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1 Soil characteristics mediate the distribution and response of boreal
2 trees to climatic variability

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12 Abstract

13 We studied the effects of the soil organic layer (SOL) accumulation on growth and
14 distribution of black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*)
15 within the Québec Clay Belt. At the landscape scale, spruce was present over a much
16 larger gradient in SOL thickness (~1 to 100 cm) than aspen (~1 to 30 cm). For trees
17 between 60 and 100 years old, SOL thickness had no effect on the basal area increment
18 (BAI) of spruce, but showed a strong and negative correlation with BAI in aspen. Radial
19 growth of black spruce was favored by higher precipitation in June of the previous
20 growing season, higher temperatures in early winter and in spring, and by low
21 temperatures in summer. SOL thickness had statistically significant but moderate effects
22 on the climate-growth relationships in spruce, apparently affecting root insulation during
23 the dormant period and water availability – during the growing period. In aspen, current
24 year June temperature was the most important factor positively correlated with growth.
25 The SOL thickness affected the relationship between the aspen growth and (a) January
26 temperature and (b) June-August monthly drought code. We predict that the response of
27 black spruce to climate change should be rather uniform across the study region, while
28 the one of aspen is likely to be strongly mediated by SOL thickness.

29 *Keywords:* climate change, biotic interactions, boreal ecosystems, limiting factors,
30 succession, dendroclimatic analyses

31 Introduction

32 Climate defines large-scale patterns of species distributions and future climatic variability
33 will likely affect the composition of vegetation cover (Heikkinen et al. 2006; Wanner et
34 al. 2008). At local scales, topography and soil conditions may be important determinants
35 of species responses to future climates, and can probably affect rate of changes in
36 vegetation cover (Lafleur et al. 2010). In the boreal forest, local scale effects may be
37 especially important since soils commonly accumulate organic matter, which strongly
38 affects nutrient cycling, tree growth rates, and dynamics of carbon stocks (Hilli et al.
39 2008). In the boreal biome, the accumulation of a soil organic layer (SOL) can
40 dramatically change site growing conditions. In the Clay Belt of northern Ontario and
41 western Quebec, Canada, clay-rich soils create favorable conditions for accumulation of
42 SOL, which can result in forest paludification, i.e., successional development leading
43 towards forested peatlands (Lecomte et al. 2006). Within this region, natural stands are
44 typically initiated by stand-replacing fires that leave an exposed mineral soil upon which
45 SOL will accumulate over time (Lecomte et al. 2006; Simard et al. 2007, 2009). SOL
46 accumulation, which occurs at average rate of 1 mm/year (Lecomte et al. 2006), increases
47 the water-holding capacity of the soil profile (Lavoie et al. 2007), thereby leading to
48 excess moisture and, ultimately, to the rise of the water table. This sequence of events
49 decreases both soil temperature and nutrient cycling rates (Oechel and Van Cleve 1986;
50 Simard et al. 2007). It also leads to lower stand productivity (Oechel and Van Cleve
51 1986; Simard et al. 2007) and in black spruce (*Picea mariana* [Miller] BSP), to more
52 frequent negative growth anomalies (Drobyshev et al. 2010).

53 Both trembling aspen (*Populus tremuloides* Michaux) and black spruce are ecologically
54 and economically important components of the Clay Belt vegetation cover (Gagnon et al.,

55 1998). Climatically induced changes in species performance may therefore have
56 substantial effects on the ecology and economics of the region (Payette and Filion 2010).
57 Climate change may affect trees directly, through relationships between weather
58 conditions and physiological processes of growth and regeneration, but also indirectly
59 through directional changes in site conditions. One such site-level factor could be the
60 accumulation of SOL, which may modify the responses of trees to future climate.

61 Spruce and aspen often occupy the same sites in the boreal landscape of western Quebec
62 and the depth of the SOL may be an important determinant of the relative importance of
63 the two species on a given site. The presence of aspen is thought to be limited on sites
64 with a thick SOL, whereas spruce can grow over much broader gradient of SOL thickness
65 (Cavard et al., 2010). Variability in SOL is also observed at much smaller scales, i.e.,
66 within single stands, which may have implications for overall stand composition.

67 In this study, we were interested in understanding the role of SOL in affecting species
68 growth and distribution at single tree and landscape scales. Previous research has shown
69 considerable differences in spruce and aspen reactions to both average and extreme
70 climate variability (Drobyshev et al., 2013) and the important role that SOL also plays in
71 affecting climate-growth relationships in pure spruce stands of the lowland forests of
72 Quebec's Clay Belt (Drobyshev et al., 2010). In the current study, we examined the
73 effects of SOL on tree growth in the mixed boreal forest and expanded the scope of our
74 previous published research to two previously unstudied tree- and landscape-scales. First,
75 we hypothesized that at the tree scale, growth diminishes with a thicker organic layer and
76 the responses differ between species (Hypothesis 1). At the landscape scale, this effect
77 would differentially restrict species distributions to sites with a certain range of SOL.
78 Second, we hypothesized that the process of SOL accumulation changes climate-growth

79 relationships in both species (Hypothesis 2). Specifically, we suggested that trees
80 growing on a thicker organic layer would have a stronger positive response to
81 temperatures and would be less sensitive to variation in precipitation, whereas trees
82 growing on sites with thin SOL would be negatively affected by warmer and drier
83 growing seasons. Lastly, we linked the dynamic role of soil conditions in modifying
84 climate-growth relationships to the discussion of species- and site-specific responses to
85 climate change.

86 Methods

87 *Study area*

88 The study area (49°03'-49°29'N; 78°46'-79°09'W) is located in the black spruce-feather
89 moss (*Pleurozium schreberi* (Brid.) Mitten) bioclimatic domain of western Quebec and
90 the Northern Clay Belt of Quebec and Ontario (Fig. 1). Most soils in the Clay Belt are
91 derived from thick clay deposits that cover the Precambrian Shield. They were left by
92 proglacial Lake Barlow-Ojibway and presently they form a vast clay plain (Veillette et al.
93 2004). The topography of the study area is flat, with a mean elevation of 250 m to 300 m
94 above sea level, with occasional bedrock hills. Half of the glaciolacustrine deposits are
95 covered by thick layers of SOL, causing forest paludification. In the absence of
96 paludification, soils of the Clay Belt are mostly luvisols and gleysols (Comité d'experts
97 sur la prospection pédologique 1998).

98 During the winter, cold continental arctic air masses dominate the study area, whereas the
99 summer climate is influenced by moist Atlantic maritime tropical air and by dry maritime
100 arctic air. According to records from the La Sarre and Joutel meteorological stations
101 (1971-2000; 41 km south and 61 km northeast of the study area, respectively), mean

102 annual temperature of the area varies between 0.1 °C and 0.7 °C. Total annual
103 precipitation is about 890 mm, with 35% falling during the growing season and 30%
104 falling as snow. Although freezing air temperatures at ground level are common during
105 the growing season, the study area is not subject to permafrost (Brown and Gangloff
106 1980).

107 The area is dominated by black spruce stands with variable height and density. Jack pine
108 (*Pinus banksiana* Lambert) and aspen are common to the region, growing in pure stands
109 or in mixed stands with black spruce. Wildfire is the main natural disturbance factor in
110 the black spruce-feather moss domain. The fire cycle in the region has increased in
111 length, from about 100 years prior to 1850 AD, to 360 years since 1920 AD (Bergeron et
112 al., 2004). Spruce and aspen colonize sites following fire and the relative importance of
113 spruce increases with greater depths of SOL (Lecomte and Bergeron 2005).

114 Eastern spruce budworm (*Choristoneura fumiferana* Clem.) exerts relatively little effect
115 on spruce population dynamics in the study area, compared to other parts of its range
116 (Gray 2008). The forest tent caterpillar (*Malacosoma disstria* Hübner) is an important
117 defoliator of aspen, but outbreaks in the study area are of short duration and relatively
118 low amplitude, occurring less frequently than south of 49°N (Cooke and Lorenzetti 2006;
119 Huang et al., 2008). Sampled stands were dominated by black spruce and aspen basal
120 area (BA) never exceeded 30% of stand BA.

