Forest mosses sensitively indicate nitrogen deposition in boreal background areas

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12

13 **Abstract**

14

15 Mosses take up nitrogen (N) mainly from precipitation through their surfaces, which makes

16 them competent bioindicators of N deposition. We found positive relationships between the

17 total N concentration (mossN%) of common terrestrial moss species (feather mosses

18 *Pleurozium schreberi* and *Hylocomium splendens*, and a group of *Dicranum* species) and

19 different forms of N deposition in 11−16 coniferous forests with low N deposition load in

20 Finland. The mosses were collected either inside (*Dicranum* group) or both inside and outside

21 (feather mosses) the forests. Deposition was monitored *in situ* as bulk deposition (BD) and

22 stand throughfall (TF) and detected for ammonium (NH_4^+-N), nitrate (NO_3^--N), dissolved

23 organic N (DON), and total N (N_{tot}, kg ha^{-1}yr^{-1}). N_{tot} deposition was lower in TF than BD

24 indicating that tree canopies absorbed N from deposition in N limited boreal stands.

25 However, mossN% was higher inside than outside the forests. In regression equations,

26 inorganic N in BD predicted best the mossN% in openings, while DON in TF explained most

27 variation of mossN% in forests. An asymptotic form of mossN% vs. TF N_{tot} curves in forests

28 and free NH_4^+-N accumulation in tissues in the southern plots suggested mosses were near

29 the N saturation state already at the N_{tot} deposition level of 3−5 kg ha^{-1}yr^{-1}. N leachate from

30 ground litterfall apparently also contributed the N supply of mosses. Our study yielded new

31 information on the sensitivity of boreal mosses to low N deposition and their response to

32 different N forms in canopy TF entering moss layer. The equations predicting the N_{tot}

33 deposition with mossN% showed a good fit both in forest sites and openings, especially in

34 case of *P. schreberi*. However, the open site mossN% is a preferable predictor of N

35 deposition in monitoring studies to minimize the effect of tree canopies and N leachate from

36 litterfall on the estimates.

37

Capsule: Mosses take up different N forms from precipitation depending on their supply

1. Introduction

The anthropogenic nitrogen (N) emissions originating from agriculture, animal husbandry and the use of fossil fuels (vehicles, energy production, industry) are dry and wet deposited onto terrestrial ecosystems as oxidized and reduced forms of N (Erisman et al. 2007, Mayer et al. 2015). Excess of N deposition has considered responsible to eutrophication of vegetation and nutrient unbalances in many habitats worldwide (Dirnböck et al. 2018). The effects of atmospheric N deposition on vegetation depend on the cumulative amount of N deposited in the past (Bernhardt-Römermann et al. 2015) and on the forms and amounts of current N deposition. In addition, the effects depend on habitat type and vary among the plant species and guilds (Perring et al. 2018). In this regard, poikilohydric mosses (bryophytes) form a distinctive group among major plant guilds of the understorey vegetation in boreal forests. Mosses lack cuticle layer and many species have large cationic exchange capacities which enable them to take up nutrients through the entire surface (Glime 2007). These properties make mosses one of the most sensitive plant groups to N deposition but also suitable organisms to be used as bioindicators (Pitcairn et al. 2006).

Terrestrial mosses take up most of nitrogen (N) they need from atmospheric wet and dry deposition (Forsum et al. 2006, Hawkins et al. 2018) although some of the N in mosses originates from the soil (Ayres et al. 2006, Liu et al. 2013). Moreover, biological fixation of atmospheric N_2 by moss-associated cyanobacteria contributes to moss N content especially in nutrient-limited northern ecosystems with a low N deposition ($< 3 - 5$ kg ha^{-1} yr^{-1}) (Rousk et al. 2013, Salemaa et al. 2019). In some experimental exposures, boreal mosses have been

63   shown to prefer ammonium (NH_4^+) and dissolved organic N (DON) over nitrate (NO_3^-) as N

64   source (Forsum et al. 2006, Nordin et al. 2006). However, mosses have an ability to also take

65   up NO_3^- from spraying solution (Solga and Frahm 2006, Hawkins et al. 2018, van den Elzen

66   et al. 2018), but NO_3^- assimilation of mosses may be suppressed by the high supply of NH_4^+

67   and DON (Liu et al. 2013). The contribution of DON (especially the amino acid component)

68   to moss N supply is suggested to be important in N limited northern ecosystems (Forsum et

69   al. 2006) and when NH_4^+ deposition is low (Liu et al. 2013). Interestingly, DON has been

70   found to serve as an important source of N also in sub-tropical epiphytic mosses growing in

71   nutrient-poor canopy habitat in cloud forests (Song et al. 2016).

72   Tree layer controls the amount and forms of atmospheric N deposition entering the moss

73   layer of boreal forests, and more knowledge on the response of terrestrial mosses to different

74   N forms in TF precipitation is needed. Tall tree canopies filter more efficiently atmospheric

75   gases (e.g. NO_2, NH_3, and HNO_3) and aerosols (e.g. NO_3^-, NH_4^+) than lower vegetation in

76   open areas due to aerodynamically rough surfaces of trees (Fowler et al. 1999, Neirynck et al.

77   2007). The dry-deposited gaseous and particulate N compounds are absorbed and retained in

78   the canopy (Fowler et al. 2009), where they are dissolved in water and converted from one

79   form to another. In addition to gaseous N compounds, water-dissolved NH_4^+ and NO_3^- may

80   be taken up by tree foliage in N-limited forests decreasing N deposition to the forest floor. In

81   high-deposition sites, NH_4^+ and NO_3^- are in turn leached from the foliage (de Schrijver et al.

82   2007, Neirynck et al. 2007), while DON is released in unpolluted or less polluted forests

83   (Mustajärvi et al. 2008, Izquieta-Rojano et al. 2016).

84   Mosses are widely used as a bioindicator for long-term trends and regional distribution of

85   total N (N_{tot}) deposition in Europe (Harmens et al. 2011, 2014; Skudnik et al. 2014, Meyer et

86   al. 2015, Kosonen et al. 2018). The lowest total N concentrations (<0.6%) of mosses

87   (mossN%) are measured in background areas in northern Europe (Poikolainen et al. 2009)

88   and Scotland with annual N_{tot} deposition <3 kg ha^{-1} yr^{-1} (Harmens et al. 2011), whereas the

89   highest mossN% (> 2.5%) are measured in areas of intensive agriculture with high NH_3

90   emissions e.g. in the UK (Pitcairn et al. 2006) and Germany (Harmens et al. 2014, Meyer et

91   al. 2015). In remote boreal areas, a possibility to apply mossN% as bioindicator of N

92   deposition instead of costly maintenance of continuous monitoring systems is of special

93   interest. However, sufficient knowledge is still lacking on how forest structure and tree

94   species composition affect the relationship between atmospheric N deposition and mossN%

95   in field conditions e.g. to enable preparation of appropriate sampling protocols for the

96   purpose.

97   In this study we investigated and modelled the relationships between the mossN% and the

98   background N deposition in boreal forests of Finland with a low N deposition in the

99   European scale. We compared the relationship between mossN% and N deposition both in

100 forest openings (bulk deposition, BD) and inside forests (TF) including different N fractions

101 in deposition (N_{tot}, NH_4^+-N, NO_3^--N and DON). We hypothesised that mossN% is equal or

102 higher in the forest than in open sites (Kluge et al. 2013, Skudnik et al. 2014, Meyer et al.

103 2015) due to 1) canopy drip of DON (Harmens et al. 2014) and 2) N leachate from litterfall

104 shed on the forest floor. In other words, we suggest that DON significantly contributes to

105 mossN% (Kielland 1997, Forsum et al. 2006, Liu et al. 2013) in northern forests with low N

106 deposition, given that the assimilation cost of organic N (amino acids) is expected to be lower

107 than that of inorganic N, especially NO_3^- (Chapin et al. 1993). Furthermore, N leaching by

108 precipitation from litterfall (senescent needles and other canopy material; Ukonmaanaho and

109 Starr 2001) may give additional input of N to mosses, and we predict a positive relationship

110 between the mossN% and the amount of N leachate at a regional scale.

111

2. Materials and methods

2.1. Study sites

Moss samples and precipitation (water and snow) were collected from intensively monitored coniferous plots in Finland (UN-ECE ICP Forests Level II network, Merilä et al. 2014) in three different inventories carried out in (1) 16 forest plots in 2009, (2) 11 forest openings in 2009−2010, and (3) in 10 forest plots in 2002−2003 (a subset of the plot network studied in 2009) (Table 1). The study sites were located along the climatic gradient between the northern latitudes 60−70°. The plots were divided into two groups, hereafter referred as "south" and "north" according to their situation in the boreal vegetation subzones of Finland (Fig. 1, Table 2). The first group consisted of the plots in the southern boreal and the second one those in the middle and northern boreal subzones. In the "north" the N deposition level is lower (Fig. 2), growing season shorter, the soil less-fertile and basal area of forests lower than in the "south" (Hilli et al. 2008). The forest data in 2009 consisted of seven Scots pine and nine Norway spruce dominated plots. Majority of the plots (12) were under conventional forest management and four (plot nos. 3, 19, 20, 21) were located in protected areas. We refer to the plots using their ICP Forests codes (Merilä et al. 2014). Basic characteristics of tree stand, understorey vegetation and soil are given in Table 2. All plots were located in background areas without any substantial nearby N emission sources, except the spruce plot Uus23S in the western coast. We excluded this plot from statistical analyses because it was an outlier due to N emissions from a fox fur farm in vicinity, but tested its effect on the shape of response curves (mossN% vs. N deposition).

