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Short-term effects of hardened wood ash and nitrogen fertilisation on understory vegetation in a Norway spruce forest in south-east Norway

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Abstract

In a fertiliser experiment in a Norway spruce forest in SE Norway, four treatments were applied in a block design with three replicates per treatment. Treatments included 3 t wood ash ha^{-1} (Ash), 150 kg nitrogen ha^{-1} (N), wood ash and nitrogen combined (Ash+N), and unfertilised control (Ctrl). Treatment effects on understory plant species numbers, single abundances of species and (summarized) cover of main species groups were studied. Two years after treatment there were no significant changes for species numbers or abundances of woody species, dwarf shrubs or pteridophytes, nor for *Sphagnum* spp. in the bottom layer. The cover of graminoids decreased in Ctrl plots. Herb cover increased significantly in Ash+N and N plots due to the increase of *Melampyrum sylvaticum*. In Ash+N plots, mosses decreased significantly in species number, while their cover increased. Moss cover also decreased significantly in N plots. The species number and cover of hepatics decreased significantly in Ash and Ash+N plots. Hepatics cover also decreased in Ctrl plots. Both the lichen number and cover decreased in Ash+N plots. Single species abundances decreased for many bryophytes in fertilised plots. To conclude, fertilisation had modest effects on vascular plants, while bryophytes were more strongly affected, especially by Ash+N.

Running head: Wood ash and N effects on understory vegetation

Keywords: Ash recycling, wood ash fertilisation, N fertilisation, vegetation, plant diversity,

Word count: 8472

Introduction

To mitigate climate change, forest fertilisation has been put forward as a means to rapidly increase forest growth and thereby CO_2 sequestration (Haugland et al. 2014; Rytter et al. 2016, Ask et al. 2021). In the Nordic countries, forest fertilisation usually takes place using mineral fertilisers containing nitrogen (N), which is generally the growth limiting element (Nilsen 2001; Nohrstedt 2001). However, peat or wood ash are also used to some extent (Nohrstedt 2001; Saarsalmi & Malkönen 2001). Ash from combustion of organic materials contains nutrients (for instance phosphorous (P), potassium (K) and calcium (Ca), Clarke et al. 2018) that, when added together with nitrogen, may further increase growth on rich mineral soil types (Hanssen et al. 2020). Even though fertilisation most often increases tree growth, both nitrogen and wood ash fertilisation may have undesirable effects on the forest ecosystem and its understory vegetation.

Nitrogen fertilisation has previously been shown to affect both abundance and species diversity in the understory. A typical finding is that nitrophilous herbs and grasses expand and that dwarf bushes, bryophytes and lichens decrease (Kellner 1993; Sullivan & Sullivan 2018), though effects may vary with site conditions (Olsson & Kellner 2006; Hedwall et al. 2014; Jacobson et al. 2020) and between species within these groups (Dirkse & Martakis 1992; Strengbom & Nordin 2008). Some fertilisation effects may last more than a decade into the next forest tree generation (Strengbom & Nordin 2008). Many earlier studies on understory vegetation report on fertilisation regimes with high doses and/or repeated fertilisation, and few have studied the effects of a single application of 150 kg N per hectare, which is the common dose applied in Norwegian forestry (Røsberg et al. 1998; Nilsen 2001; Haugland et al. 2014; see also Hedwall et al. 2018). Fertilisation effects may also vary along both local environmental and regional climatic gradients and are more pronounced on nutrient-poor than on nutrient-rich sites (Olsson & Kellner 2006). Most reported studies in Nordic countries are from Sweden and Finland (Sullivan & Sullivan 2018) while there are only a few studies on understory vegetation effects in Norway, where there is considerable variation in forest understory vegetation due to strong local and regional gradients in topography, soil nutrients and climatic conditions (Økland 1996). Effects on vascular plants have been reported by some authors to be moderate, and few effects have been observed 10 years after less intensive fertilisation (Kellner 1993; Nohrstedt 1998). Effects on bryophytes have been reported to persist for 15 to 18 years (Olsson & Kellner 2006) after multiple fertilisations.

After ash fertilisation, some negative effects on the understory vegetation, especially bryophytes, have been reported (Kellner & Weibull 1998; Jacobson & Gustafsson 2001; Pitman 2006; Ozolinčius et al. 2007; Dynesius 2012), though Jäppinen &Hotanen (1990) found only minor effects on bryophytes after application of 3 t ha^{-1} of wood ash. As emphasized by Hart et al. (2019), the effects of wood ash treatment on understory vegetation thus vary between studies. However, long-lasting effects on ground vegetation may occur, and visible changes have been reported even after 50 years in peatland forest (Moilanen et al. 2002). The effects of ash fertilisation on the understory depend on how the ash is pre-treated, on the dose applied and on the environmental conditions at the site (Aronsson & Ekelund 2004; Augusto et al. 2008) and may differ between species and taxonomic groups (Dynesius 2012). Ash pellets seem to cause fewer negative effects on understory vegetation than crushed ash (Dynesius 2012). Hardening is recommended for crushed ash, in order to reduce negative effects caused by the high reactivity of untreated crushed wood ash (Karltun et al. 2008). Doses used in wood ash fertilisation experiments vary, ranging from 1 to 44 t ha^{-1} (Pitman 2006; Augusto et al. 2008). According to The Swedish Forest Agency's guidelines (2008), the negative environmental effects will be limited for doses up to 3 t hardened ash ha^{-1}. Effects may partly be due to changes in soil humus chemistry (Huotari et al. 2015), since soil nutrients are important for the variation in understory vegetation in Norway spruce forests (Økland 1996), and partly due to the osmotic effect that causes bryophytes to dry out when the salt load on the bryophyte surface becomes too high. In our study on the effects of wood ash and N fertilisation on soil solution and soil humus chemistry (Clarke et al. 2018), we found that the supply of 3 t ha^{-1} self-hardened wood ash increased soil pH, base saturation and exchangeable concentrations (after extraction with 1 M NH_4NO_3) of several elements in the soil humus layer while exchangeable concentrations (1 M NH_4NO_3) of other elements decreased.

Bryophytes constitute a major part of the plant diversity in northern Norway spruce [*Picea abies* (L.) Karst.] forests (cf. Økland 1996). Although there are concerns about negative effects on the understory vegetation and plant diversity, especially for the bryophytes, few studies exist on either ash fertilisation effects (Augusto et al. 2008; Dynesius 2012; Huotari et al. 2015) or on effects of a single dose of nitrogen (Haugland et al. 2014) in Norway spruce forests.

