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RESEARCH ARTICLE

Alpine restoration: planting and seeding of native species facilitate vegetation recovery

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Vegetation recovery in severely disturbed alpine ecosystems can be accelerated through active restoration measures. This study evaluated the short-term effects of two restoration treatments, planting of propagated native *Salix* (willow) shrubs in three different densities (1, 2.5, and 4 plants/m^2) and seeding of the native grass *Festuca ovina* (sheep fescue), in a disturbed alpine heathland. We evaluated natural vegetation recovery (i.e. vegetation cover, vascular plant species richness, and *Salix* recruitment) in permanent plots, 5 years after the implementation of restoration measures. The results showed that both treatments had positive but different effects on vegetation recovery; *Salix* plantings (with densities ≥2.5 plants/m^2) increased vascular plant species richness and recruitment of *Salix* seedlings, whereas seeding of *F. ovina* increased bottom and field layer cover. Our results also show the importance of soil conditions for vegetation recovery, as moister plots with a higher percentage of fine soil substrate had a higher vegetation cover and vascular plant species richness. This study shows that different restoration treatments can work complementary and also highlights the importance of considering different indicators of vegetation recovery when evaluating the effectiveness of restoration measures.

Key words: alpine heathland restoration, *Festuca ovina*, native grass, native shrubs, natural vegetation recovery, *Salix* plantings, soil moisture, soil substrate

Implications for Practice

- In severely disturbed alpine sites, a combination of restoration treatments improves short-term natural recovery of vegetation.
- Planting of native *Salix* shrubs accelerates recovery of vascular plant species richness and increases *Salix* recruitment, with higher planting densities being more effective.
- Seeding of native *Festuca ovina* can complement the *Salix* treatment to increase bottom and field layer cover.
- Improving soil conditions by increasing the amount of fine soil substrate contributes to a faster natural vegetation recovery.

Introduction

Natural recovery of vegetation after disturbance in alpine ecosystems can take decades to centuries due to the harsh environmental conditions, short growing seasons, and slow rate of biological processes that characterize these high-altitude areas (Willard et al. 2007; Krautzer et al. 2012). Recovery proceeds faster under favorable environmental conditions, such as a fine soil substrate and optimal soil moisture levels (Evju et al. 2012; Rydgren et al. 2013; Mehlhoop et al. 2018) and can be accelerated through active restoration measures such as restoring terrain and soil conditions, fertilizing, seeding, or planting (Forbes & Jefferies 1999; Krautzer et al. 2012; Hagen & Evju 2013).

A method that has gained interest among restoration ecologists in recent years, is the use of nurse plants that facilitate the establishment, survival, and/or growth of other plants in disturbed environments through positive interactions, such as trapping of seeds or buffering of physical stresses, e.g. direct sunlight or wind (Bertness & Callaway 1994; Padilla & Pugnaire 2006; Gómez-Aparicio 2009). Nurse plants thereby offer the potential for enhanced vegetation recovery on disturbed terrain in environments with harsh abiotic conditions, such as alpine areas.

Studies on *Salix* (willow) shrubs in alpine ecosystems have demonstrated a nurse effect on other plant species through the provision of suitable microclimatic conditions and enhanced over-winter survival (Totland & Esaete 2002; Dona & Galen 2007; Endo et al. 2008). The *Salix* genus has been used in restoration efforts (Densmore & Holmes 1987; Kuzovkina & Quigley 2005; Aradóttir et al. 2007; Hagen 2007) because it harbors pioneer species that can colonize bare, severely degraded,

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dry, or nutrient-poor soils (Kuzovkina & Quigley 2005). Established *Salix* plants can improve soil conditions by facilitating the re-establishment of soil organisms (Sylvain & Mosseler 2017), thereby indirectly enhancing microbial decomposition and nutrient cycling and increasing the complexity of biotic interactions (Sylvain & Mosseler 2017). This may in turn increase the resilience of the ecosystem to future disturbances (Sylvain & Wall 2011). *Salix* plants are usually fast-growing, produce large quantities of viable seeds (Forbes & Jefferies 1999), and can easily be propagated via cuttings (Houle & Babeux 1998; Hagen 2002; Aradóttir et al. 2007), which allows for the use of native plant material that is usually better adapted to site-specific environmental conditions (Krautzer et al. 2012).

So far, no studies have compared effects of planting density on natural vegetation recovery. Experiments and theoretical models have shown that plant–plant facilitation is density-dependent and peaks at intermediate neighbor densities (Chu et al. 2008; Zhang & Tielbörger 2020). This peak shifts toward higher densities with increasing levels of abiotic stress (Zhang & Tielbörger 2020). However, even in stressful alpine environments, where facilitation might be expected, neighboring vegetation can hinder seedling recruitment and growth through competition (Tingstad et al. 2015; Klanderud et al. 2017). An understanding of planting density effects is thus vital for the development of successful restoration methods, and would also increase cost-effectiveness, as plant material for propagation can be limited in certain areas and propagation is costly.

Seeding of native plant species is traditionally considered a less costly and time-consuming approach to vegetation recovery than propagation of plants from cuttings. Seeded species are often fast-growing grasses that rapidly provide a vegetation cover (Hagen & Evju 2013). However, the effectiveness of grasses as nurse plants is ambiguous and context dependent, presumably because their life-form enables them to compete efficiently for resources (Choi & Wali 1995; Maestre et al. 2001; Gretarsdottir et al. 2004; Gómez-Aparicio 2009; Rydgren et al. 2013; Hagen et al. 2014). The few studies that found positive effects of native or artificially introduced grasses on vegetation recovery (e.g. Choi & Wali 1995; Maestre et al. 2001) were performed in sites with low nutrient availability (Gómez-Aparicio 2009), which suggests that grasses could function as nurse plants in nutrient-limited alpine environments.

Studies with commercially available seeds of *Festuca rubra* (red fescue) in alpine areas, however, showed that the grass increased vegetation cover but impeded the establishment of native species (Hagen & Evju 2013; Hagen et al. 2014). A complementary greenhouse experiment examining the effects of *F. rubra* and *F. ovina* (sheep fescue) on seedling establishment of *Betula nana* (dwarf birch) in different types of soils showed that germination and survival were less suppressed by *F. ovina* than by *F. rubra* (Hagen et al. 2014). Seedling establishment was highest when seeded without the grasses, yet, in coarse soil, *B. nana* seedlings survived only in the presence of *F. ovina* (Hagen et al. 2014). This suggests that the grass might act as a nurse plant in rough terrain. However, results from controlled greenhouse experiments cannot be directly translated to a field setting, where environmental conditions are more dynamic (Verdú & Traveset 2005; Rydgren et al. 2017). Field studies with *F. ovina* in alpine areas have shown that the grass rapidly provides a vegetation cover when seeded as a monoculture (Rydgren et al. 2017) and that seed mixtures including *F. ovina* can develop into large, persistent populations (Rydgren et al. 2011; Rydgren et al. 2016). However, examinations of the effects of seeded *F. ovina* monocultures on species richness have not yet been performed. Furthermore, studies on comparisons and combinations of the different efforts (planting of shrubs and seeding of grasses) on alpine vegetation recovery are lacking.

