1 **Title:**

2 Lichens facilitate seedling recruitment in alpine heath

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4 **Running title:**

5 Lichen-facilitated seedling recruitment

6

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30 KS, BJG, GRS, HH and KON designed the study; KS, KON and BJG did field work; KS

31 performed the laboratory experiment; KON, ØHO and KS analyzed the data; KON and KS

32 wrote the paper with inputs from all authors.

33

36

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38 The authors have no conflict of interest to report.

39

Data Availability Statement:

41 The two datasets analyzed in the current study are available in Supporting Information as

42 Appendix S5 and S6.

43

44

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:

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69   In harsh environments like alpine dwarf-shrub and lichen heaths, the presence of lichens and

70   the resulting amelioration of the microclimate seems more important for vascular plant

71   recruitment than are allelopathic effects often reported in lab experiments. We might

72   therefore expect most terricolous lichens, depending on the plant species in focus, to facilitate

73   rather than hamper the early stages of plant recruitment into lichen-dominated arctic-alpine

74   heath vegetation.

75

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; Larson, 1987; Crittenden, 2000; 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 1200 g m^{-2} (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 N_2-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, 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.

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104   allelopathy), by mechanisms related to the lichens' physical structure, or by harsh

105   environmental conditions (Fig. 1).

106   In summer, lichen heaths often experience droughts, which Moles and Westoby

107   (2004) identified as the second most important cause of seedling mortality. On the other

108   hand, lichens modify microclimatic conditions in ways that may support seedling survival, as

109   they maintain soil moisture (Broll, 2000; Kershaw & Rouse, 1971; Molina-Montenegro et al.,

110   2013) and prevent extreme temperatures due to high reflectivity and low thermal conductivity

111   (Kershaw, 1977; Broll, 2000). Lichens furthermore reduce wind erosion and plant

112   evapotranspiration through shelter effects (Molina-Montenegro et al., 2013).

113   The physical structure of lichens may have contrasting effects on plant recruitment.

114   Lichen mats act as efficient seed traps (Sedia & Ehrenfeld, 2003), but can also prevent seeds

115   or seedlings from reaching the ground. A classic example is Allen's (1929) observation of

116   seedlings pulled out of the soil by repeated lichen thalli expansion and contraction driven by

117   fluctuations in moisture. Some species (e.g. *Cladonia stellaris)* have upright, branched,

118   shrub-like thalli, and form very thick and dense mats with low light penetration and high

119   insulation capacity. Others (e.g. *Flavocetraria nivalis*) form upright, but thinner and more

120   open mats that provide less thermal insulation (Crittenden, 2000), but may be easier for seeds

121   and seedlings to penetrate. However, most lichen-plant recruitment interaction studies under

122   field conditions have focused on *Cladonia* spp. (e.g. Allen, 1929; Brown & Mikola, 1974;

123   Hawkes & Menges, 2003; M. M. Kytöviita & Stark, 2009; Sedia & Ehrenfeld, 2003) in

124   various vegetation types, whereas less is known about the interactions between other

125   ecologically successful genera of terricolous lichens (e.g. *Cetraria*, *Stereocaulon* and

126   *Alectoria*; Crittenden, 2000) and plant species that co-occur in arctic-alpine vegetation.

127   Lichen secondary metabolites may also inhibit establishment and growth of vascular

128   plants. Direct lichen allelopathic effects may inhibit germination, radicle and hypocotyl

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growth (Hobbs, 1985; Latkowska, Bialczyk, Lechowski, & Czaja-Prokop, 2008; Nishitoba,

Nishimura, Nishiyama, & Mizutani, 1987; Peres, Mapeli, Faccenda, 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 have 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: (1) Is soil microclimate (i.e. temperature and moisture) affected by

lichen species and lichen mat thickness? Is (2) seedling recruitment and (3) 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: (4) Is seed germination affected by lichen

allelopathy? To reveal the importance of lichen allelopathy under natural conditions we

154 asked: (5) Are the same lichen-plant interactions detected for seed germination in the

155 laboratory and seedling recruitment in the field?

156

157 **Methods**

158 **Study site**

159 The field study was conducted at an exposed dwarf-shrub and lichen heath, surrounded by

160 subalpine birch forest in the mountains of Dovrefjell, Central Norway, close to Kongsvoll

161 Biological Station (c. 930 m a.s.l., 62°18′5.75517″N, 9°36′24.00385″E). The bedrock at the

162 site consists of lightly eroded actinolite-hornblende amphibolite (Geological Survey of

163 Norway, https://www.ngu.no/en/, accessed 11.07.17). The vegetation is dominated by

164 *Empetrum nigrum* ssp. *hermaphroditum, Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea*,

165 *Betula nana* and *Salix glauca*, and the lichens *Alectoria ochroleuca* and *Flavocetraria*

166 *nivalis*. Such dwarf-shrub and lichen heaths predominantly occur above the forest line, but

167 can also be found on locally exposed areas within subalpine forests like our study site

168 (Fremstad, 1998) (see Appendix S1 for photo from the study site). The studied dwarf-shrub

169 and lichen heath is thus representative for such vegetation in general, and the findings

170 especially relevant for arctic-alpine areas where these heaths are widespread.

171 Dovrefjell has a slightly continental climate with short warm summers and long cold

172 winters. At the weather station Fokstugu (930 m a.s.l.) *c*. 26 km south of the study site, the

173 mean annual precipitation was 435 mm (Førland, 1993) and mean annual temperature -0.1°C

174 (Aune, 1993) for the period 1961–1990. For the same period, the warmest month was July

175 with average monthly temperature 9.8°C and the coldest was January, with -8.8°C (Aune,

176 1993).