In this study we examined short-term effects of fertilisation with a single dose of self-hardened wood ash and nitrogen, alone and in combination, on understory vegetation in a boreal Norway spruce forest. We compared plant diversity, cover of plant groups, and plant species abundances before and after treatment, and hypothesised that there are no pre- to post-treatment effects in: (1) plant species numbers in different species groups and in total, (2) sum cover of plant groups and (3) plant species abundances.

Materials and Methods

We set up a block design field trial involving experimental treatment with wood ash and N in a Norway spruce forest at the Bærøe farm in Hobøl municipality (see Clarke et al. 2018 and Hanssen et al. 2020 for more details), south-eastern Norway (latitude 59.56˚N, longitude 10.95˚E, altitude 195-215 m a.s.l.) Mean annual temperature and precipitation at a nearby meteorological station at Ås for the period 1st May 2005 – 30th April 2015 (i.e. before and including the study period) were 6.4 °C and 899 mm, respectively (Norwegian Meteorological Institute; https://seklima.met.no/observations/). The soil type is variable, with podzol/cambisol in thin moraine deposits that overlie Precambrian gneiss. The terrain is relatively flat with an average inclination of 8.3°. The study area is positioned within the southern boreal vegetation zone and belongs to the slightly oceanic vegetation section (Moen 1999). This productive Norway spruce forest has site index G20-G23 (Tveite 1977) and was planted after logging in the 1950s and thinned in 2006/2007. The average standing volume at the time of fertilisation was 302 m^3 ha^{-1}, the basal area was 30 m^2 ha^{-1}, the dominant height was 21.8 m and the number of stems 850 ha^{-1} (Hanssen et al. 2020).

We used 12 treatment plots, each 25 m x 25 m including a 5 m buffer zone. Within the 15 m x 15 m inner area in each of the 12 treatment plots five 1-m^2 vegetation plots were randomly placed and permanently marked, giving a total of 60 vegetation plots. Each 1-m^2 vegetation plot was divided into 16 subplots, each 25 cm x 25 cm.

Four treatments were applied in a randomised block design with three replicates for each treatment: (i) untreated control (Ctrl), (ii) 3 t ha^{-1} ash (Ash), (iii) 3 t ha^{-1} ash + 150 kg ha^{-1} N given as ammonium nitrate (Ash+N) and (iv) 150 kg ha^{-1} N as ammonium nitrate (N). A map showing the layout of the plots is given in Fig. 1. Ash and ammonium nitrate were manually applied on the soil surface in 2013, ammonium nitrate at the end of May and ash at the end of June. The ammonium nitrate fertiliser used was Opti-KAS Skog (Yara) with 27% N (NO_3^- and NH_4^+ both 13.5%), 5% Ca, 2.4% Mg and 0.2% B. The wood ash was granulated self-hardened bottom ash from the sawn timber producer Bergene Holm; its chemical composition is given in Table 1.

All 60 vegetation plots were analysed before treatment in 2012 and after treatment in 2015. We used two different species abundance measures for all species present in each of the 60 1 m^2 vegetation plots: (1) subplot frequency (Økland 1988); presence/absence in each of 16 subplots, and (2) percentage (0-100 %) cover.

Logging was performed in parts of the forest surrounding the study area during the winter of 2014-2015. We consider it unlikely that this felling affected the understory vegetation significantly before the field work was performed in June 2015.

Statistical analysis

We used non-parametric tests to assess possible treatment effects on the understory vegetation. Wilcoxon signed ranks tests (Salkind 2007) were used to test for possible pre- to post-treatment changes in: (i) species numbers within species groups, (ii) cover sum within species groups, and (iii) species abundance (subplot frequency and percentage cover). Wilcoxon tests were not performed when changes occurred in less than five plots. Statistical significance was defined as $p < 0.05$. The statistical package SPSS (IBM, New York, USA) was used for the statistical analysis.

Nomenclature

Naming of vascular plants, bryophytes, and lichens follows the Norwegian Species Nomenclature Database (http://www2.artsdatabanken.no/artsnavn/Contentpages/Hjem.aspx). Exceptions are: Vascular plants: *Dryopteris expansa* agg. may include *D. expansa* (C.Presl.) Fraser-Jenkins & Jermy, *D. dilatata* (Hoffm.) A. Gray, and *D. carthusiana* (Vill.) Fuchs. Mosses: *Hypnum cupressiforme* agg. may include *H. cupressiforme* Hedw., *H. andoi* A.J.E.Sm., *H. jutlandicum* Holmen & Warncke and *H. resupinatum* Spruce. *Plagiothecium laetum* includes var. *secundum* (Lindb.) Frisv. et al. (= *P. curvifolium* Limpr.) *Rhytidiadelphus squarrosus* agg. includes *R. squarrosus* (Hedw.) Warnst. and *R. subpinnatus* (Lindb.) Hepatics: *Lophozia ventricosa* agg. may include *L. ventricosa* (Dicks.), *L. silvicola* Buch and Dum. and *L. longiflora* (Nees) Schiffn.

Lichens: *Cladonia chlorophaea* agg. may include *C. chlorophaea* (Flörke ex Sommerf.) Spreng., *C. cryptochlorophaea* Asah., and *C. grayi* Merr. ex Sandst., while *Cladonia coniocraea* agg. may include *C. coniocraea* (Flörke) Spreng. and *C. ochrochlora* Flörke.

Results

Total number of species recorded

In 2012, before the fertilisation treatment, a total of 69 species were recorded in the 60 vegetation plots. This included 24 vascular plants, 43 bryophytes and 2 lichens. In 2015, two years after the fertilisation treatment, we recorded 67 species in total: 23 vascular plants, 42 bryophytes and 2 lichens.

Pre- to post-treatment changes in species numbers

In the Ctrl plots, there were no significant pre- to post-treatment (2012 to 2015) changes in species number for any species group. Species numbers for vascular plant species groups did not change significantly from pre- to post-treatment for any of the treatments. The total number of bryophytes decreased significantly in all fertilised plots, with the strongest decrease in Ash+N plots ($p = 0.001$; Table 2). The number of hepatics decreased significantly in Ash plots ($p = 0.016$) and in Ash+N plots ($p = 0.004$), while the number of mosses decreased significantly only in Ash+N plots ($p = 0.022$). The total species number decreased significantly in all fertilised plots due to the decrease in bryophytes, most strongly in Ash+N plots.

Pre- to post treatment changes in cover sum of species within different species groups

The cover sum of herbs (Table 3) increased significantly in both Ash+N plots ($p = 0.009$) and in N plots ($p = 0.020$), while graminoids decreased significantly in Ctrl plots ($p = 0.007$). For hepatics the cover sum decreased significantly in Ctrl plots ($p = 0.023$), but even more in Ash plots ($p = 0.004$) and Ash+N ($p = 0.005$). The cover sum of mosses increased significantly in Ash+N plots ($p = 0.016$) but decreased in plots fertilised with N only ($p = 0.05$). The cover sum of lichens decreased significantly in Ash+N plots ($p = 0.009$).