The aim of this study was to investigate the short-term effects (5 years after implementation) of two restoration measures on natural vegetation recovery in a severely disturbed alpine heathland: (1) planting of native *Salix* in three different densities (1, 2.5, and 4 plants/m^2) and (2) seeding of native *F. ovina*. Natural vegetation recovery was assessed using vegetation cover, vascular plant species richness, and *Salix* recruitment. Additionally, we investigated the role of soil conditions (soil moisture and amount of fine soil substrate) in natural vegetation recovery. We also examined whether *Salix* planting density, seeding of *F. ovina*, and soil conditions affected the performance of the planted *Salix* (i.e. cover and growth in the period 2014–2019).

Methods

Study Site

The study site used to be an ammunition testing area (400 × 600 m) in the former Hjerkinn firing range in the Dovre Mountains, Central Norway (62°13′33.6”N 9°27′43.2″E [WGS]; 1,060 m a.s.l.; Fig. S1). The firing range, located in one of the last largely intact high mountain ecosystems in Europe (Norwegian Environment Agency 2012), covers an area of 165 km^2 and was used as a military training area from 1923 to 2008. In 1999, the Norwegian Parliament announced to close down the firing range and restore the area to its “original, natural state” (Ministry of Defence 1998–1999). To reach this goal, restoration activities were carried out by the Norwegian Defence Estates Agency from 2009 to 2020.

The geology is characterized by calcium-poor glacial till overlying Precambrian metamorphic and igneous bedrock (Geological Survey of Norway 2019). The average annual temperature (1986–2016) at the nearest weather station (Fokstugu, 973 m a.s.l.) is 0.6°C, with an annual precipitation of 516.9 mm (Norwegian Meteorological Institute 2019). The vegetation is dominated by alpine dwarf-shrub heath, wetlands, and barren land (Moen & Odland 1999). Dominant shrub species are *Salix glauca* (grayleaf willow), *S. lapponum* (downy willow), and *S. phylicifolia* (tea-leaved willow; Elven & Fremstad 2018).

Experimental Design

Prior to restoration, the former ammunition testing area consisted of compacted gravel and sand and was void of organic soil and vegetation (Fig. S2). The restoration included removal of undetonated ammunition, creation of small-scale relief (Fig. S3), and stirring of the soil. In 2014, a total of 25,000 *Salix*

plants (*S. glauca*, *S. lapponum* and *S. phylicifolia*) was planted in 12 fields within the study site, ranging between 300 and 1,200 m^2 in size and in total covering approximately 4% of the study site, with an average density of 2.5 plants/m^2. Around each plant, 1 L of nutrient-rich commercial soil was added. In addition, an area of 6 ha (ca. 25% of the study site) was fertilized (20 g/m^2) and seeded with *Festuca ovina* (20 g/m^2). All plant material had been propagated from native, local plants; *Salix* from cuttings obtained in 2013 and *F. ovina* from local seeds (Martinsen & Oskarsen 2010). The planted and seeded areas partially overlap (Fig. 1).

The study was carried out in 10 out of 12 planted fields (see Fig. 1), four of which were also seeded with *F. ovina*. Before planting in 2014, we established three permanent experimental blocks (5 × 5 m) with approximately 5 m distance subjectively within each field, aiming to minimize environmental differences between blocks. Prior to planting we randomly assigned the blocks to one of three *Salix* planting densities: high (4 plants/m^2), medium (2.5 plants/m^2), or low (1 plant/m^2). In each block, we systematically placed five monitoring plots (0.5 × 0.5 m) with a planted *Salix* in the center (Fig. 2). The plots were permanently marked.

To investigate the effect of *Salix* plantings on vegetation development, we established 10 control blocks (with five plots in each; Fig. 2) in non-planted areas in 2019; one paired to each of the 10 planted fields. Control blocks were located at distances of circa 10 m from the planted fields and had the same seeding treatment (non-seeded or seeded with *F. ovina*) and a similar topography, aspect, and soil substrate as the experimental blocks in their respective paired fields. In total, the study included 150 experimental plots with *Salix* plants and 50 control plots.

Data Collection

In 2014, shortly after planting of the *Salix*, all experimental plots were photographed from a height of 1 m. From these pictures, cover percentages of the *Salix* plants in the center of the plots in 2014 were obtained with ImageJ software based on pixel cover (Schneider et al. 2012), as field-based estimates were not available. In 2019, we estimated percent cover of the same *Salix* plants with a vegetation analysis frame (0.5 × 0.5 m) in the field. A comparison of picture- and field-based estimates from several plots in 2019 showed that estimates obtained with the different methods were in close agreement. We multiplied cover estimates (proportions) by the surface area of the plot to obtain absolute measures of *Salix* cover (cm^2). *Salix* growth between 2014 and 2019 was calculated by subtracting *Salix* cover in 2014 from *Salix* cover in 2019.

At the start of the experiment in 2014, naturally established vegetation cover (i.e. excl. planted *Salix*) was negligible (<1%) in all plots. In 2019, we estimated the percentage of total vegetation cover (incl. planted *Salix* and seeded *F. ovina*) as well as cover of the bottom layer (bryophytes and lichens), field layer (herbs, incl. seeded *F. ovina*), and shrub layer (incl. planted *Salix* individuals rooted in or growing into the plot) in all plots. We recorded vascular plant abundances as subplot frequencies by registering presence/absence of each species in 16 subplots (12.5 × 12.5 cm) per plot. Presence was based on vertical projection (i.e. incl. species not rooted within the subplot). For the *Salix* genus, we distinguished between planted individuals and naturally established seedlings to be able to estimate *Salix* recruitment. We estimated the percentage of fine soil substrate (sand, silt, and/or clay; ø < 2 mm) in each plot based on visual observations and touch. For each plot, volumetric soil moisture content—hereafter referred to as soil moisture—of the upper 5 cm of soil was calculated as the average of three measurements taken with a moisture meter (Delta-T Devices type HH2 with SM300 sensor). Fieldwork was carried out in August 2019. All soil moisture measurements were taken on the same overcast day (23 August 2019).

Data Analysis

We calculated *Salix* recruitment as the percentage of subplots per plot that harbored at least one *Salix* seedling. Species richness of vascular plants was counted as the number of unique species per plot, excluding planted *Salix* individuals, seeded *F. ovina*, and unidentified seedlings. Plants identified to the genus level were not counted as a species if an identified species of that genus was present in the plot.

We used linear mixed-effect models (LMMs) and a generalized linear mixed-effect model (GLMM) to analyze the data. First, we investigated whether *Salix* cover in 2014 varied between plots, as such differences at the start of the experiment should be accounted for in the analysis of 2019 data. An LMM with *Salix* cover in 2014 as dependent variable, *Salix* planting density (high, medium, low) and seeding (non-seeded or seeded) as fixed factors, and field as a random factor (to incorporate the nested study design of blocks in fields), showed that there had been no such differences (Table S1).