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8

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-occuring lichen and plant species; Hobbs, 1985), have seeds (bulbils for *B. vivipara,* hereafter referred to as seeds) of different sizes which might affect their recruitment potential, and have seedlings 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, *P. sylvestris,* seeds were supplied by The Norwegian Forest Seed Center and originated from Oppdal at *c*. 600–650 m a.sl., *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 *D. octopetala* was used only in the laboratory and *B. vivipara* only in the field experiment. See The Norwegian Biodiversity Information Centre (NBIC) (https://www.biodiversity.no/, accessed 23.10.18) for unified nomenclature of lichen and plant species.

Field experiment

In the field, seventeen plastic trays ($56 \times 26 \times 8$ 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 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 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 *C. stellaris* and *C. arbuscula,* coherent mats were collected and transplanted into the plots. As *A. ochroleuca*, *C. islandica*, *F. nivalis,* and *S. 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 *P. sylvestris* with only 10 seeds and *S. 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 approximately 365 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.

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228   In late May 2014, temperature loggers (NexSens Micro-T DS1921G) were placed 0.5

229   cm below the soil surface in each plot to measure the soil temperature every second hour.

230   Soil moisture (% volumetric soil water content) was measured once in each plot during

231   overcast conditions after rain (26.08.14) and again during dry conditions on a sunny day after

232   one day without rain (28.08.14) with a hand-held 5 cm long soil moisture probe set to option

233   "organic soil" (TRIME-PICO, IMKO GmbH, Ettlingen, Germany). In late August and early

234   September 2014, the temperature loggers were collected and the seedlings harvested. Mean,

235   maximum and minimum temperatures were calculated for the period 13.06.14–31.08.14.

236   Seedlings were identified, counted, rinsed in water to remove soil fragments, and oven dried

237   at 70°C for 72 hours. All seedlings of each species from each plot were weighed together to

238   obtain a measure of average dry seedling biomass (mg). The thickness of the lichen mats

239   (average of 3 measurements from soil surface to highest lichen thallus point at different fixed

240   locations) was measured for each plot at the end of the experiment (Table 1).

241

242   **Laboratory experiment**

243   In the laboratory, samples of each of the six lichen species were cleaned of debris, dried, and

244   crushed with a hand blender. Two grams of crushed lichen was added underneath filter paper

245   in five Petri dishes for each of the ten species sown and a control. Thirty seeds, except for *P.*

246   *sylvestris* with 10 and *S. glauca* with 15 seeds, were placed on the filter paper and 6 ml of

247   distilled water was added. The controls had only filter paper, water and seeds. The Petri

248   dishes were sealed with parafilm and kept in darkness at 3°C for 12 weeks. After this cold

249   stratification, the Petri dishes were transferred to growth chambers (Percival E-36L) for 6

250   weeks with 20 hours daylight (representative for mid-June growing season photoperiod in

251   central Norway) with approx. 200 µm m^{-2} s^{-1} photosynthetically active radiation at 20°C, and

252   4 hours darkness at 10°C. Every week, 2 ml of distilled water was added, and the Petri dishes

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253   were rotated within the chamber. More water (1–2 ml) was added if signs of desiccation on

254   the filter paper occurred. Germinated seeds were counted and then removed from the Petri

255   dishes weekly over six weeks.

256

257   **Statistical analyses**

258   To test whether the soil microclimate was affected by the lichen treatments (question 1), we

259   fitted linear mixed-effects models with Gaussian errors and with each microclimate

260   parameter (mean soil temperature, maximum soil temperature, minimum soil temperature,

261   soil moisture wet day and soil moisture dry day) as response variable, lichen treatment, lichen

262   mat thickness and their interaction as fixed effects, and tray as random factor.

263   To test if seedling recruitment in the field experiment was affected by the lichen

264   treatments (question 2), we fitted a generalized linear mixed-effects model with binomial

265   errors and logit link-function, with proportion seedling recruitment as response variable,

266   lichen treatment, lichen mat thickness, plant species and their interaction as fixed factors, and

267   tray and plot (nested within trays) as random factors. In this analysis, plot was also included

268   in the random structure because of several observations (i.e. plant species) per plot. Numbers

269   of seeds sown for each species were added as weights in the models. For *V. myrtillus*, the

270   only species with external seed influx from the control plots without sowing, the mean influx

271   (0.7 seedling) was subtracted from the data prior to the analyses. Estimates were back-

272   transformed (from logit scale to probability scale) to obtain recruitment rates, and these rates

273   are presented in figures and text as they account for the nested structure of our experimental

274   design.

275   Similarly, to test if seedling biomass was affected by the lichen treatments (question

276   3), we fitted linear mixed-effects models with average seedling weight as response variable,

277   lichen treatment, lichen mat thickness, plant species and their interactions as fixed factors,

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278   and tray and plot (nested within trays) as random factors. Seedling numbers were added as

279   weights in the model because the number of recruited seedlings (i.e. the sample size) varied

280   among plant species and plots. Two species were excluded from the field recruitment and

281   growth analyses: *B. nana* because of low emergence rates in all treatments, and *S. glauca*

282   because most seedlings were dead when counted and harvested in autumn (see Appendix S2

283   for counts of live and dead seedlings).

284   To test if seed germination in the lab was affected by lichen treatments (question 4),

285   we fitted a generalized linear model with binomial errors and logit link-function, with the

286   proportion of germinated seeds as response variable, and lichen treatment, plant species and

287   their interaction as fixed factors. Estimates were back-transformed to obtain germination

288   rates.

