Climate-induced growth responses and tree-line shifts of boreal conifers in the alpine and polar tree-line ecotone in Finnish Lapland

Klimabedingte Wachstumsreaktionen und Baumgrenzverlagerungen borealer Koniferen im alpinen und polaren Baumgrenzökoton Finnisch-Lapplands

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Summary

At the northern margins of the boreal regions bordering the sub-Arctic, trees as a life form grow close to the limit of their ecological range and have to cope with low temperatures, low nutrient supply, and sparse light conditions during winter. The growing season lasts less than five months during which trees need to pass through all vegetative and reproductive stages. In the transition zone from closed forests to bare fell tops and open tundra, conifers form the outermost edge of their distribution area in the tree-line ecotone, which is characterized by harsh climatic conditions and disturbance regimes, challenging tree growth by frost, wind and snow load. The mortality rate is high and sequences of several favourable years are needed to grow and successfully establish sustainably high seed crops for natural regeneration.

Here, temperature is found to be the limiting parameter for growth and regeneration, hence a temperature rise under current warming is expected to considerably improve the growing conditions for conifers (Kauppi et al. 2014; Salminen and Jalkanen 2015). Under mild winters, early springs and increasing summer temperatures, trees and shrubs are predicted to establish more successfully, regionally replacing graminoids in the alpine oroarctic tundra by higher vegetation (Juntunen et al. 2002; Jia et al. 2003; Goetz et al. 2011; Jeong et al. 2012; Walker et al. 2012; Pearson et al. 2013; Aakala et al. 2014). An expansion of conifers beyond the recent tree-line position may affect the microclimate and carbon fluxes of the ecosystem, potentially influencing large-scale circulation changes in Arctic regions (Jeong et al. 2012; Miller and Smith 2012; Pearson et al. 2013; Zhang et al. 2013). Estimating vegetation shifts in these regions is consequently of high scientific interest and is also in the focus of the present project.

In Finnish Lapland, a monitoring project was established already in 1983 to monitor regeneration and growth of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) regularly in five-year intervals along elevation gradients aligned along a North-South transect. Thereby, changes in the regeneration success, mortality and volume of growing stock of conifers in a changing environment were to

be detected. The analysis was, however, restricted on the local plots and time frames, lacking a continuous and large-scale analysis of tree-line changes. The aim of the present study was therefore to supplement the monitoring study by dendroecological sampling and remote sensing. In a first step, the outcomes of the monitoring project during 1983–2009 were analysed and published in cooperation with the Natural Resources Institute Finland Luke (publication I). Afterwards, a dendroecological sampling was performed on six of the pine-dominated sites to measure growth rates and to create long-term site chronologies. Climate-growth responses of pine was analysed by computing Pearson correlation functions with relevant climatic parameters. Thereby, inter-annual growth variations and long-term growth trends were analysed and compared between mature and juvenile trees and between a northern and southern region (publication II). Finally, satellite images were acquired for the pine-dominated sites and analysed for large-scale vegetation changes around the monitoring sites (publication III). This was done by using the Normalized Difference Vegetation Index (NDVI) and a land cover classification using Random Forests.

The monitoring study indicated increasing volumes of growing stock for both spruce- and pine-dominated stands in all of the studied sites and elevation zones. An increase in height and diameter of adult trees (> 2 m) was assumed to exceed the mortality rate, leading towards a densification of the established forest stands. The number of tree stems, saplings and seedlings increased also in nearly all spruce-dominated sites, predominantly in the open stands of higher elevations. The stem numbers of pine stagnated or even decreased in all locations and elevation zones, pointing towards a high mortality rate and high sensitivity of pine seedlings to abiotic and biotic disturbances.

The dendroecological analysis revealed that stand structure and thermal conditions during the growing season affect pine-tree growth, especially during juvenile ages. Radial growth rates correlated highly negative with the occurrence of cold and frost days during the onset of the growing season predominantly in the north of the study region, while the impact of temperature diminished at the more rapidly warming southern sites. The site chronologies showed growth responses to climatic variations

until the 1980s, but not during the current warming period. Increasing radial growth trends could be detected since 2000 in the juvenile trees of the southern sites, while the mature and northern trees did not respond significantly to the current warming. We assume that warmer and wetter conditions during winter, inducing high snow loads, wind damages, diseases and frost damage during spring, to possibly counteract the benefits of climate warming.

The applied remote sensing approaches included NDVI change detection and land-cover classification. However, neither method revealed clear trends for advancing conifer tree lines towards open fell tops or treeless heath vegetation. Instead, we found evidence for densification of open forest stands at lower elevations and an expansion of deciduous vegetation at higher elevations into previously vegetation-free or sparsely covered fell tops. Increasing stand density was detected mostly in the southern, pine-dominated sites, while the northern sites indicated greening trends near the fell tops. Based on the evidence provided by the different applied approaches, we conclude that the pine forests first increase volume and seed production, before pine seedlings eventually may invade into the tundra. Under the current climatic conditions for pine, with low survival rates beyond the tree line, a high amount of seeds would be necessary to increase the survival rate of seedlings in open sites. However, we found climate warming and prolongation of the growing season predominantly in the southern regions, where forest densification and production of new seed trees might on long sight enable coniferous forests to expand towards open sites. In the north, warming rates are small, expanding the growing season for only a few days towards an earlier onset of spring. Here, the environmental conditions are still harsh enough to mask the benefits of climate warming and so far only promote the expansion of shrubs and mountain birch forests towards the open tundra. When climate warming continues also here, it is possible that pine seeds will survive sheltered in the forest-line zone before passing the critical stage of sapling size to gradually replace the deciduous vegetation.

Zusammenfassung

Titel: Klimabedingte Wachstumsreaktionen und Baumgrenzverlagerungen borealer Koniferen im alpinen und polaren Baumgrenzökoton Finnisch-Lapplands

Die subpolare Zone der Nordhemisphäre bildet den Übergang vom borealen Nadelwald zur offenen Tundra und repräsentiert in der polaren und alpinen Baumgrenze die nördlichsten und höchstgelegenen Vorkommen baumförmiger Vegetation. Ganzjährig niedrige Temperaturen, ein geringes Licht- und Nährstoffangebot sowie eine kurze Vegetationsperiode erfordern eine hohe Adaption der Vegetation an widrige klimatische Bedingungen. Die Hauptbaumarten der Borealis sind in der Lage, lange Kälteperioden zu überdauern und sich während anhaltender klimatischer Gunstphasen zu reproduzieren. In diesem Rahmen sind die Länge der Vegetationsperiode sowie die Ausprägung der Juli-Temperatur für Zuwachs und Reproduktion ausschlaggebend, die sich bereits bei geringen Temperaturänderungen stark verändern können (Kauppi et al. 2014; Salminen and Jalkanen 2015). Der Fund subfossiler Kiefern nördlich und oberhalb der Baumgrenze weist auf ein ehemals größeres Verbreitungsgebiet borealer Gehölzvegetation und damit eine klimasensitive Reaktion der Koniferen hin. Milde Winter, verlängerte Vegetationsperioden und ganzjährig höhere Temperaturen erschaffen ökosystemare Bedingungen, wie sie sonst in niedrigeren Breiten- und Höhenlagen gefunden werden. Im derzeitigen Klimaoptimum wird daher eine Ausweitung der Nadelwaldbestände, insbesondere für das polare und alpine Baumgrenzökoton prognostiziert (Juntunen et al. 2002; Jia et al. 2003; Goetz et al. 2011; Jeong et al. 2012; Walker et al. 2012; Pearson et al. 2013; Aakala et al. 2014).

Bisherige Forschungsergebnisse weisen bereits auf eine erhöhte Biomasseproduktion zuvor spärlich bewachsener Tundraareale hin, die jedoch als art- und standortspezifisch eingestuft werden. Externe Störgrößen, wie Wind- und Schneebruch, Schädlingsbefall sowie Rentierbeweidung limitieren den Verjüngungserfolg häufig und erschweren die Prognostizierung borealer Waldgrenzentwicklung (Juntunen und Neuvonen 2006; Heikkinen et al. 2002). Zudem kann aufgrund der großen Ausdehnung des borealen Nadelwaldgürtels bei Einzelstudien

häufig nur auf die lokalen Bedingungen geschlossen werden, was einen räumlichen Vergleich erschwert. Ziel des Projektes ist es daher, anhand verschiedener Methoden Wachstum und Ausbreitung ausgewählter Nadelbaumarten im Untersuchungsraum Finnisch-Lappland zu betrachten, um Aussagen zum Wachstumsverhalten auf mehreren zeitlichen und räumlichen Ebenen treffen zu können.

In Finnisch-Lappland wurden bereits im Jahr 1983 Monitoringflächen zur Erfassung des Bestandsvolumen und der Verjüngungsrate von Waldkiefer (*Pinus sylvestris* L.) und Fichte (*Picea abies* (L.) H. Karst.) errichtet. Im Abstand von fünf Jahren wurden beide Parameter entlang eines Nord-Süd-Transekts auf insgesamt dreizehn Standorten an Höhengradienten von der Waldzone bis zur Baumgrenzzone erfasst und auf standortspezifische Trends hin untersucht. Im ersten Teil des Dissertationsprojekts wurden die Ergebnisse des Bestandsmonitorings von 1983 bis 2009 ausgewertet und zusammen mit dem Natural Resources Institute Finland Luke publiziert (Publikation I). Sechs Kiefernstandorte des Monitorings wurden anschließend dendroökologisch analysiert und auf jährliche Zuwachsänderungen, Klimakorrelationen sowie langzeitliche Wachstumstrends untersucht. Vorteil der dendroökologischen Untersuchungen waren die jährliche Auflösung des Jahrringbreitenzuwachses sowie die zeitliche Abdeckung der Analysen bis zum Beginn des 19. Jahrhunderts. Das Radialwachstum wurde auf Unterschiede zwischen jungen und alten Bäumen sowie zwischen nördlichen und südlichen Standorten hin untersucht (Publikation II). Satellitenaufnahmen der Kiefernstandorte ermöglichten eine großräumige Analyse der Untersuchungsgebiete außerhalb der Monitoringplots (Publikation III). Anhand des Normalized Difference Vegetation Index (NDVI) und einer Random Forest-Oberflächenklassifizierung wurden Veränderungen in Art und Bedeckungsgrad der Vegetation bewertet.

Das Bestandsmonitoring ergab einen signifikanten Zuwachs im Bestandsvolumen für beide Baumarten an allen Standorten. Dies lässt vermuten, dass der Zuwachs und Anteil gesunder adulter Bäume (> 2 m Höhe) die Mortalitätsrate übersteigt und die Ausweitung des Bestandsvolumens durch die derzeitigen klimatischen Bedingungen begünstigt wird. Im Gegensatz dazu zeigte die

Individuenzahl ein art- und standortspezifisches Bild. Die Individuenzahlen der Sämlinge, junger und adulter Bäume stieg auf fichtendominierten Standorten kontinuierlich an, insbesondere in den offeneren Waldbeständen der oberen Höhenstufen. Bei der Kiefer konnten hingegen nur stagnierende oder sinkende Individuenzahlen festgestellt werden, die auf eine hohe Mortalitätsrate junger Kiefern zurückzuführen sind. Die Kiefer zeigte damit eine hohe Sensibilität gegenüber externen Störungen im Sämlingsstadium an.

In der dendroökologischen Analyse wurden die Bestandsstruktur und thermische Bedingungen während der Vegetationsperiode als limitierende Faktoren ermittelt. Das Radialwachstum korrelierte insbesondere an den nördlichen Standorten des Untersuchungsgebietes negativ mit der Zahl kalter und frostiger Tage während der einsetzenden Vegetationsperiode im Frühjahr. Die Korrelation mit der Temperatur nahm hingegen an den wärmeren Südstandorten im Laufe der letzten Jahrzehnte ab. Die Standortchronologien bezeugten eine hohe Sensitivität des Radialwachstums für die Temperatur bis in die 1980er Jahre, die jedoch überraschenderweise während der derzeitigen Warmphase abnahm. Lediglich Kiefern jüngeren Alters zeigten eine signifikant positive Wachstumsänderung auf den Südstandorten, während eine vergleichbare Wachstumsreaktion bei adulten Bäumen und auf den Nordstandorten ausblieb. In Hinblick auf die in Teil II präsentierten Ergebnisse wird von einer Überlagerung des klimatischen Signals durch externe Störgrößen ausgegangen. Milde und nasse Winter gehen mit erhöhter Schneelast, Kronenbruch und Frostschäden während des Frühjahrs sowie der Ausbreitung von Pilzinfektionen einher und könnten einen klimabedingten Wachstumszuwachs überdeckt haben.

Die Satellitenbildfernerkundung konnte keine Ausweitung der Nadelwaldbestände feststellen. Der NDVI belegte eine Vegetationszunahme auf bereits begrünten Flächen, insbesondere ursprünglich lichter Nadelwaldbestände im Süden und offener Fjellkuppen im Norden. Der Anstieg des NDVIs über Nadelwaldbeständen kann auf eine Zunahme der Vitalität und/oder Biomasse zurückgeführt werden und deckt sich mit einer durch das Monitoring festgestellten Zunahme des Bestandsvolumens. Eine Verschiebung der Baumgrenze nach Norden oder in höhere Höhenstufen konnte nicht

beobachtet werden. Eine Begrünung der offenen Fjellkuppen wurde in Hinblick auf die Spektraldaten auf eine Ausweitung der Birkenwaldbestände und Strauchvegetation zurückgeführt, nicht aber auf den Vorstoß der Koniferen in die offene Tundra.

Das Gesamtbild, das sich aus den Ergebnissen aller Teilstudien ergibt, beschreibt eine eher verhaltene Reaktion der Kiefer auf die regionale Klimaerwärmung. Die Fichte verzeichnet sowohl im Bestandsvolumen als auch hinsichtlich der Verjüngung eine positive Entwicklung und lässt eine Ausweitung der Fichtenwaldbestände in Finnisch-Lappland erwarten. Diese Annahmen sind jedoch ausschließlich auf die Ergebnisse einer einzelnen Untersuchungsmethode begründet. Der Verjüngungs- und Wachstumserfolg der Kiefer ist hingegen stark Standort- und Störungsabhängig, wie sowohl das Monitoring, die dendroökologische Analyse als auch die Satellitenbildauswertung erkennen lassen. Hier konnte bisher noch keine eindeutige Tendenz der Kiefernwaldentwicklung aus den Ergebnissen abgeleitet werden. Die Resultate der Studie belegen eine Verdichtung der Kiefernbestände, die nachfolgend adulte, vitale Samenbäume aus dem bislang noch recht jungen Baumgrenzökoton hervorbringen kann. Eine zeitverzögerte Baumgrenzverschiebung durch natürlich Verjüngung kann daher angenommen werden, sobald eine Verbesserung der klimatischen Bedingungen und eine Abnahme der externen Störungen eintritt und die Mortalitätsrate junger Kiefern verringert.

List of publications

I. Franke, A.K., Aatsinki, P., Hallikainen, V., Huhta, E., Hyppönen, M., Juntunen, V., Mikkola, K., Neuvonen, S. and P. Rautio. 2015. Quantifying changes of the coniferous forest line in Finnish Lapland during 1983–2009. *Silva Fennica* 49 (5): 1–18.

II. Franke, A.K., Bräuning, A., Timonen, M. and P. Rautio. 2017. Growth response of Scots pines in polar-alpine tree-line to a warming climate. *Forest Ecology and Management* 399: 94–107.

III. Franke, A.K., Feilhauer, H., Bräuning, A., Rautio, P. and M. Braun. Remotely sensed estimation of forest area change in the polar and alpine tree-line ecotone in Finnish Lapland during the last three decades. *Submitted to Forest Ecology and Management.*

Author’s contribution to the Publications

Publication I

Title: Quantifying changes of the coniferous forest line in Finnish Lapland during 1983–2009
Published in: Silva Fennica in 2015
Co-authors: Pasi Aatsinki, D.Sc. (For.) Ville Hallikainen, PhD Esa Huhta, D.Sc. (For.) Mikko Hyppönen, Vesa Juntunen, Kari Mikkola, Dr. Seppo Neuvonen, PhD Pasi Rautio

Contribution: The monitoring of the sampling plots, thus the data acquisition was done by field workers of Finnish Forest Research Institute (Metla) during 1983−2009. The first results of the project were published in 2002 and 2006 by, i.a., Vesa Juntunen and Seppo Neuvonen. The datasets until 2009 were statistically analysed by Ville Hallikainen who computed and visualised the results for the publication in Table 2−4 and in Figure 6 and 7. Ville Hallikainen was also author of the chapter 2.2. Kari Mikkola was responsible for the Table 1, and the Figures 1 and 2. Figure 4 was designed by Jouni Hyvärinen. The first author designed the Figure 3 and modified the Figures 1, 4 and 5. The subsequent publication covered the findings of the entire study during 1983−2009. All chapters of the publication, excluding the chapter 2.2, were written by the first author and submitted to *Silva Fennica* in responsibility of the first author. The research stay in Finland during 2014−2015 was applied by the author and gently funded by DAAD. All co-authors confirmed their contributions as stated above.

Publication II

Title: Growth response of Scots pines in polar-alpine tree-line to a warming climate.
Published in: Forest Ecology and Management in 2017
Co-authors: Prof. Dr. Achim Bräuning, Mauri Timonen, PhD Pasi Rautio

Contribution: The author planned and conducted the field work for the dendroecological sampling in Finnish Lapland and acquired funding by Luke, FGG, FAU and DAAD. During the two weeks of sampling, the author was supported by Hannu Herva and Jari Hietanen. The subsequent data preparation, ring-width measurement and statistical analysis were entirely done by the author in the laboratories of Luke in Finland and the Institute of Geography in Germany. The findings were published by the author in *Forest Ecology and Management*. The author was responsible for all chapters of the article and the entire process of article publication. The co-authors supported the author with their expertise during the analysis and during the publication process. All co-authors confirmed their contributions as stated above.

Publication III

Title:	Remotely sensed estimation of forest area change in the polar and alpine tree-line ecotone in Finnish Lapland during the last three decades
Submitted to:	Forest Ecology and Management in 2019
Co-authors:	Prof. Dr. Hannes Feilhauer, Prof. Dr. Achim Bräuning, PhD Pasi Rautio, Prof. Dr. Matthias Braun

Contribution: The author acquired the datasets for the analysis by open source and applied for high-resolution satellite data from the BlackBridge Science Archive (RESA) in 2014 which was granted. The data preparation, analysis and visualization of the data were entirely done by the author with technical support by Prof. Dr. Hannes Feilhauer. The author was again responsible for all chapters of the following article and the entire process of article publication. The co-authors supported the author with their expertise during the analysis and during the publication process. All co-authors confirmed their contributions as stated above.

Abbreviations and acronyms

ANOVA	Analysis of Variance
AVHRR	Advanced Very High Resolution Radiometer
BP	Before present
C	Celsius
cm	centimeter
CO_2	Carbon dioxide
DAAD	Deutscher Akademischer Austauschdienst
d.d.	degree days
DEM	Digital Elevation Model
DOY	Day of the year
dpi	dots per inch
df	degrees of freedom
E	East
EFINORD	North European Regional Office of European Forest Institute
ECAD	European Climate Assessment and Dataset
EPS	Expressed population signal
EROS	Earth Resources Observation Satellite
ESRI	Environmental Systems Research Institute
F	Forest zone
FAU	Friedrich-Alexander University Erlangen-Nuremberg
FGG	Fränkische Geographische Gesellschaft
FI	Finland
Fig.	Figure
FJ	Fjell zone
FL	Forest-line zone
FMI	Finnish Meteorological Institute
ha	hectare
GDD	Growing Degree Days
IPCC	Intergovernmental Panel of Climate Change

km	kilometer
Luke	Luonnonvarakeskus/Natural Resources Institue of Finland
m	meter
m a.s.l.	meters above sea level
Metla	Metsäntutkimuslaitos
mm	millimeter
MODIS	Moderate-resolution Imaging Spectroradiometer
MS	Mean sensitivity
N	North
NAO	North Atlantic Oscillation
NASA	National Aeronautics and Space Administration
NDVI	Normalized Difference Vegetation Index
NDVI-RE	Red Edge Normalized Difference Vegetation Index
NIR	Near Infrared
NLS	National Land Survey of Finland
NoJ	Northern Juvenile pines
NoM	Northern Mature pines
n.s.	not statistically significant
OAC	Overall Accuracy
OLI	Operational Land Imager
PA	Producer’s accuracy
P-N	northern pine region
P-S	southern pine region
RBar	inter-series correlation
RCS	Regional Curve Standardization
RESA	Rapid Eye Science Archive
sig.	statistically significant
SNR	signal to noise ratio
SoJ	Southern Juvenile pines
SoM	Southern Mature pines
std	standard deviation
S-E	eastern spruce region

S-W	western spruce region
T	Temperature
TM	Thematic Mapper
TL	Tree-line zone
TOA	Top of Atmosphere
UA	User’s accuracy
USGS	U.S. Geological Survey
Y_0	year of germination

The months are abbreviated:

Jan	January
Feb	February
Mar	March
Apr	April
May	May
Jun	June
Jul	July
Aug	August
Sept	September
Oct	October
Nov	November
Dec	December

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PhD thesis

1 Introduction

The recent decades, starting from the 1980s were the warmest 30-year period of the last 1400 years in the Northern Hemisphere, with temperatures increasing approximately by 0.85 °C since 1880 (IPCC 2014a). In Europe, the highest temperature increase was detected in the high latitudes over Scandinavia since the 1980s, which is described as a phenomenon called Arctic Amplification. Due to internal feedback processes, temperatures in the Arctic have increased twice as fast as in the mid-latitude regions. The temperature rise in Finland was about +2.3 °C since the mid-19th century, reaching even +5.0 °C during the winter season (Finnish Meteorological Institute [FMI] 2016). When the sea ice melts in the Arctic Ocean and snow coverage is reduced over terrestrial surfaces, the albedo from darker, ice-free surfaces is significantly reduced, absorbing more heat from solar radiation than before (Myeni et al. 1997). The climate-induced changes of the surface characteristics in high-latitude regions lead to a net-warming effect, which in turn amplifies environmental response (Jeong et al. 2012). The warming has taken place mostly during the winter and spring-time seasons (Klein Tank et al. 2002; ACIA 2005; Høgda et al. 2013; Aakala et al. 2014; IPCCa 2014; IPCCb 2014), eventually prolonging the growing season towards an earlier onset of spring. Besides, annual precipitation has increased in Northern Europe and climatic extremes, such as hot days during summer became more frequent (IPCCb 2014).

Plants in the high-latitude boreal forest zone and arctic tundra have to deal with adverse environmental conditions, like a short growing season, low temperatures and nutrient supply as well as sparse light in winter (Kallio 1986; Heikkinen et al. 2002). Environmental changes as enhanced temperatures or additional water supply may change the length of the growing conditions remarkably, especially in the alpine and polar tree-line ecotone, where trees grow at the limit of their ecological range. The forest-line ecotone of the boreal zone separates treeless tundra from closed boreal forests and is one of the Earth's largest vegetation transition zones, extending more than 13 000 km around the Northern Hemisphere (Callaghan et al. 2002). Trees need to pass through all phenological phases from bud break to seed production in short growing seasons of regionally less than three months, and produce sufficient seed crops during sequences of favourable years (Langer 2010; Seo et al. 2010). In this regard, temperature is the dominant regulating factor for growth and survival of the tree vegetation (Esteban et al. 2000; Heikkinen et al. 2002; Juntunen et al. 2002); hence, already small temperature changes can increase seed production, seedling establishment and tree growth significantly (Kallio et al. 1986; Varmola et al. 2004; Grace et al. 2002; Hilli et al. 2008). Findings of sub-fossil pine trunks beyond the current tree line refer to a warmer-than-present climate between 8 000 and 4 000 BP, and a forest line located already at higher altitudes and latitudes than today (Eronen et al. 2002; Heikkinen et al. 2002; Seppä et al. 2002; Kultti et al. 2006) which then retreated again during a subsequent colder period to the present extent (Aakala et al. 2014). Under current warming, a return of the alpine and polar forest line to the previous distribution limit is expected, expanding coniferous forests towards the open tundra.

A vegetation shift from tundra to forest vegetation may additionally change the surface reflectance values, especially during the snow-covered season when a high conifer and shrub abundance potentially reduces the albedo over otherwise closed snow pack (Harding et al. 2002; Chapin et al. 2005; Sturm et al. 2005; Moody et al. 2007; Pearson et al. 2013). The forest cover absorbs more incoming solar radiation than tundra vegetation also during the summer months, and may lead due to increasing evapotranspiration to a higher moisture content of the troposphere (Swann et al. 2010; Jeong et al. 2012). This, in turn induces a net-warming effect of the ecosystem and potentially promotes large-scale circulation changes in Arctic regions (Callaghan et al. 2002; Jeong et al. 2012; Miller and Smith 2012; Pearson et al. 2013; Zhang et al. 2013). Conversely, massive amounts of carbon are stored in needles and woody stems of conifers, whereas the carbon sequestration of graminoids or shrub vegetation is lower (Watson 2000; Sturm et al. 2005; Wramneby et al. 2010). The expansion of woody vegetation has thus to be taken into account when analysing potential changes of global carbon fluxes. Determining the course and extent of vegetation shifts in the high-latitude regions is therefore of high interest for policymakers and forest management, and for modelling future prospects of climate change.

Evidence for increasing photosynthetic activity in the high latitudes of the Northern Hemisphere was already detected by satellite observation and related to prolonged growing seasons and higher temperatures during winter and spring (Myeni et al. 1997; Wilmking et al. 2004; Soja et al. 2007; Jeong et al. 2012). A *greening of the Arctic* was found to arise predominantly from expanding shrub communities and graminoids with increasing leaf areas, while the conifers showed inconsistent response to warming (Sturm et al. 2001; Wielgolaski 2005; Bunn and Goetz 2006; Lopatin et al. 2006; Forbes et al. 2010; Goetz et al. 2011; McManus et al. 2012; Hofgaard et al. 2012; Zhang et al. 2013). The responses to rising temperatures were species- and site specific and not homogeneous during the 20th century. While growth response and tree-line advance were detected during the mid 20th century, a similar trend was partly missing in the beginning of the 21st century (Linderholm et al. 2003; Dalen and Hofgaard 2005; Holtmeier and Broll 2011). Contrariwise, in some sites, conifers responded also positively to warming during the recent years, depending on location and slope exposition (Danby and Hik 2007; Hallikainen et al. 2007). Environmental disturbances, as pest outbreak or increasing snow damage (Gregow et al. 2011; Jalkanen 2003; Holtmeier 2005; Heikkinen et al. 2002) and site composition may eventually mask the benefits of climate warming and lead to varying responses within the same tree species.

From the above it is evident that further research is needed to reliably estimate vegetation changes and the adaptation of boreal conifers to climate change. However, the boreal forest zone is the most extensive forest belt in the world and field-based studies can only cover a very limited area of the entire vegetation zone. In most studies, only one method is used to analyse environmental changes in a certain study site, while the relation to the surrounding environment or further outcomes of differing methods in the same area are missing. The project aims to combine three different methods to change the perspective on environmental changes from micro- to macro-scale in the boreal forests of Fennoscandia. In Finnish Lapland, a monitoring project was established already in 1983 to monitor regeneration and growth of Scots pine and Norway spruce regularly in five-year intervals along elevation gradients aligned along a North-South transect. Changes in the regeneration success, mortality and volume of growing stock of conifers in changing environments were quantified. The analysis was, however, restricted to the established plots and time frames on forest-stand level, lacking of a continuous and large-scale measurement of tree-line changes. Growth responses may vary between sites, between different age classes of trees and between years, being eventually affected by temporal disturbance regimes. A more detailed view on the very complex boreal forest biome is consequently required when analysing growth responses of conifers to climate change. Within the project, it was therefore planned to complement the monitoring data by dendroecological sampling and remote sensing, with the focus on Scots pine as a key species in the polar and alpine tree-line ecotone in Finnish Lapland, to extend the temporal and spatial perspective of the plot-based monitoring approach. The combination of methods allows an upscaling from the micro-scale level of tree individuals by tree-ring analysis, to the dynamics of whole tree stands by monitoring towards the macro-scale level by remote sensing.

The major aims of this dissertation thesis are:

1. to analyse the latest data sets of the monitoring project and to assess possible site-specific trends in the volume of growing stock and tree numbers of Scots pine and Norway spruce in the study area.

2. to analyze long-term growth trends of Scots pine by differentiating between the growth of juvenile and mature trees in a northern and southern distribution area.

3. to extend the study area around the monitoring sites by remote sensing. Thereby, the local findings of 1) and 2) should be set in a regional context, with special attention on possible relocations of the pine tree line and on possible changes in the vegetation pattern.

2 The study area

2.1 The climate zonation of Finland

Finnish Lapland is the largest administrative and northernmost region of Finland, located between latitudes 65° and 70° N and longitudes 20° and 30° E in Northern Europe (Fig. 1). Between Russia in the East and Norway and Sweden in the West and North, Finnish Lapland belongs to the circumboreal region that stretches across Eurasia and North America. The high-latitude regions are characterized by sparse light during winter when the sun does not rise above the horizon for up to 51 days in the northernmost corner of Finland during the polar night (FMI 2016). Mean day lengths of 4 hours near Lake Inari (Johannessen 1970) shorten the light availability noticeably, before the sun rises again towards the spring-time season. During summer, days are bright with sunshine of up to 24 hours, compensating partially the deficit in net radiation during the winter season (Johannessen 1970). However, the sun angles are low and the outgoing solar radiation exceeds in total the incoming radiation, forming an annual energy deficit in the Polar Regions north of 60° N. The seasonality of the solar angle is one factor of the climatic gradient from South to North, causing a related zonation of vegetation patterns in Finnish Lapland.

Secondly, the proximity to the North Atlantic Ocean, the Gulf of Bothnia and the Scandinavian mountain range impacts the climatic conditions in Finnish Lapland and forms highly varying weather conditions over the year (Linderholm et al. 2010; Mikkonen et al. 2014). The Gulf Stream, which comes from the North Atlantic Ocean towards Western Europe, heats up the Norwegian Sea and the Arctic Ocean and evens out the temperatures in Northern Europe, which tend to be several degrees warmer than temperatures in North America in the same latitudes (Kallio et al. 1986; Autio and Heikkinen 2002). Warm and moist air masses are transported from North America to Northern Europe with the westerly winds of the Polar front, crossing the Scandinavian mountains towards the East (Johannessen 1970). The western, windward exposed sites of the Scandes are characterized by a maritime climate under influence of high rainfalls, with wet and mild winters. After crossing the Scandes, warmer and drier air masses underlying a föhn-effect reach interior Lapland in the leeward position of the mountain range (Autio and Heikkinen 2002). During warm days in the summer months, the Atlantic air masses may heat up again by latent heat fluxes on their way to the East and bring convective rainfalls to central Lapland (Johannessen 1970).

The strength of the westerly winds is described by the North Atlantic Oscillation (NAO) index measuring the average air pressure difference between the Icelandic low and the Azore’s high (Linderholm et al. 2010). During a positive mode of the NAO index, the westerly winds are strong, transporting warmer and wetter air masses towards interior Lapland and promote warm and wet conditions during the winter season. During the negative mode of the NAO index, the climate is dominated by continental air masses from Russia, leading to cold and dry winters even towards the coastal regions (Linderholm et al. 2010). Temporarily, anticyclones in the Polar front form high-pressure systems crossing Lapland from continental Eurasia and bring stable continental conditions to Lapland for weeks. Then, the summer months are dominated by hot and dry periods, while freezing temperatures prevail during winter. In such situations, the climate of Finnish Lapland is characterized by rapidly changing weather conditions, high cloud coverage from the Atlantic Ocean and high temperature amplitudes between the seasons.

Depending on the exact location within Finnish Lapland, the growing conditions for plants may vary between sites. The climate is more maritime in the northern and southern coastal regions under the influence of the North Atlantic Ocean, but (sub) continental towards interior Finland in proximity to the extensive landmasses of Russia (Hämet-Ahti 1963; Autio and Heikkinen 2002; Linderholm et al. 2010). The landscape in Finland is characterized by gently sloping hills between 200 and 500 m a.s.l. (Kultti et al. 2006; Publication I) which do not form climatic barriers within Finnish Lapland. Hence, the climate changes gradually from South to North, resulting in large-scale homogeneous vegetation patterns.

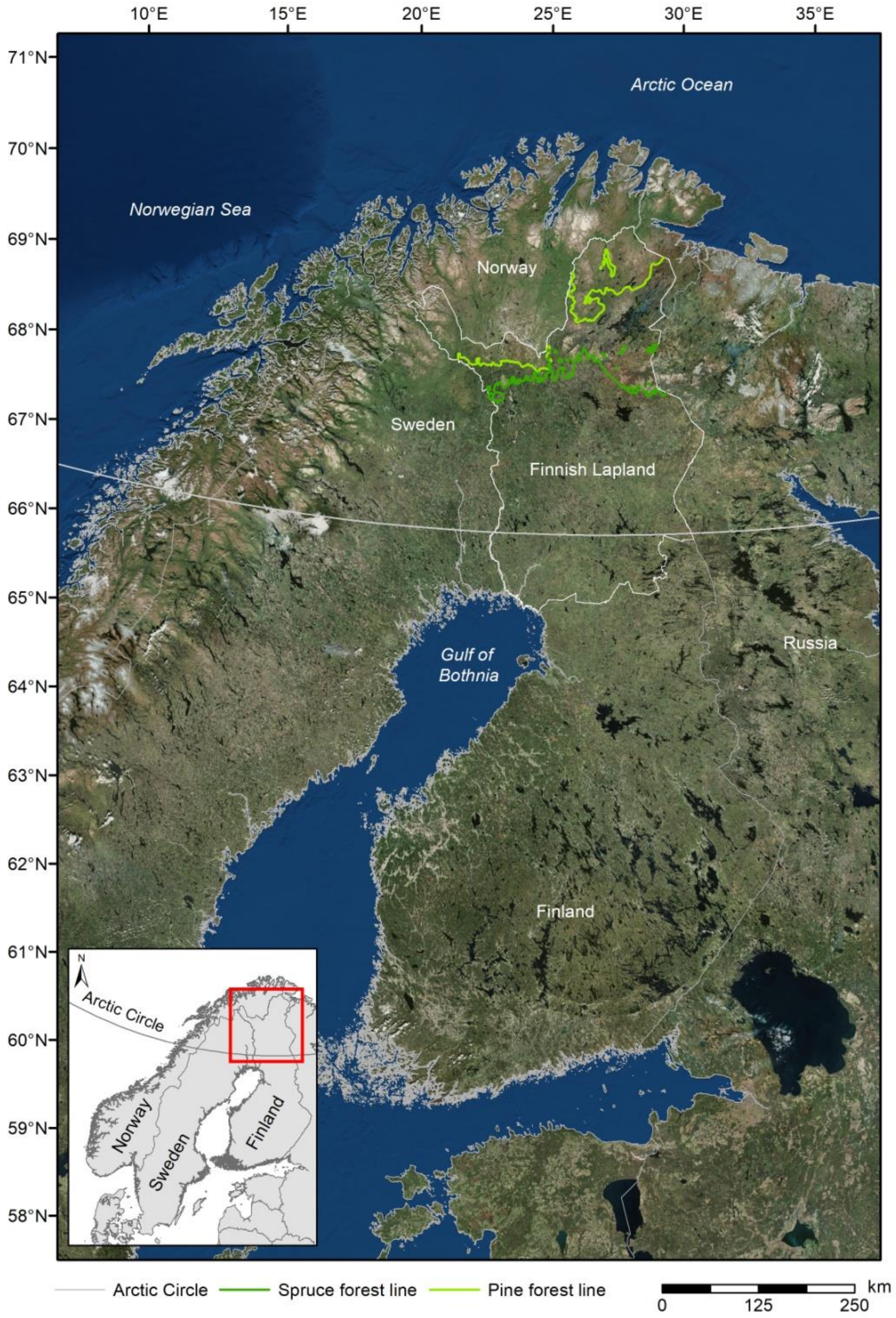

Figure 1. Location of the study area Finnish Lapland displayed with the local Spruce forest line (dark green) and Pine forest line (light green) and the position of the Arctic Circle (Layer source: ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community).

