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4 **Title:** Connecting potential frost damage events identified from meteorological records to radial  
5 growth variation in Norway spruce and Scots pine

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21 **Author contributions:** SS had the main responsibility in planning the study, conducting the  
22 analysis and writing the manuscript. HH, HM and PN participated in planning the study. HH

23 advised in the statistical methods, SH advised in the tree-ring methods and TR advised in the  
24 frost damage issues. HM, PN, MT and SH provided the data. SS, HH, HM, PN, SH and TR  
25 contributed in writing the manuscript.

26 **Key message:** Conifer radial growth reductions may be related to unusual snow conditions or a  
27 mismatch between frost hardiness level and minimum temperature, but not typically to low  
28 winter temperature extremes.

29 **Abstract:** The aim of the study was to examine if temperature conditions potentially causing  
30 frost damage have an effect on radial growth in Norway spruce and Scots pine. We hypothesized  
31 that frost damage occurs and reduces radial growth after 1) extreme cold winter temperatures, 2)  
32 frost hardiness levels insufficient to minimum temperatures, and 3) the lack of insulating snow  
33 cover during freezing temperatures, resulting in increased frost and decreased temperatures in  
34 soil. Meteorological records were used to define variables describing the conditions of each  
35 hypothesis and a dynamic frost hardiness model was used to find events of insufficient frost  
36 hardiness levels. As frost damage is likely to occur only under exceptional conditions, we used  
37 generalized extreme value distributions (GEV) to describe the frost variables. Our results did not  
38 show strong connections between radial growth and the frost damage events. However,  
39 significant growth reductions were found at some Norway spruce sites after events insufficient  
40 frost hardiness levels and, alternatively, after winters with high frost sum of snowless days. Scots  
41 pine did not show significant growth reductions associated with any of the studied variables.  
42 Thus, radial growth in Norway spruce may be more sensitive to future changes in winter  
43 conditions. Our results demonstrate that considering only temperature is unlikely to be sufficient  
44 in studying winter temperature effects on tree growth. Instead, understanding the effects of

45 changing temperature and snow conditions in relation to tree physiology and phenology is  
46 needed.

47 **Keywords:** tree growth, tree-rings, frost damage, extreme value distributions, frost hardness

## 48 **1. Introduction**

49 During the last century, winter temperatures in northern Europe have increased more than the  
50 annual average temperatures (IPCC 2014, Mikkonen et al. 2015). The effects of climate change  
51 are not restricted to winter time temperature only. Changes in length of snow season, snow  
52 properties and soil temperatures have also been documented and these trends are likely to  
53 continue in the future (Venäläinen et al. 2001, Helama et al. 2011, Liston and Hiemstra 2011).

54 In northern Europe, growing season temperature is the main factor affecting annual variations of  
55 tree growth, while the effects of winter temperatures are considered to be minor (e.g., Briffa et  
56 al. 2002). However, contradicting results regarding the effects of winter conditions have been  
57 reported. For example, several studies on Norway spruce (*Picea abies* (L.) Karst.) have shown  
58 negative correlations between radial growth and winter temperatures, suggesting that years with  
59 cold winter temperatures are associated with higher radial growth (Jonsson 1969, Miina 2000,  
60 Mäkinen et al. 2000, Helama and Sutinen 2016). These patterns appear to be species-specific, as  
61 studies with Scots pine (*Pinus sylvestris* L.) have found positive or non-significant correlations  
62 between ring-width series and winter temperatures (Jonsson 1969, Miina 2000).

63 The mechanisms of how low temperatures are related to radial growth are not fully understood.  
64 Connections between frost events and reduced growth have been explained by changes in  
65 resource allocation for replacing the damaged tissues, as well as reduced resource collection  
66 (e.g., reduced photosynthesis due to needle damage), which could reduce growth in the following  
67 summer (Dittmar et al. 2006, Príncipe et al. 2017). However, trees growing in cold environments  
68 are adapted to harsh winters. Therefore, the relationship between low temperatures and tree  
69 growth is not likely to be linear. Instead, growth reductions can only be expected after extreme  
70 events that exceed the conditions trees are acclimated to. This poses a challenge on the research

71 methods, as classical statistical methods are not well suited for studying rare events (Katz et al.  
72 2005). Statistical distributions defined by the majority of observations near the center of the  
73 distribution are not likely to describe well the characteristics of the distribution tails (i.e., minima  
74 and maxima). The statistical theory of extreme values resolves this problem, as the generalized  
75 extreme value distributions (GEV) specifically describe the form of distribution tails (Gaines and  
76 Denny 1993, Coles 2001, Katz et al. 2005).

77 The study of extreme and rarely occurring events is challenging also from the biological point of  
78 view and identifying biologically meaningful extremes is not straightforward (Gutschick and  
79 BassiriRad 2003, Babst et al. 2012, Frank et al. 2015). Gutschick and BassiriRad (2003)  
80 suggested that extreme events should be defined based on the acclimation capacity of the studied  
81 organism. As organism's ability to tolerate extreme conditions typically changes in time, using  
82 purely environmental variables in defining the extremes is insufficient. For example, the  
83 potential damage caused by cold temperatures depends on the frost hardiness of tree tissues  
84 (Leinonen 1996, Hänninen 2016). Late frost events in spring, when the frost hardiness of trees  
85 has already decreased, are typical causes of frost damage, and have been linked to abrupt growth  
86 declines prior to tree death (Vanoni et al. 2016). Even though the occurrences of low  
87 temperatures are expected to decrease (IPCC 2014), some studies suggest that frost damage in  
88 trees may increase with warmer springs and larger temperature fluctuations (Cannell and Smith  
89 1986, Hänninen 1991, Augspurger 2013).

90 The effects of winter temperatures on boreal trees are mediated by the characteristics of the  
91 snowpack. As snow forms an insulating layer, lack of snow cover combined with freezing  
92 temperatures leads to low soil temperatures and deep soil frost (Groffman et al. 2001, Hardy et  
93 al. 2001). In both Scots pine and Norway spruce, severe soil frost conditions have been

94 connected to needle loss and reduced growth (Tikkanen and Raitio 1990, Kullman 1991, Solantie  
95 2003, Tuovinen et al. 2005). Helama et al. (2013) showed that low soil temperatures as well as  
96 deep snowpack in spring were associated with lower radial growth of Scots pine. Furthermore,  
97 artificially increased soil frost, especially if soil thawing in spring is delayed, has been found to  
98 be related to higher fine-root mortality (Gaul et al. 2008, Repo et al. 2014), reduced starch  
99 content in needles (Repo et al. 2011) and delayed growth onset (Jyske et al. 2012) in Norway  
100 spruce, as well as defoliation in Scots pine (Jalkanen 1993).