289   Finally, we used a Spearman rank correlation test to test for correlation between the

290   field recruitment and laboratory germination estimates (question 5). Control treatments were

291   excluded and only the seven plant species shared in both experiments were included.

292   To visualize the lichen-plant interactions in the field recruitment and lab germination

293   experiment, and explore possible clusters, we constructed heat maps with hierarchical

294   clustering (two-dimensional representations where the recruitment and germination estimates

295   of all combinations of plant species and lichen treatments are shown with colors and ordered

296   by similarity) with the gplots R package (Warnes et al., 2019). Dendrograms were

297   constructed with hierarchical agglomerate Ward clustering based on Jaccard dissimilarities

298   calculated in the vegan R package (Oksanen et al., 2017). Number of clusters for the lichen

299   treatment and plant species dendrograms were manually chosen based on their separation

300   heights and by visual inspection of the clusters' ecological meaning.

301   For question 1–4, model selection was based on the Akaike information criterion

302   (AIC, see model selection results in Appendix S3). Small-sample corrected AIC (AIC_c) was

303 used for model selection in question 1. Anova and summary tables of models presented in the

304 manuscript are in Appendix S4. Differences in soil microclimate among lichen treatments

305 were tested using multiple comparisons with the Tukey method in the multcomp R package

306 (Hothorn, Bretz, & Westfall, 2008). For the mixed models (seed germination and seedling

307 recruitment and biomass) we used the emmeans R package for pairwise comparisons (Lenth,

308 2017). All statistical analyses were done in R 3.1.2 (R Core Team 2015). Mixed-effect

309 models were fitted with the lme4 R package (Bates, Mächler, Bolker, & Walker, 2015).

310 Primary data is available in Appendix S5 (seedling recruitment and seedling biomass in field)

311 and Appendix S6 (seed germination in lab).

312

313 **Results**

314 **Soil microclimate – field experiment**

315 Lichen treatment was a better predictor of all soil microclimate variables than was lichen mat

316 thickness (Appendix S3). The presence of lichens reduced mean and maximum soil

317 temperatures and increased minimum soil temperatures compared to the bare soil control

318 (Fig. 2a). Temperature buffering was strongest beneath *C. stellaris* and *C. arbuscula* (Fig.

319 2a), which had the thickest mats (Table 1). This was especially evident for maximum

320 temperature, which differed by more than 20°C between *C. stellaris* (24.9°C, 95% CI = 21.6

321 – 28.3) and the bare soil control (45.7°C, 95% CI = 42.6 – 48.8; Fig. 2a).

322   Soil moisture differed between treatments under dry conditions, but not under wet

323 conditions (Fig. 2b). On the dry and sunny day, the driest soils occurred in the bare soil

324 control (8.6%, 95% CI = 6.9 – 10.3) and beneath *C. islandica* (8.6%, 95% CI = 6.6 – 10.7),

325 whereas the soils beneath *A. ochroleuca* (13.1%, 95% CI = 11.2 – 15.0) and *C. stellaris*

326 (12.6%, 95% CI = 10.7 – 14.5) were moister (Fig 2c).

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Seedling recruitment – field experiment

The effects of the lichen treatments on seedling recruitment were complex and plant species-specific (Fig. 3), as demonstrated by strongest statistical support for the model including the plant-lichen treatment interaction (Appendix S3). For some plant species (*B. vivipara* and *L. 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 (Fig. 3). Most species had recruitment rates below 40%, except *P. sylvestris* with recruitment rates approaching 80% (Fig. 3).

Based on their effect on seedling recruitment, the lichen treatments cluster into three groups: one with bare soil control only, one with *C. stellaris* only, and a third with the remaining five lichen species (Fig. 3b, Appendix S7). The bare soil controls stand out with overall low recruitment, and not a single seedling of *B. vivipara* and *L. spicata* recruited here (Fig. 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 *C. stellaris* supported low recruitment of many plant species, whereas for *A. flexuosa* the recruitment in *C. stellaris* was comparatively high (Fig. 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 *S. paschale*, especially *S. virgaurea* (Fig. 3).

15

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 *P. sylvestris* and *S. virgaurea* had heavier seedlings (Fig. 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 (Fig. 3), there were no statistically detectable differences among treatments (Fig. 4). *Cladonia stellaris* clearly affected the growth of *P. sylvestris* negatively, and weight of the seedlings here were only half the weight of the heaviest seedlings found in *S. paschale* and *A. ochroleuca* (Fig. 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 (Fig. 5a). The lichen treatments' species-specific influence on seed germination is also demonstrated in the heat map in Fig. 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.

For two plant species (*S. acaulis* and *V. myrtillus*) we found interesting patterns concerning lichen secondary compounds. Germination of *S. acaulis* was clearly enhanced in *C. islandica* and *S. paschale* (Fig. 5a), the only two lichens without usnic acid (Table 1), whereas *Vaccinium myrtillus* germinated best in *F. nivalis* and *C. islandica*, which are the only lichens with protolichesterinic acid (Appendix S2).

16

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.

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 on bare soil. Importantly, the effects of lichen mats on seedling recruitment and
growth were species-specific, and for *C. stellaris*, a lichen with thick and dense mats, the
overall facilitative effect was replaced by restrained recruitment and growth conditions for
many plant species.

