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Short-term effects of *Salix* plantings and seeding of *Festuca ovina* on vegetation recovery in a disturbed alpine heathland in the Dovre Mountains, Norway

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Foreword

First of all, I would like to thank my supervisors Dagmar Hagen and Marianne Evju from the Norwegian Institute for Nature Research (NINA) for providing me the opportunity to be involved in this restoration project for my master’s thesis, for sharing their knowledge and fieldwork experience with me, and for guiding me through the data analysis and the writing process. I would also like to thank my supervisor Kari Klanderud from the Norwegian University of Life Sciences (NMBU) for her guidance and for all the useful feedback. It was a luxury to have three supervisors. Furthermore, I would like to thank Anne Mehlhoop for her assistance in the field and for keeping an eye on the muskoxen, and I would like to thank Siri Lie Olsen and Tommy Prestø for their help with the identification of plant species. I would also like to express my thanks to Svein Solli, Dan Osrønningen, and the other people from the Norwegian Defence Estates Agency (NDEA) as well as to the helicopter pilots, for the good care and the safe transport to and from the fieldwork site. I would like to thank the Villreinsenter for providing me with accommodation during the fieldwork period, and I would like to thank Jake MacDougald for answering my English related questions. I would like to extend a huge thank you to Joris Stuurop for visiting me in Hjerkinn with the drone, for helping with the processing of the drone imagery, for being my field assistant for a week, and for all his support during my master programme. I would also like to express my thanks to my family and friends for supporting me throughout my studies. And last but not least, I would like to thank the muskoxen of Hjerkinn for the excitement they caused with their regular visits. To all that I have mentioned above: tusen takk for hjelpen!

Abstract

Alpine ecosystems are particularly vulnerable to anthropogenic disturbances and have a slow natural recovery rate. Open questions remain as to which forms of active restoration measures could accelerate alpine ecosystem recovery from severe disturbances. This study evaluated the short-term effects of two restoration treatments – planting of propagated *Salix* shrubs in three different densities (1, 2.5 and 4 plants/m^2) and seeding of the grass *Festuca ovina* – on vegetation recovery in a disturbed alpine heathland in the Dovre Mountains, Norway. In addition, the relationships between soil moisture and vegetation recovery, and between soil substrate and vegetation recovery were investigated. Measurements were obtained in permanent monitoring plots, five years after implementation of the measures. Results showed that the effectiveness of the restoration treatments depended on the metric used to assess vegetation recovery. *Salix* plantings with higher densities had a higher naturally recovered vascular plant diversity and a higher *Salix* recruitment but the plantings did not affect naturally established vegetation cover. Seeding of *F. ovina* resulted in a higher bottom and field layer cover but did not affect vascular plant diversity. Vegetation recovery was positively related to soil moisture and fine soil substrate. Exploratory aerial photography suggested that the large-scale revegetation pattern in the study site was linked to artificially created topography. If the outlined restoration goal is to increase both vascular plant diversity and vegetation cover, this study suggests that planting and seeding might be used complementary to each other and in conjunction with improving soil water retention capacity and creating artificial relief.

Key words: ecological restoration, vegetation recovery, short-term monitoring, alpine heathland, Dovre Mountains, *Salix*, *Festuca ovina*.

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1. Introduction

1.1 Ecological restoration

Worldwide, there is a rapid loss of biodiversity and intact ecosystems due to anthropogenic disturbances (Cardinale et al., 2012; Díaz et al., 2019; Sala et al., 2000). When disturbances are severe, ecosystems might collapse and reach an altered state from which they cannot return to their original state without human intervention (Suding et al., 2004). In such scenarios, ecological restoration – defined as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Society for Ecological Restoration International Science & Policy Working Group [SER], 2004) – could be performed. An ecosystem is considered ‘recovered’ or ‘restored’ when it has reached a self-sustainable state that is resilient to environmental stress and disturbances (SER, 2004).

1.2 Alpine ecosystems

Alpine ecosystems are particularly vulnerable to anthropogenic disturbances (Willard et al., 2007). These high-altitude areas are characterised by harsh environmental conditions such as low temperatures, high precipitation, high evaporation, and increased exposure to wind compared to lower-altitude areas (Krautzer et al., 2012). Also typical for alpine areas are long periods of snow cover, short growing seasons, large differences in seasonal light availability and rapid transitions between seasons (Ernakovich et al., 2014). Soil temperatures are low throughout the year, which leads to a slow rate of microbial decomposition of organic matter (Krautzer et al., 2012). This in turn limits the amount of inorganic nutrients in the soil that is available for plant growth (Krautzer et al., 2012). The dry, nutrient-poor soils and the low temperatures constrain plant growth and strongly influence the type of species that establish in these areas (Monson et al., 2001; Theurillat et al., 2003); alpine ecosystems are typically dominated by lichens and low vegetation such as bryophytes, herbs, and shrubs (Ernakovich et al., 2014). Another consequence of the slow rate of biological processes is that plant regeneration in alpine areas is slow, and natural recovery from severe disturbances can take decades or even centuries (Krautzer et al., 2012; Rydgren et al., 2011; Willard et al., 2007). Research has shown that despite the generally slow recovery of vegetation in alpine areas, revegetation proceeds faster under favourable environmental conditions, such as a fine soil substrate, optimal soil moisture levels, and the presence of (small-scale) topography (Evju et al., 2012; Mehlhoop et al., 2018; Rydgren et al., 2013). Recovery times could thus be shortened by implementing active restoration measures that accelerate the natural revegetation process, such as restoring terrain and soil conditions, in addition to fertilizing, seeding, and planting (Forbes & Jefferies, 1999; Hagen & Evju, 2013; Krautzer et al., 2012).

1.3 Nurse plants in alpine restoration

Both interspecific competition and facilitation are known to play a role in the formation of plant communities (Callaway & Walker, 1997). At high altitudes, where abiotic stress levels are high, plant interactions are often positive (Callaway et al., 2002). Beneficial interactions between plants constitute for example the trapping of seeds of various species, or enabling the establishment of other species by buffering physical stresses – such as shading against direct sunlight or sheltering from cold winds (Bertness & Callaway, 1994; Padilla & Pugnaire, 2006). Plants that facilitate the establishment, survival, and/or growth of other plant species by providing such 'safe sites', are called 'nurse plants' (Gómez-Aparicio, 2009; Padilla & Pugnaire, 2006). In recent years, the positive effects of nurse plants on revegetation processes have gained interest among restoration ecologists. There has been a shift in focus from more traditional restoration techniques – such as reducing competition by undesirable plant species – towards techniques that use facilitative plant interactions to restore degraded ecosystems (Gómez-Aparicio, 2009).

Several factors come into consideration when nurse plants are used in restoration. Regarding the selection of nurse plants, it is recommended to use seeds or material from local plant species that are adapted to the harsh environmental conditions and that are likely to grow and reproduce without further human assistance (Grant et al., 2011; Krautzer et al., 2012). Native species are preferred because introduced non-native species might compete for space and resources with native species (Hagen et al., 2014; Padilla & Pugnaire, 2006) and thereby alter the trajectory of the site towards an undesirable climax state (Walker & Shiels, 2012). Pioneer species could be suitable nurse plants, as these can cope with the often unfavourable conditions for establishment in severely disturbed sites (Dalling, 2008) and are often wind- or self-pollinated rather than insect-pollinated, which increases the chance of reproductive success in harsh or barren environments where pollinator abundance is (initially) low (Walker & del Moral, 2003).

A genus that has shown potential for the restoration of alpine areas, is *Salix* (Densmore & Holmes, 1987; Hagen, 2007; Kuzovkina & Quigley, 2005). The *Salix* genus is commonly used in restoration efforts in different types of ecosystems and it harbours a wide variety of species that cover a large range of biomes, which often allows for the selection of a species that is native to the disturbed area (Kuzovkina & Quigley, 2005). *Salix* plants are usually fast-growing, produce large quantities of viable seeds (Forbes & Jefferies, 1999), and can easily be propagated via cuttings (Hagen, 2002; Houle & Babeux, 1998). Furthermore, *Salix* can colonize bare ground (Kuzovkina & Quigley, 2005; Schramm, 1966), and several species have shown to establish in severely degraded soils (e.g. soils with only a thin layer of topsoil, a high degree of compaction, or high metal concentrations), or acid, wet, dry, or nutrient-poor soils (Kuzovkina & Quigley, 2005). The ability to survive unhospitable conditions makes *Salix* plants suitable pioneer plants for the restoration of severely disturbed areas (Kuzovkina & Quigley, 2005). Moreover, research has shown that *Salix* can improve the soil conditions in degraded sites by facilitating the re-establishment of soil organism communities (Sylvain & Mosseler, 2017), leading to enhanced microbial decomposition and nutrient cycling and a higher complexity of biotic interactions, which in turn increases the resilience of the ecosystem to future disturbances (Sylvain & Wall, 2011).

Although *Salix* has widely been used in restoration efforts and has shown to act as a nurse plant in alpine areas (e.g. Dona & Galen, 2007; Endo et al., 2008), there are aspects of its use that have not yet been studied. A study by Hagen (2003) showed for example that planting density of *Salix* in restoration sites did not affect the plants' own survival, biomass or growth during the first years after planting, but it is unknown whether planting density affects the plants' function as nurse plants (i.e., if higher planting densities result in a more rapid recovery of the vegetation). As plant propagation can be costly, it would be beneficial to know what planting density is minimally required to achieve outlined restoration goals.

Seeding of plant species is a less costly restoration approach compared to the propagation of plant material. Seeded species are often fast-growing grasses that rapidly provide a vegetation cover (Hagen & Evju, 2013). However, findings about the effectiveness of grasses as nurse plants are ambiguous and seem to be context dependent (Choi & Wali, 1995; Gómez-Aparicio, 2009; Gretarsdottir et al., 2004; Hagen et al., 2014; Maestre et al., 2001; Rydgren et al., 2013). A meta-analysis of studies on plant interactions in ecosystem restoration showed that the effectiveness of plants as nurse plants might depend on their life-form; whereas shrubs were effective nurse plants in all types of studied ecosystems, herbs – and particularly grasses – showed mainly negative effects on vegetation development in terms of emergence, survival, growth, and density of other species (Gómez-Aparicio, 2009). This could be explained by the fact that grasses have fibrous root systems, a higher root to shoot ratio and a shallower rooting depth than shrubs, which enables them to compete more efficiently for resources (Canadell et al., 1996; Gómez-Aparicio, 2009). The few studies that did find positive effects of grasses on vegetation recovery (e.g. Choi & Wali, 1995) were performed in sites with low nutrient availability (Gómez-Aparicio, 2009). This suggests that grasses could potentially function as nurse plants in alpine environments, where resources are typically scarce.

Studies with commercially available seeds of *Festuca rubra* in alpine areas, however, showed that this grass species outcompeted rather than facilitated the establishment of native species, and thereby had a negative effect on species diversity (Hagen, 2003; Hagen et al., 2014). A complementary greenhouse experiment that compared the effects of *F. rubra* and *F. ovina* on the establishment of *Betula nana* showed that establishment was more suppressed by *F. rubra* than by *F. ovina* (Hagen et al., 2014). This suggests that *F. ovina* might be a more suitable candidate for alpine restoration. Nonetheless, seedling establishment was highest under non-seeded conditions, which suggests that none of the grasses functioned as a nurse plant (Hagen et al., 2014). However, as mentioned by Rydgren et al. (2017), the performance of a species under controlled greenhouse conditions cannot be directly translated to a field setting, where environmental conditions such as nutrient and water supply are more dynamic (see e.g.Verdú & Traveset, 2005). Field studies are thus required to assess the performance of a species in the field. A short-term field study on the performance of seeded *F. ovina* in an alpine area showed that the grass rapidly provided a vegetation cover, particularly when seeded as a monoculture (Rydgren et al., 2017). Effects of the grass on species diversity in a field setting, however, are still unknown. Field studies performed thus far have only assessed the effects of seed mixtures including *F. ovina* (Rydgren et al., 2011; Rydgren et al., 2016) rather than the effects of the grass seeded as a monoculture.

1.5 Aims and objectives

The aim of this study was to evaluate the short-term effects of two restoration treatments, namely the planting of *Salix* shrubs in three different densities and the seeding of *F. ovina*, on vegetation recovery in a severely disturbed alpine heathland. All species are native to the study area and propagated from local plants through cuttings and seeds. In addition, the relationships between soil moisture and vegetation recovery, and between soil substrate and vegetation recovery were investigated. The study site was situated in a former military firing range in the Dovre Mountains in Norway. Prior to restoration interventions, the site was completely void of vegetation cover. Measurements were performed in permanent monitoring plots, five years after implementation of the treatments. Metrics used for vegetation recovery were vegetation cover and vascular plant diversity. Additionally, *Salix* development in terms of cover, growth, and recruitment was studied. Lastly, exploratory research with aerial photography was performed to assess the influence of small-scale topography on vegetation recovery at a larger scale, encompassing the entire study site.

Based on the existing literature, it is expected that the planted *Salix* shrubs function as nurse plants. I therefore hypothesize that: (1) naturally established vegetation cover and vascular plant diversity are lowest in non-planted control plots and increase with increasing density of planted *Salix*; (2) *Salix* planting density does not affect *Salix* cover or growth at this early stage, but plots with higher planting densities have a higher *Salix* recruitment due to the higher densities of *Salix* (nurse) plants. Based on the literature about seeding of *F. ovina*, I hypothesize that: (3) seeded plots have a higher field layer cover than non-seeded plots, (partly) due to the cover of *F. ovina* itself, but a lower vascular plant diversity and *Salix* recruitment due to the inhibition of seedling establishment by *F. ovina*. Concerning the environmental conditions, I hypothesize that: (4) fine soil substrate and soil moisture are positively related to vegetation recovery, and that small-scale topography is related to vegetation recovery at a larger scale.