101 Our aim was to examine if exceptional temperature conditions, potentially causing frost damage  
102 to trees, have an effect on the radial growth of Norway spruce and Scots pine. In our analysis, we  
103 took into account both biological and statistical challenges in studying extreme events. We tested  
104 three hypotheses, suggesting that frost damage occurs and reduces radial growth after (1)  
105 extreme cold winter temperatures (TMIN), (2) insufficient level of frost hardiness compared to  
106 minimum temperatures (REL\_TMIN), and (3) lack of insulating snow cover during freezing  
107 temperatures, resulting in low soil temperatures (FROSTSUM). The first hypothesis represents a  
108 simple extreme in temperature, whereas the two latter hypotheses also consider physiological  
109 state of a tree and the processes of the studied system. We expect the results to differ for Norway  
110 spruce and Scots pine as previous results have shown different patterns for the two species.

## 111 **2. Material and methods**

### 112 ***2.1 Data***

#### 113 *2.1.1 Tree-ring data*

114 The tree-ring data used in the study was compiled from previously collected Norway spruce and  
115 Scots pine data sets. In all data sets, the sampled sites were located in national parks or other

116 unmanaged forests. In the Norway spruce data set, 47 stands were sampled from southern  
117 Finland to the Arctic spruce timberline (Fig. 1). At each site, one to two increment cores were  
118 taken at 1.3 meter height from up to 15 dominant trees. For a detailed description of the Norway  
119 spruce data set see Mäkinen *et al.* (2000) and Mäkinen *et al.* (2001). The Scots pine data set  
120 contained 20 sites in southern and northern Finland (Helama et al. 2013). The number of trees  
121 sampled per site ranged from 9 to 120, and one to two cores were taken from each tree.

122 Annual tree-ring widths were measured from all cores to the nearest 0.01 mm with a light  
123 microscope. Cross-dating of the ring-width series was performed visually and verified  
124 statistically using computer program COFECHA (Holmes 1983) and the *dplR* package (Bunn  
125 2010, Bunn et al. 2015) of R software (version 3.3.1, R Core Team 2016). The samples that  
126 could not be cross-dated were excluded from the data (see Supplement 1 for the final number of  
127 trees per site).

128 To remove trends related to tree age and stand dynamics, we standardized the ring-width series  
129 using a spline function with 50% frequency cut-off in 67% of the length of the tree-ring series  
130 (Cook and Peters 1981, Speer 2010). Ring-width indices (RWI) were then formed by dividing  
131 the measured ring-widths with the values of the fitted spline function, and temporal  
132 autocorrelation was removed with first-order autoregressive model. After this, site-wise average  
133 chronologies were formed by calculating annual averages from all trees at a site with Tukey's  
134 biweight robust mean. Chronologies were cropped to cover years 1922-1997 (common years of  
135 all chronologies).

### 136 *2.1.2 Weather data*

137 Daily mean and minimum temperatures from four weather stations in Finland and from Karasjok  
138 weather station in Norway (Fig. 1) were used. Years 1927 and 1945 had a lot of missing values

139 and were excluded from further analysis using the weather station data (Table 1). If daily mean  
140 temperature was not available, it was calculated from the individual temperature measurements  
141 and daily minimum temperatures using the equations of Finnish Meteorological Institute (FMI  
142 2016). Data from the closest weather station to each tree-ring site was used in the analysis (see  
143 Suppl. 1 for details).

144 In addition to weather station data, gridded data of snow depth and daily mean temperature were  
145 used (Aalto et al. 2016). This data set has a resolution of  $10 \times 10 \text{ km}^2$  and it is available from  
146 year 1961 onwards.

## 147 ***2.2 Defining potential frost damage events***

148 To test the hypotheses we used the weather data to define three variables describing conditions  
149 potentially causing frost damage to trees (referred to as “frost variables” from now on, Table 1).  
150 Minimum winter temperature (TMIN) was calculated as the minimum of daily minimum  
151 temperatures. Relative minimum temperature (REL\_TMIN) was calculated as the difference  
152 between the modelled daily frost hardiness and daily minimum temperature. The frost hardiness  
153 value describes the temperature in which 50% of needle area is damaged (Leinonen 1996, see  
154 section 2.3). Frost sum of snowless days (FROSTSUM) was used to describe the variation in soil  
155 frost between years. It was calculated as the sum of daily temperature averages below  $0 \text{ }^\circ\text{C}$   
156 during the days without snow cover. While TMIN and REL\_TMIN variables were calculated for  
157 each site by using the weather data from the closest meteorological station, FROSTSUM was  
158 calculated from the grid data (daily average temperature and snow depth), using the grid cell in  
159 which the site was located. As the grid data was only available from year 1961, the analysis  
160 using the FROSTSUM variable covered a shorter time period (1962 to 1997), whereas TMIN



161 and REL\_TMIN variables were available for the whole time period covered by the tree-ring  
162 chronologies (1922 to 1997, Table 1).

163 In all three variables, low values represent potentially damaging conditions to trees. For the  
164 TMIN and FROSTSUM variables, annual values covered a time period from previous year July  
165 to the growth year June, while in the REL\_TMIN variable only time period from January to May  
166 was considered (Table 1).

### 167 ***2.3 Frost hardiness model***

168 The daily level of frost hardiness was calculated with a dynamic needle frost hardiness model  
169 developed by Leinonen (1996) for Scots pine. The model output describes the temperature in  
170 which 50% of needle area would be damaged. The model uses daily mean and minimum  
171 temperature and night length as inputs to calculate the stationary frost hardiness, i.e. the target  
172 level of hardiness in the prevailing environmental conditions. The frost hardiness approaches the  
173 stationary level with the delay. Thus, the rate of change in frost hardiness is calculated from the  
174 frost hardiness of the previous day and the stationary level of frost hardiness (Fig. 2).

175 In order to use the model for Norway spruce, as well as different provenances of Scots pine, we  
176 made some modifications to the model. In Leinonen's model, the amount at which  
177 environmental conditions affect stationary frost hardiness is controlled by hardening competence  
178 (Fig. 2), which is determined from an annual cycle model with daily mean temperature as input.  
179 Hardening competence varies so that the effect of environmental conditions (i.e., daily minimum  
180 temperature and night length) on frost hardiness is strongest during the rest phase (hardening  
181 competence = 1) and weakest during active growth phase (hardening competence = 0). As  
182 different species and provenances within species have different annual cycles, we could not use  
183 the same annual cycle model for all of our sites. While Leinonen (1996) calculated frost

184 hardiness for each day of the year and modelled the full annual cycle dynamically, we decided  
185 only include a time period from January to May. Similar restriction to modelled time-period was  
186 used by Hänninen et al. (2001). We assumed that in the beginning of the year trees were in  
187 quiescence and that hardening competence was 0.9. These assumptions were based on studying  
188 the frost hardiness values calculated using Leinonen's original method with the full annual cycle  
189 model. By restricting the covered time period we were able to take into account different timing  
190 of spring phenology between species and provenances without reparametrizing the whole annual  
191 cycle model.