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

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399   controls did not have higher recruitment rates of small-seeded species (such as *L. spicata*, *S.*

400   *acaulis* and *V. myrtillus*). Furthermore, large temperature fluctuations can also be detrimental

401   for seedlings (e.g. Cavieres, Badano, Sierra-Almeida, & Molina-Montenegro, 2007), and the

402   low recruitment we observed on bare soil may partly represent seedling mortality during

403   summer. On bare soil, maximum temperatures reached 45°C, 10 – 20 degrees higher than

404   within the lichen mats, and soil drying was pronounced.

405   Under dry conditions, *C. islandica* was the only lichen below which the soil was as

406   dry as in the bare soil controls. Lichen water absorption and retaining abilities may vary

407   among species (Larson, 1979), and depend on morphology (Larson, 1981) and thallus size

408   (Gauslaa & Solhaug, 1998). Our focal lichen species varied extensively in morphology, and

409   lichen species was a better predictor of soil microclimate than was lichen mat thickness in

410   itself. For instance, the soil beneath *C. islandica* became much drier than beneath *S. paschale*,

411   which has thinner mats. This could be due to poor water retention of *C. islandica* combined

412   with its open mat structure and dark color.

413

414   **Lichens facilitate seedling recruitment**

415   We found that the presence of lichens increased seedling recruitment rates compared to

416   recruitment on bare soil. High seedling numbers within lichen mats have also been reported

417   for subarctic forests (Brown & Mikola, 1974; den Herder, Kytoviita, & Niemela, 2003;

418   Steijlen, Nilsson, & Zackrisson, 1995; Zackrisson, Nilsson, Steijlen, & Hornberg, 1995), and

419   for the treeline ecotone (Dufour-Tremblay, De Vriendt, Lévesque, & Boudreau, 2012). The

420   recruitment rates within lichens observed in our study (below 40% for all species except *P.*

421   *sylvestris*) is within the expectations for such systems (Graae et al., 2011; Steijlen et al.,

422   1995), and therefore contrasts with the negative effects of lichen physical structure and

423   allelopathy on seedling recruitment as reported by Hobbs (1985), Hawkes and Menges

18

424   (2003), and Sedia and Ehrenfeld (2003) at lower elevations, and possibly more benign

425   environments. Hawkes and Menges (2003) found, however, that the negative effect of lichens

426   was weaker under more severe environmental stress. Indeed, on exposed heaths dominated by

427   terricolous lichens, the vegetation is sparse and the sheltering effect of lichens may be an

428   advantage for seedling recruitment in accordance with the Stress Gradient Hypothesis

429   (Bertness & Callaway, 1994).

430   The increased importance of facilitation in stressful habitats could explain the lower

431   recruitment observed on bare soils, as bare soils otherwise tend to promote seedling

432   recruitment, also in arctic-alpine vegetation (Lembrechts et al., 2016; Milbau, Shevtsova,

433   Osler, Mooshammer, & Graae, 2013). However, recruitment is often better in small gaps, or

434   for big gaps, close to the edge and not in the center, especially in harsh environments

435   (Lembrechts, Milbau, & Nijs, 2015; Houle & Filion, 2003). The bare soil plots in our study

436   were quite big and comparable to the severe disturbances performed by Evju et al. (2012) on

437   exposed heaths where few seedlings recruited. Furthermore, the ability of lichens to trap

438   seeds (Sedia & Ehrenfeld, 2003) is important in wind-exposed sites like lichen heaths. This

439   could explain the low recruitment of *S. glauca* and *S. virgaurea* on bare soils in our study, as

440   both species have seeds with hairy appendages that could easily be blown away.

441   Only lichen species with dense and thick mats (e.g. *C. stellaris*) seem to negatively

442   affect plant recruitment. This may be caused by a combination of seeds not being able to

443   reach the soil and seedlings not being able to emerge through the mat. Plant species with long

444   and thin cotyledons (e.g. the graminoid *A. flexuosa*) may establish more successfully in thick

445   and dense mats (cf. the observations of Sydes and Grime (1981) of seedlings emerging in leaf

446   litter).

447

448

19

Lichens affect seedling growth

Dense and thick lichen mats (e.g. *C. stellaris*) seem to negatively affect seedling growth of many plant species. Seedling growth of the treeline-forming *P. sylvestris* (Körner, 2012) was clearly reduced in *C. 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 *P. sylvestris* into low-alpine *C. stellaris*-dominated heaths. Brown and Mikola (1974) also reported reduced growth of *P. sylvestris* seedlings within *C. 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 *C. stellaris*) on *P. 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 *C. stellaris*, low light availability rather than allelopathy during the initial phase of stem and root elongation contributed to the growth reduction of *P. sylvestris* and other species in our field experiment.

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 *S. acaulis*, *S. glauca* and *V. 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 were seemingly affected by lichen secondary compounds acting alone: *S. acaulis* with higher germination in lichens devoid of usnic acid (*C. islandica* and *S. paschale*), and *V.*

20

474 *myrtillus* with highest germination in protolichesterinic-producing lichens (*C. islandica* and

475 *F. nivalis*). The allelopathic effect of certain metabolites may vary among plant species

476 (Peres et al., 2009), and plant responses to different lichen species may be complicated by

477 mutual adaptation of plants and lichens (Hobbs, 1985). In our study, however, the lichen

478 secondary metabolites were not distinguished from one another or from other compounds,

479 and we cannot ascertain which compounds affected germination. *Stereocaulon paschale*, for

480 instance, has N_2-fixing cyanobacteria (Kytöviita & Crittenden, 2007), potentially resulting in

481 more available nitrogen (Nash 2008), which in turn may increase germination (Baskin &

482 Baskin, 2014) and plant growth (Körner, 2003). Although not apparent for all plant species

483 (but for *S. acaulis* and *S. virgaurea*), this could have contributed to high germination in the

484 lab as well as recruitment and growth in the field in association with *S. paschale* compared to

485 most of the other lichen species.

