RESEARCH ARTICLE

Determinants of tree seedling establishment in alpine tundra

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Abstract

Questions: Changes in climate and herbivory pressure affect northern alpine ecosystems through woody plant encroachment, altering their composition, structure and functioning. The encroachment often occurs at unequal rates across heterogeneous landscapes, hinting at the importance of habitat-specific drivers that either hamper or facilitate woody plant establishment. Here, we assess: (1) the invasibility of three distinct alpine plant community types (heath, meadow and *Salix* shrubland) by *Pinus sylvestris* (Scots pine); and (2) the relative importance of biotic (above-ground interactions with current vegetation, herbivory and shrub encroachment) and microclimate-related abiotic (soil temperature, moisture and light availability) drivers of pine seedling establishment success.

Location: Dovrefjell, Central Norway.

Methods: We conducted a pine seed sowing experiment, testing how factorial combinations of above-ground removal of co-occurring vegetation, herbivore exclusion and willow transplantation (simulated shrub encroachment) affect pine emergence, survival and performance (new stem growth, stem height and fraction of healthy needles) in three plant communities, characteristic of alpine tundra, over a period of five years.

Results: Pine seedling emergence and survival were similar across plant community types. Herbivore exclusion and vegetation removal generally increased pine seedling establishment and seedling performance. Within our study, microclimate had minimal effects on pine seedling establishment and performance. These results illustrate the importance of biotic resistance to seedling establishment.

Conclusion: Pine seedlings can easily establish in alpine tundra, and biotic factors (above-ground plant interactions and herbivory) are more important drivers of pine establishment in alpine tundra than abiotic, microclimate-related, factors. Studies aiming to predict future vegetation changes should thus consider local-scale biotic interactions in addition to abiotic factors.

1 | INTRODUCTION

Northern high-latitude ecosystems are strongly affected by climate change due to fast and intense warming (Elmendorf et al., 2015) and because their biota are limited by low temperatures (Michelsen et al., 2011; Vanneste et al., 2017). Ongoing changes in climate and herbivore pressure are affecting the species composition of these systems in several ways. For example, treelines, the lower boundaries of tundra ecosystems, are expected to advance in elevation and latitude, but the observed trends vary (Millar et al., 2004; Dalen and Hofgaard, 2005). In addition, shrubs (e.g. birch, willow and alder) are expanding in tundra communities worldwide (Myers-Smith et al., 2011; Frost and Epstein, 2014; Vanneste et al., 2017; Bjorkman et al., 2018), yet there are again exceptions (García Criado et al., 2020). Interestingly, shrubs often facilitate tree establishment in tundra (Castro et al., 2004; Akhalkatsi et al., 2006; Chen et al., 2020). Thus, woody species have the potential to expand in these ecosystems (Myers-Smith et al., 2011), resulting in vegetation shifts from open herbaceous or dwarf-shrub-dominated to closed shrub-dominated communities that potentially are beneficial for tree establishment as well. However, it is still poorly understood in which situations and to what extent these shifts will occur.

Previous work has shown that woody encroachment occurs at unequal rates across heterogeneous alpine landscapes (Wookey et al., 2009; García Criado et al., 2020). Variation is thought to depend on the invasibility (i.e., susceptibility to the establishment of new species) of current communities, a characteristic determined by the interplay between biotic and abiotic factors (Graae et al., 2011; Milbau et al., 2013). Invasibility is often assumed to be driven by resistance from the receiving community (Bruno, Stachowicz, and Bertness, 2003; Bulleri, Bruno, and Benedetti-Cecchi, 2008). However, facilitation (i.e., positive biotic interactions) is suggested to be common across ecosystems with effects at least as strong as other factors shaping plant communities (Maestre et al., 2009; McIntire and Fajardo, 2014). For example, tree recruitment in tundra is often facilitated by shrub, tree or krummholz canopies (Castro et al., 2004; Akhalkatsi et al., 2006; Chen et al., 2020), though varying with the canopy-forming and recruiting tree species (Körner, 2012; Liang et al., 2016). This facilitation seems predominantly important in early recruitment phases (Cranston and Hermanutz, 2013; Brodersen et al., 2019). Amelioration of abiotic growing conditions (e.g. protection against temperature extremes, high irradiance and wind) during vulnerable recruitment stages is an important mechanism behind this facilitation (Akhalkatsi et al., 2006; Holmgren et al., 2015; Chen et al., 2020). Conversely, dense ground covers of herbaceous plants mainly suppress tree seedling recruitment by shading (Loranger, Zotz, and Bader, 2017). These plant–plant interactions are expected to shift from competitive to facilitative with increasing abiotic stress level (Choler, Michalet, and Callaway, 2001;

Callaway et al., 2002; Blonder et al., 2018), suggesting that environmentally benign communities are less invasible than are more stressful communities.

Natural and anthropogenic disturbances, such as bare soil patches resulting from trampling, human recreation or transport, landslides or rock falls, are another strong driver of tree seedling recruitment in alpine habitats (Hättenschwiler and Körner, 1995; Munier et al., 2010; Tremblay and Boudreau, 2011). Small-scale disturbances, by removing or reducing the abundance of competitors, generate new microhabitats suitable for seedling emergence and establishment (Milbau et al., 2013; Nystuen et al., 2014; Lembrechts et al., 2016). However, severe disturbances can counteract the benefits of reduced competition, for instance when it leads to too hot and too dry soils that can be detrimental for tree seedlings (Kambo and Danby, 2018; Nystuen et al., 2019).

Browsing, grazing and trampling by herbivores such as ungulates and small rodents also create disturbances, and have therefore been suggested to indirectly facilitate plant recruitment in tundra (Ims Vistnes and Nellemann, 2008; Tremblay and Boudreau, 2011; Milbau et al., 2013). However, other studies have detected the opposite effect: experimental herbivore exclusion increased seedling establishment (Olofsson et al., 2009; Munier et al., 2010; Ravolainen et al., 2014). Herbivory can thus either increase or reduce the invasibility of a plant community, thereby either stimulating or reducing tree seedling establishment.

Alpine tundra vegetation comprises a patchwork of distinct community types that differ in abiotic conditions created by strong gradients of environmental stress. In low-alpine areas of Fennoscandia, typical topographical gradients occur from harsh wind-exposed and dry heaths to more benign sheltered shrublands, meadows and snowbeds (Graae et al., 2011). Consequently, new species trying to establish in these communities will not only be subjected to differences in abiotic stress but also to differences in biotic interactions with co-occurring plant species, soil biota and herbivores.