To investigate the effects of planting of *Salix* and seeding of *F. ovina* on natural vegetation recovery, we constructed LMMs (for the dependent variables total vegetation, bottom, field and shrub layer cover, and *Salix* recruitment) and a GLMM (for the dependent variable vascular plant species richness) with *Salix* planting density (high, medium, low, control) and seeding (non-seeded or seeded) as fixed factors and field as a random factor. To investigate the role of soil conditions in natural vegetation recovery, soil moisture and fine soil substrate (continuous variables, centered and scaled) were included as covariates in all models. To examine whether *Salix* planting density, seeding of *F. ovina*, and soil conditions affected performance of the planted *Salix*, we constructed LMMs for the dependent variables *Salix* cover and growth (2014–2019) with the same fixed factors, covariates, and random factor as those included in the LMMs and GLMM for natural vegetation recovery.

Model parameters were estimated with the maximum likelihood method. We performed backward stepwise model selection for each (G)LMM by successively removing non-significant terms and comparing alternative models with the Akaike information criterion (AIC). If the change in AIC-value between two models was small ($|\Delta AIC| < 2$), the most parsimonious model was selected. If this model contained the fixed factor *Salix* density, a Tukey HSD test for post-hoc comparisons

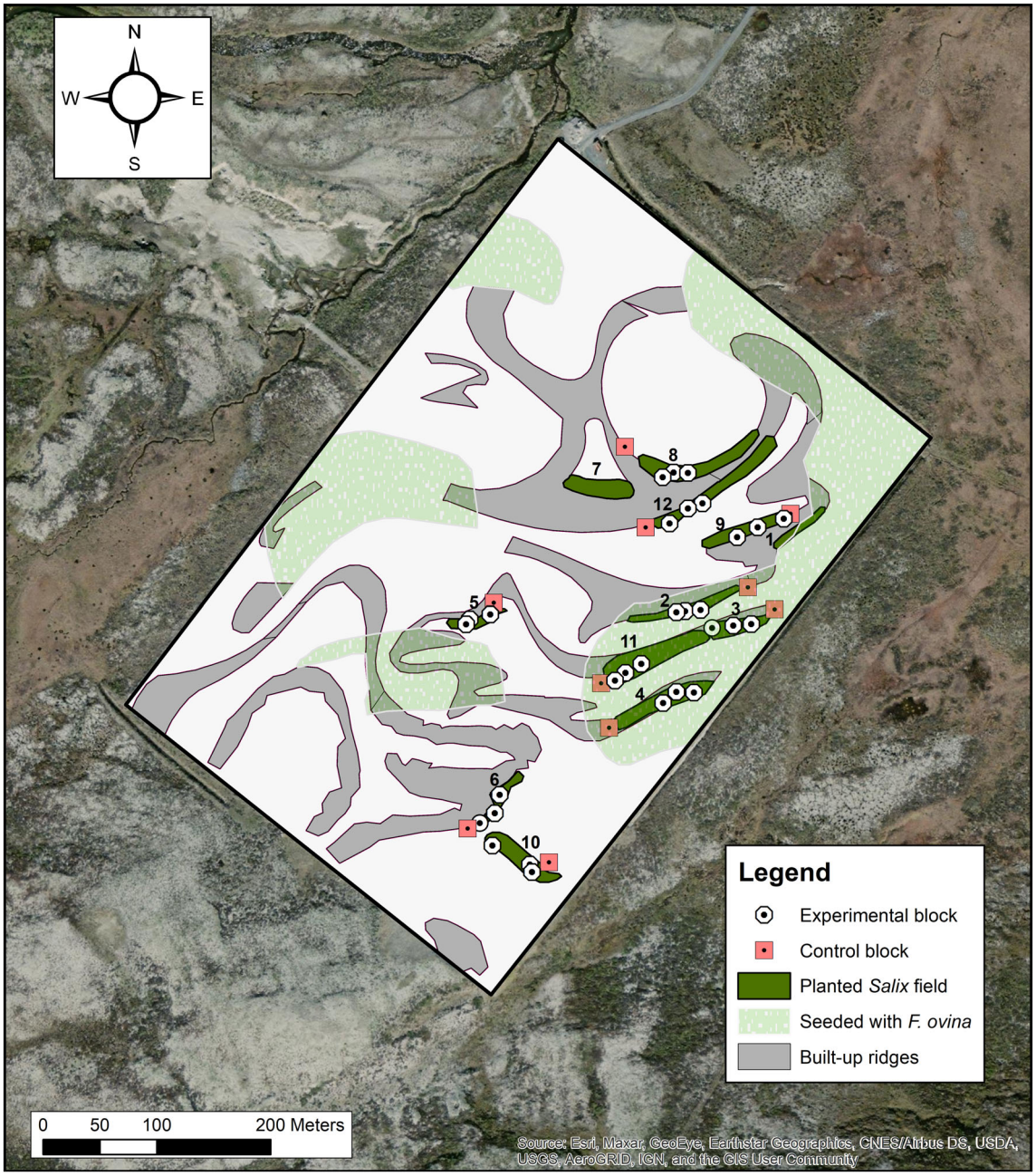

Figure 1. Schematic overview of the study site (400 × 600 m) in the former Hjerkinn firing range in the Dovre Mountains. Of the 12 fields with *Salix* plantings, 10 fields contain experimental blocks (with plots), and a non-planted control block (with plots) outside the field, as illustrated in Figure 2.

was run. Only the final models are presented. All figures show raw data.

To meet model assumptions of linearity, normality, and homogeneity of variance, we transformed *Salix* cover in 2014 and 2019 (square root transformation), *Salix* recruitment (logit transformation), and total vegetation, bottom, field and shrub layer cover (logit transformation). From the dataset for *Salix* recruitment, an outlier was removed because it caused a violation of model assumptions. We also removed one outlier from the datasets for total vegetation and field layer cover. The GLMM for vascular plant species richness was run with a Poisson error distribution.

Five plots were excluded from all analyses; three because the *Salix* plant had died and two because soil moisture measurements could not be taken due to soil compaction. We had challenges relocating six plots in 2019 and established new plots in the vicinity of the original plots. As the *Salix* plants in these plots were not identical to the plants in the plots from 2014, we removed the plots from the *Salix* growth analysis but retained them in all other analyses. Two more plots were removed from

