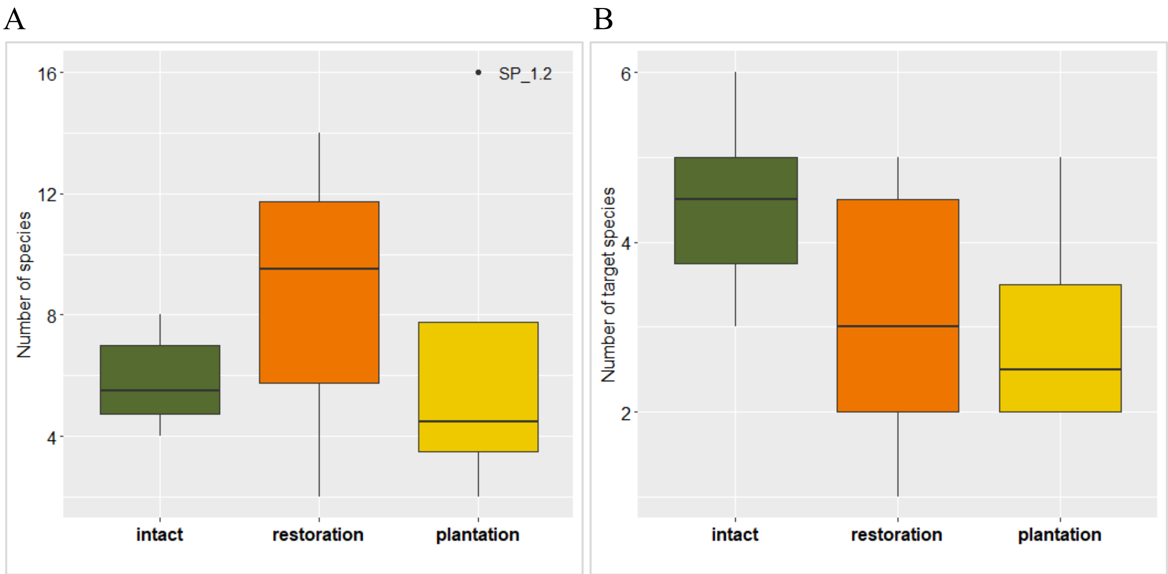

Figure 7: Number of species of the site types intact (green), restoration (orange), and plantation (yellow). Graph A shows the number of all species and graph B the number of target species only. The boxplots show the median (vertical line inside the box), the first quartile (lower end of the box), the third quartile (upper end of the box), the minimum and maximum seed density (lower and upper end of the whiskers, respectively), except outliers that are shown individually (dots labeled with the sample ID).

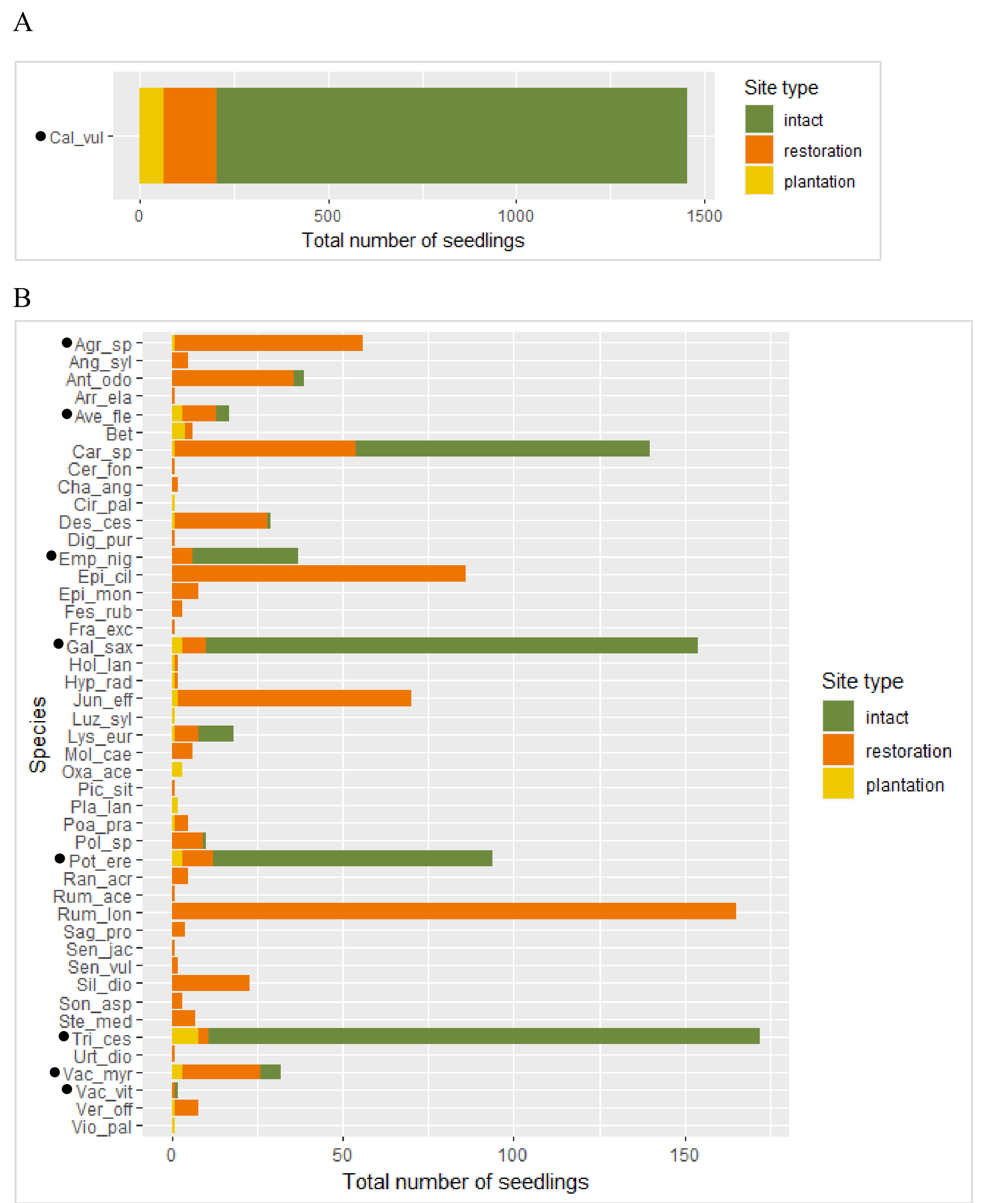

Figure 8: Species abundances of the CH-samples categorized into the site types intact (green), restoration (orange), and plantation (yellow). Graph A shows the abundance of *Calluna vulgaris* only, and graph B the abundance of all other species. For full names of the species, see Appendix Table A3. Target species are marked with a dot in front of the species name abbreviation.

The DCA showed a similar pattern: Intact sites were grouped close to each other, while the plantations and restoration sites were more widely distributed (compare Appendix Fig. A3). The ellipse of the intact sites and the plantations overlapped to a large extent in the DCA and the NMDS, while the ellipses of the restoration sites and the plantations had a smaller overlap. In the ordination of the DCA, the ellipse of the intact sites was fully positioned in the ellipse of the plantation (Appendix Fig. A3-A). Similar to the NMDS, the target species were plotted close to the intact sites in the DCA (Appendix Fig. A3-B). However, only the NMDS1-axis and the DCA1-axis were correlated ($T = 0.75$; $p < 0.001$) and not the NMDS2-axis and the DCA2-axis ($T = 0.14$; $p = 0.371$).

Environmental variables

The environmental variables explained only 30.57% of the variation in the species composition. The results of the RDA showed that only the elevation (meters above sea level) of the sample sites had a significant effect on the variation ($F(1) = 4.36$; $p = 0.005$) in the optimal model (AIC = -14.28).

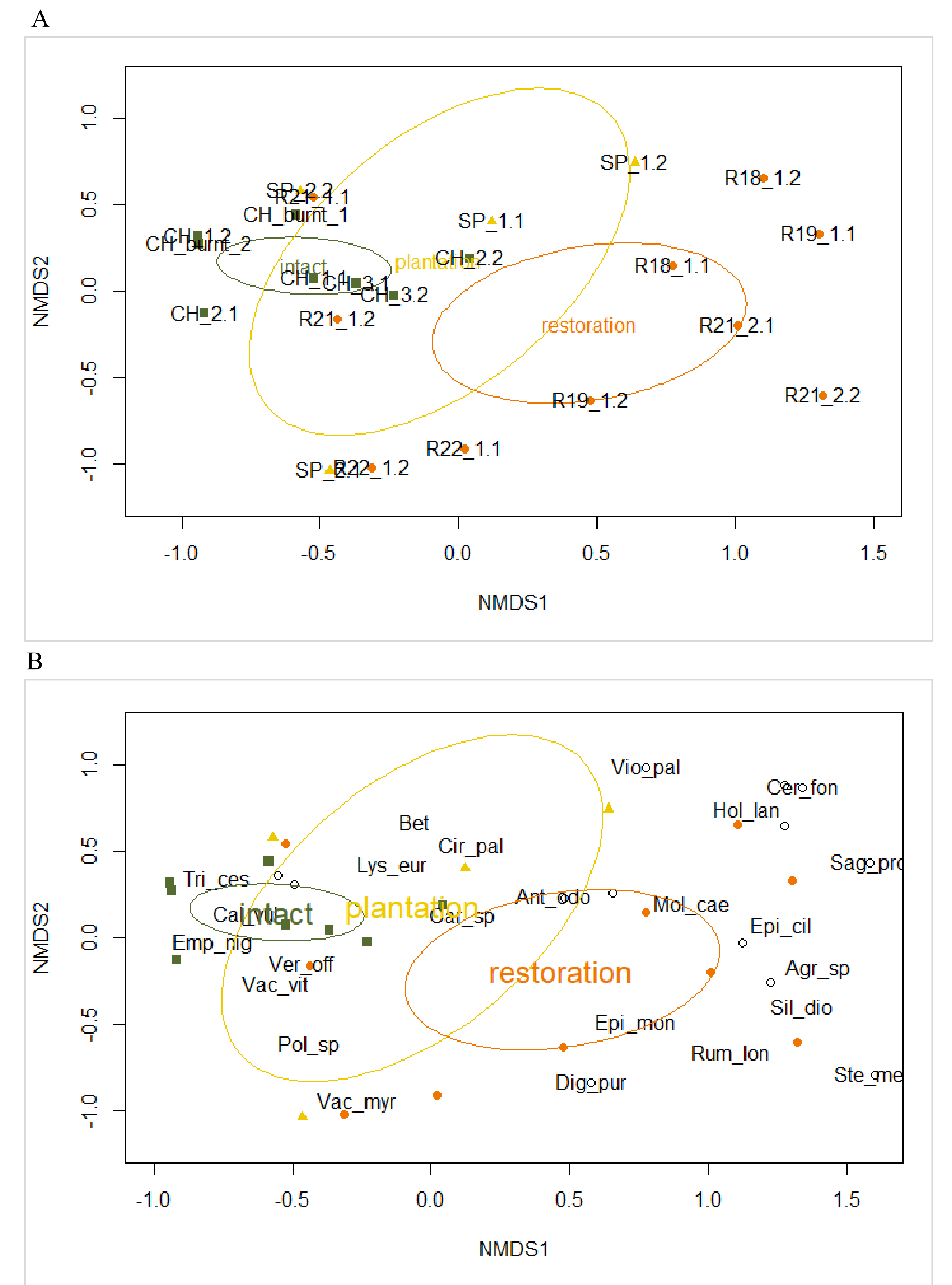

Figure 9: Ordination of the Non-Metric Multidimensional Scaling (NMDS) for the species compositions of the intact sites (green squares), restoration sites (orange points), and plantations (yellow triangles) for the coastal heathland samples; stress value = 0.08. The ellipses show the standard error for each site type in the according color. Additionally, the samples are labeled with their sample ID in (A), and abundant species are labeled in (B) (for full names, see Appendix Table A3).

Calcareous Meadow Samples

Seed density

A total of 638 seedlings germinated from the 18 M-samples. The seed density of the intact site with a mean of 55.5±44.69 seeds/L was significantly higher than the seed density of the restoration site with a mean of 25.42±35.60 seeds/L ($H(1) = 4.246$; $p = 0.039$; Fig. 11-A). The highest seed density from intact site, and overall, was recorded for sample M_1.3, with 120 seeds/L, and the lowest seed density of the intact site was recorded for sample M_1.2 with 12 seeds/L (Fig. 10). The lowest seed density from the restoration site, and overall, was recorded for sample RM_1.2 with 1 seed/L only. Two outliers with a high number of germinated seedlings from the restoration site were recorded: RM_2.1 (109 seeds/L) and RM_4.2 (84 seeds/L). Most of the seedlings in RM_2.1 were target species, while most of the seedlings in RM_4.2 were non-target species (Fig. 10).

Similarly, the seed density of target species from the intact site was significantly higher than the seed density of the restoration site ($H(1) = 6.8914$; $p = 0.0087$; Fig. 11-B). For the intact site, most seedlings were from target species with a mean seed density of 49.33±41.60 seeds/L, and for the restoration site a mean of 14.75±27.09 seeds/L was recorded (Table 4).

The number of germinated seedlings was significantly lower when the estimated moss cover of the trays after around five weeks since the start of the germination trial was higher, if the outlier RM_2.1 was excluded ($F(1,15) = 7.32$; $p = 0.016$; Appendix Fig. A5).

Table 4: Mean seed density and standard deviation of the samples from the calcareous meadow ecosystem in number of seeds per liter and converted for comparison with other studies in number of seeds per m² for both site types (intact site and restoration site) for all species and target species only.

