1   **Soil warming and CO₂ enrichment induce biomass shifts in alpine treeline vegetation**

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3   Running head: treeline plant biomass under global change

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ABSTRACT

Responses of alpine treeline ecosystems to increasing atmospheric CO_2 concentrations and global warming are poorly understood. We used an experiment at the Swiss treeline to investigate changes in vegetation biomass after 9 years of free air CO_2 enrichment (+200 ppm; 2001-2009) and 6 years of soil warming (+4°C; 2007-2012). The study contained two key treeline species, *Larix decidua* and *Pinus uncinata*, both approximately 40 years old, growing in heath vegetation dominated by dwarf shrubs. In 2012, we harvested and measured biomass of all trees (including root systems), above-ground understorey vegetation and fine roots. Overall, soil warming had clearer effects on plant biomass than CO_2 enrichment, and there were no interactive effects between treatments. Total plant biomass increased in warmed plots containing *Pinus* but not in those with *Larix*. This response was driven by changes in tree mass (+50%), which contributed an average of 84% (5.7 kg m^{-2}) of total plant mass. *Pinus* coarse root mass was especially enhanced by warming (+100%), yielding an increased root mass fraction. Elevated CO_2 led to an increased relative growth rate of *Larix* stem basal area but no change in the final biomass of either tree species. Total understory above-ground mass was not altered by soil warming or elevated CO_2. However, *Vaccinium myrtillus* mass increased with both treatments, grass mass declined with warming, and forb and nonvascular plant (moss and lichen) mass decreased with both treatments. Fine roots showed a substantial reduction under soil warming (-40% for all roots <2 mm in diameter at 0-20 cm soil depth) but no change with CO_2 enrichment. Our findings suggest that enhanced overall productivity and shifts in biomass allocation will occur at the treeline, particularly with global warming. However, individual species and functional groups will respond differently to these environmental changes, with consequences for ecosystem structure and functioning.

INTRODUCTION

As boundary ecosystems between mountain forests and alpine tundra, high-elevation treelines are expected to be especially sensitive to global change (Körner, 2012; Smith *et al.*, 2009). In particular, increases in atmospheric CO_2 concentration and the associated global warming could alter plant growth and species composition at treeline, with important consequences for ecosystem structure and functioning. While knowledge about how other ecosystem types might respond to these environmental changes has advanced rapidly in recent years (e.g. Dieleman *et al.*, 2012), it remains unclear if these findings apply to alpine treeline ecosystems in the temperate zone. The environment at temperate treelines is characterized by a long snow cover duration, low and sometimes even freezing temperatures during the growing season, and low availability of soil nutrients (particularly N) due to low-temperature constraints on decomposition and mineralization (Körner, 2012). Integration of treeline ecosystems into large-scale modelling efforts is additionally difficult because relatively little is known about biomass distribution at treeline among different tree species and plant growth forms or about allocation of biomass to above- and below-ground structures (Bolliger *et al.*, 2008; Devi *et al.*, 2008; Elkin *et al.*, 2013).

Despite clear evidence from observational studies that high-elevation ecosystems are impacted by ongoing environmental change (Cannone *et al.*, 2007; Dullinger *et al.*, 2012), we are aware of only three other experiments that have applied CO_2 enrichment in this setting. A late-successional sedge community (Körner *et al.*, 1997) and a mix of glacier forefield pioneer species (Furka Pass, 2440 m a.s.l.; Inauen *et al.*, 2012) were studied at alpine sites in the Central Swiss Alps, and a subalpine *Picea abies* forest community was studied in a model ecosystem study (Hättenschwiler & Körner, 1998). These three studies showed no enhanced above-ground plant productivity after multiple years of CO_2 enrichment but some evidence of greater allocation to below-ground biomass.

75   In general, CO_2 research from near-natural environments at lower elevations has

76   suggested no or only moderate plant productivity responses to CO_2 enrichment when total

77   plant biomass and cover have reached a steady state (Körner, 2006; Norby & Zak, 2011).

78   Further, many experiments spanning several years have shown initially positive plant growth

79   responses to elevated CO_2 that decline over time, particularly in forests (Körner, 2006;

80   Leuzinger et al., 2011; but see McCarthy et al., 2010; Norby et al., 2010). Increased

81   allocation to below-ground productivity has been reported in some longer-term CO_2

82   enrichment studies, including enhanced fine root production in a system where no sustained

83   above-ground growth stimulation was observed (Norby et al., 2004). This shift in allocation

84   has been interpreted as one of several ways in which plants achieve greater N uptake to

85   balance extra carbon assimilated under elevated CO_2 (Luo et al., 2004; Norby et al., 2010).

86   However, knowledge from field studies about below-ground plant productivity responses to

87   CO_2 enrichment is often limited to fine root dynamics, especially for trees, due to obvious

88   difficulties in assessing root system growth in situ and to the destructive nature of major

89   below-ground sampling efforts.

90   Compared to CO_2 enrichment field experiments, there is a slightly longer and more

91   widespread history of warming studies in mid-latitude alpine environments (e.g. Kudernatsch

92   et al., 2008; Kudo & Suzuki, 2003). Meta-analyses of warming studies in subarctic, arctic and

93   alpine tundra ecosystems have reported enhanced plant growth or reproductive output with

94   increased temperatures but have also indicated large heterogeneity across species or growth

95   form, location, and experimental duration (Arft et al., 1999; Dormann & Woodin, 2002;

96   Elmendorf et al., 2012; Walker et al., 2006). Additionally, in contrast to the general trend

97   observed in CO_2 enrichment studies, the magnitude of warming effect size on tundra

98   vegetation has been found to increase linearly with experimental duration (Elmendorf et al.,

99   2012). Despite the rich literature about impacts of climate change in tundra environments,

100   high-elevation studies in the temperate zone have been vastly underrepresented in synthesis

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efforts. Further, few experimental warming studies have been conducted in high-elevation environments including trees. This research gap is critical because the upper elevational limit of trees (i.e., alpine treeline) is thought to be primarily caused by low temperature inhibiting tree growth processes despite an adequate carbon supply (Körner, 2012). In older trees, heating of individual *Pinus mugo* ssp. *uncinata* branches (Lenz *et al.*, 2013) and of the apical shoot of *Picea abies* (Petit *et al.*, 2011) have shown enhanced growth of the individual warmed tissue, and a field study warming entire *Picea glauca* seedlings with passive open-top chambers resulted in increased height growth (Danby & Hik, 2007). Findings from these previous experimental studies suggest that above-ground tree growth processes are indeed limited by low temperature at the alpine treeline, yet the consequences of warmer growing conditions on the entire tree biomass are largely unknown.

Meta-analyses including a wider spectrum of ecosystem types and regions have indicated overall enhanced above-ground plant productivity with experimental warming (Dieleman *et al.*, 2012; Rustad *et al.*, 2001), including in tree species from temperate and boreal regions (Way & Oren, 2010). Biomass of coarse or fine roots has often been unresponsive to experimental warming, yielding a lower proportion of below-ground biomass in some cases (Dieleman *et al.*, 2012; Way & Oren, 2010). This altered biomass allocation may be caused, at least partially, by increased N availability with warming, i.e., plants do not need to invest as much into below-ground structures involved in nutrient acquisition (Melillo *et al.*, 2011).

CO_2 emissions from anthropogenic sources and long-term temperature increases are linearly related (Stocker *et al.*, 2013), and understanding potential interactive effects between these factors is essential for improving predictions of how ecosystems will be impacted by global change (Dieleman *et al.*, 2012). However, simultaneous manipulation of CO_2 level and temperature is challenging in high-elevation and high-latitude ecosystems, especially at sites with trees, due to logistical and financial constraints, and few such experiments exist. In two

127 separate closed-top chamber studies of boreal forest ecosystems, radial growth of 20-year-old

128 *Pinus sylvestris* was stimulated by CO_2 enrichment but not by air warming (Kilpelainen *et al.*,

129 2005) and neither CO_2 enrichment nor air warming altered the growth of *c.* 40-year-old *Picea*

130 *abies* at natural low nutrient availability (Kostiainen *et al.*, 2009; Sigurdsson *et al.*, 2013).

131 Whereas no interactions between CO_2 enrichment and warming were reported in these studies

132 of trees, a positive CO_2 x warming interactive effect on NPP was observed over 3 years for

133 arctic tussock tundra vegetation in Alaska, potentially due to increased ecosystem sink

134 strength at higher temperatures (Oechel *et al.*, 1994). Clearly, it remains uncertain if and how

135 these two global change factors will interact to influence different plant groups or species in

136 cold ecosystems in alpine and arctic locations.

137 To our knowledge, the Stillberg experiment located near Davos, Switzerland is the only

138 existing CO_2 enrichment study of an alpine treeline ecosystem (Hättenschwiler *et al.*, 2002).