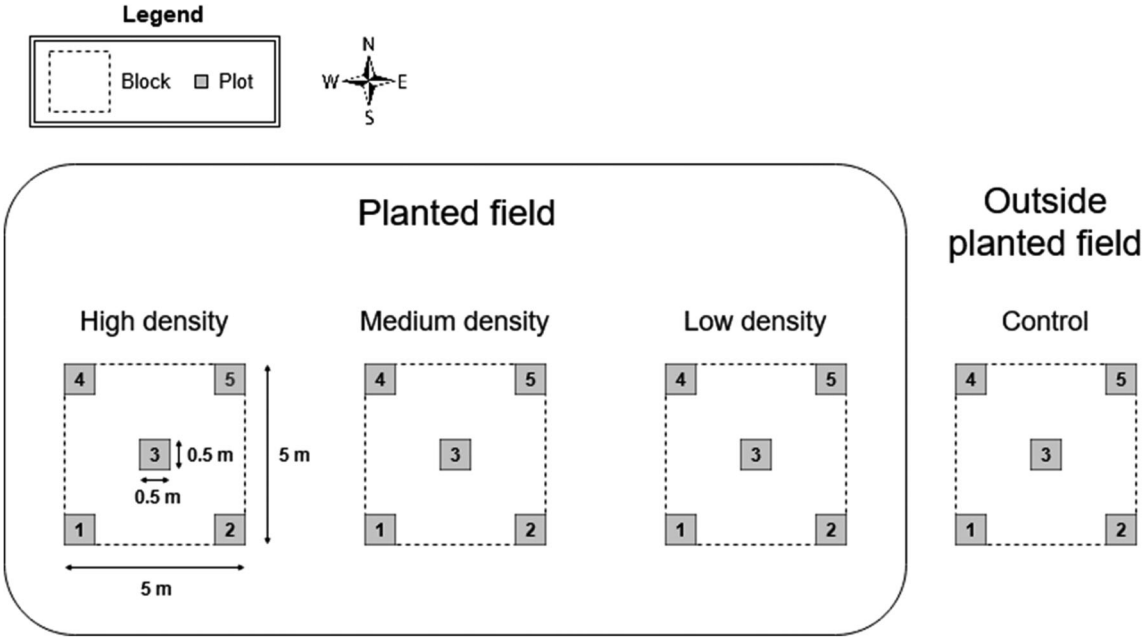

Figure 2. Schematic diagram of a planted field with three permanent experimental blocks (5 × 5 m) with *Salix* plantings in different densities: high (4 plants/m^2), medium (2.5 plants/m^2), and low (1 plant/m^2). The spatial order of the three densities differs per field. The distance between blocks is 5 m (not to scale in diagram). Each block contains five permanent plots (0.5 × 0.5 m) placed systematically. Outside the field, a control block (with plots) is situated.

the *Salix* cover (2014) and *Salix* growth analysis because data from 2014 were missing. From the bottom layer cover analysis, one plot was removed due to missing data. The shrub layer cover analysis was performed without control plots because the shrub cover in these plots was negligible (<0.1%) and inclusion led to a violation of model assumptions.

Data pre-processing and analysis were performed in RStudio (RStudio Team 2015) with R (R Core Team 2019). Statistical analyses were performed with the packages "lme4" (Bates et al. 2015), "lmerTest" (Kuznetsova et al. 2017), and "multcomp" (Hothorn et al. 2008). Marginal and conditional R^2 values (R^2_m and R^2_c) were obtained with the package "sjPlot" (Lüdecke 2020). The package "performance" (Lüdecke et al. 2020) was used to check for collinearity among fixed factors and covariates in each (G)LMM prior to model selection based on variance inflation factor (VIF) values.

Results

Salix Performance and Recruitment

Salix survival rate from 2014 to 2019 was 98.0%. Three of the 150 monitored *Salix* plants had died (one in high, one in medium, one in low planting density), two of which within the first year (Glomb 2016).

Salix cover in 2019 ($\bar{X}$ [SD] = 192 [121] cm^2) was not affected by *Salix* planting density or seeding and showed no relationship with soil moisture, but a tendency to increase with amount of fine soil substrate ($p = 0.067$; Table S2; Fig. S4A). From 2014 to 2019, 93.5% of the *Salix* plants ($N = 139$) showed a positive growth, 2.9% a negative growth, and 3.6% no growth. *Salix* growth (141 [114] cm^2) was not affected by *Salix* planting density or seeding and showed no relationship with soil moisture or fine soil substrate (Table S2; Fig. S4B).

Salix recruitment (% subplots with ≥1 seedling) was best explained by a model that included *Salix* planting density and soil moisture (Table S3). Recruitment was lowest in control plots and increased with increasing *Salix* density (Fig. 3); only the difference between high and medium density plots, and between low density and control plots was not significant (Table S4). Recruitment increased with increasing soil moisture ($p < 0.001$) but showed no relationship with fine soil substrate. Seeding had no effect on recruitment.

Vegetation Cover

Total vegetation cover was best explained by the full model including all variables (Table S5). Total vegetation cover was significantly lower in control plots than in plots with *Salix* plantings, but there were no significant differences between high, medium, and low density plots (Table S6; Fig. 4A). Seeding had a significant positive effect on total vegetation cover ($p = 0.004$; Fig. 4A), and the cover increased with increasing soil moisture ($p < 0.001$) and amount of fine soil substrate ($p = 0.005$).

Bottom layer cover (i.e. bryophytes; lichens covered <0.1%) was best explained by a model including seeding and soil moisture (Table S5). Seeding had a positive effect on bottom layer cover ($p < 0.001$; Fig. 4B), and the cover increased with increasing soil moisture ($p < 0.001$). Bottom layer cover showed a tendency to increase with increasing amount of fine soil substrate ($p = 0.056$), but this variable was removed during model

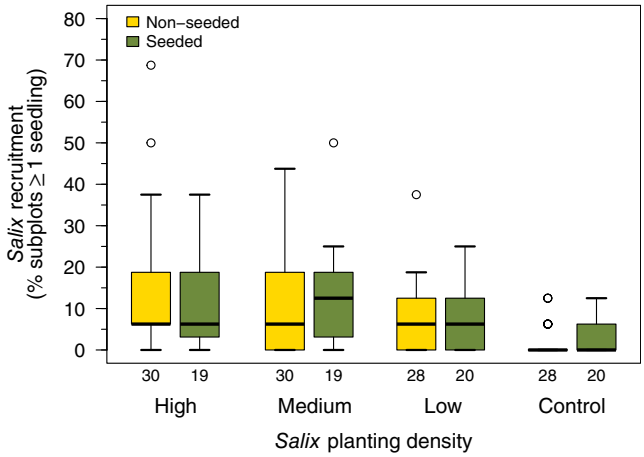

Figure 3. Boxplots showing *Salix* recruitment (% subplots with ≥1 seedling), grouped by *Salix* planting density (high = 4 plants/m^2, medium = 2.5 plants/m^2, low = 1 plant/m^2, and control = no planted *Salix*) and seeding treatment (non-seeded or seeded with *F. ovina*). Number of plots per combination of treatments is shown below each boxplot.

selection due to the non-significant *p*-value. *Salix* planting density had no effect on bottom layer cover.

Field layer cover was best explained by a model including seeding, soil moisture and fine soil substrate (Table S5). Seeding had a positive effect on field layer cover ($p = 0.009$; Fig. 4C), and field layer cover increased with increasing soil moisture ($p < 0.001$) and amount of fine soil substrate ($p = 0.005$). *Salix* planting density had no effect on field layer cover.

The shrub layer consisted of only the planted *Salix*; the contribution of established seedlings of *Salix* and other shrub species was negligible (<0.1%). Control plots had a negligible shrub layer cover (<0.1%) and were excluded from the analysis. Neither *Salix* planting density nor seeding had an effect on shrub layer cover (Fig. 4D). Shrub layer cover showed no relationship with soil moisture but a tendency to increase with amount of fine soil substrate ($p = 0.092$; Table S5).