	Intact site	**Restoration site**
All species		
Mean no. of seeds/L	55.5±44.69	25.42±35.60
Mean no. of seeds/m²	2,775	1,271
Target species		
Mean no. of seeds/L	49.33±41.60	14.75±27.09
Mean no. of seeds/m²	2,467	738

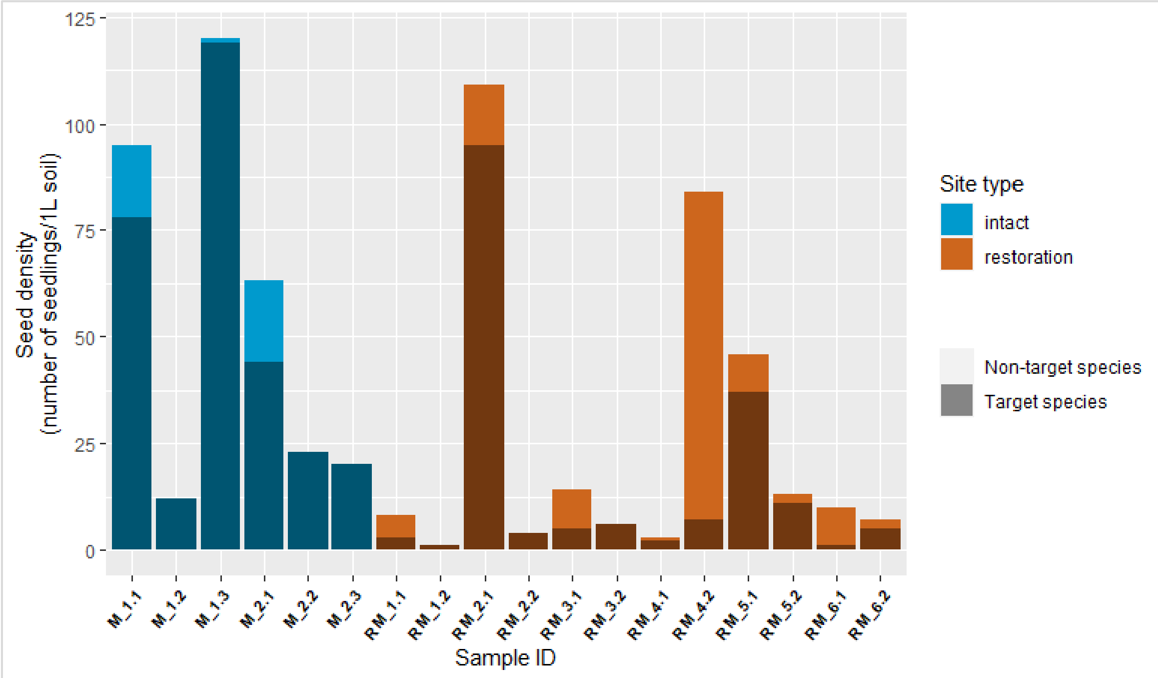

Figure 10: Seed density (number of germinated seedlings per 1 liter of soil) for each M-sample. Each bar shows the part of target species (light-grey cover), and the part of non-target species (no cover) that add to the total seed density.

Number of species and abundance

The intact site recorded a significantly higher number of species than the restoration site for all species (Kruskal-Wallis rank sum test: $H(1) = 6.71$; $p = 0.0095$; Fig. 12-A), and target species (Kruskal-Wallis rank sum test: $H(1) = 11.57$; $p < 0.001$; Fig. 12-B). The intact site had a mean number of 8.5±3.51 species in total, and 7.5±2.88 target species, while the restoration site had a mean number of 3.5±2.78 species in total, and a mean number of 1.67±1.50 target species.

The most abundant species was *Agrostis capillaris* with a total of 147 seedlings that germinated during the trial. 66 seedlings of *A. capillaris* germinating in samples from the intact site, and 81 seedlings from the restoration site (Fig. 13 and Appendix Table A4). Following in descending order, *Stellaria graminea* (107 seedlings), *Senecio viscosus* (92 seedlings), *Hypericum maculatum* (79 seedlings), *Achillea millefolium* (28 seedlings), *Trifolium repens* (21 seedlings), *Campanula rotundifolia* (20 seedlings), *Urtica dioica* (18 seedlings), *Avenella flexuosa* (18 seedlings), and *Poa compressa* (16 seedlings) had the highest abundances. Most of the seedlings of *S. graminea*, and all seedlings of *A. millefolium*, *A. flexuosa*, *C. rotundifolia*, *P. compressa*, *T. repens*, and *U. dioica* germinated in samples from the intact site, while seedlings of *S. viscosus*, and *H. maculatum* only germinated in samples from the restoration site (Fig. 13 and Appendix Table A4).

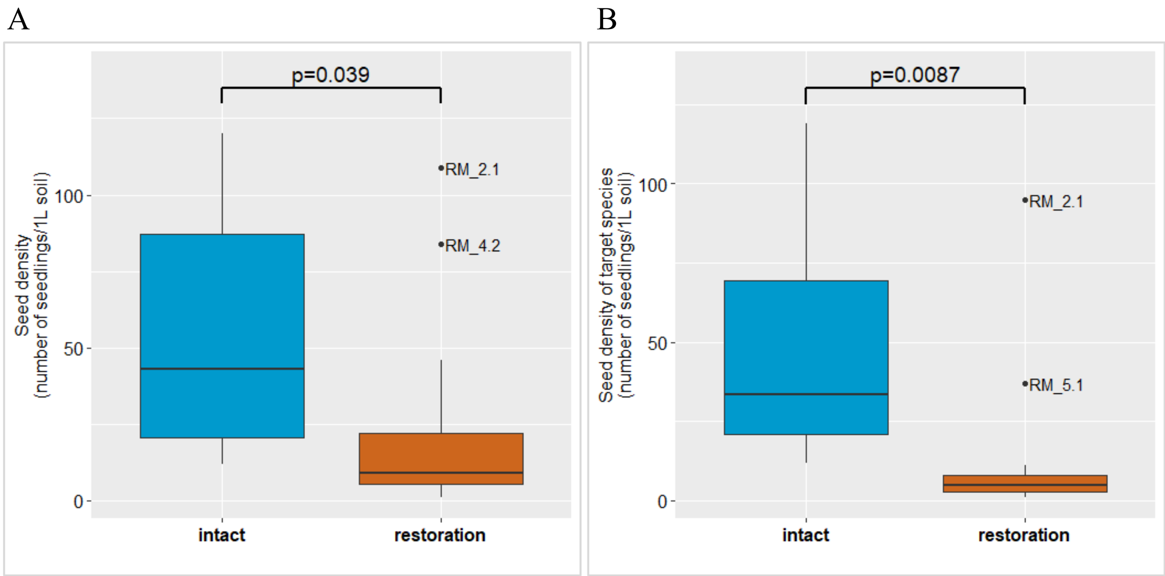

Figure 11: Seed densities (number of germinated seedlings per 1 liter of soil) of the site types intact (blue), and restoration (orange). Graph A shows the seed density for all germinated seedlings and graph B for the seedlings of target species only. The boxplots show the median (vertical line inside the box), the first quartile (lower end of the box), the third quartile (upper end of the box), the minimum and maximum seed density (lower and upper end of the whiskers, respectively), except outliers that are shown individually (dots labeled with the sample ID). Additionally, the *p*-values from the Kruskal-Wallis rank sum test for significant differences in seed density are shown above the boxplots.

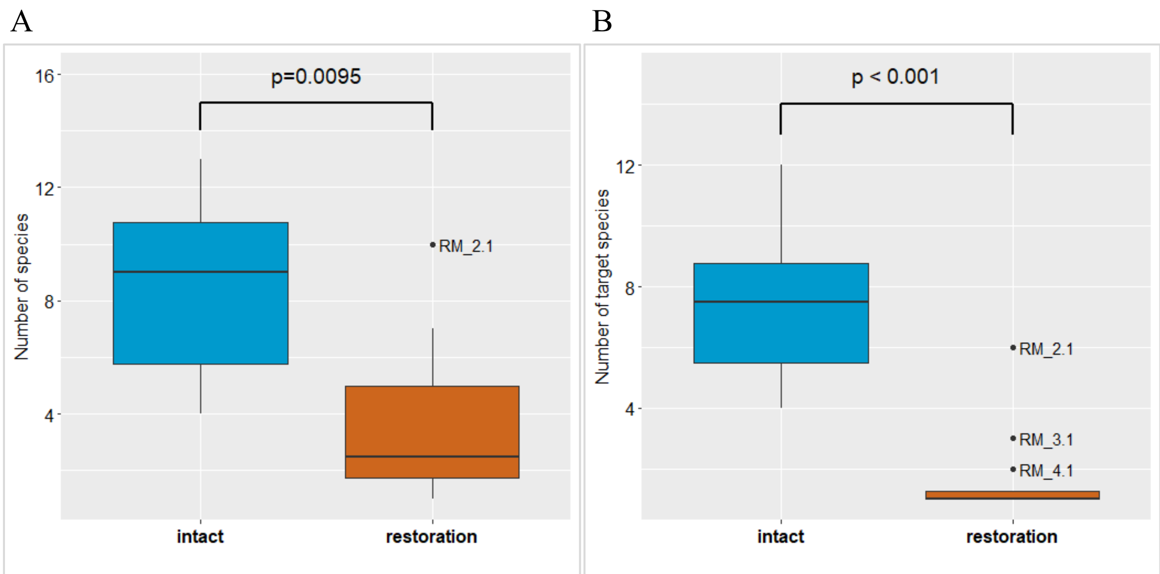

Figure 12: Number of species for the site types intact (blue), and restoration (orange). Graph A shows the number of all species and graph B the number of target species only. The boxplots show the median (vertical line inside the box), the first quartile (lower end of the box), the third quartile (upper end of the box), the minimum and maximum seed density (lower and upper end of the whiskers, respectively), except outliers that are shown individually (dots labeled with the sample ID). Additionally, the *p*-values from the Kruskal-Wallis rank sum test for significant differences in number of species are shown above the boxplots.

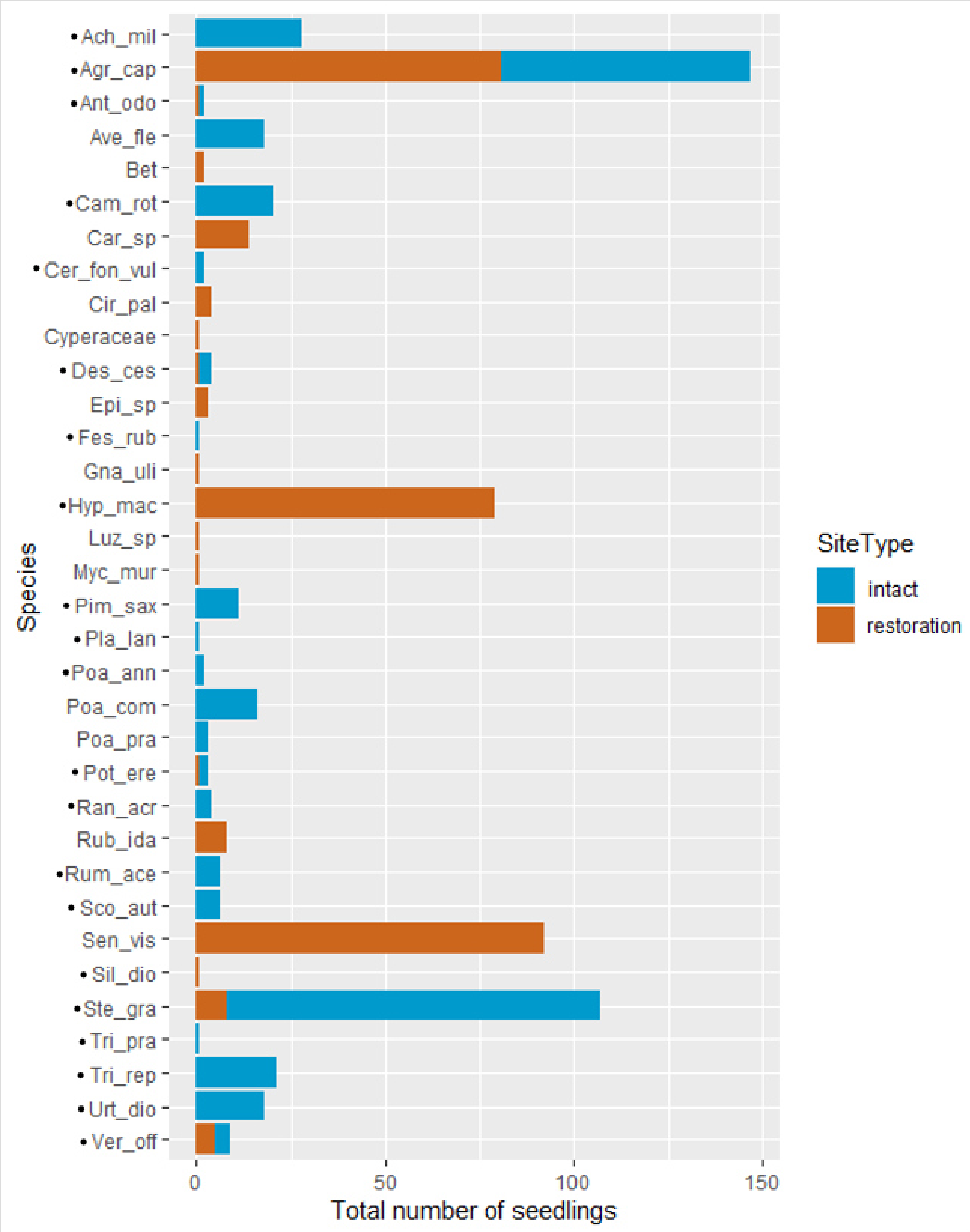

Figure 13: Species abundances of all the M-samples categorized into the site types intact (blue) and restoration (orange). For full names of the species, see Appendix Table A4. Target species are marked with a dot in front of the species name abbreviation.

Species composition

The NMDS showed each a clear grouping of the samples from the intact site and the restoration site (Fig. 14). This indicates that the species composition of the samples within the two types was similar, but the species composition of the intact site was different to the species composition of the restoration site. The results of the PerMANOVAs showed a significant difference in species composition between the intact site and the restoration site ($F(1,16) = 3.82$; $p = 0.003$).

