

Doctoral thesis

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Kristin Odden Nystuen

Drivers of plant recruitment in alpine vegetation

NTNU
Norwegian University of Science and Technology
Thesis for the Degree of
Philosophiae Doctor
Faculty of Natural Sciences
Department of Biology



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Trondheim, November 2020

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Kristin Odden Nystuen

September, 2020

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Papers I-V

LIST OF PAPERS

- I. **Nystuen, K.O.**, Evju, M., Rusch, G.M., Graae, B.J. & Eide, N.E. 2014. Rodent population dynamics affect seedling recruitment in alpine habitats. *Journal of Vegetation Science* 25: 1004-1014.
- II. Opedal, Ø.H., **Nystuen, K.O.**, Hagen, D., Holien, H., Sørensen, M.V., Lang, S., Lindmo, S., Strimbeck, G.R. & Graae, B.J. Herbivores reduce the invasibility of alpine plant communities. Manuscript.
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- IV. Marsman, F., **Nystuen, K.O.**, Opedal, Ø. H., Foest, J.J., Sørensen, M.V., De Frenne, P., Graae, B.J., & Limpens, J. 2020. Determinants of tree-seedling recruitment in alpine tundra. *Journal of Vegetation Science*: doi:10.1111/jvs.12948
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Author contributions

Paper I: NEE initiated and designed the field setup; NEE, KON and BJG designed the present study; KON performed fieldwork; KON and ME analyzed the data; KON wrote the paper in collaboration with ME, GMR, BJG and NEE.

Paper II: KON, MVS, GRS, HH, DH and BJG participated in the design of the experiment; KON, ØH, MVS, BJG, HH, SL, GRS and SL performed fieldwork; ØH analyzed the data and wrote the manuscript together with KON and BJG and with inputs from all authors.

Paper III: KON, MVS, HH, GRS and BJG designed the study. All authors performed fieldwork. ØHO and KON analyzed the data. KON and ØHO wrote the manuscript with contributions from all authors.

Paper IV: KON, MVS and BJG designed and established the experiments in 2013. KON, ØO and BJG recorded pine seedling emergence and survival until 2016. FM, JF and ØO recorded pine survival and performance in 2018. Collection of environmental data was done primarily by KON, MVS, ØO and BJG until 2017 and by FM, JF and ØO in 2018. PDF and JL participated for shorter periods. 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.

Paper V: KS, BJG, GRS, HH and KON designed the study; KS, KON and BJG did fieldwork; KS performed the laboratory experiment; KON, ØHO and KS analyzed the data; KON and KS wrote the paper with input from all authors.

All authors consent that their work is presented in this thesis.

ABSTRACT

Changes in climate and grazing from wild and domestic herbivores influence alpine vegetation, resulting in recent upward migration of species and changes in plant community composition. Seedling recruitment has an essential role in the dynamics and structure of plant communities but the seedling phase is also a major bottleneck in a plant's life. In this thesis, which consists of studies from alpine plant communities in the Norwegian Scandes, I explore how the abiotic environment as well as interactions between standing vegetation and herbivores affect plant recruitment success and failure.

Using an observational and an experimental study, strong effects of the standing vegetation, and presence of vertebrate herbivores on plant recruitment dynamics are shown. Rodents indirectly increased seedling recruitment through their disturbances, creating suitable microsites for seedling emergence. However, the direct effects of vertebrate herbivores on seedling recruitment were negative: In a five-year-seed sowing experiment, seedling survival and establishment rates were higher, and seedling community composition different inside cages inaccessible to herbivores. Thus, herbivory on seedlings lowers recruitment success in alpine communities. The standing vegetation is another strong filter that inhibits plant recruitment. In undisturbed alpine vegetation, fewer seedlings emerged, fewer survived, and the composition of seedling communities was different than where the standing vegetation was disturbed. We identified seedling emergence as the most crucial recruitment phase, and recorded only 2.3% emergent seedlings of the 36, 960 seeds sown in undisturbed vegetation. However, the negative effect of vegetation was less pronounced in a low-productive heath with high abiotic stress. A common garden experiment in a similarly stressful heath revealed mainly facilitative interactions between lichens and seedling recruitment. The positive interactions were potentially related to amelioration of the heath microclimate by the lichens. In addition, shrub cover affected recruitment patterns, and seedling composition changed along a gradient from sparse to dense *Salix* shrub canopies with dense canopies favoring broadleaf forbs. The abiotic environment influenced recruitment of the sown plant species differently, and sometimes emergence and survival within species differently. Conditions associated with dense shrub covers (i.e. warmer temperatures in winter, cooler temperatures in summer, and less light) reduced recruitment success of many species.

Although seedling recruitment success depends on the abiotic environment, this thesis demonstrates the additional relevance of vertebrate herbivores, through creation of suitable sites for emergence and later through seedling herbivory, and strong, mainly negative effects of the standing vegetation on this critical life phase. A changing climate may therefore indirectly affect plant recruitment patterns through effects on the vegetation (e.g. increased shrub growth and decrease in lichen cover), or through effects on herbivores (e.g. rodent population dynamics). The changing herbivore impact during plant recruitment phases as well as the plant species' different environmental constraints, underline the value of long-term experiments with multiple species for understanding dynamics of alpine plant communities.

SAMMENDRAG

Endringer i klima og beitetrykk fra husdyr og ville planteetere påvirker vegetasjonen i fjellet. Noen arter øker i utbredelse, mens andre er i nedgang, noe som igjen fører til nye sammensetninger av plantesamfunn. Rekruttering av nye planteindivid fra frø bidrar til disse vegetasjonsendringene, men er også en sårbar fase i plantenes liv. Hovedformålet med denne avhandlingen har derfor vært å undersøke hvordan frøspiring, samt etablering og overlevelse av frøplanter avhenger av abiotiske faktorer, beiting og den eksisterende vegetasjonen i fjellet.

Feltstudier viste at påvirkning fra beitedyr og den eksisterende vegetasjonen er svært viktig for rekrutteringssuksessen til planter i fjellet. Beite og andre forstyrrelser fra smågnagere åpner opp vegetasjonen og legger til rette for frøspiring. Beite er derimot negativt for frøplantene senere i livet. I et felteksperiment med frøspiring på Dovrefjell overlevde færre frøplanter utenfor enn innenfor bur, noe som tyder på at sau, smågnagere, rein eller andre dyr har beitet på frøplantene. Den eksisterende vegetasjonen var oftest et hinder for frørekruttering. I uforstyrret fjellvegetasjon var det både færre frøplanter som spirte, færre som overlevde og en annen artssammensetning enn der hvor vegetasjonen var fjernet. Spiring og første vekstsesong var den mest kritiske fasen, og av 36 960 sådde frø i uforstyrret vegetasjon var det bare 2,3% av frøplantene som var i live ved slutten av deres første vekstsesong. Type vegetasjon påvirket også spiresuksessen til artene, og i en lite produktiv hei med høyt abiotisk stressnivå var den negative påvirkningen på spiring lavest. Vi undersøkte også hvordan matter av ulike arter lav påvirket frørekruttering i en annen hei med tilsvarende høyt stressnivå. Her viste resultatene at lavene la til rette for frørekruttering, antagelig på grunn av det mer gunstige mikroklimaet for frøplantene inne i lavmattene, sammenlignet med på bar jord. Innad i et vierkratt påvirket buskdekningen de rekrutterende planteartene ulikt. Dette førte til en endring i sammensetning av frøplanter fra plott med sparsomt til tett buskdekke, hvor tett buskdekke favoriserte urter med store blader. Responsen på det abiotiske miljøet i vierkrattet var ulik mellom artene, og i noen tilfeller også ulik for spiring og overlevelse innen samme art. Resultatene våre tyder på at miljøforhold som korrelerer med økt dominans av busker kan ha en negativ effekt på frørekruttering hos mange plantearter.

Selv om sjansen for å lykkes med frørekruttering i fjellet avhenger av det abiotiske miljøet, viser denne studien at også type vegetasjon og beite er avgjørende for denne kritiske fasen i plantenes liv. Klimaendringene kan derfor indirekte ha innvirkning på frørekruttering, via påvirkning på vegetasjonen slik som økt vekst i busksjiktet og via effekter på dyr slik som mindre uttalte smågnagersvingninger i fjellet. At beite indirekte legger til rette for frøspiring, men senere kan ta livet av frøplantene, samt frøplantenes artsspesifikke responser på beite, vegetasjonstyper og abiotiske faktorer, demonstrer viktigheten av langtidseksperimenter med flere arter for å forstå rekrutteringsdynamikk i fjellet.

INTRODUCTION

Recently, arctic-alpine tundra vegetation has experienced several changes, including increased dominance of shrubs, declines in terricolous lichen covers (i.e. lichens growing on soil) and upward shifts of species ranges (Myers-Smith et al. 2011; Fraser et al. 2014; Vanneste et al. 2017; Steinbauer et al. 2018; Bjorkman et al. 2019; Løkken et al. 2019). Important drivers are climate and herbivory, as well as their interactions, but the trends are not ubiquitous and the underlying processes are often not fully understood (Martin et al. 2017; Myers-Smith & Hik 2018; Bjorkman et al. 2019). Although most species in tundra vegetation are long-lived, seedling recruitment is frequent and has an essential role in the dynamics and structure of tundra plant communities (Welling & Laine 2000; Büntgen et al. 2015). However, the seedling stage (i.e. seed germination, seedling survivorship and seedling growth) are major bottlenecks in a plant's life, and few seeds develop into seedlings that survive to adulthood (Leck et al. 2008). There are a multitude of factors that prevent seeds from germinating and seedlings from establishing that can be viewed as environmental filters. These filters can be either abiotic or biotic (e.g. competition, herbivory, availability of mycorrhiza symbionts, allelopathy), and act alone or together with varying effects in space and time. Seeds are well-protected by the seed coat and can sometimes persist in seed banks for years, decades or even centuries (McGraw et al. 1991; Molau & Larsson 2000; Arroyo et al. 2004; Schwienbacher et al. 2010). Seedlings, on the other hand, have limited resource reserves and are highly susceptible to resource limitation in contrast to older plants with larger energy reserves and better access to belowground resources like water and nutrients, and to light (Leck et al. 2008). Consequently, seedlings have a narrow tolerance to the abiotic environment (Moles & Westoby 2004b; Fenner & Thompson 2005). The seedling stage is also when herbivory is thought to have the strongest effect on plant survival, because of the small size and limited regrowth capacity of seedlings (Hanley 1998). This intense environmental filtering makes the seedling stage of special interest for community dynamics. In the following I will therefore describe important environmental filters acting on plant recruitment in tundra vegetation, that being abiotic factors, interactions with the standing vegetation and herbivores.

Abiotic factors and plant recruitment

Abiotic characteristics like light, moisture, temperature, wind exposure, and availability of nutrients are crucial for plant recruitment (Chambers 1995; Walck et al. 2011). While germination take place over a wider range of abiotic conditions, establishment conditions are often narrower, resulting in strong environmental filtering at this stage (Donohue et al. 2010). For instance, warmer temperatures may increase seed germination (Milbau et al. 2009; Klady et al. 2011; Walck et al. 2011), but increase subsequent seedling mortality (Hobbie & Chapin III 1998; Shevtsova et al. 2009; Milbau et al. 2017). When compared to established plants, the shallow root depth in emerging seedlings makes them more vulnerable to desiccation, and droughts are consequently among the most frequent causes of seedling mortality (Bell & Bliss 1980; Moles & Westoby 2004b). This vulnerability to extreme conditions sometimes results in more seedlings surviving in more protected microsites (e.g. within vegetation, behind a rock or below a shrub canopy). However, impaired performance is often the price to pay for this 'protection', at least for trees recruiting in tundra (Grau et al. 2013; Lett 2017; Angulo et

al. 2019). This brings us to another important aspect, namely interspecific variation of environmental tolerance, which in turn can be explained by traits of seeds and seedlings. For instance, traits of conifer seedlings may be an adaptation to recruiting in microsites with high irradiance and temperature fluctuations that are superior to traits of broadleaf forb seedlings recruiting under the same conditions (Brodersen et al. 2019). Generally, larger-seeded species are better at recruiting under conditions where water, nutrient and light are scarce than smaller-seeded species (Moles & Westoby 2004a; Körner 2012). Monitoring seedlings and the abiotic environment they experience may reveal the most determining factors for both recruitment success and failure, as well as how they vary across ontogeny. This will probably differ among species, as well as being mediated by the vegetation in which they recruit.

Vegetation-plant recruitment interactions

Fennoscandian tundra vegetation comprises a patchwork of different vegetation types. On a local scale the vegetation types are primarily distributed along topographical gradients with differing abiotic conditions (Billings 1987). These vegetation types differ in invasibility (i.e. the susceptibility to colonization by new species – either natives or aliens; Burke & Grime 1996), which in turn can explain the high variation in seedling densities among tundra habitats (Welling & Laine 2000, 2002). For instance, communities made up of perennial, clonal species support fewer recruits than those dominated by species with no or ineffective vegetative reproduction (Welling & Laine 2000, 2002; Gough 2006; Graae et al. 2011). Whether these differences in invasibility derive from the species, other aspects of the environment, or a combination is however not clear. Furthermore, successful seedling emergence of most species depend on disturbances creating gaps or ‘safe sites’ with limited competition (Grubb 1977; Milbau et al. 2013; Lembrechts et al. 2016). Also, seedling growth and survival usually benefit from competitive release from the vegetation, depending on season and ontogenetic stage (Germino et al. 2002; Loranger et al. 2017). Sources of disturbances in tundra vegetation are diverse with varying spatial and temporal impact. Examples include grazing and trampling from lemmings and voles (Sætnan et al. 2009; Olofsson et al. 2012), disturbances caused by grazing and trampling from bigger mammals (Vistnes & Nellemann 2008; Dufour-Tremblay & Boudreau 2011), melting-water, cryoturbation (Sutton et al. 2006; Frost et al. 2013) and vegetation die-off after frost-damage (Bjerke et al. 2017).

The vegetation also mediates how susceptible seeds and seedlings are to the abiotic environment. Whether vegetation-seedling interactions are facilitative or competitive, may depend on the environmental context (Callaway et al. 2002; Wipf et al. 2006). Facilitative mechanisms are considered most important in stressful habitats and include amelioration of the microenvironment (e.g. buffering of extreme temperatures, retention of soil moisture, accumulation of snow, and protection from wind and radiation). Competitive interactions (e.g. for space, nutrients, light, water) on the other hand, are considered most common in productive and environmentally benign vegetation (Bertness & Callaway 1994). Nevertheless, Milbau et al. 2013 demonstrated that the standing vegetation limited early seedling recruitment not only in productive habitats (i.e. meadows and *Salix*-shrub dominated communities), but also in more stressful tundra habitats (i.e. lichen and dwarf-shrub heaths).

Competitive interactions may therefore dominate also in stressful tundra. However, when one take into account that seedlings in tundra grow slowly and remain small and vulnerable over many growing seasons (Billings & Mooney 1968; Venn et al. 2009), prevailing competitive interactions with the vegetation may shift to facilitation of the abiotic environment under stressful events (Grau et al. 2013; Jaroszynska 2019), and thereby sustain seedlings in a long-term perspective.

Species that dominate the vegetation are potentially also strong drivers of the invasibility. Mat-forming terricolous lichens dominate wind-swept ridges and heaths in continental tundra areas where they color the landscape light yellow (Ahti 1977; Crittenden 2000). A low number of seedlings in lichen-dominated tundra vegetation (Graae et al. 2011; Evju et al. 2012) suggests it is difficult for plants to recruit here, which in turn could relate to negative interactions with lichens. Firstly, lichen produce secondary metabolites for varied purposes, among them possible allelopathic action towards co-occurring vegetation (Pyatt 1967; Brown & Mikola 1974; Sedia & Ehrenfeld 2003). Secondly, the physical structure of lichen mats can prevent seeds and root radicles of germinating seeds to reach the soil, as well as prevent emerging seedlings to penetrate the lichen mat (Allen 1929; Zamfir 2000). On the other hand, the physical structure of lichens may facilitate plant recruitment through amelioration of the harsh microclimate in lichen-dominated tundra vegetation (e.g. maintenance of soil moisture, buffering of extreme temperatures, shelter towards wind and snowdrift; Kershaw & Rouse 1971; Broll 2000; Molina-Montenegro et al. 2013). It is still an open question whether the terricolous lichens' competition or potential facilitation is most important for recruiting plants.

Canopy-forming deciduous *Salix* shrubs dominate in more sheltered and mesic tundra vegetation. Shrubs can alter the microenvironment by reducing the light availability (Totland et al. 2004), increasing the amount of litter (Becklin et al. 2012), decreasing summer temperatures (Myers-Smith & Hik 2013). They tend to support less dense understory plant covers with different species compositions compared to adjacent open tundra vegetation (Pajunen et al. 2011). Therefore, it is surprising to find high seedlings numbers and high seedling species richness in *Salix* understories (Graae et al. 2011). When exactly filtering of these recruits takes place, as well as how species of different growth forms are affected, is therefore of interest. While interactions between shrubs and recruiting tree species are extensively studied (e.g. Jumpponen et al. 1998; Cranston & Hermanutz 2013; Kambo & Danby 2018; Angulo et al. 2019; Chen et al. 2020), those among smaller woody and herbaceous species are less so. Tree seedlings often benefit from recruiting under a shrub canopy, although interaction outcomes depend on the shrub and tree species in question (Castro et al. 2004; Akhalkatsi et al. 2006; Chen et al. 2020). In the long term, shrub presence and competition can decrease seedling growth (Angulo et al. 2019). With the recent increases of erect shrubs in many tundra areas (Frost et al. 2014; Vanneste et al. 2017; Bjorkman et al. 2019) it's timely to explore shrub-mediated plant recruitment dynamics in more detail.

Other vegetation properties such as amount of litter and mosses also contribute to spatial variation in seedling numbers (Rusch & Fernández-Palacios 1995). Thick moss mats can limit germination and seedling survival, but may also provide moist refuges under droughts or protect against frost (Jeschke & Kiehl 2008; Eckstein et al. 2011; Jaroszynska 2019). Litter often suppress seedling emergence, whereas seedling survival can be both

positively and negatively affected, depending on the amount of litter, the species, and the habitat in question (Xiong & Nilsson 1999; Eckstein et al. 2011; Loydi et al. 2013). Thus, there is still much to learn about the interactions between seedlings and surrounding vegetation in tundra vegetation.

Herbivores and plant recruitment

Patterns of plant recruitment in tundra also depend on herbivores. On one hand, grazing, browsing, and trampling suppress and disturb the standing vegetation, providing ‘safe sites’ with reduced competition for seedlings to emerge (e.g. Watt & Gibson 1988; Ericson et al. 1992; Eskelinen & Virtanen 2005; Dufour-Tremblay & Boudreau 2011). Seedlings may further benefit from herbivory through competitive release from the standing vegetation (Hanley 1998). On the other hand, the seedling stage is highly vulnerable to grazing, trampling, and burial. The direction of plant community development can develop differently due to herbivore selectivity and the seedlings’ tolerance to mechanical damage and defoliation (Eskelinen 2008; Barton & Hanley 2013; Bognounou et al. 2018). Trampling, however, does not discriminate between species. Long-term studies are necessary to explore the importance of positive versus negative impacts of herbivores on plant recruitment.

The herbivores in Fennoscandian tundra vary in their effects on plant recruitment. The high-amplitude population cycles of voles and lemmings create pulsed inputs of disturbances and nutrients (Turchin & Batzli 2001) likely increasing the invasibility of the vegetation (Ericson et al. 1992), whereas seeds and seedlings may be less affected by rodents in years in-between population peaks. Domestic sheep are abundant in alpine areas of Norway in summer (Speed et al. 2019). They graze selectively, preferably in herbaceous-rich vegetation (Rekdal 2001; Kausrud et al. 2006), so that seedlings here perhaps are especially vulnerable to grazing. However, seedlings in heaths – where sheep prefer to rest (Kausrud et al. 2006) – are prone to trampling and mechanical damage. Wild or semi-domestic reindeer is another big herbivore present in Fennoscandian tundra year-round. In winter, the reindeer mainly consume lichens, and their grazing and digging for lichens in heaths may also damage seedlings (Rekdal & Angeloff 2015). Both reindeer and sheep selectively browse deciduous tree seedlings (den Herder & Pekka 2003; Speed et al. 2012), whereas big mammal herbivory on conifer and herbaceous seedlings is less studied.

The susceptibility to herbivory can indirectly be driven by the cover of vegetation. For example, seedlings in sparsely vegetated patches may be easier to detect than those within tall vegetation. As such, seedlings under dense and continuous shrub canopies are probably less accessible to big herbivores (Castro et al. 2004; Grau et al. 2013). However, the opposite counts for small herbivores, that may spend more time feeding under a protective shrub canopy (Royo & Carson 2008). How well seedlings tolerate herbivory may also depend on microsite characteristics. Shaw et al. (2013) demonstrated that seedling regrowth after vole herbivory was greater in gaps than in intact vegetation, probably as a result of less competition in gaps. The impact of herbivores on plant recruitment is therefore complex, mediated through both abiotic and biotic microsite properties, and may shift during recruitment phases, depending on the plant and the herbivore in question.

AIM AND QUESTIONS

The overall aim of this thesis is to explore the drivers of plant recruitment in alpine communities, with special emphasis on how post-dispersal recruitment phases are affected through interactions with herbivores and the standing vegetation, and by the abiotic environment. Specifically, I ask these questions:

- 1) How do herbivores affect seedling recruitment indirectly through grazing and disturbances on the standing vegetation (Paper I), and directly through trampling and herbivory on seeds and seedlings (Papers II – IV)?
- 2) Does the standing vegetation inhibit or facilitate plant recruitment when considering recruiting plants and:
 - i) intact vs. disturbed vegetation in heath, meadow, and *Salix* shrubland vegetation (Papers II – IV)?
 - ii) shrub canopy cover (Paper III)?
 - iii) shrub introduction (Paper II, IV)?
 - iv) terricolous lichens (Paper V)?
- 3) How does the abiotic environment affect plant recruitment (Papers II – IV) as well as conifer tree-seedling performance (Paper IV), and does this change during ontogenetic shifts (i.e. seedling emergence, survival, and establishment)?

METHODS

General approaches

This thesis is based on three different approaches. First, an observational survey of rodent activity and seedling abundance (Paper I). Second, a field experiment assessing interactions among recruiting plants and disturbances, herbivores, abiotic factors, and shrub introduction in different vegetation types (Papers II-IV). Third, a combined laboratory and common garden field experiment assessing interactions among plant recruitment and lichens (Paper V). The field work was conducted between 2011 and 2018 at 10 sites in common, low-alpine Fennoscandian vegetation around 700 – 1300 m a.s.l. in the Scandes, Norway (Fig.1, Table 1).

The study sites

The studies were performed in two mountain regions of the Norwegian Scandes, Børgefjell and Dovrefjell (Fig. 1). Three study sites are located in Børgefjell, whereas the other seven are located in Dovrefjell (Fig. 1, Table 1). Each site in Paper I comprises six transects covering either sheltered heath and/or snowbed vegetation at different locations, whereas the sites in Paper II-V are confined to one vegetation type and a smaller area (see location and photos in Fig. 1, Table 1). See the papers for thorough study site descriptions.

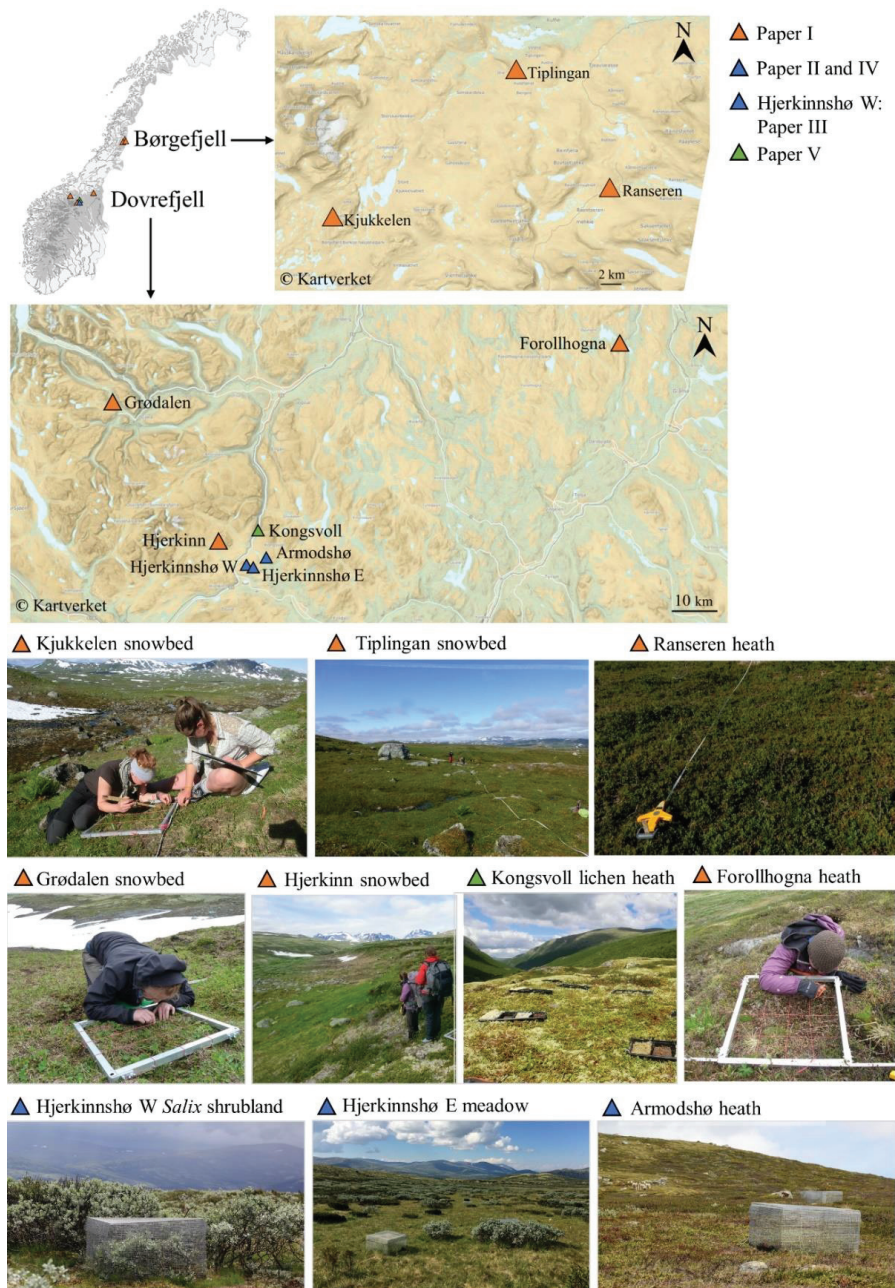


Figure 1. Map of Norway with mountainous areas in dark grey and location of the 10 study sites in the two mountain regions Børgefjell and Dovrefjell, as well as photos from the study sites: **Kjukkelen snowbed**: looking for seedlings, **Tiplingan snowbed**: measuring tape transect, **Ranseren heath**: measuring tape transect, **Grødalen snowbed**: looking for seedlings, **Hjerkinnsjø W**: standing in a lichen heath looking down at a snowbed-transect, **Kongsvoll lichen heath**: some of the experimental trays with lichens and bare soil, **Forollhogna heath**: looking for seedlings, **Hjerkinnsjø W Salix shrubland**: a caged plot to exclude vertebrate herbivores, **Hjerkinnsjø E meadow**: looking down the meadow site dominated by herbs and cryptogams with scattered *Salix* canopies, **Armodshø heath**: looking up at two caged plots and sheep (left) in the dwarf-shrub-dominated vegetation

Table 1. Overview of the study regions and sites, the studied vegetation type, altitude, latitude and longitude and the papers in which they are included.

Region Site	Vegetation type	Altitude (m a.s.l.)	Latitude and longitude	Paper
<i>Børgefjell</i>				
Kjukkelen	Sheltered heath and snowbed	704 – 914	65°9'44.95104" N, 13°49'14.80424" E	I
Tiplingan	Sheltered heath and snowbed	751 – 914	65°15'25.24247" N, 14°4'53.14911" E	I
Ranseren	Sheltered heath and snowbed	841 – 968	65°11'8.51491" N, 14°13'20.35542" E	I
<i>Dovre fjell</i>				
Grødalen	Sheltered heath and snowbed	1052 – 1236	62°31'39.48613" N, 8°56'17.83733" E	I
Hjerkinn	Sheltered heath and snowbed	1188 – 1326	62°17'11.86987" N, 9°26'51.94492" E	I
Forollhogna	Sheltered heath and snowbed	923 – 1044	62°44'11.96714" N, 11°6'11.71481" E	I
Kongsvoll	Lichen- and dwarf-shrub heath	c. 930	62°18'5.75517" N, 9°36'24.00385" E	V
Hjerkinnshø W	<i>Salix</i> shrubland	1188 – 1210	62°14'29.60657" N, 9°35'41.55917" E	II, III, IV
Hjerkinnshø E	Meadow	1152 – 1162	62°14'9.8096" N, 9°37'21.45197" E	II, IV
Armodshø	Dwarf-shrub heath	1135 – 1145	62°15'37.09447" N, 9°40'35.3892" E	II, IV

The herbivores

Lemmings (*Lemmus lemmus*) and voles (*Microtus agrestis*, *M. oeconomus* and *Myodes rufocanus*) are important rodents in both study regions that exhibit cyclic population dynamics. The regions experienced a high population peak in 2010-2011, followed by a low-density year in 2012. At Dovrefjell, the populations also had build-ups in 2013 and 2017 resulting in low rodent peaks in 2014 and 2018 (Framstad 2019). Dovrefjell has a long history of summer grazing and browsing by domestic sheep (*Ovis aries*) (Hagen et al. 2006; NIBIO 2017) and has wild populations of reindeer (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*). Muskox herbivory is relevant only for study site Hjerkinn in Paper I. Børgefjell is an important area for reindeer husbandry (Evju et al. 2010). Other herbivores include hare (*Lepus timidus*) and ptarmigans (*Lagopus lagopus* and *L. muta*).

The studies

Observational study of rodent activity and seedling abundance (Paper I)

The first paper explores how the cyclic population dynamics of lemmings and voles affect plant regeneration during a rodent peak year (2011), and in the following low-density year (2012). In both years, we recorded abundance of emergent seedlings and rodent activity (i.e. grazing marks and feces) in 270 snowbed and sheltered heath-plots, divided between two mountain regions (Børgefjell and Dovrefjell), six study sites (Table 1), and 36 transects (see schematic method summary in Fig. 2 and detailed description of the methods in Paper I).

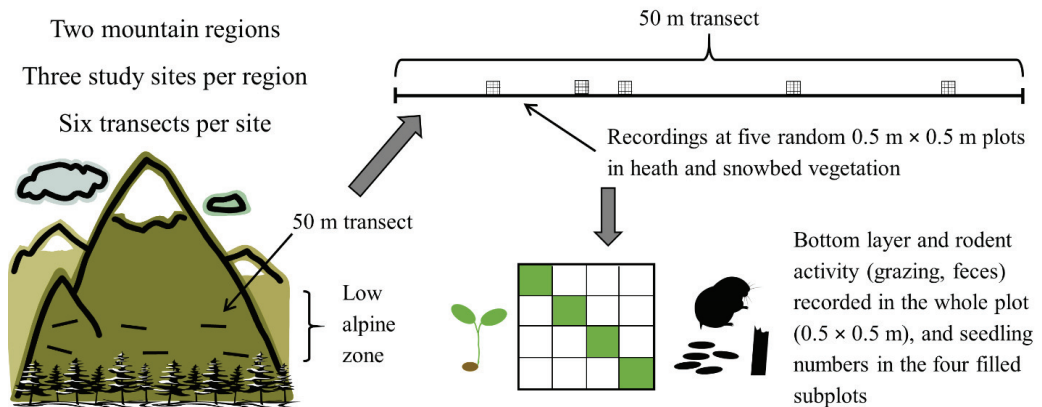


Figure 2. Schematic summary of the observational setup in Paper I where we recorded rodent activity and naturally occurring seedling abundance over two years.

Experimental herbivore exclusion, shrub introduction and disturbance in different vegetation types (Paper II)

In the second paper we explore how plant recruitment is affected by herbivore exclusion, shrub introduction, disturbances, the abiotic environment and seed addition at a meadow, heath and *Salix* shrubland site. In 2013, we placed 32 plots (25×25 cm) within each site for experimental exclusion herbivores and shrub introduction. With a 2×2 factorial design, we protected half of the plots from small and large vertebrate herbivores by $80 \times 80 \times 60$ cm cages with lids (Fig 3B), and in half of the caged and half of the open plots we planted five c. 10 cm tall *Salix* saplings (from a mixed cultivation of *Salix glauca* and *S. lapponum* not determined to species) to simulate shrub expansion (Fig. 3C). The *Salix* shrub introduction into the already shrub-covered *Salix* shrubland site acted as a control. At each plot, we established four seedling subplots (12.5×12.5 cm) for a 2×2 factorial experiment including disturbance (i.e. removal of above-ground vegetation) and seed sowing (Fig 3A). A seed mixture of 14 plant species was sown in each of the two seeded subplots in late autumn 2013. We recorded seedling emergence in all seedling subplots in autumn 2014, as well as seedling emergence and seedling survival in 2015, 2016, and 2018. Microenvironmental measurements included soil surface temperatures in intact vegetation and disturbed unseeded subplots, litter cover in all subplots, and snow depth in all plots. See detailed description of the methods in Paper II.

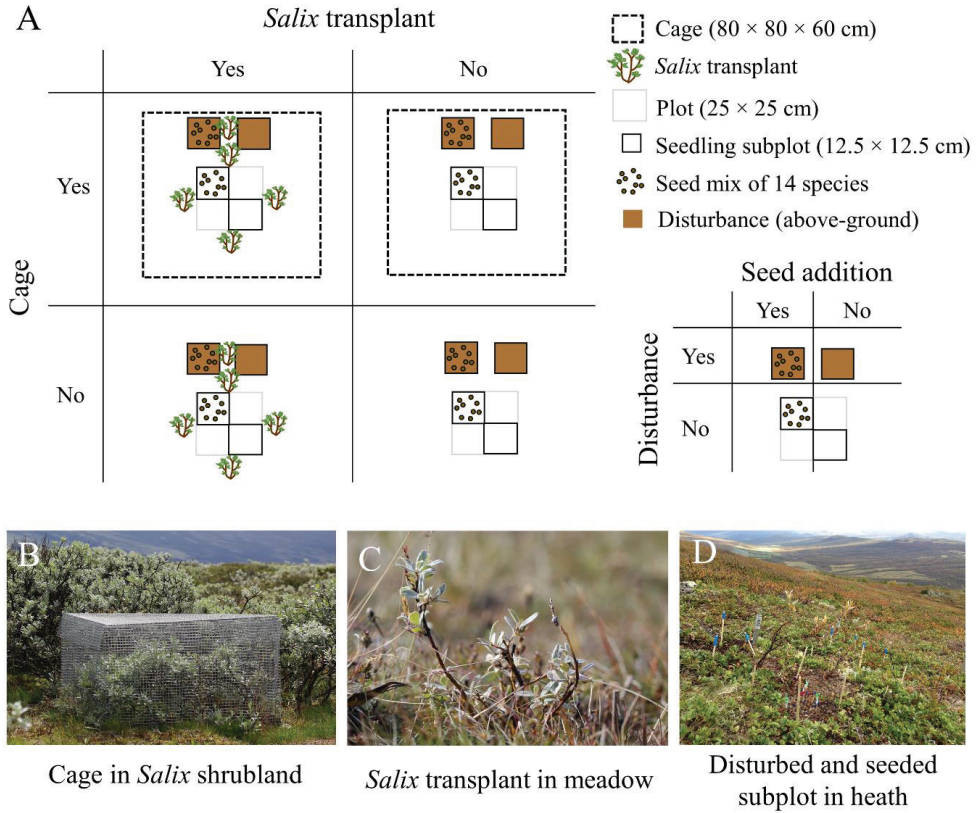


Figure 3. (A) Schematic representation of the 2×2×2×2 factorial experimental design in Papers II – IV with cages excluding vertebrate herbivores, *Salix* transplants simulating shrub expansion, disturbance removing above-ground competition from standing vegetation, and seed addition. Treatments were replicated eight times in a *Salix*-dominated shrubland community, an herb- and cryptogam dominated meadow, and an *Empetrum*-dominated heath in the low-alpine zone (Paper III include the *Salix* shrubland and disturbed subplots only). We recorded seedling emergence, survival, and establishment over five years in the seedling subplots. Photos B-D show the plant communities and treatments: (B) a cage at the *Salix* shrubland site, (C) a *Salix* shrub (c. 9 cm tall) at the meadow site two years after planting, and (D) a disturbed and seeded subplot with plot and seedling markers at the heath site three years after sowing.

Seed sowing along a gradient in shrub cover (Paper III)

The third paper explores more in detail how plant recruitment is affected by the microenvironment and shrub covers. We used the same experimental setup as in Paper II, but focused on the disturbed subplots at the *Salix* shrubland site only (Fig. 3A, B). This site is south-facing and located close to Gamle Kongeveg at Hjerkinshø, Dovrefjell (Fig. 1, Table 1). The 32 plots comprised a gradient from sparse to dense deciduous shrub cover (Fig. 4), recorded as number of hits from point intercept analysis (Goodall 1952) with 25 pins distributed across a 25×25 cm square. We monitored seedling emergence, survival, and establishment in the disturbed subplots over five years (see Fig. 4 for photo of emergent seedlings in a disturbed seeded subplot). We also recorded microenvironmental factors, including light availability, soil moisture, litter cover, regrowth cover, and soil surface temperature on subplot level, as well as snow depth on plot level. See detailed description of the methods in Paper III.

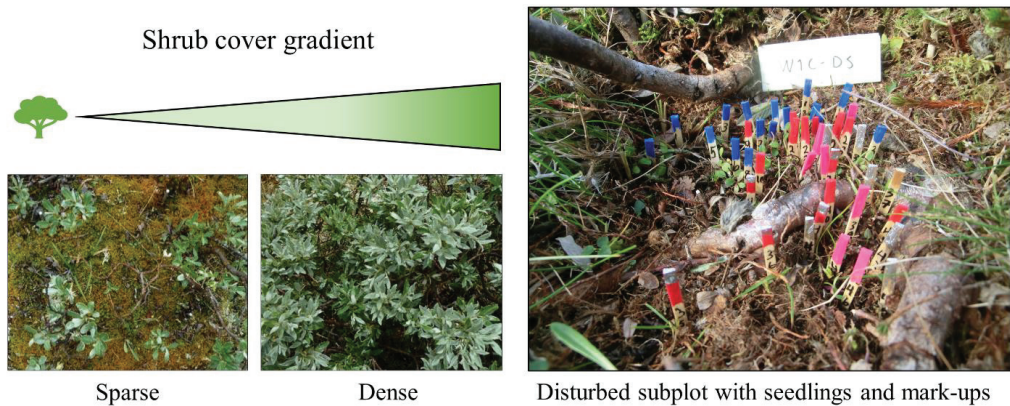


Figure 4. Schematic summary of the experimental setup in Paper III. In a *Salix* shrubland we established plots with different deciduous shrub cover densities and removed above-ground vegetation in small understory subplots (12.5×12.5 cm) where we sowed seeds of 14 different species and recorded seedling emergence and survival over five years. The right photo shows a disturbed subplot with emergent seedlings and color-coded markups in autumn 2014.

Tree-seedling establishment and performance in tundra vegetation (Paper IV)

In the fourth paper we explore the importance of biotic (competition from above-ground vegetation and herbivory) and abiotic factors on establishment and performance of the coniferous subalpine tree *Pinus sylvestris* in tundra. We used the similar experimental setup as in Paper II (described in Fig. 3), but in addition to emergence and survival over five years, we recorded *P. sylvestris* seedling height, new stem growth, and fraction healthy needles in the fifth year. For the abiotic environment, we measured soil surface temperatures, soil moisture, snow depth, and light availability. See detailed description of the methods in Paper IV.

Laboratory and common garden field experiment with lichens (Paper V)

In the fifth paper we explore how terricolous lichens interact with plant recruitment through allelopathy, physical mechanisms, and microclimate. In autumn, we established a common garden experiment in a lichen- and dwarf-shrub heath at Kongsvoll (Fig.1, Table 1) where seeds of ten vascular plant species were sown in mats of six lichen species and bare soil controls (see schematic method summary in Fig. 5). The following year we recorded growing season soil temperature and moisture, and end-of-growing season seedling recruitment and biomass. We tested the effect of lichen secondary compounds (Fig. 5A) on seed germination in a growth chamber experiment with the same plant and lichen species. See detailed description of the methods in Paper V.

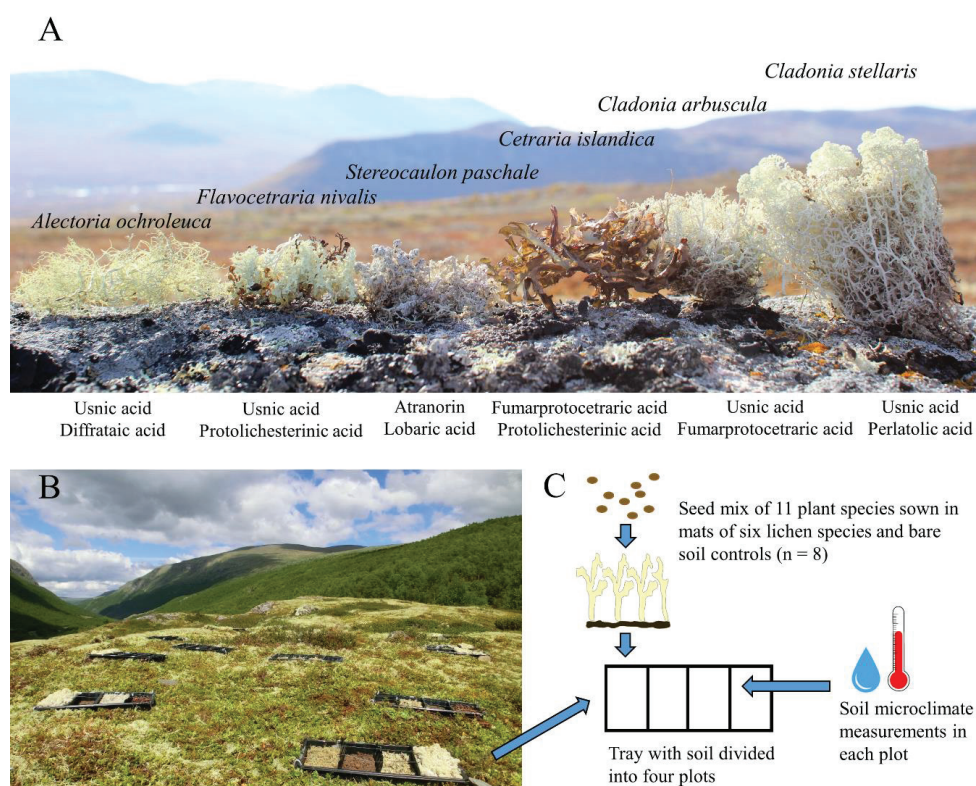

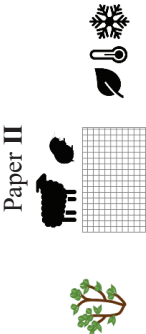
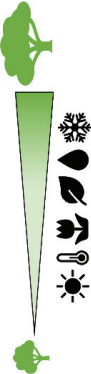
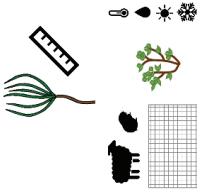
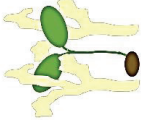


Figure 5. Schematic summary of the common garden field experiment in Paper V. (A) Group photo of the six terricolous lichens (i.e. lichens growing on soil) used in the common garden and laboratory experiment, and the secondary metabolites they produce. Notice the difference between the lichens in mat height, density and color, resulting in different environments for recruiting plants. (B) Photo from the lichen- and dwarf-shrub heath c. 930 m a.s.l. at Kongsvoll, Dovrefjell with some of the experimental trays. (C) Schematic representation of the common garden experiment where we sowed seeds of 11 plant species into plots with soil and lichens (eight replicates), or only soil (controls). In the growing season we recorded soil moisture on a wet and dry day, and soil surface temperature continuously on plot level.

Table 2. Summary of the study designs and data collected for the five papers presented in this thesis.

Study design		Data collected
Paper I		Observational study of 270 plots in snowbed and heath vegetation along 36 transects divided between six study sites and the two mountain regions Borgefjell and Dovrefjell.
Paper II		Sowing of 14 plant species in intact vegetation and gaps, with and without <i>Salix</i> shrub introduction, and with and without herbivore exclusion at a meadow, heath, and <i>Salix</i> shrubland site at Dovrefjell
Paper III		Sowing of 14 plant species in gaps along a shrub-cover gradient in <i>Salix</i> -dominated shrubland vegetation at Dovrefjell.
Paper IV		Sowing of <i>Pinus sylvestris</i> in intact vegetation and gaps, with and without herbivore exclusion, and with and without <i>Salix</i> shrub introduction at meadow, heath, and <i>Salix</i> shrubland site at Dovrefjell.
Paper V		<div>1) Sowing of 12 plant species into mats of six lichen species and bare soil controls in a common garden experiment at a lichen- and dwarf-shrub heath at Kongsvoll, Dovrefjell- Laboratory experiment of seed germination in petri dishes with lichen thalli and water.</div> <div>2) Laboratory: counts of germinated seeds.</div>

MAIN RESULTS AND DISCUSSION

Rodents with cyclic population dynamics promote seedling recruitment in alpine tundra

Our observational study of seedlings and rodent activity (Paper I) revealed that lemmings and voles in peak densities create numerous microsites suitable for seedling recruitment through grazing, trampling, feces deposition, and digging. More seedlings emerged in snowbed and heath plots with high rodent activity, similar to the correlation Ericson et al. (1992) found between willow ramet ages and peaks in vole cycles in forests. Although voles and lemmings are not believed to prefer seedlings in early development (Shaw et al. 2010), it is probable that they in peak densities damage and kill many seedlings through trampling or herbivory (Eskelinen 2008; Sætnan et al. 2009; Bognounou et al. 2018). The peak year was followed by a collapse of the rodent populations, but their disturbances (e.g. runways, feces, cutting of dwarf-shrubs) were still visible in the vegetation in the low-density year (Fig. 6A). Seedlings therefore continued to emerge in these ‘safe sites’, resulting in higher seedling numbers in the low-density year than in the previous peak year (Fig. 6A, D), comparable to the high seedling densities Freedman et al. (1982) found in an abandoned lemming burrow complex. Surprisingly, disturbances from rodents were equally important for recruitment in heaths and snowbeds, despite the more favorable germination conditions offered by snowbeds (Gough 2006; Graae et al. 2011). As such, the cyclic population dynamics of small rodents provide recurrent opportunities for seed regeneration every third to fifth year in otherwise low-invasible alpine plant communities (Milbau et al. 2013). We expect that especially herbaceous, short-lived, ruderal species with small seeds in need of high light levels for germination rely on such openings in the vegetation for successful regeneration and population persistence (Grime et al. 1981; Freedman et al. 1982). Thus, rodents with cyclic population dynamics are a unique and important driver of seedling recruitment patterns in tundra vegetation through creation of suitable sites for seedling emergence.

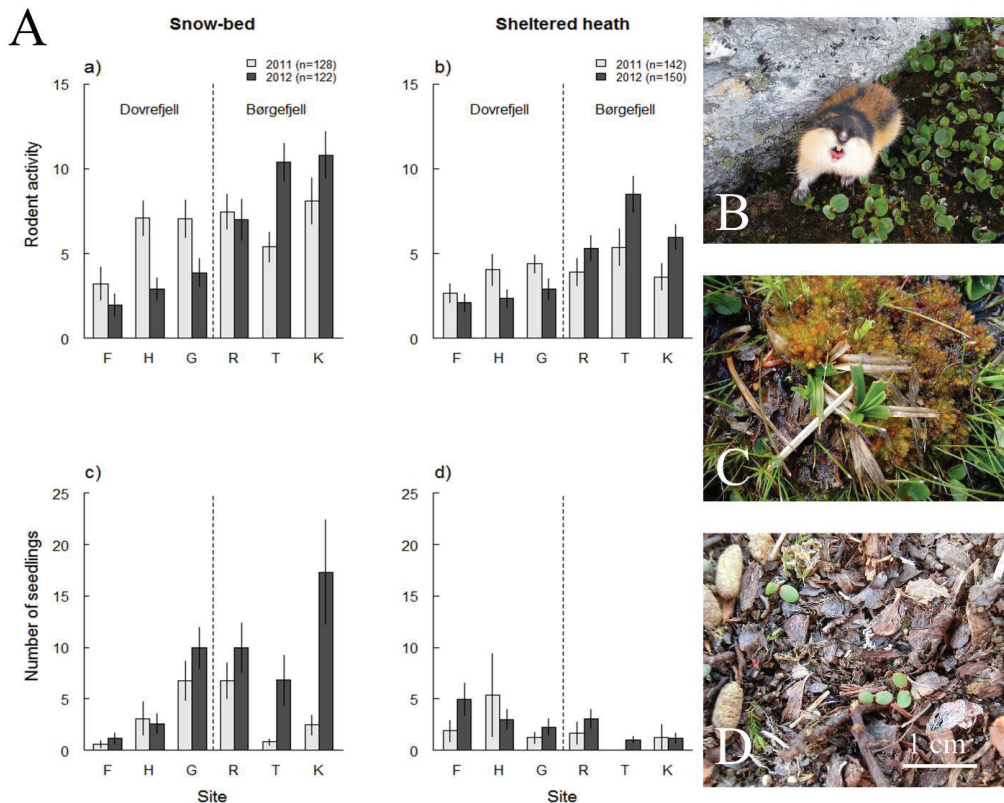


Figure 6. Main results and photos related to Paper I on rodent-plant recruitment interactions in alpine tundra. (A) Records of rodent activity and seedling numbers with barplots of mean (\pm SE) observed rodent activity based on number of subplots (0-16) with feces (a, b) and number of seedlings (c, d) in snowbed and sheltered heath vegetation in the two study regions and six study sites (Dovre: F = Forollhogna, H = Hjerkin, G = Grødalen, Borgefjell: R = Ranseren, T = Tipling and K = Kjukkelen) in the rodent population peak year 2011 (light grey bars) and in the low-density year 2012 (dark grey bars). The rodent activity (i.e. feces frequency) in Borgefjell was higher in 2012 than 2011 because the rodent populations here collapsed later than in Dovre, so that rodents were abundant and continued to deposit feces also after the 2011-census in Borgefjell (see Fig. 1 in Paper I). Nevertheless, few live rodents were observed in both mountain regions in summer 2012. Photos B-D were taken during records and show: (B) a quick-tempered Norwegian lemming photographed by Elin Brattström in Borgefjell during the peak year 2011, and (C) a grazed *Carex* plant, and (D) a rodent runway with old rodent feces (left) and three small seedlings photographed in Borgefjell in the low-density year 2012.

Seedling herbivory decreases invasibility and shapes seedling communities

The experimental exclusion of herbivores by cages in Papers II – IV made it possible to investigate the importance of large and small vertebrate herbivores for plant recruitment in alpine tundra. The effect of herbivore exclusion on seedling emergence was limited (except for *Pinus sylvestris*; Paper IV), but in the following years more seedlings died in plots exposed to herbivores in the heath and meadow sites (Paper II). The herbivore effect got stronger and stronger over the years, and eventually led to different seedling communities in caged and plots accessible to herbivores in the fifth year (Fig. 7, Paper II). Especially species attractive to herbivores such as *Solidago virgaurea*, *Ranunculus acris*, *Bistorta vivipara*, *Pinus sylvestris*, and *Anthoxanthum nipponicum* (Rekdal 2001; Eskelinen 2008) had more recruited seedlings inside cages, indicating that selective grazing rather than accidental trampling have filtered the recruits.

The cages excluded all vertebrate herbivores (rodents, sheep, reindeer, birds), but we found some heterogeneity among sites that may result from differential use by herbivores. Whereas seedlings within dense shrub vegetation may be difficult to access and escape large-mammal herbivory (Pajunen et al. 2011), a shrub canopy may allow lemmings and voles to escape predators and result in rodents spending more time feeding under shrubs (Sætnan et al. 2009). Lemmings and voles at Dovrefjell experienced moderate population peaks in the experimental study's second (2014) and fifth year (2018) (Framstad 2019). In contrast to the regular summer grazing pressure by sheep, the impact of rodents is closely linked to their population cycles (Paper I). The first population peak coincided with seed addition in late 2013 (build-up phase) and seedling emergence in 2014, and the second peak in 2018 with records of final seedling establishment (see rodent runway in Fig. 8C). Rodents prefer large seedlings (Hulme 1994), and Shaw et al. (2010) found that small willow seedlings were of little interest to voles. Indeed, in the first three years when seedlings remained small, only *Pinus sylvestris* and *Anthoxanthum nipponicum* recruited more successfully in absence of herbivores in the *Salix* shrubland, compared to all but one species in the meadow and the heath (Paper II). Both plants are attractive to rodents (Sætnan et al. 2009; Soininen et al. 2013; Bognounou et al. 2018). By the fifth year, however, seedlings of most species had grown bigger (pers. obs.) and possibly more attractive to the rodents that increased in abundance during the moderate population peak in 2018 (Hulme 1994; Shaw et al. 2010). Accordingly, we found more survivors in caged plots with shrub introduction, compared to plots accessible to herbivores with shrub introduction, also in the *Salix* shrubland. However, the positive effect of cages on seedling survival was not evident in the plots without shrub introduction in the *Salix* shrubland (Fig. 7). Sheep herbivory may have been more pronounced in meadow and heath vegetation. First, seedlings in lower-statured habitats without a shrub canopy are easier to detect and access for big herbivores such as sheep. Second, the constant grazing pressure from sheep corresponds to the steady decline in seedling numbers in plots accessible to herbivores at the heath and meadow sites (Paper II). Although we cannot ascertain which herbivores that grazed the seedlings in our experiment, we suggest that rodents are of greatest importance within dense shrub-dominated vegetation (Pajunen et al. 2011), whereas sheep and rodents (when abundant) together are important in lower-statured alpine vegetation.

The proximity to plants attractive to herbivores may also have affected the seedlings' chance of being grazed (Palmer et al. 2003). *Salix* spp. are commonly grazed early in the growing season by sheep (Mobæk et al. 2012; Speed et al. 2013). The small *Salix* plants we experimentally introduced to imitate shrub expansion in meadow and heath vegetation, did indeed have browsing marks from herbivores (unpublished data). *Salix* shrubs are probably easier to detect than seedlings, and may have attracted sheep and increased the risk of grazing also on surrounding vegetation. The higher seedling mortality in intact meadow plots with shrub introduction than plots without shrub introduction, could be a result of this (Paper II). This was however not evident in disturbed plots, perhaps because seedlings on bare soil are easier to detect - independent of the presence of *Salix* shrubs - and thus more likely to be eaten (see Fig. 8B of *Anthoxanthum nipponicum* seedlings in a disturbed heath plot that probably have been grazed by sheep). Thus, recruitment success may indirectly depend of herbivory through the presence of other attractive species.

Seedlings are generally thought to be inferior competitors to adult plants, and grazing may indirectly favor seedling recruitment by keeping down or eliminating competitors in the established vegetation and preventing competitive exclusion (Chambers 1993; Clear Hill & Silvertown 1997). To this end, we expected the absence of herbivores to favor growth of the standing vegetation on the expense of seedling recruitment. However, we did not detect such a trend, probably because the seed sowing was initiated just after set-up of the cages reported in Papers II – IV and because alpine vegetation grows slowly (Billings 1987; Körner 2003) and had not yet responded strongly to the herbivory release (Sørensen et al. 2018).

In this thesis, I demonstrate that vertebrate herbivores indirectly promote seedling recruitment through increased availability of suitable microsites for emergence, whereas herbivores directly reduce the invasibility of alpine vegetation through seedling herbivory. Our results add to previous studies highlighting seedling herbivory as a key biotic driver of community assembly (Eskelinen 2008; Barton & Hanley 2013; Eskelinen et al. 2016), and to studies demonstrating how herbivory can buffer climate-driven vegetation changes (Speed et al. 2012; Kaarlejärvi et al. 2015; Kaarlejärvi et al. 2017), by for instance limiting tree regeneration into tundra (Munier et al. 2010; Bognounou et al. 2018).

ESTABLISHED SEEDLINGS AND HERBIVORES

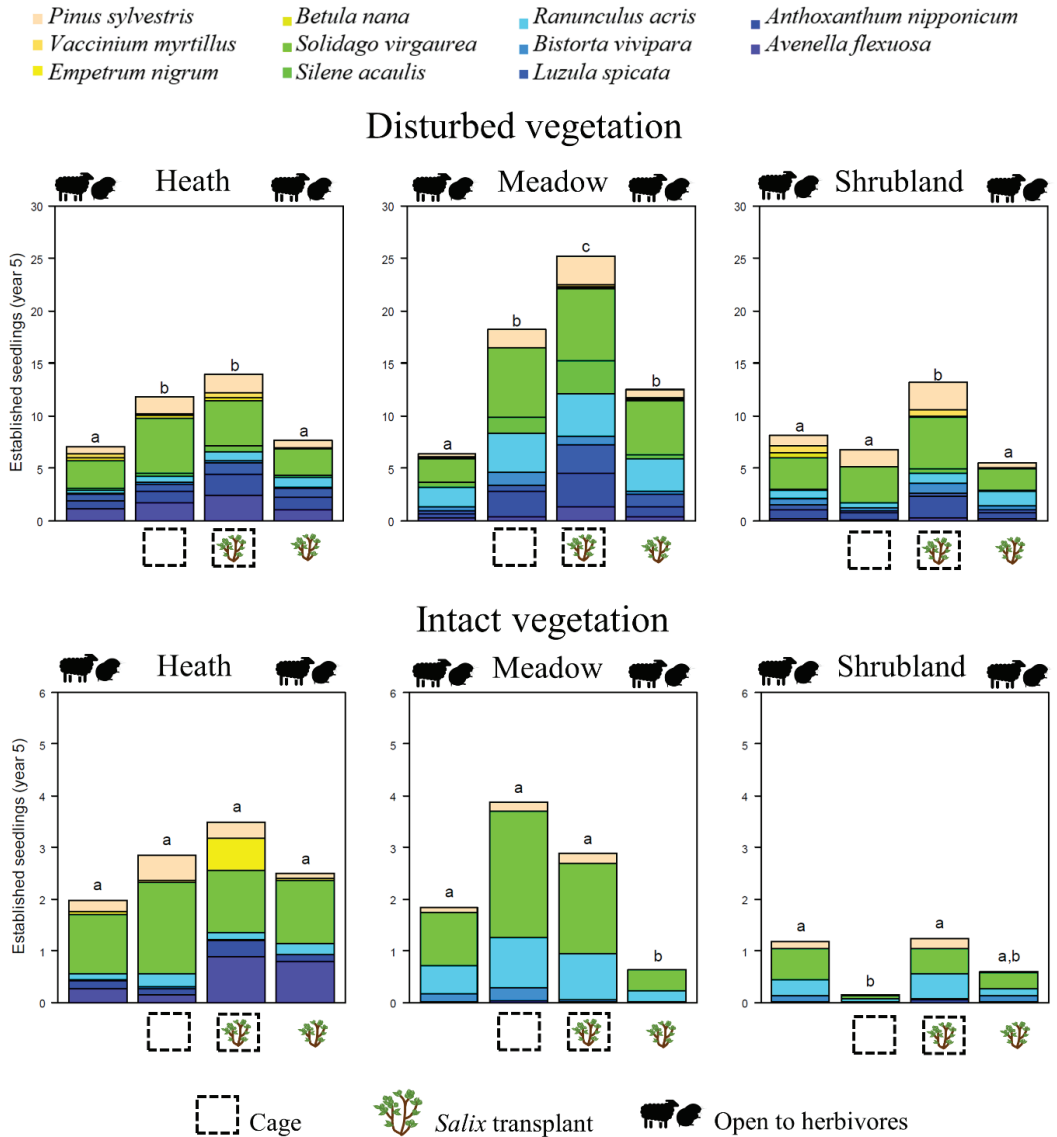


Figure 7. Seedling establishment in the study's fifth year in disturbed (i.e. vegetation removal) and intact vegetation with and without cages and shrub introduction (*Salix* transplant) at a heath, meadow and *Salix* shrubland site. Different letters indicate >95% posterior support. Figure adapted from Paper II.

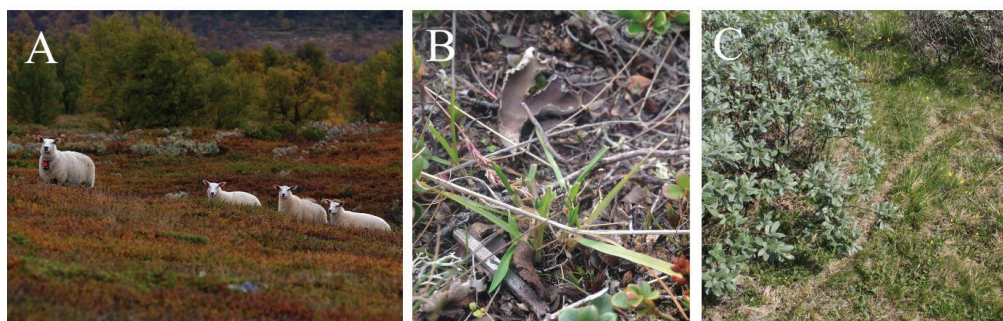


Figure 8. Sights and tracks of herbivores at the study sites with experimental herbivore exclusion (Papers II and IV): (A) sheep near the heath site in September 2014 photographed by Benjamin Blonder; (B) grazed *Anthoxanthum nipponicum* seedlings in a disturbed plot at the heath in August 2016; and (C) a rodent runway in the *Salix* shrubland in June 2014.

Intact alpine vegetation has low invasibility

The disturbance treatment in Papers II – IV made it possible to investigate biotic interactions between seedlings and the surrounding vegetation. We found that intact vegetation had low invasibility to the sown species, especially at the *Salix* shrubland site (Fig. 9, 10, Paper II, IV). The vegetation exerted strong filtering effect already at seedling emergence. Fewer, and less than a third of the number of seedlings, emerged in intact compared to disturbed plots (Fig. 9, 10, Paper II). However, bias to detect grass seedlings in graminoid-abundant meadow and *Salix* shrubland plots may have under-estimated emergence of *Avenella flexuosa* and *Anthoxanthum nipponicum*. Furthermore, we detected strong filtering by the standing vegetation also on seedling survival (60% of the seedlings in intact vegetation died over the two first years). This eventually led to different composition of established seedling communities after five years between vegetation types, and demonstrates how important both identity of the receiving vegetation and the recruiting species is for recruitment success in tundra (Graae et al. 2011).

Interestingly, the negative effect of vegetation cover on seedling recruitment was less pronounced at the heath than at the meadow and *Salix* shrubland sites (Fig. 9, 10, Paper II). This is surprising considering the reported low seedling numbers in dwarf-shrub heaths (Welling & Laine 2000) and the negative effects of the abundant species *Empetrum nigrum* on seed germination and seedling growth of certain species (Zackrisson & Nilsson 1992; Bråthen et al. 2010). Because of the high abiotic stress level in heaths, seedlings that emerge within vegetation experience a modified and probably less stressful environment than those emerging in disturbed plots (Renard et al. 2016; Paper IV). This can explain the relatively high seedling diversity and numbers in intact heath vegetation compared to in intact *Salix* shrubland vegetation (Paper II). The lichen-facilitated seedling emergence in a similarly stressful lichen- and dwarf-shrub heath is an outstanding example of positive interactions among the standing vegetation and recruiting plants in exposed tundra vegetation (Paper V). Still, considerably more seedlings emerged and established in disturbed compared to that of intact subplots also in the heath (Paper II). Although seedlings may benefit from vegetation-

protection against the above-ground environment, they still compete for light and below-ground resources like nutrients and water. Lichens don't compete for below-ground resources like vascular plants, and this release from below-ground competition can have contributed to the high seedling emergence success within lichen mats in Paper V.

This thesis demonstrates, both observationally (Paper I) and experimentally (Papers II and IV) that plant community identity is a strong filter of recruitment success in the absence of disturbances. Particularly productive alpine tundra dominated by erect shrubs with thick ground layers of bryophytes and tundra dominated by dense swards of herbaceous species, have low invasibility.