Here, we explored the mechanisms underlying tree invasibility in alpine tundra in a full-factorial pine seed sowing experiment manipulating canopy cover, herbivore exclusion and shrub introduction in three alpine plant communities differing in abiotic stress. Treatment effects on emergence, survival and performance of Scots pine (*Pinus sylvestris*) and microclimatic conditions were monitored for five years. To explore the relative importance of biotic and abiotic drivers, we assessed the effects of community type, vegetation removal, herbivore exclusion, shrub introduction and microclimate on the establishment, growth and survival of pine seedlings, and whether these effects vary among distinct community types, over a period of five years. We compared treatment effects on the invasibility of a heath, a meadow and a *Salix* shrubland, three representative plant community types at an alpine tundra site in Central

Norway (Dovrefjell) (Sørensen, et al., 2018). Specifically, we asked: (1) whether the invasibility by *P. sylvestris* differed among the three distinct plant community types; and (2) what the relative importance is of biotic (above-ground interactions with current vegetation, herbivory and shrub encroachment) and abiotic (soil temperature, soil moisture and light availability) drivers for the establishment success of pine seedlings. We expected that abiotic stressors are more important in the harsh heath environment, while biotic drivers are more important in the environmentally more benign *Salix* shrubland.
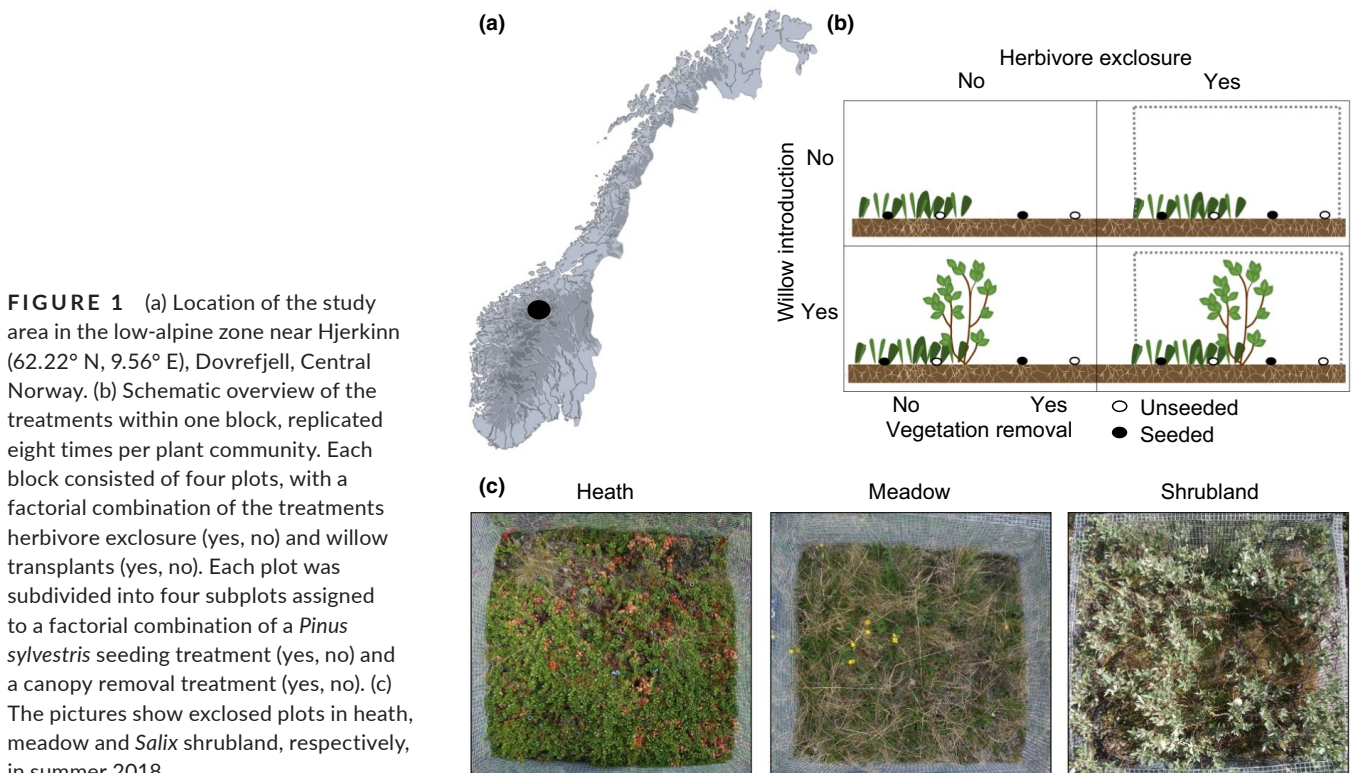
2 | MATERIALS AND METHODS

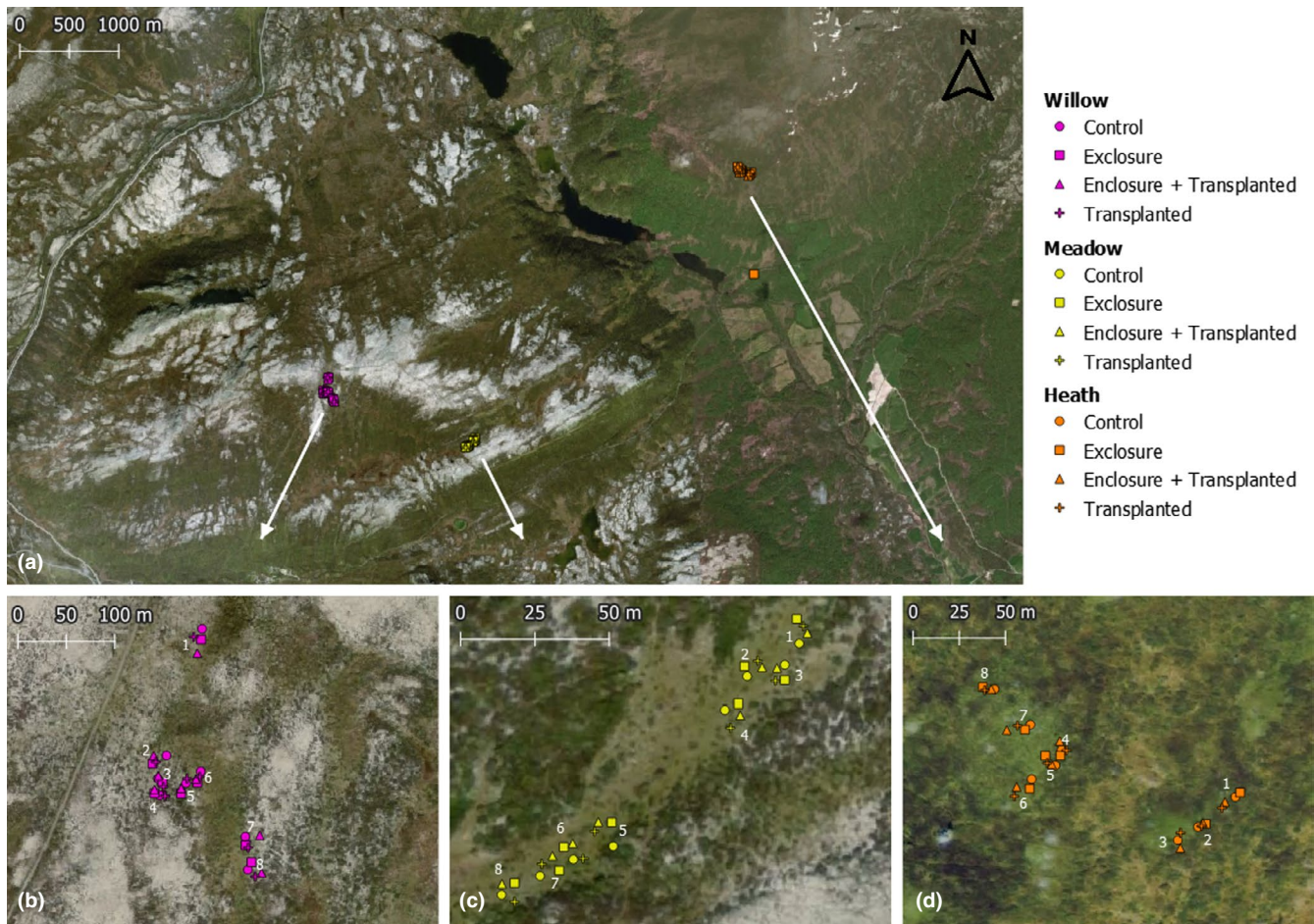### 2.1 | Study site and plant community description