121 *Field data collection*

122 We used forest inventory data from the Lake Matagami Lowland ecoregion (ecoregion
123 6a, Fig. 1), which had been gathered by the Quebec Ministry of Natural Resources
124 (MNRQ) in 1996. A total of 1309 circular permanent sampling plots (PSP) of 400 m²

125 were sampled every 250 m along 1.5 km transects in the ecoregion. In each PSP, all trees
126 with a diameter greater than 10 cm at breast height were identified and their frequencies
127 were tabulated into 2 cm-wide diameter classes. Subplots of 40 m² area were used to
128 identify and measure trees with a diameter < 10 cm. SOL thickness was assessed through
129 visual examination of the soil profile on a representative point within each of the sampled
130 stands, following the standard protocol of the Ministry of natural resources of Quebec
131 (MRNQ 1994). Specifically, estimation of SOL thickness was based on the examination
132 of soil density, colour, and texture.

133 Our dendrochronological and soil sampling reflected our interest in tree level effects of
134 micro-site conditions on climate-growth relationships. For logistical reasons, we worked
135 within sites in the field, but we considered trees (rather than sites) as single sampling
136 units. We obtained data on growth and corresponding soil properties for each of the
137 sampled trees, avoiding any data aggregation to the site level.

138 During 2008 and 2009, we sampled ten mixed black spruce and aspen stands that have
139 developed on soils of varying SOL thickness (Table 1, Fig. 1). The sites were distributed
140 within the following three sub-areas: Villebois (VIL), Selbaie (SEL), and Wawagosisic
141 (WAW). Although average SOL thickness at each site varied between 2.41 and 15.55 cm
142 (Table 1), sampled trees were found on SOL thicknesses ranging from 1 to 23 cm.

143 In each of the ten sites, we established 10 to 19 circular 0.063 ha plots, the number of
144 which depended upon the availability of aspen and black spruce trees on the site (total
145 $n_{\text{plots}} = 145$; Table 1). A plot was positioned around a living and healthy looking aspen
146 tree and encompassed at least one of the canopy spruces. Thus, one aspen and one black
147 spruce tree (nearest to the aspen tree) were sampled per plot. All aspens were canopy

148 dominants, while the spruce trees were in co-dominant positions. For each of the selected
149 trees, two cores were extracted from opposite sides of the trunk (i.e., at 180° degrees to
150 one another), at 30 cm above the ground surface. This stump height, rather than breast
151 height (1.3 m), was selected for the collection of more precise age data.

152 For both datasets (MNRQ data and newly sampled sites), no data were available on aspen
153 origin, although it is likely that considerable proportion of aspen trees in both datasets
154 were of seed origin. Two lines of evidence support this suggestion. First, the selected
155 stands were post-fire regenerated and were dominated by spruce prior to last fire. Second,
156 in field we observed aspen as stand-alone trees not growing in clumps, which otherwise
157 could indicate regeneration through sprouting. An unpublished study (Bergeron et al,
158 unpublished data) on aspen post-fire regeneration at a site within our study area indicated
159 that more than a half (59%) of the canopy aspen trees originated from seeds. A
160 considerable proportion of sprouting in aspen regeneration was likely due to ability of
161 aspen roots to survive fires, especially in clay-rich soils which are characteristic of the
162 study region. We believe that this proportion generally hold in sites of the current study.

163 *Climate data*

164 Dendroclimatic analyses utilized climate data generated in BioSIM 10.0 (Régnière 1996),
165 which is a set of spatially-explicit bioclimatic models that use a database of climate
166 station records at daily resolution. For each sampling site, we interpolated data from the
167 ten closest weather stations and adjusted for differences in latitude, longitude, and
168 elevation between weather stations and the site location. Given the density of
169 meteorological stations was lower during the first half of the 20th century, the mean
170 distance between stations and the sampling sites decreased since that time (from 400 km

171 to < 200 km). Due to short distances between sites within each of the three sub-areas
172 (usually < 20 km), we aggregated climate data for each of three sub-areas (SEL, VIL and
173 WAW, Fig. 1) by averaging data from the respective sites. Climate variables included
174 monthly mean temperature (°C), monthly total precipitation (mm), total degree-days (> 5
175 °C), and cumulative degree days, which were calculated by summing degrees exceeding
176 the 5 °C mean daily temperature. Also, we calculated Monthly Drought Code (MDC),
177 considering the period from May to October and using monthly maximum temperature
178 and seasonal precipitation amounts.

179 *Soil data and analyses*

180 In summer 2009, SOL volumetric moisture (m^3/m^3) was measured at the interface
181 between SOL and the mineral soil surface at 10 randomly selected points on each site.
182 Measurements were taken at an average depth of 6.2 cm and were performed using a soil
183 moisture sensor (ThetaProbe ML2x, Delta-T Devices, Cambridge, UK), from which the
184 apparent dielectric constant of the substrate was determined. Five measurements were
185 taken at every point and the two most extreme values were later excluded to calculate a
186 mean SOL moisture content for the plot.

187 Soil temperatures were recorded by thermochron data loggers (iButton DS1921G, Maxim
188 Electronics, Dallas, TX) that were placed between the SOL and mineral soil in 30 plots of
189 different sites that were distributed along the SOL thickness gradient. The 30 data loggers
190 recorded soil temperature every 255 minutes for 12 months (August 2009 to August
191 2010).

192 We dug three pits that were about 20 cm away from each of the sampled trees, measured
193 SOL thickness (cm), and sampled both the organic layer (SOL) and mineral soil for

194 analyses. The mineral soil was sampled from 5 to 15 cm below the interface between the
195 SOL and mineral soil. To determine mineral soil texture, we conducted a particle size
196 analysis ($n_{\text{samples}} = 290$). Portions of three soil samples that had been taken around each
197 tree were composited, air-dried, and sieved to pass a 2 mm mesh screen. The texture of
198 the resulting fine earth fraction (percentage sand, silt and clay) was determined using the
199 hydrometer method of Bouyoucos (Carter 2008). Water content of the field-moist mineral
200 soil was determined gravimetrically by drying subsample at 105 °C to constant mass
201 (Topp 1993).

202 Remaining portions of SOL samples were sieved to pass a 4 mm-mesh screen, and oven-
203 dried at 40 °C for 60 h. We determined total carbon (C, %), total nitrogen (N, %), total
204 sulphur (S, %), total phosphorus (P, %), and pH in 0.1 M CaCl₂, following protocols
205 (Laganière et al. 2010) that were established by the Soils Laboratory of the Laurentian
206 Forestry Centre, Canadian Forest Service (Québec City, QC).

207 *Tree-ring data*

208 The tree cores and cross-sections were prepared and measured following standard
209 dendrochronological methods (Cook and Kairiukstis 1990). The samples were first
210 mounted in wooden blocks, sanded, and visually cross-dated using the skeleton plot
211 method (Stokes and Smiley 1968). Ring-widths were then measured using a Velmex
212 micrometer (Velmex Incorporated, Bloomfield, NY) controlled by TSAP-Win
213 Professional (version 0.55, Rinntech, Heidelberg, Germany) at a precision of 0.01 mm.
214 Data quality was validated in the program COFECHA (Grissino-Mayer 2001).

215 To obtain tree-ring chronologies with amplified high frequency variability, the series
216 were detrended in the ARSTAN program (Cook and Krusic 2005), using a 32-year cubic

217 smoothing spline with a 50% frequency response. By dividing the original chronology
218 values by the predicted values, the ring widths were transformed into index values. To
219 remove temporal autocorrelation, the series were prewhitened by autoregressive
220 modeling. Residual single-tree chronologies were computed to analyze climate-growth
221 relationships in single trees of both species (black spruce, $n = 145$; aspen, $n = 143$).

222 *Statistical analyses and hypothesis testing*

223 To test Hypothesis 1, the effect of SOL thickness on spruce and aspen distributions at the
224 landscape level was tested with forest inventory data. We regressed basal area ($\text{m}^2 \text{ha}^{-1}$)
225 of each species against SOL thickness that had been measured in every PSP. To further
226 test the hypothesis, we examined the effect of SOL thickness on the absolute basal area
227 increment (BAI) in a regression analysis with cumulative BAI over the last 25 years
228 (1982 through 2008), using BAI and soil thickness data that were collected at the level of
229 single trees in our study sites. To avoid a confounding effect of age on SOL, we removed
230 the youngest (< 60 -years-old) and oldest (> 100 -years-old) trees from our dataset, which
231 tended to grow on very thin or thick SOL, respectively. In our dataset, two “independent”
232 factors (tree age and SOL) exhibited strong interdependence, with Pearson product-
233 moment correlation (r) coefficients approaching 0.7 (for spruce, $r = 0.66$; for aspen, $r =$
234 0.67). These r values directly pointed to the difficulty in separating the unique effects of
235 SOL and tree age using the entire data set. Even when considering one of the variables as
236 a covariate, the analysis still faced a problem of collinearity (Kleinbaum et al. 2008).
237 Limiting the range of tree ages considerably reduced the strength of the age-SOL
238 thickness relationship (spruce: $r = 0.28$; aspen: $r = 0.20$) and reduced the total dataset by
239 32 % in the case of spruce and by 31% in the case of aspen.