139 The study is additionally unique for simultaneously manipulating CO_2 concentration and soil

140 temperature for *c.* 40-year-old individuals of two key high-elevation tree species, *Larix*

141 *decidua* and *Pinus uncinata*, in a replicated factorial experimental design (Hagedorn *et al.*,

142 2010). After 9 years of free air CO_2 enrichment (2001-2009) and 6 years of soil warming

143 (2007-2012), including 3 years of the treatments applied in combination (2007-2009), we

144 conducted a complete final harvest of the experiment. With this harvest effort, we were able

145 to evaluate cumulative effects of multiple years of CO_2 enrichment, soil warming and the

146 combined treatments on plant biomass and to provide novel comparative above- and below-

147 ground biomass measures for two major treeline tree species and the associated understorey

148 plant community. Additionally, we measured tree stem radial growth on entire stem discs to

149 study tree above-ground growth responses to the treatments over the entire 12 years of the

150 experiment.

151 We hypothesized that (i) both treatments led to an increase in total tree and understorey

152 plant biomass. We expected positive biomass responses to the combined treatment to be more

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153   than additive if the soil warming treatment alleviated constraints on the CO_2 growth response

154   associated with low temperature. In addition, we hypothesized that (ii) CO_2 enrichment and

155   soil warming had opposing effects on the root mass fraction (RMF) of the trees, with CO_2

156   enrichment increasing RMF due to an increased nutrient demand associated with a sustained

157   photosynthetic enhancement of both *Larix* and *Pinus* (Streit *et al.*, 2014). In contrast,

158   evidence of increased nitrogen availability during the initial 3 years of soil warming (Dawes

159   *et al.*, 2011a) led us to expect a reduced RMF in trees growing in warmed soils.

160

161   **MATERIALS AND METHODS**

162   *Site and experimental setup*

163   The study site was located at Stillberg, Davos in the Central Alps, Switzerland (9° 52'

164   E, 46° 46' N, 2180 m a.s.l.) on a NE-exposed 25-30° slope slightly above the current treeline

165   in the region (Barbeito *et al.*, 2012). The site was situated within a 5 ha long-term

166   afforestation research area where tree seedlings were planted into the intact dwarf shrub

167   community in 1975 by the Swiss Federal Institute for Forest, Snow and Landscape Research

168   (WSL). From 1975 to 2012, the mean annual precipitation was 1155 mm and the mean annual

169   air temperature was 2.1°C. For the same period, the main growing season months (June-

170   August) had a mean precipitation of 444 mm and a mean air temperature of 9.2°C. Soil types

171   are sandy Ranker and Podzols (Lithic Cryumbrepts and Typic Cryorthods), derived from

172   siliceous Paragneis parent material and dominated by a 5-20 cm thick organic Humimor layer

173   (Bednorz *et al.*, 2000). Experimental plots for the study were established in spring 2001 when

174   a free air CO_2 enrichment (FACE) experiment was initiated (Hättenschwiler *et al.*, 2002). A

175   total of 40 plots were created, each 1.1 m^2 in area, 20 with a *Larix decidua* L. (European

176   larch) individual in the centre and 20 with a *Pinus mugo* ssp. *uncinata* Ramond (mountain

177   pine) individual in the centre. To accommodate the logistics of CO_2 distribution, the plots

178   were assigned to 10 groups, five of which were exposed to elevated CO_2 while the remaining

7

179   five groups received no supplementary CO_2. The trees were *c.* 40 years old in 2012 but were

180   not taller than 4 m and were sparsely distributed so did not form a closed canopy. A dense

181   cover of understorey vegetation dominated by ericaceous dwarf shrubs surrounded the tree

182   stem in each plot.

183   CO_2 enrichment (ambient concentration +200 ppm) was supplied throughout each

184   vegetation period (*c.* beginning of June to end of September) from 2001-2009. The setup and

185   performance of the FACE system have been described in detail previously (Dawes *et al.*,

186   2011b; Handa *et al.*, 2006; Hättenschwiler *et al.*, 2002). In spring 2007, one plot of each tree

187   species was randomly selected from each of the 10 CO_2 treatment groups and assigned a soil

188   warming treatment, yielding a completely randomized split-plot design. Warming was

189   accomplished using 420-W heating cables laid on the ground surface underneath the dwarf

190   shrub layer, with a distance of 5 cm between neighbouring cables (details about the heating

191   system are given in Hagedorn *et al.*, 2010). The warming treatment was applied during the

192   entire snow-free period in 2007-2011 and from 2 June to 8 August in 2012 (Table S1). Soil

193   warming increased the growing season mean soil temperature at 5 cm depth by an average of

194   3.6°C over the 6 seasons of heating (Table S1). Increased air temperatures were detected

195   within the dwarf shrub canopy (0.9°C at 20 cm above ground) but no temperature difference

196   was detected at 50 cm height (Hagedorn *et al.*, 2010). Soil warming had a slight drying effect

197   on the soil organic layer during the first three years of treatment, but this effect was not

198   apparent in later years (Table S1). The soil matric water potential at 5 cm depth was always

199   above -300 hPa in all plots, indicating overall very moist soil conditions (Dawes *et al.*, 2014).

200

201   *Understorey above-ground biomass*

202   Understorey vegetation from the entire plot area was clipped at the ground surface at the

203   beginning of August in 2012. The harvested vegetation was separated into individual species

204   for dwarf shrubs (excluding dead ramets) and into plant functional groups of graminoids,

205 forbs, and nonvascular plants (mosses and lichens) for the remaining species. This material

206 was dried and weighed to obtain the dry mass of each species or functional group (expressed

207 as g m^{-2}). All plant samples were dried at 70°C for 48h or until weights stabilized.

208

209 *Fine root mass*

210   To estimate fine root mass, we sampled soils down to 20 cm depth in early August of

211 2012 after understorey vegetation was removed. For 0-5 cm soil depth (Oe+Oa horizons) we

212 took 8 cores, each 5 cm in diameter, evenly distributed across the area of each plot; for 5-10

213 cm depth (Oa horizon) we took 6 cores, each 4.4 cm in diameter; and for 10-20 cm depth (Oa

214 and mineral soil) we took 6 cores, each 2 cm in diameter. Samples from each soil layer were

215 bulked at the plot level, and all fine roots were separated from the soil samples using a 4 and a

216 2 mm sieve. Roots were then washed using a 50 μm mesh and separated by size class (<0.5

217 mm and 0.5-2 mm in diameter) for the 0-5 and 5-10 cm depths where almost all roots

218 occurred. Samples were then dried and weighed, and mass values were scaled up to g m^{-2}

219 from the sampling area. Accurate separation of fine roots into individual plant species or

220 functional types was not possible, and thus mass data represented plot-level estimations of all

221 species combined.

222

223 *Tree biomass and basal area increments*

224   Tree material above the ground surface was harvested at the beginning of August in

225 2012. All needles and branches (<1 cm in diameter for *Larix* and <1.5 cm for *Pinus*, including

226 new shoots formed in 2012) were removed from the main stem and oven dried. Needles were

227 then separated from the branches and the dry mass of each compartment was measured. The

228 main stem material was cut into *c*. 15 cm long sections with a circular saw (minimal mass

229 loss), dried and weighed. The entire coarse root system of each tree (i.e. roots > *c*. 2 mm in

230 diameter) was carefully excavated in mid August (after soil core sampling), dried and

231 weighed. Data from all tree compartments were combined to calculate the following biomass

232 data for each tree: wood mass (main stem and branches); needle mass (all needles were

233 formed in 2012 for deciduous *Larix*; needles formed in 2012 and in previous years were

234 bulked for evergreen *Pinus*); above-ground mass (main stem, branches and needles), below-

235 ground mass (coarse root system); and total tree biomass (above- and below-ground). We

236 additionally calculated the leaf mass fraction (LMF, total needle mass divided by total tree

237 mass) and root mass fraction (RMF, coarse root system mass divided by total tree mass) for

238 each tree.

239   Three to four stem discs were cut from the lower section of each tree stem (5-20% of

240 total tree height) for detailed tree ring measurements. Each disc was progressively sanded to a

241 grit of 400 and scanned at a resolution of 1200 dpi (Epson Expression 10000 XL, Seiko

242 Epson, Nagano, Japan). Tree ring width was measured along 12 equally-spaced radii on each

243 disc using the software WinDENDRO (version 2008g, Regent Instruments Inc., Québec,

244 Canada). Ring width measurements were averaged at the disc level and then used to calculate

245 annual basal area increments of each disc for each year from 2000-2012. We used basal area

246 values averaged over the three to four discs for each tree in statistical analyses.

247

248 *Total plant biomass per land area unit*

249   Tree density in the experimental area (pooled across *Larix decidua* and *Pinus uncinata*)

250 was one tree per 1.14 m^2 in 2005 (P. Bebi, unpublished data), indicating that the experimental

251 plot area of 1.1 m^2 was realistic for the actual tree density at the site. We therefore estimated

252 total plant biomass on a land area basis (g m^{-2}) by combining tree above-ground and coarse

253 root mass (scaled down from g 1.1 m^{-2} to g m^{-2}), understorey above-ground mass and fine root

254 mass.