SEEDLING EMERGENCE PATTERNS

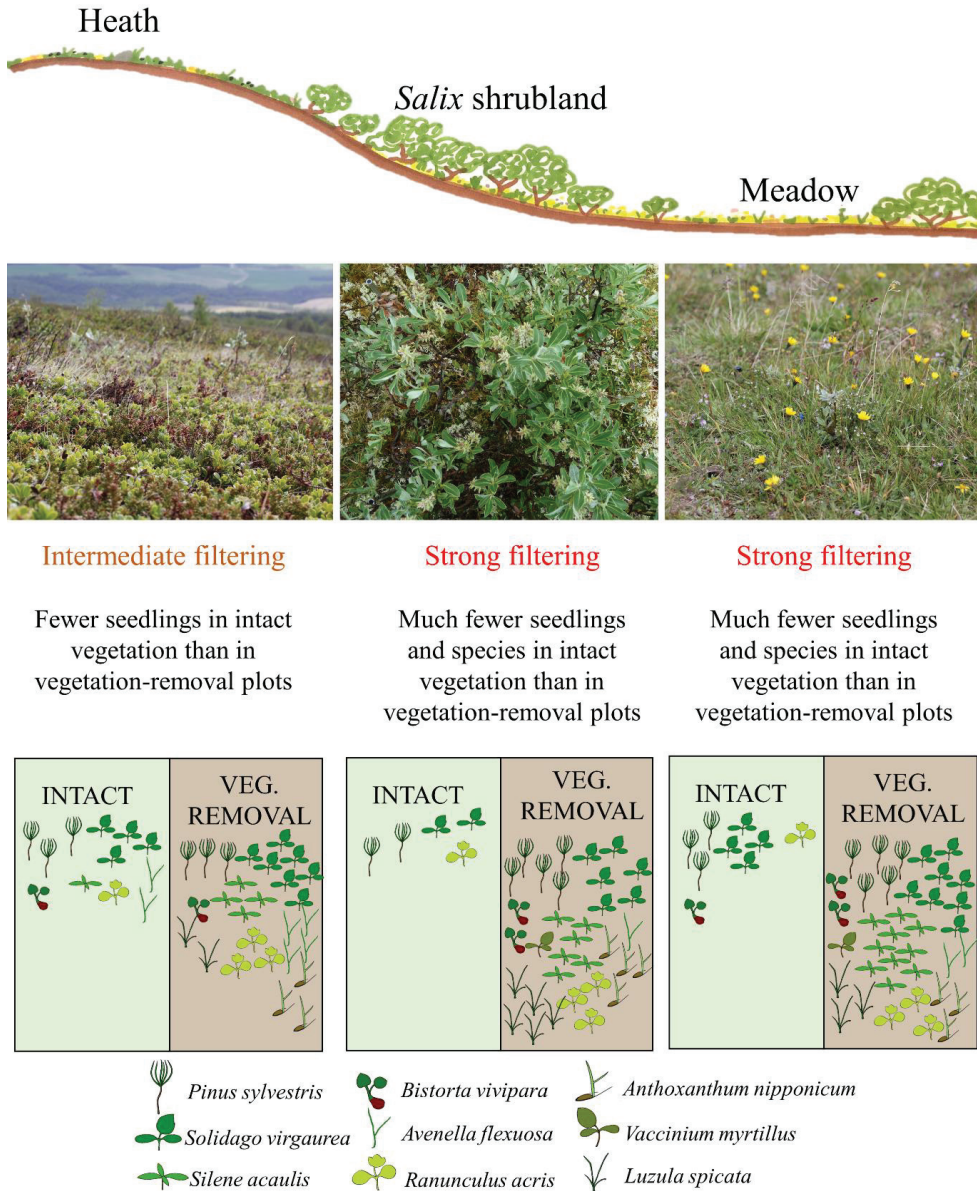


Figure 9. Alpine vegetation is a strong filter of seedling emergence success. This schematic illustration shows emergence of nine species after seed addition in intact and disturbed vegetation in three common low-alpine plant communities distributed along a topographic gradient with differing abiotic conditions as reported in Paper II and IV. The disturbance removing above-ground vegetation resulted in higher emergence within each community. Number of seedlings are based on average seedling emergence over the three first years after seed addition in caged plots inaccessible to herbivores. *Ranunculus acris* emerged primarily the second year after sowing. *Salix* shrubland photo by Mia Vedel Sørensen.

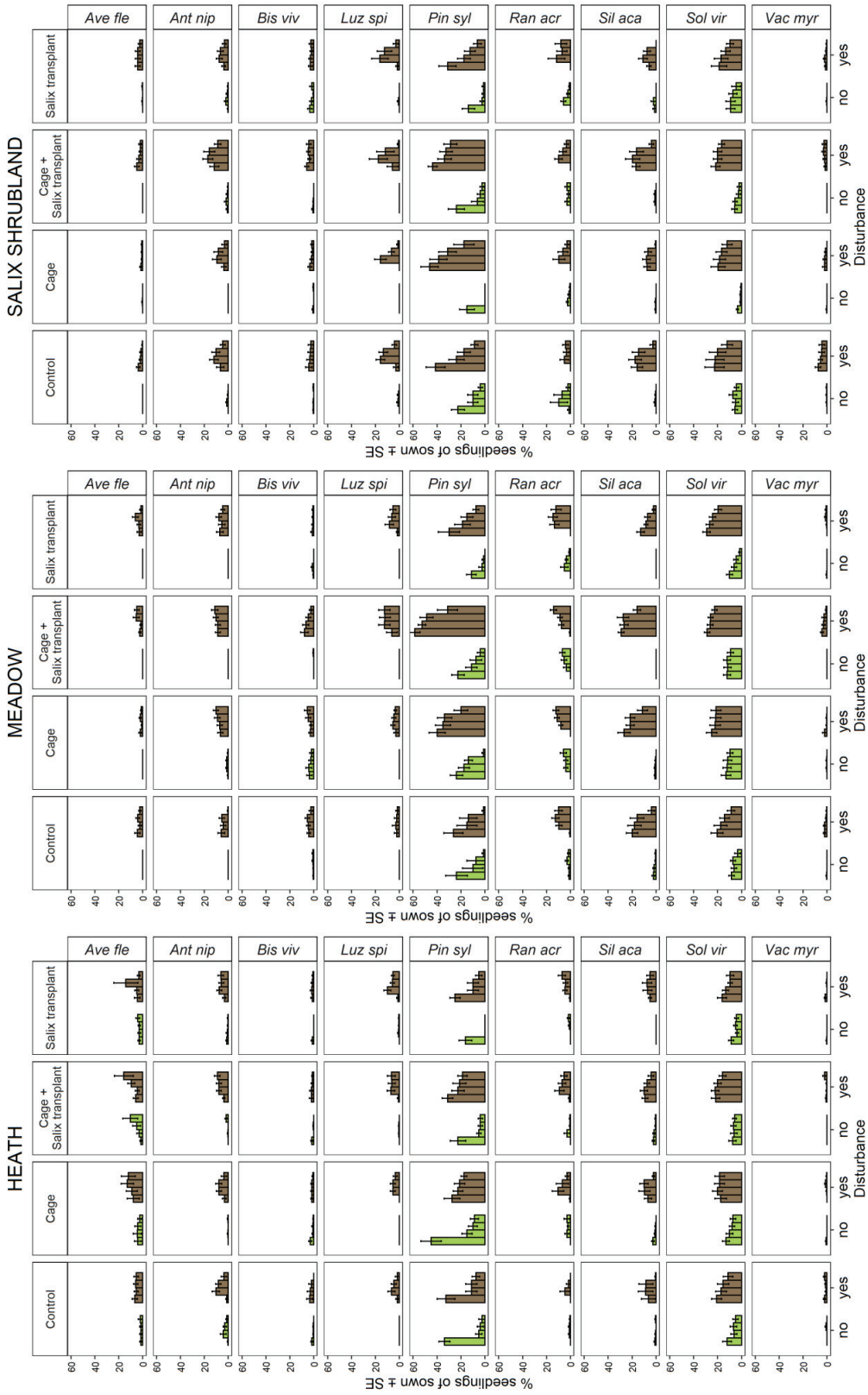


Figure 10. Seedlings alive in the seeded subplots (mean \pm SE percentage of sown seeds) in year one, two, three and five after sowing. Years are shown as the four successive bars in similar color. Only nine of the 14 species are shown, as the other species failed or nearly failed to recruit.

Low invasibility also to a conifer tree species of intact alpine vegetation

Intact alpine tundra vegetation had low invasibility to the conifer tree *Pinus sylvestris*. In contrast to the other focal species, the strongest filtering happened during survival, and not emergence. In fact, *Pinus sylvestris* was successful emerging within vegetation, especially heath vegetation and lichen mats (Fig. 11A, Papers IV and V). Seedlings from large seeds tolerate hazards like competition from intact vegetation, shade and drought better than seedlings from small seeds (Westoby et al. 2002), and also tend to have higher survival early during establishment (Moles & Westoby 2004a). The big seeds of *P. sylvestris* – about six times heavier than those of the other focal species (Paper V) – probably contributed to its successful emergence. However, vegetation filtering over the next four years was strong. More than six times as many *P. sylvestris* seedlings died in intact vegetation compared to that in disturbed vegetation, resulting in few established pines in intact *Salix* shrubland and meadow vegetation in the fifth year (Fig. 11B, Paper IV). Our findings are supported by other studies reporting mainly negative effects of vegetation on tree recruitment in tundra (Hättenschwiler & Körner 1995; Loranger et al. 2017; Frei et al. 2018; Lett & Dorrepaal 2018). It is therefore not surprising that also pine performance was negatively affected by the vegetation presence. The pine seedlings in intact heath and *Salix* shrub – but not meadow – vegetation had a lower fraction healthy of needles than those in disturbed vegetation (Paper IV). Thus, how well seedlings perform is to a great extent driven by the type of vegetation in which they grow. We demonstrate the importance of vegetation identity on pine seedling growth also in Paper V, where biomass of pine seedlings differed among lichen species monocultures already at the end of their first growing season.

Our results suggest that *P. sylvestris* recruitment in alpine tundra is inhibited by above-ground vegetation in productive and environmentally benign plant communities, with the strongest filtering happening after the first growing season. Less productive and environmentally harsh vegetation is easier to invade, and in such conditions most lichens facilitate early recruitment phases of *P. sylvestris*.

PINUS SYLVESTRIS RECRUITMENT PATTERNS

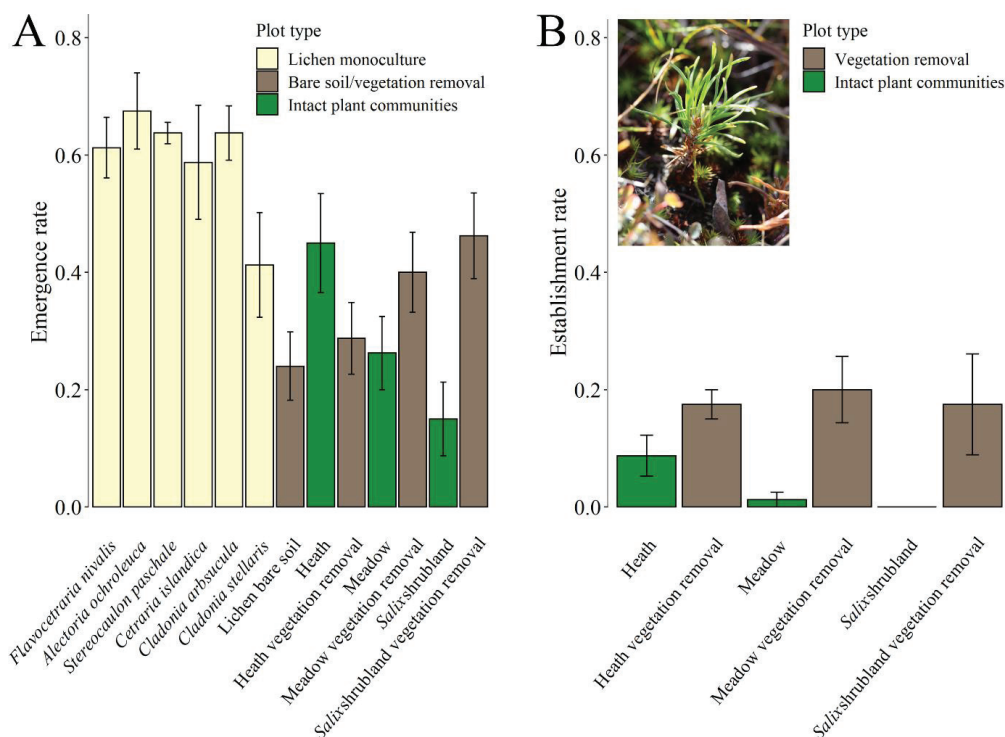


Figure 11. *Pinus sylvestris* (A) seedling emergence and (B) establishment rate (mean \pm SE, $n=8$) in monocultures of six lichen species and on bare soil controls in a dwarf-shrub and lichen heath (Paper V: emergence only) and in three intact alpine plant communities with neighboring disturbed (i.e. vegetation-removal) plots (Paper IV: data from caged plots without shrub introduction only). Seedling emergence was recorded at the end of the first growing season and establishment rate in the fifth growing season. Photo of a five-year old established *P. sylvestris* seedling in a caged, disturbed plot in the *Salix* shrubland.

Seedling communities vary along gradients in Salix shrub cover

In Paper **III** we investigated how seedlings in disturbed plots were affected by the microenvironment and shrub covers in a *Salix*-dominated shrubland. We found that the recruiting species responded uniquely to the shrub-cover gradient with its related variation in microenvironment. As a result, in the fifth year we observed a turnover of established sown seedling communities from sparse to dense canopies favoring broadleaf forbs (Fig. 12A, left), similar to what has been described for adult plant covers (Pajunen et al. 2011). Nevertheless, establishment of additional four species was facilitated by dense shrub covers when only considering the independent effect of shrub covers (i.e. the marginal effect with the other microenvironmental variables set to their mean value; Fig. 12A, right). These species may benefit from the presence of the shrub through for example better nutrient availability, moisture retention and temperature buffering (Chen et al. 2020), but be disfavored by other aspects associated with dense shrub covers. Increased litterfall, less light, warmer soil surface temperatures in winter, and colder soil surface temperatures in summer are all more pronounced below dense shrubs (Becklin et al. 2012; Myers-Smith & Hik 2013; Barrio et al. 2016; Bueno et al. 2016; Wallace & Baltzer 2019), and did indeed affect one or more of the studied recruitment phases of all species negatively (Paper **III**). The ongoing expansion of shrubs in many tundra areas strongly modifies the microenvironment and occurrence and performance of other plant species (Pajunen et al. 2011; Wallace & Baltzer 2019; Kitagawa et al. 2020), and our results show that much of this filtering happens during the first five years of recruitment.

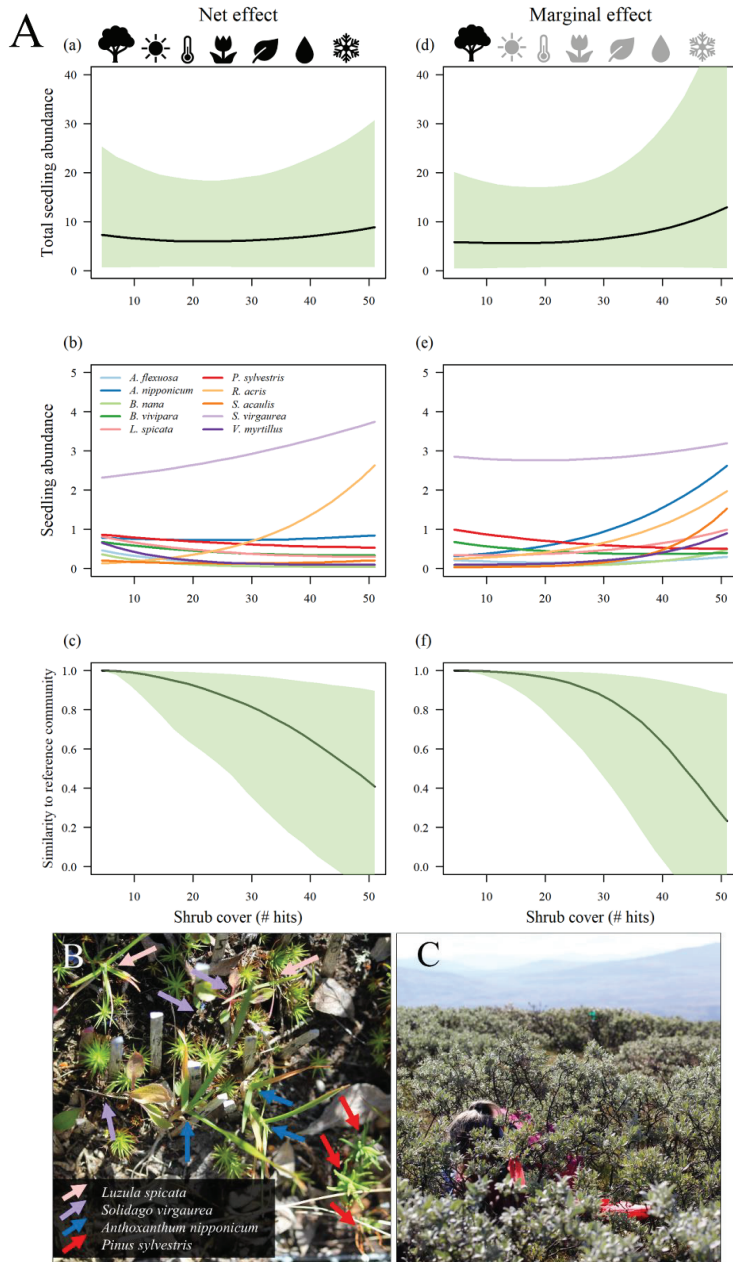


Figure 12. Main results and photos related to Paper III on plant recruitment-shrub interactions in tundra. (A) Shrubs affected the composition of established seedling communities in disturbed plots along a gradient in shrub cover (# hits from point intercept vegetation analysis), with different outcomes when assessing the net effect of shrubs (left) with associated variation in microenvironmental variables and the marginal (independent) effect of shrubs (right). The shrub cover's effect on seedling community composition in (c) and (f) is measured as similarity (Pearson correlation) relative a reference community below the sparsest shrub canopy (5 hits, far left). See Paper III for more details. (B) A diverse community of mainly three years old seedlings with markups in a disturbed, seeded subplot at the *Salix* shrubland in August 2016. (C) Scientists experience a different environment than usual as well when looking for seedlings within shrub canopies, here during recordings at the *Salix* shrubland in August 2016.

Experimental introduction of shrubs in heath and meadow vegetation has mixed effects

The effects of experimental introduction of *Salix* shrubs were inconsistent, weak and hard to predict when looking at all sown species (Paper II). However, in paper IV we found that more pine *Pinus sylvestris* seedlings emerged in plots with *Salix* shrub introduction when combined with disturbed vegetation at the heath and meadow sites (Fig. 13). Pine seedling survival was also higher in plots with shrub introduction at all sites in the disturbed vegetation-plots. Because the shrub introduction did not affect the microclimate (i.e. soil temperatures, soil moisture or light availability; Paper IV), the pine seedling facilitation in disturbed vegetation in the open communities could result from other shrub-mediated conditions not measured in our study. For example, increased nutrient availability (Chen et al. 2020), accumulation of ectomycorrhizal fungi (Nara & Hogetsu 2004) or simply disturbances or other artefacts associated with planting of the *Salix* shrubs. The introduced shrubs were still small three years after planting and had probably invested in below-ground growth during these years. We expect more above-ground growth after 6-7 growing seasons (Rytter 2001; Hagen & Skrindo 2010), and simultaneously stronger interactions among the introduced *Salix* shrubs and plant recruits.



Figure 13. The introduced *Salix* shrubs simulating shrub expansion in the heath and meadow sites in Papers II and IV: (A) A introduced *Salix* shrub in the heath two years after planting. (B) A caged heath plot in August 2014 with arrows pointing to *Salix* shrubs planted in early spring the same year. (C) The *Salix* shrubs seemed to facilitate pine seedling emergence and survival in disturbed vegetation in the meadow and the heath sites (Paper IV), here represented by a two-year old pine seedling in a disturbed plot with *Salix* shrub introduction in August 2016.

Lichens modify the microenvironment and support seedling emergence in heath vegetation

We found negative associations among seedling and lichen occurrences in Paper I, and investigated potential mechanisms behind this in field experiment in a lichen- and dwarf-shrub heath and a lab experiment Paper V. However, in the field experiment we found that lichen mats generally support seedling emergence. Alpine plants rely increasingly on protection from surrounding vegetation as the abiotic environment get harsher (Callaway et al. 2002). The higher emergence within lichens compared to on bare soil, probably acts through lichen-mediated amelioration of the microenvironment experienced by seedlings (e.g. water retention, temperature buffering and wind protection; Paper V; Fig. 14). Interestingly, we found species-specific interactions between lichens and seedlings in terms of seedling numbers and growth both in the field (Fig. 14) and in the lab (Paper V). In the field, positive interactions prevailed (e.g. among *Stereocaulon paschale* and plants; Fig. 14D), although the thick and dense *Cladonia stellaris*-mats hampered recruitment of most species (Fig. 14C). Our findings support that lichen allelopathy under natural conditions has limited ecological importance for seedling recruitment (Stark & Hyvärinen 2003; Kytöviita & Crittenden 2007; Kytöviita & Stark 2009; Favero-Longo & Piervittori 2010), even though the outcome may be different for later life stages, in less stressful habitats, or between other plant and lichen species.

A

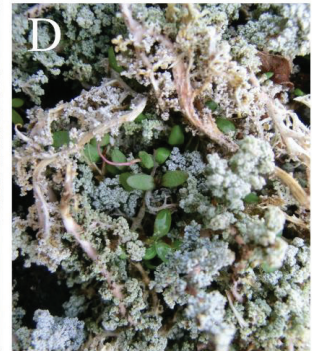
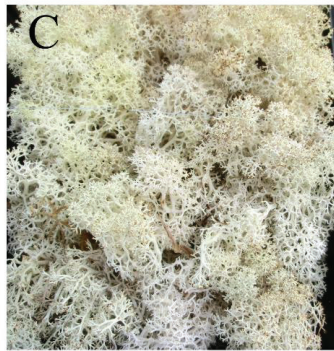
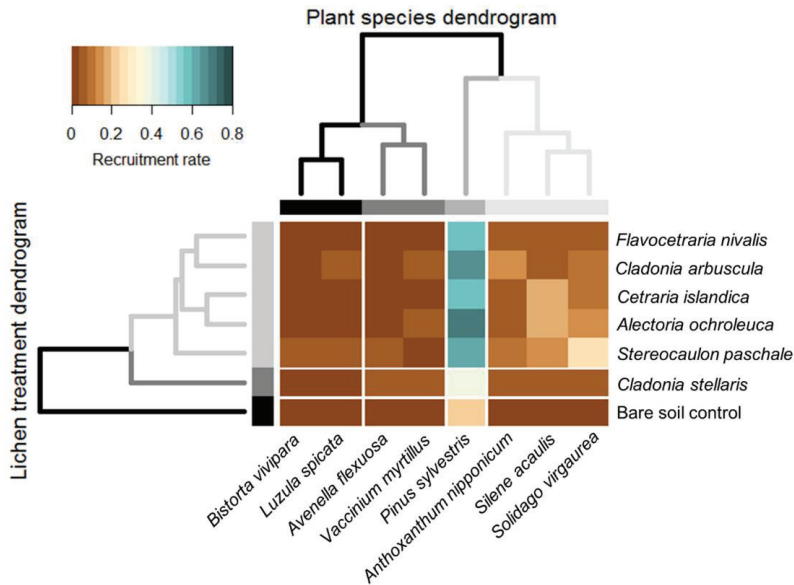


Figure 14. Interactions between recruiting plants and lichens in Paper V illustrated with: (A) a heatmap of mean seedling recruitment in the lichens treatments (i.e. the six lichen species and bare soil controls) with clustering of plant species (top) and lichen treatments (left) in the common garden experiment (Paper V). (B) A bare soil control plot in early summer 2014 with many newly emerged seedlings. Most seedlings that emerged on bare soil did not survive until the end of the first growing season, and recruitment rates were generally higher within lichens. The seedlings probably benefitted from the lichen-mediated microclimate with higher soil moisture and less extreme temperatures. (C) Low recruitment of many plants in *Cladonia stellaris* can be a combination of seeds and seedlings not being able to penetrate the dense mat (mean thickness \pm SE: 6.7 ± 1.1 cm), as well as low light availability far down in the mat (Zamfir 2000). (D) Many *Solidago virgaurea* seedlings recruited and grew big within *Stereocaulon paschale*, the only lichen with N_2 -fixing cyanobacteria, which could result in higher nitrogen-availability affecting germination and growth positively.

Importance of abiotic factors depend on recruiting species and the microsite

In Paper II we investigated the effects of abiotic variables on a broad scale across the three plant communities (Fig. 3). Interestingly, higher maximum summer temperatures increased seedling survival rates of species in disturbed plots in particular (Paper II). Seedlings are often more responsive to abiotic conditions like temperature when local vegetation is removed (Grau et al. 2013; Okano & Bret-Harte 2015; Lembrechts et al. 2017). That high summer temperatures promote seedling survival in the comparably cooler *Salix* shrubland makes sense and are confirmed in Paper III. However, as high temperatures often are associated with increased risk of desiccation, the positive effect on survival also in the warmer heath and meadow sites are surprising (see Paper IV for comparison of the abiotic environment at the tree study sites). Furthermore, seedling emergence, survival and establishment success was lower in plots with a thin snow cover (Paper II). This probably arises from the differing winter conditions at our study sites. While the snow cover in meadow and shrubland vegetation is deep and stable in winter, snow cover in heath vegetation is thinner and more unstable (Fig. 15A). The seedlings at the heath site are therefore more prone to detrimental false spring events (Fig. 15B), as well as low winter temperatures (Fig. 15A, Paper IV) that may result in root injury and higher mortality (Weih & Karlsson 2002). Thus, the abiotic variables' importance and impact on recruiting plants probably differ between plant community types.

In paper III we investigated how the abiotic environment affected seedling recruitment in disturbed plots within a *Salix*-dominated shrubland. Soil surface temperatures emerged as the major predictor of recruitment success overall. Seedling emergence, survival and establishment increased along the gradient in mean summer temperature (8.1 – 11.5°C), whereas it decreased along the gradient in mean winter temperature (-2.1 – 0.5°C). Reasons for the higher recruitment success in plots with sub-zero average winter temperatures could be lower susceptibility of seeds and seedlings to fungal attacks (Graae et al. 2008; Graae et al. 2011) or lower seedling winter maintenance respiration (Ögren 1997; Nobrega & Grogan 2007) in the coldest plots. Seedling responses to the other abiotic variables were species-specific (Paper III). Moreover, seedling emergence and later survival did sometimes respond differently (Paper III), suggesting contradicting effects of the environment during recruitment referred to as seed-seedling conflicts (Schupp 1995; Cranston & Hermanutz 2013; Lett & Dorrepaal 2018). Abiotic conditions associated with dense shrub covers (i.e. less light, cooler summer and warmer winter temperatures) affected one or more of the studied recruitment phases of the focal species negatively. Thus, climate-driven shrub expansion in tundra will have complex filtering effects on species recruiting in the shrub understory.

The effects of abiotic variables on pine seedling emergence and survival, as well as performance (i.e. fraction healthy needles and seedling height) were studied in detail in paper IV. The pine seedlings grew taller in plots where less light was available, for instance when emerging in thick bryophyte mats in intact *Salix* shrubland-plots. Most of these tall pine seedlings also had very thin stems. Such growth is a common plant response to try reach better light conditions (i.e. etiolation), which will disappear if the light demands are fulfilled (Angulo et al. 2019). We also detected relationships between abiotic variables and seedling survival and fraction healthy needles, but the estimated effects were weak (Paper V). Compared to the strong effects of biotic drivers like vegetation disturbances, vegetation

identity, and herbivores, the abiotic variables had only limited effects on pine recruitment success. Biotic drivers do often have stronger effects on seedling emergence and survival success than abiotic variables do (Lett 2017). To predict future distributions of species in tundra, it is therefore important to evaluate local biotic drivers such as herbivore pressure in addition to climate trends (Løkken et al. 2019).

In this thesis we show that the abiotic environment is important for recruitment success in alpine vegetation, although the importance depends on the recruiting species in question and the recruitment phase studied, and the impact often is mediated by the vegetation (e.g. presence or absence of vegetation).

WINTER AND SPRING CONDITIONS

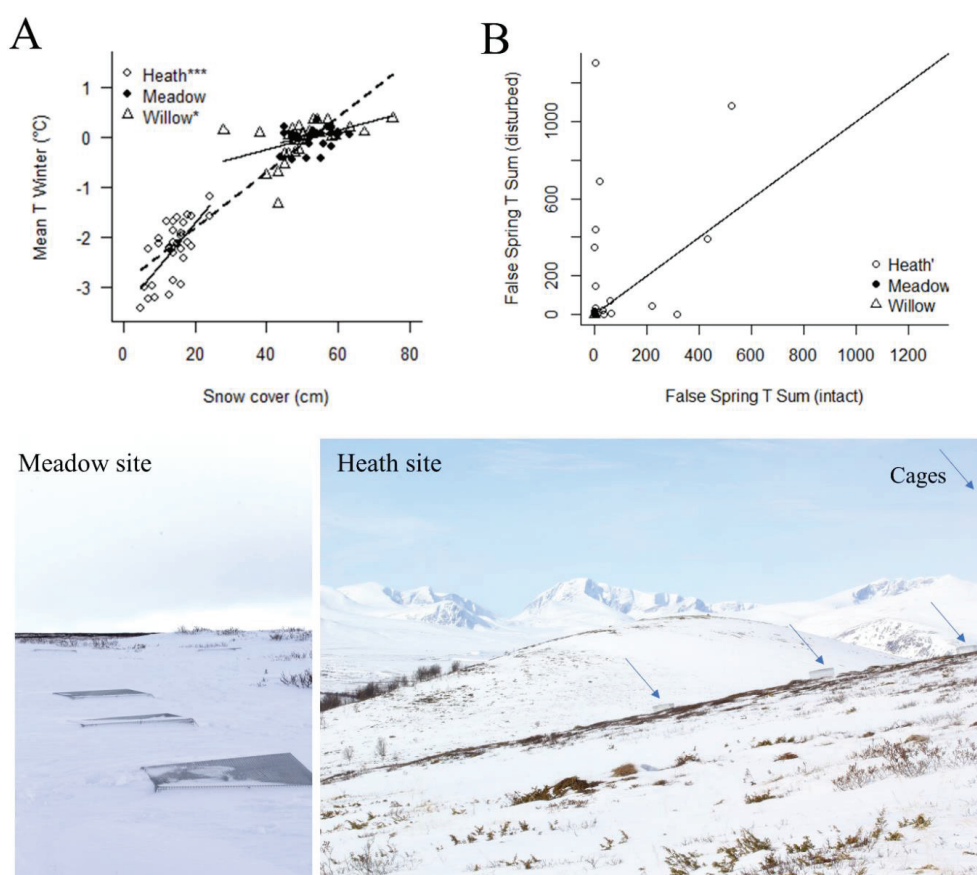


Figure 15. Differing winter and spring conditions in tundra vegetation, here demonstrated through: (A) the effects of snow depth on average winter temperatures and (B) comparison of false spring temperature sums recorded in paired intact and disturbed plots at the heath, meadow and *Salix* shrubland site. Asterisks following site names in (A) indicate significance of correlation tests between snow depth and temperature per plot. Photos are from snow depth measurements 3rd of April 2016.

SYNTHESIS AND PERSPECTIVES

The aim of this thesis was to explore drivers of post-dispersal recruitment phases in alpine tundra, and among the drivers explored we found vegetation type and presence of vertebrate herbivores to be most important for regeneration success and failure. Although processes concerning seeds and seedlings may seem insignificant on landscape level, they eventually are important to plant community assembly, dynamics and persistence. Rodent disturbances during population peak years increase seedling emergence. Seedling herbivory, on the other hand, is a selective filter lowering success of preferred species. In intact vegetation, fewer seedlings emerge, fewer survive, and filtering of seedling community composition is stronger, compared to that in vegetation-free plots. We found trends for stronger vegetation filtering in environmentally benign compared to stressful alpine habitats. On the microscale on which this study operated, abiotic drivers like soil surface temperatures affect recruitment success, but seem subordinate to biotic drivers (i.e. competition from the vegetation and herbivory), at least for *Pinus sylvestris* recruitment success in tundra. We identified seedling emergence as the most crucial recruitment phase. Despite these general patterns, it should be kept in mind that the few species studied herein interacted uniquely with the filters explored. Which consequences expansion of erect shrubs, declines in lichen covers, more frequent warm spells in summer, more frequent thaw-freeze events in winter, or changes in herbivore densities will have for plant recruitment, therefore depend on regenerative traits of the species in question, the microsite qualities, and – the inevitable – chance.

The significance of vertebrate herbivores for recruitment success is perhaps the most important to stress from this thesis. In Paper I we demonstrate a unique impact of fluctuating small rodent populations on plant regeneration in tundra habitats. Even though the observational study in this thesis do not show the long-term impacts on plant community processes, it is reasonable to suppose that the population fluctuations are important promoting plant coexistence (Barton & Hanley 2013). Recurring high, intermediate and low-herbivory years likely let plants with varying regeneration strategies establish and coexist in the standing vegetation (Warner & Chesson 1985; Chesson 1986). Moreover, these opportunities for successful sexual regeneration are important for both plant migration and persistence in changing tundra environments (Stenström 2000; Alsos et al. 2007). However, Scandinavian tundra has over the three past decades experienced more frequent rain-on-snow events resulting in either collapse of, or water freezing, in the subnivean space where rodents hide, feed and breed in winter (Ims et al. 2008; Kausrud et al. 2008). Periods with less pronounced population cycles in some areas in Fennoscandia may partly be attributed to such unstable winter conditions (Ehrich et al. 2020). The absence of high-density rodent disturbances in combination with a warmer climate may result in more plant biomass, less suitable microsites for seedling emergence and more competitive interactions between the standing vegetation and seedlings (Vuorinen et al. 2017). Long-term studies including data on identity and survival of seedlings naturally emerging in sites with high and low rodent activity would further our understanding of how rodents contribute to structure tundra vegetation.

Our results suggest that rodents, together with other herbivores such as sheep, further affect recruitment dynamics through selective herbivory and/or trampling as seedlings grow bigger (Papers II-IV; Shaw et al. 2010). In tundra, the implications of seedling herbivory have received by far less attention than that of herbivory on the standing vegetation, yet the strongest effect of herbivory on plant survival is thought to be at the seedling stage (Hulme 1994). Invertebrate seedling herbivory is probably also underrated in tundra vegetation, and as such is a hot topic for further studies. In Dovrefjell moth larvae (*Epirrita autumnata* and *Operophtera brumata*) were abundant in 2015-2017 (Framstad 2019). Although most common in subalpine birch forest, we also observed larvae at our alpine study sites where they could have killed or lowered performance of preferred seedlings both inside and outside cages. While rodents, and probably bigger vertebrate herbivores, prefer large seedlings, insects and mollusks prefer small seedlings (Hanley 1998). It would be interesting to investigate these potentially complementary negative effects of vertebrate and invertebrate herbivory on plant recruitment with setups similar to those differing between effects of small and large vertebrate herbivores (e.g. Olofsson et al. 2004; Ravolainen et al. 2014). Moreover, measuring characteristics of seedlings relevant in the face of herbivore attack such as investment in anti-herbivore defenses (i.e. seedling palatability) may further help understand plant recruitment-herbivore interaction outcomes (Herms & Mattson 1992; Hanley 1998).

The results from this thesis are confined to a short period in time and the environmental drivers acting during that period. Dendroecological approaches extend the temporal aspect and provide insights in decades or even centuries of previous woody recruitment dynamics related to climate (Büntgen et al. 2015; Nielsen 2017) and herbivore-disturbances (Ericson et al. 1992). Furthermore, to fully understand seedling recruitment patterns, seed production, seed bank dynamics and seed dispersal should be considered in addition to the post-dispersal phases studied herein. For example flowering and seed set are highly dependent on climatic conditions and may vary dramatically among years (Chambers 1995; Arft et al. 1999).

The drivers investigated in this thesis, i.e. the abiotic environment, herbivory, and existing vegetation are not exclusive of drivers important for seedling recruitment in tundra. For instance, how the seedling stage is affected by below-ground interactions deserves more attention. Positive associations include mycorrhizal symbionts, which are mediated by vegetation cover and composition (Nara & Hogetsu 2004; Becklin et al. 2012; Koorem et al. 2012). Despite the limited ecological importance of lichen allelopathy on seedling recruitment in Paper V, allelopathic interactions may still be relevant and lower recruitment success of certain species (Zackrisson et al. 1995; Dufour-Tremblay et al. 2012; Angers-Blondin et al. 2018).

Although seedling survival is crucial for recruitment success, long-term plant persistence also depends on growth, and factors that promote survival do not necessarily promote growth (Lett & Dorrepaal 2018). For instance, *Solidago virgaurea* emergence, but not growth was facilitated by *Stereocaulon paschale* in Paper V. Furthermore, at the end of the field experiment in Paper II, we observed large differences in seedling size within the focal species, as well as grazing marks on certain seedlings. Despite being alive during the last census, nonlethal grazing can reduce seedling vigor and competitive ability and increase the risk of competitive exclusion on a longer-term (Barton & Hanley 2013). Moreover,

species tolerance to herbivory differ (Barton 2013), and the negative impact of nonlethal grazing is likely stronger in extant vegetation than in disturbed sites (Shaw et al. 2013). Long-term monitoring is therefore necessary and should ideally include seedling performance records in addition to survival, as well as environmental monitoring. The established experiment at Dovrefjell (Papers **II** and **IV**) is a good foundation for future work, and it remains to see how the sown seedlings survive and perform with respect to the introduced *Salix* plants and herbivore exclusion on a longer term.

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Paper I



Norwegian lemming. Artist: Kine Odden Nystuen



Rodent population dynamics affect seedling recruitment in alpine habitats

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Abstract

Questions: How do rodents with cyclic population dynamics affect seedling recruitment in alpine habitats? Does disturbance from rodents have larger implications on seedling recruitment in some plant communities than in others?

Location: Snowbeds and sheltered heaths in the low-alpine zone in areas of Borgefjell and Dovrefjell, Norway.

Methods: We recorded seedling emergence, rodent activity and cover of mosses, lichens, litter and bare ground in 270 plots in snowbeds and sheltered heaths in a rodent population peak year and in the following low-density year.

Results: Seedling recruitment was positively correlated with disturbances from lemmings and voles in both years. More seedlings emerged in the low-density year than in the year of the population peak. Snowbeds had higher seedling recruitment than the sheltered heaths, but both habitats were equally affected by disturbances from rodents.

Conclusions: Rodent activity created gaps and increased seedling emergence in these alpine plant communities, particularly in the year after the rodent peak, both in snowbeds and sheltered heath habitats. Our study therefore suggests that regeneration patterns in alpine vegetation are tightly linked to the population cycles of lemmings and voles, which peak in density at 3- to 5-yr intervals.

Introduction

Disturbances, i.e. the mechanisms that limit plant biomass by causing its partial or total destruction (*sensu* Grime 2001), are important in shaping plant communities (Pickett et al. 1999; Walker 2012). In arctic-alpine communities, both abiotic and biotic disturbances are important. Disturbances from herbivores can even counteract climate-driven vegetation change (Post & Pedersen 2008; Olofsson et al. 2009). It is therefore of interest to reveal both the direct (through grazing) and indirect (e.g. creation of microsites for seedling recruitment through trampling) impacts of herbivore disturbances on plant communities to more fully understand the dynamics of tundra communities and to better predict the responses to climate change.

Small rodents strongly affect plant community structure, diversity and ecosystem functioning (Hulme 1994; Olofsson et al. 2005; Rebollo et al. 2013). For instance, North American pocket gophers (*Thomomys bottae*) and plateau zokors (*Myospalax fontanierii*) act as ecosystem engineers by generating distinct patterns of soil heterogeneity (Reichman & Seabloom 2002; Zhang et al. 2003). In Scandinavia, the cyclic fluctuation in small-rodent population densities observed in the Norwegian lemming (*Lemmus lemmus*) and the voles *Microtus agrestis*, *Myodes rufocanus* and *Microtus oeconomus*, create a cyclic disturbance regime that regularly has high impacts on the vegetation cover in arctic-alpine habitats (Stenseth 1999; Ims & Fuglei 2005), which are even visible on satellite images (Olofsson et al. 2012). Their effect on tundra plant communities has been

shown to be stronger than that of large herbivores (Olofsson et al. 2004). In addition to the plant biomass they consume, these arctic-alpine rodents also impact their habitats through activities such as trampling, cutting, burrowing (Hambäck et al. 1998; Turchin & Batzli 2001) and through deposition of urine and faeces, which increases the overall nitrogen availability (McKendrick et al. 1980; Jonasson 1992).

Bare soil offers space for colonization (Rusch & Fernández-Palacios 1995), and rodent disturbances are expected to increase the availability of vegetation gaps, thus creating suitable microsites for seedling emergence (Eskelinen & Virtanen 2005; Mayer & Erschbamer 2011), even though successful recruitment can take decades (Forbis et al. 2004). Austrheim et al. (2007) found that the amount of exposed soil was positively related to rodent grazing in alpine habitats. On the other hand, high frequencies and intensities of disturbance could also cause high seedling mortality due to herbivory and trampling (Weltzin et al. 1997; Munier et al. 2010).

Abiotic factors such as temperature, light, moisture, wind and the availability of nutrients are crucial for seedling emergence (Grubb 1977; Chambers 1995). Seedling density varies in tundra vegetation, with high germination in moist and productive habitats, declining with increasing levels of environmental stress (Bell & Bliss 1980; Milbau et al. 2013). Vegetation composition in alpine habitats also affects recruitment dynamics, with the number of emerging seedlings being closely related to the regenerative strategy of the species in the mature vegetation (Welling & Laine 2000). Fewer seedlings emerge in heath vegetation, which is dominated by perennial clonal species compared to meadows and snowbeds with high forb richness (Gough 2006; Graae et al. 2011).

Lemmings and vole species use tundra habitats differently, depending on the availability of preferred food plants and the distribution of snow (Batzli 1975; Sætnan et al. 2009). Snowbeds and heaths are habitats frequently used by both lemmings and voles (Moen et al. 1993). Disturbances could be expected to have a higher impact on recruitment in habitats with favourable germination conditions as in snowbeds, whereas abiotic factors may be more limiting in heath vegetation. The role of rodent disturbances on seedling recruitment in snowbeds has been studied (Eskelinen & Virtanen 2005), but the relative importance of disturbance for the recruitment of plants in snowbeds vs. heaths has not yet been explored.

In addition to the presence of bare ground caused by disturbance, the cover of mosses, lichens and litter can contribute to spatial variation in seedling numbers (Rusch & Fernández-Palacios 1995). Cover of mosses and lichens is often found to be inhibitory for germination and seedling survival, depending on the plant species (Hobbs 1985; Zamfir 2000; Eckstein et al. 2011; Soudzilovskaia et al.

2011). Lemming grazing can decrease the cover and abundance of mosses (Virtanen et al. 1997; Austrheim et al. 2007). On the other hand, lichens are non-preferred forage and likely unaffected by rodent herbivory (Virtanen 2000; Soininen et al. 2013), but could be affected by trampling. Depending on habitat productivity (Suding & Goldberg 1999) and litter amount (Loydi et al. 2013), litter can inhibit (Dalling & Hubbell 2002) or have no influence (Welling & Laine 2000; Forbis 2009) on seedling emergence. Some studies suggest that grazing and other rodent activities prevent the accumulation of plant litter (Sirotnak & Huntly 2000; Virtanen 2000), while Moen et al. (1993) found that winter lemming grazing in snowbeds increases the amount of litter. Lemmings and voles could therefore also indirectly have an impact on alpine plant recruitment through potential interactions with the bottom layer, which – to the best of our knowledge – are not well explored in the literature.

In this study, we investigated the impacts of lemmings and voles on the recruitment of new plant individuals in alpine habitats. We collected data on seedling emergence and rodent activity in two alpine habitats; snowbeds and sheltered heaths, in the low-alpine zone in two mountain regions in Norway in a rodent peak population year and in the following low-density year. We expected that: (1) disturbances from lemmings and voles would enhance seedling emergence, as their activity would affect the ground cover and create vegetation gaps that provide microsites suitable for recruitment; (2) this effect would be stronger the year after a rodent population peak when little direct disturbances such as trampling and grazing were exerted; (3) the number of seedlings emerging would differ between habitats according to differences in the degree of use by rodents; and (4) at equal levels of rodent disturbance, seedling recruitment would be higher in snowbeds than in sheltered heaths, since snowbeds have more favourable conditions for seedling recruitment.

Methods

Study sites

The study was carried out in two mountain regions: Dovrefjell (62°29' N, 9°40' E) in central Norway and Børgefjell (65°27' N, 14°10' E), ca. 350 km further north (Appendix S1). Both regions are characterized by having large ranges in altitude and precipitation, and in each region, three study sites were established in the low-alpine zone. At Dovrefjell, the Forollhogna site is located within the Forollhogna National Park, whereas the Hjerkin and Grødalen sites are located within the Dovrefjell-Sunddalsfjella National Park. At Børgefjell, all three sites (Kjukkelen, Tipling and Ranseren) are located within the Børgefjell National Park. The characteristics of the study sites are shown in Table 1.

Lemmings and voles are present in both study regions. Over the past 20 yr, rodents in Børgefjell have had regular population peaks, while in Dovrefjell the peaks have been rather irregular, with comparatively low densities until recently (Fig. 1). Both regions experienced a peak in 2010–2011, followed by a low-density year in 2012. Note that the numbers in Fig. 1 are from the trapping of rodents during autumn (September), whereas records of rodent activity in this study are from June to August. The peak in Dovrefjell started to build up earlier, and also appears to have crashed earlier compared to Børgefjell, which resulted in the low catch seen for Dovrefjell in autumn 2011 (Framstad 2013). Børgefjell is an important area for reindeer husbandry (Evju et al. 2010), while Dovrefjell has wild populations of reindeer and muskoxen, as well as a long history of extensive grazing by sheep (Hagen et al. 2006).

Sampling and field design

At each site, we subjectively located a total of nine transects of 50 m each in habitats without tall shrubs at three altitudinal levels in the low-alpine zone (Fig. 2). We observed the vegetation at each meter along the transect and classified it as either ridge, exposed heath, sheltered heath or snowbed habitat, with this study focusing on snowbeds and sheltered heaths. The snowbed habitat occurs in depressions and has a short growing season due to long-lasting snow cover. The vegetation is dominated by herbs, graminoids and mosses, and by *Salix herbacea* L. in late-melting areas. The sheltered heath habitat is located in sites with comparatively more exposed topography with earlier snow melt, and is dominated by the dwarf shrubs *Empetrum nigrum* subsp. *hermaphroditum* (Lange ex Hagerup) Böcher and *Vaccinium myrtillus* L.

For this study, we randomly selected plots of snowbed and sheltered heath habitat along the transects. In most cases, each transect had five plots, but sometimes up to ten or only one plot were selected, depending on the

occurrence of the habitat type. Vegetation and rodent activity were recorded within each plot (a 0.5 m × 0.5 m quadrat divided into 16 subplots). In 2011 vegetation records included the total number of seedlings present without recording the species identity, but including adult individuals of annual plants (primarily *Euphrasia* spp.) in four pre-selected subplots. We recorded the number of subplots per plot with grazing marks, tunnels and faeces (each with a range of 0–16). The percentage cover of bottom layers (mosses, litter and bare soil) was visually estimated for the entire plot. The records were repeated in 2012; however, the bottom layer cover was recorded in the four seedling subplots only, and we also included the cover of lichens. Since the plots were not permanently marked in the first summer, exact relocation was not possible in 2012. The total number of plots was 270 in 2011 and 272 in 2012, which is roughly balanced between sites and habitats (Appendix S2).

The fieldwork in 2011 was conducted in late June and in August in Dovrefjell, and in July in Børgefjell. In 2012, the fieldwork was carried out in July in Dovrefjell, where late snowmelt resulted in many waterlogged plots with newly exposed vegetation in two of the sites, and in the first half of August in Børgefjell (see Appendix S3 for more details on sample timing).

Statistical analyses

We used two indices as a measure of rodent activity in the plots. The first was based on records of rodent faeces only, and calculated as the number of subplots with faeces (range 0–16). The second index was based on independent records of faeces, grazing marks and tunnels present in the 16 subplots (range 0–48). All analyses were conducted with both measures of rodent activity.

To assess possible differences in the level of rodent activity between habitats and years, we used a zero-inflated generalized linear mixed model (ZIGLMM) fitted with the

Table 1. Characteristics of the study sites in: (a) Dovrefjell and (b) Børgefjell with latitude and longitude, altitudinal range, mean annual temperature, mean July and January temperature, annual precipitation and bedrock composition. Temperature and precipitation data are from the period between 1961–1990, interpolated to the centre of each site based on data from surrounding weather stations; see Tveito et al. (2005) for details.

Site	Lat. and Long.	Altitude (m a.s.l.)	Mean Annual Temp. (°C)	Mean July Temp. (°C)	Mean Jan Temp. (°C)	Annual Precip. (mm)	Bedrock
(a) Dovrefjell							
Grødalen	62°53' N, 8°93' E	1052–1236	−0.4	5.7	−5.5	864	Amphibolite and mica schists
Hjerkinn	62°29' N, 9°40' E	1188–1326	−2.6	6.7	−11.8	787	Precambrian metamorphosed rock, patches of gneiss and grit
Forollhogna	62°72' N, 11°09' E	923–1044	−0.9	7.4	−9.0	1010	Micaceous gneiss
(b) Børgefjell							
Kjukkelen	65°17' N, 13°81' E	704–914	−2.2	7.7	−11.5	1237	Micaceous gneiss and mica schists
Tiplingan	65°27' N, 14°10' E	751–905	−2.2	7.9	−11.8	1033	Gneiss and granite
Ranseren	65°19' N, 14°26' E	841–968	−2.5	7.6	−12.0	961	Quartz-diorite

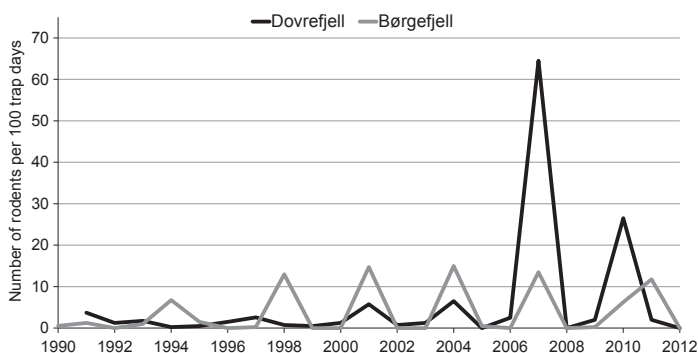


Fig. 1. Rodent abundance in Børgefjell (light grey line) and Dovrefjell (black line) based on the number of lemmings and voles caught during 100 trap days in September each year from 1990/1991 until 2012. The rodent populations peaked in both regions in 2010–2011, but crashed earlier in Dovrefjell (low catch in autumn 2011). The oscillations are historically stable in Børgefjell, while they have been almost absent in Dovrefjell until recent years; source: Framstad (2013).

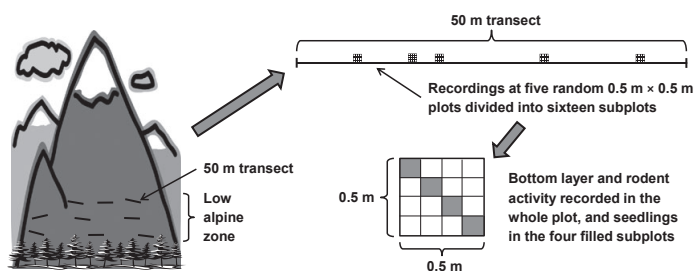


Fig. 2. Schematic representation of the sampling design. To the left is a study site with nine 50-m transects in the low-alpine zone. At the top right is a zoom-in of one transect with five randomly chosen plots. On bottom right, a plot (0.5 m × 0.5 m) divided into 16 subplots where bottom layer and rodent activity records were obtained. On the four subplots on the plot diagonal (filled squares), the number of seedlings and adult individuals of annual species was counted.

‘glmmadmb’ function in the ‘glmmADMB’ package (Fournier et al. 2012) with a Poisson error structure; consequently, all estimates are on a log scale. We used a generalized linear mixed model to account for the spatial dependency between plots within the same transect and a zero-inflated model because the rodent activity records had many plots with no signs from rodents (108 out of 544). The minimally adequate model was found by model simplification based on a comparison of AIC values and Wald tests.

We tested whether seedling emergence was related to rodent activity and whether the correspondence differed between habitats and years. We used seedling counts as the response variable and rodent activity (Hypotheses 1 and 2), study region and habitat (Hypothesis 3) as explanatory variables, including two-way interactions (testing Hypothesis 4). The cover of bottom layers was included as covariates (lichen, litter, moss and bare ground), and

separate models for 2011 and 2012 were constructed. The seedling counts were zero-inflated (many plots with no seedlings; Appendix S4), over-dispersed for the non-zero data, and non-independent (spatial dependency between plots within the same transect), thus ZIGLMMs with a negative binomial error structure ‘NB1’ were used, with transect as a random effect. The minimally adequate model for each year was found by successively including explanatory variables and two-way interactions. Comparison of AIC values and Wald tests were used for model selection.

Two outliers, a heath plot at Hjerkind in 2011 with 90 seedlings, and a snowbed plot at Kjukkelen in 2012 with 70 seedlings, were excluded from the analyses because they had a large influence on the outcome of the analyses.

All statistical analyses were done using the software R, version 2.15.1 (R Foundation for Statistical Computing, Vienna, AT, USA).

Results

Regional and between-year differences in rodent activity

The two indices of rodent activity produced similar results in the analyses, although only the results from analyses performed with records of rodent faeces are presented here.

Rodent activity was higher in 2012 than in 2011 ($\beta \pm \text{SE}$: 0.158 ± 0.052 ; Table 2), and the difference in rodent activity between 2011 and 2012 was smaller in Dovrefjell than in Børgefjell (significant study region \times year interaction; Table 2). In the low-density year 2012, tunnels, holes, faeces and litter caused by lemmings and voles were still visible in the vegetation (Fig. 3a, b), despite the fact that the rodent populations had crashed (Fig. 1).

Impact of rodent activity on seedling emergence

In 2011, a total of 665 seedlings were recorded in 99 plots, and no seedlings were found in the remaining 171 plots (Appendix S5), but there were more seedlings in Dovrefjell than in Børgefjell ($\beta \pm \text{SE}$: 1.520 ± 0.484 ; Table 3a), 415 and 250, respectively. Furthermore, rodent activity significantly explained the number of seedlings found in both regions ($\beta \pm \text{SE}$: 0.086 ± 0.038 ; Table 3a).

In 2012, a total of 1232 seedlings were observed in 152 plots, of which 543 were in Børgefjell and 689 in Dovrefjell, and in 120 plots no seedlings were found (Appendix S5). In contrast to 2011, there was no difference between regions in the number of seedlings emerged ($\beta \pm \text{SE}$: 0.319 ± 0.298 , $P = 0.285$), but in 2012, seedling emergence was also positively related to rodent activity ($\beta \pm \text{SE}$: 0.086 ± 0.023 ; Table 3b). In general, the number of seedlings recorded in the rodent low-density year was higher in plots which had

experienced a high level of rodent activity before the populations crashed.

Interaction of ground cover and rodent activity on seedling recruitment

In 2011, the amount of bare ground was positively associated with seedling emergence ($\beta \pm \text{SE}$: 0.110 ± 0.032 ; Table 3a). There was a small positive main effect of litter cover on seedling emergence ($\beta \pm \text{SE}$: 0.023 ± 0.011 ; Table 3a), although with a negative interaction between rodent activity and litter cover, thereby suggesting that seedling emergence was highest in plots with a high rodent activity when litter cover was low. No effects on seedling numbers of moss cover were detected.

In contrast to 2011, there were no effects of bare ground and cover of litter on seedling emergence found in 2012, but the seedling number was negatively related to the cover of lichens ($\beta \pm \text{SE}$: -0.031 ± 0.015 ; Table 3b). A small negative interaction between rodent activity and moss cover suggested that fewer seedlings emerged in plots with high rodent activity when the moss cover was high.

Interaction of rodent activity and habitat on seedling recruitment

Rodent activity was higher in snowbeds than in sheltered heaths ($\beta \pm \text{SE}$: 0.181 ± 0.059 ; Table 2, Fig. 3a,b). In 2011, the seedling number was higher in snowbeds than in sheltered heaths ($\beta \pm \text{SE}$: 1.933 ± 0.474 ; Table 3a, Fig. 3c,d), although the difference between habitats was smaller in Dovrefjell than in Børgefjell (significant region \times habitat interaction; Table 3a). As in 2011, significantly more seedlings were found in 2012 in snowbeds compared to sheltered heath habitats ($\beta \pm \text{SE}$: 0.637 ± 0.222 ; Table 3b, Fig. 3c,d), but in this case the differences between habitats were similar in both regions (no significant region \times habitat interaction; Table 3b).

We did not find any differences in either year between habitats on the effect of rodent activity on seedling emergence (no significant rodent activity \times habitat interaction; Table 3a,b).

Discussion

This study reveals that small rodent population dynamics are an important driver of seedling recruitment patterns in alpine plant communities and that the disturbance from rodents is equally important for recruitment in snowbeds and sheltered heaths, even though seedling emergence in general is higher in snowbeds. Rodent activity interacts with bottom layers, including the cover of litter and

Table 2. Zero-inflated generalized linear mixed model (ZIGLMM with Poisson distribution) of rodent activity (records of faeces) as a function of habitat, study region, year and an interaction between study region and year ($n = 544$). The reference level (intercept) is the study region of Børgefjell and the habitat sheltered heath. The transect is the model's random factor with $n = 57$. The parameter estimates of random effects are not shown.

Fixed Effects	Estimate	SE	Z-Value	P-Value
Intercept	1.703	0.113	15.07	<0.001***
Habitat (Snowbed vs. Heath)	0.181	0.059	3.08	0.002**
Study Region (Dovrefjell vs. Børgefjell)	-0.301	0.160	-1.89	0.059
Year (2012 vs. 2011)	0.158	0.052	3.07	0.002**
Study Region \times Year 2012	-0.584	0.089	-6.60	<0.001***

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, $^{\circ}P < 0.1$.

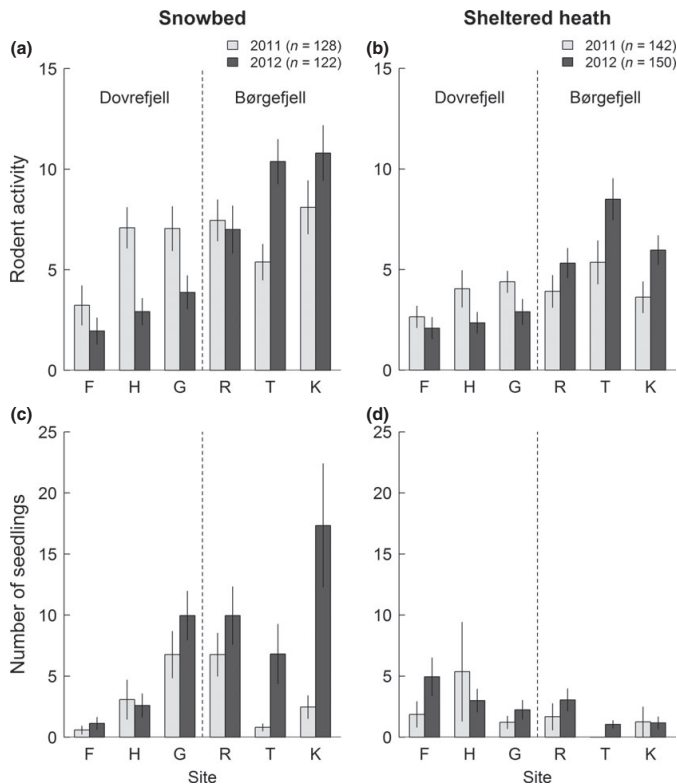


Fig. 3. Mean observed rodent activity based on records of faeces (range 0–16) (a, b) and number of seedlings (c, d) in snowbed and sheltered heath habitat in the six study sites (in Dovrefjell: F, Forollhogna; H, Hjerkinn; and G, Grødalen and in Børgefjell: R, Ranseren; T, Tiplingan; and K, Kjukkelen) in 2011 (light grey bars) and 2012 (dark grey bars). Vertical lines show ± 1 SE from the mean.

mosses, thereby also indirectly influencing seedling recruitment.

Seedling emergence and rodent disturbance

We revealed the positive effects of rodent activity on the number of seedlings in both the population peak and the low-density year, as found by Eskelinen & Virtanen (2005). The availability of open space is one of the main limitations for seed regeneration in many plant communities (Grubb 1977), including arctic-alpine communities (Welling & Laine 2002; Graae et al. 2011). Our results indicate that disturbances from rodents in peak densities (e.g. herbivory, grubbing for rhizomes, trampling in tunnels, digging holes, cutting of vegetation) create gaps in the vegetation where seedlings can emerge. Much of the influence of herbivores on plant communities is assumed to be indirectly caused through the alteration of abiotic factors (Mulder 1999). For example, disturbed plots

experience more temperature fluctuations than closed vegetation (Graae et al. 2011), which is important for breaking seed dormancy for many species (Fenner & Thompson 2005). A higher light availability due to biomass removal is also beneficial for germination, particularly for small-seeded species (Grime et al. 1981), and several species also respond to light quality, germinating only in gaps and not when light is filtered through the canopy (Silvertown 1980; Smith 1985). Furthermore, the substantial amounts of faeces deposited in peak years could have a positive fertilization effect on seedling survival and growth (Chambers et al. 1990).

The impact of rodent disturbances on seedling recruitment appears to be a function of the ground cover. In accordance with Suding & Goldberg (1999), we found a small, positive effect of litter cover on seed recruitment in the peak year, but there was also a small, negative interaction between rodent activity and litter, indicating that fewer seedlings emerged in plots with high rodent activity

Table 3. Zero-inflated generalized linear mixed models (ZIGLMMs with negative binomial 'NB1' distribution) of seedling counts as a function of region, habitat and bottom layer covers in: (a) the peak year 2011 and (b) in the low-density year 2012. The reference level (intercept) is the study region of Børgefjell and the habitat sheltered heath. The transect is the models' random factor with $n = 54$ in 2011 and $n = 55$ in 2012. The parameter estimates of random effects are not shown.

Fixed Effects	Estimate	SE	Z-Value	P-Value
(a) 2011 (Peak Year)				
Intercept	-1.511	0.490	-3.08	0.002**
Rodent Activity	0.086	0.038	2.28	0.023*
Habitat (Snowbed vs. Heath)	1.933	0.474	4.08	<0.001***
Study Region (Dovre fjell vs. Børgefjell)	1.520	0.484	3.14	0.002**
Study Region (Dovre fjell × Habitat Snowbed)	-1.315	0.554	-2.37	0.018*
Bare Ground	0.110	0.032	3.48	<0.001***
Litter	0.023	0.011	1.99	0.047*
Rodent Activity × Litter	-0.004	0.001	-2.52	0.012*
(b) 2012 (Low-Density Year)				
Intercept	0.472	0.274	1.72	0.085'
Rodent Activity	0.086	0.023	3.78	<0.001***
Habitat (Snowbed vs. Heath)	0.637	0.222	2.87	0.004**
Lichen	-0.031	0.015	-2.11	0.035*
Moss	0.006	0.005	1.11	0.268
Rodent Activity × Moss	-0.002	0.001	-2.74	0.006**

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ' $P < 0.1$.

when the amount of litter was high. To some extent, these results are contradictory, indicating that both litter and rodent activity facilitate seedling emergence, although to a lesser extent when both litter cover and rodent activity are high. Lemming disturbance can result in a three-fold increase in litter due to the cutting of graminoids and mosses (Moen et al. 1993). Thus, litter accumulation due to high rodent activity may counteract the positive effects of disturbance on seedling emergence, as high litter amounts may inhibit seedling recruitment (Loydi et al. 2013).

A negative effect of lichen cover on seedling emergence was found in the low-density year (lichen cover was not recorded in the peak year), and several factors related to the presence of lichens could contribute to the observed pattern: lichens prevail in dry environments, where the gap quality could be expected to be comparably low, a dense lichen cover reduces light availability and several lichen species have allelopathic effects (Hobbs 1985; Lawrey 1986; Zamfir 2000). Mosses usually suppress seedling emergence (Eckstein et al. 2011; Soudzilovskaia et al. 2011), but in this study no main effect of moss cover on seedling emergence was found. Both herbivory and other

activities by rodents could potentially suppress the negative effect of mosses by reducing the thickness of the moss carpet (Moen et al. 1993; Virtanen 2000).

Rodent population dynamics and consequences for plant recruitment

As predicted, we found higher seedling recruitment rates in the low-density year compared to the peak year. Small rodents often have a substantial impact on seed populations through seed predation (Hulme 1994; Fox 2011). Seeds are indeed common in the diet of field voles, but not for lemmings (Sætnan et al. 2009), and it is possible that seed predation during the peak year may have contributed to lower seedling recruitment rates. Although seedling herbivory by lemmings and voles is considered to be negligible (Olofsson et al. 2005; Shaw et al. 2010), it is probable that high rodent activity resulted in both seedling herbivory and damage to seedlings in the peak year, hence contributing to the lower number of seedlings compared to the low-density year. Moreover, many seedlings were observed in tunnels that were still visible among the vegetation during the low-density year (K.O. Nystuen, pers. obs.). Vegetative growth in alpine areas is a slow process (Evju et al. 2012), and gaps created during the peak year could therefore be expected to still be available in the subsequent growing season, thus providing opportunities for successful seedling emergence when the disturbance intensity is lower. Between-year differences in recruitment could also be a result of differences in the availability of seeds in the seed bank or of other abiotic factors not measured, such as rainfall or temperature.

The cyclic population dynamics of lemmings and voles constitutes a disturbance regime with extensive disturbance and gap formation taking place at peaks typically occurring every third to fifth year (Angerbjörn et al. 2001). Consequently, seedling recruitment patterns in arctic-alpine habitats should be reflected by the rodent population cycles, with an especially high recruitment in the year following a peak (Ericson et al. 1992). Recurrent disturbances resulting in opportunities to reproduce by seeds every third to fifth year, followed by years with a much lower disturbance level, could be important to maintain species richness in arctic-alpine habitats by providing frequent opportunities for recruitment (Warner & Chesson 1985; Chesson 1986) and by preventing competitive exclusion (Chesson 1986; Chambers 1993). The rodent population cycles have been fading out in many places in Scandinavia and in the rest of Europe over the past two decades (Ims et al. 2008; Kausrud et al. 2008; Cornulier et al. 2013), and the absence of the regular disturbance regime could be hypothesized to influence plant recruitment patterns in these sites. In our southern study region

of Dovrefjell, major rodent population peaks have been absent between 1989 (Gjershaug 1996) and 2006 (Fig. 1). If the absence of predictable rodent cycles had resulted in a loss of – or reduced – population sizes of plant species dependent on the regular creation of open space for recruitment, lower seedling numbers could have been expected in Dovrefjell than in Borgefjell. However, our results suggest no such effect. The lack of differences in seedling emergence between the two regions could be due to few species and small populations relying on frequent disturbances in these arctic-alpine habitats, therefore comprising only a minor portion of the bulk of seedlings emerging in gaps. Another reason could be the importance of other sources of disturbance in arctic-alpine habitats, such as frost heave, snowmelt and grazing, as well as trampling from large herbivores, which may contribute to creating microsites for seedling emergence independently of small rodents. The additional positive effect of bare soil on seedling numbers in the peak year supports this, and is in line with the results from Shaw et al. (2010).