Pre- to post-treatment abundance changes for individual plant species

Pre- to post-treatment changes in subplot frequencies and cover for individual species are presented in the Appendix, Tables (i) and (ii) respectively. We comment only on subplot frequency changes in the text below since this is a more suitable abundance measure for most bryophytes (cf. Økland 1988). Of the vascular plants, only the herb *Melampyrum sylvaticum* showed significant pre- to post-treatment change, with an increase in subplot frequencies in Ash+ N plots (p = 0.002). In Fig. 2 the numbers of cryptogam species with significant decrease and increase in subplot frequency are presented.

The pleurocarpous moss *Sciuro-hypnum starkei* decreased significantly in Ctrl plots (p = 0.001), Ash plots (p = 0.03) and N plots (p = 0.002), while *Sciuro-hypnum reflexum* decreased in the N plots. *Hylocomium splendens* increased significantly in both Ctrl plots (p = 0.004) and Ash plots (p = 0.045). *Hypnum cupressiforme agg.*, on the other hand, decreased significantly only in Ash+N plots (p = 0.018). There were significant decreases for *Plagiothecium laetum* not only in Ash+N plots (p = 0.019) and N plots (p = 0.001), but also in the Ctrl plots (p = 0.001). *Pleurozium schreberi* increased significantly in subplot frequency in both Ctrl and Ash plots (p = 0.017 for both).

Several acrocarpous moss species of the genus *Dicranum* decreased significantly in either Ash plots or Ash+N plots, or both. *Dicranum fuscescens agg.* and *D. majus* decreased significantly in Ash+N plots (p = 0.024 and p = 0.020, respectively), while *D. majus* also increased significantly in the Ctrl plots (p = 0.005). *D. polysetum* decreased significantly (p = 0.010) only in Ash plots, whereas *D. scoparium* decreased significantly in both Ash (p = 0.002) and Ash+N (p = 0.003) plots. *Pohlia nutans* had low abundance in the treatment plots and decreased significantly only in the Ctrl plots (p = 0.042). *Polytrichastrum formosum* decreased significantly only in the Ash plots (p = 0.046) while *Tetraphis pellucida* decreased significantly in Ctrl plots (p = 0.041) and in Ash+N plots (p = 0.007).

Of the hepatics, *Barbilophozia attenuata* decreased significantly in both Ash plots (p = 0.026) and in Ash+N plots (p = 0.027). *Lepidozia reptans* decreased significantly in Ash+N plots (p=0.039), whereas *Lophocolea heterophylla* decreased significantly in all plot types (p = 0.011, p = 0.027, p = 0.007 and p = 0.036 for the Ctrl plots, Ash plots, Ash+N plots and N plots, respectively).

Only two lichen species were found within the plots. *Cladonia chlorophaea* agg. decreased significantly in all treatment plots except the Ctrl plots (p = 0.034, p = 0.006 and p = 0.025 for the Ash plots, Ash+N plots and N plots, respectively). *Cladonia coniocraea* agg. decreased significantly (p = 0.009) only in Ash+N plots.

None of the species recorded are on the Norwegian red list of rare or endangered species.

Discussion

Vascular plants

Effects of wood ash and nitrogen fertilisation on understory vegetation in boreal forests reported from other studies vary (Hart et al. 2019). In the present study, the fertilisation effects on vascular plants were limited for all three treatments (Ash, Ash+N and N), as also reported by Skrindo & Økland (2002) and Ozolinčius et al. (2007). Two years after treatment, we found no significant pre- to post-treatment change in species number for any group of vascular plants. However, the species number of vascular plants in the 1-m^2 plots was low (on average 5.3 per plot) already before fertilisation treatment.

Abundances of the dwarf shrubs *Vaccinium myrtillus* and *V. vitis-idaea* neither decreased nor increased significantly for any of the treatments in our study. Some studies report a decrease in abundance of dwarf shrubs after N fertilisation (Strengbom et al. 2001; Strengbom & Nordin 2008), though a recent study by Jacobson et al. (2020) from Scots pine sites in Sweden found an increase of the two above-mentioned species in fertilised plots compared to control plots. Responses of dwarf shrubs to N addition may partly be related to effects on tree growth and canopy closure (Sullivan & Sullivan 2018). The canopy at our spruce forest site was, however, already closed before treatment. Dwarf shrubs have been reported to decrease in abundance also after ash fertilisation in some studies, with effects depending on dose, ash type and species (Levula et al. 2000; Jacobson & Gustafsson 2001; Arvidsson et al. 2002). However, ash doses up to 3 t ha^{-1}, as used in our experiment, have mostly not given significant effects on dwarf shrub abundances. The abundances of dwarf shrubs were relatively low in our study already before treatment; the most abundant dwarf shrub *V. myrtillus* had mean subplot frequency 5 and mean cover 6.3 % per vegetation plot, and an uneven distribution between plots. *V. myrtillus* had an average subplot frequency of 12.5 in 20 of the 1-m^2 plots and 1.3 for the remaining 40 plots, and an average cover of 22.3 % in 15 of the plots, 0.84 % in the remaining 45 plots.

Nitrophilous herbs and grasses have been reported to increase in abundance in response to repeated applications of nitrogen in Scandinavian boreal forests (Sullivan & Sullivan 2018). In our study, with a single application, the cover sum for herbs increased significantly in both N and Ash+N plots due to the increase of one species, while no graminoid species decreased nor increased significantly in abundance in these treatment plots. For ash treatment, increased abundance for some herb and grass species has earlier been reported in some studies (Gyllin & Kruuse, 1996; Arvidsson et al. 2002) and increased biomass for *Avenella flexuosa* has recently been reported for a young Norway spruce stand (Brandtberg et al. 2021).

Of the vascular plants only the annual herb *Melampyrum sylvaticum* increased significantly in abundance, in the Ash+N and N plots. Since this hemiparasite each year must reproduce via seeds (Dalrymple 2007) its abundance may vary somewhat depending on year-to-year variation in climatic conditions, whether these are favourable for seed dispersal. Yet, in contrast to *M. pratense,* which had no significant abundance change, *M. sylvaticum* is typically more abundant in somewhat nutrient-rich sites (Økland 1996), indicating that the Ash+N and N treatments contributed to the abundance increase due to the increase in soil nutrients, possibly mostly due to the increase in nitrogen. Jacobson & Gustafsson (2001) observed that *Melampyrum* spp. increased somewhat in cover after treatment with crushed ash in a Swedish pine forest. However, to our knowledge significantly increased abundance for *M. sylvaticum* has not been reported in other studies after treatment with ash or ash plus nitrogen. Many of the ash fertilisation experiments in the Nordic countries have however been performed in pine forests, where *M. sylvaticum* is less abundant.