135

136   *2.2. Collecting and N% determination of moss samples*

137

138   We used three subsamples of moss data in investigating the relationship of mossN% and

139   atmospheric N deposition in Finland (Table 1). Forest mosses and stand TF deposition were

140   collected within the same ICP Forests Level 2 plots. Open site mosses and bulk deposition

141   were collected from the two separate forest openings in the vicinity of each other and the

142   Level 2 forest plots within the same study area.

143

144   Subsample 1 (forest plots, 2009)

145

146   The data consists of three moss species, two feather mosses *Pleurozium schreberi* and

147   *Hylocomium splendens*, and a group of acrocarpous *Dicranum* species (mainly *D. polysetum*

148   in the south and *D. polysetum*, *D. scoparium* and *D. fuscenscens* in the north) collected from

149   16 ICP Forests Level II plots during Jul−Aug in 2009. The moss layer was partly shaded by

150   tree canopies inside the forests (Table 2). We took 28 area based moss samples (30 cm x 30

151   cm) from each plot. The samples located systematically along the four sides of the ground

152   vegetation monitoring subplot (30 m x 30 m), and the distance between two samples was 3−6

153   m. All vegetation including ground litter and humus layer was removed as one piece and

154   stored frozen before biomass separation in a laboratory. Some dwarf shrubs, herbs or grasses

155   grew above the moss layer in most samples.

156

157   All plant species were carefully separated wearing clean laboratory gloves on hands.

158   Altogether 1−8 joint samples were formed per moss species for chemical analysis. Moss thalli

159   were divided into upper green part and lower decomposing yellow-green part. The upper part

160   (length 4 cm) had generally 2.5 - 3 annual growths in Jul−Aug. The samples were dried in

161   60°C temperature, weighed and grinded, and the mossN% of upper parts was determined

162   using the CHN analyser (LECO) (Parkano lab, the Finnish Forest Research Institute, FFRI,

163   nowadays Luke).

164

165   Subsample 2 (forest openings, 2009−2010)

166

167   This data consisted of moss samples from forest openings in the vicinity of the ICP Forests

168   Level II plots (*P. schreberi* from 9 and *H. splendens* from 8 sites) collected as a part of

169   "European Moss Survey" (ICP Vegetation 2010, Meyer et al. 2015). The moss samples were

170   collected at least 10 m distance from the nearest trees so that TF precipitation had minimal

171   effect on their N content. Altogether 4–6 moss samples were taken from different points of

172   the open site and combined to form a sample of 2 g dry weight per site. Moss samples with

173   three annual growths were dried at 35°C, grained and mossN% was determined using the

174   modified micro Kjeldahl method (Kubin and Siira 1980) in the Muhos lab, FFRI. The

175   Kjeldahl method might give slightly lower mossN% values than LECO CHN (because it

176   underestimates the amount of NO_3^-). However, an earlier nationwide survey of forest

177   mossN% in Finland (Poikolainen et al. 2009), basing on the modified Kjeldahl method,

178   provided rather similar values for mossN% we received by LECO CHN for forest mosses in

179   the current study. Furthermore, the Muhos lab participated in the international quality

180   assurance test and its results on mossN% reference material agreed well with recommended

181   values (Harmens et al. 2014). In the data analyses we used the average mossN% of the

182   samples collected monthly during May– Sep, (5 months) in 2009 or 2010. The missing moss

183   data in some open sites was substituted by modelled values basing data from the other sites

184   (details in 2.4.).

185

186   Subsample 3 (forest plots, 2002−2003)

187

188   Moss samples (*H. splendens*, *P. schreberi* and *Dicranum* spp.) were collected from 10 ICP

189   Forests Level II plots in Jul 2002 or Aug 2003. The sampling protocol was similar as

190   described above for the subsample 1. We reanalysed the total N concentration of stored moss

191   powder in 2017 and determined separately nitrite + nitrate ($NO_2^- + NO_3^-$) and NH_4^+

192   concentrations. For the $NO_2^- + NO_3^-$ and NH_4^+ analyses, 50 ml of deionized water was added

193   to 0.25 g of ground moss. The samples were vigorously shaken by hand, after which they

194   were kept (horizontally) in a shaker for 16 h (250 rpm), centrifuged for 15 min (4000 rpm),

195   and filtered through a 0.45-µm Millipore filter (Millex HA, cellulose esters; Merck KGaA,

196   Darmstadt, Germany). The $NO_2^- + NO_3^-$ and NH_4^+ concentrations were measured with a

197   Thermo Scientific Gallery Plus Automated Photometric Analyser at the Lammi Biological

198   Station, University of Helsinki, following the SFS-EN ISO 13395 and SFS-EN ISO 11732

199   standards of the International Organization for Standardization. As the $NO_2^- + NO_3^-$

200   concentrations of moss samples were below the detection limit of the analyser (<10 µg l^{-1}, i.e.

201   < 2 µg $NO_2^- + NO_3^-$ -N g^{-1} dw), the amount of water-soluble DON was calculated by

202   subtracting NH_4^+ -N from total N.

203

204   *2.3. Precipitation, N deposition measurements and N leaching data*

205

206   Monitoring data on the amount of precipitation and chemical composition of bulk deposition

207   (BD) in the open areas was available for 14 ICP Level II plots including the outlier plot

208   Uus23S (Mustajärvi et al. 2008). In two areas (Juupajoki plot nos 10, 11, and Punkaharju 16,

209   17), where pine and spruce plots were located close to each other, there was one common plot

210   for open area deposition measurements for the pine and spruce plots (Suppl. Table S.1).

211   Stand TF data was available for all 16 plots. As the moss samples for chemical analysis had

212   app. 2.5−3 annual growths, we used the corresponding three-year-period in calculating the

213   mean annual deposition. We used the deposition period of 2007−2009 for the moss data from

214   2009 and 2010 (growth 2009 was unfinished in the latter year) and the periods of 2000-2002

215   or 2001-2003 for the moss data from 2002 and 2003, respectively. The use of three-year

216   means diminished the effect of annual variation in the amounts of precipitation and N

217   deposition. There were not increasing or decreasing temporal trends in the N_{tot} deposition

218   either in BD or TF across 2000 – 2010, but annual variation in precipitation controlled the

219   amount of N deposition in collectors (Suppl. Fig. S.1).

220

221   TF was collected within the forest stand with systematically located 20 rainfall collectors

222   resulting in an area based estimate for the forest floor, and BD in the nearby open area with 3

223   rainfall collectors (funnel, diameter 20 cm), during the snow-free period. During winter, 6–10

224   (TF) and 2 (BD) snow collectors (diameter 36 cm) were used. Besides wet-deposition, the

225   collectors probably caught some dry deposition during the 2–4 weeks collecting periods.

226   Deposition samples were filtered (membrane filter, 0.45 µm). Total N was determined by

227   flow injection analysis (FIA) (the Vantaa lab, FFRI), and NH_4^+-N and NO_3^--N by ion

228   chromatography (IC) (the Rovaniemi lab, FFRI), both laboratories were internationally

229   accredited. DON deposition was calculated by subtracting the measured NH_4^+-N and NO_3^--N

230   from the total N. The sampling procedure for the deposition measurements, including

231   laboratory analyses, is described in detail in Mustajärvi et al. (2008).

232

233   We used available data of the annual mass of litterfall fractions and their N amounts (kg ha^{-1}

234   yr^{-1}) for 11 plots (Uus23S excluded) provided by the study of Ukonmaanaho et al. (2008).

235   Based on this data, we modelled the amount of N in the leachate from litterfall (kg ha^{-1} yr^{-1})

236 as 6% from the total N in litterfall according to a short-term experiment (Aug-Sep)

237 (Ukonmaanaho and Starr 2001).

238

239 **3. Data analysis**

240

241 We used area based N deposition values (kg ha^{-1} yr^{-1}) consisting of information on both the N

242 concentration in precipitation and amount of precipitation in the data analysis. The amount of

243 N_{tot} in BD and TF within the study areas (open site vs. forest site) and the amount of NH_4^+-N

244 and NO_3^--N within BD and TF were compared by paired t tests. Furthermore, we tested the

245 effect of zone (north, south) and tree species on the amount of DON in TF using ANOVA

246 and post-hoc Tukey's t-tests.