192 To account for the differences in spring phenology between Scots pine and Norway spruce, as  
193 well as different Scots pine provenances, we modified the parameter controlling spring  
194 dehardening based on previous results from provenance tests (Beuker 1994). In quiescent and  
195 active growth phases hardening competence is calculated using a parameter  $FU_{crit}$  that defines  
196 the amount of forcing units ( $FU$ ) needed to accumulate for bud burst to occur. We defined the  
197 value of  $FU_{crit}$  for different provenances of Scots pine and Norway spruce based on temperature  
198 sums (with 5 °C threshold) required for bud burst reported from provenance tests (Beuker 1994).  
199 First, we calculated the accumulation of  $FU$  from the beginning of year to the day that  
200 temperature sum reached the value required for bud burst in years 1950 to 2013. Then,  $FU_{crit}$   
201 was defined as mean of these annual  $FU$  values (Supplement 2).

202 As the frost hardiness value for each day is calculated based on the change from the previous  
203 day, we needed to define the frost hardiness level for January 1<sup>st</sup>. We did this by starting the frost  
204 hardiness modelling from the beginning of December, assuming the frost hardiness to be equal to  
205 the stationary frost hardiness in December 1<sup>st</sup> (Fig. 3).

## 206 **2.4 Defining extreme years – Generalized extreme value distributions**

207 Generalized extreme value distributions (GEVs) were used to define thresholds for identifying  
208 years with exceptional winter conditions to which the trees would not be well acclimated to. We  
209 fitted GEVs to the three frost variables separately in each weather station (or in each site for  
210 FROSTSUM variable), using the R package *extRemes* (Gilleland and Katz 2011).

211 For the TMIN and REL\_TMIN variables we fitted the GEVs with the block maxima approach,  
212 i.e. the variables represented an extreme within certain time window (Table 1). GEVs have three  
213 parameters, location parameter ( $\mu$ ), scale parameter ( $\sigma$ ) and shape parameter ( $\xi$ ). The shape  
214 parameter defines the shape of the distributions, so that  $\xi = 0$  corresponds to a light tailed  
215 (Gumbel) distribution,  $\xi > 0$  to a heavy tailed (Fréchet) distribution, and  $\xi < 0$  a bounded  
216 (Weibull) distribution (Coles 2001, Katz et al. 2005).

217 Since the FROSTSUM variable is a sum of conditions within a season, the block maxima  
218 approach was not applicable with it. Therefore, we chose to use a “peaks over threshold” (POT)  
219 approach, where the extreme value distribution is fit to values exceeding a chosen threshold.  
220 These values should have an approximate generalized Pareto (GP) distribution, with two  
221 parameters, scale ( $\sigma$ ) and shape ( $\xi$ ), which have same interpretations as with the GEV  
222 distributions. In this case  $\xi = 0$  corresponds to light-tailed (exponential) distribution,  $\xi > 0$  to a  
223 heavy tailed (Pareto) distribution, and  $\xi < 0$ , a bounded (beta) distribution (Katz et al. 2005).

224 The extreme value distributions typically handle maximum values, and as we were interested in  
225 the minima, all distributions were fitted to the inverse values of the original variables (see Katz  
226 et al. 2005). To account for the warming trend in temperatures, we tested including year as a  
227 covariate for the GEV parameters. In total, we tested three types of GEVs: 1) no covariates, 2)

228 year as a covariate for the location parameter, and 3) year as a covariate for location and scale  
229 parameters. We compared these three with Akaike Information Criteria (AIC, Akaike 1974), and  
230 selected GEVs without any covariates, as they had the lowest AIC values in a majority of  
231 weather stations (sites in FROSTSUM) for all frost variables.

232 In identifying the extreme years in each frost variables we used a ten year return level, defined  
233 from the extreme value distributions. The ten-year return level means that values lower than this  
234 level can be expected to occur on average once every ten years (Coles 2001). For the three frost  
235 variables, the ten year return level was calculated for each weather station (site in FROSTSUM)  
236 and each year exceeding this threshold was defined as an extreme year in the frost variable in  
237 question.

## 238 ***2.5 Statistical analysis***

239 We fitted two linear regression models separately to all site chronologies. With the first model  
240 (“dummy model”) we tested if RWIs were lower in years with low values of the three frost  
241 variables (i.e., values lower than the 10-year return level), while also taking into account the  
242 effect of summer temperature on radial growth. The first model was formulated as

$$243 \quad RWI_t = \beta_0 + \beta_1 SummerT_t + \beta_2 Frost\_RL10_t + \varepsilon_t, \quad (1)$$

244 where  $RWI_t$  is the value of RWI chronology in year  $t$ ,  $SummerT_t$  is the mean temperature of  
245 June (Norway spruce) or July (Scots pine) in year  $t$ , and  $Frost\_RL10_t$  is a dummy variable (0/1)  
246 describing whether the value of the frost variable (TMIN, REL\_TMIN or FROSTSUM) was  
247 lower than the 10-year return level in year  $t$ .

248 In the second model (“slope model”) we also included a continuous frost variable (TMIN,  
249 REL\_TMIN or FROSTSUM) and its interaction with the  $Frost\_RL10$  dummy variable to test if

250 the severity of the frost conditions was related to the radial growth variation. The second model  
251 was formulated as

$$252 \quad RWI_t = \beta_0 + \beta_1 SummerT_t + \beta_2 Frost\_RL10_t + \beta_3 Frost_t + \beta_4 Frost\_RL10_t Frost_t + \varepsilon_t, \quad (2)$$

253 where  $Frost_t$  was the continuous frost variable in year  $t$ . Logarithm transformations were tested  
254 for the continuous variables but they did not change the outcomes of the models. In both models  
255 the FROSTSUM variable was scaled to mean of zero and standard deviation of one in order to  
256 have the model coefficients in similar magnitudes as the other two frost variables. Correlations  
257 between explanatory variables in the models were low and in most cases statistically non-  
258 significant.

259 In order to test if the slope model had a better fit to the data compared to the dummy model, the  
260 models were compared with likelihood ratio test within each site (using R function *anova*). All  
261 analyses were conducted using the statistical software R (R Core Team 2016).

