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Quantifying changes of the coniferous forest line in Finnish Lapland during 1983–2009

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Highlights

- Volume of the growing stock of spruce and pine has increased in forests and in timber lines during the past 26 years.
- Spruce stem numbers increased on average, while pine stem numbers remained stable and location-specific variation was observed.
- Presuming that the ongoing trend of increasing temperature will remain, the enhanced forest regeneration and growth may result in extension of forests in the future.

Abstract

The boreal timber- and tree-line forests grow in harsh environmental conditions in their outermost distribution limit. Here even small environmental changes may cause dramatic changes in the distribution of tree species. We examined changes of the forest lines of Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) in Finnish Lapland five times during 1983–2009. We monitored the number of stems and the volume of the growing stock in thirteen different locations in forest-line areas. The linear temporal trends and the variations of these response variables were used as indicators of a possible change during the study period. Spruce showed a significant increase both in the volume of the growing stock (up to 40% increase) and in the total stem number (up to 100% increase). A significant increase in the volume of the growing stock was observed in the pine data as well (up to 70% increase), whereas the stem number stagnated or even decreased. The results suggest that spruce needs favourable conditions to have an abundant regeneration, but after the establishment the seedlings seem to be more resistant against biotic and abiotic disturbances than pine seedlings. The increasing stand volume might result in a climate-related northward and upward extension of forests in the future. However, our results show that responses in the boreal forest line are species and location specific and a more favourable climate does not necessarily lead to an advance of the coniferous forest line.

Keywords *Pinus sylvestris*; *Picea abies*; tree line; environmental change; forest regeneration; stand volume

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1 Introduction

The forest-line ecotone of the boreal zone, which separates treeless areas from closed boreal forests, is one of the Earth's largest vegetation transition zones, extending more than 13 000 km around the Northern Hemisphere (Callaghan et al. 2002). Boreal vegetation has adapted to adverse environmental conditions, such as a short growing season, low temperatures and nutrient supply as well as sparse light during winter (Kallio et al. 1986; Heikkinen et al. 2002). In Finnish Lapland, for example, the growing season lasts less than four months during which trees need to pass through all vegetative (bud break, annual growth) and reproductive (flowering, cone production) stages (Seo et al. 2010). In northern boreal forests, the temperature during the growing season is the main factor that influences the growth and survival of coniferous species (Esteban and Jackson 2000; Heikkinen et al. 2002; Juntunen et al. 2002). Even small temperature changes might cause strong response e.g. in growth or bud burst (Grace et al. 2002; Linkosalo et al. 2009; Høgda et al. 2013; Salminen and Jalkanen 2015). Favourable conditions also allow abundant seed production leading to higher regeneration and seedling establishment (Hilli et al. 2008). Consequently, tree survival and growth in forest-line areas can be used as indicators for a change of the environmental conditions (Karlsen et al. 2005).

The analysis of the sub-fossil Scots pine (*Pinus sylvestris* L.) trunks coming from north of the current coniferous forest line in Finland suggests a warmer-than-present climate between 8 000 and 4 000 BP, and a forest line located at higher altitudes and latitudes compared to the present (Seppä et al. 2002; Kultti et al. 2006). However, the pine forests retreated during a subsequent colder period to the present lower altitudes and more southern latitudes. Hence a warming climate might result in an advance of the current forest line to approach the previous distribution limit (Aakala et al. 2014). This makes forest-line monitoring important because recently rising temperatures and prolonged growing-seasons as well as varying amounts of precipitation have been observed in Finland (Klein Tank et al. 2002; Tietäväinen et al. 2010; Mikkonen et al. 2014).

As the latest decade (2001–2010) was the warmest one in Finland since the beginning of temperature measurements (starting in the 1840's, Finnish Meteorological Institute 2014; Mikkonen et al. 2014; see also Fig. 1), we expect to see an advance of the forest line assuming that the regeneration correlates positively with temperature. During the last 50 years, the climate has been favourable enough for the regeneration of forests in the forest-line areas (Holtmeier 2005; Hyppönen et al. 2013). Previous studies in our study area have indicated that seedling establishment has been at least satisfactory and the mortality of seedlings has remained rather low (Juntunen et al. 2002; Juntunen and Neuvonen 2006).

Several environmental factors determine the regeneration and death of trees at the forest line affecting the balance between increase and decrease of the volume of the growing stock in a stand. These factors are assumed to be related to prevailing climatic conditions at the forest line. Favourable climatic conditions support seedling production and tree growth. However, a changing climate may also create adverse conditions, which may increase death of trees via disturbances, for example, by increasing storm and snow damage (Gregow et al. 2011), large temperature variations (Heikkinen et al. 2002) and providing favourable conditions for the outbreak of pests and diseases (Jalkanen 2003; Holtmeier 2005).

In this paper we investigate changes at forest lines of Scots pine and Norway spruce (*Picea abies* (L.) H. Karst.) during a 26-year period. We monitored the number of stems and the volume