247

248 We calculated open site/forest site mossN% ratios to nine study areas having moss samples

249 from the both habitats. Then we modelled the missing mossN% values for open sites (five

250 open sites in *H. splendens* and seven in *P. schreberi*) by multiplying forest mossN% values

251 using this ratio (cf. Meyer et al. 2015). We used tree-species specific average ratios for *P.*

252 *schreberi* and the overall average for *H. splendens*.

253

254 We used four-factor ANOVA in testing the effect of moss species (*P. schreberi*, *H.*

255 *splendens*), habitat (open site, forest), zone (northern, southern part of the country) and

256 dominant tree species (pine, spruce) and their two-factor interactions on the mossN% (13

257 plots with two coexisting moss species). Similarly, we used three-factor ANOVA in testing

258 the effect of moss species (three coexisting species in forest habitat), zone and tree species

259 and their two-factor interactions on mossN% (13 forest plots, 2009) and on free NH_4^+-N

260 concentration in moss tissues (10 forest plots, 2002−2003). Pairwise comparisons between

261   the moss species after ANOVA were made by post-hoc Tukey's t-tests. Assumption of

262   normal distribution of the data in using parametric tests was checked by Shapiro-Wilk

263   normality tests and the data was log (x+1) transformed when needed. We analysed the

264   relationship between the averages of mossN% and amount of N leachate calculated separately

265   to the pine and spruce stands in the north and south using Spearman rank correlation. The

266   tests were carried out using the STATISTIX 10.0 program (2013).

267

268   We fitted linear logarithmic models (lm) for the three moss species in order to study the

269   response of mossN% (y variable) to different N forms in deposition (x variable). Separate

270   species-specific models were calculated for mossN% in open site vs. BD, and for mossN% in

271   forest site vs. TF. We used total N ($N_{tot} = NH_4^+$-N + NO_3^--N+ DON), inorganic N ($N_{inorg} =$

272   NH_4^+-N + NO_3^--N) or individually NH_4^+-N, NO_3^--N and DON as explanatory variables.

273   Interaction between N_{inorg} and DON, tree species (pine, spruce) and N_{tot}, as well as DON and

274   stand basal area were tested. We answered the hypothesis arguing DON contributes

275   significantly to mossN% in forest habitats by comparing two models, the first having only

276   N_{inorg} as a predictor, and the second having both N_{inorg} and DON as predictors of the

277   mossN%. Linear logarithmic models (lm) were used also in analysing the response of NH_4^+-

278   N and total N% of tissues of feathermosses (average of *H. splendens* and *P. schreberi*) to

279   increasing N_{tot} in TF deposition (data 2002-2003).

280

281   Finally, we studied how well N_{tot} deposition (y) in background forests in Finland could be

282   predicted according to mossN% of the three moss species (x). We made separate lm

283   logarithmic models for open site (BD vs. feather mosses) and forest site (TF vs. feather

284   mosses and *Dicranum* spp.) data. We used the species-specific as well as average mossN%

285   values of *H. splendens* and *P. schreberi* as predictors in the models. The goodness of fit was

286 evaluated according to adjusted R^2 values in all models. We used the R statistical

287 environment in constructing the models (R core team 2017).

288

289

290 **4. Results**

291

292 *4.1. Amount and chemistry of N deposition and N leachate from litterfall*

293

294 The N_{tot} in BD increased from 1.2 to 4.8 kg ha^{-1} yr^{-1} along the latitudinal gradient from north

295 to south (Fig. 2a, Table S.1). The N_{tot} was higher in BD than in TF ($p < 0.01$), but the average

296 difference was smaller in the north (0.3 kg ha^{-1} yr^{-1}, $p < 0.05$) than in the south (0.8 kg^{-1} ha^{-1}

297 yr^{-1}, $p<0.01$). The absolute (Fig. 2a,b) and relative amounts (Fig. S.2a,b) of different N forms

298 varied between BD and TF. In BD, the proportion of N_{inorg} was 70–85% of N_{tot}, whereas in

299 TF it was ca. 60% in the north and only 40% in the southernmost plots. The amount of NO_3^--

300 N was higher than that of NH_4^+-N in both BD and TF ($p<0.001$). Only in the outlier plot

301 Uus23S (excluded from the tests above) NH_4^+-N was remarkable higher than NO_3^--N in TF

302 (Fig. 2b). The amount of DON increased from north to south in TF, and it was higher in

303 spruce than pine stands in the south ($p < 0.05$) (Table S.2a-c). The amount of N leached from

304 the tree litter varied from 0.3 – 0.6 kg ha^{-1} yr^{-1} in the north and from 0.7 – 2.3 kg ha^{-1} yr^{-1} in

305 the south (Fig. 2c).

306

307 *4.2. Effect of site, zone, tree species and litterfall on mossN%*

308

309 In all species sampled from forests, the average mossN% was higher in the southern than

310 northern part of the country ($p<0.05$) (Fig. 3a, Table 2), and in spruce than pine stands

311 (p<0.05) (Fig. 3b). *H. splendens* and *P. schreberi* had similar average mossN% values, but

312 *Dicranum* spp. had higher mossN% than the feather mosses in forests (p<0.05). The average

313 mossN% of *P. schreberi* and *H. splendens* was higher in forest (range 0.8−1.7%) than in open

314 site habitats (0.5−1.2%) both in pine and spruce dominated areas (p<0.001) (Fig. 3a,b). The

315 mossN% of feather mosses was higher in spruce than pine dominated areas also in open site

316 habitats in the southern part of country (p<0.05) (Fig. 3b, for ANOVA see Table S.3a,b).

317 Moreover, the mossN% of feather mosses tended to increase with increasing amount of N

318 leachate from litterfall (p < 0.08) when compared as average values in pine and spruce stands

319 in the south and north. The outlier plot Uus23S was not included in the data analysis

320 presented here.

321

322 *4.3. Response of mossN% to total N deposition at open and forest sites*

323

324 In the open sites, the mossN% of both feather moss species increased almost linearly with

325 increasing N_{tot} in BD (Fig. 4a,b). The R^2 value of the open site model (mod1B) was higher

326 for *P. schreberi* (81%) than for *H. splendens* (52%) (Table 3a,b). Similarly, the mossN% of

327 both feather moss species and *Dicranum* spp. sampled from forests increased with increasing

328 N_{tot} in stand TF (Fig. 4a-c). However, here the response followed an asymptotic curve

329 showing a slight decrease in the N accumulation rate at higher TF N_{tot} levels. R^2 value for *P.*

330 *schreberi* (73%) was higher than those for *H. splendens* (60%) and *Dicranum* spp. (54%) in

331 the mod1TF equations (Table 3a-c). When the outlier plot Uus23S was included to these

332 models, the shape of the curves did not change compared to the basic models without Uus23S

333 (Fig. 4a-c; for Model tables see Suppl. Table S.4a,b). For *P. schreberi* the fit of the mod1B

334 was higher (R^2 81%) than that of mod1TF (73%), but opposite was true for *H. splendens*

335 (Table 3a,b).

336

337 *4.3.1. The effect of tree species in the response models*

338

339 The dominant tree species (pine or spruce) surrounding the forest openings had no

340 statistically significant effect when added as the second predictor with N_{tot} in the models of

341 feather mosses (mod2B, Table 3a,b). However, mossN% (especially in *H. splendens*) tended

342 to increase higher with increasing N_{tot} deposition in openings surrounded by spruce than by

343 pine in the southern part of the country (Fig. S.3). Similar effect of the tree species was found

344 in forest sites. Here interaction between N_{tot} and tree species (p<0.06-0.08) in equations of

345 *P.schreberi* and *Dicranum* spp. (mod2TF) showed higher accumulation rate of mossN% in

346 spruce than in pine dominated stands (Table 3a-c, Fig. S.3).

347

348 *4.3.2. MossN% in relation to different forms of N deposition and stand basal area*

349

350 N_{inorg} of BD explained most variation in mossN% of the both feather moss species in forest

351 openings in one-predictor models (mod6B). Adding DON of BD as the second predictor was

352 not significant and did not increase the R^2 values of the models (mod7B) (Table 3a,b). On the

353 other hand, N_{inorg} of TF in forest sites had relatively low R^2 values (21 – 39%) in one-

354 predictor models (mod6TF) for all three moss species, whereas TF DON as the second

355 predictor was highly significant (p<0.01) and it explained most variation in mossN%

356 (mod7TF, Table 3). When TF DON was included to the models, TF N_{inorg} changed to be an

357 insignificant predictor. There was no interaction between N_{inorg} and DON in either BD or TF

358 models (not shown). However, the effect of TF DON on mossN% was controlled by the

359 forest structure, being higher in the stands with larger basal area (significant interaction

360 DON: Basal area in modTF8 in all moss species) (Table 4, Fig.S.4). In the case of *P.*

361 *schreberi* also N_{inorg} had a small positive effect (p<0.10) on mossN% when the effect of DON

362 was linked in the interaction term with basal area.