The study was conducted in the low-alpine zone near Hjerkinn (62.22° N, 9.56°E) at Dovrefjell, Central Norway, a part of the Scandes mountains (Figure 1a). Here, Scots pine (*Pinus sylvestris* L., Pinaceae, hereafter referred to as pine) exist as scattered trees up to the tree line, which is dominated by birch (*Betula pubescens* ssp. *czerepanovii (N.I.Orlova) Hämet-Ahti*) (See The Norwegian Biodiversity Information Centre (NBIC) (https://www.biodiversity.no/, accessed 5 October 2020) for unified nomenclature of plant species.), and smaller pine individuals occur sporadically above the treeline. The field sites are all located on podzolic soils around 1,100 m above sea level just above the local treeline. In the period between January 2013 and December 2018, the mean February and July temperatures were −6.4°C and 11.5°C, respectively, and the annual mean precipitation was 531 mm at the closest weather station (Hjerkinn

II, 1,012 m a.s.l., 62.22° N, 9.54° E; Norwegian Meteorological Institute, eklima.met.no). Study sites were selected within three common alpine plant community types in the alpine tundra ecosystem: (1) evergreen dwarf-shrub heath dominated by *Empetrum*; (2) meadow with mixed herbaceous vegetation of grasses, forbs and cryptogams; and (3) deciduous shrubland dominated by *Salix* sp. with a heterogenous ground layer rich in bryophytes and lichens (see Appendix S1, Table S1, for community characteristics and species composition). The three plant communities were situated on different mountain slopes with similar aspect and elevation and located within 5 km of each other (Figure 2), thus sharing roughly the same macroclimate. All sites are subjected to low-intensity summer grazing by Norwegian white sheep (*Ovis aries*) (Norwegian Institute of Bioeconomy Research: http://kilden.skogoglandskap.no/), and animal husbandry has probably been present in the area for about 400 years BC (Risbøl, Stene, and Sætren, 2011). Wild grazers present in the study area include voles (*Microtus agrestis*, *Microtus oeconomus*, and *Myodes rufocanus*), lemmings (*Lemmus lemmus*), hares (*Lepus timidus*), ptarmigan (*Lagopus lagopus* and *Lagopus muta*), moose (*Alces alces*) and wild reindeer (*Rangifer tarandus*).

2.2 | Study design

The experiment was established in 2013 as a randomized block design within each of the three plant communities, with eight replicates (blocks) per treatment (Sørensen, et al., 2018). The eight blocks were randomly located in each plant community. Within each block, four plots (25 cm × 25 cm) were randomly assigned to a full-factorial

FIGURE 1 (a) Location of the study area in the low-alpine zone near Hjerkinn (62.22° N, 9.56° E), Dovrefjell, Central Norway. (b) Schematic overview of the treatments within one block, replicated eight times per plant community. Each block consisted of four plots, with a factorial combination of the treatments herbivore exclosure (yes, no) and willow transplants (yes, no). Each plot was subdivided into four subplots assigned to a factorial combination of a *Pinus sylvestris* seeding treatment (yes, no) and a canopy removal treatment (yes, no). (c) The pictures show exclosed plots in heath, meadow and *Salix* shrubland, respectively, in summer 2018

FIGURE 2 (a) Spatial configuration of the three vegetation communities, and spatial configuration of plots within communities (b) *Salix* shrubland, (c) Meadow and (d) Heath

combination of herbivore exclosure (no, yes) and willow transplantation (no, yes), resulting in four treatment combinations (Figure 1b). Each plot was split into four subplots (12.5 cm × 12.5 cm) which received a full-factorial combination of a vegetation-removal treatment (no, yes) and a sowing treatment (no, yes) (Figure 1c).

Willow saplings, *Salix glauca* and *Salix lapponum*, were transplanted into half of the plots to simulate shrub expansion. The willows were collected in the vicinity of the field sites in October 2013, stored at 0°C until January 2014, and thereafter cultivated by clonal propagation in greenhouses during the rest of the winter. In June 2014 the plants were pruned to measure approximately 10 cm in height, and transplanted into the experimental fields, five transplants per plot, right next to the 12.5 cm × 12.5 cm subplots. It was difficult to differentiate between *Salix glauca* and *Salix lapponum*, and the two species were therefore randomly distributed among the plots (the two species commonly occur in mixed stands in the study area). To exclude herbivores, 80 cm × 80 cm × 50 cm cages were placed permanently over half of the plots. The cages were constructed from galvanized iron with a mesh size of 1.27 cm × 1.27 cm, and buried 5–10 cm into the soil (Sørensen, et al., 2018).

In all seeded subplots, 10 pine seeds were sown in late autumn 2013. Seeds were supplied by the Norwegian Forest Seed Center,

and originated from a natural forest near Oppdal (600–650 m above sea level), 50 km north of the study sites. While seeding, a cardboard box was placed around the subplot to protect against wind and to make sure that the subplot received exactly 10 seeds. The unseeded subplots provide an experimental control for spontaneous emergence at the study sites and were not used directly in the analysis. In half of the subplots, all above-ground biomass of all co-occurring plants was removed to ground level to reduce above-ground interactions of surrounding species with the pine seedlings. Vegetation removal was done with a knife, leaving soil and roots intact.

In summary, the experiment comprised three community types × eight blocks × two vegetation-removal treatments × two herbivore treatments × two willow transplant treatments × two sowing treatments = 384 subplots.

2.3 | Seedling emergence, survival, and performance

Pine seedling emergence was monitored yearly in all subplots during summer or early autumn from 2014 to 2016. The emerged seedlings were assigned a unique ID, marked with a toothpick

and marked on a seedling map, so that every seedling could be followed individually. Litter was removed to facilitate seedling counts, and subsequently replaced. In the first growing season (2014), vegetative regrowth was trimmed back. In the summer of 2018, the total number of seedlings per subplot was recorded (number of seedlings per subplot was counted independently by two observers; results were the same). *Emergence probability* was defined per seeded subplot as the total number of emerged seedlings in the seeded subplots from 2014 to 2016, corrected for the seedlings that emerged in the unseeded subplots (only two across all control plots), divided by the total number of seeds sown (10 per subplot). *Survival probability* was defined for each subplot as the fraction of seedlings that survived until the 2018 census, calculated as the total number of seedlings present in 2018 divided by the total number of emerged seedlings from 2014–2016. When more seedlings were present in 2018 than had emerged during 2014–2016 (fraction > 1), we assigned a value of 1 to the subplot.

In 2018 only, the performance of the pine seedlings was quantified in terms of their growth and condition. *Pine seedling performance* was measured in three ways: stem height, new stem growth and the fraction of healthy needles per seedlings. Stem height was measured as the length of the stem from the soil to the highest point of the stem, pressing the measuring stick firmly into the ground to minimize the deviation due to the moss layer. New stem growth was defined as the length of the green part of the main stem, which indicates the yearly seedling growth (Holmgren et al., 2015). The fraction of healthy needles per seedling was based on the colour of the needles. Colour change in needles is a good indicator of stress and nutrient deficiency in *Pinus sylvestris* (Hytönen and Wall, 2006). All needles were counted and scored as either 'healthy' (when the needle was fresh and green) or 'unhealthy' (when the needle had turned yellow or brown) and the fraction of healthy needles was monitored per seedling. Seedlings that were missing, or had only brown needles, were scored as dead.