Seedling emergence and habitat type

In accordance with our predictions, we found more seedlings in snowbeds than in sheltered heaths. In addition, we expected that a certain disturbance level would result in more seedlings emerging in snowbeds than in sheltered heaths, as the seed rain is higher and germination conditions comparatively better in snowbeds than in sheltered heaths (Graae et al. 2011) where seedling emergence may be hindered by environmental constraints such as drought (Welling & Laine 2002). We also found that rodent activity was higher in snowbeds compared to sheltered heaths, but in contrast to our expectations, no interaction between rodent activity and habitat was found. Our results are in concordance with Olofsson et al. (2005), who found no difference in the impact of experimental disturbance on recolonization in low (heath) and high (birch forest) productive mountain habitats, but in contrast to Evju et al. (2012), who found a larger increase in seedling numbers in sheltered heaths than in snowbeds after severe experimental disturbance.

The lack of a significant rodent activity–habitat interaction could be due to within-habitat differences of snowbeds in our study. The snowbeds in the study ranged from productive, dominated by graminoids and forbs with a high seedling emergence, to late-melting and less productive snowbeds dominated by mosses and *Salix herbacea*, where fewer seedlings are expected to emerge (Welling & Laine 2000). The latter is a preferred winter habitat for lemmings, and is thus expected to have high rodent activity (Moen et al. 1993). The small, though significant, negative interaction between rodent activity and moss cover in

the low-density year points to lower seedling numbers in plots with a high moss cover and high rodent activity, compared to plots with a low moss cover and high rodent activity. This further indicates that variable seedling numbers in snowbeds, due to within-habitat differences, could contribute to explaining the absence of rodent activity–habitat interactions. Additionally, the 2012 records in Dovrefjell (especially in two of the sites) were carried out shortly after snowmelt (Appendix S3), and several snowbed plots were waterlogged; thus, seedling emergence in snowbed plots may be somewhat underestimated.

Even though the overall rodent activity was higher in snowbeds compared to sheltered heaths, the relatively high rodent activity recorded in both habitats (Fig. 3a,b) suggests that additional factors contribute to limit seedling emergence. Relevant factors are seed availability and gap quality (Grubb 1977; Dullinger & Hülber 2011). The total number of seedlings varied largely among the study plots, also within habitats (Appendices S4 and S5), and in some plots no seedlings were present at all despite high rodent activity. Such a large spatial variation in seedling abundance is a common feature in arctic-alpine (Forbis 2003) as well as in other systems (Aguir et al. 1992). The spatial structure of seeds, including both the seed rain and the seed bank, is highly clumped and heterogeneously distributed in space (Rusch & Fernández-Palacios 1995; Molau & Larsson 2000). Shelter effects of microrelief or neighbour plants, resulting in a highly variable microclimate within short distances, might also contribute to the clumping of seedlings (Diemer 1992; Graae et al. 2012).

This study shows that rodent dynamics are an important structuring factor of the vegetation through recruitment. Studies, including data on the species identity of seedlings and the mature vegetation, would further help to understand the effect of rodent disturbances and of the loss of rodent population peaks (Ims et al. 2008; Kausrud et al. 2008) on species assemblage processes, species richness patterns and the invasibility of alpine plant communities. Knowledge about these processes is also important in order to understand the effects of drivers such as climate change, which may enhance the rate of change in alpine vegetation.

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Supporting Information

Additional supporting information may be found in the online version of this article:

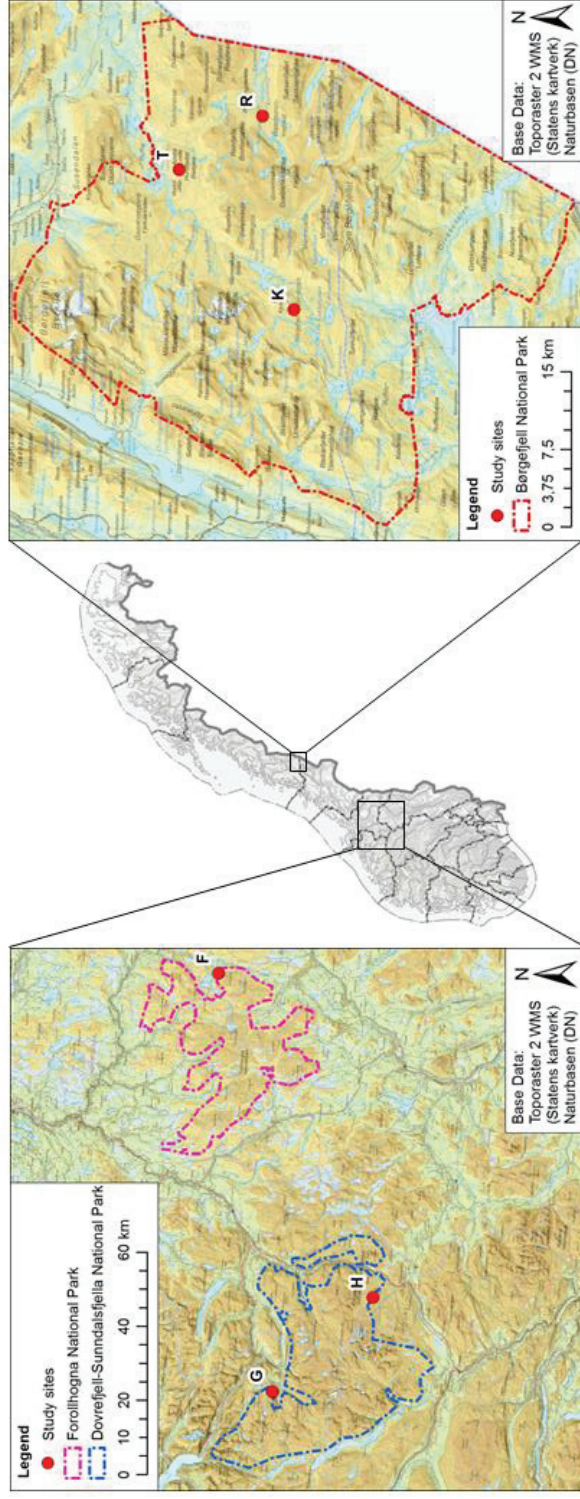
Appendix S1. Map of the study sites and the study regions' location in Norway.

Appendix S2. Table showing the distribution of plots among study sites, habitats and year.

Appendix S3. Table with detailed information on data sampling time.

Appendix S4. Histograms with frequency distribution of seedlings in the recorded plots.

Appendix S5. Table with details on seedling occurrences (mean \pm SE, total number, number of plots with no seedlings) for all combinations of habitat, study region and year.

















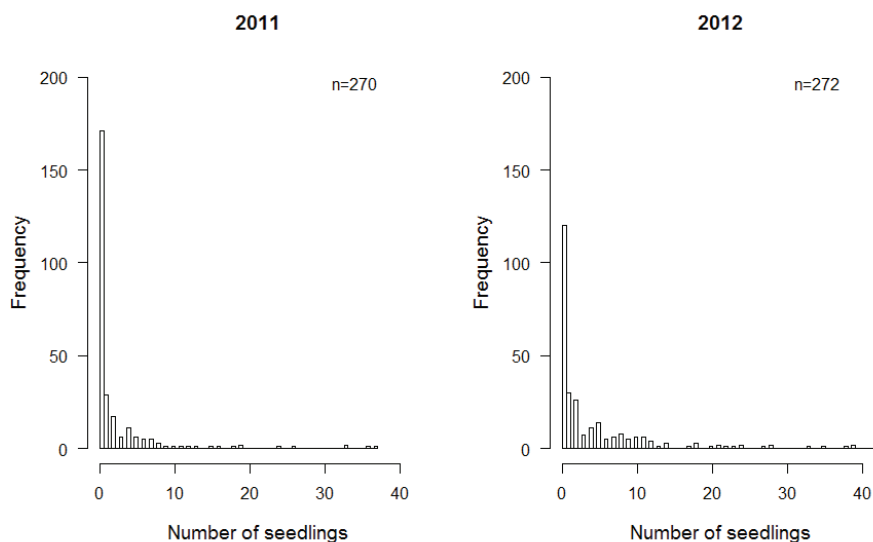
Appendix S1: The study regions of Dovrefjell to the left and Børgefjell to the right. The study sites in each region are marked with red dots. In Dovrefjell, the study sites are: G - Grødalen, H - Hjerkin and F - Forollhogna. In Børgefjell, the sites are: K - Kjukkelen, T - Tiplingan and R - Ranseren. Note that the scales in the two regional maps differ.

Appendix S2. Distribution of plots among study sites and habitats. Numbers from 2011 is written first with numbers from 2012 following in brackets.

	Dovre fjell			Børgefjell			Total
	Forollhogna	Grødal	Hjerkinn	Kjøkkelen	Ranseren	Tiplingan	
Sheltered heath	23 (22)	23 (20)	22 (20)	27 (35)	25 (31)	22 (22)	142 (150)
Snow-bed	22 (21)	21 (24)	23 (25)	19 (15)	22 (16)	21 (21)	128 (122)
Total	45 (43)	44 (44)	45 (45)	46 (50)	47 (47)	43 (43)	270 (272)

Appendix S3. Overview of when field work (grey shading) was conducted during summer in the sites in a) the rodent peak year 2011 and b) the low-density year 2012.

	June	July	August
a) Peak year 2011			
Forollhogna			
Hjerlenn			
Grødalen			
Ranseren			
Tiplingan			
Kjukkelen			
b) Low density year 2012			
Forollhogna			
Hjerlenn			
Grødalen			
Ranseren			
Tiplingan			
Kjukkelen			



Appendix S4. Frequency distribution of the number of seedlings found in the plots in a) 2011 (n=270) and b) 2012 (n=272). In 2011 there were no seedlings in 171 plots and seedling occurrences in 99. In 2012 no seedlings were observed in 120 plots, while occurrences were recorded in 152 plots.

Appendix S5. Observed mean number of seedlings with standard error (SE), total number of seedlings, number of plots without seedling emergence, and total number of recorded plots for all combinations of habitat, study region and year.

	No. of seedlings (mean \pm SE)	Total no. of seedlings	No. of plots without seedlings	Total no. of plots
Sheltered heaths Børgefjell 2011	1.0 \pm 0.6	76	67	74
Sheltered heaths Børgefjell 2012	1.8 \pm 0.4	159	36	88
Sheltered heaths Dovrefjell 2011	1.4 \pm 0.4	99	39	68
Sheltered heaths Dovrefjell 2012	3.5 \pm 0.7	214	25	62
Snow-beds Børgefjell 2011	2.8 \pm 0.7	174	34	62
Snow-beds Børgefjell 2012	9.0 \pm 1.6	460	32	52
Snow-beds Dovrefjell 2011	3.4 \pm 0.9	226	31	66
Snow-beds Dovrefjell 2012	4.6 \pm 0.9	329	27	70
Børgefjell 2011	1.8 \pm 0.5	250	98	136
Børgefjell 2012	4.5 \pm 0.7	619	68	140
Dovrefjell 2011	2.5 \pm 0.5	325	73	133
Dovrefjell 2012	4.1 \pm 0.6	543	52	132

Paper II



Grazing sheep. Artist: Kine Odden Nystuen

Herbivores reduce the invasibility of alpine plant communities

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Abstract

Through changes in climate and other environmental factors, alpine tundra ecosystems are subject to increased cover of erect shrubs, reduced predictability of rodent dynamics, and changes in wild and domesticated herbivore densities. To predict the dynamics of these ecosystems, we need to understand how these simultaneous changes affect alpine vegetation. In the long term, vegetation dynamics depend critically on seedling recruitment. We study drivers of alpine plant seedling recruitment in a field experiment where we manipulated the opportunity for plant-plant interactions through vegetation removal and introduction of willow transplants, the occurrence of herbivory through caging of plots, and then sowed 14 species into the plots. We replicated the experiment in three common alpine vegetation types and recorded seedling emergence and survival over five years. Herbivore exclusion had strong positive effects on the recruitment success of vascular-plant seedlings. This effect arose primarily via reduced seedling mortality in plots from which herbivores had been experimentally excluded and became noticeably stronger over time. In contrast, we detected no consistent effects of experimental willow shrub introduction on seedling recruitment. These results demonstrate that large and small herbivores can affect alpine plant seedling recruitment negatively by trampling and feeding on seedlings. Importantly, these effects became stronger over time, underlining the importance of long-term studies for understanding the dynamics of alpine plant communities subject to changes in the biotic and abiotic environment.

Keywords: climate change, herbivory, seedling recruitment, shrub encroachment, species interactions, vegetation dynamics

Introduction

Arctic-alpine tundra ecosystems are thought to be disproportionately affected by ongoing environmental changes (Björk & Molau, 2007; Vowles, Lovehø, Molau, & Björk, 2017). Beyond direct effects of increasing temperatures on plant physiology, important indirect effects are expected to arise via changes in land use and in species interactions within and between trophic levels (Austrheim & Eriksson, 2001; Körner, 2003; Olofsson et al., 2009; Vowles et al., 2017). One prominent example of expected changes in species interactions is the negative effects of ongoing shrub encroachment on many understorey plants (Mod & Luoto, 2016; Pajunen, Oksanen, & Virtanen, 2011; Wallace & Baltzer, 2019). Increased shrub cover ('shrubification') increases vegetation productivity and changes the nutrient and carbon dynamics of tundra heath and meadow vegetation (Sørensen et al., 2018b). Beyond these plant-plant interactions, it is also increasingly clear that patterns of vegetation change depend on interactions among trophic levels, notably herbivory (Kaarlejärvi, Eskelinen, & Olofsson, 2017; Olofsson et al., 2009). In alpine Fennoscandia, recent changes in herbivore communities include less predictable population cycles of small rodents (Ehrich et al., 2020; Framstad, 2019; Kausrud et al., 2008), and changes in the abundance and composition of large wild and free-ranging domestic herbivores (Austrheim, Solberg, & Mysterud, 2011; Speed, Austrheim, Kolstad, & Solberg, 2019). A better understanding of the direct and indirect effects of species interactions within and between trophic levels will be important for understanding the future dynamics of arctic-alpine ecosystems.

The vast majority of arctic-alpine plants are long-lived and slow-growing, and vegetation changes in these regions are therefore often slow (Billings, 1987; Körner, 2003; Morris & Doak, 1998). Although clonal species can persist for long periods, long-term vegetation dynamics depend increasingly on changes in community composition and hence successful seedling recruitment. Seedling recruitment is expected to depend on microclimatic conditions (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011) and on species interactions (Fayolle, Violle, & Navas, 2009; Milbau, Shevtsova, Osler, Mooshammer, & Graae, 2013; Nystuen et al., 2019), both of which are likely to be affected by ongoing environmental changes. While seed production and germination in cold biomes are often found to respond positively to warmer temperatures, at least when sufficient soil moisture is available (Klady, Henry, & Lemay, 2011; Milbau, Graae, Shevtsova, & Nijs, 2009; Walck et al., 2011), seedling survival and establishment are in turn thought to be sensitive to droughts associated with warm weather (Fenner & Thompson, 2005; Leck, Parker, & Simpson, 2008;

Moles & Westoby, 2004). Predicting the net effect of environmental change on seedling recruitment is therefore complicated (Shevtsova et al., 2009).

Seedling recruitment may depend in important ways on plant-plant interactions, which are expected to differ among plant community types. For example, plant communities dominated by strong competitors, such as grasslands, are normally thought to be less invisable than are those dominated by ruderal species (Burke & Grime, 1996; Lett, Dorrepaal, & Fox, 2018a). The relative success of competitive species is likely to depend on the frequency of disturbances creating gaps in the vegetation, because gaps provide ‘safe sites’ where competition is limited, thus allowing seedling recruitment (Graae et al., 2011; Grubb, 1977; Lembrechts et al., 2016; Milbau et al., 2013). Therefore, if environmental changes affect the frequency of disturbances, this can change the invasibility of the vegetation and consequently lead to a shift in community composition.

The ongoing expansion of erect shrub communities in arctic-alpine regions (Elmendorf et al., 2012; García Criado, Myers-Smith, Bjorkman, Lehmann, & Stevens, 2020; Myers-Smith et al., 2011) may modify competitive interactions compared to those occurring in low-growing vegetation types such as meadows and heaths. The net effect of erect shrub expansion on plant recruitment in tundra depends on the extent of shrub cover, the shrub and plant species studied, and the recruitment phase in question (Cranston & Hermanutz, 2013; Dona & Galen, 2007; Dufour-Tremblay, De Vriendt, Levesque, & Boudreau, 2012; Jumpponen, Mattson, Trappe, & Ohtonen, 1998). For example, shrubs trap snow and thereby create stable winter conditions known to benefit seedling survival for boreal species (Dona & Galen, 2007; Lett et al., 2018b). However, light reduction is among the principal factors explaining low tree seedling occurrence (Dufour-Tremblay et al., 2012; Jumpponen et al., 1998) and growth (Cranston & Hermanutz, 2013) in tundra systems. Furthermore, shrubs may affect seedling recruitment through indirect effects, as when tall shrubs outcompete dwarf shrubs, graminoids or cryptogams (Pajunen et al., 2011), thereby allowing seedlings to recruit on the bare soil in the moist microclimate under the shrub canopy (Graae et al., 2011).

The fate of recruiting plants in shrub-dominated vegetation may depend directly or indirectly on herbivory. For example, herbivory can affect the competitive capacity of the extant vegetation, and the frequency of vegetation gaps. Indeed, vegetation gaps are often associated with mammal activities such as burrowing and trampling (Ericson, Elmqvist, Jakobsson, Danell, & Salomonson, 1992; Nystuen, Evju, Rusch, Graae, & Eide, 2014; Watt & Gibson, 1988), and herbivory may therefore indirectly increase the invasibility of the

vegetation (Eskelinen & Virtanen, 2005; Olofsson, 2006; Olsen & Klanderud, 2014). However, small size and limited storage make seedlings highly vulnerable to trampling and herbivory. Herbivores can kill or reduce the performance of preferred species in arctic-alpine vegetation (Bognounou et al., 2018; Eskelinen, 2008), although these effects may be weak compared to the positive effects of disturbances and consumption of extant vegetation (Eskelinen & Virtanen, 2005). Compared to other ecosystems, seedlings in tundra are small and grow slowly, and are therefore of little interest to mammalian herbivores during their first years (Shaw et al. 2010). Therefore, herbivore-induced seedling mortality may be less important in tundra compared to other community types (Clark, Poulsen, & Levey, 2012; Hanley, 1998; Hulme, 1994). However, slow recovery of vegetation subject to trampling may increase the importance of herbivore-induced disturbances.

To predict the joint outcome of shrub expansion and changes in herbivore pressure on the successional pathways in alpine vegetation we need a more mechanistic understanding of seedling recruitment processes. To this end, we sowed 14 species into plots in a full-factorial plant recruitment experiment where we manipulated the opportunity for plant-plant interactions through vegetation removal and introduction of willow transplants, and the occurrence of herbivory through caging of plots. Because alpine terrains comprise a patchwork of distinct vegetation types, and invasibility is thought to differ among these, we replicated the experiment in three common alpine vegetation types: a meadow snowbed, a *Salix* shrubland, and a dwarf-shrub heath. If plant-plant interactions are important for seedling recruitment, we expect recruitment success to differ among vegetation types and between controls and experimentally encroached plots. We also expect that seedling emergence and establishment is greater when seeds are sown into experimental gaps in the extant vegetation. If herbivory is important, we expect greater mortality of emerged seedlings and consequently reduced establishment success in those plots exposed to natural herbivory.

Materials and Methods

Study sites

The study area is located in the low-alpine vegetation zone around 1100 m a.s.l. near Hjerkin, central Norway (Fig. 1A). The climate in the area is continental, with short warm summers and long cold winters (Moen, 1998; Supplementary Materials, Figure S1, Table S1). We established study sites on three neighbouring mountain slopes representative of three

common tundra vegetation types: a dwarf-shrub-dominated heath, an herb- and cryptogam-dominated meadow, and a *Salix*-dominated shrubland (Fig. 1A, Table S2).

The study sites experience low-intensity summer grazing and browsing by domestic sheep (NIBIO, 2017). Wild herbivores present in the study area include voles (*Microtus agrestis*, *M. oeconomus* and *Myodes rufocanus*), lemmings (*Lemmus lemmus*), hare (*Lepus timidus*), ptarmigan (*Lagopus lagopus* and *L. muta*), moose (*Alces alces*) and the occasional passing of reindeer (*Rangifer tarandus*). The small rodents exhibit cyclic population dynamics (Stenseth & Ims, 1993) with population build-ups in 2013 and 2017 resulting in moderate rodent peaks in 2014 and 2018 (Framstad, 2019). The herbivores use the different vegetation types differently, with potential consequences for plant recruitment. Heaths are important resting sites for sheep, but are not preferred for grazing (Kausrud, Mysterud, Rekdal, Holand, & Austrheim, 2006). Sheep grazing is more intense in the more productive meadow and shrub vegetation rich in herbaceous plants preferred by sheep (Kausrud et al., 2006). Seedlings in open plots are therefore exposed to sheep herbivory but may also experience reduced biotic competition as a result of grazing on the extant vegetation. Within dense shrub vegetation, understorey plants may be difficult to access and thereby escape large-mammal herbivory (Pajunen et al., 2011), while smaller herbivores may benefit from shelter below shrub canopies. Winter herbivory by lemmings and voles is expected to be most important at the meadow and shrub sites, as rodents prefer habitats with a thick, insulating snow cover (Sætnan, Gjershaug, & Batzli, 2009).

Experimental setup and study design

In late June 2013 we placed 32 plots (25 × 25 cm) within the fairly homogenous vegetation at each site (see Table S2 for further description of the study sites). The plots were assigned to a 2×2 factorial experiment comprising exclusion of herbivores with cages and planting of *Salix*, resulting in four treatment combinations with eight replicates per site (Fig. 1c). At each plot, we established four subplots (12.5 × 12.5 cm) for a 2×2 factorial experiment comprising disturbance and seed sowing. The two disturbed subplots were placed c. 15 cm outside the 25 × 25 cm plot to avoid interference with other ongoing experiments, while the two intact subplots were inside the 25 × 25 cm plot (Fig. 1C).

In early July 2013, cages (80 × 80 × 50 cm with a lid) excluding small and large vertebrate herbivores were placed over one half of the plots (Fig. 1C, D). The cages were made from galvanized steel mesh with mesh size 1.27 × 1.27 cm, small enough to keep out small rodents (Grellmann, 2002; Moen, Lundberg, & Oksanen, 1993; Olofsson, Hulme,

Oksanen, & Suominen, 2005) and dug 5 to 10 cm into the ground. To simulate shrub encroachment, we planted five rooted *Salix* cuttings into one half of the plots (Fig. 1C, E). We used cuttings from a mixed cultivation of *Salix glauca* and *S. lapponum*. Branches were collected in the vicinity of the field sites in October 2013, and transported to a plant nursery (Norske Naturplanter AS, Færvik, Norway) for cultivation. The branches were stored at 0°C until January 2014 and then divided into c. 10 cm long cuttings and planted vertically in commercial plant soil for rooting. They were kept cool in the greenhouse during winter to promote below-ground growth. In May 2014 they were planted in 10 cm diameter pots, top twigs were cut to promote lateral branching, and the pots moved outside for hardening (Hagen & Evju, 2014). In June 2014, the top twigs were trimmed to c. 10 cm before planting in the field. We planted one *Salix* cutting along each of the four plot edges, and a fifth cutting between the two disturbed subplots (Fig. 1C). Two hundred of the 240 *Salix* cuttings were still alive three years after transplantation, but most of these remained rather small (<18 cm; Table S3).

In the disturbed subplots, all aboveground vegetation was cut at soil surface to mimic a severe small-scale disturbance event (Fig. 1C, F). In all seeded subplots, we sowed seeds from 14 plant species common in subalpine and low-alpine vegetation (Fig. 1B). These species were chosen because they represent a variety of growth forms (tree, shrub, dwarf-shrub, graminoid and forb) and seedling morphologies and have seeds (bulbils for *Bistorta vivipara*, hereafter referred to as seeds) and seedlings of different sizes which might affect their recruitment potential and resistance to herbivory and environmental stress. The species have easily distinguishable seedlings facilitating field identification. Seeds were collected in the study area when ripe during autumn 2013. The fleshy fruits of *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium myrtillus* were kept in a refrigerator before they were gently squashed in a bowl of water to separate fruit flesh and seeds. The seeds were stored in paper bags at room temperature. *Pinus sylvestris* seeds were supplied by The Norwegian Forest Seed Center, collected at Oppdal c. 600–650 m a.s.l., about 40 km north of the study sites.

A mixture of 30 seeds per focal plant species was sown in each of the two seeded subplots in late autumn 2013 (Fig. 1B), except for *Pinus sylvestris* with only 10 seeds because of known high germination capacity (82%) and large seedling size, and *Salix glauca* with only 15 seeds due to limited seed availability. During sowing, a c. 20 cm tall cardboard frame was placed around the subplots to shelter from wind and avoid spilling of seeds (see Eskelinen & Virtanen, 2005). We sowed the *Betula nana* and *Betula pubescens* ssp. *tortuosa* seeds in spring 2014 because they matured after the other seeds were sown. To ensure that the *Betula*

seeds experienced conditions similar to those of the already sown seeds, we kept them in paper bags under snow during winter (*c.* 8 km from the study site). Each seeded subplot received a total of 385 seeds with a seed density of 2.5 seeds per cm². This density is higher than the expected natural seed rain in alpine vegetation (Graae et al., 2011; Molau & Larsson, 2000). Because germination success in tundra is low (Graae et al., 2011), we increased the probability of successful seedling emergences by sowing many seeds. One unseeded disturbed and one unseeded intact subplot served as controls for natural seedling emergence.

We recorded seedling emergence in all seeded and unseeded subplots in autumn 2014. Each seedling was determined to species and marked with a toothpick adjacent to the seedling. We drew a map of each subplot with seedling positions to ease identification in later years. The subplots were resurveyed for seedling survival and for newly emerged seedlings in July 2015 and in August 2016. The toothpicks were removed after the 2016 survey. In August 2018, we counted the number of seedlings still alive.

Microenvironmental data

Although our focus here is on the effects of the plot-level experimental treatments (herbivore exclusion, willow introduction) on seedling recruitment, we controlled for variation in relevant microenvironmental variables. To this end, we recorded soil surface temperatures in intact vegetation and in the disturbed unseeded subplots, litter cover in all subplots and snow depth in all plots. Soil surface temperature (°C at *c.* 1 cm depth) was logged at four-hour-intervals with temperature sensors (Micro-T DS1921G, Maxim Integrated Products, Sunnyvale, California). Temperatures were logged in intact vegetation from autumn 2013 onwards, and in the disturbed unseeded subplots (representative of disturbed subplots in general) from summer 2016 onwards. We extracted absolute minimum and maximum temperatures and computed mean temperatures for summer (July and August) and winter (January and February). We estimated litter cover (%) visually for each subplot during the seedling censuses. We measured snow depth (cm) at four points per plot with avalanche probes in 2015 (March 14), 2016 (April 2), 2017 (March 11) and 2018 (April 19). If cages or marking sticks were not visible, we located the plots with the aid of a handheld GPS receiver (3 m precision).

Hierarchical joint modelling of seedling emergence, mortality and establishment

We analysed the structure and dynamics of the seedling assemblages emerging in each seeded plot using Bayesian latent-variable joint species distribution models (Hierarchical Modelling

of Species Communities framework; Ovaskainen et al., 2017), implemented in the Hmsc 3.0 R package (Tikhonov et al., 2020). This approach allowed us to model the effects of the experimental treatments on the dynamics of all species jointly, while accounting for the non-independence of seeds sown into the same plot. To assess treatment effects and whether these varied among sites, we fitted four distinct models, separately for disturbed and intact subplots. In each model, we excluded very rare species occurring less than 8 times in the response matrix (across all sites).

First, we modelled the effects of the experimental treatments (willow introduction, herbivore exclusion) on seedling emergence in the first year following sowing (and vegetation removal for the disturbed subplots). We refer to seedling emergence as seed germination and seedling survival until census time. Treatment effects were allowed to vary among sites by including a treatment \times site interaction. Environmental covariates included year-specific mean and maximum summer temperatures, mean and minimum winter temperatures, snow cover, and litter cover. The temperature variables were strongly correlated across years (Fig. S2), which allowed us to replace a few missing values with the mean value (across years) for that plot.

Second, we modelled seedling survival rate between census years, including the number of seedlings in the focal plot in year $t-1$ as an additional explanatory variable describing density-dependent mortality.

Finally, we analysed the seedling assemblages of all sown species alive in the third and fifth year after sowing (2016 and 2018, respectively), which integrates both first-year emergence, later emergence, and survival. We refer to the assemblage of sown species in these later censuses, independently of their age class, as established seedlings.

All models were fitted with a probit link function, and we thus modelled rates of emergence, survival, and establishment. We ran 2 independent MCMC chains of 30000 iterations with the first 10000 discarded as burnin, and a thinning interval of 20 iterations. We assessed model convergence qualitatively by investigation of posterior trace plots, and quantitatively by computing effective sample sizes and potential scale reduction factors (Table S4). We computed the explanatory power of the model as the square correlation coefficient (r^2) between the observed and predicted seedling abundances in each plot.

Interpreting the model results

Our Bayesian analytical approach is analogous to a more typical analysis of variance approach to analysing factorial experiments but differs in how statistical support is evaluated.

To assess patterns of variation in seedling recruitment success across sites and treatments, we interpreted the model output as follows. First, we performed variance component analyses for each model, which allowed us to partition the explained variation (as given by the r^2) into contributions of each fixed and random effect (latent variable). The variance components can be directly compared among models, and allow us to ask, for example, whether the distribution of variance within and among sites differ for the intact and disturbed subplots. While our focus is on interpreting effect sizes, we assessed statistical support for treatment effects within each site by computing posterior support values for the pairwise differences between treatments, i.e. the proportion of posterior samples for which pairwise differences were positive (for positive effects), or negative (for negative effects). Because the vegetation types were not replicated within our design, we do not test statistically for differences among vegetation types (i.e. sites).

Results

Seedling emergence

In intact vegetation, 596 seedlings emerged during the first growing-season following sowing. Most of the variance in seedling emergence occurred among sites, while differences among the plot-level experimental treatments were limited (Table 1). Neither herbivore exclusion nor willow introduction detectably affected the number of emerged seedlings at the meadow and shrubland sites, but fewer seedlings tended to emerge in experimentally shrub-encroached plots at the heath site (Fig. 2).

When the intensity of above-ground competition was reduced by sowing seeds into artificial gaps, the overall emergence rate was much higher with a total of 1895 emerged seedlings. Furthermore, the emergence rates in gaps were more similar across sites than in the plots with intact vegetation, as indicated by a much smaller site-level variance component (11.1% vs. 35.3% for disturbed and intact plots, respectively; Table 1). The effects of herbivore exclusion and willow introduction on seedling emergence in the gaps differed among sites (Fig. 3). At the meadow site, the greatest number of seedlings emerged within the exclosed, shrub-encroached plots. At the shrubland site fewer seedlings emerged within the encroached, open plots, while at the heath site emergence rates were not detectably different among treatments.

Seedling mortality

In intact vegetation, mortality rates were high during the second and third year of the study (mean = 0.57). The largest proportions of variance were explained by the environmental variables representing variation in soil surface temperatures, litter cover and snow depth within and among sites (Table 1, Fig. S5), as well as the treatments and their contrasting effects across sites (Table 1; site-by-treatment interaction). At the heath and meadow sites, mortality rates tended to be lower in exclosed plots (Fig. 2). At the shrubland site, mortality rates were higher in the exclosed, non-encroached plots, and in the non-exclosed, encroached plots. We detected only a limited signal of density-dependent mortality (Table 1, Fig. S5).

Patterns of mortality in the disturbed plots were broadly similar to those observed in intact vegetation. Mortality rates were markedly lower in all exclosed plots at the heath and meadow sites, but not at the shrubland site (Fig. 3), and mortality was largely independent of seedling density (Table 1, Fig. S9).

Seedling establishment

In the third year of the study, the composition of the established seedling assemblages in intact vegetation differed among sites but were broadly similar across treatments (Fig. 2). More seedlings remained at the heath and meadow sites, with a weakly supported tendency towards more seedlings in the exclosed plots. At the shrubland site few seedlings remained, especially in the exclosed, non-encroached plots. These trends remained similar after five years, although the tendency towards greater seedling numbers in exclosed plots at the heath and meadow sites became slightly stronger (Fig. 2).

Compared to the intact vegetation plots, the seedling assemblages of the disturbed plots in the third year of the study tended to be more similar across sites (Table 1, Fig. 3). Overall, a greater number of seedlings tended to occur in exclosed plots, especially at the meadow site. This pattern became even stronger after five years, when the seedling assemblages of all exclosed plot types were statistically different from those of the control plots, except the exclosed, non-encroached plots at the shrubland site (Fig. 3).

Discussion

In a five-year field study, we have demonstrated consistent positive effects of herbivore exclusion on the establishment of vascular-plant seedlings in both intact and experimentally disturbed alpine vegetation. The effect of herbivory on seedling establishment arose primarily

via reduced seedling mortality in plots from which herbivores had been experimentally excluded. In contrast, we detected no consistent effects of experimental shrub encroachment on seedling recruitment. The effect of herbivore exclusion became noticeably stronger over time, underlining the importance of long-term studies for understanding the dynamics of alpine plant communities subject to changes in the biotic and abiotic environment.

Strong effects of natural vegetation type and cover on seedling recruitment

Several observations support a strong impact of natural vegetation cover on seedling recruitment. First, seedling emergence in intact vegetation during the first growing season varied much more among sites (i.e. dominant vegetation types) than did emergence in disturbed plots. Second, these differences remained after four years of ‘filtering’ by extant vegetation and by abiotic conditions, suggesting a principal role of vegetation type and associated environmental variation in determining invasibility (Evju, Hagen, & Hofgaard, 2012). Third, across all vegetation types, a much greater number of seedlings emerged in disturbed subplots than in intact subplots. The latter finding adds to a growing literature suggesting strong effects of disturbances on seedling emergence and establishment (e.g. Klanderud et al., 2017; Lembrechts et al., 2016; Milbau et al., 2013; Tingstad, Olsen, Klanderud, Vandvik, & Ohlson, 2015). Interestingly, while emergence in intact vegetation tended to occur at a higher rate at the heath site than at the meadow and shrubland sites, the trend was opposite for plots from which vegetation had been removed (Figs. 2, 3). In other words, the effect of vegetation removal was stronger at the meadow and shrubland sites, suggesting that these vegetation types are less invasible (Marsman et al., 2020). The reduced emergence in disturbed gaps at the heath site compared to the meadow and shrubland sites could relate either to the harsh environment characterizing dwarf-shrub heaths (Cooper et al., 2004), or possibly to allelopathic effects of the dominant species *Empetrum nigrum* (González et al., 2015; Zackrisson & Nilsson, 1992). Notice though that the inverse pattern was observed for seeds sown into intact vegetation, suggesting that other factors more than outweigh any allelopathic effect of the local vegetation.

Reduced invasibility, as indicated by stronger vegetation-removal effects, at the meadow and shrubland sites compared to the heath site may relate to the dense understories characterizing these sites. At the meadow site, dense root systems could lead to intense belowground competition and lower seedling performance (Germino, Smith, & Resor, 2002; Loranger, Zotz, & Bader, 2017), yet the reduced mortality at the meadow suggests that the lack of gaps for emergence is probably the main limitation, as suggested by Gough (2006) for

tussock tundra. The competitive effect of aboveground vegetation is more obvious at the shrubland site, where emergence was low and mortality high in intact vegetation. Many studies have tried to link the harshness of the environment to the importance of gaps and microclimate for seedling recruitment. The ‘stress gradient hypothesis’ predicts that seedling recruitment under harsh climatic conditions is facilitated by surrounding vegetation through microclimatic buffering, whereas seedling recruitment in more benign microclimates is limited by competitive inter-specific interactions (Brooker et al., 2007; Callaway et al., 2002; Maestre, Callaway, Valladares, & Lortie, 2009). Most studies assessing seedling recruitment along assumed stress gradients have suggested that competition is the principal driver, while evidence for facilitative interactions is scarce (Graae et al., 2011; Milbau et al., 2013; but see Venn & Morgan 2009). Our results corroborate this view because we find far more emergent and a tendency for more surviving seedlings in the disturbed plots irrespective of harshness of the microclimate as indicated by vegetation types, although seedlings in disturbed plots may be more vulnerable during extreme weather events than those in more protected microsites (e.g. within vegetation).

Effects of herbivory on invasibility increase over time

Our herbivore exclusion treatment allowed us to study the impact of large and small mammalian herbivores on seedling recruitment. While we detected only limited effects of herbivore exclusion on first-year emergence, these effects became apparent when considering seedling survival during the two subsequent years at the heath and meadow sites, but not at the shrubland site. The differential mortality between exclosed and open plots led to differences in the seedling assemblages of these plot types in the third year of the study, and the effects became even clearer in the fifth year (Figs. 2, 3). Although we cannot ascertain the exact causes of mortality, several observations suggest that seedling mortality in open meadow and heath plots results from selective grazing rather than accidental trampling. First, sheep are important and abundant large herbivores in the study area and are generally thought to graze selectively. Indeed, three species known to be attractive to sheep (*A. flexuosa*, *A. nipponicum* and *S. virgaurea*; Rekdal, 2001) recruited more successfully within exclosures. Second, the positive effect of herbivore exclusion on seedling survival was stronger in disturbed plots, perhaps because seedlings on bare soil are easier to detect and thus more likely to be eaten. Because the experimental seeds were sown shortly after the exclosures were established, and changes in alpine vegetation are slow (Billings, 1987; Körner, 2003; Morris & Doak, 1998), we could not rule out any positive impacts of herbivores on

recruitment through competitive release from the standing vegetation, as Eskelinen and Virtanen (2005) have suggested for snowbed vegetation. Nevertheless, these results demonstrate a strong effect of herbivores on seedling recruitment, and that these effects become increasingly important over time. These findings add to the emerging consensus that herbivores play an important role in buffering environmental-change-induced changes to tundra vegetation (Eskelinen, Saccone, Spasojevic, & Virtanen, 2016; Kaarlejärvi et al., 2017; Kaarlejärvi, Hoset, & Olofsson, 2015; Munier, Hermanutz, Jacobs, & Lewis, 2010; Speed, Austrheim, Hester, Mysterud, & Ejrnaes, 2012), and are consistent with a recent meta-analysis suggesting that effects of global-change experiments such as ours escalate over time (Komatsu et al., 2019).

Because our herbivore exclosures excluded both large (sheep, reindeer) and small (rodents) herbivores, we cannot directly separate their effects. Previous work in tundra systems suggest that ungulates and rodents may have complementary effects (Ravolainen, Brathen, Yoccoz, Nguyen, & Ims, 2014) and that rodents may sometimes be the key herbivores affecting the vegetation dynamics in these systems (Nystuen et al., 2014; Olofsson, Hulme, Oksanen, & Suominen, 2004). However, the weaker herbivory effect at the shrubland site, where we expected rodents to be of greater importance than sheep, suggests that this is not necessarily a general pattern. These findings must also be interpreted in light of the reduced frequency of high rodent peaks in the study area, which may lead to dramatic changes in recruitment patterns (Nystuen et al. 2014).

Weak effects of experimental shrub encroachment

We detected no consistent positive or negative effect of willow introduction on seedling recruitment. Although recruitment patterns in plots receiving willow transplants differed from corresponding control plots in a few cases (Figs. 2, 3), these apparent effects were largely idiosyncratic and hard to explain as the outcome of willow-seedling interactions. For example, the apparent effect of willow introduction on seedling emergence at the shrubland site (where any effect of willow introduction at all is surprising) weakened over time, so that the willow-introduction plots became more similar to the controls (Fig. 3). It is also possible that the observed effect of willow introduction arose from disturbance associated with the planting of willows, rather than any effect of the introduced willows *per se*. We therefore conclude that the effect of willow introduction over the first five years of the experiment is at best weak and hard to predict. We suspect that the lack of detectable effects is related to investment in belowground biomass and slow above-ground growth of the introduced

willows, as also indicated by limited effects of the willow introduction on plot-level carbon cycling (Sørensen et al., 2018a) and pine seedling performance (Marsman et al., 2020) in parallel studies. We expect accelerated aboveground growth of the transplanted willows after 6-7 growing seasons (Hagen & Skrindo, 2010; Rytter, 2001).

Conclusions and implications for vegetation dynamics

Despite some heterogeneity in effects across sites, our results strongly suggest that herbivores play an important role in reducing the invasibility of alpine plant communities. This provides a clear example of an indirect effect of changes in climate and land-use on biotic community dynamics, because changes in herbivore communities are directly related to climate (e.g. rodent population dynamics) and human land-use (e.g. summer sheep grazing vs. wild ungulate harvesting regimes). One open question is how recruitment patterns such as those described in this study translate into long-term vegetation dynamics. For example, despite substantial recruitment, herbaceous plants are rare in alpine heath vegetation, suggesting strong biotic or abiotic filters acting at a later stage. However, it is unclear whether these patterns will prevail under novel climatic conditions in the future, such as the expected increases in temperature and changes in precipitation regimes.

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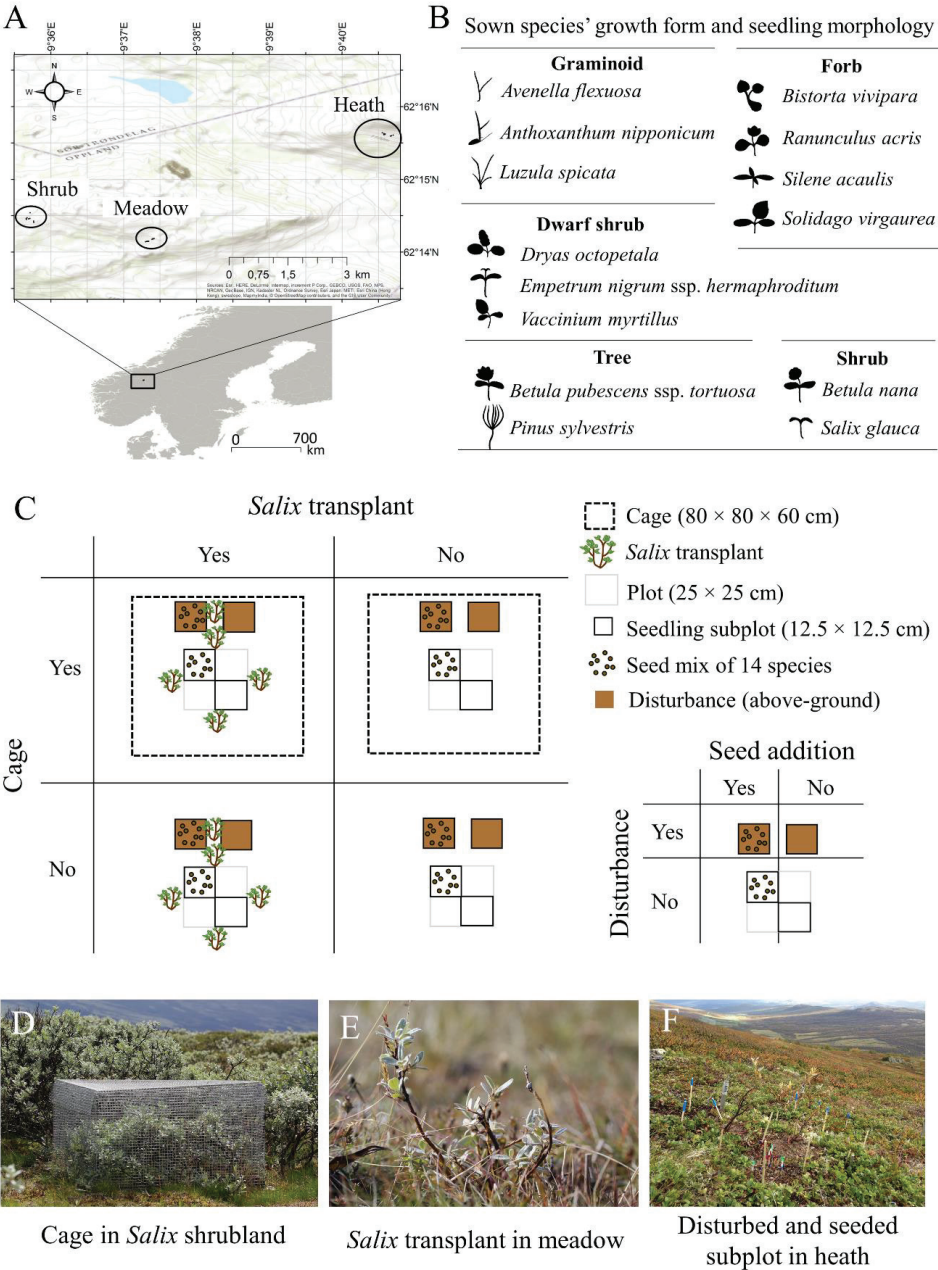
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Table 1. Variance partitioning for joint models of seedling emergence, mortality, and establishment in intact and disturbed plots. Variance components are given as percentages of the total explained variation (given by r^2). The parameter $N(t-1)$ is the number of seedlings in the focal plot in the previous year (i.e. density dependence).

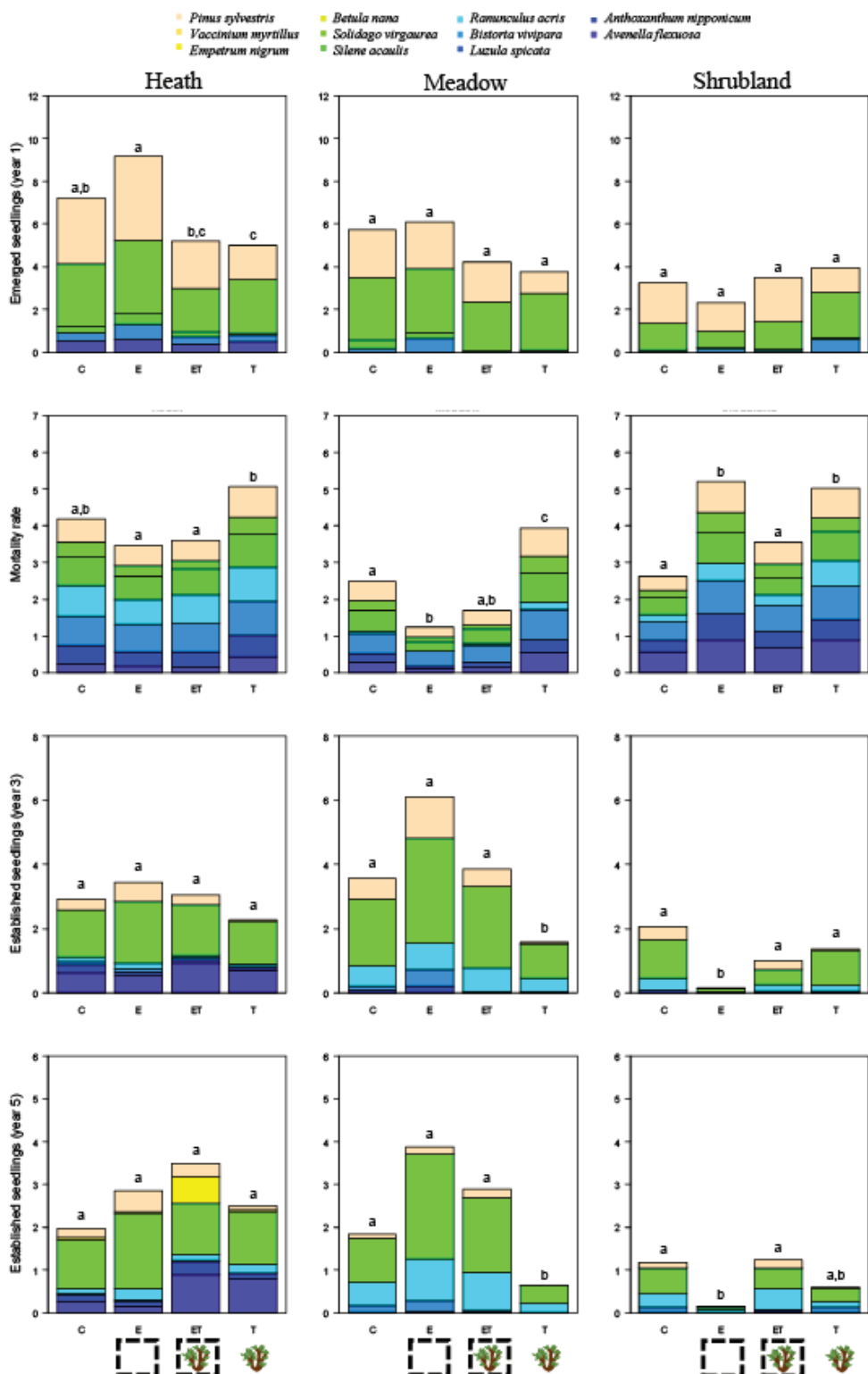
Model	Plot type	r^2	Fixed effects					Random effects		
			Environment	$N(t-1)$	Site	Treatment	Site \times Treatment	Year	Plot	Census
Emergence year 1										
	Intact	69%	21.0%		35.3%	4.8%	11.6%		27.3%	
	Disturbed	67%	25.8%		11.1%	7.4%	12.8%		42.9%	
Mortality year 2-3										
	Intact	75%	38.9%	5.4%	9.0%	11.5%	18.2%	4.4%	6.9%	5.7%
	Disturbed	70%	22.6%	3.0%	8.0%	14.4%	13.4%	7.5%	12.4%	18.7%
Establishment year 3										
	Intact	70%	25.8%		24.5%	5.5%	16.2%		28%	
	Disturbed	70%	24.7%		16.2%	4.8%	7.3%		46.9%	
Establishment year 5										
	Intact	68%	29.1%		36.2%	5.1%	10.9%		18.6%	
	Disturbed	67%	21.9%		17.4%	7.8%	12.8%		40.1%	

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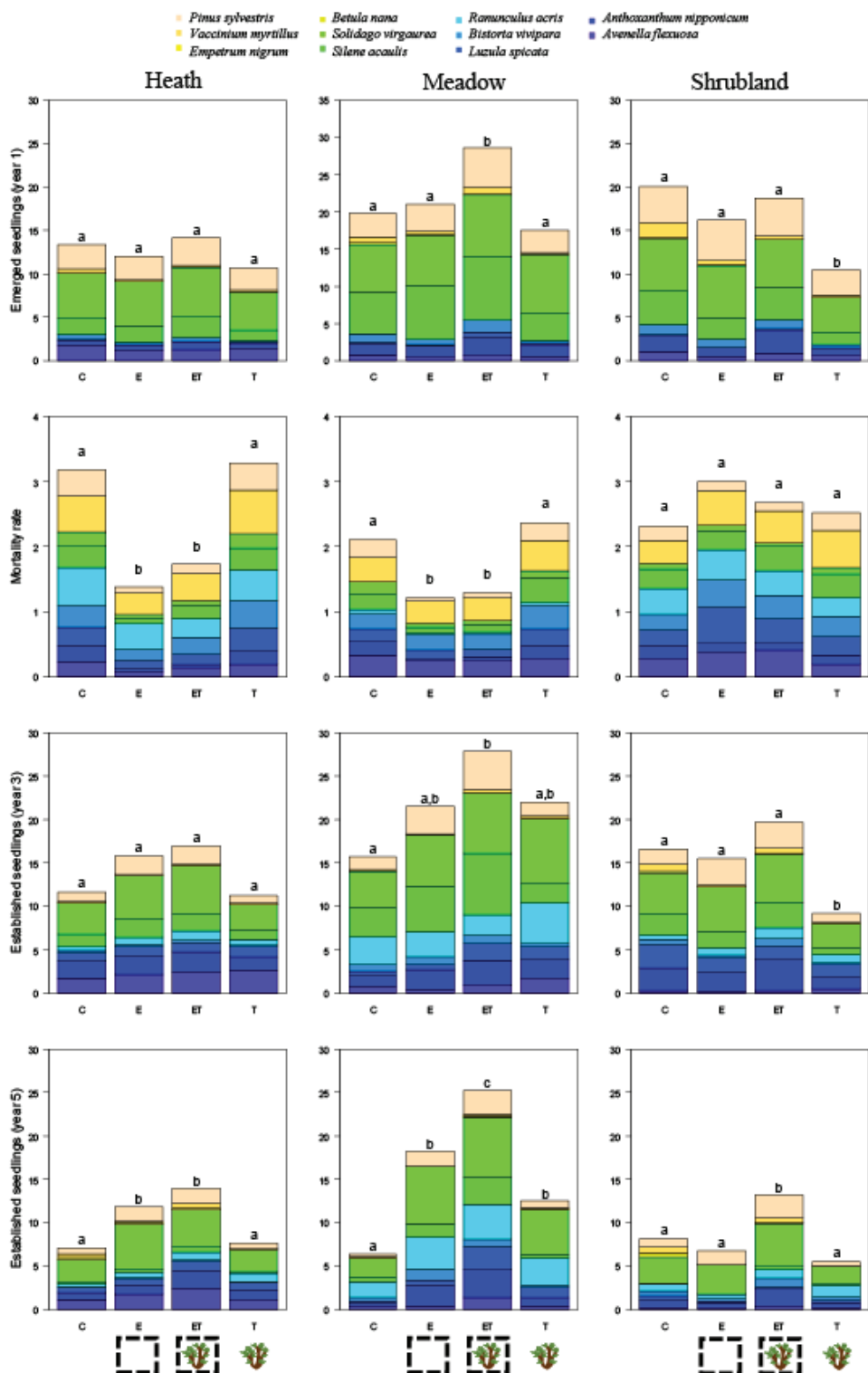


702
703 Figure 1. Graphical summary of the experiment. (A) Location of the study area and the three study
704 sites near Hjerkind, Dovrefjell, central Norway. (B) List of the 14 vascular plant species sown in the
705 seeding experiment and their growth forms. (C) Schematic representation of the factorial
706 experimental design with *Salix* transplants simulating shrub encroachment, cages excluding
707 vertebrate herbivores, disturbance eliminating above-ground competition from standing vegetation,
708 and seed addition. Treatments were replicated eight times at each of the three sites. We recorded
709 seedling emergence, survival and establishment over five years in the seedling subplots. Photos
710 show the plant communities and treatments: (D) a cage at the *Salix* shrubland site, (E) a *Salix*
711 transplant (c. 9 cm tall) at the meadow site two years after planting, and (F) a disturbed and seeded
712 subplot with plot and seedling markers at the heath site three years after sowing.



713

714 Figure 2. Effects of experimental treatments on seedling recruitment in intact vegetation.
 715 Treatments are C = control, E = herbivore exclusion, ET = herbivore exclusion + willow
 716 introduction, T = willow introduction. Different letters indicate >95% posterior support.



717

718 Figure 3. Effects of experimental treatments on seedling recruitment in disturbed vegetation
 719 (experimental gaps). Treatments are C = control, E = herbivore exclusion, ET = herbivore exclusion
 720 + willow introduction, T = willow introduction. Different letters indicate >95% posterior support.

Herbivores reduce the invasibility of alpine plant communities

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SUPPLEMENTARY MATERIALS

Table S1. Precipitation (mm) and temperature (°C) through the study period 2013 – 2018

Table S2. Summary of sites and vegetation

Table S3. *Salix* transplant survival (number of individuals) and height (mean \pm SE) in open and caged plots in 2017, three years after planting.

Table S4. Summary of MCMC sampling parameters.

Figure S1. Daily total precipitation (mm) and average air temperature (°C) through the study period 2013 – 2018.

Figure S2. Pearson correlations of temperature variables for (A) disturbed and (B) intact vegetation across years.

Figure S3. Seedlings alive in the seeded subplots (mean \pm SE percentage of sown seeds) in year one, two, three and five after sowing. Years are shown as the four successive bars in similar colour.

Appendix 1 (Fig. S4 - S11). Patterns of support for positive (red) and negative (blue) effects of microenvironmental variables, sites, treatments, and the site \times treatment interaction.

Table S1. Precipitation (mm) and temperature (°C) through the study period 2013 – 2018. Data are from the weather station Hjerkin II, 1012 m a.s.l., 62.221°N, 9.542°E, Norwegian Meteorological Institute, eklima.met.no. Temperatures are calculated based on daily means. The growing season is defined as the months June – September.

	2013	2014	2015	2016	2017	2018
Annual precipitation (mm)	365.1	439.8	662.7	659.3	595.1	468.3
Growing season precipitation (mm)	107.4	191.9	260.8	264.3	268.2	222.3
February temperature (°C)	-8.3 ± 0.9	-4.2 ± 0.7	-3.7 ± 0.6	-6.5 ± 0.5	-6.1 ± 1.0	-9.8 ± 0.9
July temperature (°C)	11.7 ± 0.4	14.1 ± 0.5	9.1 ± 0.6	10.1 ± 0.4	9.5 ± 0.4	14.3 ± 0.5

Table S2. Study site description based on Sørensen et al. (2017) and Sørensen et al. (2019).

	Heath	Meadow	Salix shrubland
Most abundant species (relative abundance %)	<i>Arctostaphylos uva-ursi</i> (31.7 %) <i>Empetrum nigrum</i> ssp. <i>hermaphroditum</i> (29.3 %) <i>Vaccinium vitis-idaea</i> (15.3 %) <i>Festuca ovina</i> (8.6 %) <i>Flavocetraria cucullata</i> (2.3 %) <i>Cladonia arbuscula/Cladonia mitis</i> (2.0 %) <i>Loiseleuria procumbens</i> (1.4 %) <i>Betula nana</i> (1.2 %) <i>Salix glauca</i> (introduced) (1.1 %)	<i>Avenella flexuosa</i> (11.4 %) <i>Festuca ovina</i> (9.5 %) <i>Anthoxanthum nipponicum</i> (7.3 %) <i>Barbilophozia lycopodioides</i> (7.2 %) <i>Deschampsia cespitosa</i> (5.3 %) <i>Stereocaulon alpinum</i> (5.1 %) <i>Thalictrum alpinum</i> (4.7 %) <i>Sanionia uncinata</i> (4.1 %) <i>Antennaria dioica</i> (3.5 %)	<i>Salix lapponum</i> (19.4 %) <i>Salix glauca</i> (13.1 %) <i>Pleurozium schreberi</i> (9.0 %) <i>Polytrichum commune</i> (8.9 %) <i>Avenella flexuosa</i> (8.0 %) <i>Hylocomium splendens</i> (7.8 %) <i>Festuca ovina</i> (5.3 %) <i>Cladonia arbuscula/Cladonia mitis</i> (2.6 %) <i>Carex bigelowii</i> (2.3 %)
Vegetation height (cm)	5.8 (SD = 2.4)	7.1 (SD = 3.5)	21.0 (SD = 13.7)
Latitude and longitude	62° 15' 37" N, 9° 40' 35" E	62° 14' 09" N, 9° 37' 21" E	62° 14' 29" N, 9° 35' 41" E
Elevation (m a.s.l.)	1135 – 1145	1152 – 1162	1188 – 1210
Snowmelt (range 2014 – 2016)	21. April – 2. May	14. – 19. May	19. May – 4. June
Snow depth (cm, average 2015-2017)	7.0 (SD = 3.0)	43.7 (SD = 5.1)	48.9 (SD = 8.9)
Soil profile	Podzolic	Podzolic	Podzolic
Sediments and bedrock	Moraine over metavolcanic rock	Moraine over shale	Moraine over metavolcanic rock
Soil pH (minimum)	3.5 (SD = 0.4)	4.4 (SD = 0.3)	3.5 (SD = 0.3)
Exposure	South	South-west	South

Note Species composition and vegetation height are based on point-intercept analyses (Goodall 1952) in each plot with 25 pins distributed across a 25 × 25 cm square at the peak of the growing season in 2014. We assigned only 1 hit per pin for cryptogam species, and 0.5 hits to species present in the plot, but not hit. Species abundances was calculated relative to the total number of vascular plant, lichen and bryophyte hits at each site. Snowmelt dates are when soil surface temperatures suddenly increased and started fluctuating. Sediment and bedrock data are retrieved from the Geological Survey of Norway (NGU 2017, Bedrock N250 and Sediments N50, Accessed September 2017. <http://geo.ngu.no/kart/kartkatalog/>). Minimum soil pH is from soil samples of all horizons down to bedrock or the BC horizon from six soil pits at the heath and meadow site, and five soil pits at the *Salix* shrubland site (see details in Sørensen et al. 2019).

Sørensen, M.V., Graae, B.J., Classen, A., Enquist, B.J. & Strimbeck, R. 2019. Drivers of C cycling in three arctic-alpine plant communities. *Arctic, Antarctic, and Alpine Research* 51: 128-147.

Sørensen, M.V., Strimbeck, R., Nystuen, K.O., Kapas, R.E., Enquist, B.J. & Graae, B.J. 2017. Draining the Pool? Carbon Storage and Fluxes in Three Alpine Plant Communities. *Ecosystems*.

Table S3. *Salix* transplant survival (number of individuals) and height (mean \pm SE) in open and caged plots in 2017, three years after planting. Height is measured at the tallest green leaf because it was difficult to know if branches without leaves were dead or alive.

	Heath	Meadow	<i>Salix</i> shrubland
Open plots			
Dead	11	11	7
Alive	29	29	33
Caged plots			
Dead	1	4	8
Alive	39	36	32
Height open plots (cm)	7.8 \pm 0.3	8.7 \pm 0.7	13.4 \pm 0.8
Height caged plots (cm)	11.2 \pm 0.5	12.4 \pm 0.7	17.4 \pm 0.9

Table S4. Summary of MCMC sampling parameters. Effective sample sizes and potential scale reduction factors (PSRF) are medians.

	Emergence year 1		Mortality year 2-3		Establishment year 3		Establishment year 5	
	Intact	Disturbed	Intact	Disturbed	Intact	Disturbed	Intact	Disturbed
Number of chains	2	2	2	2	2	2	2	2
Iterations per chain	30000	30000	30000	30000	30000	30000	30000	30000
Transient	10000	10000	10000	10000	10000	10000	10000	10000
Samples per chain	1000	1000	1000	1000	1000	1000	1000	1000
Total samples	2000	2000	2000	2000	2000	2000	2000	2000
Effective sample size								
Beta	1326.9	1121.6	1531.3	1456.5	724.4	872.8	695.0	885.4
Omega (Year)			2000.0	2000.0				
Omega (Plot)	707.7	610.1	1767.0	896.8	137.5	649.2	382.9	360.4
Omega (Census)			1891.7	899.3				
PSRF								
Beta	1.002	1.001	1.001	1.000	1.006	1.003	1.003	1.008
Omega (Year)			1.016	1.006				
Omega (Plot)	1.059	1.002	1.006	1.002	1.051	1.011	1.018	1.136
Omega (Census)			1.012	1.005				

Supplementary figures

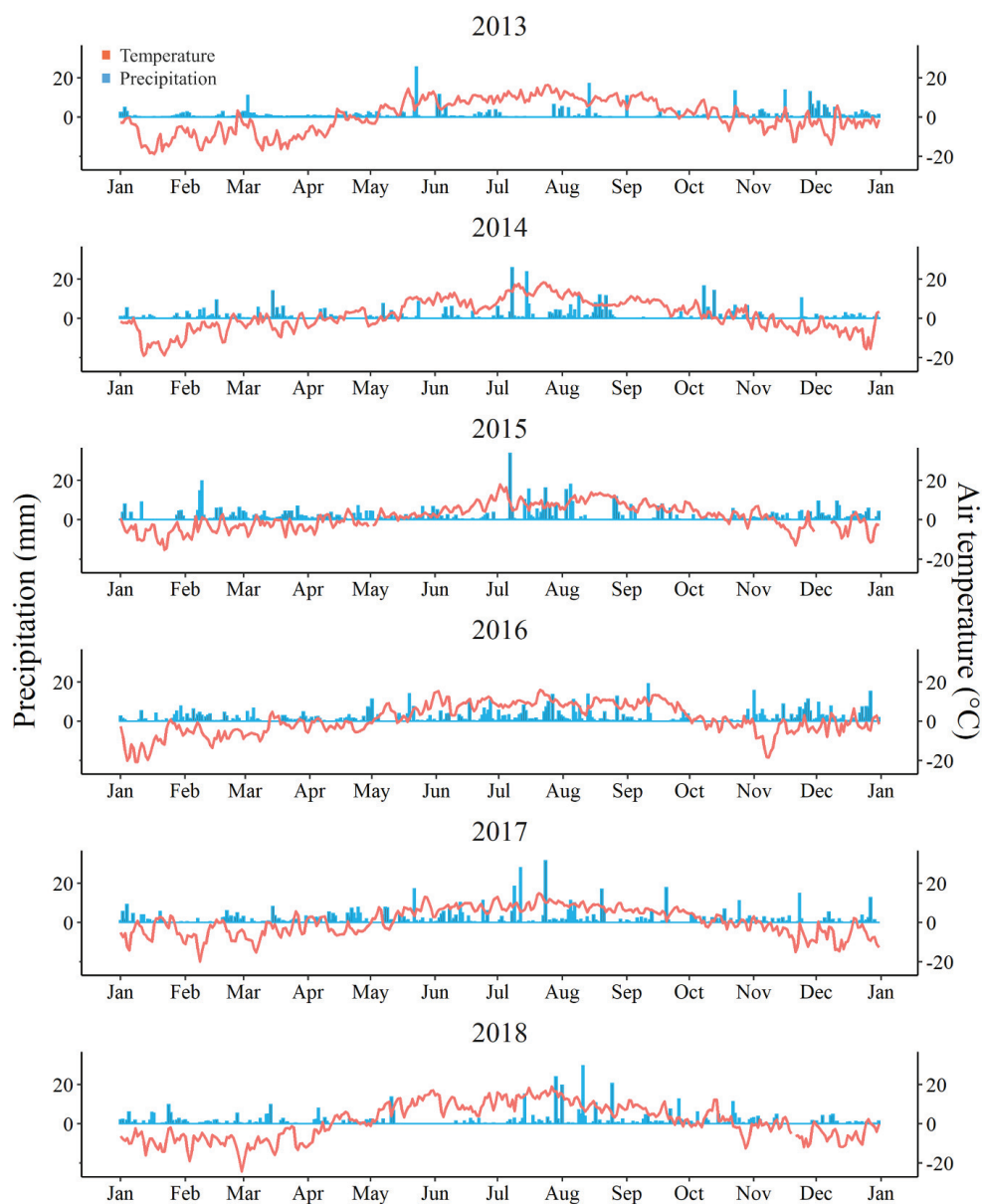
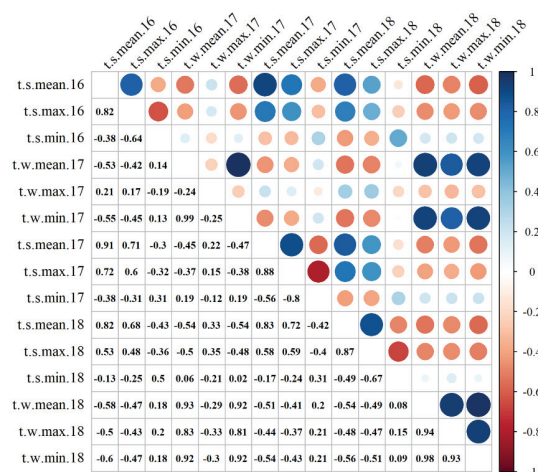


Figure S1. Daily total precipitation (mm) and average air temperature (°C) through the study period 2013 – 2018. Data are from the nearest weather station Hjerkin II, 1012 m a.s.l., 62.221°N, 9.542°E, 4 – 8 km from the study sites (Norwegian Meteorological Institute, eklima.met.no).