486   The germination responses to lichens observed in the lab were only partly confirmed

487 in the field, suggesting a minor effect of lichen allelopathy on seed regeneration under natural

488 conditions. We did not measure secondary metabolites under field conditions, but concerning

489 *C. stellaris* and usnic acid, Stark et al. (2007) found no traces in rainwater percolated through

490 the mat or in the soils beneath. Our findings therefore support recent studies suggesting that

491 allelopathic effects of lichens on vascular plants under natural conditions are weaker than

492 traditionally thought (Favero-Longo & Piervittori, 2010; Stark et al., 2007).

493

494 **Conclusions and implications for vegetation dynamics**

495 Our study shows that lichens facilitate recruitment of vascular plants in dwarf-shrub and

496 lichen heaths, but also that lichen-plant interactions are likely to be species-specific. Overall,

497 the observed lichen-driven modification of microclimate indicates more benign conditions for

498 seedling recruitment. Together, these findings suggest that the ecological importance of

21

499   lichen allelopathy under natural conditions might be overestimated based on the findings in

500   laboratory experiments, at least in stressful habitats. We might therefore expect most lichens

501   to facilitate rather than hamper vegetation changes in dry tundra heaths. While lichens may

502   facilitate recruitment of seedlings of some species in harsh environments, the effect of lichens

503   may be different for later life stages. High seedling mortality during the first years is common

504   on heaths as well as other tundra habitats (Graae et al. 2011; Milbau et al. 2013), and for

505   heaths associated with low winter temperatures (Milbau et al. 2013). The lichen mats may

506   protect against very low winter temperatures, though, as observed during summer for the

507   species with thick mats. For herbaceous species with broad leaves, re-emerging through the

508   densest lichen mats every spring could get harder as they grow bigger. When seedlings

509   eventually grow past the protective lichen canopy, their survival may depend on adaptations

510   to conserve water and withstand wind-erosion and low temperatures, especially on the most

511   exposed heaths.

512   Nevertheless, vascular plants are expanding at the cost of terricolous lichens e.g. in

513   low-arctic Canada (Fraser et al., 2014) due to increase of tall- and dwarf shrubs, and on

514   Scandinavian low-alpine summits due to increase of the shrub *B. nana* (Vanneste et al.,

515   2017). Accumulation of leaf litter from deciduous shrubs, or other plant litter, can result in

516   death of fruticose lichens (Cornelissen et al., 2001). This suggests that certain vascular plants,

517   and especially those adapted to drought and/or with prostrate growth forms, such as *B. nana*

518   (de Groot, Thomas, & Wein, 1997), are able to expand and outcompete shade-intolerant

519   lichens in heaths despite the stressful environment.

520

521

22

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List of appendices

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 manuscript.

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 Fig. 3 and Fig. 5 with heights.

Tables

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 lobed and leaf-like thalli with dorsiventral morphology), mat thickness in the field experiment (mean ± 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)	Secondary metabolites*
Flavocetraria nivalis	Cetrarioid	1.9 ± 0.2	Usnic acid and protolichesterinic acid
Alectoria ochroleuca	Fruticose	1.9 ± 0.4	Usnic acid and diffractaic acid
Stereocaulon paschale	Fruticose	2.1 ± 0.2	Atranorin and lobaric acid
Cetraria islandica	Cetrarioid	2.6 ± 0.3	Fumarprotocetraric acid and protolichesterinic acid
Cladonia arbuscula	Fruticose	3.8 ± 0.3	Usnic acid and fumarprotocetraric acid
Cladonia stellaris	Fruticose	6.8 ± 0.4	Usnic acid and perlatolic acid

Vascular plant species	Growth form	Seed mass (mg)**	
Anthoxanthum nipponicum	Graminoid	0.4878	
Avenella flexuosa	Graminoid	0.5	
Betula nana	Shrub	0.3184	
Bistorta vivipara	Forb	2.73	
Dryas octopetala	Dwarf shrub	0.706	
Luzula spicata	Graminoid	0.259	
Pinus sylvestris	Tree	6.0	
Salix glauca	Shrub	0.163	
Silene acaulis	Forb	0.3	
Solidago virgaurea	Forb	0.55	
Vaccinium myrtillus	Dwarf shrub	0.3	

*Info on secondary metabolites from Krog, Østhagen, and Tønsberg (1980) and Holien and Tønsberg (2008).

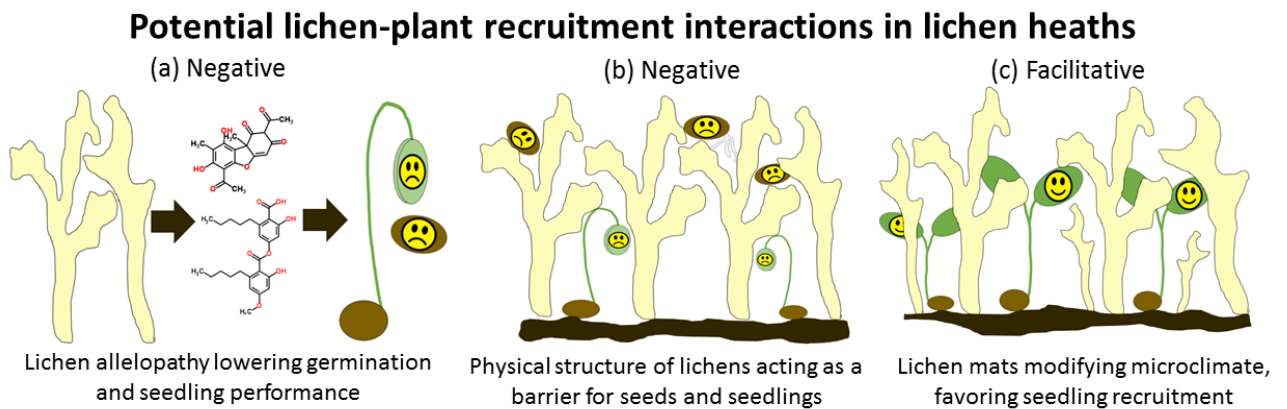**Seed mass data accessed from Royal Botanic Gardens Kew. (2018) Seed Information Database (SID).