255

256 *Statistical analysis*

257   We assessed treatment effects on plant biomass and tree stem radial growth (basal area)

258   with linear mixed effects models fitted with REstricted Maximum Likelihood (REML). The

259   random effects structure of all statistical models reflected the experimental design, where

260   individual plots (i.e. one tree) were nested within 20 soil warming treatment groups nested

261   within 10 CO_2 treatment groups. For all biomass response variables (tree compartments,

262   understorey above-ground parts, fine roots and total plant biomass), we included soil warming

263   treatment (unwarmed or warmed), CO_2 level (ambient or elevated), tree species (*Larix* or

264   *Pinus*), and all interactions between these variables as fixed effects in statistical models and

265   tested for significance using Type I conditional F tests (Pinheiro & Bates, 2000). Results were

266   never sensitive to the order in which fixed factors were fit in the models. All 20 plots

267   containing a *Larix* tree were included in analyses (n=5 for each CO_2 and warming treatment

268   combination). Three *Pinus* trees died during the CO_2 enrichment period: one ambient CO_2,

269   unwarmed; one ambient CO_2, warmed; and one elevated CO_2, unwarmed. These plots were

270   excluded from analyses of tree biomass and total plant biomass (n=4 for these treatment

271   groups) but were included for analyses of understorey above-ground and fine root biomass

272   (n=5; results did not change if these plots were excluded).

273   In models for tree and total plant biomass, we included tree basal area after the 2006

274   growing season (BA2006), immediately before the soil warming treatment was initiated, as a

275   covariate to account for pre-warming differences in tree size. Although using BA2006 as a

276   covariate was most appropriate for testing effects of soil warming and interactive effects

277   between the CO_2 and warming treatments, doing so could underestimate effects of elevated

278   CO_2 on biomass if substantial CO_2-induced gains occurred in 2001-2006. We therefore

279   additionally applied a second model for each biomass variable where basal area after the 2000

280   growing season (BA2000) was used as a covariate to account for pre-CO_2 enrichment

281   differences in tree size, and CO_2, tree species and CO_2 x tree species (but not soil warming)

282   were included as fixed effects. No pre-treatment information was available for biomass

283   allocation ratios of the trees (LMF and RMF).

284   Estimates of cover for each plant species present in each experimental plot were made

285   in 2005, thereby providing information about understorey plant composition at that pre-

286   warming time point. The percentage cover of each species was classified as <1%, 1-4%, 5-

287   14%, 15-24%, 25-49%, 50-74% or 75-100%. We used the mid-point of each cover category

288   as a covariate in analyses of the above-ground biomass of different understorey species and

289   plant functional groups, acknowledging that doing so would not capture any CO_2 effects that

290   occurred before 2005. Fine root mass measured using soil cores sampled in autumn of 2002-

291   2004 (data presented in Handa *et al.*, 2008) did not differ between CO_2 or soil warming

292   treatment groups and showed no relationship with fine root mass in 2012, and therefore we

293   completed fine root mass analyses of different size classes and depths without considering

294   these earlier data.

295   *Tree stem basal area growth rate*. Flexible nonlinear models such as a power-law are

296   preferred for modelling plant growth because relative growth rate (RGR) frequently slows as

297   plants increase in size (e.g. Evans, 1972; Philipson *et al.*, 2012). However, non-linear models

298   could not be fit successfully with our tree basal area dataset. We therefore modelled tree stem

299   radial growth as the log of basal area through time using linear mixed effects models, where

300   the slope represents RGR (Paine *et al.*, 2012). To evaluate the degree to which RGR differed

301   between species and treatment groups, we analyzed the log of tree basal area using separate

302   models for two key periods in the 12-year experiment. For the CO_2 enrichment period

303   (beginning of 2001 to end of 2009), models included CO_2 level, tree species, treatment year

304   (continuous variable) and all interactions as fixed effects. For the soil warming period

305   (beginning of 2007 to final harvest in 2012, including the 2007-2009 period with combined

306   CO_2 and warming treatments), we included warming treatment and all associated interactions

307   as additional fixed effects. We applied a residual auto-correlation structure (auto-regressive

308   model of order 1, corAR1) to account for violation of independence of residuals from

309   repeated basal area measurements on a given tree.

310   For all statistical analyses, we log-transformed response variables where necessary to

311   meet assumptions of normality and homoscedasticity of the residuals. In addition, we

312   accounted for cases where the residual variance differed between levels of the treatments or

313   between tree species by using the VarIdent argument (Pinheiro et $al.$, 2008). We considered

314   fixed effects significant at $P<0.05$. Due to relatively low replication and therefore statistical

315   power, we additionally designated P-values ≥ 0.05 but <0.10 as marginally significant. All

316   analyses were performed using R version 2.15.2 (R Development Core Team, 2012) and

317   mixed-effects models were fitted using the nlme package (Pinheiro et $al.$, 2008). All estimates

318   of treatment differences reported in the main article reflect statistical analyses by showing

319   model estimates for a standardized 2006 (pre-warming treatment) or 2000 (pre-CO_2

320   treatment) tree stem basal area for total plant biomass and tree biomass compartments and

321   model estimates for a standardized 2005 cover value for understorey plants. However,

322   information provided about different biomass contributions in this treeline ecosystem in

323   general were derived from raw data, which is provided in Tables S2 and S3.

324

325   **RESULTS**

326   *Total plant biomass per unit land area*

327   Total plant biomass summed to 6.67 ± 0.42 kg m^{-2} (mean of all plots ± 1 SE), with 54%

328   (3.65 ± 0.28 kg m^{-2}) in tree above-ground mass, 30% (2.04 ± 0.16 kg m^{-2}) in tree coarse root

329   mass, 4% (0.26 ± 0.02 kg m^{-2}) in above-ground understorey mass and 12% (0.71 ± 0.05 kg m^{-}

330   ^{2}) in fine root mass (Tables S2 and S3). As trees were by far the largest contributors to plot-

331   level biomass, tree stem basal area at the end of 2006 (BA2006; immediately before the soil

332   warming treatment was initiated), strongly influenced total plant biomass ($F_{1,12}=175.65$,

333    $P<0.001$). Accounting for this pre-warming variability in tree basal area, total plant biomass

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increased in warmed plots ($F_{1,8}$=14.23, P=0.006), mainly in plots containing *Pinus* (warming

x tree species interaction: $F_{1,12}$=17.61, P=0.001; Fig. 1). The total plant biomass response to

warming was driven by responses in tree above-ground and tree coarse root mass, as neither

total understorey above-ground mass nor fine root mass showed increases with soil warming

(see below). Irrespective of plot tree species and warming treatment, CO_2 enrichment (after

2006) did not significantly influence total plant biomass ($F_{1,8}$=0.07, P=0.795; Fig. 1). This

result did not change even if tree basal area at the end of 2000, just before the FACE

experiment was initiated, was used as a covariate in models testing effects of CO_2 enrichment

and plot tree species ($F_{1,24}$=5.24, P=0.031 for BA2000 covariate). In this second analysis,

mean total plant biomass was 7492 g m^{-2} (±1SE: 6454 - 8696) in elevated CO_2 plots with

Larix compared to 5659 g m^{-2} (±1SE: 4848 - 6605) in ambient CO_2 plots with *Larix*, but this

difference was not statistically significant due to large variability ($F_{1,8}$=1.09, P=0.327). Total

plant biomass was greater in plots with *Larix* than in those with *Pinus* in statistical models

accounting for pre-warming differences in tree size (marginally significant: $F_{1,12}$=4.69,

P=0.051; Fig. 1).

Understorey above-ground biomass

　　　Averaged over all plots, dwarf shrub species contributed 239±19 g m^{-2} (88%) out of

271±17 g m^{-2} of total understorey above-ground biomass, and *V. myrtillus* was the greatest

contributor in most plots (mean 121±9 g m^{-2} or 45%; Figs 2,3, Table S2). Taking into account

cover estimates from 2005 (included as a covariate in statistical models of understorey

biomass), total above-ground mass of understorey vegetation was not significantly altered by

soil warming, elevated CO_2 or the combined treatments, but the relative contributions of

individual species and functional groups changed significantly (Fig. 2). The total mass of all

dwarf shrubs increased with warming in plots with a *Larix* individual (marginally significant

warming x tree species interaction: $F_{1,14}$=3.55, P=0.081) but showed no effect of CO_2

14

360   enrichment ($F_{1,8}$=2.19, P=0.177; Fig. 2). For the three dominant dwarf shrub species, *V.*

361   *myrtillus* above-ground mass was enhanced by soil warming ($F_{1,8}$=6.79, P=0.031) and by CO_2

362   enrichment after 2005 (marginally significant: $F_{1,8}$=4.23, P=0.074), whereas neither *V.*

363   *gaultherioides* nor *E. hermaphroditum* mass was significantly affected by the treatments (Fig.