240 We calculated residuals from the age versus BAI regressions to fully remove age effects.
241 These tree-specific residuals were then regressed against SOL, using a linear mixed-
242 effects model with location parameter (defined at the level of sub-areas - Selbaie,
243 Villebois, and Wawagasic) as a random variable in the R package *nlme* (Pinheiro and
244 Bates 2000). To compare the strength of SOL effect on BAI between two species we
245 evaluated *b* coefficients representing the slope of the respective regression lines. We
246 applied Mann-Whitney U-tests (Hollander and Wolfe 1999) to the bootstrapped (Efron
247 and Tibshirani 1993) distributions of *b*. We performed bootstrapping in the R package
248 *boot* (Canty 2002) and used the R function *wilcox* to calculate Mann-Whitney U-test
249 statistics.

250 To test Hypothesis 2, we first used response function analyses to identify significant
251 relationships between climate variables and the tree-ring chronologies and, second,
252 assessed the effects of SOL on these relationships. The initial set of climate variables
253 included mean monthly temperatures and monthly total precipitation spanning from May
254 of the previous year to August of the current growth year, the thermal sum above 5 °C (in
255 degree-days), and seven composite climate variables. The composite variables included
256 seasonal Monthly Drought Codes (MDC) for four periods (June-August of the previous
257 year, September-October of previous year, April-May of current year, June-August of
258 current year) and three seasonal precipitation amounts (September-November for the
259 previous year, December-March, April-May).

260 The response functions were calculated between single-tree residual chronologies and
261 climate variables in the software package DendroClim 2002 (Biondi and Waikul 2004).
262 Significance of the response function coefficients was tested at the 0.05 level through
263 bootstrapping. Since the coefficients were obtained through principal component analysis

264 (PCA), they represented a unique contribution of single climate variables to the climate-
265 growth relationships.

266 We regressed SOL thickness, which was available for each sampled tree, against
267 correlation coefficients for the growth of that tree versus the climate variables, which
268 showed significant response function correlations with at least 10% of spruce or aspen
269 trees. The rationale for selecting such a low cut-off value was our concern that climate-
270 growth relationships might have been strongly affected by the range of the SOL gradient
271 that was covered by the current study. In other words, a small percentage of trees
272 showing a significant response may not adequately reflect the SOL effect within a larger
273 geographical context due to the fact that the sampled gradient in SOL thickness was
274 smaller than the one observed in the study region. Lack of significant effect in this study,
275 therefore, may be a result of sampling strategy which did not cover a wider gradient.

276 Selection of a low cut-off value was therefore intended to address this issue, while still
277 providing for filtering of the initial set of variables.

278 To avoid dependency of correlation coefficients on a particular setup of response function
279 analysis, we used Spearman rank correlation coefficients (r_s) to regress them against SOL
280 thickness. In addition, we also considered that in the absence of fire, SOL thickness may
281 increase over time at different rates (Simard et al. 2007) and, therefore, the recorded SOL
282 thickness might not adequately represent retrospective differences in SOL among trees.

283 To minimize this effect, the correlations were calculated for 1982-2007, i.e., the most
284 recent 25 years with both available climate and tree-ring data. In doing this, we
285 considered SOL as a temporally stable characteristic of tree growth condition and used it
286 as an independent variable in regression analyses. We therefore assumed that SOL

287 thickness was stable over the analyzed period (1982-2007) and was equal to the value
288 that was measured during field sampling.

289 Results

290 *Soil characteristics*

291 SOL thickness was significantly correlated with soil chemical properties (Table 2). In
292 particular, sites with thicker SOL had lower pH and both higher C/N ratio and soil
293 moisture. Mineral soil texture, expressed as percentages of sand, silt and clay, did not
294 exhibit a significant correlation with SOL thickness. To relate SOL accumulation to the
295 soil properties and to identify the main sources of variability in the soils data, we
296 included 10 soil variables and tree age in a principal component analysis (PCA). The
297 PCA used only trees with a complete set of measured variables ($n = 284$).
298 PCA used a correlation matrix and the values normalized to z-scores, since the variables
299 were expressed in different units and across different numerical scales. The first four
300 principal components (PCs) that were extracted from the data had eigenvalues > 1.0
301 (Kaiser's criterion) and accounted for 77.8% of variation in the dataset. The first two PCs
302 explained 28.4% and 19.9% of the total variance, respectively (Fig. 2).

303 The PCA confirmed the pattern that was previously observed between SOL and mineral
304 soil variables in correlation and regression analyses. SOL thickness was closely
305 associated with low values for both pH and N content, and tended to be associated with
306 heavier soils, as reflected by the similar loadings of the SOL and clay content of the
307 mineral soil on the PC1.

308 Average annual soil temperature varied between 2 and 6 °C, and June temperatures varied
309 between 2.5 and 12.5 °C (Fig. 3, Fig. SI1 in the *Supplementary Information*). The SOL

310 thickness was negatively related to mean soil temperature (Fig. 3A), although this effect
311 was not significant ($p = 0.095$). The SOL thickness had no effect on minimum annual soil
312 temperature (Fig. 3B, $p = 0.489$), but was strongly and negatively correlated to the
313 maximum soil temperature (Fig. 3C, $p < 0.001$).

314 *SOL thickness influence on tree distribution and BAI*

315 The effect of SOL thickness on species distributions across the landscape, as revealed by
316 analysis of the MRNQ dataset, was more evident for aspen than for spruce (Fig. 4).

317 Spruce was present on sites with SOL thicknesses that were up to 100 cm in depth,
318 whereas the distribution of aspen was limited by a threshold value of about 30 cm depth.

319 At the tree scale, a negative effect of SOL on BAI was absent in spruce BAI ($p = 0.980$),

320 whereas it was strong and significant in aspen ($p < 0.001$, Fig. 5). Bootstrapping of b

321 coefficients ($n = 1000$) revealed that 95% of their values fell between -0.631 and 0.115

322 for spruce, and between -4.63 and -2.80 for aspen. Consequently, the estimated slope

323 coefficients for the two species were significantly different (Mann-Whitney z value 12.2,

324 $p < 0.001$).

325 *Dendroclimatic analyses*

326 Spruce generally showed a positive response to current spring temperature, and a
327 negative response to May temperatures of the previous year and to summer temperatures

328 in the current year (Fig. 6). June precipitation of the previous year was positively

329 correlated with spruce growth, whereas wetter conditions in May had a negative effect.

330 For aspen, the two most important factors were June temperature of the current year (a

331 positive correlation) and August precipitation of the previous year (a negative response).

332 Aspen growth was positively related to drier August in the previous year, a wetter spring

333 in the current year, as indicated by significant effect of MDC for April-May, and the sum
334 of accumulated temperatures during the current growing season.

335 Correlations between growth and the selected climate variables, calculated for single
336 trees, were regressed against SOL thickness measured at these trees, using location as
337 random variable. We used only climate variables that were significant for at least 10% of
338 the response function analyses that were performed on single trees (Fig. 6). For spruce,
339 SOL thickness was significantly related to December temperatures recorded in the
340 previous year and was almost significant with respect to March precipitation of the
341 current year (Table 3, Fig. 7). However, the regressions explained a small amount of
342 variability in respective correlation coefficients ($< 10\%$, Table 3). All regressions
343 revealed a tendency for the correlation coefficient to decline with an increase in SOL
344 thickness.

345 For aspen, two variables showed significant relationship with SOL thickness: current year
346 January temperature and current year MDC for July-August. Linear regression explained
347 more variation in aspen than in spruce, with R^2 values ranging between 13 and 15%
348 (Table 3). Significant regressions indicated an increasingly positive effect of January
349 temperature and summer aridity along the gradient of increasing SOL thickness.