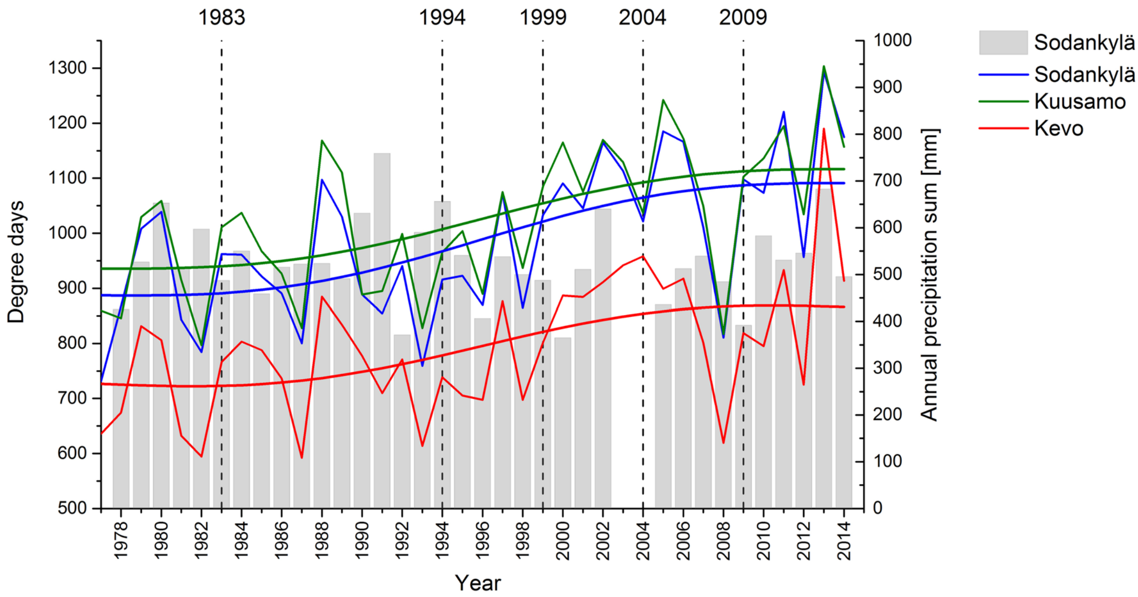

Fig. 1. Effective temperature sums (+4 °C threshold) in Kuusamo, Sodankylä and Kevo and annual precipitation sums (columns) in Sodankylä from 1977 to 2013. The climate datasets (thin lines, columns) are provided in a yearly resolution by European Climate Assessment & Dataset (Klein Tank et al. 2002) and smoothed by using a Fast Fourier Transformation (thick lines).

of the growing stock in forest-line areas in Finnish Lapland during 1983–2009. The linear temporal trends and the variations of these response variables were used as indicators of a possible change. First responses of the coniferous forest lines to a changing environment have been already observed in the first part of the study during 1983–1999 (Juntunen et al. 2002). Here we predict an increase in the number of stems and the volume of the growing stock of pine and spruce in the forest-line ecotone in response to the increased summertime temperatures during the past decade.

2 Materials and methods

2.1 Study area, sampling design and measurements

In our study area in Finnish Lapland, coniferous forest lines are alpine or polar-alpine and they occur over an area spanning 400 km in the south-north direction (Juntunen et al. 2002). These forest lines vary in nature from the Southern to the Northern Lapland. In Southern Lapland forest lines are clearly alpine forest lines and occur on scattered fells in the midst of continuous boreal forest. The northern forest lines are found on higher altitudes as well but are mostly a result of harsh growing conditions on high latitudes, where the boreal forest meets the mountain birch forest zone (*Betula pubescens* Ehrh.) forming the outermost limit of forest vegetation (Hämet-Ahti 1963). The regional climate is mostly (sub)continental with cold winters and relatively warm summers (Tuhkanen 1980).

The forest-line monitoring project is being carried out by the Finnish Forest Research Institute (from beginning of 2015, Natural Resources Institute Finland) and the universities of Helsinki, Oulu and Turku (Kallio et al. 1986). To monitor the forest lines in Finnish Lapland the area was divided into four regions on the basis of predominant tree species and geographical areas (Juntunen et al. 2002). The pine-dominated areas were divided into a northern and a southern region (P-N and P-S), and the spruce-dominated areas into a western and an eastern region (S-W and S-E). Each region

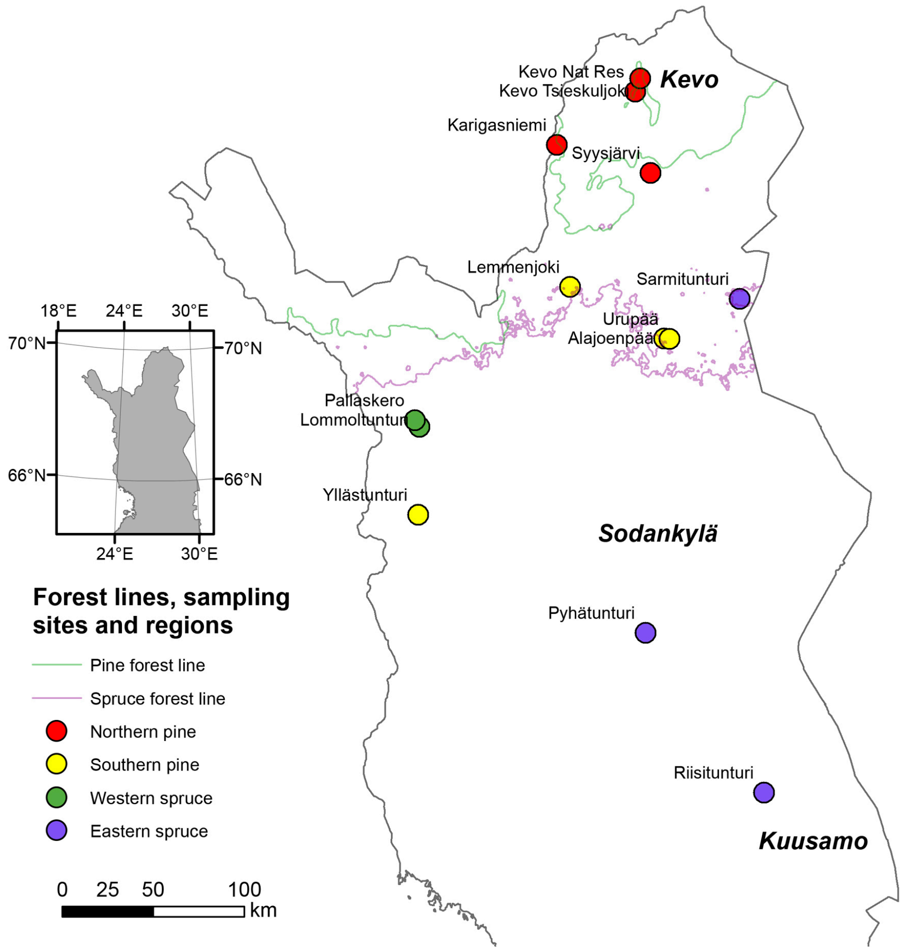

Fig. 2. Monitoring locations of spruce and pine in Finnish Lapland as well as the forest lines of both species. The locations were divided on the basis of predominant species and geographical areas into a northern and southern region of pine and into a western and eastern region of spruce.