Version 7.1. Retrieved from: http://data.kew.org/sid/ (October 2018).

Figures

Potential lichen-plant recruitment interactions in lichen heaths

(a) Negative — Lichen allelopathy lowering germination and seedling performance

(b) Negative — Physical structure of lichens acting as a barrier for seeds and seedlings

(c) Facilitative — Lichen mats modifying microclimate, favoring seedling recruitment

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.
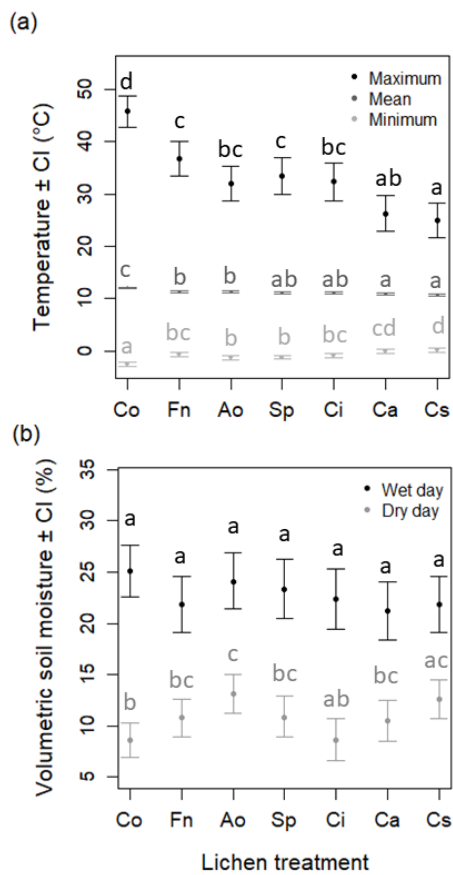
**Figure 2:** Estimated soil microclimate conditions in the field experiment with temperature (maximum, mean and minimum) (a) and moisture (wet and dry day) (b) with 95% confidence intervals for each lichen treatment. Treatments with no letters in common are significantly different ($p < 0.05$), tested 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*.

(a) Field seedling recruitment barplots
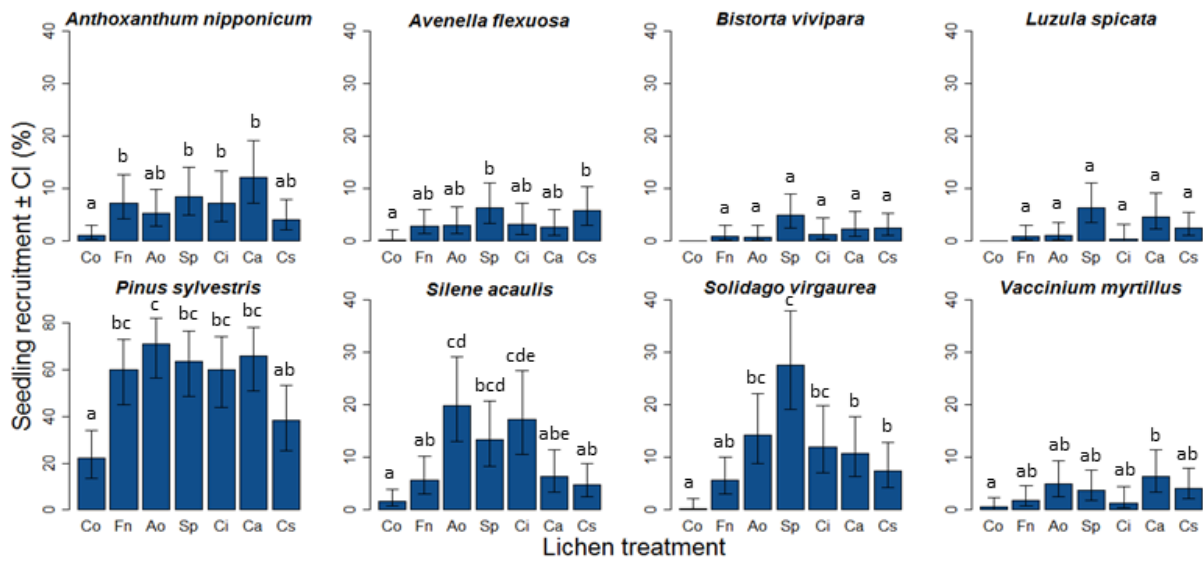
(b) Field seedling recruitment heatmap
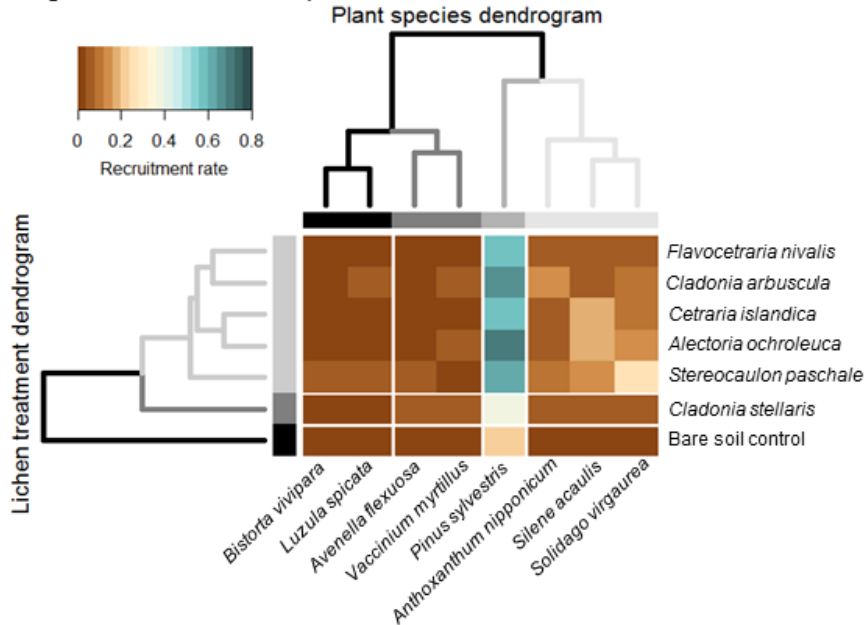
Figure 3: Seedling recruitment in the field experiment across lichen treatments. (a) Barplots showing mean estimated seedling recruitment and 95% confidence intervals. Notice that the recruitment scale of *P. sylvestris* differ from the other plant species. The lichen treatments are ordered by increasing 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) Heat map of mean estimated seedling recruitment rates in the lichen treatments with clustering of