350 Discussion

351 Although being regularly acknowledged, the variability in tree response to climate has
352 often been difficult to quantify, partly because of variation in microsite conditions at the
353 scale of single trees. In this study, we analyzed the effects of succession-driven change in
354 the soil organic layer (SOL) to address these methodological issues, by using data
355 collected at the tree-level. We identified two spatial levels at which SOL variability

356 affected spruce and aspen populations. Landscape level (10^4 to 10^5 ha) analysis indicated
357 negative effects of increased SOL for both species, confirming our first hypothesis. SOL
358 thickness limited the distribution of trembling aspen, as this tree species was rarely found
359 in the stands growing on SOL that was more than 30 cm thick. SOL effects on black
360 spruce distribution were less apparent, although 76% of spruce stands were located on
361 sites where the thickness of SOL did not exceed 30 cm. In the case of spruce, the 30 cm
362 threshold, which appeared as a change in the slope of cumulative function (Fig. 4), was
363 likely an effect of sampling bias. The inventory data were collected in forest stands that
364 had been deemed to be productive according to criteria that were established by the
365 MRNQ. Aspen trees are characteristic of productive sites (typically understood to be
366 stands with at least 30 m^3 per ha of wood volume), while spruce is present on both
367 productive and non-productive sites. Consequently, a change in response at the 30 cm
368 SOL thickness might represent a shift towards non-productive habitats, which would be
369 then underrepresented in the MRNQ dataset.

370 Two factors appeared important in limiting aspen abundance on sites with high SOL: (a)
371 difficulties with initial establishment of seedlings, and (b) sub-optimal conditions for
372 biomass accumulation, possibly leading to increased mortality rates. Since no stand
373 history data were available for the sites in the Matagami region, we could not evaluate the
374 effect of SOL on initial aspen establishment, although our field observations and
375 published results from other studies (Johnstone and Chapin 2006; Belleau et al. 2007;
376 Shenoy et al. 2011) have strongly pointed to the importance of this factor. In a study of
377 seedling survivorship rates in North American boreal trees, trembling aspen exhibited the
378 strongest negative relationship between SOL thickness and survivorship, compared to
379 seedlings of black spruce, lodgepole pine (*Pinus contorta* ssp. *latifolia* Engelmann

380 Critchfield), and jack pine (Table 4 in Greene et al. 2007). Origin of aspen regeneration
381 did not appear important in this context. Accumulation of SOL will likely have a negative
382 effect on aspen recruitment whether through limiting seed establishment or through
383 reducing sucker initiation in sites prone to waterlogging (Maini and Horton 1964; Green
384 et al. 2006).

385 At the level of single trees ($\sim 10^{-3}$ ha), SOL thickness had no effect on spruce basal area
386 increment (BAI), but showed a strong and negative correlation with BAI in aspen (Fig.
387 5). We can explain this pattern by the greater sensitivity of aspen to SOL variability and
388 by the limited gradient in SOL thickness. Over the larger SOL gradients and on larger
389 spatial scales, the accumulation of SOL has been previously shown to cause declines in
390 spruce productivity (Landhäusser et al. 2001; Simard et al. 2007).

391 Species specific responses to increasing SOL thickness were likely driven by changes in
392 physical and chemical properties of the soils (Table 2, Fig. 2; Oechel and Van Cleve
393 1986; Lavoie et al. 2007; Simard et al. 2007, 2009). SOL accumulation causes the water
394 table level to rise and soil temperature to decrease (Fig. 3; Oechel and Van Cleve 1986).
395 With respect to changes in chemical properties, SOL accumulation led to general soil
396 acidification and increased C/N ratios (Table 2, Fig. 2). Differences in SOL effects on the
397 two species, in turn, were probably related to differences in root system response to
398 changes in SOL. Black spruce has a shallow root system, which is mostly located within
399 the uppermost 20 cm of organic horizons. As organic matter accumulates, spruce will
400 form new adventitious roots, which maintain tree nutrient uptake (Burns and Honkala
401 1990a; Krause and Morin 2005). In contrast, aspen is characterized by a root system that
402 is deeper than that of black spruce, the development of which is strongly influenced by
403 both the physical and chemical properties of the soil (Burns and Honkala 1990b).

404 SOL accumulation also led to lower soil summer temperatures (possibly through changes
405 in soil moisture, Fig. 3), which might add to differences in species response to SOL.
406 Spruce and aspen have different optimum temperatures for root growth, with the
407 temperature optimum for black spruce being lower than that for aspen (viz., 16 °C vs. 19
408 °C, Peng and Dang 2003). A comparative study of seedling performance in aspen and
409 white spruce (*Picea glauca* (Moench) Voss) had shown that decreased soil temperatures
410 lowered root growth in spruce, but had no effect on its leaf and shoot growth and
411 assimilation. In contrast, aspen seedlings that had been similarly subjected to decreased
412 soil temperatures exhibited a decline in overall assimilation rates, and leaf and shoot
413 growth, and cessation in root growth (Landhäusser et al. 2001).

414 We propose that the 30 cm SOL thickness threshold affecting aspen distribution may be a
415 result of an abrupt change in soil properties with the increase in water table height above
416 the mineral soil surface (Simard et al. 2007). The elevated water table would
417 subsequently submerge root systems, potentially inducing anaerobic conditions which
418 would eventually cause the death of the roots (Kozłowski 1997). The relationship
419 between SOL thickness and aspen distribution might have also reflected a negative effect
420 of aspen litter on the accumulation of organic matter (Légaré et al. 2005). However, we
421 did not consider this effect as being important in the current study since our results
422 indicated that aspen rarely grew on thick SOL and that its regeneration appeared to be
423 limited by thick SOL accumulations.

424 *Climate sensitivity of radial growth*

425 Our results demonstrated differences in response to climate for spruce and aspen growing
426 on the same sites, supporting our second hypothesis. The two main differences were

427 growth reactions to spring and summer temperatures. Spruce exhibited a positive
428 response to spring temperatures and a negative response to summer temperatures (Fig. 6),
429 suggesting a positive effect was accrued by an earlier onset of the growing season, while
430 drought conditions during summer imposed a negative effect. In turn, aspen showed a
431 positive response to summer temperatures, indicating the importance of summer warmth
432 for various physiological processes.

433 For spruce, annual variations in radial growth were influenced by early-winter, spring and
434 growing season temperatures. It was difficult to interpret the link between SOL and the
435 temperature-growth relationship for December of the previous year (Fig. 7), which was
436 probably related to an effect of SOL on the root temperature regime and to differences in
437 rooting depth along SOL gradient. Positive effects of increasing spring temperatures,
438 which were also demonstrated in pure spruce stands (Drobyshev et al. 2010), were likely
439 caused by an early onset of photosynthesis and, in turn, a longer growing season (Chen et
440 al. 1999, Baldocchi et al. 2005). Finally, negative correlations with current summer
441 temperatures, together with positive effects of June precipitation in the previous year,
442 indicated that black spruce might suffer from drought stress during the summer, a pattern
443 that was suggested earlier for pure spruce stands in the Clay Belt region (Drobyshev et al.
444 2010). The shallow root system of black spruce, which was confined to the unsaturated
445 surface layers of SOL (upper 20 cm), apparently tended to dry out more rapidly than the
446 underlying mineral soil during summer drought-prone conditions (Rothwell et al. 1996).
447 Interestingly, low summer temperatures (*Supplementary Information*, Fig. S11) generally
448 did not appear to limit black spruce growth.

449 For aspen, a positive growth response relative to June mean temperature dominated the
450 pattern of climate-growth relationships (Fig. 6). A late autumn in the previous growing

451 season may decrease the frost resistance of aspen (Lapointe-Garant et al. 2010) due to
452 late activation of mechanisms responsible for such resistance, e.g. changes in levels of
453 abscisic acid and dehydrins (Welling et al. 2002). Similar effect of increased autumn
454 temperatures has been shown to be important in silver birch (*Betula pendula* Roth,
455 Puhakainen et al. 2004). A positive influence of both June temperature and degree-days
456 for the current growing season suggested that trembling aspen growth might be limited by
457 the temperature sum during the physiologically active part of the year. In our study
458 region, a number of important physiological processes occur in aspen during June,
459 including budburst, and root, leaf and shoot growth (Fahey and Hughes 1994;
460 Landhäusser et al. 2001, 2003; Fréchette et al. 2011). June is the period of leaf extension
461 in this species (Zhai et al. 2012) and it has been shown that spring temperatures are
462 crucial in affecting carbon fixation of aspen forests in Canada (Chen et al. 1999).