364   3). In contrast to dwarf shrub mass, graminoid ($F_{1,8}$=6.80, P=0.031), forb ($F_{1,8}$=4.77,

365   P=0.060; marginally significant), and nonvascular (moss and lichen) species ($F_{1,8}$=9.49,

366   P=0.015) mass were all lower in warmed than in unwarmed plots (Fig. 2). Forbs additionally

367   experienced a negative CO_2 effect, but only in plots with *Larix* (CO_2 x tree species

368   interaction: $F_{1,14}$=8.52, P=0.011), and mosses and lichens showed a slight overall decline in

369   plots that had received supplementary CO_2 (marginally significant: $F_{1,8}$=3.87, P=0.085; Fig.

370   2). The interaction between CO_2 and warming treatments was not significant for any of the

371   species or functional groups tested. Plots with *Pinus* had a greater total above-ground

372   understorey mass ($F_{1,14}$=6.24, P=0.026) and dwarf shrub mass ($F_{1,14}$=8.97, P=0.010) than

373   plots with *Larix*, largely due to tree species effects on the mass of *V. myrtillus* ($F_{1,14}$=16.43,

374   P=0.001) and *V. gaultherioides* ($F_{1,14}$=14.23, P=0.002), whereas plot tree species did not

375   affect the mass of other functional groups (Figs 2,3).

376

377   *Fine root biomass*

378   Fine root mass measurements from soil core samples revealed that the majority of roots

379   were in the uppermost 5 cm of the organic layer (61±3% of total fine root mass; mean pooled

380   across warming treatments, CO_2 levels and plot tree species). An average of 33±2% of roots

381   occurred at 5-10 cm depth and only 6±1% occurred at 10-20 cm depth (Fig. 4). Total fine root

382   mass (<2 mm diameter, 0-20 cm depth) showed a substantial reduction in plots with warmed

383   soil ($F_{1,8}$=38.38, P<0.001), with 555±55 g m^{-2} compared to 889±55 g m^{-2} in unwarmed plots,

384   pooled across CO_2 levels and plot tree species. This effect was apparent at depths of 0-5 cm

385   ($F_{1,8}$=25.25, P=0.001) and 5-10 cm ($F_{1,8}$=6.84, P=0.031), both within the organic layer,

386 although in the shallower depth class it occurred primarily in plots with *Pinus* (warming x tree

387 species interaction: $F_{1,14}=5.63$, $P=0.033$; Fig. 4). There was no change in fine root mass (total

388 or at individual depths) in plots previously exposed to elevated CO_2, and interactive effects

389 involving CO_2 were not statistically significant. There were no treatment effects at 10-20 cm

390 depth where only a small fraction of fine roots grew (Fig. 4). We did not detect differences in

391 the vertical distribution of fine root associated with soil warming, CO_2 enrichment or tree

392 species, suggesting an overall decline in fine root mass with warming rather than a

393 redistribution to deeper soil depths.

394   Averaged across all plots and pooled over the top 10 cm of organic soil, 32±2% of the

395 total fine root mass consisted of roots <0.5 mm in diameter. Reductions in fine root mass with

396 warming occurred both in roots <0.5 mm in diameter ($F_{1,8}=34.41$, $P<0.001$) and in roots 0.5-2

397 mm in diameter ($F_{1,8}=16.85$, $P=0.003$; Fig. S1). Warming-induced decreases were stronger in

398 plots with *Pinus* than with *Larix* (warming x tree species interaction), both for roots <0.5 mm

399 in diameter ($F_{1,13}=11.42$, $P=0.005$) and for roots 0.5-2 mm in diameter ($F_{1,12}=9.63$, $P=0.009$;

400 Fig. S1). In plots with *Larix*, roots <0.5 mm additionally experienced a decline in elevated

401 CO_2 plots (warming x tree species x CO_2 interaction: $F_{1,15}=5.52$, $P=0.033$; Fig. S1). Neither

402 size class showed a significant overall difference in mass associated with the different plot

403 tree species.

404

405 *Tree biomass and biomass allocation*

406   Accounting for pre-treatment differences in tree size (by fitting BA2006 as a covariate

407 in statistical models), soil warming had a significant positive effect on all tree biomass

408 variables tested: total, above-ground, needle, wood and coarse root mass. Treatment group

409 estimates and linear mixed-effects model results are given in Table 1. Additionally, there was

410 a warming x tree species interactive effect for each compartment, indicating that overall soil

411 warming effects were primarily due to increased biomass of *Pinus* but not *Larix* trees (Table

412   1). Trees that grew under elevated CO_2 did not have significantly enhanced biomass

413   compared to trees exposed to ambient CO_2 for any of the compartments analyzed (Table 1),

414   irrespective of soil warming treatment or tree species, even in models where BA2000 was

415   used as a covariate instead of BA2006 (Table 2). *Larix* trees that were exposed to elevated

416   CO_2 tended to have greater mass of all compartments compared to trees that experienced

417   ambient CO_2 (by *c*. +50%), but these differences were not statistically significant (Table 2).

418   Relative to tree size in 2006, *Larix* trees had greater total, above-ground and wood mass than

419   *Pinus* trees, whereas needle mass was greater for the evergreen species *Pinus* and coarse root

420   mass did not differ between tree species (Table 1).

421   Tree biomass allocation to needles (LMF) did not show a significant effect of soil

422   warming, CO_2 enrichment or the interaction between these treatments (Fig. 5).

423   Unsurprisingly, LMF was greater for evergreen *Pinus* (13.0±0.8%, averaged across CO_2 and

424   warming treatments) than for deciduous *Larix* (6.3±0.2%; $F_{1,11}$=78.19, *P*<0.001; Fig. 5). Root

425   mass fraction (RMF) was enhanced for trees growing in warmed plots ($F_{1,8}$=6.96, *P*=0.030),

426   and a warming x tree species interaction ($F_{1,13}$=5.77, *P*=0.032) revealed that this effect mainly

427   applied to *Pinus* trees (42±2% in warmed plots compared to 34±1% in unwarmed plots; Fig.

428   5). Overall, *Pinus* trees had a slightly greater RMF (38±2%) compared to *Larix* trees (33±5%;

429   $F_{1,13}$=11.40, *P*=0.005; Fig. 5). Trees that grew under ambient and elevated CO_2 did not differ

430   significantly in RMF and there were no significant interactive effects involving CO_2 level.

431   Biomass relationships can change with increasing tree size and may indirectly lead to

432   treatment effects (e.g. Gebauer *et al.*, 1996), but we found that biomass allocation ratios

433   showed no relationship with absolute tree biomass or with tree height (data not shown).

434

435   *Tree stem radial growth*

436   Increases in (log) tree stem basal area over time indicated species-specific positive RGR

437   responses to the two experimental treatments. For the 2001-2009 period (analysis of CO_2 and

438   tree species effects), trees exposed to elevated CO_2 did not show an overall significant

439   difference in basal area compared to trees grown under ambient CO_2, including at the

440   beginning of the experiment (CO_2 effect on model intercept: $F_{1,8}$=2.80, P=0.133; Fig. 6a).

441   However, elevated CO_2 had a positive effect on RGR (CO_2 x year interaction: $F_{1,329}$=6.34,

442   P=0.012), primarily for *Larix* trees (trend of CO_2 x tree species x year interaction: $F_{1,329}$=2.35,

443   P=0.127; Fig. 6a). For the 2007-2012 period where we additionally analyzed effects of soil

444   warming and associated interactive effects, trees already exposed to elevated CO_2 for 6 years

445   had a larger basal area than those growing under ambient CO_2 conditions but this difference

446   did not continue to increase (positive CO_2 effect on model intercept ($F_{1,8}$=5.67, P=0.044) but

447   no CO_2 x year interactive effect ($F_{1,214}$=0.83, P=0.364); Fig. 6b). *Pinus* trees in warmed plots

448   had an increased RGR compared to those in unwarmed plots, whereas *Larix* RGR was not

449   responsive to soil warming (marginally significant warming x tree species x year interaction;

450    $F_{1,214}$=3.80, P=0.053; Fig. 6b). There were no interactive effects between CO_2 and soil

451   warming treatments. RGR was lower for *Pinus* than for *Larix* (tree species x year interaction)

452   during both 2001-2009 ($F_{1,329}$=48.38, P<0.001) and 2007-2012 ($F_{1,214}$=7.93, P=0.005).

453   However, *Pinus* trees had a greater stem basal area than *Larix* at the beginning of the

454   experiment and this initial difference persisted throughout the 2001-2009 period ($F_{1,25}$=12.81,

455   P=0.001; Fig. 6a).

456

457   **DISCUSSION**

458   *Enhanced treeline vegetation biomass after six years of soil warming*

459   Our 12-year field experiment showed that higher summer soil temperatures led to shifts

460   in biomass production among plant species and functional groups at the alpine treeline.