Cold winters and relatively warm summers define a growing season length of < 4 months (+ 5 °C threshold), with July as the warmest month of the year (Seo et al. 2010). The growing season begins in the end of May in northernmost Lapland (FMI 2016), when the daily mean temperatures permanently exceed 5 °C (Tveito et al. 2001). The temperature sum varies from 823 degree days in the southernmost part of the area (long-term average [1981–2010] in Sodankylä) to < 600 degree days in the north (long-term average [1981–2010] in Kevo). The mean annual temperature varies from -3 °C in north-eastern Lapland to 1 °C near the Gulf of Bothnia (Fig. 2; Autio and Heikkinen 2002; FMI 2016). The winter temperatures are on average -12 to -14 °C and can reach even -45 °C to -50 °C in continental Lapland (FMI 2016). The summers are generally cool and cloudy, not exceeding mean daily temperatures of 12 °C to 14 °C (FMI 2016).

Mean annual rainfall varies in northern Finland between 400 and 600 mm (Fig. 2; FMI 2016), resulting in a humid climate in the entire study area due to low evaporation rates (Autio und Heikkinen 2002). Highest monthly precipitation sums but also highest evaporation rates occur in July and August (Vajda and Venäläinen 2005), while the lowest monthly precipitation sums occur in March (Autio and Heikkinen 2002). Much precipitation (about 40 %, Langer 2010; Kultti et al. 2006) falls as snow during the winter season and forms a closed snow cover during October to May or even June (Autio and Heikkinen 2002; Kultti et al. 2006). The number of days with snow cover increases towards the north of Lapland, where snow depth is still high in May, delaying the start of the growing season (Fig. 2; FMI 2016). The season with highest wind speeds is the winter season (FMI 2016).

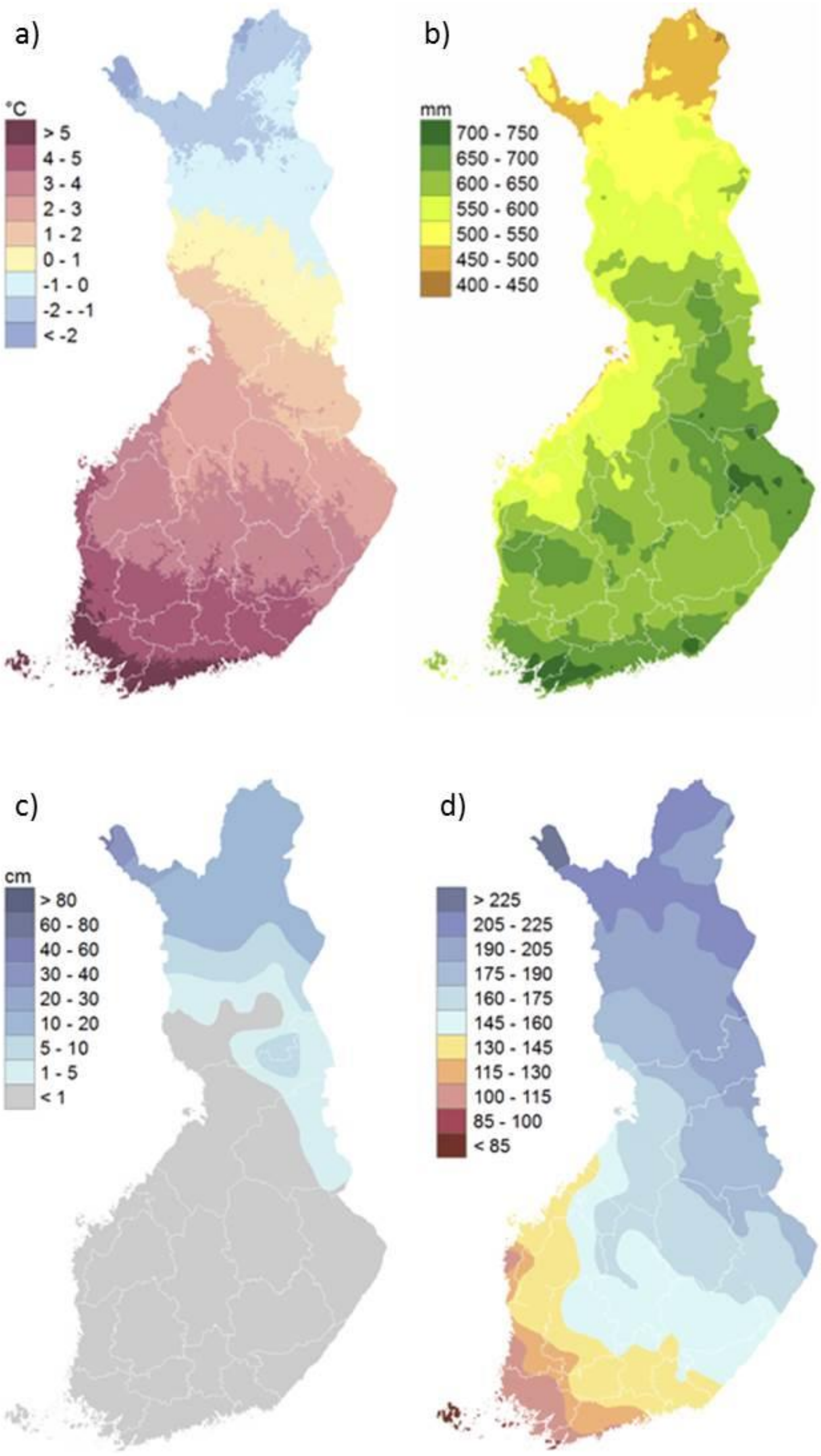

Figure 2. Annual mean temperature (a), annual mean precipitation sum (b), snow depth in May (c) and average number of days with snow cover (d) in Finland during 1981–2010 (Maps: FMI 2016).

2.2 The vegetation distribution patterns in the study area

Finnish Lapland belongs to the boreal forest region which stretches in a circumpolar belt across North America and Eurasia, accounting for approximately one third of the global forest abundance. During the 9th National Forest Inventory of Finland (1996–2003), 20.34 million ha of the Finnish land area were attributed to forest land, thereof 9.17 million ha being located in North Finland (Tomppo et al. 2011). The dominating tree species are the conifers Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.), while Silver birch (*Betula pendula* Roth) and Mountain birch (*Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti) form the deciduous forest belts in the upper altitudes and latitudes (Kultti et al. 2006; Tomppo et al. 2011) (Fig. 3).

The proportion of pine-dominated forests of the entire forest area (65.9 %) exceeds the proportion of spruce-dominated forests (22.0 %) significantly. The proportion of spruce decreases from South (31.0 %) to North (15.0 %), since pine was favored in planting throughout the 1960s and 1970s due to its high quality saw timber, forming now relatively young pine forests in silvicultural stands (Tomppo et al. 2011). While low temperatures and low availability of light as well as a shortage of nutrients in poor soils limit tree growth in the high-latitude regions (Sutinen and Niemelä 2000), conifers have adapted well to these adverse conditions. The formation of evergreen needles allows conifers to immediately start photosynthesis when the temperature exceeds the respective threshold during spring (Wehberg 2007). The pillared growth form maximizes the surface for light exploitation during low sun angles and reduces the risk of crown breaks due to heavy snow load during the winter season (Parachnowitsch 1993).

During the growing season, conifers store photosynthetic products such as carbohydrates and prepare for dormancy when the temperature falls and the day length shortens towards autumn (Sutinen and Niemelä 2000). Photosynthetic activity decreases strongly when night frosts occur or when daytime temperature drops below zero (Kolari et al. 2007). The water content in the tissues decreases and substances protecting the cell membranes accumulate within the cells to accomplish the frost hardiness of the trees. Due to the reduced surface of the needle leaves with thick cuticle and closing stomata during winter, trees are already protected to a certain extent from frost drought during freezing winter temperatures. However, when the temperature rises in spring, water becomes available from the soil and in the tissues, reducing the frost hardiness of the trees for starting photosynthetic activity. Depending on latitude, bud break in Lapland begins during early to mid-May (Salminen and Jalkanen 2015). During this time, the tissues are on risk to be damaged by spring frosts and hence are sensitive to rapidly changing daily temperatures, as to be found in regions under maritime conditions (Cannell and Smith 1986; Sutinen and Niemelä 2000; Salminen and Jalkanen 2015).

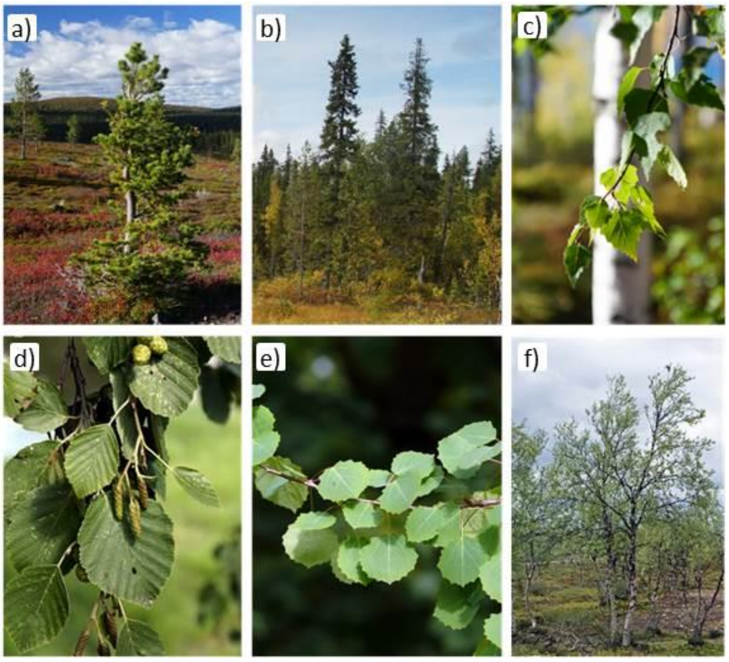

Figure 3. Abundant tree species in Finnish Lapland: a) Scots pine (Pinus sylvestris L.), b) Norway spruce (*Picea abies* (L.) H. Karst.), c) Silver birch (*Betula pendula* Roth), d) Grey alder[1] (*Alnus incana* (L.) Moench), e) Eurasian aspen[1] (*Populus tremula* L.), and f) mountain birch[1] (*Betula pubescens* Ehrh. ssp. czerepanovii (Orlova) Hämet-Ahti) (up left to bottom right).[1]

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[1] Data source: Lehmuskallio, J.NatureGate. URL: www.luontoportti.com

In northernmost Lapland, in proximity to the coast, deciduous tree species gradually replace the coniferous forest by subarctic birch and shrub communities and form an extensive mountain birch forest belt beyond the coniferous forest line (Juntunen et al. 2002). Contrariwise to North America and North Asia, deciduous species represent the northernmost occurrence of tree vegetation in Europe (Heikkinen et al. 2002; Wehberg 2007). The deciduous mountain birch is better adapted to the unsteady maritime climate with strong winds during the winter season, and to the shallow substrates on the fells (Hämet-Ahti 1963). The deciduous leaves shed during the autumn season and eliminate the risk of frost drought or wind damage during the harsh winter (Oksanen 1995; Wielgolaski 2005). On exposed sites, birch grows in low, multi-stemmed growth forms sheltered from strong winds and ice abrasion under the snow cover, and is able to produce sufficient seed crops already under low summer temperatures (Wehberg 2007; Jepsen et al. 2009). The proportion of birch in the Finnish forest is 10.2 % (Tomppo et al. 2011), mixed with Grey alder (*Alnus incana* (L.) Moench), Eurasian aspen (*Populus tremula* L.), Black alder (*Alnus glutinosa* (L.) Gaertn.) or Mountain-ash (*Sorbus aucuparia* L.), in valleys or near river shores (Kultti et al. 2006; Wehberg 2007) (Fig. 4).

In upper elevations beyond the birch forest, dwarf-shrub communities including mountain bearberry (*Arctostaphylos alpina* (L.) Spreng.), crowberry (*Empetrum nigrum* ssp. *hermaphroditum* L.), purple mountain heather (*Phyllodoce caerulea* (L.) Bab.), European blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.), dwarf birch (*Betula nana* L.), and mosses characterize the alpine (oroarctic) tundra (Hämet-Ahti 1963; Oksanen and Virtanen 1995; Holtmeier et al. 1996; Kultti et al. 2006; Wehberg 2007). The humus layer on the fell tops is shallow and poor of nutrients, and the sites at fell tops are highly exposed to wind pressure. The bare soil and fell rocks are often free of higher vegetation and partly covered by lichens. The subarctic tundra is missing in the territory of Finland and extends beyond the birch forest line towards northernmost Norway.

Figure 4. Abundant shrub species in Finnish Lapland: a) mountain bearberry[1] (*Arctostaphylos alpina* (L.) Spreng.), b) crowberry (*Empetrum nigrum* ssp. *hermaphroditum* L.), c) Heather (*Calluna vulgaris* (L.) HULL), d) Reindeer lichen (*Cladonia rangiferina* (L.) Weber ex F.H.Wigg)), e) European blueberry (*Vaccinium myrtillus* L.), f) dwarf birch (*Betula nana* L.), g) lingonberry (*Vaccinium vitis-idaea* L.), and h) Arctic Kidney Lichen (*Nephroma arcticum* (L.) Torss.) (upper left to bottom right).

2.3 The tree-line ecotone in Finnish Lapland

From low basins to the fell tops of Lapland, the growth conditions for plants become harsher, being characterized by stronger winds, declining temperatures, and more shallow substrates. At the tree line, tree vegetation reaches its uppermost distribution limit and is gradually replaced by birch and shrub vegetation before the bare, lichen-covered fell tops set in. The coniferous forest line follows an isoline of effective temperature sums of 600 degree days in Finnish Lapland (Fig. 5) and is positioned in lower latitudes and elevations than the birch forest line (Heikkinen et al. 2002; Kultti et al. 2006). It is of polar-alpine or alpine character and reaches altitudinal limits of 460 m a.s.l. in the southernmost sites, while it drops down to 190 m a.s.l. in the northernmost sites of the study area (Juntunen et al. 2002). While the forest zone is characterized by dense stands with closed canopies, the canopy closure in the forest-line zone ceases (Hustich 1948; Heikkinen et al. 2002) towards the tree-line zone with between-tree distances of up to 100 m. Single trees or small groups of conifers are mixed with patches of birch, shrubs and fell heath. In southern Lapland, alpine forest lines are more prominent, since pine and spruce are still the dominant tree species. The closed coniferous forest belt reaches the deciduous and shrub vegetation in higher elevations and is gradually replaced by the fell vegetation. In northern Lapland, where the outermost distribution limit of pine and spruce is reached, coniferous forest is restricted to small patches in open stands in the lower elevations among the northwards expanding mountain birch belt (Juntunen et al. 2002). Forest lines in the fell area are of polar-alpine character.

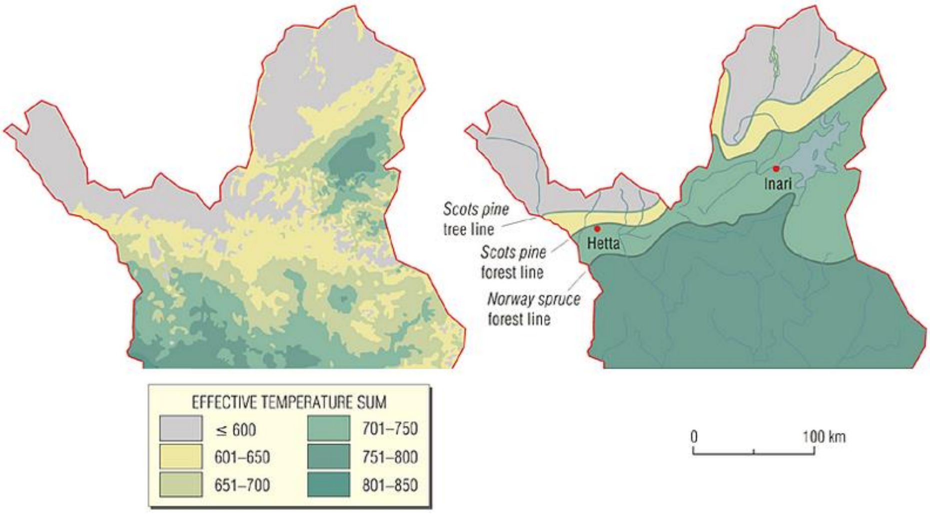


Figure 5. Effective temperature sums and related position of the forest line of Scots pine and Norway spruce in Finnish Lapland (Source: Heikkinen et al. 2002).

Topographic conditions may alter the position of the forest line upwards the fell tops or northwards by providing climatically sheltered sites in valleys or depressions in the mountain birch forest belt (Seppä 1996; Heikkinen et al. 2002; Sutinen et al. 2012). In northern Utsjoki and Kevo, which actually belong to the subarctic birch zone, solitary pines and pine forest stands occur far above and north of the coniferous tree line (Fig. 5; Holtmeier et al. 1996; Holtmeier 2005). They remain partly as relicts from ancient forest lines, which had previously spread under warmer climate far more north than today (Holtmeier et al. 1996). Young pine stands also result from forest plantations of the Finnish Forest Institution Metsähallitus (Wehberg 2007).

The trees in the tree-line zone are considerably smaller in size and often characterized by signs of damage due to snow loads and strong winds in the crown tops (Heikkinen et al. 2002; Holtmeier 2005). The growth forms are, however, mostly upright, reaching growth heights of tree size. With increasing altitude and latitude, only single trees of severely crippeled and partially ground-level growth appear in the forest-tundra boundary, representing the krummholz zone (Holtmeier 1981). The outermost abundance of krummholz represents the tree-species line which hence differs from the tree-line zone. The temperature amplitude is much higher in the open, sparsely vegetated fell areas, where solar radiation heats up the soil during day- and summertime, while during nights and winter the bare ground turns rapidly cold (Autio and Heikkinen 2002; Vajda and Venäläinen 2005; Sutinen et al. 2011). In lower elevations, a closed vegetation cover protects the soil from heating up and keeps the warmth longer when air temperatures fall. The temperature amplitude is hence moderate in the forest stands and the depth and length of soil frost is reduced (Vajda and Venäläinen 2005). Based on interception and shadowing by the vegetation cover, the sites with vegetation are generally more humid than the open, wind-exposed sites on the fells. Under low temperatures and sparsely active soil fauna, pedogenesis is restricted due to low decomposition rates and sparse vegetation cover, resulting in nutrient-poor soils (Kultti et al. 2006). Fertile ground is much rarer in northern Finland and in the tree-line ecotone than in southern Finland and in the forested areas (Wehberg 2007; Tomppo et al. 2011). The snow cover is generally higher in the forest area, where it accumulates and melts up several weeks later than in the exposed, wind-blown and sparsely vegetated fell tops (Autio and Heikkinen 2002; Vajda and Venäläinen 2005).

Especially young pines invading into open sites beyond the forest line are at risk to die in early stages, when growing unprotected from a sheltering snow cover. The snow cover provides wind shelter, a higher soil temperature during winter, and water supply in spring (Dalen and Hofgaard 2005). The survival rates of seedlings increase when being protected under a dense winter snowpack or in the sheltered birch and pine forest stands (Bolli et al. 2007; Holtmeier and Broll 2011). When uncovered by strong winds, seedlings in open sites are at risk for wind, frost damage and reindeer browsing and were found to die on exposed ground (Middleton et al. 2008; Holtmeier and Broll 2011). A compact and long-lasting snow cover may under moist conditions, on the other hand, increase the risk of snow blight infection (*Phacidium infestans* P. Karst) (Jalkanen 2007; Kullman 2007; Holtmeier and Broll 2011; Barbeito et al. 2012) which also reduces the survival rate of seedlings under dense snow cover. Under these conditions, a high amount of coniferous seeds and seedlings die before reaching maturity. Big seed crops by seed-producing old pines in a sequence of favourable years are needed to enhance the survival rate of seedlings in the tree-line zone (Juntunen and Neuvonen 2006) which form new seed trees in and beyond the treeline. In the subarctic biomes, temperature has the main impact on growth and even small temperature changes might promote growth and seed formation for natural regeneration during sequences of favourable years (Heikkinen et al. 2002; Karlsen et al. 2005; Juntunen and Neuvonen 2006; Linkosalo et al. 2009; Høgda et al. 2013; Salminen and Jalkanen 2015). Mild winters, early springs and increasing summer temperatures in warmer periods are expected to improve the growing conditions in Finnish Lapland, particularly in the harsh tree-line ecotone (Kauppi et al. 2014), initiating increased radial growth and seedling establishment probably even beyond the recent treeline under a warming climate (Aakala et al. 2014).

3 Recent developments induced by climate change

The climate in Finnish Lapland underlies a high annual and inter-annual variability and the climate since the early 20th century was characterized by alternations of warmer and cooler periods affecting tree growth (Tuomenvirta 2000). When temperatures increased after the Little Ice Age towards the warm 1930s (Mikkonen et al. 2014), a maximum of natural regeneration was observed until the 1980s (Holtmeier et al. 1996; Autio and Heikkinen 2002; Tuomenvirta 2000; Dalen and Hofgaard 2005; Holtmeier 2005;

Aakala et al. 2014). The seedlings established during this period form the recent tree lines in Finnish Lapland which are of relatively young ages (Holtmeier et al.1996; Sutinen et al. 2012). The mean temperature was quite constant between 1940 and 1970, but rose significantly after 1990, initiating the warmest decade in Finland since the beginning of meteorological measurements (starting in the 1840’s, FMI 2016; Kauppi et al. 2014; Mikkonen et al. 2014).

The annual mean temperature in Finland has risen during 1847–2013 by over 2 °C, exceeding the globally detected trend twice (Mikkonen et al. 2014). The warming has taken place mostly during the winter season (Nov–Jan) and spring-time season (Mar–May), extending the length of the growing season towards an earlier onset of spring (Fig. 6) (see also Kellomäki et al. 1997; Tietäväinen et al. 2010; Høgda et al. 2013; Mikkonen et al. 2014; Salminen and Jalkanen 2015). An earlier start of the growing season of about 12 days was detected, however, predominantly in the southern regions of Fennoscandia, while the northern regions showed a mostly stable or only modest earlier start of the growing season of 2–4 days (Høgda et al. 2013). In addition, the advance of the starting date of the growing season was highest until the 1990s but slowed down and stabilized during the following decades (Høgda et al. 2013). In terms of humidity, increasing precipitation sums were measured during the autumn and winter season, promoting mild and wet winter conditions (Klein Tank et al. 2002; Mikkonen et al. 2014), while the enhanced evaporation rate under warmer temperatures lead to drier conditions during the summer season (Tuomenvirta 2000; Langer 2010). As a result of increasing evaporation rates above warming land and ocean surfaces, slightly increasing cloud coverage was detected in Finland during the last decades (Fig. 6), reducing the sunshine hours during the growing season.

Under the effects of rapid warming, an advance of coniferous tree lines towards the ancient distribution limit was expected. Evidence for a greening arctic were already detected by several field investigations in the boreal region, and correspond to modelled climate-growth simulations for an ongoing warming (Juntunen et al. 2002; Kullman 2007; Middleton et al. 2008; Sutinen et al. 2012; Jeong et al. 2012; Pearson et al. 2013; Aakala et al. 2014; Kauppi et al. 2014): The Finnish National Forest Inventory observed an increase of the forest area by 9 % between 1964 and 2003, predominantly in the northern regions (Tomppo et al. 2011). The volume of the growing stock increased for the main tree species in Finland, including, however, also productive forest land and afforested areas (Fig. 7). According to an experiment of Juntunen et al. (2002), the basal area of conifers as a function of diameter in breast height has increased within study plots in Northern Finland about 1.6 m^2 ha^{-1} in the closed forest stands, 2.3 m^2 ha^{-1} near the forest line, and about 0.2 m^2 ha^{-1} at the tree line. Pensa et al. (2006) detected an increase of height increment, needle production and radial growth of Scots pine near the northern timberline in Lapland since the 1990s. Furthermore, new tree seedlings were found in the northern areas where heath has been the dominant vegetation type (Harsch et al. 2009; Holtmeier 2005; Holtmeier and Broll 2011; Juntunen and Neuvonen 2006; Kullman 2007). The timing of leaf bud burst and flowering advanced towards earlier spring in deciduous tree vegetation (Linkosalo et al. 2009; Salminen and Jalkanen 2015).

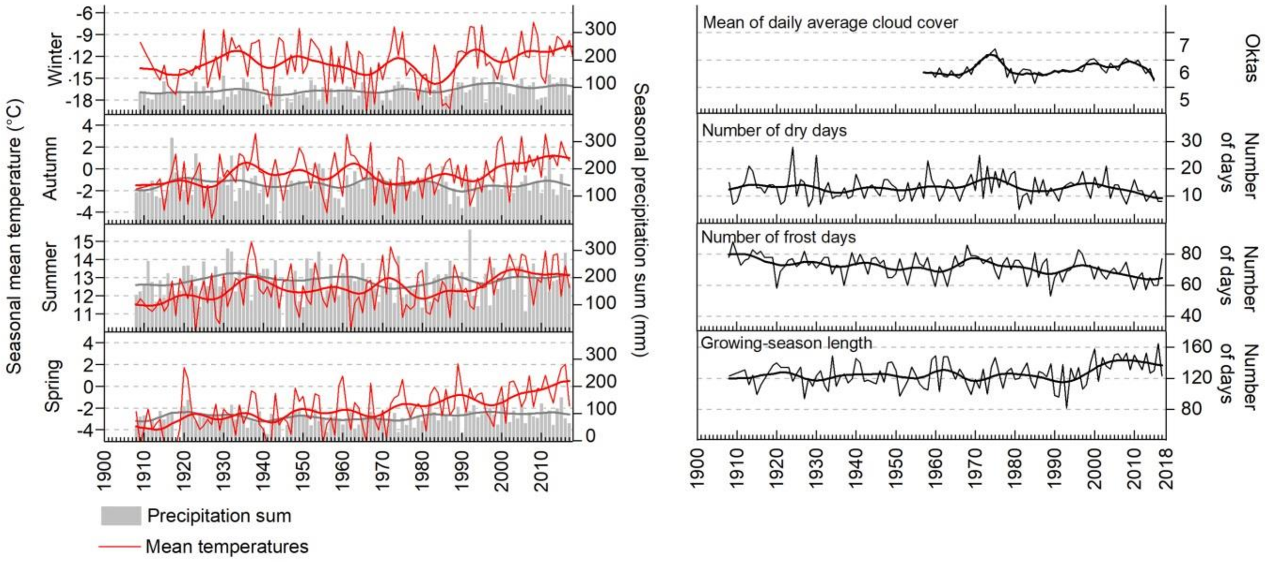


Figure 6. Mean temperature and precipitation sum (left panels) plotted seasonally for the spring (Mar–May), summer (Jun–Aug), autumn (Sept–Nov) and winter seasons (Dec–Feb); and growth-relevant climate parameters (right panels; growing-season length; number of frost days (T < 0 °C), number of dry days (daily precipitation sum < 1 mm), mean of daily average cloud cover) in Sodankylä during 1908–2018 (Dataset: Klein Tank et al. 2002). All series were smoothed by using a 5-points Fast Fourier Transformation.

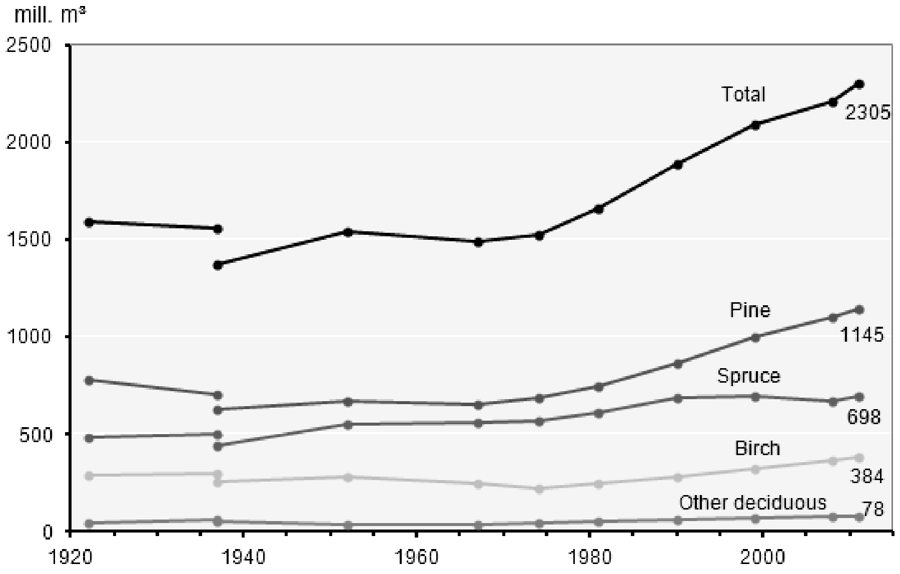


Figure 7. Volume of the growing stock by tree species groups in Finland during 1922–2011 (Metla 2012).

In contrast, Holtmeier et al. (1996) found that seedling establishment increased solely in close proximity to old and healthy seed trees and under open canopies in sheltered stands. In dense forest stands with a closed canopy or in open unsheltered areas, comparable trends were missing (Holtmeier and Broll 2011). Also in greater distance to the seed tree, the seedling density decreased rapidly. According to Hallikainen et al. (2007), pine seedling densities increased remarkably in the southern part of Finnish Lapland, while the populations were instable and tree recruitment was more problematic in the North. Aakala et al. (2014) found that tree recruitment and density advanced rapidly in the 1970s and 1980s, but returned to lower levels in the 1990s. This is in accordance with Dalen and Hofgaard (2005) who mentioned low numbers of pines younger than 10 years in the tree-line zone. In western Fennoscandia, the radial growth of pine showed a reduced sensitivity to temperature during the second half of the 20th century (Linderholm et al. 2003), while trees in the East responded positively to warming. While pine showed limited expansion, the birch tree line was found to advance considerably (Middleton et al. 2008; Hofgaard et al. 2012).

Tree-line responses were thereby highly species- and site-specific and influenced by factors including microclimate, topography, soil, water supply and biotic stress (Heikkinen et al. 2002; Dalen and Hofgaard 2005; Holtmeier 2005; Bunn and Goetz 2006; Danby and Hik 2007). The warming climate of the last decades did not automatically enhance growth and regeneration in the coniferous tree-line ecotone as expected when considering ancient tree lines under a warmer climate. Previous studies in our study area have indicated, however, 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). We aimed to examine the course of tree-line dynamics and vegetation shifts in more detail by studying the vegetation changes in Finnish Lapland and differentiating between sites, altitudes, tree ages and vegetation types.

4 Methods

Within the framework of the present project, three different methodologies were applied to examine growth changes and changes in the spatial extension of conifers in selected locations in the coniferous tree-line biome in Finnish Lapland. Each of the three methods is regarded as a single subproject (Part I–III), which create stand-alone results (Table 1). The results of the individual parts are, however, synthesized to answer the main research questions.

Part I. Monitoring changing biomass of long-term study plots
Part II. Dendroecological analysis of climate-growth responses in ring-width data
Part III. Remote sensing of changing vegetation patterns

The starting point of the investigation was a forest-line monitoring project carried out by Luke and the universities of Helsinki, Oulu and Turku (Kallio et al. 1986). Thirteen study locations were established within the project in 1983 across Finnish Lapland to monitor growth and regeneration of Scots pine and Norway spruce in five-year intervals over several decades (Fig. 8). Part I of the project evaluates the findings of the monitoring project until 2015 and presents the results in a first publication.

Part II focussed on the pine-dominated locations of the monitoring project. Dendroecological sample cores were taken from mature and juvenile Scots pines along elevation gradients in the monitoring sites (red and yellow points in Fig. 8). Aim of the subproject was a climate-growth analysis to examine the long-term growth response of pines of different ages to climate warming and to detect the most relevant impact factors on pine growth during the recent decades. The second publication presents the results of the dendroecological findings. Part I and the field and laboratory work of Part II were carried out in the Luke institute in Rovaniemi / Finland, while the data analysis of Part II and entire Part III were conducted at FAU in Erlangen / Germany.

Part III was again based on the pine-dominated locations of the monitoring project and analysed large-scale changes of vegetation patterns and possible tree-line shifts by applying remote sensing techniques. The results were presented in a third publication and related in a synthesis to the findings of Part I and II. A brief overview of the methods used in the subprojects is provided below, while the detailed materials and methods are described in the respective publications in the Appendix.