The species in the NMDS showed that most species associated with calcareous meadows were placed close to the samples from the intact site (e.g., Agr_cap: *Agrostis capillaris*, Ant_odo: *Anthoxanthum odoratum*, Cer_fon_vul: *Cerastium fontanum* subsp. *vulgare*, Pla_lan: *Plantago lanceolata*, Pot_ere: *Potentilla erecta*, Ran_acr: *Ranunculus acris*, Sco_aut: *Scorzoneroides autumnalis*, and Tri_rep: *Trifolium repens*; Figure 14-B). The DCA showed a similar pattern with a grouping of the intact and the restoration site, and the location of target species close to the intact site (Appendix Fig. A6). The NMDS1-axis and the DCA1-axis ($T = 0.76$; $p < 0.001$) and the NDMS2-axis and DCA2-axis ($T = 0.43$; $p = 0.012$) correlated significantly.

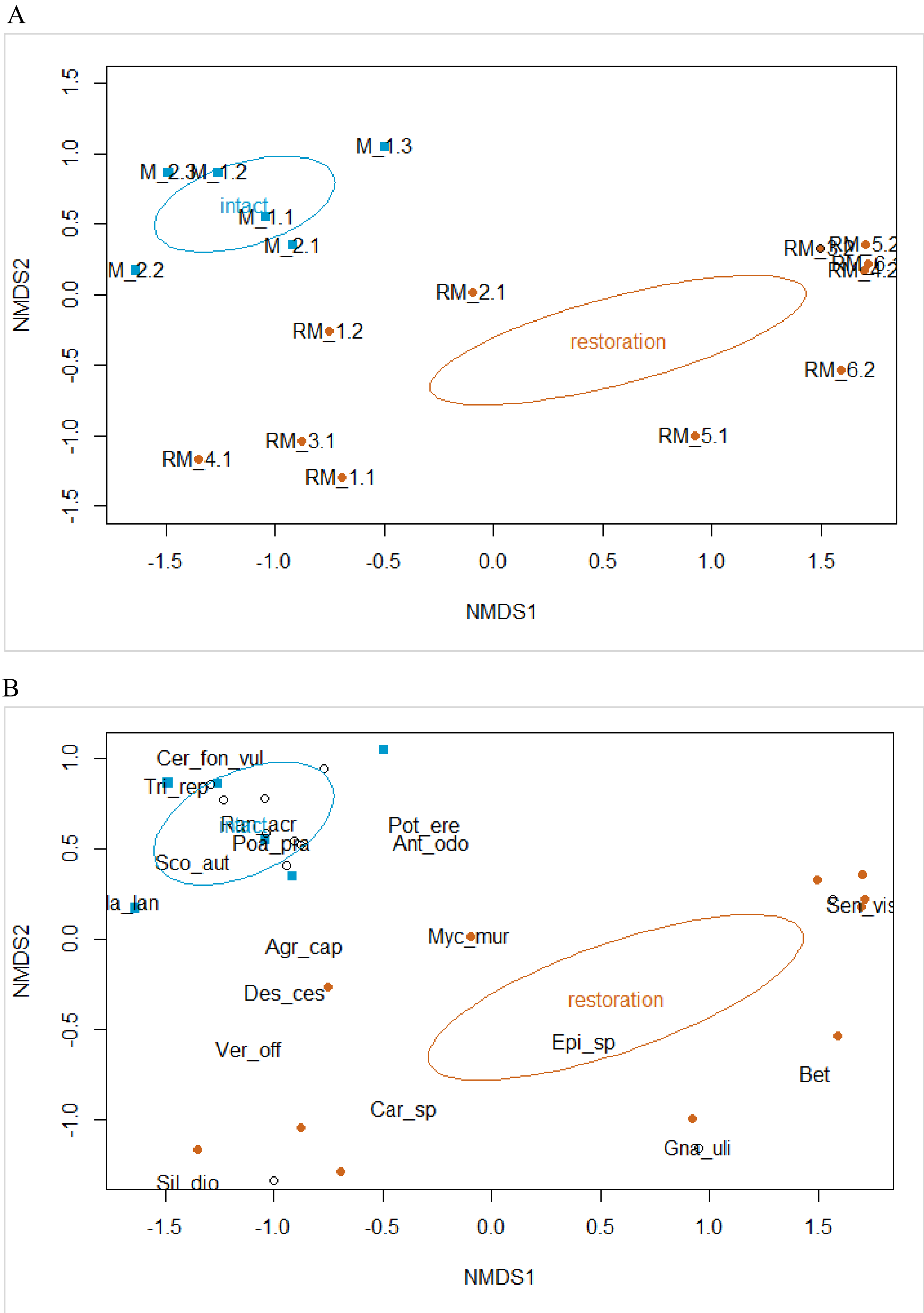

Figure 14: Ordination of the Non-Metric Multidimensional Scaling (NMDS) for the species compositions of the intact site (blue squares), and restoration site (orange points) for the calcareous meadow samples; stress value = 0.012. The ellipses show the standard error for each site type in the according color. Additionally, the samples are labeled with the sample ID in graph A, and abundant species are labeled in graph B (for full names, see Appendix Table A4).

Environmental variables

The environmental variables explained only 31.68% of the variation in the species composition. The results of the RDA showed that in the optimal model (AIC = -5.79) the elevation (in meters above sea level) of the sampling sites ($F(1) = 3.15$; $p = 0.01$), and the slope of the sampling sites ($F(1) = 2.99$; $p = 0.02$) had a significant effect on the variation. The linear model for elevation against the number of target seedlings showed a significant trend towards more target seedlings at lower elevations, i.e. in or closer to the intact site ($F(1,15) = 6.57$; $p = 0.022$; Fig. 15).

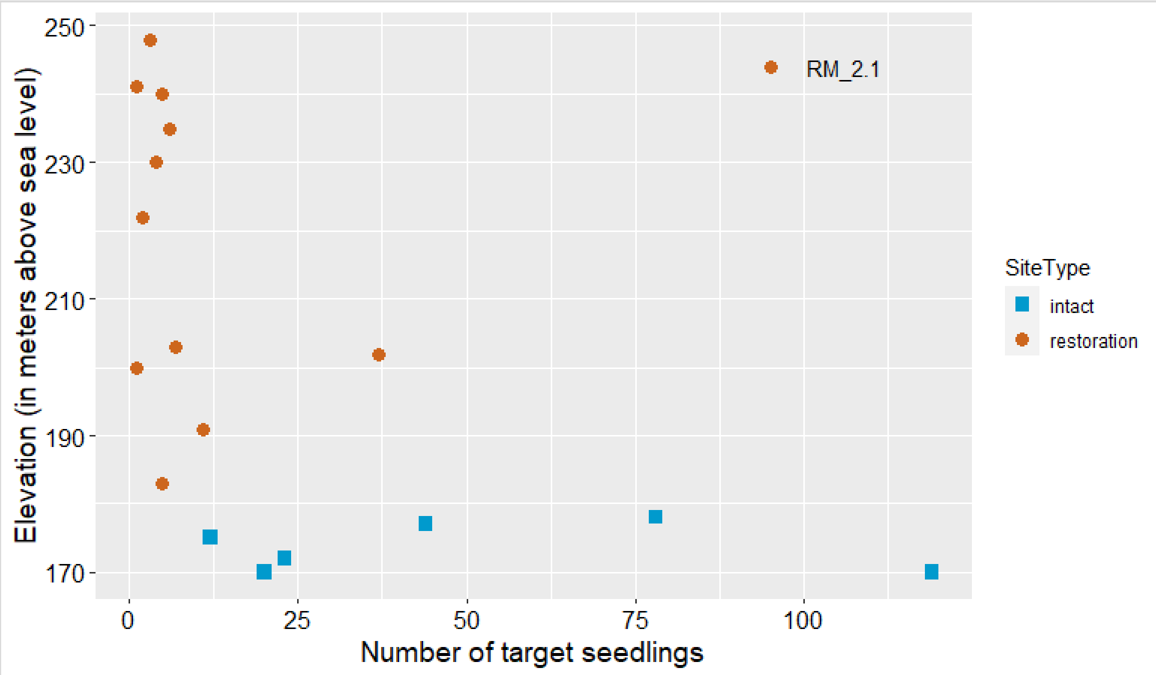

Figure 15: Number of target seedlings (x-axis) plotted against the elevation in meters above sea level (y-axis) of the site types intact (blue squares), and restoration (orange dots) for the calcareous meadow samples. One outlier is shown labeled with the sample ID.

Discussion

Seed Density and Species Composition

Coastal heathland

As predicted, the highest seed density was recorded for the samples from intact sites, with most seedlings from target species. The seeds of *Calluna* were most abundant in the samples from the intact sites, which is not surprising as *Calluna* is a dominant species and sometimes considered a keystone species for coastal heathland ecosystems (Bratli et al., 2022; Måren et al., 2010). The samples from the burnt sites especially showed a high density of viable seeds. This could be due to the response of *Calluna* seeds to smoke, as found by Måren et al. (2010), and it matches the high seed density of *Calluna* during the first two years after burning compared to the following years found by Måren and Vandvik (2009).

Galium saxatile, *Potentilla erecta*, and *Trichophorum cespitosum* were abundant in the SSB of intact sites and present, but in smaller numbers, in the restoration sites and plantations, which might be expected as they are a species commonly found in coastal heathlands (Bratli et al., 2022). However, *G. saxatile* was only present in the aboveground vegetation of the intact coastal heathland site on Silda (Nielsen, 2023). Even though seeds of *G. saxatile* are short-term persistent (Ludewig et al., 2021), it is uncertain why it was more abundant in the soil samples from this study than in the aboveground vegetation. One idea that might be worth researching in following studies is whether there is a similar effect on the germination of *G. saxatile* seeds as on the germination of *Calluna* seeds following exposure to smoke (Måren et al., 2010), as the highest abundance of *G. saxatile* seedlings was found in the sample CH_burnt_1. Interestingly, in a study by Måren and Vandvik (2009), *T. cespitosum* was absent from the SSB, which they attributed to *T. cespitosum* forming transient seed banks. The results of this study suggest otherwise, despite the application of comparable methods, such as sampling in spring, and the set-up of the germination trial. This difference could indicate that there are even more site-specific differences or seasonal variations depending on the weather conditions during previous years, and that we have yet to understand the variation of SSBs fully.

Nielsen (2023) recorded 24 more vascular plant species in the aboveground vegetation of intact sites, which were not found in the SSB. Most of the species found in the aboveground vegetation that are not found in the SSB are rather rare, i.e. only found at one or two sites in the aboveground vegetation, while most of the species found in the aboveground vegetation and the SSB are more common species. Therefore, I consider the aboveground vegetation and the SSB of the intact sites to be quite similar because all species except one (*Polygonum* sp.), which were found in the SBB, were present in the aboveground vegetation on Silda or Vågsøy. Notably, it is common to find fewer species in the SSB than in the aboveground vegetation because of species that have a transient seed bank, i.e. the seeds do only persist in the soil for a short time, and plants that disperse vegetatively (Ludewig et al., 2021; Måren & Vandvik, 2009; Mitlacher et al., 2002).

The samples from the restoration sites and plantations had as expected lower seed densities, with the lowest mean for the Sitka spruce plantations. The mean seed density of the Sitka spruce plantations recorded in this study (21 seeds/L or 1,050 seeds/m²) corresponds to results found in other studies. Mitlacher et al. (2002) recorded a mean seed density of 1,106 seeds/m² for abandoned and overgrown grassland, and Bisteau and Mahy (2005) recorded a mean seed density of 1,508 seeds/m² for a pine forest. Hill and Stevens (1981) found that the samples from the oldest Sitka spruce plantations (41-43 years old) had a lower seed density than younger plantations. The lower seed densities that are found in plantations shows that the number of viable seeds in the SSB decreases over time as probably the seeds stay dormant for too long or the change in the environmental conditions cause degradation of the seeds in the soil. Hence, this could explain the low seed density found in this study, as the plantations are about 50 years old.

Furthermore, the mossy soil recorded in the plantations might have played a role. The soil samples consisted of a large extent of dead organic moss matter that could decrease the seed density to the extent of one liter in comparison to the more decomposed, dense soil of the samples from intact and restoration sites. A high percentage of moss cover developed in the trays with samples from the plantations during the germination trial, which could have inhibited seed germination to a certain extent, e.g., due to shadow caused by the moss (Bele et al., 2019; Drake et al., 2018; Jeschke & Kiehl, 2008).

Restoration sites varied more in seed density and species composition. While some contained almost no target species, other sites had quite a lot. One outlier (R21_2.2) with a higher seed density due to many seedlings of *Rumex longifolius* stood out which could be due to the close location of the sampling site to houses and roads on Silda (Fig. 3 and Appendix Table A1). *Juncus effusus* very abundant in the restoration sites, categorized as an early successional by Måren and Vandvik (2009), which can be supported by the results of this study.

During the germination trial, seeds of *Calluna* and a few other plant species germinated from the plantation on Vågsøy while they were not present in the aboveground vegetation (Nielsen, 2023). The sampling process included handling the soil with a hand shovel, which created a mechanical disturbance of the soil (Appendix Fig. A1-A and B), and exposure of the soil samples to more light during the germination trial, which likely initiated seed germination (Gimingham, 1972). The germination of seeds from the plantation samples indicates that seeds of the coastal heathland ecosystem are still viable in the SSB of the plantations and shows that the SSB has the potential to re-vegetate the restoration area after deforestation of the plantations. This is supported by the findings of Saure et al. (2023) that *Calluna* seeds germinated immediately after clear-felling. These findings of viable *Calluna* seeds in the soil of about 50-year-old plantations confirm the longevity of the species that was found in other studies (Granstrom, 1988; Ludewig et al., 2021). Another indication that the *Calluna* seeds from the plantation are from the SSB rather than from spatial seed dispersal from close areas is the location of the plantation where the samples SP_1.1 and SP_1.2 were taken. There is no direct coastal heathland vegetation in the vicinity of the sampling site, but a meadow south of the area (see Appendix, Table A1), but still target species from coastal heathland ecosystems like *Calluna*, *Galium saxatile*, *Avenella flexuosa*, *Potentilla erecta*, and *Trichophorum cespitosum* germinated from these two samples, agreeing with Måren and Vandvik (2009) that the SSB act as refuges in the ecosystem.