Of the 16 studies of nitrogen fertilisation effects from Nordic countries reviewed by Sullivan & Sullivan (2018), only six were performed in *Picea abies* forests and none of these in Norway. To our knowledge, ash fertilisation experiments have not previously been performed on mineral soil in Norway in any forest type. Our study was performed in a productive Norway spruce forest, on mineral soils relatively rich in nutrients (Clarke et al. 2018; Hanssen et al. 2020). The study by Olsson & Kellner (2006) indicated that long-term fertilisation effects are more pronounced at nutrient-poor than nutrient-rich sites. It is likely that the nutrient-rich soils in our study, in combination with only one single relatively low fertilisation dose, have contributed to the limited effects on vascular plants.

Bryophytes

As in several other studies (Skrindo & Økland 2002; Strengbom et al 2001; Jacobson and Gustafsson 2001; Moilanen et al 2002; Ozolinĉius et al. 2007), bryophytes were negatively affected by fertilisation in our study. We found that ash and ash plus nitrogen fertilisation resulted in a decrease in the species numbers and abundances for bryophytes, mainly due to a decrease in the number and abundances of hepatic species and mosses. For N fertilisation, there was a decrease in the total number of bryophyte species.

Since bryophytes have their main uptake of water and nutrients via their aboveground surface, which lacks a well-developed cuticle, they are directly exposed and vulnerable to both ash and N fertilisation (Skrindo & Økland 2002; Jacobson & Gustafsson 2001; Huotari et al. 2015). In addition, in N-fertilised plots indirect effects may arise through greater canopy cover, reducing radiation and throughfall precipitation (Skrindo & Økland 2002; Strengbom et al. 2001). However, Hedwall et al. (2010) found no response of bryophytes to changes in the canopy cover and related the decrease to direct effects of the fertilisation.

Some other studies have reported a decrease in the abundances of bryophytes after application of ash (Kellner & Weibull 1998; Jacobsson & Gustafsson 2001; Moilanen et al 2002; Ozolinĉius et al. 2007) or with ash in combination with nitrogen (Ozolinĉius et al. 2007). Even though the treatment effects depend on ash dosage, bryophyte species, forest type, and environmental conditions, several bryophyte species may be damaged shortly after the ash treatment (Jacobson 1997; Kellner & Weibull 1998; Dynesius 2012) due to the increased alkalinity (Huotari et al. 2015).

While the moss cover sum increased significantly in plots fertilised with ash plus nitrogen, no individual moss species increased significantly in abundance after this treatment. However, the abundance of two pleurocarpous mosses *Hylocomium splendens* and *Pleurozium schreberi* increased significantly in the ash fertilised plots as well as in the control plots, indicating that other factors than fertilisation may have affected their growth. Some of the largest forest mosses, such as *H. splendens,* are favoured by longer growth seasons due to increased temperature (cf. Økland & Halvorsen 2020). Possibly these species are also less harmed by ash treatment than many other bryophytes (Kellner & Weibull 1998), although they have been reported to be negatively affected by N fertilisation (Olsson & Kellner 2006). However, in our experiment they neither increased nor decreased significantly in N fertilised plots.

In a short-term ash experiment on ground-living bryophyte transplants and on wood inhabiting bryophytes in boreal spruce forests in Sweden, Dynesius (2012) found the responses to crushed ash to depend on the species' pH ecology and phylogenetic position. While Dynesius (2012) reported growth two months after fertilisation for two species belonging to *Brachytheciacea*, we found that two years after fertilization *Sciuro-hypnum starkei* (synonymous name *Brachythecium starkei*) had decreased significantly, not only in plots fertilised with either ash or nitrogen, but also in the control plots, while *S. reflexum* decreased in N fertilised plots, and *H. cupressiforme agg.* decreased in Ash+N plots. We find it unlikely that this change is an effect of pH ecology, and relate it more to availability of suitable microhabitats, as all three species are favoured by the presence of small, branched harvesting residues lying directly on the forest floor (cf. Økland et al. 2016). While small branches typically are abundant on the forest floor after thinning and logging of the tree stand, their availability tends to decrease due to decomposition of the small branches, and by overgrowth of larger and more competitive moss species. In this study, the reduced availability of small branches in 2015 relative to 2012 probably contributed to the decrease for *S. starkei* in the control plots, where *H. splendens* increased most.

Dynesius (2012) found that the clearest negative responses to ash fertilisation were for species in the moss genera *Sphagnum*, *Tetraphis*, and *Dicranum* and the hepatic genus *Barbilophozia.* At our study site, *Sphagnum* spp. had low abundances before fertilisation in all 1-m^2 plots except two, thus we could not test for abundance changes for these species. However, we observed significant decrease for *Tetraphis pellucida* in plots fertilised with both ash and nitrogen, but also a weaker decrease in the control plots, indicating a simultaneous reduction in suitable microhabitats. We also observed a significant decrease after fertilisation for *Dicranum* species, two species in plots fertilised with ash, and three species in plots fertilised with both ash and nitrogen. However, one of these species, *D. majus*, also increased significantly in the control plots.

Even though the total cover of hepatics decreased slightly in control plots in this study, the decrease was much stronger in plots fertilised with either ash or ash plus nitrogen. We observed significant decrease in abundance for some hepatic species, e.g. *Barbilophozia attenuate* and *Lepidozia reptans,* while *Lophocolea heterophyllla* decreased in plots fertilised with nitrogen. Since hepatic species normally occur scattered in the forest floor (Økland 1996), abundance changes cannot be tested for all species. However, the decrease in cover sum and species numbers of hepatics emphasizes the vulnerability of this species group to ash and nitrogen fertilisation. Hepatics, which usually are small species with only one cell-layer thick leaves, are particularly vulnerable to environmental changes caused by fertilisation such as the increased concentrations of base cations on the bryophyte surface causing damage via osmotic effects (Huotari et al. 2015). Most hepatic species are dependent on open microhabitats; “pockets” in the forest bottom layer (cf. Økland 1996). As they do not reproduce and grow as fast as larger forest bryophytes, they may not easily reappear at a site when they have once disappeared, as has been observed in spruce forest monitoring sites in Norway (Økland & Halvorsen 2020).