Vascular Plant Species Richness

In total, 38 vascular plant species—of which 34 identified to species and 4 to genus level—were observed in the plots (Table S7). Vascular plant species richness was best explained by a model including *Salix* planting density, soil moisture, and

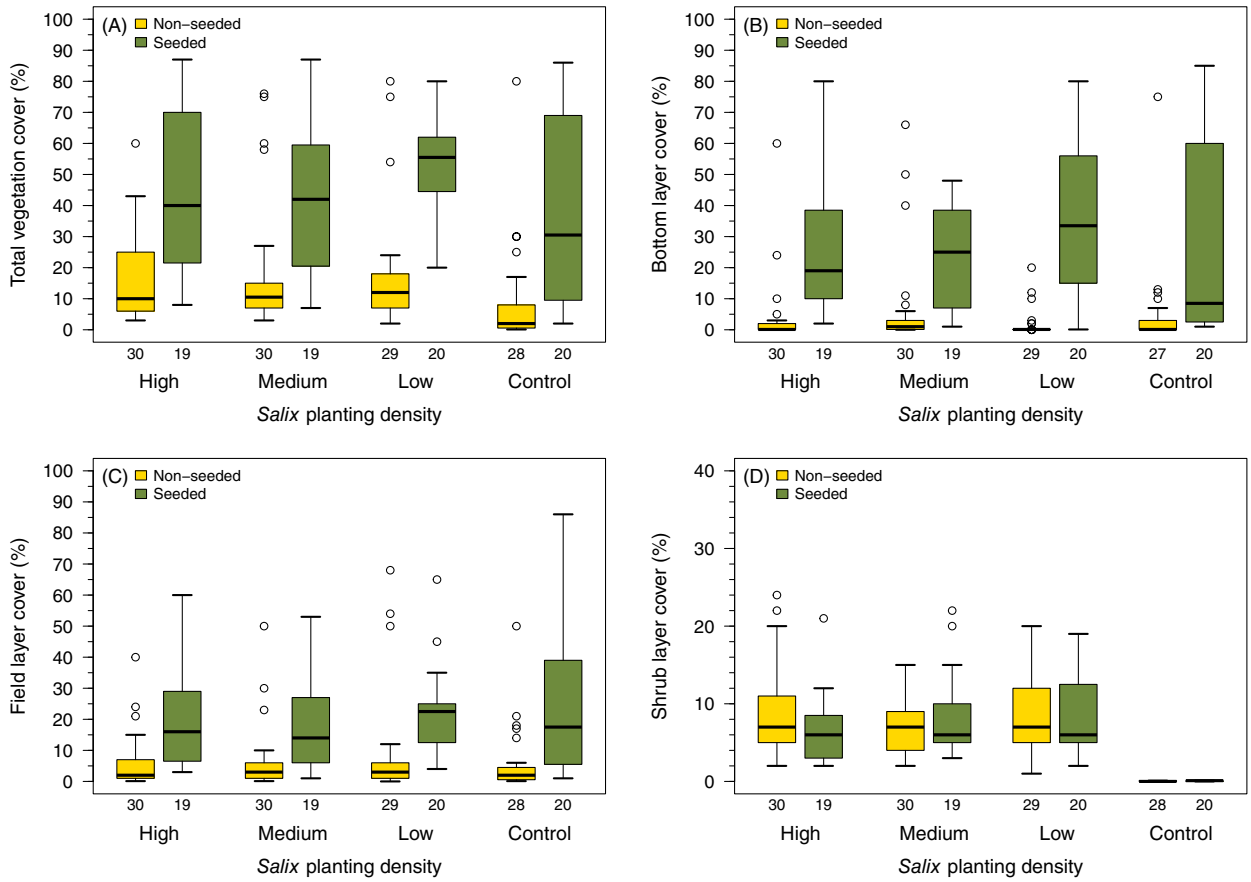

Figure 4. Boxplots showing (A) total vegetation cover (%), (B) bottom layer cover (%), (C) field layer cover (%), and (D) shrub layer cover (%), grouped by *Salix* planting density (high = 4 plants/m^2, medium = 2.5 plants/m^2, low = 1 plant/m^2, and control = no planted *Salix*) and seeding treatment (non-seeded or seeded with *F. ovina*). Number of plots per combination of treatments is shown below each boxplot. The scale of the y-axis differs across the figures.

fine soil substrate (Table S8). Species richness was lowest in control plots and increased with increasing *Salix* density (Fig. 5), but only the difference between control and high, and between control and medium density plots was significant ($p < 0.001$ and $p = 0.025$, respectively; Table S9). Species richness increased with increasing soil moisture ($p = 0.024$) and amount of fine soil substrate ($p < 0.001$). Seeding had no effect on species richness.

Discussion

This study shows the importance of active restoration measures for initiating natural vegetation recovery in severely disturbed alpine heathland. Five years after implementation, planting of native *Salix* and seeding of native *Festuca ovina* both had positive but different effects on vegetation recovery. *Salix* plantings—if minimally 2.5 plants/m^2—increased vascular plant species richness and *Salix* recruitment but had no effect on naturally established vegetation cover, whereas seeding of *F. ovina* resulted in a higher bottom and field layer cover but did not affect vascular plant species richness. Our results also show the importance of soil conditions for vegetation recovery, as moister plots with a higher percentage of fine soil substrate had a higher recovery of vegetation cover and vascular plant species richness.

Effects of *Salix* Planting Density on *Salix* Performance and Recruitment

The high survival rate of the *Salix* plantings confirmed that the plants were able to cope with harsh environmental conditions and severely degraded soils, as previous studies have also shown (e.g. Densmore & Holmes 1987; Kuzovkina & Quigley 2005; Hagen 2007). We found that neither cover nor growth of the planted *Salix* was affected by planting density, in line with Hagen (2003), which suggests that none of the 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.

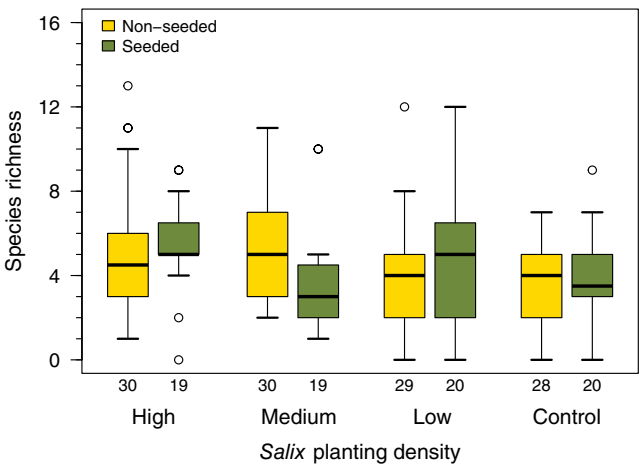

Figure 5. Boxplots showing vascular plant species richness, grouped by *Salix* planting density (high = 4 plants/m^2, medium = 2.5 plants/m^2, low = 1 plant/m^2, and control = no planted *Salix*) and seeding treatment (non-seeded or seeded with *F. ovina*). Number of plots per combination of treatments is shown below each boxplot.