(A)



(B)

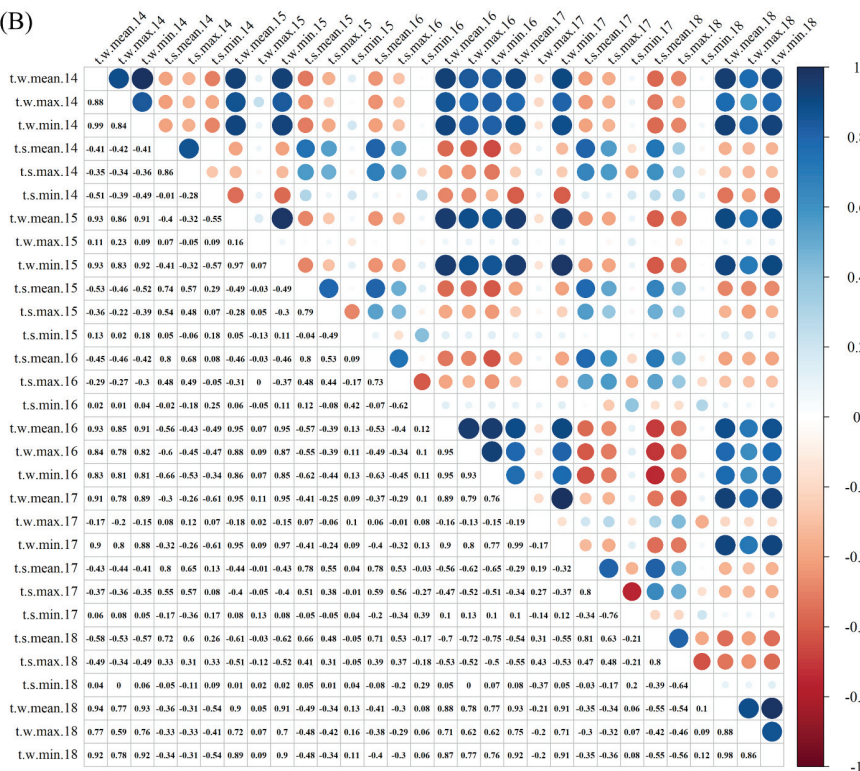


Figure S2. Pearson correlations of temperature variables for (A) disturbed and (B) intact vegetation across years. Temperatures were logged in intact vegetation from autumn 2013 onwards, and in disturbed vegetation from summer 2016 onwards. Numbers correspond to recording year, “w” to winter and “s” to summer.

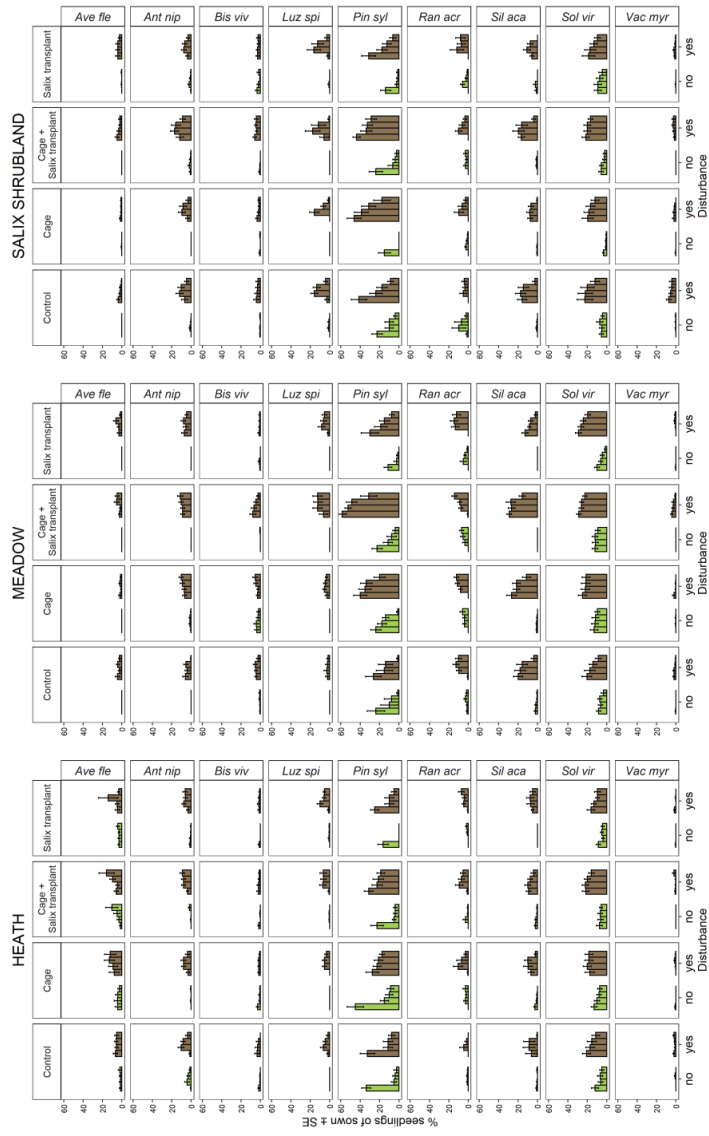


Figure S3. Seedlings alive in the seeded subplots (mean \pm SE percentage of sown seeds) in year one, two, three and five after sowing. Years are shown as the four successive bars in similar colour. Only nine of the 14 species are shown, as the other species failed or nearly failed to recruit.

Appendix 1: Posterior support for individual covariates

The following figures (Fig. S4 - S11) illustrate patterns of support for positive (red) and negative (blue) effects of microenvironmental variables, sites, treatments, and the site×treatment interaction. Treatment abbreviations are C = control, E = exclosure (cage), T = willow transplants, ET = exclosure + transplant. Parameters with at least 95% posterior support are shown.

Fig. S4. Emergence first year, intact plots

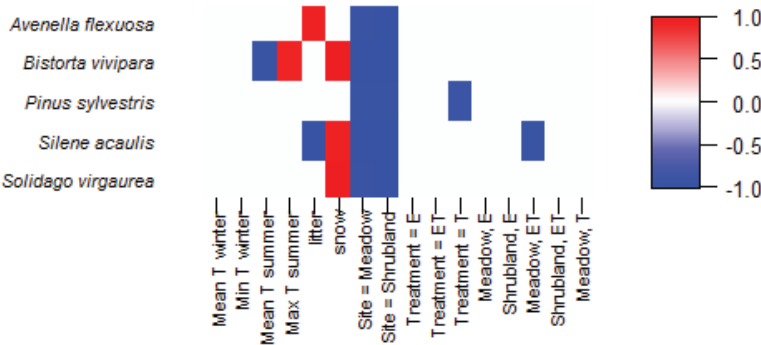


Fig. S5. Mortality year 2-3, intact plots

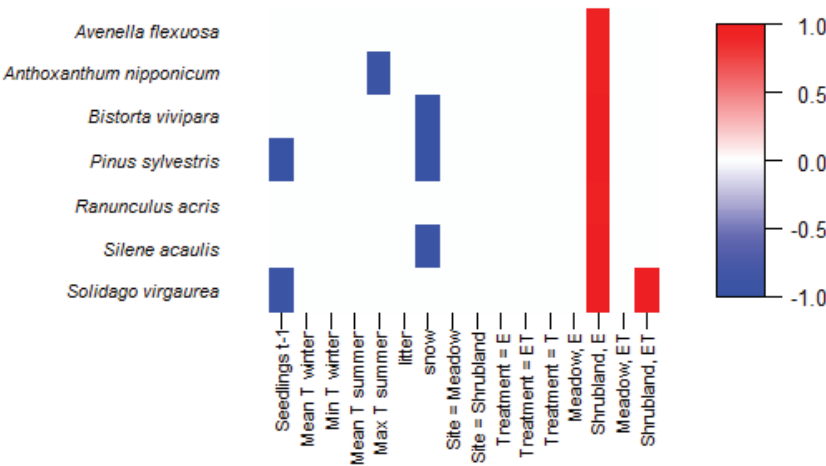


Fig. S6. Establishment year 3, intact plots

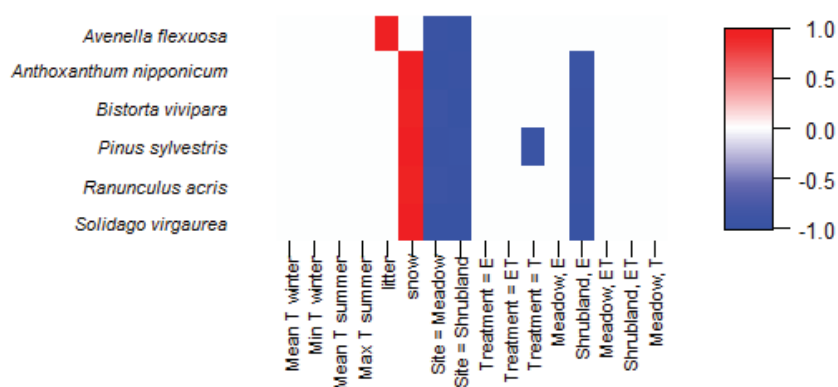


Fig. S7. Establishment year 5, intact plots

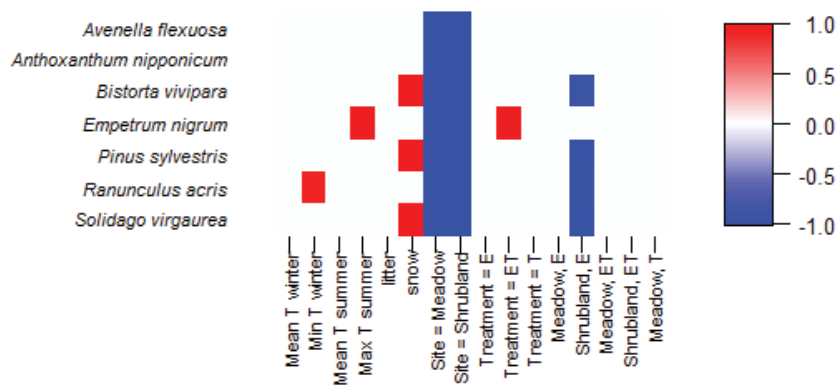


Fig. S8. Emergence first year, disturbed plots

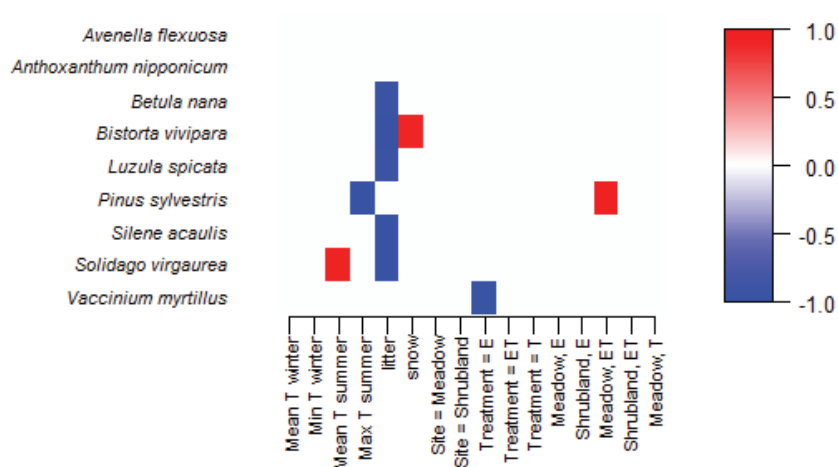


Fig. S9. Mortality year 2-3, disturbed plots

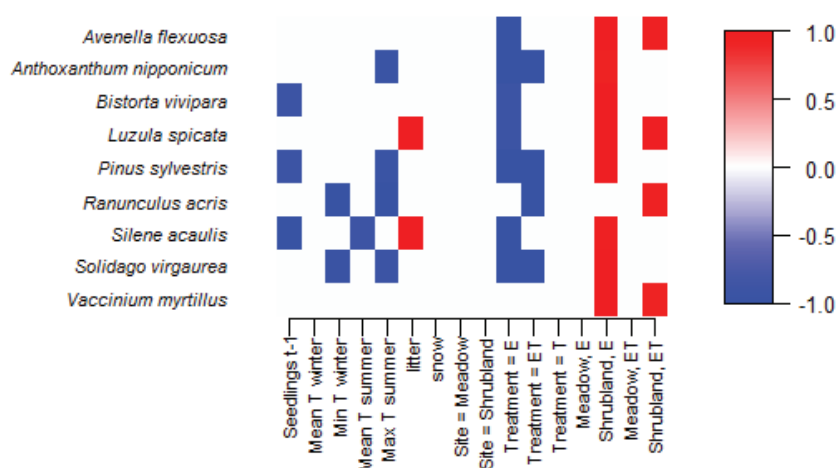


Fig. S10. Establishment year 3, disturbed plots

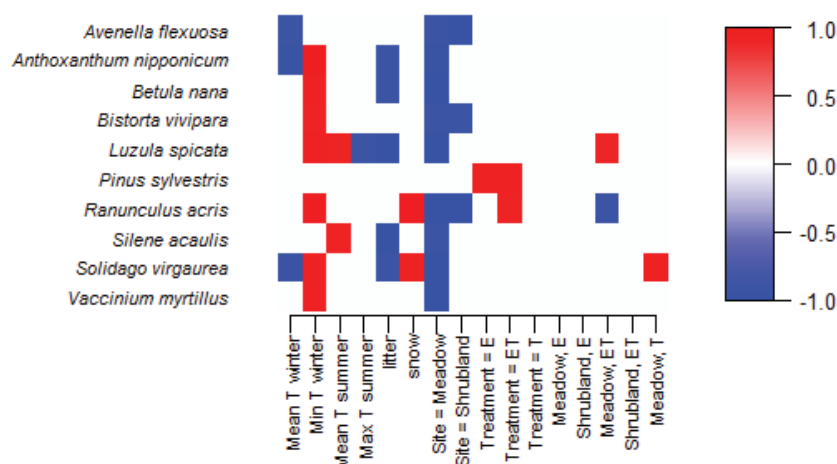
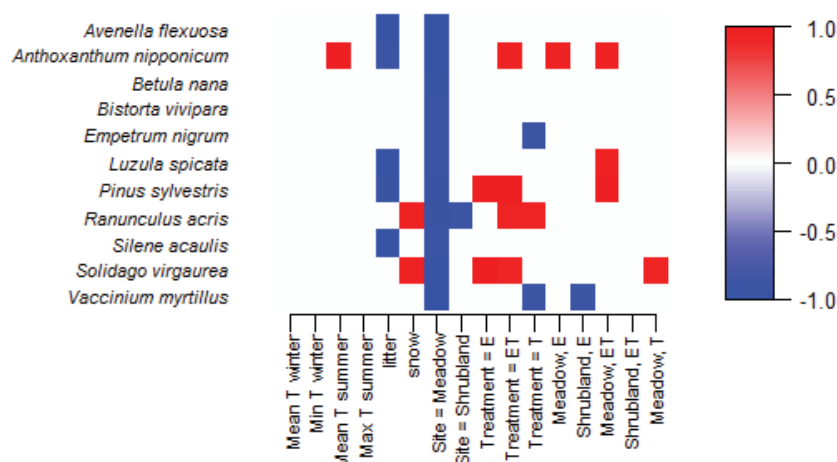


Fig. S11. Establishment year 5, disturbed plots



Paper III



A warm summer day at the *Salix* shrubland site

The effects of shrub cover and microenvironment on plant recruitment in alpine shrub-dominated vegetation

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Abstract

Canopy-forming shrubs in tundra strongly affect the composition and abundance of adult plant understories, but the filtering effect of shrub canopies on plant recruitment stages is less well understood. We asked how deciduous shrub canopies affect the understory microenvironment, and in turn seedling emergence, survival and establishment. We conducted a five-year field experiment in an alpine *Salix* shrub-dominated community in the mountains of Dovrefjell, Central Norway. Seeds of 14 different plant species were sown into disturbed gaps along a gradient in shrub cover, and seedling emergence and survival was recorded in late summer over the three first years, and final seedling establishment after five years. We found that our gradient in shrub cover mainly affected the microenvironment through small effects on light availability and soil surface temperatures in summer and winter. Soil surface temperature was most important for recruitment, and average summer and winter temperature had consistently positive and negative effects, respectively, on recruitment of many species. Many species emerged less successfully in plots where litter was abundant, and survived better at high light availability. The plant species responded uniquely to the shrub cover gradient and the associated variation in the microenvironment, resulting in a turnover in species composition of seedling communities from sparse to dense shrub canopies, with dense canopies favoring broadleaf forbs. Conditions associated with shrub-modified microenvironments, including increased leaf litterfall, low soil surface temperatures in summer, and high soil surface temperatures in winter, affected one or more of the studied recruitment phases negatively. Our results therefore demonstrate how the expansion of erect shrubs in tundra may have complex filtering effects on recruitment of understory plant species communities.

Keywords:

Abiotic, herbivory, competition, conifer, facilitation, filtering, graminoid, disturbance, regeneration, regrowth, seed germination, shrub expansion, snow depth, soil moisture, ontogenetic shift

Introduction

Canopy-forming deciduous shrubs have expanded into many tundra ecosystems over recent decades (Myers-Smith et al. 2011; Elmendorf et al. 2012; Scharnagl et al. 2019; García Criado et al. 2020). Erect shrub canopies alter the understory microenvironment and tend to support less dense and otherwise distinct understory plant communities compared to neighboring open and less dense shrub patches (Totland et al. 2004; Pajunen et al. 2011; Wallace & Baltzer 2019). However, the habitat affinities of mature plants do not necessarily correspond to the characteristics of ‘safe sites’ for plant recruitment (Schupp 1995; Körner 2003). Successful establishment of new individuals is a prerequisite for long-term plant presence and community changes. It is therefore important also to consider how plant recruitment is affected by shrubs and the microenvironments associated with them. Such knowledge would contribute to a better understanding of community dynamics in shrub-dominated arctic-alpine vegetation and help predict the rate of change and the future of arctic-alpine plant communities.

Shrubs in arctic-alpine ecosystems influence the understory microenvironment in many ways. Depending on their height, density and species, shrubs alter light availability (Totland et al. 2004; Bueno et al. 2016), accumulation of snow (Sturm et al. 2001) and litter (Shaver et al. 2001; Wallace & Baltzer 2019), soil moisture (Bueno et al. 2016; Wallace & Baltzer 2019) and soil temperature (Sturm et al. 2001; Holmgren et al. 2015; Chen et al. 2020). Shrub expansion and natural variation in shrub abundance across heterogeneous alpine landscapes thus create a range of microenvironments for recruiting plants. These microenvironments may exert different effects on the regenerative phases of seed germination, seedling emergence and seedling survival (Schupp 1995; Cranston & Hermanutz 2013; Körner & Hiltbrunner 2017; Lett & Dorrepaal 2018). Differences among species in their response to the microenvironment (Moles & Leishman 2008; Shevtsova et al. 2009) further complicate generalization about plant recruitment dynamics below shrub canopies.

Mesic shrub communities dominated by erect *Salix* shrubs are widespread (Hultén & Fries 1986) and functionally important components (Schickhoff et al. 2002) of arctic-alpine Fennoscandian vegetation (Myers-Smith 2011) that recently have increased in biomass, cover and abundance (Forbes et al. 2010; Hedenås et al. 2011; Myers-Smith 2011). High seedling emergence rates and seedling species richness within *Salix* communities suggest that they are highly invasible (Milbau et al. 2013), but long-term dynamics eventually depend on seedling survival. Interactions among shrubs and tree-seedling recruitment in tundra is well studied (e.g. Jumpponen et al. 1998; Cranston & Hermanutz 2013; Kambo & Danby 2018; Angulo et al. 2019; Chen et al. 2020). However, we are not aware of long-term studies monitoring recruitment of different plant functional groups in shrub-dominated tundra.

The microenvironment under *Salix* canopies may affect seedling recruitment and establishment both positively and negatively. In winter, a thick, stable snow cover results in alpine soil top layers with temperatures around or just below 0°C (Bueno et al. 2016). These relatively high temperatures can increase germination rates (Milbau et al. 2009), but may be harmful for young seedlings (Graae et al. 2011). In summer, increased shading from shrub canopies results in less available light and lower temperatures (Myers-Smith & Hik 2013),

which may on the one hand lower the seedlings' photosynthetic gain (Kitajima & Fenner 2000; Cranston & Hermanutz 2013), but on the other hand protect seedlings from potential desiccation and extreme temperatures (e.g. leading to low-temperature photoinhibition) (Ball et al. 1991; Germino & Smith 1999; Moles & Westoby 2004; Holmgren et al. 2015). The large amounts of leaf litter produced by the deciduous *Salix* species (Becklin et al. 2012) can further increase shading, as well as constituting a physical barrier for seedlings emerging below the litter layer, or for seeds germinating above the litter layer to reach the soil (Facelli & Pickett 1991; Dalling & Hubbell 2002). *Salix* leaf litter may also release allelopathic compounds that negatively affect plant nutrient acquisition (Becklin et al. 2012). The interactions between *Salix* shrub canopies and *adult* plants in terms of presence, abundance, and biomass range from positive to negative, depending on the species considered (Jumpponen et al. 1998; Totland & Esæte 2002; Totland et al. 2004; Pajunen et al. 2011). However, we know less about the interactions between *recruitment phases* and *Salix* shrub canopies with their associated microenvironments, including the assessment of which recruitment phases are subject to stronger environmental filtering.

Small-scale disturbance leading to competitor-free gaps within the vegetation increase recruitment of most species, as demonstrated experimentally several times in arctic-alpine vegetation (Eskelinen & Virtanen 2005; Gough 2006; Graae et al. 2011; Evju et al. 2012; Lembrechts et al. 2016). Small gaps favoring recruitment may occur due to herbivores (Dufour-Tremblay & Boudreau 2011; Nystuen et al. 2014), cryoturbation (Sutton et al. 2006; Frost et al. 2013), or other disturbances. Gaps provide competitive release from above-ground vegetation, as well as distinct microenvironments compared to the surrounding vegetation, often resulting in higher establishment success (Chambers 1995; Bullock 2000). For instance, in a seed addition study over a steep environmental gradient in dry tundra, only 0.9% percent of the seeds sown into intact vegetation emerged, in contrast to 12.8% in disturbed gaps (Graae et al. 2011). While the importance of small gaps for recruitment is well established, the mechanistic understanding of the environmental drivers of successful seedling recruitment in gaps is still limited.

In this study, we investigate how gradients in shrub cover and microenvironment affect seedling emergence, survival, and establishment by sowing 14 local plant species into experimental gaps in an heterogeneous alpine *Salix* shrubland community. Specifically we ask: (1) How does *Salix* shrub cover modify the microenvironment? (2) How are seedling emergence, survival, and establishment affected by the microenvironment and shrub cover, and does seedling response differ among species? and (3) How does seedling establishment vary along a gradient in shrub cover with and without associated variation in microclimate?

Methods

Study site

The study was conducted in a low-alpine *Salix* shrubland site at about 1200 m a.s.l. at Dovrefjell, Central Norway (Fig. 1a, b). Dovrefjell has a slightly continental climate, with short warm summers and long cold winters (vegetation section C1; Moen 1998). For the study years, 2013 – 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, 1012 a.s.l., 62.221°N, 9.542°E, Norwegian Meteorological Institute, eklima.met.no; see Appendix S1 for daily precipitation and average temperature over the study period). The site has a podzolic soil profile and is situated on a thick layer of till deposits from glacial moraines over metavolcanic bedrock (NGU 2017).

The shrubland site was dominated by the erect deciduous willows *Salix glauca* L. and *Salix lapponum* L. In addition to willows, the deciduous shrub *Betula nana* L. was present in the shrub canopy (less than 11% of the total shrub biomass). The understory was dominated by the graminoids *Avenella flexuosa* (L.) Drejer, *Festuca ovina* L. and *Carex bigelowii* Torr. ex Schwein. and the forbs *Solidago virgaurea* L., *Saussurea alpina* (L.) DC. and *Galium boreale* L. The ground layer differed among plots and comprised either lichens, bryophytes, or both. The lichens were mainly the reindeer lichens *Cladonia arbuscula* (Wallr.) Flot./*Cladonia mitis* Sandst. (here treated as a single morphospecies) and *Cladonia stellaris* (Opiz) Pouzar & Vezda, and the bryophytes *Pleurozium schreberi* (Willd. Ex Brid.) Mitt., *Polytrichum commune* Hedw. and *Hylocomium splendens* Hedw. Schimp.

The study site experiences low-intensity summer grazing and browsing by domestic sheep (NIBIO 2017). Voles (*Microtus agrestis*, *M. oeconomus* and *Myodes rufocanus*), lemmings (*Lemmus lemmus*), hare (*Lepus timidus*), ptarmigan (*Lagopus lagopus* and *L. muta*). Moose (*Alces alces*) are also present in the study area, and wild reindeer (*Rangifer tarandus*) occasionally pass through. The voles and lemmings exhibit cyclic population dynamics, with population build-ups in 2013 and 2017 resulting in low rodent peaks in 2014 and 2018 (Framstad 2019).

Experimental setup

The current study is part of a long-term study (established in 2013) of shrub expansion effects on alpine plant communities and carbon dynamics with experimental herbivore exclusion and willow introduction into the *Salix* shrubland site and two sites located within plant communities without a shrub canopy (Sørensen et al. 2018). At each site, we established 32 plots (25 × 25 cm), half of which were protected from herbivores by placing cages (80 × 80 × 60 cm) in summer 2013 (Appendix S2). In half of the caged and half of the open plots we planted five c. 10 cm tall *Salix* saplings (from a mixed cultivation of *Salix glauca* and *Salix lapponum* not determined to species) in spring 2014 to simulate shrub expansion (Sørensen et al. 2018). The willow introduction into the already shrub-covered *Salix* shrubland site acted as a control in the long-term study, and we did not expect this treatment to affect seedling recruitment at this site. We placed the 32 plots in the *Salix* shrubland in c. 40 cm tall shrub canopies so they would fit inside the cages. In each plot, we recorded deciduous shrub cover

in each plot as the total number of hits using the point intercept method (Goodall 1952), with 25 pins distributed across a 25×25 cm square. Records made at the peak of the growing season in 2014 and 2016, as well as early in the growing season in 2015, revealed a gradient in shrub canopy cover among plots (Fig 1, Table 1). In this study we explore patterns of plant recruitment along this gradient, focusing on the direct influence of shrub cover as well as indirect effects through shrub-cover related variation in microenvironmental variables. We also consider the effect of herbivore exclusion.

Seedling recruitment experiment

Approximately 15 cm outside the 25×25 cm plot, on each side of a *Salix* transplant, we established two “seedlings subplots” (12.5×12.5 cm) where all above-ground vegetation was cut at soil surface to mimic severe small-scale disturbance events (Appendix S2, Fig. 2). We placed the subplots adjacent to the plot to avoid interference with other measurements. One of the subplots served as a control for natural seedling emergence (Appendix S2). In the other subplot, we sowed seeds of 14 plant species (Fig. 2). The species were chosen to represent a range of growth forms, seed sizes and abundances in alpine and subalpine plant communities, and we thus expected their regeneration to be affected differently by shrub cover and the microenvironment. For example, six of the sown species (*D. octopetala*, *E. nigrum* ssp. *hermaphroditum*, *S. acaulis*, *L. spicata*, *B. pubescens* and *P. sylvestris*) are not present as mature individuals in the *Salix* shrubland, and we expected these species to recruit less successfully. Moreover, the species have easily distinguishable seedlings.

We collected seeds within a 9 km radius of the study sites when they matured during autumn 2013. The seeds were stored in paper bags at room temperature, except the fleshy fruits of *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium myrtillus* which were stored for seven days in a refrigerator at 5°C and then gently squashed in a bowl of water to separate seeds and fruit flesh. Seeds of *Pinus sylvestris* were supplied by The Norwegian Forest Seed Center, with origin from Oppdal at c. 600–650 m a.s.l., c. 40 km north of the study site.

We sowed a mixture of 30 seeds each of the 14 focal plant species into one disturbed subplot within each plot in late autumn 2013. For *Pinus sylvestris* we used only 10 seeds because of known high germination capacity (82%) and large seedling size, while only 15 seeds were used for *Salix glauca* due to limited seed availability. Both the *Betula nana* and *Betula pubescens* ssp. *tortuosa* seeds were sown in spring 2014 because the adultplants’ fruits matured after the other seeds were sown. We wanted the *Betula* sp. seeds to experience similar conditions as the other seeds, and they were therefore kept under the snow at Kongsvold (c. 8 km from the study site) during winter. This resulted in a total of 385 seeds sown per subplot and a seed density of 2.5 seeds per cm². This density is higher than the expected natural seed rain in alpine vegetation (Molau & Larsson 2000; Graae et al. 2011) and was chosen to increase the probability of successful seedling emergence. We placed a c. 20 cm tall cardboard frame around the subplots before sowing to shelter from wind and avoid spilling of seeds (see Eskelinen & Virtanen 2005). We sprayed the subplots with water after the seeds were sown to avoid them being blown away when removing the cardboard shelter.

We recorded seedling emergence in all subplots between August 25 and September 12, 2014. We determined each seedling to species and put a toothpick adjacent to them for

markup. For each subplot, we drew a map with seedling positions to ease identification in later years. We resurveyed the subplots for seedling survival and for newly emerged seedlings in July 2015 and August 2016. The toothpicks were removed after the 2016 survey. In August 2018, seedlings still alive were counted.

Microenvironmental data

Light intensity (photosynthetically active radiation – PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured three times, in August and September 2016 and in August 2018 under diffuse conditions, with a LI-190S quantum sensor (LI-COR Inc., Lincoln, Nebraska, USA). In each plot, we first measured light intensity above the shrub canopy, and then as close to the ground as possible in the disturbed gap under similar sun conditions. We then computed light availability for seedlings as percent difference in PAR above the canopy and below the understory (Table 1).

Soil moisture (% volumetric soil water content) at 5 cm depth was measured with a hand-held soil moisture probe (TRIME-PICO, IMKO GmbH, Ettlingen, Germany) with one measurement in the disturbed control subplot. We measured moisture in all subplots on days with stable and dry weather: August 10 and September 9, 2016, and on July 24, 2018.

We visually estimated the percent cover of litter and vegetative regrowth (i.e. recolonization of lichens, bryophytes and vascular plants) for each subplot during the seedling censuses.

We measured snow depth with avalanche probes in 2015 (March 14), 2016 (April 2) and 2017 (March 11), as the mean of four repeated measures per plot. We used a handheld GPS receiver (3 m precision) to locate plots if cages or marking sticks were not visible.

Temperature sensors (Micro-T DS1921G, Maxim Integrated Products, Sunnyvale, California) continuously logged soil surface temperatures ($^{\circ}\text{C}$ at *c.* 1 cm depth) at four-hour intervals. We logged temperatures from summer 2016 and onwards. We extracted absolute minimum and maximum temperatures and computed mean temperature for summer (July and August) and winter (January and February) as explanatory variables.

Statistical analyses

Hierarchical joint modelling of seedling emergence, survival and establishment

We analysed the structure and dynamics of each seeded, disturbed subplot using Bayesian latent-variable joint species distribution models (Hierarchical Modelling of Species Communities framework; Ovaskainen et al. 2017), implemented in the Hmsc 3.0 R package (Tikhonov et al. 2020). This approach allowed us to model the effects of shrub cover and microenvironmental variables on the dynamics of all species jointly, while accounting for the non-independence of seeds sown into the same subplot.

First, we explored the effect of shrub cover (number of *Salix* spp. including *Salix* transplants and *B. nana* hits in the point intercept analyses) on microenvironmental variables (Table 1) over the study's first three years. We fitted a normally-distributed Hmsc model with microenvironmental variables as response matrix, shrub cover as fixed effect, and plot, year and census (plot-year combination) as random (latent) effects.

To identify the effects of shrub cover and microenvironmental variables on seedling emergence, survival and establishment following disturbance and seeding, we fitted a total of

four “seedling recruitment” Hmsc models (one for first year emergence, one for second year emergence, one for survival, and one for establishment). In each model, we excluded rare species occurring less than 8 times in the response matrix. Four species were excluded from all analyses because they failed or nearly failed to emerge (*B. pubescens* ssp. *tortuosa*, *E. nigrum* ssp. *hermaphroditum*, *D. octopetala* and *S. glauca*). However, *D. octopetala* and *S. glauca* germinated in growth chambers in a study with seeds from the same source as this study (Nystuen et al. 2019). To account for the study design, we included herbivore exclusion (caged vs. open) as fixed effect in addition to shrub cover and the microenvironmental variables.

First, we modelled the effects of shrub cover, microenvironment, and herbivore exclusion on seedling emergence during the first year. *Ranunculus acris* germinated primarily in the second year and was therefore not included. We included plot as random variable to account for the non-independence of seeds sown into the same plot.

Similarly, we modelled seedling emergence during the second year, while accounting for the seeds already germinated during the first year. We included plot as a random effect, and only the five species with considerable emergence. We did not model seedling emergence in the third year because of few emergent seedlings (Table 2).

For seedling survival, we modelled survival rates between the first and second and the second and third census year. We also included the total abundance of seedlings (of all species) the previous year (year $t-1$) as a fixed effect to account for density-dependent seedling survival. Plot, year and census (plot-year combination) were random effects.

For seedling establishment in the final census year, five years after sowing, we included all seedlings alive at census time. We therefore refer to seedling establishment as seedling emergence and survival until the final census year, independently of age class.

All seedling recruitment models were fitted with a probit link function, and we thus modelled rates of emergence, survival, and establishment. We ran 2 independent MCMC chains of 30000 iterations with the first 10000 discarded as burn-in, and a thinning interval of 20 iterations. We assessed model convergence qualitatively by investigation of posterior trace plots, and quantitatively by computing effective sample sizes and potential scale reduction factors (Appendix S3). We computed the explanatory power of the seedling recruitment models as the squared correlation coefficient (r^2) between the observed and predicted seedling abundances in each plot. To assess the extent of overfitting, we performed 4-fold cross-validation where we sequentially obtained predictions for $\frac{1}{4}$ of the plots based on a model trained on data from the remaining $\frac{3}{4}$ of the plots (Table 3).

For the seedling recruitment models, we evaluated the relative effects of shrub cover and each microenvironmental variable based on the posterior mean parameter estimates and each variable’s contribution to the explained variance (Ovaskainen et al. 2017). Although cross-validation suggested some overfitting for most models (Table 4), we decided to keep all variables in the models so that we could directly compare the effects across recruitment phases. We therefore focus on the variation explained by the models rather than making predictions outside the observed parameter space.

Three temperature sensors were lost during our study, one in 2017 and two in 2018. We replaced missing values with mean temperatures from the remaining plots, as Hmsc does not handle missing predictor values.

Established seedling communities along a shrub cover gradient

We used the parameters of the seedling establishment model to predict seedling communities along a gradient of increasing shrub cover in two ways. First, to assess the net effect of shrub cover and associated variation in microenvironment, we let the microenvironmental variables vary according to their observed correlation with shrub cover along the gradient. Second, to assess the marginal (independent) effect of shrub cover, the microenvironmental variables were set to their mean value.

Results

Salix shrub canopies modify light availability and soil surface temperatures

The understories of more densely shrub-covered plots tended to be darker (i.e. had less available light), less cold in winter, and colder in summer (i.e. had lower average and maximum temperatures; Fig. 2, Table 4), whereas the remaining aspects of the microenvironment assessed were not detectably affected by shrub cover (Table 4, Appendix S4).

Seedling emergence depends mainly on litter cover and soil surface temperatures

Eight species emerged at a substantial rate (mean = 12.0%, range = 3.0 – 40.0%) in the first year following seed sowing (Table 2). *Ranunculus acris* germinated primarily in the second year. No species emerged at a rate of more than 1.6% in the third year (Table 2). A total of 1051 seedlings emerged over the three first years, with 636 seedlings the first year, 367 the second and 48 the third year. Over the same period, 111 seedlings of the focal species emerged spontaneously in the disturbed control subplots without sowing, of which 63 were *Luzula* spp. and 14 *R. acris* (Appendix S5). For the other focal species, spontaneous emergence totaled less than eight seedlings over the three years.

For first-year seedling emergence, the Hmsc model explained 72.9% (mean r^2 over species) of the overall variation (Table 3). The largest proportions of variance were explained by litter cover (15.1%) and by soil temperatures (14.2%; Fig. 4a). Shrub cover alone explained on average only 2.2% of the variance, and *S. virgaurea* was the only species detectably affected with more seedlings emerging below the densest shrub canopies. All species but one emerged at a greater rate in plots with nearly no litter. Soil temperatures were important for emergence of most species (Fig. 4a). Average summer temperatures had consistent positive effects on emergence while average winter temperatures had negative effects. The remaining microenvironmental variables each explained 4% or less of the variance in emergence patterns, but still affected certain species (Fig. 4a).

For second-year seedling emergence, the Hmsc model explained 86.1% of the overall variation (Table 3). Soil surface temperatures and cover of vegetative regrowth from the neighboring vegetation explained the greatest proportions of variance (Appendix S6). Effects of soil temperatures on emergence were similar to those observed in the first year. Cover of vegetative regrowth from neighboring vegetation favored emergence of most species. Emergence of *R. acris* and *L. spicata* was favored by shrub cover (Appendix S6).

Seedling survival depends mainly on soil surface temperatures and light availability

Seedling survival during the second and third year of the study varied among species (mean = 70%, range = 40 – 93%), but the rate of survival for each species was generally similar in the second and third year. Exceptions were *A. flexuosa* and *B. vivipara* that survived better the second year and *L. spicata* that survived better the first year (Table 2).

The seedling survival model explained 56.2% of the overall variation (Table 3), and soil surface temperatures explained the largest proportions of variance (11%; Fig. 4b). Shrub cover did not explain much variance, but seedlings of four species were more likely to survive under dense shrub canopies (*A. flexuosa*, *A. nipponicum*, *L. spicata* and *P. sylvestris*:

Fig. 4b). In winter, three species were more likely to survive in the on average coldest plots with sub-zero temperatures (*A. flexuosa*, *A. nipponicum* and *P. sylvestris*). Five species were more likely to survive in plots with high light availability (*A. nipponicum*, *L. spicata*, *P. sylvestris*, *S. virgaurea* and *V. myrtillus*). The remaining microenvironmental variables each contributed to less than 2.5% of the variance in seedling survival, but still affected certain species (Fig. 4b).

Seedling establishment depends mainly on soil surface temperatures

The established sown seedling communities five years after sowing comprised a total of 369 seedlings of 10 species. Establishment rates varied among species (mean = 4.8%, range = 1.2 – 15.3%) and *P. sylvestris* and *S. virgaurea* established most successfully (Table 2).

The seedling establishment model explained 78.7% of the overall variation (Table 3). Soil surface temperatures (22%) and litter cover (10.2%) explained the largest proportions of variance (Fig. 4c). The rate of establishment increased along the 3.5°C gradient in mean summer temperature. In winter, establishment success of five species (*A. flexuosa*, *A. nipponicum*, *L. spicata* and *V. myrtillus*) was highest in the on average coldest plots. Litter suppressed establishment of four species (*A. nipponicum*, *P. sylvestris*, *S. acaulis* and *S. virgaurea*). Three species established more successfully below dense shrub canopies (*A. nipponicum*, *R. acris* and *S. acaulis*). The remaining microenvironmental variables also affected establishment of many species (Fig. 4c).

Established seedling communities along a gradient of shrub cover: some species win, most lose or are unaffected

The total number of established seedlings was similar along the gradient in shrub cover when including associated variation in the microenvironment (Fig. 5a, net effect). Considering each plant species separately, however, the net effect of shrub cover ranged from positive to negative (Fig. 5b, Appendix S7). Establishment of two species (*R. acris* and *S. virgaurea*) was clearly favoured by increasing shrub cover, while establishment of six species (*A. flexuosa*, *B. nana*, *B. vivipara*, *L. spicata*, *P. sylvestris*, and *V. myrtillus*) was slightly disfavoured (Fig. 5b, Appendix S7). The species-specific responses led to distinct predicted seedling communities at opposite ends of the shrub cover gradient, although these predictions were associated with considerable uncertainty (Fig. 5c).

The total number of seedlings tended to be higher below the densest shrubs when assessing the isolated shrub effect with microenvironmental variables set to their mean value (Fig. 5d, marginal effect). Most species exhibited different trends for the net and marginal effect of shrub cover (Fig 5b, e), suggesting that the overall effect of shrub cover may be driven as much by indirect effects associated with modification of the microenvironment.

Trends were similar for open and caged plots (Fig. 5, Appendix S8), with the exception of more *P. sylvestris* and *S. virgaurea* seedlings, and fewer *L. spicata* seedlings in cages. This suggests that the impact of herbivory on seedling recruitment is modest at this site.

Discussion

Our study of seedling recruitment into experimental disturbed gaps below short-statured alpine *Salix* shrub canopies has shown that shrub cover affects the composition of established seedling communities after five years. We also demonstrated that the microenvironment is important for recruiting seedlings, but only a few important aspects of the microenvironment covaried consistently with shrub cover. Soil surface temperatures emerged as a key predictor of recruitment success for most species. Recruitment was favored by warm average temperatures in summer and disfavored by warm average temperatures in winter. The importance of other microenvironmental variables depended on the recruitment phase and species in question, suggesting species-specific drivers that can in turn explain the overall turnover in established seedling communities along the shrub-cover gradient.

Minor impacts of erect, short-statured shrub canopies on the microenvironment

Variation in *Salix* shrub canopy density had only minor effects on the understory microenvironment. We did not detect the expected relationship between shrub cover and litter cover (Table 3), even though canopy-forming deciduous shrubs are known to contribute substantial amounts of litterfall in shrub-dominated communities (Becklin et al. 2012; Wallace & Baltzer 2019). In our study, litter input from species other than shrubs probably interfered with this relationship. In winter, the mean soil temperatures below the densest shrub canopies increased to above freezing which can be significant for seed and seedling fates. The lack of strong microenvironmental modification by the canopy could be caused by the relatively short-statured (c. 40 cm tall) *Salix* shrubs at our study site. Other factors not accounted for may also have counteracted the expected patterns. Shading from the thick and dense cryptogam layer surrounding the disturbed subplots could have buffered the shrub canopy effects. Other studies have found substantial differences in microenvironments below shrub canopies compared to measurements in either adjacent shrub-free plots (Totland & Esaete 2002; Totland et al. 2004; Myers-Smith & Hik 2013; Wallace & Baltzer 2019) or above canopies (Williams et al. 2014) but did not investigate changes along canopy cover gradients as we did here. In one of the few gradient studies similar to ours, Sturm et al. (2001) demonstrated increased snow trapping by the tallest and densest canopies along a gradient. An extended gradient including taller and denser canopies in more sheltered tundra locations (e.g. in depressions and along rivers and streams) would be likely to reveal greater microenvironmental variation than detected in this study.

Soil surface temperatures are important for seedling recruitment in alpine shrub-dominated vegetation

Soil surface temperature emerged as an important microenvironmental variable for the recruitment phases in our alpine *Salix* shrub-dominated community. The effect of increasing temperature along the 3.5°C gradient in mean summer temperature was consistently positive, and many species emerged and established more successfully in the warmest plots. Even though responses often are species-specific (Shevtsova et al. 2009), tundra warming experiments report higher germination in warmer conditions (Hobbie & Chapin III 1998;

Munier et al. 2010), but also that the positive effect of warmer temperature may be counteracted by higher mortality later in the growing season (Milbau et al. 2017). This did not seem to be the case in our study, as the warmest plots contained more living seedlings of most species at the end of the first growing season. Buffering of extreme temperatures by the shrub canopy is one possible explanation for this finding. However, in the second growing season, two species emerged less successfully in plots with high maximum temperatures (*R. acris* and *V. myrtillus*), and *R. acris* emergence appeared to benefit from the presence of a shrub canopy. Emerging seedlings with less developed root systems are sensitive to weather conditions, and during the ~ 6 day long period in mid-July 2015 with daily temperature averages around 20°C and no rain (Appendix S1), many newly emerged seedlings in the most exposed plots probably died. This is further supported by the more successful *R. acris* emergence under dense shrubs buffering high temperatures. Our results add to studies demonstrating that interannual variation in climate (Jaroszynska 2019) as well as the species' susceptibility to the microenvironment (Shevtsova et al. 2009) are important for recruitment success.

Seedling emergence, survival and establishment of some species increased under cold (sub-zero) average winter soil temperatures. Graae et al. (2008) found that more seeds were attacked by fungi when stratified under relatively high temperatures. Fungal attacks may be more frequent in warm winter conditions (Graae et al. 2011) and could have increased seed and seedling mortality in our study as well. Another reason could be the higher plant-associated winter respiration below thick snow where soils are warmer (Nobrega & Grogan 2007). Seedlings may have died because of increased maintenance respiration resulting in depleted carbohydrate reserves in the plots experiencing the warmest winter conditions (Ögren 1997). Even though not relevant for all species, above-freezing soil surface temperatures in winter seem to disfavor recruitment of certain plants in *Salix*-dominated tundra.

Litter complicates seedling emergence

Litter, ranging in cover from 3 – 100%, had consistent negative effects on seedling emergence for all but one species, survival of one, and establishment of four species. Litter is indeed known to hamper seedling emergence (Galvánek & Lepš 2012), whereas outcomes for later recruitment phases are species-dependent and mixed (Goldberg & Werner 1983; Facelli & Pickett 1991; Sayer 2006; Eckstein et al. 2011). In our study, the seeds were sown on newly exposed soil in late autumn, and the litter must thus have accumulated on top of the seeds. High litter cover often coincides with a thick litter layer. Failure of emerging seedlings to penetrate the litter layer, or germination failure due to reduced light availability below the litter layer, might have resulted in fewer successful emergences in litter-covered subplots (Donath & Eckstein 2010). *Avenella flexuosa*, the only species where seedling emergence was unaffected and not constrained by litter, might benefit from its thin and long graminoid cotyledons, which are good at penetrating litter (Sydes & Grime 1981). Our results suggest that litter below alpine shrub canopies act as an emergence filter on most species.

Light availability promotes seedling survival in shrub-dominated vegetation

Two species emerged less successfully in high-light understories, yet five species survived better under these conditions. In the most shaded subplots only 11% of the light measured above the canopy reached the seedlings, as opposed to 68% in the lightest plots (Table 1). For *V. myrtillus*, our results are in line with those of Eriksson and Fröborg (1996), who found that seedling survival increased along a gradient from forest to moist, open bog. Two graminoids (*A. nipponicum*, *L. spicata*) and a forb (*S. virgaurea*) that occur mostly in open habitats as adults, as well as the shade-intolerant conifer *P. sylvestris*, survived better in plots with high light availability. Our results indicate a positive effect of light availability on seedling survival in shrub-dominated alpine tundra, and that shrub densification resulting in less available light may therefore be detrimental for seedling survival of some species.

Broadleaf forbs win while many other species recruit less successfully under dense shrub canopies

Given that disturbances are present in the understory, our study shows that recruitment success of certain plant species depends on the density of the shrub canopy. Furthermore, the effects of the microenvironment on seedling recruitment discussed above suggest that variation in shrub cover not only affects seedlings directly, but also indirectly through shrub-related variation in the microenvironment (see also Blonder et al. 2018; Kitagawa et al. 2020). Despite apparent facilitative effects of shrub canopies in isolation on recruitment (Fig. 4 and Fig. 5: marginal effect), only *R. acris* and *S. virgaurea* established more successfully below the densest canopies when considering the predicted joint effect of shrub cover and associated environmental variation (Fig 5b: net effect). Also, the facilitative effect of shrubs on *A. nipponicum* survival and establishment seem to be limited compared to the effects of colder average summer temperatures, warmer average winter temperatures and less light with increasing shrub cover. Similar trade-offs when recruiting under shrubs in tundra is commonly reported in trees experiencing reduced growth, but better survival, under shrubs (Castro et al. 2004; Grau et al. 2012; Kambo & Danby 2018).

The two forbs that benefitted from emerging under the densest shrub covers have relatively high specific leaf area expected to be advantageous under shaded conditions, but less so in exposed conditions (Dahlgren et al. 2006). Because broadleaf seedlings have the whole leaf surface towards the sun, they are more exposed to high leaf temperatures during the day and radiative heat loss during cold nights, as well as wind damage (Brodersen et al. 2019). Shrub canopies cool the air and soil, reduce wind speed and can also increase nutrient accumulation (Holmgren et al. 2015; Chen et al. 2020). The shrub-facilitated forb-seedling emergence in our study can help explain why forbs are generally successful below *Salix* shrub canopies in tundra, as indicated by comparatively high presence and cover (Pajunen et al. 2011).

Six species established less successfully under the most dense shrub canopies (*A. flexuosa*, *B. nana*, *B. vivipara*, *L. spicata*, *P. sylvestris* and *V. myrtillus*), and one species (*S. acaulis*) established at a very low rate along the shrub cover gradient. Three of these species are not present as adults in the *Salix* shrubland (*L. spicata*, *P. sylvestris* and *S. acaulis*), but also species abundant as mature plants in the standing vegetation established less successfully

under dense canopies (*A. flexuosa*, *B. nana* and *B. vivipara*). Thus, densification and infilling of shrub-free patches within shrub-dominated communities, reducing light availability and temperatures and increasing litter inputs, can make it harder for even locally abundant plants to recruit. This underlines the contrasting requirements of the recruitment phase and the adult phase of plants (Schupp 1995; Angulo et al. 2019; Malfasi & Cannone 2020). Additionally, dense shrub canopies may limit plant recruitment through increased below-ground root competition (Holmgren et al. 2015; Mudrák et al. 2016).

One key finding of our study is that the critical microenvironmental factors varied among different recruitment stages (see also Cranston & Hermanutz 2013). For instance, *Silene acaulis* is a forb growing in dense cushions adapted to open and windy tundra habitats and is evidently capable of emerging but experienced high mortality below *Salix* shrub canopies (Graae et al. 2011). Expansion of shrub-dominated communities may therefore decrease the area suitable for successful establishment of typical tundra species and increase the area suitable for recruitment of shade-adapted, boreal species (Dona & Galen 2007; Wallace & Baltzer 2019; Kitagawa et al. 2020). Still, even for shade-adapted species, the shrub facilitation seems to cease when the shrub cover gets too dense (Liang et al. 2016; Kambo & Danby 2018).

More *P. sylvestris* and *S. virgaurea* seedlings established under shrubs when protected from vertebrate herbivores. Seedlings below shrub canopies are less accessible to trampling and consumption by large herbivores (Castro et al. 2004; Grau et al. 2013), but on the other hand more easily accessible for small rodents that hide from predators and spend more time feeding under canopies. We observed disturbances from voles and lemmings in the study's second (2014) and fifth year (2018) when they peaked in abundance (Framstad 2019). *Pinus sylvestris* and *S. virgaurea*, with their big seeds and seedlings (Nystuen et al. 2019), are evidently especially prone to herbivory (cf. the observations in forests of Royo & Carson 2008). Thus, how shrubs affect the spatial variation in vertebrate herbivory also interacts with plant recruitment in shrub-dominated tundra.

In conclusion, dense shrub canopies may limit or promote seedling recruitment through many different mechanisms, depending on the recruiting species. In particular, higher amounts of litter, lowered soil surface temperatures in summer and higher soil surface temperatures in winter tend to reduce seedling establishment success through negative effects on at least one of the studied recruitment phases. Obtaining a mechanistic understanding of the main factors filtering seedling establishment under shrub canopies thus requires more experimental studies or larger and longer-term observational studies.

Tables

Table 1. Shrub cover and microenvironmental variable means, standard deviations and ranges for the 32 subplots.

Variable		Period	Mean	SD	Range
Shrub cover (# hits)		2014	25.5	14.4	2.0 – 58.0
		2015	23.5	10.0	4.0 – 44.5
		2016	25.4	12.7	6.0 – 60.5
		All years	24.8	10.8	4.5 – 51.0
Temperature (°C)	Summer mean	2016	8.7	0.6	7.6 – 9.8
		2017	8.6	0.7	7.4 – 10.2
		2018	13.2	1.1	11.4 – 15.4
		All years	10.7	0.8	8.1 – 11.5
	Summer min	2016	2.7	0.9	0.0 – 4.0
		2017	2.7	1.0	0.0 – 4.0
		2018	5.1	0.9	2.5 – 6.5
		All years	3.4	0.8	1.3 – 4.7
	Summer max	2016	16.4	2.7	12.5 – 23.0
		2017	18.9	4.3	13.5 – 33.5
		2018	25.9	5.0	22.0 – 41.5
		All years	20.2	3.3	15.8 – 28.5
	Winter mean	2017	-0.2	0.6	-2.1 – 0.5
		2018	0.1	0.4	-1.8 – 0.5
		All years	-0.1	0.5	-2.1 – 0.5
	Winter min	2017	-1.5	1.2	-5.0 – 0.0
		2018	-0.5	0.7	-2.5 – 0.5
		All years	-1.1	1.0	-5.0 – 0.0
Snow depth (cm)		2015	49.7	17.4	24.0 – 94.0
		2016	47.2	6.7	38.0 – 64.0
		2017	49.7	8.8	28.0 – 75.0
		All years	48.9	9.0	37.3 – 75.3
Light availability (%)		Aug 2016	30.5	16.3	4.8 – 66.1
		Sep 2016	41.5	19.2	12.1 – 80.1
		2018	31.0	14.8	3.1 – 74.0
		All years	34.3	13.0	8.7 – 55.9
Soil moisture (%)		Aug 2016	26.5	6.6	18.2 – 53.0
		Sep 2016	22.7	8.5	9.7 – 48.5
		Jul 2018	20.2	5.9	12.9 – 36.3
		All years	23.1	5.9	15.6 – 44.1
Litter cover (%)		2014	31.5	25.9	3.0 – 95.0
		2015	52.0	23.5	5.0 – 100.0
		2016	47.0	27.4	10.0 – 95.0
		All years	43.5	18.6	11.0 – 83.3
Regrowth cover (%)		2014	24.0	19.3	0.0 – 90.0
		2015	27.0	17.3	3.0 – 60.0
		2016	37.5	24.1	0.0 – 85.0
		All years	29.3	14.4	6.0 – 60.0

Table 2. Seedling emergence, survival and establishment percentages (mean \pm SE) for the 14 focal plant species in the seed sowing experiment.

Plant species	Emergence (%)			Survival (%)		Establishment (%)
	Year 1	Year 2	Year 3	Year 1-2	Year 2-3	Year 5
<i>Avenella flexuosa</i> (L.) Drejer	3.5 \pm 0.8	0.6 \pm 0.3	0.1 \pm 0.1	50.0 \pm 10.0	84.0 \pm 9.0	1.5 \pm 0.4
<i>Anthoxanthum nipponicum</i> Honda	6.5 \pm 1.4	6.2 \pm 1.1	1.1 \pm 0.7	88.0 \pm 6.0	76.0 \pm 7.0	5.0 \pm 1.1
<i>Betula nana</i> L.	0.6 \pm 0.4	0	0.4 \pm 0.3	50.0 \pm 29.0	0	1.2 \pm 0.6
<i>Betula pubescens</i> ssp. <i>tortuosa</i> (Ledeb.) Nyman	0	0	0			0
<i>Bistorta vivipara</i> (L.) Delarbre	4.0 \pm 0.9	0.7 \pm 0.3	0.5 \pm 0.3	57.0 \pm 10.0	78.0 \pm 9.0	2.7 \pm 0.8
<i>Dryas octopetala</i> L.	0.1 \pm 0.1	0	0	100.0	0	0
<i>Empetrum nigrum</i> ssp. <i>hermaphroditum</i> (Hagerup) Böcher	0	0	0			0
<i>Luzula spicata</i> (L.) DC.	2.6 \pm 1.3	11.0 \pm 2.2	0.9 \pm 0.5	91.0 \pm 6.0	56.0 \pm 7.0	2.3 \pm 0.8
<i>Pinus sylvestris</i> L.	40.0 \pm 3.4	0	0	67.0 \pm 5.0	81.0 \pm 5.0	15.3 \pm 3.1
<i>Ranunculus acris</i> L.	0	8.2 \pm 2.3	0.2 \pm 0.2		40.0 \pm 9.0	4.6 \pm 1.5
<i>Silene acaulis</i> (L.) Jacq.	11.0 \pm 18.0	7.5 \pm 1.7	1.6 \pm 0.6	57.0 \pm 8.0	64.0 \pm 7.0	1.7 \pm 0.8
<i>Salix glauca</i> L.	0	0	0			0
<i>Solidago virgaurea</i> L.	20.0 \pm 2.9	0.6 \pm 0.3	0.6 \pm 0.3	93.0 \pm 2.0	91.0 \pm 3.0	12.6 \pm 1.8
<i>Vaccinium myrtillus</i> L.	2.9 \pm 0.8	1.0 \pm 0.4	0.6 \pm 0.4		52.0 \pm 12.0	1.8 \pm 0.7

Table 3. The plant recruitment models' explanatory power (r^2) and predictive power from 4-fold cross-validation (r^2_{cv}) for plant species.

Species	Emergence year 1 r^2 (r^2_{cv})	Emergence year 2 r^2 (r^2_{cv})	Survival year 2 and 3 r^2 (r^2_{cv})	Establishment year 5 r^2 (r^2_{cv})
<i>Avenella flexuosa</i>	0.46 (0.01)		0.67 (0.05)	0.76 (0.29)
<i>Anthoxanthum nipponicum</i>	0.89 (0.02)	0.85 (0.00)	0.47 (0.02)	0.74 (0.21)
<i>Betula nana</i>				0.91 (0.01)
<i>Bistorta vivipara</i>	0.86 (0.24)		0.50 (0.03)	0.73 (0.00)
<i>Luzula spicata</i>	0.97 (0.12)	0.86 (0.07)	0.50 (0.01)	0.61 (0.03)
<i>Pinus sylvestris</i>	0.29 (0.00)		0.42 (0.06)	0.76 (0.20)
<i>Ranunculus acris</i>		0.93 (0.37)	0.73 (0.36)	0.79 (0.11)
<i>Silene acaulis</i>	0.78 (0.00)	0.94 (0.00)	0.87 (0.18)	0.74 (0.03)
<i>Solidago virgaurea</i>	0.93 (0.06)		0.47 (0.03)	0.92 (0.01)
<i>Vaccinium myrtillus</i>	0.71 (0.00)	0.71 (0.04)	0.44 (0.00)	0.91 (0.01)

Table 4. Parameter estimates and variance partitioning for effects of shrub cover (number of shrub hits in point-intercept analysis) on microenvironmental variables. r^2 is explanatory power, r^2_{CV} is predictive power as evaluated by 4-fold cross-validation over plots. Estimates with at least 90% posterior support are in bold.

Microenvironmental variable	Estimate (95% CI)	r^2	r^2_{CV}	Fixed effect (%)	Random effects (%)			Un-explained
				Shrub cover	Plot	Year	Census	
Temp winter mean (°C)	0.006 (-0.002, 0.013)	85.9	0.0	4.0	79.0	1.2	1.7	14.1
Temp winter min (°C)	-0.001 (-0.012, 0.009)	99.2	2.1	0.6	97.5	0.3	0.8	0.8
Temp summer mean (°C)	-0.01 (-0.022, 0.002)	85.9	40.4	2.9	8.5	34.8	39.7	14.1
Temp summer max (°C)	-0.033 (-0.076, 0.008)	99.0	23.2	2.3	0.8	16.8	79.0	1.0
Temp summer min (°C)	0.005 (-0.008, 0.018)	69.2	3.6	1.9	46.6	16.3	4.4	30.8
Light availability (%)	-0.072 (-0.203, 0.020)	15.9	0.2	11.4	1.6	1.2	1.7	84.1
Soil moisture (%)	-0.001 (-0.014, 0.012)	100.0	13.7	0.0	100.0	0.0	0.0	0.0
Litter cover (%)	-0.04 (-0.160, 0.073)	0.4	16.0	0.3	0.0	0.0	0.0	99.6
Regrowth cover (%)	-0.033 (-0.132, 0.055)	4.3	10.5	2.5	0.6	0.7	0.5	95.7
Snow depth (cm)	-0.009 (-0.106, 0.087)	19.4	8.0	5.0	12.2	0.8	1.4	80.6

Figures

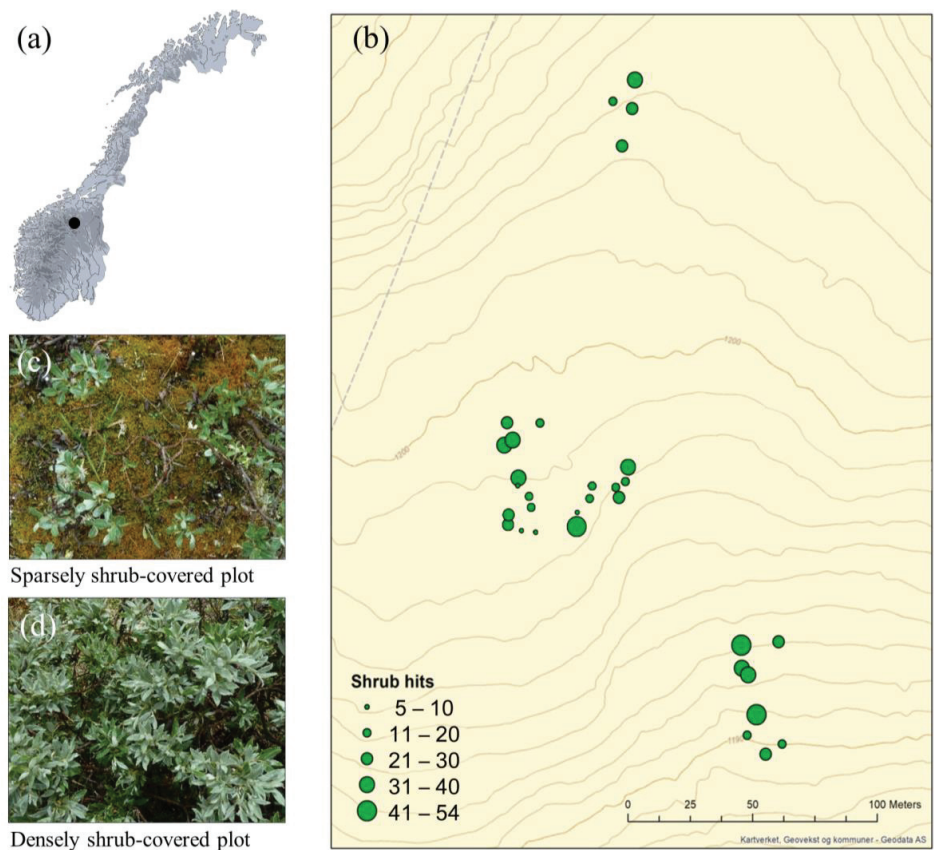


Figure 1. Study site information with (a) the study area’s location in Norway, (b) location and shrub cover (mean number of hits in point intercept vegetation analysis) of the 32 plots and photographs of a (c) sparsely (5 hits on average) and (d) densely shrub-covered plot (54 hits on average).