2. Materials and Methods

2.1 Study site

The study site is a former military ammunition test field (400 x 600 m) in the Hjerkinn firing range in the Dovre Mountains, Central Norway (62°13'33.6"N 9°27'43.2"E [WGS]), situated at an elevation of approximately 1060 m a.s.l. (Norwegian Mapping Authority, 2019). It is located in one of Europe’s last largely intact high mountain ecosystems (Directorate for Nature Management, 2012), surrounded by nature conservation areas (Figure 1).

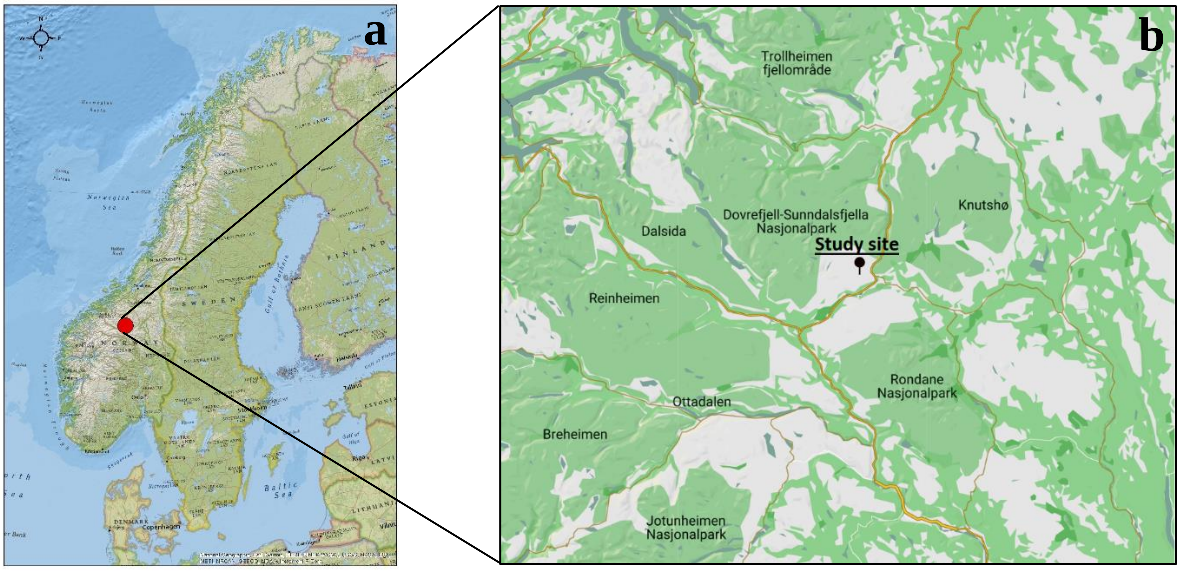

Figure 1. a) Location of the Dovre Mountains (red dot) in Central Norway, b) location of the study site in the Dovre Mountains, surrounded by nature conservation areas (green colour). Sources: a) ESRI ArcMap[1], b) Google Maps, 2020.

The Hjerkinn firing range covers an area of 165 km^2 and was used as a military training area from 1923 to 2005. In 1999, the Norwegian Parliament announced to close down the firing range to restore the area to its “original, natural state” (Ministry of Defence, 1998-99). To reach this goal, the Hjerkinn Restoration Project (Hjerkinn PRO) was initiated, managed by the Norwegian Defence Estates Agency. Parts of the project that concern nature restoration are performed in collaboration with the Norwegian Institute for Nature Research (NINA). The project started in 2009 and will be finished in 2020 (Hagen & Evju, 2013; Norwegian Defence Estates Agency, 2019). It is thus far the largest restoration project ever initiated in Norway.

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[1] Map made by collaboration between Esri, USGS, HERE, Garmin, FAO, NOAA, National Geographic, UNEP-WCMC, NASA, ESA, METI, NRCAN, GEBCO, and increment P Corp.

The geology of the Hjerkinn area is characterised by calcium-poor glacial till overlying Precambrian metamorphic and igneous bedrock (Geological Survey of Norway, 2019; Hagen, 2007). The average annual temperature for the period 1986 – 2016 at the nearest weather station (Fokstugu, 973 m a.s.l.) was 0.6°C, the average annual growing season length (number of days with an average temperature ≥ 5°C) was 129 days, and the annual precipitation during this period was 516.9 mm (Norwegian Meteorological Institute, 2019).

Prior to restoration interventions, the ecosystem of the study site had been severely disturbed. Due to the physical destruction of vegetation and soil, the terrain consisted of compacted gravel and sand, and it lacked organic material and vegetation cover (Hagen & Evju, 2014; Figure 2). The relatively intact vegetation of the area surrounding the study site is dominated by dwarf shrub heath and lichens (Hagen, 2007; Hagen & Evju, 2013). Dominant shrub species are *Salix glauca*, *S. lapponum* and *S. phylicifolia* (Hagen, 2003). In the surrounding area, numerous bogs and fens can be found (Hagen, 2007).

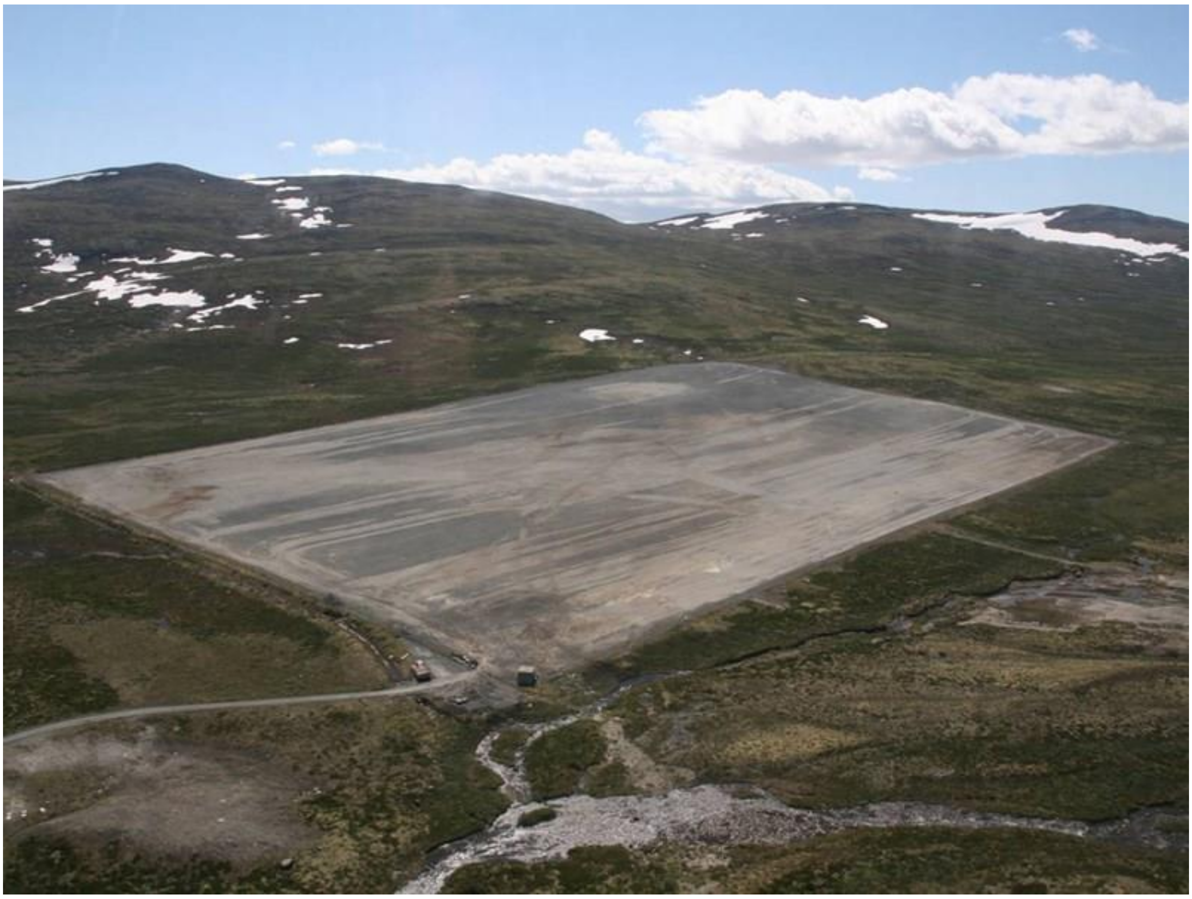


Figure 2. The study site in the Hjerkinn firing range in 2011, prior to restoration interventions. Source: Norwegian Defence Estates Agency.

2.2 Performed restoration interventions

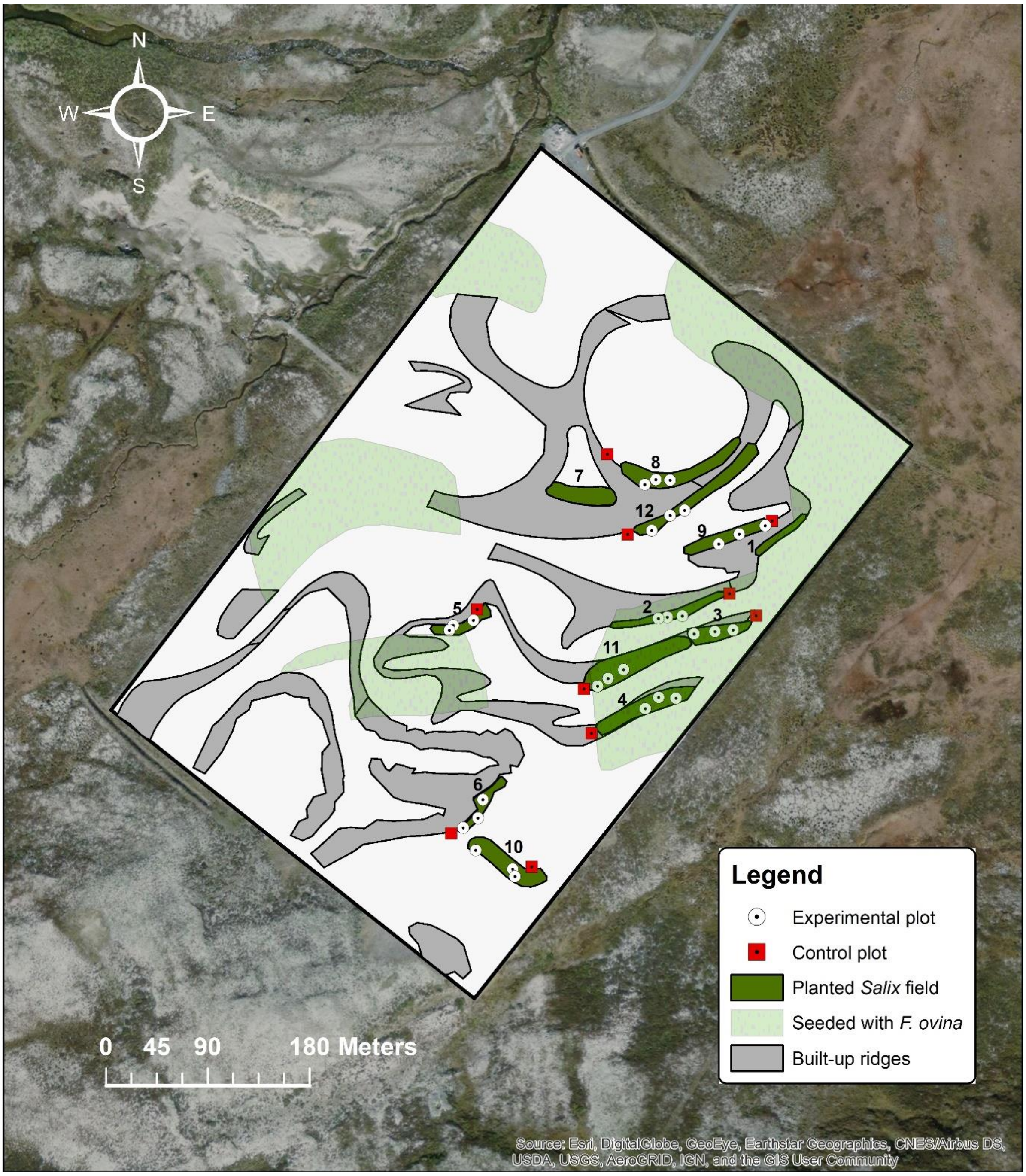
The restoration of the former test field started with the clearing of unexploded ammunition by the Norwegian Defence Estates Agency. After clearance, the previously flat terrain was provided with small-scale relief. In certain parts of the site, soil was excavated and used in other places to create ridges, mixed with soil from local gravel pits. The rest of the site was harrowed to loosen the compacted soil. Terrain development was completed in 2013 (Hagen & Evju, 2014).

In autumn 2013, cuttings from three *Salix* species (*S. glauca*, *S. lapponum* and *S. phylicifolia*) were obtained from local mother plants and propagated in a greenhouse. In June and September 2014, a total of 25 000 of these propagated *Salix* plants were planted in the study site with an overall density of 2.5 plants per square meter (Hagen & Evju, 2014). The plants were divided over 12 fields, covering approximately 4% of the study site (Figure 3). Around each plant, one litre of commercial, nutrient rich soil was added to increase the probability of plant survival. In August 2014, an area of 6 ha (ca. 25% of the study site) was fertilised (20 kg/da) and seeded manually with the local grass species *F. ovina* (Hagen & Evju, 2014). The seeds were propagated from seeds that had been hand-collected in Hjerkinn (Martinsen & Oskarsen, 2010) and seeded with a density of approximately 20 kg/da. The planted and seeded areas partially overlap (Figure 3).