## 262 **3. Results**

### 263 ***3.1 GEVs and extreme year classification***

264 In the GEVs fitted to TMIN and REL\_TMIN variables, all shape parameters ( $\xi$ ) were negative,  
265 corresponding to a Weibull distribution. In FROSTSUM variable, the shape parameter values  
266 ranged from positive to negative, indicating different shapes of distributions at different sites (see  
267 Fig. 4 for examples).

268 The years classified as extreme years based on the GEVs were not identical at different weather  
269 stations (Fig. 5). However, in the TMIN variable several years were consistently classified as  
270 extreme years in several weather stations, for example 1940 (4 stations), 1956 (3 stations), 1966

271 (4 stations) and 1987 (3 stations). In the REL\_TMIN variable, there was more variation between  
272 the weather stations, whereas the extreme years for spruce and pine were very similar (Fig. 5).

273 In the FROSTSUM variable, gridded weather data was used instead of weather station data and,  
274 therefore, the GEVs were fitted for each site separately and the extreme years differed between  
275 sites (Fig. 6a). Per site, two to seven years were classified as extreme years (Fig. 6b).

### 276 **3.2 Connections between RWI and frost variables**

277 The connections between the frost variables and ring-width indices (RWI) showed different  
278 patterns for Norway spruce and Scots pine. In the Norway spruce dummy models, the extreme  
279 TMIN variable (i.e., *Frost\_RL10* in Eq. 1 with TMIN as frost variable) showed positive  
280 coefficients in the majority of sites (43 of 47 sites), and it was statistically significant in the 16 of  
281 the total 47 spruce sites (all significant coefficients in northern Finland, Fig. 7). This indicates  
282 that radial growth was in fact higher after winters with exceptionally cold minimum temperature.  
283 For Scots pine, none of the coefficients for extreme TMIN variable were significant in the  
284 dummy models (Fig. 7).

285 The extreme REL\_TMIN variable (i.e., *Frost\_RL10* in Eq. 1 with REL\_TMIN as frost variable)  
286 showed negative coefficients in the Norway spruce dummy models at 43 of the 47 sites (Fig. 5),  
287 suggesting lower radial growth in years in which minimum temperature had been exceptionally  
288 close to the modelled frost hardness levels. However, the coefficients were statistically  
289 significant only at two sites, located in northern and central Finland. In comparison, in the Scots  
290 pine models the three sites (of total 20 pine sites) where the REL\_TMIN coefficient was  
291 significant, but the effect was positive, indicating higher radial growth in those years.

292 The extreme FROSTSUM variable (i.e., *Frost\_RL10* in Eq. 1 with FROSTSUM as frost  
293 variable) showed negative coefficients in the Norway spruce dummy models at 33 of the 47 sites  
294 (i.e., lower growth in the years with exceptionally high frost sum of snowless days), but the  
295 variable was only significant in the models of seven sites (Fig. 5). For Scots pine, the  
296 FROSTSUM variable was not significant in the dummy models at any of the twenty sites.

297 In the slope models, positive coefficients for the frost variables during extreme years (sum of  $\beta_3$   
298 and  $\beta_4$  in Eq. 2) suggest that radial growth decreased with decreasing values of the frost  
299 variables. However, both positive and negative coefficients were found in sites where the  
300 likelihood ratio test showed a significant improvement compared to the dummy model. For  
301 Norway spruce, positive coefficients in slope models that significantly improved the dummy  
302 model fit were only found in the FROSTSUM model in six sites in northern Finland, and for  
303 Scots pine only at one site both in TMIN and FROSTSUM variables (Fig. 8). Slope models with  
304 negative coefficients (i.e. radial growth increasing with decreasing values of frost variables) were  
305 found at one Scots pine site in REL\_TMIN variable and at seven closely located Norway spruce  
306 sites in FROSTSUM variable (Fig. 8). In other cases the likelihood ratio test did not show  
307 significant improvement of model fit from the simpler dummy model.

## 308 **4. Discussion**

309 Our results did not show very strong connections between radial growth and the potential frost  
310 damage events defined using meteorological data. However, our hypotheses of reduced growth  
311 after events of insufficient level of frost hardiness (REL\_TMIN) and after winters with high frost  
312 sum of snowless days (FROSTSUM) were supported by the results from some of the Norway  
313 spruce sites. Reductions in radial growth were related only to those variables that took frost

314 hardiness or snow cover into account, whereas year with low minimum winter temperatures  
315 showed statistically significant growth increases at some sites. Therefore, our results highlight  
316 that, when studying winter climate effects on tree growth, physiological and other processes  
317 affecting the studied system need to be carefully considered instead of using purely  
318 environmental variables.

319 While the results for Norway spruce gave some support for our hypotheses about extreme  
320 relative minimum temperatures and frost sums of snowless days being harmful for growth during  
321 the following growing season, the results for Scots pine were generally statistically non-  
322 significant or even opposite to the original hypotheses. This agrees with our original expectation  
323 of between-species differences and is in line with previous studies (Jonsson 1969, Miina 2000).  
324 The different patterns found for the two species are likely to be related to differences in winter  
325 time physiology. For example, Beuker et al. (1998) reported weaker frost hardiness of Norway  
326 spruce buds compared to Scots pine, and Linkosalo et al. (2014) showed that Norway spruce  
327 photosynthesis was reactivated during warm winter spells more readily, whereas the cold  
328 inhibition of photosynthetic light reactions was stronger in Scots pine.

329 The results supporting our hypotheses were statistically significant only in a minority of study  
330 sites. Therefore, conclusions about the results should be made with caution. The differences in  
331 statistical significance between the sites may be at least partly related to the spatial variability of  
332 minimum temperatures and snow cover. Due to a need for long time series the distance between  
333 some study sites and the weather stations was rather large and, therefore, the weather data is  
334 likely to be less representative of the conditions at these sites (Fig. 1, Supplement 1). In addition,  
335 the resolution of the gridded data used for calculating FROSTSUM (10 x 10 km<sup>2</sup>) may hide  
336 local, more fine-scale variation in snow cover. Therefore, the used weather data may not



337 accurately describe the local conditions at the study sites, especially since minimum  
338 temperatures vary locally with topographic variation and proximity of water bodies (Jarvis and  
339 Stuart 2001). It is possible that the sites showing a significant effect of the frost variables on  
340 RWI are more sensitive to frost, due to factors that were not taken into account in the statistical  
341 analysis. The different results between sites may also be related to tree age. Tuovinen et al.  
342 (2005) showed that severe soil frosts in northern Finland in winter 1986-1987 did not affect  
343 radial growth in mature Scots pines (approx. 130 years), whereas younger trees (approx. 45  
344 years) showed increase in water stress for two years, as well as suppressed radial growth for 6 to  
345 7 years after the exceptionally harsh winter conditions.