463 *Effects of SOL on growth response to climate*

464 SOL modified the response of spruce and aspen to climatic variability over the observed
465 gradient of SOL thickness (1-26 cm), supporting our second hypothesis and suggesting
466 that both species biology and microsite properties controlled tree response to climate. Our
467 results further suggested that a statistically significant relationship between a given
468 climate variable and growth may only occur over a limited portion of the respective
469 gradient, a finding which highlighted the dynamic nature of climate-growth relationships
470 in mixed spruce-aspen forests. The effect of SOL thickness on climate-growth
471 relationships, however, appeared limited with only moderate amounts of variability in
472 correlation coefficient being accounted for (Table 3). Effects of SOL accumulation on
473 growth responses may be more visible during the period of anomalous climate conditions.
474 A previous study has demonstrated a positive relationship between SOL thickness and the

475 frequency of negative growth anomalies (negative pointer years) in pure spruce stands of
476 Quebec Clay belt (Drobyshev et al. 2010).

477 In spruce, the gradient in SOL thickness explained more than 5% of variability for only
478 two analyses, which involved December temperatures of the previous year and March
479 precipitation of the current year. In particular, trees on shallow SOL showed a positive
480 response to December temperatures of the previous year, whereas trees on deeper SOL (>
481 15 cm) tended to show a negative response (Fig. 7). Lower winter temperatures may have
482 been associated with elevated risk of frost damage to the roots. An increase in SOL
483 thickness would then translate into more effective insulation of the roots (Bigras 1997;
484 Gornall et al. 2007), thereby largely offsetting the positive effect of elevated
485 temperatures. Direct measurements of soil temperatures (Fig. 3), however, did not
486 support this assumption, as minimum soil temperatures were not related to SOL thickness
487 (Fig. 3B). We speculate that minimum soil temperatures might have been controlled by
488 variation in snow cover, which is spatially unrelated to SOL thickness.

489 A trend towards an increasingly negative effect of March precipitation on increasing SOL
490 was the most pronounced effect of SOL thickness for spruce trees. We can relate the
491 observed effect to the tree water balance at the start of the growing season and to the
492 onset of the growing season. Higher amounts of March precipitation, which would imply
493 greater accumulations of snow, likely improved water availability for trees on low SOL,
494 which dried more rapidly in spring and would subject trees to greater soil water deficits
495 later in the growing season (Hofgaard et al. 1999). Microsites with thick SOL apparently
496 experienced greater water availability (as it might be suggested by a greater accumulation
497 of SOL itself), diminishing the importance of the link between spring snow accumulation
498 and soil water deficit later in the season.

499 In aspen, SOL effects had greater explanatory power than in spruce, generally indicating
500 a greater sensitivity of this species to SOL accumulation. It remains unclear as to what
501 was the mechanism causing the effect of SOL on the relationship between growth and
502 January temperature. A significant regression with summer MDC (Table 3, Fig. 7)
503 suggested that greater spring or summer aridity tended to have an increasingly positive
504 effect along the SOL thickness gradient. We can explain this effect by greater aridity
505 decreasing water saturation of the soil profile. Water saturation may have promoted
506 hypoxic conditions, which would result in mortality of aspen roots (Kozlowski 1997).
507 Our results indicated that aspen, unlike spruce, generally avoided moisture-saturated
508 soils. Apart from aspen's greater sensitivity to waterlogging, the observed pattern might
509 have been due to variation in soil nutrient conditions. On drier sites, organic matter
510 decomposes at higher rates (Davidson and Janssens 2006; Domisch *et al.*, 2006), which
511 might also benefit aspen growth.

512 *Conclusion - species- and site-specific response to climate change*

513 Complex growth responses to annual weather present a challenge for interpretation of
514 future climate impacts on vegetation in the Québec Clay Belt. Three possible pathways of
515 climate impact on future growth and distribution of trees include (a) direct effects on
516 growth, (b) indirect effects through changes in soil conditions, and (c) indirect effects
517 through changes in natural disturbance regimes. The relative importance of these effects
518 is still not clear; however, soil conditions appear to play a crucial role across the whole
519 range of potential interactions between tree growth and climate. Overall, future climatic
520 changes will probably shift the relative abundance of these species. Since the thickness of
521 SOL plays an important role in controlling tree growth, we would not expect future

522 climate to cause spatially large and temporally dramatic changes in regional vegetation
523 cover, as has been predicted in some studies (Malcolm *et al.*, 2005). Under conditions of
524 increasing SOL accumulation, the dominance of spruce over the aspen will likely
525 increase, whereas we would expect an increased proportion of mixed stands in the
526 landscape with declining SOL thickness. In case climate conditions favour northward
527 expansion of aspen's distributional range, soil conditions may limit these dynamics.

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- 745

746 **Table 1.** Characteristics of sampled sites distributed within three sub-areas: Selbaie
 747 (SEL), Villebois (VIL), and Wawagosic (WAW). Means and standard deviations are
 748 given for SOL (Soil Organic Layer) thickness, pH, and C/N ratio. pH and C/N values are
 749 given for the part of the soil profile located within 5 and 15 cm below the interface
 750 between the SOL and mineral soil.

Site	Geographic coordinates	Mineral soil texture class	SOL thickness, cm	pH _{CaCl2}	C/N ratio	Number of plots
SEL1	N 49.47, W 79.02	Clay	15.55 ± 3.84	3.59 ± 0.38	36.0 ± 8.55	10
SEL2	N 49.38, W 79.03	Clay	4.49 ± 1.22	4.12 ± 0.50	31.1 ± 2.91	16
SEL3	N 49.32, W 79.08	Clay loam	2.45 ± 0.80	4.19 ± 0.28	25.0 ± 2.07	10
VIL1	N 49.05, W 79.13	Clay	9.05 ± 2.68	2.97 ± 0.16	40.4 ± 7.90	19
VIL2	N49.05, W 79.11	Clay	5.07 ± 1.28	4.18 ± 0.42	28.6 ± 1.91	19
VIL3	N 49.10, W 79.15	Clay loam	2.84 ± 1.30	4.05 ± 0.31	24.0 ± 2.40	18
VIL4	N 49.10, W 79.15	Sandy loam	2.57 ± 0.91	3.62 ± 0.22	24.9 ± 1.61	10
WAW1	N 49.22, W 79.78	Clay	12.25 ± 3.55	2.98 ± 0.21	43.7 ± 1.57	17
WAW2	N 49.17, W 79.80	Clay	4.29 ± 0.97	4.25 ± 0.23	24.8 ± 2.93	15
WAW3	N 49.18, W 79.78	Clay	2.41 ± 0.67	4.33 ± 0.21	20.62 ± 1.57	11

751

752

753 **Table 2.** Spearman correlations (r_s) among soil variables at the level of single trees.

754 Values of C, N, S, and P were percentages by mass (see *Methods* section for details).

755

Variables	Organic layer								Mineral soil		
	SOL thickness	SOL vol. moisture	C	N	C/N	S	P	pH _{CaCl2}	Water content	Clay	Silt
SOL vol. moist.	0.31										
C	0.45	0.22									
N	-0.42	0.01	0.27								
C/N	0.70	0.14	0.41	-0.73							
S	-0.29	0.07	0.38	0.89	-0.56						
P	-0.16	-0.18	0.09	0.12	-0.08	0.12					
pH _{CaCl2}	-0.68	-0.08	-0.43	0.50	-0.78	0.30	0.03				
Water content	0.16	-0.44	0.18	-0.08	0.22	-0.01	0.15	-0.29			
Clay	0.08	-0.06	0.00	-0.28	0.28	-0.26	0.05	-0.04	0.13		
Silt	0.08	0.13	0.02	0.05	-0.05	-0.03	-0.12	0.13	-0.55	-0.10	
Sand	-0.13	-0.05	-0.02	0.19	-0.19	0.23	0.04	-0.06	0.28	-0.73	-0.61

756

757 SOL vol. moist. – volumetric moisture of soil organic layer, C - total carbon, N - total

758 nitrogen, S - total sulphur, P - phosphorus, water content - mineral soil water content;

759 Clay, Silt, and Sand - percentages of clay, silt, and sand in mineral soil, respectively.

760 Correlations in boldface type are significant at $p < 0.05$, $n = 288$.

761

762 Table 3. Summary of linear mixed-effects models of SOL thickness versus regression
 763 slope coefficients (b) representing climate-growth relationships in black spruce and
 764 trembling aspen. Listed climatic variables significantly affected the growth of at least
 765 10% of trees in each species (see Fig. 6). “Temp”, “Prec”, and “Prev” indicate monthly
 766 average temperature, total monthly precipitation, and previous growing season,
 767 respectively. Results are for trees that are 60- to 100-years-old, for the period 1982-2007.
 768 Significant regressions, indicated in bold, are presented graphically in Fig. 7.