461   Enhanced biomass of *Pinus* trees exposed to warmed soil (50% for total tree mass and over

462   100% for coarse root mass alone) was the most pronounced response to either soil warming or

463   CO_2 enrichment, and this response drove an increase in total plant biomass on a land area

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464   basis. The roots of most trees extended a considerable distance outside of the 1.1 m^2 plot area

465   by the time of the harvest, and it is therefore feasible that the growth response of *Pinus* would

466   have been even greater if the entire root system had been warmed to the same extent. Similar

467   to our findings, *Picea abies* in a boreal forest showed an increase in cumulative stem volume

468   production by 115% after 6 years of 5°C soil warming in summer combined with advanced

469   soil thawing and snowmelt during spring (Strömgren & Linder, 2002). We intentionally did

470   not manipulate snowmelt dynamics in our experiment, and therefore the observed growth

471   enhancement of *Pinus* was due to warmer soils alone without a potential additional effect of

472   advanced or longer growing season. Our findings regarding *Pinus* support observational

473   studies showing that treelines have advanced to higher elevations in a number of regions

474   during the past century as warming has occurred (Hagedorn *et al.*, 2014; Harsch *et al.*, 2009).

475   Our warming treatment only increased soil temperatures and air temperatures near the

476   ground surface, yet *Pinus* growing in warmed plots had an increased above-ground biomass

477   and a greater RGR of stem basal area (Table 1 and Fig. 6). In their soil warming study of

478   boreal *Picea abies*, Strömgren and Linder (2002) attributed above-ground growth stimulation

479   to increased nitrogen mineralization. Mineral nitrogen contents in the soil increased during

480   the initial 3 years of soil warming at our treeline site (Dawes *et al.*, 2011a), which might have

481   contributed to overall enhanced growth of *Pinus*. However, *Pinus* trees might have shown a

482   larger growth response, and *Larix* might have also had enhanced growth, if air at canopy

483   height was additionally warmed. In support of this possibility, seedlings of *Larix decidua* and

484   *Pinus uncinata* exposed to partial cooling of either roots or shoots in a climate chamber

485   experiment were found to have considerably decreased growth relative to seedlings growing

486   completely at warmer temperatures (Hoch, 2013).

487   The lack of a response to soil warming by *Larix* in what is often assumed to be a low

488   temperature-limiting environment for tree growth was surprising. At our treeline site, *Larix*

489   needles and new shoots were frequently damaged by freezing events during the growing

490   season (Rixen *et al.*, 2012), so it is possible that extreme air temperatures influence the

491   growth of this species more than mean growing season temperatures. Additionally, in

492   excavating the tree root systems we found that *Larix* coarse roots grew deeper in the soil (*c.*

493   uppermost 20 cm) than *Pinus* coarse roots (*c.* uppermost 10 cm), irrespective of treatment.

494   Therefore, it is possible that a smaller proportion of *Larix* (coarse) roots experienced the

495   warming treatment, which might have contributed to the lack of growth response of this

496   species.

497   In the understorey layer, we found differences between functional groups in response to

498   soil warming, with increased dwarf shrub biomass (driven by the +35% response of *V.*

499   *myrtillus*) but reduced mass of herbaceous plants (–35%) and of mosses and lichens (–85%).

500   Above-ground understorey vegetation made only a minor contribution to total plant biomass

501   in this treeline site where trees were planted densely 40 years ago. However, trees are

502   generally sparser at unplanted treeline locations in the same region as our study site (Hefti &

503   Bühler, 1986), and changes in the community composition of low-stature vegetation could

504   have large impacts on the structure of such ecosystems. Despite the relatively dense tree

505   cover, we found no correlation between understorey biomass and variables representing tree

506   size (height, total biomass, leaf mass; data not shown). Thus, we would expect similar

507   responses of low-stature plants in 'natural' treelines and in tundra ecosystems just above the

508   treeline.

509   Michelsen *et al.* (2012) found that two decades of open-top chamber (OTC) warming of

510   treeline heath vegetation in subarctic Sweden (Abisko) led to a doubling in shrub cover and a

511   considerable reduction in moss and lichen cover. More broadly, a meta-analysis of the

512   International Tundra Experiment (ITEX), with most sites in subarctic and arctic regions,

513   indicated that warming by OTCs in locations with relatively high summer temperatures and/or

514   wet soils (as at our site) led to enhanced productivity of shrubs but a tendency of reduced

515   abundance of graminoids, mosses and lichens (Elmendorf *et al.*, 2012). Therefore, our results

516   suggest that understorey vegetation within temperate alpine treeline ecosystems will follow

517   the general patterns predicted for arctic treeline and tundra sites under climate warming,

518   despite differences in daylight distribution, terrain, and species composition between these

519   regions.

520

521   *Low and species-specific biomass responses to nine years of CO_2 enrichment*

522   In contrast to tree responses to soil warming, stem basal area measurements revealed

523   that *Larix* (but not *Pinus*) trees exposed to elevated CO_2 had a greater RGR of basal area

524   during the CO_2 enrichment period from 2001-2009 (Fig. 6a). However, *Larix* trees in plots

525   treated with elevated CO_2 no longer had an enhanced RGR during the 2007-2012 period

526   (including 3 years of enrichment; Fig. 6b) and did not have significantly increased biomass

527   above or below ground in 2012, although there was a clear trend in this direction (Table 2).

528   These results suggest both a decline in the growth response to CO_2 after the first 6 years of

529   enrichment and a lack of carry-over effects in years after enrichment stopped. Our results of

530   CO_2-induced enhanced stem radial growth in *Larix* only that declined during the last few

531   years of enrichment confirm preliminary findings from ring width measured on microcores

532   sampled when the experiment was ongoing (Dawes *et al.*, 2011b; Handa *et al.*, 2006). A

533   declining size of the growth response over time has similarly been found in other CO_2

534   enrichment studies of trees (e.g. Norby *et al.*, 2010). In our treeline experiment, this response

535   pattern could not be attributed to photosynthetic down-regulation (Streit *et al.*, 2014) and

536   there was no evidence of increasing nitrogen limitation under elevated CO_2 (Dawes *et al.*,

537   2013). Instead, *Larix* trees that were growing under elevated CO_2 were more severely

538   damaged by a freezing event during the early growing season in 2007 than those growing at

539   ambient CO_2 (Rixen *et al.*, 2012). This effect might have contributed to smaller CO_2-induced

540   RGR gains in the final years of enrichment and ultimately reduced the CO_2 effect on biomass.

541   There were few indications of CO_2-induced increases in understorey vegetation, where

542   no enhancement was observed for any functional group and *Vaccinium myrtillus* was the only

543   individual dwarf shrub species to show a moderate positive biomass response. We even

544   observed negative biomass responses to CO_2 enrichment in forb above-ground mass in plots

545   with *Larix* (*c*. -50%) and in moss and lichen mass irrespective of the tree species present in

546   the plot (*c*. -80%). Similarly, alpine glacier forefield species showed a 35% decrease in above-

547   ground biomass when exposed to elevated CO_2 for 3 years (Inauen *et al.*, 2012). In our study,

548   the decline in biomass of functional groups that make only a minor contribution to total plant

549   biomass could indicate that elevated CO_2 led to increased competition within the understorey

550   layer, particularly from *V. myrtillus*.

551   The unresponsiveness of total plant biomass to elevated CO_2 in a treeline ecosystem is

552   consistent with findings from previous studies of alpine and montane ecosystems in the Alps

553   (Hättenschwiler & Körner, 1998; Inauen *et al.*, 2012; Körner *et al.*, 1997). More broadly,

554   there was no productivity response after several years of CO_2 enrichment by heath vegetation

555   in a subarctic birch forest (Olsrud *et al.*, 2010), by mature deciduous temperate forest trees

556   (Bader *et al.*, 2013) or by vegetation in a desert ecosystem (Newingham *et al.*, 2013). The

557   long-term steady state of total biomass on a land area basis in all of these studies may explain

558   this lack of productivity enhancement (Körner, 2006).

559

560   *Lack of interaction between soil warming and CO_2 enrichment*

561   We found no interactive effects between CO_2 enrichment and soil warming, which

562   implies that these two environmental changes will have independent effects on treeline

563   vegetation. This result additionally suggests that direct low soil temperature limitations on

564   growth processes did not control biomass responses to CO_2 enrichment. As observed for

565   *Pinus* in our treeline study, *Picea abies* trees in a boreal forest showed no response to elevated

566   CO_2, even when air was warmed (Sigurdsson *et al.*, 2013). Conversely, similar to *Larix* in our

study, boreal *Pinus sylvestris* showed a significant enhancement of tree ring width under elevated CO_2 but no such change with warmer air and no interactive effects (Kilpelainen *et al.*, 2005). Results from these previous studies suggest that the lack of a positive CO_2 x warming interactive effect on tree growth in our experiment was not simply because soil was warmed instead of air, but it remains unclear whether such an interaction might have occurred if temperatures in the entire system were increased.