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773   plants (top) and lichen treatments (left). The plant and lichen dendrogram were cut at

774   manually chosen heights (see Appendix S7).

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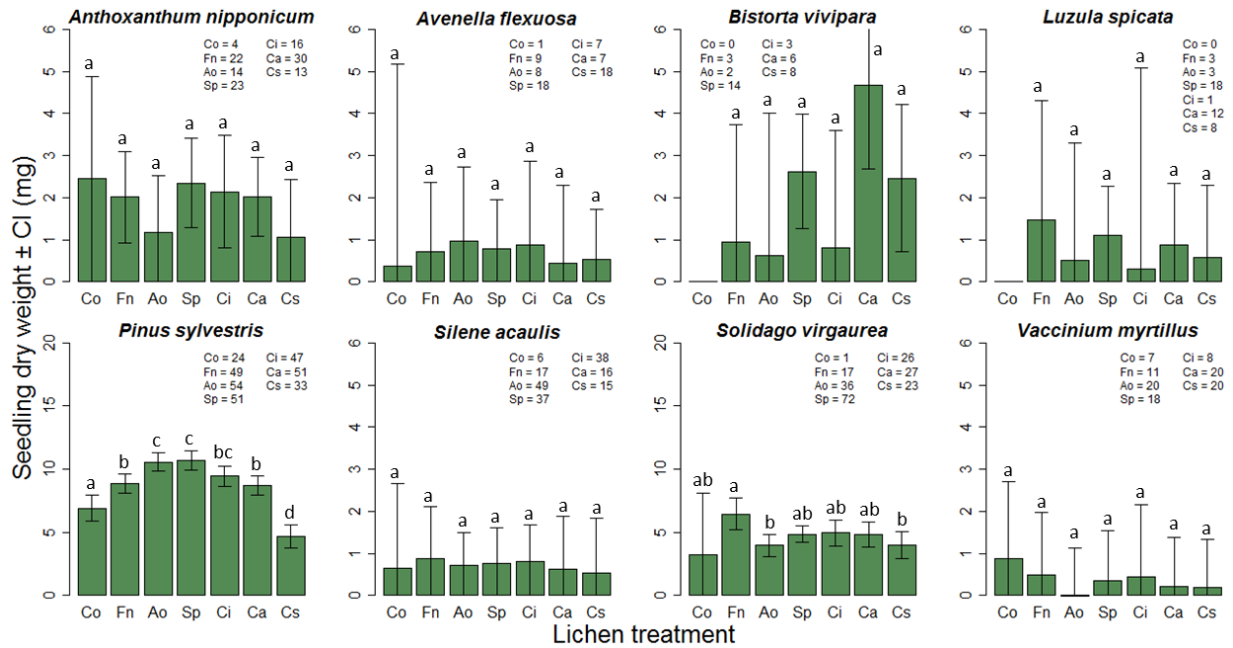
777

778   **Figure 4:** Estimated biomass (mg dry weight) of the emerged seedlings in the field

779   experiment across lichen treatments with 95% confidence intervals. Notice that the seedling

780   weight scale of the heavy *P. sylvestris* and *S. virgaurea* differ from the six other plant

781   species. Legends show number of seedlings emerged in each lichen treatment. The lichen

782   treatments are ordered by increasing mat thickness and abbreviated as follows: Co; Control

783   (bare soil), Fn; *Flavocetraria nivalis*, Ao; *Alectoria ochroleuca*, Sp; *Stereocaulon paschale*,

784   Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*. Treatments with

785   no letters in common are significantly different ($p < 0.05$), as revealed by pairwise

786   comparisons.