2.3 Establishment of experimental and control plots

At the start of the experiment in 2014, permanent experimental plots were established in 10 of the 12 fields to monitor the effects of two restoration treatments (planting of *Salix* and seeding of *F. ovina*) on the revegetation process. In each of the 10 monitored fields, three 5 x 5 m plots were established by planting *Salix* individuals in different densities: one plot with a high (4 plants/m^2), one with a medium (2.5 plants/m^2), and one with a low planting density (1 plant/m^2), as illustrated in Figure 4. Each planting density was assigned randomly to one of the plots. The distance between plots was approximately 5 m. Within each plot, five permanent 0.5 x 0.5 m subplots were established with a *Salix* plant as midpoint and marked with small metal poles in the corners. Of the 10 monitored fields, 4 were situated in areas seeded with *F. ovina* (Figure 3).

In 2019, we established 10 permanent control plots outside the planted fields (one paired to each of the 10 monitored fields; Figure 3) to allow for a comparison of the revegetation process in experimental plots with, and in control plots without planted *Salix*. The control plots were established according to the criteria stated in section 2.4 and had the same design as the experimental plots (Figure 4). In total, the study design contains 150 experimental and 50 control subplots.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 3. Schematic overview of the study site (400 x 600 m) in the Hjerkinn firing range in the Dovre Mountains. Of the 12 fields with *Salix* plantings, 10 fields contain experimental plots (plus a control plot outside the field) according to the design shown in Figure 4.

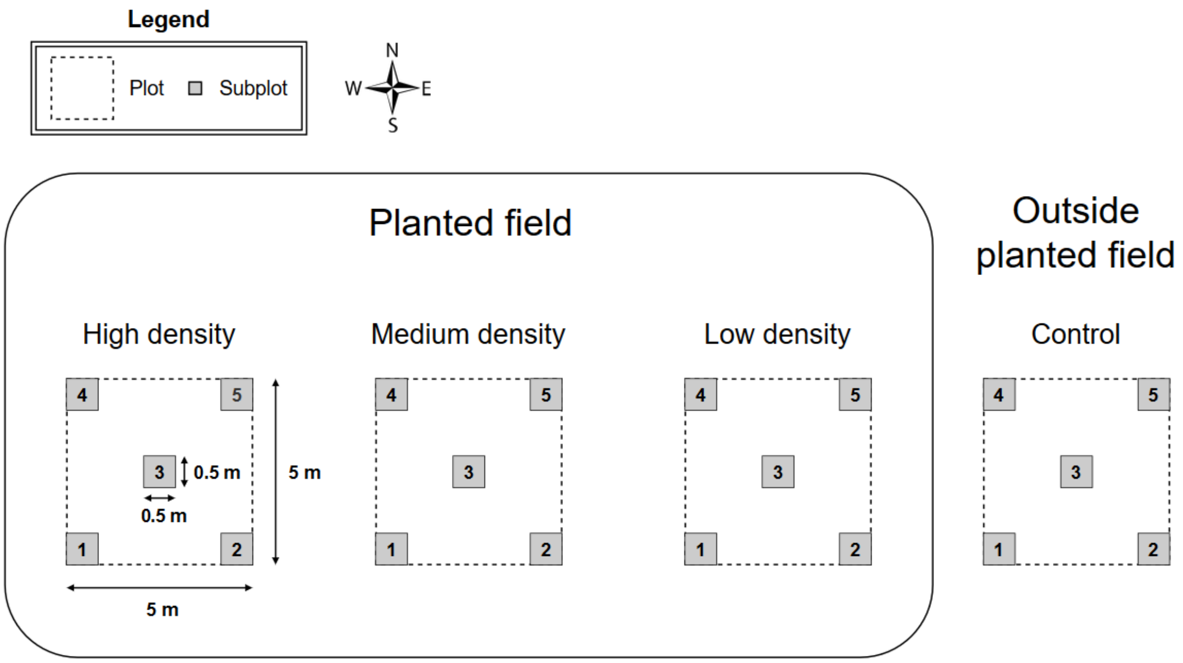


Figure 4. Schematic diagram of the study design. Each of the 10 monitored planted fields contains three permanent experimental plots (5 x 5 m) with *Salix* plantings in different densities: high (4 plants/m^2), medium (2.5 plants/m^2), and low (1 plant/m^2). The spatial order of the three densities differs per field. The distance between plots was 5 m (not to scale in diagram). Each plot contains five subplots (0.5 x 0.5 m). Outside each of the 10 fields, a control plot (without planted *Salix*) was established with the same design as the experimental plots.

2.4 Establishment criteria for control plots

The control plots were established in non-planted areas that fulfilled four criteria, mentioned in order of importance:

1) The seeding treatment (non-seeded or seeded with *F. ovina*) was the same as the seeding treatment in the planted field that the control plot was paired to.
2) The terrain – with respect to topography, aspect, and soil substrate – was similar to the terrain of the experimental plots in the planted field that the plot was paired to.
3) The distance from the border of the planted field to the midpoint of the control plot was approximately 10 m. This distance was considered large enough to reduce a potential effect of the *Salix* plantings in the field on vegetation development in the control plot, but small enough to minimize differences in terrain conditions.
4) The control plot should not be located closer to another field than to the field that it was paired to.

If no area could be found that fulfilled both criteria 2 and 3, criterion 2 was prioritized, and the 10 m distance stated in criterion 3 could be reduced up to a minimum of 4.5 m. This was decided because field observations suggested that terrain conditions had a larger influence on the revegetation process in the control plot than the distance to the planted field had on a scale of several meters. The establishment procedure is illustrated in Appendix A.

2.5 Data collection

Data collection took place in August 2019. All data were collected for both experimental and control subplots. Only *Salix* cover estimates were obtained solely for experimental subplots. In addition, each subplot was photographed from a height of 1 m.

2.5.1 Salix cover and growth

For each experimental subplot, I estimated *Salix* cover as a percentage of the subplot area covered by the vertical projection of the plant onto the ground. Estimates were made with a 0.5 x 0.5 m vegetation analysis frame that was divided into 16 equally sized units (Figure 5a), and obtained only for the *Salix* plant in the centre of the subplot (the 'monitored' *Salix* plant). Other *Salix* plants that had grown into or established in the subplot were not included in the estimate. Cover percentages were later turned into proportions and multiplied by the total surface area of the subplot (2500 cm^2) to obtain an absolute measure of *Salix* cover (in cm^2).

To determine *Salix* growth since the start of the experiment, cover estimates for 2014 were required. Because these data were not available, I made estimates based on pictures of the subplots including vegetation analysis frame in 2014 (Figure 5b). With ImageJ software (Schneider et al., 2012), I delineated the *Salix* cover within a frame, turned it into a polygon (Figure 5c), and calculated it as a percentage of the subplot area based on pixel cover. A comparison of photo- and field-based estimates from several subplots in 2019 showed that estimates obtained with the different methods were in close agreement. Finally, the estimates for *Salix* cover in 2014 were turned into absolute measures and *Salix* growth between 2014 and 2019 (cm^2) was calculated by subtracting *Salix* cover in 2014 from *Salix* cover in 2019.

Figure 5. a) Subplot (0.5 x 0.5 m) with vegetation analysis frame (divided into 16 equally sized units) in 2019, b) the same subplot with frame in 2014 (source: M. Evju), c) the subplot picture from 2014 in ImageJ software, with a polygon of *Salix* cover (white colour).

2.5.2 Vegetation cover, plant litter, and bare soil

I estimated the total vegetation cover as a percentage of the subplot area. Estimates were made with the vegetation analysis frame and based on the vertical projection of the vegetation onto the ground. Likewise, I obtained cover estimates for each of the vegetation layers separately: the bottom layer (bryophytes and lichens), the field layer (forbs and graminoids, including the seeded *F. ovina*), and the shrub layer (including planted *Salix* individuals rooted in or growing into the subplot). The different vegetation layers could overlap and therefore their sum could exceed the estimate for the total vegetation cover. I also estimated the percentage of plant litter (both loose and attached to plants, but not litter located underneath vegetation), and the percentage of bare soil (including soil covered with biological soil crust) in the subplot. For each subplot, the sum of the total vegetation cover, plant litter, and bare soil was 100%. If a factor was present but comprised less than 1% of the subplot area, it was noted as 0.1%.

2.5.3 Species subplot frequency

For each of the 16 units of the vegetation analysis frame, we identified the occurring vascular plant species, including those that were not rooted within the unit. For each species, the subplot frequency was counted as the total number of units of the subplot that the species occurred in. Plant identification was based on Mossberg and Stenberg (2019) and Lid and Lid (1994) and done to the species level, or if not possible to the genus level. If plants were too small to be identified, they were counted as monocot or dicot seedlings. For the *Salix* genus, a distinction was made between the monitored *Salix* plant, other planted *Salix* individuals that had grown into the subplot, and *Salix* seedlings (individuals that were only a few centimetres in height). The subplot frequency of bryophytes, lichens, and biological soil crust was counted but these individuals were not identified further.

2.5.4 Soil substrate composition and soil moisture

For each subplot, I determined the soil substrate composition based on three substrate classes: 1) stones (⌀ > 5 cm), 2) gravel (⌀ = 2 mm – 5 cm), and 3) fine soil substrate: sand, silt, and/or clay (⌀ < 2 mm). I used the vegetation analysis frame to estimate the percentage of soil belonging to each of the classes. The sum of the three classes was 100%. Distinctions between substrate classes were made based on visual and tactile observations.

I measured the volumetric soil moisture content (%) – hereafter referred to as soil moisture – of the upper 5 cm of soil with a moisture meter (Delta-T Devices type HH2 with a SM300 sensor) and an accuracy of 1 decimal. All measurements were taken on an overcast day without precipitation (August 23, 2019). Per subplot, three measurements were taken in the shape of a triangle with the monitored *Salix* as midpoint, at distances of approximately 15 cm from the plant. The average of the three measurements was taken as the soil moisture content for that subplot. For control subplots, measurements were taken as if there were a *Salix* plant in the centre.

2.5.5 Aerial photography (UAV)

Aerial photographs of the entire study site (400 x 600 m) were taken to get an impression of the revegetation process at a larger scale. Photographs were taken by Joris Stuurop with an unmanned aerial vehicle (UAV), the Parrot Anafi, from a height of 60 m above the take-off site at the midpoint of the study site. Photo overlap was set to 85%.

We used Pix4Dmapper (version 4.5) to create an orthomosaic of the photos and to generate a digital surface model (DSM). Adobe Photoshop (version 21) was used to emphasize the vegetation patterns on the orthomosaic. First, blue colours were exaggerated (+100 on the yellow-blue colour scale, -55 on the cyan-red colour scale) to create contrast between the vegetation and darker terrain features. Subsequently, the remaining dark terrain features were replaced in colour by increasing the lightness of its specific colour range. Lastly, a threshold was set to create a binary black and white image, the threshold corresponding roughly to the lightest colour of the vegetation (hence, black stands for vegetation, white for bare terrain).

The resulting black and white image of vegetation cover was overlain onto a slope map created from the DSM with ESRI ArcMap (version 10.6), showing only the black colours (vegetation).

2.6 Data pre-processing

Data pre-processing was done in Microsoft Excel (version 2003), and in RStudio (version 1.2.5001; RStudio Team, 2015) with R (version 3.6.1; R Core Team, 2019).

2.6.1 Vascular plant diversity

For each subplot, I obtained two measures of vascular plant diversity (Shannon index): species diversity and genus diversity. The diversity measures were based on the subplot frequency of the species and genera and calculated in RStudio with the vegan package (Oksanen et al., 2019). Excluded from the calculations were planted *Salix* individuals (but not seedlings), seeded *F. ovina*, and unidentified monocot and dicot seedlings. For genera that harboured several congeners in the study site, plants identified to the genus level were treated as a separate species if an identified species of that genus was present in the same subplot (e.g. *Cerastium* sp. was considered as a separate species if *Cerastium alpinum* was present). This was decided because there were numerous small plants that could not be identified to the species level, but that were considered important to include in the diversity estimates given the early stage of the restoration process and the scarce vegetation in the study site.

2.6.2 Exclusion of subplots, outlier, and missing data

Three subplots were excluded from all analyses because the *Salix* plant had died or had been dug out by a muskox, and it was uncertain how this might have affected the revegetation process (a fourth subplot in which the *Salix* had died, was not relocated correctly in 2019). For the analysis of *Salix* growth, another seven subplots were excluded (five because the subplots had been relocated incorrectly in 2019, and two because pictures from 2014 were missing). The five incorrectly relocated subplots were included in all other analyses because there was no reason to assume that the *Salix* plants in these subplots differed significantly from the *Salix* plants in the original subplots, which had been placed randomly. For the analysis of shrub layer cover, control subplots were excluded because the shrub layer cover in these subplots was negligible (< 0.1%), and inclusion led to a violation of the assumptions of linearity, normality, and homogeneity of variance. The analysis for *Salix* recruitment was run both with and without an outlier that caused a violation of the homogeneity of variance assumption, as the outlier was presumably the result of natural variation and could therefore not simply be disregarded. Missing data was handled with the pairwise deletion method.

2.6.3 Transformation of dependent variables

Some of the dependent variables were transformed to meet the assumptions of linearity, normality and homogeneity of variance required for the statistical models (section 2.7). The type of transformation (logarithmic or square root) was selected based on a visual inspection of the residual plots of the model and suggestions by Pallant (2010) based on the distribution of the dependent variable. To perform a logarithmic transformation on vegetation cover variables, which contained values of zero, a value of 1 was added to the original values.