363

364 The distinct effects of DON in open and forest sites are clearly seen in the shape of the

365 response curves of mossN% vs N form (Fig. 4a-c). The range of DON (on x axis) in the

366 forest sites was twice as wide as that in the open sites. Thus, in the open sites the effect of

367 DON on mossN% was minimal whereas N_{inorg} dominated the N_{tot} deposition pattern. On the

368 other hand, DON determined the shape of mossN% vs. N_{tot} curve in the forest sites. The

369 location of the outlier plot Uus23S was distant from the response curves of mossN% vs BD in

370 the open sites, but it fitted quite well to the curves of mossN% vs. TF N_{tot} or TF N_{inorg} based

371 on the forest data (Fig. 4a-c).

372

373 *4.4. Free NH_4-N in moss tissues (forest data 2002-2003)*

374

375 An analysis of N forms in mosses collected from the forest plots (2002−2003) showed that

376 most N (average 98.8%) was assimilated into organic N compounds. However, we found a

377 small amount of free NH_4^+-N (1.2%) in tissues. The concentration of NH_4^+-N was higher in

378 the southern than in northern stands (p<0.001), and in spruce than in pine stands (p<0.001) in

379 each three moss species (Suppl. Fig. S.5, Table S.3c). Average NH_4^+-N as well as total N

380 concentration of the feather mosses increased with increasing TF N_{tot} deposition according to

381 an asymptotic curve (Fig. 5, Table S.5).

382

383 *4.5. Predicting N_{tot} deposition for background forest areas by mossN%*

384

385   Equations predicting the N_{tot} deposition in background forests of Finland according to

386   average mossN% of the feather moss species gave high fit for both open (R^2=73%) and forest

387   site habitats (R^2=79%) (Fig. 6, Suppl. Table S.6). *P. schreberi* predicted slightly higher BD

388   N_{tot} estimates than *H. splendens* for open sites, but the TF N_{tot} estimates of the two species

389   were almost similar for forest sites. *Dicranum* spp. predicted lower TF N_{tot} than feather

390   mosses for forests.

391

392

393   **5. Discussion**

394

395   We found clear positive relationship between the mossN% of and N_{tot} deposition in

396   background forest areas along an extensive north-south gradient in Finland. The N_{tot}

397   deposition was lower in forest TF than in open site BD, indicating that tree canopies filtered

398   and absorbed dry and wet-deposited N in northern N-limited forests (Mustajärvi et al. 2008).

399   On the other hand, mossN% was higher within forest stands than in forest openings.

400   Corresponding difference in mossN% concentrations between the two types of growing sites

401   has also been observed in Slovenia (Skudnik et al. 2014) and in Germany (Kluge et al. 2013,

402   Meyer et al. 2015), but there – unlike in Finland – N_{tot} deposition was much higher in forests

403   (rich with NH_4^+-N and NO_3^--N) than in open sites. The possible reasons for the observed

404   mossN% pattern in our study are: (1) Mosses prefer certain forms of N (e.g. amino acids in

405   DON) the amounts of which are higher in TF than in BD (cf. Harmens et al. 2014); (2) a part

406   of N accumulating in mosses originates from N leachates of litterfall (Ukonmaanaho and

407   Starr 2001) not included in BD or TF; (3) biological N_2 fixation of moss-associated bacteria

408   (Salemaa et al. 2019); (4) translocation of N from senescing tissues to new moss growth

409   (Eckstein and Karlsson 1999, Salemaa et al. 2008), and (5) differences in moss growth rates

410 due to differences in abiotic and biotic factors between geographical areas and forest types

411 (Harmens et al. 2011).

412

413 *5.1. The effect of different N forms on mossN%*

414

415 Our results suggested that differences in the deposition chemistry and supply of different N

416 forms between the open and forest sites affected the uptake of N from precipitation by

417 mosses. At the open sites inorganic forms of N in deposition explained the accumulation of N

418 in mosses, whereas DON explained almost completely the variation of mossN% in forest

419 sites. These correlative results gave indirect evidence for moss affinity to DON and supported

420 the hypothesis that the canopy drip of DON greatly contributed to mossN% in forests.

421 However, mosses seemed to have an ability to absorb both inorganic and organic N forms

422 depending on the region and stand structure. NH_4^+-N and NO_3^--N in BD correlated positively

423 with mossN%, but it is difficult to conclude which inorganic N form was preferred by mosses

424 based on the correlative approach. The effect of N_{inorg} also in forest site was observed in the

425 outlier 'fox farm' plot (Uus23S), where the annual NH_4^+-N deposition was 3.3 kg ha^{-1} higher

426 in TF than in BD most probably because dry-deposited NH_3 and NH_4^+ were washed down

427 from the spruce canopy. Here the mossN% of *P. schreberi* was 2.2% in forest and 1.4% in

428 opening.

429

430 Depending on the conditions, amino acids in DON may contribute substantially to N

431 sequestration of mosses (Wiedermann et al. 2009, Liu et al. 2013) although they only account

432 for a small proportion of the bioavailable fraction of DON (Neff et al. 2002). DON usually

433 accounts for about 20 to 65% of total N in wet deposition (Cornell et al. 2003). In the Finnish

434 background forests, DON formed nearly a half (>40%) of the N_{tot} in TF, whereas its share

435   was only 20% in BD. We did not analyse the composition of DON, but mosses apparently

436   took up amino acids, such as glycine (Song et al. 2016), as they can be absorbed easily into

437   moss cells through cation exchange capacity and proton (H^+) pump (Glime et al. 2007).

438

439   *5.2. The effect of tree species and stand basal area on mossN%*

440   The average mossN% of the studied moss species was higher in spruce than in pine stands.

441   Furthermore, the accumulation rate of N in mosses in relation to N_{tot} was slightly higher

442   under the spruce than pine canopies and increased with increasing stand basal area. Both the

443   characteristics of tree species and the site fertility regulated the composition of TF in forests.

444   Especially in the southern spruce stands, tree canopies modified the N in TF so that DON

445   leached from the canopies compensated the inorganic N retained therein (Mustajärvi et al.

446   2008). The greater needle mass (i.e. greater leaf area) of southern spruce stands in

447   comparison to those of pine (Merilä et al. 2014) enable spruce crowns to capture more N_{inorg}

448   from dry and wet deposition than pine crowns. In addition, the higher fertility level of spruce

449   dominated site types (Tamminen 2000, Lukina et al. 2018) may result in larger amount of

450   DON leaching in TF in spruce than in pine stands. N_{inorg} in TF explained the mossN% of *P.*

451   *schreberi* at forest sites when interaction term DON:basal area was included in the model.

452   This is reasonable particularly in northern stands which are sparser and have smaller canopy

453   coverage (Table 2) in comparison to southern stands. It is noteworthy, that tree species of the

454   surrounding forest also tended to influence mossN% in open site models in the southern part

455   of the country, although the sampling plots were treeless. This kind of tree effect may be

456   caused by litterfall or the fertility level of the site.

457

458   *5.3. Effect of litterfall, N_2 fixation, N translocation and microclimate on mossN%*

459

460   Aboveground litterfall (shed leaves, branches and bark) of trees and understorey vegetation is

461   an important pathway of nutrient return in the forest ecosystem. According to Ukonmaanaho

462   et al. (2008) N return from needle litter of coniferous stands is ca. 5 and 7–14 kg N ha^{-1} yr^{-1}

463   in the northern and in the southern Finland, respectively. During autumn and winter, litterfall

464   enter new decomposable material and water-extractable N on the forest floor (Ukonmaanaho

465   and Starr 2001, Hilli et al. 2008). As predicted, the modeled estimates for the amount of N

466   leachate for our forest plots tended to show a positive relationship with mossN% at the

467   regional scale. N leachate contributes to internal cycling of N in forests and it may partly

468   explain the higher mossN% at forest than at open sites.

469

470   In a previous study carried out partly in the same forest plots as the present study, the activity

471   of cyanobacteria hosted by mosses was highest in the northern plots having low N deposition,

472   and ceased in the south (Salemaa et al. 2019). Because light level regulates the activity of

473   cyanobacteria, it is probable that N_2 fixation is higher in mosses growing at open than forest

474   sites. In contrast, N translocation to the new growth of mosses may be faster in moist

475   conditions expressing as higher mossN% in forests than at open sites.

476

477   *5.4. The impact of low N deposition on mossN%*

478

479   Large-scale European data has provided evidence of asymptotic relationship between the

480   mossN% and N deposition (Harmens et al. 2014). The data from Finland (open site data of *P.*

481   *schreberi*, also used in our study) represented background areas with the lowest bulk N

482   deposition. The Finnish data was within the initial linear part of the asymptotic response

483   curve and showed a good fit with the model. The models of all three moss species at open

484   sites had high R^2 values also in the current analyses. The best fit was found for the

485   relationship between N% of *P. schreberi* and the amount of N_{inorg} in BD ($R^2 = 82\%$).

486   Similarly, in a Swiss study by Kosonen et al. (2018) mossN% of *P. schreberi* and *Hypnum*

487   *cupressiforme* showed a good relationship with N originating from dry deposited NH_3 and

488   from precipitation (DON excluded; $R^2=81\%$). The mossN% was generally slightly higher in

489   Switzerland than in Finland, probably due to the higher contribution of dry-deposited NH_3 to

490   mossN% at the Swiss sites (Kosonen et al. 2018).