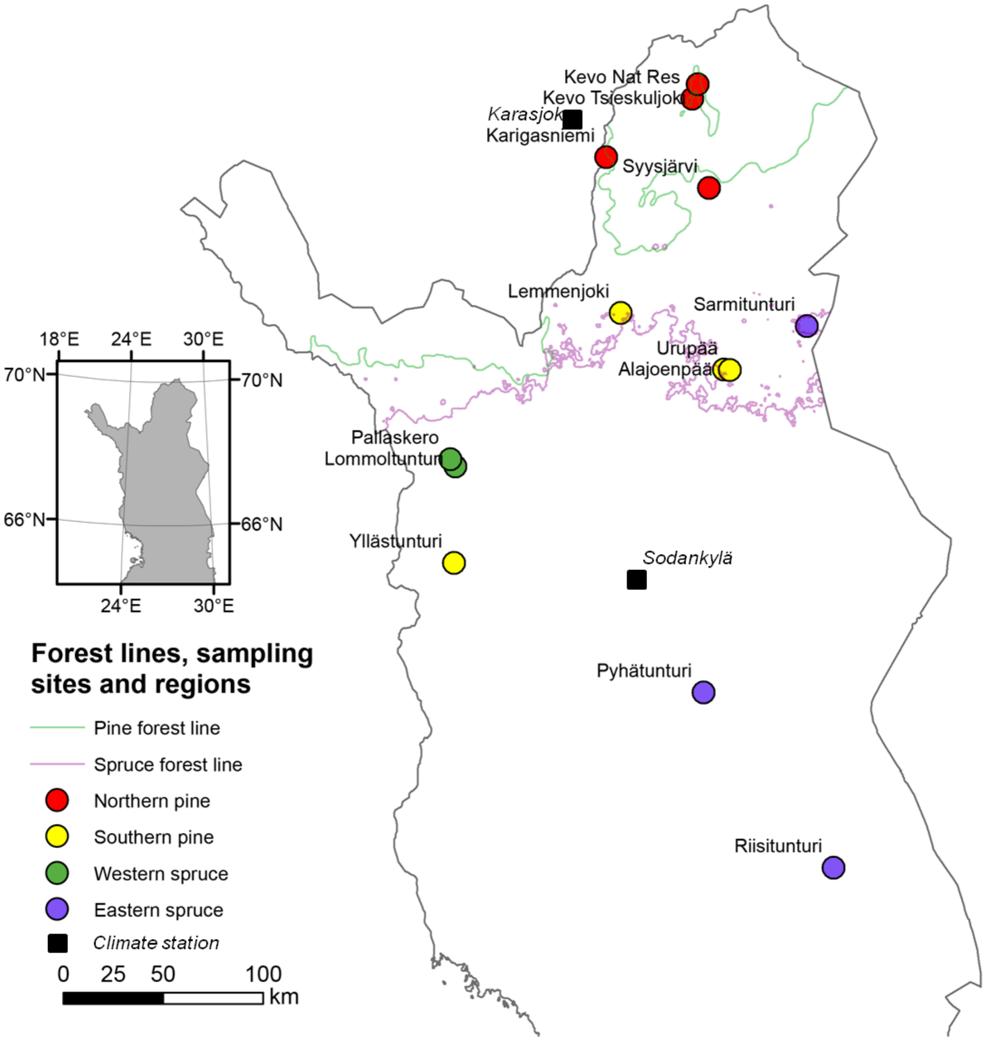


Figure 8. Study locations of the monitoring project (I). The dendroecological sampling (II) and satellite-based analysis (III) were based on the pine-dominated study locations exclusively. Climate data were derived from the climate stations Sodankylä and Karasjok.

Table 1. Summary of the data and subprojects in the present work.

Subproject	Data type	Period	Locations	Data analyzer
I. Monitoring	Stem number of living trees (≥ 2 m height), saplings (< 2 m – ≥ 1.3 m), seedlings (height < 1.3 m) of Scots pine and Norway spruce Volume of growing stock of living trees (> 2 m height) of Scots pine and Norway spruce	1983 1994 1999 2004 2009	Scots pine: Kevo Tsieskuljoki Kevo nat. res. Karigasniemi Syysjärvi Lemmenjoki Saariselkä: Urupää and Alajoenpää Yllästunturi Norway spruce: Lommoltunturi Pallaskero Sarmitunturi Pyhätunturi Riisitunturi	Monitoring: field workers of Metla/Luke Statistics: V. Hallikainen Analysis and publication: A.K. Franke, P. Aatsinki, V. Hallikainen, E. Huhta, M. Hyppönen, V. Juntunen, K. Mikkola, S. Neuvonen, P. Rautio
II. Dendroecology	Ring-width measurements of 963 Scots pines Climatic datasets of Sodanyklä / Finland Karasjok / Norway	1800–2017 continuously	Scots pine: Kevo nat. res. Syysjärvi Lemmenjoki Saariselkä: Urupää and Alajoenpää Yllästunturi	Sampling: A.K. Franke, H. Herva, J. Hietanen Laboratory work: A.K. Franke Analysis: A.K. Franke Publication: A.K. Franke, A. Bräuning, M. Timonen, P. Rautio
III. Remote sensing	satellite images of Landsat-5 Landsat-8 RapidEye	1984–2017 sporadically	Kevo nat. res. Karigasniemi Syysjärvi Lemmenjoki Saariselkä Yllästunturi	Data acquisition: A.K. Franke Analysis: A.K. Franke Publication: A.K. Franke, H. Feilhauer, A. Bräuning, P. Rautio, M. Braun

4.1 Stand monitoring of Scots pine and Norway spruce

The monitoring project was established in 1983 across Finnish Lapland to monitor growth and regeneration of Scots pine and Norway spruce in five-year intervals over several decades. The study area Finnish Lapland 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 (red points and yellow points in Fig. 8), and the spruce-dominated areas into a western and an eastern region (green points and blue points in Fig. 8). The northern pine-sites are located on the northern timberline or in enclaves of pine forests within the mountain-birch belt. Mountain birch is the common species in the northern sites even at the lower elevations and the coniferous tree line reaches altitudes of 180 to 275 m a.s.l. on the fells (Juntunen et al. 2002). The climate is relatively maritime compared to the southern pine-sites. The southern sites are located within the extended boreal forest zone, where conifers dominate the landscape and tree lines are of alpine character in altitudes of 340 to 410 m a.s.l. (Juntunen et al. 2002). The tree-line sites border on dry fell heath or scattered mountain birch stands. The spruce-dominated sites are located in more continental regions of Finnish Lapland towards interior Finland or sheltered by the Scandinavian Mountains by maritime influence. Tree lines reach 445 to 480 m a.s.l. in the western sites, and 370 to 440 m a.s.l. in the eastern sites (Juntunen et al. 2002). The eastern sites stretch across 330 km in north-south direction.

Each region included two to four study locations, giving a total of 13 locations (eight for Scots pine and five for Norway spruce) in northern Finland, all situated on mineral soil types in dry or semi-dry heath (Juntunen et al. 2002). Each of the locations consisted of a sample system of three rows of three circular sample plots (area of 300 m^2 or 500 m^2 towards the tree line) along an altitudinal gradient from forest to tree line (Fig. 9). These three rows were located in at least 100 m distance from each other and differed in vegetation patterns, tree height and stand density. They can therefore be considered as independent sites. 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 the *forest-line zone* (in the monitoring project synonymously used as *timberline zone*), which is defined as the altitudinal limit at which the forest canopy closure ceases (Hustich 1948). The lowest row was established in a closed forest stand representing the characteristics of the *forest zone*. Within these plots, two items were monitored: (1) the number of living trees ($\geq$ 2 m height), saplings ($<$ 2 m and $\geq$ 1.3 m) and seedlings (height $<$ 1.3 m) and (2) the height and diameter at breast height of all trees ($>$ 2 m) within a plot which were used to compute the volume of the growing stock. After the establishment of the plots in 1983, the monitoring was repeated in 1994, 1999, 2004 and 2009.

Climate datasets were provided by the European Climate Assessment & Dataset from 1977 to 2014 for Kevo, Kuusamo and Sodankylä (Klein Tank et al. 2002). To characterize the climatic conditions during the growing season, the annual precipitation sums and the effective temperature sums in degree days were plotted with Fast Fourier Transformation smoothing splines. The degree days were computed for each location during 1961−1990 from a climatic grid, since there were no meteorological stations near the study plots.

For statistical analysis, the average of three plots in each zone was used to provide a reliable estimate for forest stand level demographic processes. Linear mixed models were calculated for two response variables: 1) The sums of the number of trees, saplings and seedlings (ha^{-1}), defined as total *stem number,* and 2) the volume of the growing stock (m^3 ha^{-1}) of trees. The models were calculated separately for pine- and spruce-dominated locations over time. Logarithmic transformation was used for the stem number and square-root transformation for the volume of growing stock to yield unbiased residuals. The model coefficients and their significances were reported. It was tested if the coefficients of time by region and by zone differed from 0 (null hypothesis: $\beta = 0$), indicating significantly increasing or decreasing trends in stem number and volume of growing stock during the 26-year study period. Part I of the study hence aimed to estimate the natural regeneration of Scots pine and Norway spruce in the selected locations and to estimate potential growth increase or growth decline of the established mature stands. The stand dynamics underlie, however, complex interactions with climatic conditions, biotic factors and disturbances, which were not examined but which could have affected the sites substantially in the years between the monitoring activities. A yearly resolution of growth responses and the detection of the most growth-relevant climatic factors were therefore subject of the second part of the study which supplemented the monitoring by dendroecological analysis of the selected sites.

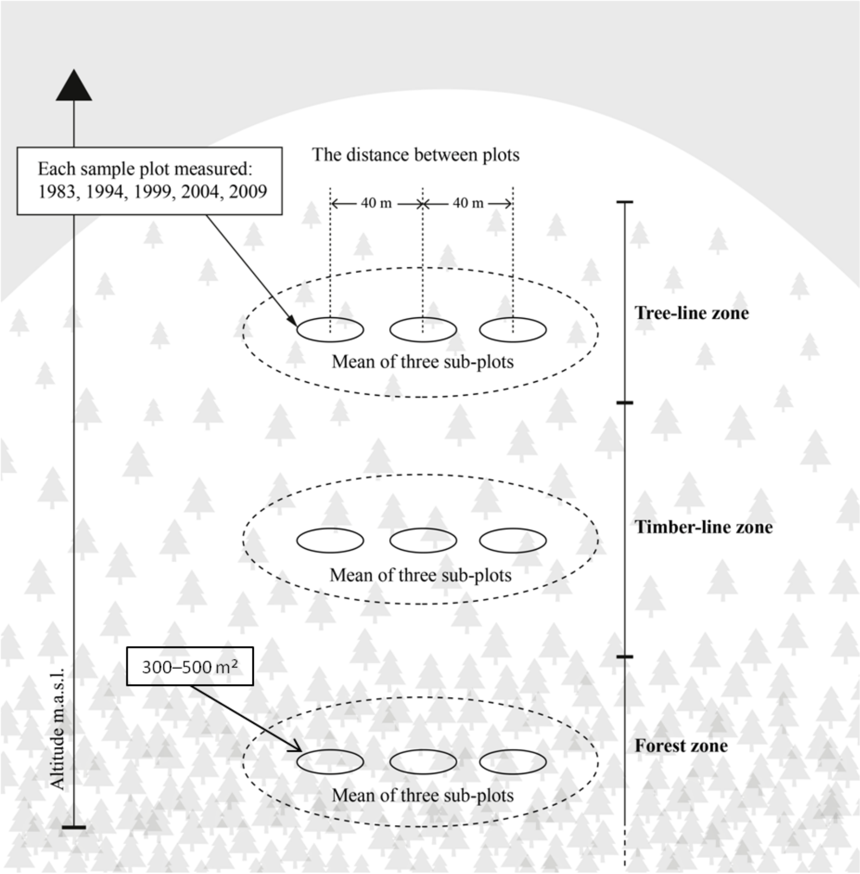


Figure 9. Sampling design in each of the 13 study locations. The sampling was done on three sample plots in forest and timber- and tree-line zones in 1983, 1994, 1999, 2004 and 2009.

4.2 Dendroecological growth analysis of Scots pine

The dendroecological sampling was related to six pine-dominated study locations of the monitoring project (Fig. 8) and carried out in August 2014 and 2015. The locations

Karigasniemi and Kevo Tsieskuljoki were excluded from the analysis to keep the sampling effort at a reasonable level. Pine trees were sampled in the forest zone, forest-line zone and tree-line zone of the monitoring locations along the contour line around the monitoring plots. Healthy solitary pine trees (> 2 m) of juvenile and mature ages which did not show any signs of damage, deformation or disease in the stem or crown shape were selected for tree-ring analysis. The sampling focussed if possible on isolated, unsheltered trees to avoid disturbance signals of changing stand structure in the tree-ring data. Two cores were collected with an increment borer at breast-height from each tree (Fig. 10). In each of the three elevation zones, 30–60 trees were sampled, generating a dataset of at most 180 sample trees for each location. The complete dataset contained a total amount of 963 sample trees. The sampled cores were scanned with a high-resolution (3200 dpi) flatbed-scanner and tree-ring widths were measured by using the software *CooRecorder* and *CDendro* (Cybis Elektronik & Data AB 2008) or, if a reliable detection of the rings was not possible in the scanned image, by using the *LINTAB*™ measuring station (Rinntech, Germany). The samples were cross-dated by site by using the software *TSAP-Win* (Rinn 2010). To reduce statistical noise and to strengthen the climatic signal, sample trees with signs of damage, compression wood or extensive parts of missing rings were excluded from further analysis. Thereby, a total amount of 905 sample trees remained for constructing the final chronologies.

We computed the mean annual growth rates of juvenile pines and tested the statistical significance by a two-way factorial analysis of variance (ANOVA) with zone and location as factors. Thereby, differences in the growth rates between different locations and elevation zones were detected. The raw ring-widths were afterwards standardized and transformed into site-specific residual chronologies by zone and location. The residual chronologies were tested by calculating Pearson correlation coefficients for similarities in the growth patterns. The residual chronologies were afterwards correlated with relevant climatic parameters by Pearson correlations. We tested the mean temperature, number of warm, cold and frost days, precipitation sum, number of snow days, average of monthly snow cover, cloud coverage, solar radiation, maximum wind speed, and the strength of the North Atlantic Oscillation (NAO) (Datasets: European Climate Assessment & Dataset [Klein Tank et al. 2002];

Norwegian Meteorological Institute and the Norwegian Broadcasting Corporation [Yr 2017]; Climate Analysis Section [Hurrell 2003]). The Pearson correlations were restricted to the time span 1950–2014, where we had the highest sample size of the tree-ring data and therefore the highest reliability.

However, examining long-term growth trends in the radial growth of Scots pine was also aim of the study. The relevant climatic parameters were plotted and analyzed by linear regression and ANOVA for significant trends during the last decades. The raw ring-widths were standardized in a second detrending step by Regional Curve Standardization (RCS), which retains long-term growth trends unrelated to age trends (Briffa et al. 1992). Therefore, we divided the tree-ring data by age / year of germination (juvenile trees: $Y_0 \geq 1950$, ranging from 1950–2014; mature trees: $Y_0 \leq 1900$, ranging from 1800–2014) and by region (north; south) and computed four chronologies: Northern mature trees and northern juvenile trees, southern mature trees and southern juvenile trees. The four groups were selected to achieve a sufficient sample size throughout each year of the chronologies. In contrast to the monitoring approach, we attributed Lemmenjoki to the northern region to ensure a similar and comparable sample size for statistical analysis in both regions. Since the forest stand composition in Lemmenjoki apparently did not differ considerably from the stand in Kevo and the Pearson correlation indicated similar climate-growth responses, this was considered to be statistically justified. The chronologies were smoothed with Fast Fourier Transformation smoothing splines to emphasize decadal variations in the growth patterns. A pointer year analysis was performed to analyze climatic event years with relative growth changes of > 20 % from the current to the next year occurring in at least 75 % of the sample trees (Schweingruber et al. 1990). The relation of growth variations to the recent warming period 1996–2014 was tested by linear regression and ANOVA. An evolutionary correlation was computed for the southern mature trees and the mean temperature, the precipitation sum, the number of frost and snow days using DendroClim software (Biondi and Waikul 2004). Thereby, the consistency of the climatic impact factors was tested during the time span of 1913–2013 with a base length of 40 years.

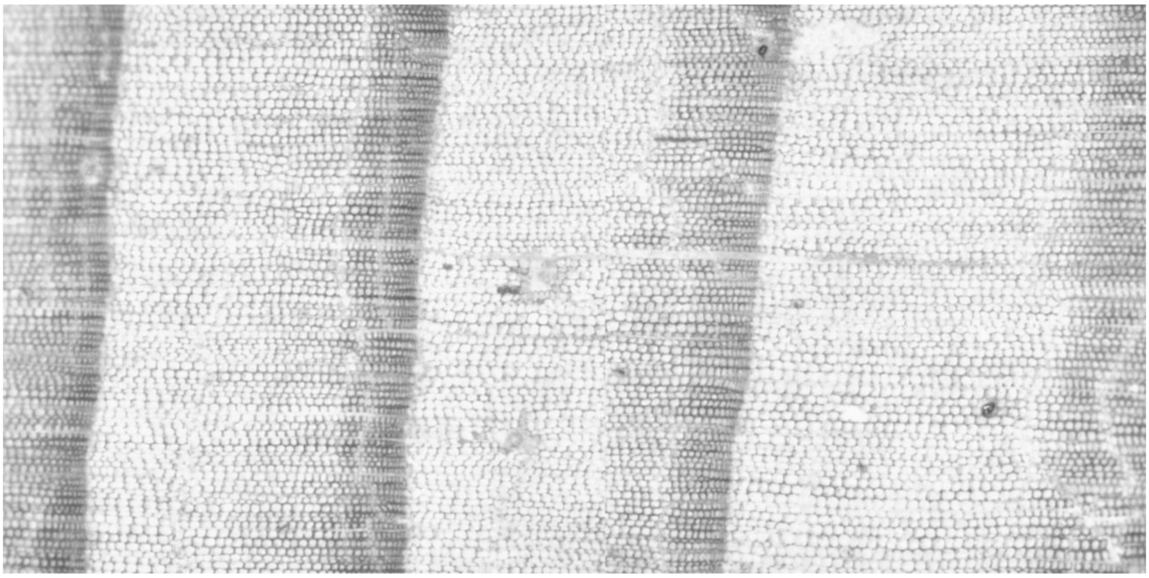


Figure 10. Tree rings within a sample core of Scots pine for ring-width measurements. The thick-walled cells of the latewood clearly mark the tree-ring border towards the wide cells of the earlywood.

4.3 Analysis of vegetation changes in multispectral imagery

While parts I and II of the thesis studied the growth changes of conifers on a plot level, the large-scale variations in vegetation patterns during the last decades was analysed by applying remote sensing techniques. Thereby it should be evaluated whether the results of the plot-based monitoring project are representative for the surrounding forest area in Finnish Lapland.

Again, the pine-dominated sites of the monitoring study were chosen for the analysis, including the location Karigasniemi. Several multiband satellite images of Landsat-5 (TM), Landsat-8 (OLI) (Datasets: USGS Earth Explorer [Landsat: U.S. Geological Survey (USGS) Earth Resources Observation and Science (EROS) Centre 2017), and RapidEye (Datasets: BlackBridge 2015) sensors were obtained during the peak growing season during 1984 to 2017 for the study area. Eleven to sixteen cloud-free images were used for each location to display the studied time period sporadically. It was not possible to obtain a scene for each year over the studied period due to high cloud coverage and incomplete data coverage. The available images were clipped to a maximum extent of 10 km x 10 km, framing the monitoring sites in the centre. The study area was thereby expanded from the small monitoring plots to a larger area, however keeping a comparable sample of the local site conditions in proximity to the studied fell. Pre-processing of all images was performed to mitigate noise by atmospheric scattering and topographic effects (Fig. 11). The subsequent analysis consisted of four steps:

(1) creating of NDVI time-series for a) the entire scene and b) for the elevation zones
(2) NDVI change detection
(3) NDVI-profiling of the elevation zones for the detection of tree-line shifts
(4) Random Forest land-cover classification

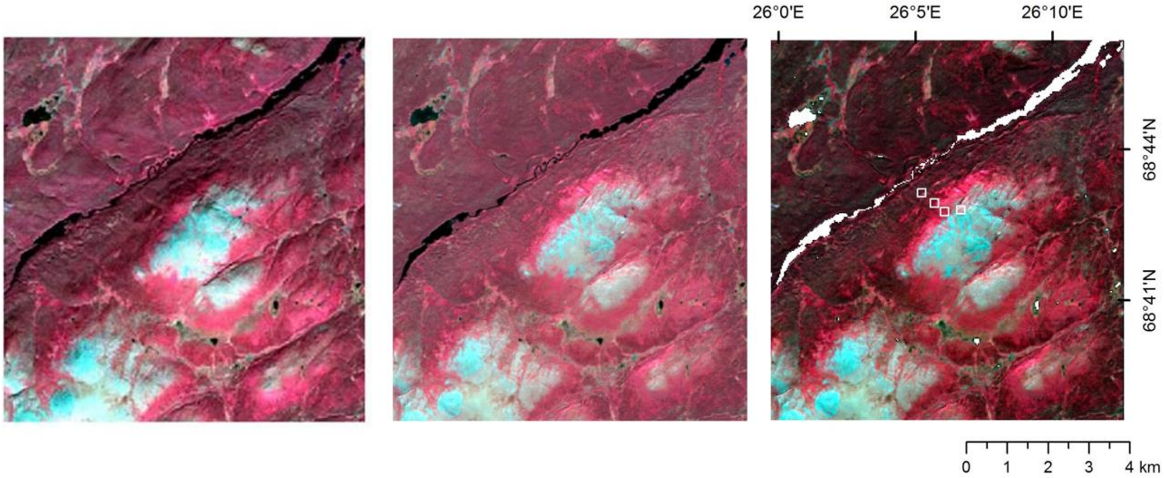


Figure 11. The clipped image of the study location Lemmenjoki in false colour imaging using the NIR band (band 4), the red band (band 3), and the green band (band 2) of Landsat-5. Blue colours indicate areas of no or sparse vegetation as fell tops while reddish colours indicate areas of different vegetation patterns. Topographic effects were removed by pre-processing (left to central image) and water bodies masked to ensure noise-free NDVI analyses (right image). Subsamples (white squares) were established in different elevation zones to compute zone-specific NDVI values.

(1a) For a first analysis of the vegetation cover, the normalized difference vegetation index (NDVI, Tucker 1979) was computed for each scene to study the density and vitality of the vegetation during the acquired year. High NDVI values indicate vital and dense vegetation, covering the underlying soil by a closed canopy, while moderate values indicate sparse or stressed vegetation (NASA 2011). An NDVI time-series was computed and plotted for each location during 1985–2017, giving a first impression of the variability of the NDVI. To enable a comparison between the NDVI-values of Landsat-5 and Landsat-8, a sensor calibration was previously executed for the imagery of Landsat-5 using the MR1-Exp-model by Villaescusa-Nadal et al. (2019).

(1b) In addition, subsamples of 10 pixels x 10 pixels (about 300 m x 300 m) were established in the different elevation zones of the monitoring project to compute an average NDVI value for each zone (white squares in Fig. 11). NDVI time-series were computed and plotted for the forest zone, the forest-line zone, the tree-line zone, and the fell top of each transect. Thereby, biomass and biomass development were analyzed on zone-specific differences.

(2) Afterwards, a bi-temporal NDVI change detection was performed. The direct comparison of two images of one location, e.g. 1985 and 2009 in Yllästunturi, enabled to assess areas of high NDVI change against low NDVI change. We used two cloud-free images of Landsat-5 of preferably similar days of the year during the peak growing season for each location. To test whether the chosen scenes were dated during the high growing season for comparison, phenology curves and variance analyses were computed with Terra MODIS datasets (Didan et al. 2015) for each location available from year 2000 to 2018. We subtracted the earlier image from the later image to reveal the rate of NDVI change for each pixel. The resulting pixel values were classified into six classes, quantifying the rate of NDVI change (from low to high): < -0.1, -0.1 to -0.05, > -0.05 to 0.0, > 0.0 to 0.05, > 0.05 to 0.1, > 0.1 to 1.0. Based on the interquartile range of the variance analysis, we assumed changes of more than ±0.05 index values to be significantly different from zero. Changes of ±0.05 index values were interpreted to be within the random variability of inter-annual and seasonal variations in the vegetation status, while exceeding values reflect significant, rapid changes in the

vegetation pattern. The two scenes were further classified into four vegetation classes: *no vegetation* (NDVI ≤ 0.5), *sparse vegetation* (NDVI > 0.5 – 0.65), *moderately dense vegetation* (NDVI > 0.65 – 0.75) and *dense vegetation* (NDVI > 0.75). Pixels attributed to another class in the two compared images should localize densification or thinning of the vegetation cover.

(3) An NDVI profile was laid across the subsamples (refer to 1b) in each study site from the forest zone to the fell top in scenes of three different years for each location (e.g. 1985, 2009, 2017). An abrupt NDVI decline in the profile was assumed to indicate the tree-line position in each site. Increasing biomass near the tree line, resulting from tree-line shifts, forest densification or shrubification of previously sparsely vegetated areas, would be displayed by NDVI increment in the upper elevation zones during the three acquisition years. In contrast, decreasing NDVI values may indicate tree-line declines or browning of the vegetation cover.

(4) Finally, a land cover classification based on Random Forest (Breiman 2001) was computed using the three selected images to detect changes in the abundance of different vegetation types. We chose five land-cover classes which were easy to distinguish without reference data from the field: water bodies, bare fell tops / non-vegetated area, sparse vegetation, deciduous vegetation, and conifer stands. Calibration polygons were established in the centre of clearly identifiable land-cover patches, where an overlap of two classes was unlikely. Reference data, such as high-resolution orthophotos (NLS 2017), datasets of the National Forest Inventories (Luke 2015), and coordinates of sample trees from the dendroecological sampling were considered if necessary to ensure the reliability of the calibration data. The pixel values for each land-cover class were extracted, defining the spectral signature of each class. In a random forest consisting of an ensemble of 500 self-learning decision trees, all pixels were assigned to a class with the highest likelihood. Accuracy assessment was conducted by using a set of validation points for each class. A map was exported for each scene and analysed against the relative percentage of each land-cover class. Thereby, expansion or reduction of land-cover classes between the years could be detected by relative extent in the image.

5 Results and Discussion

The results are described in detail in the original publications I–III, attached in Appendix. The main findings of each publication will be presented and discussed here and synthesized in chapter six.

5.1 Development of stand volume and stem number in the study area

The results of the site monitoring indicated an increasing volume of the growing stock (trees > 2 m height) in all locations and elevation zones (Table 4 in Publication I). For spruce, the increase was higher in the western region with 40 % compared to the eastern region with 27 %. The increase was significant only in the forest zone and forest-line zone (Table 4 and Fig. 6 in Publication I). The volume of the growing stock of pine increased significantly in the northern region up to 70 % and in the southern region up to 56 %. The increasing trend was especially strong in the forest zone and the forest-line zone, while the increase in the tree-line zone was only marginal (Table 4 and Fig. 7 in Publication I). An increasing volume of the growing stock means a higher increment and survival of trees compared to the rate of dieback. The results indicate that the growing conditions are favourable enough for trees beyond the sapling stage to increase the stand volume of both spruce and pine stands. Since the volume of growing stock changed only slightly in the tree-line zone in nearly all locations, environmentally harsh conditions in the tree-line zone still seem to partly mask the benefits of climate warming. For spruce, we assume the mild and more maritime climate in the western region to favour increasing stand volumes, while the eastern, continental sites challenge tree growth by strongly varying temperatures and lower water supply. For the pine-dominated sites, the increase in stand volume was higher in the northern locations than in the southern locations, despite of the more challenging climatic conditions for tree growth in the north. The northern pine stands are of relatively young ages (Tomppo et al. 2011), and probably have not yet reached their climax in age and stand volume. Increasing tree heights and diameters, and a higher survival rate of trees exceeding the sapling stage, account for an increasing volume of the growing stock in stand monitoring.

Regarding the stem number as an estimation of the natural regeneration, we found species-specific differences: The stem number of spruce, including trees, saplings and seedlings, significantly increased in the forest-line and tree-line zones, whereas the forest zone remained stable (Table 4 and Fig. 6 in Publication I). We assume open stands to provide more space, nutrients and light for seedlings than the dense forest stands. The increase of the stem number was much higher in the west (+ 100 %) than in the east (+ 44 %) of Finland (Fig. 12), pointing towards milder and more favourable conditions in the west. Increasing stem numbers in the tree- and forest-line zones indicate favourable conditions for seed production, establishment and survival of spruce in the last decades, predominantly in open stands at higher elevations. It seems that spruce is tolerant against abiotic and biotic disturbances and has an advantage under the currently warming conditions. A northward and upward expansion of the spruce forest line by forest densification and establishment of new seed trees can be expected wherever the soil conditions, such as nutrient supply, allow (Hyppönen et al. 2013; Sutinen et al. 2012). In the forest zone at lower elevations, stem numbers increased only slightly and climate warming seems not to have a similar effect on tree regeneration. Between-tree competition and a seed bed formed by thick moss and humus layers may restrict successful seedling establishment and result in stagnating stem numbers in the dense forest zone. The potential of natural regeneration has possibly already reached its limits (see also Juntunen and Neuvonen 2006; Hallikainen et al. 2007).

In contrast to spruce, the pine-stem numbers stagnated or even decreased in all locations and showed no clear trends in any of the zones (Table 4 and Fig. 7 in Publication I). When separating the northern and southern pine regions, a significant decline in the pine stem number of 49 % was found in the southern regions, while the increase of 17 % in the north was not significant (Fig. 13).

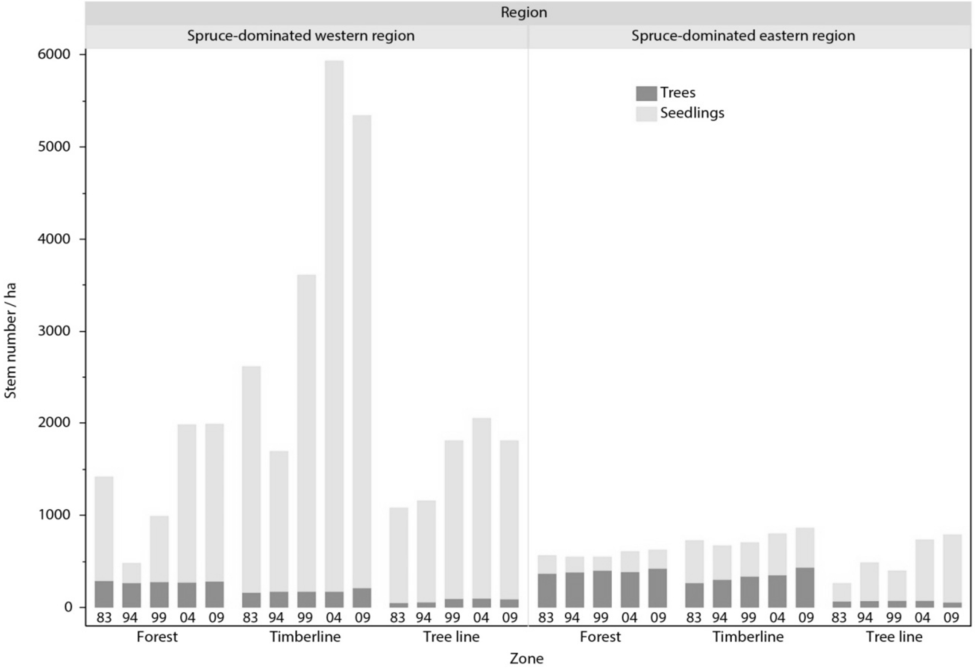


Figure 12. Stem numbers of Norway spruce in the forest zone, timberline zone and tree-line zone for the western and eastern study region (Figure: Mikko Hyppönen).

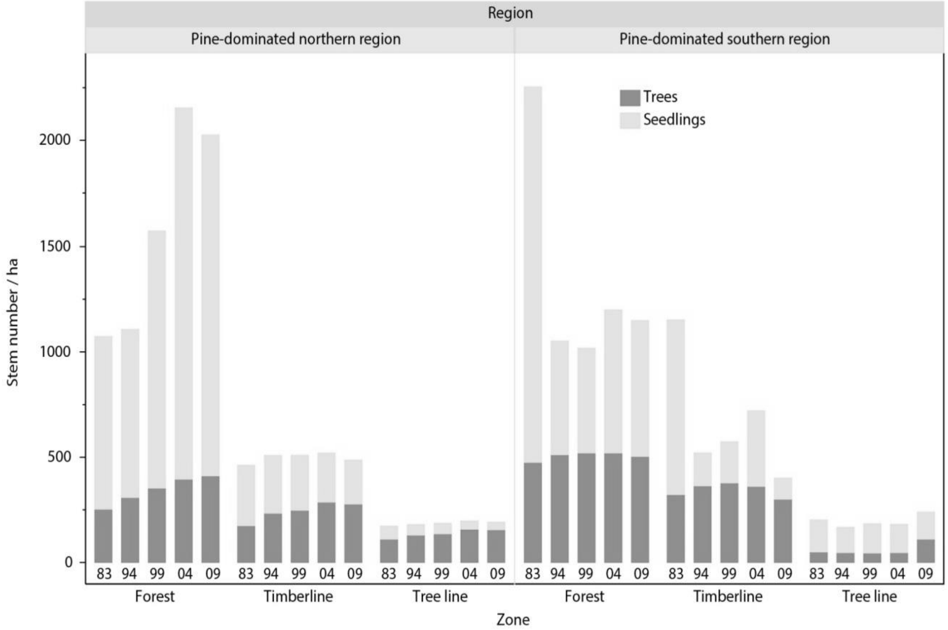


Figure 13. Stem numbers of Scots pine in the forest zone, timberline zone and tree-line zone for the northern and southern study region (Figure: Mikko Hyppönen).

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) as a result of high mortality of pine seedlings during the years 1983–2004 (Juntunen et al. 2002; Juntunen and Neuvonen 2006). In the subsequent years, only a low recovery of stem numbers by seedlings establishment was detected. In the northern region, both tree and seedling numbers increased slightly in the tree-line and forest-line zones, while the increment was enhanced in the forest zone. However, none of these trends was statistically significant; hence the stem number was statistically interpreted as stable in all zones.

With regard to further studies of pine in the polar and alpine tree-line ecotone, pine seedlings were found to be more vulnerable to disturbances during the seedlings stage compared to spruce. Pines in the southern locations are often hit by fungal diseases such as Scleroderris canker (*Gremmeniella abietina* (Lagerb.) Morelet) and the snow blight (*Phacidium infestans* P. Karst), which benefit from the mild and wet conditions during the winter season (Fig. 14). Especially small pine seedlings growing under a thick and wet snow cover are at risk to suffer from snow blight infestation and die after defoliation (Jalkanen 2007). Infestation by pathogens is predicted to increase under enhanced winter precipitation, especially if the density of seedlings within the snowpack is high and air circulation is limited (Holtmeier and Broll 2011). The European pine sawfly (*Neodiprion sertifer* Geoffr.) is also predicted to have more outbreaks in Finnish Lapland due to a reduced mortality of the eggs under milder winter temperatures (Virtanen et al. 1996; Neuvonen et al. 1999; Veteli et al. 2005). The decline in pine stem number occurred simultaneously with a high mortality of pine seedlings detected in Finnish Lapland to arise from fungal disease (Niemelä et al. 1987; Juntunen and Neuvonen 2006; Holtmeier and Broll 2011).

Mild and wet winters enhance furthermore the risk of frost damage during an early start of the growing season (Cannell and Smith 1986) or during frost events in autumn (Tuovinen et al. 2005). Large temperature fluctuations during winter and spring influence the frost-hardiness of pine and enhance the risk of frost-damage induced mortality (see also Hänninen 1991; Leinonen 1995; Repo et al. 1996; Tuovinen et al. 2005). Especially on the fell tops, seedlings are frequently uncovered from snow by strong winds and are at higher risk to die from climatic disturbances. Ground frosts were found to damage the fine roots of young pine seedlings substantially, limiting the uptake of nutrients and water even in the upcoming years (Tuovinen et al. 2005). Besides, winter desiccation kills the foliage of saplings and juvenile trees when the water-uptake is restricted in frozen soils under otherwise warming air temperatures (Kullman 2001). These disturbances occur predominantly in open sites, where trees grow exposed without protecting stand composition or snow cover. The temperature variations decrease from open tundra to sheltering forest stands and are noticeably lower under snow coverage. In the closed forest, where temperature variations are lower, and frost, wind and ice abrasion have minor impact, seedlings experience lower mortality rates than in exposed sites, as our findings indicate (Fig. 7 in Publication I). Seedlings may also in exposed sites grow undisturbed, as soon as the snow cover is thick enough to protect the tissues from wind and frost. However, according to Martz et al. (2016), the snow conditions recently changed under climate warming and promoted the risk of frost damage, mitigating the effect of climate warming (see also Domisch et al. 2018).