Fig. 3. Examples of the forest stands in the a) forest zone (Yllästunturi), b) timber-line zone (Kevo) and c) tree-line zone (Urupää) (Photos by Seppo Neuvonen and Anna Franke).

includes two to four locations, giving a total of 13 locations (Scots pine 8 and Norway spruce 5) in northern Finland (Fig. 2). The 13 locations were carefully chosen to cover the whole area of Lapland but at the same time avoiding locations where the topography or soil factors would affect the results. At the same time places where marks of past disturbances were present were excluded. The mean age of the studied stands was not possible to record as the age of seedlings, saplings and trees varied from 1-year old seedlings to several hundred years old trees. Hence we presume that the age of the studied stands in the beginning of the monitoring was the same as the age of the dominant trees. According to the sample cores taken from the old trees for another project in the studied locations the stand age varied from 200 to 400 years in forest and timber-line zones and from 150 to 200 years in tree-line zone (Fig.3).

Each of the locations consists of a system of three rows of three circular sample plots along an altitudinal gradient from forest to tree line (Fig. 4). These three rows were located in at least 100 meters distance from each other and differed in vegetation pattern, tree height and stand density and can therefore be considered as independent stands (Fig. 5, Table 1). The number of analyzed forest stands is therefore 39. The distance between the centres of adjacent monitoring plots was 40 m. The row in the highest altitude was established within the **tree-line zone**, just below the tree line, where the distance between solitary trees was higher than 2 m but did not exceed 100 m. The second row was established in **timber-line zone**, which is defined here as the altitudinal limit at which the forest canopy closure ceases (Hustich 1948). The lowest row was then established in a forest stand

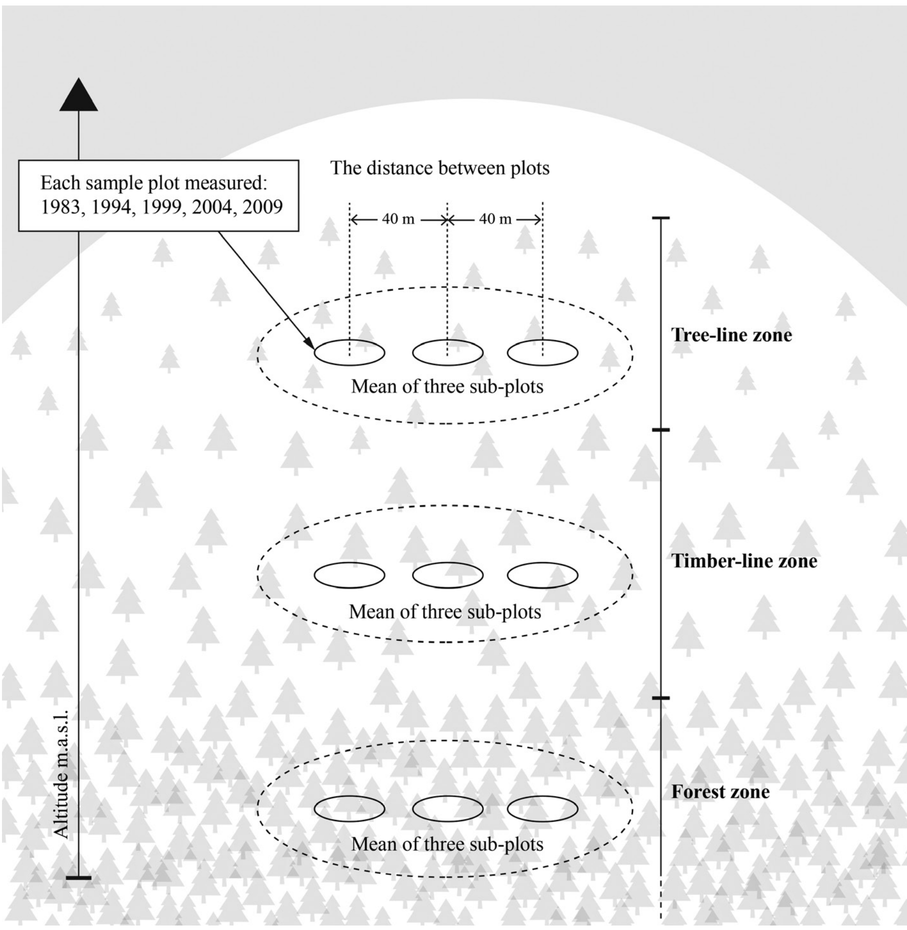

Fig. 4. Sampling design in each of the 13 locations. The sampling was done on three sample plots in forest and timber- and tree-line zones in 1983, 1994, 1999, 2004 and 2009.