491

492   Overall, bulk sampler measurements include only a part of the total amount of the reactive N

493   included in fine particles and gases incorporated on foliar surfaces of plants i.e., the sampling

494   method overestimate wet deposition but underestimate dry deposition (Loubet et al. 2009,

495   Meyer et al. 2015). Our sample plots (except one outlier) were located in background areas

496   far from agricultural and livestock sites and roads, and therefore the amount of dry deposition

497   on the plots was most probably low. On the other hand, in natural boreal ecosystems, both

498   low temperatures and rainfall limit the ability of mosses to assimilate excess N_{inorg} and to

499   allocate it into new biomass.

500

501   In the response models of the joint European data the mossN% did not greatly respond to

502   increasing NH_4^+-N deposition of over 12 kg $ha^{-1}yr^{-1}$, and wet bulk N deposition of over 20

503   kg $ha^{-1}yr^{-1}$ (Harmens et al. 2014). According to Pitcairn et al. (1998) mossN% is saturated to

504   a level of ca. 2% when the wet BD is ca. 20 kg N ha^{-1} yr^{-1}. However, Pitcairn et al. (2006)

505   concluded mosses cannot reach high N concentrations in the field conditions when

506   precipitation is high, unless rainfall constantly contains large concentrations of N. In Finland,

507   N_{tot} deposition is remarkably lower than the N levels mentioned above. At open sites the

508   relationships between mossN% and N_{tot} in BD were linear and the highest mossN% was 1 –

509   1.2%. However, at forest sites the accumulate rate of N in mosses started to decline when N

510   deposition was only 3 – 5 kg ha^{-1} yr^{-1} and the highest mossN% c.a. 1.4 – 2.0%. Also free

511   NH_4^+-N accumulated in mosses in the southern forests at this N deposition level suggesting

512   mosses were near the N saturation state at these sites. Thus, our data suggests that the boreal

513   mosses were achieving the N saturated state at much lower level than 20 kg ha^{-1} yr^{-1} when

514   growing under the effects of tree canopies and litterfall.

515

516   *5.5. Predicting N deposition based on mossN%*

517

518   The nationwide surveys on mossN% in *H. splendens* in Finland reflected well the known

519   decreasing gradient of N deposition from south to north at the country level, but the

520   correlation with the modelled N deposition was fairly weak (Poikolainen et al. 2009). The

521   authors suggested that in addition to N deposition, the variability in a range of site and stand

522   characteristics cause variation in mossN%. In the present study, we were able to quantify the

523   relationship between mossN% and N_{tot} in more detail because N deposition was measured at

524   the moss sampling sites (TF) or in their vicinity (BD).

525

526   At open sites, the linear pattern of accumulation of N in mosses with increasing N_{tot}

527   deposition gives evidence of their high bio-indicator value at conditions of fairly low N

528   deposition. This finding justifies using the open site equations in modelling N_{dep} particularly

529   in remote boreal areas, where it is not possible to maintain continuous N_{dep} monitoring

530   systems. Mosses growing in forests took up N from TF precipitation passing tree and dwarf

531   shrub canopies and from litterfall. Because these processes are controlled by many

532   environmental factors (e.g. stand structure, amount of dry deposition and precipitation, and

533   temperature), we recommend using the equations calculated from the open site data. We also

534   recommend using *P. schreberi* in field studies when possible because its equations showed

535   the best fit between the mossN% and N deposition at both open and forest sites.

536

537   **6. Conclusions**

538

539   Given the low precipitation and low N deposition at the Finnish sites as well as higher

540   mossN% in forests than in openings, it is probable that TF at background sites was enriched

541   with N forms (e.g. amino acids in DON) readily taken up by mosses. This was reflected as a

542   lowered N uptake efficiency of mosses at higher N exposure levels. The view is supported by

543   the asymptotic form of the accumulation curves of the N_{tot} and NH_4-N in tissues vs. N

544   deposition, suggesting mosses in forests were approaching N saturation at TF N_{tot} of 3–4 kg

545   ha^{-1} yr^{-1}. Corresponding level of N deposition has been found to turn off N_2 fixation of

546   cyanobacteria associated with mosses (Salemaa et al 2019). The accumulation of NH_4^+-N in

547   moss tissue may indicate that the supply of N_{inorg} exceeds the ability of mosses to assimilate

548   and allocate N into biomass production i.e. the moss growth is no longer N limited. However,

549   it should be noted that a part of the N accumulated in mosses apparently came from the N

550   leachate from litterfall emphasizing the effect of internal N flux of the forest ecosystem.

551   According to Bobbink et al. (2010) and Bobbink and Hettelingh (2011) critical N load for

552   eutrophication, i.e. slow changes in the structure and function of boreal forests, may take

553   place already at N deposition levels < 5 kg ha^{-1} yr^{-1}. This level is near the suggested N

554   saturation point of the boreal mosses in our study. However, more research is needed for

555   understanding what kind of roles mosses have in the internal N flux and eutrophication

556   process of boreal ecosystems.

557

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565

566

567   Appendix: Supplementary Figures and Tables

568

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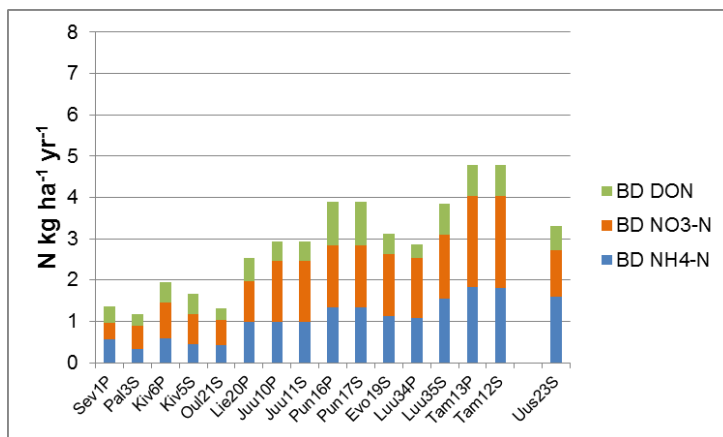750   Phytologist 181, 208-217. https://doi.org/10.1111/j.1469-8137.2008.02628.x

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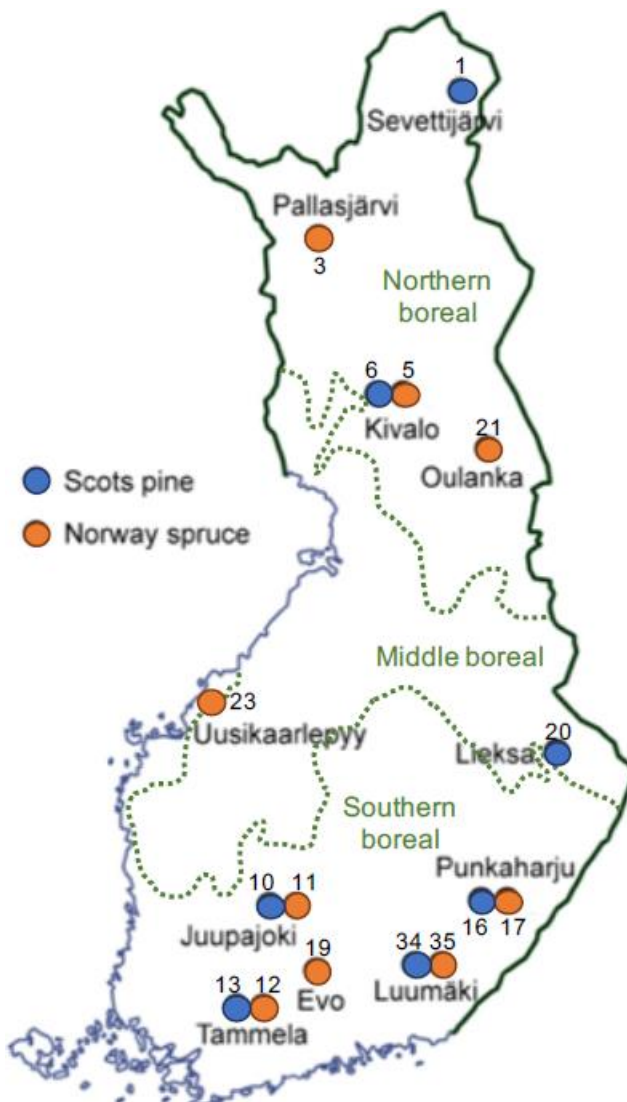
Figure 1. Location of the plots and distribution of the vegetation zones in Finland. ICP
Forests plot code shown. In the data analysis "south" = southern boreal and "north" =
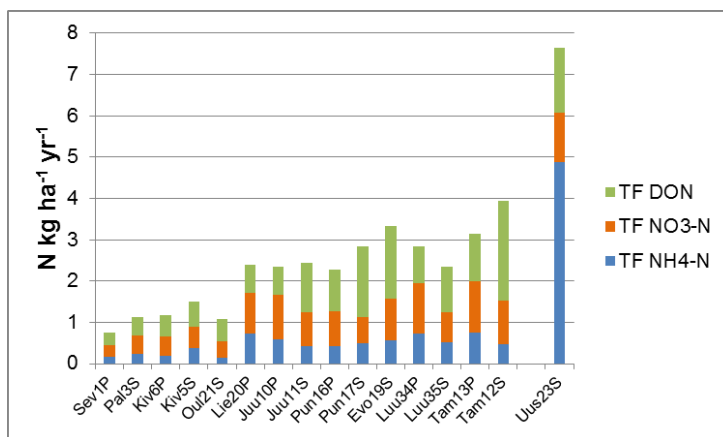middle and northern boreal subzones.