Lichens

Only two lichens occurred at our spruce study site, *Cladonia chlorophaea* and *C. coniocraea*. Both decreased significantly in plots fertilised with both ash and nitrogen, while *C. chlorophaea* also decreased in the plots fertilised with ash alone. Lower abundances after treatment with ash and/or nitrogen compared with control plots were also found by Hart et al. (2019), who emphasized that lichens are sensitive to high concentrations of nitrogen, and that they rapidly absorb water and dissolved elements including heavy metals. Decreased abundances in response to nitrogen fertilisation for some lichen species were also found by Skrindo & Økland (2002) and Hedwall et al. (2010), among others.

Conclusions

Two years after fertilisation we found limited effects on vascular plants, while there was a decrease in diversity and abundances for bryophytes and lichens. These changes are most probably due to the elevated ion concentrations on the moss and lichen surfaces that typically occur after the application of both ash and nitrogen (cf. Kellner and Weibull 1998). Hepatic species seem to be vulnerable to fertilisation with ash, but even more to fertilisation with both ash and nitrogen. The few species that also decreased in the control plots indicate that other factors also contributed, e.g. decrease in suitable microhabitats, possibly partly due to an ongoing succession after thinning in 2006/2007. Our results suggest that negative fertilisation effects on the understory vegetation are more pronounced when adding both ash and nitrogen than when adding ash or nitrogen alone. However, our study was performed in a relatively productive spruce forest site in south-eastern Norway. Since fertilisation effects depend on several factors, experimental studies on how ash and nitrogen fertilisation affect understory vegetation and plant diversity along local and regional gradients in environmental and climatic conditions are needed. We also need to study how long the effects on understory vegetation will last.

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Disclosure statement

The authors report there are no competing interests to declare.

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Table 1. Element concentrations (dry weight basis) and pH in the ash used in the field experiment. Data from Dibdiakova and Horn (2014) and email from J Dibdiakova; unreferenced.

Element	Concentration	Element	Concentration	Element	Concentration	Element	Concentration
C (%)	0.3	Cd (mg/kg)	3.0	Mg (g/kg)	37.3	Sc (mg/kg)	3.9
N (%)	<0.1	Cl (mg/kg)	0.1	Mn (g/kg)	33.1	Se (mg/kg)	12.0
pH	11.6	Co (mg/kg)	18.6	Mo (mg/kg)	6.5	Si (g/kg)	40.7
Al (g/kg)	8.9	Cr (mg/kg)	127.9	Na (g/kg)	0.2	Sr (g/kg)	2.1
As (mg/kg)	0.6	Cu (mg/kg)	20.7	Ni (mg/kg)	50.3	Ti (mg/kg)	367.5
Ba (g/kg)	10.5	Fe (g/kg)	4.6	P (g/kg)	24.2	V (mg/kg)	10.1
Be (mg/kg)	4.6	K (g/kg)	8.2	Pb (mg/kg)	11.9	Y (mg/kg)	3.9
Ca (g/kg)	437.2	Li (mg/kg)	19.9	S (g/kg)	0.9	Zn (g/kg)	0.1

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Table 2. Changes in number of species in different species groups at the Bærøe forest site from 2012 (pre-treatment) to 2015 (post-treatment). Four treatments: Ctrl - control, Ash - ash fertilised, Ash+N – ash plus nitrogen fertilised, N –nitrogen fertilised. m12 and m15 are mean species numbers in 2012 and 2015 respectively, n+ is the number of plots with increase in number of species, while n- denotes the number of plots with decrease in species number. p is the probability that the median change is not significantly different from 0 versus the two-tailed alternative (Wilcoxon signed rank tests, p ≤ 0.05 in bold, significant reduction in italic).

	Ctrl					Ash					Ash+N					N				
	m12	m15	n-	n+	p	m12	m15	n-	n+	p	m12	m15	n-	n+	p	m12	m15	n-	n+	p
Woody species	1.4	1.4	3	3	1.000	1.3	1.1	4	1	0.180	1.3	1.2	2	0	0.157	1.3	1.2	4	2	0.414
Dwarf shrubs	0.7	0.7	3	3	1.000	0.7	0.8	1	2	0.564	0.7	0.9	0	2	0.157	0.9	1.0	0	2	0.157
Pteridophytes	0.3	0.1	2	0	0.157	0.4	0.3	1	0	0.317	0.3	0.3	1	0	0.317	0.5	0.4	1	0	0.317
Herbs	1.7	1.9	1	4	0.157	1.7	1.9	2	3	0.480	1.1	1.7	2	7	0.058	1.4	1.4	2	3	1.000
Graminoids	1.2	1.1	4	2	0.414	1.3	1.1	3	0	0.083	1.1	1.1	1	2	0.564	0.9	0.9	1	1	1.000
All vascular plants	5.3	5.3	5	5	1.000	5.5	5.2	6	3	0.506	4.6	5.2	3	7	0.075	4.9	4.9	3	3	0.914
Mosses	11.7	10.7	7	4	0.245	9.3	8.5	7	4	0.126	10.1	9.2	***9***	***3***	***0.022***	11.7	10.7	10	4	0.058
Sphagnum spp.	*0.1*	0.1	0	0	1.000	*0.4*	0.5	0	1	0.317	0.5	0.3	2	0	0.157	*0.4*	0.3	1	1	0.655
Hepatics	1.9	1.7	3	1	0.194	2.1	0.9	***8***	***1***	***0.016***	2.8	1.3	***10***	***0***	***0.004***	3.5	2.7	9	4	0.087
All bryophytes	13.7	12.5	9	4	0.160	11.7	9.9	***9***	***2***	***0.020***	13.3	10.9	***14***	***1***	***0.001***	15.6	13.7	***11***	***4***	***0.034***
Lichens	0.9	0.5	6	2	0.107	0.9	0.7	3	1	0.317	1.1	0.4	***8***	***0***	***0.009***	0.7	0.5	3	0	0.083
Total species number	19.9	18.3	9	3	0.181	18.1	15.8	***12***	***2***	***0.018***	19.1	16.5	***12***	***2***	***0.003***	21.3	19.1	***11***	***4***	***0.032***

Table 3. Changes in (summarized) percentage cover for species groups at the Bærøe forest site from 2012 (pre-treatment) to 2015 (post-treatment). Four treatments: Ctrl - control, Ash - ash fertilised, Ash+N – ash plus nitrogen fertilised, N – nitrogen fertilised. m12 and m15 are mean percentage cover for each species group in 2012 and 2015 respectively, "+" is the number of plots with increase, while "-" denotes the number of plots with decrease. p is the probability that the median change is not significantly different from 0 versus the two-tailed alternative (Wilcoxon signed rank tests, p ≤ 0.05 in bold, significant reduction in italic). Mean percentage cover for each year is given for each group and treatment type.