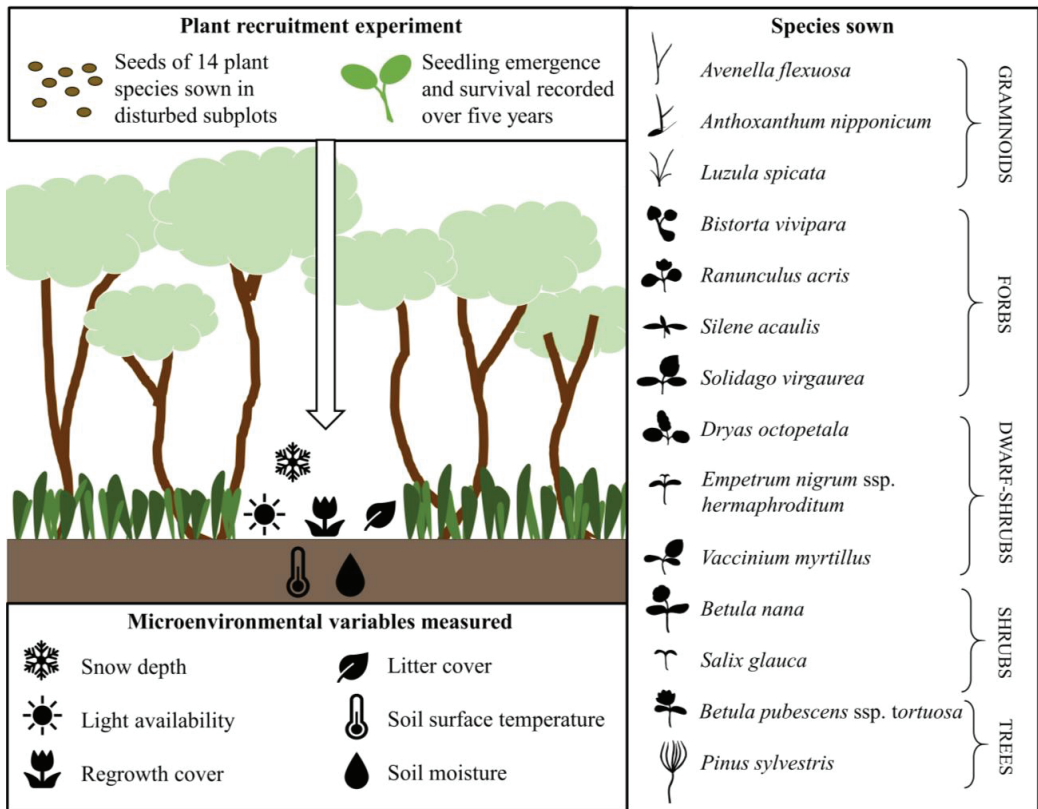


Figure 2. Schematic representation of the experimental design in the *Salix* shrubland with a shrub-covered plot with a 12.5×12.5 cm disturbed subplot into which we sowed a seed mix of 14 plant species and recorded seedling emergence, survival and establishment over 5 years, as well as a set of microenvironmental variables hypothesized to affect seedling recruitment.

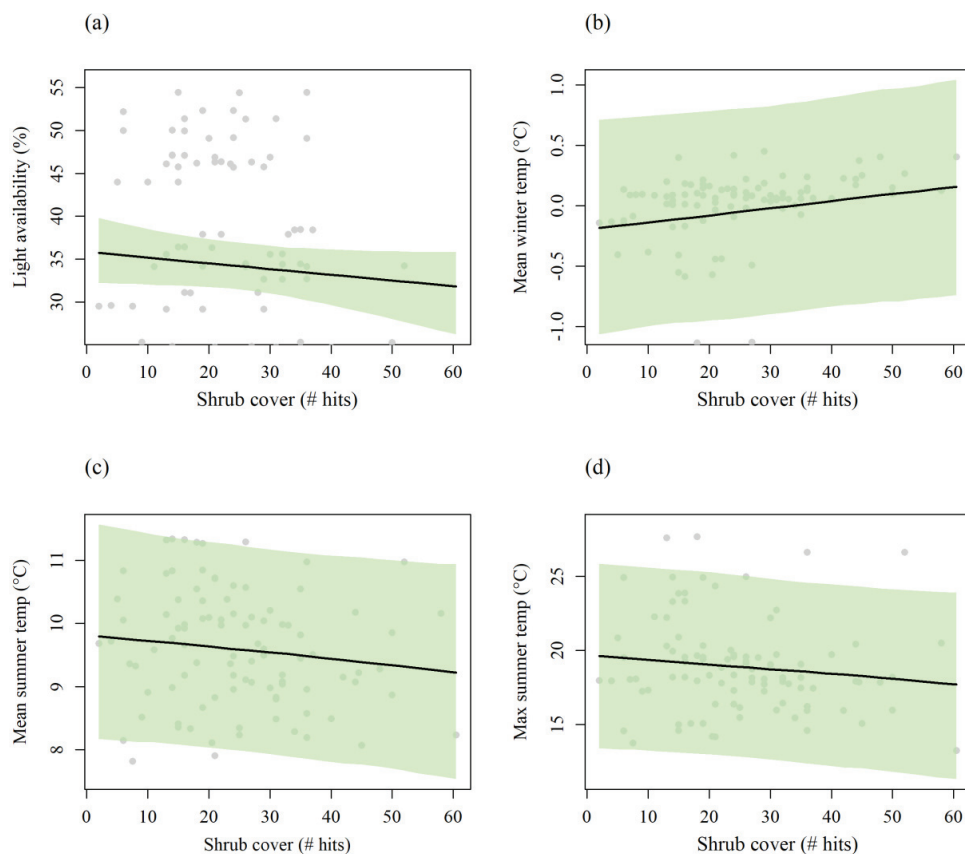
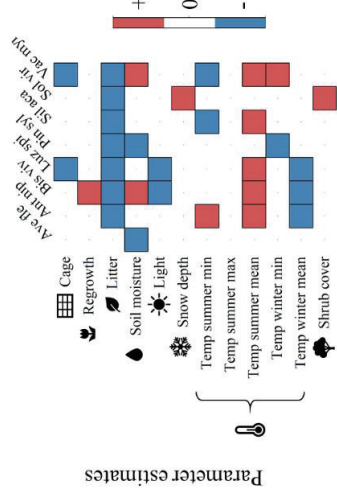
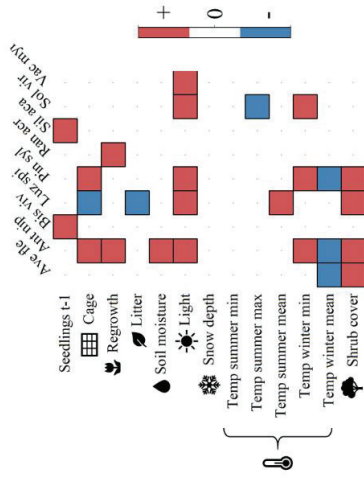


Figure 3. Predicted effects of shrub canopy cover (# hits from point intercept vegetation analysis) with 95% credible intervals on (a) light availability and soil surface temperatures for (b) means in winter, (c) means in summer and (d) maximums in summer in disturbed subplots ($n = 32$) over three years.

(a) Seedling emergence



(b) Seedling survival



(c) Seedling establishment

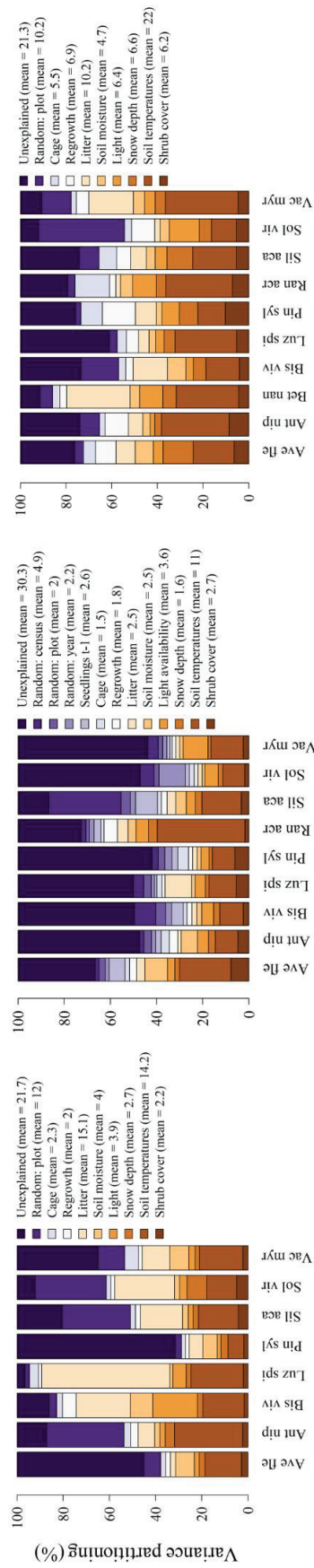
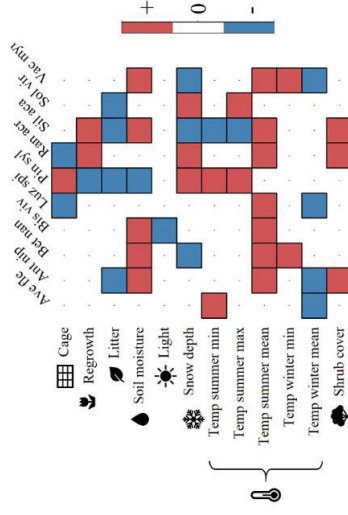


Figure 4. Summary of Hmsc results for each plant species for first-year seedling emergence (top), seedling survival (middle) and seedling establishment (bottom) with variance partitioning of fixed (i.e. shrub cover and microenvironmental variables) and random effects (lower panels), and parameter estimates visualized as negative (blue) or positive (red) effects of microenvironmental variables on the recruitment phases (upper panels). For visual clarity parameters with less than 90% posterior support are set to zero. The random variable plot ($n = 32$) is included in variance partitioning of all models, while only the survival model – with data over two years – have year ($n = 2$) and census ($n = 64$; plot and year combinations) as additional random variable.

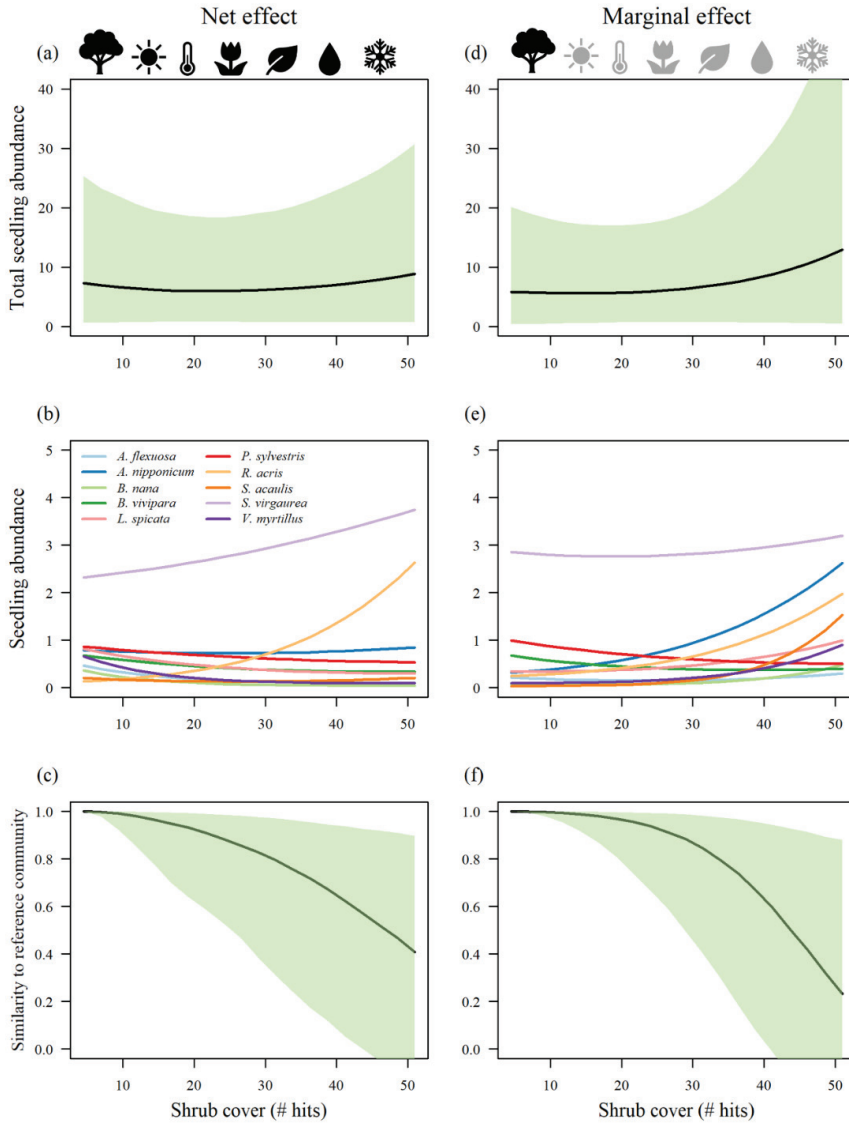


Figure 5. Predicted composition of established seedling communities along a gradient in shrub cover (# hits from point intercept vegetation analysis) in terms of total abundance of established seedlings with 95% credible intervals (a, d), established seedling abundance per species (b, e, see Appendix S7 for credible intervals), and sown seedling community composition (c, f) in open plots. The effect of shrub cover on seedling community composition is measured as similarity (Pearson correlation) relative to the reference community below the sparsest shrub canopy (5 hits, far left). For the net effect the microenvironmental variables were set to covary along the shrub-cover gradient (left), whereas for the marginal (independent) shrub cover-effect they were set to their mean value (right).

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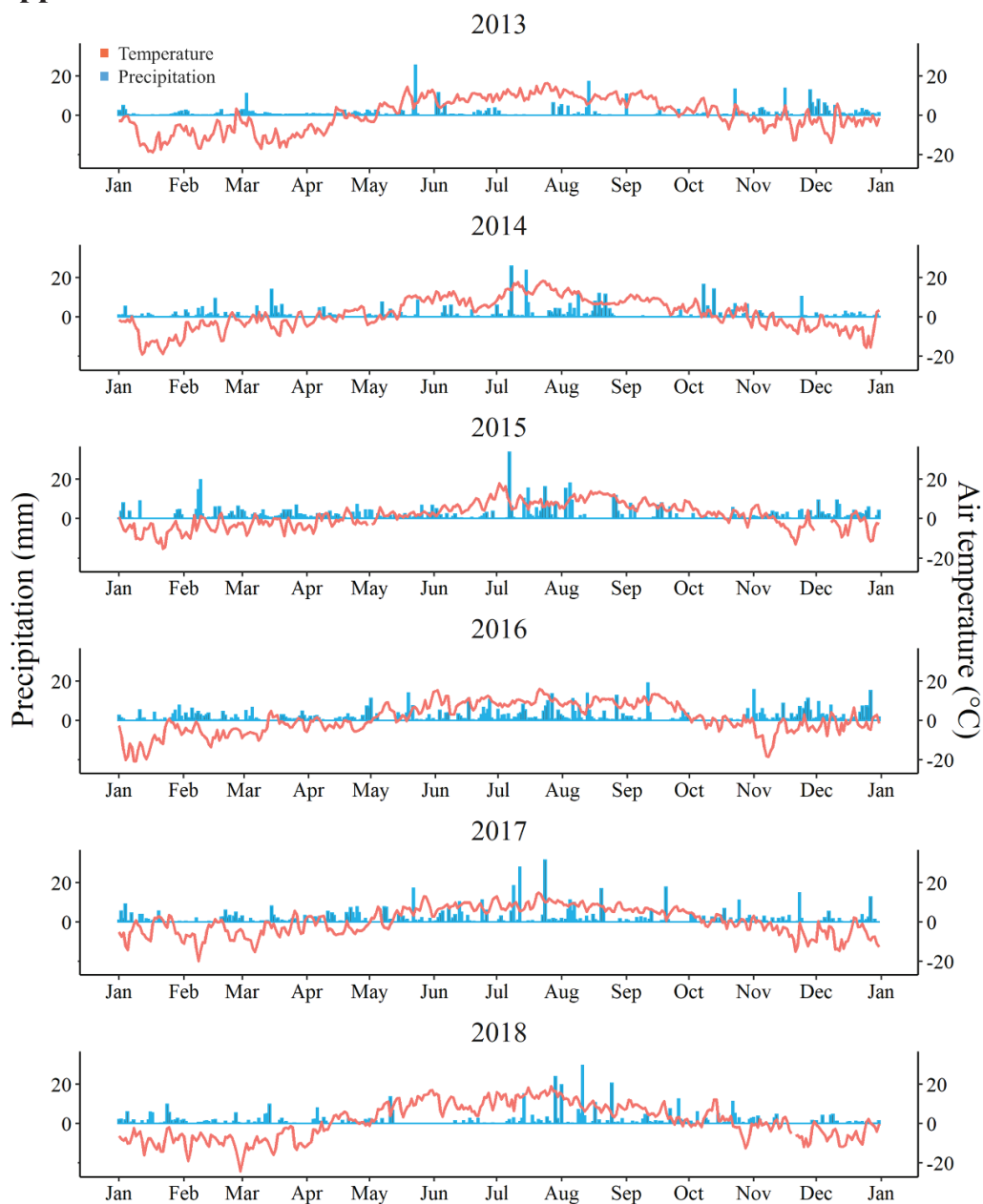
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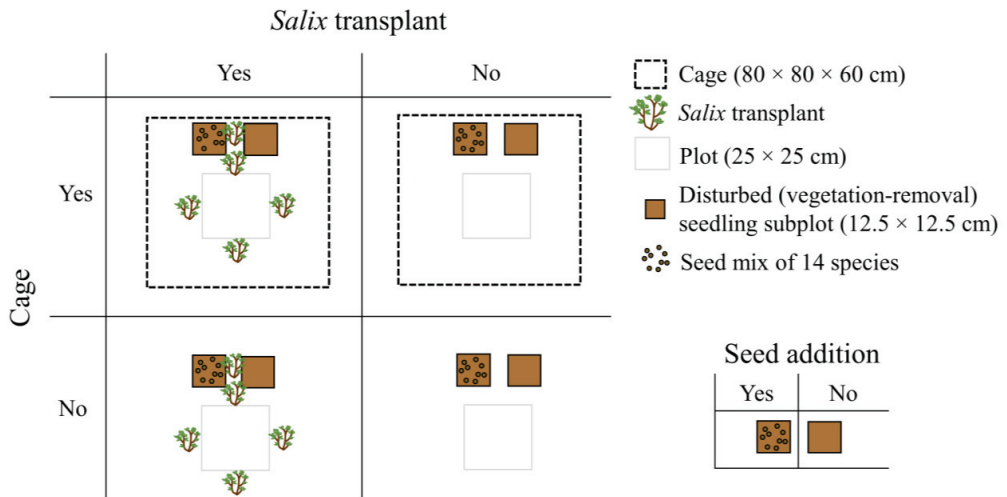
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Appendices



Appendix S1. Daily total precipitation (mm) in blue and average air temperature (°C) in red over the study period 2013-2018 from the nearest weather station Hjerkind II, 1012 m a.s.l., 62.221°N, 9.542°E, 4 – 8 km from the study sites (Norwegian Meteorological Institute, eklima.met.no).

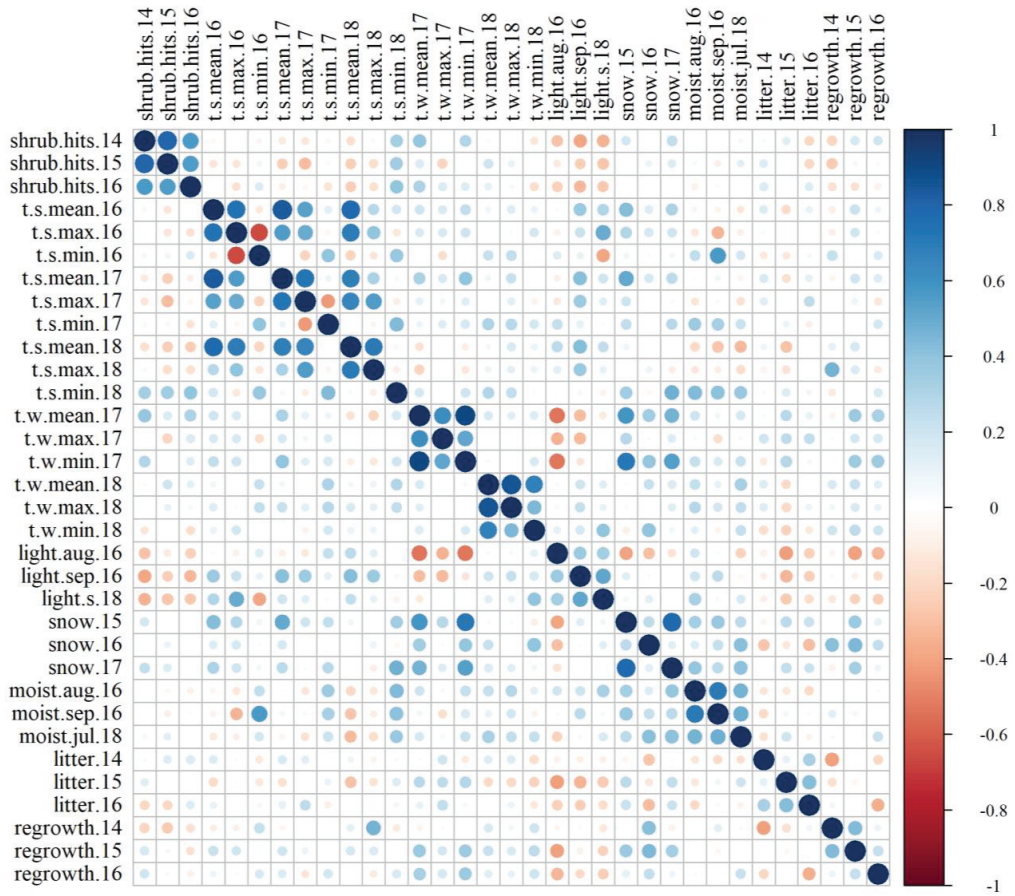


Appendix S2. Schematic representation of the 2×2×2 experimental design with *Salix* shrub transplants, cages excluding vertebrate herbivores, and seed addition. Each plot consisted of two seedling subplots where above-ground vegetation was removed. In the seedling subplots, we recorded seedling emergence, survival and establishment over five years. Treatments were replicated eight times, resulting in 64 seedling subplots in total.

Appendix S3. Summary of MCMC sampling parameters. Effective sample sizes and potential scale reduction factors (PSRF) are medians.

	Shrub cover year 1, 2 and 3	Emergence year 1	Emergence year 2	Survival year 2 and 3	Establishment year 5
Number of chains	2	2	2	2	2
Iterations per chain	30000	30000	30000	30000	30000
Transient	10000	10000	10000	10000	10000
Samples per chain	1000	1000	1000	1000	1000
Total samples	2000	2000	2000	2000	2000
Effective sample size					
Beta	2000.0	1787.9	1629.0	2000.0	936.7
Omega (Year)	2000.0			2000.0	
Omega (Plot)	1983.3	999.1	919.0	1909.1	423.2
Omega (Census)	2000.0			1847.0	
PSRF					
Beta	1.001	1.001	1.001	1.001	1.004
Omega (Year)	1.007			1.006	
Omega (Plot)	1.006	1.004	1.002	1.008	1.007
Omega (Census)	1.005			1.002	

Correlations shrub cover (# hits) and microenvironmental variables



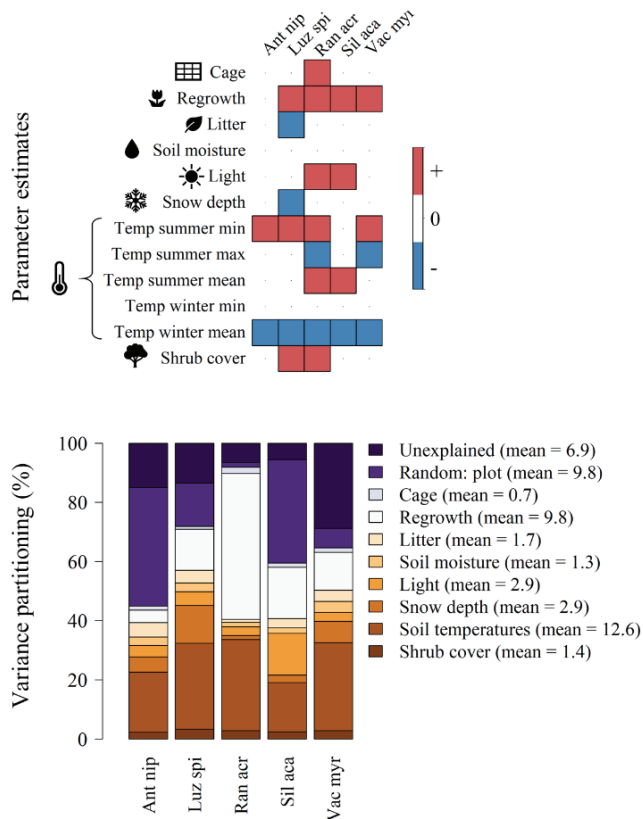
Appendix S4. Correlations of shrub cover (# hits) and microenvironmental variables for disturbed plots in the *Salix* shrubland. Numbers correspond to recording year, “w” to winter and “s” to summer.

Appendix S5. Natural seedling emergence in disturbed control subplots (n=32) over the three first year with total number of emerged seedlings, mean number of seedlings and maximum number of seedlings recorded in a subplot. Additionally, number of subplots where seedlings emerged is shown (n). Only emergence of the 14 species used in the seeding experiment is presented.

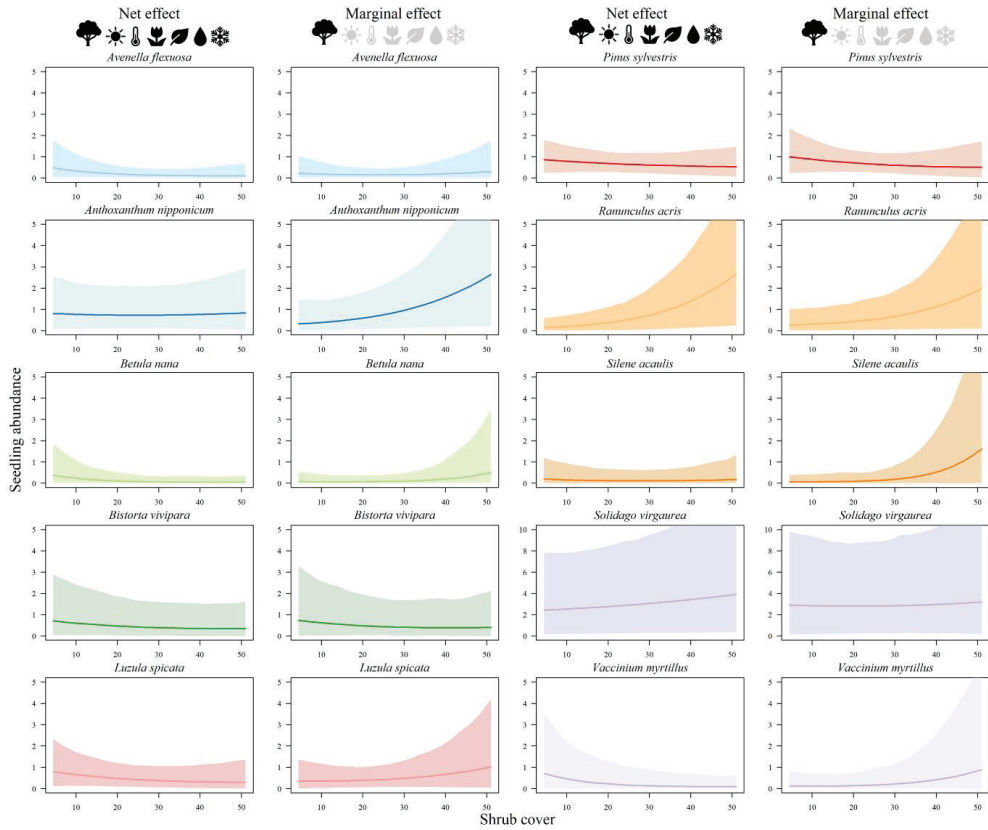
Species	Year 1				Year 2				Year 3			
	Total	Mean	Max	n	Total	Mean	Max	n	Total	Mean	Max	n
<i>Avenella flexuosa</i>	2	0.06	1	2	1	0.03	1	1	5	0.16	5	1
<i>Anthoxanthum nipponicum</i>	0	0.00	0	0	3	0.09	1	3	0	0.00	0	0
<i>Betula nana</i>	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0
<i>Betula pubescens</i>	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0
<i>Bistorta vivipara</i>	2	0.06	1	2	2	0.06	1	2	1	0.03	1	1
<i>Dryas octopetala</i>	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0
<i>Empetrum nigrum</i>	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0
<i>Luzula spicata</i> ¹	3	0.09	2	2	56	1.75	19	10	4	0.13	2	3
<i>Pinus sylvestris</i>	2	0.06	2	1	0	0.00	0	0	0	0.00	0	0
<i>Ranunculus acris</i>	0	0.00	0	0	13	0.41	7	6	1	0.03	1	1
<i>Silene acaulis</i>	0	0.00	0	0	2	0.06	1	2	0	0.00	0	0
<i>Salix glauca</i>	0	0.00	0	0	0	0.00	0	0	0	0.00	0	0
<i>Solidago virgaurea</i>	6	0.19	2	4	0	0.00	0	0	1	0.03	1	1
<i>Vaccinium myrtillus</i>	3	0.09	2	2	1	0.03	1	1	3	0.09	2	2

¹ Could be other *Luzula* species

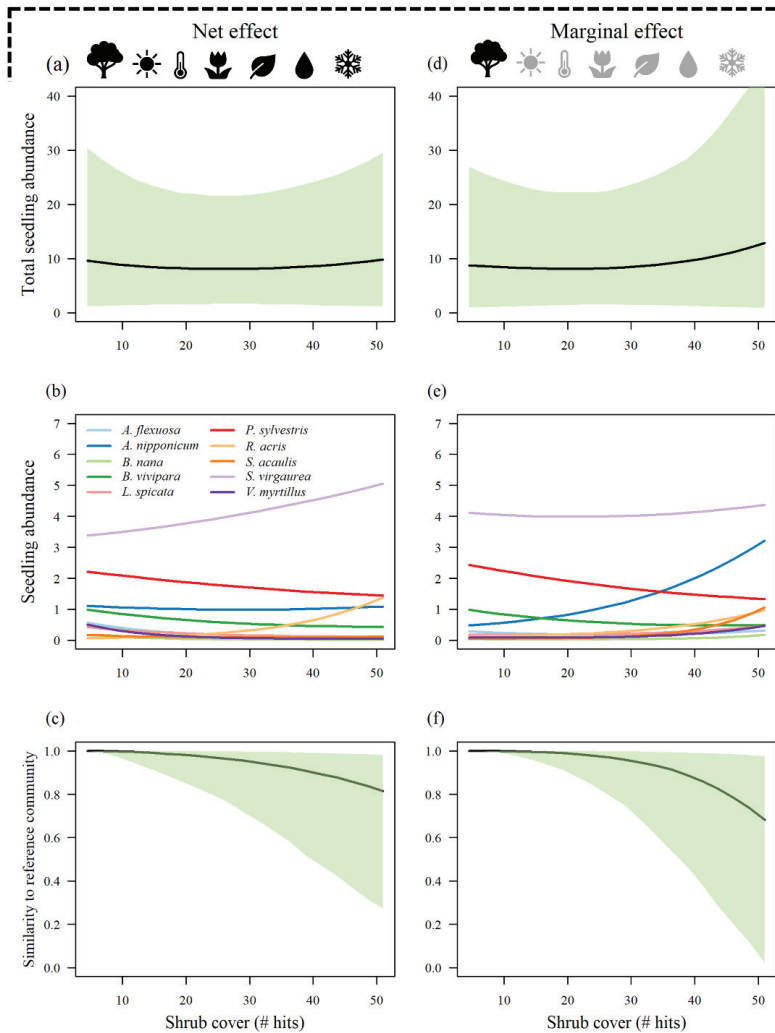
Seedling emergence second year



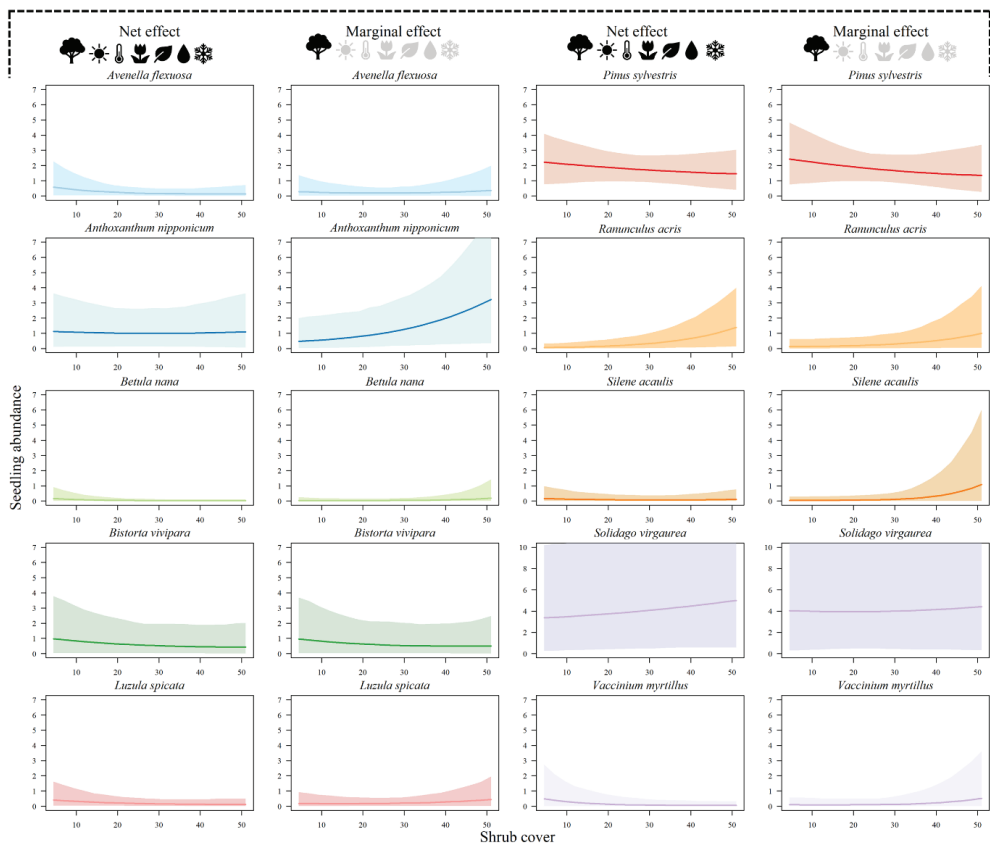
Appendix S6. Second-year seedling emergence Hmsc-results for the five species with considerable emergence (*Anthoxanthum nipponicum*, *Luzula spicata*, *Ranunculus acris*, *Silene acaulis* and *Vaccinium myrtillus*). Variance partitioning of microenvironmental variables and random effects (left) and parameter estimates visualized as negative (blue) or positive (red) effects of microenvironmental variables on the second-year seedling emergence (right).



Appendix S7. Predicted composition of established seedling abundance per species along a gradient in shrub cover (# hits from point intercept vegetation analysis) in **open plots** with 95% credible intervals. For the net effect the microenvironmental variables were set to covary along the shrub-cover gradient, whereas for the marginal (independent) effect they were set to their mean value.



Appendix S8. Predicted composition of established seedling communities along a gradient in shrub cover (# hits from point intercept vegetation analysis) in terms of total abundance of established seedlings with 95% credible intervals (a, d), established seedling abundance per species (b, e, see Appendix S9 for credible intervals), and sown seedling community composition (c, f) **inside cages**. The effect of shrub cover on seedling community composition is measured as similarity (Pearson correlation) relative the reference community below the sparsest shrub canopy (5 hits, far left). For the net effect the microenvironmental variables were set to covary along the shrub-cover gradient (left), whereas for the marginal (independent) shrub cover-effect they were set to their mean value (right).



Appendix S9. Predicted composition of established seedling abundance per species along a gradient in shrub cover (# hits from point intercept vegetation analysis) in **caged plots** with 95% credible intervals. For the net effect the microenvironmental variables were set to covary along the shrub-cover gradient, whereas for the marginal (independent) effect they were set to their mean value.

Paper IV



A cage protecting pine seedlings from herbivores in the heath. Artist: Kine Odden Nystuen

Title:

Determinants of tree seedling establishment in alpine tundra

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28

29 **Abstract**

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

39 **Location:** Dovrefjell, Central Norway.

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

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

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

55

56 **Keywords:** *Pinus sylvestris*, aboveground competition, herbivory, invasibility, microclimate,
57 alpine tundra, exclosure, shrub encroachment

58

59 **Introduction**

60 Northern high-latitude ecosystems are strongly affected by climate change due to fast and
61 intense warming (Elmendorf et al., 2015) and because their biota are limited by low
62 temperatures (Michelsen, Syverhuset, Pedersen, & Holten, 2011; Vanneste et al., 2017).
63 Ongoing changes in climate and herbivore pressure are affecting the species composition of
64 these systems in several ways. For example, treelines, the lower boundaries of tundra
65 ecosystems, are expected to advance in elevation and latitude , but the observed trends vary
66 (Dalen & Hofgaard, 2005; Millar, Westfall, Delany, King, & Graumlich, 2004). In addition,
67 shrubs (e.g. birch, willow and alder) are expanding in tundra communities worldwide
68 (Bjorkman et al., 2018; Frost & Epstein, 2014; Myers-Smith et al., 2011; Vanneste et al., 2017),
69 yet there are again exceptions (García Criado, Myers-Smith, Bjorkman, Lehmann, & Stevens,
70 2020). Interestingly, shrubs often facilitate tree establishment in tundra (Akhalkatsi, Abdaladze,
71 Nakhutsrishvili, & Smith, 2006; Castro, Zamora, Hódar, & Gómez, 2004; Chen, Yang, Wang,
72 Sun, & Schöb, 2020). Thus, woody species have the potential to expand in these ecosystems
73 (Myers-Smith et al., 2011), resulting in vegetation shifts from open herbaceous or dwarf-shrub-
74 dominated to closed shrub-dominated communities that potentially are beneficial for tree
75 establishment as well. However, it is still poorly understood in which situations and to what
76 extent these shifts will occur.

77 Previous work has shown that woody encroachment occurs at unequal rates across
78 heterogeneous alpine landscapes (García Criado et al., 2020; Wookey et al., 2009). Variation is
79 thought to depend on the invasibility (*i.e.* susceptibility to the establishment of new species) of

current communities, a characteristic determined by an interplay between biotic and abiotic factors (Graae et al., 2011; Milbau, Shevtsova, Osler, Mooshammer, & Graae, 2013). Invasibility is often assumed to be driven by resistance from the receiving community (Bruno, Stachowicz, & Bertness, 2003; Bulleri, Bruno, & 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, Callaway, Valladares, & Lortie, 2009; McIntire & Fajardo, 2014). For example, tree recruitment in tundra is often facilitated by shrub, tree or krummholz canopies (Akhalkatsi et al., 2006; Castro et al., 2004; 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 (Brodersen et al., 2019; Cranston & Hermanutz, 2013). Amelioration of abiotic growing conditions (e.g. protection against temperature extremes, high irradiance and wind) during vulnerable recruitment stages are important mechanisms behind this facilitation (Akhalkatsi et al., 2006; Chen et al., 2020; Holmgren et al., 2015). Conversely, dense ground covers of herbaceous plants mainly suppress tree seedling recruitment by shading (Loranger, Zotz, & Bader, 2017). These plant-plant interactions are expected to shift from competitive to facilitative with increasing abiotic stress level (Blonder et al., 2018; Callaway et al., 2002; Choler, Michalet, & Callaway, 2001), suggesting that environmentally benign communities are less invisable 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 & Körner, 1995; Munier, Hermanutz, Jacobs, & Lewis, 2010; Tremblay & Boudreau, 2011). Small-scale disturbances, by removing or reducing the abundance of competitors, generate new microhabitats suitable for seedling emergence and establishment (Lembrechts et al., 2016; Milbau et al., 2013; Nystuen, Evju, Rusch, Graae, &

Eide, 2014). 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 & 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 & Nellemann, 2008; Milbau et al., 2013; Tremblay & Boudreau, 2011). However, other studies have detected the opposite effect: experimental herbivore exclusion increased seedling establishment (Munier et al., 2010; Olofsson et al., 2009; Ravolainen, Bråthen, Yoccoz, Nguyen, & Ims, 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 5 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, Strimbeck, 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.

Materials and methods

Study site and plant community description

The study was conducted in the low-alpine zone near Hjerkin (62.22°N, 9.56°E) at Dovrefjell, Central Norway, a part of the Scandes mountains (Fig. 1a). Here, Scots pine (*Pinus sylvestris* L., Pinaceae, hereafter referred to as pine) exists as scattered trees up to the tree line, which is dominated by birch (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman), and smaller pine individuals occur sporadically above the treeline. The field sites are all located on podzolic soils around 1100 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 (Hjerkin II, 1012 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

155 shrubland dominated by *Salix sp.* with a heterogenous ground layer rich in bryophytes and
156 lichens (see Appendix S1, Table S1, for community characteristics and species composition).
157 The three plant communities were situated on different mountain slopes with similar aspect and
158 elevation and located within 5 km of each other (Fig. 2), thus sharing roughly the same
159 macroclimate. All sites are subjected to low-intensity summer grazing by Norwegian white
160 sheep (*Ovis aries*) (Norwegian Institute of Bioeconomy Research:
161 <http://kilden.skogoglandskap.no/>), and animal husbandry has probably been present in the area
162 since about 400 years BC (Risbøl, Stene, & Sætren, 2011). Wild grazers present in the study
163 area include voles (*Microtus agrestis*, *M. oeconomus*, and *Myodes rufocanus*), lemmings
164 (*Lemmus lemmus*), hares (*Lepus timidus*), ptarmigan (*Lagopus lagopus* and *L. muta*), moose
165 (*Alces alces*) and wild reindeer (*Rangifer tarandus*).

166

167 ***Study design***

168 The experiment was established in 2013 as a randomised block design within each of the three
169 plant communities, with eight replicates (blocks) per treatment (Sørensen, Strimbeck, et al.,
170 2018). The eight blocks were randomly located in each plant community. Within each block,
171 four plots (25 × 25 cm) were randomly assigned to a full-factorial combination of herbivore
172 exclosure (no, yes) and willow transplantation (no, yes), resulting in four treatment
173 combinations (Fig. 1b). Each plot was split into four subplots (12.5 × 12.5 cm) which received
174 a full-factorial combination of a vegetation removal treatment (no, yes) and a sowing treatment
175 (no, yes) (Fig. 1c).

176 Willow saplings, *Salix glauca* and *Salix lapponum*, were transplanted into half of the plots
177 to simulate shrub expansion. The willows were collected in the vicinity of the field sites in
178 October 2013, stored at 0 °C until January 2014, and thereafter cultivated by clonal propagation

179 in greenhouses during the rest of the winter. In June 2014 the plants were pruned to measure
180 approximately 10 cm in height, and transplanted into the experimental fields, five transplants
181 per plot, right next to the 12.5×12.5 cm subplots. It was difficult to differentiate between *S.*
182 *glauca* and *S. lapponum*, and the two species were therefore randomly distributed among the
183 plots (the two species commonly occur in mixed stands in the study area). To exclude
184 herbivores, $80 \times 80 \times 50$ cm cages were placed permanently over half of the plots. The cages
185 were constructed from galvanised iron with a mesh size of 1.27×1.27 cm, and buried 5 to 10
186 cm into the soil (Sørensen, Graae, et al., 2018).

187 In all seeded subplots, 10 pine seeds were sown in late autumn 2013. Seeds were supplied
188 by the Norwegian Forest Seed Center, and originated from a natural forest near Oppdal (600-
189 650 m above sea level), 50 km north of the study sites. While seeding, a cardboard box was
190 placed around the subplot to protect against wind and to make sure that the subplot received
191 exactly 10 seeds. The unseeded subplots provide an experimental control for spontaneous
192 emergence at the study sites and were not used directly in the analysis. In half of the subplots,
193 all aboveground biomass of all co-occurring plants was removed to ground level to reduce
194 above-ground interactions of surrounding species with the pine seedlings. Vegetation removal
195 was done with a knife, leaving soil and roots intact.

196 In summary, the experiment comprised 3 community types \times 8 blocks \times 2 vegetation
197 removal treatments \times 2 herbivore treatments \times 2 willow transplant treatments \times 2 sowing
198 treatments = 384 subplots.

199

200 *Seedling emergence, survival, and performance*

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

203 and marked on a seedling map, so that every seedling could be followed individually. Litter
204 was removed to facilitate seedling counts, and subsequently replaced. In the first growing
205 season (2014), vegetative regrowth was trimmed back. In the summer of 2018, the total number
206 of seedlings per subplot was recorded (number of seedlings per subplot were counted
207 independently by two observers; results were the same). **Emergence probability** was defined
208 per seeded subplot as the total number of emerged seedlings in the seeded subplots from 2014
209 to 2016, corrected for the seedlings that emerged in the unseeded subplots (only 2 across all
210 control plots), divided by the total number of seeds sown (10 per subplot). **Survival probability**
211 was defined for each subplot as the fraction of seedlings that survived until the 2018 census,
212 calculated as the total number of seedlings present in 2018 divided by the total number of
213 emerged seedlings from 2014-2016. When more seedlings were present in 2018 than had
214 emerged during 2014-2016 (fraction > 1), we assigned a value of 1 to the subplot.

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

227

228 *Microclimate*

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

231 **Soil temperature** was measured with iButton temperature loggers (Maxim Integrated
232 Products, Sunnyvale, CA, USA) placed in plastic bags, sealed with duct tape, and placed in a
233 slot circa 1 cm into the soil beneath the soil surface. The loggers recorded the temperature at 4-
234 hour intervals from 19 June 2016 to 28 July 2018. Each plot had two sensors placed in the
235 unseeded subplots, one in the subplot with the vegetation removed, and one in the vegetated
236 subplot. To focus on the extreme conditions across the year, two seasons were distinguished in
237 the study, referred to as winter and summer, which include the temperatures of the months
238 February (from 2017 and 2018) and July (from 2016, 2017 and 2018), respectively. For both
239 periods and for each subplot, we computed the mean temperature (T_{mean}) as the average
240 temperature per logger, minimum temperature (T_{min}) as the 1st percentile of the temperature
241 measurements, and maximum temperature (T_{max}) as the 99th percentile of the temperature
242 measurements during the period.

243 **Soil moisture** (% volumetric soil water content) was measured with a hand-held moisture
244 meter (TRIME-PICO, IMKO GmbH, Ettlingen, Germany) in August and September 2016, and
245 in July 2018. Two repeated measurements were taken in the unseeded intact and unseeded
246 vegetation-removal subplots to avoid disturbing the seedlings in the seeded subplots. The
247 moisture measurements were made on the same day in all subplots, and always on days with
248 stable and dry weather, after a dry period of at least 4 days. All measurements were averaged
249 per subplot.

250 **Light availability** was measured with a LICOR Li-190R Quantum light sensor connected
251 to a Squirrel SQ2010 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.

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: $y \sim \text{removal} \times \text{exclusion} \times \text{transplant}$.

275 To test for effects of plant community type and treatment on microclimate (soil temperature,
276 moisture and light availability), we fitted LMMs with Gaussian error distributions (see
277 Appendix S2). Some of the soil temperature variables exhibited multicollinearity. Therefore,
278 we analysed only maximum summer temperature (which correlated with mean summer
279 temperature, $r = 0.85$) and minimum winter temperature (which correlated with mean winter
280 temperature, $r = 0.98$), because temperature extremes are most likely to limit establishment. We
281 also analysed soil moisture and light availability. Block and plot (nested within block) were
282 treated as random factors. As above, we fitted models for each community when treatment
283 effects differed among communities.

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

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

297

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

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 (Fig. 3).

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, Fig. 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.

Vegetation removal effect on pine establishment

Seedling emergence increased with vegetation removal at the *Salix* shrubland ($\chi^2=33.65$, $p<0.001$, Table 2, Fig. 3) and at 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. Pattern 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 at the heath ($F=10.26$, $p=0.001$, Table 2, Fig. 3) and at 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, Fig. 3) and at the *Salix* shrubland site especially when vegetation removal was combined with herbivore exclusion (interaction removal \times enclosure: $F=7.80$, $p=0.007$). New stem growth was not affected by the treatments.

Herbivore effect on pine establishment

Pine emergence increased when herbivores were excluded at the meadow ($\chi^2=8.66$, $p=0.003$, Table 2, Fig. 3) and at 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 3, Table S3.1, Fig. 3). At 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 at the heath and *Salix* shrubland ($\chi^2=4.17$, $p=0.041$, $\chi^2=6.63$, $p=0.010$, respectively, Table 2, Fig. 3), but not at the meadow.

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 (Fig. 3). More seedlings emerged in encroached plots (i.e. plots with transplanted willows) when vegetation was also removed at the heath and meadow ($\chi^2=7.16$, $p=0.007$ and $\chi^2=8.34$, $p=0.004$, respectively), and at 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, Fig. 3). Pines grew less tall in encroached plots at the *Salix* shrubland ($\chi^2=5.56$, $p=0.022$), while other effects on pine performance depended on complex interactions (Table 2, Fig. 3).

Biotic treatments 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, Fig. 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, Fig. 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, Fig. 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, Fig. 4).

367 *Relationship between pine establishment and microclimate*

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

374

375 **Discussion**

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

385

386 *Pine seedling establishment into alpine plant communities and vegetation interaction effect*

387 In intact vegetation, pine seedlings emerged and survived about equally well in all three alpine
388 tundra community types we considered, but establishment rates were generally low. This low
389 invasibility of intact tundra vegetation is in line with previous studies reporting predominantly
390 negative effects of tundra vegetation on tree seedling recruitment (Hättenschwiler & Körner,

1995; Lett & Dorrepaal, 2018; Loranger et al., 2017). 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 acts through competition for light, nutrients, water and space, but could also relate to allelopathy or higher susceptibility to pathogen infections in dense vegetation (Lett & Dorrepaal, 2018; Loranger et al., 2017; Sedia & Ehrenfeld, 2003).

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 at the heath were taller in intact than vegetation removal subplots, perhaps due to facilitation through protection from, for instance, strong abrasive winds during periods with shallow snow cover (Batllori, Camarero, Ninot, & Gutiérrez, 2009; McIntire, Piper, & Fajardo, 2016; Piper et al., 2016). Also at 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 understory ground layers of lichens or bryophytes (mean thickness \pm SD in mm: 73.7 ± 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 & Danby, 2018), but this

was not evident for the performance measures in our study. Since we found the 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.

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 & 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 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 (Bougnounou, Hulme, Oksanen, Suominen, & Olofsson, 2018; Olofsson, E. Hulme, Oksanen, & Suominen, 2004). These results add to previous studies (Bougnounou et al., 2018; Boulant, Kunstler, Rambal, & Lepart, 2008; Moen, Lundberg, & Oksanen, 1993; Munier et al., 2010; Post & Pedersen, 2008) in suggesting that herbivory may be important in limiting tree regeneration in alpine tundra ecosystems.

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

Willow introduction resulted in higher pine seedling emergence at 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 (Fig 4), and transplants were relatively small. Therefore, their effect on invasibility observed here may not relate to amelioration of microclimatic conditions as previously suggested (Holmgren et al., 2015; Sturm et al., 2005). 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 CO₂ levels due to more soil respiration (Strimbeck, Graae, Lang, & Sørensen, 2019). Disentangling the mechanisms behind this apparent facilitative effect will require further studies as the introduced willows grow larger.

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 ecological 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 (Fig. 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.

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 2013; 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. Aboveground 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.

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484 **Author contribution statement**

485 KON, MVS and BJG conceived and designed the experiments. FM, JF, KON, PDF, BJG, ØO
486 and MVS performed the fieldwork. FM analysed the data and wrote the manuscript. JL, BJG,
487 PDF, KON, ØO, JF and MVS contributed to the writing. All authors read and approved the
488 final manuscript.

489

490 **Data availability statement**

491 The data used for the analyses is available at Figshare. DOI: 10.6084/m9.figshare.12846089.

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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. The minimal models were obtained by stepwise backward elimination of least significant explanatory variables, starting from a full model with three-way interactions, until all terms were significant or part of a significant interaction. The full model is shown in Appendix S2. 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.

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

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. Sample size $n = 1920$ 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.

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

*variable is natural log-transformed

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. Minimal models were obtained by stepwise backward elimination of least significant explanatory variables. Full models are shown in Appendix S2. Sample size $n = 1920$ 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.

Response variable															
Explanatory variable	Emergence probability (log odds)			Survival probability (log odds)			Stem height (log mm)*			New stem growth (log mm)**			Healthy needles (fraction of total)		
	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				-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

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

Fig 1 (a) Location of the study area in the low-alpine zone near Hjerkind (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 enclosure (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.

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

Fig 3 Effects of experimental treatments on pine emergence, survival and performance in seeded subplots in the three different plant communities after 5 year (means \pm standard error). (a, b, c) Pine emergence per seeded subplot, as fraction of seeds sown (10 seeds per subplot), (d, e, f) pine survival per seeded subplot as fraction of emerged pines, (g, h, i) mean stem height per pine seedling, (j, k, l) mean new stem growth per pine seedling and (m, n, 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.

Fig 4 Effects of experimental treatments on microclimate in the three different plant communities (means \pm 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 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.

Fig 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.

Supplementary material

Appendix S1: Community description

Appendix S2: Details on the data analysis

Appendix S3: Results from the (generalised) linear models

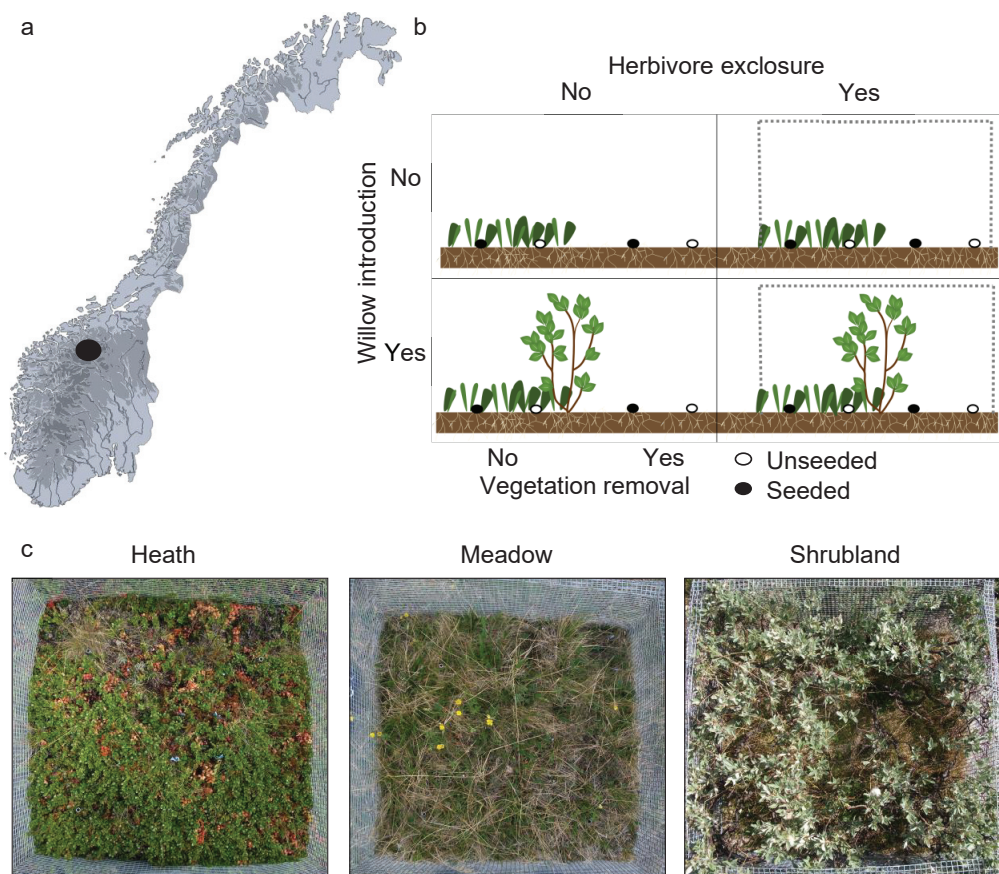


Figure 1.

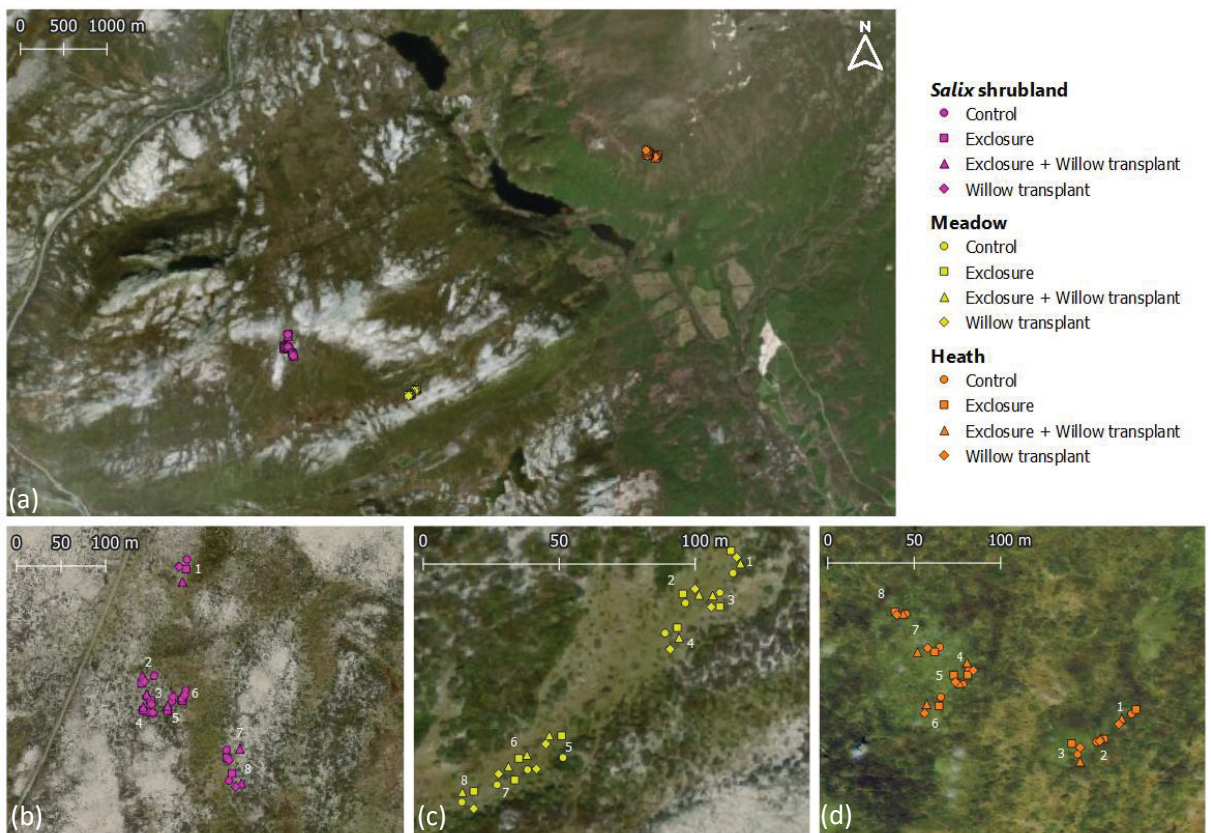


Figure 2.

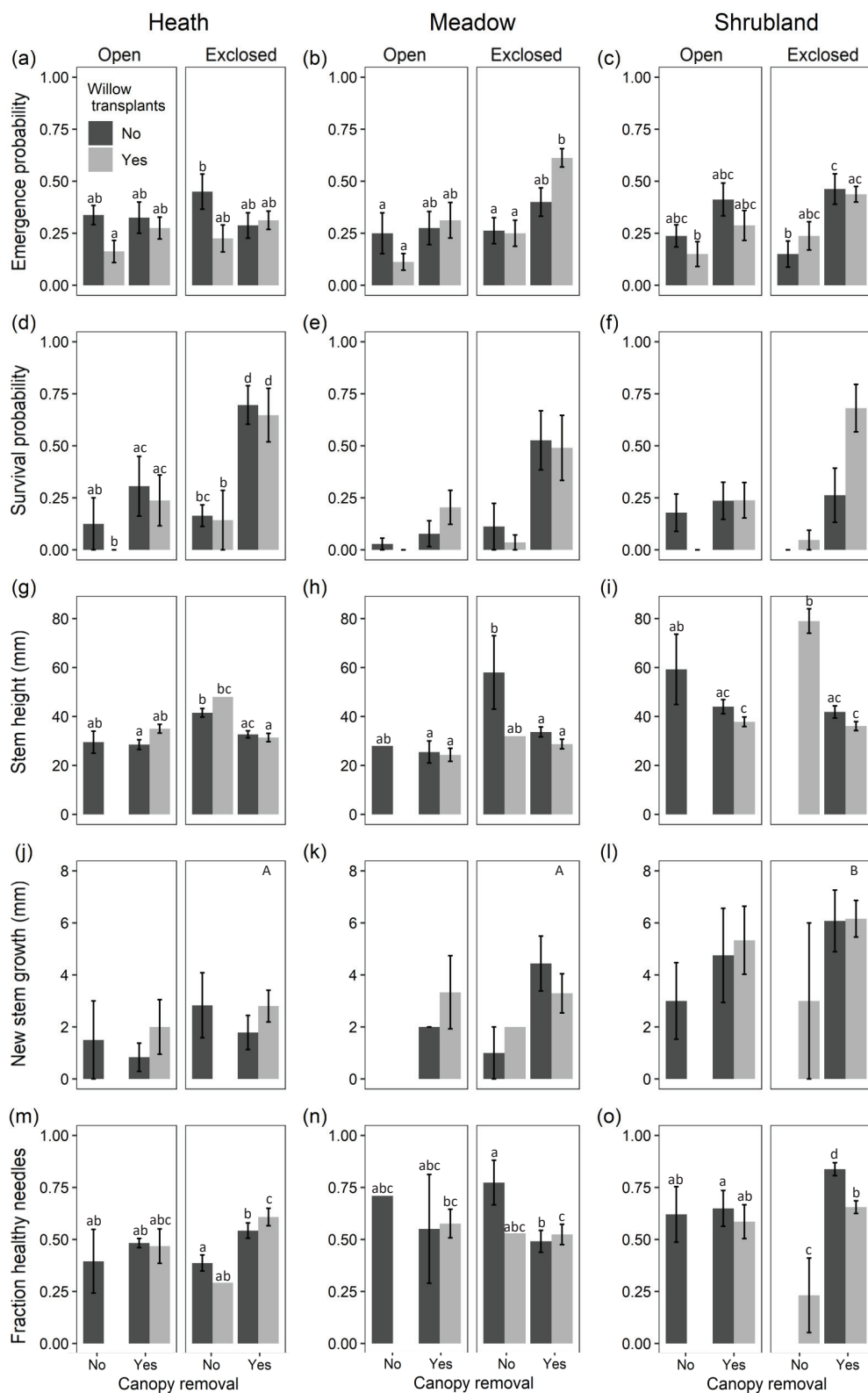


Figure 3.

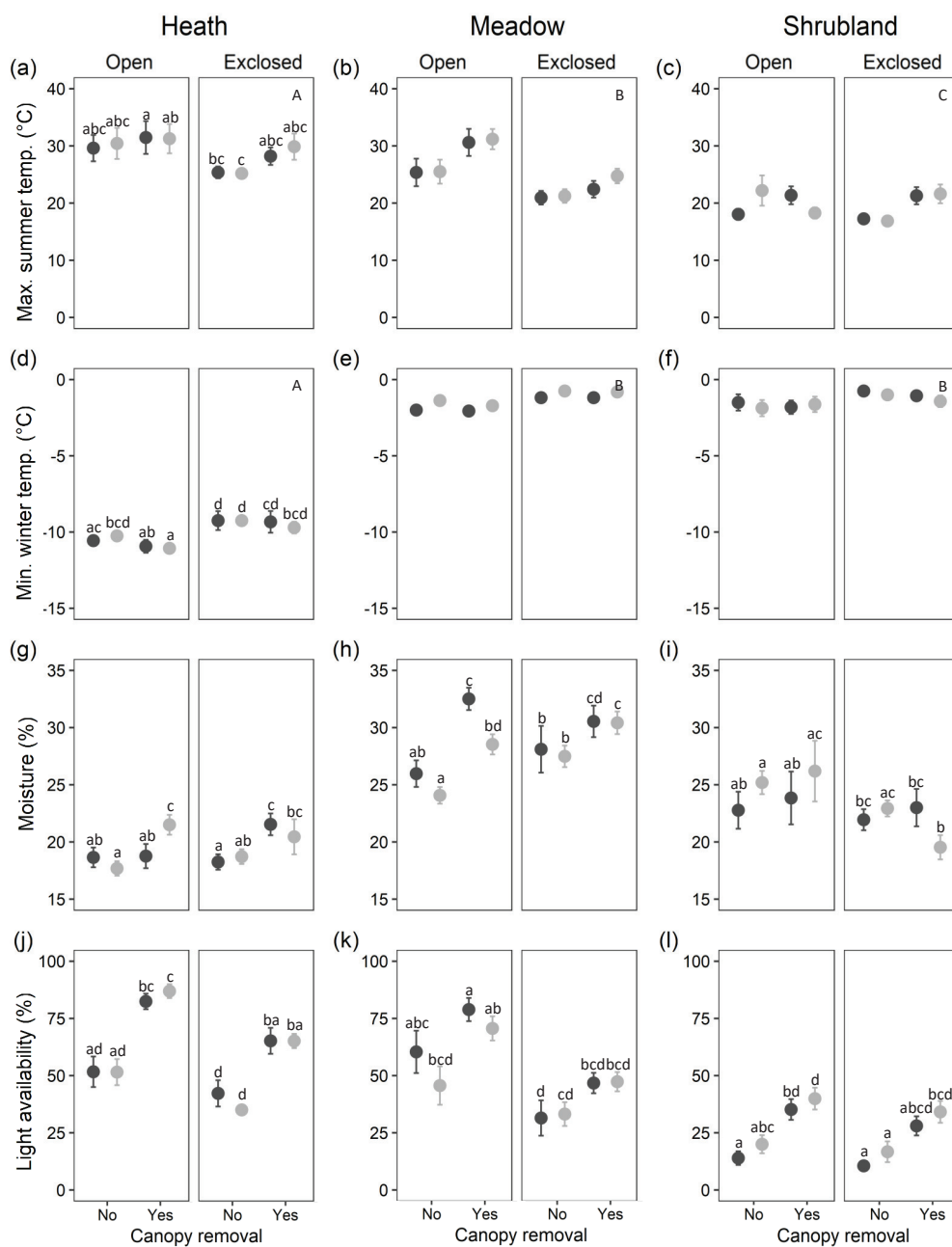


Figure 4.