Plots with higher planting densities had a higher recruitment of *Salix* seedlings. This could be due to: (1) a higher abundance of *Salix* and thus of catkins, which some of the plants produced already in 2015, 1 year after planting (D. Hagen, personal observation); (2) enhanced wind- or insect-pollination resulting from smaller distances between plants; or (3) positive density-dependent nurse effects of *Salix* on conspecific seedling emergence and survival; a phenomenon known to occur in harsh environments (Bertness & Callaway 1994; Loayza et al. 2017). Our results show that in the short term, *Salix* plantings with high (4 plants/m^2) and medium (2.5 plants/m^2) densities significantly increase *Salix* recruitment compared to low-density plantings (1 plant/m^2) and non-planted control plots. The *Salix* shrub layer might thus develop more rapidly in plots with higher *Salix* planting densities (≥2.5 plants/m^2), unless conspecific competition occurs at a later stage. This does not seem improbable, as plant interactions can shift from facilitation to competition with changes in ontogeny (Miriti 2006).

Effects of *Salix* Plantings on Natural Vegetation Recovery

Planting of *Salix* increased total vegetation cover, but not the cover of the bottom or field layer. Thus, the higher total vegetation cover was due to the simple presence of the planted *Salix*. Our study thus suggests that there is limited to no facilitative effect of *Salix* plantings on the natural development of vegetation cover. We found, however, that higher *Salix* planting densities (2.5 and 4 plants/m^2) increased vascular plant species richness. Due to the slow plant growth in alpine areas (Krautzer et al. 2012), we would expect that the newly established plants do not contribute a quantitatively discernible amount of vegetation cover at this early stage. This could explain why the higher species richness in plots with higher *Salix* planting densities did not coincide with a higher vegetation cover. Our results could also mean that *Salix* facilitates establishment and survival, but not growth of other species. This explanation 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). It would, however, be in contrast with a study on low alpine vegetation that showed a positive effect of naturally occurring *Salix lapponum* canopies on vegetative growth of alpine plants, implying a sheltering effect (Totland & Esaete 2002). At the same time, Totland and Esaete (2002) found lower plant densities inside *S. lapponum* canopies, suggesting that plant establishment rates were lower, presumably due to lower availability of photosynthetically active radiation (PAR). At this stage, our *Salix* plants are small compared to naturally occurring *Salix* thickets in alpine heath, and might therefore provide insufficient shelter for the facilitation of vegetative growth while enabling higher establishment rates due to a considerably smaller reduction in PAR. As the facilitating effects of *Salix* might change over time and with

changes in plant size, this is an important point to follow up in long-term monitoring.

An alternative explanation for our findings could be that *Salix* plantings with higher densities allow a larger number of species and individuals to establish while only a limited number of individuals of each species survives due to competition for space or resources, causing the facilitative effect to not be visible in terms of vegetation cover. However, this explanation seems improbable due to the scarce vegetation cover (and low competition) in many of the plots.

Our results seem nevertheless promising for future vegetation recovery, as seedling establishment and survival are suggested to be more important than growth in early stages of restoration programs given the generally low seedling survival rate in degraded ecosystems (Gómez-Aparicio 2009). This might be particularly important in alpine areas, where seedling survival is a bottleneck for species establishment (Graae et al. 2011). As higher *Salix* planting densities seem to be more effective in terms of enhancing species establishment, investing in plant propagation might increase the likelihood of achieving short-term restoration targets.

Effects of Seeded *F. ovina* on Natural Vegetation Recovery

Seeding with *F. ovina* increased the field layer cover, most likely due to the contribution of *F. ovina* itself, which was present in 90.9% of the seeded subplots but in only 39.9% of the non-seeded subplots. Seeded plots also had a higher bottom layer (i.e. bryophyte) cover than non-seeded plots. 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 (e.g. Bergamini et al. 2001; van der Wal et al. 2005; Boch et al. 2018). Other studies have found positive effects of forbs and grasses on bryophyte cover that were attributed to favorable changes in microclimate that enhanced bryophyte photosynthesis, such as an increase in ambient moisture and changes in temperature (Ingerpuu et al. 2005; Fergus et al. 2017). According to Ingerpuu et al. (2005), such facilitative effects are likely to prevail at low vascular plant covers. Mean total vegetation cover in our plots was 28%, which makes it reasonable to assume that *F. ovina* had positive effects on bryophyte cover.

Seeding of *F. ovina* did not have negative effects on vascular plant species richness or *Salix* recruitment and thereby provides more promising results than the commercially available *Festuca rubra* that impeded the establishment of native species in previous studies in the Hjerkinn firing range (see Hagen & Evju 2013; Hagen et al. 2014). Our findings, in combination with those of Rydgren et al. (2017), suggest that seeding of native grass species could be an effective method to increase vegetation cover in early stages of restoration projects without hindering the natural recovery of vascular plant species richness. The fact that neither performance of the *Salix* plantings nor *Salix* recruitment was negatively affected by *F. ovina*, combined with the finding that field layer cover (existing largely of *F. ovina*) was not negatively affected by *Salix* plantings, suggests that planting and seeding can be used simultaneously. Thus, if the restoration goal is to increase both species richness and vegetation cover, the methods could be used complementary to each other.

Relationships Between Soil Conditions and Natural Vegetation Recovery

Plots with a higher moisture content in the upper 5 cm of soil had a higher recovery of bottom and field layer and total vegetation cover compared to drier plots. These findings are in line with Evju et al. (2012), who found a positive relationship between vegetation recovery and soil moisture in disturbed alpine plots, and can be explained by the influence of soil moisture on plant productivity through the regulation of photosynthetic activity and nutrient availability (Johnson & Caldwell 1975; Bowman & Fisk 2001; Körner 2003; Winkler et al. 2016; Fath 2018).

Moister plots also had a higher vascular plant species richness and *Salix* recruitment. Soil moisture is important for seed germination and early seedling development (Fay & Schultz 2009; Mosseler et al. 2014), as newly established plants are small and shallow-rooted and therefore dependent on the upper soil layer for water supply. As species differ in their sensitivity to water and nutrient stress (Bowman & Fisk 2001), moister plots might enable the establishment of a wider range of species and thereby yield a higher species richness. Soil moisture showed no relationship with cover and growth of the planted *Salix*, likely because these have more developed root systems that enable the plants to obtain water from deeper soil layers.

Plots with a higher percentage of fine soil substrate had a higher recovery of field layer cover, total vegetation cover, and vascular plant species richness. This is in line with previous studies (e.g. Rydgren et al. 2013; Mehlhoop et al. 2018) and can be explained by the fact that finer soils generally have higher water retention and nutrient holding capacities than coarse soils (Nebel & Wright 1993; Hornberger et al. 1998), which facilitates plant growth. In addition, finer soils allow for a more downward root growth (Popova et al. 2016) and thereby facilitate growth to deeper soil layers with a more constant water supply. Fine soil substrate also showed a tendency to promote cover of the bottom layer and the planted *Salix*, suggesting that these layers might develop more rapidly in finer soils. The findings of this study strongly suggest that an improvement of soil conditions such as soil penetrability and soil water retention and nutrient holding capacities by increasing the amount of fine soil substrate can contribute to a faster natural vegetation recovery in degraded sites.