More broadly, a meta-analysis including various ecosystem types indicated that combining these treatments often yielded results that were less than additive, possibly because reduced root biomass resulting from increased nutrient availability in warmed soils can make plants more susceptible to periodic droughts (Dieleman *et al.*, 2012). It is therefore notable that in our experiment, where soil moisture was permanently high, we did not observe any antagonistic effects of experimental CO_2 enrichment and soil warming. However, we acknowledge that potential interactive effects operating over longer time scales, such as altered nutrient availability, would not necessarily have been captured in our study. Understanding longer-term dynamics between CO_2 enrichment and increased temperatures remains as an important goal for global change research in various ecosystem types (Dieleman *et al.*, 2012).

Shifts in biomass allocation under soil warming but not with CO_2 enrichment

We found that soil warming led to an increased RMF, at least for *Pinus* trees. This finding was contrary to our hypothesis that trees growing in warmed plots would experience improved nitrogen availability and therefore invest less biomass into below-ground structures. Instead, our results suggest that warming directly ameliorated low temperature limitations on (coarse) root growth and that this change had a stronger effect on tree growth allocation than altered nitrogen availability over 6 years of warming. On the typically steep slopes at the alpine treeline, these larger root systems could improve tree stability in the face of natural

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593   hazards such as snow avalanches, shallow landslides and rockfall (Mao *et al.*, 2014;

594   Schönenberger, 1978).

595   In contrast, we found a considerable (*c.* 40%) decline in (bulk) fine root mass with soil

596   warming, especially in plots with *Pinus* despite the increased RMF of this tree species. Fine

597   roots are primarily responsible for nutrient uptake, and the warming treatment in our study led

598   to increased mineral N in the soil (Dawes *et al.*, 2011a). Therefore, reduced investment into

599   nutrient acquisition by vegetation as a whole in warmed plots could explain this negative

600   response in fine root mass. Similarly, 6 years of soil warming in a temperate lowland forest

601   had a negative impact on fine root standing crop, which the authors attributed to increased N

602   mineralization associated with the warming treatment (Zhou *et al.*, 2011).

603   Exposure to elevated CO_2 did not lead to a shift in RMF in either tree species and there

604   was no effect of CO_2 enrichment on fine root mass. This result is in contrast to reports of an

605   increased RMF under elevated CO_2 for montane *Picea abies* saplings (Hättenschwiler and

606   Körner 1998) and for glacier forefield vegetation (Inauen *et al.*, 2012). A decrease in leaf N

607   concentration under elevated CO_2 occurred in these two previous studies, and the shift in

608   RMF was interpreted as a response to increased nutrient demand associated with

609   photosynthetic enhancement. Although both *Larix* and *Pinus* exhibited sustained stimulation

610   of photosynthesis over the 9 years of enrichment in our study (Streit *et al.*, 2014), N

611   concentrations in needles and mineral N contents in soils showed no sign of a decline in N

612   availability due to elevated CO_2 (Dawes *et al.*, 2013). We therefore attribute the

613   unresponsiveness in biomass allocation under CO_2 enrichment in our treeline system to

614   minimal changes in nitrogen dynamics with the treatment. As in our study, there was no

615   evidence of sustained enhanced belowground allocation in a mature deciduous-mixed forest

616   (based on fine roots; Bader *et al.*, 2013) or in a desert (Newingham *et al.*, 2013), both systems

617   where elevated CO_2 did not reduce N availability (Newingham *et al.*, 2013; Schleppi *et al.*,

618   2012).

619   In conclusion, our results suggest that enhanced productivity at the alpine treeline is

620   likely to occur in the future, especially as a result of global warming. Further, individual

621   species and functional groups at the treeline will probably respond differently to increasing

622   temperatures and rising CO_2 concentrations, with *Pinus* more responsive to warmer soils,

623   *Larix* more responsive to elevated CO_2, and a shift toward increasing dwarf shrub dominance

624   in the understorey with both environmental changes. In addition, the lack of interactive effects

625   between the two treatments suggests that increasing CO_2 concentrations and temperatures

626   might largely have independent effects on treeline vegetation. Finally, our results suggest that

627   changes in vegetation biomass allocation might occur with warmer soils, with larger tree root

628   systems (at least of *Pinus*) but a decline in total fine root mass. As a whole, these changes in

629   treeline vegetation productivity and community composition associated with ongoing shifts in

630   environmental conditions are likely to have important consequences for the structure of these

631   high-elevation ecosystems and the ecosystem services they provide.

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SUPPORTING INFORMATION LEGENDS

Table S1. Climatic conditions and effects of the soil heating treatment on soil temperature

and moisture during each of the 6 years of treatment

Table S2. Plant biomass per unit land area, including total biomass and contributions from

understorey above-ground parts and fine roots, for each combination of CO_2 level, soil

warming treatment and plot tree species

Table S3. Tree biomass (total, needles, above-ground wood and coarse roots) for each

combination of CO_2 level, soil warming treatment and plot tree species

Figure S1. Mass of fine roots separated into <0.5 mm and 0.5-2 mm diameter size classes for

each combination of CO_2 level, soil warming treatment and plot tree species

838 **Table 1.** Tree total biomass and biomass of tree needles, woody above-ground parts and

839 coarse roots. Mean values ±1 SE intervals for each CO_2 level (ambient, elevated), soil

840 warming treatment (unwarmed, warmed) and tree species (*Larix decidua, Pinus uncinata*) are

841 listed (n = 4-5). Values reflect statistical analyses by showing model estimates (±1 SE) for

842 each compartment for a standardized tree stem basal area in the pre-warming year 2006 (947

843 mm^2, mean of all trees). Results from the linear mixed-effects models are shown to the right

844 of biomass estimates.

845

Tree compartment	Tree species	CO_2 treatment	Warming treatment	-1 SE (g m^{-2})	Estimate (g m^{-2})	+1 SE (g m^{-2})	Fixed effect	DF	*F*	*P*
Total	*Larix*	Ambient	Unwarmed	5521	6197	6956	BA2006	1, 12	144.06	<.001
			Warmed	5493	6163	6916	Temp	1, 8	22.21	0.002
		Elevated	Unwarmed	4767	5761	6961	CO_2	1, 8	0.00	0.981
			Warmed	5777	6977	8426	Tree	1, 12	4.47	0.056
	Pinus	Ambient	Unwarmed	3650	4097	4600	Temp x CO_2	1, 8	0.18	0.683
			Warmed	6373	7149	8019	Temp x Tree	1, 12	29.75	<.001
		Elevated	Unwarmed	2955	3651	4512	CO2 x Tree	1, 12	1.24	0.288
			Warmed	4899	5919	7152	Temp x CO_2 x Tree	1, 12	0.65	0.436
Needles	*Larix*	Ambient	Unwarmed	294	379	489	BA2006	1, 12	27.07	0.000
			Warmed	231	297	382	Temp	1, 8	5.89	0.041
		Elevated	Unwarmed	290	370	472	CO_2	1, 8	0.00	0.979
			Warmed	339	431	548	Tree	1, 12	9.34	0.010
	Pinus	Ambient	Unwarmed	287	376	491	Temp x CO_2	1, 8	0.00	0.995
			Warmed	824	1075	1404	Temp x Tree	1, 12	6.90	0.022
		Elevated	Unwarmed	333	445	595	CO2 x Tree	1, 12	0.73	0.410
			Warmed	608	776	989	Temp x CO_2 x Tree	1, 12	2.02	0.181
Wood	*Larix*	Ambient	Unwarmed	3335	3739	4191	BA2006	1, 12	163.58	<.001
			Warmed	3351	3755	4209	Temp	1, 8	4.69	0.062
		Elevated	Unwarmed	2978	3550	4233	CO_2	1, 8	0.01	0.931
			Warmed	3419	4075	4856	Tree	1, 12	41.76	<.001
	Pinus	Ambient	Unwarmed	2112	2369	2656	Temp x CO_2	1, 8	0.03	0.879
			Warmed	2941	3296	3695	Temp x Tree	1, 12	15.79	0.002
		Elevated	Unwarmed	1637	1989	2417	CO2 x Tree	1, 12	2.75	0.123
			Warmed	2122	2529	3016	Temp x CO_2 x Tree	1, 12	0.59	0.459
Coarse roots	*Larix*	Ambient	Unwarmed	1777	2028	2316	BA2006	1, 12	68.12	<.001
			Warmed	1793	2046	2335	Temp	1, 8	20.99	0.002
		Elevated	Unwarmed	1531	1857	2254	CO_2	1, 8	0.07	0.802
			Warmed	2025	2454	2975	Tree	1, 12	0.41	0.532
	Pinus	Ambient	Unwarmed	1144	1308	1496	Temp x CO_2	1, 8	0.56	0.474
			Warmed	2429	2774	3168	Temp x Tree	1, 12	19.92	0.001
		Elevated	Unwarmed	1001	1247	1555	CO2 x Tree	1, 12	0.39	0.546
			Warmed	2123	2575	3124	Temp x CO_2 x Tree	1, 12	0.63	0.444

846

847

848 **Table 2.** Tree total biomass and biomass of tree needles, woody above-ground parts and

849 coarse roots. Mean values ± 1 SE intervals for each CO_2 level (ambient, elevated) and tree

850 species (*Larix decidua, Pinus uncinata*) are listed (n = 8-10). Values reflect statistical

851 analyses by showing model estimates (± 1 SE) for each compartment for a standardized tree

852 stem basal area in the pre-CO_2 enrichment year 2000 (329 mm^2, mean of all trees). Results

853 from the linear mixed-effects models are shown to the right of biomass estimates.