758

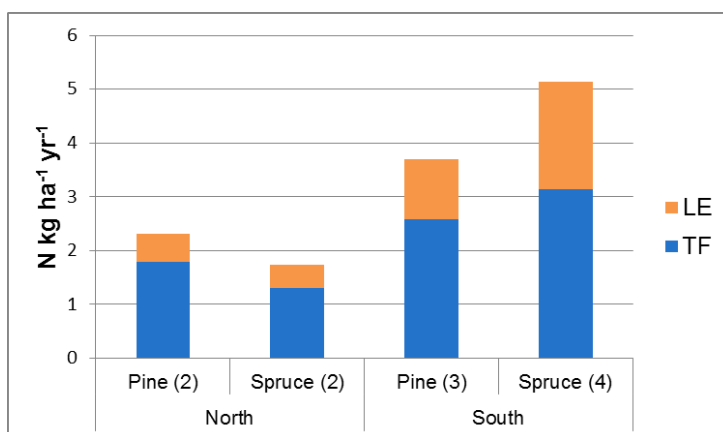759   a)

760

761   b)

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763   c)

764

765   Figure 2. Amount of different N forms in a) bulk (BD) and b) throughfall (TF) deposition (averages
766   across 2007-2009, see Suppl. Table S.2). Plots ordered according to N latitude (Table 2) from north to
767   south (left – right). P = Scots pine and S = Norway spruce in the plot names. Plot Uus23S is an outlier
768   and positioned far right. c) Average amount of N_{tot} in TF and in leachate (LE) from litterfall (shed
769   needles and other canopy material) in the southern and northern pine and spruce plots (number of
770   plots in parenthesis). The amount of N in LE was calculated as 6% from the N of litterfall
771   (Ukonmaanaho and Starr 2001).

772   a)
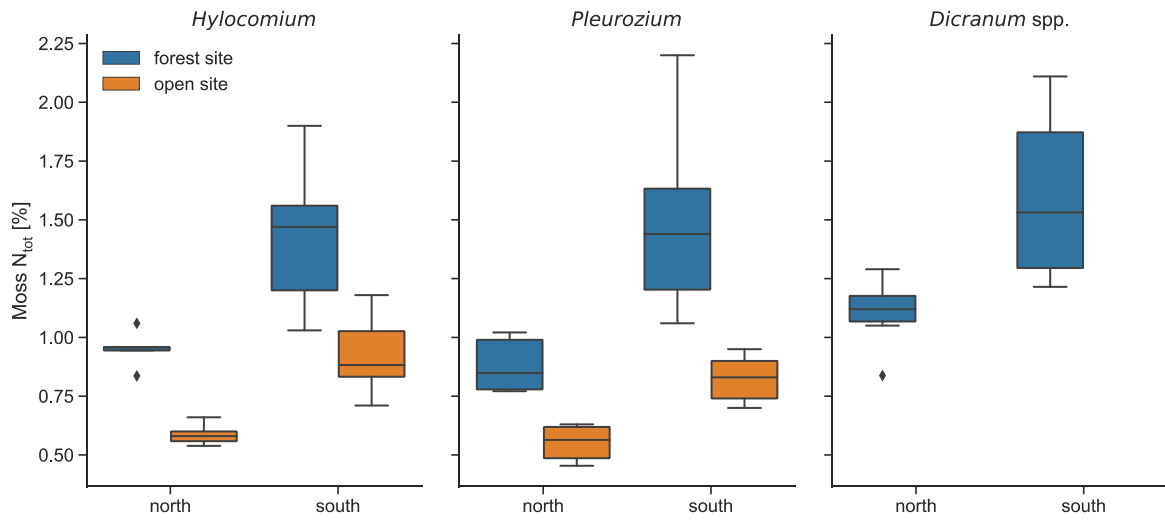
773

774   b)
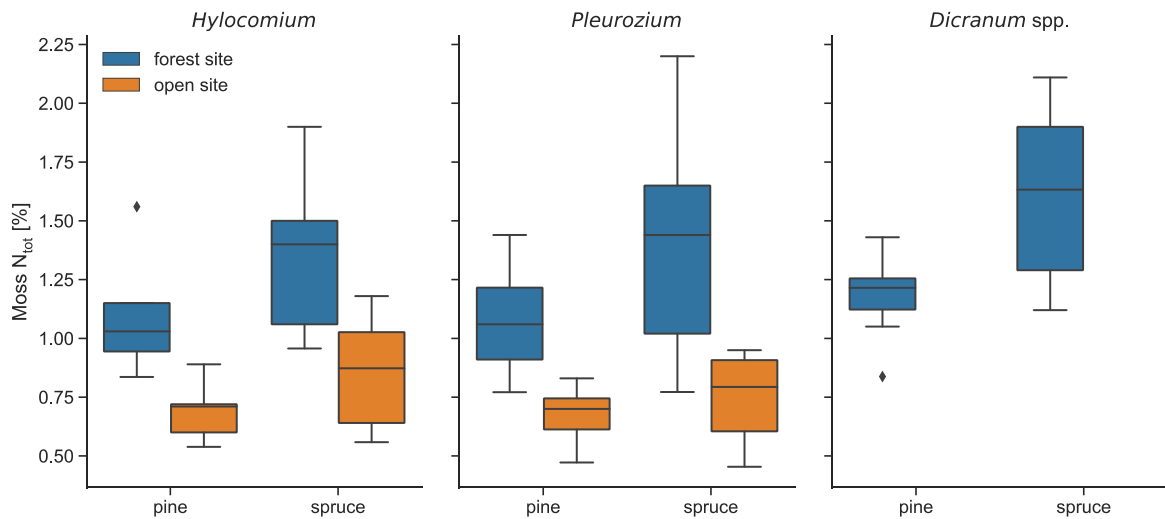
775

776   Figure 3. Box-plot diagrams of total mossN% of three species (*Pleurozium schreberi*,
777   *Hylocomium splendens* and *Dicranum* spp.) collected from forests and open sites a) in
778   northern vs. southern parts of Finland and b) in Scots pine vs. Norway spruce dominated
779   areas. Middle line in a box is a median, the box shows 75 % and 25 % percentiles, and the
780   whiskers denote 97.5 % and 3.5 % percentiles.
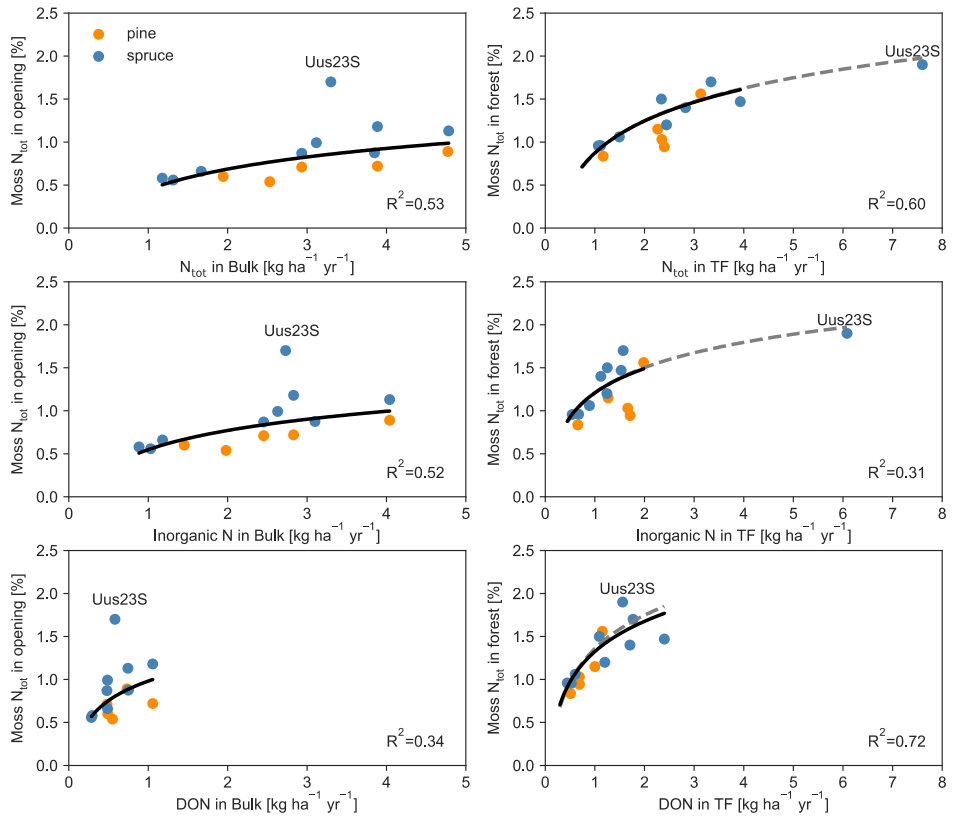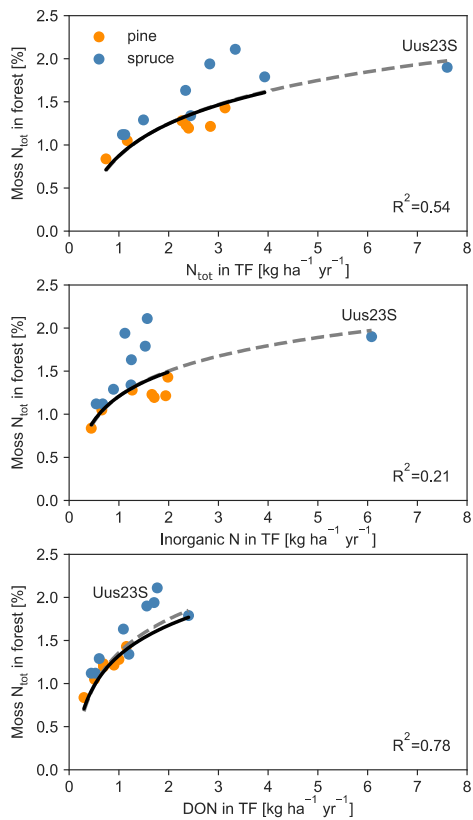
781