346 The way our frost variables were defined limits the type of cases included in the analysis. For  
347 example, TMIN and REL\_TMIN variables only accounted for the lowest daily values within the  
348 season. However, especially in the case of TMIN it might have been also relevant to consider,  
349 for example, the length of longer time periods with low minimum temperatures. Winter  
350 conditions may also affect the growth of the following growing season in many ways that are not  
351 all included in our hypotheses. For example, warm winters may lead to respiratory losses,  
352 especially in Norway spruce, if trees initiate photosynthetic activity before sufficient availability  
353 of light (Linkosalo et al. 2014). This could be one potential mechanism behind pattern of higher  
354 radial growth after low winter temperatures, which was observed in this study, as well as in  
355 earlier studies (Jonsson 1969, Miina 2000, Mäkinen et al. 2000). However, more research would  
356 be needed to understand if this correlative pattern is related to the winter time conditions or some  
357 other factors.

358 To refrain from parametrizing the full annual cycle model and to reduce the potential  
359 uncertainties associated with it, we modelled frost hardiness only for a restricted time period

360 from January to May (see Hänninen et al. 2001 for similar approach). However, events of  
361 insufficient frost hardiness may occur also if temperatures drop before trees have developed  
362 adequate hardiness levels after the growing season (Sutinen et al. 2001). For example, Mikola  
363 (1952) suggested that autumn frosts were likely a major cause for the considerable growth  
364 reductions of Scots pine in the early 20<sup>th</sup> century in northern Finland. Therefore, our results do  
365 not cover possible frost damage events occurring outside of the chosen time-frame. Further  
366 development and parametrization of frost hardiness models would demand more studies on the  
367 topic.

368 The effects of snowpack on trees are more complex than accounted for in the FROSTSUM  
369 variable. Especially the timing of soil thaw may be influential to tree physiology and growth.  
370 Helama et al. (2013) showed that high soil temperature and low snow depth in spring, rather than  
371 in winter, are connected to increased Scots pine radial growth of the following growing season.  
372 Similarly, artificially delayed thawing of soil frost affected the physiology of mature Norway  
373 spruce trees (Repo et al. 2007, Repo et al. 2011) and Scots pine saplings (Repo et al. 2005, Repo  
374 et al. 2008). Physiological changes were more evident when increased soil frost was combined  
375 with delayed thawing than after increased soil frost alone (Repo et al. 2011, Martz et al. 2016).  
376 In further studies, the characteristics of snowpack need to be considered in more detail.

377 The frost hardiness model used in the study was originally developed to describe frost hardiness  
378 in Scots pine needles in central Finland, but it has later been used also for other tree species and  
379 locations (e.g., Morin and Chuine 2014). However, the parametrization of the model for new  
380 species and even other provenances is challenging (see Hänninen 2016). In this study, we used  
381 information of temperature sums needed for bud burst in different provenances of Norway  
382 spruce and Scots pine to calibrate the parameter that controls the changes in hardening

383 competence in spring. Despite these modifications, several parameters in the model are based on  
384 Scots pine data. Therefore, the model is likely to be less suitable for Norway spruce and also for  
385 Scots pine in northern Finland. It should also be noted, that the model describes the frost  
386 hardiness of needles, but phenology and frost hardiness differ between tree organs. For example,  
387 frost hardiness in plant roots is typically lower than in shoots (Sakai & Larcher 1987, Delpierre  
388 et al. 2016). In addition, the shape of the relationship between severity of frost damage and the  
389 difference of minimum temperature and frost hardiness is a sigmoidal curve, where the curve's  
390 slope parameter depends on frost hardiness (Leinonen 1996). Our analysis did not take this into  
391 account, as the REL\_TMIN variable only considered the difference between daily minimum  
392 temperature and the level of frost hardiness.

393 The use of the extreme value distributions enabled us to identify the thresholds for extreme  
394 events so that they would correspond to occurrence of extreme conditions that the trees are  
395 adapted to. However, the choice of the threshold used for classifying extreme years (return level  
396 of ten years) was partly driven by practical necessities. A ten-year reoccurrence rate for an event  
397 is rather high from an evolutionary point of view, and a use of a stricter classification threshold  
398 would have been ecologically justified. Yet, to analyse the existing data we needed to define the  
399 threshold so that the number of years classified as extreme years is sufficient. To overcome this  
400 issue, we fitted the slope model, where a more flexible model behaviour was allowed with the  
401 interaction of a continuous frost variable and the dummy variable describing if a year was  
402 defined as an extreme or not. Thus, the model covered a situation where the defined threshold  
403 was too low to represent a biologically meaningful extreme and, therefore, the reduction in RWI  
404 would increase with decreasing values of the frost variables. However, with the slope model also  
405 the number of years included in the analysis is a challenge, as the study period may not

406 necessarily contain years with truly extreme conditions in the studied variables. This is probably  
407 reflected to our results, where the slope model only supported our hypotheses on a few sites,  
408 mainly in the case of FROSTSUM variable in Norway spruce sites in northern Finland.

## 409 **5. Conclusions**

410 Our results show, that instead of extremely cold winters, Norway spruce growth is potentially  
411 reduced after events of insufficient frost hardiness or after winters with high sum of freezing  
412 temperatures without insulating snow cover. However, Scots pine growth reductions were not  
413 connected to any of the studied variables. Therefore, it seems that radial growth in Norway  
414 spruce may be more sensitive to variable winter temperatures compared to Scots pine.

415 Our results demonstrated that using purely environmental variables, such as minimum  
416 temperature, is unlikely to be sufficient in studying winter temperature effects on tree growth.  
417 Instead, understanding the effects of changing temperature and snow conditions in relation to  
418 tree physiology and phenology is needed.

419 The long time series of growth variation provided by tree-ring data is especially beneficial in  
420 studying rarely occurring events, such as frost events leading to tree damage. However, equally  
421 long time series of tree phenology data or frost damage observations are often not available.  
422 Similarly, long meteorological data records exists only for a limited number of weather stations  
423 and, thus, data on local climatic conditions at the study sites is typically lacking. Therefore, to  
424 understand the effects of changing winter conditions on tree growth, tree-ring studies should be  
425 combined with modelling approaches as well as physiological and experimental studies.

426 **Conflict of interest**

427 The authors declare that they have no conflict of interest.

428 **Acknowledgements**

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431 Drebs from the Finnish Meteorological Institute for providing us with pre-1960s weather data.