Figure 14. Infestation of pine seedlings with the snow blight (*Phacidium infestans* P. Karst) (Photo: Risto Jalkanen).

Further damage to pine seedlings is often caused by reindeer (*Rangifer tarandus tarandus* L.), when it is grazing the reindeer lichens (*Cladonia spp.*) in pine dominated forests in winter (Heikkinen et al. 2002; Holtmeier 2005; Vajda and Venäläinen 2005; Holtmeier and Broll 2011). Reindeer, when browsing for lichens or rubbing their antlers against small trees, massively damage pines in the critical small stages and may cause numerous loss of healthy seedlings to the new generation (Fig. 15). The reduction of thick lichen layers on the ground means furthermore the reduction of soil insulation and enhances in turn the risk of ground frosts in herding areas (Tuovinen et al. 2005). Spruce is less affected by reindeer, since it grows in forests where lichens play only a minor role in the understory.

Figure 15. Small pine saplings are on risk to be damaged by reindeer grazing or antler rubbing

When pine trees have passed the seedling and sapling stage, they have to resist a severe crown-snow loading which is the major reason for tree breakage in the tree-line ecotone in northern Finland (Fig. 16) (Marchand 1987; Jalkanen and Konôpka 1998; Lehtonen et al. 2014). This is in accordance with Holtmeier (2005) who found most of the pines, invading into the tundra during the mid-20th century, to show crippled growth forms. Spruce is, due to its slim crown shape, better protected against massive snow loading, whereas the shape of pine crown facilitates snow damage. Besides, the branches of mature trees growing beyond the protecting snow cover are at higher risk to suffer from winter desiccation under mild temperatures during the winter season (Kullman 2001). The impact of these disturbances might explain the stagnating stem numbers in the open tree-line and timberline zone. In the forest zone, where seedlings and trees have more shelter from wind and strongly varying temperatures, stem numbers increased slightly, pointing towards a slightly higher survival rate of pine compared to the upper elevations.

Figure 16. Crippled growth forms of pine trees by wind and snow pressure in the tree-line zone near Yllästunturi.

The results of the monitoring study suggest that the volume of the growing stock increases in all sites, indicating a densification of the already established forest stands. The natural regeneration is highly site- and species-specific in its response to currently changing environmental conditions. Spruce needs favourable conditions for abundant regeneration, but after the establishment the seedlings seem to be relatively tolerant against biotic and abiotic disturbances. In contrast, stagnating stem numbers of pine seedlings indicate high seedling mortality or less successful establishment and survival of trees in juvenile stages (Juntunen and Neuvonen 2006). Under these conditions, a climate-related northward and upward extension is conceivable for Norway spruce, but seems to be still limited for Scots pine which needs high seed crops to enhance the survival rate of new seedlings (Hilli et al. 2008).

When interpreting these results, it has to be taken account, that the monitoring underlies some methodological limitations which might have affected on the outcomes of the study. The selected sites were chosen in 1983 with regard to similar soil properties, representative forest composition and the absence of human or severe natural disturbance regimes. During the years of monitoring, some of the locations were, however, impacted by civil constructions, such as roads, skiing areas or the expansion of settlements and agricultural land. This was especially apparent in Yllästunturi, where the skiing area is nowadays in very close proximity to the monitoring sites and an impact of the human activities cannot be entirely excluded. We found furthermore reindeer grazing on the monitoring plots, where originally no grazing territory was registered. Biotic and abiotic disturbances were not recorded during the field-based monitoring, hence the impact of external disturbances on the results cannot be quantified.

5.2 Long-term site- and age-specific growth response of Scots pine to climate warming

The dendroecological analysis highlighted site- and age-specific differences in pine growth. The growth rates of sampled juvenile pines (being > 2 m high) were highest in the southern locations and in the tree-line zones (Fig. 3 and Table 2 in Publication II).

The effect of the elevation zone on growth was higher in the southern locations than in the northern locations, which was confirmed by a significant interaction of location and zone (Table 1 in Publication II). The results indicated in statistics modelling improved growth conditions for juvenile pines in the southern study area and a significant effect of the stand structure on growth, most likely by competition for light, nutrients and water. Open forest stands in the forest-line and tree-line zones seem to promote rapid radial growth in juvenile pines. Naturally, the effect of elevation is more dominant in the southern locations, where the gradient in the stand structure from closed forests to open fells is distinct (Fig. 17). In contrast, in close proximity to the polar tree-line ecotone with scattered and sparse stands, these elevation effects diminish. Even if we aimed to sample isolated, unsheltered trees, stand structure had a significant effect on the growth rates of young pines, favouring annual radial increment in thinned or more open stands (see also Varmola et al. 2004).

Figure 17. The tree-line zone of the southern location Urupää in Saariselkä differs remarkably from the dense stands of the extended forest zone in the background. Pines in the upper elevations are of younger ages and thinner and more slow-growing than in the forest zone.

The residual site chronologies revealed similar growth variations during 1950 to 2014, and the correlation coefficients were moderate or high between all sites (Fig. 4 and Table 4 in Publication II). Highest correlation coefficients (≥ 0.7) were found between sites of the same location and between sites of adjacent locations, such as Alajoenpää and Urupää. Lower correlation values (0.3–0.69) were found between distant locations, such as Kevo and Yllästunturi. The correlation values point to slight differences in growth variations between northern and southern locations, hence a latitudinal gradient of changing environmental conditions from south to north. However, since peaks and depressions occurred simulanously in the chronology pattern in all sites, we assume equal climatic parameters to affect pine growth homogenously throughout the study area during distinct years.

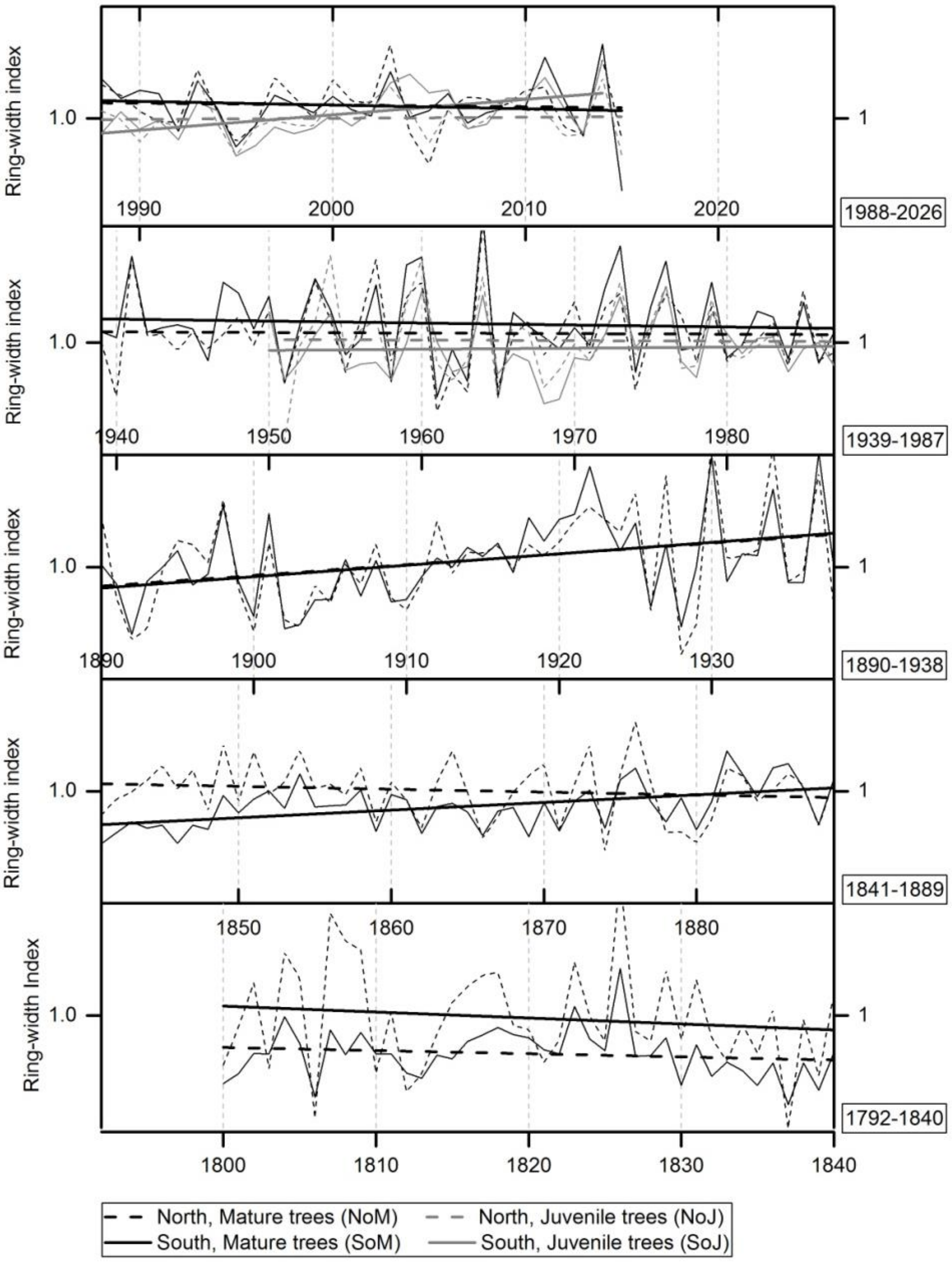
The most relevant climatic parameters for radial growth were detected by Pearson correlations. Throughout the studied period 1950−2014, radial growth correlated significantly with mean temperature in July and temperatures during the previous and current spring season (Mar–May) (Fig. 5 in Publication II). Negative correlations were found with the number of cold days in May and July and frost days in May and March (Table 5 in Publication II). Moving correlations between the growth of southern mature pine trees and July temperatures revealed constantly high values during 1950–2013, while correlations between growth and temperatures and frost days in May declined (Fig. 10 in Publication II). Pine seems to be still very sensitive to the temperature regime during the growing season, being however less sensitive to temperatures during the beginning of the growing season in mature ages. This might be caused by a prolonged growing season under climate warming in the south, improving the growth conditions in May. Kauppi et al. (2014) detected an increment of the annual growing degree days over 20 % since 1960, and Høgda et al. (2013) quantified their number to about 19.3 days, promoting our assumption. We assume that the number of frost days, however, is still highly relevant for juvenile pine trees and trees in the northern locations (Table 5 in Publication II), a factor not included in the moving correlation analysis. Elevated temperatures during late winter cause needles to deharden earlier, thus enhancing the risk of frost damage during an early onset of spring (Leinonen 1995). Ground frosts were found to damage roots and tissues of young trees in particular, which show growth declines in the tree-ring widths in the following growing season due to water stress, limited nutrient uptake and defoliation (Tuovinen et al. 2005). This is more problematic in open, unsheltered stands in the north and tree-line zones, and for trees in the sensitive sapling and seedling stages (Repo et al. 1996). In contrast, ring widths of mature trees were found to be not affected by severe frost events (Tuovinen et al. 2005).

Negative correlations of radial growth were also found with the number of snow days and average monthly snow cover in April and May (Table 5 in Publication II). The number of snow days in April had an increasingly negative impact on the adult pine trees in the south compared to previous decades (Fig. 10 in Publication II). A high number of snow days during spring delays the onset of the growing season and enhances the risk of fungal diseases under a wet and deep snow cover. Moreover, mild and wet winter conditions enhance heavy snow loads in the crowns and promote the risk of crown breakage (Rogers 1990; Hurrell 1995). In contrast, high precipitation sums had a positive impact on pine growth during May in the north, but a negative impact during July in the south (Table 5 in Publication II). Trees growing on low, dry substrates in the north might benefit from ample water supply during the growing season (see also Henttonen et al. 2014), while higher precipitation in the south might go along with water saturation and hypoxia of soils when the water supply exceeds the drainage. Besides, increased precipitation sums promote the risk of fungal diseases both in the south and the north.

Those climatic variables which showed a significant impact on pine growth were examined for long-term trends during the last century (Table 6 and Fig. 6 in Publication II). The temperature increased significantly, predominantly in winter and spring and in Sodankylä in the south, while the temperature increase was moderate in Karasjok in the north. Precipitation sums increased significantly in Sodankylä during winter and May, mostly during the second half of the century. This is in accordance with high winter temperatures and precipitation sums accompanying maximum NAO index values since the 1990s. It was additionally found that the snow cover in April decreased during the 1980s and 1990s, indicating an earlier start of the growing season (Fig. 6 in Publication II).

The long-term variations in the RCS-chronologies were found to be simultaneous to the temperature course during the growing season, with growth increments during the warm periodes 1800–1830, 1920–1940, 1950–1960 and mid 1970s (Fig. 18; Fig. 7 in Publication II). With the temperature rise during the early 1900s, the radial growth of mature trees exceeded the standardized mean of 1.0, reaching maximum growth indices in the warm 1930s. We found growth depressions during unfavourable summer conditions in 1995, after 2006 and 2013, whereas increasing July temperatures during 1996–2004 promoted peaks in the growth index. However, a consistent response of tree growth to the exceptional warm decades after 1990 was missing (Fig. 7 and Fig. 8 in Publication II). The southern juvenile trees showed significantly increased growth since 1996, while neither the southern mature trees nor the northern juvenile and mature trees displayed similar growth trends (Fig. 18). This was surprising, since we expected a prominent growth trend like in the warm 1930s.

The findings of the dendroecological analysis strengthen our assumption that abiotic and biotic disturbances overrule or accompany the effects of climate warming. Further studies found trees in the boreal biome to respond less sensitive to temperature today than during the 20th century, which is in accordance with a decreasing occurrence of pointer years in our analysis (Fig. 9 in Publication II) (see also Wilmking et al. 2004; Briffa et al. 1998). This phenomenon is widely discussed as the “divergence problem” in northern boreal regions (Wilmking et al. 2004; D’Arrigo et al. 2007; Büntgen et al. 2009). While site chronologies based on tree-ring data could model the temperature course until the mid 20th century, the current warming is underestimated in the tree-ring data, indicating a reduced temperature sensitivity of the trees. Drought stress, varying onset of snowmelt, time-dependent response, or global dimming is discussed to possibly overrule the effects of climate warming on tree growth (D’Arrigo et al. 2007). Thereafter, trees respond more individually to site-specific factors which bias the climatic signal. According to D’Arrigo et al. (2007), the divergence problem is caused by “end-effects” of chronology building. Trees, when responding highly sensitive to temperature or site conditions, may show opposing effects in the single tree-ring series. When averaged into one chronology, the series-specific effects override each other.



	NoM	SoM	NoJ	SoJ
1988-2026:	n.s.	n.s.	n.s.	sign.
1939-1987:	n.s.	n.s.	n.s.	n.s.
1890-1938:	sign.	sign.		
1841-1889:	n.s.	sign.		
1792-1840:	n.s.	n.s.		

Figure 18. Regional curve standardization chronologies of Scots pine with linear regressions for region (north, south) and age (mature trees: $Y_0 < 1900$, juvenile trees: $Y_0 \geq 1950$). The significance levels ($p < 0.05$) were listed in the table below.

We identified the thermal conditions, such as sufficient temperatures during the growing season and a low number of cold and frost days during spring to be important for tree growth when including both juvenile and mature trees in the analysis (Table 5 in Publication II). According to our findings (Table 6 and Fig. 6 in Publication II) and further studies (Høgda et al. 2013; Salminen and Jalkanen 2015), the warming happened predominantly in the south of Lapland, most likely prolonging the duration of the growing season and improving the conditions for tree growth during the spring-time season (see also Høgda et al. 2013; Salminen and Jalkanen 2015). It is possible that juvenile trees in the southern region benefit from the improved conditions, showing the related growth increment (Fig. 8 in Publication II). Mild winters, warm summers and sufficient water supply promote tree growth in juvenile ages, when trees have passed the critical seedlings stage but have not yet reached their biological climax. A climatic sensitivity can therefore be stated for juvenile ages. In the northern region, where the temperature increase was modest (Table 6 in Publication II) and the growing season duration remained stable, growth conditions have not yet improved to the same degree (Fig. 8 in Publication II). Trees grow here at the edge of their outermost distribution limit, where the forests are scattered and the open canopies cannot provide sufficient shelter against wind, frost, and ice abrasion. The juvenile trees of the north did not respond with accelerated growth to the last warm decades, hence the warming was obviously insufficient to accelerate growth.

However, since we detected growth increments in the tree-ring data of juvenile trees in the southern locations, we expected similar growth response to warming of mature trees which were, however, missing (Fig. 7 and Fig. 8 in Publication II). As in the context of the divergence problem, we assume that disturbances, such as wind, frost events during autumn and spring, drought or diseases accompany climate warming and to overrule a common climate signal in the tree-ring data. We assume predominantly mild and wet winter conditions and higher cloud coverage under high NAO indices since the 1990s masked the benefits of climate warming. Positive NAO index values lead to distinctively higher temperatures and precipitation sums during the winter months (Table 6 and Fig. 6 in Publication II). This most likely promoted heavy snow loads and wind pressure in the crown tops, challenging the vitality of trees even for the following summers. Broken crown tops and growth deformations were visible across the entire study area in the tree-line zones. Winter desiccation stresses tree vitality additionally during early onsets of spring, when rising temperatures promote water loss through the needles while water uptake is restricted in frozen soils (Martz et al. 2016). Seo et al. (2011) assumed changing snow conditions to be causative for missing growth response in northern Lapland. It is furthermore likely that mature trees have reached their climax of growth under rising temperatures, while further environmental factors, such as water supply and soil properties rather regulate additional growth increment.

Some limitations of the chosen methods have to be mentioned also to evaluate the outcomes of the study correctly. During sampling, we noticed that the forest zone and forest-line zone, where the monitoring plots were established, did not differ distinctively from each other. Effects of elevation and stand structure might therefore have been suppressed partly when comparing the forest with the forest-line zone. When the plots were established in 1983, the forest stands of the forest-line zone might have been more open than today, hence more different from the stand composition of the forest zone. Challenging for dendroecological sampling was also the differentiation of mature and juvenile trees in the field, since e.g. in the northern locations and upper zones, thin and slow-growing trees were already several decades old. In addition, many of the mature trees showed broken tree tops or signs of damage and had to be excluded from sampling and analysis. Thereby, we finally had considerably less mature trees than juvenile trees in the analysis, being known to be more sensitive to non-climatic factors in the tree-ring data. We addressed this limitation by using different approaches to analyse the tree-ring data: The direct comparison of the growth rates was restricted to juvenile trees exclusively, and the residual chronologies had to be cut to a time span of high sample number. For the long-term analysis, we chose the RCS method for detrending which is known to be less sensitive to the biological age curve of the trees, and classified the samples by region and age to preferably un-mix site- and age-specific signals.

5.3 Vegetation greening and tree-line dynamics detected in satellite imagery

Studying the pine-dominated sites of the monitoring project by remote sensing emphasized the location-specific differences in the forest composition from south to north. The southern sites were clearly identified in the satellite images by conifers in closed and extended forest stands in the lower elevations, while deciduous vegetation was abundant in valleys, near water bodies, and in the transition zone between forest and fell vegetation (Fig. 5b in Publication III). Here, the deciduous vegetation often formed a dense vegetation belt around the fell tops, which has to be considered when discussing the establishment of pine seedlings beyond the tree line. In contrast, the vegetation on the fell tops was formed by dwarf shrubs and lichens on barren rock, as indicated by high reflectance values compared to the surrounding forest canopy. The northern sites were dominated by deciduous vegetation, spreading from the lower elevations to the upper fell zones, where sparse sub-arctic vegetation occurred (Fig. 5a in Publication III). Coniferous forest was restricted to small patches in open stands in the lower zones, and was not easy to distinguish from sparse deciduous or shrub vegetation. In proximity to the polar pine forest line, conifers reach their outermost distribution limit within the polar mountain birch forest.

The mean NDVI was highest in scenes with a high abundance of dense and vital deciduous vegetation, and was lower in scenes with extensive coniferous stands (Fig. 3 in Publication III). The NDVI of the forest and tree-line zones exceeded therefore partly the value of the forest zone (Fig. 4 in Publication III). The NDVI showed high inter-annual variability during the study period 1985–2017 in all locations, indicating differences in the vitality and abundance of vegetation between the years. Naturally, images taken in the beginning of the growing season in the end of June revealed lower NDVI values than images retrieved in July and August. This was particularly distinct in the northern sites, emphasizing the effect of the growing-season course on the vegetation stage. While the NDVI indicated slightly increasing values during the study period in the southern locations, no statistically significant trend was detected in the northern sites (Fig. 3 and Fig. 4 in Publication III). Despite sensor calibration between Landsat-5 and Landsat-8, our data indicated a sudden increase of the NDVI from Landsat-5 to Landsat-8, which might naturally occur from land cover changes, but might also be caused by remaining sensor-specific differences (Roy et al. 2016).

The NDVI change detection provided a better understanding of spatial variations of vegetation patterns. In Kevo, Saariselkä and Yllästunturi, the number of pixels showing increasing NDVI values exceeded the number of pixels with decreasing NDVI values considerably about 14–30 % (Table 2 in Publication III). In Karigasniemi and Lemmenjoki, the number of pixels of increasing NDVI values was only 2–4 % higher than the number of pixels of decreasing values. In Syysjärvi, slightly more pixels showed decreasing values. All sites except of Syysjärvi experienced a decreasing proportion of *sparse* or *moderate vegetation*, while the percentage of *moderate* or *dense vegetation* increased (Fig. 6 in Publication III). These were areas close to the fell tops, particularly in the northern sites, or open stands in the lower elevations in the southern sites which were previously covered by sparse vegetation. These findings support our assumption of a densification of previously open forest stands by e.g. an increase in the volume of growing stock (Publication I; see also Masek 2001; Hofgaard et al. 2012; Manninen et al. 2019). Decreasing NDVI values were mostly located in areas with anthropogenic impact, such as reinstalled streets, parking lots or skiing areas, but also from clear cuttings that were found around Syysjärvi and Yllästunturi (Fig. 5a/b in Publication III). But also river terrace erosion or areas affected by biotic disturbances, such as moth outbreaks defoliating the deciduous tree vegetation in Karigasniemi during 2009 and 2013, were mapped by NDVI decline or a reduction in vegetation cover (Fig. 5a/b in Publication III).

Vegetation indices, such as the NDVI, are very sensitive to inter-annual and seasonal variations of the species’ phenology. The temperature regime, water supply, or the time of bud burst affect species-specific phenology, hence the reflectance values, and may distort the bi-temporal NDVI change detection, especially when using it for the estimation of vegetation expansion. Selecting accidentally one exceptional year for NDVI change detection, when the vegetation is extraordinary vital or un-vital may distort the interpretation of the resulting outcomes. Recently established open or dry forest stands near the forest edge may for instance be accidentally attributed to sparse fell vegetation while the forest is actually expanding. Therefore, only scenes dating during the peak of the growing season and not during the critical period of initiating or ceasing growing season were used for analysis. The phenology curves derived from MODIS data during 2000–2018 indicated a comparable state of the vegetation development for the analysis (Fig. A3 in Publication III). In addition, when computing the NDVI for open forests with scattered stand canopies like in the tree-line ecotone, the signal not only includes the index values of the forest vegetation, but also of the understory vegetation (Lopatin et al. 2006). This cannot be avoided and has to be considered in the interpretation of the results. However, by selecting scenes of similar dates during the high growing season which were of non-exceptional character regarding the climatic conditions, we widely ensured that the vegetation's phenology was comparable for vegetation change analysis. We used the NDVI as a tool to estimate the vegetation density and supplemented the analysis with a Random Forest land-cover classification, which is less sensitive to short-term variations in the phenology.

Based on the accuracy assessment, the classification results of the Random Forest land-cover classification were regarded as reliable. However, the occurrence of mixed pixels, accumulating reflectance values of several land-cover types may distort precise land-cover classification. Transition zones formed by a high percentage of mixed vegetation and mixed pixels are assigned by maximum likelihood to one land-cover class. The remaining vegetation types were excluded, leading to potential misclassifications. Since we did not have validation sites in the field in problematic transition zones, these errors did not occur in our quality assessment. The overall accuracy overrates the quality of the models. The presented results are consequently treated as indicators of possible trends: If pixels in the transition zone change their land cover class from the previous to the current year, we estimate the probability of the new land cover class to be more likely.

The Random Forest classification results revealed minor variations in the vegetation pattern of the southern sites, but more distinct changes towards the North (Fig. 8 in Publication III). In Yllästunturi, the abundance of conifers decreased slightly due to clear-cuttings, detected in sharply delimited patterns in the south western forest stands (Fig. A2b in Publication III). In Saariselkä, more pixels were attributed to conifers in the lower elevations from 1987 to 2014, while the sparse vegetation decreased in abundance. In Lemmenjoki, sparse vegetation was most likely replaced by deciduous vegetation while the abundance of conifers remained stable. These changes were, however, of minor degree and pointed to a densification of the forest stands than to an expansion of conifers towards higher elevations. In accordance with these results, no tree-line shifts were detected in the NDVI profile of the southern locations, displaying the position of the tree line unchanged over the study period (Fig. 7 in Publication III).

In the northern sites, the Random Forest classification revealed more distinct variations in the vegetation pattern (Fig. 8 in Publication III). Syysjärvi and Karigasniemi showed increasing class size in the sparse vegetation, while deciduous and coniferous vegetation decreased. This decline was, however, only minor until 2004/2009, but prominent until 2014/2016. The decline was attributed to biotic disturbances, such as clear cuttings and civil constructions in Syysjärvi and moth infestation in Karigasniemi, defoliating extensive birch forest stands during 2009–2013 (Fig. A2a in Publication III). In Kevo, the area of sparse vegetation was clearly replaced by deciduous and partly even coniferous forest, pointing towards the establishment of higher plants in previously sparsely covered areas. In none of the northern locations a clear tree-line advance could be detected by NDVI profiling along the elevation gradient (Fig. 7 in Publication III).

Neither the NDVI profiles nor the Random Forest land-cover classification showed clear trends for rising and expanding tree lines of coniferous tree species towards the treeless boreal heath or to alpine tundra. In the northern locations, we found increasing NDVI values to result rather from the expansion of sparse and deciduous species (Fig. 8 and Fig. A2a in Publication III). Fast growing shrub vegetation, heaths and lichens are better adapted to the harsh conditions in the tree-line ecotone and consequently are the first to establish on bare ground. Mountain birch is less sensitive to snow loads, spring frosts and nutrient-poor substrates of the fell tops and able to grow larger seed crops of only a few seed trees under adverse conditions (Wehberg 2007). Increasing temperatures and moisture conditions during summer seem to promote growth and germination of deciduous species which were found to spread towards the northern and upper habitats (Fig. 5a and Fig. A2a in Publication III). Our findings correspond with results from studies in the polar tree-line ecotone which found greening trends beyond the polar-alpine tree line arising mostly from expanding birch forest and shrub vegetation (Sturm et al. 2001; Tømmervik et al. 2005; Wielgolaski 2005; Forbes et al. 2010; Goetz et al. 2011), while very limited advance of conifers to higher elevations was detected (Masek 2001; Bunn and Goetz 2006; Holtmeier and Broll 2011; Hofgaard et al. 2012).

Dense understory vegetation might, however, hinder successful seed establishment and growth of pine seedlings (Hyppönen et al. 2013) by competition for water, nutrients and light. Pine seedlings do not find a proper seed bed or space to grow beyond the seedling stage. A dense birch forest, as in the upper elevations in Lemmenjoki, in Syysjärvi or Karigasniemi, might limit possible tree-line advance to higher altitudes and latitudes. Birch forest stands which are open enough and provide areas with bare ground for seedling establishment may, in contrast, provide shelter from wind, ice-abrasion and frost damage since soil temperatures are higher under high shrub abundance (Sturm et al. 2005). Then, pine seedlings can grow sheltered in the birch forests, gradually replacing deciduous by coniferous vegetation when reaching adult ages. The structure and expansion of the surrounding mountain birch forest belt might therefore be of high relevance for potential tree-line shifts (Fig. 19).

However, transition zones are formed by a high percentage of mixed vegetation and accumulate the reflectance values of several land-cover types in mixed pixels which are assigned by maximum likelihood to one land-cover class. The remaining vegetation types are excluded, leading to potential misclassifications. It is possible that initiating reforestation of the upper and northern sites is not yet visible in the satellite data. These errors do not occur in our quality assessment, thus the overall accuracy overrates the quality of the models (Table A2 in Publication III). The presented results are consequently treated as indicators of possible trends and are expected to give an estimation of observed land-cover changes under a warming climate.

Figure 19. Mountain birch belt in the forest-line zone of Lemmenjoki (left) and the study location Syysjärvi (right), potentially limiting the establishment of pine seedlings by competition.

6 Synthesis

From the results of all three subprojects, we draw the following conclusions to reflect on the major aims of the study:

(1) The volume of the growing stock of both spruce and pine is increasing in the established forest stands, since the survival and growth of conifers exceeds the mortality rate under current climate warming. This leads to a densification of the established forest stands.

(2) The growth rates of the individual trees have not changed significantly under current warming in the study area, hence the sensitivity to temperature decreased at least in mature ages and might be exceeded by other growth limiting factors, such as biotic or abiotic disturbances.

(3) The spruce stem numbers increased significantly during the study period, indicating a densification and expansion of the spruce forest stands. The pine seedling establishment and survival underlies a high mortality rate by disturbances accompanying climate warming, and is currently not successful enough to allow pine expansion beyond the recent tree-line position.

(1) The first conclusion is mainly based on the findings of the monitoring studies and the remote sensing results. The volume of the growing stock (trees ≥ 2 m height) increased in both spruce- and pine-dominated sites, predominantly in the forest and forest-line zone, while only slight increase was found in the tree-line zone (Table 4, Fig. 6 and Fig 7 in Publication I). An increasing volume of the growing stock means that trees naturally increase in height and diameter, while the mortality rate is low. The forest is in a positive imbalance. In the upper elevations, where trees reach their distribution limit, disturbance regimes by frost, wind and snow pressure enhance the mortality rate and possibly mask the favourable conditions of climate warming. These findings are in accordance with increasing NDVI values in the lower elevations detected by remote sensing (Fig. 5b and Fig. 6 in Publication III). In the southern locations,

increasing NDVI values were predominantly detected in previously sparse and open forest stands in the lower elevations, while no trends were detected in the upper elevations or the northern locations (Fig. 5a/b and Fig. 6 in Publication III). Also in the dendroecological sampling, we found increasing ring width indices for juvenile pines in the southern locations, but not in the northern sites and for mature ages. For mature trees, moving correlations indicated a decreased sensitivity of mature pines to unfavourable conditions during the early growing season (Fig. 7 and 8 in Publication II). We thereby assume enhanced growth of the juvenile trees and a lower mortality of the adult trees under more favourable conditions to result in a densification of the established forest stands in the lower elevations.

It is surprising, that the monitoring study was the only analysis to detect increasing stand volumes also in the northern sites. As mentioned in chapter 5.1, we assume the juvenile ages of the northern stands to cause this result. Trees recently exceeding stand heights of 2 m are added to the computation of the volume of the growing stock, increasing the stand volume sustainably. Based on the mean age of 40–50 years (Table 3 in Publication II), we assume the juvenile trees to originate from high tree recruitment of the 1970s (Aakala et al. 2014) which now reach tree sizes over 2 m. This does not mean that the trees grow faster, as the dendroecological analysis shows, but rather that the juvenile trees gain naturally growth heights over 2 m towards adult ages with possibly higher survival rates. However, this effect was not seen in the satellite data over the northern pine forests (Fig. 5b in Publication III). It is possible, that the relatively scattered pine-forest canopies within the mountain birch belt impede a clear detection of changing stand volumes. However, this does not mean that the volume of the growing stock is not increasing by the survival and continuous growth of the established individuals also in the northern locations. Concluding the first hypothesis, grown-up trees seem to generally benefit from the current growth conditions, showing constant growth and high survival rates to increase the forest stand densities in the study area, predominantly in the southern sites and the lower elevations.

(2) An increasing volume of the growing stock does, however, not automatically mean that trees grow more rapidly under current warming as revealed by the dendroecological analysis. The radial growth of mature trees exceeded the standardized

mean in the warm 1920s and remained on a constant level afterwards (Fig. 7 in Publication II), showing no growth increase in response to the recent warm decades. The moving correlation and pointer year analysis even revealed a decreasing sensitivity of mature pine growth to spring temperatures and the occurrence of frost days during spring in the south (Fig. 9 and Fig. 10 in Publication II). Further warming does not necessarily increase the radial growth of mature trees, as soon as other environmental factors provide limitations for growth. We assume water supply, stand composition and disturbance regimes to recently affect growth to a higher extent.

The juvenile trees, instead, showed increasing index values in the southern locations of the study area, responding most likely to a prolonged and warmer growing season (Fig. 7 and Fig. 8 in Publication II). In juvenile ages, trees are particularly sensitive to temperature and the climatic conditions during the growing season. Hence, warm summer temperatures, mild winters with an early start of the growing season might improve the growing conditions for juvenile pines sustainably. In the south, where temperature rose rapidly and juvenile trees grow more sheltered within mature forest stands, the warming climate promoted increasing growth trends for pine. In the northern locations, the warming was remarkably below the southern level and trees grow more exposed in scattered stands on open sites near the polar tree line. Here, no growth acceleration was detected during the recent years comparable to the southern trees. Again, we assume that the temperature rise was not sufficient to compensate the harsh growing conditions of the high latitudes.

(3) When discussing the growth of juvenile trees, it has to be highlighted that "juvenile" refers here to tree sizes differing significantly from the seedlings stage. While juvenile trees are already several decades old and have reached tree heights over 2 m, seedlings grow close to the ground and have developed only few branches. The stem number in the monitoring study included seedlings and saplings besides mature trees and should thus give estimates of the regeneration success of spruce and pine. The stem numbers increased in the spruce-dominated sites in all locations and zones significantly (Table 4 and Fig. 6 in Publication I), indicatin a successful seed production, establishment and survival of spruce seedlings under the current environmental conditions. A densification and even expansion of spruce by the

establishment of new seed trees even in the tree-line zone is therefore a possible scenario. Since we have no additional data for spruce from remote sensing or dendroecological analysis, we have to base this assumption on the monitoring data exclusively.