2.7 Statistical analyses

Statistical analyses were carried out in RStudio (RStudio Team, 2015) with R (R Core Team, 2019) and the packages lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), multcomp (Hothorn et al., 2008), and performance (Lüdecke et al., 2020).

Linear mixed-effect models (LMMs) were used to investigate the effects of the two restoration measures – planting of *Salix* and seeding of *F. ovina* – on the dependent variables (1) *Salix* cover, (2) *Salix* growth, (3) *Salix* recruitment, (4) total vegetation cover, (5) bottom layer cover, (6) field layer cover, (7) shrub layer cover, (8) vascular plant species diversity, and (9) vascular plant genus diversity. Fixed factors were *Salix* density (categorical variable) and seeding of *F. ovina* (binary variable). Covariates were soil moisture and fine soil substrate (continuous variables, standardised with the function *scale*). To incorporate the nested study design (plot nested in field) in the model, field number was included as a random factor. Model parameters were estimated with the maximum likelihood method. The significance level for all analyses was 0.05. The model for *Salix* recruitment was based on count data (seedling subplot frequency) and therefore run with a Poisson distribution. Each LMM was checked for collinearity among fixed factors and covariates based on variance inflation factor (VIF) values with the function *check_collinearity*.

For each LMM, backward stepwise model selection was used to eliminate nonsignificant variables from the model. The full model included all fixed factors, covariates, and the random factor. Per step, an alternative model was created by removing the nonsignificant fixed factor or covariate with the highest *p*-value from the model. Model selection ended when the Akaike information criterion (AIC) value of the newest model was higher than that of the previous model. If the absolute change in AIC-value between two models was small ($|\Delta AIC| < 2$), the model with the fewest variables was selected. Only the final model was presented. If this model contained the fixed factor *Salix* density, a Tukey HSD test for post-hoc comparisons was run for this variable.

Before running the LMMs for *Salix* cover and growth, a LMM for *Salix* cover in 2014 was run – with fixed factors *Salix* density and seeding, and random factor field number – to ensure that there had been no differences in *Salix* cover between subplots with different *Salix* densities or between subplots with different seeding treatments at the start of the experiment that should be controlled for.

3. Results

3.1 *Salix* development

By 2019, there was a total loss of 4 of the 150 monitored *Salix* individuals that had been planted in 2014, resulting in a survival rate of 97.3%. Three of these plants had been located in seeded areas and had already died or had been dug out by a muskox within the first year (Glomb, 2016). The loss was approximately evenly distributed across the *Salix* densities. Theoretically, *Salix* survival rate could be lower because five subplots were not relocated correctly in 2019.

3.1.1 Salix cover

The LMM for *Salix* cover in 2014 showed that there was no difference in cover between subplots with different *Salix* densities, nor between subplots with different seeding treatments at the start of the experiment ($p > .050$ in both cases; results not shown). *Salix* cover in 2019, grouped by *Salix* density and seeding treatment, is shown in Figure 6. Model selection resulted in a model with only the variable fine soil substrate (for test output, see Appendix B) but this relationship was not significant ($p = .067$). There was no effect of *Salix* density or seeding on *Salix* cover, and *Salix* cover showed no relationship with soil moisture.

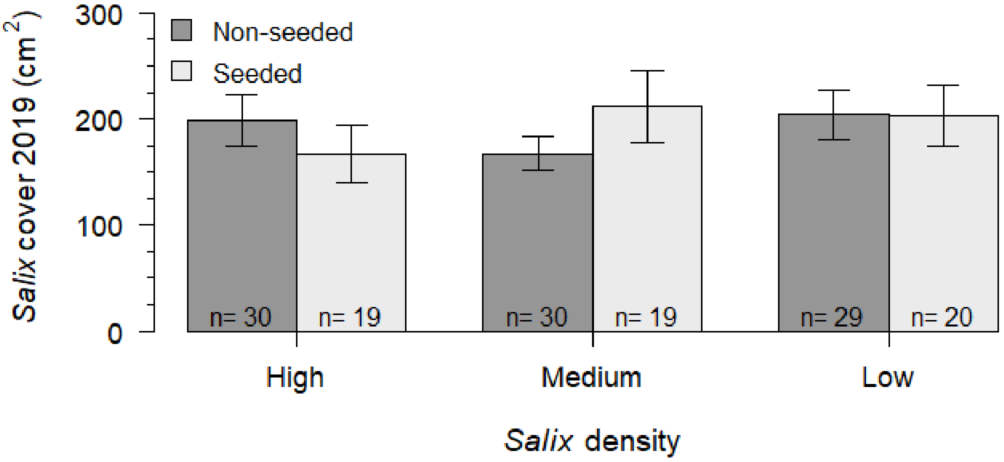


Figure 6. Mean (± *SE*) *Salix* cover in 2019 (cm^2), grouped by *Salix* density (high = 4 plants/m^2, medium = 2.5 plants/m^2, and low = 1 plant/m^2) and seeding treatment (non-seeded or seeded with *F. ovina*); *n* denotes the number of subplots per combination of treatments. Figure is based on the raw data.

3.1.2 Salix growth (2014-2019)

Salix growth between 2014 and 2019, grouped by *Salix* density and seeding treatment, is shown in Figure 7. In 2019, 130 of the 139 plants included in the analysis showed an increase in cover, 4 plants showed a decrease and 5 plants showed no change compared to 2014. Model selection resulted in a model containing only the variable soil moisture (Appendix B) but this relationship was not significant (p = .157). There was no effect of *Salix* density or seeding on *Salix* growth, and *Salix* growth showed no relationship with the percentage of fine soil substrate in the subplot.

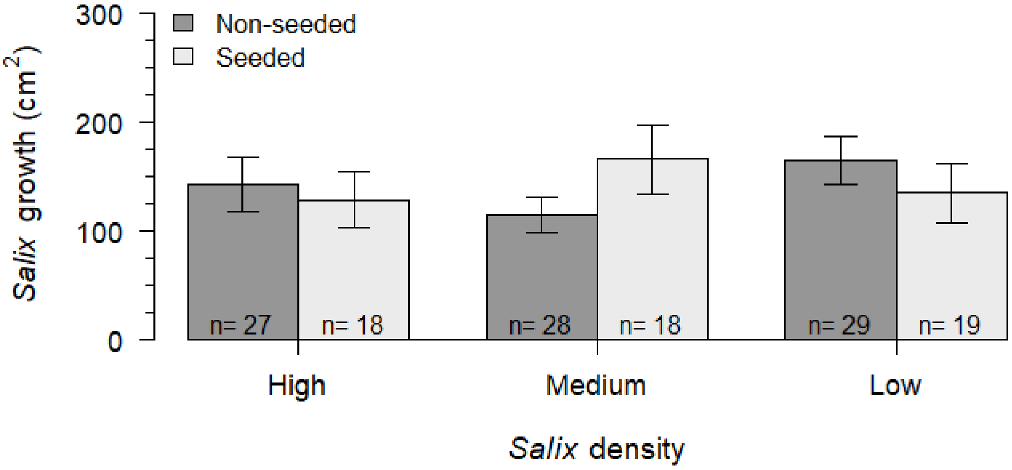


Figure 7. Mean (± *SE*) *Salix* growth between 2014 and 2019 (cm^2), grouped by *Salix* density (high = 4 plants/m^2, medium = 2.5 plants/m^2, and low = 1 plant/m^2) and seeding treatment (non-seeded or seeded with *F. ovina*); *n* denotes the number of subplots per combination of treatments. Figure is based on the raw data.

3.1.3 Salix recruitment

Salix recruitment for the dataset without outlier is shown in Figure 8a, grouped by *Salix* density and seeding treatment. *Salix* recruitment for this dataset was best predicted by a model including the variables *Salix* density and soil moisture (Appendix C, Table C1). *Salix* density had a significant effect on *Salix* recruitment; recruitment (pooled over seeding treatments) was lowest in control plots and increased with increasing *Salix* density. Post-hoc comparisons showed that all *Salix* densities except high and medium differed significantly from each other in terms of recruitment (p < .050; Tukey HSD test output in Appendix C, Table C2). Furthermore, *Salix* recruitment showed a significant positive relationship with soil moisture (p < .001; Appendix C, Table C1; Figure 8b). There was no effect of seeding on

Salix recruitment, and *Salix* recruitment showed no relationship with the percentage of fine soil substrate in the subplot.

Model selection for the dataset with outlier resulted in a model with the same (significant) variables (Appendix D, Table D1). However, inclusion of the outlier resulted in a higher mean recruitment in the low *Salix* density (*M* = 1.31 [*SD* = 2.01] compared to *M* = 1.08 [*SD* = 1.29] in the dataset without outlier) so that in addition to the high and medium density, also the low and medium *Salix* density did not differ significantly from each other in terms of recruitment (*p* = .053; Tukey HSD test output in Appendix D, Table D2). The bar chart with *Salix* recruitment for this dataset is not shown.

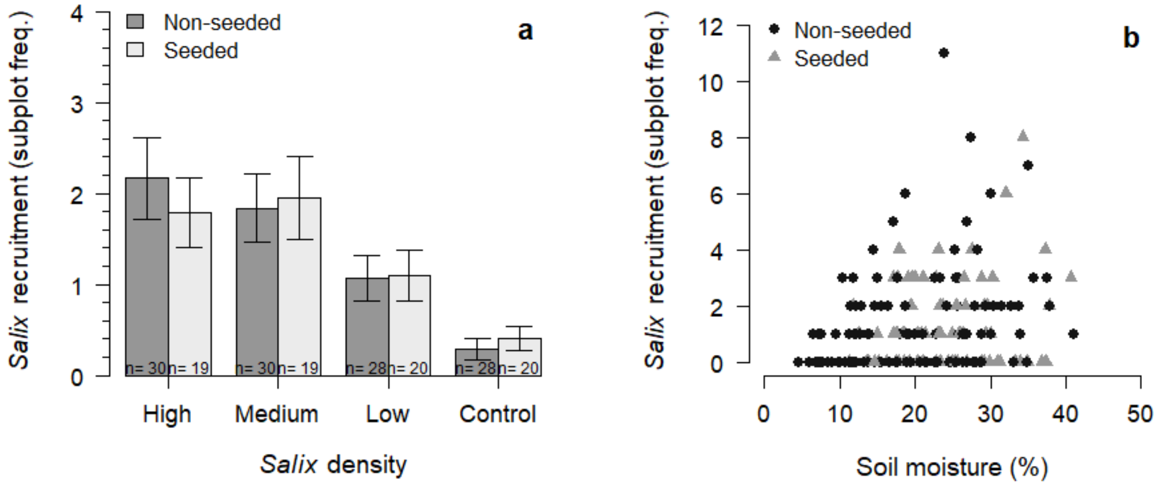


Figure 8. a) Mean (± *SE*) *Salix* recruitment (seedling subplot frequency), grouped by *Salix* density (high = 4 plants/m^2, medium = 2.5 plants/m^2, low = 1 plant/m^2, and control = no planted *Salix*) and seeding treatment (non-seeded or seeded with *F. ovina*); *n* denotes the number of subplots per combination of treatments, b) relationship between *Salix* recruitment (seedling subplot frequency) and soil moisture (%; *p* < .001), coloured by seeding treatment. Figures are based on the raw data from the dataset without outlier.

3.2 Vegetation cover

3.2.1 Total vegetation cover

The percentage of total vegetation cover, grouped by *Salix* density and seeding treatment, is shown in Figure 9a. Total vegetation cover was best predicted by the full model including all variables (Appendix E, Table E1). *Salix* density did not have a significant effect on total vegetation cover; post-hoc comparisons showed that the cover (pooled over seeding treatments) was significantly lower in the control plots than in high, medium, and low *Salix* density plots (*p* < .001 in all cases) but no significant differences were found between high, medium and low density plots (*p* > .050 in all cases; Tukey HSD test, Appendix E, Table E2). Seeding had a significant positive effect on total vegetation cover, such that the cover (pooled over *Salix* density treatments) was higher in seeded than in non-seeded subplots (*p* = .004). Furthermore, total vegetation cover showed a significant positive relationship with soil moisture (*p* < .001; Appendix E, Table E1; Figure 10a) and with the percentage of fine soil substrate in the subplot (*p* = .016; Appendix E, Table E1; Figure 10b).

3.2.2 Bottom layer cover

The percentage of bottom layer cover, grouped by *Salix* density and seeding treatment, is shown in Figure 9b. The bottom layer consisted mainly of bryophytes; the contribution of lichens to the cover was negligible (< 0.1%). Bottom layer cover was best predicted by a model including seeding, soil moisture, and fine soil substrate (Appendix E, Table E1). A significant positive effect of seeding was found, such that the bottom layer cover (pooled over *Salix* density treatments) was higher in seeded than in non-seeded subplots (*p* < .001). Furthermore, bottom layer cover showed a significant positive relationship with soil moisture (*p* < .001; Appendix E, Table E1; Figure 10c) and with the percentage of fine soil substrate in the subplot (*p* = .044; Appendix E, Table E1; Figure 10d). *Salix* density had no effect on bottom layer cover.

3.2.3 Field layer cover

The percentage of field layer cover, grouped by *Salix* density and seeding treatment, is shown in Figure 9c. Field layer cover was best predicted by a model including seeding, soil moisture and fine soil substrate (Appendix E, Table E1). A significant positive effect of seeding was found, such that the field layer cover (pooled over *Salix* density treatments) was higher in seeded than in non-seeded subplots (*p* = .008). The difference in field layer cover between seeded and non-seeded subplots is illustrated with pictures in Appendix F. Furthermore, field layer cover showed a significant positive relationship with soil moisture (*p* < .001; Appendix E, Table E1; Figure 10e) and with the percentage of fine soil substrate in the subplot (*p* = .003; Appendix E, Table E1; Figure 10f). *Salix* density had no effect on field layer cover.