2.4 | Microclimate

To quantify microclimatic conditions, we measured soil temperature, soil moisture and light availability for every subplot.

Soil temperature was measured with iButton temperature loggers (Maxim Integrated Products, Sunnyvale, CA, USA) placed in plastic bags, sealed with duct tape, and placed in a slot circa 1 cm into the soil beneath the soil surface. The loggers recorded the temperature at four-hour intervals from 19 June 2016 to 28 July 2018. Each plot had two sensors placed in the unseeded subplots, one in the subplot with the vegetation removed, and one in the vegetated subplot. To focus on the extreme conditions across the year, two seasons were distinguished in the study, referred to as winter and summer, which include the temperatures of the months February (from 2017 and 2018) and July (from 2016, 2017 and 2018), respectively. For both periods and for each subplot, we computed the mean temperature (T_{mean}) as the average temperature per logger, minimum temperature

(T_{min}) as the first percentile of the temperature measurements, and maximum temperature (T_{max}) as the ninety ninth percentile of the temperature measurements during the period.

Soil moisture (% volumetric soil water content) was measured with a hand-held moisture meter (TRIME-PICO32, IMKO GmbH, Ettlingen, Germany) in August and September 2016, and in July 2018. Two repeated measurements were taken in the unseeded intact and unseeded vegetation-removal subplots to avoid disturbing the seedlings in the seeded subplots. The moisture measurements were made on the same day in all subplots, and always on days with stable and dry weather, after a dry period of at least four days. All measurements were averaged per subplot.

Light availability was measured with a Li-190R Quantum light sensor (LI-COR, Lincoln, NE, USA) connected to a Squirrel SQ2010 (Grant Instruments Ltd, Cambridge, UK) data logger. In every unseeded subplot (both intact and vegetation removed) the light was measured above the canopy (approximately 80 cm above the ground) and below the canopy, resting the sensor on the soil surface. Measurements below and above the canopy were taken immediately after each other, ensuring similar ambient light conditions, and all measurements per community were taken on the same day. The light measurements were made in overcast, dry weather. Light availability was calculated as the percentage of light reaching through the canopy and thus available for seedlings.

2.5 | Data analysis

The invasibility of the study sites to pine seedlings were tested with linear mixed models (LMMs) with Gaussian error distributions or generalized linear mixed models (GLMMs) with binomial error distributions (see Appendix S2). As measures of invasibility we used the variables emergence probability, survival probability, stem height, new stem growth and fraction of healthy needles of the pine seedlings. First, we fitted models for each response variable with community (with levels heath, meadow and *Salix* shrubland), treatment (compound variable with $2^3 = 8$ levels; unique combinations of vegetation removal, herbivore exclusion, and willow introduction) and their interaction as fixed effects. Depending on the observational unit of the model (either subplot or pine seedling), block, plot (nested within block) and subplot (nested within plot and block) were treated as random factors (see Appendix S2). Because our focal community types were concentrated in one site, we focused our hypothesis testing on the treatment effects, and their possible variation among communities. A significant interaction between community and treatment provided evidence that the treatment effects differed among communities. To further explore these differences, we fitted models for each community separately following: $y \sim$ removal × exclusion × transplant.

To test for effects of plant community type and treatment on microclimate (soil temperature, moisture and light availability), we fitted LMMs with Gaussian error distributions (see Appendix S2). Some of the soil temperature variables exhibited multicollinearity.

Therefore, we analyzed only maximum summer temperature (which correlated with mean summer temperature, $r = 0.85$) and minimum winter temperature (which correlated with mean winter temperature, $r = 0.98$), because temperature extremes are most likely to limit establishment. We also analyzed soil moisture and light availability. Block and plot (nested within block) were treated as random factors. As above, we fitted models for each community when treatment effects differed among communities.

To test how the abiotic factors affected pine invasibility, we fitted LMMs or GLMMs with the invasibility variables (emergence probability, survival probability, stem height, new stem growth and fraction of healthy needles) as response variables and community type and the environmental variables (maximum summer temperature, minimum winter temperature, soil moisture and light availability) as explanatory variables.

Minimal adequate models were obtained by stepwise backward elimination of least-significant explanatory variables, starting from a full model with all interactions, alternately dropping terms until all terms were significant or part of a significant interaction. For each step, we assessed significance of terms with F-tests (LMMs) or likelihood-ratio chi-square tests (for the GLMMs). Random structure remained identical during the backward elimination. Pairwise differences between treatments and communities were further analyzed by multiple-comparison tests, using Tukey's honest significant difference when the data were normally distributed and Dunn's test when the data were not normally distributed.

Statistical analyses were performed in R version 3.4.4, using the functions lmer and glmer from the package *lme4* (Bates et al., 2014) for model fitting, the function drop1 from the base package for backward selection, and the function dunn.test from package *dunn. test* (Dinno and Dinno, 2017) for performing Dunn's tests.

3 | RESULTS

A total of 578 pine seedlings (30% of sown seeds) emerged during the first three years of the experiment and 159 (almost 30%) of the emerged seedlings survived until the fifth year. Mean emergence and survival rates tended to be similar across the three communities (Figure 3).

3.1 | Differences in treatment effects on pine establishment among communities

The effects of the treatments on seedling emergence and performance differed among communities, while effects on seedling