(a) Lab seed germination barplots
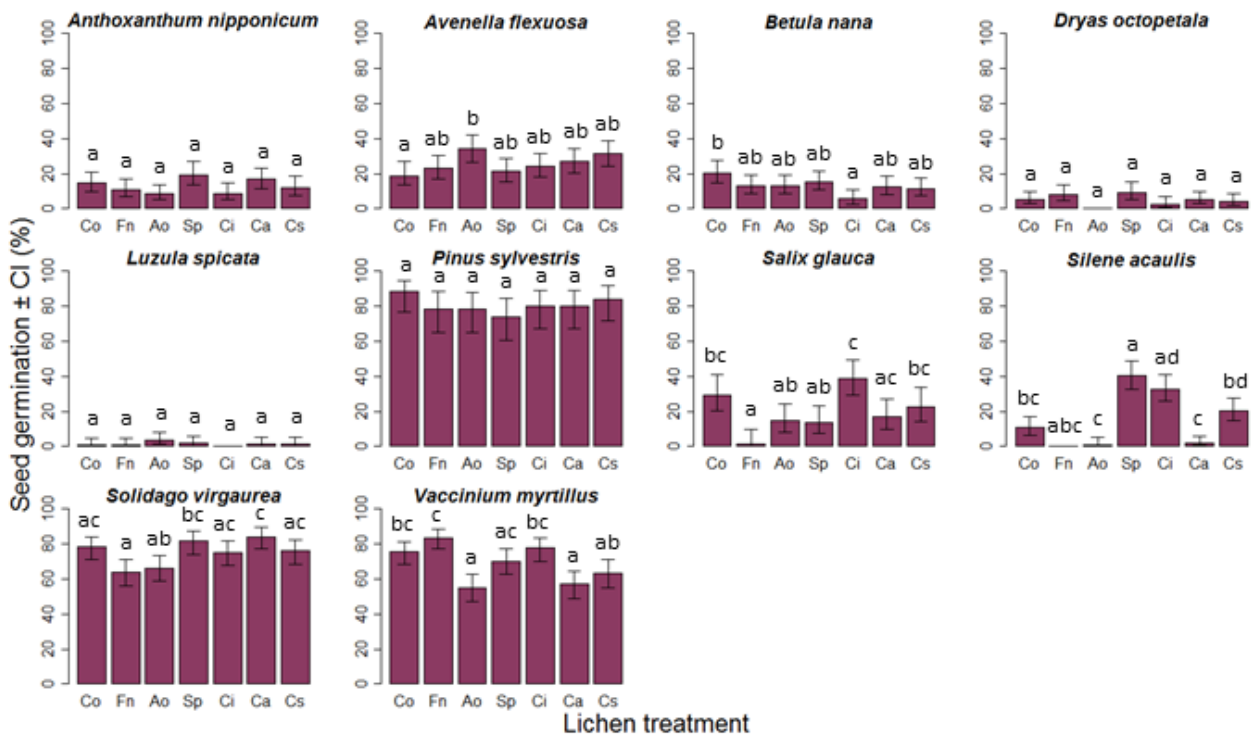
(b) Lab seed germination heatmap
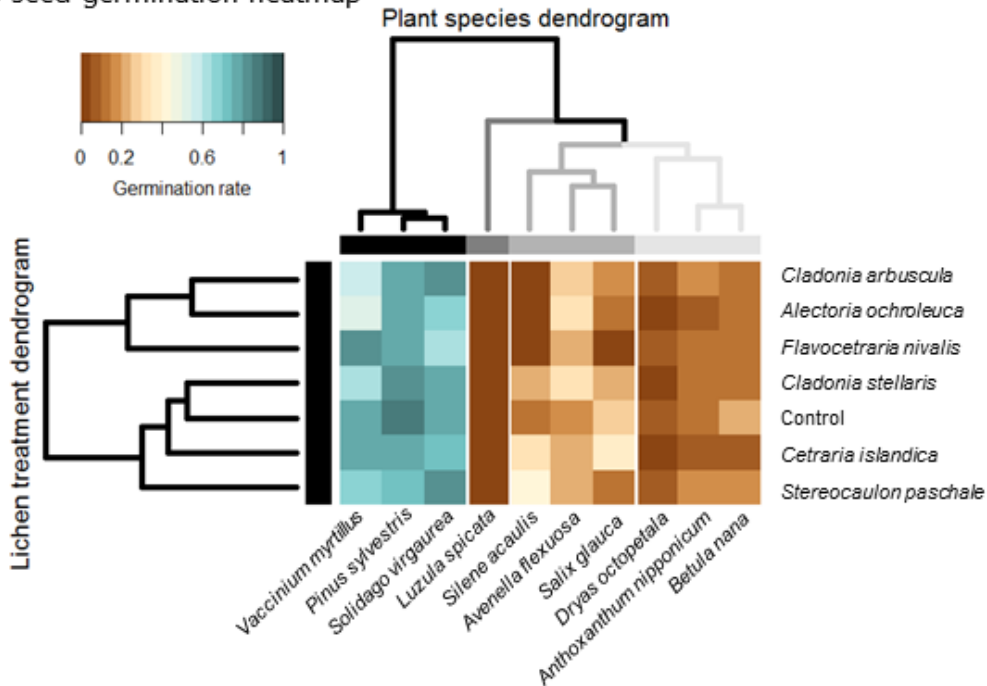
Figure 5: Seed germination in the laboratory experiment across lichen treatments. (a)

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

39

793   different ($p < 0.05$), as revealed by pairwise comparisons. (b) Heat map of mean estimated

794   mean germination rates in the lichen treatments with clustering of plants (top) and lichen

795   treatments (left). The lichen treatment dendrogram did not separate until height 0.38 and

796   supported no ecologically meaningful clustering of the lichens (see Appendix S7).