Variable	b	p	R^2
<i>Picea mariana</i> , $n = 96$			
Temp prev. May	$-5.17 * 10^{-3}$	0.259	0.034
Temp prev Dec	$-1.12 * 10^{-2}$	0.043	0.077
Temp April	$9.72 * 10^{-3}$	0.119	0.000
Temp June	$4.02 * 10^{-3}$	0.513	0.012
Temp July	$-2.88 * 10^{-3}$	0.652	0.000
Prec prev June	$-1.11 * 10^{-2}$	0.064	0.016
Prec prev Aug	$-2.71 * 10^{-3}$	0.634	0.007
Prec March	$-1.15 * 10^{-2}$	0.053	0.092
Prec May	$8.56 * 10^{-3}$	0.108	0.000
MDC April_May	$-9.75 * 10^{-4}$	0.820	0.000
Snow cover prev Sept-Nov	$3.82 * 10^{-4}$	0.938	0.000
<i>Populus tremuloides</i> , $n = 98$			
Temp prev Nov	$1.51 * 10^{-3}$	0.809	0.019
Temp Jan	$1.66 * 10^{-3}$	0.003	0.146
Temp June	$-5.15 * 10^{-3}$	0.445	0.000
Temp Aug	$5.77 * 10^{-4}$	0.933	0.005
Prec prev Aug	$-6.31 * 10^{-3}$	0.412	0.137
MDC Apr-May	$1.16 * 10^{-2}$	0.100	0.134
MDC June-Aug	$1.64 * 10^{-2}$	0.043	0.130
Degree-days (above 5 °C)	$3.52 * 10^{-4}$	0.954	0.000

769 Figures

770 Fig. 1. The study was located within the Québec Clay Belt (indicated in grey in the map
771 insert) north of Rouyn-Noranda, in the Spruce-Moss Bioclimatic Domain. Study sites are
772 shown as open squares.

773 Fig. 2. Soil variable scores projected onto the first two principal components (PC1 and
774 PC2). The variables included tree age (Age), SOL thickness (SOL_thi), SOL volumetric
775 soil moisture (SOL_hum), total carbon (C), total nitrogen (N), carbon/nitrogen ratio
776 (C/N), total sulphur (S), phosphorus (P), SOL pH in CaCl₂ (pH), mineral soil water
777 content (Mineral_hum), and percentages of sand (Sand) and clay (Clay) in the mineral
778 soil. Amount of the variability in the dataset, explained by each axis, is shown at axis
779 captions of the respective.

780 Fig. 3. Effects of SOL on average summer temperature (A), minimum (B) and maximum
781 (C) soil temperature, and an example of soil temperature variability during 12 months
782 (D). For B and C, the data are the absolute maximum and minimum values recorded by
783 each sensor during its complete recording period. For D, the temperature records are from
784 two data loggers: T02 buried under 22 cm of SOL (black dotted line) and T17 buried
785 under 2.5 cm of SOL (solid grey line).

786 Fig. 4. Basal area (BA, m²/ha) of aspen (A) and black spruce (B) in the study plots,
787 plotted against SOL thickness (cm). A threshold of 30 cm SOL, in relation to aspen
788 distribution, is shown as a dashed line. Data are for the Lake Matagami lowland
789 ecoregion, Western Québec. Note the differences in scales of the vertical axis in the two
790 panels.

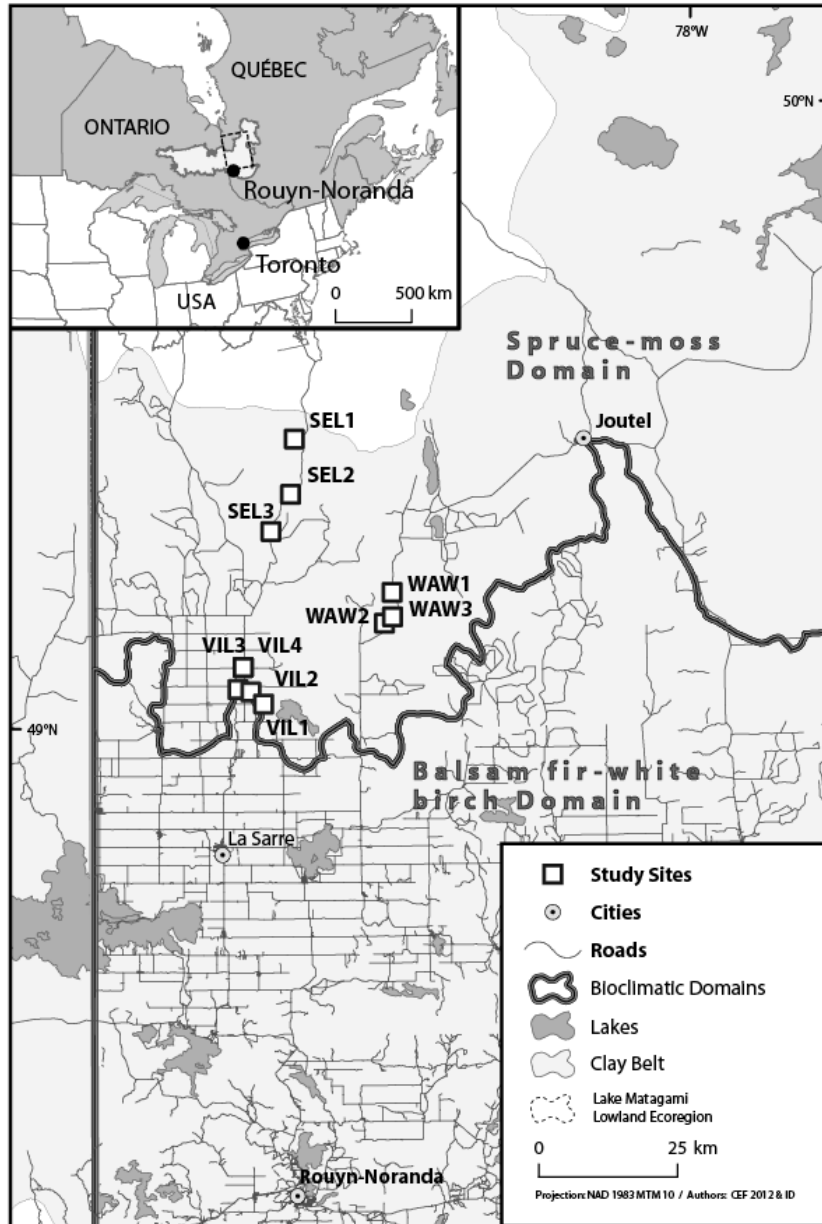
791 Fig. 5. Cumulative basal area growth index (Y) of black spruce and trembling aspen over
792 a 20-year period as a function of soil organic layer (SOL) thickness (X), adjusted for
793 differences in age, for black spruce (solid line) and trembling aspen (dashed line). Note
794 the logarithmic scale of the vertical axis.

795 Fig. 6. Proportions of spruce and aspen trees displaying significant positive (white bars)
796 and negative (black bars) response function coefficients for growth versus climate
797 variables ($n = 145$ trees). Monthly climate variables are mean temperature and total
798 precipitation from the previous May to August of the current growth year. Seasonal
799 climate variables are: monthly drought code (MDC) from previous June to previous
800 August, from previous September to previous October, from April to May, and from June
801 to August; precipitation from previous September to previous November, from previous
802 December to March, and from April to May; and total number of degree-days for the
803 previous year (DD-1) and for the current year (DD). The dashed line refers to the 10%
804 threshold used for including a variable in the regression with SOL thickness (Fig. 7).