3.2.4 Shrub layer cover

The percentage of shrub layer cover, grouped by *Salix* density and seeding treatment, is shown in Figure 9d. At this stage, the shrub layer consisted of only the planted *Salix* individuals; the contribution of newly established seedlings of *Salix* and other shrub species was negligible (< 0.1%). Model selection resulted in a model containing only the variable fine soil substrate (Appendix E, Table E1) but this relationship was not significant ($p = .056$). There was no effect of *Salix* density or seeding on shrub layer cover, and shrub layer cover showed no relationship with soil moisture.

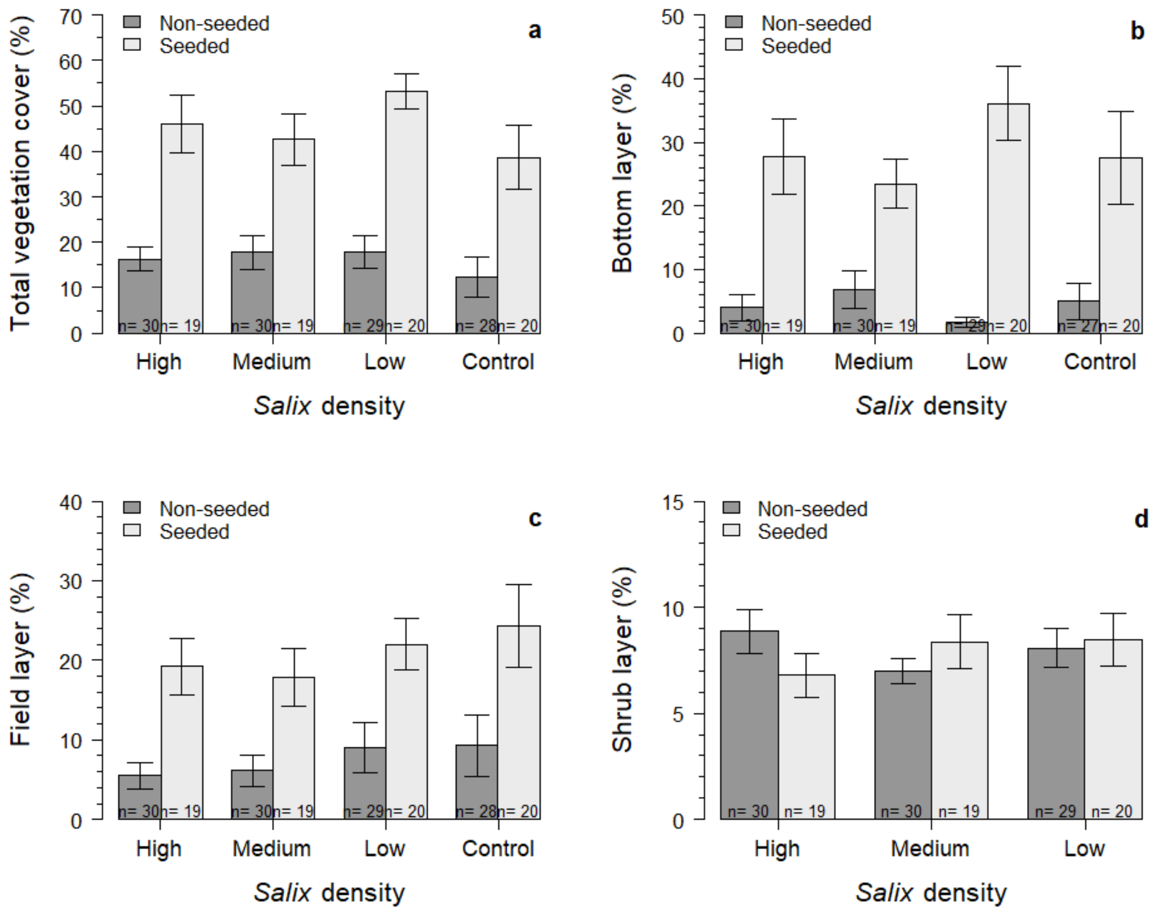


Figure 9. Mean (± *SE*) a) total vegetation cover (%), b) bottom layer cover (%), c) field layer cover (%), and d) shrub layer cover (%), grouped by *Salix* density (high = 4 plants/m^2, medium = 2.5 plants/m^2, low = 1 plant/m^2, and control = no planted *Salix*) and seeding treatment (non-seeded or seeded with *F. ovina*); *n* denotes the number of subplots per combination of treatments. The scale of the y-axis differs across the figures. Figures are based on the raw data.

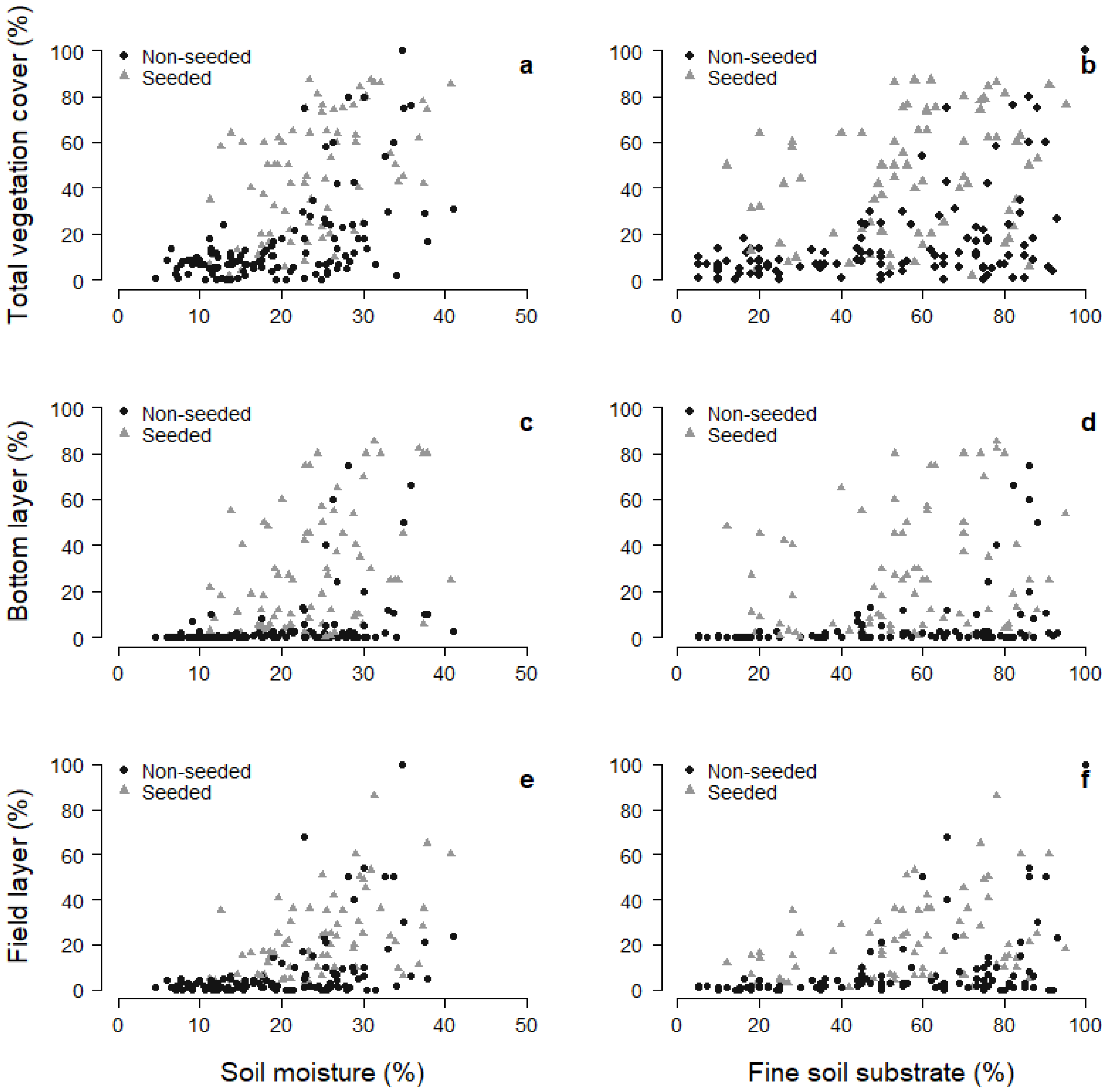


Figure 10. Relationship between total vegetation cover (%) and a) soil moisture (%), b) fine soil substrate (%); relationship between bottom layer cover (%) and c) soil moisture (%), d) fine soil substrate (%); relationship between field layer cover (%) and e) soil moisture (%), f) fine soil substrate (%). All relationships were significant ($p < .050$). Data points are coloured by seeding treatment (non-seeded or seeded with *F. ovina*). Figures are based on the raw data.

3.3 Vascular plant diversity

In total, 38 different species belonging to 29 different genera were observed in the study site. A list with the abundance of each species in terms of the total number and percentage of subplots and units that the species was present in, is provided in Appendix G.

Of all species, *Deschampsia cespitosa* was the most abundant; it was present in 71.1% of the subplots and in 31.4% of all units in the study. Other observed graminoids, ranked by the percentage of subplots that they occurred in, were *Luzula* sp. (28.4%), *Agrostis* sp. (16.2%), *Poa* sp. (16.2%), and *F. rubra* (15.7%). Also present were single individuals of less common species such as *Calamagrostis lapponica* spp. *lapponica*. Among forbs, *Sagina saginoides* (54.3%) and *Cerastium* sp. (48.7%) were the most abundant, followed by *Rumex acetosella* (19.8%). *Equisetum arvense* had a high abundance in moist subplots. The most common shrubs were seedlings of *Salix* sp. (55.8%) and *Betula nana* (46.2%).

Vascular plant species diversity (Shannon index), grouped by *Salix* density and seeding treatment, is shown in Figure 11a. Vascular plant species diversity was best predicted by a model including *Salix* density, soil moisture, and fine soil substrate (Appendix H, Table H1). *Salix* density had a significant effect on species diversity; the diversity (pooled over seeding treatments) was lowest in control plots and increased with increasing *Salix* density. However, post-hoc comparisons showed that only the difference between high *Salix* density plots and control plots was significant ($p = .010$; Tukey HSD test, Appendix H, Table H2). Furthermore, vascular plant species diversity showed a significant positive relationship with soil moisture ($p = .025$; Appendix H, Table H1; Figure 11b) and with the percentage of fine soil substrate in the subplot ($p < .001$; Appendix H, Table H1; Figure 11c). Seeding had no effect on species diversity.

Model selection for genus diversity resulted in a model with the same (significant) variables (Appendix I, Table I1) and similar differences in diversity between *Salix* densities (Figure not shown). Post-hoc comparisons showed that in terms of genus diversity, both high and medium *Salix* density plots differed significantly from control plots ($p < .050$; Tukey HSD test output in Appendix I, Table I2).

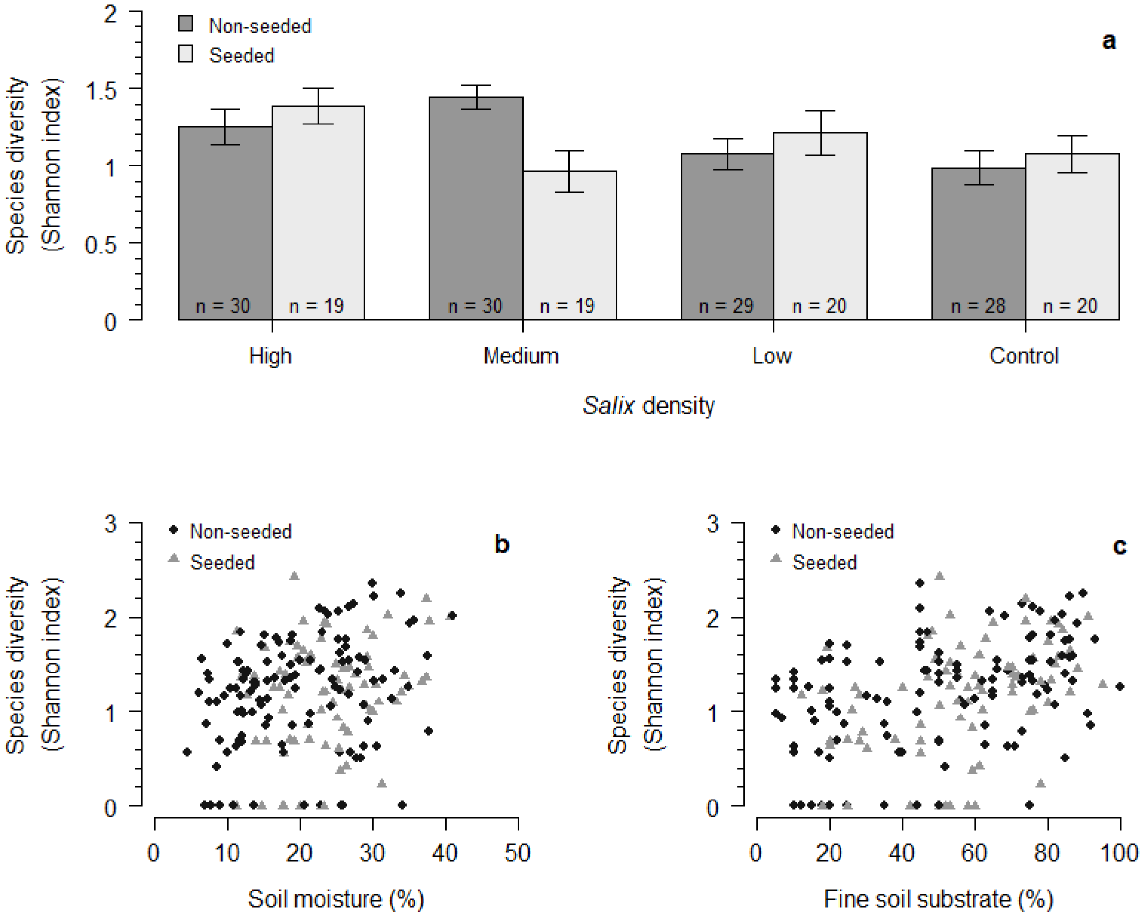


Figure 11. a) Mean (± *SE*) vascular plant species diversity (Shannon index), grouped by *Salix* density (high = 4 plants/m^2, medium = 2.5 plants/m^2, low = 1 plant/m^2, and control = no planted *Salix*) and seeding treatment (non-seeded or seeded with *F. ovina*); *n* denotes the number of subplots per combination of treatments. Below: relationship between vascular plant species diversity (Shannon index) and b) soil moisture (%, $p = .025$), c) fine soil substrate (%, $p < .001$). Data points are coloured by seeding treatment. All figures are based on the raw data.