	Ctrl					Ash					Ash+N					N				
	m12	m15	-	+	P	m12	m15	-	+	p	m12	m15	-	+	p	m12	m15	-	+	P
Woody species	3.1	3.6	5	7	0.805	3.3	4.1	5	6	0.319	4.7	5.3	3	5	0.779	2.9	3.9	5	5	0.878
Dwarf shrubs	4.0	6.8	3	7	0.076	6.7	9.1	2	7	0.131	8.4	9.7	3	4	0.672	6.9	8.3	1	7	0.119
Pteridophytes	7.1	1.5	4	0	0.066	0.7	0.5	3	1	0.257	1.1	0.4	2	0	0.180	1.7	0.9	4	0	0.068
Herbs	5.1	3.8	4	5	0.402	3.4	5.5	8	4	0.843	2.9	9.1	**3**	**11**	**0.009**	3.1	4.4	**1**	**8**	**0.020**
Graminoids	5.9	2.5	***9***	***0***	***0.007***	10.0	9.7	8	5	0.780	3.9	3.9	4	4	0.833	4.3	4.9	2	4	0.236
Mosses	59.7	58.6	9	5	0.285	60.0	67.2	4	11	0.147	53.5	63.9	**3**	**10**	**0.016**	59.8	54.2	***11***	***2***	***0.050***
Sphagnum spp.	0.1	0.1	0	0	1.000	1.4	1.0	1	1	0.655	5.5	2.6	3	0	0.109	0.4	0.4	1	2	0.564
Hepatics	3.3	2.3	***8***	***2***	***0.023***	4.9	1.9	***11***	***1***	***0.004***	3.4	1.3	***10***	***0***	***0.005***	5.5	3.6	9	4	0.081
Lichens	0.9	0.5	6	2	0.107	0.9	0.7	3	1	0.317	1.2	0.5	***8***	***0***	***0.009***	0.7	0.5	3	0	0.083

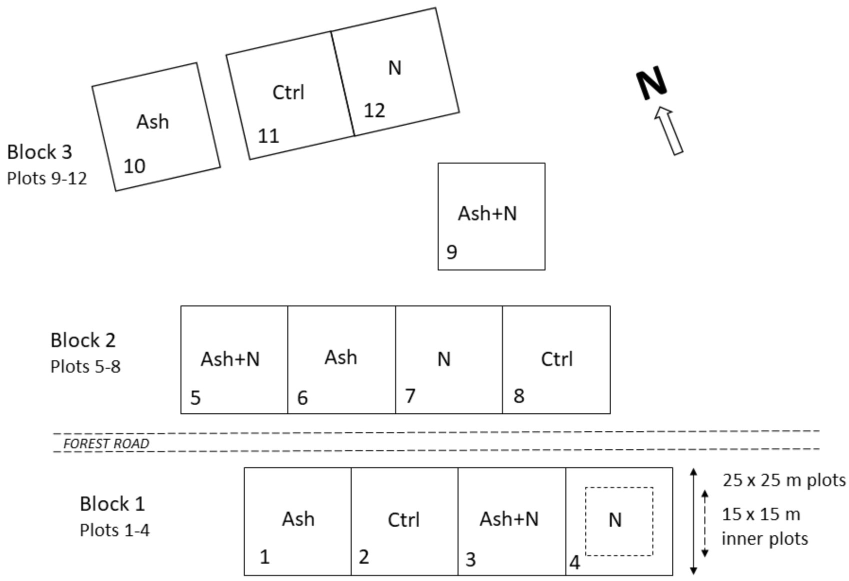

Fig. 1. Map of the plot layout.

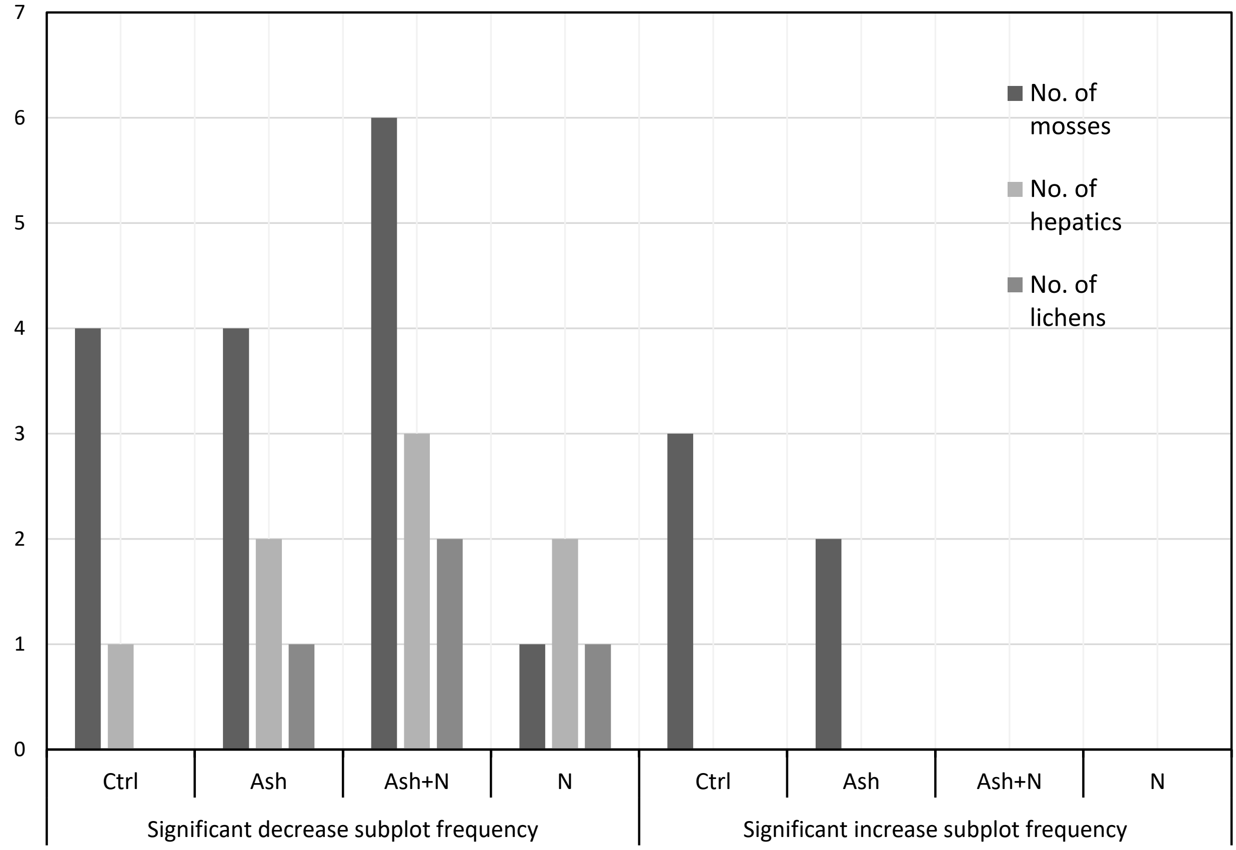

Fig. 2. Number of cryptogams with significant changes in sub-plot frequencies. Four treatments: Ctrl - control, Ash - ash fertilised, Ash+N – ash plus nitrogen fertilised, N – nitrogen fertilised.