For pine, the monitored stem number did not significantly increase in any of the locations and zones during the studied time span (Table 4 and Fig. 7 in Publication I). As discussed in chapter 5.1, we assume a high mortality of pine seedlings caused by biotic and abiotic disturbances to cause this result (see also Aakala et al. 2014). Moreover, dense underground vegetation of shrubs, mosses and dense birch forest belts hinders the establishment of pine seedlings which need bare grounds and open canopies for successful germination (Hyppönen et al. 2013). A successful establishment and growth of pine seedlings would, however, be required for an expansion of the tree line into the open tundra. Holtmeier et al. (1996) found that seedling establishment increased solely in close proximity to old and healthy seed trees and under open canopies in sheltering stands. In greater distance to the seed tree in open unsheltered areas, the seedling density decreases rapidly (Holtmeier and Broll 2011). In open forest stands in lower elevations, seed trees can form appropriate seed crops during favourable years, which then establish sheltered but without competition for nutrients and light in openings within the forest stand. This is in accordance with our findings of the remote sensing study, since we detected increasing NDVI values predominantly in previously more open forest stands, but not in the upper elevations and latitudes. When seeds are transported by the wind up to one kilometre towards open tundra beyond the dense mountain birch belt and germinate on proper sites, increasing numbers of seedlings and trees are not unlikely. These individuals were then small in size and most likely not yet visible in the satellite data. Enhanced and successful seed production as in the 1970s, and the survival of the seedlings forming new seed trees beyond the recent tree line would be the base for forest expansion. With regard to the monitoring results (Publication I), this scenario seems impeded under the current growing conditions, considering the abiotic and biotic disturbances summarized in Figure 20.

Based on these considerations, we draw the following conclusions: Climate warming basically improves the growth conditions of conifers by warmer soil and air temperatures, sufficient water supply and CO_2 fertilization in the polar and alpine tree-line ecotone of Finnish Lapland. These benefits may, under undisturbed conditions, increase the seed production and germination of conifers which possibly invade into the open sites of fell tops and treeless boreal heath. Tendencies of accelerated growth and increasing stand volumes were found in the results, pointing, however, to species- and site-specific response to warming below the expected level. Besides the benefits of warming temperatures, also unfavourable conditions tend to occur more frequently under a changing climate.

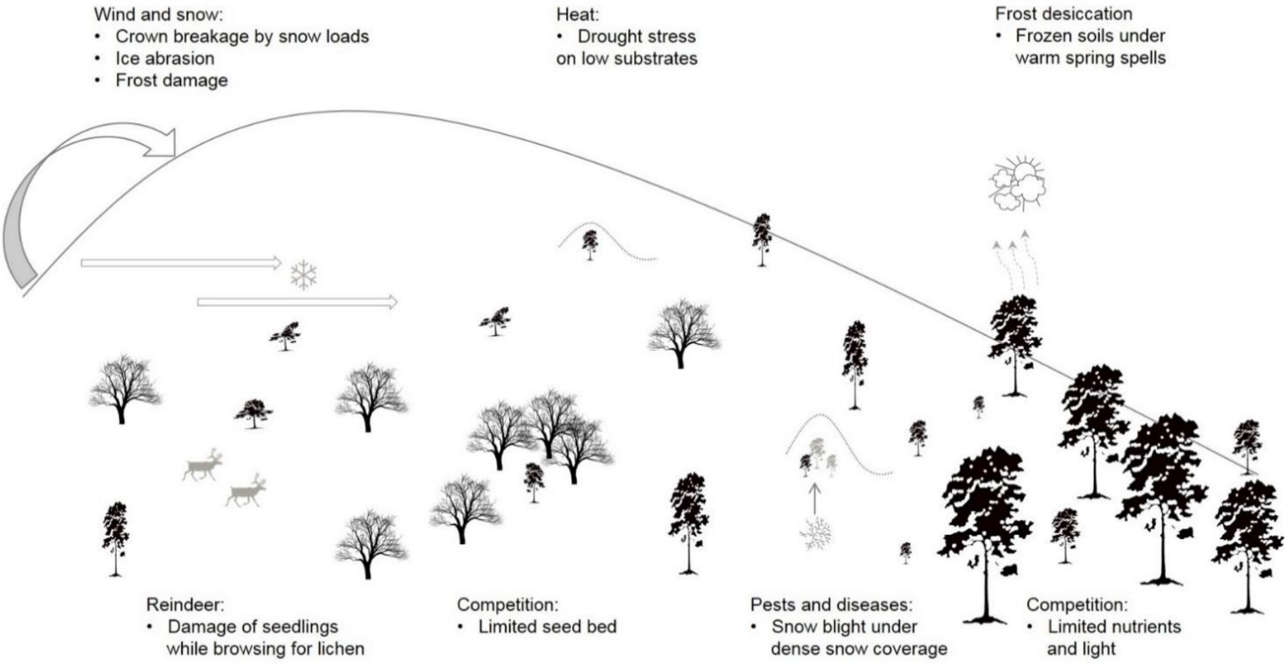


Figure 20. Biotic and abiotic disturbance regimes in the alpine and polar tree-line ecotone in Finnish Lapland affecting the potential of tree-line advance by survival and natural regeneration of pines.

The conifers in the alpine and polar tree-line ecotone grow rather slow, and an expansion of coniferous forest might happen with time delay after the onset of enhanced warming. According to Hallikainen et al. (2007), successful regeneration requires more than 10 years in the study area. Under the current conditions for pine, with low survival rates beyond the tree line, high seed crops would be necessary to enhance the survival rate of seedlings in open sites (Juntunen and Neuvonen 2006; Danby and Hik 2007; Holtmeier and Broll 2011). When seeds grow sheltered in the forest-line zone and pass the critical stage of sapling size, it is likely that pine stands gradually replace the deciduous vegetation (Middleton et al. 2008). We assume the pine forests to first increase the stand volume and seed production, before invading continuously into the tundra as far as climate warming continues. We assume the vegetation shift to first occur in southern Lapland, until the growing conditions are also favourable enough in the north. For spruce, both increasing stand volumes and stem numbers were found in all studied sites and an immediate expansion of spruce forest abundance is more likely than for pine.

To bring our findings in a global context, we draw a picture, which is representative not only for Fennoscandia but also for other alpine and polar tree-line sites around the globe. In boreal regions, such as Fennoscandia, Alaska, Canada and Siberia, tree-line shifts were found to be highly dependent on topography and water supply and varied between different species. Kullman and Öberg (2009) detected tree-line rise rather in wind-sheltered and steep concave slopes, while wind-exposed sites revealed less or no tree-line shift. According to Lloyd and Fastie (2002), ring-width measurements on tree-line sites in Alaska indicated increasing radial growth during 1900–1950, but not afterwards. After the 1950s, growth decreased in nearly all sites, except of the more humid sites of the Alaska Range. Drought stress was here supposed to effect tree growth negatively. This assumption coincides with the findings of Mamet et al. (2018), who found the spruce tree line in Siberia and North America to shift from the warmer, drier sites towards cooler, drier sites. Infilling of the spruce forest was detected in the more northern sites under wetter conditions, while the dry southern sites experienced a thinning of the tree-line sites. Northwards tree-line shifts would then not be linked to a promotion of tree growth by higher temperatures, but rather to an adaption of the spruce’s ecological niche in Siberia and North America (Mamet et al. 2018).

In the western Himalaya, infilling of silver fir stands by individuals younger than 100 years resulted in a densification of the established forest stands (Singh et al. 2018), as also detected in our results. It seems that predominantly growth increments and higher survival rates of juvenile trees beyond the seedling stage cause detected forest densifications. As in our study, no upslope advance occurred in the western Himalaya, possibly as a result of drought stress due to increasing evapotranspiration under rising temperatures (Singh et al. 2018). Increasing population densities without tree-line movement were also detected for Smith fir on the Tibetan Plateau (Liang et al. 2011) and for Schrenk spruce in the Central Tianshan Mountains (Wang et al. 2006). Tree-line changes in the Swiss Alps were also related predominantly to land use changes, and only to a minor percentage to climate change (Gehring-Fasel et al. 2007). Interestingly, in Quebec, Canada, growth forms of spruce shifted from deformed krummholz to erect individuals, indicating the absence of external disturbances (Payette et al. 1985; Gamache and Payette 2004). While many older trees in our study area showed signs of damage as flag trees or krummholz, the younger individuals, e.g. in Saariselkä were of upright growth (Fig. 17). A higher survival rate of the juvenile trees might lead to tree-line infilling and possibly delayed to a forest expansion. This might happen, however, rather slow (see also Dullinger et al. 2004; MacDonald et al. 2007) and is dependent on the occurrence of further limiting environmental drivers of growth, such as water supply during the growing season.

To capture this process, we encourage ongoing monitoring activity and the observation of the boreal tree-line ecotone by remote sensing to provide continuous information about the density and vitality of the coniferous region. By supplementing the monitoring by dendroecological sampling and remote sensing, we chose a study approach which was innovative for the study area in Finnish Lapland. Thereby, we were able to draw a distinctively more detailed picture of the growth dynamics of pine in the study area than we could have done with monitoring solely. We found that the growth response of the individual pines was age-specific and not as strong as the increasing volume of growing stock would have hypothesized. The growth response of pine could be evaluated back until 1800 by dendroecology, setting the recent growth response of pine into a longer temporal context. It could be shown that the growth response of the boreal forest and alpine (oroarctic) tundra did not occur to the expected extent under global warming, and that modelling overestimated progressive tree-line advance at least for our study region. The remote sensing confirmed the hypothesis of limited forest expansion which was already assumed from the monitoring observations. By remote sensing, it was possible to set the plot-based findings of the monitoring study into a more regional context and show site-specific differences in the vegetation changes. The methodical combination therefore helped to understand recent growth dynamics of conifers in Finnish Lapland and gave evidence for the complex interactions in the tree-line ecotone.

However, some improvements and supplementary data are suggested for further studies in the tree-line ecotones. Field-based reference data of the vegetation composition help to interpret the spectral signatures of mixed pixels in satellite-based land cover classifications. Validation plots should be established for different land-cover classes, such as heath- and birch-dominated plots, open coniferous forest and wetlands, in order to identify the major vegetation class covered by one pixel with higher validity. This is especially important for the open sites of the tree-line ecotone to clearly identify the position of the forest line in recent but also ancient sceneries. Neither by plot-based monitoring nor by remote sensing it was furthermore possible to detect the seedling density in the open tundra or the numbers of conifers in the krummholz zone near the tree-species line. These areas beyond the tree line were not covered by the monitoring plots, and single seedlings would not be visible in our satellite data due to a low resolution of the imageries. Suggested that single seedlings migrated on proper sites into the open tundra as a response to climate warming, we could not have detected that effect in our data. Studying single seedling establishment beyond the tree line requires field observations which also track the survival rate of the seedlings for several years until tree size. We therefore advise to additionally study the disturbance regimes more deeply to derive better estimates of the regeneration success and to predict possible tree-line shifts in the future. We suggest to establish study plots in different tree line sites, supplemented by temperature loggers in the air and soil layer. This would enable to capture ground frost events and root zone conditions continuously during the studied time span and to correlate these events e.g. with the seedling mortality. Further variables to record in the field were the snow depths, and the onset of snow coverage and snow melt. Also here, more detailed information about the vegetation composition would be helpful for field-based stand monitoring. This should contain in particular information about the ground layer composition and understory vegetation by vegetation mapping to evaluate the seed bed and stand competition for the seedling establishment. These suggestions, however, acquire a study design being more laborious and time-consuming compared to the presented stand monitoring. However, a study design based on different methods captures more information about the complex tree-line dynamics than the focus on only one variable would do. Such a combined approach is needed to better understand the environmental drivers of prospective changes of the tree-line position.

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Appendix - Original publications

Publication I – page 101–129

Franke A.K., Aatsinki P., Hallikainen V., Huhta E., Hyppönen M., Juntunen V., Mikkola, K., Neuvonen S. and P. Rautio. 2015. Quantifying changes of the coniferous forest line in Finnish Lapland during 1983–2009. *Silva Fennica* 49 (5): 1–18. DOI: 10.14214/sf.1408.

Publication II – page 130–168

Franke, A. K., Bräuning, A., Timonen, M. and P. Rautio. 2017. Growth response of Scots pines in polar-alpine tree-line to a warming climate. *Forest Ecology and Management* 399: 94–107. DOI: 10.1016/j.foreco.2017.05.027.

Publication III – page 169–211

Franke, A. K., Feilhauer, H., Bräuning, A., Rautio, P. and M. Braun. 2018. Remotely sensed estimation of forest expansion in the polar and alpine tree-line ecotone in Finnish Lapland during the last three decades. Submitted to *Forest Ecology and Management*.

Publication I

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

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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

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 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 temperature s during the past decade.

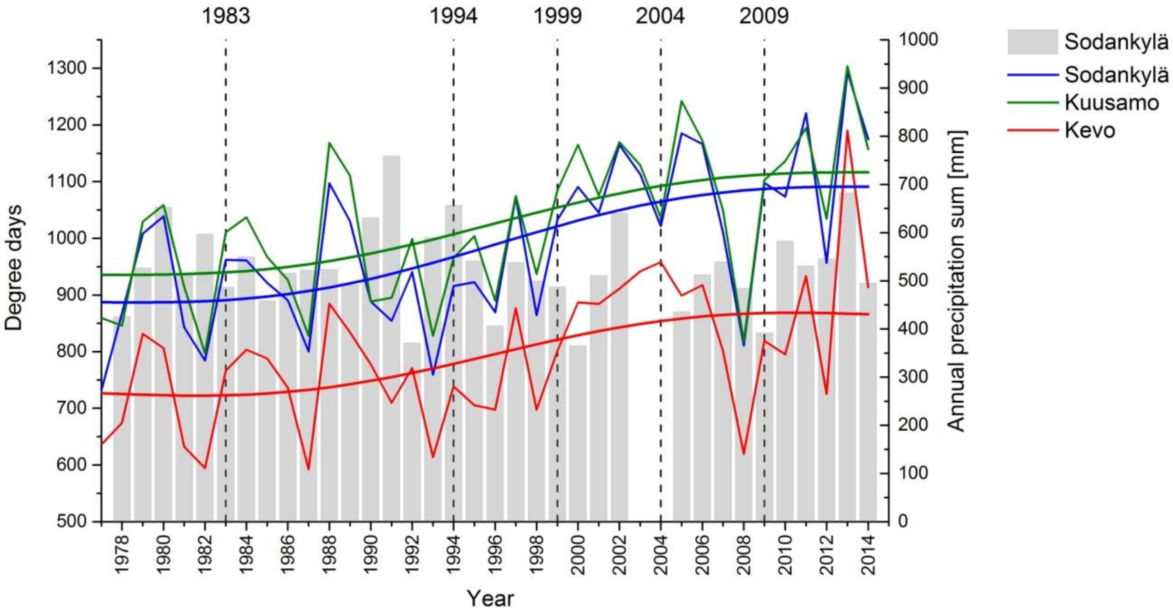

Figure 1. Effective temperature sums (+4°C threshold) in Kuusamo, Sodankylä and Kevo and annual precipitation sums (columns) in Sodankylä from 1977 to 2013. The climate datasets (thin lines, columns) are provided in a yearly resolution by European Climate Assessment & Dataset (Klein Tank et al. 2002)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

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 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, samplings 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 timberline ones and from 150 to 200 years in tree line zone (Fig.3).

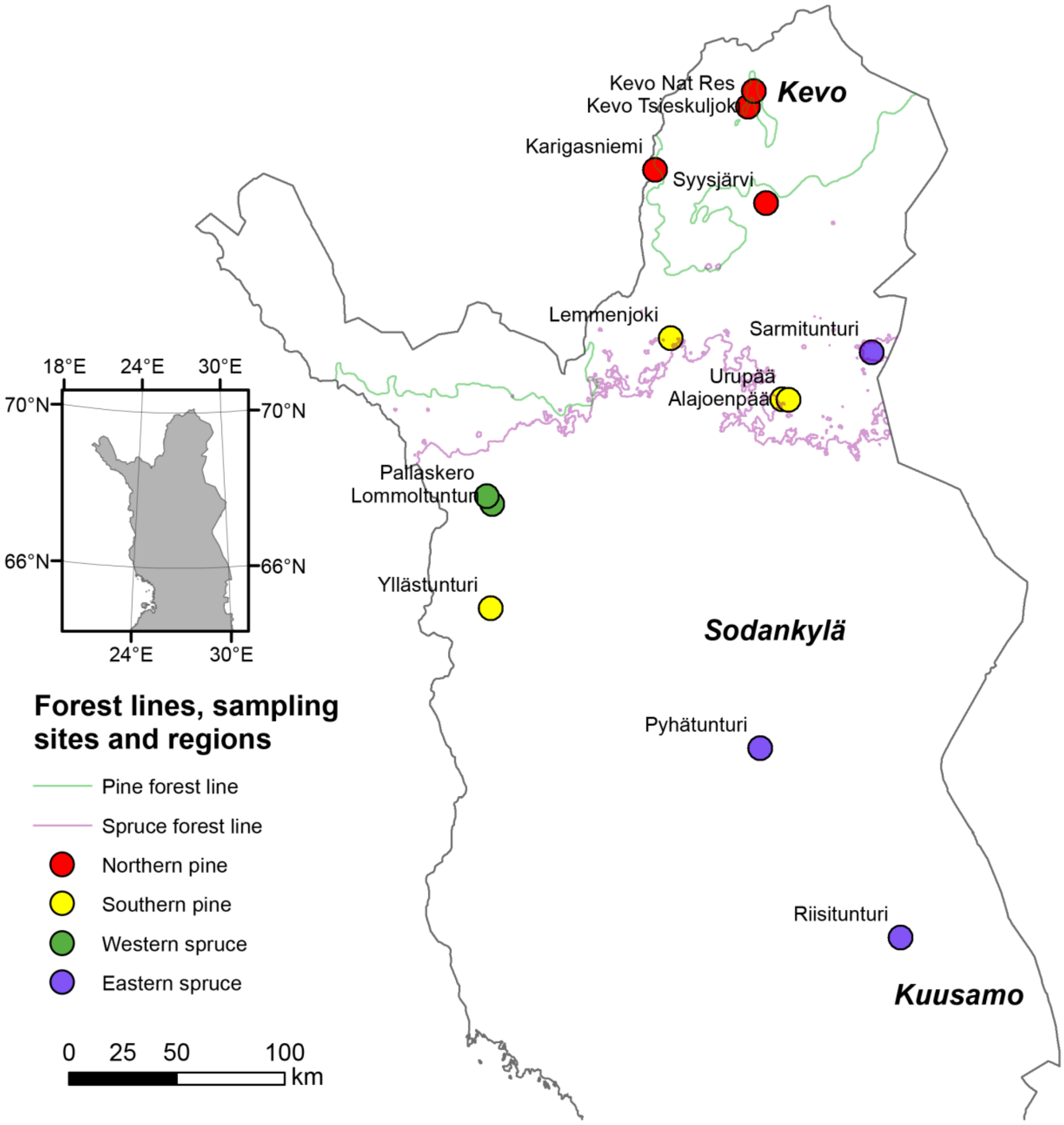

Figure 2. Monitoring locations of spruce and pine in Finnish Lapland as well as the forest lines of both species. The locations were divided on the basis of predominant species and geographical areas into a northern and southern region of pine and into a western and eastern region of spruce.

Figure 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).

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 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.

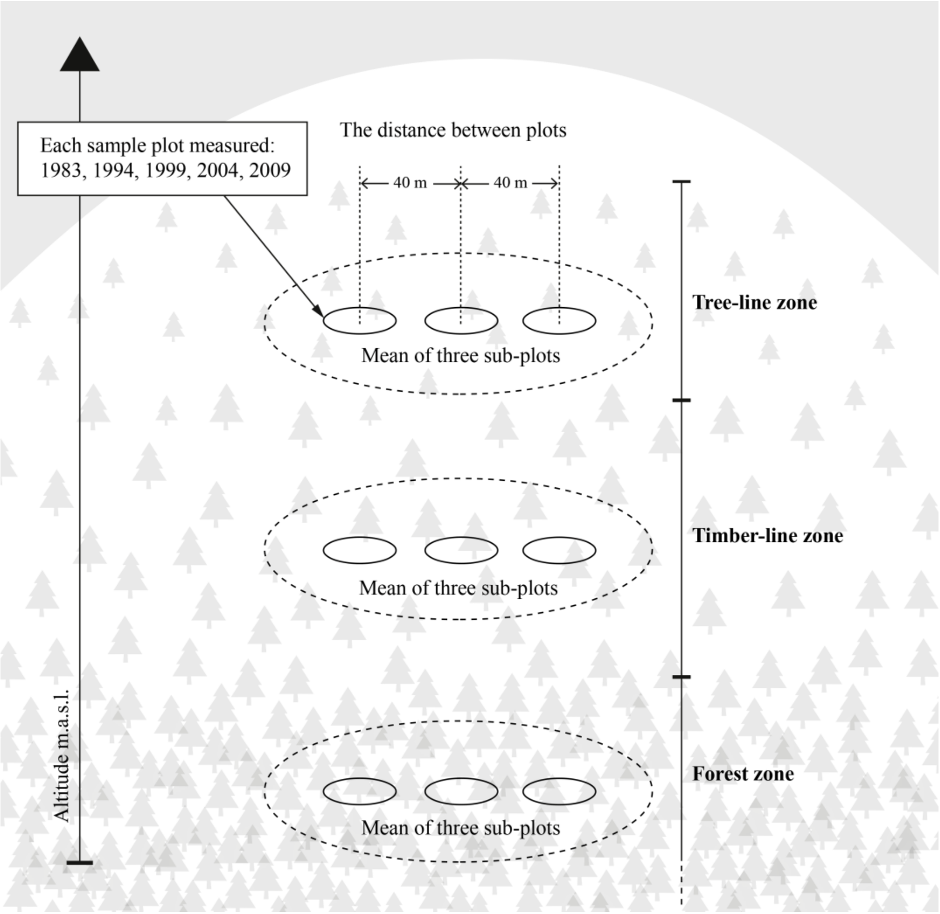

Figure 4. Sampling design in each of the 13 locations. The sampling was done on three sample plots in forest and timber- and tree-line zones in 1983, 1994, 1999, 2004 and 2009.

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.

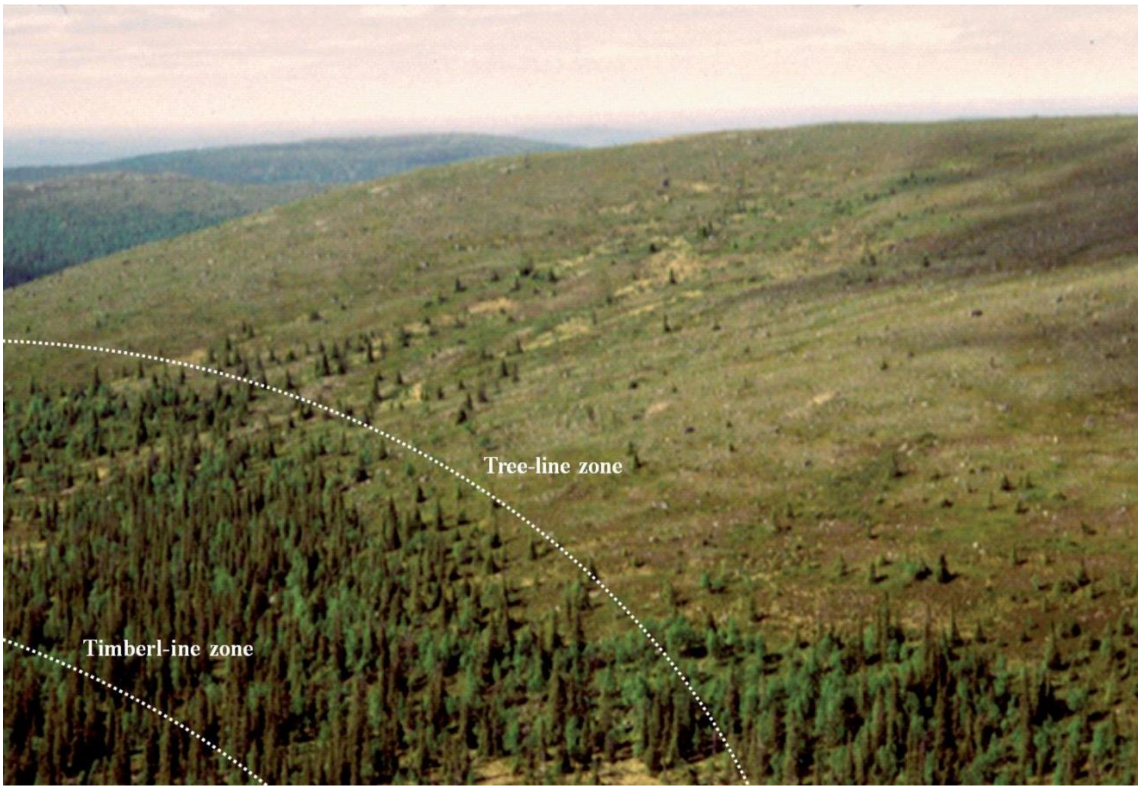

Figure 5. Example of a sampling location (Sarmitunturi) showing the position of the timber-line and tree-line zones (Photo by Raimo Sutinen). The forest zone is located further downhill and therefore not shown in the photo.

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 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.

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).

				Altitude (m a.s.l.)				Horizontal distance (m) between	
Location	Latitude	Longitude	Dominant conifer[1]	Forest zone	Timber line	Tree line	Temperature sum (d.d. 5°C)	Forest and timber line	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.

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:

(1)

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

, where

$\mathrm{sqrt}(\hat{y}_{ijt})$ = 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)

$\beta_{0,\ldots,}\beta_5$ = 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).

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 (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 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.

Table 2. The estimates and Likelihood-ratio tests of the models for Norway spruce, t-values for the coefficients and $\chi2$ – 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			

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 →

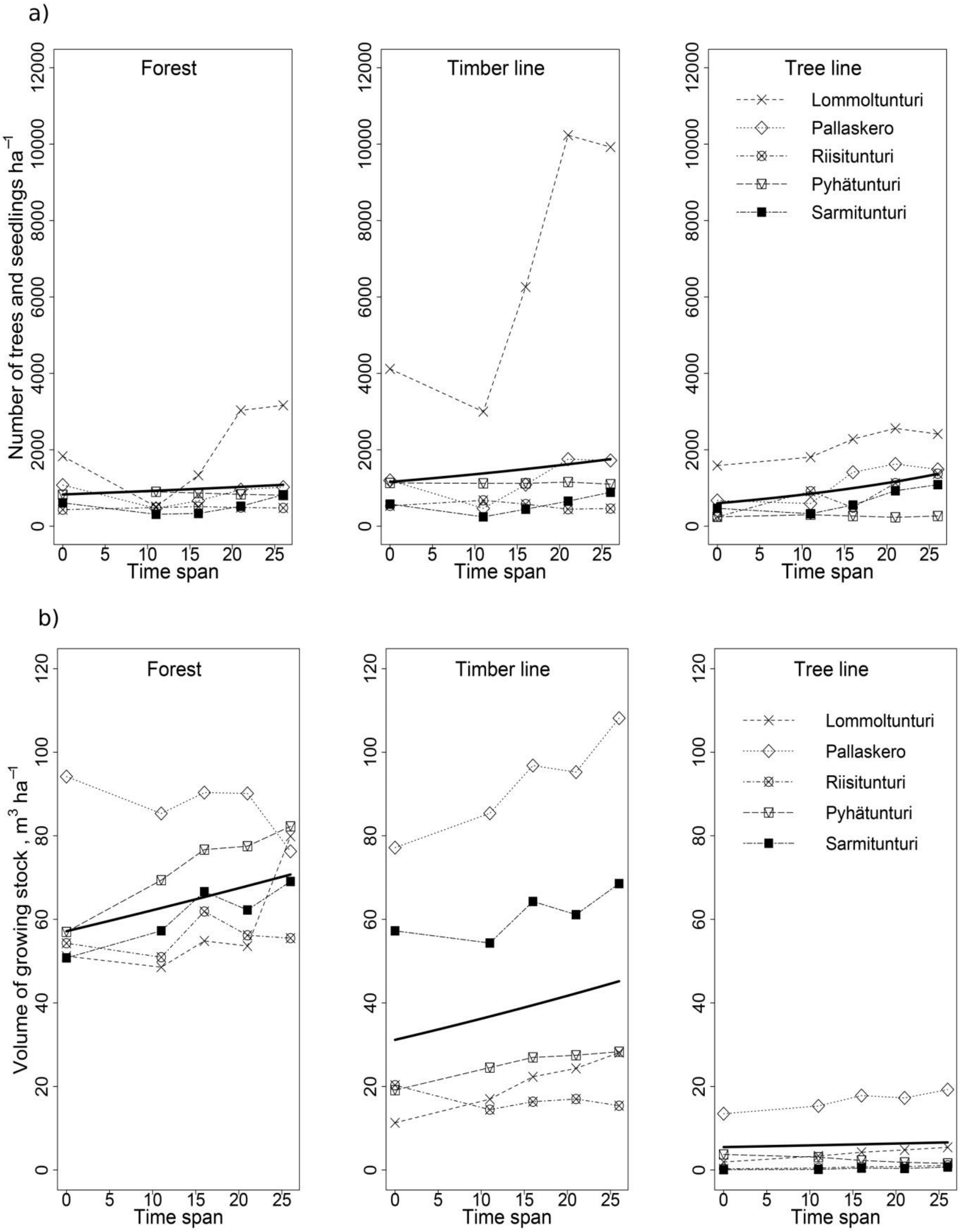

Figure 6. The stem number ha^{-1} (a) and volume of growing stock m^3 ha^{-1} (b) of spruce during the study in each location (raw data) as well as the predicted values of the models for each zone (thick line).

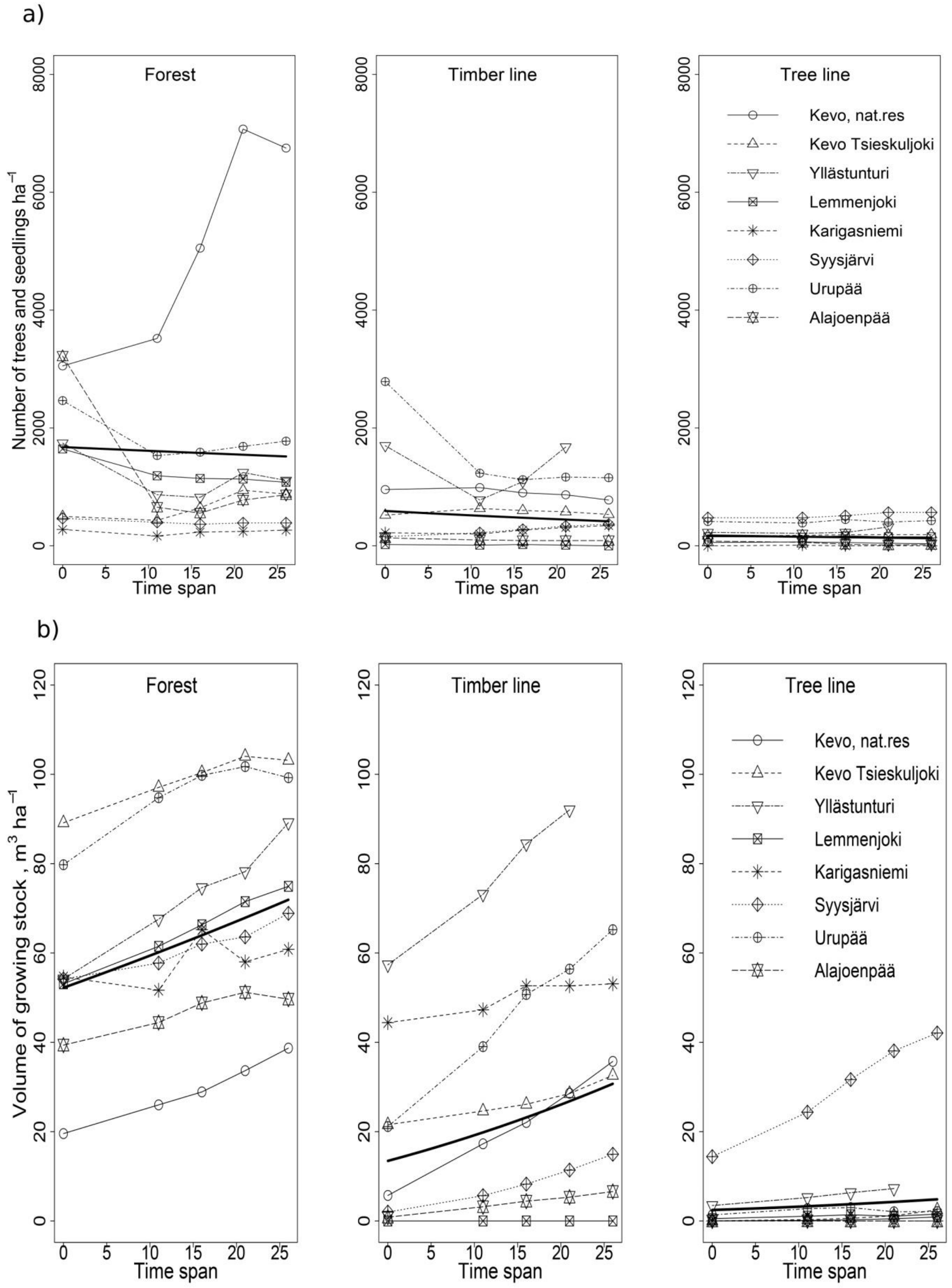

Figure 7. The stem number ha^{-1} (a) and volume of growing stock m^3 ha^{-1} (b) of pine during the study in each location (raw data) as well as the predicted values of the models for each zone (thick line).

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) has 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 timberline 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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Publication II

Growth response of Scots pines in polar-alpine tree-line to a warming climate

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Abstract

Coniferous trees at the alpine and polar tree lines of the Northern Hemisphere represent the outermost limit of their ecological range. Under such conditions, even small temperature variations may cause growth responses, which therefore can be used as indicators for changing environmental conditions. In this study we analysed the radial growth of Scots pine (*Pinus sylvestris* L.) along a latitudinal and altitudinal gradient at six locations in the polar and alpine tree-line ecotone in Finnish Lapland. We evaluated the effect of climatic trends on pine growth in relation to tree age and region, specifying a northern and a southern region in the study area. We found a response of Scots pine to climatic variations until the 1980s, but not to the current warming period. Increasing growth trends could be detected since 2000 in the radial growth of southern located trees, predominantly of juvenile ages, while the northern trees did not respond significantly to the current warming. In the north recent warmer and wetter conditions during winter time, inducing snow loads, wind damages, diseases and frost damages possibly masked the benefits of warmer conditions. The missing link between warming and radial growth would affect the use of tree-rings as proxy for past climate and for predictions for forest extension in polar-alpine tree-line sites.