805 Fig. 7. Interactions between climate-growth relationships, expressed as Spearman rank
806 correlations (r_s) between climate variables and radial growth, and SOL thickness for
807 black spruce and trembling aspen. Climate variables were selected through response
808 function analysis (Fig. 6). Significant ($p < 0.05$) correlations are indicated by white
809 circles, and non-significant ones, by black circles. Regression lines are shown for each
810 analysis. Presented climatic variables significantly affected growth of at least 10% of
811 trees in one of the species in response function analyses (see Fig. 6). Prefix “p” indicates
812 variables of the previous growing season. A summary of the analyses is given in Table 3.

813

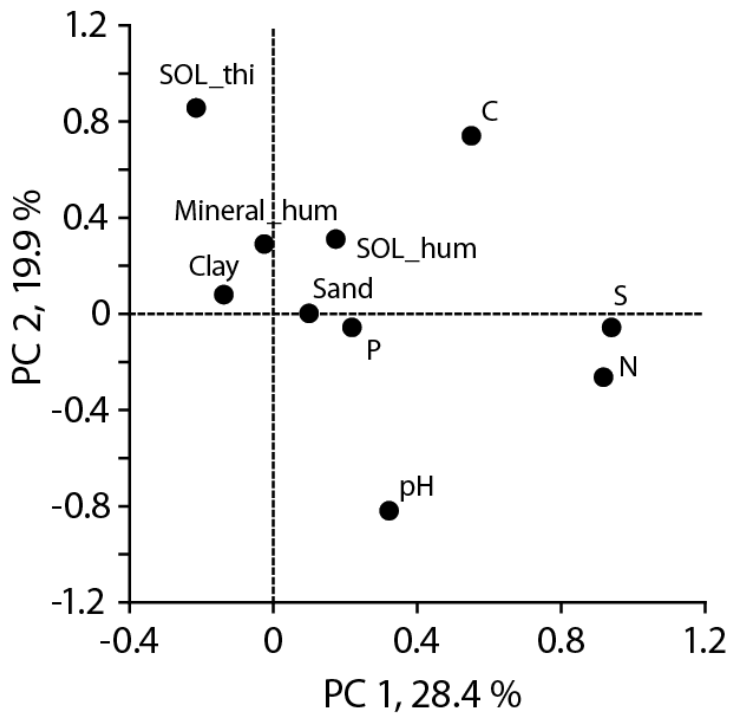
814 Fig. 1.



815

816 Fig. 2

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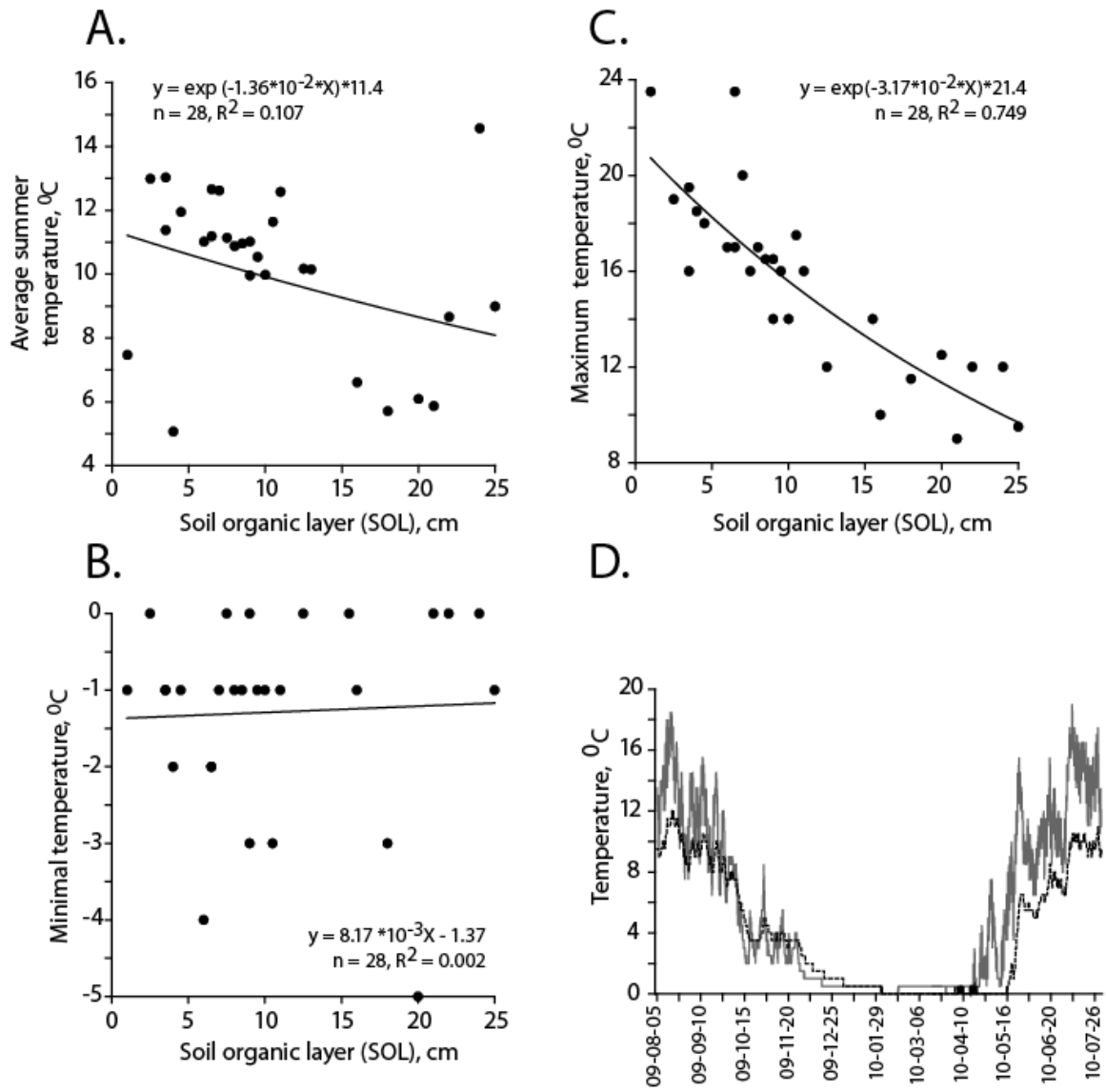


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820 Fig. 3.

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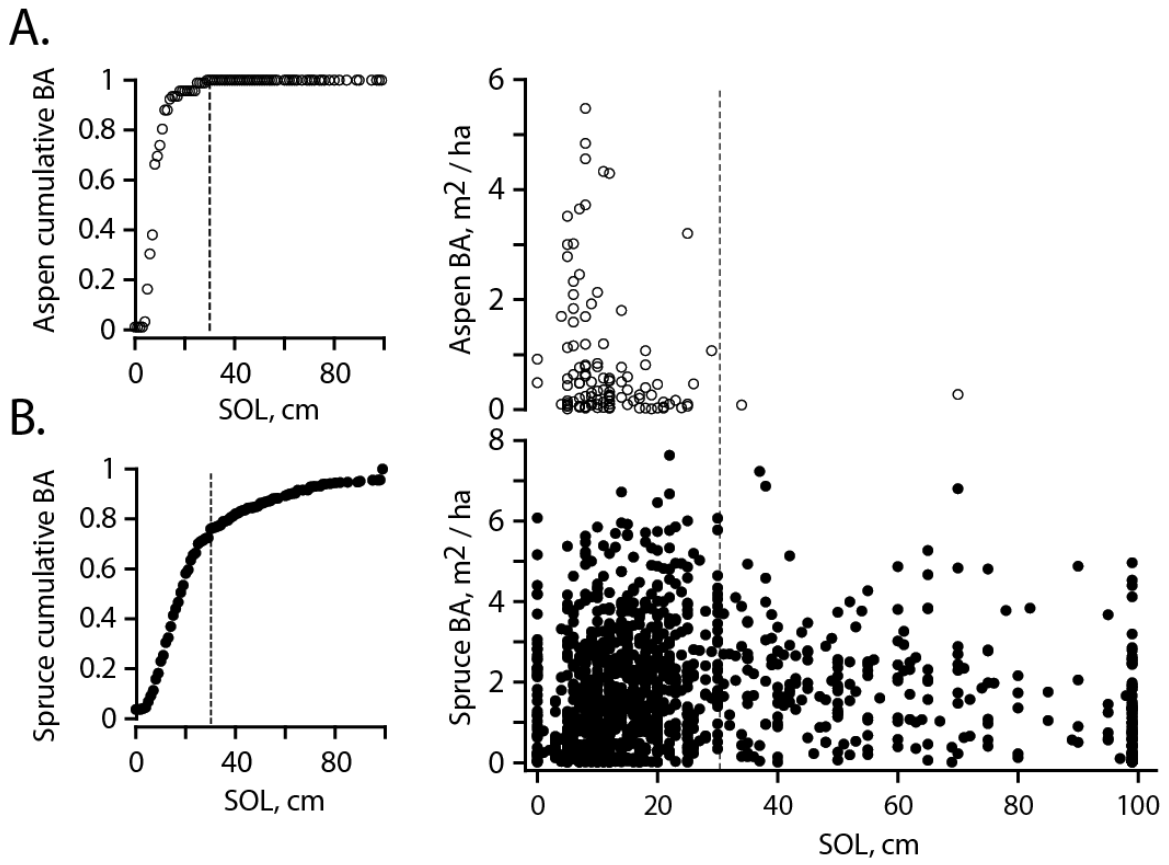
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823 Fig 4.