854

Tree compartment	Tree species	CO_2 treatment	-1 SE (g)	Estimate (g)	+1 SE (g)	Fixed effect	DF	*F*	*P*
Total	*Larix*	Ambient	4183	5031	6052	BA2000	1, 24	4.67	0.041
		Elevated	6076	7259	8673	CO2	1, 8	1.39	0.272
	Pinus	Ambient	4150	5034	6106	Tree	1, 24	0.68	0.418
		Elevated	4547	5520	6701	CO2:Tree	1, 24	1.24	0.277
Needles	*Larix*	Ambient	222	285	364	BA2000	1, 24	15.71	0.001
		Elevated	355	450	569	CO2	1, 8	0.99	0.349
	Pinus	Ambient	466	605	784	Tree	1, 24	4.89	0.037
		Elevated	523	679	882	CO2:Tree	1, 24	0.83	0.371
Wood	*Larix*	Ambient	2648	3164	3781	BA2000	1, 24	1.98	0.172
		Elevated	3741	4445	5283	CO2	1, 8	1.00	0.347
	Pinus	Ambient	2089	2514	3026	Tree	1, 24	6.87	0.015
		Elevated	2086	2513	3027	CO2:Tree	1, 24	2.41	0.133
Coarse roots	*Larix*	Ambient	1345	1632	1980	BA2000	1, 24	5.23	0.031
		Elevated	2010	2419	2910	CO2	1, 8	2.21	0.175
	Pinus	Ambient	1454	1782	2186	Tree	1, 24	0.00	0.978
		Elevated	1798	2207	2709	CO2:Tree	1, 24	0.38	0.542

855

856

FIGURE LEGENDS

858

859 **Figure 1.** Plant biomass per unit of land area for each combination of CO_2 level (A =

860 ambient, E = elevated) and soil warming treatment (C = unwarmed soil, W = warmed soil) in

861 plots containing a *Larix decidua* (left) or *Pinus uncinata* (right) tree (n = 4-5). Total plant

862 biomass (filled circles) is shown, as well as contributions from tree above-ground parts (filled

863 squares), understorey above-ground parts (filled triangles), tree coarse roots (open squares),

864 and fine roots (<2 mm diameter) bulked for all plant species (open triangles). The figure

865 reflects statistical analyses by showing model estimates (±1 SE) for a standardized 2006 (pre-

866 warming treatment) tree stem basal area (947 mm^2, mean of all trees) for total plant biomass

867 and tree biomass components and model estimates for a standardized 2005 total (sum of all

868 species) vegetation cover (105%, mean of all plots) for understorey biomass.

869

870 **Figure 2.** Total plot understorey above-ground biomass and contributions from different

871 functional groups (each shown in a separate panel): dwarf shrub, graminoid, forb and

872 nonvascular (moss and lichen). Different scales are used for each panel to highlight treatment

873 differences. Values reflect statistical analyses by showing model predictions (±1 SE) for a

874 standardized vegetative cover value (%) of each functional group in the pre-warming year

875 2005. Estimates for each combination of CO_2 level (A = ambient, E = elevated), soil warming

876 treatment (C = unwarmed, W = warmed) and plot tree species (*Larix decidua*, *Pinus uncinata*)

877 are shown (n = 5), and values are expressed per unit of land area.

878

879 **Figure 3.** Above-ground biomass of the three dominant dwarf shrub species: *Vaccinium*

880 *myrtillus* (circles), *Vaccinium gaultherioides* (triangles) and *Empetrum hermaphroditum*

881 (squares). Values reflect statistical analyses by showing model predictions (±1 SE) for a

882 standardized vegetative cover value (%) of each individual species in the pre-warming year

883   2005. Estimates for each combination of CO_2 level (A = ambient, E = elevated), soil warming

884   treatment (C = unwarmed, W = warmed) and plot tree species (*Larix decidua*, *Pinus uncinata*)

885   are shown (n = 5), and values are expressed per unit of land area.

886

887   **Figure 4.** Mass of fine roots (<2 mm diameter) at soil depths of 0-5 cm (top panels), 5-10 cm

888   (middle panels) and 10-20 cm (bottom panels). Mean values ±1 SE for each combination of

889   CO_2 level (A = ambient, E = elevated), soil warming treatment (C = unwarmed, W = warmed)

890   and plot tree species (*Larix decidua*, *Pinus uncinata*) are shown (n = 4-5), and values are

891   expressed per unit of land area.

892

893   **Figure 5.** Leaf mass fraction (LMF, needle mass divided by total tree mass; top panels) and

894   root mass fraction (RMF, coarse root mass divided by total tree mass; bottom panels) of trees.

895   Mean values ±1 SE for each combination of CO_2 level (A = ambient, E = elevated), soil

896   warming treatment (C = unwarmed, W = warmed) and plot tree species (*Larix decidua*, *Pinus*

897   *uncinata*) are shown (n = 4-5).

898

899   **Figure 6.** Increases in tree stem basal area through time, with mean values ±1 SE (estimated

900   from statistical models) shown for individual treatment groups and years. *Larix decidua* is

901   shown in top panels and *Pinus uncinata* is shown in bottom panels. In **(a)**, basal area during

902   the CO_2 enrichment period (end of 2000 (i.e., beginning of 2001) to end of 2009) is shown for

903   trees exposed to ambient (dashed lines) and elevated (solid lines) CO_2 (n=8-10). In **(b)**, basal

904   area during the soil warming period (end of 2006 (i.e., beginning of 2007) to harvest in

905   summer 2012), including the 2007-2009 period when both CO_2 enrichment and soil warming

906   were applied, is shown for trees treated with ambient (left panels) or elevated (right panels)