3.4 Large-scale revegetation patterns in the study site

The DSM of the study site (Figure 12) showed that the large-scale revegetation pattern was linked to topography. Vegetation cover seemed to be highest in the depressed areas flanked by slopes, i.e., along the built-up ridges. The orthomosaic of the study site is shown in Appendix J.

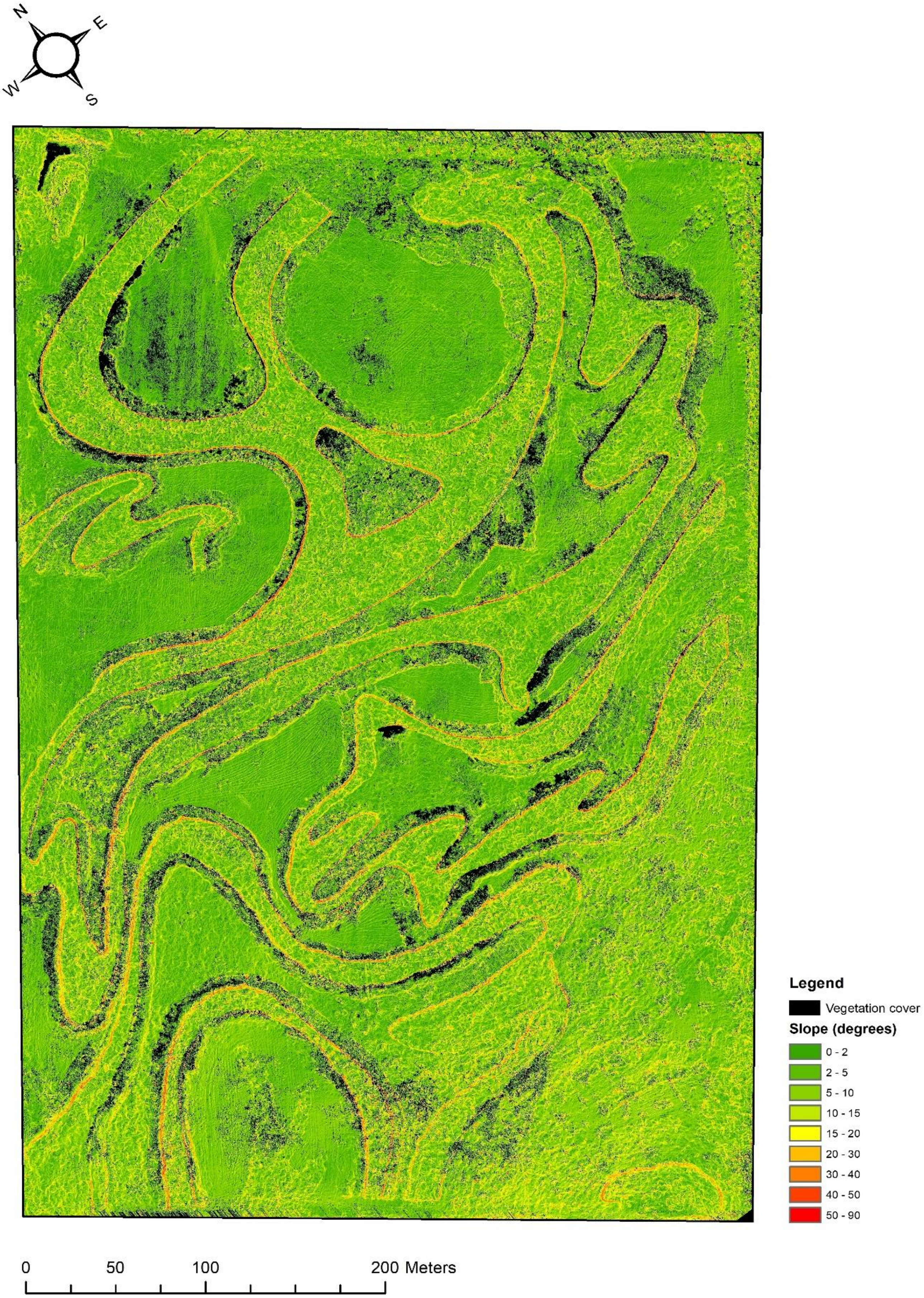


Figure 12. Digital surface model (DSM) of the study site (400 x 600 m) in the Hjerkinn firing range, showing the relationship between vegetation cover and slope in 2019.

4. Discussion

The results of this study showed that five years after implementation of the restoration treatments in the study site – a disturbed alpine heathland in the Dovre Mountains – the propagated *Salix* plants had a positive effect on vascular plant diversity but they had no effect on vegetation cover in terms of natural recovery. Seeding of *F. ovina* on the other hand, resulted in a higher bottom and field layer cover, while it did not affect vascular plant diversity. The results also showed that environmental conditions – soil moisture and the percentage of fine soil substrate in the subplot – were strongly related to vegetation recovery. At a larger scale, encompassing the entire study site, small-scale topography seemed to play a role in the revegetation process.

4.1 Effects of planted *Salix* on vegetation recovery

There was a high survival rate of the *Salix* plantings since the start of the experiment. A few single plants died, mainly in the first year after planting, which suggests that this has been the most critical phase for survival, a finding similar to earlier studies (Hagen, 2003; Mosseler et al., 2014). The high survival rate confirms that the *Salix* plants are able to cope with harsh environmental conditions and severely degraded soils with a thin layer of topsoil, as other studies have shown as well (e.g. Densmore & Holmes, 1987; Hagen, 2007; Kuzovkina & Quigley, 2005). The selected *Salix* species (*S. glauca*, *S. lapponum* and *S. phylicifolia*) thus seem suitable to be used as pioneer plants in alpine restoration efforts.

Plots with *Salix* plantings had, regardless of planting density, a higher total vegetation cover than control plots, but not a higher bottom nor field layer cover. The higher total vegetation cover was likely due to the presence of the shrub layer (i.e., the planted *Salix* itself) that was absent in control plots, rather than due to a facilitative effect of *Salix* plantings on the natural recovery of other vegetation. Furthermore, higher *Salix* planting densities did not result in a higher vegetation cover.

Vascular plant diversity on the other hand, was lowest in control plots and increased with increasing *Salix* density, but differences were small. Only control plots and plots with sufficiently high *Salix* densities (4 plants/m^2 in the case of species diversity, and 2.5 or 4 plants/m^2 in the case of genus diversity) differed significantly from each other. Possible explanations for this could be that *Salix* plantings must be sufficiently dense to provide a considerable number of safe sites or a notable improvement of soil conditions that facilitates the establishment of a wider range of species and genera. The findings imply that if *Salix* plants are used in restoration efforts to enhance vascular plant diversity, planting densities should be minimally 2.5 plants per square meter and preferably higher to attain a significant effect.

The increase in vascular plant diversity in plots with high and medium *Salix* densities did not coincide with an increase in field layer (or total vegetation) cover. Possible explanations for this are: (1) the number of species (and genera) and the number of established plants is higher, but due to the slow plant growth in alpine areas (Krautzer et al., 2012), the newly established plants do not yet contribute a quantitatively discernible amount of vegetation cover at this early stage. (2) *Salix* facilitates establishment and survival, but not growth of other species. This would be in line with a meta-analysis of studies on plant interactions in ecosystem restoration that revealed that nurse plants often facilitate establishment and survival of other species, but have neutral or negative effects on further growth (Gómez-Aparicio, 2009). Seedling establishment and survival are suggested to be more important than growth in early stages of restoration programs because of the low seedling survival rate in degraded ecosystems (Gómez-Aparicio, 2009). This might be even more important for the restoration of alpine areas, where seedling survival is a bottleneck for species establishment (Graae et al., 2011). (3) A larger number of individuals and species establishes, but due to competition for space and/or resources, only a limited number of individuals of each species survives. Although all three explanations would fit the field observation that there were numerous small plants, the third explanation seems improbable due to the scarce vegetation cover in many of the subplots. As the findings of this study showed that higher planting densities of *Salix* resulted in a higher vascular plant diversity but not a higher naturally established vegetation cover, hypothesis 1 is only partly confirmed.

In line with the findings of Hagen (2003), neither cover nor growth of the *Salix* plants was affected by planting density. This finding confirms the expectation that none of the planting densities used in this study (1, 2.5 and 4 plants/m^2) results in competition or facilitation among *Salix* plants during early stages of restoration. This might be explained by the fact that the plants were still small (mean *Salix* cover was 192 cm^2) and distances between plants were relatively large. The possibility exists that competitive or facilitative interactions will occur at a later stage, when further growth results in smaller distances between plants. *Salix* recruitment was lowest in control plots and increased with increasing *Salix* density. An explanation for the positive effect of *Salix* density on recruitment could be a higher seed production due to higher plant abundance and/or enhanced wind- or insect-pollination resulting from the smaller distances between plants. Worth noting is that in 2015, one year after planting, some of the small *Salix* plants already produced catkins (Hagen, personal communication). Furthermore, it could be that seedling establishment and survival were higher due to the higher densities of (*Salix*) nurse plants. Such positive density-dependent effects of nurse plants on seedling survival have been found to occur in harsh environments (Bertness & Callaway, 1994). The higher recruitment in plots with higher planting densities might lead to a more rapid development of the (*Salix*) shrub layer – if no competition occurs. The findings of this study support hypothesis 2 that *Salix* planting density does not affect *Salix* cover or growth at this stage, but that plots with higher planting densities have a higher *Salix* recruitment. Important to note, however, is that the two datasets for *Salix* recruitment (with and without outlier) provided slightly different results. Regardless, a conclusion that can be derived from both datasets is that the presence of *Salix* plantings significantly increased *Salix* recruitment compared to recruitment in control plots, and that high planting densities (4 plants/m^2) were more effective than low planting densities (1 plant/m^2).

4.2 Effects of seeded *F. ovina* on vegetation recovery

Plots seeded with *F. ovina* had a higher field layer cover than non-seeded plots. Most likely, this was largely due to the contribution of *F. ovina* itself, which was present in 90.9% of the total number of seeded subplot units whereas it was present in only 39.9% of all non-seeded subplot units. It is unknown whether *F. ovina* facilitated the establishment and growth of other graminoids and forbs, as cover percentages were estimated only for the field layer in its entirety, including *F. ovina*. Furthermore, seeded plots had a higher bottom layer (i.e., bryophyte) cover. This finding contradicts the large number of studies that show negative effects of vascular plants on bryophyte cover due to competition for light or space, among other reasons (e.g. Bergamini et al., 2001; Boch et al., 2018; Startsev et al., 2008; van der Wal et al., 2005). There are however a few studies that did find positive effects of forbs and grasses, including *Festuca pratensis*, on bryophyte cover (Fergus et al., 2017; Ingerpuu et al., 2005). These effects were attributed to changes in microclimate such as an increase in ambient moisture and changes in temperature, that might optimise conditions for bryophyte photosynthesis and thereby outweigh any negative effects caused by vascular plant cover

(Fergus et al., 2017; Ingerpuu et al., 2005). In the study of Ingerpuu et al. (2005), where the mean vascular plant cover was 40%, the positive effects prevailed at low vascular plant densities. As the mean total vegetation cover in the Hjerkinn study site was considerably lower (ca. 28% including both vascular plants and bryophytes), it seems reasonable to assume that similar effects of *F. ovina* facilitated the development of bryophyte cover.

Contrary to the expectations, neither *Salix* recruitment nor vascular plant diversity was affected by seeding of *F. ovina*. This suggests that, in contrast with the greenhouse experiment conducted by Hagen et al. (2014), *F. ovina* does not inhibit (nor facilitate) the establishment of other vascular plant species. These contradictory findings might be explained by the fact that environmental conditions in the field, such as nutrient and water supply, are more dynamic and presumably more constraining on plant growth (Verdú & Traveset, 2005); hence, the growth and thereby the competitive abilities of *F. ovina* might be more confined in the field. The results of this study provide only partial support for hypothesis 3 that seeding of *F. ovina* increases the field layer cover but negatively affects vascular plant diversity. These findings, in combination with a field study showing that *F. ovina* rapidly provides a vegetation cover when seeded as a monoculture (Rydgren et al., 2017), suggest that seeding of the grass could be an effective method to increase vegetation cover in early stages of restoration projects within the species' native range without negatively affecting vascular plant diversity. The species provides thereby more promising results than its congener *F. rubra* that was used in a pilot study in Hjerkinn and that showed a negative effect on species diversity (Hagen & Evju, 2013). Furthermore, the development of the monitored *Salix* plants and shrub layer cover (all *Salix* plants in the subplot) were not affected by seeding, which suggests that the two methods (planting of *Salix* and seeding of *F. ovina*) can be used simultaneously.