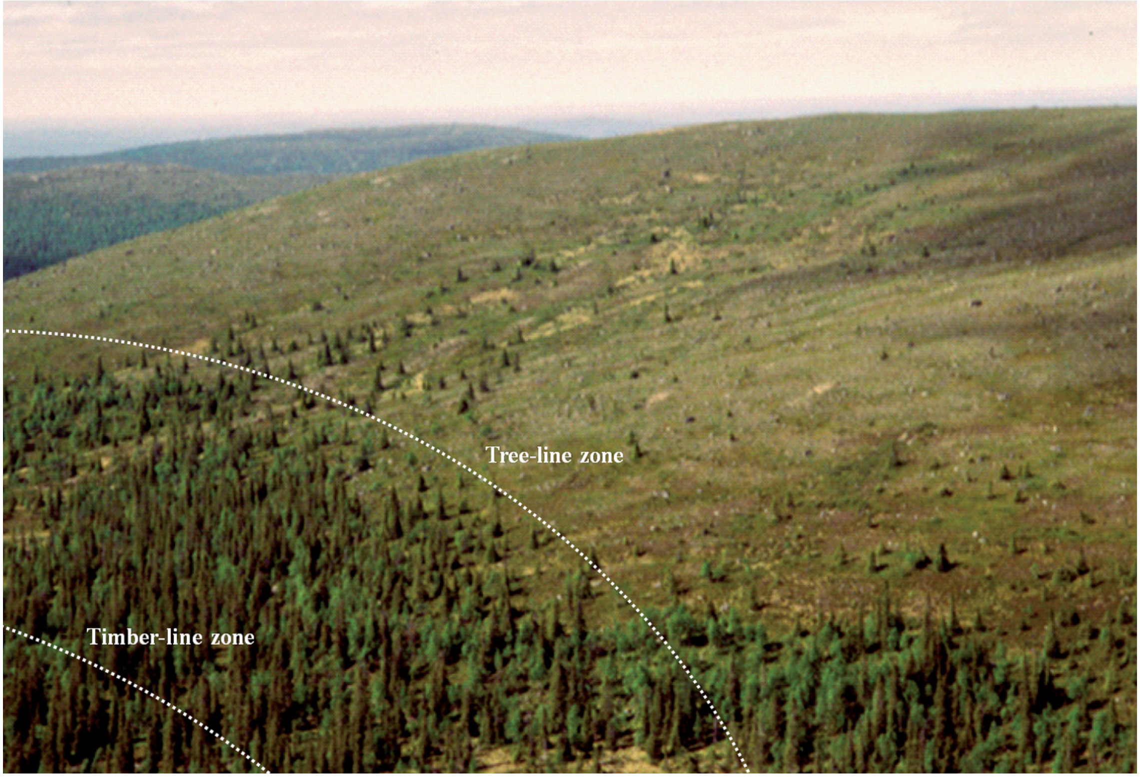

Fig. 5. Example of a sampling location (Sarmitunturi) showing the position of the timber-line and tree-line zones (Photo by Raimo Sutinen). The forest zone is located further downhill and therefore not shown in the photo.

representing the characteristics of the **forest zone**. It was placed so that its vertical distance from the timber-line row was at least 20 m, or its horizontal distance over 100 m, or both. The **forest-line area** in this study contains the entire transition belt in general, extending from closed coniferous forests up to fell heaths. The total number of the plots in the experiment is 117 (nine plots in each 13 locations). Most of the plots have an area of 300 m^2 (radius 9.8 m); however, in the places where there were only a few trees, 500 m^2 plots (radius 12.6 m) were used (Table 1). The average of three plots in each zone was used in the statistical analysis, because it gives a reliable estimate for forest stand level demographic processes in our study locations. Therefore, the original values (counts and measurements) per sample plot have been transformed to the values per hectare.

After the establishment of the plots in 1983, monitoring was repeated in 1994, 1999, 2004 and 2009. The monitoring on the plots includes the number of living trees (≥ 2 m height), saplings (< 2 m and ≥ 1.3 m) and seedlings (height < 1.3 m) as well as measurements of the height and diameter at breast height of all trees within a plot to compute the volume of the growing stock with the KPL-software (Heinonen 1994). The volume of the growing stock includes only trees over 2 meters, (i.e. not seedlings and saplings). In this study an increasing growing stock denotes that the volume increment of a forest stand exceeds the loss of volume due to mortality and represents, therefore, a positive in-balance of growth.

The climate datasets are provided in a yearly resolution by European Climate Assessment & Dataset from 1977 to 2014 for Kevo, Kuusamo and Sodankylä (Klein Tank et al. 2002, http://www.ecad.eu). To characterize the climatic conditions during the growing season we used the effective temperature sum expressed in degree days and the annual precipitation sum. The degree day as a linear temperature sum is based on daily mean temperature minus the threshold value of +4 °C, used by the database for continental Europe. The results were not fitted to the threshold value for Finland (+5 °C) in this context because the threshold does not affect the detected trends

Table 1. Coordinates, altitude, temperature sum, and horizontal distance between the zones in each location. Coordinates and temperature sums are focused on the timber-line zones. The average temperature sums (+5 °C threshold) were provided in a climatic grid (1961–90 standard period) by using the model of Ojansuu and Henttonen (1983).

Location	Latitude	Longitude	Dominant conifer[1]	Altitude (m a.s.l.) Forest zone	Altitude (m a.s.l.) Timber line	Altitude (m a.s.l.) Tree line	Temperature sum (d.d. 5 °C)	Horizontal distance (m) between Forest and timber line	Horizontal distance (m) between Timber line and tree line
Kevo Tsieskuljoki	69°41’ N	26°59’ E	P	110	180	190	773	310	180
Kevo, nat. res	69°45’ N	27°03’ E	P	185	210	225	741	230	100
Karigasniemi	69°25’ N	25°53’ E	P	225	275	420	770	840	810
Syysjärvi	69°17’ N	27°12’ E	P	215	220	225	781	1280	11460
Lemmenjoki	68°43’ N	26°06’ E	P	285	375	415*	782	460	130
Urupää	68°28’ N	27°26’ E	P	315	340	370*	745	140	210
Alajoenpää	68°28’ N	27°22’ E	P	340	380	400*	748	250	270
Ylläs	67°34’ N	24°11’ E	P	380	410	465*	900	240	210
Lommoltunturi	68°00’ N	24°09’ E	S	410	445	465*	874	250	120
Pallaskero	68°02’ N	24°06’ E	S	465	480	500*	892	220	110
Sarmitunturi	68°39’ N	28°23’ E	S	340	370	410*	842	150	160
Pyhätunturi	67°01’ N	27°07’ E	S	380	400	420	914	300	260
Riisitunturi	66°13’ N	28°33’ E	S	420	440	460*	943	120	190

[1] Dominant conifer species: P = pine, S = spruce.
* Indicates that a larger sample plot area (500 m^2) has been used.

and it is likely to cause only minor differences in the resulting temperature sums. Since there were no meteorological stations near the study plots, we used a climatic grid of temperature sums (+5 °C threshold) to receive the temperature sum for each location. The grid data was computed by using the model of Ojansuu and Henttonen (1983) for averaging the temperature sums within the period from 1961–90.