Keywords: Pinus sylvestris; tree line; environmental change; growth response; latitudinal and altitudinal gradient; tree age; dendroecology

1 Introduction

Coniferous trees at the alpine and polar tree lines of the Northern Hemisphere grow close to the limit of their ecological range. They have adapted to low temperatures, short growing seasons, and harsh conditions during winter (Heikkinen et al. 2002; Seo et al. 2010). In northern Fennoscandia, where water is sufficiently provided and the competition for light and nutrients is lower than in dense forests, temperature is the most regulating and limiting factor for growth and regeneration (Briffa et al. 1990; Esteban and Jackson 2000; Heikkinen et al. 2002; Juntunen et al. 2002). Under such conditions, even small temperature variations may cause growth responses, which therefore can be used as indicators for changing environmental conditions (Grace et al. 2002; Linkosalo et al. 2009; Høgda et al. 2013; Salminen and Jalkanen 2015).

Findings of sub-fossil logs of Scots pine beyond the current timberline refer to a warmer climate and the existence of ancient forests at higher altitudes and latitudes than today (Autio and Heikkinen 2002; Eronen et al. 2002; Kultti et al. 2006). Since atmospheric warming has been observed in the 20th and 21st centuries in the entire Northern Hemisphere, but particularly in high-latitude regions during the winter season (Klein Tank et al. 2002; ACIA 2005; Høgda et al 2013; Aakala et al. 2014; IPCCa 2014; IPCCb 2014), a response of tree growth and tree regeneration is expected with ongoing increasing temperatures. In fact, a greening of the arctic has already been detected in several studies due to a densification and upward and northward expansion of the forest area (e.g. Jeong et al. 2012; Pearson et al. 2013).

This trend may have both positive and negative feedbacks on the global climate system. On the one hand, the enrichment of biomass in the previously sparsely covered tree-line ecotone and the replacement of graminoids by shrub and tree vegetation lead to increasing carbon sequestration compensating anthropogenic emissions (Watson 2000). On the other hand, forest vegetation absorbs incoming solar radiation to a greater extent than alpine fjell vegetation, predominantly during the snow-covered season. This may cause a net warming effect in ecosystems and on larger scale initiate circulation changes in Arctic regions (Grace et al. 2002; Wramneby et al. 2010; Jeong et al. 2012; Miller and Smith 2012; Zhang et al. 2013). Tree abundance additionally increases evapotranspiration, resulting in enhanced moisture in the troposphere and further global warming (Swann et al. 2010; Jeong et al. 2011; Pearson et al. 2013).

More research is needed to reliably estimate the adaptation of conifers to a changing climate and to derive realistic models of forest expansion into current tundra and alpine regions. Consequently the aim of the present study is to analyse the growth of Scots pine (*Pinus sylvestris* L.) in the polar and alpine tree-line ecotones in Finnish Lapland in relation to regional climate. In order to do this: (1) We investigated tree growth along an altitudinal gradient at six locations to determine spatial growth differences of pines across northern Finland. We evaluated the effect of latitude and altitude on current pine growth and detected the most relevant climatic drivers. (2) We also investigated the impact of long-term climatic trends on pine growth with regard to age and region in Finnish Lapland. We hypothesized that tree growth has increased during the last decades due to more favourable growth conditions especially in the northern region, where temperature is the most limiting environmental factor. We expected the climate-sensitive and fast-growing juvenile trees to respond to a greater extent with increasing radial growth to warming temperatures than mature trees.

2 Material and Methods

2.1 Study area

In the study area in Finnish Lapland, coniferous tree lines are of alpine or polar-alpine character and located on gently sloping hills with altitudinal limits of 200–500 m a.s.l.

The forest-line ecotone is primarily formed by a widespread homogenous vegetation pattern of Scots pine and Mountain birch (*Betula pubescens* subsp. *czerepanovii*) (Heikkinen et al. 2002; Kultti et al. 2006). The regional climate is influenced by the North Atlantic Ocean and the Scandes Mountain range, with a maritime climate in the coastal regions and (sub)continental conditions towards interior Finland (Linderholm et al. 2010). Cold winters and relative warm summers define a growing season of less than four months (+ 5°C threshold) including July as the warmest month of the year. The temperature sum varies from 800–900 degree days in the south to < 600 degree days in the north of the study area. The annual mean precipitation varies from 300 mm in the winter period and 700 mm in the summer period (Finnish Meteorological Institute 2016). Due to low temperatures and evaporation rates, sufficient water supply is provided in the entire study area (Autio and Heikkinen 2002). A permanent snow cover lasts from October to May (Kultti et al. 2006).

2.2 Sampling design and data preparation

The sampling was carried out in August 2014 and 2015 in six locations in Finnish Lapland (Fig. 1), where a long-term tree line monitoring project had already been established in 1983 by the Finnish Forest Research Institute (Metla) and the universities of Oulu, Helsinki and Turku (Juntunen et al. 2002). The project was designed to study regeneration and stand volume in both the polar and the alpine tree-line ecotone and is now complemented by this study. The locations were chosen on a latitudinal gradient from northern to southern Lapland and included three sampling plots each, placed along an altitudinal gradient in the closed forest zone, the forest-line zone and near the tree line (Fig. 2), resulting in total of 18 sites. The three sampling plots in each location were located close but in at least 100 meters distance from each other and differed in vegetation pattern, tree height and stand density (Fig. 2). The forest-line zone was defined here as the altitudinal limit where the forest canopy closure ceases (Hustich 1948), whereas the tree-line zone was characterized by between-tree distances of more than 2 m up to 100 m. The tree-line zone was located at 450 m a.s.l. in the southernmost location and at 200 m a.s.l. in the northernmost location. Healthy solitary pine trees of various ages which did not show any sign of damage, deformation or disease were chosen for the dendroecological sampling. To avoid remarkable signals of the stand structure in the tree-ring data, we focussed on isolated, unsheltered trees for sampling. We recorded each sample tree and bored two cores with an increment borer at breast-height. In each site, 30–60 trees were sampled, generating a dataset of at most 180 sample trees for each location. The dataset contained a total amount of 963 sample trees.

The sampled increment cores were mounted on sample holders and polished with sandpaper and razor blades to make wood anatomical structures and tree-ring boundaries clearly visible. The samples were scanned with a high-resolution (3200 dpi) flatbed-scanner and the ring-widths measured by using the software *CooRecorder* and *CDendro* (Cybis Elektronik & Data AB 2008). If a reliable detection of the rings was not possible in the scan, the ring-width measurement was performed by using the *LINTAB*™ measuring *station (Rinntech, Germany). The samples were divided into groups by site and cross-dated within the groups by using the software TSAPWin* (Rinn 2010). The cross-dating contributed to detect measuring errors, missing rings, and to evaluate the synchronicity of the single series. To reduce statistical noise and to strengthen the climatic signal, sample trees with signs of damage, compression wood or extensive parts of missing rings were excluded from further analysis. Thereby, a total amount of 905 sample trees remained for constructing the final chronology.

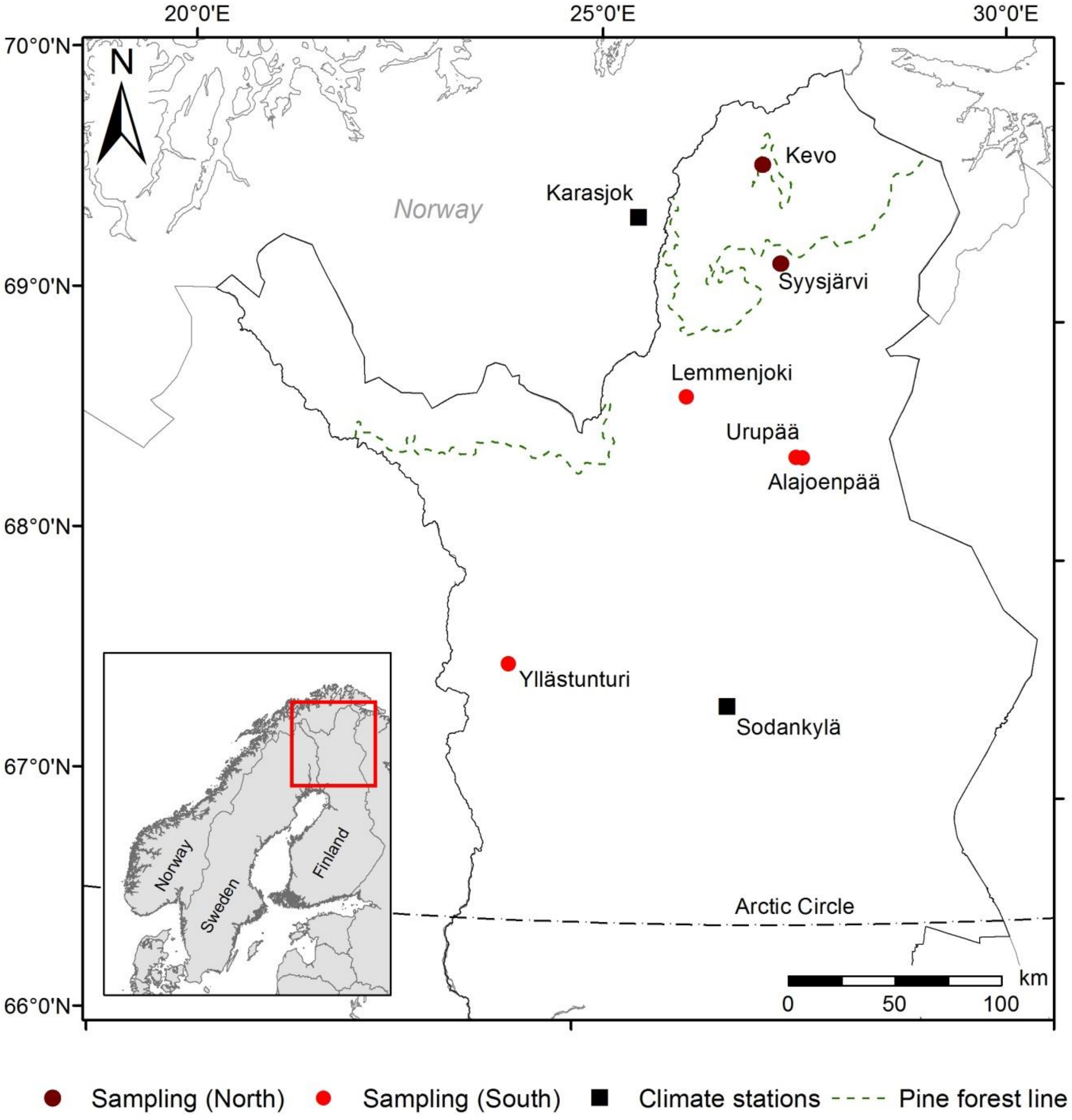

Figure 1. Position of the Scots pine forest line, the sampling locations and the climate stations used in this study.

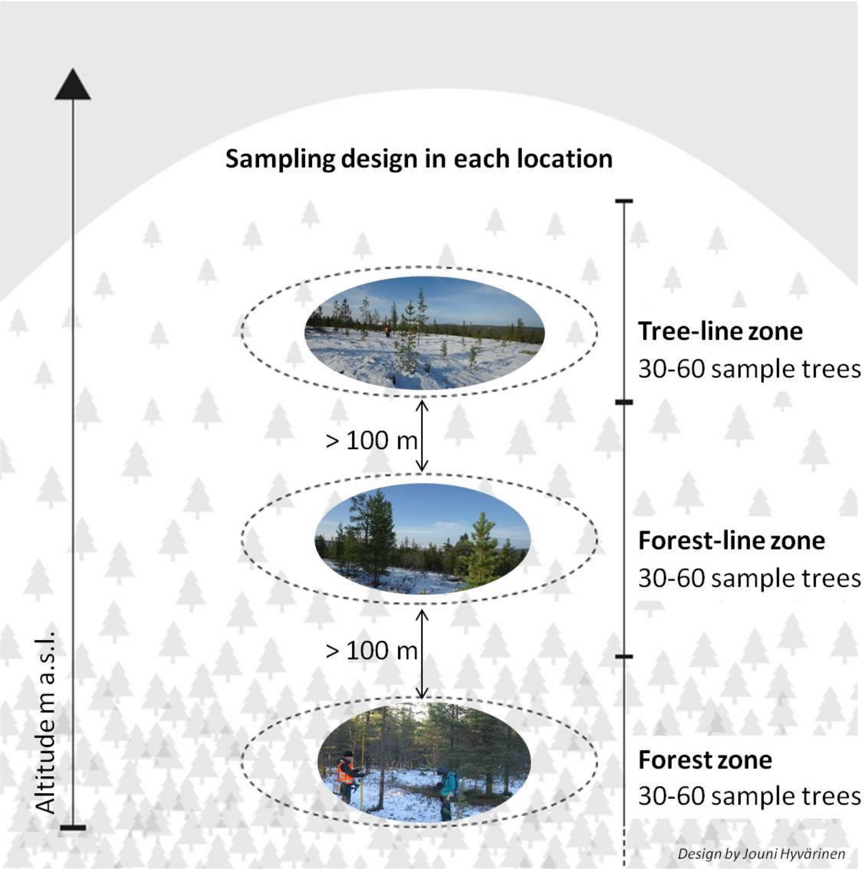

Figure 2. Sampling design for Scots pine in each of the six sampling locations. Tree-ring sampling was carried out in the forest zone, the forest-line zone, and the tree-line zone and included trees of mature and juvenile ages.

2.3 Tree-ring analysis: Site-specific growth variations

The ring-width measurements were used to compute the mean annual growth rate of pine, the annual increase in the stem radius, for each of the 18 sample plots. This was done in order to point out site-specific differences in the climate, stand structure or disturbance regime. The computation was based solely on juvenile trees, established in the forest stands after 1950, since they reflect the impact of climate and stand structure with a high sensitivity in the tree-ring data. Furthermore, the mean growth rate of mature trees would be affected by the biological age curve, forming wide rings in fast-growing juvenile ages but narrow rings in the mature ages. By using only juvenile ages we aimed to reduce the impact of the biological age. The statistical significance of the results was tested by the two-way factorial analysis of variance (ANOVA) with zone and location as factors on a confidence level of $p < 0.05$.

For further analysis, we transformed the raw ring-widths of all mature and juvenile samples of each site into a site-specific residual chronology to enable a comparison of the high-frequency growth-pattern. Since this method eliminated the age effect, trees of all ages were included. The age-related growth trends and non-climatic noise, such as local disturbance events by pests or diseases were first removed from the tree-ring data by standardization *with the dplR package* in R version 3.2.0 (Bunn et al. 2015). Dimensionless tree-ring indices were derived by dividing each measured ring-width value by the expected value of the growth curve (Cook and Holmes 1986). Since no uniform age-trend was visible in the predominantly juvenile samples, a relatively flexible smoothing spline function of 30 years and a frequency cut-off of f = 0.5 was fitted to the individual series. The individual index series were then averaged by site into 18 residual chronologies (Cook and Holmes 1986), being cleaned from autocorrelation for the climate analysis. Descriptive statistics, such as the mean tree age, mean sensitivity (MS) and signal-to-noise ratio (SNR) were computed. The Expressed Population Signal (EPS), as a function of sample size and mean inter-series correlation (RBar), indicated the reliability of the chronology (adequate when EPS ≥ 0.85) (Wigley et al. 1984). The sample size was not equally distributed between the sites and through time, since some sites were characterized by sparse tree vegetation and juvenile age stands, covering mostly the recent decades. We therefore used a 64-year period from 1950 to 2014 to generate comparable datasets for the subsequent analysis. The residual chronologies 1950–2014 were tested by Pearson correlation coefficient on similarities in the growth pattern. High correlation values expressed a similar year-to-year variation between the sites, whereas low correlations pointed to differing growth curves.

The relation between the growth pattern and the relevant climate parameters during 1950–2014 were tested by Pearson correlation coefficient. As variables we chose the site chronologies and relevant climate parameters in a monthly resolution of the current and the previous year. We tested the mean temperature, the number of warm, cold and frost days, the precipitation sum, the number of snow days, the average of monthly snow cover, the cloud coverage, the solar radiation and the maximum wind speed. Since there were no meteorological stations near the study plots, the climate datasets were provided for Sodankylä by the European Climate Assessment & Dataset (Klein Tank et al. 2002) and for Karasjok by the joint online weather service from the *Norwegian* Meteorological Institute and the *Norwegian* Broadcasting Corporation (Yr 2017). Observations from Karasjok (Norway) were correlated with the northern site chronologies (of Kevo and Syysjärvi), whereas Sodankylä (Finland) was correlated with the southern site chronologies (of Lemmenjoki, Alajoenpää, Urupää and Yllästunturi). The North Atlantic Oscillation (NAO) Index was provided in a quarterly resolution by the Climate Analysis Section (Hurrell 2003). Only the correlation coefficients showing statistically significant relation ($p < 0.05$) between relevant climate variables and tree growth were presented in the results.

2.4 Tree-ring analysis: Trend analysis and climate

The mean temperature and the precipitation sum were plotted for the winter period (Oct–Mar) and the summer period (Apr–Sep) and complemented with Fast Fourier Transformation smoothing splines in order to detect long-term variations on the example of Sodankylä. The recent warming period, where the July temperature exceeded the average remarkably in 1996 until 2014, was highlighted for the growth-trend analysis. Linear regressions as an estimation of the climatic trends were computed for temperature and precipitation and tested for statistical significance by ANOVA on a confidence level of $p < 0.05$. This was done for the temperature of the entire time span (1908–2014) and of the recent warming period (1996–2014), respectively.

To see whether the long-term climatic trends are detectable in the tree-ring data as well, we used another method of chronology building. The raw data were prepared to preserve low-frequency information excluding the biological age-trend. The Regional Curve Standardization (RCS) was used in the dplR package of R version 3.2.0 (Bunn et al. 2015) for standardization which fitted a single average biological growth curve to each individual ring-width series (Briffa et al. 1992). The indexed series were then separated by age by the year of germination (juvenile trees: $Y_0 \geq 1950$, ranging from 1950–2014; mature trees: $Y_0 \leq 1900$, ranging from 1800–2014) and region (north; south) and averaged into four RCS chronologies. To ensure a clear separation of the age classes, middle-aged trees, germinated during 1901–1949, were excluded. The RCS chronologies were plotted with Fast Fourier Transformation smoothing splines in order to visualize long-term variation. The response to the recent warming period 1996–2014, was tested by linear regression. The significance of the linear regression was tested by ANOVA.

A pointer year analysis was performed on the datasets by using the Becker algorithm (Becker et al. 1994) in R version 3.2.0 (Bunn et al. 2015) to detect climatic event years. A pointer year was defined here as a relative growth change of > 20 % (recommended for alpine timberlines by Schweingruber et al. 1990) from the current to the next year occurring in at least 75 % of the sample trees. The analysis was performed on all sampled trees within each location for the period of 1800–2014, starting with a minimum sample size of ten trees. Finally, an evolutionary correlation was computed using DendroClim software (Biondi and Waikul 2004) to test the consistency of the climatic impact factors during the last decades. For the evolutionary correlation analysis southern mature trees were chosen as an example. In this analysis the radial growth was correlated with the mean temperature, the precipitation sum, the number of frost and snow days (measured in Sodankylä meteorological station) within a period starting in previous April and ending in current October during the time span of 1913–2013 with a base length of 40 years.

3 Results

3.1 Site-specific growth variations

The growth-rate analysis indicated a statistically significant effect of location, zone and their interaction on pine growth during 1950–2014 (Table 1). The impact of zone on pine growth depended on the location in the study area, being higher in the southern region than in the northern region. Elevation effects occurred predominantly in the southern locations, such as Yllästunturi and Urupää. Highest growth rates were found in the tree-line zones in all locations except in Syysjärvi, whereas the lowest values occurred in the forest zones (Fig. 3, Table 2). While the growth in the tree-line zones indicated a latitudinal gradient, the forest zone did not show similar effects.

The high-frequency growth pattern, covering the period from 1950 to 2014, was found to be quite similar in all site chronologies, revealing homogeneous variations during the past 64 years (Fig. 4). The mean ages ranged from approximately 40 years in the more recent forest stands of the tree-line zone to 111.26 years in the older stands of the forest zone (Table 3). The mean sensitivity, as an estimation of the high-frequency growth variability, and the inter-series correlation (RBar) values were similarly low in all chronologies (Table 4). High EPS (expressed population signal) values indicated a sufficient sample size and reliability of the datasets, exceeding the recommended threshold of 0.85 for the whole time span. The signal to noise ratio (SNR) as an estimation of the common climatic signal was slightly higher in the southern than in the northern region and decreased in the southern locations from the forest to the tree-line zone. This might also be an effect of lower number of trees in one northern location, as the SNR is also affected by sample size.

Table 1. Analysis of variance for the effect of location and zone, and their interaction on the mean annual growth of juvenile Scots pine trees.

Source	Sum of Squares	df	F	Sig.
Location	8.41	5	13.72	<0.001
Zone	31.03	2	126.54	<0.001
Location * Zone	15.97	10	13.03	<0.001
Error	75.89	619		

Table 2. The mean annual growth rate with standard error, sample size (amount of sample trees) and mean age of juvenile Scots pines during 1950–2015 in different locations and zones.

	Zone/location	Mean growth rate (mm)	Standard error (mm)	Sample size	Mean age
Zones	Tree-line zone	1.67	± 0.024	248	42.13
	Forest-line zone	1.51	± 0.025	232	43.86
	Forest zone	1.10	± 0.030	157	50.09
Locations	Kevo	1.33	± 0.049	53	35.53
	Syysjärvi	1.47	± 0.030	145	43.73
	Lemmenjoki	1.37	± 0.034	114	40.96
	Alajoenpää	1.62	± 0.032	123	45.04
	Urupää	1.37	± 0.039	99	49.22
	Yllästunturi	1.57	± 0.036	103	50.28

Slight regional differences recurred in correlations between the growth patterns of different sites, although the correlation coefficients were relatively high in most cases (Table 4). Strongest correlations were found between sites of the same location and between sites of adjacent locations, such as Alajoenpää and Urupää. Low correlation values were found between distant locations, such as Kevo and Yllästunturi. Site Lemmenjoki showed low correlations with all other sites due to slightly deviant growth patterns.

The climate-growth analysis indicated a significant correlation of pine growth in all sites with parameters related to temperature (Fig. 5, Table 5). The highest correlation values were found with the mean temperature of the current year’s July at all sites, especially in the forest-line zone in the south and the forest zone in the north (Fig. 5). The mean temperature of the previous year’s May and the current year’s March revealed a significant growth impact in nearly all sites, while the current April and May correlated with at least some of the sites significantly. The number of warm days during the previous May and the current March and July had a positive impact on the radial growth, especially in the northern sites (Table 5). In nearly all of the sites a negative correlation was found between the site chronologies and the occurrence of cold days in

May and July and with the occurrence of frost days in May. The site chronologies in the northern sites had a negative correlation with cold and frosty days in March, while in the southern sites negative correlations were found with the number of cold days in August. High precipitation sums during current year’s May had a positive effect on tree growth in the north, whereas precipitation during July had a negative impact in the south. The number of snow days and the average monthly snow cover during current year’s April and May correlated highly negatively with all site chronologies. The NAO Index during the winter season had a positive impact on tree growth predominantly at southern sites.

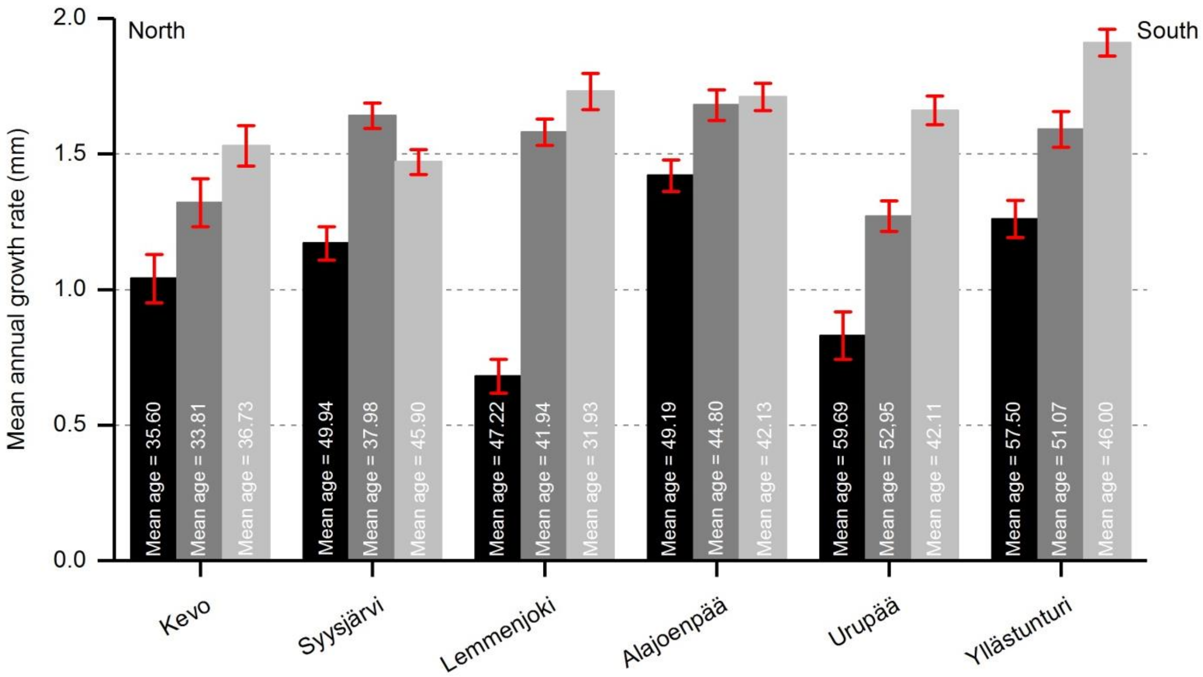

Figure 3. Mean annual growth rates (grey columns) with standard errors (red bars) and mean ages of juvenile Scots pines during 1950–2015. The statistical differences between the zones and locations are presented in Tables 1 and 2. The mean age is indicated within each bar.

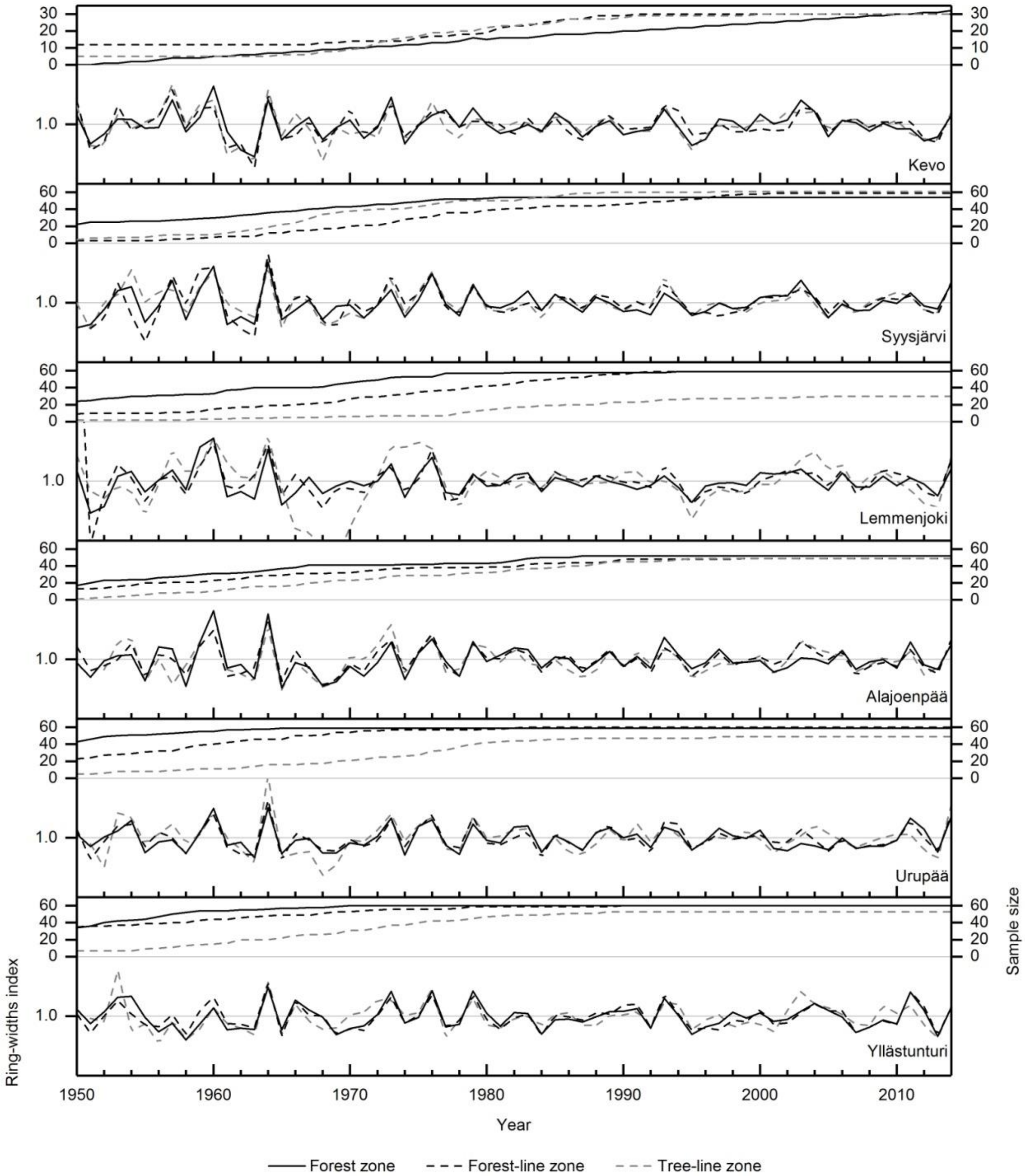

Figure 4. Residual site chronologies of ring-width indices of Scots pine, plotted separately for the forest zone, the forest-line zone and the tree-line zone for the period of 1950–2014. The sample size in the upper part of each panel displays the number of sample trees through time of the corresponding chronology.

Table 3. Statistics of local and regional master chronologies: Altitude, sample size (number of sample trees), time span, mean age, mean sensitivity (MS), inter-series correlation (RBar), expressed population signal (EPS) and signal-to-noise ratio (SNR).

Detrending	Location	Zone	Region	Altitude [m a.s.l.]	Sample size	Mean age	Time span	MS	RBar	EPS	SNR
Smoothing Spline	Kevo	Treeline	North	190	30	68.73	1950–2014	0.19	0.24	0.86	6.07
	Syysjärvi	Treeline	North	225	61	50.73	1950–2014	0.17	0.29	0.95	17.89
	Kevo	Forest line	North	180	30	86.47	1950–2014	0.21	0.21	0.85	5.55
	Syysjärvi	Forest line	North	220	59	46.48	1950–2014	0.18	0.27	0.93	12.64
	Kevo	Forest	North	110	32	107.78	1950–2014	0.19	0.22	0.88	7.04
	Syysjärvi	Forest	North	215	54	111.62	1950–2014	0.20	0.23	0.93	14.11
	Lemmenjoki	Treeline	South	415	30	37.33	1950–2014	0.21	0.25	0.84	5.27
	Alajoenpää	Treeline	South	400	49	43.49	1950–2014	0.22	0.23	0.91	9.58
	Urupää	Treeline	South	370	49	48.63	1950–2014	0.20	0.23	0.91	9.90
	Yllästunturi	Treeline	South	465	53	51.64	1950–2014	0.20	0.28	0.94	14.64
	Lemmenjoki	Forest line	South	375	59	46.22	1950–2014	0.20	0.25	0.93	13.28
	Alajoenpää	Forest line	South	380	49	55.42	1950–2014	0.20	0.28	0.94	14.46
	Urupää	Forest line	South	340	60	72.12	1950–2014	0.19	0.30	0.96	22.74
	Yllästunturi	Forest line	South	410	60	88.88	1950–2014	0.20	0.29	0.96	22.14
	Lemmenjoki	Forest	South	285	59	105.75	1950–2014	0.19	0.21	0.93	13.36
	Alajoenpää	Forest	South	340	52	80.48	1950–2014	0.22	0.22	0.92	11.86
	Urupää	Forest	South	315	59	81.97	1950–2014	0.19	0.27	0.96	21.34
	Yllästunturi	Forest	South	380	60	89.85	1950–2014	0.20	0.31	0.96	25.80
Detrending	Region	Age			Sample size	Mean age	Time span	MS	RBar	EPS	SNR
RCS	North	Mature (= NoM)			54	189.06	1800–2014	0.26	0.31	0.95	20.75
	North	Juvenile (= NoJ)			205	40.91	1950–2014	0.18	0.14	0.95	20.23
	South	Mature (= SoM)			73	171.97	1800–2014	0.25	0.27	0.96	21.70
	South	Juvenile (SoJ)			435	46.24	1950–2014	0.20	0.10	0.97	34.73

Table 4. Correlations between the chronologies of the forest zone (F), forest-line zone (FL) and tree-line zone (TL) of each location. Symbols for correlation coefficients: ● (≥ + 0.7),◍ (≥ + 0.5),○ (≥ + 0.3),◌ (< + 0.3).