782   a) *Pleurozium schreberi*
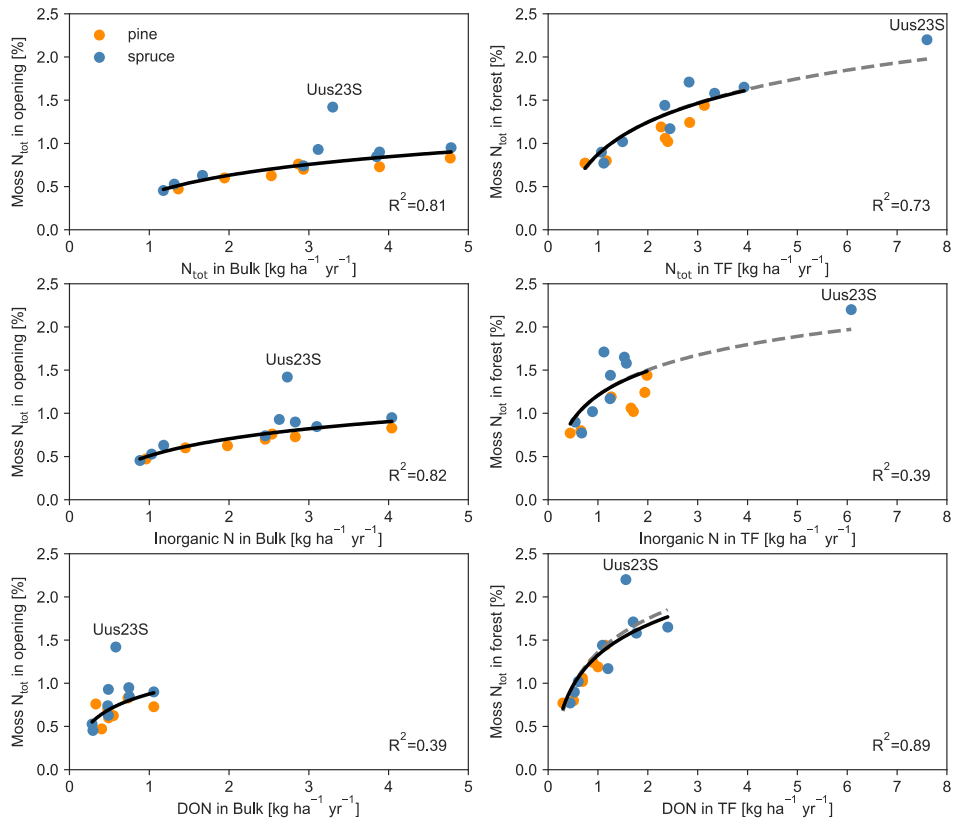
783

784   b) *Hylocomium splendens*

785

786

787   c) *Dicranum* spp.

788

789   Figure 4. Total mossN% in relation to different N forms (N_{tot}, N_{inorg} and DON) in bulk
790   (samples from openings) and in throughfall (TF) deposition (samples from forests) for a)
791   *Pleurozium schreberi*, b) *Hylocomium splendens* and c) *Dicranum* spp. (only forest samples).
792   Dominant tree species in the sampling site given in the point colour.The outlier plot Uus23S
793   (near a fox farm), marked as a point in figures, is excluded in the basic models (solid line),
794   but included in the extended TF models (dashed line). R^2 value tells the fit of the basic
795   model. Model tables for response curves in Supplement Table S.4a,b.

796
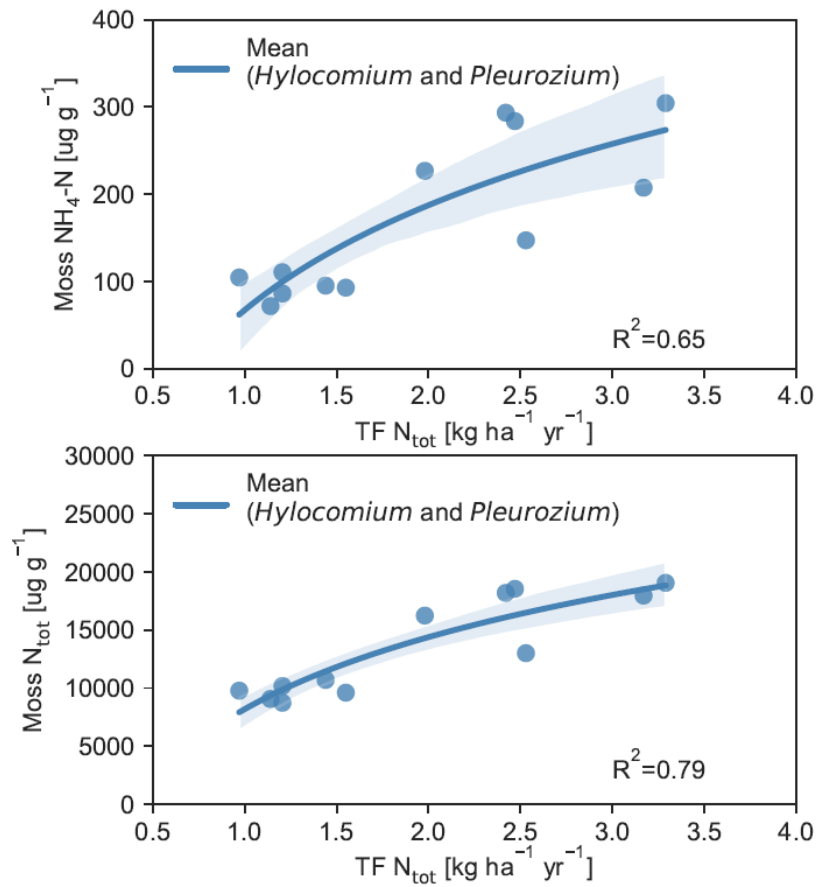
Figure 5. Accumulation curves with 95 % confidence intervals for a) NH_4^+-N and b) N_{tot} (µg g$^-$^{1}) in moss tissues (mean of *P. schreberi* and *H. splendes, years 2002 or 2003*) vs. TF N_{tot} deposition.