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Appendix

Table (i). Changes in the subplot frequency for vascular plants, bryophytes and lichens in plots from 2012 (pre-treatment) to 2015 (post-treatment) at the Bærøe forest site. Four treatments: Ctrl - control, Ash - ash fertilised, Ash+N – ash plus nitrogen fertilised, N – nitrogen fertilised. m12 and m15 are mean subplot frequencies in 2012 and 2015 respectively, n+ is the number of plots with increase, while n- denotes the number of plots with decrease. p is the probability that the median change is not significantly different from 0 versus the two-tailed alternative (Wilcoxon signed rank tests, p ≤ 0.05 in bold, significant reduction in italic).

	Ctrl					**Ash**					**Ash+N**					**N**				
	m12	**m15**	**n-**	**n+**	**p**	**m12**	**m15**	**n-**	**n+**	**p**	**m12**	**m15**	**n-**	**n+**	**p**	**m12**	**m15**	**n-**	**n+**	**p**
Picea abies	7.6	7.8	6	4	0.877	6.5	6.0	8	4	0.159	8.6	7.5	4	2	0.207	8.3	8.6	5	8	0.643
Vaccinium myrtillus	3.3	3.9	4	6	0.215	5.9	6.3	2	6	0.393	6.0	6.1	0	2		4.7	5.1	2	7	0.365
Maianthemum bifolium	0.3	0.2	2	0		1.1	1.6	1	4	0.131	0.2	0.2	0	0		1.3	2.1	0	3	
Melampyrum pratense	3.6	5.5	3	8	0.075	3.9	3.6	5	5	0.837	3.5	2.0	5	5	0.441	3.7	3.5	6	7	0.752
Melampyrum sylvaticum	3.7	3.1	4	5	0.514	2.4	4.0	4	4	0.440	3.1	5.8	**0**	**12**	**0.002**	3.0	3.6	3	4	0.391
Luzula pilosa	2.4	1.6	6	5	0.621	5.5	5.6	3	3	0.915	0.7	0.9	2	4	0.458	0.7	0.6	1	3	
Brachythecium salebrosum	0.6	0.2	3	2	0.336	0.0	0.0	0	0		0.2	0.1	1	0		0.5	0.0	3	0	
Dicranum fuscescens	0.2	0.3	1	2		0.6	0.7	3	2	0.890	1.1	0.3	***6***	***0***	***0.024***	1.1	0.9	6	6	0.773
Dicranum majus	11.0	12.7	**1**	**11**	**0.005**	12.1	11.1	5	3	0.136	12.9	10.9	***8***	***1***	***0.020***	10.9	10.1	11	2	0.112
Dicranum polysetum	1.9	2.1	5	6	0.490	1.6	0.7	***8***	***0***	***0.010***	1.5	0.5	6	1	0.061	1.3	0.5	4	1	0.074
Dicranum scoparium	9.9	10.1	7	5	0.873	8.3	5.4	***12***	***1***	***0.002***	6.9	5.3	***12***	***1***	***0.003***	9.5	8.1	9	6	0.138
Hylocomium splendens	7.3	9.8	**1**	**11**	**0.004**	8.4	9.7	**2**	**8**	**0.045**	9.8	10.5	4	7	0.263	10.7	11.8	4	7	0.152
Hypnum cupressiforme agg.	2.7	2.3	7	3	0.441	0.3	0.3	2	2		2.5	1.6	***8***	***1***	***0.018***	1.9	1.4	7	2	0.369
Plagiomnium affine	0.9	0.6	2	0		1.3	0.8	4	1	0.131	0.1	0.2	0	1		0.9	0.6	3	0	
Plagiothecium denticulatum	1.1	0.9	5	2	0.389	0.3	0.0	3	0		0.7	0.2	3	0		1.9	1.1	6	3	0.151
Plagiothecium laetum agg.	8.3	2.6	***14***	***0***	***0.001***	3.3	2.8	8	4	0.237	5.1	2.4	***9***	***1***	***0.019***	8.4	3.9	***15***	***0***	***0.001***
Plagiothecium undulatum	0.9	0.6	4	1	0.157	2.5	2.9	0	4		2.2	2.3	1	1		1.1	1.1	2	1	
Pleurozium schreberi	12.9	14.5	**1**	**8**	**0.017**	12.7	14.1	**1**	**8**	**0.017**	11.4	11.9	4	6	0.442	14.5	14.5	4	3	1.000
Pohlia nutans	1.5	0.4	***5***	***0***	***0.042***	0.3	0.3	2	1		0.3	0.4	2	2		0.6	0.4	3	3	0.518
Polytrichastrum formosum	6.1	6.1	4	5	0.904	4.3	3.1	***5***	***1***	***0.046***	5.5	5.2	3	0		5.1	5.0	4	3	0.931
Ptilium crista-castrensis	0.7	0.8	2	4	0.739	1.1	1.1	0	1		0.2	0.1	1	0		0.9	0.6	3	1	
Sciuro-hypnum reflexum	2.2	1.6	4	4	0.573	0.7	0.7	2	2		1.6	1.3	4	3	0.606	2.5	0.8	***9***	***2***	***0.024***
Sciuro-hypnum starkei	9.1	3.8	***15***	***0***	***0.001***	5.9	3.7	***7***	***1***	***0.029***	5.6	6.6	6	6	0.570	7.1	2.4	***13***	***1***	***0.002***
Tetraphis pellucida	1.5	0.8	***5***	***0***	***0.041***	1.5	1.2	3	1		2.0	0.9	***9***	***0***	***0.007***	2.2	1.8	4	3	0.527
Sphagnum girgensohnii	0.2	0.3	0	1		1.9	1.5	2	2		2.6	1.7	4	1	0.174	0.5	0.7	1	3	
Barbilophozia attenuata	0.3	0.2	1	1		0.8	0.1	***6***	***0***	***0.026***	1.8	0.3	***6***	***0***	***0.027***	1.6	1.1	3	1	
Lophocolea heterophylla	5.6	2.5	***8***	***1***	***0.011***	2.3	0.2	***6***	***0***	***0.027***	3.9	1.7	***10***	***1***	***0.007***	5.0	2.9	***9***	***2***	***0.036***
Lepidozia reptans	0.5	0.1	3	0	0.102	0.2	0.1	2	1		0.9	0.1	***5***	***0***	***0.039***	2.0	1.5	4	3	0.610