2.2 Statistical analysis

Linear mixed models were used in the modelling of the data. Separate models were calculated for two response variables: 1) The volume of the growing stock (m^3 ha^{-1}) and 2) total number of trees, saplings and seedlings (ha^{-1}), in the following used as "stem number". These two models were calculated separately for Scots pine- and Norway spruce -dominated locations. The response variables were calculated by summing the values (number of stem and the volume of the growing stock) of spruces and pines in each sample plot. Logarithmic (ln) transformation was used for the stem number and square-root transformation for the volume of the growing stock. These transformations yielded the most unbiased residuals (no trends, consistent variances) for the models. The model for the volume of the growing stock can be expressed as following:

$$sqrt(\hat{y}_{ijt}) = \beta_0 + \beta_1 x_{1(i)} + \beta_2 x_{2(ij)} + \beta_3 x_{3(ijt)} + \beta_4 x_{1(i)} * x_{3(ijt)} + \beta_5 x_{2(ij)} * x_{3(ijt)} + \mu_{1(i)} + \mu_{2(ij)} + \varepsilon_{ijt} \quad (1)$$

, where

$sqrt(\hat{y}_{ijt})$ = Estimated square root of the volume of the growing stock (separate models for the locations dominated by Scots pine and Norway spruce)

$x_{1(i)}$ = Fixed predictor of region (levels: northern, southern (Scots pine), western, eastern (Norway spruce))

$x_{2(ij)}$ = Fixed predictor of zone (levels: forest, timber line, tree line)

$x_{3(ijt)}$ = Fixed predictor of time (0 – 26 years, 0 denotes year 1983 and 26 year 2009 respectively)

$\beta_0,...,\beta_5$ = Coefficients of the fixed effects and interactions of the fixed effects

$\mu_{1(i)}$ = Random effect of location (Scots pine: 8 locations; Norway spruce: 5 locations)

$\mu_{2(ij)}$ = Random effect of zone nested within location

ε_{ijt} = Random error (*t*, denoting repeated measures), nested within zone (*j*). Autoregressive (AR-1) error, heterogeneous variances for each repeated measures time points were estimated.

Compound symmetry was used as the random error structure in the log-transformed models for the stem number, instead of the autoregressive structure based on likelihood-ratio tests and residuals (minimizing bias). The same model structure based on the experimental design was used in all of the models and all the coefficients and their significances were reported, including the two-way interaction terms (formula 1). The three way interaction of region, zone and time could not be tested due to convergence problems.

In addition we tested if the coefficients of time by region and by zone differ from 0 (results are presented in Table 4, null hypothesis: $\beta = 0$). These tests indicate if the stem number as well as the volume of the growing stock has increased, decreased or remained stable during the 26-year period. The tests and the coefficients in the tables 2–4 were generated by the models using the transformed response. However, the fitted values presented in the text and figures were transformed back to the original scale (exponential and power transformations). The values of the exponential transformations were corrected using Snowdon's (1991) ratio estimator and those of power transformation by adding variances of the random parts to the transformed values.

In addition to the linear trends, the second-order polynomial of time and its interactions with region and zone were tested as the additional terms in the models for the volume of growing stock, but they were not significant at 5% risk level. Thus, only the linear trends are presented here. Significant polynomial terms would indicate an accelerative increase or decrease in the volume of growing stock.

R statistical environment (R Core Team 2013) was used in the modelling. Used packages were nlme (Pinheiro et al. 2013), Car (Fox and Weisberg 2011) and lsmeans (Lenth 2014).

Table 2. The estimates and Likelihood-ratio tests of the models for Norway spruce, t-values for the coefficients and χ2 – values for the Likelihood ratio tests are presented in t/Chisq. Tests show the significance of the variables in the model and the significance of the coefficients related to the reference categories (given in parentheses). A non-significant interaction term means that the coefficients do not differ from the coefficient of reference category.

Variable / term	Coefficient	Std. error	Df	t/Chisq	p
Norway spruce, number of trees and seedlings ha^{-1}					
Intercept	7.000	0.376	56/1	18.62/346.54	0.000
Region (ref. Western)			1	4.28	0.039
-Eastern	-0.854	0.412	3	-2.07	0.130
Zone (ref. Forest)			2	3.70	0.157
-Timber line	0.333	0.342	8	0.97	0.359
-Tree line	-0.325	0.342	8	-0.95	0.370
Time	0.018	0.010	56/1	1.77/3.13	0.077
Region*Time			1	1.81	0.179
-Eastern*Time	-0.013	0.010	56	-1.35	0.184
Zone*Time			2	3.49	0.175
-Timber line*Time	0.006	0.012	56	0.48	0.630
-Tree line*Time	0.021	0.012	56	1.80	0.077
Random effects	Estimate	Cl 95%			
Location	0.107	0.007 – 1.682			
Zone nested Location	0.187	0.061 – 0.579			
Error (compound symmetry)	0.141	0.098 – 0.205			
Norway spruce, volume of tree stock, m^{3}ha^{-1}					
Intercept	7.970	1.073	56/1	7.43/55.19	0.000
Region (ref. Western)			1	0.65	0.420
-Eastern	-1.031	1.278	3	-0.81	0.479
Zone (ref. Forest)			2	67.50	0.000
-Timber line	-2.056	0.717	8	-2.87	0.021
-Tree line	-5.812	0.717	8	-8.10	0.000
Time	0.043	0.010	56/1	4.27/18.21	0.000
Region*Time			1	2.85	0.091
-Eastern*Time	-0.017	0.010	56	-1.69	0.097
Zone*Time			2	8.10	0.017
-Timber line*Time	0.012	0.012	56	1.04	0.301
-Tree line*Time	-0.021	0.012	56	-1.77	0.082
Random effects	Estimate	Cl 95%			
Location	1.530	0.197 – 11.853			
Zone nested within Location	1.186	0.443 – 3.177			
Error (ARH-1, phi=0.55)	0.398	0.165 – 0.957			

3 Results

We detected a significant increase in the stem number of spruce in timber- and tree-line zones, whereas the forest zone remained stable (Fig. 6a, Tables 2 and 4). Even though the stem number of spruce increased in both western and eastern regions the increase was much higher in the west (on average 1 389 stems ha^{-1} in 1983 and 2 826 ha^{-1} in 2009, i.e. over 100% increase) compared to the east (591 stems ha^{-1} in 1983 and 850 ha^{-1} in 2009, i.e. 44% increase). The volume of the spruce growing stock (m^3 ha^{-1}) showed also increasing trends over the whole observation period in all zones, although the increase in the tree-line zone was statistically only marginally significant

Table 3. The estimates and Likelihood-ratio tests of the models for Scots pine, t-values for the coefficients and χ2 – values for the Likelihood ratio tests are presented in t/Chisq. Tests show the significance of the variables in the model and the significance of the coefficients related to the reference categories (given in parentheses). A non-significant interaction term means that the coefficients do not differ from the coefficient of reference category.