Region			**Northern region**						**Southern region**											
	Location		Kevo			Syysjärvi			Lemmenjoki			Alajoenpää			Urupää			Yllästunturi		
		Zone	TL	FL	F	TL	FL	F	TL	FL	F	TL	FL	F	TL	FL	F	TL	FL	F
Northern region	Kevo	TL																		
		FL	●																	
		F	●	●																
	Syysjärvi	TL	●	◍	●															
		FL	●	●	●	●														
		F	●	◍	●	●	●													
Southern region	Lemmenjoki	TL	◍	○	○	◍	◍	○												
		FL	○	○	○	○	●	◌	○											
		F	●	●	●	●	●	●	○	◍										
	Alajoenpää	TL	◍	◍	◍	●	◍	●	◍	●	●									
		FL	●	◍	●	●	●	●	◍	◍	●	●								
		F	◍	◍	◍	●	●	●	◍	○	●	●	●							
	Urupää	TL	◍	◍	◍	●	●	●	◍	◍	◍	●	●	●						
		FL	◍	◍	●	●	●	●	○	○	●	●	●	●	●					
		F	◍	◍	◍	●	◍	●	○	○	●	●	●	●	●	●				
	Yllästunturi	TL	○	◍	○	◍	◍	◍	○	◍	○	◍	◍	◍	◍	◍	◍			
		FL	◍	◍	◍	●	●	◍	○	○	◍	◍	●	●	◍	●	●	●		
		F	○	○	◍	◍	◍	◍	◌	○	◍	◍	●	◍	◍	●	●	●	●	

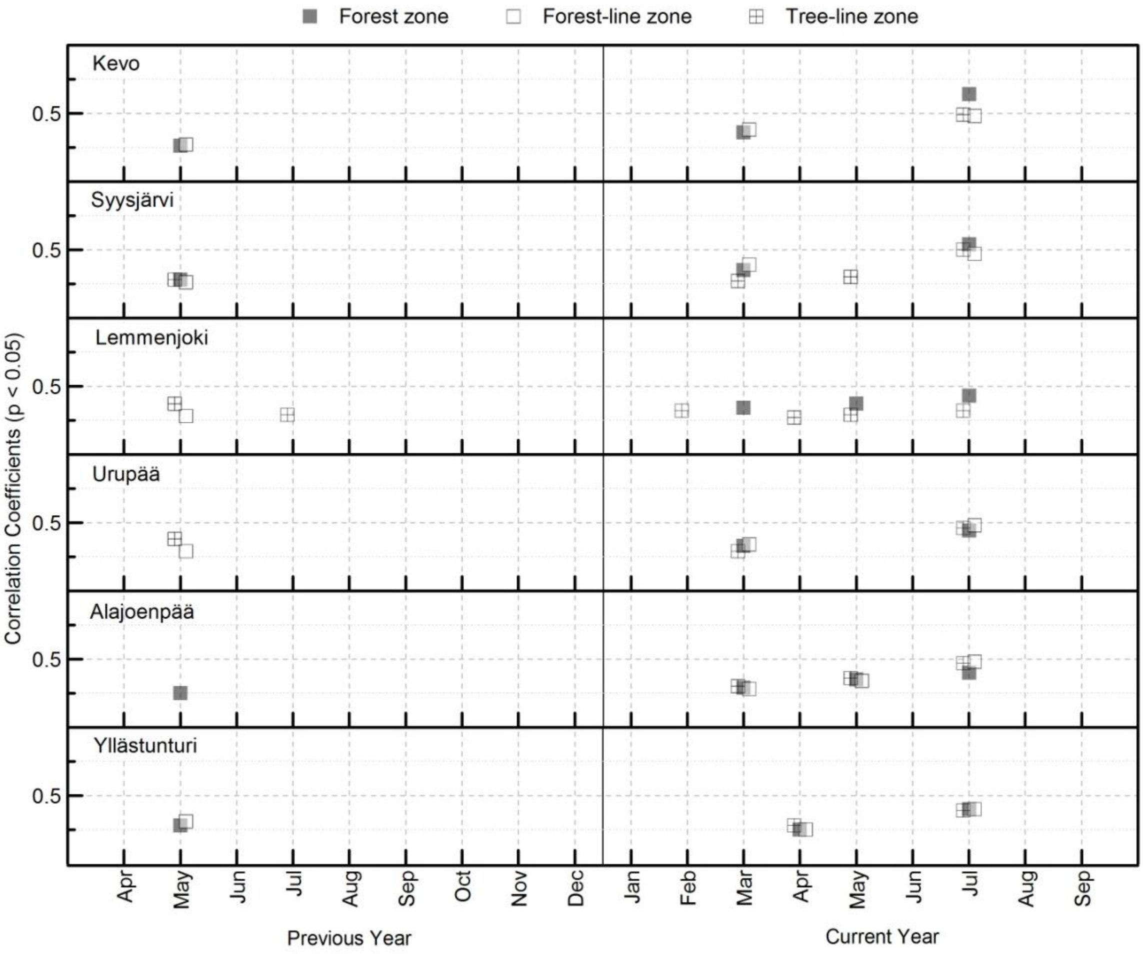

Figure 5. Pearson's correlation coefficients between residual chronologies of pine and monthly mean temperatures of the current and the previous year. Only significant values ($p < 0.05$) are plotted for each location and zone.

Table 5. Results of the Pearson correlation (*r*) of the site chronologies in tree-line zone (TL), forest-line zone (FL), forest zone (F) with the growth-relevant climatic variables of the current and the previous year during 1950–2014.

🟤 ($r \geq +0.5$), 🟠 ($+0.3 \leq r < 0.5$), ○ ($+0.1 \geq r < +0.3$), ● ($r \leq -0.3$), ◎ ($-0.1 \geq r > -0.3$)

		Region	**Northern region**						**Southern region**											
		Location	Kevo			Syysjärvi			Lemmenjoki			Alajoenpää			Urupää			Yllästunturi		
Climatic parameter	**Month**	**Zone**	TL	FL	F	TL	FL	F	TL	FL	F	TL	FL	F	TL	FL	F	TL	FL	F
Number of warm days (T_{mean} > 90th percentile of daily mean temp.)	May$_{\text{previous}}$		🟠	🟠	🟠	🟠	🟠	🟠	○	○		○	○	🟠	🟠	🟠	○	🟠	🟠	
	Mar$_{\text{currrent}}$			○	🟠	○	🟠	🟠			🟠	🟠	🟠	🟠	○	○	○			
	Jul$_{\text{current}}$		🟠	🟠	🟤	🟠	🟠	🟤	🟠		🟠	🟠	🟠	🟠	🟠	🟠	🟠	○	○	
Number of cold days (T_{mean} < 10th percentile of daily mean temp.)	Mar$_{\text{current}}$			◎	◎		●	◎												
	May$_{\text{current}}$		◎	◎	◎	●	◎	●	●	◎	●	●	●	●	●	●	◎	◎	●	
	Jul$_{\text{current}}$			◎	●	◎		●			◎	●	●	●	●	●	●	◎	◎	●
	Aug$_{\text{current}}$				◎						◎	●	◎		◎	◎		◎		
Number of frost days (T < 0 °C)	Mar$_{\text{current}}$				●	●	●	●												
	May$_{\text{current}}$		●		●	●	●	●	●		●	●	●	●	●	◎	◎		◎	
Precipitation sum	May$_{\text{current}}$		🟠	○	🟠	🟠	🟠	🟠						○	○			○		
	Jul$_{\text{current}}$												◎	◎		●	◎		●	◎
Number of snow days (snow depth ≥ 1 cm)	Apr$_{\text{current}}$				◎	●	◎	●	●	●	●	●	●	●	◎	●	●		●	
	May$_{\text{current}}$		●	◎			●	●	●		●				◎					
Average of monthly snow cover	Mar$_{\text{current}}$							◎		●	◎	◎	◎		◎			●	●	◎
	Apr$_{\text{current}}$			◎		◎	●	●	◎	●	●	●	●		●	◎		●	●	●
	May$_{\text{current}}$		●				◎	◎	◎	●			◎							
NAO index	Nov$_{\text{previous}}$–Jan$_{\text{current}}$		○		○		○	○	○		○	🟠	🟠	🟠	🟠	🟠	🟠		🟠	

3.2 Long-term trend analysis

The mean annual temperature and precipitation sum were examined by linear regression to detect possible long-term trends. The annual mean temperature increased significantly ($p < 0.05$) at the climate station of Sodankylä (1908–2014: +1.92 °C; 1996–2014: +1.57 °C), and the warming was highest during the winter and springtime seasons (Table 6). The July temperature exceeded the average temporarily in the 1930s and permanently after 1996. We hence selected this recent warming period 1996–2014 for the subsequent growth-trend analysis, although a slight decrease in the July temperature was detected during the last decade (Fig. 6, Table 6). The winter season displayed increasing temperatures in the 1930s and constantly after 1988 (Fig. 6). Karasjok indicated a slight, non-significant increase in the annual mean temperature in the north (1908–2014: +0.80 °C; 1996–2014: +0.88 °C). In Karasjok the warming of the entire time span (1908–2014) was highest during the summer period, while during 1996–2014 it was highest in the winter period (Table 6). The warming rate of Karasjok was lower than in Sodankylä. The precipitation sums in Sodankylä increased significantly during the winter period (1908–2014: +40.37 mm) and during May (1908–2014: +12.57 mm) (Table 6), while the increase was highest during the second half of the 20th century (Fig. 6).

Both the NAO index and the number of snow days, presumably affecting the start of the growing season, were additionally chosen from the correlation analysis and plotted with smoothing splines to detect decadal variations (Fig. 6). The NAO Index revealed a maximum in the 1990s during the winter period, going synchronously with a high winter mean temperature and precipitation sum. The number of snow days showed a tendency of reduced snow cover in April during the 1980s and 1990s, indicating an earlier start of the growing season during this period.

Table 6. Changes of mean temperature in Sodankylä and Karasjok and the precipitation sum in Sodankylä during the 20th century (Datasets: Klein Tank et al. 2002; Yr 2017). A linear regression provided an estimation of the year-to-year change by the slope of the trend line. The linear regressions for temperature were computed for the entire time span (1908–2014) and for the recent warming period (1996–2014), respectively. Statistically significant trends, tested by ANOVA ($p < 0.05$), are marked with an asterisk (*).

Parameter	Climate station	Time span	Annual	Winter period	Summer period	May	July
Mean temperature (°C)	Sodankylä	per year	+ 0.0179*	+ 0.0182*	+ 0.0157*	+ 0.0242*	+ 0.0072
		1908–2014	+ 1.92*	+ 1.95*	+ 1.68*	+ 2.59*	+ 0.77
		per year	+ 0.0827*	+ 0.1082	+ 0.0906*	+ 0.2195*	+ 0.0329
		1996–2014	+ 1.57*	+ 2.06	+ 1.72*	+ 4.17*	+ 0.63
	Karasjok	per year	+ 0.0075	+ 0.0002	+ 0.0129*	+ 0.0195*	+ 0.0046
		1908–2014	+ 0.80	+0.02	+ 1.38*	+ 2.09*	+ 0.49
		per year	+ 0.0463	+ 0.1025	+ 0.0354	+ 0.146*	– 0.0575
		1996–2014	+ 0.88	+ 1.95	+ 0.67	+ 2.77*	– 1.09
Precipitation sum (mm)	Sodankylä	per year	+ 0.3881	+ 0.3773*	– 0.0055	+ 0.1175*	+ 0.1381
		1908–2014	+ 41.53	+ 40.37*	– 0.59	+ 12.57*	+ 14.78

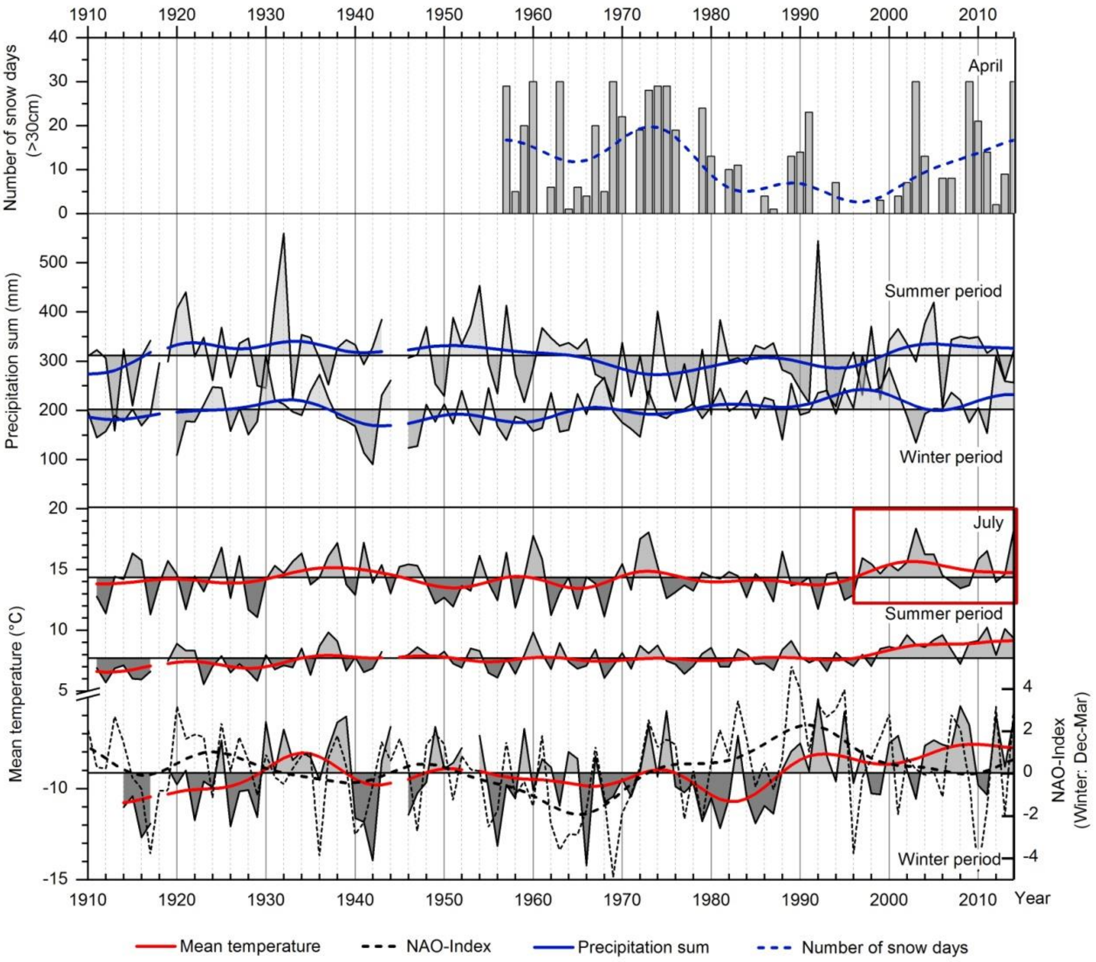

Figure 6. Mean temperature of the summer period (Apr–Sept), the winter period (Oct–Mar) and July in Sodankylä during 1908–2014 (Dataset: Klein Tank et al. 2002); precipitation sum of the summer period (Apr–Sept) and the winter period (Oct–Mar) in Sodankylä during 1908–2014 (Dataset: Klein Tank et al. 2002); the number of snow days of April during 1957–2014 (Dataset: Klein Tank et al. 2002); and the North Atlantic Oscillation Index of the winter period (Dec–Mar) during 1908–2014 (Dataset: Hurrell 2003). All data series were smoothed by using a Fast Fourier Transformation. The recent warming period based on the July temperature is marked (red box) for the trend analysis (cf. Figure 8).

We tested whether the detected climatic trends are reflected in the detrended tree-ring data as well. The regional curve standardization (RCS) chronologies covered a time span of 64 years for juvenile trees and 214 years for mature trees and exceeded the recommended EPS-threshold value of 0.85 in all cases (Table 3). The mean sensitivities (MS) were similar in the North and the South whereas the MS was slightly higher in the mature ages (MS_{north} = 0.26, MS_{south} = 0.25) than in the juvenile ages (MS_{north} = 0.18, MS_{south} = 0.20). The inter-series correlation (RBar) values were higher in the mature ages (Table 3), while the signal to noise ratio (SNR) was highest in the southern juvenile trees. The long-term growth pattern revealed some common decadal variation in both the north and the south, showing high growth indices during 1800–1830, 1920–1940, 1950–1960 and the mid-1970s (Fig. 7). Growth depressions occurred in the 1830s, 1892, the 1900s, 1910, the late 1920s and the early 1960s. The index values of the mature trees recovered after the depression in 1902, reaching maximum values in the 1930s and remaining afterwards on an above-average level. No significant response was detected during the recent warming period after 1996 (Fig. 8), revealing rather low and less variable growth indices in both regions (Fig. 7). The juvenile trees displayed a similar growth pattern in both regions, with higher variation before 1980 (Fig. 7). A significant growth increment was detected in the growth of southern juvenile trees since 1996, but not in northern juvenile trees (Fig. 8).

The pointer year analysis indicated negative event years during the 1830s and the early 1900s and positive event years over the entire time span with the exception of the periods 1845–1875 and 1980–2014 (Fig. 9). During these periods the tree-ring data did not respond synchronously to climatic events. The evolutionary correlation indicated high positive correlations of the southern mature tree growth with the temperature in July during the entire time span while the correlation with the May temperature decreased and diminished until 2013, having the highest impact during the 1950s (Fig. 10). The precipitation sum indicated a negative impact on tree growth in February and July, predominantly during the 1970s and after 2000. Positive correlations with the precipitation sum were found in August during 1958–1973. The number of frost days in May had a negative impact on tree growth during the entire time span, being lowest towards the end of the study period. The number of snow days in April started to correlate negatively with tree growth in 2003.

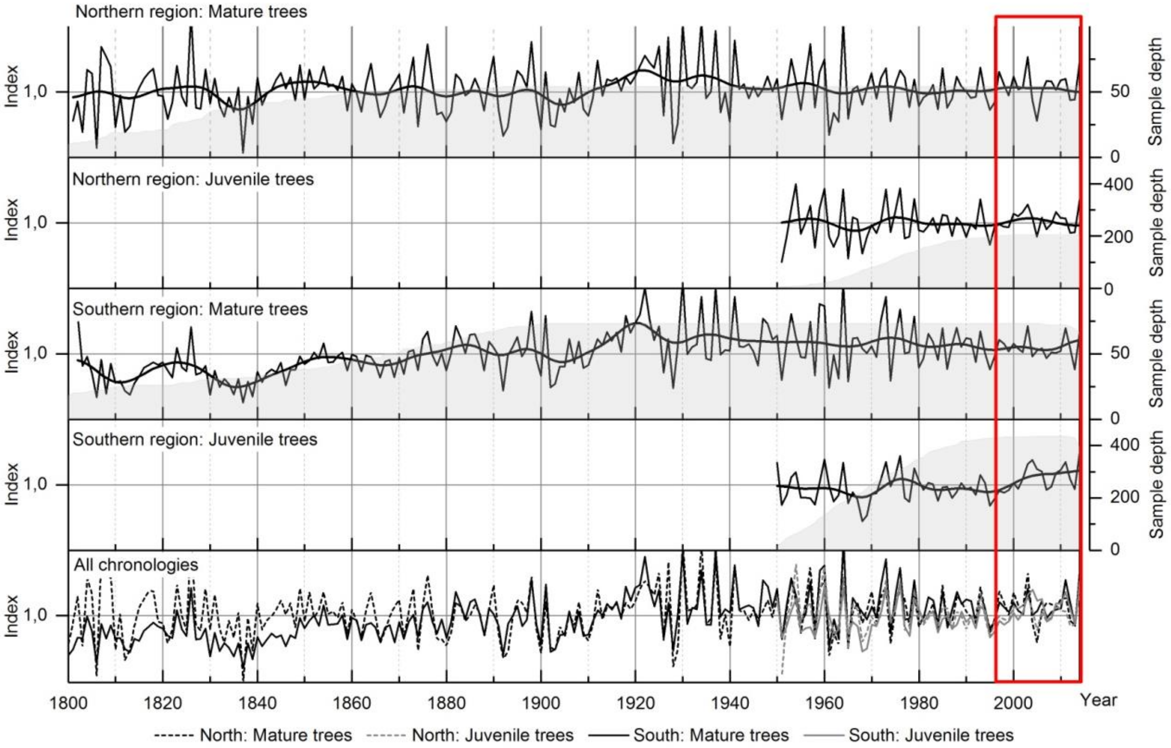

Figure 7. RCS chronologies of Scots pine specified for region (north, south) and age (mature trees: $Y_0 \leq 1900$, juvenile trees: $Y_0 \geq 1950$). Since dimensionless, adjusted growth indices were derived from the raw-data to remove non-climatic trends, the chronologies fluctuate around the value 1.0. Smoothing splines (bold lines) were fitted to the chronologies by using a Fast Fourier Transformation. Grey shaded areas indicate numbers of trees included in the chronologies. The current warming period, detected in Figure 6, is marked for the subsequent trend analysis (Figure 8).

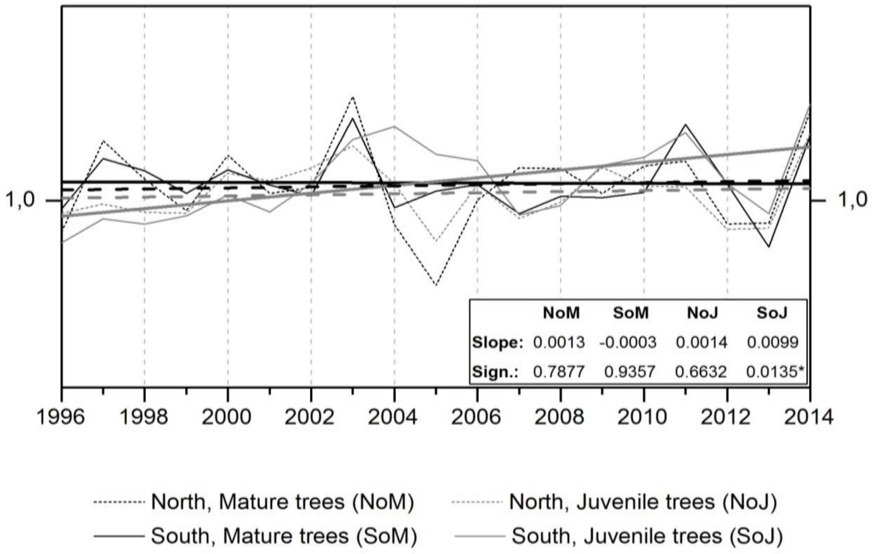

Figure 8. The regional curve standardization chronologies of Scots pine with linear regression for region (north, south) and age (mature trees: Y0 ≤ 1900, juvenile trees: Y0 ≥ 1950). The period (1996–2014) was chosen on the basis of the recent warming detected in the July mean temperature (Figure 6). Statistically significant trends ($p<0.05$) are marked with an asterisk (*).

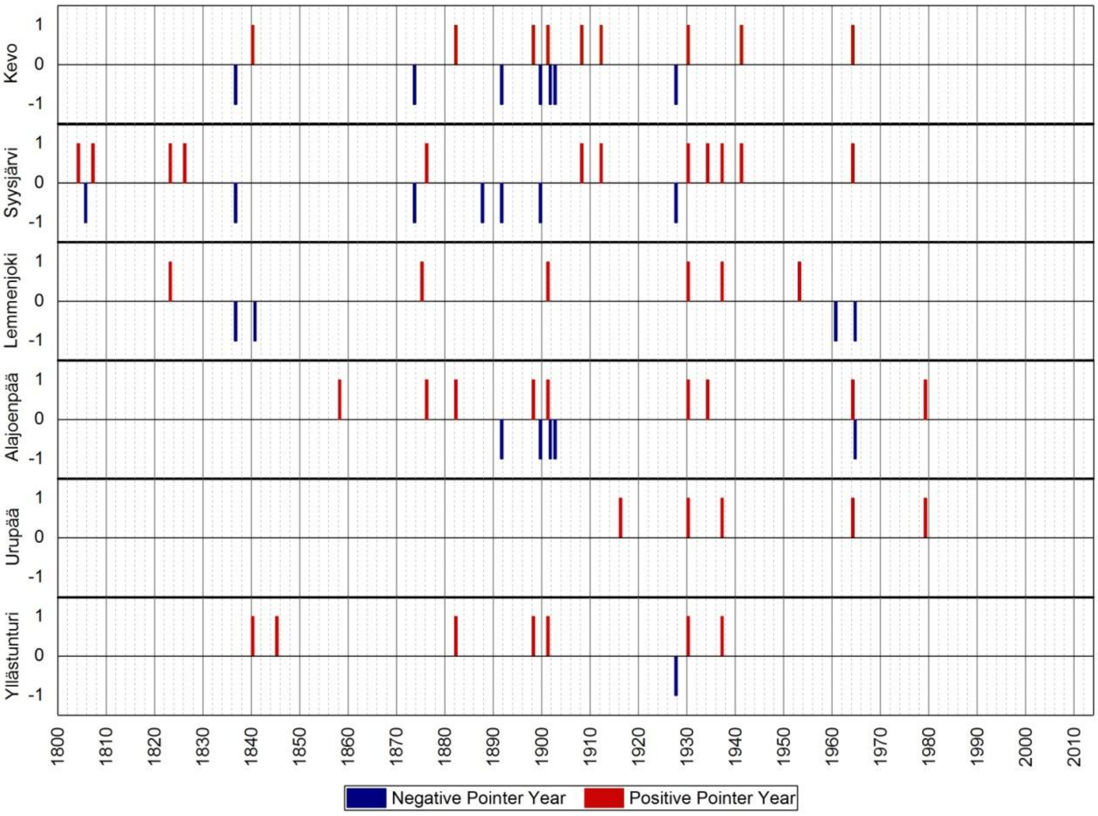

Figure 9. Occurrence of positive and negative pointer years (relative growth variation of > 20 %) in the tree-ring datasets of each location during 1800–2014, occurring in at least 75 % of the sample trees. The minimum sample size was set to ten trees.

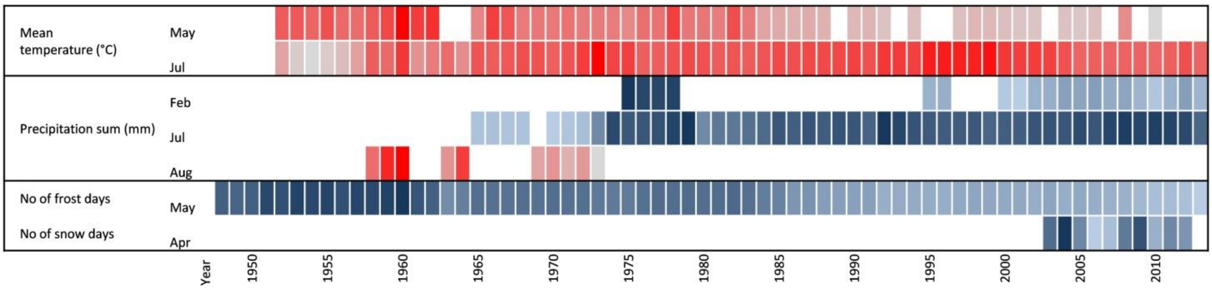

Figure 10. Computation of evolutionary correlation between the radial growth of southern mature trees and selected climatic variables in DendroClim software (Biondi and Waikul 2004). The strength of the correlations vary from positive (red) to negative (blue) values and from high (dark) to low (light) values. Only months revealing a statistically significant correlation ($p < 0.05$) during the study period are presented.

4 Discussion

We found moderate spatial differences in the growth of Scots pine in the polar-alpine tree-line in Finnish Lapland. We found a significant effect of location and zone and their interaction on pine growth. Not surprisingly a latitudinal gradient was seen in the mean annual growth rate in the tree-line zone with higher growth rates in the south. In the northern parts of the polar tree-line ecotone, tree growth is more limited due to low temperature and disturbances, such as frost events in the early growing season and heavy snow load during winter (Seo et al. 2010).

The forest-line zones and forest zones did, however, not show similar latitudinal gradients but relatively low growth rates instead. We assume that factors related to stand structure overrule the climate signal detected in the tree-line zone. The forest-line zones and forest zones are characterized by denser forest stands, where especially juvenile trees have to deal with between-tree competition for nutrients and light. Even if mostly isolated sample trees were chosen, a reduced availability of light might decelerate the growth rate of juvenile trees in comparison with the tree-line zone. Differences in stand structure and topography turned out to cause a high variability between the locations, masking the climate signal and a corresponding latitudinal gradient. Sites with a dense understory and stand structure, as observed in the southern locations and Lemmenjoki, are characterized by relatively low growth rates in the forest zones. Since the forest stands become sparser towards the upper zones, effects of stand structure diminish.

The impact of elevation turned out to be more prominent in the southern locations, which was confirmed by a significant interaction of location and zone in ANOVA. The stand structure of southern locations changed remarkably from the densely covered more temperate forest zone towards the sparsely covered, harsh tree-line zone. In close proximity to the polar tree-line ecotone in the north, these elevation effects diminish. The entire tree-line ecotone is affected here by harsher climatic conditions and sparsely covered with tree vegetation. Our assumption was confirmed by the analysis of the residual chronologies which did not indicate any significant elevation effects on tree growth (Figure 4, Table 4). While also mature trees are included here, the effects of stand structure on radial growth diminish. Site-specific differences occur as well predominantly in a latitudinal gradient from south to north, expressed by lower correlations between distant locations (Table 4). As an exception, Lemmenjoki indicated low correlations with all other, even adjacent sites. The forest-line and tree-line zone of Lemmenjoki were characterized by high abundance of the Mountain birch while the sparsely distributed pine trees were visibly formed by wind and snow loads. Although we focussed on healthy, undamaged sample trees, stress-induced impacts might have resulted in a deviating growth pattern. These findings confirmed our assumption of climate-induced regional differences and stand-induced local differences in the growth-rate analysis.

The differences in the growth rates between 1950–2014 might, however, indicate current growth dynamics as well, being induced by environmental changes. More favourable conditions due to increasing temperatures might have promoted tree growth predominantly in the harsh tree-line zone and in climate-sensitive juvenile ages. We therefore took a closer look on the long-term growth trends of both young and mature pines in our study area. We found that, in fact, the decadal variance of pine growth reflected the climatic course to a high extent, following warm and cold conditions with equivalent growth indices. With the temperature rise during the early 1900s, the radial growth of mature trees exceeded the standardized mean of 1.0, reaching maximum growth indices in the warm 1930s. The 1930s were found to be exceptionally warm (Fig. 6) (Gunnarson et al. 2011; McCarroll et al. 2013), promoting growth increment even in the harsh north (Lindholm et al. 1996; Briffa et al. 1998; ACIA 2005; Gunnarson et al. 2011; McCarroll et al. 2013). Several studies detected a synchronous rapid increase in stand densities particularly in the north, most likely promoted by a sequence of favourable summers for tree recruitment (e.g. Dalen and Hofgaard 2005; Danby and Hik 2007). After 1940/1950 both recruitment and radial growth were found to decrease in relation to declining temperatures (Danby and Hik 2007; Dalen and Hofgaard 2005). Depressions in radial growth, such as in 1892, the 1900s, the late 1920s, and the 1960s, originated from a sequence of frosty winters or cool summers with an early onset of a harsh winter, being partly induced by volcanic eruptions (Pohtila 1980, McCarroll et al. 2013). Our datasets display both the corresponding climatic events and decadal variations in July temperature until the 1980s in the radial growth.

Since pine growth reflected variations of July temperature until 1980 and revealed high correlations with temperature-related variables in the climate-growth analysis (cf. Fig. 5 and Table 5), we expected similar growth responses during the recent warming period. In fact, we found growth depressions during unfavourable summer conditions in 1995, after 2006 and 2013, whereas increasing July temperatures during 1996–2004 promoted peaks in the growth index (Fig. 7). However, we expected a more prominent growth trend during the current warm period in comparison to the warm 1930s. The southern juvenile trees indicated increased growth since 1996 (Fig. 8 and Fig. 9), while neither the southern mature trees nor the northern juvenile and mature trees displayed similar growth trends. A clear common response of pine growth towards the recent warm decades was missing both in the RCS chronologies and the pointer year analysis (see also: Briffa et al. 1998; Linderholm 2002; Linderholm et al. 2003; Dalen and Hofgaard 2005; Bolli et al. 2007; Danby and Hik 2007).

The reduced sensitivity might be related to the “divergence problem”, which has been discovered earlier in other studies in the boreal region (e.g. Wilmking et al. 2005; D’Arrigo et al. 2007; Büntgen et al. 2009). The divergence problem describes the weakening of the climate-growth response during the last decades in the tree-ring datasets of higher latitudes where tree rings do not indicate the warming climate anymore (Wilmking et al. 2005). Apparently other climatic or environmental drivers than temperature, such as precipitation or biotic stresses, mask the current climatic signal (Wilmking et al. 2005; D’Arrigo et al. 2007; Büntgen et al. 2009).

Our results suggest that warm periods brought not only ameliorated growth conditions but also restrictions in the form of e.g. changes in normal winter snow cover, frost events or snow loads breaking tree tops especially in the north. In accordance with other studies (e.g. Hurrell 1995; Cook et al. 2002; ACIA 2005; Linderholm and Chen 2005), we found increasing temperatures and precipitation sums during the winter season after 1990, presumably masking the benefits of a warming climate (Fig. 6). Increasing winter precipitation enhance the snow load in trees and the risk for storm-induced crown breakage especially at high altitudes and latitudes (Marchand 1987; Gregow et al. 2011) and in mature trees (Jalkanen and Konôpka 1998; Lehtonen et al. 2014). Many trees with severe crown damage were observed in the study area with close proximity to the polar and alpine tree-line. The North Atlantic Oscillation has shown to have a strong climatic impact during positive anomalies on the winter season and tree growth in Fennoscandia (Linderholm et al. 2003; Helama et al. 2009; Lindholm et al. 2014), transporting warm and moist air masses by strong winds to interior Lapland. These conditions are assumed to eventually promote crown breakage or stress (Rogers 1990; Hurrell 1995) and could have masked the effect of synchronously rising temperatures during the 1990s even in healthy pines. On the other hand, the outbreak of diseases during wet winters limits tree growth in juvenile ages effectively (Juntunen and Neuvonen 2006; Holtmeier and Broll 2011). Fungal diseases, such as Scleroderris canker (*Gremmeniella abietina* (Lagerb.) Morelet) or the snow blight (*Phacidium infestans* P. Karst), as well as insects during summer, such as the European pine sawfly (*Neodiprion sertifer* Geoffr.) benefit from warmer and wetter conditions and decrease tree growth (Veteli et al. 2005). The evolutionary correlation seemed to confirm our findings by revealing negative relation of precipitation and snow on tree growth during the last decades (Fig. 10).

We also detected a negative impact of frost events on pine growth during March–May in the south and during April–May in the north. Changing snow condition, like rain on snow events creating an ice encasement or absence of snow cover, have found to increase the seedling damage and dying of annual shoots (Martz et al. 2016). When pine activates growth and bud burst during an early onset of spring, the frost-hardiness is considerably reduced (Cannell and Smith 1986; Linderholm 2001; Salminen & Jalkanen 2015) and temperature variations might cause severe growth depressions. This phenomenon appears predominantly in open forest stands of the polar and alpine tree-line ecotone where trees are less sheltered. In the more temperate southern part of the study area, where especially juvenile trees were sheltered and a more constant stand climate was provided, frost and cold temperatures had less effect (Dalen and Hofgaard 2005). Frost damages have been predicted to increase under ongoing warming (Hänninen 1991; Leinonen 1995; Repo et al. 1996, Høgda et al. 2001) which was supported in our data by the negative impact of frost days in March and May on growth (Table 5) and the absence of thick snow cover during the 1990s (Fig. 6). The evolutionary correlation indicated a slightly declining impact of frost events in May on the southern mature trees during the last decades, resulting most likely from warming springtime seasons (Fig. 10).

The fact that tree-rings did not reflect the temperature during the recent warm decades asks for caution when using tree-rings as proxy for past climate. Several factors might mask the climatic signal, resulting in misleading predictions. However, it is worth noting that the present results are not necessarily an indicator for missing biomass increment or forest expansion. While established trees do currently not reflect the current climate warming, seedling recruitment and survival might benefit from more favourable conditions. For example, Kullmann (2007) detected a divergence between the climate response found in the tree-ring datasets and the seedling recruitment. While currently warming temperatures caused increasing stand density and northward forest migration, a response was not seen in the radial growth in Kullman's (2007) data. Also Franke et al. (2015) found, that even though the volume of tree stock of pines increased during 1983–2009 in the study locations used in the present study, the number of trees and seedlings did not. Hence, tree-ring datasets indicate the growth response of conifers to a changing environment, but are not necessarily a suitable indicator to conclude to dynamics of the tree-line position.

5 Conclusions

We found a response of pine tree-rings to climatic variations until the 1980s, but not to the current warmer period. For example, the growth increment that was seen during the warm 1930s was not seen during the later warmer periods. Only the juvenile pines in the southern part of the study area seemed to respond with enhanced radial growth. Warmer and wetter winter seasons, leading to enhanced snow loads, winds, diseases and frost damages, have possibly created environmental conditions that mask the effects of the large climatic trend. The ongoing climate warming seemed to not be sufficient to compensate abiotic and biotic pressures affecting tree growth, especially in the northern part of the study area. In the southern part we found some indications for positive response to warming climate, as the ring-width of juvenile trees increased during the past quarter of a century.