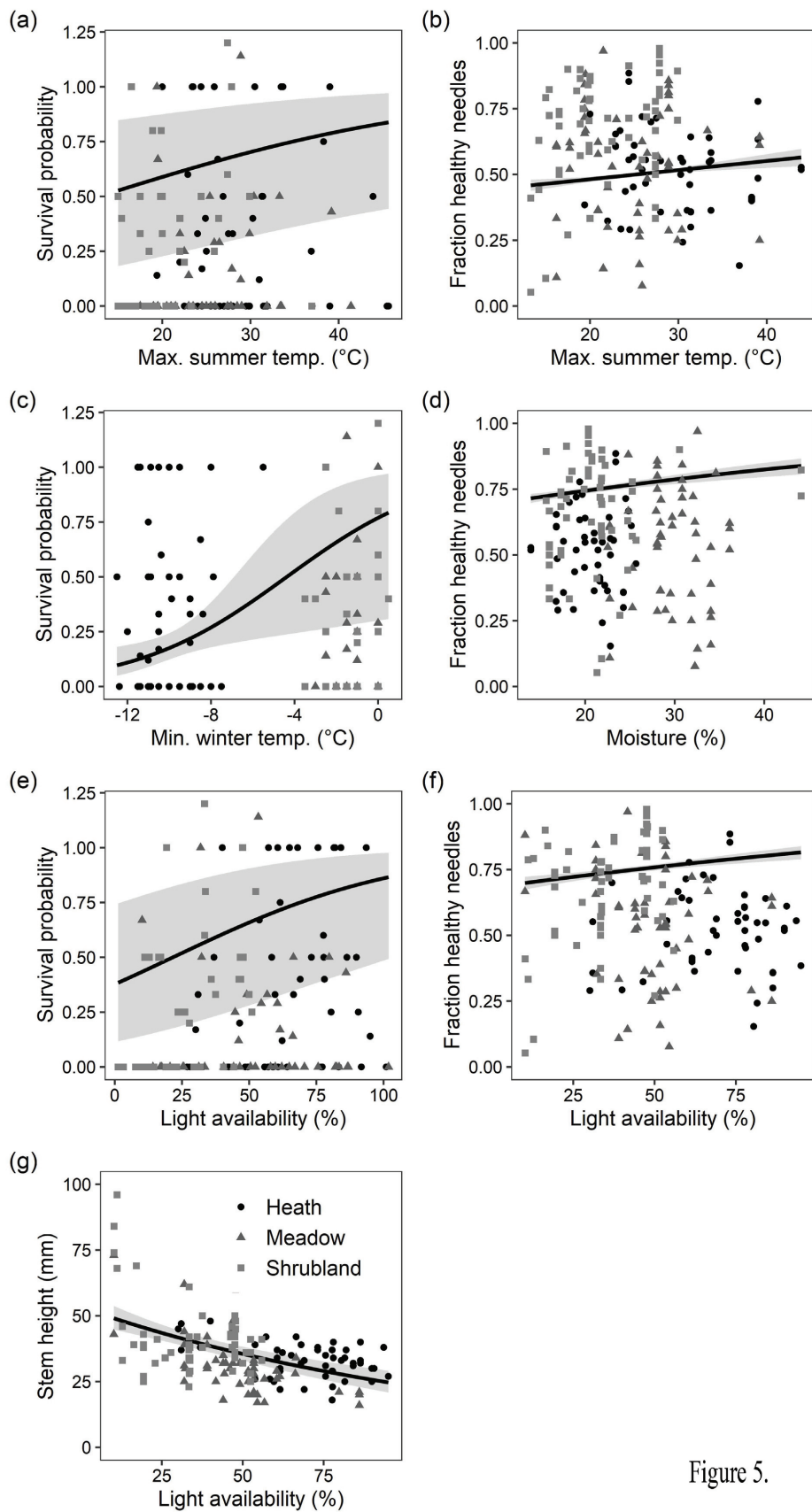


Figure 5.

Supporting information to the paper

Marsman, F. et al. Determinants of tree seedling establishment in alpine tundra. *Journal of Vegetation Science*.

Appendix S1. Plant community description

Table S1 Plant community description based on Sørensen et al. (2018).

Plant community	Heath	Meadow	Shrubland
Exposure	South facing	Southwest facing	South facing
Snow depth (average '15-'17)	6.95 ± 6.76 cm	43.69 ± 9.83 cm	48.85 ± 11.78 cm
Snowmelt (range '14-'16)	21 April to 2 May	14 to 19 May	19 May to 4 June
Vegetation height (average '14, '15)	6.2 ± 2.2 cm	7.3 ± 3.1 cm	20.2 ± 10.6 cm
Abundant species (relative abundance (%)) [*]	Low evergreen dwarf shrubs	Forbs and graminoids	Deciduous shrub canopy
	<i>Empetrum nigrum</i> L. (39.0)	<i>Deschampsia cespitosa</i> (L.) P. Beauv. (17.0)	<i>Salix glauca</i> L. (36.7)
	<i>Arctostaphylos uva-ursi</i> (L.) Spreng. (34.8)	<i>Avenella flexuosa</i> (L.) Drejer (13.9)	<i>Salix lapponum</i> L. (15.8)
	<i>Vaccinium vitis-idaea</i> L. (16.1)	<i>Anthoxanthum nipponicum</i> Honda (12.0)	<i>Avenella flexuosa</i> (L.) Drejer (16.7)
	Lichens	<i>Festuca ovina</i> L. (11.6)	<i>Saussurea alpina</i> L. DC. (4.8)
	<i>Flavocetraria cucullata</i> (Bellardi) Kamefelt & Thell (44.4)	<i>Carex bigelowii</i> Torr. ex Schwein. (8.5)	<i>Carex bigelowii</i> Torr. ex Schwein. (3.9)
	<i>Cladonia mitis</i> ** (Sandst.) Ruoss (22.2)	<i>Thalictrum alpinum</i> L. (7.7)	<i>Vaccinium myrtillus</i> L. (3.5)
	<i>Alectoris ochroleuca</i> (Hoffm.) A. Massal. (8.3)	<i>Antennaria dioica</i> (L.) Gaertn. (3.9)	<i>Galium boreale</i> L. (3.2)
	<i>Cladonia rangiferina</i> (L.) F. H. Wigg. (5.6)	<i>Leontodon autumnalis</i> L. (3.1)	<i>Festuca ovina</i> L. (2.3)
	<i>Cladonia sensu lato gracilis</i> (L.) Willd. (5.6)	<i>Ranunculus acris</i> L. (3.1)	<i>Trientalis europaea</i> L. (2.3)
	<i>Cetraria islandica</i> (L.) Ach. (2.8)	<i>Saussurea alpina</i> L. DC. (3.1)	Lichens
	Bryophytes	<i>Astragalus alpinus</i> L. (2.3)	<i>Cladonia mitis</i> ** (Sandst.) Ruoss (37.0)
	<i>Polytrichum</i> sp (42.1)	<i>Achillea millefolium</i> L. (1.9)	<i>Cladonia stellaris</i> (Opiz) Pouzar & Vezda (24.1)
	<i>Dicranum flexicaule</i> Brid. (26.3)	<i>Agrostis capillaris</i> L. (1.5)	<i>Cladonia stygia</i> (Fr.) Ruoss (14.8)
	<i>Polytrichum juniperinum</i> Hedw. (15.8)	Lichens***	<i>Cladonia rangiferina</i> (L.) F. H. Wigg. (7.4)
	<i>Ceratodon purpureus</i> (Hedw.) Brid. (5.3)	<i>Stereocaulon alpinum</i> Laurer ex Funck (73.1)	Bryophytes
		<i>Cetraria islandica</i> (L.) Ach. (25.0)	<i>Pleurozium schreberi</i> Hedw. (28.3)
		Bryophytes**	<i>Polytrichum commune</i> (20.8)
		<i>Hylocomium splendens</i> (Hedw.) Schimp. (24.5)	<i>Hylocomium splendens</i> (Hedw.) Schimp. (18.9)
		<i>Barbilophozia lycopodioides</i> (Wallr.) Loeske (18.6)	
		<i>Aulacomnium palustre</i> (Hedw.) Schwa'gr. (16.7)	
		<i>Hylocomiastrum pyrenaicum</i> Spruce (12.7)	
		<i>Sanionia uncinata</i> (Hedw.) Loeske (9.8)	
		<i>Pleurozium schreberi</i> (Willd. Ex Brid.) Mitt. (6.9)	

Mean characteristics ± SD of the *Empetrum*-dominated dwarf shrub heath (Heath), meadow (Meadow), and the *Salix*-dominated shrubland (Shrubland) in Dovre Mountains, Central Norway. Vascular and cryptogam species listed are the most abundant in each of the communities in 2014*, calculated with a 90% threshold of cumulative relative abundance. Relative abundance (%) is indicated in parenthesis for each species.

* Relative abundance to total abundance was found with the pin-point method and assessed separately for vascular, lichen, and bryophyte species. In each plot, we recorded total number of hits of species using the point intercept method, with 25 pins distributed across a 25 × 25 cm square.

** Can also be *Cladonia arbuscula* (Wallr.) Rabenh.

*** Cryptogams in meadow only for blocks 1–7.

References

Sørensen, M. V., Strimbeck, R., Nystuen, K. O., Kapas, R. E., Enquist, B. J., & Graae, B. J. (2018). Draining the pool? Carbon storage and fluxes in three alpine plant communities. *Ecosystems*, 21(2), 316-330.
doi:10.1007/s10021-017-0158-4

Supporting information to the paper

Marsman, F. et al. Determinants of tree seedling establishment in alpine tundra. *Journal of Vegetation Science*.

Appendix S2. Details on the data analysis

Details on the data analysis

For the response variables containing proportional data (emergence probability, survival probability and fraction of healthy needles) we fitted generalised linear mixed models (GLMMs) with a Binomial error distribution (Table S2). For the growth response variables (stem height and new stem growth) linear mixed models (LMMs) were fitted with Gaussian error distributions (Table S2). To improve normality and homoscedasticity of the residuals stem height was $\ln(x)$ -transformed, and new stem growth $\ln(x+1)$ -transformed. First, we fitted models for each response variable with community (with levels heath, meadow and *Salix*), treatment (compound variable with 2³ levels (unique combinations of vegetation removal, herbivore exclusion, and willow transplants) and their interaction as fixed effects. 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: $y \sim \text{removal} \times \text{exclusion} \times \text{transplant}$ (Table S2).

For all microclimatic variables (maximum summer temperature, minimum winter temperature, soil moisture and light availability) we fitted LMMs with Gaussian error distributions (Table S2). To improve normality and homoscedasticity of the residuals maximum summer temperature and soil moisture were $\ln(x)$ -transformed.

In the third set of models the effect of the microclimatic variables on pine invasibility was tested. The pine variables were inserted as response variables with the same error distributions and transformations as in the first set of models (Table S2).

Table S2: Overview of full model structure.

Response variable	Transformation	Distribution	Explanatory variables	Random structure
Emergence rate	no	Binomial	C × treatment	Block/plot
Survival probability	no	Binomial	C × treatment	Block/plot
Stem height	ln(x)	Gaussian	C × treatment	Block/plot/subplot
New stem growth	ln(x+1)	Gaussian	C × treatment	Block/plot/subplot
Fraction of healthy needles	no	Binomial	C × treatment	Block/plot/subplot
Emergence rate	no	Binomial	R × E × T (for each community separate)	Block/plot
Survival probability	no	Binomial	R × E × T (for all communities combined)	Block/plot
Stem height	ln(x)	Gaussian	R × E × T (for each community separate)	Block/plot/subplot
New stem growth				
Fraction of healthy needles	no	Binomial	R × E × T (for each community separate)	Block/plot/subplot
Max. summer temp. (MS)	ln(x)	Gaussian	C × treatment	Block/plot
Min. winter temp. (MW)	no	Gaussian	C × treatment	Block/plot
Soil moisture (SM)	ln(x)	Gaussian	C × treatment	Block/plot
Light availability (LA)	no	Gaussian	C × treatment	Block/plot
Max. summer temp. (MS)	ln(x)	Gaussian	R × E × T (for each community separate)	Block/plot
Min. winter temp. (MW)	no	Gaussian	R × E × T (for each community separate)	Block/plot
Soil moisture (SM)	ln(x)	Gaussian	R × E × T (for each community separate)	Block/plot
Light availability (LA)	no	Gaussian	R × E × T (for each community separate)	Block/plot
Emergence rate	no	Binomial	C + MS + MW + SM + LA	
Survival probability	no	Binomial	C + MS + MW + SM + LA	
Stem height	ln(x)	Gaussian	C + MS + MW + SM + LA	
New stem growth	ln(x+1)	Gaussian	C + MS + MW + SM + LA	
Fraction of healthy needles	no	Binomial	C + MS + MW + SM + LA	

Key to the abbreviations:

C – community, R – canopy removal, E – herbivore exclosure, T – willow transplant introduction
MS – maximum summer temperature, MW – minimum winter temperature, SM – soil moisture, LA – light availability

Appendix S3. Results from the (generalised) linear models

Table S3.1 Summary of the (generalised) linear models describing direct and interactive effects of plant community and treatment (compound variable with $2^3 = 8$ levels representing unique combinations of vegetation removal, herbivore exclusion, and willow introduction) on pine emergence, pine survival, stem height, new stem growth and fraction of healthy needles. Sample size $n = 1920$ for pine emergence, $n = 578$ for pine survival and $n = 159$ for stem height, new stem growth and fraction healthy needles.

Explanatory variable	Response variable									
	Emergence probability (log odds)		Survival probability (log odds)		Stem height (log mm)*		New stem growth (log mm)**		Healthy needles (fraction of total)	
	χ^2	p	χ^2	p	F	P	F	p	χ^2	p
Community							11.2	<0.001		
Treatment			118.5	<0.001						
Community × treatment	42.7	<0.001			1.92	0.048			26.1	0.006

*variable is natural log-transformed, **variable is natural log(x+1)-transformed

Table S3.2: Summary of the linear models describing direct and interaction effects of plant community and treatment (compound variable with $2^3 = 8$ levels representing unique combinations of vegetation removal, herbivore exclusion, and willow introduction) on the microclimate variables (maximum summer temperature, minimum winter temperature, soil moisture and light availability). Sample size $n = 192$ for all variables.

Explanatory variable	Response variable							
	Max. temp. summer (log °C)*		Min. temp. winter (°C)		Soil moisture (log %)*		Light availability (%)	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Community	38.75	<0.001	499.48	<0.001				
Treatment	6.80	<0.001	5.54	<0.001				
Community × treatment					3.54	<0.001	2.20	0.012

*variable is natural log-transformed

Table S3.3: Parameter estimates from the selected minimal linear models describing direct and interaction effects of vegetation removal (R), herbivore exclosure (E), and willow transplants (T) on maximum summer temperature and minimum winter temperature. The minimal models were obtained by stepwise backward elimination of least significant explanatory variables, starting from a full model with three-way interactions, until all terms were significant or part of a significant interaction. Full models are shown in Appendix S2. 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.

Explanatory variable	Response variable					
	Max. temp. summer (log °C)*			Min. temp. winter (°C)		
	Est.±SE	F	p	Est.±SE	F	p
Intercept	3.17±0.04					
Vegetation removal (R)	0.12±0.02	22.87	<0.001	-0.22±0.07	10.37	0.002
Herbivore exclosure (E)	-0.12±0.03	17.14	<0.001	0.89±0.17	26.69	<0.001

*variable is natural log-transformed

Table S3.4: Parameter estimates from the selected minimal models describing direct and interaction effects of vegetation removal (R), herbivore exclosure (E), and willow transplants (T) on soil moisture and light availability in the heath, meadow and *Salix* shrubland. Sample size $n = 192$ for both variables. 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.

Explanatory variable	Response variable					
	Soil moisture (log %)*			Light availability (%)		
	Est.±SE	χ^2	p	Est.±SE	F	p
Heath						
Intercept	2.92±0.05			53.24±2.94		
Vegetation removal (R)	0.00±0.05			29.82±2.52	140.34	<0.001
Herbivore exclosure (E)	-0.02±0.06			-16.25±3.74	18.93	<0.001
Transplants (T)	-0.05±0.06					
R × E	0.16±0.07					
R × T	0.19±0.07					
E × T	0.08±0.09					
R × E × T	-0.29±0.10	8.12	0.008			
Meadow						
Intercept	3.26±0.02			54.77±3.99		
Vegetation removal (R)	0.15±0.03	23.83	<0.001	18.23±3.82	22.77	<0.001
Herbivore exclosure (E)				-24.20±4.96	23.81	<0.001
Salix shrubland						
Intercept	3.12±0.05			12.41±2.40		
Vegetation removal (R)				19.03±2.72	48.89	<0.001
Herbivore exclosure (E)	-0.02±0.05					
Transplants (T)	0.10±0.05			5.77±2.81	4.23	0.048
E × T	-0.16±0.08	4.23	0.044			


*variable is natural log-transformed

Paper V



The common garden experiment

Lichens facilitate seedling recruitment in alpine heath

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Abstract

Questions: How do mat thickness, physical structure and allelopathic properties of terricolous mat-forming lichens affect recruitment of vascular plants in dwarf-shrub and lichen heath vegetation?

Location: The mountains of Dovrefjell, central Norway.

Methods: In autumn, seeds of ten vascular plant species were collected and sown in a common garden experiment with mats of six lichen species and bare soil controls as experimental treatments. We recorded growing season soil temperature and moisture, and seedling recruitment and growth after one year. The effect of lichen secondary compounds on germination was tested in a growth chamber experiment and compared to the lichen–plant interactions detected under field conditions.

Results: The lichen mats buffered extreme soil temperatures and soil drying in dry weather, with soils below the thickest mats (*Cladonia stellaris* and *C. rangiferina*) experiencing the lowest temperature fluctuations. Seedling recruitment and seedling growth in the field and seed germination in the lab were species-specific. Seedling recruitment rates were overall higher within lichen mats than on bare soil, but the c. 6.5-cm-thick mats of *C. stellaris* reduced recruitment of many species. The lab experiment suggested no overall strong effect of lichen allelopathy on seed germination, and effects on seed germination were only moderately correlated with the lichen–plant interactions observed for seedling recruitment in the field.

Conclusions: In harsh environments like alpine dwarf-shrub and lichen heaths, the presence of lichens and the resulting amelioration of the microclimate seem more important for vascular plant recruitment than are allelopathic effects often reported in lab experiments. We might therefore expect most terricolous lichens, depending on the plant species in focus, to facilitate rather than hamper the early stages of plant recruitment into lichen-dominated arctic-alpine heath vegetation.

KEYWORDS

Alectoria, *Cetraria*, *Cladonia* heath, *Flavocetraria*, ground lichen, lichen secondary metabolites, lichen–plant interaction, microclimate, seedling emergence, soil moisture, *Stereocaulon*, tundra, vascular plant colonization

*Shared first author.

1 | INTRODUCTION

Terricolous lichens (i.e., lichens growing on soil) dominate the vegetation of roughly 8% of terrestrial ecosystems, among them arctic and alpine heaths (Ahti, 1977; Crittenden, 2000; Larson, 1987; Nash, 2008). The species composition and abundance of terricolous lichens on arctic-alpine heaths vary with elevation, topography, and continentality (Haapasaari, 1988). Lichens are particularly dominant in convex parts of exposed and well-drained heaths (Crittenden, 2000; Vistnes & Nellemann, 2008), where standing lichen biomass can reach 1,200 g/m² (Nellemann, Jordhøy, Støen, & Strand, 2000). Terricolous lichens are ecologically important as the main food resource for reindeer and caribou in winter (Boertje, 1984; Danell, Utsi, Palo, & Eriksson, 1994) and contribute substantially to the arctic-alpine carbon pool (Lange, Hahn, Meyer, & Tenhunen, 1998). Species with N₂-fixing cyanobacteria, such as *Stereocaulon* spp., further contribute to nitrogen enrichment of the often N-deficient heaths (Crittenden, 1989).

Recent studies report declines in lichen abundance in arctic-alpine areas (Fraser, Lantz, Olthof, Kokelj, & Sims, 2014; Løkken, Hofgaard, Dalen, & Hytteborn, 2019; Maliniemi, Kapfer, Saccone, Skog, & Virtanen, 2018; Vanneste et al., 2017; Vuorinen et al., 2017), often driven by expansion of vascular plants, and in particular shrubs (Cornelissen et al., 2001; Fraser et al., 2014; Vanneste et al., 2017). Whether the negative effects of vascular plants on lichen communities are mediated by expansion of the already established plants within or close to lichen mats, or by colonizing plants from outside, is not known. Many lichens are indeed sensitive to shading from plants or their litter (Palmquist, Jonsson, & Nash, 2008), whereas the low seedling densities often reported on arctic-alpine lichen heaths (Evju, Hagen, & Hofgaard, 2012; Graae et al., 2011) suggest it is difficult for plants to recruit here. Plant recruitment in lichen heaths may be hampered by lichen secondary metabolites (i.e., allelopathy), by mechanisms related to the lichens' physical structure, or by harsh environmental conditions (Figure 1).

In summer, lichen heaths often experience droughts, which Moles and Westoby (2004) identified as the second most important cause of seedling mortality. On the other hand, lichens modify microclimatic conditions in ways that may support seedling survival, as they maintain soil moisture (Broll, 2000; Kershaw & Rouse, 1971; Molina-Montenegro et al., 2013) and prevent extreme temperatures due to high reflectivity and low thermal conductivity (Broll, 2000; Kershaw, 1977). Lichens furthermore reduce wind erosion and plant evapotranspiration through shelter effects (Molina-Montenegro et al., 2013).

The physical structure of lichens may have contrasting effects on plant recruitment. Lichen mats act as efficient seed traps (Sedia & Ehrenfeld, 2003), but can also prevent seeds or seedlings from reaching the ground. A classic example is Allen's (1929) observation of seedlings pulled out of the soil by repeated lichen thalli expansion and contraction driven by fluctuations in moisture. Some species (e.g., *Cladonia stellaris*) have upright, branched, shrub-like thalli and form very thick and dense mats with low light penetration and high insulation capacity. Others (e.g., *Flavocetraria nivalis*) form upright, but thinner and more open mats that provide less thermal insulation (Crittenden, 2000), but may be easier for seeds and seedlings to penetrate. However, most lichen-plant recruitment interaction studies under field conditions have focused on *Cladonia* spp. (Allen, 1929; Brown & Mikola, 1974; Hawkes & Menges, 2003; Kytöviita & Stark, 2009; Sedia & Ehrenfeld, 2003) in various vegetation types, whereas less is known about the interactions between other ecologically successful genera of terricolous lichens (e.g., *Cetraria*, *Stereocaulon* and *Alectoria*; Crittenden, 2000) and plant species that co-occur in arctic-alpine vegetation.

Lichen secondary metabolites may also inhibit establishment and growth of vascular plants. Direct lichen allelopathic effects may inhibit germination, radicle and hypocotyl growth (Hobbs, 1985; Latkowska, Białczyk, Lechowski, & Czaja-Prokop, 2008; Nishitoba, Nishimura, Nishiyama, & Mizutani, 1987; Peres, Mapeli, Faccenda,

Potential lichen-plant recruitment interactions in lichen heaths

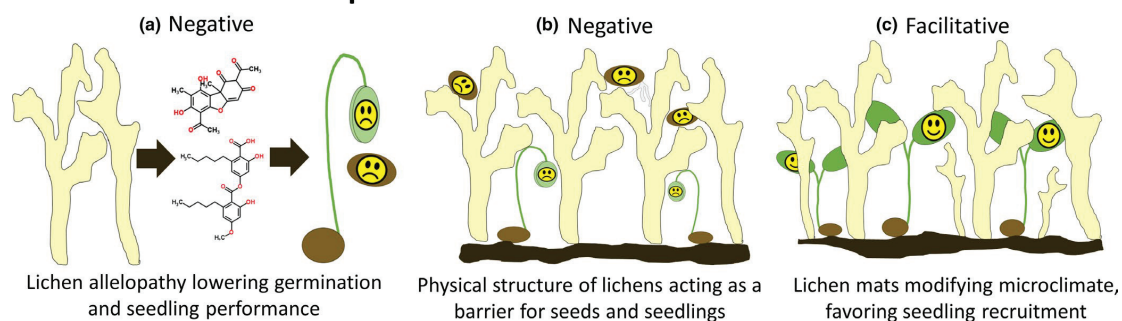


FIGURE 1 Visual representation of how lichens may affect the recruitment phase of vascular plants. In scenario (a) lichen allelopathy inhibits seed germination and early seedling development and reduces the number of mycorrhizae associations of the seedling. In scenario (b) the physical structure of lichen mats prevents seeds and root radicles of germinating seeds from reaching the soil, and emerging seedlings may fail to penetrate the lichen mat. In scenario (c) lichens may facilitate plant recruitment by modifying the microclimate, in particular shelter against wind, extreme temperatures, and drought, which are harmful for emerging seedlings



Gomes, & Honda, 2009; Pyatt, 1967; Sedia & Ehrenfeld, 2003; Tigre et al., 2012). Importantly, most findings of allelopathy are results from in vitro experiments, often with pure lichen compounds at high concentrations, and clear evidence for lichen allelopathy under natural conditions is scarce (Favero-Longo & Piervittori, 2010). Under field conditions, allelopathy has been suggested to indirectly affect seedling growth by inhibition of soil microorganisms and mycorrhizal fungi (Brown & Mikola, 1974; Fisher, 1979; Sedia & Ehrenfeld, 2003), although the generality of these findings has been challenged (Kytöviita & Stark, 2009; Stark & Hyvärinen, 2003; Stark, Kytöviita, & Neumann, 2007). Furthermore, the allelopathic effects depend on the specific secondary compounds and plant species in focus (Brown & Mikola, 1974; Favero-Longo & Piervittori, 2010; Hobbs, 1985; Peres et al., 2009).

Whether the lichens' negative effects via allelopathy and physical structure or facilitation via amelioration of the microclimate is more important for plant recruitment is an open question. Therefore, we here combine field and laboratory experiments to investigate how terricolous lichens affect the early recruitment phase of plants in dwarf-shrub and lichen-dominated heath vegetation typical for arctic-alpine areas. We test the response of plant species with different growth forms, seed sizes and seedling morphologies, which we expect to interact uniquely with the lichen species. In a field experiment, we aimed to answer the following questions: (a) is soil microclimate (i.e., temperature and moisture) affected by lichen species and lichen mat thickness? Is (b) seedling recruitment and (c) seedling growth affected by lichen species and lichen mat thickness? Because allelopathy is hard to distinguish from other factors under natural conditions, we conducted a complementary laboratory experiment where we asked: (d) is seed germination affected by lichen allelopathy? To reveal the importance of lichen allelopathy under natural conditions we asked: (e) are the same lichen-plant interactions detected for seed germination in the laboratory and seedling recruitment in the field?

2 | METHODS

2.1 | Study site

The field study was conducted at an exposed dwarf-shrub and lichen heath, surrounded by subalpine birch forest in the mountains of Dovrefjell, Central Norway, close to Kongsvoll Biological Station (c. 930 m a.s.l., 62°18'5.75517" N, 9°36'24.00385" E). The bedrock at the site consists of lightly eroded actinolite-hornblende amphibolite (Geological Survey of Norway, <https://www.ngu.no/en/>, accessed 11 July 2017). The vegetation is dominated by *Empetrum nigrum* ssp. *hermaphroditum*, *Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea*, *Betula nana* and *Salix glauca*, and the lichens *Alectoria ochroleuca* and *Flavocetraria nivalis*. Such dwarf-shrub and lichen heaths predominantly occur above the forest line, but can also be found on locally exposed areas within subalpine forests like our study site (Fremstad, 1997) (see Appendix S1 for a photo from the study site). The studied dwarf-shrub and lichen heath is

thus representative for such vegetation in general and the findings especially relevant for arctic-alpine areas where these heaths are widespread.

Dovrefjell has a slightly continental climate with short warm summers and long cold winters. At the weather station Fokstugu (930 m a.s.l.) ca. 26 km south of the study site, the mean annual precipitation was 435 mm (Førland, 1993) and the mean annual temperature -0.1°C (Aune, 1993) for the period 1961–1990. For the same period, the warmest month was July with an average monthly temperature of 9.8°C , and the coldest was January, at -8.8°C on average (Aune, 1993).

2.2 | Lichen and seed material

In a parallel field and laboratory experiment, we studied the interactions between six locally abundant terricolous lichen species: *Alectoria ochroleuca*, *Cetraria islandica*, *Cladonia arbuscula*, *Cladonia stellaris*, *Flavocetraria nivalis* and *Stereocaulon paschale* and 11 vascular plant species: *Anthoxanthum nipponicum*, *Avenella flexuosa*, *Betula nana*, *Bistorta vivipara*, *Dryas octopetala*, *Luzula spicata*, *Pinus sylvestris*, *Salix glauca*, *Silene acaulis*, *Solidago virgaurea* and *Vaccinium myrtillus* common in subalpine and low-alpine vegetation. These 11 plant species were chosen because they represent a variety of growth forms (tree, shrub, dwarf-shrub, graminoid and forb), have been observed as adult plants growing within terricolous lichens (negative effects of lichen secondary metabolites on plant recruitment are more likely to have developed in co-occurring lichen and plant species; Hobbs, 1985), have seeds (bulbils for *Bistorta vivipara*, hereafter referred to as seeds) of different sizes which might affect their recruitment potential, and have seedlings that are easy to distinguish from each other. The lichen species were chosen because of their dominance in arctic-alpine vegetation, and because they produce different secondary metabolites, have different growth forms (fruticose vs. cetrarioid) and physical structure of their mats (e.g., height and density), resulting in a variety of microenvironments for the recruiting plant species (Table 1).

The lichens and seeds were collected close to the study site in September and October 2013. For one species, *Pinus sylvestris*, seeds were supplied by The Norwegian Forest Seed Center originating from Oppdal at c. 600–650 m a.s.l., c. 35 km north of the study site. We planned to use all plant and lichen species in both the laboratory and field experiment, but due to seed limitation *Dryas octopetala* was used only in the laboratory and *Bistorta vivipara* only in the field experiment. See The Norwegian Biodiversity Information Centre (NBIC) (<https://www.biodiversity.no/>, accessed 23 October 2018) for unified nomenclature of lichen and plant species.

2.3 | Field experiment

In the field, seventeen plastic trays (56 × 26 × 8 cm) were divided into four plots each, for a total of 68 plots. Each plot was filled with one liter of commercial garden soil. The trays had holes to drain water, and the vegetation underneath was removed so that the plots were

TABLE 1 Characteristics of lichen and vascular plant species used in the study, including growth form (fruticose here referring to lichens with upright, shrub-like thalli with cylindrical branches, and cetrarioid to lichens with upright, modified lobes and leaf-like thalli with dorsiventral morphology), mat thickness in the field experiment (mean \pm SE, $n = 8$ except for 7 in *C. islandica*) and secondary metabolites of the lichen species, and growth form and seed mass (mg) of the plant species. The lichen species are listed by increasing mat thickness

Lichen species	Growth form	Mat thickness (cm \pm SE)	Secondary metabolites ^a
<i>Flavocetraria nivalis</i>	Cetrarioid	1.9 \pm 0.2	Usnic acid and protolichesterinic acid
<i>Alectoria ochroleuca</i>	Fruticose	1.9 \pm 0.4	Usnic acid and diffractaic acid
<i>Stereocaulon paschale</i>	Fruticose	2.1 \pm 0.2	Atranorin and lobaric acid
<i>Cetraria islandica</i>	Cetrarioid	2.6 \pm 0.3	Fumarprotocetraric acid and protolichesterinic acid
<i>Cladonia arbuscula</i>	Fruticose	3.8 \pm 0.3	Usnic acid and fumarprotocetraric acid
<i>Cladonia stellaris</i>	Fruticose	6.8 \pm 0.4	Usnic acid and perlatolic acid
Vascular plant species	Growth form	Seed mass (mg) ^b	
<i>Anthoxanthum nipponicum</i>	Graminoid	0.4878	
<i>Avenella flexuosa</i>	Graminoid	0.5	
<i>Betula nana</i>	Shrub	0.3184	
<i>Bistorta vivipara</i>	Forb	2.73	
<i>Dryas octopetala</i>	Dwarf-shrub	0.706	
<i>Luzula spicata</i>	Graminoid	0.259	
<i>Pinus sylvestris</i>	Tree	6.0	
<i>Salix glauca</i>	Shrub	0.163	
<i>Silene acaulis</i>	Forb	0.3	
<i>Solidago virgaurea</i>	Forb	0.55	
<i>Vaccinium myrtillus</i>	Dwarf-shrub	0.3	

^aInfo on secondary metabolites from Krog, Østhagen, and Tønsberg (1994) and Holien and Tønsberg (2008).

^bSeed mass data accessed from Royal Botanic Gardens Kew (2018). Seed Information Database (SID), Version 7.1. Retrieved from: <http://data.kew.org/sid/> (October 2018).

at level with the surrounding vegetation. Each of the six lichen species had eight replicate plots randomly assigned to the trays. Two types of controls were used with ten replicates each: (a) bare soil where seeds were sown and (b) bare soil without seeds to control for external seed influx (see Appendix S1 for a field design figure). At least one plot per tray was assigned to a control treatment, and each lichen species had one replicate per tray only.

For *Cladonia stellaris* and *Cladonia arbuscula*, coherent mats were collected and transplanted into the plots. As *Alectoria ochroleuca*, *Cetraria islandica*, *Flavocetraria nivalis*, and *Stereocaulon paschale* form less coherent mats, the plots were filled with several smaller lichen samples representing how they naturally grow. A mixture of 30 seeds from each of the 10 plant species, except for *Pinus sylvestris* with only 10 seeds and *Salix glauca* with only 15 seeds due to limited seed availability, was sown on top of each lichen species and bare soil sowing control plot (the "lichen treatments") in October 2013. This gives a total of 265 seeds per plot, and as each plot was $\sim 365 \text{ cm}^2$, the seed density was 0.73 seeds per cm^2 . This density is higher than the expected natural seed rain in such vegetation (Graae et al., 2011; Molau & Larsson, 2000) and ensured that seed availability would not constrain seedling recruitment. String was tied in a grid over the trays to prevent the lichens from being blown out. From October to May the trays were placed in a sheltered scrub community dominated by *Salix* spp., graminoids and bryophytes at the study

site to reduce wind exposure during winter and were moved c. 35 m to a neighboring exposed dwarf-shrub and lichen heath in late May, which is the most representative environment for the lichen species used in this experiment.

In late May 2014, temperature loggers (Micro-T DS1921G, Maxim Integrated Products, Sunnyvale, CA, USA) were placed 0.5 cm below the soil surface in each plot to measure the soil temperature every second hour. Soil moisture (% volumetric soil water content) was measured once in each plot during overcast conditions after rain (26 August 2014) and again during dry conditions on a sunny day after one day without rain (28 August 2014) with a hand-held 5 cm long soil moisture probe set to option "organic soil" (TRIME-PICO32, IMKOGmbH, Mannheim, Germany). In late August and early September 2014, the temperature loggers were collected and the seedlings harvested. Mean, maximum and minimum temperatures were calculated for the period 13 June 2014–31 August 2014. Seedlings were identified, counted, rinsed in water to remove soil fragments, and oven-dried at 70°C for 72 hr. All seedlings of each species from each plot were weighed together to obtain a measure of average dry seedling biomass (mg). The thickness of the lichen mats (average of three measurements from soil surface to highest lichen thallus point at different fixed locations) was measured for each plot at the end of the experiment (Table 1).

2.4 | Laboratory experiment

In the laboratory, samples of each of the six lichen species were cleaned of debris, dried, and crushed with a hand blender. Two grams of crushed lichen was added underneath filter paper in five Petri dishes for each of the ten species sown and a control. Thirty seeds, except for *Pinus sylvestris* with 10 and *Salix glauca* with 15 seeds, were placed on the filter paper and 6 ml of distilled water was added. The controls had only filter paper, water and seeds. The Petri dishes were sealed with parafilm and kept in darkness at 3°C for 12 weeks. After this cold stratification, the Petri dishes were transferred to growth chambers (E-36L, Percival Scientific, Perry, IA, USA) for six weeks with 20-hr daylight (representative for mid-June growing season photoperiod in central Norway) with $\sim 200 \mu\text{m m}^{-2} \text{s}^{-1}$ photosynthetically active radiation at 20°C and 4-hr darkness at 10°C. Every week, 2 ml of distilled water was added, and the Petri dishes were rotated within the chamber. More water (1–2 ml) was added if signs of desiccation on the filter paper occurred. Germinated seeds were counted and then removed from the Petri dishes weekly over 6 weeks.

2.5 | Statistical analyses

To test whether the soil microclimate was affected by the lichen treatments (question 1), we fitted linear mixed-effects models with Gaussian errors and with each microclimate parameter (mean soil temperature, maximum soil temperature, minimum soil temperature, soil moisture wet day and soil moisture dry day) as response variable, lichen treatment, lichen mat thickness and their interaction as fixed effects, and tray as random factor.

To test if seedling recruitment in the field experiment was affected by the lichen treatments (question 2), we fitted a generalized linear mixed-effects model with binomial errors and logit link-function, with proportion seedling recruitment as response variable, lichen treatment, lichen mat thickness, plant species and their interaction as fixed factors, and tray and plot (nested within trays) as random factors. In this analysis, plot was also included in the random structure because of several observations (i.e., plant species) per plot. Numbers of seeds sown for each species were added as weights in the models. For *Vaccinium myrtillus*, the only species with external seed influx from the control plots without sowing, the mean influx (0.7 seedling) was subtracted from the data prior to the analyses. Estimates were back-transformed (from logit scale to probability scale) to obtain recruitment rates, and these rates are presented in the figures and text as they account for the nested structure of our experimental design.

Similarly, to test if seedling biomass was affected by the lichen treatments (question 3), we fitted linear mixed-effects models with average seedling weight as response variable, lichen treatment, lichen mat thickness, plant species and their interactions as fixed factors, and tray and plot (nested within trays) as random factors. Seedling numbers were added as weights in the model because the number of recruited seedlings (i.e., the sample size) varied among

plant species and plots. Two species were excluded from the field recruitment and growth analyses: *Betula nana* because of low emergence rates in all treatments, and *Salix glauca* because most seedlings were dead when counted and harvested in autumn (see Appendix S2 for counts of live and dead seedlings).

To test if seed germination in the lab was affected by lichen treatments (question 4), we fitted a generalized linear model with binomial errors and logit link function, with the proportion of germinated seeds as response variable, and lichen treatment, plant species and their interaction as fixed factors. Estimates were back-transformed to obtain germination rates.

Finally, we used a Spearman rank correlation test to test for correlation between the field recruitment and laboratory germination estimates (question 5). Control treatments were excluded and only the seven plant species shared in both experiments were included.

To visualize the lichen–plant interactions in the field recruitment and lab germination experiment and explore possible clusters, we constructed heatmaps with hierarchical clustering (two-dimensional representations where the recruitment and germination estimates of all combinations of plant species and lichen treatments are shown with colors and ordered by similarity) with the *gplots* R package. Dendrograms were constructed with hierarchical agglomerate Ward clustering based on Jaccard dissimilarities calculated in the *vegan* R package. Numbers of clusters for the lichen treatment and plant species dendrograms were manually chosen based on their separation heights and by visual inspection of the clusters' ecological meaning.

For question 1–4, model selection was based on the Akaike information criterion (AIC, see model selection results in Appendix S3). Small-sample corrected AIC (AIC_c) was used for model selection in question 1. Anova and summary tables of models presented in the manuscript are in Appendix S4. Differences in soil microclimate among lichen treatments were tested using multiple comparisons with the Tukey method in the *multcomp* R package. For the mixed models (seed germination and seedling recruitment and biomass) we used the *emmeans* R package for pairwise comparisons. All statistical analyses were done in R 3.1.2 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). Mixed-effect models were fitted with the *lme4* R package. Primary data is available in Appendix S5 (seedling recruitment and seedling biomass in field) and Appendix S6 (seed germination in lab).

3 | RESULTS

3.1 | Soil microclimate — field experiment

Lichen treatment was a better predictor of all soil microclimate variables than was lichen mat thickness (Appendix S3). The presence of lichens reduced mean and maximum soil temperatures and increased minimum soil temperatures compared to the bare soil control (Figure 2a). Temperature buffering was strongest beneath *Cladonia stellaris* and *Cladonia arbuscula* (Figure 2a), which had the thickest mats (Table 1). This was especially evident for

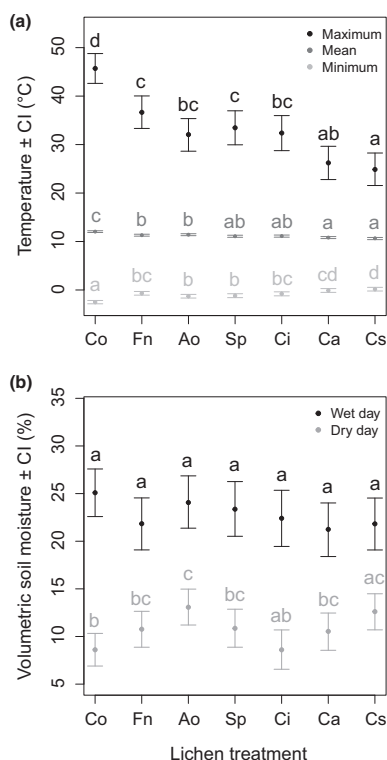


FIGURE 2 Estimated soil microclimate conditions in the field experiment with temperature (maximum, mean and minimum) (a) and moisture (wet and dry day) (b) with 95% confidence intervals for each lichen treatment. Treatments with no letters in common are significantly different ($p < 0.05$), tested using multiple comparisons with the Tukey method. The lichen treatments are ordered by increasing mat thickness and abbreviated as follows: Co; Control (bare soil), Fn; *Flavocetraria nivalis*, Ao; *Alectoria ochroleuca*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*

maximum temperature, which differed by more than 20°C between *Cladonia stellaris* (24.9°C, 95% CI = 21.6–28.3) and the bare soil control (45.7°C, 95% CI = 42.6–48.8; Figure 2a).

Soil moisture differed between treatments under dry conditions, but not under wet conditions (Figure 2b). On the dry and sunny day, the driest soils occurred in the bare soil control (8.6%, 95% CI = 6.9–10.3) and beneath *Cetraria islandica* (8.6%, 95% CI = 6.6–10.7), whereas the soils beneath *Alectoria ochroleuca* (13.1%, 95% CI = 11.2–15.0) and *Cladonia stellaris* (12.6%, 95% CI = 10.7–14.5) were moister (Figure 2b).

3.2 | Seedling recruitment — field experiment

The effects of the lichen treatments on seedling recruitment were complex and plant species-specific (Figure 3), as demonstrated by strongest statistical support for the model including

the plant–lichen treatment interaction (Appendix S3). For some plant species (*Bistorta vivipara* and *Luzula spicata*) the lichen species did not seem to affect the recruitment, whereas for the other six plant species recruitment rates were overall higher and differed between lichen species, or between some lichen species and the bare soil control (Figure 3). Most species had recruitment rates below 40%, except *Pinus sylvestris* with recruitment rates approaching 80% (Figure 3).

Based on their effect on seedling recruitment, the lichen treatments cluster into three groups: one with bare soil control only, one with *Cladonia stellaris* only, and a third with the remaining five lichen species (Figure 3b; Appendix S7). The bare soil controls stand out with overall low recruitment, and not a single seedling of *Bistorta vivipara* and *Luzula spicata* recruited here (Figure 3a). Many germinating seeds were observed on the bare soil controls during early summer (Kristin O. Nystuen, pers. obs.), suggesting high post-germination mortality. Compared to other lichen species, *Cladonia stellaris* supported low recruitment of many plant species, whereas for *Avenella flexuosa* the recruitment in *Cladonia stellaris* was comparatively high (Figure 3). The remaining five lichens supported higher recruitment overall, but still depending on the plant species in focus. Some of the species had relatively high recruitment rates within *Stereocaulon paschale*, especially *Solidago virgaurea* (Figure 3).

3.3 | Seedling growth — field experiment

The lichen treatments' effects on seedling growth were species-dependent, as indicated by strongest statistical support for the model with lichen treatment–plant species interaction in Appendix S3. Most plant species had small seedlings below 5 mg in dry weight, whereas *Pinus sylvestris* and *Solidago virgaurea* had heavier seedlings (Figure 4). Seedling weight of these two species was also detectably affected by the lichen treatments, whereas for the remaining six species, with fewer recruited seedlings (Figure 3), there were no statistically detectable differences among treatments (Figure 4). *Cladonia stellaris* clearly affected the growth of *Pinus sylvestris* negatively, and weight of the seedlings here was only half the weight of the heaviest seedlings found in *Stereocaulon paschale* and *Alectoria ochroleuca* (Figure 4).

3.4 | Seed germination — laboratory experiment

Seed germination in the Petri dishes differed among plant species, and the lichen species had species-specific effects on the plant species (strongest statistical support for the model with plant–lichen treatment interaction; Appendix S3). Six out of ten plant species were detectably affected by the lichen treatments (Figure 5a). The lichen treatments' species-specific influence on seed germination is also demonstrated in the heatmap in Figure 5b, where the lichen dendrogram did not separate until height 0.38 (Appendix S7), indicating that the treatments have few common effects on seed germination.

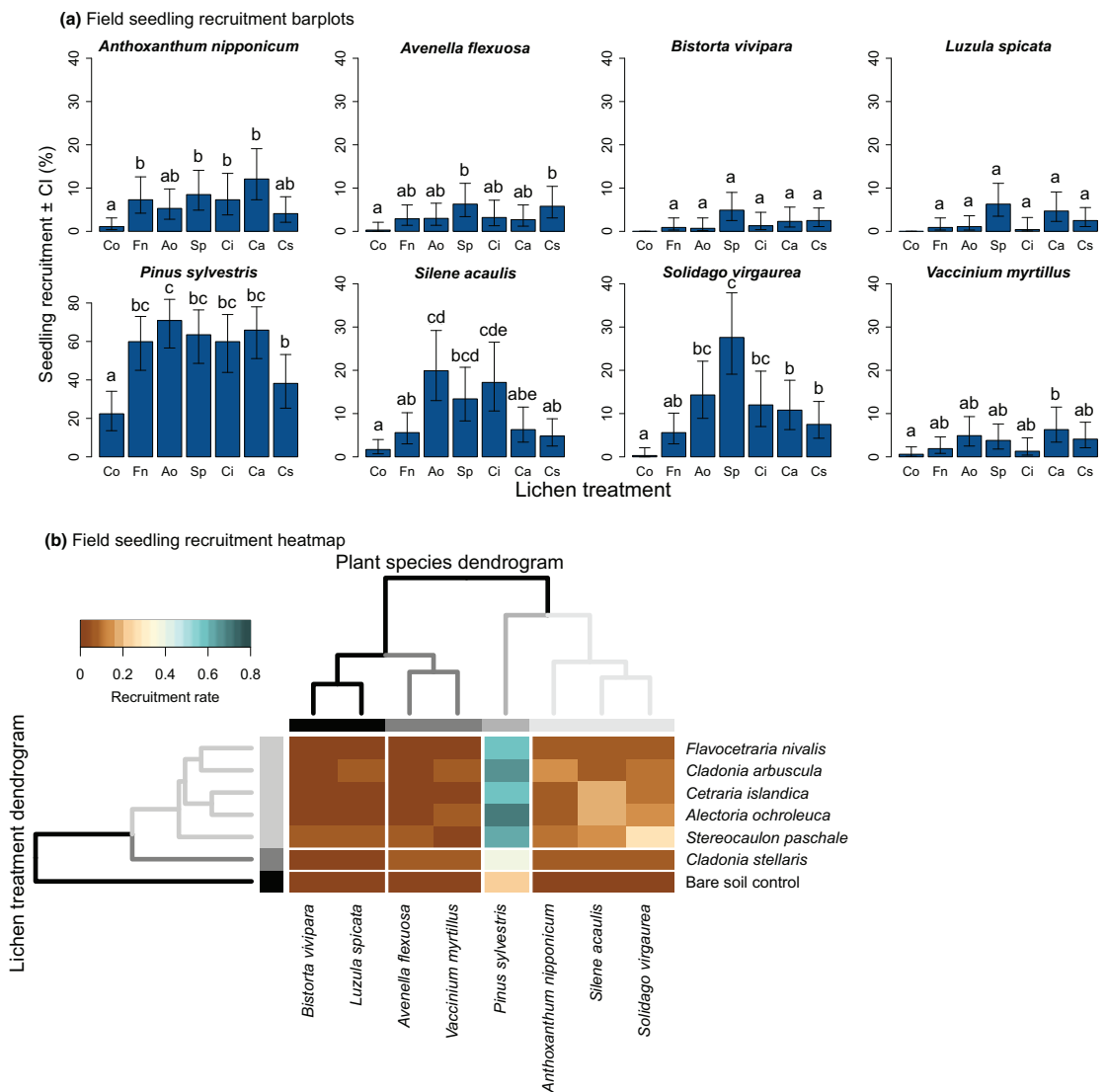


FIGURE 3 Seedling recruitment in the field experiment across lichen treatments. (a) Barplots showing mean estimated seedling recruitment and 95% confidence intervals. Notice that the recruitment scale of *Pinus sylvestris* differs from that of the other plant species. The lichen treatments are ordered by increasing mat thickness and abbreviated as follows: Co; Control (bare soil), Fn; *Flavocetraria nivalis*, Ao; *Alectoria ochroleuca*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*. Treatments with no letters in common are significantly different ($p < 0.05$), as revealed by pairwise comparisons. (b) Heatmap of mean estimated seedling recruitment rates in the lichen treatments with clustering of plants (top) and lichen treatments (left). The plant and lichen dendrograms were cut at manually chosen heights (see Appendix S7)

For two plant species (*Silene acaulis* and *Vaccinium myrtillus*) we found interesting patterns concerning lichen secondary compounds. Germination of *Silene acaulis* was clearly enhanced in *Cetraria islandica* and *Stereocaulon paschale* (Figure 5a), the only two lichens without usnic acid (Table 1), whereas *Vaccinium myrtillus* germinated best in *Flavocetraria nivalis* and *Cetraria islandica*, which are the only lichens with protolichesterinic acid (Table 1).

3.5 | Comparison between field and laboratory results

Estimated recruitment rates in the field and germination rates in the laboratory were moderately correlated (Spearman's $\rho = 0.45$, $p = 0.003$), indicating only partial correspondence between the field and laboratory results.

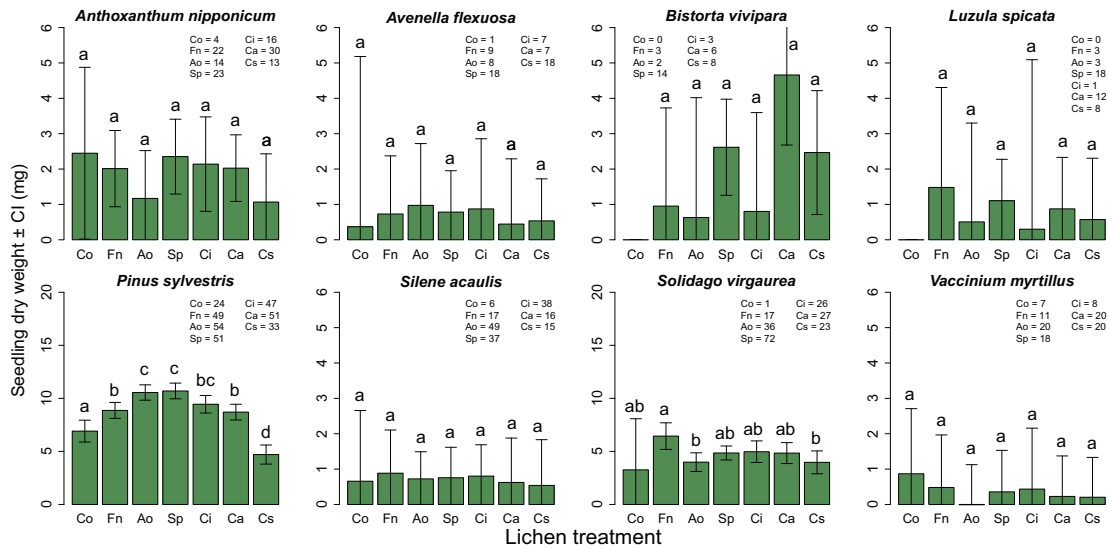


FIGURE 4 Estimated biomass (mg dry weight) of the emerged seedlings in the field experiment across lichen treatments with 95% confidence intervals. Notice that the seedling weight scale of the heavy *P. sylvestris* and *S. virgaurea* differs from those of the six other plant species. Legends show number of seedlings emerged in each lichen treatment. The lichen treatments are ordered by increasing mat thickness and abbreviated as follows: Co; Control (bare soil), Fn; *Flavocetraria nivalis*, Ao; *Alectoria ochroleuca*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*. Treatments with no letters in common are significantly different ($p < 0.05$), as revealed by pairwise comparisons

4 | DISCUSSION

This study suggests that terricolous lichens facilitate rather than prevent seedling recruitment under stressful, natural conditions and that the effects of lichens on seedling recruitment are related more to their physical structure and resulting microclimate modifications than to allelopathy. The lichen mats prevent large temperature fluctuations and conserve soil moisture, and this may have caused the increased recruitment we observed within lichen mats compared to bare soil. Importantly, the effects of lichen mats on seedling recruitment and growth were species-specific, and for *Cladonia stellaris*, a lichen with thick and dense mats, the overall facilitative effect was replaced by restrained recruitment and growth conditions for many plant species.

4.1 | Damped microclimatic variation under lichens

Microclimatic conditions strongly affect plant species distributions in alpine habitats and are known to vary across small distances (Graae et al., 2012; Opedal, Armbruster, & Graae, 2015; Scherrer & Körner, 2011). Our results suggest that some of this small-scale variation may be related to variation in lichen cover and assemblages, because the lichen species differ in their effect on microclimate. In general, temperatures beneath lichens were less extreme than on the bare soil controls. Large temperature fluctuations are favorable for germination of many species, especially those with small seeds and low competitive ability (Fenner & Thompson, 2005). However, despite having the largest

temperature fluctuations, the bare soil controls did not have higher recruitment rates of small-seeded species (such as *Luzula spicata*, *Silene acaulis* and *Vaccinium myrtillus*). Furthermore, large temperature fluctuations can also be detrimental for seedlings (Cavieres, Badano, Sierra-Almeida, & Molina-Montenegro, 2007), and the low recruitment we observed on bare soil may partly represent seedling mortality during summer. On bare soil, maximum temperatures reached 45°C, 10–20 degrees higher than within the lichen mats, and soil drying was pronounced.

Under dry conditions, *Cetraria islandica* was the only lichen below which the soil was as dry as in the bare soil controls. Lichen water absorption and retaining abilities may vary among species (Larson, 1979) and depend on morphology (Larson, 1981) and thallus size (Gauslaa & Solhaug, 1998). Our focal lichen species varied extensively in morphology, and lichen species was a better predictor of soil microclimate than was lichen mat thickness in itself. For instance, the soil beneath *Cetraria islandica* became much drier than beneath *Stereocaulon paschale*, which has thinner mats. This could be due to poor water retention of *Cetraria islandica* combined with its open mat structure and dark color.

4.2 | Lichens facilitate seedling recruitment

We found that the presence of lichens increased seedling recruitment rates compared to recruitment on bare soil. High seedling numbers within lichen mats have also been reported for subarctic forests (Brown & Mikola, 1974; den Herder, Kytöviita, & Niemela,

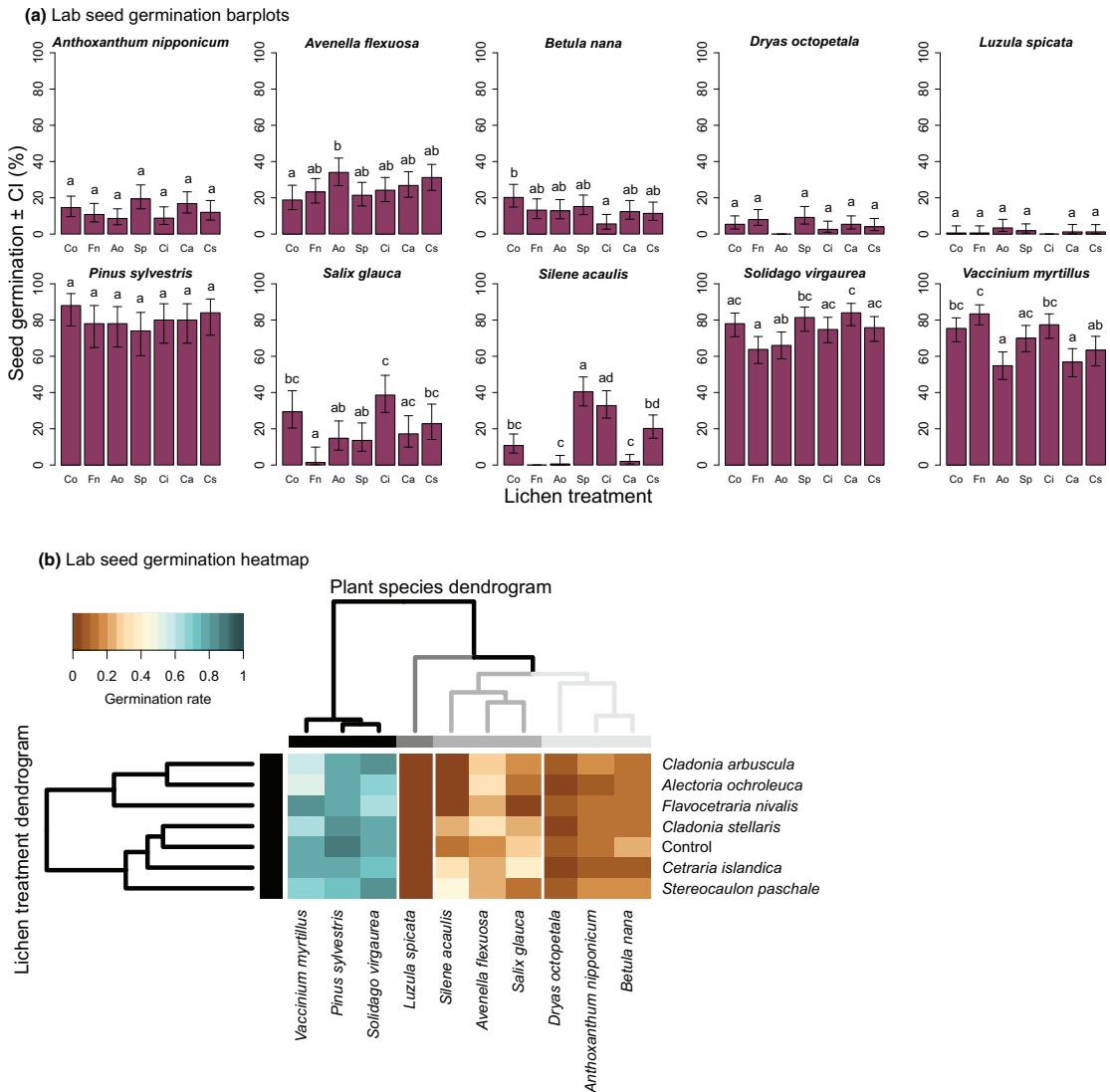


FIGURE 5 Seed germination in the laboratory experiment across lichen treatments. (a) Barplots showing mean estimated seed germination and 95% confidence intervals. The lichen treatments are abbreviated as follows: Co; Control (water only), Fn; *Flavocetraria nivalis*, Ao; *Alectoria ochroleuca*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*. Treatments with no letters in common are significantly different ($p < 0.05$), as revealed by pairwise comparisons. (b) Heatmap of mean estimated mean germination rates in the lichen treatments with clustering of plants (top) and lichen treatments (left). The lichen treatment dendrogram did not separate until height 0.38 and supported no ecologically meaningful clustering of the lichens (see Appendix S7)

2003; Steijlen, Nilsson, & Zackrisson, 1995; Zackrisson, Nilsson, Steijlen, & Hornberg, 1995) and for the treeline ecotone (Dufour-Tremblay, De Vriendt, Lévesque, & Boudreau, 2012). The recruitment rates within lichens observed in our study (below 40% for all species except *Pinus sylvestris*) are within the expectations for such systems (Graae et al., 2011; Steijlen et al., 1995) and therefore contrast with the negative effects of lichen physical structure and allelopathy on seedling recruitment as reported by Hawkes and

Menges (2003), Hobbs (1985), and Sedia and Ehrenfeld (2003) at lower elevations, and possibly more benign environments. Hawkes and Menges (2003) found, however, that the negative effect of lichens was weaker under more severe environmental stress. Indeed, on exposed heaths dominated by terricolous lichens, the vegetation is sparse and the sheltering effect of lichens may be an advantage for seedling recruitment in accordance with the Stress Gradient Hypothesis (Bertness & Callaway, 1994).



The increased importance of facilitation in stressful habitats could explain the lower recruitment observed on bare soils, as bare soils otherwise tend to promote seedling recruitment, also in arctic-alpine vegetation (Lembrechts et al., 2016; Milbau, Shevtsova, Osler, Mooshammer, & Graae, 2013). However, recruitment is often better in small gaps, or for big gaps, close to the edge and not in the center, especially in harsh environments (Houle & Filion, 2003; Lembrechts, Milbau, & Nijs, 2015). The bare soil plots in our study were quite big and comparable to the severe disturbances performed by Evju et al. (2012) on exposed heaths where few seedlings recruited. Furthermore, the ability of lichens to trap seeds (Sedia & Ehrenfeld, 2003) is important in wind-exposed sites like lichen heaths. This could explain the low recruitment of *Salix glauca* and *Solidago virgaurea* on bare soils in our study, as both species have seeds with hairy appendages that could easily be blown away.

Only lichen species with dense and thick mats (e.g., *Cladonia stellaris*) seem to affect plant recruitment negatively. This may be caused by a combination of seeds not being able to reach the soil and seedlings not being able to emerge through the mat. Plant species with long and thin cotyledons (e.g., the graminoid *Avenella flexuosa*) may establish more successfully in thick and dense mats [cf. the observations of Sydes and Grime (1981) of seedlings emerging in leaf litter].

4.3 | Lichens affect seedling growth

Dense and thick lichen mats (e.g., *Cladonia stellaris*) seem to affect seedling growth of many plant species negatively. Seedling growth of the treeline-forming *Pinus sylvestris* (Körner, 2012) was clearly reduced in *Cladonia stellaris* compared to lichen species forming thinner mats, and this reduced growth, as well as the low recruitment rates, could slow down potential upward migration of *Pinus sylvestris* into low-alpine *Cladonia stellaris*-dominated heaths. Brown and Mikola (1974) also reported reduced growth of *Pinus sylvestris* seedlings within *Cladonia stellaris* and suggested that allelopathy restricted ectomycorrhiza formation. In a later study, Kytöviita and Stark (2009) found no negative effect of usnic acid (one of the secondary metabolites in *Cladonia stellaris*) on *Pinus sylvestris* growth and suggested other compounds or lichen structure as explanations for the reduced growth. Zamfir (2000) found that light availability decreased dramatically as they moved down the thick (c. 6 cm) lichen mats of *Cladonia* spp., with only about 7% of the available light reaching the soil below. We therefore suggest that for *Cladonia stellaris*, low light availability rather than allelopathy during the initial phase of stem and root elongation contributed to the growth reduction of *Pinus sylvestris* and other species in our field experiment.

4.4 | Limited lichen allelopathic effects on seed germination

Our laboratory experiment assessing allelopathic effects of lichens suggests no consistent negative effect on seed germination. Some species were more sensitive to the lichen treatments (such as *Silene acaulis*, *Salix glauca* and *Vaccinium myrtillus*), demonstrating

the importance of species-specific effects as shown by Escudero, Martínez, de la Cruz, Otálora, and Maestre (2007) and Favero-Longo and Piervittori (2010). In our study only germination of two plant species was seemingly affected by lichen secondary compounds acting alone: *Silene acaulis* with higher germination in lichens devoid of usnic acid (*Cetraria islandica* and *Stereocaulon paschale*), and *Vaccinium myrtillus* with highest germination in protolichetzerinic-producing lichens (*Cetraria islandica* and *Flavocetraria nivalis*). The allelopathic effect of certain metabolites may vary among plant species (Peres et al., 2009), and plant responses to different lichen species may be complicated by mutual adaptation of plants and lichens (Hobbs, 1985). In our study, however, the lichen secondary metabolites were not distinguished from one another or from other compounds, and we cannot ascertain which compounds affected germination. *Stereocaulon paschale*, for instance, has N_2 -fixing cyanobacteria (Kytöviita & Crittenden, 2007), potentially resulting in more available nitrogen (Nash, 2008), which in turn may increase germination (Baskin & Baskin, 2014) and plant growth (Körner, 2003). Although not apparent for all plant species (but for *Silene acaulis* and *Solidago virgaurea*), this could have contributed to high germination in the lab as well as recruitment and growth in the field in association with *Stereocaulon paschale* compared to most of the other lichen species.

The germination responses to lichens observed in the lab were only partly confirmed in the field, suggesting a minor effect of lichen allelopathy on seed regeneration under natural conditions. We did not measure secondary metabolites under field conditions, but concerning *Cladonia stellaris* and usnic acid, Stark et al. (2007) found no traces in rainwater percolated through the mat or in the soils beneath. Our findings therefore support recent studies suggesting that allelopathic effects of lichens on vascular plants under natural conditions are weaker than traditionally thought (Favero-Longo & Piervittori, 2010; Stark et al., 2007).