Other species such as *Agrostis* spp. were more often present in the SSB than in the aboveground vegetation. The high abundance and presence of *Agrostis* spp. seedlings in the SSBs is likely because seeds of *Agrostis capillaris* are calculated to be short-term persistent by Ludewig et al. (2021), and seeds of *A. capillaris* and other *Agrostis* species are found in high abundance in other studies (Ludewig et al., 2021; Måren & Vandvik, 2009; Mitlacher et al., 2002).

While the species composition of the SSB and the aboveground vegetation appeared rather similar for the intact sites, more differences occurred when comparing the aboveground vegetation and the SSBs of the restoration sites and plantations. Nielsen (2023) found that the aboveground vegetation of the restoration site from 2018 on Silda was most similar to the control coastal heathland sites compared to the other restoration sites, which appeared not to be the case for the SSB. The results from the SSB of the restoration site from 2018 on Silda were more different from the samples from intact coastal heathland than, for example, the SSB of the site that was deforested in 2021 (see Fig. 9-A). This raises the question of whether the vegetation prior to the plantation of this site was possibly not coastal heathland but a different ecosystem type, such as a mire, while the current aboveground vegetation established from seeds from surrounding areas. For the plantation on Vågsøy, Nielsen (2023) found only one vascular plant species, *Lysimachia europaea*, while at least five species were recorded in the SSB of the plantation site close to the plots for the analysis of the aboveground vegetation and many of the seeds were target species. The results of this study indicate that the seeds of target species, and especially *Calluna*, were persistent and still viable in the soil. It supports the assumption of Nielsen (2023) that seeds of *Calluna* from the SSB contributed to revegetation of restoration sites.

Calcareous meadow

Similarly to the coastal heathland ecosystem, the results of the calcareous meadow ecosystem met the main expectations that the restoration site showed a lower seed density than the intact site. The mean seed density of the intact meadow recorded in this study (2,775 seeds/m²) is coherent with the results of Mitlacher et al. (2002) of 3,453 seeds/m² in the upper 5 cm of the soil. Bisteau and Mahy (2005) and Mitlacher et al. (2002) recorded higher seed densities for the restoration sites than the intact sites, which is an opposite trend to the results of this study. In comparison to Mitlacher et al. (2002), this could be explained by the time since restoration, as restoration was more recent in this study and, hence, was in a different stage during sampling. However, in the study by Bisteau and Mahy (2005), the time since restoration was also four years, as it was in Voss. Environmental factors, such as climate and soil composition, could also have caused differences in seed density, but it remains unclear why an opposite trend is recorded in this study.

Even though large numbers of seedlings germinated in some samples from the restoration site, the mean seed density of the restoration site was significantly lower than the mean seed density of the intact site. RM_2.1 had a very high seed density of *A. capillaris*, which was found to be abundant other studies (for example, Ludewig et al., 2021; Rosef, 2008). Interestingly, according to Bratli et al. (2022), *Hypericum maculatum* is a typical species for calcareous pastures but was only found here in the samples from the restoration site. Another sample from the restoration site with a high seed density was RM_4.2 due to a high number of *Senecio viscosus* seedlings. *S. viscosus* is an invasive species in Norway (Alm et al., 2023) and has been found frequently in the aboveground vegetation of the restoration site in Voss (Helle et al., unpublished).

While *A. capillaris* and *H. maculatum* are target species and, therefore, desired in the SSB, the high abundance of *S. viscosus* points out the vulnerability of restoration sites to new invasive species (see, for example, Matthews et al., 2009). Invasive species are important to consider during restoration, as they might impact the SSB in the long term (Gioria et al., 2012). *Rubus idaeus* and *Betula pubescens* which are considered "problem species" in semi-natural meadows (Bär et al., 2023, pp. 13-14), have been found in the restoration site of this project. Even though they are not invasive species, they should receive attention to ensure restoration success.

In comparison to the aboveground vegetation analysis by Helle et al. (unpublished), around 44 more species were found in the aboveground vegetation than in the SSB. Even though there were more plots for the aboveground vegetation than soil samples taken, this result is consistent with other studies that found lower species richness in the SSB (Bisteau & Mahy, 2005). Only few species were found in the SSB, but not in the aboveground vegetation, including *Cirsium palustre, Gnaphalium uliginosum, Mycelis muralis, Poa compressa,* and *Urtica dioica*. Overall, the results of this thesis agree with the findings of other studies, such as Matus et al. (2003), that the species found in the SSB were rather ordinary.

While Ludewig et al. (2021) found that the invasive Lupin species does not affect the seed density, and hence, the SSB can be used for restoration, this might not be the case for the study site in Voss. The type of plant, i.e. whether it is a herbaceous or a woody plant, appears to be relevant and causes a different effect on the SSB. Spruce might rather be considered a "transformer" species (Richardson et al., 2000, p. 98), changing the conditions, such as density of the canopy, of the ecosystem to a larger extent than Lupin. The results of this study rather support the results found by Bisteau and Mahy (2005), where grassland has been afforested. Even though a native species was planted in their study site, they found fewer species in the *Pinus*-stand than in the intact grassland.

<u>Spruce Seeds</u>

The number of Sitka spruce seedlings was much lower than expected, with only one seedling germinated from the CH-samples during the trial. As Nielsen (2023) recorded seedlings of Sitka spruce for all the restoration sites, and Vesterbukt (2019) found a high re-establishment of Sitka spruce after deforestation, a much higher number of Sitka spruce seedlings was expected. It is unclear why so few seedlings were found in the SSB, but this might indicate that sampling the soil for a germination trial in the lab is not the best method to examine the germination of Sitka spruce seeds.

There was no record of Norwegian spruce seedlings from the M-samples in the SSB and the analysis of the aboveground vegetation in Voss by Helle et al. (unpublished). This might indicate a low spruce establishment from seeds in Voss, but it certainly cannot be neglected during the restoration process.

Environmental Factors

Another critical factor for evaluating potential restoration success is the spatial arrangement of the restoration sites to the intact sites. Bisteau and Mahy (2005) and Dutoit and Alard (1995) point out that spatial connectivity of intact sites to restoration sites plays an important part in the restoration of grasslands due to seed dispersal from intact sites to restoration sites. The trend of a higher number of target seedlings closer to the intact meadow shown in the results of this study indicates that the viable seeds might have not persisted over time in the SSB, but were rather dispersed from the intact meadow to the restoration site. This could have happened either by wind or sheep, as the whole area in Voss was grazed. Thus, the surrounding vegetation might play a more significant role in the restoration success than the SSB for the area in Voss.

The influence of surrounding vegetation on the restoration sites on Vågsøy and Silda is challenging to discuss, as the intact and restoration sites were distributed rather complexly and the landscape was more a mosaic of coastal heathland ecosystems and other ecosystems. The influence of the elevation on the seed densities indicated by the RDA were probably due to the general higher location of the intact coastal heathland sites with high seed densities compared to the restoration sites and plantations. It can be assumed that the plantations were established at lower elevations closer to infrastructure for practical reasons.

Future Perspectives and Practical Applications

Coastal heathland

The results of this study indicate that the target species of coastal heathlands are viable in the soil of Sitka spruce plantations. This suggests that the SSB can provide potential for restoration of these areas. However, it is important to note that the seed densities in the plantations and restoration sites were significantly lower than in the intact sites, indicating that restoration efforts may need to consider more than just the passive use of the SSB. Given that coastal heathland ecosystems are traditionally reliant on burning and grazing, these measures should be integrated into future studies and restoration efforts. Previous studies have shown an increased germination of *Calluna* seeds following exposure to smoke (Måren et al., 2010), especially when the seeds have not been exposed to fire recently (Bargmann et al., 2014). As the seed density of the burnt coastal heathland sites is highest in this study, I suggest that the restoration sites on Vågsøy and Silda should be burnt like the intact coastal heathland traditionally. Both, grazing and burning, has to be moderate because a too high frequency can cause that grasses take over and too low frequency that more shrub and woodland species establish (Hobbs & Gimingham, 1987).

Despite the low number of Sitka spruce seedlings that established during in the germination trial of this study, their establishment through the SSB is likely and can also be seen in the aboveground vegetation analysis (Nielsen, 2023). Vesterbukt (2018) recommends grazing by sheep (more precisely "gammelnorsk sau") to reduce re-establishment of Sitka spruce. Additionally, possible re-establishment of Sitka spruce in restoration sites after burning should be given special attention to adapt measures.

Calcareous meadow

Overall, the results support previous studies on SSB for restoration of meadows, which show that the SSB of grassland species is not sufficient for restoration. Due to the increased seed density, especially of the target species, of samples from the restoration site that were close to the intact area, future measures should focus on the improvement of spatial dispersal of seeds. Therefore, grazing by sheep should be continued with free movement of the sheep between the intact site and the restoration site because sheep disperse seeds over space and increase species richness (Benthien et al., 2016; Kuiters & Huiskes, 2010).

To inhibit the establishment of invasive species in the restoration site, additional treatment and input of target seeds might be necessary. Bucharova and Krahulec (2020) found the combination of herbicide-treatment and the addition of seeds from native plants to be a successful tool to prevent the invasive *Rumex alpinus* from reinvasion through its seed bank. The results of this study indicate that *Senecio viscosus* establishes from its seed bank in high densities in some patches of the restoration site and could become a problem during the restoration process, which is why a similar additional treatment might be necessary. An overall input of additional seeds by transferring hay from the intact site is often connected with a high effort and some studies doubt its efficiency (Maccherini & Santi, 2012) while others claim that it is a helpful tool to increase target species (Hofmann et al., 2020). Therefore, transferring hay can be useful for the area of the restoration site that is further away from the intact site.

Suggestions for Improvement, Limitations, and Source of Errors

The large amount of work and space required during sampling and the germination trial was limiting the extent of the thesis. Initially, it was planned to extract and sort the seeds from the soil prior to the germination trial to be able to compare the density of viable seeds to those that were not germinating. It is particularly interesting to find out whether fewer seeds are viable in the SSB of plantations, or whether the density of the seeds is overall lower and the condition of the soil may play a bigger role. This could be done in a larger frame with more time capacity. As mentioned previously, it might be worth sampling restoration areas before and after burning the sites to compare the germination of seeds exposed to smoke to those that were not. It can be expected that more target species, especially *Calluna*, will germinate from the burnt restoration sites, which could support the restoration process.

The limited space caused some samples to be stored in the freezer and exposed to additional cold-stratification. If more space is available, the sample number could be increased in order to equalize the number of samples from the different site types. Furthermore, some improvements in the methodology can be made. Given the high number of seedlings germinated during the trial, the constant light supply appeared not to have affected the trial, possibly due to the high amount of natural light during summer in Norway. However, to improve the methodology, more natural conditions could be created by interrupting the light supply for a couple of hours. The sampling methodology used for this thesis limits the ability to differentiate whether the seeds originated from the soil and hence were time dispersed from the previous vegetation of the site or dispersed over space from surrounding vegetation, which might be especially relevant for the meadow as dispersal over space appears to be more relevant for the restoration site in Voss.

Conclusion

The results of this thesis were able to answer the questions posed. The analysis showed a clear trend of higher seed density in the SSBs from intact sites and a difference in species composition with more target species found in intact sites for both ecosystems. However, this thesis highlights differences between the potential of SSB for restoration of coastal heathlands and calcareous meadows. The viable seeds of target species found in plantations of Sitka spruce on former coastal heathland gives reason to assume that the SSBs of the coastal heathland ecosystem have the potential to contribute to the restoration process. Future measures should include moderate grazing by sheep between intact and restoration sites and burning of the restoration sites to increase germination of *Calluna* seeds.

The SSB of the restoration site of the calcareous meadow ecosystem appears to be not sufficient for restoration as the species in the SSB are rather ordinary and only present in low densities. Here, the spatial dispersal of seeds from the intact site to the restoration site should be improved by free movement of sheep between the two sites. Additional input of seeds can be useful for more distant part of the restoration site and to inhibit problem species to establish in the restoration site.

Together with the aboveground vegetation analyses by Nielsen (2023) and Helle et al. (unpublished), the results give a in depth understanding of the restoration process of these two areas. The knowledge gained can be used to adapt measures for both restoration projects and provide guidance for comparable projects.