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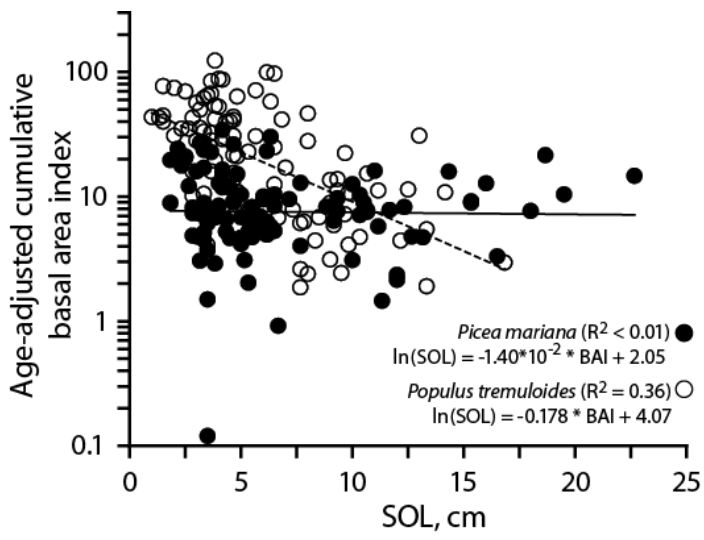


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828

829 Fig. 5.

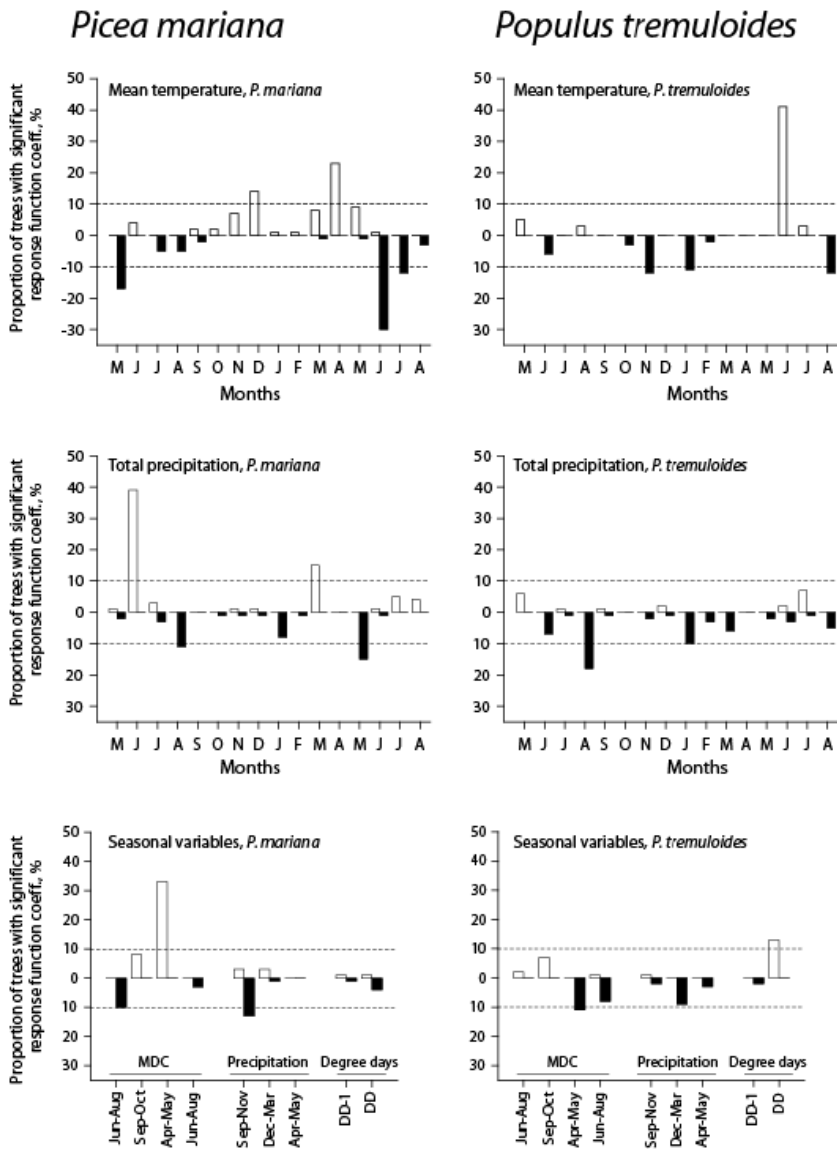
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831

832 Fig. 6.

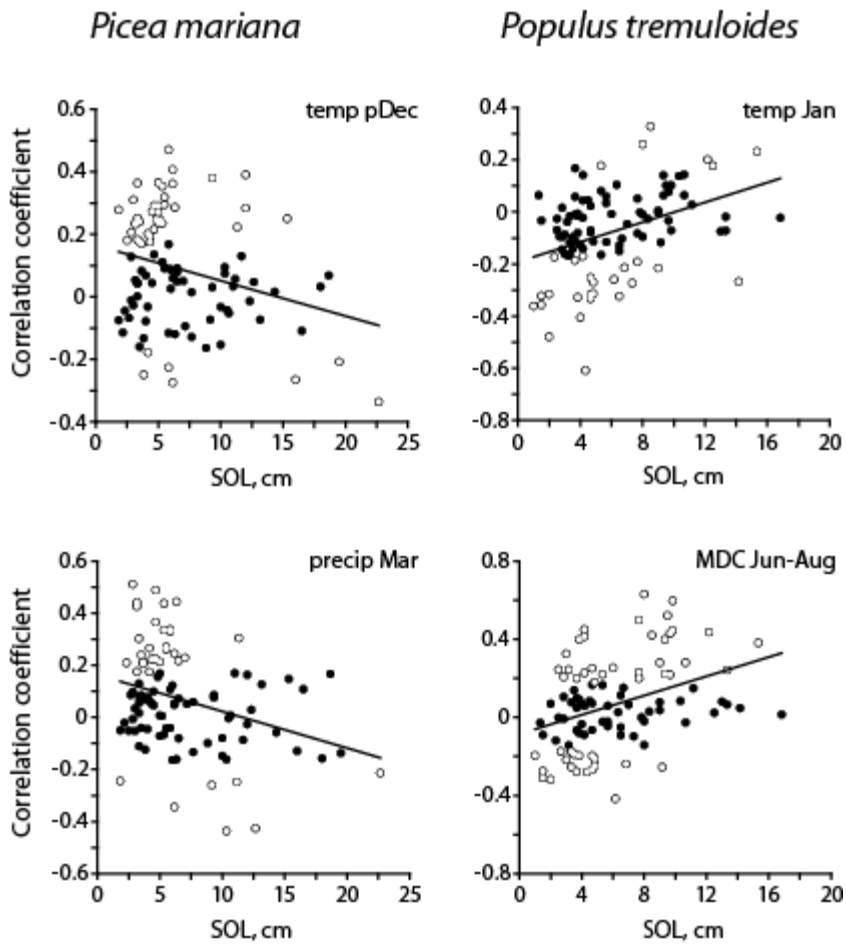
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834

835

Fig. 7.



836

Supplementary Information for the paper

Soil characteristics mediate distribution and response of boreal trees to climatic variability, by Gewehr et al.

Fig. S11. Distribution of annual and June temperatures measured by IButton sensors in the studied sites (see details in the *Methods* section).