survival were consistent (Appendix 3, Table S3.1, Figure 3). In the following analyses, the three-way interactions among vegetation removal, herbivore exclusion and willow introduction were never statistically significant, and we focus only on direct and two-way interaction effects.
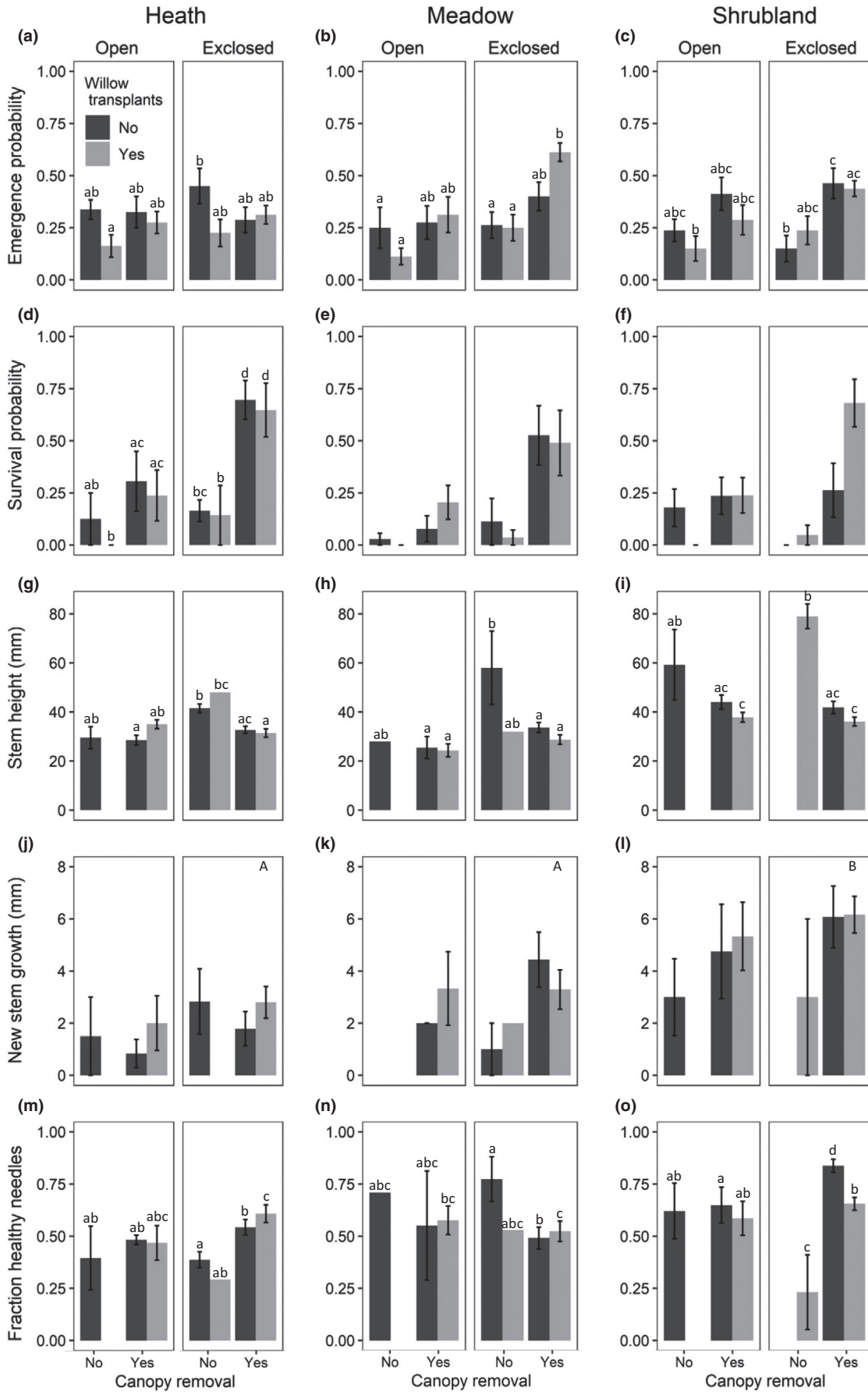
3.2 | Vegetation-removal effect on pine establishment

Seedling emergence increased with vegetation removal in the *Salix* shrubland ($\chi^2 = 33.65$, $p < 0.001$, Table 2, Figure 3) and in the heath and meadow when vegetation removal was combined with willow introduction (interaction removal $\times$ transplant: $\chi^2 = 7.16$, $p = 0.007$, $\chi^2 = 8.34$, $p = 0.004$, respectively). Seedling survival also increased with vegetation removal combined with willow introduction (interaction removal $\times$ transplant: $\chi^2 = 10.27$, $p = 0.001$), irrespective of community. In vegetation-removed subplots 6.4 times more seedlings survived than in subplots with vegetation intact. Patterns of seedling performance differed from those observed for seedling emergence and survival, and depended on the performance variable measured. The pines had greater fractions of healthy needles in vegetation-removed subplots than in intact subplots on the heath ($F = 10.26$, $p = 0.001$; Table 2, Figure 3) and in the *Salix* shrubland when vegetation removal was combined with willow introduction (interaction removal $\times$ transplant: $F = 5.88$, $p = 0.015$). In contrast, pines grew taller in intact subplots at the heath community ($F = 10.99$, $p = 0.002$; Table 2, Figure 3) and at the *Salix* shrubland site especially when vegetation removal was combined with herbivore exclusion (interaction removal $\times$ exclosure: $F = 7.80$, $p = 0.007$). New stem growth was not affected by the treatments.

3.3 | Herbivore effect on pine establishment

Pine emergence increased when herbivores were excluded in the meadow ($\chi^2 = 8.66$, $p = 0.003$; Table 2, Figure 3) and in the *Salix* shrubland when herbivore exclusion was combined with willow introduction (interaction exclusion $\times$ transplant: $\chi^2 = 3.92$, $p = 0.048$). Pine seedling survival increased when protected from herbivores ($\chi^2 = 15.76$, $p < 0.001$) for all communities. The effect of herbivore exclusion on stem height was inconsistent among sites (Appendix S3; Table S3.1, Figure 3). /in the shrubland and heath, the effect depended on complex interactions with vegetation removal and willow introduction, respectively, while we detected no effect at the meadow. When herbivores were excluded, pine seedlings had greater fractions of healthy needles on the heath and *Salix* shrubland

FIGURE 3 Effects of experimental treatments on pine emergence, survival and performance in seeded subplots in the three different plant communities after fiveyear (means ± standard error). (a–c) Pine emergence per seeded subplot, as fraction of seeds sown (10 seeds per subplot); (d–f) pine survival per seeded subplot as fraction of emerged pines; (g–i) mean stem height per pine seedling; (j–l) mean new stem growth per pine seedling; and (m–o) mean fraction healthy needles per pine seedling. Different letters represent statistically significant differences between treatments (lower case) or communities (upper case) (Tukey HSD or Dunn's test, $p < 0.05$). For survival probability, hypothesis testing was performed jointly across the three communities

Heath

(a) Open | Exclosed

(d)

(g)

(j)

(m)

Meadow

(b) Open | Exclosed

(e)

(h)

(k)

(n)

Shrubland

(c) Open | Exclosed

(f)

(i)

(l)

(o)

($\chi^2 = 4.17$, $p = 0.041$, $\chi^2 = 6.63$, $p = 0.010$, respectively; Table 2, Figure 3), but not in the meadow.

3.4 | Willow transplant effect on pine establishment

The effect of willow introduction on seedling emergence and survival depended on complex interactions with vegetation removal and herbivore exclusion (Figure 3). More seedlings emerged in encroached plots (i.e., plots with transplanted willows) when vegetation was also removed from the heath and meadow ($\chi^2 = 7.16$, $p = 0.007$ and $\chi^2 = 8.34$, $p = 0.004$, respectively), and in the shrubland when herbivores were also excluded ($\chi^2 = 3.92$, $p = 0.048$). At all sites, seedlings survived better in encroached plots when vegetation was also removed (Table 1, Figure 3). Pines grew less tall in encroached plots in the *Salix* shrubland ($\chi^2 = 5.56$, $p = 0.022$), while other effects on pine performance depended on complex interactions (Table 2, Figure 3).

3.5 | Biotic treatment effects on microclimate

Compared to the *Salix* shrubland, the heath was warmer in summer and colder in winter and the meadow community was generally intermediate. The effects of the treatments on the temperature variables were consistent among communities (Appendix 3, Table S3.2). Vegetation removal increased maximum summer temperatures ($F = 22.78$, $p < 0.001$, Appendix 3, Table S3.3, Figure 4) and decreased minimum winter temperatures ($F = 10.37$, $p = 0.002$). Maximum summer temperatures were generally lower inside the exclosures ($F = 17.14$, $p < 0.001$, Appendix 3, Table S3.3, Figure 4), and minimum winter temperatures were higher in exclosed plots compared to open plots ($F = 26.69$, $p < 0.001$). Treatment effects on soil moisture were highly variable among communities (Appendix 3, Table S3.2, Figure 4). Vegetation removal increased light availability at all communities and in the exclosed plots light availability was also lower at the heath and meadow (Appendix 3, Table S3.4, Figure 4).