4.3 Relationships between environmental conditions and vegetation recovery

4.3.1 Soil moisture

Subplots with a higher moisture content in the upper five centimetres of soil had a higher bottom and field layer cover, as well as a higher total vegetation cover compared to dryer subplots. These findings are in line with findings from another study on revegetation in disturbed alpine plots, in which recovery was positively related to soil moisture conditions (Evju et al., 2012). This relationship could possibly be explained by the influence of soil moisture on plant productivity through the regulation of photosynthetic activity and nutrient availability (Bowman & Fisk, 2001; Fath, 2018; Johnson & Caldwell, 1975; Körner, 2003; Winkler et al., 2016). In general, an increase in soil moisture leads to increased photosynthetic activity, as long as the optimum moisture content for photosynthesis is not exceeded (Xu & Zhou, 2011).

Subplots with moister soils also had a higher *Salix* recruitment, which might be explained by the importance of soil moisture for seed germination and early seedling development (Fay & Schultz, 2009; Mosseler et al., 2014). *Salix* cover and growth on the other hand, showed no relationship with soil moisture. This difference between *Salix* seedlings and adult plants might be explained by rooting depth. Seedlings have shallow roots and are therefore dependent on the upper soil layer for their water supply. This upper layer is, especially in bare, exposed terrain, highly sensitive to short-timescale weather conditions (e.g. radiation, precipitation, and wind) that cause rapid fluctuations in moisture content (National Research Council, 2009). Such fluctuations could result in periodic water and nutrient shortages (Fath, 2018) that might negatively affect seedling survival. *Salix* plantings on the other hand, have more developed root systems that can reach depths of 40 to 45 cm (Rytter & Hansson, 1996) and thereby enable the plants to obtain water from deeper soil layers with a more stable water content. In contrast with the seedlings, the plants show therefore no relationship with moisture content in the upper soil layer.

Rooting depth might also explain the positive relationship between soil moisture and vascular plant diversity, as many of the species were small, newly established herbs with presumably shallow root systems. As species differ in their sensitivity to water and nutrient stress (Bowman & Fisk, 2001), another explanation for the higher diversity might be that higher moisture levels enable the establishment of a wider range of species, including species that are more sensitive to water and nutrient stress.

Although it seems logical that soil moisture positively influenced vegetation recovery in the study site, it should be noted that the relationship between soil moisture and vegetation is likely to be two-directional as vegetation is also known to influence soil moisture content by affecting soil water retention capacity, by altering radiative energy transfer between the soil and atmosphere, and by actively taking part in the water cycle through evapotranspiration (Aalto et al., 2013; Asbjornsen et al., 2011).

4.3.2 Soil substrate

Subplots with a higher percentage of fine soil substrate had a higher bottom and field layer cover, total vegetation cover, and vascular plant diversity. This is in line with findings of previous studies (e.g. Mehlhoop et al., 2018; Rydgren et al., 2013) and could be explained by the fact that finer soils in general have a higher water retention and nutrient holding capacity than coarse soils (Hornberger et al., 1998; Nebel & Wright, 1993). Thus, in finer soils, plants have a lower chance of experiencing water stress and nutrient shortages. In addition, soils with finer substrate allow a more downward root growth compared to coarse soils, in which larger particles must be circumnavigated (Popova et al., 2016), and thereby facilitate root growth to deeper soil layers with a more constant water supply. An exception however would be clay soils, as these often have a high bulk density as a result of compaction, and compact soil has been found to hamper root penetration (Popova et al., 2016). Only the non-existent relationship between *Salix* recruitment and fine soil substrate could not be explained. Nevertheless, the positive relationships between fine soil substrate and the different vegetation recovery metrics in this study strongly suggest that an improvement of soil conditions (i.e., improving the soil water retention capacity by increasing the amount of fine soil substrate) could contribute to a faster vegetation recovery in degraded sites.

4.3.3 Small-scale topography

The fact that vegetation cover in the study site seemed to be highest in the depressed areas flanked by slopes, i.e., along the built-up ridges, suggests that also small-scale topography of the restoration site plays a role in the revegetation process. This is in line with findings from previous studies (Jones & del Moral, 2005; e.g. Jumpponen et al., 1999; Rydgren et al., 2013). Jumpponen et al. (1999) found that concave surfaces had a greater overall plant recruitment than convex or plateau surfaces. This might be explained by the influence of topography on wind speed, as wind is an important seed dispersal mechanism in alpine areas (Tackenberg & Stöcklin, 2008). In depressions, wind velocities are lower, which results in an accumulation of wind-dispersed seeds in those areas that are flanked by slopes (Reichman, 1984). Also, terrain might influence seed germination and plant growth indirectly by influencing the distribution of soil moisture in the landscape. In alpine areas, small-scale depressions accumulate more snow than the surrounding areas, which results in moister conditions upon snowmelt in spring (DeWalle & Rango, 2008). Additionally, overland flow of rain- and/or snowmelt water is collected in depressions (Hayashi et al., 2003). Lastly, in depressions, the groundwater table is generally located closer to the surface than in higher areas (Woo, 2012), meaning that plants have to root less deep to reach moist soil layers. As terrain conditions seem to play a crucial role in the revegetation process in Hjerkinn, it can be concluded that artificially creating relief to increase the number of safe sites for seedling establishment is an important tool in ecosystem restoration.

The findings of this study support hypothesis 4 that fine soil substrate and soil moisture are positively related to vegetation recovery, and that small-scale topography is related to recovery at a larger scale. As the role of topography was only assessed exploratory and not related to more detailed observations of vegetation recovery, it would be interesting to study the influence of this factor in more detail in future monitoring studies.

4.4 Conclusion

The results of this study showed that five years after implementation, both restoration treatments (planting of propagated *Salix* and seeding of *F. ovina*) had a positive effect on the revegetation process, but their effectiveness depended on the metric that was used to estimate vegetation recovery. *Salix* plantings mainly increased vascular plant diversity, whereas seeding of *F. ovina* increased the field and bottom layer cover. If the outlined restoration goal is to increase both vascular plant diversity and vegetation cover (of all vegetation layers), planting and seeding might be used complementary to each other. To significantly increase vascular plant diversity, *Salix* planting densities should be minimally 2.5 plants per square meter. Furthermore, based on the results of this study, it is suggested that the effectiveness of the treatments could be increased by improving the soil water retention capacity to facilitate plant growth, and by creating small-scale topography to facilitate the accumulation and germination of wind-dispersed seeds. It should be emphasized that these results only showed the short-term effects of the implemented treatments. Long-term monitoring should be performed to gain an understanding of the effects on vegetation recovery on a longer timescale.

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Appendices

Appendix A

Establishment of control plots

Schematic overview of the establishment procedure for the control plots in the study site in the Hjerkinn firing range in 2019. In total, 10 control plots were established: one paired to each of the 10 monitored fields with Salix plantings. Establishment occurred according to the criteria stated in section 2.4. A schematic diagram is shown on the next page (Figure A).

Step 1.

Within a field, the three experimental plots were located roughly on a line. This imaginary line through the plots was extended in both directions by walking up to 15 m beyond the border of the field. The 15 m long strips of terrain (with a width of 5 m, equal to the width of the plots) on both sides of the field were visually examined in terms of similarity to the terrain of the plots (see Figure A, step 1).

Step 2.

Starting from the border of the field, 10 m were measured with a measuring tape in the direction that was considered most suitable for the establishment of the control plot (see Figure A, step 2).

Step 3.

If the spot at 10 m distance from the field met the establishment criteria, a stick was thrown in the air. The landing point (indicated with ‘X’) would be the midpoint of the control plot (i.e., the midpoint of control subplot 3), as illustrated in Figure A, step 3. If the spot at 10 m distance from the field did not meet establishment criteria 2 (similar terrain conditions) and 3 (a distance of 10 m between the border of the planted field and the midpoint of the control plot), criterion 2 was prioritised; hence, the distance stated in criterion 3 was gradually reduced from 10 m up to a minimum of 4.5 m, until a spot was found that met the criteria.

Appendix is continued on the next page.

Appendix A (continued)

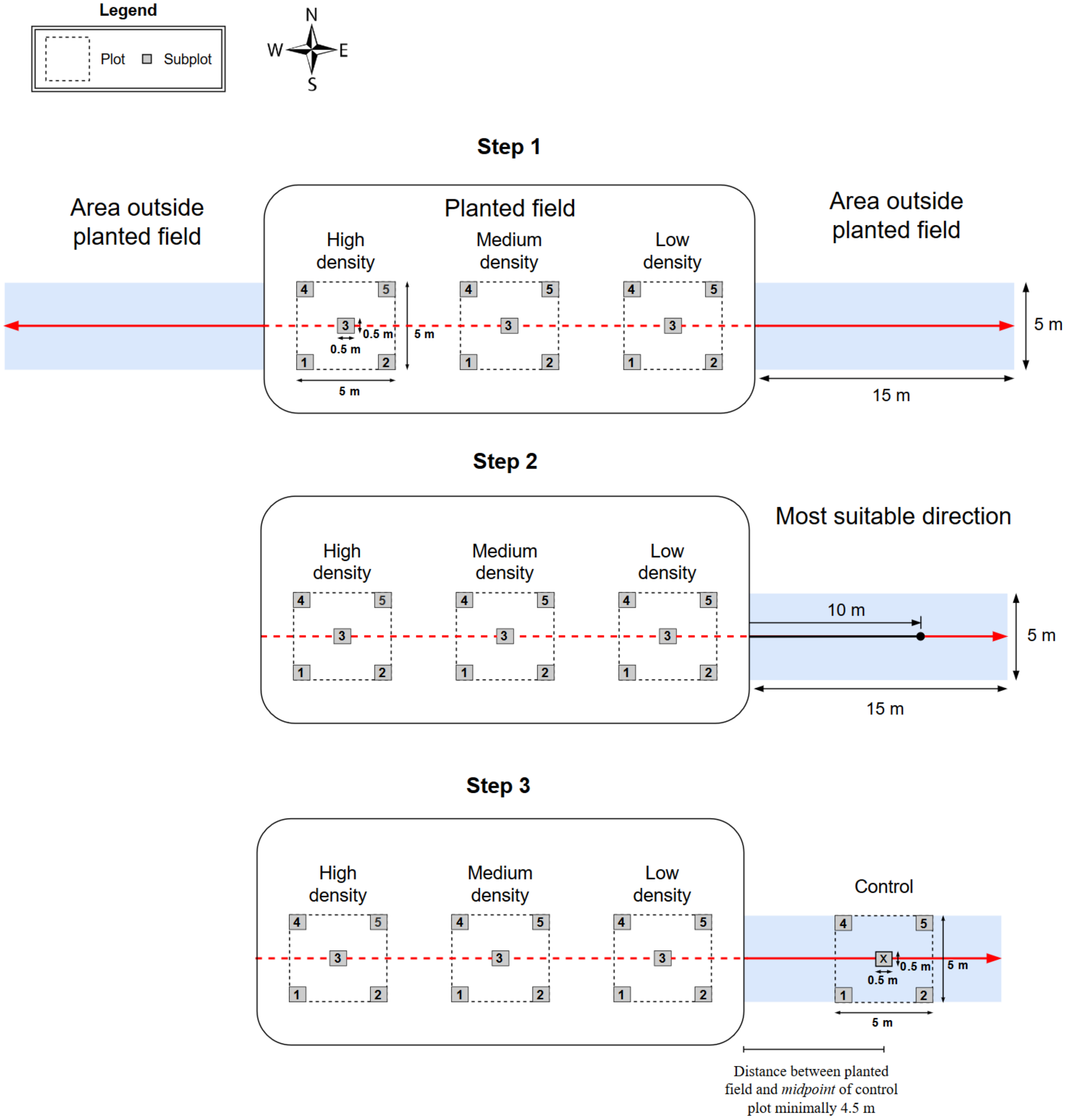

Figure A. Schematic diagram of the establishment procedure for the control plots.

Appendix B

Test output *Salix* cover and growth

Table B. Output of the final LMMs (resulting from model selection) for the dependent variables Salix cover in 2019 (cm^2); square root transformed, and Salix growth 2014 – 2019 (cm^2). The full model included the fixed factors Salix density and seeding, and the standardised covariates soil moisture and fine soil substrate. Parameter estimates of the random factor (field number) are not shown.

Dependent variable	**Independent variable**	**Estimate**	***SE***	***df***	***t*-value**	***p*-value**
Salix cover 2019	Intercept	13.212	0.343	147.000	38.477	< .001***
	Fine soil substrate	0.626	0.339	147.000	1.845	.067
Salix growth 2014-2019	Intercept	140.793	9.646	139.000	14.596	< .001***
	Soil moisture	14.068	9.881	139.000	1.424	.157

Note. * *p* < .050, ** *p* < .010, *** *p* < .001

Appendix C

Test output *Salix* recruitment – Dataset without outlier

Table C1. Output of the final LMM (resulting from model selection) for the dependent variable Salix recruitment (seedling subplot frequency). The model was run with a Poisson distribution on the dataset without outlier. The full model included the fixed factors Salix density (H = high, M = medium, L = low, and C = control) and seeding, and the standardised covariates soil moisture and fine soil substrate. The intercept refers to the average for the high Salix density treatment. Parameter estimates of the random factor (field number) are not shown.