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Appendix

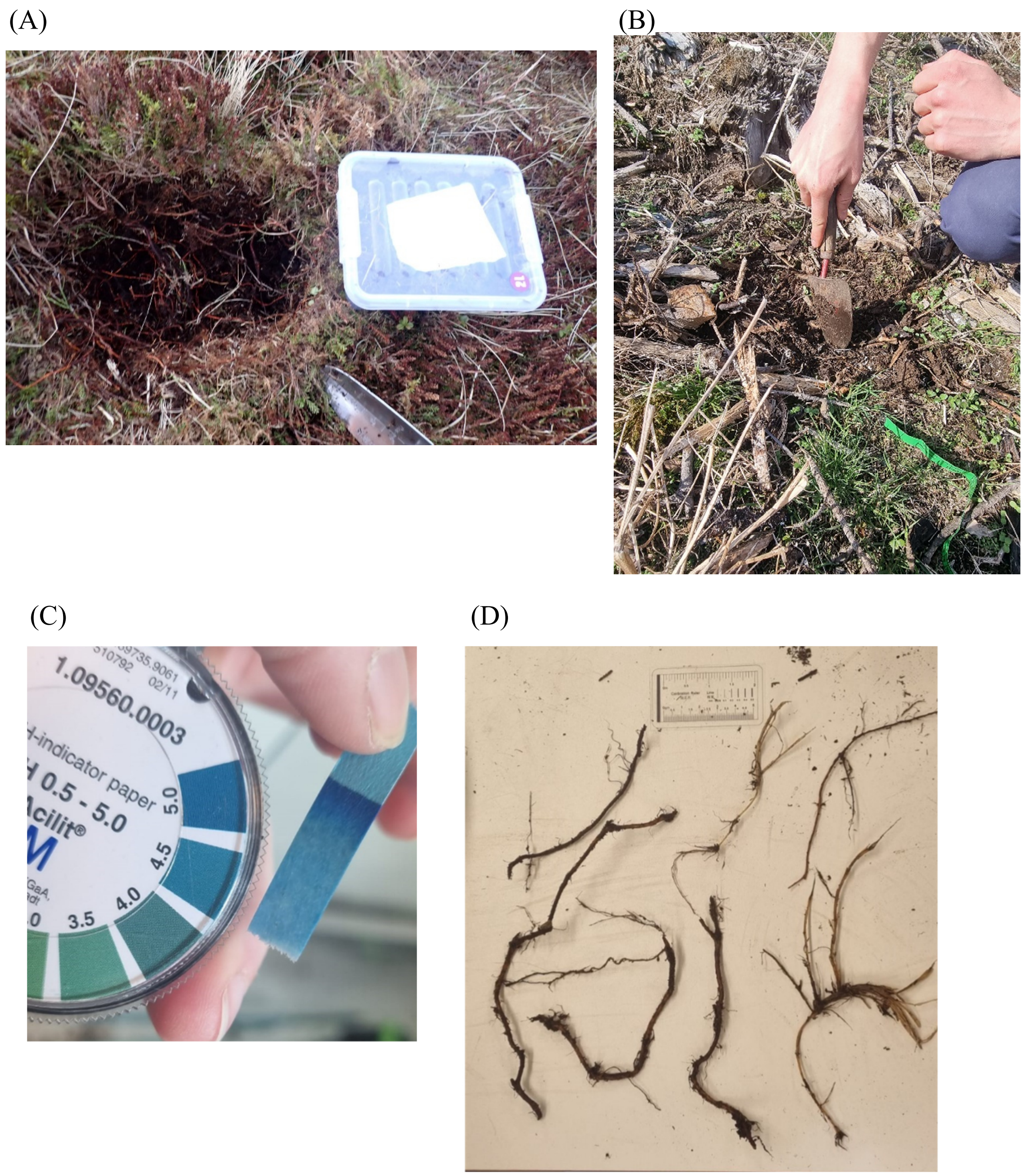

Figure A1: (A) Removed vegetation for soil sampling from coastal heathland ecosystem on Vågsøy; (B) taking soil samples in Voss; (C) measuring pH-value with pH-indicator paper; (D) example of the roots that were removed from the soil sample in the lab.

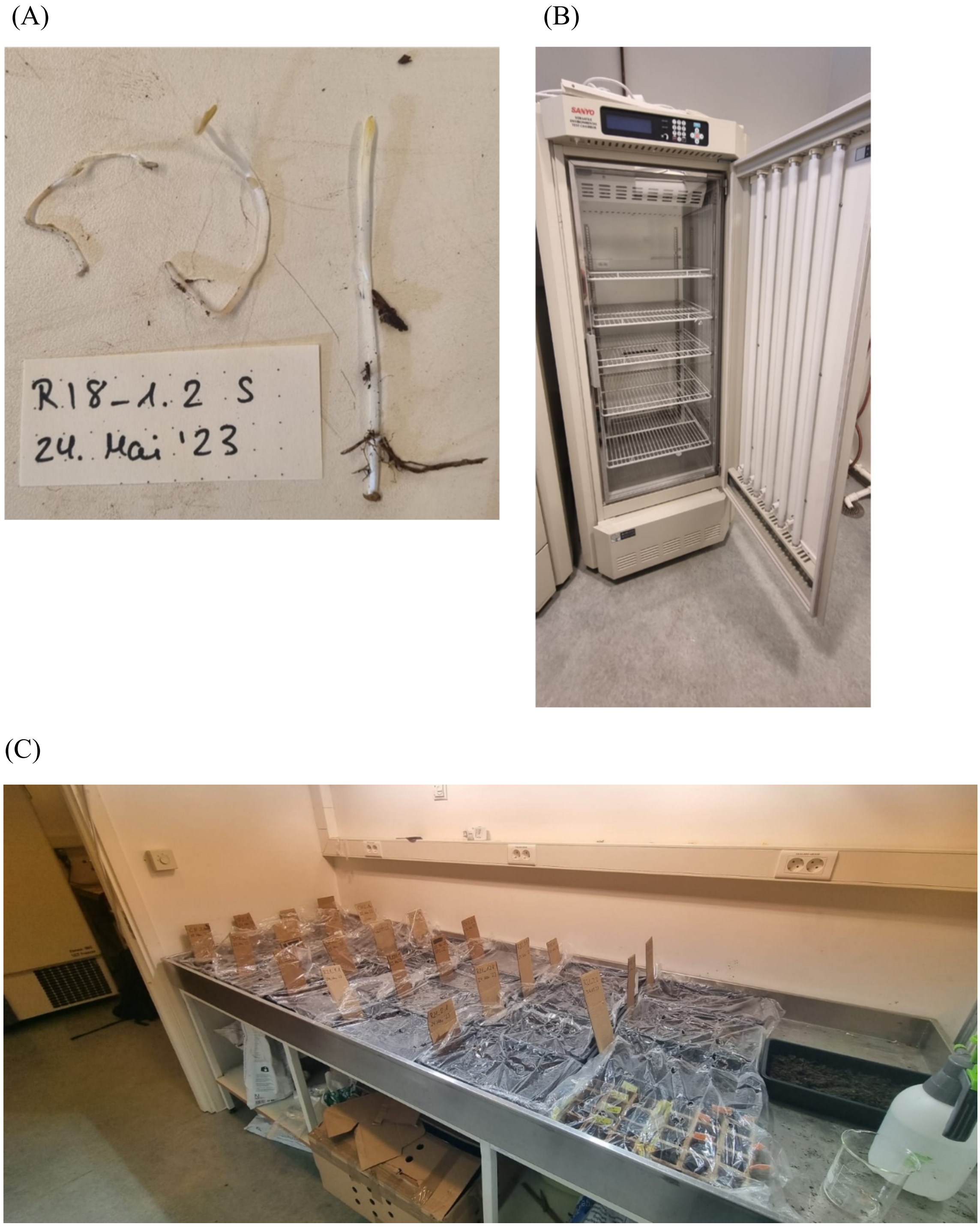

Figure A2: (A) Example of the seedlings that already sprouted before the start of the germination trial (these were kept in separate planting pots); (B) environmental test chamber for the M-samples with two trays per compartment; (C) setup of the germination trial on the bench (CH-samples).

Table A1: Overview of the sampling sites, environmental variables, and notes from the field and lab for all samples from the coastal heathland ecosystem.

Sample ID	Site Description	Site Type	Notes on site
CH_1.1	intact coastal heathland	intact	
CH_1.2	intact coastal heathland	intact	
CH_2.1	intact coastal heathland	intact	
CH_2.2	intact coastal heathland	intact	
CH_3.1	intact coastal heathland	intact	
CH_3.2	intact coastal heathland	intact	
CH_burnt_1	intact and burnt coastal heathland	intact	burnt one week before sampling
CH_burnt_2	intact and burnt coastal heathland	intact	burnt one week before sampling
R18_1.1	restoration site	restoration	deforestation in 2018
R18_1.2	restoration site	restoration	deforestation in 2018
R19_1.1	restoration site	restoration	deforestation in 2019
R19_1.2	restoration site	restoration	deforestation in 2019
R21_1.1	restoration site	restoration	deforestation in 2021
R21_1.2	restoration site	restoration	deforestation in 2021
R21_2.1	restoration site	restoration	deforestation in 2021
R21_2.2	restoration site	restoration	deforestation in 2021
R22_1.1	restoration site	restoration	deforestation in 2022
R22_1.2	restoration site	restoration	deforestation in 2022
SP_1.1	Sitka spruce plantation	plantation	Sitka spruce was planted during 1970s and early 1980s
SP_1.2	Sitka spruce plantation	plantation	Sitka spruce was planted during 1970s and early 1980s
SP_2.1	Sitka spruce plantation	plantation	Sitka spruce was planted during 1970s and early 1980s
SP_2.2	Sitka spruce plantation	plantation	Sitka spruce was planted during 1970s and early 1980s

Table A1 continuing.

Sample ID	Location	Notes on location	Longitude	Latitude
CH_1.1	Vågsøy	distance to closest road around 220 m, located in a wide coastal heathland area	5,0280100°E	62,0026510°N
CH_1.2	Vågsøy	distance to closest road around 220 m, located in a wide coastal heathland area	5,0282490°E	62,0025990°N
CH_2.1	Vågsøy	distance to closest road around 90 m, located in a wide coastal heathland area	5,0358900°E	61,9997520°N
CH_2.2	Vågsøy	distance to closest road around 90 m, located in a wide coastal heathland area	5,0356140°E	61,9998430°N
CH_3.1	Silda	hiking path 3 m far from sampling spot	5,1902750°E	62,0145120°N
CH_3.2	Silda	hiking path 5m far from sampling spot	5,1901460°E	62,0145350°N
CH_burnt_1	Vågsøy	distance to closest road around 53 m, located in a wide coastal heathland area	5,0185540°E	62,0007890°N
CH_burnt_2	Vågsøy	distance to closest road around 90 m, located in a wide coastal heathland area	5,0175610°E	62,0007090°N
R18_1.1	Silda	close to sea (20 m distance); nearest hiking path 50m	5,1970650°E	62,0078900°N
R18_1.2	Silda	close to sea (32 m distance); nearest hiking path 40m	5,1969821°E	62,0079946°N
R19_1.1	Silda	3 m far from road and 30m far from (farm)house	5,2029850°E	62,0167570°N
R19_1.2	Silda	16 m far from road (1 m from path) and 40m far from (farm)house	5,2032470°E	62,0167220°N
R21_1.1	Vågsøy	about 67 m distance to farmland	5,0395700°E	61,9926340°N
R21_1.2	Vågsøy	about 82 m distance to farmland	5,0391570°E	61,9929347°N
R21_2.1	Silda	close to houses (62 m)	5,1970280°E	62,0127740°N
R21_2.2	Silda	close to houses (68 m)	5,1969450°E	62,0127910°N
R22_1.1	Silda	close to sea (80 m distance); nearest hiking path 50m	5,1848800°E	62,0127630°N
R22_1.2	Silda	close to sea (80 m distance); nearest hiking path 34m	5,1851823°E	62,0130649°N
SP_1.1	Vågsøy	about 9 m deep in the plantation, bordering a meadow to the south	5,0449010°E	61,9913020°N
SP_1.2	Vågsøy	about 5 m deep in the plantation, bordering a meadow to the south	5,0451020°E	61,9912540°N
SP_2.1	Vågsøy	about 33 m deep in the plantation	5,0250700°E	62,0227070°N
SP_2.2	Vågsøy	about 22 m deep in the plantation	5,0249820°E	62,0226020°N

Table A1 continuing.

Sample ID	**pH**	**Slope (in degree)**	**Slope Orientation**	**Elevation (in meters asl.)**	**Start of germination trial**	**Weight (g) of the sample (=1 L of soil)**	**Comments from the lab**
CH_1.1	5	7	South-east	407	22. May 2023	450	Germination of seedlings, some grasses (22.05.2023)
CH_1.2	4.5	7	South-east	408	22. May 2023	NA	
CH_2.1	5	17	West	414	23. May 2023	NA	
CH_2.2	4.5	18	West	415	23. May 2023	524	
CH_3.1	4.5	22	Nord-west	46	23. May 2023	264	
CH_3.2	5	23	Nord-west	44	23. May 2023	334	a lot of seedlings
CH_burnt_1	5	13	South-west	333	23. May 2023	485	
CH_burnt_2	5	9	South-west	334	23. May 2023	NA	
R18_1.1	5	7	North-west	2	23. May 2023	NA	
R18_1.2	5	3	North-west	2	24. May 2023	333	
R19_1.1	5	4	North	10	24. May 2023	385	
R19_1.2	4.5	4	North	10	23. May 2023	500	
R21_1.1	4.5	26	South	227	24. May 2023	697	
R21_1.2	5	23	South	239	24. May 2023	244	
R21_2.1	4.5	19	South-east	26	24. May 2023	659	2 cones; many germinated seeds
R21_2.2	4.5	14	South-east	27	24. May 2023	427	
R22_1.1	5	8	West	12	24. May 2023	540	
R22_1.2	5	21	West	18	24. May 2023	415	
SP_1.1	5	18	South	185	23. May 2023	143	
SP_1.2	5	18	South	184	23. May 2023	656	
SP_2.1	4.5	19	North-east	182	23. May 2023	216	
SP_2.2	5	25	North-east	185	23. May 2023	284	

Table A1 continuing.