TABLE 1 Parameter estimates from the selected minimal linear model describing direct and interaction effects of vegetation removal (R), herbivore exclosure (E), and willow transplants (T) on survival probability

Explanatory variable	Response variable		
	Survival probability (log odds)		
	Est. ± SE	**χ^2**	**p**
Intercept	−3.46 ± 0.47		
Vegetation removal (R)	1.79 ± 0.39		
Herbivore exclosure (E)	1.50 ± 0.38	15.76	<0.001
Transplants (T)	−1.77 ± 0.75		
R × T	2.22 ± 0.77	10.27	0.001

3.6 | Relationship between pine establishment and microclimate

None of the microclimatic variables detectably affected pine emergence. Seedling survival tended to increase with warmer maximum summer temperature, minimum winter temperature and light availability, although the estimated effects were weak (Table 3, Figure 5). Seedlings in plots characterized by high maximum summer temperatures, moister soils and higher light availability had greater fractions of healthy needles. Furthermore, seedlings grew taller in plots where less light was available. All of the estimated effects were weak.

4 | DISCUSSION

We detected strong effects of biotic factors (above-ground interactions with the co-occurring vegetation, and herbivory) on pine seedling survival, and broadly similar yet less clear effects on pine emergence patterns. Furthermore, pine seedling performance (stem height and fraction of healthy needles) was enhanced when herbivores were excluded and when above-ground vegetation was removed in two of the investigated communities. In contrast, despite clear differences in microclimate among the three focal community types (heath, meadow and *Salix* shrubland) we detected limited differences in invasibility among communities over a five-year study period. These results suggest that biotic factors are of greater importance than are abiotic factors in determining pine seedling invasibility into alpine plant communities.

4.1 | Pine seedling establishment in alpine plant communities and vegetation interaction effect

In intact vegetation, pine seedlings emerged and survived about equally well in all three alpine tundra community types we considered, but establishment rates were generally low. This low invasibility of intact tundra vegetation is in line with previous studies reporting predominantly negative effects of tundra vegetation on tree seedling recruitment (Hättenschwiler and Körner, 1995; Loranger et al., 2017; Lett and Dorrepaal, 2018). As expected, experimental reduction of competition through vegetation removal strongly increased invasibility. Vegetation removal had positive effects on emergence in the *Salix* shrubland and in the heath and meadow communities when combined with willow introduction. Seedling survival was considerably better at all three sites when canopies were removed when this effect was combined with willow introduction. This illustrates biotic resistance of alpine plant communities also for later life stages of the pine seedlings. The negative effects of tundra vegetation on tree seedling recruitment probably act through competition for light, nutrients, water and space, but could also relate to allelopathy or higher susceptibility to pathogen infections in dense vegetation (Sedia and Ehrenfeld, 2003; Loranger et al., 2017; Lett and Dorrepaal, 2018).

TABLE 2 Parameter estimates from the selected minimal (generalised) linear models describing direct and interaction effects of vegetation removal (R), herbivore exclosure (E), and willow transplants (T) on pine emergence, stem height and fraction of healthy needles in the heath, meadow and *Salix* shrubland

	Response variable								
	Emergence probability (log odds)			Stem height (log mm)[*]			Healthy needles (fraction of total)		
Explanatory variable	Est. $\pm$ SE	χ^2	p	Est. $\pm$ SE	F	p	Est. $\pm$ SE	χ^2	p
Heath									
Intercept	−0.44 $\pm$ 0.20			3.52 $\pm$ 0.08			−0.95 $\pm$ 0.30		
Vegetation removal (R)	−0.40 $\pm$ 0.24			−0.23 $\pm$ 0.07	10.99	0.002	0.88 $\pm$ 0.26	10.26	0.001
Herbivore exclosure (E)				0.19 $\pm$ 0.07			0.49 $\pm$ 0.23	4.17	0.041
Transplants (T)	−1.01 $\pm$ 0.26			0.26 $\pm$ 0.10					
R × T	0.95 $\pm$ 0.36	7.16	0.007						
E × T				-0.30 $\pm$ 0.12	6.73	0.012			
Meadow									
Intercept	−1.52 $\pm$ 0.26			3.34 $\pm$ 0.06			0.23 $\pm$ 0.18		
Vegetation removal (R)	−0.41 $\pm$ 0.25								
Herbivore exclosure (E)	0.77 $\pm$ 0.25	8.66	0.003						
Transplants (T)	−0.52 $\pm$ 0.33								
R × T	1.07 $\pm$ 0.37	8.34	0.004						
Salix shrubland									
Intercept	−1.30 $\pm$ 0.21			3.99 $\pm$ 0.11			0.79 $\pm$ 0.40		
Vegetation removal (R)	1.04 $\pm$ 0.18	33.65	<0.001	−0.22 $\pm$ 0.13			0.01 $\pm$ 0.45		
Herbivore exclosure (E)	−0.09 $\pm$ 0.25			0.53 $\pm$ 0.20			0.83 $\pm$ 0.30	6.63	0.010
Transplants (T)	−0.57 $\pm$ 0.26			−0.15 $\pm$ 0.06	5.56	0.022	−2.67 $\pm$ 0.78		
R × E				−0.59 $\pm$ 0.21	7.80	0.007			
R × T							2.05 $\pm$ 0.81	5.88	0.015
E × T	0.73 $\pm$ 0.36	3.92	0.048						

Note: Sample size n = 1,920 for pine emergence, and n = 159 for stem height and fraction healthy needles. The reference level (intercept) is no exclosure, no transplants and vegetation not removed, and parameter estimates give contrasts from the reference level. Only those factors and interactions included in the minimal models are reported.

 *Variable is natural log-transformed.

Furthermore, pine seedlings in intact vegetation had a lower fraction of healthy needles than in vegetation removal subplots in heath and in *Salix* shrubland when combined with the introduction of willow transplants, suggesting a negative impact of the standing vegetation on tree seedling performance. On the other hand, seedlings in the heath were taller in intact than in vegetation removal subplots, perhaps due to facilitation through protection from, for instance, strong abrasive winds during periods with shallow snow cover (Batllori et al., 2009; McIntire, Piper, and Fajardo, 2016; Piper et al., 2016). Also in the *Salix* shrubland, when protected from herbivores, seedlings grew taller in intact subplots than vegetation-removal subplots. In addition to the presence of a shrub canopy, the *Salix* shrubland is characterized by relatively thick understorey ground layers of lichens or bryophytes (mean thickness $\pm$ *SD* in mm: 73.7 $\pm$ 30.6). Therefore, the greater height of the seedlings in undisturbed *Salix* shrubland could be attributed to the need of outgrowing this ground layer to reach high-light conditions. Consistent with this hypothesis, we found that the *Salix* shrub community was

associated with the lowest light availability of all three communities. Decreased tree growth is often the cost of recruiting below shrubs (Castro et al., 2004; Kambo and Danby, 2018), but this was not evident for the performance measures in our study. Since we found a strong interaction between vegetation removal and willow introduction, *Salix* shrublands might provide favourable regeneration sites, provided that gaps and enough light are available in the vegetation.