Lophozia ventricosa agg.	0.2	0.0	1	0		0.2	0.0	2	0		0.3	0.1	3	0		0.5	0.4	4	1	0.480
Plagiochila asplenoides	2.1	2.7	1	5	0.168	4.5	3.5	6	2	0.065	2.1	1.5	6	1	0.054	2.7	3.2	2	5	0.161
Cladonia chlorophaea agg.	1.0	0.7	5	2	0.206	1.5	0.7	***5***	***0***	***0.034***	1.5	0.7	***9***	***0***	***0.006***	0.8	0.5	***5***	***0***	***0.025***
Cladonia coniocraea agg.	1.1	0.3	5	1	0.058	1.5	0.7	5	1	0.072	1.5	0.6	***8***	***0***	***0.009***	1.1	0.6	5	1	0.096

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Table (ii). Changes in percentage cover for vascular plants, bryophytes and lichens in plots from 2012 (pre-treatment) to 2015 (post-treatment) at Bærøe forest site. Four treatments: Ctrl - control, Ash - ash fertilised, Ash+N – ash plus nitrogen fertilised, N –nitrogen fertilised. m12 and m15 are mean percent cover in 2012 and 2015 respectively, n+ is the number of plots with increase, while n- denotes the number of plots with decrease. P is the probability that the median change is not significantly different from 0 versus the two-tailed alternative (Wilcoxon signed rank tests, P ≤ 0.05 in bold, significant reduction in italic).

	Ctrl					**Ash**					**Ash+N**					**N**				
	m12	**m15**	**n-**	**n+**	**p**	**m12**	**m15**	**n-**	**n+**	**p**	**m12**	**m15**	**n-**	**n+**	**p**	**m12**	**m15**	**n-**	**n+**	**P**
Picea abies	2.5	3.0	2	5	0.380	2.7	3.7	3	5	0.136	3.8	4.4	3	5	0.673	2.5	3.6	3	5	0.623
Vaccinium myrtillus	3.9	6.7	3	7	0.076	6.5	8.9	2	7	0.072	8.0	8.9	3	4	0.672	6.5	7.9	1	6	0.147
Melampyrum pratense	1.7	1.6	3	4	1.000	1.5	1.3	4	4	1.000	1.3	1.2	4	5	1.000	1.1	1.0	2	5	0.861
Melampyrum sylvaticum	2.5	1.3	4	5	0.755	1.0	3.5	4	5	0.437	1.5	7.7	**0**	**12**	**0.002**	1.7	3.1	**1**	**6**	**0.048**
Avenella flexuosa	4.7	1.6	4	1	0.104	6.1	4.4	6	1	0.128	1.9	3.1	0	3	0.109	3.7	4.3	1	3	
Luzula pilosa	0.9	0.6	4	1	0.157	2.7	4.1	4	4	0.360	0.4	0.4	1	1	1.000	0.3	0.3	0	1	
Dicranum fuscescens	0.1	0.2	1	2		0.2	0.3	1	2		0.4	0.1	***4***	***0***	***0.046***	0.6	0.7	2	4	0.414
Dicranum majus	8.5	10.6	2	10	0.049	12.2	8.9	***11***	***3***	***0.025***	14.6	15.4	8	6	0.950	4.3	6.6	1	6	0.089
Dicranum polysetum	0.7	0.6	2	1	0.564	0.6	0.3	5	1	0.102	0.5	0.3	2	0	0.157	0.4	0.3	1	0	
Dicranum scoparium	6.7	6.3	5	7	0.636	2.9	1.7	***6***	***1***	***0.048***	2.5	1.5	***8***	***0***	***0.011***	2.7	1.3	***6***	***2***	***0.048***
Hylocomium splendens	7.9	10.2	**1**	**10**	**0.007**	13.1	19.7	**1**	**12**	**0.002**	9.6	14.7	5	7	0.271	16.4	16.7	7	6	0.972
Hypnum cupressiforme agg.	0.7	0.6	3	1		0.2	0.3	1	2		0.9	0.7	0	2	0.705	0.7	0.4	6	1	0.059
Plagiothecium laetum agg.	1.6	0.7	***8***	***0***	***0.008***	0.9	0.9	2	1		0.7	0.7	1	0	0.317	1.9	1.1	4	0	
Pleurozium schreberi	16.7	18.4	5	9	0.244	18.9	28.1	**3**	**12**	**0.011**	12.1	17.1	4	9	0.054	18.6	17.5	8	7	0.798
Polytrichastrum formosum	9.5	5.2	***7***	***0***	***0.018***	5.2	3.5	4	1	0.223	5.2	5.2	6	3	0.553	7.9	4.8	5	2	0.121
Sciuro-hypnum reflexum	0.5	0.5	1	2		0.3	0.3	1	1		0.4	0.5	1	2	0.564	0.7	0.4	5	1	0.103
Sciuro-hypnum starkei	2.3	1.1	***8***	***0***	***0.010***	1.7	0.9	4	1	0.102	2.3	2.9	2	3	0.686	1.6	0.7	***8***	***0***	***0.008***
Tetraphis pellucida	0.5	0.3	3	0		0.9	0.4	3	0		0.7	0.3	6	1	0.059	0.7	0.5	3	0	
Barbilophozia attenuat	0.1	0.1	1	0		0.4	0.1	***5***	***0***	***0.025***	0.6	0.1	***5***	***0***	***0.034***	0.5	0.5	0	0	
Lophocolea heterophylla	1.3	0.5	***5***	***0***	***0.038***	0.5	0.1	***6***	***0***	***0.014***	0.7	0.5	3	0	0.083	0.9	0.5	5	1	0.096
Lepidozia reptans	0.2	0.1	**1**	**0**		0.1	0.1	2	1		0.5	0.1	***5***	***0***	***0.034***	0.5	0.5	3	3	1.000
Plagiochila asplenoides	1.2	1.2	1	1		3.5	1.5	***7***	***0***	***0.017***	0.8	0.3	***6***	***0***	***0.020***	2.3	1.4	2	2	
Cladonia chlorophaea agg.	0.5	0.3	4	1	0.180	0.5	0.3	3	0		0.7	0.2	***7***	***0***	***0.008***	0.3	0.1	3	0	
Cladonia coniocraea agg.	0.3	0.1	4	1	0.180	0.4	0.5	0	1		0.5	0.3	5	1	0.102	0.4	0.4	1	1	