Sample ID	Notes on the Surrounding Vegetation
CH_1.1	*Empetrum nigurm, Juncus squarrosus, Calluna vulgaris, Vaccinium vitis-idaea, Trichophorum cespitosum* ssp. *cespitosum, Nardus stricta, Vaccinium myrtillus*
CH_1.2	*E. nigurm, J. squarrosus, C. vulgaris, V. vitis-idaea, T. cespitosum ssp. cespitosum, N. stricta, V. myrtillus;* Sprouts*: V. myrtillus*
CH_2.1	*E. nigrum, C. vulgaris, Carex vaginata* cf, *V. vitis-idaea, Arctostaphylos alpina, V. myrtillus*
CH_2.2	*E. nigrum, C. vulgaris, C. vaginata* cf, *V. vitis-idaea, A. alpina, V. myrtillus, Luyula sylvatica, Juniperus communis, T. cespitosum ssp. cespitosum, Loiseleuria procumbens, J. squarrosus*
CH_3.1	*C. vulgaris, J. communis, V. vitis-idaea, Molinia caerulea, Avenella flexuosa, E. nigrum, L. sylvatica, Sorbus aucuparia, Pinus sylvestris, C. vaginata, Sorbus hybrida, Populus tremula, V. myrtillus, Aira praecox*
CH_3.2	*C. vulgaris, J. communis, V. vitis-idaea, M. caerulea, A. flexuosa, E. nigrum, L. sylvatica, S. aucuparia, P. sylvestris, C. vaginata, S. hybrida, P. tremula, V. myrtillus, A. praecox*
CH_burnt_1	*C. vulgaris, E. nigrum, C. vaginata, V. vitis-idaea, J. communis, L. sylvatica, Erica cinerea, J. squarrosus, T. cespitosum ssp. cespitosum*
CH_burnt_2	*C. vulgaris, E. nigrum, C. vaginata, V. vitis-idaea, J. communis, L. sylvatica, E. cinerea, J. squarrosus, T. cespitosum ssp. cespitosum*
R18_1.1	*M. caerulea, C. vulgaris, Lonicera periclymenum, A. flexuosa, V. myrtillus, S. aucuparia, Picea sitchensis*
R18_1.2	*A. flexuosa, M. caerulea, Succisa pratensis, S. aucuparia, P. sitchensis, Betula sp., Deschampsia cespitosa, Veronica officinalis, C. vulgaris, Angelica archangelica, Rumex acetosa, Cirsium plaustre*
R19_1.1	*A. archangelica, M. caerulea, Ribes uva-crispa, D. cespitosa, A. flexuosa, Chamerion angustifolium, Salix sp., R. acetosa, Peucedanum palustre/Anthriscus sylvestris* cf, *Hypochaeris radicata, C. vulgaris, E. nigrum, V. myrtillus, V. officinalis, L. sylvatica, Betula sp., Eriophorum vaginatum*
R19_1.2	*A. archangelica, M. caerulea, R. uva-crispa, D. cespitosa, A. flexuosa, C. angustifolium, Salix sp., R. acetosa, P. palustre/A. sylvestris* cf, *H. radicata, C. vulgaris, E. nigrum, V. myrtillus, V. officinalis, L. sylvatica, Betula* sp., *E. vaginatum*
R21_1.1	*P. sitchensis, Primula veris, A. flexuosa, V. vitis-idaea, C. vaginata, Anemone nemorosa, M. caerulea, Viola canina, D. cespitosa, J. communis, C. vulgaris, E. cinerea, V. myrtillus, Narthecium ossifragum;* Sprouts*: Veronica canina*
R21_1.2	*P. sitchensis, P. veris, A. flexuosa, V. vitis-idaea, C. vaginata, A. nemorosa, M. caerulea, V. canina, D. cespitosa, J. communis, C. vulgaris, E. cinerea, V. myrtillus, Narthecium ossifragum;* Sprouts*: V. canina*
R21_2.1	*H. radicata, R. repens, C. pallescens/vaginata* cf, *R. idaeus, Deschampsia cespitosa, Ribes uva-crispa, Chamerion angustifolium, Rumex longifolius, Luyula congesta, Sambucus racemosa, M. cearulea, Succisa pratensis, Sambucus aucuparia, Ilex aquifolium, Geranium robertianum, R. acetosa;* Sprouts*: P. sitchensis* (8)
R21_2.2	*H. radicata, Ranunculus repens, C. pallescens/vaginata* cf, *R. idaeus, D. cespitosa, R: uva-crispa, C. angustifolium, R. longifolius, Luzula congesta, S. racemosa, M. cearulea, S. pratensis, S. aucuparia, I. aquifolium, G. robertianum, R. acetosa*
R22_1.1	*P. sitchensis, V. officinalis, M. caerulea, S. aucuparia, Pinus mugo, C: vulgaris, J. communis, Cardamine pratensis ssp. paludosa, Geranium robertianum;* Sprouts*: P. sitchensis, C. pratensis ssp. paludosa, V. officinalis, G. robertianum, S. aucuparia, V. vitis-idaea*
R22_1.2	*S. aucuparia, S. racemosa, Epilobium ciliatum, R. uva-crispa, L. periclymenum, R. acetosa, P. sitchensis, V. officinalis, M. caerulea, P. mugo, C. vulgaris, J. communis, C. pratensis ssp. paludosa, G. robertianum;* Sprouts*: P. sitchensis* (2)
SP_1.1	*P. sitchensis, V. myrtillus, Oxalis acetosella, V. vitis-idaea*; mossy-soil
SP_1.2	*P. sitchensis, V. myrtillus, O. acetosella, V. vitis-idaea*; mossy-soil
SP_2.1	*P. sitchensis, O. acetosella*; mossy soil and stone
SP_2.2	*P. sitchensis, O. acetosella, V. vitis-idaea*; mossy soil and stone

Table A2: Overview of the sampling sites, environmental variables, and notes from the lab for all samples from the calcareous meadow ecosystem.

Sample ID	Site Description	Site Type	Notes on sample	Location
M_1.1	calcareous meadow	intact		Voss
M_1.2	calcareous meadow	intact		Voss
M_1.3	calcareous meadow	intact		Voss
M_2.1	calcareous meadow	intact		Voss
M_2.2	calcareous meadow	intact		Voss
M_2.3	calcareous meadow	intact		Voss
RM_1.1	restoration site	restoration	deforestation in 2019	Voss
RM_1.2	restoration site	restoration	deforestation in 2019	Voss
RM_2.1	restoration site	restoration	deforestation in 2019	Voss
RM_2.2	restoration site	restoration	deforestation in 2019	Voss
RM_3.1	restoration site	restoration	deforestation in 2019	Voss
RM_3.2	restoration site	restoration	deforestation in 2019	Voss
RM_4.1	restoration site	restoration	deforestation in 2020	Voss
RM_4.2	restoration site	restoration	deforestation in 2020	Voss
RM_5.1	restoration site	restoration	deforestation in 2020	Voss
RM_5.2	restoration site	restoration	deforestation in 2020	Voss
RM_6.1	restoration site	restoration	deforestation in 2020	Voss
RM_6.2	restoration site	restoration	deforestation in 2020	Voss

Table A2 continuing.

Sample ID	Longitude	Latitude	pH	Slope (in degree)	Slope Orientation	Elevation (in meters asl.)
M_1.1	6,4572010°E	60,6400200°N	5	16	South-east	178
M_1.2	6,4572330°E	60,6399220°N	5	17	South-east	175
M_1.3	6,4575320°E	60,6398700°N	4.5	19	South-east	170
M_2.1	6,4575620°E	60,6401450°N	5	18	South-east	177
M_2.2	6,4576160°E	60,6399660°N	4.5	19	South-east	172
M_2.3	6,4579270°E	60,6399110°N	4.5	20	South-east	170
RM_1.1	6,4559550°E	60,6417140°N	4.5	7	South	248
RM_1.2	6,4561710°E	60,6413950°N	4.5	13	South	241
RM_2.1	6,4566830°E	60,6417030°N	4.5	14	South	244
RM_2.2	6,4571250°E	60,6414230°N	4.5	20	South	230
RM_3.1	6,4548230°E	60,6413400°N	4.5	15	South	240
RM_3.2	6,4545530°E	60,6411140°N	4.5	12	South	235
RM_4.1	6,4554300°E	60,6405400°N	4.5	26	South-east	222
RM_4.2	6,4553490°E	60,6401510°N	5	23	South-east	203
RM_5.1	6,4565900°E	60,6406050°N	5	17	South-east	202
RM_5.2	6,4569460°E	60,6403540°N	4.5	27	South-east	191
RM_6.1	6,4578400°E	60,6407570°N	4.5	25	South-east	200
RM_6.2	6,4581730°E	60,6404820°N	5	22	South-east	183

Table A2 continuing.

Sample ID	Comments from the lab	Start of germination trial	Weight (g) of the sample (=1 L of soil)
M_1.1		25. May 2023	779
M_1.2	compact, roots	15. September 2023	680
M_1.3		25. May 2023	650
M_2.1		25. May 2023	800
M_2.2	lots of roots, compact	15. September 2023	873
M_2.3	lots of roots, compact	15. September 2023	687
RM_1.1		25. May 2023	441
RM_1.2	small roots, loose soil	15. September 2023	458
RM_2.1		25. May 2023	651
RM_2.2	no big roots	15. September 2023	694
RM_3.1		25. May 2023	444
RM_3.2	a lot of needles	15. September 2023	452
RM_4.1		25. May 2023	NA
RM_4.2	a lot of woody debris	15. September 2023	580
RM_5.1		25. May 2023	563
RM_5.2	few small roots	15. September 2023	609
RM_6.1		25. May 2023	433
RM_6.2	small roots, woody debris	15. September 2023	633

Table A3: Table of all vascular plant species that germinated from the soil seed bank of the coastal heathland ecosystem during the trial, including their abbreviation, and the number of seedlings that germinated in each sample.

Abbreviation	**Species name**	**CH_1.1**	**CH_1.2**	**CH_2.1**	**CH_2.2**	**CH_3.1**	**CH_3.2**	**CH_burnt_1**	**CH_burnt_2**
Agr_sp	*Agrostis* sp.	0	0	0	0	0	0	0	0
Ang_syl	*Angelica sylvestris*	0	0	0	0	0	0	0	0
Ant_odo	*Anthoxanthum odoratum*	0	0	0	0	1	0	2	0
Arr_ela	*Arrhenatherum elatius*	0	0	0	0	0	0	0	0
Ave_fle	*Avenella flexuosa*	0	0	0	3	0	1	0	0
Bet	*Betula*	0	0	0	0	0	0	0	0
Cal_vul	*Calluna vulgaris*	72	14	145	103	59	194	277	388
Car_sp	*Carex* sp.	2	0	0	10	0	74	0	0
Cer_fon	*Cerastium fontanum*	0	0	0	0	0	0	0	0
Cha_ang	*Chamerion angustifolium*	0	0	0	0	0	0	0	0
Cir_pal	*Cirsium palustre*	0	0	0	0	0	0	0	0
Des_ces	*Deschampsia cespitosa*	0	0	0	1	0	0	0	0
Dig_pur	*Digitalis purpurea*	0	0	0	0	0	0	0	0
Emp_nig	*Empetrum nigrum*	1	22	2	0	0	1	0	5
Epi_cil	*Epilobium ciliatum*	0	0	0	0	0	0	0	0
Epi_mon	*Epilobium montanum*	0	0	0	0	0	0	0	0
Fes_rub	*Festuca rubra*	0	0	0	0	0	0	0	0
Fra_exc	*Fraxinus excelsior*	0	0	0	0	0	0	0	0
Gal_sax	*Galium saxatile*	0	0	0	0	0	24	118	2
Hol_lan	*Holcus lanatus*	0	0	0	0	0	0	0	0
Hyp_rad	*Hypochaeris radicata*	0	0	0	0	0	0	0	0
Jun_eff	*Juncus effusus*	0	0	0	0	0	0	0	0
Luz_syl	*Luzula sylvatica*	0	0	0	0	0	0	0	0
Lys_eur	*Lysimachia europaea*	1	0	0	2	2	0	5	0
Mol_cae	*Molinia caerulea*	0	0	0	0	0	0	0	0
Oxa_ace	*Oxalis acetosella*	0	0	0	0	0	0	0	0
Pic_sit	*Picea sitchensis*	0	0	0	0	0	0	0	0
Pla_lan	*Plantago lanceolata*	0	0	0	0	0	0	0	0
Poa_pra	*Poa pratensis*	0	0	0	0	0	0	0	0
Pol_sp	*Polygonum* sp.	0	0	1	0	0	0	0	0
Pot_ere	*Potentilla erecta*	6	1	0	6	34	34	0	1
Ran_acr	*Ranunculus acris*	0	0	0	0	0	0	0	0
Rum_ace	*Rumex acetosa*	0	0	0	0	0	0	0	0
Rum_lon	*Rumex longifolius*	0	0	0	0	0	0	0	0
Sag_pro	*Sagina procumbens*	0	0	0	0	0	0	0	0
Sen_jac	*Senecio jacobea*	0	0	0	0	0	0	0	0
Sen_vul	*Senecio vulgaris*	0	0	0	0	0	0	0	0
Sil_dio	*Silene dioica*	0	0	0	0	0	0	0	0
Son_asp	*Sonchus asper*	0	0	0	0	0	0	0	0
Ste_med	*Stellaria media*	0	0	0	0	0	0	0	0
Tri_ces	*Trichophorum cespitosum*	13	42	4	8	0	0	87	7
Urt_dio	*Urtica dioica*	0	0	0	0	0	0	0	0
Vac_myr	*Vaccinium myrtillus*	1	0	0	3	1	1	0	0
Vac_vit	*Vaccinium vitis-idaea*	0	0	0	0	0	0	1	0
Ver_off	*Veronica officinalis*	0	0	0	0	0	0	0	0
Vio_pal	*Viola palustris*	0	0	0	0	0	0	0	0
	indeterminate	11	27	37	25	30	54	13	42

Table A3 continuing.