5 | CONCLUSIONS AND IMPLICATIONS FOR VEGETATION DYNAMICS

Our study shows that lichens facilitate recruitment of vascular plants in dwarf-shrub and lichen heaths, but also that lichen–plant interactions are likely to be species-specific. Overall, the observed lichen-driven modification of microclimate indicates more benign conditions for seedling recruitment. Together, these findings suggest that the ecological importance of lichen allelopathy under natural conditions might be overestimated based on the findings in laboratory experiments, at least in stressful habitats. We might therefore expect most lichens to facilitate rather than hamper vegetation changes in dry tundra heaths. While lichens may facilitate recruitment of seedlings of some species in harsh environments, the effect of lichens may be different for later life stages. High seedling mortality during the first years is common on heaths as well as other tundra habitats (Graae et al., 2011; Milbau et al., 2013), and for heaths associated with low winter temperatures (Milbau et al., 2013). The lichen mats may protect against very low winter temperatures, though, as observed

during summer for the species with thick mats. For herbaceous species with broad leaves, re-emerging through the densest lichen mats every spring could get harder as they grow bigger. When seedlings eventually grow past the protective lichen canopy, their survival may depend on adaptations to conserve water and withstand wind erosion and low temperatures, especially on the most exposed heaths.

Nevertheless, vascular plants are expanding at the cost of terrestrial lichens, e.g., in low-arctic Canada (Fraser et al., 2014) due to increase of tall and dwarf shrubs, and on Scandinavian low-alpine summits due to increase of the shrub *Betula nana* (Vanneste et al., 2017). Accumulation of leaf litter from deciduous shrubs, or other plant litter, can result in death of fruticose lichens (Cornelissen et al., 2001). This suggests that certain vascular plants, and especially those adapted to drought and/or with prostrate growth forms, such as *Betula nana* (de Groot, Thomas, & Wein, 1997), are able to expand and outcompete shade-intolerant lichens in heaths despite the stressful environment.

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CONFLICT OF INTEREST

The authors have no conflict of interest to report.

AUTHOR CONTRIBUTION

KS, BJG, GRS, HH and KON designed the study; KS, KON and BJG did fieldwork; KS performed the laboratory experiment; KON, ØHO and KS analyzed the data; KON and KS wrote the paper with input from all authors.

DATA AVAILABILITY

The two datasets analyzed in the current study are available as Appendices S5 and S6.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Schematic figure and photo of the field design.

Appendix S2 Figure with number of live and dead seedlings in the lichen treatments after one year.

Appendix S3 Table with model selection results for the four first research questions in the study.

Appendix S4 ANOVA and summary statistic tables of the models presented in the paper.

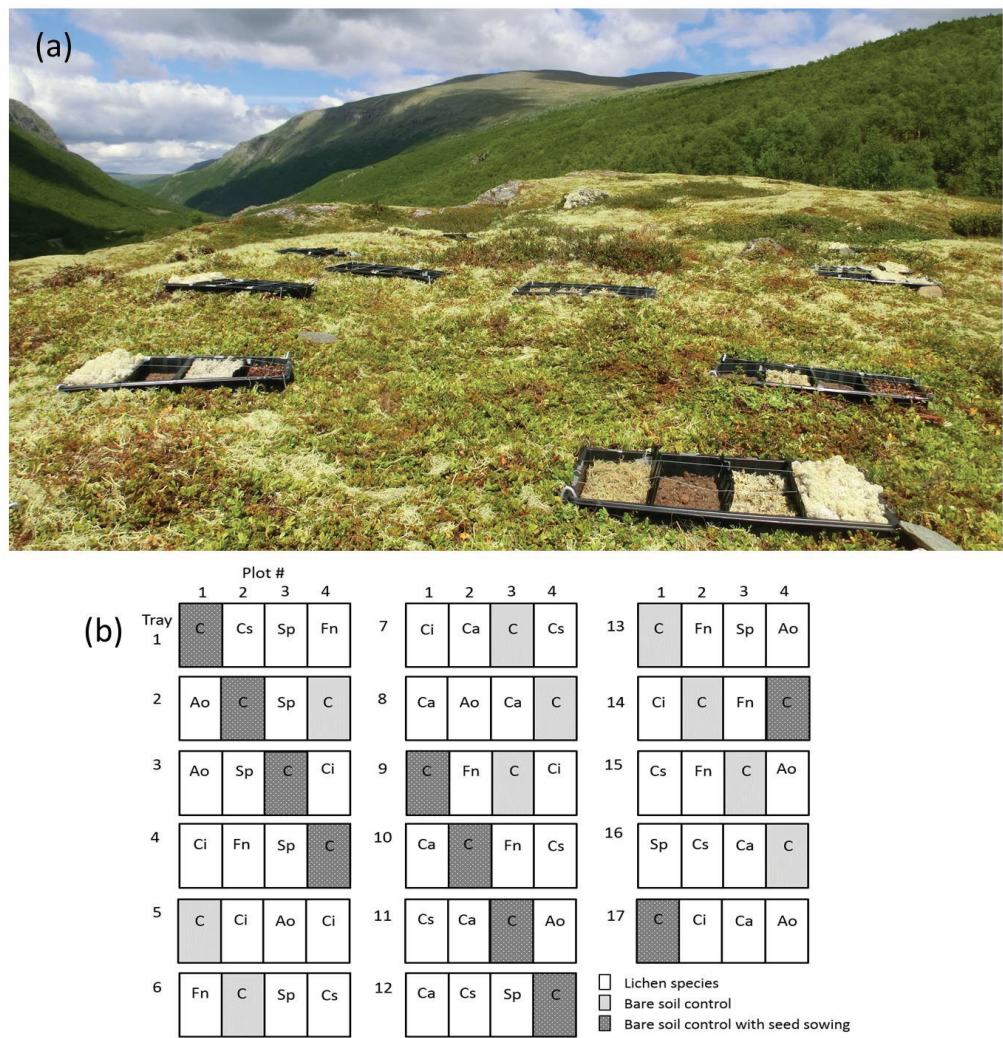
Appendix S5 Seedling recruitment and biomass data for the field experiment.

Appendix S6 Seed germination data for the laboratory experiment.

Appendix S7 Dendrograms for lichen treatments and plant species used in Figures 3 and 5 with heights.

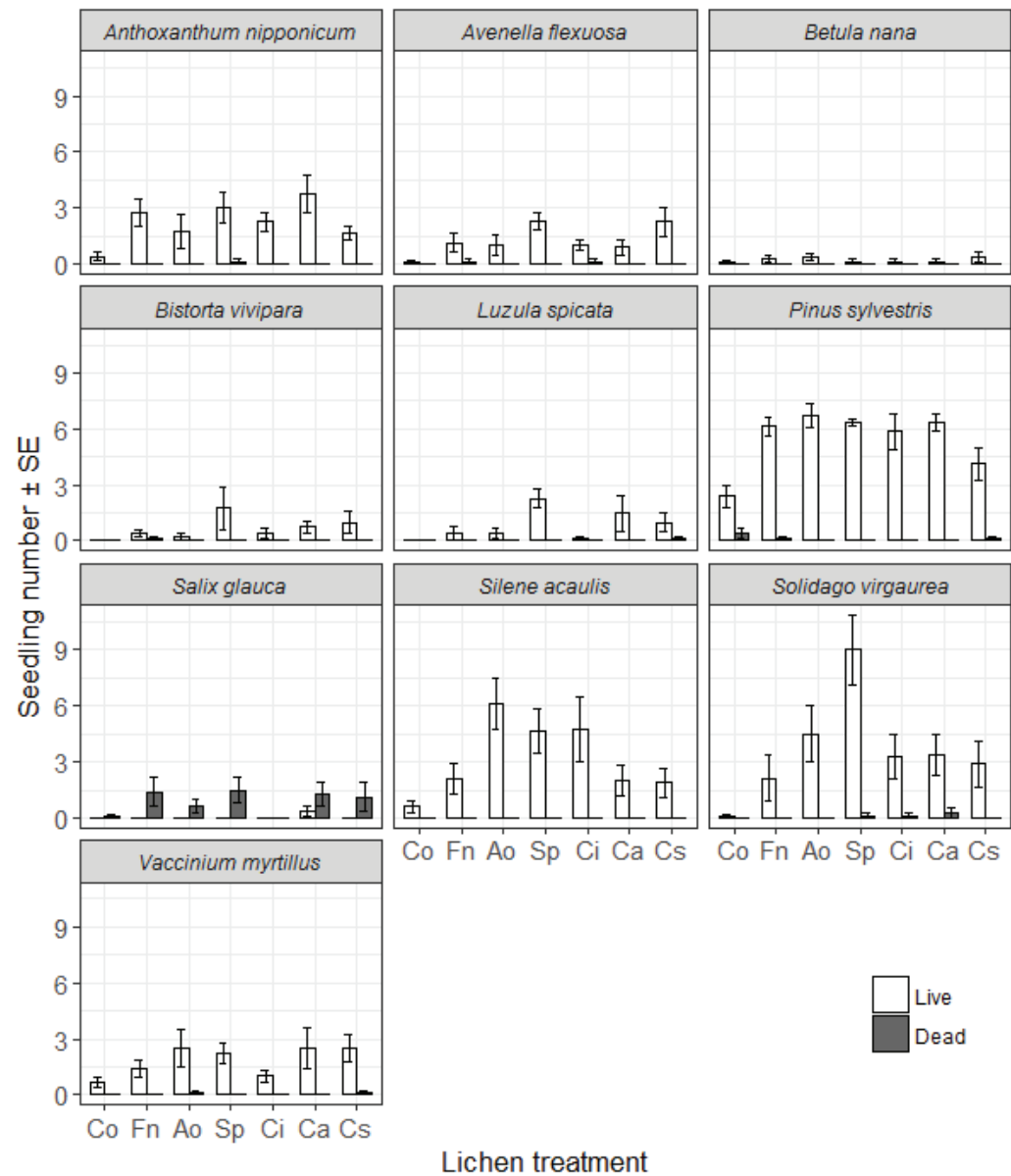
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Supporting information to the paper: Nystuen, K.O., Sundsdal, K. et al. Lichens facilitate seedling recruitment in alpine heath. *Journal of Vegetation Science*.



Appendix S1: Photo from the study site (a) and a schematic representation of the field design (b). The photo (a) shows the dwarf-shrub and lichen heath at c. 930 m a.s.l. surrounded by subalpine birch forests with some of the trays. The field design in (b) show the 17 trays divided into four plots each with different treatments. White plots are the lichen treatments replicated eight times and abbreviated Ao; *Alectoria ochroleuca*, Fn; *Flavocetraria nivalis*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*. Light gray plots are bare soil controls without seeds to control for external seed influx, and the dark gray plots bare soil controls with seed sowing. Both types of control had 10 replicates.

Supporting information to the paper: Nystuen, K.O., Sundsdal, K. et al. Lichens facilitate seedling recruitment in alpine heath. *Journal of Vegetation Science*.



Appendix S2: Mean number of live (white) and dead (grey) seedlings \pm SE in the different lichen treatments during autumn census one year after sowing (n=8). We sowed 30 seeds of each plant species, except *P. sylvestris* with 10 and *S. glauca* with 15 seeds. The lichen treatments are abbreviated as follows: Co; Control (bare soil), Ao; *Alectoria ochroleuca*, Fn; *Flavocetraria nivalis*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*.

Supporting information to the paper: Nystuen, K.O., Sundsdal, K. et al. Lichens facilitate seedling recruitment in alpine heath. *Journal of Vegetation Science*.

Appendix S3: Model selection results for models representing the first four research questions. Fixed effects, number of parameters (k), log-likelihood value (logLik), AIC value (AIC_c for soil microclimate models in question 1) and Δ AIC value (a measure of each model, relative to the selected model) are given for all models. The models are ranked by decreasing statistical support, and summary statistics from the selected models are presented in Appendix S5. The model specifications follow R syntax, with “+” referring to only main effects, and “ \times ” to main effects and their interactions. For the fixed effects, “lichen” refers to lichen treatment, “plant” to plant species, and “mat thickness” or “thickness” only to thickness of the lichen mats.

Question	Response variable	Fixed effects	k	logLik	AIC	Δ AIC
Field experiment						
1. Soil microclimate	<i>Mean temperature</i>	lichen	9	-9.0	39.8	0.0
		lichen + mat thickness	15	-9.0	42.8	3.0
		lichen \times mat thickness	10	-1.7	45.4	5.6
		mat thickness	4	-24.0	56.8	16.9
		constant	3	-44.1	94.7	54.9
	<i>Maximum temperature</i>	lichen	9	-164.7	351.4	0.0
		lichen + mat thickness	10	-164.5	353.9	2.5
		lichen \times mat thickness	15	-159.7	361.3	10.0
		mat thickness	4	-181.9	372.6	21.3
		constant	3	-199.7	405.8	54.5
	<i>Minimum temperature</i>	lichen	9	-43.8	109.4	0.0
		lichen + mat thickness	10	-43.8	112.4	3.0
		lichen \times mat thickness	15	-41.3	124.6	15.2
		mat thickness	4	-62.7	134.3	24.8
		constant	3	-82.7	171.8	62.4
	<i>Soil moisture wet conditions</i>	lichen	9	-133.7	289.3	0.0
		mat thickness	4	-141.7	292.2	2.9
		constant	3	-133.7	292.3	3.0
		lichen + mat thickness	10	-144.2	294.8	5.5
		lichen \times mat thickness	15	-132.5	306.9	17.6
	<i>Soil moisture dry conditons</i>	lichen	9	-141.1	308.3	0.0
		mat thickness	4	-156.9	319.6	11.6
		lichen + mat thickness	10	-156.0	320.0	11.7
		constant	3	-153.5	327.1	18.8
		lichen \times mat thickness	15	-150.6	331.3	23.0
2. Seedling recruitment		lichen \times plant	58	-720.5	1557.0	0.0
		lichen \times plant + mat thickness	59	-720.5	1559.0	2.0
		lichen \times plant + plant \times mat thickness	66	-714.7	1561.4	4.4
		lichen \times mat thickness + plant \times thickness	64	-718.3	1564.6	7.6
		lichen \times mat + plant \times mat + lichen \times plant	71	-712.5	1567.1	10.1
		lichen \times plant \times mat thickness	106	-685.4	1582.8	25.8
		lichen + plant \times mat thickness	24	-777.0	1602.0	45.0
		lichen \times mat + plant \times mat	29	-774.7	1607.3	50.3

	lichen + plant	16	-791.6	1615.1	58.1
	lichen + plant + mat thickness	17	-791.6	1617.1	60.1
	lichen × mat thickness + plant	22	-789.2	1622.4	65.4
	plant × mat thickness	18	-804.7	1645.3	88.3
	plant + mat thickness	11	-817.3	1656.7	99.7
	plant	10	-820.2	1660.4	103.4
	lichen	9	-1397.7	2813.3	1256.3
	lichen + mat thickness	10	-1397.7	2815.3	1258.3
	lichen × mat thickness	15	-1395.3	2820.7	1263.7
	mat thickness	4	-1423.8	2855.7	1298.7
	constant	3	-1426.7	2859.3	1302.3
3. Seedling growth	lichen × plant	57	-484.0	1082.0	0
	lichen × plant + mat thickness	58	-483.8	1083.6	1.6
	lichen × plant + lichen × mat thickness	63	-479.6	1085.3	3.3
	lichen × plant + plant × mat thickness	65	-480.5	1091.0	9.0
	lichen × mat + plant × mat + lichen × plant	70	-475.9	1091.8	9.8
	lichen + plant + plant × mat thickness	25	-533.6	1117.1	35.1
	lichen × thickness + plant × thickness	30	-530.1	1120.1	38.2
	lichen × plant × mat thickness	103	-459.0	1124.1	42.1
	lichen + plant	17	-546.0	1126.0	44.0
	lichen + plant + mat thickness	18	-546.0	1128.0	46.0
	lichen + plant + lichen × mat thickness	23	-542.6	1131.1	49.1
	plant × mat thickness	19	-550.5	1138.8	56.8
	plant + mat thickness	12	-558.8	1141.5	59.6
	plant	11	-563.6	1149.2	67.3
	mat thickness	5	-807.9	1625.8	543.8
	constant	4	-811.8	1631.6	549.6
	lichen	10	-806.4	1632.6	550.8
	lichen + mat thickness	11	-806.4	1634.8	552.8
	lichen × mat thickness	16	-805.8	1643.7	561.7
Laboratory experiment					
4. Seed germination	lichen × plant	70	-780.9	1701.7	0
	lichen + plant	16	-960.9	1953.7	252.0
	plant	10	-2714.5	1997.3	295.6
	lichen	7	-988.7	5443.0	3741.3
	constant	1	-2732.0	5466.0	3764.3

Supporting information to the paper: Nystuen, K.O., Sundsdal, K. et al. Lichens facilitate seedling recruitment in alpine heath. *Journal of Vegetation Science*.

Appendix S4: Anova and summary statistic tables of the models presented in the manuscript.

Table 1: Summary statistics of the models explaining soil temperatures (mean, maximum and minimum), linear mixed effects models with lichen treatment as fixed effect and tray as random factor. The reference level (intercept) is bare soil control.

Fixed effect	Mean			Maximum			Minimum		
	Estimate	SE	t-value	Estimate	SE	t-value	Estimate	SE	t-value
Intercept	12.042	0.090	133.98	45.705	1.631	28.01	-2.512	0.183	-13.73
Fn	-0.738	0.132	-5.60	-9.055	2.011	-4.50	1.823	0.243	7.51
Ao	-0.635	0.131	-4.84	-13.644	1.969	-6.93	1.222	0.239	5.12
Sp	-0.960	0.137	-7.02	-12.240	2.075	-5.90	1.331	0.251	5.31
Ci	-0.928	0.136	-6.81	-13.323	2.047	-6.51	1.719	0.248	6.93
Ca	-1.230	0.133	-9.28	-19.485	2.058	-9.47	2.414	0.247	9.76
Cs	-1.377	0.132	-10.40	-20.840	2.052	-10.15	2.679	0.247	10.86

Table 2: Anova tables of the models explaining soil temperatures (mean, maximum and minimum), linear mixed effects models with lichen treatment as fixed effect and tray as random factor.

	Df	Mean			Maximum			Minimum		
		Sum Sq	Mean Sq	F-value	Sum Sq	Mean Sq	F-value	Sum Sq	Mean Sq	F-value
lichen	6	5281.70	754.53	8932.4	2148.8	358.12	23.34	35.716	5.9527	25.95

Table 3: Summary statistics of the models explaining soil moisture (wet and dry day), linear mixed effects models with lichen treatment as fixed effect and tray as random factor. The reference level (intercept) is bare soil control.

Fixed effect	Wet day			Dry day		
	Estimate	SE	t-value	Estimate	SE	t-value
Intercept	25.090	1.328	18.895	8.609	0.858	10.04
Fn	-3.251	1.661	-1.957	2.152	1.118	1.93
Ao	-1.028	1.627	-0.632	4.476	1.098	4.08
Sp	-1.728	1.714	-1.008	2.258	1.155	1.96
Ci	-2.684	1.691	-1.587	0.011	1.141	0.01
Ca	-3.844	1.698	-2.264	1.907	1.141	1.67
Cs	-3.267	1.694	-1.929	3.987	1.138	3.51

Table 4: Anova tables of the models explaining soil moisture (wet and dry day), linear mixed effects models with lichen treatment as fixed effect and tray as random factor.

	Df	Rainy day			Sunny day		
		Sum Sq	Mean Sq	F-value	Sum Sq	Mean Sq	F-value
lichen	6	86.09	14.348	1.3657	125.83	20.971	4.3435

Table 5: Summary statistics of the model explaining seedling recruitment in the field experiment, a generalized linear mixed-effects model with binomial errors and logit link-function, where lichen treatment and plant species and their interaction were fixed factors and tray and plot (nested within trays) were random factors. The reference level (intercept) is lichen treatment bare soil control and plant *Ant nip*.

Fixed effects	Estimate	SE	Z-value
Intercept	-4.477	0.538	-8.32
Fn	1.942	0.606	3.21
Ao	1.598	0.628	2.55
Sp	2.098	0.602	3.49
Ci	1.933	0.624	3.10
Ca	2.491	0.598	4.17
Cs	1.328	0.633	2.10
Ave fle	-1.400	1.121	-1.25
Bis viv	-16.635	40.033	-0.42
Luz spi	-16.666	34.934	-0.48
Pin syl	3.234	0.560	5.77
Sil aca	0.415	0.652	0.64
Sol vir	-1.400	1.121	-1.25
Vac myr	-0.702	0.871	-0.81
Fn × Ave fle	0.422	1.195	0.35
Ao × Ave fle	0.803	1.211	0.66
Sp × Ave fle	1.077	1.169	0.92
Ci × Ave fle	0.519	1.214	0.43
Ca × Ave fle	-0.195	1.203	-0.16
Cs × Ave fle	1.758	1.185	1.48
Fn × Bis viv	14.521	40.038	0.36
Ao × Bis viv	14.614	40.038	0.37
Sp × Bis viv	16.038	40.034	0.40
Ci × Bis viv	14.884	40.038	0.37
Ca × Bis viv	14.880	40.035	0.37
Cs × Bis viv	16.117	40.036	0.40
Fn × Luz spi	14.551	34.938	0.42
Ao × Luz spi	15.056	34.937	0.43
Sp × Luz spi	16.343	34.935	0.47
Ci × Luz spi	13.804	34.947	0.39
Ca × Luz spi	15.639	34.935	0.45
Cs × Luz spi	16.147	34.937	0.46
Fn × Pin syl	-0.296	0.652	-0.45
Ao × Pin syl	0.534	0.676	0.79
Sp × Pin syl	-0.303	0.649	-0.47
Ci × Pin syl	-0.288	0.668	-0.43
Ca × Pin syl	-0.588	0.641	-0.92
Cs × Pin syl	-0.567	0.675	-0.84
Fn × Sil aca	-0.705	0.737	-0.96
Ao × Sil aca	1.072	0.729	1.47
Sp × Sil aca	0.097	0.711	0.14
Ci × Sil aca	0.559	0.726	0.77

Ca × Sil aca	-1.129	0.730	-1.55
Cs × Sil aca	-0.259	0.763	-0.34
Fn × Sol vir	1.110	1.172	0.95
Ao × Sol vir	2.489	1.170	2.13
Sp × Sol vir	2.813	1.152	2.44
Ci × Sol vir	1.948	1.171	1.66
Ca × Sol vir	1.276	1.158	1.10
Cs × Sol vir	2.037	1.179	1.73
Fn × Vac myr	-0.700	0.992	-0.71
Ao × Vac myr	0.622	0.959	0.65
Sp × Vac myr	-0.153	0.950	-0.16
Ci × Vac myr	-1.049	1.080	-0.97
Ca × Vac myr	-0.012	0.931	-0.01
Cs × Vac myr	0.702	0.962	0.73

Table 6: Anova table of the model explaining seedling recruitment in the field experiment, a generalized linear mixed-effects model with binomial errors and logit link-function, where lichen treatment and plant species and their interaction were fixed factors and tray and plot (nested within trays) were random factors.

	Df	Sum Sq	Mean Sq	F-value
lichen	6	19.16	3.19	3.19
plant	7	1000.27	142.90	142.90
lichen × plant	42	125.75	2.99	2.99

Table 7: Summary statistics of the model explaining seedling biomass in the field experiment, a linear mixed-effects model with plant species, lichen treatment, and their two-way interaction as fixed factors, and tray and plot (nested within trays) as random factors. The reference level (intercept) is lichen treatment bare soil control and plant *Ant nip*.

Fixed effects	Estimate	SE	t-value
Intercept	2.448	1.239	1.98
Fn	-0.435	1.356	-0.32
Ao	-1.278	1.418	-0.90
Sp	-0.097	1.352	-0.07
Ci	-0.308	1.414	-0.22
Ca	-0.421	1.329	-0.32
Cs	-1.380	1.421	-0.97
Ave fle	-2.080	2.750	-0.76
Bis viv	1.399	1.101	1.27
Luz spi	-0.496	1.095	-0.45
Pin syl	4.466	1.325	3.37
Sil aca	-1.790	1.568	-1.14
Sol vir	0.817	2.715	0.30
Vac myr	-1.579	1.549	-1.02
Fn × Ave fle	0.797	2.915	0.27
Ao × Ave fle	1.883	2.967	0.63
Sp × Ave fle	0.512	2.856	0.18
Ci × Ave fle	0.814	2.999	0.27
Ca × Ave fle	0.498	2.933	0.17
Cs × Ave fle	1.548	2.889	0.54
Fn × Bis viv	-2.459	1.865	-1.32
Ao × Bis viv	-1.940	2.145	-0.90
Sp × Bis viv	-1.133	1.390	-0.82
Ci × Bis viv	-2.737	1.912	-1.43
Ca × Bis viv	1.236	1.550	0.80
Fn × Luz spi	-0.035	1.870	-0.02
Ao × Luz spi	-0.168	1.919	-0.09
Sp × Luz spi	-0.750	1.339	-0.56
Ci × Luz spi	-1.344	2.750	-0.49
Ca × Luz spi	-0.655	1.386	-0.47
Fn × Pin syl	2.386	1.467	1.63
Ao × Pin syl	4.916	1.521	3.23
Sp × Pin syl	3.881	1.461	2.66
Ci × Pin syl	2.841	1.526	1.86
Ca × Pin syl	2.213	1.441	1.54
Cs × Pin syl	-0.830	1.546	-0.54
Fn × Sil aca	0.662	1.754	0.38
Ao × Sil aca	1.344		0.77
Sp × Sil aca	0.196	1.701	0.12
Ci × Sil aca	0.452	1.751	0.26
Ca × Sil aca	0.387	1.742	0.22
Cs × Sil aca	1.261	1.821	0.69
Fn × Sol vir	3.614	2.832	1.28

Ao × Sol vir	2.002	2.826	0.71
Sp × Sol vir	1.685	2.779	0.61
Ci × Sol vir	2.015	2.838	0.71
Ca × Sol vir	1.999	2.794	0.72
Cs × Sol vir	2.085	2.845	0.73
Fn × Vac myr	0.047	1.792	0.03
Ao × Vac myr	0.401	1.771	0.23
Sp × Vac myr	-0.415	1.732	-0.24
Ci × Vac myr	-0.126	1.893	-0.07
Ca × Vac myr	-0.220	1.710	-0.13
Cs × Vac myr	0.716	1.777	0.40

Table 8: Anova table of the model explaining seedling biomass in the field experiment, a linear mixed-effects model with plant species, lichen treatment, and their two-way interaction as fixed factors, and tray and plot (nested within trays) as random factors.

Fixed effect	Df	Sum Sq	Mean Sq	F-value
lichen	6	356.19	59.36	10.16
plant	7	12008.01	1715.43	293.47
lichen × plant	40	795.95	19.90	3.40

Table 9: Summary statistics of the model explaining seed germination in the lab experiment, a generalized linear model with binomial errors and logit link-function, where lichen treatment and plant species and their interaction were fixed factors. The reference level (intercept) is lichen treatment control and plant Ant nip.

Fixed effects	Estimate	SE	z-value
Intercept	-1.766	0.231	-7.64
Ao	-0.597	0.372	-1.61
Ca	0.166	0.318	0.52
Ci	-0.572	0.370	-1.55
Cs	-0.226	0.341	-0.66
Fn	-0.345	0.350	-0.99
Sp	0.342	0.310	1.10
Ave fle	0.303	0.312	0.97
Bet nan	0.392	0.308	1.27
Dry oct	-1.097	0.429	-2.56
Luz spi	-3.344	1.082	-3.09
Pin syl	3.759	0.493	7.63
Sal gla	0.890	0.343	2.59
Sil aca	-0.345	0.350	-0.99
Sol vir	3.032	0.304	9.98
Vac myr	2.886	0.299	9.65
Ao × Ave fle	1.397	0.460	3.04
Ca × Ave fle	0.292	0.423	0.69
Ci × Ave fle	0.893	0.465	1.92
Cs × Ave fle	0.898	0.437	2.05
Fn × Ave fle	0.611	0.451	1.35
Sp × Ave fle	-0.180	0.424	-0.43
Ao × Bet nan	0.052	0.489	0.11
Ca × Bet nan	-0.748	0.452	-1.66
Ci × Bet nan	-0.879	0.551	-1.59
Cs × Bet nan	-0.451	0.473	-0.95
Fn × Bet nan	-0.165	0.471	-0.35
Sp × Bet nan	-0.687	0.435	-1.58
Ao × Dry oct	-16.676	1167.940	-0.01
Ca × Dry oct	-0.166	0.602	-0.28
Ci × Dry oct	-0.188	0.728	-0.26
Cs × Dry oct	-0.089	0.649	-0.14
Fn × Dry oct	0.766	0.586	1.31
Sp × Dry oct	0.232	0.554	0.42
Ao × Luz spi	2.360	1.208	1.95
Ca × Luz spi	0.533	1.335	0.40
Ci × Luz spi	-14.455	1167.941	-0.01
Cs × Luz spi	0.925	1.340	0.69
Fn × Luz spi	0.345	1.536	0.22
Sp × Luz spi	0.769	1.261	0.61
Ao × Pin syl	-0.130	0.667	-0.19
Ca × Pin syl	-0.773	0.645	-1.20
Ci × Pin syl	-0.034	0.672	-0.05

Cs × Pin syl	-0.108	0.674	-0.16
Fn × Pin syl	-0.382	0.655	-0.58
Sp × Pin syl	-1.289	0.624	-2.06
Ao × Sal gla	-0.277	0.555	-0.50
Ca × Sal gla	-0.862	0.509	-1.69
Ci × Sal gla	0.984	0.507	1.94
Cs × Sal gla	-0.117	0.507	-0.23
Fn × Sal gla	-3.034	1.074	-2.83
Sp × Sal gla	-1.315	0.523	-2.51
Ao × Sil aca	-2.401	1.151	-2.09
Ca × Sil aca	-1.944	0.712	-2.73
Ci × Sil aca	1.966	0.486	4.05
Cs × Sil aca	0.964	0.477	2.02
Fn × Sil aca	-17.680	1167.940	-0.02
Sp × Sil aca	1.380	0.439	3.14
Ao × Sol vir	0.022	0.455	0.05
Ca × Sol vir	0.226	0.435	0.52
Ci × Sol vir	0.394	0.459	0.86
Cs × Sol vir	0.102	0.438	0.23
Fn × Sol vir	-0.354	0.436	-0.81
Sp × Sol vir	-0.132	0.423	-0.31
Ao × Vac myr	-0.330	0.448	-0.74
Ca × Vac myr	-1.013	0.405	-2.50
Ci × Vac myr	0.683	0.459	1.49
Cs × Vac myr	-0.345	0.426	-0.81
Fn × Vac myr	0.839	0.455	1.85
Sp × Vac myr	-0.615	0.405	-1.52

Table 10: Anova table of the model explaining seed germination in the lab experiment, a generalized linear model with binomial errors and logit link-function, where lichen treatment and plant species and their interaction were fixed factors.

Fixed effects	Sum Sq	Df	F-value	Pr(>F)
lichen	55.754	6	3.584	0.002
plant	3512.156	9	150.500	<0.001
lichen × plant	359.006	54	2.564	<0.001
residuals	726.026	280		

tray	plot	lichen	plant	seeds	seedlings	living	dead	tot.weight.mg	s.weight	t.min	t.max	t.mean	moist.wet	moist.dry	mat.thickness
2	1	Ao	Ant_alp	30	1	1	0	0.58	0.58	-1.50	35.00	11.69	20.11	12.67	2.23
3	1	Ao	Ant_alp	30	3	3	0	2.72	0.91	-1.00	28.00	11.24	15.06	10.39	3.67
15	4	Ao	Ant_alp	30	3	3	0	4.90	1.63	-1.00	29.00	10.83	23.65	11.91	1.33
17	4	Ao	Ant_alp	30	7	7	0	12.44	1.78	-0.50	29.50	11.34	30.95	15.28	3.00
5	3	Ao	Ant_alp	30	0	0	0	NA	NA	-1.00	33.50	11.67	24.20	8.96	1.00
8	2	Ao	Ant_alp	30	0	0	0	NA	NA	-0.50	31.50	11.49	24.06	14.64	0.63
11	4	Ao	Ant_alp	30	0	0	0	NA	NA	-2.50	44.00	11.97	17.95	11.79	0.97
13	4	Ao	Ant_alp	30	0	0	0	NA	NA	-2.50	37.00	11.08	24.70	16.08	2.53
8	1	Ca	Ant_alp	30	1	1	0	0.29	0.29	0.00	25.50	10.49	27.39	12.27	4.10
10	1	Ca	Ant_alp	30	2	2	0	1.03	0.52	-0.50	26.50	11.10	25.90	11.63	3.80
8	3	Ca	Ant_alp	30	5	5	0	4.93	0.99	0.50	29.00	11.07	20.30	10.23	5.20
16	3	Ca	Ant_alp	30	4	4	0	7.80	1.95	0.00	26.00	11.17	20.00	8.51	2.27
11	2	Ca	Ant_alp	30	3	3	0	9.23	3.08	0.00	28.50	10.51	16.29	9.46	4.23
7	2	Ca	Ant_alp	30	6	6	0	9.32	1.55	0.50	25.00	10.84	20.85	9.07	3.73
12	1	Ca	Ant_alp	30	9	9	0	23.89	2.65	-0.50	25.50	10.44	24.76	14.09	3.60
17	3	Ca	Ant_alp	30	0	0	0	NA	NA	0.00	24.00	10.74	23.52	14.92	3.80
4	1	Ci	Ant_alp	30	2	2	0	1.50	0.75	-0.50	35.50	11.62	27.47	7.07	NA
7	1	Ci	Ant_alp	30	1	1	0	2.81	2.81	-0.50	36.00	11.20	30.11	7.24	3.17
5	2	Ci	Ant_alp	30	3	3	0	3.00	1.00	-1.00	36.50	11.31	22.58	7.90	1.23
3	4	Ci	Ant_alp	30	2	2	0	4.17	2.09	-0.50	26.50	11.00	17.06	6.89	3.13
14	1	Ci	Ant_alp	30	5	5	0	9.88	1.98	-0.50	29.50	10.86	22.68	8.48	2.57
9	4	Ci	Ant_alp	30	3	3	0	10.04	3.35	-0.50	30.00	11.09	25.15	7.17	3.63
5	4	Ci	Ant_alp	30	2	2	0	NA	NA	-1.50	38.00	11.30	17.39	9.85	1.90
17	2	Ci	Ant_alp	30	0	0	0	NA	NA	-0.50	32.50	11.12	23.18	9.05	3.10
14	4	Co	Ant_alp	30	1	1	0	2.07	2.07	-3.00	41.50	12.12	24.81	6.23	0.00
3	3	Co	Ant_alp	30	2	2	0	3.51	1.76	-1.50	36.00	11.90	24.90	5.15	0.00
9	1	Co	Ant_alp	30	1	1	0	3.75	3.75	-2.50	56.50	12.06	20.41	5.08	0.00
1	4	Co	Ant_alp	30	0	0	0	NA	NA	-3.00	37.00	11.35	30.37	7.92	0.00
2	2	Co	Ant_alp	30	0	0	0	NA	NA	-3.00	53.00	12.38	18.97	7.21	0.00
4	4	Co	Ant_alp	30	0	0	0	NA	NA	-3.00	39.00	12.00	28.25	8.96	0.00
10	2	Co	Ant_alp	30	0	0	0	NA	NA	-3.00	45.00	12.21	34.77	17.21	0.00
11	3	Co	Ant_alp	30	0	0	0	NA	NA	-2.50	44.50	11.90	16.51	7.17	0.00
12	4	Co	Ant_alp	30	0	0	0	NA	NA	-3.00	46.50	11.91	26.83	7.05	0.00
17	1	Co	Ant_alp	30	0	0	0	NA	NA	-1.00	39.50	11.62	30.07	12.47	0.00
12	2	Cs	Ant_alp	30	1	1	0	0.05	0.05	0.50	25.00	10.70	24.36	19.35	6.40
7	4	Cs	Ant_alp	30	1	1	0	0.20	0.20	0.50	24.00	10.78	20.41	12.96	8.30

6	4 Cs	Ant_alp	30	2	2	0	0.23	0.12	0.00	23.00	10.83	23.98	11.19	6.83
16	2 Cs	Ant_alp	30	1	1	0	0.57	0.57	0.00	22.00	10.43	20.25	9.98	5.67
10	4 Cs	Ant_alp	30	2	2	0	0.63	0.32	0.00	28.50	10.66	32.63	15.70	8.30
1	2 Cs	Ant_alp	30	3	3	0	5.28	1.76	0.00	23.00	10.71	21.42	16.16	6.57
15	1 Cs	Ant_alp	30	3	3	0	6.90	2.30	0.50	25.50	10.76	15.95	9.88	5.43
11	1 Cs	Ant_alp	30	0	0	NA	NA	NA	0.00	23.00	10.31	18.13	8.52	6.67
13	2 Fn	Ant_alp	30	1	1	0	0.30	0.30	-1.50	52.50	12.08	16.40	9.86	3.10
4	2 Fn	Ant_alp	30	1	1	0	3.39	3.39	-0.50	32.50	11.32	23.82	10.72	1.50
10	3 Fn	Ant_alp	30	4	4	0	4.13	1.03	-1.00	31.50	10.90	27.75	19.47	1.67
14	3 Fn	Ant_alp	30	2	2	0	5.67	2.84	-0.50	30.50	11.05	19.47	8.58	1.60
9	2 Fn	Ant_alp	30	3	3	0	6.77	2.26	-1.50	44.00	11.70	27.48	7.80	2.17
1	1 Fn	Ant_alp	30	5	5	0	10.11	2.02	0.50	25.00	11.07	22.09	14.94	1.93
15	2 Fn	Ant_alp	30	6	6	0	14.59	2.43	-0.50	38.00	10.97	19.76	9.30	1.33
6	1 Fn	Ant_alp	30	0	0	NA	NA	NA	-1.00	35.50	11.36	23.40	6.84	1.50
13	3 Sp	Ant_alp	30	1	1	0	1.54	1.54	-2.50	42.00	11.31	18.84	8.03	3.40
2	3 Sp	Ant_alp	30	1	1	0	2.56	2.56	-2.00	39.00	11.40	16.63	8.83	2.10
1	3 Sp	Ant_alp	30	3	3	0	5.55	1.85	-0.50	31.50	11.11	22.02	11.00	1.77
16	1 Sp	Ant_alp	30	3	2	1	7.91	3.96	-1.00	34.50	10.96	20.90	12.23	2.03
4	3 Sp	Ant_alp	30	6	6	0	10.18	1.70	-0.50	25.50	11.20	27.43	11.36	1.50
3	2 Sp	Ant_alp	30	6	6	0	10.63	1.77	-1.00	30.50	11.20	25.68	10.39	1.67
6	3 Sp	Ant_alp	30	5	5	0	17.90	3.58	-0.50	29.50	11.34	24.21	12.85	2.33
12	3 Sp	Ant_alp	30	0	0	NA	NA	NA	-1.50	33.00	10.22	24.93	9.93	2.17
15	4 Ao	Ave_fle	30	1	1	0	0.49	0.49	-1.00	29.00	10.83	23.65	11.91	1.33
8	2 Ao	Ave_fle	30	3	3	0	1.53	0.51	-0.50	31.50	11.49	24.06	14.64	0.63
13	4 Ao	Ave_fle	30	4	4	0	3.95	0.99	-2.50	37.00	11.08	24.70	16.08	2.53
2	1 Ao	Ave_fle	30	0	0	NA	NA	NA	-1.50	35.00	11.69	20.11	12.67	2.23
3	1 Ao	Ave_fle	30	0	0	NA	NA	NA	-1.00	28.00	11.24	15.06	10.39	3.67
5	3 Ao	Ave_fle	30	0	0	NA	NA	NA	-1.00	33.50	11.67	24.20	8.96	1.00
11	4 Ao	Ave_fle	30	0	0	NA	NA	NA	-2.50	44.00	11.97	17.95	11.79	0.97
17	4 Ao	Ave_fle	30	0	0	NA	NA	NA	-0.50	29.50	11.34	30.95	15.28	3.00
8	1 Ca	Ave_fle	30	1	1	0	0.01	0.01	0.00	25.50	10.49	27.39	12.27	4.10
8	3 Ca	Ave_fle	30	1	1	0	0.03	0.03	0.50	29.00	11.07	20.30	10.23	5.20
7	2 Ca	Ave_fle	30	2	2	0	0.72	0.36	0.50	25.00	10.84	20.85	9.07	3.73
12	1 Ca	Ave_fle	30	3	3	0	1.76	0.59	-0.50	25.50	10.44	24.76	14.09	3.60
10	1 Ca	Ave_fle	30	0	0	NA	NA	NA	-0.50	26.50	11.10	25.90	11.63	3.80
11	2 Ca	Ave_fle	30	0	0	NA	NA	NA	0.00	28.50	10.51	16.29	9.46	4.23
16	3 Ca	Ave_fle	30	0	0	NA	NA	NA	0.00	26.00	11.17	20.00	8.51	2.27

17	3	Ca	Ave_fle	30	0	0	0	0	NA	NA	0.00	24.00	10.74	23.52	14.92	3.80
14	1	Ci	Ave_fle	30	1	1	1	0	0	0.56	0.56	-0.50	29.50	10.86	8.48	2.57
4	1	Ci	Ave_fle	30	1	1	1	0	0	0.87	0.87	-0.50	35.50	11.62	7.07	NA
9	4	Ci	Ave_fle	30	2	2	2	0	0	0.95	0.48	-0.50	30.00	11.09	25.15	3.63
5	4	Ci	Ave_fle	30	2	2	2	0	0	1.26	0.63	-1.50	38.00	11.30	17.39	1.90
17	2	Ci	Ave_fle	30	1	1	1	0	0	3.39	3.39	-0.50	32.50	11.12	23.18	3.10
3	4	Ci	Ave_fle	30	2	1	1	1	1	NA	NA	-0.50	26.50	11.00	17.06	3.13
5	2	Ci	Ave_fle	30	0	0	0	0	0	NA	NA	-1.00	36.50	11.31	22.58	1.23
7	1	Ci	Ave_fle	30	0	0	0	0	0	NA	NA	-0.50	36.00	11.20	30.11	3.17
17	1	Co	Ave_fle	30	1	1	1	0	0	0.44	0.44	-1.00	39.50	11.62	30.07	0.00
1	4	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-3.00	37.00	11.35	30.37	0.00
2	2	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-3.00	53.00	12.38	18.97	0.00
3	3	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-1.50	36.00	11.90	24.90	0.00
4	4	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-3.00	39.00	12.00	28.25	0.00
9	1	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-2.50	56.50	12.06	20.41	0.00
10	2	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-3.00	45.00	12.21	34.77	0.00
11	3	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-2.50	44.50	11.90	16.51	0.00
12	4	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-3.00	46.50	11.91	26.83	0.00
14	4	Co	Ave_fle	30	0	0	0	0	0	NA	NA	-3.00	41.50	12.12	24.81	0.00
10	4	Cs	Ave_fle	30	1	1	1	0	0	0.01	0.01	0.00	28.50	10.66	32.63	8.30
16	2	Cs	Ave_fle	30	1	1	1	0	0	0.15	0.15	0.00	22.00	10.43	20.25	5.67
11	1	Cs	Ave_fle	30	3	3	3	0	0	0.90	0.30	0.00	23.00	10.31	18.13	6.67
12	2	Cs	Ave_fle	30	2	2	2	0	0	1.37	0.69	0.50	25.00	10.70	24.36	6.40
1	2	Cs	Ave_fle	30	3	3	3	0	0	1.38	0.46	0.00	23.00	10.71	21.42	6.57
6	4	Cs	Ave_fle	30	1	1	1	0	0	1.45	1.45	0.00	23.00	10.83	23.98	6.83
15	1	Cs	Ave_fle	30	7	7	7	0	0	4.60	0.66	0.50	25.50	10.76	15.95	5.43
7	4	Cs	Ave_fle	30	0	0	0	0	0	NA	NA	0.50	24.00	10.78	20.41	8.30
15	2	Fn	Ave_fle	30	1	1	1	0	0	1.01	1.01	-0.50	38.00	10.97	19.76	1.33
1	1	Fn	Ave_fle	30	2	2	2	0	0	1.25	0.63	0.50	25.00	11.07	22.09	1.93
13	2	Fn	Ave_fle	30	3	2	2	1	0	1.91	0.96	-1.50	52.50	12.08	16.40	3.10
10	3	Fn	Ave_fle	30	4	4	4	0	0	2.74	0.69	-1.00	31.50	10.90	27.75	1.67
4	2	Fn	Ave_fle	30	0	0	0	0	0	NA	NA	-0.50	32.50	11.32	23.82	1.50
6	1	Fn	Ave_fle	30	0	0	0	0	0	NA	NA	-1.00	35.50	11.36	23.40	1.50
9	2	Fn	Ave_fle	30	0	0	0	0	0	NA	NA	-1.50	44.00	11.70	27.48	2.17
14	3	Fn	Ave_fle	30	0	0	0	0	0	NA	NA	-0.50	30.50	11.05	19.47	1.60
2	3	Sp	Ave_fle	30	1	1	1	0	0	0.48	0.48	-2.00	39.00	11.40	16.63	2.10
16	1	Sp	Ave_fle	30	2	2	2	0	0	0.87	0.44	-1.00	34.50	10.96	20.90	2.03

3	2 Sp	Ave_fle	30	1	1	0	1.08	1.08	-1.00	30.50	11.20	25.68	10.39	1.67
13	3 Sp	Ave_fle	30	3	3	0	1.59	0.53	-2.50	42.00	11.31	18.84	8.03	3.40
12	3 Sp	Ave_fle	30	2	2	0	1.73	0.87	-1.50	33.00	10.22	24.93	9.93	2.17
6	3 Sp	Ave_fle	30	2	2	0	2.26	1.13	-0.50	29.50	11.34	24.21	12.85	2.33
1	3 Sp	Ave_fle	30	5	5	0	3.41	0.68	-0.50	31.50	11.11	22.02	11.00	1.77
4	3 Sp	Ave_fle	30	2	2	0	4.63	2.32	-0.50	25.50	11.20	27.43	11.36	1.50
3	1 Ao	Bet_nan	30	1	1	0	0.83	0.83	-1.00	28.00	11.24	15.06	10.39	3.67
17	4 Ao	Bet_nan	30	1	1	0	0.88	0.88	-0.50	29.50	11.34	30.95	15.28	3.00
8	2 Ao	Bet_nan	30	1	1	0	NA	NA	-0.50	31.50	11.49	24.06	14.64	0.63
2	1 Ao	Bet_nan	30	0	0	0	NA	NA	-1.50	35.00	11.69	20.11	12.67	2.23
5	3 Ao	Bet_nan	30	0	0	0	NA	NA	-1.00	33.50	11.67	24.20	8.96	1.00
11	4 Ao	Bet_nan	30	0	0	0	NA	NA	-2.50	44.00	11.97	17.95	11.79	0.97
13	4 Ao	Bet_nan	30	0	0	0	NA	NA	-2.50	37.00	11.08	24.70	16.08	2.53
15	4 Ao	Bet_nan	30	0	0	0	NA	NA	-1.00	29.00	10.83	23.65	11.91	1.33
7	2 Ca	Bet_nan	30	1	1	0	0.03	0.03	0.50	25.00	10.84	20.85	9.07	3.73
8	1 Ca	Bet_nan	30	0	0	0	NA	NA	0.00	25.50	10.49	27.39	12.27	4.10
8	3 Ca	Bet_nan	30	0	0	0	NA	NA	0.50	29.00	11.07	20.30	10.23	5.20
10	1 Ca	Bet_nan	30	0	0	0	NA	NA	-0.50	26.50	11.10	25.90	11.63	3.80
11	2 Ca	Bet_nan	30	0	0	0	NA	NA	0.00	28.50	10.51	16.29	9.46	4.23
12	1 Ca	Bet_nan	30	0	0	0	NA	NA	-0.50	25.50	10.44	24.76	14.09	3.60
16	3 Ca	Bet_nan	30	0	0	0	NA	NA	0.00	26.00	11.17	20.00	8.51	2.27
17	3 Ca	Bet_nan	30	0	0	0	NA	NA	0.00	24.00	10.74	23.52	14.92	3.80
7	1 Ci	Bet_nan	30	1	1	0	0.01	0.01	-0.50	36.00	11.20	30.11	7.24	3.17
3	4 Ci	Bet_nan	30	0	0	0	NA	NA	-0.50	26.50	11.00	17.06	6.89	3.13
4	1 Ci	Bet_nan	30	0	0	0	NA	NA	-0.50	35.50	11.62	27.47	7.07 NA	
5	2 Ci	Bet_nan	30	0	0	0	NA	NA	-1.00	36.50	11.31	22.58	7.90	1.23
5	4 Ci	Bet_nan	30	0	0	0	NA	NA	-1.50	38.00	11.30	17.39	9.85	1.90
9	4 Ci	Bet_nan	30	0	0	0	NA	NA	-0.50	30.00	11.09	25.15	7.17	3.63
14	1 Ci	Bet_nan	30	0	0	0	NA	NA	-0.50	29.50	10.86	22.68	8.48	2.57
17	2 Ci	Bet_nan	30	0	0	0	NA	NA	-0.50	32.50	11.12	23.18	9.05	3.10
1	4 Co	Bet_nan	30	1	1	0	0.01	0.01	-3.00	37.00	11.35	30.37	7.92	0.00
2	2 Co	Bet_nan	30	0	0	0	NA	NA	-3.00	53.00	12.38	18.97	7.21	0.00
3	3 Co	Bet_nan	30	0	0	0	NA	NA	-1.50	36.00	11.90	24.90	5.15	0.00
4	4 Co	Bet_nan	30	0	0	0	NA	NA	-3.00	39.00	12.00	28.25	8.96	0.00
9	1 Co	Bet_nan	30	0	0	0	NA	NA	-2.50	56.50	12.06	20.41	5.08	0.00
10	2 Co	Bet_nan	30	0	0	0	NA	NA	-3.00	45.00	12.21	34.77	17.21	0.00
11	3 Co	Bet_nan	30	0	0	0	NA	NA	-2.50	44.50	11.90	16.51	7.17	0.00

12	4 Co	Bet_nan	30	0	0	0	NA	NA	-3.00	46.50	11.91	26.83	7.05	0.00
14	4 Co	Bet_nan	30	0	0	0	NA	NA	-3.00	41.50	12.12	24.81	6.23	0.00
17	1 Co	Bet_nan	30	0	0	0	NA	NA	-1.00	39.50	11.62	30.07	12.47	0.00
11	1 Cs	Bet_nan	30	1	1	0	0.01	0.01	0.00	23.00	10.31	18.13	8.52	6.67
1	2 Cs	Bet_nan	30	2	2	0	0.16	0.08	0.00	23.00	10.71	21.42	16.16	6.57
6	4 Cs	Bet_nan	30	0	0	0	NA	NA	0.00	23.00	10.83	23.98	11.19	6.83
7	4 Cs	Bet_nan	30	0	0	0	NA	NA	0.50	24.00	10.78	20.41	12.96	8.30
10	4 Cs	Bet_nan	30	0	0	0	NA	NA	0.00	28.50	10.66	32.63	15.70	8.30
12	2 Cs	Bet_nan	30	0	0	0	NA	NA	0.50	25.00	10.70	24.36	19.35	6.40
15	1 Cs	Bet_nan	30	0	0	0	NA	NA	0.50	25.50	10.76	15.95	9.88	5.43
16	2 Cs	Bet_nan	30	0	0	0	NA	NA	0.00	22.00	10.43	20.25	9.98	5.67
1	1 Fn	Bet_nan	30	1	1	0	0.41	0.41	0.50	25.00	11.07	22.09	14.94	1.93
9	2 Fn	Bet_nan	30	1	1	0	0.47	0.47	-1.50	44.00	11.70	27.48	7.80	2.17
4	2 Fn	Bet_nan	30	0	0	0	NA	NA	-0.50	32.50	11.32	23.82	10.72	1.50
6	1 Fn	Bet_nan	30	0	0	0	NA	NA	-1.00	35.50	11.36	23.40	6.84	1.50
10	3 Fn	Bet_nan	30	0	0	0	NA	NA	-1.00	31.50	10.90	27.75	19.47	1.67
13	2 Fn	Bet_nan	30	0	0	0	NA	NA	-1.50	52.50	12.08	16.40	9.86	3.10
14	3 Fn	Bet_nan	30	0	0	0	NA	NA	-0.50	30.50	11.05	19.47	8.58	1.60
15	2 Fn	Bet_nan	30	0	0	0	NA	NA	-0.50	38.00	10.97	19.76	9.30	1.33
1	3 Sp	Bet_nan	30	1	1	0	0.10	0.10	-0.50	31.50	11.11	22.02	11.00	1.77
2	3 Sp	Bet_nan	30	0	0	0	NA	NA	-2.00	39.00	11.40	16.63	8.83	2.10
3	2 Sp	Bet_nan	30	0	0	0	NA	NA	-1.00	30.50	11.20	25.68	10.39	1.67
4	3 Sp	Bet_nan	30	0	0	0	NA	NA	-0.50	25.50	11.20	27.43	11.36	1.50
6	3 Sp	Bet_nan	30	0	0	0	NA	NA	-0.50	29.50	11.34	24.21	12.85	2.33
12	3 Sp	Bet_nan	30	0	0	0	NA	NA	-1.50	33.00	10.22	24.93	9.93	2.17
13	3 Sp	Bet_nan	30	0	0	0	NA	NA	-2.50	42.00	11.31	18.84	8.03	3.40
16	1 Sp	Bet_nan	30	0	0	0	NA	NA	-1.00	34.50	10.96	20.90	12.23	2.03
3	1 Ao	Bis_viv	30	1	1	0	0.34	0.34	-1.00	28.00	11.24	15.06	10.39	3.67
15	4 Ao	Bis_viv	30	1	1	0	1.62	1.62	-1.00	29.00	10.83	23.65	11.91	1.33
2	1 Ao	Bis_viv	30	0	0	0	NA	NA	-1.50	35.00	11.69	20.11	12.67	2.23
5	3 Ao	Bis_viv	30	0	0	0	NA	NA	-1.00	33.50	11.67	24.20	8.96	1.00
8	2 Ao	Bis_viv	30	0	0	0	NA	NA	-0.50	31.50	11.49	24.06	14.64	0.63
11	4 Ao	Bis_viv	30	0	0	0	NA	NA	-2.50	44.00	11.97	17.95	11.79	0.97
13	4 Ao	Bis_viv	30	0	0	0	NA	NA	-2.50	37.00	11.08	24.70	16.08	2.53
17	4 Ao	Bis_viv	30	0	0	0	NA	NA	-0.50	29.50	11.34	30.95	15.28	3.00
11	2 Ca	Bis_viv	30	1	1	0	2.26	2.26	0.00	28.50	10.51	16.29	9.46	4.23
7	2 Ca	Bis_viv	30	1	1	0	2.82	2.82	0.50	25.00	10.84	20.85	9.07	3.73

17	3 Ca	Bis_viv	30	2	2	0	4.68	2.34	0.00	24.00	10.74	23.52	14.92	3.80
12	1 Ca	Bis_viv	30	2	2	0	18.60	9.30	-0.50	25.50	10.44	24.76	14.09	3.60
8	1 Ca	Bis_viv	30	0	0	0	NA		0.00	25.50	10.49	27.39	12.27	4.10
8	3 Ca	Bis_viv	30	0	0	0	NA		0.50	29.00	11.07	20.30	10.23	5.20
10	1 Ca	Bis_viv	30	0	0	0	NA		-0.50	26.50	11.10	25.90	11.63	3.80
16	3 Ca	Bis_viv	30	0	0	0	NA		0.00	26.00	11.17	20.00	8.51	2.27
3	4 Ci	Bis_viv	30	1	1	0	0.48	0.48	-0.50	26.50	11.00	17.06	6.89	3.13
7	1 Ci	Bis_viv	30	2	2	0	1.51	0.76	-0.50	36.00	11.20	30.11	7.24	3.17
4	1 Ci	Bis_viv	30	0	0	0	NA		-0.50	35.50	11.62	27.47	7.07 NA	
5	2 Ci	Bis_viv	30	0	0	0	NA		-1.00	36.50	11.31	22.58	7.90	1.23
5	4 Ci	Bis_viv	30	0	0	0	NA		-1.50	38.00	11.30	17.39	9.85	1.90
9	4 Ci	Bis_viv	30	0	0	0	NA		-0.50	30.00	11.09	25.15	7.17	3.63
14	1 Ci	Bis_viv	30	0	0	0	NA		-0.50	29.50	10.86	22.68	8.48	2.57
17	2 Ci	Bis_viv	30	0	0	0	NA		-0.50	32.50	11.12	23.18	9.05	3.10
1	4 Co	Bis_viv	30	0	0	0	NA		-3.00	37.00	11.35	30.37	7.92	0.00
2	2 Co	Bis_viv	30	0	0	0	NA		-3.00	53.00	12.38	18.97	7.21	0.00
3	3 Co	Bis_viv	30	0	0	0	NA		-1.50	36.00	11.90	24.90	5.15	0.00
4	4 Co	Bis_viv	30	0	0	0	NA		-3.00	39.00	12.00	28.25	8.96	0.00
9	1 Co	Bis_viv	30	0	0	0	NA		-2.50	56.50	12.06	20.41	5.08	0.00
10	2 Co	Bis_viv	30	0	0	0	NA		-3.00	45.00	12.21	34.77	17.21	0.00
11	3 Co	Bis_viv	30	0	0	0	NA		-2.50	44.50	11.90	16.51	7.17	0.00
12	4 Co	Bis_viv	30	0	0	0	NA		-3.00	46.50	11.91	26.83	7.05	0.00
14	4 Co	Bis_viv	30	0	0	0	NA		-3.00	41.50	12.12	24.81	6.23	0.00
17	1 Co	Bis_viv	30	0	0	0	NA		-1.00	39.50	11.62	30.07	12.47	0.00
15	1 Cs	Bis_viv	30	1	1	0	0.77	0.77	0.50	25.50	10.76	15.95	9.88	5.43
16	2 Cs	Bis_viv	30	2	2	0	5.90	2.95	0.00	22.00	10.43	20.25	9.98	5.67
1	2 Cs	Bis_viv	30	5	5	0	13.11	2.62	0.00	23.00	10.71	21.42	16.16	6.57
6	4 Cs	Bis_viv	30	0	0	0	NA		0.00	23.00	10.83	23.98	11.19	6.83
7	4 Cs	Bis_viv	30	0	0	0	NA		0.50	24.00	10.78	20.41	12.96	8.30
10	4 Cs	Bis_viv	30	0	0	0	NA		0.00	28.50	10.66	32.63	15.70	8.30
11	1 Cs	Bis_viv	30	0	0	0	NA		0.00	23.00	10.31	18.13	8.52	6.67
12	2 Cs	Bis_viv	30	0	0	0	NA		0.50	25.00	10.70	24.36	19.35	6.40
4	2 Fn	Bis_viv	30	1	1	0	0.20	0.20	-0.50	32.50	11.32	23.82	10.72	1.50
6	1 Fn	Bis_viv	30	1	1	0	0.96	0.96	-1.00	35.50	11.36	23.40	6.84	1.50
1	1 Fn	Bis_viv	30	2	1	1	1.77	1.77	0.50	25.00	11.07	22.09	14.94	1.93
9	2 Fn	Bis_viv	30	0	0	0	NA		-1.50	44.00	11.70	27.48	7.80	2.17
10	3 Fn	Bis_viv	30	0	0	0	NA		-1.00	31.50	10.90	27.75	19.47	1.67

13	2 Fn	Bis_viv	30	0	0	0 NA	NA	-1.50	52.50	12.08	16.40	9.86	3.10
14	3 Fn	Bis_viv	30	0	0	0 NA	NA	-0.50	30.50	11.05	19.47	8.58	1.60
15	2 Fn	Bis_viv	30	0	0	0 NA	NA	-0.50	38.00	10.97	19.76	9.30	1.33
16	1 Sp	Bis_viv	30	6	6	0	18.66	3.11	-1.00	34.50	20.90	12.23	2.03
1	3 Sp	Bis_viv	30	8	8	0	23.19	2.90	-0.50	31.50	22.02	11.00	1.77
2	3 Sp	Bis_viv	30	0	0	0 NA	NA	-2.00	39.00	11.40	16.63	8.83	2.10
3	2 Sp	Bis_viv	30	0	0	0 NA	NA	-1.00	30.50	11.20	25.68	10.39	1.67
4	3 Sp	Bis_viv	30	0	0	0 NA	NA	-0.50	25.50	11.20	27.43	11.36	1.50
6	3 Sp	Bis_viv	30	0	0	0 NA	NA	-0.50	29.50	11.34	24.21	12.85	2.33
12	3 Sp	Bis_viv	30	0	0	0 NA	NA	-1.50	33.00	10.22	24.93	9.93	2.17
13	3 Sp	Bis_viv	30	0	0	0 NA	NA	-2.50	42.00	11.31	18.84	8.03	3.40
2	1 Ao	Luz_spi	30	1	1	0	0.39	0.39	-1.50	35.00	20.11	12.67	2.23
11	4 Ao	Luz_spi	30	2	2	0	0.77	0.39	-2.50	44.00	17.95	11.79	0.97
3	1 Ao	Luz_spi	30	0	0	0 NA	NA	-1.00	28.00	11.24	15.06	10.39	3.67
5	3 Ao	Luz_spi	30	0	0	0 NA	NA	-1.00	33.50	11.67	24.20	8.96	1.00
8	2 Ao	Luz_spi	30	0	0	0 NA	NA	-0.50	31.50	11.49	24.06	14.64	0.63
13	4 Ao	Luz_spi	30	0	0	0 NA	NA	-2.50	37.00	11.08	24.70	16.08	2.53
15	4 Ao	Luz_spi	30	0	0	0 NA	NA	-1.00	29.00	10.83	23.65	11.91	1.33
17	4 Ao	Luz_spi	30	0	0	0 NA	NA	-0.50	29.50	11.34	30.95	15.28	3.00
8	3 Ca	Luz_spi	30	1	1	0	0.19	0.19	0.50	29.00	20.30	10.23	5.20
10	1 Ca	Luz_spi	30	1	1	0	0.64	0.64	-0.50	26.50	25.90	11.63	3.80
17	3 Ca	Luz_spi	30	2	2	0	2.22	1.11	0.00	24.00	23.52	14.92	3.80
7	2 Ca	Luz_spi	30	8	8	0	7.08	0.89	0.50	25.00	20.85	9.07	3.73
8	1 Ca	Luz_spi	30	0	0	0 NA	NA	0.00	25.50	10.49	27.39	12.27	4.10
11	2 Ca	Luz_spi	30	0	0	0 NA	NA	0.00	28.50	10.51	16.29	9.46	4.23
12	1 Ca	Luz_spi	30	0	0	0 NA	NA	-0.50	25.50	10.44	24.76	14.09	3.60
16	3 Ca	Luz_spi	30	0	0	0 NA	NA	0.00	26.00	11.17	20.00	8.51	2.27
9	4 Ci	Luz_spi	30	1	1	0	0.88	0.88	-0.50	30.00	25.15	7.17	3.63
3	4 Ci	Luz_spi	30	0	0	0 NA	NA	-0.50	26.50	11.00	17.06	6.89	3.13
4	1 Ci	Luz_spi	30	0	0	0 NA	NA	-0.50	35.50	11.62	27.47	7.07 NA	
5	2 Ci	Luz_spi	30	0	0	0 NA	NA	-1.00	36.50	11.31	22.58	7.90	1.23
5	4 Ci	Luz_spi	30	0	0	0 NA	NA	-1.50	38.00	11.30	17.39	9.85	1.90
7	1 Ci	Luz_spi	30	0	0	0 NA	NA	-0.50	36.00	11.20	30.11	7.24	3.17
14	1 Ci	Luz_spi	30	0	0	0 NA	NA	-0.50	29.50	10.86	22.68	8.48	2.57
17	2 Ci	Luz_spi	30	0	0	0 NA	NA	-0.50	32.50	11.12	23.18	9.05	3.10
1	4 Co	Luz_spi	30	0	0	0 NA	NA	-3.00	37.00	11.35	30.37	7.92	0.00
2	2 Co	Luz_spi	30	0	0	0 NA	NA	-3.00	53.00	12.38	18.97	7.21	0.00