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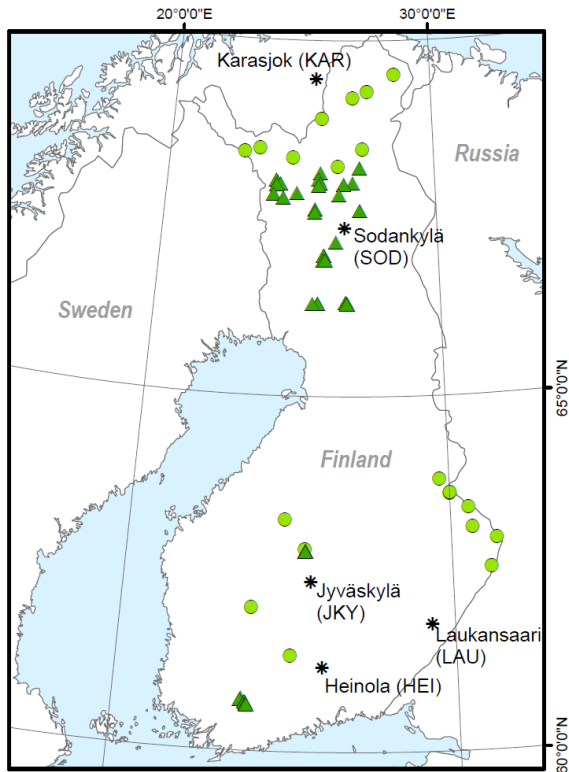
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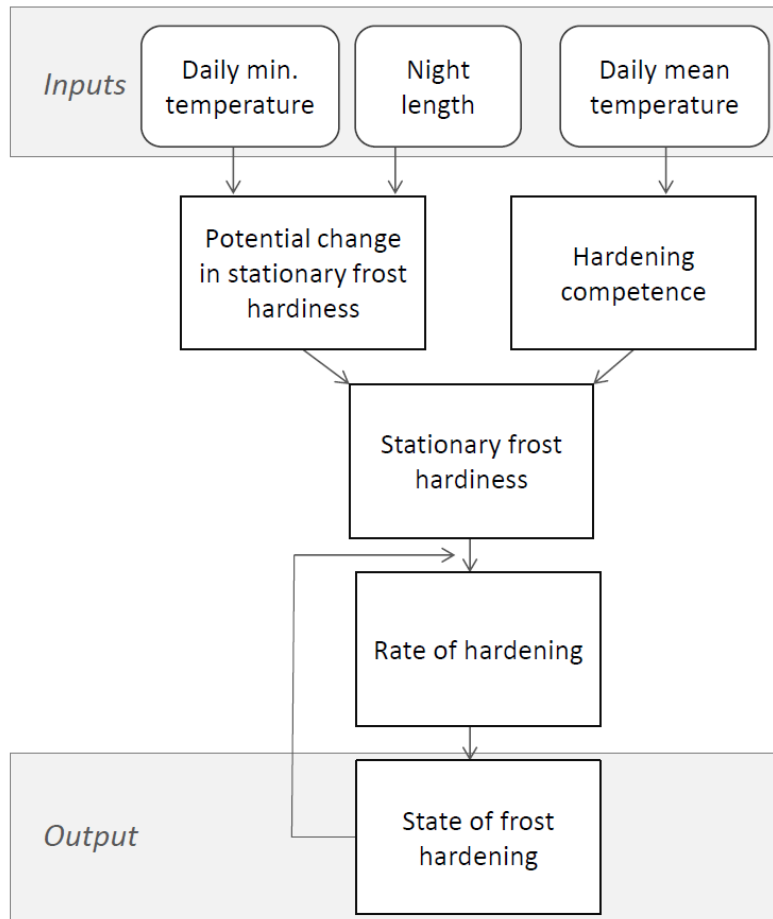
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599 **Figures**



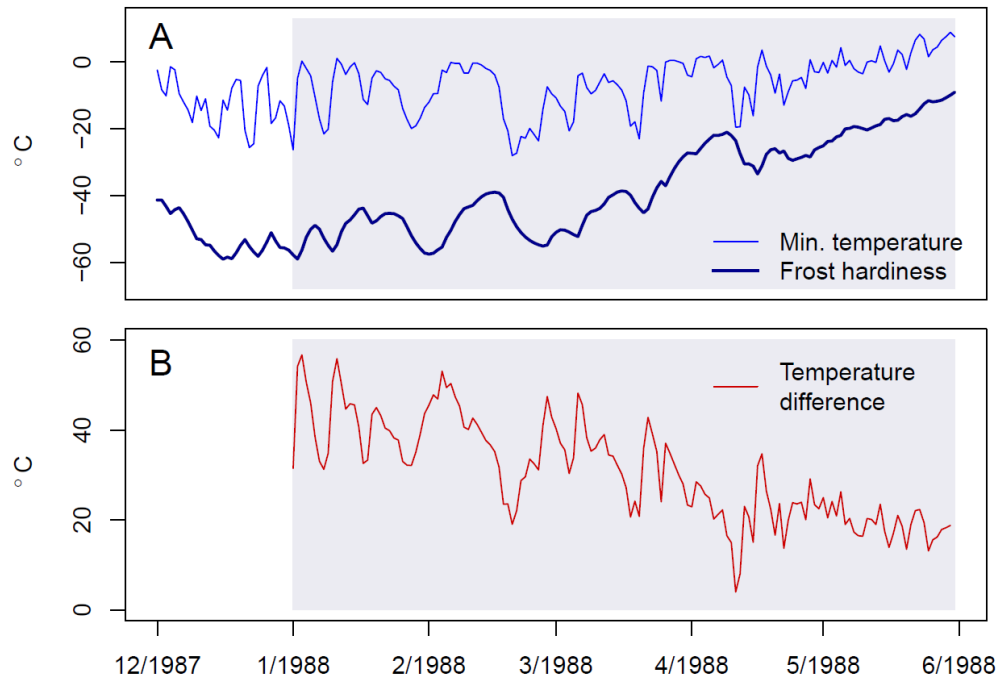
600 ● Scots pine sites ▲ Norway spruce sites \* weather stations

601 **Fig. 1** Locations of the Norway spruce (triangles) and Scots pine (circles) study sites and weather  
602 stations (asterisks). Note that some of the site symbols are on top of each other (especially the  
603 spruce sites in southern Finland).