Abbreviation	Species name	R18_1.1	R18_1.2	R19_1.1	R19_1.2	R21_1.1	R21_1.2	R21_2.1	R21_2.2	R22_1.1	R22_1.2
Agr_sp	*Agrostis* sp.	0	0	14	0	0	0	9	32	0	0
Ang_syl	*Angelica sylvestris*	0	0	5	0	0	0	0	0	0	0
Ant_odo	*Anthoxanthum odoratum*	35	0	1	0	0	0	0	0	0	0
Arr_ela	*Arrhenatherum elatius*	0	1	0	0	0	0	0	0	0	0
Ave_fle	*Avenella flexuosa*	0	3	5	1	0	0	1	0	0	0
Bet	*Betula*	0	1	1	0	0	0	0	0	0	0
Cal_vul	*Calluna vulgaris*	1	0	2	22	76	6	3	0	9	22
Car_sp	*Carex* sp.	43	0	5	3	1	0	1	0	0	0
Cer_fon	*Cerastium fontanum*	0	1	0	0	0	0	0	0	0	0
Cha_ang	*Chamerion angustifolium*	0	0	0	2	0	0	0	0	0	0
Cir_pal	*Cirsium palustre*	0	0	0	0	0	0	0	0	0	0
Des_ces	*Deschampsia cespitosa*	0	0	9	0	0	0	8	10	0	0
Dig_pur	*Digitalis purpurea*	0	0	0	1	0	0	0	0	0	0
Emp_nig	*Empetrum nigrum*	0	0	0	1	0	0	1	0	2	2
Epi_cil	*Epilobium ciliatum*	8	9	44	2	0	0	8	15	0	0
Epi_mon	*Epilobium montanum*	1	1	1	1	0	0	1	2	1	0
Fes_rub	*Festuca rubra*	0	0	0	0	0	0	3	0	0	0
Fra_exc	*Fraxinus excelsior*	0	0	0	0	0	0	0	0	0	1
Gal_sax	*Galium saxatile*	0	0	0	1	4	0	0	0	0	2
Hol_lan	*Holcus lanatus*	0	0	1	0	0	0	0	0	0	0
Hyp_rad	*Hypochaeris radicata*	0	0	0	0	0	0	0	1	0	0
Jun_eff	*Juncus effusus*	0	68	0	0	0	0	0	0	0	0
Luz_syl	*Luzula sylvatica*	0	0	0	0	0	0	0	0	0	0
Lys_eur	*Lysimachia europaea*	2	4	0	0	1	0	0	0	0	0
Mol_cae	*Molinia caerulea*	6	0	0	0	0	0	0	0	0	0
Oxa_ace	*Oxalis acetosella*	0	0	0	0	0	0	0	0	0	0
Pic_sit	*Picea sitchensis*	0	0	0	0	0	0	0	0	0	1
Pla_lan	*Plantago lanceolata*	0	0	0	0	0	0	0	0	0	0
Poa_pra	*Poa pratensis*	0	0	4	0	0	0	0	0	0	0
Pol_sp	*Polygonum* sp.	0	0	0	6	0	0	0	0	0	3
Pot_ere	*Potentilla erecta*	1	0	0	0	8	0	0	0	0	0
Ran_acr	*Ranunculus acris*	0	0	5	0	0	0	0	0	0	0
Rum_ace	*Rumex acetosa*	0	0	0	0	0	0	0	1	0	0
Rum_lon	*Rumex longifolius*	4	0	0	0	0	0	2	158	1	0
Sag_pro	*Sagina procumbens*	0	0	4	0	0	0	0	0	0	0
Sen_jac	*Senecio jacobea*	0	0	0	0	0	0	0	0	0	1
Sen_vul	*Senecio vulgaris*	0	0	0	0	0	0	0	2	0	0
Sil_dio	*Silene dioica*	2	0	0	0	0	0	0	21	0	0
Son_asp	*Sonchus asper*	0	0	0	0	0	0	0	3	0	0
Ste_med	*Stellaria media*	0	0	0	0	0	0	0	7	0	0
Tri_ces	*Trichophorum cespitosum*	0	0	0	0	0	0	3	0	0	0
Urt_dio	*Urtica dioica*	0	0	0	0	0	0	1	0	0	0
Vac_myr	*Vaccinium myrtillus*	0	0	0	6	0	0	0	3	4	10
Vac_vit	*Vaccinium vitis-idaea*	0	0	0	0	0	0	0	0	0	1
Ver_off	*Veronica officinalis*	0	0	0	0	0	7	0	0	0	0
Vio_pal	*Viola palustris*	0	0	0	0	0	0	0	0	0	0
	indeterminate	1	0	4	0	0	0	0	1	0	3

Table A3 continuing.

Abbreviation	**Species name**	**SP_1.1**	**SP_1.2**	**SP_2.1**	**SP_2.2**	**Total**
Agr_sp	*Agrostis* sp.	0	1	0	0	**56**
Ang_syl	*Angelica sylvestris*	0	0	0	0	**5**
Ant_odo	*Anthoxanthum odoratum*	0	0	0	0	**39**
Arr_ela	*Arrhenatherum elatius*	0	0	0	0	**1**
Ave_fle	*Avenella flexuosa*	0	3	0	0	**17**
Bet	*Betula*	3	0	0	1	**6**
Cal_vul	*Calluna vulgaris*	6	2	2	53	**1456**
Car_sp	*Carex* sp.	0	1	0	0	**140**
Cer_fon	*Cerastium fontanum*	0	0	0	0	**1**
Cha_ang	*Chamerion angustifolium*	0	0	0	0	**2**
Cir_pal	*Cirsium palustre*	1	0	0	0	**1**
Des_ces	*Deschampsia cespitosa*	0	1	0	0	**29**
Dig_pur	*Digitalis purpurea*	0	0	0	0	**1**
Emp_nig	*Empetrum nigrum*	0	0	0	0	**37**
Epi_cil	*Epilobium ciliatum*	0	0	0	0	**86**
Epi_mon	*Epilobium montanum*	0	0	0	0	**8**
Fes_rub	*Festuca rubra*	0	0	0	0	**3**
Fra_exc	*Fraxinus excelsior*	0	0	0	0	**1**
Gal_sax	*Galium saxatile*	0	3	0	0	**154**
Hol_lan	*Holcus lanatus*	0	1	0	0	**2**
Hyp_rad	*Hypochaeris radicata*	1	0	0	0	**2**
Jun_eff	*Juncus effusus*	0	2	0	0	**70**
Luz_syl	*Luzula sylvatica*	0	1	0	0	**1**
Lys_eur	*Lysimachia europaea*	0	1	0	0	**18**
Mol_cae	*Molinia caerulea*	0	0	0	0	**6**
Oxa_ace	*Oxalis acetosella*	0	3	0	0	**3**
Pic_sit	*Picea sitchensis*	0	0	0	0	**1**
Pla_lan	*Plantago lanceolata*	0	2	0	0	**2**
Poa_pra	*Poa pratensis*	0	1	0	0	**5**
Pol_sp	*Polygonum* sp.	0	0	0	0	**10**
Pot_ere	*Potentilla erecta*	1	0	0	2	**94**
Ran_acr	*Ranunculus acris*	0	0	0	0	**5**
Rum_ace	*Rumex acetosa*	0	0	0	0	**1**
Rum_lon	*Rumex longifolius*	0	0	0	0	**165**
Sag_pro	*Sagina procumbens*	0	0	0	0	**4**
Sen_jac	*Senecio jacobea*	0	0	0	0	**1**
Sen_vul	*Senecio vulgaris*	0	0	0	0	**2**
Sil_dio	*Silene dioica*	0	0	0	0	**23**
Son_asp	*Sonchus asper*	0	0	0	0	**3**
Ste_med	*Stellaria media*	0	0	0	0	**7**
Tri_ces	*Trichophorum cespitosum*	0	7	0	1	**172**
Urt_dio	*Urtica dioica*	0	0	0	0	**1**
Vac_myr	*Vaccinium myrtillus*	0	0	3	0	**32**
Vac_vit	*Vaccinium vitis-idaea*	0	0	0	0	**2**
Ver_off	*Veronica officinalis*	0	1	0	0	**8**
Vio_pal	*Viola palustris*	0	1	0	0	**1**
	indeterminate	0	0	0	1	**249**

Table A4: Table of all vascular plant species that germinated from the soil seed bank of the calcareous meadow ecosystem during the trial, including their abbreviation, and the number of seedlings that germinated in each sample.

Abbreviation	Species name	M_1.1	M_1.2	M_1.3	M_2.1	M_2.2	M_2.3
Ach_mil	*Achillea millefolium*	20	0	6	0	1	1
Agr_cap	*Agrostis capillaris*	13	4	25	10	11	3
Ant_odo	*Anthoxanthum odoratum*	0	0	1	0	0	0
Ave_fle	*Avenella flexuosa*	0	0	1	17	0	0
Bet	*Betula*	0	0	0	0	0	0
Cam_rot	*Campanula rotundifolia*	0	0	16	0	2	2
Car_sp	*Carex* sp.	0	0	0	0	0	0
Cer_fon_vul	*Cerastium fontanum* ssp. *vulgare*	0	2	0	0	0	0
Cir_pal	*Cirsium palustre*	0	0	0	0	0	0
	Cyperaceae (indet.)	0	0	0	0	0	0
Des_ces	*Deschampsia cespitosa*	1	0	0	2	0	0
Epi_sp	*Epilobium* sp.	0	0	0	0	0	0
Fes_rub	*Festuca rubra*	0	0	0	1	0	0
Gna_uli	*Gnaphalium uliginosum*	0	0	0	0	0	0
Hyp_mac	*Hypericum maculatum*	0	0	0	0	0	0
Luz_sp	*Luzula* sp.	0	0	0	0	0	0
Myc_mur	*Mycelis muralis*	0	0	0	0	0	0
Pim_sax	*Pimpinella saxifraga*	4	0	7	0	0	0
Pla_lan	*Plantago lanceolata*	0	0	0	0	1	0
Poa_ann	*Poa annua*	0	0	2	0	0	0
Poa_com	*Poa compressa*	15	0	0	1	0	0
Poa_pra	*Poa pratensis*	2	0	0	1	0	0
Pot_ere	*Potentilla erecta*	0	0	2	0	0	0
Ran_acr	*Ranunculus acris*	4	0	0	0	0	0
Rub_ida	*Rubus idaeus*	0	0	0	0	0	0
Rum_ace	*Rumex acetosa*	0	0	6	0	0	0
Sco_aut	*Scorzoneroides autumnalis*	5	0	0	0	1	0
Sen_vis	*Senecio viscosus*	0	0	0	0	0	0
Sil_dio	*Silene dioica*	0	0	0	0	0	0
Ste_gra	*Stellaria graminea*	29	4	51	12	1	2
Tri_pra	*Trifolium pratense*	0	0	1	0	0	0
Tri_rep	*Trifolium repens*	0	2	1	1	5	12
Urt_dio	*Urtica dioica*	1	0	1	16	0	0
Ver_off	*Veronica officinalis*	1	0	0	2	1	0
	indeterminate	0	0	0	0	0	0

Table A4 continuing.

Abbreviation	Species name	RM_1.1	RM_1.2	RM_2.1	RM_2.2	RM_3.1	RM_3.2	RM_4.1	RM_4.2	RM_5.1	RM_5.2	RM_6.1	RM_6.2	Total
Ach_mil	*Achillea millefolium*	0	0	0	0	0	0	0	0	0	0	0	0	**28**
Agr_cap	*Agrostis capillaris*	3	1	76	0	1	0	0	0	0	0	0	0	**147**
Ant_odo	*Anthoxanthum odoratum*	0	0	1	0	0	0	0	0	0	0	0	0	**2**
Ave_fle	*Avenella flexuosa*	0	0	0	0	0	0	0	0	0	0	0	0	**18**
Bet	*Betula*	0	0	0	0	0	0	0	0	1	0	0	1	**2**
Cam_rot	*Campanula rotundifolia*	0	0	0	0	0	0	0	0	0	0	0	0	**20**
Car_sp	*Carex* sp.	1	0	8	0	4	0	0	0	1	0	0	0	**14**
Cer_fon_vul	*Cerastium fontanum* ssp. *vulgare*	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Cir_pal	*Cirsium palustre*	0	0	0	0	0	0	0	0	4	0	0	0	**4**
	Cyperaceae (indet.)	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Des_ces	*Deschampsia cespitosa*	0	0	0	0	1	0	0	0	0	0	0	0	**4**
Epi_sp	*Epilobium* sp.	0	0	2	0	0	0	0	0	1	0	0	0	**3**
Fes_rub	*Festuca rubra*	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Gna_uli	*Gnaphalium uliginosum*	0	0	0	0	0	0	0	0	1	0	0	0	**1**
Hyp_mac	*Hypericum maculatum*	0	0	8	4	0	6	0	7	37	11	1	5	**79**
Luz_sp	*Luzula* sp.	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Myc_mur	*Mycelis muralis*	0	0	1	0	0	0	0	0	0	0	0	0	**1**
Pim_sax	*Pimpinella saxifraga*	0	0	0	0	0	0	0	0	0	0	0	0	**11**
Pla_lan	*Plantago lanceolata*	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Poa_ann	*Poa annua*	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Poa_com	*Poa compressa*	0	0	0	0	0	0	0	0	0	0	0	0	**16**
Poa_pra	*Poa pratensis*	0	0	0	0	0	0	0	0	0	0	0	0	**3**
Pot_ere	*Potentilla erecta*	0	0	1	0	0	0	0	0	0	0	0	0	**3**
Ran_acr	*Ranunculus acris*	0	0	0	0	0	0	0	0	0	0	0	0	**4**
Rub_ida	*Rubus idaeus*	2	0	0	0	5	0	1	0	0	0	0	0	**8**
Rum_ace	*Rumex acetosa*	0	0	0	0	0	0	0	0	0	0	0	0	**6**
Sco_aut	*Scorzoneroides autumnalis*	0	0	0	0	0	0	0	0	0	0	0	0	**6**
Sen_vis	*Senecio viscosus*	0	0	3	0	0	0	0	77	1	1	9	1	**92**
Sil_dio	*Silene dioica*	0	0	0	0	0	0	1	0	0	0	0	0	**1**
Ste_gra	*Stellaria graminea*	0	0	8	0	0	0	0	0	0	0	0	0	**107**
Tri_pra	*Trifolium pratense*	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Tri_rep	*Trifolium repens*	0	0	0	0	0	0	0	0	0	0	0	0	**21**
Urt_dio	*Urtica dioica*	0	0	0	0	0	0	0	0	0	0	0	0	**18**
Ver_off	*Veronica officinalis*	0	0	1	0	3	0	1	0	0	0	0	0	**9**
	indeterminate	0	0	0	0	0	0	0	0	0	1	0	0	**1**