3	3 Co	Luz_spi	30	0	0	0	0	NA	NA	-1.50	36.00	11.90	24.90	5.15	0.00
4	4 Co	Luz_spi	30	0	0	0	0	NA	NA	-3.00	39.00	12.00	28.25	8.96	0.00
9	1 Co	Luz_spi	30	0	0	0	0	NA	NA	-2.50	56.50	12.06	20.41	5.08	0.00
10	2 Co	Luz_spi	30	0	0	0	0	NA	NA	-3.00	45.00	12.21	34.77	17.21	0.00
11	3 Co	Luz_spi	30	0	0	0	0	NA	NA	-2.50	44.50	11.90	16.51	7.17	0.00
12	4 Co	Luz_spi	30	0	0	0	0	NA	NA	-3.00	46.50	11.91	26.83	7.05	0.00
14	4 Co	Luz_spi	30	0	0	0	0	NA	NA	-3.00	41.50	12.12	24.81	6.23	0.00
17	1 Co	Luz_spi	30	0	0	0	0	NA	NA	-1.00	39.50	11.62	30.07	12.47	0.00
7	4 Cs	Luz_spi	30	1	1	0	0	0.41	0.41	0.50	24.00	10.78	20.41	12.96	8.30
15	1 Cs	Luz_spi	30	2	2	0	0	0.82	0.41	0.50	25.50	10.76	15.95	9.88	5.43
11	1 Cs	Luz_spi	30	1	1	0	0	0.91	0.91	0.00	23.00	10.31	18.13	8.52	6.67
1	2 Cs	Luz_spi	30	4	4	0	0	2.47	0.62	0.00	23.00	10.71	21.42	16.16	6.57
6	4 Cs	Luz_spi	30	0	0	0	0	NA	NA	0.00	23.00	10.83	23.98	11.19	6.83
10	4 Cs	Luz_spi	30	0	0	0	0	NA	NA	0.00	28.50	10.66	32.63	15.70	8.30
12	2 Cs	Luz_spi	30	0	0	0	0	NA	NA	0.50	25.00	10.70	24.36	19.35	6.40
16	2 Cs	Luz_spi	30	1	0	1	NA	NA	NA	0.00	22.00	10.43	20.25	9.98	5.67
1	1 Fn	Luz_spi	30	3	3	0	0	3.94	1.31	0.50	25.00	11.07	22.09	14.94	1.93
4	2 Fn	Luz_spi	30	0	0	0	0	NA	NA	-0.50	32.50	11.32	23.82	10.72	1.50
6	1 Fn	Luz_spi	30	0	0	0	0	NA	NA	-1.00	35.50	11.36	23.40	6.84	1.50
9	2 Fn	Luz_spi	30	0	0	0	0	NA	NA	-1.50	44.00	11.70	27.48	7.80	2.17
10	3 Fn	Luz_spi	30	0	0	0	0	NA	NA	-1.00	31.50	10.90	27.75	19.47	1.67
13	2 Fn	Luz_spi	30	0	0	0	0	NA	NA	-1.50	52.50	12.08	16.40	9.86	3.10
14	3 Fn	Luz_spi	30	0	0	0	0	NA	NA	-0.50	30.50	11.05	19.47	8.58	1.60
15	2 Fn	Luz_spi	30	0	0	0	0	NA	NA	-0.50	38.00	10.97	19.76	9.30	1.33
12	3 Sp	Luz_spi	30	2	2	0	0	0.68	0.34	-1.50	33.00	10.22	24.93	9.93	2.17
3	2 Sp	Luz_spi	30	2	2	0	0	0.84	0.42	-1.00	30.50	11.20	25.68	10.39	1.67
13	3 Sp	Luz_spi	30	3	3	0	0	2.32	0.77	-2.50	42.00	11.31	18.84	8.03	3.40
4	3 Sp	Luz_spi	30	2	2	0	0	2.51	1.26	-0.50	25.50	11.20	27.43	11.36	1.50
6	3 Sp	Luz_spi	30	2	2	0	0	2.59	1.30	-0.50	29.50	11.34	24.21	12.85	2.33
1	3 Sp	Luz_spi	30	2	2	0	0	2.78	1.39	-0.50	31.50	11.11	22.02	11.00	1.77
16	1 Sp	Luz_spi	30	5	5	0	0	9.21	1.84	-1.00	34.50	10.96	20.90	12.23	2.03
2	3 Sp	Luz_spi	30	0	0	0	0	NA	NA	-2.00	39.00	11.40	16.63	8.83	2.10
8	2 Ao	Pin_syl	10	5	5	0	0	41.12	8.22	-0.50	31.50	11.49	24.06	14.64	0.63
13	4 Ao	Pin_syl	10	6	6	0	0	47.84	7.97	-2.50	37.00	11.08	24.70	16.08	2.53
5	3 Ao	Pin_syl	10	6	6	0	0	58.79	9.80	-1.00	33.50	11.67	24.20	8.96	1.00
2	1 Ao	Pin_syl	10	7	7	0	0	60.05	8.58	-1.50	35.00	11.69	20.11	12.67	2.23
17	4 Ao	Pin_syl	10	5	5	0	0	60.07	12.01	-0.50	29.50	11.34	30.95	15.28	3.00

11	4	Ao	Pin_syl	10	6	6	0	62.74	10.46	-2.50	44.00	11.97	17.95	11.79	0.97
15	4	Ao	Pin_syl	10	9	9	0	109.82	12.20	-1.00	29.00	10.83	23.65	11.91	1.33
3	1	Ao	Pin_syl	10	10	10	0	131.46	13.15	-1.00	28.00	11.24	15.06	10.39	3.67
12	1	Ca	Pin_syl	10	6	6	0	26.55	4.43	-0.50	25.50	10.44	24.76	14.09	3.60
10	1	Ca	Pin_syl	10	4	4	0	26.96	6.74	-0.50	26.50	11.10	25.90	11.63	3.80
7	2	Ca	Pin_syl	10	6	6	0	49.82	8.30	0.50	25.00	10.84	20.85	9.07	3.73
16	3	Ca	Pin_syl	10	8	8	0	53.42	6.68	0.00	26.00	11.17	20.00	8.51	2.27
8	3	Ca	Pin_syl	10	6	6	0	54.57	9.10	0.50	29.00	11.07	20.30	10.23	5.20
11	2	Ca	Pin_syl	10	7	7	0	57.73	8.25	0.00	28.50	10.51	16.29	9.46	4.23
8	1	Ca	Pin_syl	10	6	6	0	75.48	12.58	0.00	25.50	10.49	27.39	12.27	4.10
17	3	Ca	Pin_syl	10	8	8	0	100.42	12.55	0.00	24.00	10.74	23.52	14.92	3.80
4	1	Ci	Pin_syl	10	6	6	0	32.35	5.39	-0.50	35.50	11.62	27.47	7.07 NA	
3	4	Ci	Pin_syl	10	7	7	0	45.89	6.56	-0.50	26.50	11.00	17.06	6.89	3.13
5	4	Ci	Pin_syl	10	5	5	0	50.39	10.08	-1.50	38.00	11.30	17.39	9.85	1.90
5	2	Ci	Pin_syl	10	5	5	0	52.46	10.49	-1.00	36.50	11.31	22.58	7.90	1.23
14	1	Ci	Pin_syl	10	7	7	0	59.77	8.54	-0.50	29.50	10.86	22.68	8.48	2.57
7	1	Ci	Pin_syl	10	9	9	0	85.01	9.45	-0.50	36.00	11.20	30.11	7.24	3.17
9	4	Ci	Pin_syl	10	8	8	0	93.82	11.73	-0.50	30.00	11.09	25.15	7.17	3.63
17	2	Ci	Pin_syl	10	0	0	0 NA	NA	-0.50	32.50	11.12	23.18	23.18	9.05	3.10
12	4	Co	Pin_syl	10	5	2	3	4.77	2.39	-3.00	46.50	11.91	26.83	7.05	0.00
14	4	Co	Pin_syl	10	1	1	0	5.13	5.13	-3.00	41.50	12.12	24.81	6.23	0.00
1	4	Co	Pin_syl	10	2	2	0	14.82	7.41	-3.00	37.00	11.35	30.37	7.92	0.00
2	2	Co	Pin_syl	10	2	2	0	16.04	8.02	-3.00	53.00	12.38	18.97	7.21	0.00
3	3	Co	Pin_syl	10	3	3	0	21.35	7.12	-1.50	36.00	11.90	24.90	5.15	0.00
9	1	Co	Pin_syl	10	5	5	0	22.76	4.55	-2.50	56.50	12.06	20.41	5.08	0.00
17	1	Co	Pin_syl	10	4	4	0	29.90	7.48	-1.00	39.50	11.62	30.07	12.47	0.00
10	2	Co	Pin_syl	10	5	5	0	51.78	10.36	-3.00	45.00	12.21	34.77	17.21	0.00
4	4	Co	Pin_syl	10	0	0	0 NA	NA	-3.00	39.00	12.00	28.25	8.96	8.96	0.00
11	3	Co	Pin_syl	10	1	0	1 NA	NA	-2.50	44.50	11.90	16.51	7.17	7.17	0.00
10	4	Cs	Pin_syl	10	2	2	0	12.12	6.06	0.00	28.50	10.66	32.63	15.70	8.30
7	4	Cs	Pin_syl	10	3	3	0	13.60	4.53	0.50	24.00	10.78	20.41	12.96	8.30
15	1	Cs	Pin_syl	10	4	4	0	18.55	4.64	0.50	25.50	10.76	15.95	9.88	5.43
11	1	Cs	Pin_syl	10	4	4	0	19.39	4.85	0.00	23.00	10.31	18.13	8.52	6.67
6	4	Cs	Pin_syl	10	6	6	0	22.77	3.80	0.00	23.00	10.83	23.98	11.19	6.83
12	2	Cs	Pin_syl	10	7	6	1	23.80	3.97	0.50	25.00	10.70	24.36	19.35	6.40
1	2	Cs	Pin_syl	10	8	8	0	44.53	5.57	0.00	23.00	10.71	21.42	16.16	6.57
16	2	Cs	Pin_syl	10	0	0	0 NA	NA	0.00	22.00	10.43	20.25	20.25	9.98	5.67

9	2 Fn	Pin_syl	10	5	5	0	31.34	6.27	-1.50	44.00	11.70	27.48	7.80	2.17
1	1 Fn	Pin_syl	10	5	5	0	31.87	6.37	0.50	25.00	11.07	22.09	14.94	1.93
14	3 Fn	Pin_syl	10	4	4	0	35.82	8.96	-0.50	30.50	11.05	19.47	8.58	1.60
6	1 Fn	Pin_syl	10	6	6	0	45.79	7.63	-1.00	35.50	11.36	23.40	6.84	1.50
13	2 Fn	Pin_syl	10	6	6	0	45.89	7.65	-1.50	52.50	12.08	16.40	9.86	3.10
15	2 Fn	Pin_syl	10	7	7	0	65.17	9.31	-0.50	38.00	10.97	19.76	9.30	1.33
10	3 Fn	Pin_syl	10	9	8	1	88.78	11.10	-1.00	31.50	10.90	27.75	19.47	1.67
4	2 Fn	Pin_syl	10	8	8	0	91.59	11.45	-0.50	32.50	11.32	23.82	10.72	1.50
2	3 Sp	Pin_syl	10	6	6	0	48.69	8.12	-2.00	39.00	11.40	16.63	8.83	2.10
12	3 Sp	Pin_syl	10	6	6	0	65.04	10.84	-1.50	33.00	10.22	24.93	9.93	2.17
13	3 Sp	Pin_syl	10	6	6	0	65.12	10.85	-2.50	42.00	11.31	18.84	8.03	3.40
4	3 Sp	Pin_syl	10	6	6	0	69.15	11.53	-0.50	25.50	11.20	27.43	11.36	1.50
6	3 Sp	Pin_syl	10	6	6	0	69.42	11.57	-0.50	29.50	11.34	24.21	12.85	2.33
3	2 Sp	Pin_syl	10	7	7	0	72.47	10.35	-1.00	30.50	11.20	25.68	10.39	1.67
1	3 Sp	Pin_syl	10	7	7	0	76.62	10.95	-0.50	31.50	11.11	22.02	11.00	1.77
16	1 Sp	Pin_syl	10	7	7	0	79.40	11.34	-1.00	34.50	10.96	20.90	12.23	2.03
2	1 Ao	Sal_gla	15	0	0	0 NA	NA	-1.50	35.00	11.69	20.11	12.67	2.23	
3	1 Ao	Sal_gla	15	3	0	3 NA	NA	-1.00	28.00	11.24	15.06	10.39	3.67	
5	3 Ao	Sal_gla	15	0	0	0 NA	NA	-1.00	33.50	11.67	24.20	8.96	1.00	
8	2 Ao	Sal_gla	15	0	0	0 NA	NA	-0.50	31.50	11.49	24.06	14.64	0.63	
11	4 Ao	Sal_gla	15	1	0	1 NA	NA	-2.50	44.00	11.97	17.95	11.79	0.97	
13	4 Ao	Sal_gla	15	0	0	0 NA	NA	-2.50	37.00	11.08	24.70	16.08	2.53	
15	4 Ao	Sal_gla	15	0	0	0 NA	NA	-1.00	29.00	10.83	23.65	11.91	1.33	
17	4 Ao	Sal_gla	15	1	0	1 NA	NA	-0.50	29.50	11.34	30.95	15.28	3.00	
1	4 Co	Sal_gla	15	0	0	0 NA	NA	-3.00	37.00	11.35	30.37	7.92	0.00	
2	2 Co	Sal_gla	15	0	0	0 NA	NA	-3.00	53.00	12.38	18.97	7.21	0.00	
3	3 Co	Sal_gla	15	0	0	0 NA	NA	-1.50	36.00	11.90	24.90	5.15	0.00	
4	4 Co	Sal_gla	15	0	0	0 NA	NA	-3.00	39.00	12.00	28.25	8.96	0.00	
5	1 Co	Sal_gla	15	0	0	0 NA	NA	-3.00	54.50	12.29	27.24	10.04	0.00	
9	1 Co	Sal_gla	15	0	0	0 NA	NA	-2.50	56.50	12.06	20.41	5.08	0.00	
10	2 Co	Sal_gla	15	0	0	0 NA	NA	-3.00	45.00	12.21	34.77	17.21	0.00	
11	3 Co	Sal_gla	15	0	0	0 NA	NA	-2.50	44.50	11.90	16.51	7.17	0.00	
12	4 Co	Sal_gla	15	1	0	1 NA	NA	-3.00	46.50	11.91	26.83	7.05	0.00	
14	4 Co	Sal_gla	15	0	0	0 NA	NA	-3.00	41.50	12.12	24.81	6.23	0.00	
17	1 Co	Sal_gla	15	0	0	0 NA	NA	-1.00	39.50	11.62	30.07	12.47	0.00	
7	2 Ca	Sal_gla	15	0	0	0 NA	NA	0.50	25.00	10.84	20.85	9.07	3.73	
8	1 Ca	Sal_gla	15	0	0	0 NA	NA	0.00	25.50	10.49	27.39	12.27	4.10	

8	3	Ca	Sal_gla	15	4	0	0	4	NA	NA	0.50	29.00	11.07	20.30	10.23	5.20
10	1	Ca	Sal_gla	15	4	0	0	4	NA	NA	-0.50	26.50	11.10	25.90	11.63	3.80
11	2	Ca	Sal_gla	15	0	0	0	0	NA	NA	0.00	28.50	10.51	16.29	9.46	4.23
12	1	Ca	Sal_gla	15	1	1	0	0	NA	NA	-0.50	25.50	10.44	24.76	14.09	3.60
16	3	Ca	Sal_gla	15	2	0	2	NA	NA	NA	0.00	26.00	11.17	20.00	8.51	2.27
17	3	Ca	Sal_gla	15	2	2	0	0	NA	NA	0.00	24.00	10.74	23.52	14.92	3.80
3	4	Ci	Sal_gla	15	0	0	0	0	NA	NA	-0.50	26.50	11.00	17.06	6.89	3.13
4	1	Ci	Sal_gla	15	0	0	0	0	NA	NA	-0.50	35.50	11.62	27.47	7.07	NA
5	2	Ci	Sal_gla	15	0	0	0	0	NA	NA	-1.00	36.50	11.31	22.58	7.90	1.23
5	4	Ci	Sal_gla	15	0	0	0	0	NA	NA	-1.50	38.00	11.30	17.39	9.85	1.90
7	1	Ci	Sal_gla	15	0	0	0	0	NA	NA	-0.50	36.00	11.20	30.11	7.24	3.17
9	4	Ci	Sal_gla	15	0	0	0	0	NA	NA	-0.50	30.00	11.09	25.15	7.17	3.63
14	1	Ci	Sal_gla	15	0	0	0	0	NA	NA	-0.50	29.50	10.86	22.68	8.48	2.57
17	2	Ci	Sal_gla	15	0	0	0	0	NA	NA	-0.50	32.50	11.12	23.18	9.05	3.10
1	2	Cs	Sal_gla	15	0	0	0	0	NA	NA	0.00	23.00	10.71	21.42	16.16	6.57
6	4	Cs	Sal_gla	15	0	0	0	0	NA	NA	0.00	23.00	10.83	23.98	11.19	6.83
7	4	Cs	Sal_gla	15	4	0	0	4	NA	NA	0.50	24.00	10.78	20.41	12.96	8.30
10	4	Cs	Sal_gla	15	0	0	0	0	NA	NA	0.00	28.50	10.66	32.63	15.70	8.30
11	1	Cs	Sal_gla	15	0	0	0	0	NA	NA	0.00	23.00	10.31	18.13	8.52	6.67
12	2	Cs	Sal_gla	15	5	0	0	5	NA	NA	0.50	25.00	10.70	24.36	19.35	6.40
15	1	Cs	Sal_gla	15	0	0	0	0	NA	NA	0.50	25.50	10.76	15.95	9.88	5.43
16	2	Cs	Sal_gla	15	0	0	0	0	NA	NA	0.00	22.00	10.43	20.25	9.98	5.67
1	1	Fn	Sal_gla	15	0	0	0	0	NA	NA	0.50	25.00	11.07	22.09	14.94	1.93
4	2	Fn	Sal_gla	15	0	0	0	0	NA	NA	-0.50	32.50	11.32	23.82	10.72	1.50
6	1	Fn	Sal_gla	15	0	0	0	0	NA	NA	-1.00	35.50	11.36	23.40	6.84	1.50
9	2	Fn	Sal_gla	15	6	0	0	6	NA	NA	-1.50	44.00	11.70	27.48	7.80	2.17
10	3	Fn	Sal_gla	15	3	0	0	3	NA	NA	-1.00	31.50	10.90	27.75	19.47	1.67
13	2	Fn	Sal_gla	15	2	0	0	2	NA	NA	-1.50	52.50	12.08	16.40	9.86	3.10
14	3	Fn	Sal_gla	15	0	0	0	0	NA	NA	-0.50	30.50	11.05	19.47	8.58	1.60
15	2	Fn	Sal_gla	15	0	0	0	0	NA	NA	-0.50	38.00	10.97	19.76	9.30	1.33
1	3	Sp	Sal_gla	15	2	0	0	2	NA	NA	-0.50	31.50	11.11	22.02	11.00	1.77
2	3	Sp	Sal_gla	15	0	0	0	0	NA	NA	-2.00	39.00	11.40	16.63	8.83	2.10
3	2	Sp	Sal_gla	15	0	0	0	0	NA	NA	-1.00	30.50	11.20	25.68	10.39	1.67
4	3	Sp	Sal_gla	15	0	0	0	0	NA	NA	-0.50	25.50	11.20	27.43	11.36	1.50
6	3	Sp	Sal_gla	15	0	0	0	0	NA	NA	-0.50	29.50	11.34	24.21	12.85	2.33
12	3	Sp	Sal_gla	15	1	0	0	1	NA	NA	-1.50	33.00	10.22	24.93	9.93	2.17
13	3	Sp	Sal_gla	15	4	0	0	4	NA	NA	-2.50	42.00	11.31	18.84	8.03	3.40

16	1 Sp	Sal_gla	15	5	0	5	NA	NA	-1.00	34.50	10.96	20.90	12.23	2.03
2	1 Ao	Sil_aca	30	1	1	0	0.78	0.78	-1.50	35.00	11.69	20.11	12.67	2.23
17	4 Ao	Sil_aca	30	1	1	0	1.60	1.60	-0.50	29.50	11.34	30.95	15.28	3.00
5	3 Ao	Sil_aca	30	3	3	0	2.77	0.92	-1.00	33.50	11.67	24.20	8.96	1.00
13	4 Ao	Sil_aca	30	9	9	0	4.39	0.49	-2.50	37.00	11.08	24.70	16.08	2.53
15	4 Ao	Sil_aca	30	10	10	0	4.88	0.49	-1.00	29.00	10.83	23.65	11.91	1.33
11	4 Ao	Sil_aca	30	6	6	0	5.33	0.89	-2.50	44.00	11.97	17.95	11.79	0.97
8	2 Ao	Sil_aca	30	10	10	0	6.02	0.60	-0.50	31.50	11.49	24.06	14.64	0.63
3	1 Ao	Sil_aca	30	9	9	0	10.17	1.13	-1.00	28.00	11.24	15.06	10.39	3.67
8	1 Ca	Sil_aca	30	1	1	0	0.26	0.26	0.00	25.50	10.49	27.39	12.27	4.10
17	3 Ca	Sil_aca	30	2	2	0	0.40	0.20	0.00	24.00	10.74	23.52	14.92	3.80
10	1 Ca	Sil_aca	30	1	1	0	0.46	0.46	-0.50	26.50	11.10	25.90	11.63	3.80
11	2 Ca	Sil_aca	30	1	1	0	0.82	0.82	0.00	28.50	10.51	16.29	9.46	4.23
12	1 Ca	Sil_aca	30	4	4	0	1.19	0.30	-0.50	25.50	10.44	24.76	14.09	3.60
7	2 Ca	Sil_aca	30	7	7	0	6.37	0.91	0.50	25.00	10.84	20.85	9.07	3.73
8	3 Ca	Sil_aca	30	0	0	0	NA	NA	0.50	29.00	11.07	20.30	10.23	5.20
16	3 Ca	Sil_aca	30	0	0	0	NA	NA	0.00	26.00	11.17	20.00	8.51	2.27
4	1 Ci	Sil_aca	30	1	1	0	0.15	0.15	-0.50	35.50	11.62	27.47	7.07	NA
5	4 Ci	Sil_aca	30	1	1	0	0.24	0.24	-1.50	38.00	11.30	17.39	9.85	1.90
5	2 Ci	Sil_aca	30	1	1	0	0.50	0.50	-1.00	36.50	11.31	22.58	7.90	1.23
14	1 Ci	Sil_aca	30	3	3	0	1.91	0.64	-0.50	29.50	10.86	22.68	8.48	2.57
17	2 Ci	Sil_aca	30	4	4	0	2.30	0.58	-0.50	32.50	11.12	23.18	9.05	3.10
7	1 Ci	Sil_aca	30	9	9	0	4.56	0.51	-0.50	36.00	11.20	30.11	7.24	3.17
9	4 Ci	Sil_aca	30	4	4	0	5.93	1.48	-0.50	30.00	11.09	25.15	7.17	3.63
3	4 Ci	Sil_aca	30	15	15	0	10.11	0.67	-0.50	26.50	11.00	17.06	6.89	3.13
17	1 Co	Sil_aca	30	1	1	0	0.67	0.67	-1.00	39.50	11.62	30.07	12.47	0.00
9	1 Co	Sil_aca	30	1	1	0	0.77	0.77	-2.50	56.50	12.06	20.41	5.08	0.00
10	2 Co	Sil_aca	30	1	1	0	0.82	0.82	-3.00	45.00	12.21	34.77	17.21	0.00
3	3 Co	Sil_aca	30	3	3	0	1.86	0.62	-1.50	36.00	11.90	24.90	5.15	0.00
1	4 Co	Sil_aca	30	0	0	0	NA	NA	-3.00	37.00	11.35	30.37	7.92	0.00
2	2 Co	Sil_aca	30	0	0	0	NA	NA	-3.00	53.00	12.38	18.97	7.21	0.00
4	4 Co	Sil_aca	30	0	0	0	NA	NA	-3.00	39.00	12.00	28.25	8.96	0.00
11	3 Co	Sil_aca	30	0	0	0	NA	NA	-2.50	44.50	11.90	16.51	7.17	0.00
12	4 Co	Sil_aca	30	0	0	0	NA	NA	-3.00	46.50	11.91	26.83	7.05	0.00
14	4 Co	Sil_aca	30	0	0	0	NA	NA	-3.00	41.50	12.12	24.81	6.23	0.00
12	2 Cs	Sil_aca	30	2	2	0	0.30	0.15	0.50	25.00	10.70	24.36	19.35	6.40
15	1 Cs	Sil_aca	30	1	1	0	0.42	0.42	0.50	25.50	10.76	15.95	9.88	5.43

11	1 Cs	Sil_aca	30	1	1	0	0.76	0.76	0.00	23.00	10.31	18.13	8.52	6.67
6	4 Cs	Sil_aca	30	2	2	0	0.87	0.44	0.00	23.00	10.83	23.98	11.19	6.83
16	2 Cs	Sil_aca	30	2	2	0	1.78	0.89	0.00	22.00	10.43	20.25	9.98	5.67
1	2 Cs	Sil_aca	30	7	7	0	3.81	0.54	0.00	23.00	10.71	21.42	16.16	6.57
7	4 Cs	Sil_aca	30	0	0	0 NA	NA	NA	0.50	24.00	10.78	20.41	12.96	8.30
10	4 Cs	Sil_aca	30	0	0	0 NA	NA	NA	0.00	28.50	10.66	32.63	15.70	8.30
10	3 Fn	Sil_aca	30	1	1	0	0.66	0.66	-1.00	31.50	10.90	27.75	19.47	1.67
9	2 Fn	Sil_aca	30	1	1	0	0.73	0.73	-1.50	44.00	11.70	27.48	7.80	2.17
4	2 Fn	Sil_aca	30	1	1	0	0.76	0.76	-0.50	32.50	11.32	23.82	10.72	1.50
13	2 Fn	Sil_aca	30	2	2	0	1.01	0.51	-1.50	52.50	12.08	16.40	9.86	3.10
14	3 Fn	Sil_aca	30	1	1	0	1.11	1.11	-0.50	30.50	11.05	19.47	8.58	1.60
15	2 Fn	Sil_aca	30	4	4	0	3.39	0.85	-0.50	38.00	10.97	19.76	9.30	1.33
1	1 Fn	Sil_aca	30	7	7	0	6.70	0.96	0.50	25.00	11.07	22.09	14.94	1.93
6	1 Fn	Sil_aca	30	0	0	0 NA	NA	NA	-1.00	35.50	11.36	23.40	6.84	1.50
4	3 Sp	Sil_aca	30	3	3	0	1.95	0.65	-0.50	25.50	11.20	27.43	11.36	1.50
13	3 Sp	Sil_aca	30	7	7	0	4.84	0.69	-2.50	42.00	11.31	18.84	8.03	3.40
12	3 Sp	Sil_aca	30	4	4	0	4.94	1.24	-1.50	33.00	10.22	24.93	9.93	2.17
1	3 Sp	Sil_aca	30	8	8	0	6.50	0.81	-0.50	31.50	11.11	22.02	11.00	1.77
6	3 Sp	Sil_aca	30	7	7	0	7.61	1.09	-0.50	29.50	11.34	24.21	12.85	2.33
16	1 Sp	Sil_aca	30	8	8	0	8.18	1.02	-1.00	34.50	10.96	20.90	12.23	2.03
2	3 Sp	Sil_aca	30	0	0	0 NA	NA	NA	-2.00	39.00	11.40	16.63	8.83	2.10
3	2 Sp	Sil_aca	30	0	0	0 NA	NA	NA	-1.00	30.50	11.20	25.68	10.39	1.67
5	3 Ao	Sol_vir	30	1	1	0	4.14	4.14	-1.00	33.50	11.67	24.20	8.96	1.00
8	2 Ao	Sol_vir	30	3	3	0	9.20	3.07	-0.50	31.50	11.49	24.06	14.64	0.63
11	4 Ao	Sol_vir	30	3	3	0	11.86	3.95	-2.50	44.00	11.97	17.95	11.79	0.97
17	4 Ao	Sol_vir	30	4	4	0	19.62	4.91	-0.50	29.50	11.34	30.95	15.28	3.00
15	4 Ao	Sol_vir	30	5	5	0	22.20	4.44	-1.00	29.00	10.83	23.65	11.91	1.33
13	4 Ao	Sol_vir	30	6	6	0	27.84	4.64	-2.50	37.00	11.08	24.70	16.08	2.53
3	1 Ao	Sol_vir	30	14	14	0	54.55	3.90	-1.00	28.00	11.24	15.06	10.39	3.67
2	1 Ao	Sol_vir	30	0	0	0 NA	NA	NA	-1.50	35.00	11.69	20.11	12.67	2.23
11	2 Ca	Sol_vir	30	3	1	2	8.50	8.50	0.00	28.50	10.51	16.29	9.46	4.23
10	1 Ca	Sol_vir	30	2	2	0	9.24	4.62	-0.50	26.50	11.10	25.90	11.63	3.80
8	3 Ca	Sol_vir	30	3	3	0	10.91	3.64	0.50	29.00	11.07	20.30	10.23	5.20
17	3 Ca	Sol_vir	30	4	4	0	14.02	3.51	0.00	24.00	10.74	23.52	14.92	3.80
8	1 Ca	Sol_vir	30	4	4	0	20.62	5.16	0.00	25.50	10.49	27.39	12.27	4.10
16	3 Ca	Sol_vir	30	3	3	0	22.31	7.44	0.00	26.00	11.17	20.00	8.51	2.27
7	2 Ca	Sol_vir	30	10	10	0	46.15	4.62	0.50	25.00	10.84	20.85	9.07	3.73

12	1	Ca	Sol_vir	30	0	0	0	0	NA	NA	-0.50	25.50	10.44	24.76	14.09	3.60
5	4	Ci	Sol_vir	30	3	3	0	0	10.59	3.53	-1.50	38.00	11.30	17.39	9.85	1.90
7	1	Ci	Sol_vir	30	3	3	0	0	17.79	5.93	-0.50	36.00	11.20	30.11	7.24	3.17
5	2	Ci	Sol_vir	30	4	4	0	0	18.94	4.74	-1.00	36.50	11.31	22.58	7.90	1.23
17	2	Ci	Sol_vir	30	8	8	0	0	41.10	5.14	-0.50	32.50	11.12	23.18	9.05	3.10
9	4	Ci	Sol_vir	30	9	8	1	0	45.92	5.74	-0.50	30.00	11.09	25.15	7.17	3.63
3	4	Ci	Sol_vir	30	0	0	0	0	NA	NA	-0.50	26.50	11.00	17.06	6.89	3.13
4	1	Ci	Sol_vir	30	0	0	0	0	NA	NA	-0.50	35.50	11.62	27.47	7.07	NA
14	1	Ci	Sol_vir	30	0	0	0	0	NA	NA	-0.50	29.50	10.86	22.68	8.48	2.57
3	3	Co	Sol_vir	30	1	1	0	0	3.24	3.24	-1.50	36.00	11.90	24.90	5.15	0.00
1	4	Co	Sol_vir	30	0	0	0	0	NA	NA	-3.00	37.00	11.35	30.37	7.92	0.00
2	2	Co	Sol_vir	30	0	0	0	0	NA	NA	-3.00	53.00	12.38	18.97	7.21	0.00
4	4	Co	Sol_vir	30	0	0	0	0	NA	NA	-3.00	39.00	12.00	28.25	8.96	0.00
9	1	Co	Sol_vir	30	0	0	0	0	NA	NA	-2.50	56.50	12.06	20.41	5.08	0.00
10	2	Co	Sol_vir	30	0	0	0	0	NA	NA	-3.00	45.00	12.21	34.77	17.21	0.00
11	3	Co	Sol_vir	30	0	0	0	0	NA	NA	-2.50	44.50	11.90	16.51	7.17	0.00
12	4	Co	Sol_vir	30	0	0	0	0	NA	NA	-3.00	46.50	11.91	26.83	7.05	0.00
14	4	Co	Sol_vir	30	0	0	0	0	NA	NA	-3.00	41.50	12.12	24.81	6.23	0.00
17	1	Co	Sol_vir	30	0	0	0	0	NA	NA	-1.00	39.50	11.62	30.07	12.47	0.00
11	1	Cs	Sol_vir	30	1	1	0	0	3.74	3.74	0.00	23.00	10.31	18.13	8.52	6.67
16	2	Cs	Sol_vir	30	1	1	0	0	4.14	4.14	0.00	22.00	10.43	20.25	9.98	5.67
7	4	Cs	Sol_vir	30	1	1	0	0	5.87	5.87	0.50	24.00	10.78	20.41	12.96	8.30
12	2	Cs	Sol_vir	30	4	4	0	0	21.52	5.38	0.50	25.00	10.70	24.36	19.35	6.40
1	2	Cs	Sol_vir	30	9	9	0	0	24.99	2.78	0.00	23.00	10.71	21.42	16.16	6.57
6	4	Cs	Sol_vir	30	7	7	0	0	30.39	4.34	0.00	23.00	10.83	23.98	11.19	6.83
10	4	Cs	Sol_vir	30	0	0	0	0	NA	NA	0.00	28.50	10.66	32.63	15.70	8.30
15	1	Cs	Sol_vir	30	0	0	0	0	NA	NA	0.50	25.50	10.76	15.95	9.88	5.43
13	2	Fn	Sol_vir	30	1	1	0	0	3.58	3.58	-1.50	52.50	12.08	16.40	9.86	3.10
4	2	Fn	Sol_vir	30	2	2	0	0	10.82	5.41	-0.50	32.50	11.32	23.82	10.72	1.50
14	3	Fn	Sol_vir	30	4	4	0	0	29.77	7.44	-0.50	30.50	11.05	19.47	8.58	1.60
1	1	Fn	Sol_vir	30	10	10	0	0	64.83	6.48	0.50	25.00	11.07	22.09	14.94	1.93
6	1	Fn	Sol_vir	30	0	0	0	0	NA	NA	-1.00	35.50	11.36	23.40	6.84	1.50
9	2	Fn	Sol_vir	30	0	0	0	0	NA	NA	-1.50	44.00	11.70	27.48	7.80	2.17
10	3	Fn	Sol_vir	30	0	0	0	0	NA	NA	-1.00	31.50	10.90	27.75	19.47	1.67
15	2	Fn	Sol_vir	30	0	0	0	0	NA	NA	-0.50	38.00	10.97	19.76	9.30	1.33
3	2	Sp	Sol_vir	30	4	4	0	0	8.65	2.16	-1.00	30.50	11.20	25.68	10.39	1.67
12	3	Sp	Sol_vir	30	4	4	0	0	16.77	4.19	-1.50	33.00	10.22	24.93	9.93	2.17

2	3 Sp	Sol_vir	30	4	4	0	21.23	5.31	-2.00	39.00	11.40	16.63	8.83	2.10
13	3 Sp	Sol_vir	30	9	9	0	29.77	3.31	-2.50	42.00	11.31	18.84	8.03	3.40
4	3 Sp	Sol_vir	30	11	10	1	40.26	4.03	-0.50	25.50	11.20	27.43	11.36	1.50
6	3 Sp	Sol_vir	30	8	8	0	45.14	5.64	-0.50	29.50	11.34	24.21	12.85	2.33
16	1 Sp	Sol_vir	30	16	16	0	78.84	4.93	-1.00	34.50	10.96	20.90	12.23	2.03
1	3 Sp	Sol_vir	30	17	17	0	117.32	6.90	-0.50	31.50	11.11	22.02	11.00	1.77
8	2 Ao	Vac_my	30	1	1	0	0.01	0.01	-0.50	31.50	11.49	24.06	14.64	0.63
5	3 Ao	Vac_my	30	1	1	0	0.18	0.18	-1.00	33.50	11.67	24.20	8.96	1.00
11	4 Ao	Vac_my	30	2	2	0	0.26	0.13	-2.50	44.00	11.97	17.95	11.79	0.97
17	4 Ao	Vac_my	30	2	2	0	0.42	0.21	-0.50	29.50	11.34	30.95	15.28	3.00
2	1 Ao	Vac_my	30	1	1	0	0.75	0.75	-1.50	35.00	11.69	20.11	12.67	2.23
15	4 Ao	Vac_my	30	4	4	0	1.24	0.31	-1.00	29.00	10.83	23.65	11.91	1.33
3	1 Ao	Vac_my	30	10	9	1	1.67	0.19	-1.00	28.00	11.24	15.06	10.39	3.67
13	4 Ao	Vac_my	30	0	0	NA	NA	-2.50	37.00	11.08	11.08	24.70	16.08	2.53
11	2 Ca	Vac_my	30	2	2	0	0.65	0.33	0.00	28.50	10.51	16.29	9.46	4.23
8	1 Ca	Vac_my	30	5	5	0	0.82	0.16	0.00	25.50	10.49	27.39	12.27	4.10
7	2 Ca	Vac_my	30	6	6	0	1.45	0.24	0.50	25.00	10.84	20.85	9.07	3.73
10	1 Ca	Vac_my	30	7	7	0	1.66	0.24	-0.50	26.50	11.10	25.90	11.63	3.80
8	3 Ca	Vac_my	30	0	0	NA	NA	0.50	29.00	11.07	11.07	20.30	10.23	5.20
12	1 Ca	Vac_my	30	0	0	NA	NA	-0.50	25.50	10.44	10.44	24.76	14.09	3.60
16	3 Ca	Vac_my	30	0	0	NA	NA	0.00	26.00	11.17	11.17	20.00	8.51	2.27
17	3 Ca	Vac_my	30	0	0	NA	NA	0.00	24.00	10.74	10.74	23.52	14.92	3.80
7	1 Ci	Vac_my	30	2	2	0	0.14	0.07	-0.50	36.00	11.20	30.11	7.24	3.17
5	2 Ci	Vac_my	30	2	2	0	0.18	0.09	-1.00	36.50	11.31	22.58	7.90	1.23
5	4 Ci	Vac_my	30	1	1	0	0.18	0.18	-1.50	38.00	11.30	17.39	9.85	1.90
17	2 Ci	Vac_my	30	1	1	0	0.75	0.75	-0.50	32.50	11.12	23.18	9.05	3.10
3	4 Ci	Vac_my	30	2	2	0	1.42	0.71	-0.50	26.50	11.00	17.06	6.89	3.13
4	1 Ci	Vac_my	30	0	0	NA	NA	-0.50	35.50	11.62	11.62	27.47	7.07	NA
9	4 Ci	Vac_my	30	0	0	NA	NA	-0.50	30.00	11.09	11.09	25.15	7.17	3.63
14	1 Ci	Vac_my	30	0	0	NA	NA	-0.50	29.50	10.86	10.86	22.68	8.48	2.57
9	1 Co	Vac_my	30	1	1	0	0.01	0.01	-2.50	56.50	12.06	20.41	5.08	0.00
10	2 Co	Vac_my	30	1	1	0	0.41	0.41	-3.00	45.00	12.21	34.77	17.21	0.00
2	2 Co	Vac_my	30	1	1	0	1.61	1.61	-3.00	53.00	12.38	18.97	7.21	0.00
1	4 Co	Vac_my	30	2	2	0	2.00	1.00	-3.00	37.00	11.35	30.37	7.92	0.00
11	3 Co	Vac_my	30	2	2	0	2.46	1.23	-2.50	44.50	11.90	16.51	7.17	0.00
3	3 Co	Vac_my	30	0	0	NA	NA	-1.50	36.00	11.90	11.90	24.90	5.15	0.00
4	4 Co	Vac_my	30	0	0	NA	NA	-3.00	39.00	12.00	12.00	28.25	8.96	0.00

12	4	Co	Vac_my	30	0	0	0	NA	NA	-3.00	46.50	11.91	26.83	7.05	0.00
14	4	Co	Vac_my	30	0	0	0	NA	NA	-3.00	41.50	12.12	24.81	6.23	0.00
17	1	Co	Vac_my	30	0	0	0	NA	NA	-1.00	39.50	11.62	30.07	12.47	0.00
7	4	Cs	Vac_my	30	2	2	0	0	0.20	0.10	0.50	24.00	20.41	12.96	8.30
11	1	Cs	Vac_my	30	1	1	0	0	0.21	0.21	0.00	23.00	10.31	8.52	6.67
10	4	Cs	Vac_my	30	3	3	0	0	0.39	0.13	0.00	28.50	10.66	15.70	8.30
15	1	Cs	Vac_my	30	2	2	0	0	0.39	0.20	0.50	25.50	10.76	9.88	5.43
1	2	Cs	Vac_my	30	2	2	0	0	0.48	0.24	0.00	23.00	10.71	16.16	6.57
12	2	Cs	Vac_my	30	8	7	1	0	1.06	0.15	0.50	25.00	10.70	19.35	6.40
6	4	Cs	Vac_my	30	3	3	0	0	1.16	0.39	0.00	23.00	10.83	11.19	6.83
16	2	Cs	Vac_my	30	0	0	0	NA	NA	0.00	22.00	10.43	20.25	9.98	5.67
10	3	Fn	Vac_my	30	1	1	0	0	0.23	0.23	-1.00	31.50	10.90	19.47	1.67
14	3	Fn	Vac_my	30	3	3	0	0	0.46	0.15	-0.50	30.50	11.05	8.58	1.60
4	2	Fn	Vac_my	30	2	2	0	0	1.10	0.55	-0.50	32.50	11.32	10.72	1.50
1	1	Fn	Vac_my	30	3	3	0	0	2.19	0.73	0.50	25.00	11.07	14.94	1.93
15	2	Fn	Vac_my	30	2	2	0	0	2.74	1.37	-0.50	38.00	10.97	9.30	1.33
6	1	Fn	Vac_my	30	0	0	0	NA	NA	-1.00	35.50	11.36	23.40	6.84	1.50
9	2	Fn	Vac_my	30	0	0	0	NA	NA	-1.50	44.00	11.70	27.48	7.80	2.17
13	2	Fn	Vac_my	30	0	0	0	NA	NA	-1.50	52.50	12.08	16.40	9.86	3.10
16	1	Sp	Vac_my	30	5	5	0	0	0.28	0.06	-1.00	34.50	10.96	12.23	2.03
6	3	Sp	Vac_my	30	3	3	0	0	0.52	0.17	-0.50	29.50	11.34	12.85	2.33
3	2	Sp	Vac_my	30	1	1	0	0	0.64	0.64	-1.00	30.50	11.20	10.39	1.67
4	3	Sp	Vac_my	30	1	1	0	0	0.70	0.70	-0.50	25.50	11.20	11.36	1.50
13	3	Sp	Vac_my	30	3	3	0	0	1.01	0.34	-2.50	42.00	11.31	8.03	3.40
1	3	Sp	Vac_my	30	2	2	0	0	2.50	1.25	-0.50	31.50	11.11	11.00	1.77
12	3	Sp	Vac_my	30	3	3	0	0	2.58	0.86	-1.50	33.00	10.22	9.93	2.17
2	3	Sp	Vac_my	30	0	0	0	NA	NA	-2.00	39.00	11.40	16.63	8.83	2.10

plant	lichen	replicate	seeds	tot.ger
Ant_alp	Ao	1	30	2
Ant_alp	Ao	2	30	1
Ant_alp	Ao	3	30	3
Ant_alp	Ao	4	30	6
Ant_alp	Ao	5	30	1
Ave_fle	Ao	1	30	8
Ave_fle	Ao	2	30	7
Ave_fle	Ao	3	30	14
Ave_fle	Ao	4	30	9
Ave_fle	Ao	5	30	13
Bet_nan	Ao	1	30	8
Bet_nan	Ao	2	30	0
Bet_nan	Ao	3	30	1
Bet_nan	Ao	4	30	5
Bet_nan	Ao	5	30	5
Dry_oct	Ao	1	30	0
Dry_oct	Ao	2	30	0
Dry_oct	Ao	3	30	0
Dry_oct	Ao	4	30	0
Dry_oct	Ao	5	30	0
Luz_spi	Ao	1	30	0
Luz_spi	Ao	2	30	0
Luz_spi	Ao	3	30	0
Luz_spi	Ao	4	30	3
Luz_spi	Ao	5	30	2
Pin_syl	Ao	1	10	8
Pin_syl	Ao	2	10	10
Pin_syl	Ao	3	10	9
Pin_syl	Ao	4	10	3
Pin_syl	Ao	5	10	9
Sal_gla	Ao	1	15	3
Sal_gla	Ao	2	15	6
Sal_gla	Ao	3	15	0
Sal_gla	Ao	4	15	1
Sal_gla	Ao	5	15	1
Sil_aca	Ao	1	30	0
Sil_aca	Ao	2	30	0
Sil_aca	Ao	3	30	0
Sil_aca	Ao	4	30	1
Sil_aca	Ao	5	30	0
Sol_vir	Ao	1	30	23
Sol_vir	Ao	2	30	17
Sol_vir	Ao	3	30	19

Sol_vir	Ao	4	30	19
Sol_vir	Ao	5	30	22
Vac_myr	Ao	1	30	23
Vac_myr	Ao	2	30	10
Vac_myr	Ao	3	30	5
Vac_myr	Ao	4	30	15
Vac_myr	Ao	5	30	29
Ant_alp	Co	1	30	8
Ant_alp	Co	2	30	3
Ant_alp	Co	3	30	3
Ant_alp	Co	4	30	4
Ant_alp	Co	5	30	4
Ave_fle	Co	1	30	9
Ave_fle	Co	2	30	6
Ave_fle	Co	3	30	8
Ave_fle	Co	4	30	2
Ave_fle	Co	5	30	3
Bet_nan	Co	1	30	9
Bet_nan	Co	2	30	5
Bet_nan	Co	3	30	8
Bet_nan	Co	4	30	5
Bet_nan	Co	5	30	3
Dry_oct	Co	1	30	2
Dry_oct	Co	2	30	2
Dry_oct	Co	3	30	3
Dry_oct	Co	4	30	0
Dry_oct	Co	5	30	1
Luz_spi	Co	1	30	0
Luz_spi	Co	2	30	0
Luz_spi	Co	3	30	1
Luz_spi	Co	4	30	0
Luz_spi	Co	5	30	0
Pin_syl	Co	1	10	10
Pin_syl	Co	2	10	10
Pin_syl	Co	3	10	9
Pin_syl	Co	4	10	8
Pin_syl	Co	5	10	7
Sal_gla	Co	1	15	14
Sal_gla	Co	2	15	1
Sal_gla	Co	3	15	6
Sal_gla	Co	4	15	1
Sal_gla	Co	5	15	0
Sil_aca	Co	1	30	0
Sil_aca	Co	2	30	3

Sil_aca	Co	3	30	6
Sil_aca	Co	4	30	5
Sil_aca	Co	5	30	2
Sol_vir	Co	1	30	24
Sol_vir	Co	2	30	23
Sol_vir	Co	3	30	27
Sol_vir	Co	4	30	24
Sol_vir	Co	5	30	19
Vac_myr	Co	1	30	21
Vac_myr	Co	2	30	20
Vac_myr	Co	3	30	16
Vac_myr	Co	4	30	27
Vac_myr	Co	5	30	29
Ant_alp	Ca	1	30	2
Ant_alp	Ca	2	30	5
Ant_alp	Ca	3	30	9
Ant_alp	Ca	4	30	0
Ant_alp	Ca	5	30	9
Ave_fle	Ca	1	30	8
Ave_fle	Ca	2	30	7
Ave_fle	Ca	3	30	9
Ave_fle	Ca	4	30	5
Ave_fle	Ca	5	30	11
Bet_nan	Ca	1	30	9
Bet_nan	Ca	2	30	4
Bet_nan	Ca	3	30	1
Bet_nan	Ca	4	30	4
Bet_nan	Ca	5	30	1
Dry_oct	Ca	1	30	0
Dry_oct	Ca	2	30	1
Dry_oct	Ca	3	30	2
Dry_oct	Ca	4	30	3
Dry_oct	Ca	5	30	2
Luz_spi	Ca	1	30	0
Luz_spi	Ca	2	30	1
Luz_spi	Ca	3	30	1
Luz_spi	Ca	4	30	0
Luz_spi	Ca	5	30	0
Pin_syl	Ca	1	10	10
Pin_syl	Ca	2	10	6
Pin_syl	Ca	3	10	9
Pin_syl	Ca	4	10	8
Pin_syl	Ca	5	10	7
Sal_gla	Ca	1	15	1

Sal_gla	Ca	2	15	8
Sal_gla	Ca	3	15	2
Sal_gla	Ca	4	15	0
Sal_gla	Ca	5	15	2
Sil_aca	Ca	1	30	0
Sil_aca	Ca	2	30	0
Sil_aca	Ca	3	30	0
Sil_aca	Ca	4	31	1
Sil_aca	Ca	5	30	2
Sol_vir	Ca	1	30	26
Sol_vir	Ca	2	30	19
Sol_vir	Ca	3	30	27
Sol_vir	Ca	4	30	24
Sol_vir	Ca	5	30	30
Vac_myr	Ca	1	30	17
Vac_myr	Ca	2	30	14
Vac_myr	Ca	3	30	14
Vac_myr	Ca	4	30	19
Vac_myr	Ca	5	30	21
Ant_alp	Ci	1	30	2
Ant_alp	Ci	2	30	3
Ant_alp	Ci	3	30	3
Ant_alp	Ci	4	30	3
Ant_alp	Ci	5	30	2
Ave_fle	Ci	1	30	6
Ave_fle	Ci	2	30	8
Ave_fle	Ci	3	30	5
Ave_fle	Ci	4	30	6
Ave_fle	Ci	5	30	11
Bet_nan	Ci	1	30	2
Bet_nan	Ci	2	30	2
Bet_nan	Ci	3	30	0
Bet_nan	Ci	4	30	2
Bet_nan	Ci	5	30	2
Dry_oct	Ci	1	30	1
Dry_oct	Ci	2	30	0
Dry_oct	Ci	3	30	0
Dry_oct	Ci	4	30	0
Dry_oct	Ci	5	30	3
Luz_spi	Ci	1	30	0
Luz_spi	Ci	2	30	0
Luz_spi	Ci	3	30	0
Luz_spi	Ci	4	30	0
Luz_spi	Ci	5	30	0

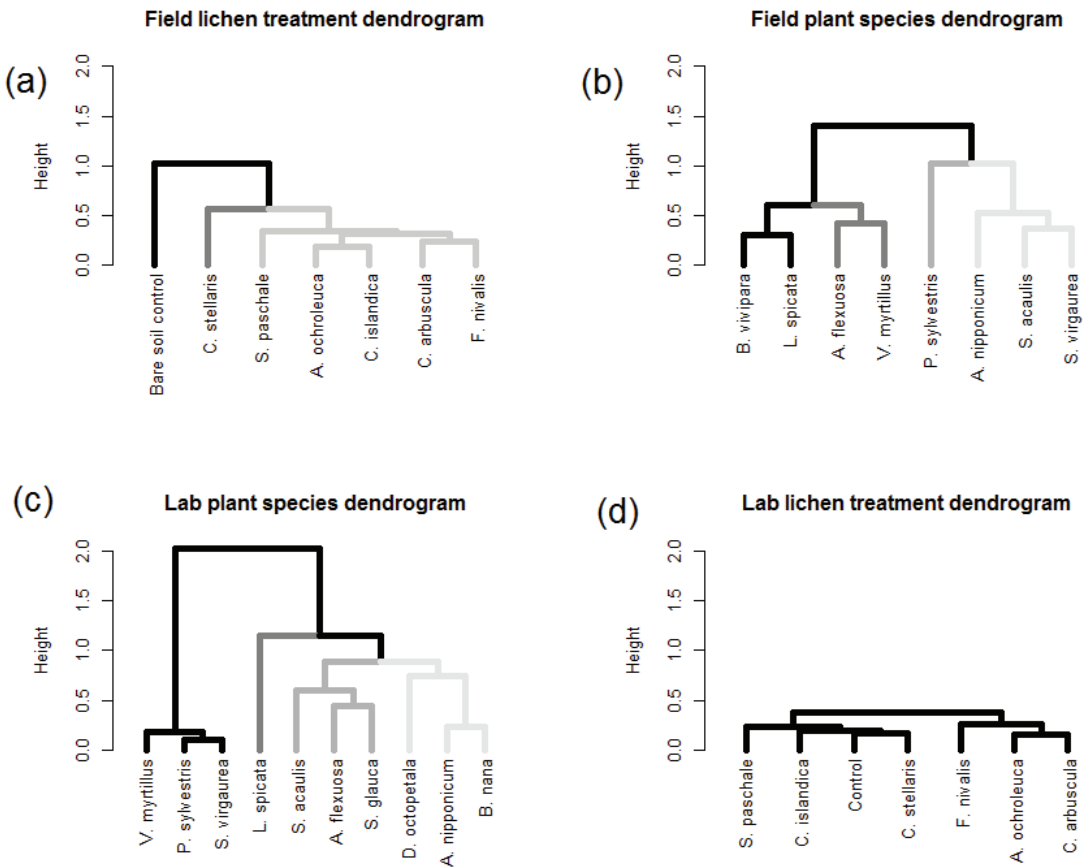
Pin_syl	Ci	1	10	6
Pin_syl	Ci	2	10	9
Pin_syl	Ci	3	10	7
Pin_syl	Ci	4	10	10
Pin_syl	Ci	5	10	8
Sal_gla	Ci	1	15	0
Sal_gla	Ci	2	15	10
Sal_gla	Ci	3	15	12
Sal_gla	Ci	4	15	2
Sal_gla	Ci	5	15	5
Sil_aca	Ci	1	30	12
Sil_aca	Ci	2	30	11
Sil_aca	Ci	3	30	9
Sil_aca	Ci	4	30	8
Sil_aca	Ci	5	30	9
Sol_vir	Ci	1	30	29
Sol_vir	Ci	2	30	20
Sol_vir	Ci	3	30	19
Sol_vir	Ci	4	30	26
Sol_vir	Ci	5	30	18
Vac_myr	Ci	1	30	28
Vac_myr	Ci	2	30	11
Vac_myr	Ci	3	30	26
Vac_myr	Ci	4	30	21
Vac_myr	Ci	5	30	30
Ant_alp	Cs	1	30	1
Ant_alp	Cs	2	30	3
Ant_alp	Cs	3	30	6
Ant_alp	Cs	4	30	2
Ant_alp	Cs	5	30	6
Ave_fle	Cs	1	30	9
Ave_fle	Cs	2	30	7
Ave_fle	Cs	3	30	13
Ave_fle	Cs	4	30	7
Ave_fle	Cs	5	30	11
Bet_nan	Cs	1	30	4
Bet_nan	Cs	2	30	5
Bet_nan	Cs	3	30	2
Bet_nan	Cs	4	30	2
Bet_nan	Cs	5	30	4
Dry_oct	Cs	1	30	0
Dry_oct	Cs	2	30	3
Dry_oct	Cs	3	30	3
Dry_oct	Cs	4	30	0

Dry_oct	Cs	5	30	0
Luz_spi	Cs	1	30	0
Luz_spi	Cs	2	30	0
Luz_spi	Cs	3	30	1
Luz_spi	Cs	4	30	0
Luz_spi	Cs	5	30	1
Pin_syl	Cs	1	10	9
Pin_syl	Cs	2	10	5
Pin_syl	Cs	3	10	9
Pin_syl	Cs	4	10	9
Pin_syl	Cs	5	10	10
Sal_gla	Cs	1	15	0
Sal_gla	Cs	2	15	10
Sal_gla	Cs	3	15	1
Sal_gla	Cs	4	15	2
Sal_gla	Cs	5	15	4
Sil_aca	Cs	1	30	4
Sil_aca	Cs	2	30	8
Sil_aca	Cs	3	30	5
Sil_aca	Cs	4	30	8
Sil_aca	Cs	5	30	5
Sol_vir	Cs	1	30	21
Sol_vir	Cs	2	30	24
Sol_vir	Cs	3	30	22
Sol_vir	Cs	4	30	22
Sol_vir	Cs	5	30	25
Vac_myr	Cs	1	30	9
Vac_myr	Cs	2	30	24
Vac_myr	Cs	3	30	8
Vac_myr	Cs	4	30	27
Vac_myr	Cs	5	30	27
Ant_alp	Fn	1	30	2
Ant_alp	Fn	2	30	3
Ant_alp	Fn	3	30	5
Ant_alp	Fn	4	30	2
Ant_alp	Fn	5	30	4
Ave_fle	Fn	1	30	5
Ave_fle	Fn	2	30	7
Ave_fle	Fn	3	30	4
Ave_fle	Fn	4	30	9
Ave_fle	Fn	5	30	10
Bet_nan	Fn	1	30	5
Bet_nan	Fn	2	30	3
Bet_nan	Fn	3	30	7

Bet_nan	Fn	4	30	1
Bet_nan	Fn	5	30	4
Dry_oct	Fn	1	30	0
Dry_oct	Fn	2	30	3
Dry_oct	Fn	3	30	5
Dry_oct	Fn	4	30	1
Dry_oct	Fn	5	30	3
Luz_spi	Fn	1	30	0
Luz_spi	Fn	2	30	1
Luz_spi	Fn	3	30	0
Luz_spi	Fn	4	30	0
Luz_spi	Fn	5	30	0
Pin_syl	Fn	1	10	9
Pin_syl	Fn	2	10	6
Pin_syl	Fn	3	10	7
Pin_syl	Fn	4	10	8
Pin_syl	Fn	5	10	9
Sal_gla	Fn	1	15	0
Sal_gla	Fn	2	15	0
Sal_gla	Fn	3	15	0
Sal_gla	Fn	4	15	0
Sal_gla	Fn	5	15	1
Sil_aca	Fn	1	30	0
Sil_aca	Fn	2	30	0
Sil_aca	Fn	3	30	0
Sil_aca	Fn	4	30	0
Sil_aca	Fn	5	30	0
Sol_vir	Fn	1	30	18
Sol_vir	Fn	2	30	22
Sol_vir	Fn	3	30	18
Sol_vir	Fn	4	30	16
Sol_vir	Fn	5	30	22
Vac_myr	Fn	1	30	23
Vac_myr	Fn	2	30	28
Vac_myr	Fn	3	30	21
Vac_myr	Fn	4	30	27
Vac_myr	Fn	5	30	26
Ant_alp	Sp	1	30	3
Ant_alp	Sp	2	30	9
Ant_alp	Sp	3	30	8
Ant_alp	Sp	4	30	6
Ant_alp	Sp	5	30	3
Ave_fle	Sp	1	30	10
Ave_fle	Sp	2	30	5

Ave_fle	Sp	3	30	8
Ave_fle	Sp	4	30	4
Ave_fle	Sp	5	30	5
Bet_nan	Sp	1	30	7
Bet_nan	Sp	2	30	4
Bet_nan	Sp	3	30	5
Bet_nan	Sp	4	30	4
Bet_nan	Sp	5	30	3
Dry_oct	Sp	1	30	3
Dry_oct	Sp	2	30	1
Dry_oct	Sp	3	30	4
Dry_oct	Sp	4	30	4
Dry_oct	Sp	5	30	2
Luz_spi	Sp	1	30	0
Luz_spi	Sp	2	30	1
Luz_spi	Sp	3	30	0
Luz_spi	Sp	4	30	1
Luz_spi	Sp	5	30	1
Pin_syl	Sp	1	10	8
Pin_syl	Sp	2	10	7
Pin_syl	Sp	3	10	7
Pin_syl	Sp	4	10	7
Pin_syl	Sp	5	10	8
Sal_gla	Sp	1	15	1
Sal_gla	Sp	2	15	4
Sal_gla	Sp	3	15	0
Sal_gla	Sp	4	15	4
Sal_gla	Sp	5	15	1
Sil_aca	Sp	1	30	10
Sil_aca	Sp	2	30	15
Sil_aca	Sp	3	30	16
Sil_aca	Sp	4	30	13
Sil_aca	Sp	5	30	7
Sol_vir	Sp	1	30	28
Sol_vir	Sp	2	30	20
Sol_vir	Sp	3	30	24
Sol_vir	Sp	4	30	24
Sol_vir	Sp	5	30	26
Vac_myr	Sp	1	30	22
Vac_myr	Sp	2	30	26
Vac_myr	Sp	3	30	17
Vac_myr	Sp	4	30	13
Vac_myr	Sp	5	30	27

Supporting information to the paper: Nystuen, K.O., Sundsdal, K. et al. Lichens facilitate seedling recruitment in alpine heath. *Journal of Vegetation Science*.



Appendix S7: Dendrograms used in the heat maps of seedling recruitment in field (Fig. 3b) and seed germination in lab (Fig. 5b) constructed with hierarchical agglomerate Ward clustering based on Jaccard dissimilarities. The dendrograms were cut at different manually chosen heights creating clusters separated with grayscale colors: the field lichen dendrogram was cut at height 0.5 (a), the field plant species dendrogram at height 0.6 (b) and the lab plant species dendrogram at height 0.8 (d). The lab lichen treatment dendrogram (c) did not separate until height 0.38 and was therefore not cut into clusters.

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i>
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympatric species of newts (<i>Triturus</i> , <i>Amphibia</i>) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskft	Dr. philos Zoology	Sociobiological studies of the rook <i>Corvus frugilegus</i>
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (<i>Trichoptera</i>) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit <i>Parus montanus</i>
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i>
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (<i>Salmo salar</i>): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (<i>Mytilus edulis</i>)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (<i>Salmo salar</i> L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose <i>Alces alces</i>
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose <i>Alces alces</i> , and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (<i>Salmo salar</i>) and brown trout (<i>Salmo trutta</i>): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie <i>Pica pica</i>
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (<i>Lynx lynx</i>) in Norway
1991	Jan Henning L'Abée Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout <i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera <i>Coregonus</i> and <i>Salvelinus</i> : Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torggrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (<i>Phleum pratense</i> L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i>
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O ⁶ -methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
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1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> .
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1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (<i>Gallinago media</i>): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i>
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (<i>Rubus idaeus</i> L.)
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1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i>
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cuckoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
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1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition
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1996	Jorunn Skjermo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjörg Einarsson	Dr. scient Zoology	Production of Atlantic salmon (<i>Salmo salar</i>) and Arctic charr (<i>Salvelinus alpinus</i>): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics
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1997	Gunvor Øie	Dr. scient Botany	Evaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybo	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper <i>Cinclus cinclus</i> in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (<i>Hylobius abietis</i>), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to soil bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i>
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (<i>Salvelinus alpinus</i> (L.)) and brown trout (<i>Salmo trutta</i> L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (<i>Salmo salar</i>) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (<i>Alces alces</i>) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls <i>Strix aluco</i> : An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Solendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker <i>Dendrocopos leucotos</i>
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (<i>Gadus morhua</i> L.) and Halibut (<i>Hippoglossus hippoglossus</i> L.)
1999	Marianne Gjaever	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (<i>Micromisistius poutassou</i>), haddock (<i>Melanogrammus aeglefinus</i>) and cod (<i>Gadus morhua</i>) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lokeus</i>
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (<i>Salmo salar</i>) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (<i>Salmo salar</i> L.) and Brown trout (<i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (<i>Cuculus canorus</i>) and its host: adaptations and counteradaptations in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (<i>Loxodonta africana</i>)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (<i>Salvelinus alpinus</i>), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (<i>Salmo trutta</i>) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (<i>Symphodus melops</i> L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (<i>Castor fiber</i>)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A ₂ in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and the Ral GTPase from <i>Drosophila melanogaster</i>
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatus</i> L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (<i>Syncerus caffer</i>) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (<i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i>)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i>
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (<i>Salmo salar</i> L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliusson	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohintanely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i>
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (<i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i>)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (<i>Fragaria x ananassa</i>): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i>
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelién	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (<i>Halichoerus grypus</i>) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected <i>Echinops</i> spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutants (POPs) in seabirds, Retinoids and α -tocopherol – potential biomarkers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on <i>Calanus finmarchicus</i>
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	<i>Acesta oophaga</i> and <i>Acesta excavata</i> – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (<i>Salmo trutta</i>) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish <i>Syngnathus typhle</i> : when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle <i>Tenebrio molitor</i> - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth <i>Heliothis virescens</i>
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (<i>Mamestra brassicae</i> L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod (<i>Gadus morhua</i> L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (<i>Struthio camelus massaicus</i>) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, <i>Taeniopygia guttata</i>
2008	Solvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (<i>Gadus morhua</i>): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	<i>Arabidopsis thaliana</i> Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in <i>Cyclamen persicum</i> . Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth <i>Heliothis virescens</i> : Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos <i>Cuculus canorus</i> and <i>Fringilla</i> finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (<i>Panthera leo</i>) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (<i>Rachycentron canadum</i>) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in <i>Arabidopsis</i> from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of <i>Eriophorum latifolium</i> , a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (<i>Gobiussculus flavescens</i>)
2011	Ann-Iren Kittang	PhD Biology	<i>Arabidopsis thaliana</i> L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in <i>Arabidopsis thaliana</i>
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (<i>Poecilia reticulata</i>): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (<i>Salmo salar</i>): The interaction between habitat and density

2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (<i>Elephas maximus</i>) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in <i>Arabidopsis</i>
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (<i>Mytilus edulis</i>): Feed requirements, storage and integration with salmon (<i>Salmo salar</i>) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (<i>Salmo trutta</i> L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in <i>Calanus finmarchicus</i>
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect <i>Heliothis virescens</i> .
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment

2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in <i>Emiliania huxleyi</i> Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in <i>Arabidopsis thaliana</i>
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (<i>Salmo salar</i>) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in <i>Calanus finmarchicus</i> – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in <i>Arabidopsis thaliana</i>
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom <i>Phaeodactylum tricornutum</i>
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog (<i>Lycaon pictus</i>) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (<i>Salmo salar</i> L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose (<i>Alces alces</i>) habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite <i>Syngamus trachea</i> in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholipase A2

2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: <i>Calanus</i> , little auks (<i>Alle alle</i>) and black-legged kittiwakes (<i>Rissa tridactyla</i>)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms <i>Phaeodactylum tricornutum</i> and <i>Seminavis robusta</i>
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in <i>Arabidopsis thaliana</i>
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (<i>Sphagnum</i>)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (<i>Gadus morhua</i> L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod <i>Calanus finmarchicus</i> in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod <i>Calanus finmarchicus</i>
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (<i>Gadus morhua</i> L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (<i>Somateria mollissima</i>)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (<i>Giraffa camelopardalis tippelskirchi</i>) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Environmental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.

2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (<i>Lycaon pictus</i>) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of <i>Tanytarsus</i> van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (<i>Sphagnum</i>)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on <i>Arabidopsis thaliana</i>
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (<i>Salmo salar</i>)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological context to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh

2019	Knut Jørgen Egelie	Phd Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	Phd Biology	Adaptive responses to environmental stochasticity on different evolutionary time-scales
2019	Kwaslema Malle Hariohay	Phd Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	Phd Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (<i>Haliaeetus albicilla</i>) nestlings
2019	Joseph Mbyati Mukeka	Phd Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	Phd Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	Phd Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	Phd Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	Phd Biology	Population dynamics under climate change and harvesting: Results from the high Arctic Svalbard reindeer
2019	Alex Kojo Datsomor	Phd Biology	The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon (<i>Salmo salar</i> L): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes
2020	Ingun Næve	Phd Biology	Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon (<i>Salmo Salar</i>) production and reproduction
2020	Rachael Morgan	Phd Biology	Physiological plasticity and evolution of thermal performance in zebrafish
2020	Mahsa Jalili	Phd Biology	Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon (<i>Salmo salar</i> L.): possible nutrionomics approaches
2020	Haiqing Wang	Phd Biology	Utilization of the polychaete <i>Hediste diversicolor</i> (O.F. Millier, 1776) in recycling waste nutrients from land-based fish farms for valueadding applications'
2020	Louis Hunninck	Phd Biology	Physiological and behavioral adaptations of impala to anthropogenic disturbances in the Serengeti ecosystems
2020	Kate Layton-Matthews	Phd Biology	Demographic consequences of rapid climate change and density dependence in migratory Arctic geese
2020	Amit Kumar Sharma	Phd Biology	Genome editing of marine algae: Technology development and use of the CRISPR/Cas9 system for studies of light harvesting complexes and regulation of phosphate homeostasis
2020	Lars Rød-Eriksen	Phd Biology	Drivers of change in meso-carnivore distributions in a northern ecosystem
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