Dependent variable	**Independent variable**	**Estimate**	***SE***	***z*-value**	***p*-value**
Salix recruitment	Intercept	0.572	0.181	3.165	.002**
	Salix density L vs. H	- 0.725	0.172	- 4.219	< .001***
	Salix density M vs. H	- 0.114	0.145	- 0.787	.431
	Salix density C vs. H	- 1.738	0.269	- 6.474	<.001***
	Soil moisture	0.386	0.082	4.730	< .001***

Note. * *p* < .050, ** *p* < .010, *** *p* < .001

Table C2. Output of the post-hoc comparisons (Tukey HSD test) for the fixed factor Salix density, run on the final LMM for the dependent variable Salix recruitment (shown in Table C1). Estimates show the difference in mean for each contrast of Salix densities.

Dependent variable	***Salix* densities contrast**	**Estimate**	***SE***	***z*-value**	***p*-value**
Salix recruitment	L vs. H	- 0.725	0.172	- 4.219	< .001***
	M vs. H	- 0.114	0.145	- 0.787	.854
	C vs. H	- 1.738	0.269	- 6.474	< .001***
	M vs. L	0.611	0.173	3.521	.002**
	C vs. L	- 1.014	0.286	- 3.544	.002**
	C vs. M	- 1.624	0.271	- 6.000	< .001***

Note. * *p* < .050, ** *p* < .010, *** *p* < .001

Appendix D

Test output *Salix* recruitment – Dataset with outlier

Table D1. Output of the final LMM (resulting from model selection) for the dependent variable Salix recruitment (seedling subplot frequency). The model was run with a Poisson distribution on the dataset with outlier. The full model included the fixed factors Salix density (H = high, M = medium, L = low, and C = control) and seeding, and the standardised covariates soil moisture and fine soil substrate. The intercept refers to the average for the high Salix density treatment. Parameter estimates of the random factor (field number) are not shown.

Dependent variable	**Independent variable**	**Estimate**	***SE***	***z*-value**	***p*-value**
Salix recruitment	Intercept	0.598	0.178	3.366	< .001***
	Salix density L vs. H	- 0.517	0.161	- 3.214	.001**
	Salix density M vs. H	- 0.107	0.145	- 0.740	.459
	Salix density C vs. H	- 1.732	0.269	- 6.448	< .001***
	Soil moisture	0.365	0.082	4.426	< .001***

Note. * *p* < .050, ** *p* < .010, *** *p* < .001

Table D2. Output of the post-hoc comparisons (Tukey HSD test) for the fixed factor Salix density, run on the final LMM for the dependent variable Salix recruitment (shown in Table D1). Estimates show the difference in mean for each contrast of Salix densities.

Dependent variable	***Salix* densities contrast**	**Estimate**	***SE***	***z*-value**	***p*-value**
Salix recruitment	L vs. H	- 0.517	0.161	- 3.214	< .007**
	M vs. H	- 0.107	0.145	- 0.740	.876
	C vs. H	- 1.732	0.269	- 6.448	< .001***
	M vs. L	0.410	0.163	2.519	.053
	C vs. L	- 1.215	0.280	- 4.342	< .001***
	C vs. M	- 1.624	0.271	- 6.000	< .001***

Note. * *p* < .050, ** *p* < .010, *** *p* < .001

Appendix E

Test output vegetation cover

Table E1. Output of the final LMMs (resulting from model selection) for the dependent variables total vegetation cover (%), bottom layer cover (%), field layer cover (%); all log-transformed, and shrub layer cover (%); square root transformed. The full model included the fixed factors Salix density (H = high, M = medium, L = low, and C = control[1]) and seeding, and the standardised covariates soil moisture and fine soil substrate. For the total vegetation cover model, the intercept refers to the average for the high Salix density treatment. Parameter estimates of the random factor (field number) are not shown. [1]The analysis for shrub layer cover did not include control plots.

Dependent variable	**Independent variable**	**Estimate**	***SE***	***df***	***t*-value**	***p*-value**
Total vegetation cover	Intercept	2.589	0.192	13.355	13.483	< .001***
	Salix density L vs. H	0.092	0.120	185.494	0.763	.447
	Salix density M vs. H	- 0.023	0.120	185.038	- 0.190	.850
	Salix density C vs. H	- 0.725	0.122	186.030	- 5.950	< .001***
	Seeded vs. non-seeded	1.033	0.282	9.939	3.663	.004**
	Soil moisture	0.374	0.068	178.188	5.488	< .001***
	Fine soil substrate	0.160	0.066	182.442	2.439	.016*
Bottom layer cover	Intercept	0.905	0.192	9.816	4.706	< .001***
	Seeded vs. non-seeded	1.823	0.306	10.000	5.963	< .001***
	Soil moisture	0.385	0.092	142.946	4.173	< .001***
	Fine soil substrate	0.184	0.091	146.660	2.028	.044*
Field layer cover	Intercept	1.514	0.202	9.909	7.504	< .001***
	Seeded vs. non-seeded	1.066	0.320	10.031	3.329	.008**
	Soil moisture	0.436	0.073	184.401	5.979	< .001***
	Fine soil substrate	0.215	0.071	186.476	3.024	.003**
Shrub layer cover	Intercept	2.698	0.067	147.000	40.040	< .001***
	Fine soil substrate	0.128	0.067	147.000	1.928	.056

Note. * $p < .050$, ** $p < .010$, *** $p < .001$

Appendix is continued on the next page.

Appendix E (continued)

Table E2. Output of the post-hoc comparisons (Tukey HSD test) for the fixed factor Salix density (H = high, M = medium, L = low, and C = control), run on the final LMM for the dependent variable total vegetation cover (shown in Table E1). Estimates show the difference in mean for each contrast of Salix densities.

Dependent variable	***Salix* densities contrast**	**Estimate**	***SE***	***z*-value**	***p*-value**
Total vegetation cover	L vs. H	0.092	0.120	0.763	.871
	M vs. H	- 0.023	0.120	- 0.190	.998
	C vs. H	- 0.725	0.122	- 5.950	< .001***
	M vs. L	- 0.114	0.121	- 0.944	.781
	C vs. L	- 0.816	0.125	- 6.555	< .001***
	C vs. M	- 0.702	0.120	- 5.828	< .001***

Note. * *p* < .050, ** *p* < .010, *** *p* < .001

Appendix F

Photographs of seeded and non-seeded subplots

Figure F. a) A seeded subplot, and b) a non-seeded subplot, both located in plots with a high *Salix* planting density.

Appendix G

List of vascular plant species

Table G. Alphabetical list of vascular plant species and genera that were observed in the study site in the Hjerkinn firing range (Dovre Mountains, Central Norway) in 2019. The table shows the total number of subplots and units that a species or genus was observed in, both as an absolute number and as a percentage of the total number of subplots (197) or units (3152**) in the study. The planted Salix species and seeded F. ovina are not included in the list. * This number includes the incorrectly located subplots but not the subplots in which the Salix plant had died or had been dug out by a muskox. ** 197 subplots x 16 units = 3152 units.*

Species	**Total number subplots**	**% of subplots**	**Total number units**	**% of units**
Agrostis sp.	32	16.2	81	2.6
Alchemilla sp.	2	1.0	2	0.1
Astragalus alpinus	7	3.6	20	0.6
Betula nana	91	46.2	188	6.0
Bistorta vivipara	2	1.0	5	0.2
Calamagrostis lapponica ssp. *lapponica*	1	0.5	1	< 0.1
Carex sp.	2	1.0	2	0.1
Cerastium alpinum	13	6.6	41	1.3
Cerastium fontanum	31	15.7	56	1.8
Cerastium sp.	96	48.7	438	13.9
Deschampsia cespitosa	140	71.1	989	31.4
Empetrum nigrum	4	2.0	4	0.1
Equisetum arvense	24	12.2	197	6.3
Euphrasia wettsteinii	1	0.5	7	0.2
Festuca rubra	31	15.7	95	3.0
Juncus arcticus	6	3.0	30	1.0
Juncus biglumis	1	0.5	1	< 0.1

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Appendix G (continued)

Species	**Number of subplots**	**% of subplots**	**Total number units**	**% of units**
Juncus trifidus	1	0.5	2	0.1
Juncus triglumis	2	1.0	3	0.1
Juncus sp.	15	7.6	27	0.9
Luzula multiflora	6	3.0	10	0.3
Luzula sp.	56	28.4	192	6.1
Poa alpina	17	8.6	32	1.0
Poa glauca	2	1.0	3	0.1
Poa pratensis	3	1.5	12	0.4
Poa sp.	32	16.2	66	2.1
Potentilla crantzii	1	0.5	3	0.1
Primula scandinavica	1	0.5	1	< 0.1
Rumex acetosella	39	19.8	193	6.1
Sagina nivalis	8	4.1	13	0.4
Sagina nodosa	9	4.6	17	0.5
Sagina saginoides	107	54.3	719	22.8
Sagina sp.	42	21.3	235	7.5
Salix herbacea (seedling)	1	0.5	1	< 0.1
Salix sp. (seedling)	110	55.8	270	8.6
Saxifraga aizoides	8	4.1	9	0.3
Silene acaulis	2	1.0	2	0.1
Stellaria borealis	5	2.5	14	0.4
Stellaria sp.	8	4.1	20	0.6
Thalictrum alpinum	1	0.5	2	0.1
Tofieldia pusilla	2	1.0	2	0.1
Trifolium repens	1	0.5	1	< 0.1
Vaccinium uliginosum	1	0.5	4	0.1
Vaccinium vitis-idaea	1	0.5	2	0.1
Viola sp.	1	0.5	1	< 0.1

Appendix H

Test output vascular plant species diversity

Table H1. Output of the final LMM (resulting from model selection) for the dependent variable vascular plant species diversity (Shannon index). The full model included the fixed factors Salix density (H = high, M = medium, L = low, and C = control) and seeding, and the standardised covariates soil moisture and fine soil substrate. The intercept refers to the average for the high Salix density treatment. Parameter estimates of the random factor (field number) are not shown.

Dependent variable	**Independent variable**	**Estimate**	***SE***	***df***	***t*-value**	***p*-value**
Vascular plant species diversity	Intercept	1.322	0.087	32.133	15.245	< .001***
	Salix density L vs. H[1]	- 0.200	0.099	185.521	- 2.028	.044*
	Salix density M vs. H	- 0.075	0.099	184.538	- 0.765	.446
	Salix density C vs. H	- 0.314	0.100	186.677	- 3.132	.002**
	Soil moisture	0.113	0.049	72.345	2.284	.025*
	Fine soil substrate	0.186	0.048	87.456	3.845	< .001***

Note. * p < .050, ** p < .010, *** p < .001

[1] This contrast was significant in the model output but not in the Tukey HSD test because the latter adjusts for multiple comparisons.

Table H2. Output of the post-hoc comparisons (Tukey HSD test) for the fixed factor Salix density, run on the final LMM for the dependent variable vascular plant species diversity (shown in Table H1). Estimates show the difference in mean for each contrast of Salix densities.

Dependent variable	***Salix* densities contrast**	**Estimate**	***SE***	***z*-value**	***p*-value**
Vascular plant species diversity	L vs. H	- 0.200	0.099	- 2.028	.178
	M vs. H	- 0.075	0.099	- 0.765	.870
	C vs. H	- 0.314	0.100	- 3.132	.010**
	M vs. L	0.125	0.099	1.257	.590
	C vs. L	- 0.113	0.102	- 1.113	.682
	C vs. M	- 0.238	0.099	- 2.402	.077

Note. * p < .050, ** p < .010, *** p < .001

Appendix I

Test output vascular plant genus diversity

Table I1. Output of the final LMM (resulting from model selection) for the dependent variable vascular plant genus diversity (Shannon index). The full model included the fixed factors Salix density (H = high, M = medium, L = low, and C = control) and seeding, and the standardised covariates soil moisture and fine soil substrate. The intercept refers to the average for the high Salix density treatment. Parameter estimates of the random factor (field number) are not shown.

Dependent variable	**Independent variable**	**Estimate**	***SE***	***df***	***t*-value**	***p*-value**
Vascular plant genus diversity	Intercept	1.240	0.081	31.138	15.342	< .001***
	Salix density L vs. H	- 0.140	0.093	184.966	- 1.513	.132
	Salix density M vs. H	- 0.035	0.092	183.918	- 0.376	.708
	Salix density C vs. H	- 0.309	0.094	186.195	- 3.286	.001**
	Soil moisture	0.098	0.046	67.965	2.128	.037*
	Fine soil substrate	0.185	0.045	82.655	4.088	< .001***

Note. * *p* < .050, ** *p* < .010, *** *p* < .001

Table I2. Output of the post-hoc comparisons (Tukey HSD test) for the fixed factor Salix density, run on the final LMM for the dependent variable vascular plant genus diversity (shown in Table I1). Estimates show the difference in mean for each contrast of Salix densities.

Dependent variable	***Salix* densities contrast**	**Estimate**	***SE***	***z*-value**	***p*-value**
Vascular plant genus diversity	L vs. H	- 0.140	0.093	- 1.513	.430
	M vs. H	- 0.035	0.092	- 0.376	.982
	C vs. H	- 0.309	0.094	- 3.286	.006**
	M vs. L	0.105	0.093	1.130	.671
	C vs. L	- 0.168	0.095	- 1.765	.291
	C vs. M	- 0.274	0.093	- 2.943	.017*

Note. * *p* < .050, ** *p* < .010, *** *p* < .001

Appendix J

Orthomosaic of the study site

Figure J. Orthomosaic of the study site (400 x 600 m) in the Hjerkinn firing range in 2019.

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