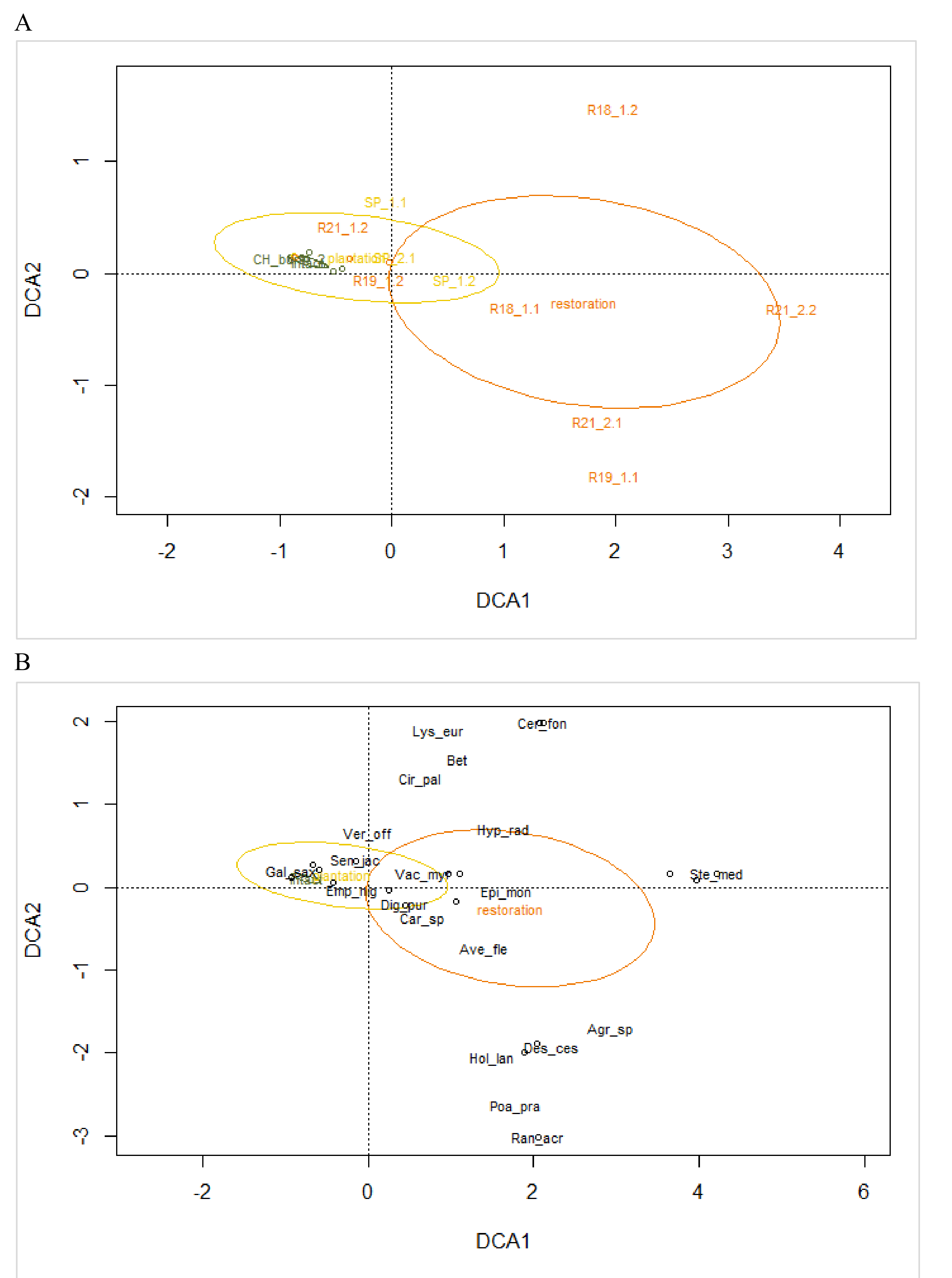

Figure A3: Ordination of the Detrended Correspondence Analysis (DCA) for the species compositions of the intact sites (green), restoration sites (orange), and plantations (yellow) for the CH-samples. The ellipses show the standard error for each group in the according color. Additionally, the samples are labeled with their sample ID in graph A, and abundant species are labeled in graph B (for full names, see Appendix Table A3).

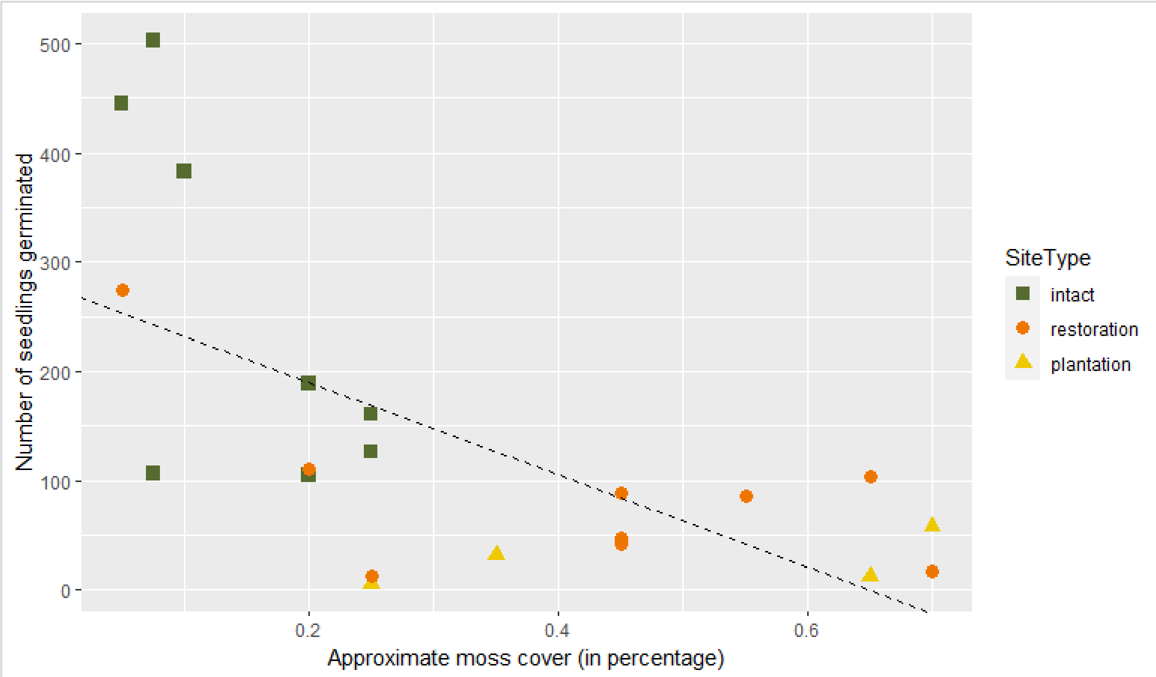

Figure A4: Number of germinated seedlings plotted against the approximate moss cover in percentage estimated five weeks after the start of the germination trial for each tray of the CH-samples. The linear regression is shown as a dotted line.

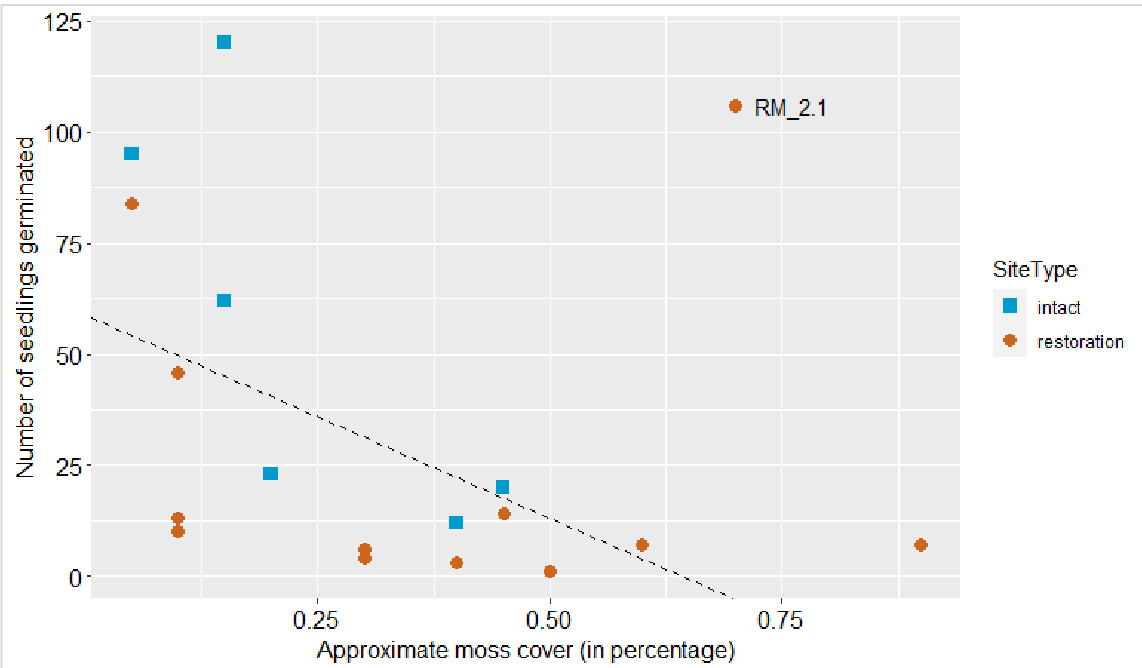

Figure A5: Number of germinated seedlings plotted against the approximate moss cover in percentage estimated five weeks after the start of the germination trial for each tray of the M-samples. The linear regression is shown as a dotted line. The outlier is labeled with the sample ID and not included in the linear regression.

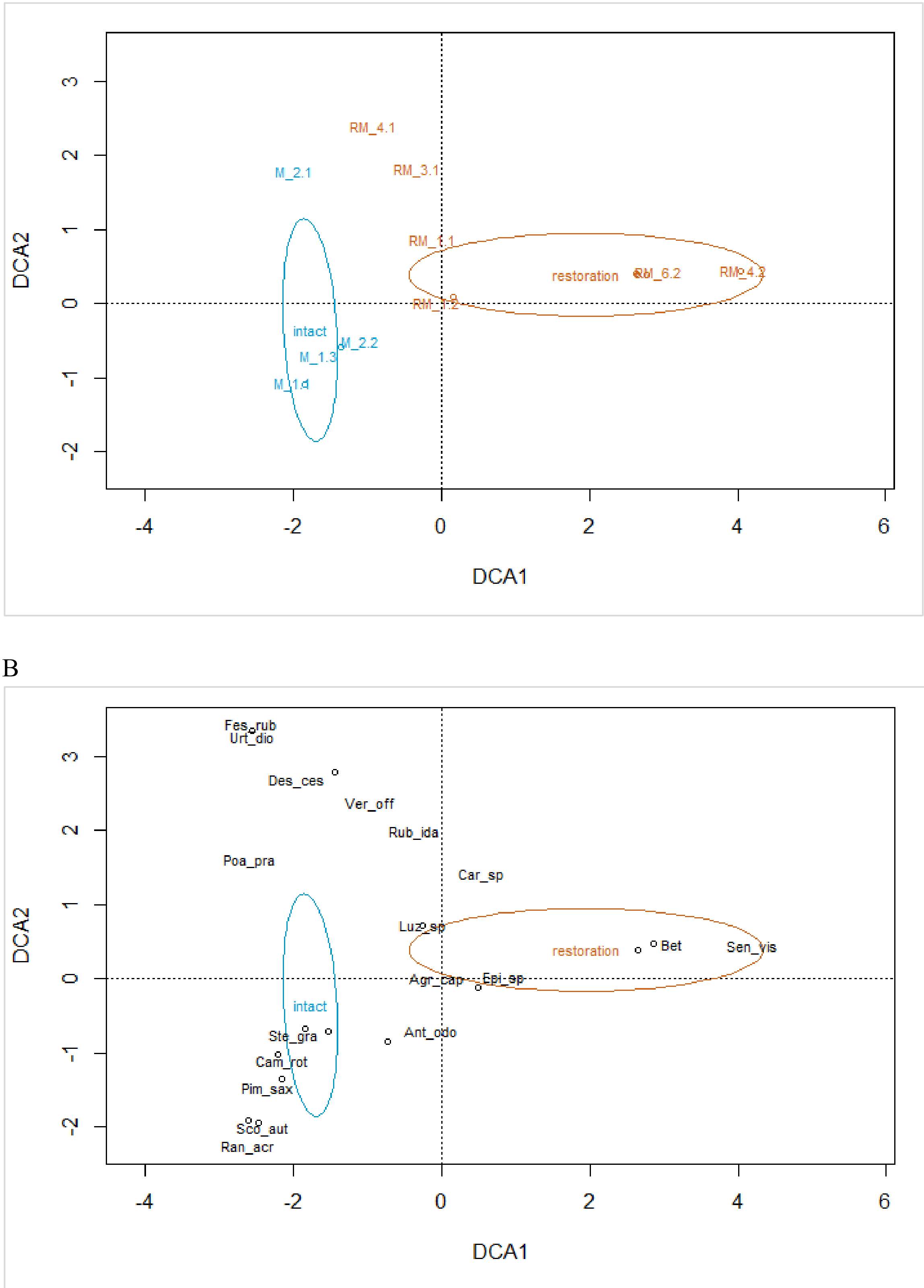

Figure A6: Ordination of the Detrended Correspondence Analysis (DCA) for the species compositions of the intact site (blue) and restoration site (orange) for the M-samples. The ellipses show the standard error for each group in the according color. Additionally, the samples are labeled with their sample ID in graph A, and abundant species are labeled in graph B (for full names, see Appendix Table A4).

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