4.2 | Herbivory reduces invasibility

We detected strong effects of experimental herbivore exclusion, suggesting that sheep, rodents and other herbivores affect pine seedling emergence, survival and performance. Rodents may also have eaten some of the experimental seeds (Nilson and Hjältén, 2003; Nystuen et al., 2014). Interestingly, the study area experienced a rodent population build-up during the year of seed sowing (2013), resulting in a
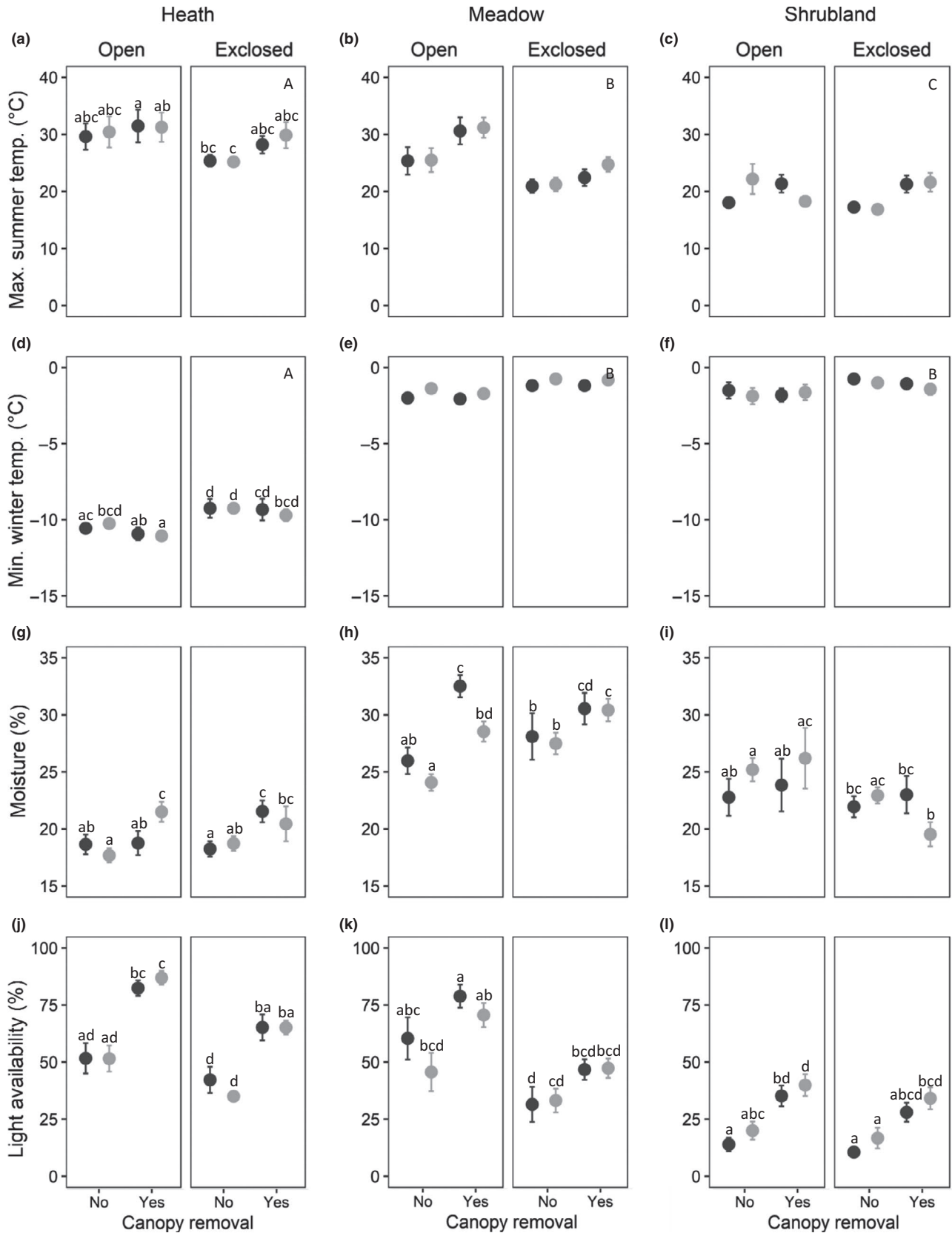
FIGURE 4 Effects of experimental treatments on microclimate in the three different plant communities (means ± standard error). (a, b, c) Mean maximum summer temperature per subplot, (d, e, f) mean minimum winter temperature per subplot, (g, h, i) mean soil moisture per subplot and (j, k, l) mean light availability per subplot. Different letters represent statistically significant differences between treatments (lower case) or communities (upper case) (Tukey's honestly significant difference [HSD] or Dunn's test, $p < 0.05$). For maximum summer temperature and minimum winter temperature, hypothesis testing was performed jointly across the three communities

TABLE 3 Parameter estimates from the selected minimal (generalised) linear models describing direct effects of community type, maximum summer temperature, minimum winter temperature, soil moisture and light availability on pine emergence, pine survival, stem height, new stem growth and fraction of healthy needles

| | Response variable | | | | | | | | | | | | | | |
| | Emergence probability (log odds) | | | Survival probability (log odds) | | | Stem height (log mm)* | | | New stem growth (log mm)** | | | Healthy needles (fraction of total) | | |
Explanatory variable	Est. ± SE	χ^2	p	Est. ± SE	χ^2	p	Est. ± SE	F	p	Est. ± SE	F	p	Est. ± SE	χ^2	p
Intercept	-0.65 ± 0.06			-1.11 ± 1.04			4.05 ± 0.10			0.84 ± 0.11			-1.35 ± 0.15		
Community					23.54	<0.001		15.62	<0.001		15.70	<0.001		552.90	<0.001
Meadow				-2.46 ± 0.96			-0.27 ± 0.06			0.33 ± 0.15			0.25 ± 0.07		
Salix shrubland				-1.00 ± 0.91			-0.07 ± 0.07			0.82 ± 0.15			1.20 ± 0.06		
Max. temp. summer				0.05 ± 0.02	5.73	0.017							0.01 ± 0.00	14.68	<0.001
Min. temp. winter				0.28 ± 0.11	6.80	0.009									
Moisture													0.02 ± 0.00	27.72	<0.001
Light availability				0.02 ± 0.01	13.23	<0.001	-0.01 ± 0.00	38.46	<0.001				0.01 ± 0.00	25.02	<0.001

Note: Minimal models were obtained by stepwise backward elimination of least significant explanatory variables. Full models are shown in Appendix S2. Sample size *n* = 1,920 for pine emergence, *n* = 578 for pine survival and *n* = 159 for stem height, new stem growth and fraction healthy needles. The reference level (intercept) is heath.

*variable is ln(x) transformed.

**variable is ln(x + 1) transformed.

(a) Survival probability vs Max. summer temp. (°C)

(b) Fraction healthy needles vs Max. summer temp. (°C)

(c) Survival probability vs Min. winter temp. (°C)

(d) Fraction healthy needles vs Moisture (%)

(e) Survival probability vs Light availability (%)

(f) Fraction healthy needles vs Light availability (%)

(g) Stem height (mm) vs Light availability (%)