Importance of Considering Different Indicators of Recovery

Our study shows that both restoration measures (planting of native *Salix* and seeding of native *F. ovina*) have the potential to initiate and accelerate natural vegetation recovery in disturbed alpine areas, but in different ways. These findings highlight the importance of considering different indicators of vegetation recovery when evaluating the effectiveness of restoration measures. Knowledge about the effects of specific measures increases the likelihood that selected measures contribute to outlined restoration targets (e.g. increasing species richness, vegetation cover, or biomass). As short-term outcomes are not necessarily reliable predictors for long-term restoration success, further monitoring is required to gain a full understanding of the long-term effects of both treatments, and their complementarity for vegetation recovery. On a longer time scale,

species composition could be an additional and informative indicator of vegetation recovery.

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References

Aradóttir ÁL, Svavarsdóttir K, Bau A (2007) Clonal variability of native willows (*Salix pylicifolia* and *Salix lanata*) in Iceland and implications for use in restoration. Icelandic Agricultural Sciences 20:61–72

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48

Bergamini A, Pauli D, Peintinger M, Schmid B (2001) Relationships between productivity, number of shoots and number of species in bryophytes and vascular plants. Journal of Ecology 89:920–929

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends in Ecology & Evolution 9:191–193

Boch S, Allan E, Humbert J-Y, Kurtogullari Y, Lessard-Therrien M, Müller J, Prati D, Rieder NS, Arlettaz R, Fischer M (2018) Direct and indirect effects of land use on bryophytes in grasslands. Science of the Total Environment 644:60–67

Bowman WD, Fisk MC (2001) Primary production. Pages 177–197. In: Bowman WD, Saestedt TR (eds) Structure and function of an alpine ecosystem: Niwot Ridge, Colorado. Oxford University Press, Oxford, United Kingdom

Choi YD, Wali MK (1995) The role of *Panicum virgatum* (switch grass) in the revegetation of iron-mine tailings in northern New York. Restoration Ecology 3:123–132

Chu C-J, Maestre FT, Xiao S, Weiner J, Wang Y-S, Duan Z-H, Wang G (2008) Balance between facilitation and resource competition determines biomass–density relationships in plant populations. Ecology Letters 11:1189–1197

Densmore RV, Holmes KW (1987) Assisted revegetation in Denali National Park, Alaska, U.S.A. Arctic and Alpine Research 19:544–548

Dona AJ, Galen C (2007) Nurse effects of alpine willows (*Salix*) enhance overwinter survival at the upper range limit of fireweed, *Chamerion angustifolium*. Arctic, Antarctic, and Alpine Research 39:57–64

Elven R, Fremstad E (2018) The genus *Salix* (willows) in Norway. Gunneria 82: 527–580

Endo M, Yamamura Y, Tanaka A, Nakano T, Yasuda T (2008) Nurse-plant effects of a dwarf shrub on the establishment of tree seedlings in a volcanic desert on Mt. Fuji, Central Japan. Arctic, Antarctic, and Alpine Research 40:335–342

Evju M, Hagen D, Hofgaard A (2012) Effects of disturbance along snow pack gradients in alpine habitats. Plant Ecology 213:1345–1355

Fath BD (2018) Encyclopedia of ecology. 2nd edition. Elsevier, Amsterdam, Netherlands

Fay PA, Schultz MJ (2009) Germination, survival, and growth of grass and forb seedlings: effects of soil moisture variability. Acta Oecologica 35:679–684

Fergus AJF, Gerighausen U, Roscher C (2017) Vascular plant diversity structures bryophyte colonization in experimental grassland. Journal of Vegetation Science 28:903–914

Forbes BC, Jefferies RL (1999) Revegetation of disturbed Arctic sites: constraints and applications. Biological Conservation 88:15–24

Geological Survey of Norway (2019) Bedrock map. https://geo.ngu.no/kart/berggrunn/ (accessed 1 May 2020)

Glomb MS (2016) Alpine heathland restoration: survival and establishment of propagated Salix planted in a disturbed site at Hjerkinn, Dovre Mountain. Master's thesis, Norwegian University of Life Sciences, Ås, Norway. http://hdl.handle.net/11250/2399563 (accessed 10 October 2019)

Gómez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology 97:1202–1214

Graae BJ, Ejrnæs R, Lang SI, Meineri E, Ibarra PT, Bruun HH (2011) Strong microsite control of seedling recruitment in tundra. Oecologia 166:565–576

Gretarsdottir J, Aradottir AL, Vandvik V, Heegaard E, Birks HJB (2004) Long-term effects of reclamation treatments on plant succession in Iceland. Restoration Ecology 12:268–278

Hagen D (2002) Propagation of native Arctic and alpine species with a restoration potential. Polar Research 21:37–47

Hagen D (2003) Assisted recovery of disturbed Arctic and alpine vegetation – an integrated approach. Norwegian University of Science and Technology, Trondheim, Norway, PhD Dissertation

Hagen D (2007) Native willows (*Salix* spp.) in restoration – a technical solution with ecological and social fidelity. Pages 139–145. In: Halldorsson G, Oddsdottir ES, Eggertsson O (eds) Effects of afforestation on ecosystems, landscape and rural development: proceedings of the AFFORNORD conference Reykholt, Iceland, June 18–22, 2005. Nordic Council of Ministers, Copenhagen, Denmark

Hagen D, Evju M (2013) Using short-term monitoring data to achieve goals in a large-scale restoration. Ecology and Society 18:11

Hagen D, Hansen T, Graae BJ, Rydgren K (2014) To seed or not to seed in alpine restoration: introduced grass species outcompete rather than facilitate native species. Ecological Engineering 64:255–261

Hornberger GM, Raffensperger JP, Wiberg PL, Eshleman KN (1998) Elements of physical hydrology. The John Hopkins University Press, Baltimore, Maryland

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical Journal 50:346–363

Houle G, Babeux P (1998) The effects of collection date, IBA, plant gender, nutrient availability, and rooting volume on adventitious root and lateral shoot formation by *Salix planifolia* stem cuttings from the Ungava Bay area (Quebec, Canada). Canadian Journal of Botany 76:1687–1692

Ingerpuu N, Liira J, Pärtel M (2005) Vascular plants facilitated bryophytes in a grassland experiment. Plant Ecology 180:69–75

Johnson DA, Caldwell MM (1975) Gas exchange of four Arctic and alpine tundra plant species in relation to atmospheric and soil moisture stress. Oecologia 21:93–108

Klanderud K, Meineri E, Töpper J, Michel P, Vandvik V (2017) Biotic interaction effects on seedling recruitment along bioclimatic gradients: testing the stress-gradient hypothesis. Journal of Vegetation Science 28:347–356

Körner C (2003) Alpine plant life: functional plant ecology of high mountain ecosystems. 2nd edition. Springer-Verlag, Berlin Heidelberg, Germany

Krautzer B, Uhlig C, Wittmann H (2012) Restoration of Arctic-alpine ecosystems. Pages 189–202. In: Van Andel J, Aronson J (eds) Restoration ecology: the new frontier. 2nd edition. Wiley-Blackwell, Chichester, West Sussex, United Kingdom

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. Journal of Statistical Software 82:1–26

Kuzovkina Y, Quigley MF (2005) Willows beyond wetlands: uses of *Salix* L. species for environmental projects. Water, Air, and Soil Pollution 162:183–204

Loayza A, Herrera-Madariaga M, Carvajal D, García-Guzmán P, Squeo F (2017) Conspecific plants are better 'nurses' than rocks: consistent results revealing intraspecific facilitation as a process that promotes establishment in a hyper-arid environment. AoB Plants 9:plx056

Lüdecke D (2020) sjPlot: data visualization for statistics in social science. R package version 2.8.7. https://CRAN.R-project.org/package=sjPlot (accessed 19 Jan 2021).