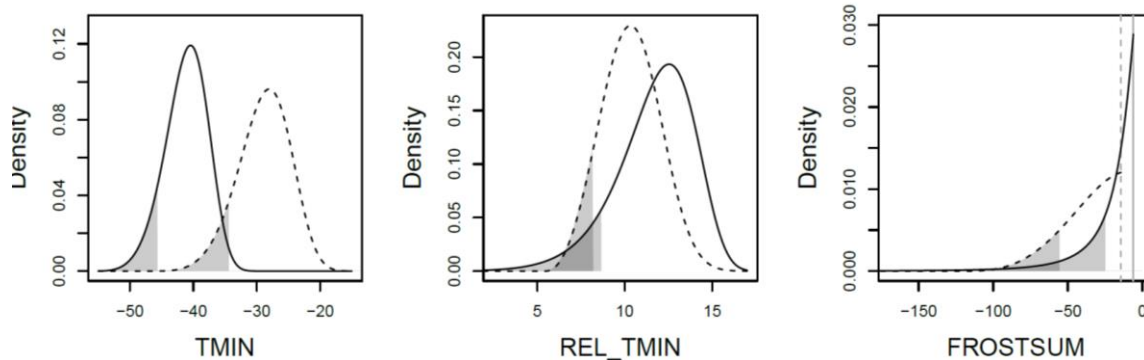
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605 **Fig. 2** Framework of the frost hardiness model (modified from Hänninen 2016). The model uses  
 606 daily minimum and mean temperatures, and night length to calculate daily level of frost  
 607 hardiness. A detailed description of the model can be found in Supplement 2.



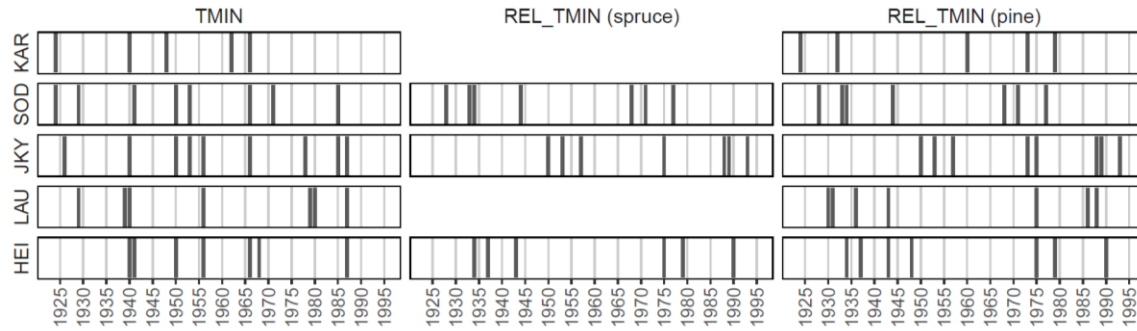
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609 **Fig. 3** Daily minimum temperature and modelled frost hardiness level (A) and the difference  
 610 between frost hardiness level and minimum temperature (B) in December 1987 to May 1988 at  
 611 Jyväskylä weather station. Year 1988 was classified as an extreme year for REL\_TMIN variable  
 612 in Jyväskylä, due to low value of REL\_TMIN (lowest difference in modelled frost hardiness and  
 613 minimum temperature in April). Only the time period from January to May (gray box) was used  
 614 for finding the REL\_TMIN variable, but frost hardiness was also calculated for previous year  
 615 December to find a suitable initial value for the beginning of January.



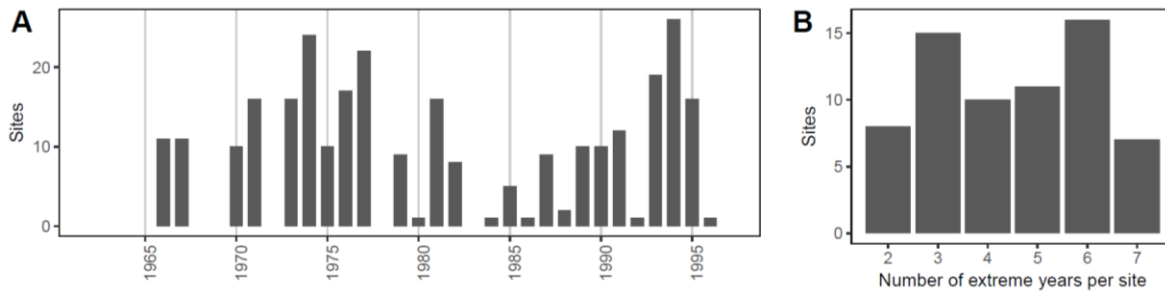
616

617 **Fig. 4** Examples of density functions of the GEV distributions for minimum winter temperature  
 618 (TMIN), minimum temperature in relation to modelled frost hardness (REL\_TMIN) and the  
 619 frost sum of snowless days (FROSTSUM). For TMIN and REL\_TMIN the GEVs of Karasjok  
 620 (solid line) and Heinola (dashed line) weather stations are presented. For FROSTSUM, example  
 621 sites from northern Finland (solid line, negative shape parameter) and southern Finland (dashed  
 622 line, negative shape parameter) are presented. The shaded areas demonstrate the values below  
 623 the 10-year return level. The vertical lines in the FROSTSUM subplot represent the thresholds  
 624 used in fitting the “peaks over threshold” distributions. Note that sub-figures have different  
 625 ranges of y-axis.