907   CO_2 and to unwarmed (black lines) or warmed (red lines) soil (n = 4-5). The dashed vertical

908   lines in **(b)** indicate the end of the CO_2 enrichment treatment (after the 2009 growing season).
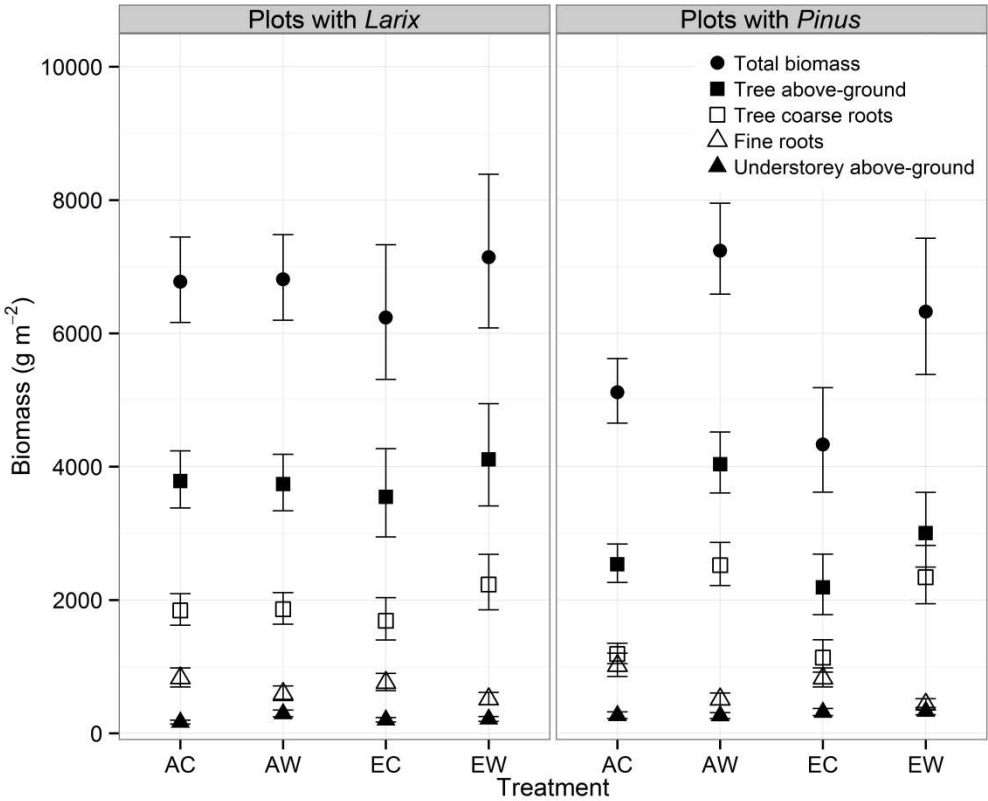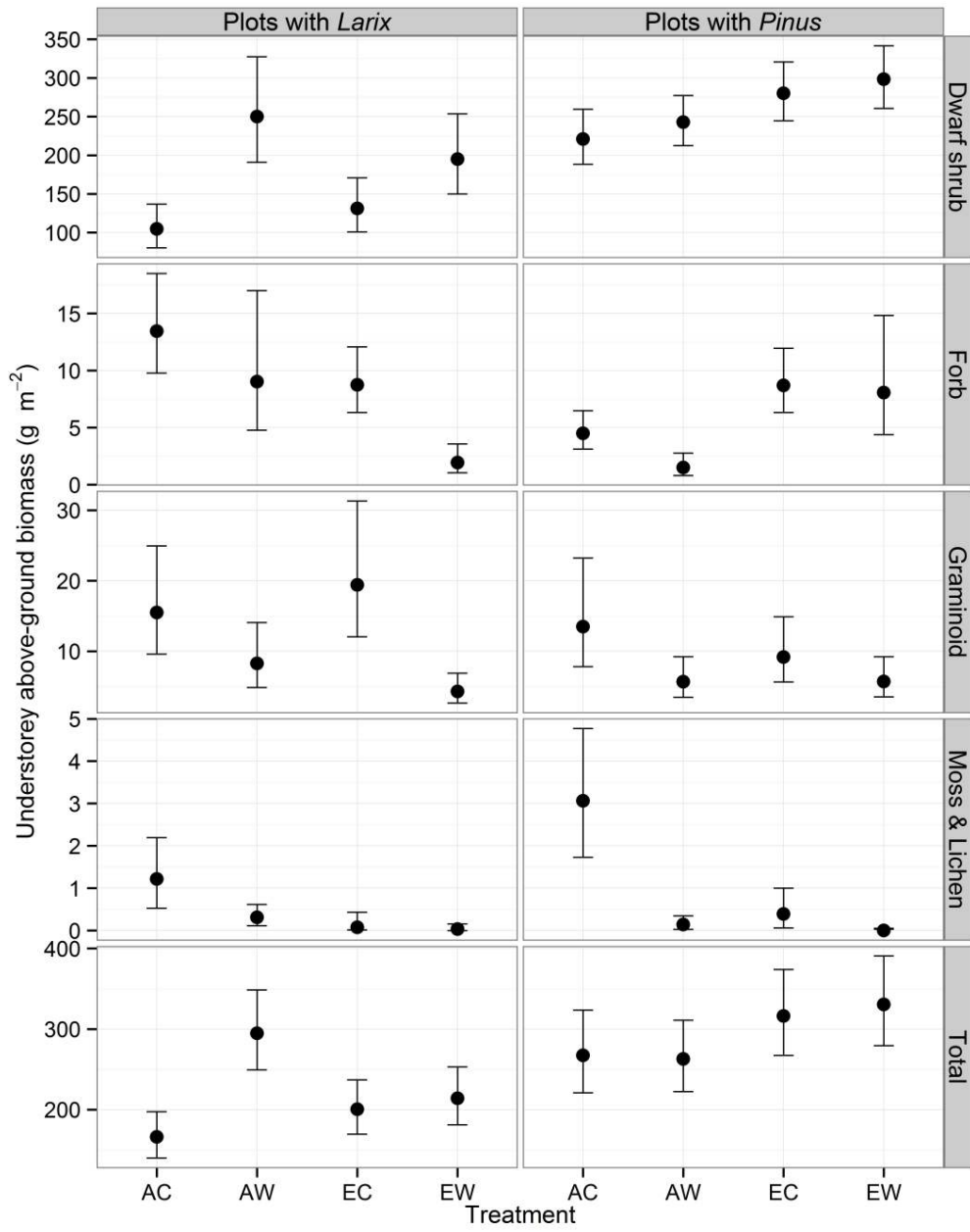
FIGURES

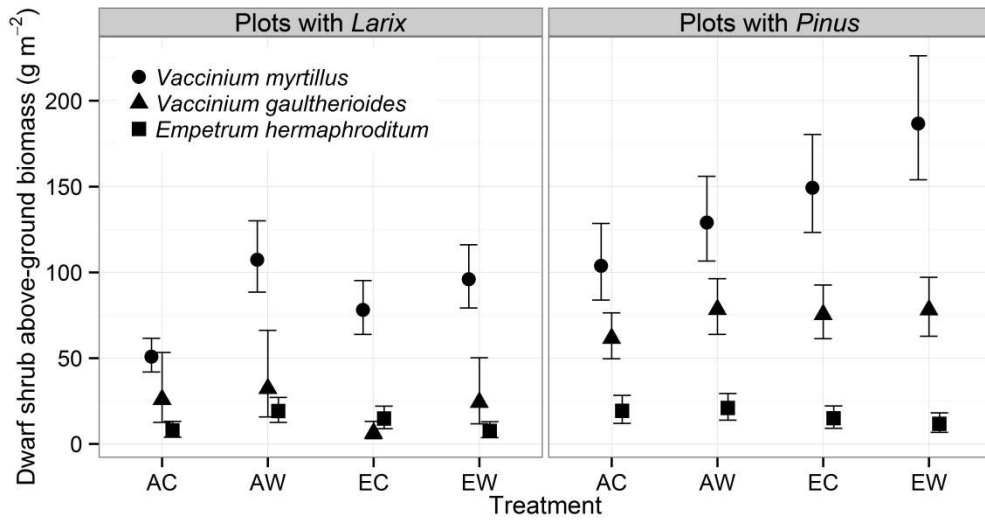**Figure 1.**

Figure 2.

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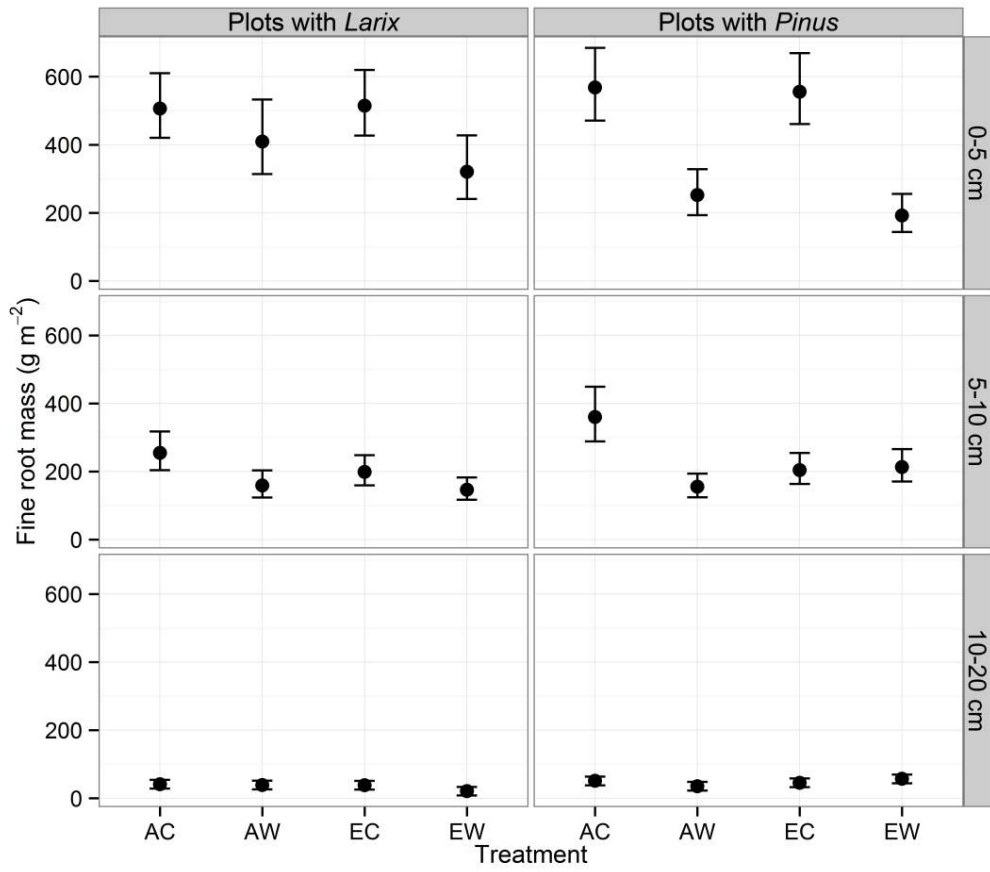
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