Lüdecke D, Makowski D, Waggoner P, Patil I (2020) Performance: assessment of regression models performance. R package. https://easystats.github.io/performance/ (accessed 19 Jan 2021).

Maestre F, Bautista S, Cortina J, Bellot J (2001) Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. Ecological Applications 11:1641–1655

Martinsen OE, Oskarsen H (2010) Multiplication of sheep fescue (*Festuca ovina*) – restoration of Hjerkinn firing range into nature conservation area. Pages 65–66. In: Hagen D, Skrindo AB (eds) Restoration of nature in Norway – a glimpse into the tematic field, professional institutions and ongoing activity. Norwegian Institute for Nature Research, Trondheim, Norway. [Oppformering av sauesvingel – tilbakeføring av Hjerkinn skytefelt til sivile formal]

Mehlhoop AC, Evju M, Hagen D (2018) Transplanting turfs to facilitate recovery in a low-alpine environment—what matters? Applied Vegetation Science 21:615–625

Ministry of Defence (1998–1999) Melding til Stortinget nr. 11: regionalt skyte- og øvingsfelt for Forsvarets avdelinger på Østlandet – Regionfelt Østlandet. Ministry of Defence, Oslo, Norway

Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94:973–979

Moen A, Odland A (1999) National atlas of Norway: vegetation. Norwegian Mapping Authority, Hønefoss, Norway

Mosseler A, Major J, Labrecque M (2014) Growth and survival of seven native willow species on highly disturbed coal mine sites in eastern Canada. Canadian Journal of Forest Research 44:340–349

Nebel BJ, Wright RT (1993) Environmental science: the way the world works. Prentice Hall, Englewood Cliffs, N.J

Norwegian Environment Agency (2012) Dovrefjell-Sunndalsfjella: united and loyal until the mountains of Dovre crumble. Norwegian Environment Agency, Trondheim, Norway

Norwegian Meteorological Institute (2019) eKlima. http://sharki.oslo.dnmi.no/portal/page?_pageid=73,39035,73_39101&_dad=portal&_schema=-PORTAL (accessed 18 Apr 2019)

Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment 4:196–202

Popova L, Van Dusschoten D, Nagel KA, Fiorani F, Mazzolai B (2016) Plant root tortuosity: an indicator of root path formation in soil with different composition and density. Annals of Botany 118:685–698

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

RStudio Team (2015) RStudio: integrated development for R. RStudio, Inc., Boston, Massachusetts

Rydgren K, Halvorsen R, Odland A, Skjerdal G (2011) Restoration of alpine spoil heaps: successional rates predict vegetation recovery in 50 years. Ecological Engineering 37:294–301

Rydgren K, Halvorsen R, Auestad I, Hamre LN (2013) Ecological design is more important than compensatory mitigation for successful restoration of alpine spoil heaps. Restoration Ecology 21:17–25

Rydgren K, Auestad I, Hamre LN, Hagen D, Rosef L, Skjerdal G (2016) Long-term persistence of seeded grass species: an unwanted side effect of ecological restoration. Environmental Science and Pollution Research 23:13591–13597

Rydgren K, Hagen D, Rosef L, Pedersen B, Aradottir AL (2017) Designing seed mixtures for restoration on alpine soils: who should your neighbours be? Applied Vegetation Science 20:317–326

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675

Sylvain ZA, Mosseler A (2017) Use of shrub willows (*Salix* spp.) to develop soil communities during coal mine restoration. Canadian Journal of Forest Research 47:1687–1694

Sylvain ZA, Wall DH (2011) Linking soil biodiversity and vegetation: implications for a changing planet. American Journal of Botany 98:517–527

Tingstad L, Olsen SL, Klanderud K, Vandvik V, Ohlson M (2015) Temperature, precipitation and biotic interactions as determinants of tree seedling recruitment across the tree line ecotone. Oecologia 179:599–608

Totland Ø, Esaete J (2002) Effects of willow canopies on plant species performance in a low-alpine community. Plant Ecology 161:157–166

Van Der Wal R, Pearce IS, Brooker RW (2005) Mosses and the struggle for light in a nitrogen-polluted world. Oecologia 142:159–168

Verdú M, Traveset A (2005) Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. Ecology 86:1385–1394

Willard BE, Cooper DJ, Forbes BC (2007) Natural regeneration of alpine tundra vegetation after human trampling: a 42-year data set from Rocky Mountain National Park, Colorado, USA. Arctic, Antarctic, and Alpine Research 39:177–183

Winkler DE, Chapin KJ, Kueppers LM (2016) Soil moisture mediates alpine life form and community productivity responses to warming. Ecology 97:1553–1563

Zhang R, Tielbörger K (2020) Density-dependence tips the change of plant–plant interactions under environmental stress. Nature Communications 11:2532

Supporting Information

The following information may be found in the online version of this article:

Figure S1. The study site is located in the former Hjerkinn firing range (indicated by orange lines) in the Dovre Mountains in Central Norway (indicated by orange square).
Figure S2. The study site—a former ammunition testing area (400 × 600 m) in the former Hjerkinn firing range—in 2011, prior to restoration interventions.
Figure S3. The study site in 2013, after the creation of small-scale relief and before implementation of the planting and seeding treatments.
Figure S4. Boxplots showing A) *Salix* cover in 2019 (cm^2) and B) *Salix* growth 2014–2019 (cm^2).
Table S1. Output of the LMM for the dependent variable *Salix* cover in 2014 (cm^2; square root transformed).
Table S2. Output of the final LMMs for the dependent variables *Salix* cover in 2019 (cm^2; square root transformed), and *Salix* growth 2014–2019 (cm^2).
Table S3. Output of the final LMM for the dependent variable *Salix* recruitment (% subplots with ≥1 seedling; logit transformed).
Table S4. Output of the post-hoc comparisons (Tukey HSD test) for the fixed factor *Salix* planting density ('H' = high, 'M' = medium, 'L' = low, and 'C' = control), run on the final LMM for the dependent variable *Salix* recruitment.
Table S5. Output of the final LMMs for the dependent variables total vegetation cover (%), bottom layer cover (%), field layer cover (%), and shrub layer cover (%); all logit transformed.
Table S6. Output of the post-hoc comparisons (Tukey HSD test) for the fixed factor *Salix* planting density ('H' = high, 'M' = medium, 'L' = low, and 'C' = control), run on the final LMM for the dependent variable total vegetation cover.
Table S7. Alphabetical list of the vascular plant species that were observed in the experimental and control plots in the study site in the former Hjerkinn firing range (Dovre Mountains, Central Norway) in 2019.
Table S8. Output of the final GLMM for the dependent variable vascular plant species richness.
Table S9. Output of the post-hoc comparisons (Tukey HSD test) for the fixed factor *Salix* planting density ('H' = high, 'M' = medium, 'L' = low, and 'C' = control), run on the final GLMM for the dependent variable vascular plant species richness.

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