Variable / term	Coefficient	Std. error	Df	t/Chisq	p
Scots pine, number of trees and seedlings ha^{-1}					
Intercept	6.577	0.695	90/1	9.43/88.90	0.000
Region (ref. Northern)			1	0.84	0.359
-Southern	0.729	0.795	6	0.92	0.395
Zone (ref. Forest)			2	10.12	0.006
-Timber line	-1.040	0.710	14	-1.47	0.165
-Tree line	-2.256	0.710	14	-3.18	0.007
Time	0.012	0.009	90/1	1.36/1.85	0.174
Region*Time			1	12.95	0.000
-Southern*Time	-0.032	0.009	90	-3.60	0.001
Zone*Time			2	0.91	0.635
-Timber line*Time	-0.010	0.011	90	-0.89	0.377
-Tree line*Time	-0.008	0.011	90	-0.74	0.464
Random effects	Estimate	Cl 95%			
Location	0.591	0.050 – 7.018			
Zone nested Location	1.876	0.882 – 3.990			
Error (compound symmetry)	0.185	0.138 – 0.248			
Scots pine, volume of tree stock, m^{3}ha^{-1}					
Intercept	7.124	1.166	90/1	6.11/37.34	0.000
Region (ref. Northern)			1	0.00	0.997
-Southern	-0.005	1.296	6	-0.00	0.997
Zone (ref. Forest)			2	24.57	0.000
-Timber line	-3.665	1.247	14	-2.94	0.011
-Tree line	-6.145	1.247	14	-4.93	0.000
Time	0.054	0.015	90/1	3.64/13.27	0.000
Region*Time			1	0.50	0.478
-Southern*Time	-0.011	0.015	90	-0.71	0.479
Zone*Time			2	5.47	0.065
-Timber line*Time	0.026	0.018	90	1.43	0.155
-Tree line*Time	-0.016	0.018	90	-0.89	0.377
Random effects	Estimate	Cl 95%			
Location	1.287	0.084 – 19.753			
Zone nested within Location	4.968	2.348 – 10.513			
Error (ARH-1, phi=0.91)	1.325	0.533 – 3.294			

Table 4. Significances (p-values) of asymptotical tests for the coefficients of the interaction terms (Time*Region or Time*Zone) in the models. Hypothesis is that the coefficients=0. The arrows denote either a significant increasing or decreasing change in time, or non-significant change (flat arrow).

Coefficient	Scots pine, number of trees ha^{-1}	Scots pine, volume of tree stock, m^{3}ha^{-1}	Norway spruce, number of trees ha^{-1}	Norway spruce, volume of tree stock, m^{3}ha^{-1}
Region: northern (pine), western (spruce)	0.327 →	0.000 ↗	0.000 ↗	0.000 ↗
Region: southern (pine), eastern (spruce)	0.000 ↘	0.000 ↗	0.026 ↗	0.000 ↗
Zone: forest	0.590 →	0.000 ↗	0.127 →	0.000 ↗
Zone: timber line	0.078 →	0.000 ↗	0.041 ↗	0.000 ↗
Zone: tree line	0.120 →	0.011 ↗	0.000 ↗	0.086 →

(Fig. 6b, Tables 2 and 4). When comparing the western and the eastern region, the western part indicated a higher gain of volume of 40% (from 31.5 m^3 ha^{-1} in 1983 to 44.0 m^3 ha^{-1} in 2009) compared to the 27% in the eastern part (from 21.6 m^3 ha^{-1} to 27.4 m^3 ha^{-1}).

On the contrary to spruce, the stem number of pine showed no clear trends in any of the zones when all the locations are considered (Fig. 7a, Tables 3 and 4). When trends for the northern and southern pine regions were studied separately, a statistically significant decline in the pine