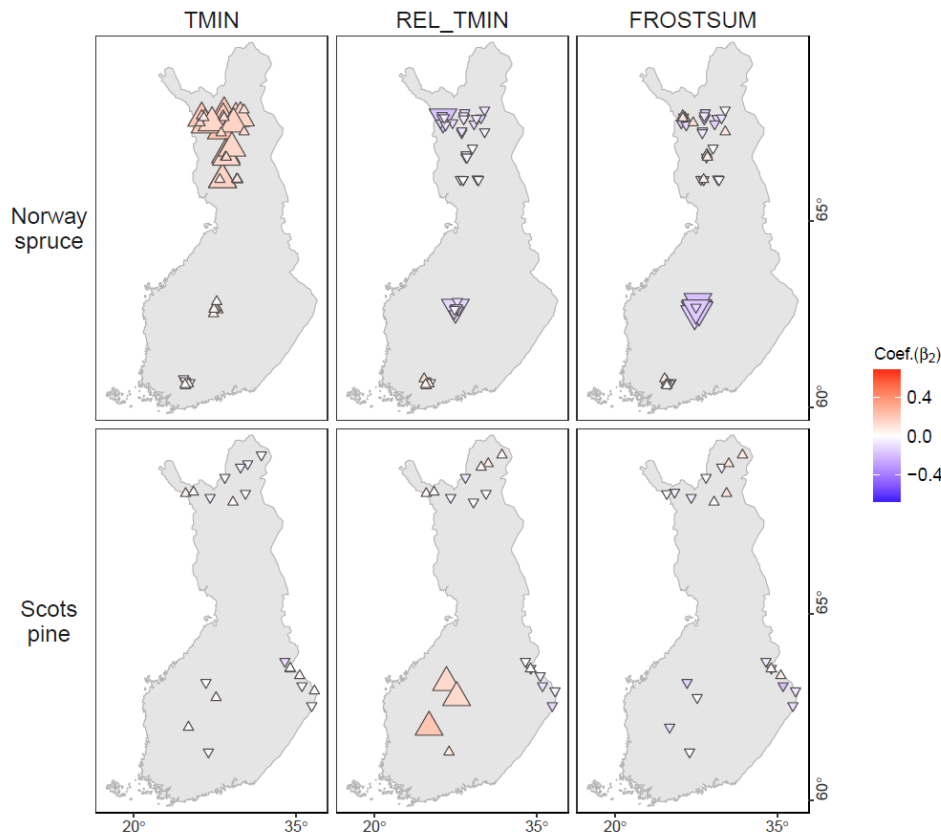
626

627 **Fig. 5** Years classified as extreme years (dark vertical bars) in the TMIN (minimum winter  
 628 temperature) and REL\_TMIN (minimum temperature in relation to modelled frost hardiness)  
 629 variables at each weather station. Names and locations of weather stations are shown in Fig. 1.  
 630 Extreme years in REL\_TMIN (spruce) are not shown for stations Karasjok (KAR) and  
 631 Laukansaari (LAU), as they were not used for any spruce sites (no spruce sites close to them, see  
 632 Fig. 1).



633

634 **Fig. 6** Number of sites in each year where FROSTSUM (i.e., the frost sum of snowless days)  
 635 variable was classified as extreme (A), and the distribution of total number of extreme years per  
 636 site (B). The FROSTSUM variable was derived from the gridded weather data for each site  
 637 separately



638

639 **Fig. 7** Coefficients and statistical significance of the frost variables in the dummy model (Eq. 1).

640 Small symbols represent statistically non-significant and large symbols significant coefficients ( $p$

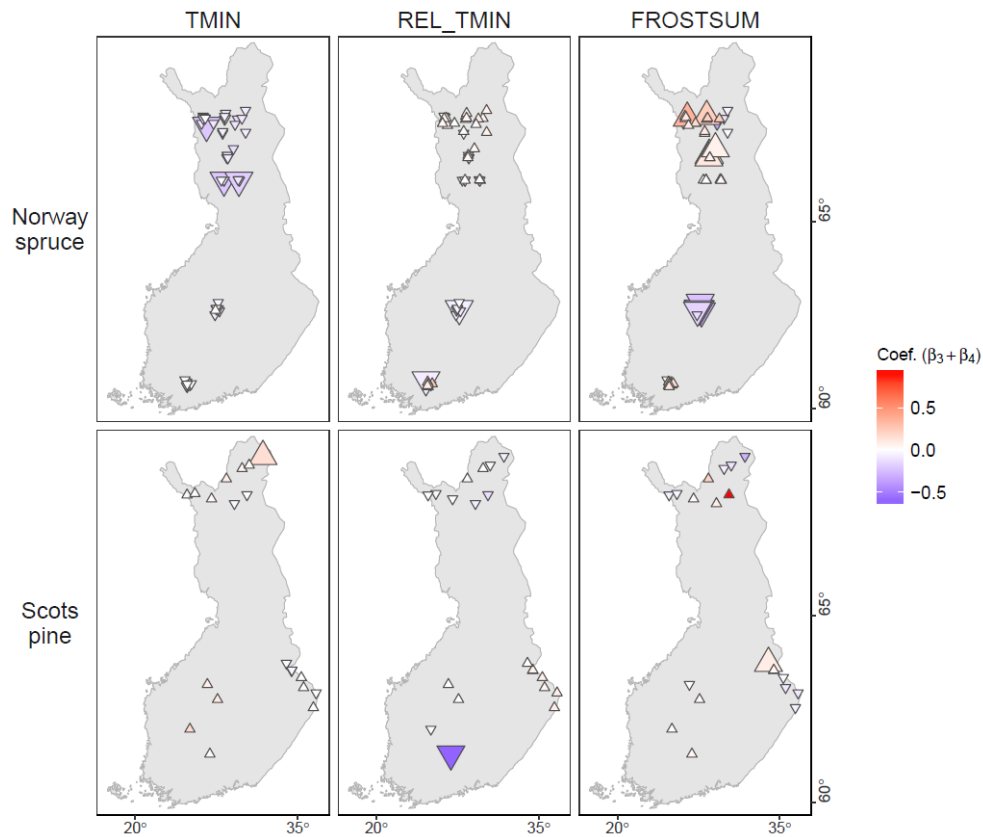
641  $< 0.05$ ). The down-facing triangles represent negative and up-facing triangles positive

642 coefficients. Note that some random variation has been added to the site coordinates so that

643 symbols of nearby sites would not cover each other. See the exact locations of sites in Fig. 1. The

644 non-significant symbols are always drawn on top of the significant ones





645

646 **Fig. 8** Results for the “slope model” (Eq. 2): Coefficients for the slope of the frost variables  
 647 during extreme years. The size of the symbol describes whether the slope model was  
 648 significantly improved compared with the dummy model ( $p < 0.05$ , likelihood ratio test results).  
 649 The down-facing triangles represent negative and up-facing triangles positive coefficients. Note  
 650 that some random variation has been added to the site coordinates so that symbols of nearby sites  
 651 would not cover each other. See the exact locations of sites in Fig. 1

652 **Tables**

653 **Table 1.** Descriptions of frost variables and their range in the whole study area.

	<b>Description</b>	<b>Covered time window</b>	<b>Source data</b>	<b>Years included</b>	<b>Range (whole study area)</b>
TMIN	Lowest daily minimum temperature	Previous July to growth year June	Weather stations	1922 to 1997 (excl. 1927, 1945)	-50 to -21.5
REL_TMIN	The smallest difference between modelled daily frost hardiness and daily minimum temperature	Growth year January to May	Weather stations	1922 to 1997 (excl. 1927, 1945)	3.1 to 16.9
FROSTSUM	Sum of temperatures below 0°C during days with no snow cover	Previous July to growth year June	FMI grid	1962 to 1997	-216.3 to 0

654

655

656 **Electronic supplementary materials**

657 **Supplementary material 1.**

658 Table S1.1 Details about the tree-ring sites, name and distance of weather stations for each site,  
659 the model coefficients for frost variables in dummy and slope models, and the 10-year return  
660 level for FROSTSUM variable in each site (return levels for other two frost variables were  
661 defined for weather stations and can be found below this table).

662 Table S1.2 10-year return levels for TMIN and REL\_TMIN variables for the weather stations.  
663 Although REL\_TMIN differed slightly for spruce and pine (different parametrization of frost  
664 hardness model) the return levels were the same.

665 Figure S1.1 Scatterplots of p-values for frost variable coefficients (dummy models) against  
666 distance between plot and the nearest weather station.

667 **Supplementary material 2.** Detailed description of the frost hardness model and the  
668 modifications made to it in this study