- ● Heath
- ▲ Meadow
- ■ Shrubland
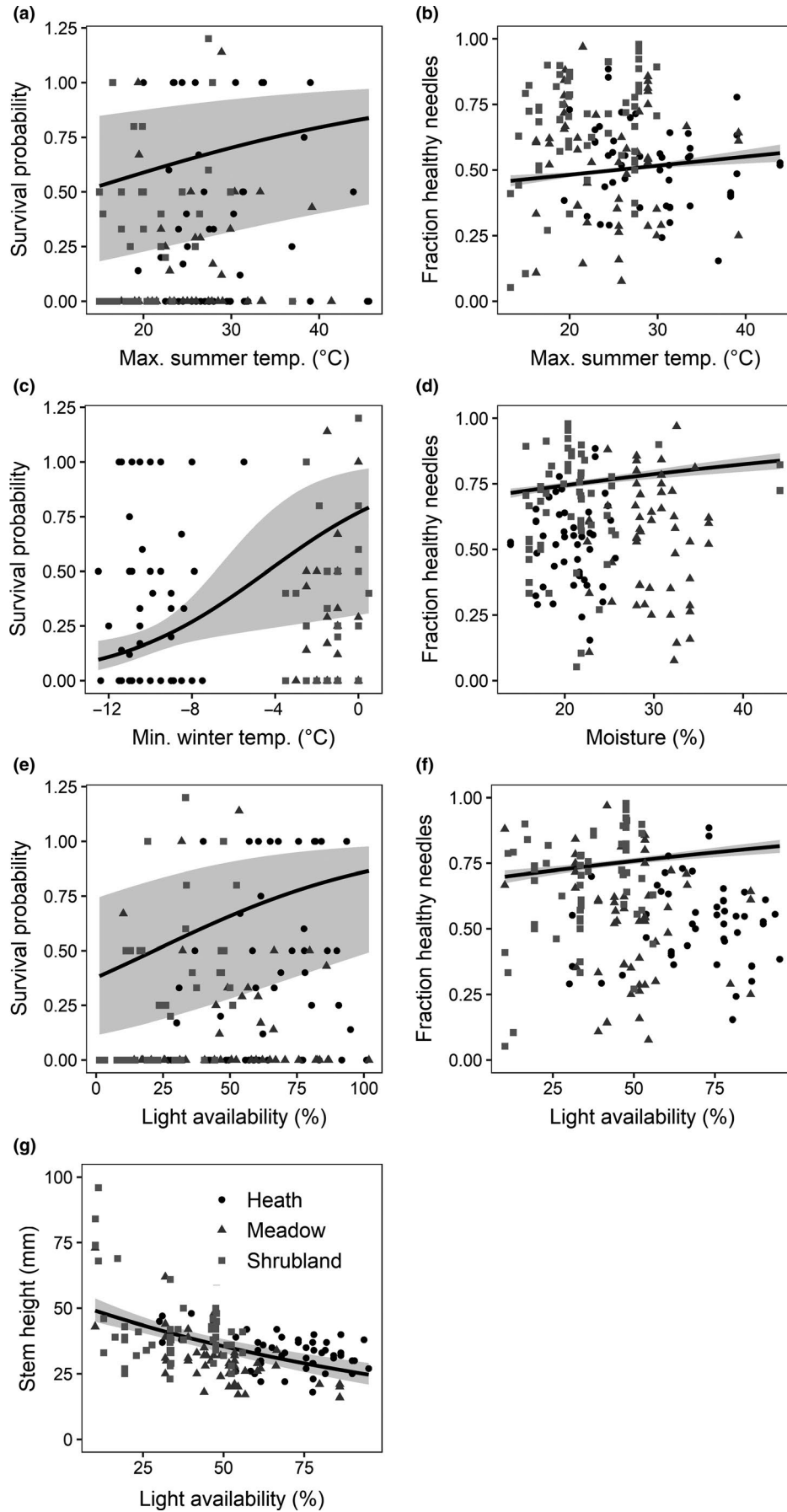
FIGURE 5 Regression plots showing the statistically significant ($p < 0.05$, Table 3) relationships between: (a) survival probability and maximum summer temperature; (b) fraction healthy needles and maximum summer temperature; (c) survival probability and minimum winter temperature; (d) fraction healthy needles and moisture; (e) survival probability and light availability;(f) fraction healthy needles and light availability; and (g) stem height and light availability. Other explanatory variables in the models are kept constant at their median values. Non-significant relationships are not shown. Shaded areas indicate 95% confidence intervals

low rodent peak in 2014 when most pine seeds germinated (Framstad, 2017). Previous studies have shown that small rodents have a stronger effect on alpine plant communities than do large herbivores (Olofsson et al., 2004; Bougnounou et al., 2018). These results add to previous studies (Moen, Lundberg, and Oksanen, 1993; Boulant et al., 2008; Post and Pedersen, 2008; Munier et al., 2010; Bougnounou et al., 2018) in suggesting that herbivory may be important in limiting tree regeneration in alpine tundra ecosystems.

4.3 | Willow introduction increases invasibility when above-ground vegetation has been removed

Willow introduction resulted in higher pine seedling emergence in the heath and meadow communities and higher pine survival in all three communities, but only when combined with vegetation removal, which could indicate facilitation from the willows on pine seedling recruitment in these short-statured vegetation types (Akhalkatsi et al., 2006; Holmgren et al., 2015; Chen et al., 2020). The introduction of willows had no detectable effect on the microclimate (Figure 4), and transplants were relatively small. Therefore, the effect observed here on invasibility may not relate to amelioration of microclimatic conditions as previously suggested (Sturm et al., 2005; Holmgren et al., 2015). Instead, this apparent facilitative effect may relate, for example, to changes in nutrient content (Chen et al., 2020), soil biota, ectomycorrhizal activity (Nara, 2006) or increased CO_2 levels due to higher soil respiration (Strimbeck et al., 2019). Disentangling the mechanisms behind this apparent facilitative effect will require further studies as the introduced willows grow larger.

4.4 | Weak effects of microclimate on invasibility

Contrary to expectations, pine seedling survival and fraction of healthy needles increased with higher maximum summer temperatures. Thus, high summer temperatures do not seem to limit seedling establishment and performance. In addition, seedling survival increased with higher minimum winter temperatures. Although temperature extremes are more ecologically meaningful for explaining seedling establishment than are temperature means, we could not distinguish with certainty between the variables, due to their correlation. Magnitudes of all microclimate effects were very small (Table 3) and statistical support was weak (Figure 5), indicating only subtle effects of abiotic factors on pine invasibility in this system. These results suggest that abiotic factors are of limited importance for pine establishment compared to the biotic drivers discussed

above. It is possible that abiotic stress is an important factor driving differences in woody encroachment at larger scales, but on the scale we operated, abiotic factors seem to play limited roles compared to biotic factors.

5 | CONCLUSIONS

Our results demonstrate that, when experimentally introduced into treeless alpine tundra, *Pinus sylvestris* seedlings have the potential to emerge and establish in all three plant community types considered. Despite successful initial establishment, the pines remained small, depending on their microsite and community characteristics (Körner, 2012; Brodersen et al., 2019). Furthermore, we provide field evidence that biotic factors are the key drivers of pine seedling establishment into the alpine tundra ecosystem. Above-ground vegetation biomass and herbivory inhibited both pine seedling establishment and performance, and this inhibition was relieved the most when both factors were removed. In contrast, seedling responses to variation in microclimate were subtle. This suggests that effects of climate on vegetation dynamics in alpine ecosystems are mediated through disturbances and herbivory. Studies aiming to predict future vegetation changes should therefore incorporate local biotic interactions in addition to abiotic factors even in alpine communities.

AUTHOR CONTRIBUTIONS
KON, MVS and BJG conceived and designed the experiments. FM, JF, KON, PDF, BJG, ØO and MVS performed the fieldwork. FM analyzed the data and wrote the manuscript. JL, BJG, PDF, KON, ØO, JF and MVS contributed to the writing. All authors read and approved the final manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Community description
Appendix S2. Details on the data analysis
Appendix S3. Results from the (generalized) linear models