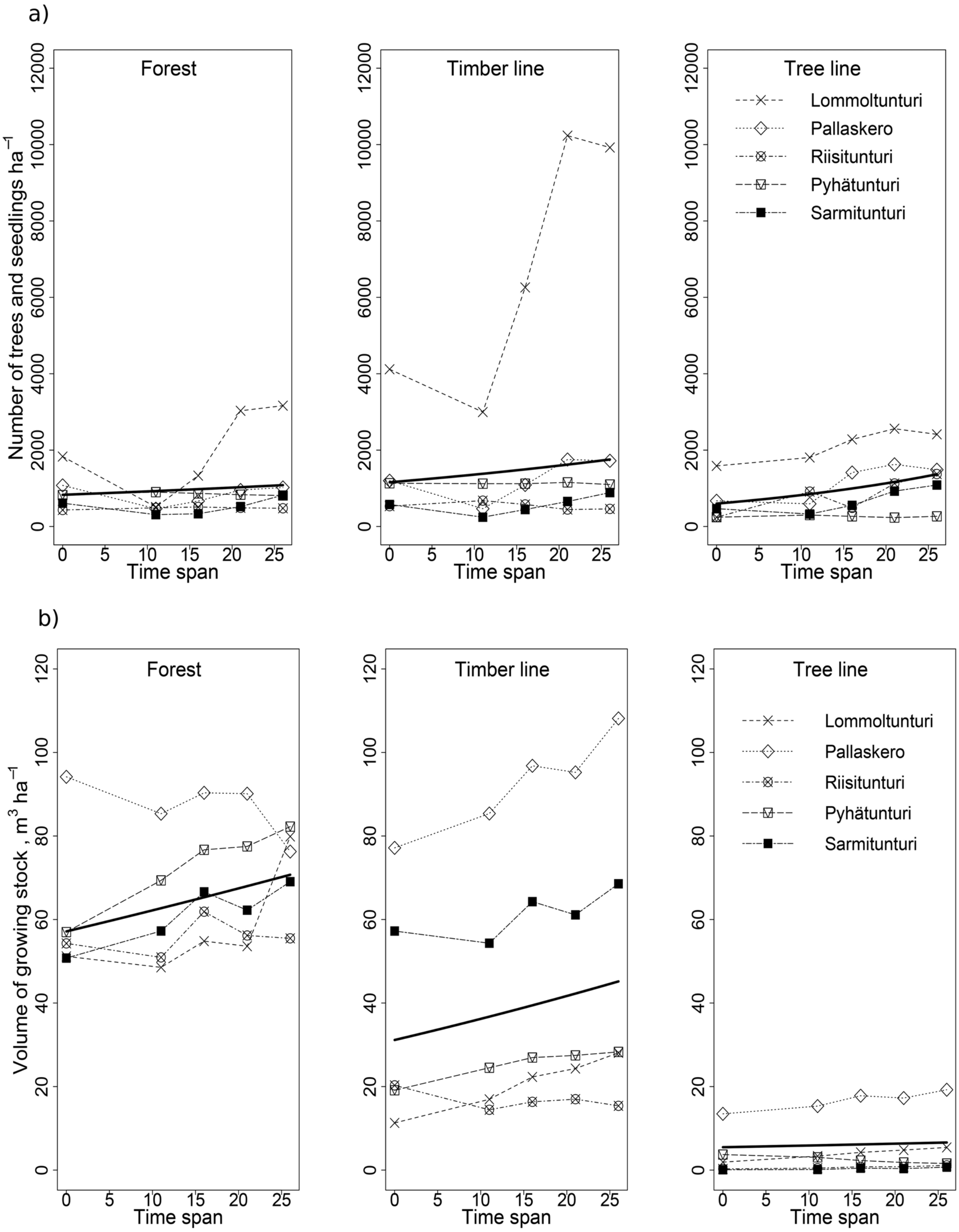

Fig. 6. The stem number ha^{-1} (a) and volume of growing stock m^3 ha^{-1} (b) of spruce during the study in each location (raw data) as well as the predicted values of the models for each zone (thick line).

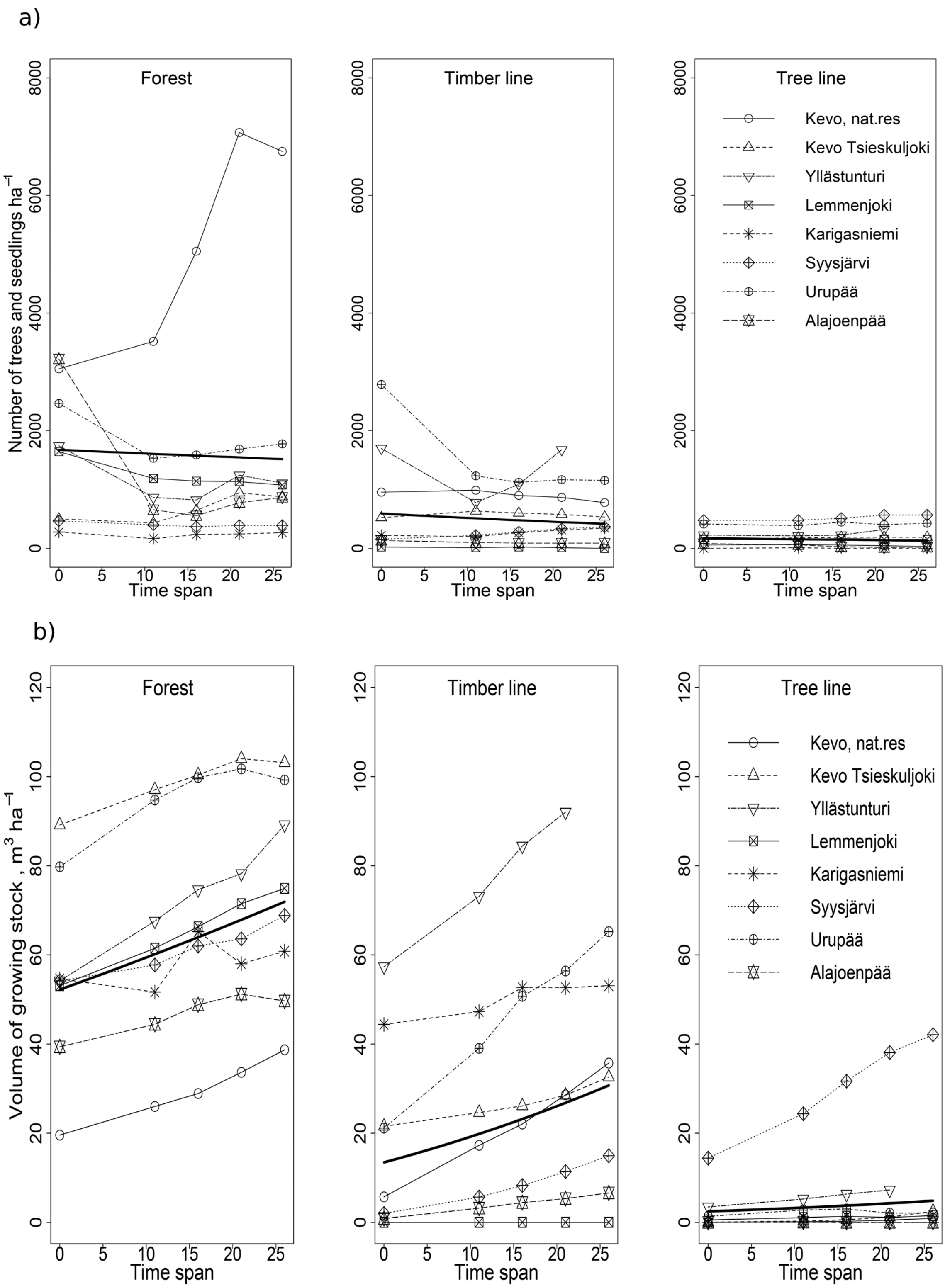

Fig. 7. The stem number ha^{-1} (a) and volume of growing stock m^{3} ha^{-1} (b) of pine during the study in each location (raw data) as well as the predicted values of the models for each zone (thick line).

number of 49% from 816 stems ha^{-1} in 1983 to 414 stems ha^{-1} in 2009 was found in the southern regions. The observed low increase of 17% from 394 stems ha^{-1} to 462 stems ha^{-1} in the northern region is not significant.

Even though the number of the pines showed no clear overall change, the volume of the pine growing stock (m^3 ha^{-1}) increased significantly in all zones in the northern and the southern regions (Fig. 7b, Tables 3 and 4). Northern and southern distribution areas revealed an increased volume of 70% (from 18.6 m^3 ha^{-1} to 33.4 m^3 ha^{-1}) in the north and 56% (from 19.5 m^3 ha^{-1} to 30.4 m^3 ha^{-1}) in the south during the study period. A noteworthy fact is that even though there was a lot of variation between the locations the trend was, especially in the forest zone and in the timber line, positive in all locations.