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803
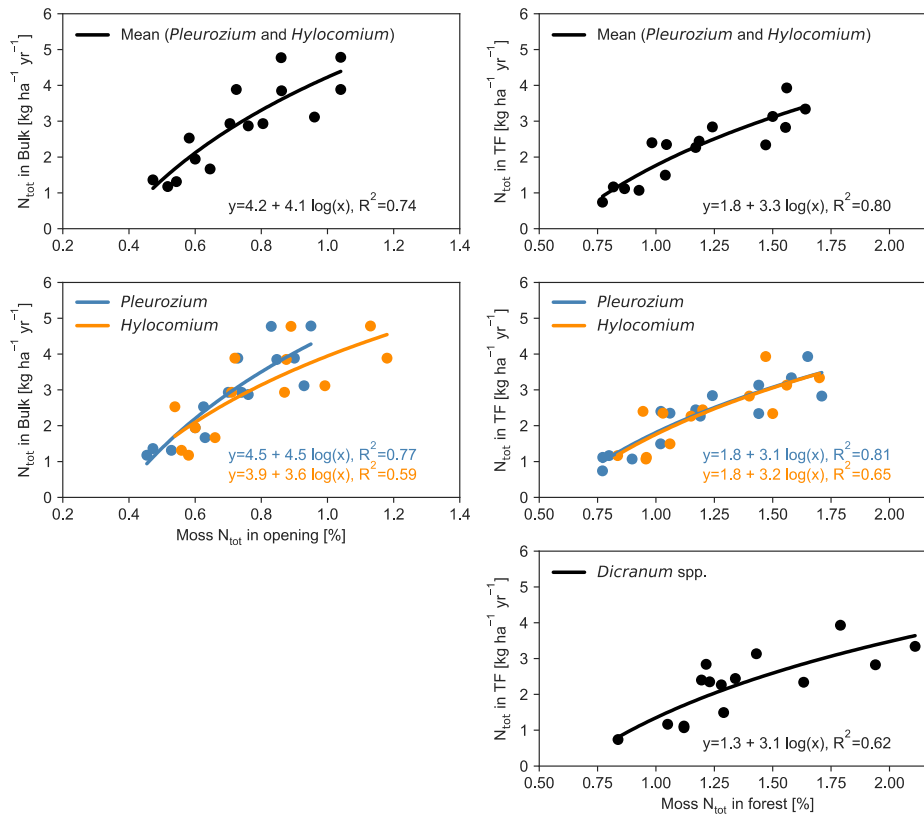
Figure 6. Response curves for the total N deposition (y) in the background forests of Finland using mossN% as a predictor (x). Left side column: bulk N_{tot} deposition vs. moss samples from forest openings and right side column: TF N_{tot} deposition vs. moss samples inside forest. Mean mossN% values of the two feather mosses is used as a preditor in models in the upper row and separate models are given for *P. schreberi* and *H. splendens* in the middle.

810

811

812   TABLES

813

Sub-sample	Habitat	Sample years of mosses	N forms in mosses	Sample years of deposition, prec.	N forms in deposition
1	Forest n = 16	2009	N_{tot}	TF: 2007 - 2009	N_{tot}, NH_4^+-N, NO_3^--N, DON
2	Opening n = 11	2009 (2010)	N_{tot}	BD: 2007 - 2009	N_{tot}, NH_4^+-N, NO_3^--N, DON
3	Forest n = 10	2002 (2003)	N_{tot}, NH_4^+-N, NO_3^--N, DON	TF: 2000 – 2002, (2001 - 2003)	N_{tot}, NH_4^+-N, NO_3^--N, DON

814

815   Table 1. Overview of measurements in the three subsamples of mosses, N deposition and
816   precipitation (prec.) in different years. n = total number of sites. Years in parenthesis include
817   2 - 3 sites. TF = throughfall, BD = bulk deposition. We calculated three-year averages of the
818   deposition values corresponding the growth period of moss shoots used in chemical
819   analyses.

820

ICP Forests plot name	Plot abbr.	N latitude	Tree species	Basal area m² ha⁻¹	Canopy cover%	Org. soil C:N	Mosses cover %	Forest Hylo sple mossN%	Pleu schr mossN%	Dicr spp. mossN%	Opening Hylo sple mossN%	Pleu schr mossN%
Sevettijärvi1P	Sev1P	69º34′	pine	13.5	35	50.2	17		0.8	0.8		0.5ᵐ
Pallasjärvi3S	Pal3S	67º59′	spruce	15.4	40	46.3	93	1.0	0.8	1.1	0.6	0.5ᵐ
Kivalo6P	Kiv6P	66º21′	pine	18.9	23	46.8	89	0.8	0.8	1.1	0.6	0.6
Kivalo5S	Kiv5S	66º19′	spruce	18.0	33	41.3	90	1.1	1.0	1.3	0.7	0.6
Oulanka21S	Oul21S	66º18′	spruce	21.0	48	53.4	90	1.0	0.9	1.1	0.6ᵐ	0.5ᵐ
Lieksa20P	Lie20P	63º09′	pine	22.3	28	52.6	93	0.9	1.0	1.2	0.5ᵐ	0.6ᵐ
Uusikaarlepyy23S*	Uus23S	63º33′	spruce	32.7	51	21.7	40	1.9	2.2	1.9	1.7	1.4
Juupajoki10P	Juu10P	61º52′	pine	23.6	29	35.4	90	1	1.1	1.2	0.7	0.7
Juupajoki11S	Juu11S	61º51′	spruce	30.4	35	34.9	57	1.2	1.2	1.3	0.9	0.7
Punkaharju16P	Pun16P	61º46′	pine	32.0	60	35.1	96	1.2	1.2	1.3	0.7	0.7ᵐ
Punkaharju17S	Pun17S	61º48′	spruce	30.8	42	31.7	75	1.4	1.7	1.9	1.2	0.9
Evo19S	Evo19S	61º14′	spruce	49.7	73	30.8	43	1.7	1.6	2.1	1ᵐ	0.9ᵐ
Luumäki34P	Luu34P	60º55′	pine	13.6	33	40.0	38		1.2	1.2		0.8ᵐ
Luumäki35S	Luu35S	60º55′	spruce	28.2	65	26.7	84	1.5	1.4	1.6	0.9ᵐ	0.8ᵐ
Tammela13P	Tam13P	60º36′	pine	29.3	34	34.0	60	1.6	1.4	1.4	0.9ᵐ	0.8ᵐ
Tammela12S	Tam12S	60º38′	spruce	33.1	69	30.5	72	1.5	1.7	1.8	1.1	1.0

821

Table 2. Stand characteristics of the forest plots and mossN% of *Hylocomium splendens* (Hylo sple), *Pleurozium schreberi* (Pleu schr) and *Dicranum* spp. (Dicr spp.) collected inside (2009) and outside (2009-2010) forests. Missing data in openings modelled (marked ᵐ). Plots ordered along the north-south gradient (N latitude). The first six plots in the list belong to "north" and the remainder ten to "south". Location of the plots marked in Fig. 1. Stand basal area and cover % mosses from the year 2009, C:N ratio of the organic soil layer from 2006 and cover% of tree canopy from 2014. Pine = *Pinus sylvestris*, spruce = *Picea abies*. *: Uus23S is an outlier plot owing to high N emissions from a nearby fox farm.

827

Model	Predictor	Bulk deposition			TF deposition		
		R^2	P values N form, stand	Interact.	R^2	P values N form, stand	Interact.
a) *Pleurozium schreberi*							
1	N$_{tot}$	80.8	0.001		73.4	0.001	
2	N$_{tot}$+Tree+N$_{tot}$:Tree	89.8	0.001, ns^T	ns	82.7	0.001, ns^T	0.08
3	NH$_4$-N	74.4	0.001		39.6	0.007	
4	NO$_3$-N	80.0	0.001		35.6	0.011	
5	DON	39.2	0.007		89.1	0.001	
6	N$_{inorg}$	81.5	0.001		39.3	0.007	
7	N$_{inorg}$+DON	80.0	0.001^i,ns^D		88.2	ns^i, 0.01^D	
8	N$_{inorg}$+DON:BA	81.9	0.001	ns	84.9	0.106	0.001
b) *Hylocomium splendens*							
1	N$_{tot}$	52.5	0.003		59.7	0.001	
2	N$_{tot}$+Tree+N$_{tot}$:Tree	83.1	0.03, ns^T	ns	66.8	0.03, ns^T	ns
3	NH$_4$-N	46.9	0.006		29.3	0.03	
4	NO$_3$-N	55.0	0.002		27.3	0.04	
5	DON	33.4	0.02		71.2	0.001	
6	N$_{inorg}$	51.8	0.01		30.2	0.03	
7	N$_{inorg}$+DON	47.4	0.08^i, ns^D		69.1	ns^i,0.003^D	
8	N$_{inorg}$+DON:BA	47.4	0.01	ns	71.6	ns^i	0.002
c) *Dicranum* spp.							
1	N$_{tot}$				53.9	0.001	
2	N$_{tot}$+Tree+N$_{tot}$:Tree				81.3	0.02,ns^T,	0.06
3	NH$_4$-N				21.5	0.05	
4	NO$_3$-N				18.1	0.06	
5	DON				78.5	0.001	
6	N$_{inorg}$				20.8	0.05	
7	Ninorg+DON				79.5	ns^i,0.001D	
8	N$_{inorg}$+DON:BA				83.4	ns^i	0.001

829

Table 3. Comparison of the models (no 1 – 8) explaining tissue N% of three moss species using different N forms and stand variables as predictors. Moss samples collected from open sites were modelled vs. bulk (BD) and those from forests vs. throughfall (TF) deposition. For *Dicranum* spp. only forest data was available. Adjusted R^2 for models and P values for predictors are given (the 1st P value is always for the 1st predictor in a model). Abbreviations: interact. = interaction term, BA = stand basal area, i = N$_{inorg}$, D = DON, T = Tree species (pine, spruce), ns = not significant. The outlier plot Uus23S omitted from the models. The model tables are given in Supplement Table S.4a.

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