4 Discussion

Our results indicated an increase in the volume of the growing stock of both spruce and pine in every zone and region, except in the case of spruce in the tree-line zone. An increasing growing stock here means that changing environmental conditions support higher reproduction, increment and survival of trees compared to the rate of dieback, leading to an advancing forest line. In other words, the studied stands were not in their climax balance, in which reproduction and growth are levelled out by death of trees, but a positive imbalance exists. The fact that the volume of the growing stocks was, on average, increasing gives a reason to assume that environmental conditions affecting growing stocks have, in general, improved since the first inventory in 1983. Temperature sums in Kuusamo, Sodankylä and Kevo as well as the amount of precipitation have risen during the study period in comparison to their long term annual mean values (1977–2013), especially during the period of 1994 to 2013 (Fig. 1). On the other hand, there was no clear indication for acceleration of the growing stock during the past decade that was the warmest decade in Finland ever recorded. In fact, in some of our study locations the growing stock has diminished during the last decade. This suggests that in addition to summer time temperature other factors have also had a strong impact on the growing stock. Kauppi et al. (2014) studied the effect of climate warming on boreal forests since 1960 and found out that in Finnish Lapland, where the annual growing degree days (GDD) have increased over 20% since 1960, the proportion of forest growth attributable to warming was around 43% whereas the rest was unrelated to warming. Kauppi et al. (2014) explained the part unrelated to warming by the factors such as forest management, increased nitrogen deposition and CO_2 concentration when the whole Finland is considered. In our study locations, however, forests are not managed and the nitrogen deposition is very low (Mustajärvi et al. 2008). All this suggests that the trends seen in the growing stocks in our study locations are a response to interactions of warmer and longer growing season as well as increased CO_2 with other abiotic and biotic factors.

On the contrary to the growing stock, the number of stems, including trees, saplings and seedlings, revealed a species and location specific response to changing environmental conditions. The significant increase in the number of spruce stems in the tree- and timber-line zones suggests that the end of the 20th century obviously provided favourable conditions for good seed years followed by good seedling establishment. The modest gain of the stem number in the forest zone is most likely a result of a between-tree competition for nutrients and light as well as of thick moss and humus layers which hinder regeneration (Juntunen and Neuvonen 2006).

Once spruce seedlings and saplings have been established successfully they seem to be more tolerant to disturbances. With regard to a significant increase of stem numbers, growth conditions near tree and timber lines seem to be favourable enough to enhance seeding, seedling establishment and survival of trees of all age classes. Supposing that prolonged growing seasons as well as higher temperatures in summer and winter times are at least partly responsible for the observed development, a northward and upward transition of spruce forest line can be expected where the geological factors, such as nutrient supply, allow this (Hyppönen et al. 2003; Sutinen et al. 2012).

In contrast to spruce, there was not a clear trend in the number of pine stems. When considering geographical regions separately, the stem number of pine in the southern part of the study area (locations Urupää, Alajoenpää and Yllästunturi) decreased especially during the first monitoring interval (1983–1994), but it is obvious that generally no large changes have taken place during the last 15 years (Fig. 7a). The strong reduction in the stem numbers in southern locations was mainly due to the high mortality of pine seedlings during 1983–2004 (Juntunen et al. 2002; Juntunen and Neuvonen 2006). Pine diebacks in the southern locations are a consequence of multiple biotic factors. Pines in these locations are often hit by the fungal diseases Scleroderris canker (*Gremmeniella abietina* (Lagerb.) Morelet) and the snow blight (*Phacidium infestans* P. Karst), as well as insects, such as the European pine sawfly (*Neodiprion sertifer* Geoffr.) (Niemelä et al. 1987; Juntunen and Neuvonen 2006; Holtmeier and Broll 2011). The European pine sawfly is predicted to have more outbreaks also in Finnish Lapland due to a reduced mortality of the eggs in milder winter temperatures (Virtanen et al. 1996; Neuvonen et al. 1999; Veteli et al. 2005).

Another biotic factor causing damage to pine seedlings is trampling by reindeer (*Rangifer tarandus tarandus* L.), when it is grazing. The reindeer population of Finland has more than doubled from about 100 000 reindeer in the beginning of the 1900s up to 265 000 in early 1990 (Väre et al. 1996) after which it has decreased to 197 000 in 2010 (Mattila 2014 a, b). Reindeer graze the reindeer lichens (*Cladonia spp.*) in pine dominated forests in winter that causes additional disturbance particularly to pine seedlings (Heikkinen et al. 2002; Holtmeier 2005; Vajda and Venäläinen 2005; Holtmeier and Broll 2011). Spruce grows in forests where lichens have only a minor role in understory and is therefore only marginally influenced by reindeer grazing.

Besides above biotic factors, seedlings are threatened by mild winters with an early start of the growing season and large temperature variations during late autumn and early spring, which influence their frost-hardiness (Cannell and Smith 1986). The risk of frost-damage induced mortality of seedlings is predicted to increase due to a warming climate and milder winter temperatures (Hänninen 1991; Leinonen 1995; Repo et al. 1996). Once trees have passed the seedling and sapling stage they have to survive from the stress of snow loading. Extreme crown-snow loading is the major reason for tree breakage at timber line in northern Finland (Marchand 1987), particularly at high altitudes and in old age-classes of the trees (Jalkanen and Konôpka 1998; Lehtonen et al. 2014). Spruce is, due to its slim crown shape, better protected against massive snow loading, whereas the shape of pine crown facilitates snow damage.

To sum up, our results show that the forests in the timber-line ecotone in Finnish Lapland are increasing in the volume of growing stock and tree number most likely due to favourable climatic conditions during the past decades. Presuming that the ongoing trend of increasing temperature will remain, the enhanced forest regeneration and growing stock in the timber- and tree line may result in a northward and upward extension of forests in the future. However, this process seems to be species specific, and in places where the pine is the main species, biotic factors or snow damage might overrule the effects of otherwise favourable environmental conditions. To evaluate the effect of abiotic and biotic factors more precisely, more detailed studies on cause-effect relationships are needed. However, results of the present monitoring study provide a valuable tool for decision-makers in forest policy, as well as a basis for further studies on factors influencing forest-line dynamics. Hence, the continuation of similar long-term studies is important to enable a reliable estimation of environmental changes in the forest-line ecotone.

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