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Publication III

Remotely sensed estimation of forest area change in the polar and alpine tree-line ecotone in Finnish Lapland during the last three decades

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Abstract

Global warming is predicted to affect ecosystems, particularly in high-latitude regions where polar amplification accelerates temperature rise and environmental changes. Here, where plants grow under adverse conditions, a warmer climate provides more favourable conditions for growth and regeneration. At the alpine and polar tree line in Finnish Lapland, rising temperatures are assumed to promote densification and expansion of conifers towards fell tops and treeless boreal heathlands beyond the recent tree-line position. In this study, we analysed vegetation changes along elevation gradients in six study sites in Finnish Lapland using multi-spectral satellite data during 1984–2017. We assessed the vegetation cover of Scots pine (Pinus sylvestris L.) stands using changes in the normalized difference vegetation index (NDVI) and RandomForest land-cover classification. We did not find clear trends for advancing coniferous tree lines towards open fell tops or treeless heath vegetation, neither by NDVI change detection nor by the land-cover classification. However, we found evidence for densification of open forest stands in lower elevations and the expansion of deciduous vegetation in higher elevations of previously vegetation-free or sparsely covered fell tops. Increasing stand density was detected mostly in the southern, pine-dominated sites, while the northern sites indicated greening trends near the fell tops.

Keywords: Pinus sylvestris; vegetation shifts; multi-spectral satellite data; NDVI; climate change

1 Introduction

Ecosystems of high-latitude regions are predicted to be affected by global warming to a higher extent than ecosystems in lower latitudes, since polar amplification accelerates and enhances the temperature rise and promotes sustainable environmental changes here. A warming climate would provide more favourable conditions for growth and regeneration of plants that are presently living under harsh conditions (Høgda et al. 2013; IPCCa 2014; IPCCb 2014; Salminen and Jalkanen 2015). In the sub-Arctic biome, conifers grow close to the limit of their ecological range and are adapted to low temperatures, low nutrient supply, and sparse light during winter. During short growing seasons, they are able to persist and even regenerate successfully to persevere in the alpine and polar tree line (Heikkinen et al. 2002).

Temperature has a major impact on tree growth and sequences of several favourable years are needed for regeneration to successfully establish sustainably high seed crops (Heikkinen et al. 2002; Karlsen et al. 2005; Juntunen and Neuvonen 2006; Franke et al. 2017). Under mild winters, early springs and increasing summer temperatures of a warming climate, trees are predicted to grow and establish more successfully in the north (Hilli et al. 2008; Kauppi et al. 2014; Salminen and Jalkanen 2015), regionally replacing graminoids in the alpine oroarctic tundra by shrub and forest vegetation (Juntunen et al. 2002; Jia et al. 2003; Goetz et al. 2011; Aakala et al. 2014). Such vegetation shift affects the microclimate of the ecosystem and might even promote wide-scale circulation changes in Arctic regions (Jeong et al. 2012; Miller and Smith

2012; Pearson et al. 2013; Zhang et al. 2013). Increasing evapotranspiration leading to higher moisture content in the troposphere (Swann et al. 2010; Jeong et al. 2012), and higher absorption of solar radiation over forested areas induce a net-warming effect of the ecosystem, particularly in the snow-covered season when a high conifer and shrub abundance potentially reduces the albedo over otherwise closed snow pack (Harding et al. 2002; Chapin et al. 2005; Sturm et al. 2005; Moody et al. 2007).

Trends towards a ‘greening arctic’ were already detected by several field surveys and modelled by climate-growth simulations predicting vegetation changes under a warming climate (Juntunen et al. 2002; Kullman 2007; Sutinen et al. 2012; Jeong et al. 2012; Pearson et al. 2013; Aakala et al. 2014). The responses were, however, found to be species-specific and influenced by factors including microclimate, topography, soil, water supply and biotic stress, which may partially mask the benefits of a warming climate (Heikkinen et al. 2002; Dalen and Hofgaard 2005; Holtmeier 2005; Bunn and Goetz 2006; Danby and Hik 2007). In some sites, coniferous stands have shown only little growth response to climatic trends, whereas shrubs were found to expand remarkably (Bunn and Goetz 2006; Hofgaard et al. 2012; McManus et al. 2012; Weijers et al. 2018).

A monitoring project established on tree-line sites in Finnish Lapland detected an increasing volume of growing stock in pine forest stands (Pinus sylvestris L.) during 1983 to 2009, while the stem number stagnated or even decreased (Franke et al. 2015). A related analysis of the pine growth rates in the study sites revealed increased radial growth in juvenile pines in southern Finnish Lapland, while mature trees and trees in northern Lapland did not show any growth response to warming (Franke et al. 2017). These findings indicate a densification of the established forest stands by maturation and low mortality rates but limited probability of tree-line shifts by natural regeneration. A complementation with satellite-based observations intends to study this hypothesis by mapping vegetation changes in the monitoring sites. Hence, the objectives of the present study are to determine temporal and spatial changes of the vegetation patterns and tree-line positions in the study sites of Finnish Lapland and to identify areas of significant changes.

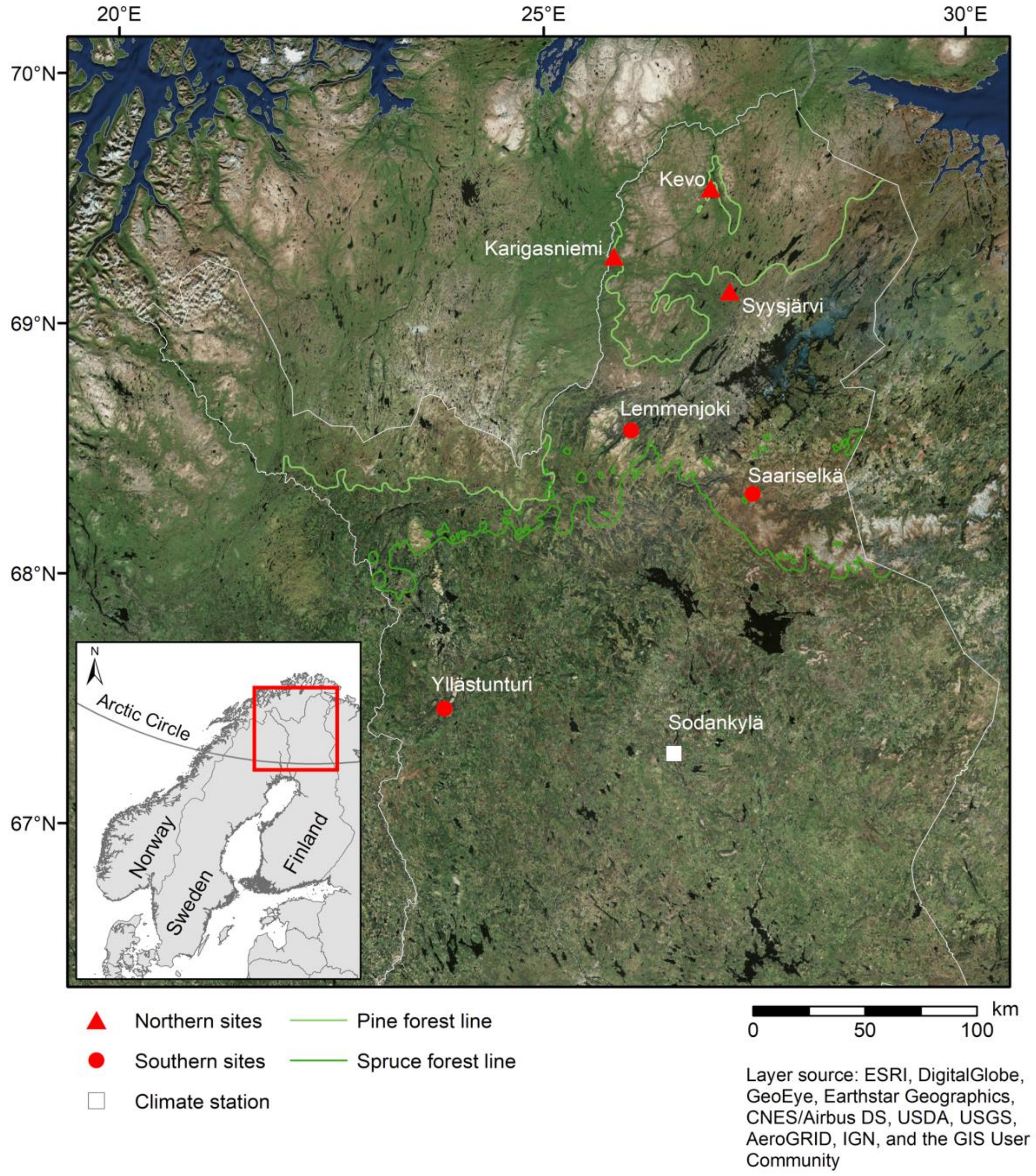
2 Methods

2.1 Site description

Six sites in Finnish Lapland were chosen for our analysis, based on the sites of the monitoring project, established in 1983 by the Finnish Forest Research Institute (Metla/Luke) and the universities of Oulu, Helsinki and Turku (Juntunen et al. 2002). The study sites were established along a latitudinal gradient from northern to southern Lapland, covering both eastern and western distribution areas of pine (Fig. 1). Most of the sites are positioned on gently sloping hills with altitudinal ranges of 200–600 m a.s.l., covering the transition from closed forest in lower altitudes to alpine (oroarctic) tundra (hereafter in the text simply termed ‘alpine tundra’) on the fell tops.

The southern sites Yllästunturi, Saariselkä and Lemmenjoki are characterized by clearly distinguishable elevation belts, including dense coniferous forest in lower elevations, upper deciduous and shrub vegetation, and mostly lichen dominated fell tops. In contrast, the coniferous forest occurs only in small patches in the northern sites Syysjärvi, Karigasniemi and Kevo, where the mountain birch forest (Betula pubescens subsp. czerepanovii Ehrh.) dominates all elevation zones. Pine reaches here at the polar tree line its northernmost distribution limit while the birch forest extends under maritime impact of the North Atlantic Ocean towards the Norwegian cost. Bare soil and rocks on the fell tops are partly covered by lichens and mosses.

At each site, the monitoring plots were previously established along an elevation gradient, covering the forest zone, the forest-line zone and the tree-line zone. In the tree-line zone single trees or small groups of conifers are smaller in size and are mixed with patches of birch and fell heath. Due to the prevailing climatic conditions, the position of the tree line varies between 450 m a.s.l. in the southernmost site and 200 m a.s.l. in the northernmost site. Cold winters and relatively warm summers define a growing season length of < 4 months (+ 5 °C threshold), with July as the warmest month of the year. The annual precipitation sum varies in northern Finland from 400 to 600 mm (Finnish Meteorological Institute 2016), providing sufficient water supply under low temperatures and low evaporation rates in the entire study area. A permanent snow cover lasts from October to late spring in May or even June (Autio and Heikkinen 2002).



Layer source: ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1. Position of the Northern study sites (triangles), Southern study sites (circles), the climate station Sodankylä, and the northern distribution limits of Scots pine forests and Norway spruce forest in the study area in Finnish Lapland.

2.2 Data acquisition and pre-processing

Several multiband satellite images were chosen to cover all of the six study sites over the time period 1985 to 2017 (Table 1). Preferably, cloud-free images of Landsat-5 (TM) and Landsat-8 (OLI) were obtained from the USGS Earth Explorer (U.S. Geological Survey (USGS) Earth Resources Observation and Science (EROS) Centre 2017) during the peak growing season between June and August with a major proportion in July. The availability of cloud-free images was limited due to the frequent cloud coverage in the high latitude regions, and during 1999−2003 no data were available. Small clouds, appearing in few cases, were masked out. In total, 11 to 16 multiband images were selected for each study site to build a continuous time series.

Table 1. Basic information on the satellite data and number of images taken by sensor for the project. For location of the study areas see Fig. 1.

		Landsat-5 (TM)	Landsat-8 (OLI)	RapidEye Level 3A
	Launched in	1984	2013	2009
	Spatial resolution	30 m	30 m	6.5 m
	Spectral bands	7 Bands	9 Bands	5 Bands
	Number of images:			
Northern sites	Kevo	13	3	2
	Karigasniemi	12	2	4
	Syysjärvi	11	2	2
Southern sites	Lemmenjoki	8	3	4
	Saariselkä	10	4	3
	Yllästunturi	9	4	2

The commercial multispectral earth observation mission RapidEye (BlackBridge 2015) provided additional high-resolution satellite data with 6.5 m resolution through the BlackBridge Science Archive (RESA) for the period from 2009 to 2015. RapidEye provides the Red Edge Band, which is very sensitive to variations in chlorophyll content and leaf structure (Weichelt et al. 2013; Schuster et al. 2012). The RapidEye data were considered in the analysis to provide additional and high-resolution field information for the recent years. Due to a high cloud-coverage, only a small amount of RapidEye scenes could be used.

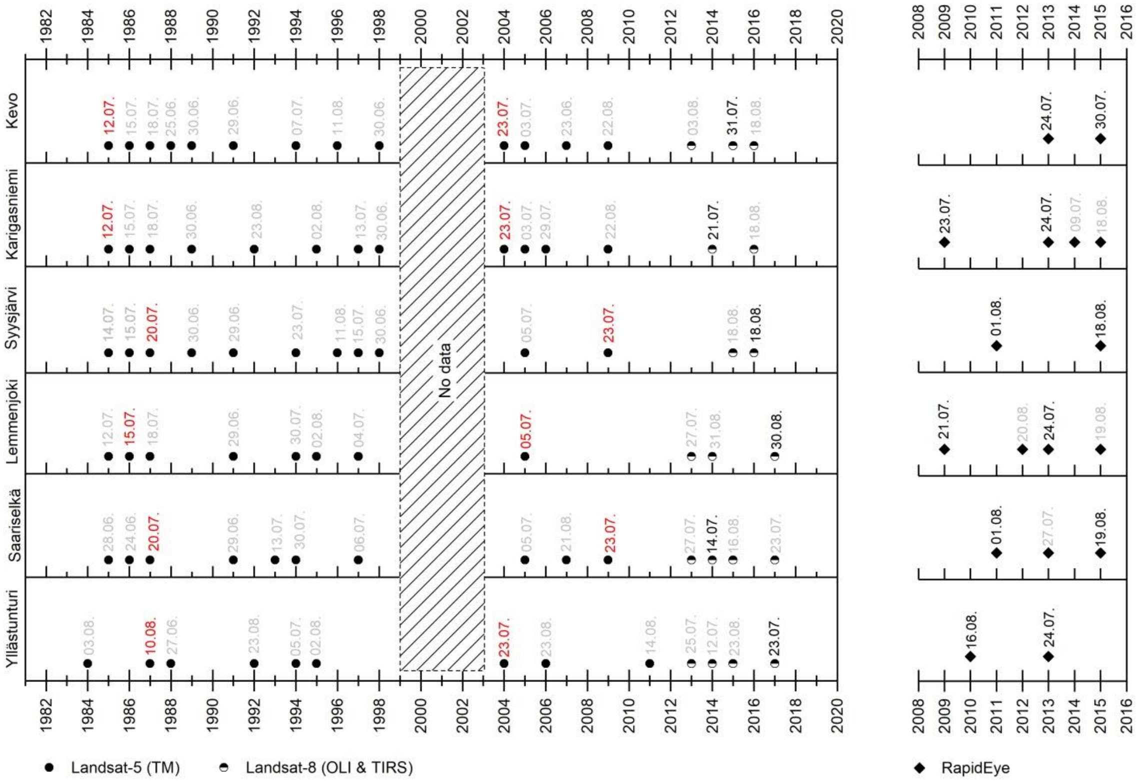


Figure 2. Acquisition dates of the Landsat-5 TM, Landsat-8 OLI, and RapidEye imagery for each study site. All displayed dates were used in the NDVI-trend analysis (Fig. 3; Fig. 4). Red values highlight the two scenes each used for NDVI change detection, black values indicate scenes used additionally for NDVI profiles and land cover classification.

Pre-processing of all images was performed to mitigate noise by atmospheric scattering and topographic effects. The image data were clipped to a maximum extent of 10 km x 10 km, framing the monitoring sites in the centre. The raw digital numbers (DN) were converted to top-of-atmosphere reflectance (TOA) using the sensor specific parameters. Atmospheric scattering was mitigated by dark object subtraction, identifying and subtracting the minimum reflectance value from each band. To eliminate topographic shadowing, a topographic normalization based on cosine correction (Teillet et al. 1982) was performed using digital elevation models (DEMs) provided by the National Land Survey of Finland Topographic Database (09/2017). Water bodies which eventually may affect the computation of vegetation indices by similar reflectance values were masked out.

2.3 Processing of NDVI-time series

The normalized difference vegetation index (NDVI, Tucker 1979) was used to study the vegetation in each of the six sites. The NDVI works as a normalized difference ratio of the red and near infrared bands (NIR) on a per-pixel basis in multiband images and is widely used as an index for vegetation greenness or photosynthetic activity:

(1)

$$\mathrm{NDVI} = \frac{(\mathrm{NIR\ band} - \mathrm{Red\ band})}{(\mathrm{NIR\ band} + \mathrm{Red\ band})}$$

The NDVI values range from -1 to +1 and indicate water, snow and ice by negative values, bare soils by values around zero and vegetation abundance by values up to +1 (NASA 2011). The mean NDVI was computed and plotted for each scene of Landsat-5 and Landsat-8, and described by standard deviations listed in Table A1 in Appendix. To enable a comparison between the NDVI-values of Landsat-5 and Landsat-8, which may show sensor-specific variations, a sensor calibration was previously executed for the imagery of Landsat-5. The red band and NIR band of Landsat-5 were corrected by using the SBAF-Exp-model and the MR1-model described in Villaescusa-Nadal et al. (2019). The NDVI was afterwards computed for the Landsat-5 imagery using the calibrated bands.

Subsamples of 10 pixels x 10 pixels (about 300 m x 300 m) were established along the elevation gradient of the monitoring sites in order to compute the mean NDVI specifically for the forest zone, the forest-line zone, the tree-line zone and the fell tops in each of the six sites. This was done both for Landsat imagery and RapidEye. For

RapidEye, the Red Edge Normalized Difference Vegetation Index (NDVI-RE) was used:

(2)

$$NDVI\text{–}RE = \frac{(NIR\ band - Red\ Edge\ band)}{(NIR\ band + Red\ Edge\ band)}$$

2.4 NDVI change detection

To analyze spatial variations within the sites, we selected two scenes each for bi-temporal NDVI change detection. The analysis was based on Landsat-5 imagery exclusively with comparable acquisition dates during the high growing season (red values in Fig. 2) in order to avoid potential sensor- and season-specific bias (Forkel et al. 2013). The seasonal comparability of the scenes was verified by phenology curves computed on Terra MODIS datasets (Didan et al. 2015) during 2000 to 2018 (Fig. A3 in Appendix; see also chapter S1 in Appendix) (refer e.g. to Huseby et al. 2005 and Baumann et al. 2017). We analyzed the MODIS data on inter-annual variation in the NDVI for the period 2000–2018. We computed the interquartile as the difference between 75th and 25th percentiles to identify the start and end date of the stable NDVI plateau where low NDVI variation indicate the period of fully developed vegetation greenness. Within this time frame, ranging from day of the year (DOY) 161–257, we computed the mean interquartile range across all locations. The mean interquartile of all locations was 0.053 index values, reflecting regular inter-annual and seasonal variations in the vegetation status.

We subtracted the earlier image from the later image to reveal the rate of NDVI change for each pixel. The resulting pixel values were classified into six classes quantifying the rate of NDVI change. Pixels changing ±0.05 index values were attributed to areas with non-significant change, while exceeding values reflected significant changes in the vegetation pattern by e.g. greening of un-vegetated area or disturbed areas. The pixels of each scene were additionally classified into four vegetation classes: no vegetation (NDVI ≤ 0.5), sparse vegetation (NDVI > 0.5 – 0.65), moderately dense vegetation (NDVI > 0.65 – 0.75) and dense vegetation (NDVI > 0.75). Pixels attributed in the second scene to another class than in the first scene should give an estimation of changes in density and vitality of the vegetation.

A profile was laid across the subsamples of the NDVI change detection in each study site to measure potential up-shifting or down-shifting of the vegetation cover by changes in NDVI. The NDVI values were extracted from both scenes of Landsat-5 and in addition from one scene of Landsat-8 and two scenes of RapidEye. The NDVI values of Landsat-5 were again modelled for comparison with Landsat-8.

2.5 Random Forest land-cover classification

Since the NDVI is not appropriate to detect changes in the expansion or reduction of land-cover classes, we concluded with a land-cover classification using the self-learning decision tree classifier Random Forest (Breiman 2001). We first computed a Principal Component Analysis (Hotelling 1933) on the stacked images of each scene to reduced the dimensionality of the multi-seasonal and multispectral signals of the differing vegetation patterns. We chose five land-cover classes which were relatively easy to distinguish without field data: water bodies, open fell tops / non-vegetated area, sparse vegetation, deciduous vegetation and conifers.

Calibration polygons were established in the centre of clearly identifiable land-cover patches, where an overlap of two classes was unlikely. Reference data, such as high-resolution orthophotos (NLS 2017) and datasets of the National Forest Inventories (Luke 2015) were considered if necessary to ensure the reliability of the calibration data. In a Random Forest consisting of an ensemble of 500 self-learning decision trees, all pixels were assigned to a class with the highest likelihood using the raster (Hijmans et al. 2016), rgdal (Bivand et al. 2017) and randomForest package (version 4.6−14) (Breiman and Cutler 2018) in R version 3.4.0. We used three scenes of both Landsat-5 and Landsat-8 to cover the period 1985–2017. Since models were built for each scene specifically, this approach diminished effects of seasonality or vitality of the vegetation, or sensor-specific variation in the classification result.

Accuracy assessment was conducted with a set of validation points, comparing predicted and observed class memberships. The overall accuracy (OAC), user’s accuracy (UA) and producer’s accuracy (PA) described the model’s accuracy (Table A2 in Appendix). However, the occurrence of mixed pixels, accumulating reflectance values of several land-cover types may lead to misclassifications in transition zones. Since we did not have validation sites in the field in problematic transition zones, these errors do not occur in our quality assessment. The extension of a specific land-cover class is thereby not interpreted as the total land cover here but as the increased probability of class abundance in these pixels.

3 Results

3.1 Site-specific vegetation patterns

We found site-specific differences in the vegetation patterns and vegetation dynamics when comparing the false-colour images of the sites (Fig. 5a/b). The southern sites Yllästunturi, Saariselkä and Lemmenjoki were dominated by conifers in closed and extended forest stands in the lower elevations, while deciduous vegetation was abundant in valleys, near water bodies, and in the transition zone between forest and fell vegetation. The vegetation on the fell tops was formed by dwarf shrubs and lichens on barren rock, indicated by high reflectance values compared to the surrounding forest canopy. These broad patterns were in the southern sites clearly distinguishable by spectral signature in the satellite images (Fig. A1 in Appendix). The northern sites Syysjärvi, Karigasniemi and Kevo were dominated by deciduous vegetation, spreading from the lower elevations to the upper fell zones where sparse sub-arctic vegetation began. Coniferous forest was restricted to small patches in open stands in the lower zones and was not easy to distinguish from sparse deciduous or shrub vegetation. The pine forest stands were open and the spectral signatures consequently mixed with the occurrence of understory vegetation (Fig. A1 in Appendix). The land cover patterns were partly small-scaled and not easy to separate, eventually distorting the land-cover classification of these sites.

3.2 NDVI time series

The mean NDVI value was highest in the northern sites Karigasniemi and Syysjärvi with a high abundance of dense and vigorous deciduous vegetation, while sites dominated by sparse or coniferous vegetation revealed lower NDVIs (Fig. 3). In all northern sites, the highest mean NDVI was found in the tree-line zone and the forest-line zone dominated by deciduous vegetation (Fig. 4). The NDVI of the forest zone, extracted from pine-dominated patches in the low elevations, showed slightly lower NDVIs. The fell tops showed lowest NDVI values in Kevo and Karigasniemi, but similar values to the tree-line zone in Syysjärvi.

In the southern sites, NDVI was constantly higher in Saariselkä than in Lemmenjoki and Yllästunturi. As in the northern sites, the NDVI increased also here from bare fell to vegetated areas. The highest NDVI values were found in the tree-line and forest-line zone in Lemmenjoki while NDVI was highest in the forest and forest-line zone in Saariselkä and Yllästunturi. The standard deviation estimated the heterogeneity of the study site, being lower in homogeneous vegetation pattern (Table A1 in Appendix). In the southern sites, the standard deviation slightly increased from the closed forest zone towards the tree-line zone, while this gradient was not observed in the northern sites.

All NDVI time series showed high inter-annual variability during the study period (Fig. 3; Fig. 4). However, no significant trends were found in the NDVI-time series of Landsat-5 in the northern sites during 1985−2009, even when considering only values from July. In contrast, NDVI in the southern sites showed increasing values, particularly in Saariselkä. NDVI increased during the recent years in the southern sites both in Landsat-8 and RapidEye images (Fig. 4). Contrarily, no changes or even decreasing values were detected during 2013−2017 in the NDVI and NDVI-RE in the northern sites Kevo and Syysjärvi. The NDVI was in all sites higher in Landsat-8 images than in images of Landsat-5.

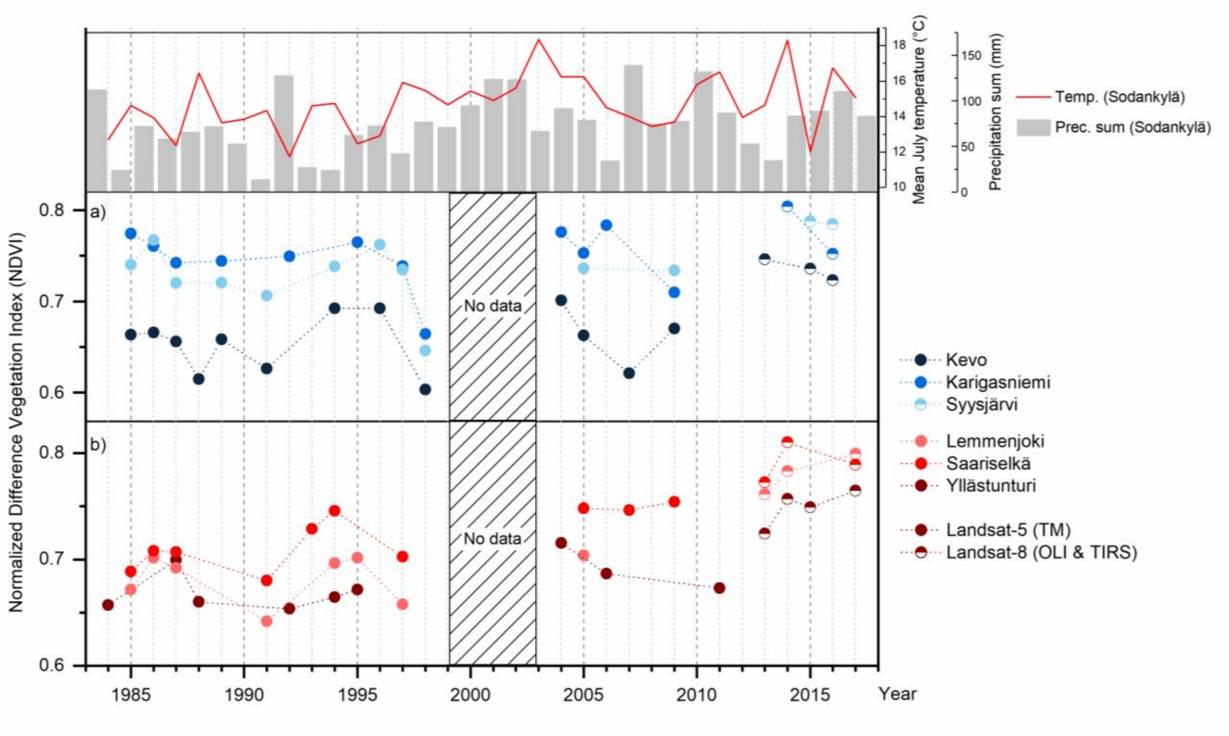


Figure 3. Mean NDVI during 1984–2017 for the northern (a) and southern (b) sites, computed from Landsat-5 and Landsat-8. The NDVI values of Landsat-5 were corrected for Landsat-8. Standard deviations are presented for each scene in Table A1 in Appendix. The mean July temperature and precipitation sum are plotted for Sodankylä in southern Lapland in the upper panel.

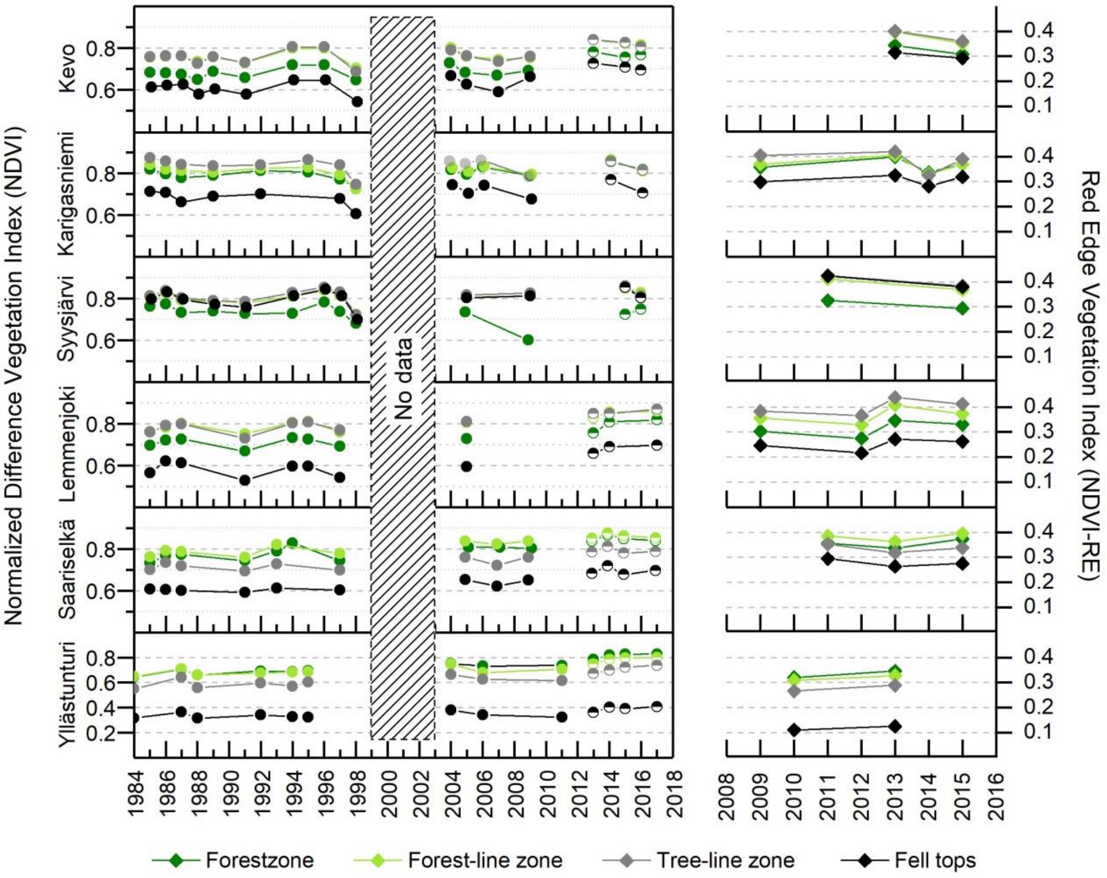


Figure 4. Mean NDVI for four elevation zones in each study site, based on sample squares positioned in each zone (Fig. 5a/b) and computed from Landsat-5 and Landsat-8 during the acquisition dates of Figure 2. The NDVI values of Landsat-5 were corrected for Landsat-8. The standard deviations for each scene are presented in Table A1 in Appendix. The mean NDVI-RE was additionally computed by elevation zone on available RapidEye images (right panel). Please refer to the legend of Figure 3 for an explanation of the sensor-specific symbols.

3.3 NDVI change detection

The distribution of NDVI change rates across all pixels from the mid-1980s to the early 2000s indicated the majority of pixels ranging with no or minor changes around ± 0.05 index values (Table 2). Major NDVI increases (> +0.05) were found in Kevo (41.34 % of all pixels), Saariselkä (48.55% of all pixels) and Yllästunturi (23.16% of all pixels), where visibly more pixels showed increasing than decreasing NDVI values (Table 2; Fig. 5a/b). In Karigasniemi and Lemmenjoki the number of pixels with increasing NDVI values exceeded the number with decreasing values only slightly (Karigasniemi: +8.62 % and -4.74%; Lemmenjoki: +6.65% and -4.76%). This proportion was inversed in Syysjärvi (+6.73% and -8.42%).

By mapping the NDVI change, we identified regions of major vegetation change (Fig. 5a/b). Decreasing NDVI values were mostly located in areas with anthropogenic impact, such as reinstalled streets, parking lots or skiing areas but also from clear cuttings that were found around Syysjärvi and Yllästunturi. Some fell tops, as in Kevo and Lemmenjoki showed decreasing NDVI values as well. Increasing NDVIs were observed predominantly in areas which were previously covered by sparse vegetation as revealed from the false-colour images. These were areas close to the fell tops, particularly in the northern sites, or open stands in the lower elevations in the southern sites.

Most sites experienced a decreasing proportion of no vegetation and sparse vegetation, while the percentage of dense vegetation increased (Fig. 6). Slight increase of pixels classified as no vegetation was found in Yllästunturi, Lemmenjoki and Syysjärvi. Syysjärvi and Karigasniemi encountered increasing proportions of moderately dense vegetation, while the other sites encountered a decreasing class percentage.

Table 2. NDVI change between two acquisition dates during the peak growing season. NDVI change of ± 0.05 index values are regarded as insignificant (grey values), while NDVI change of index values higher or below 0.05 are regarded as meaningful (black values). The relative number of pixels is given in percentage for each NDVI change class in each site.

NDVI change (index values)		Relative number of changed pixels (%)					
		Kevo 1985–2004	Karigasniemi 1985–2004	Syysjärvi 1987–2009	Lemmenjoki 1986–2005	Saariselkä 1987–2009	Yllästunturi 1987–2004
↗	>0.1 to 1.0	8.14	1.10	0.83	0.20	10.90	4.57
	> 0.05 to 0.1	33.20	7.52	5.90	6.45	37.65	18.59
→	> 0.0 to 0.05	40.50	38.90	38.29	48.10	41.27	45.18
	> -0.05 to 0.0	13.14	47.75	46.55	40.50	8.33	24.41
↘	-0.1 to -0.05	3.50	4.08	6.56	4.49	0.88	4.62
	< 0.1	1.53	0.66	1.86	0.27	0.97	2.62

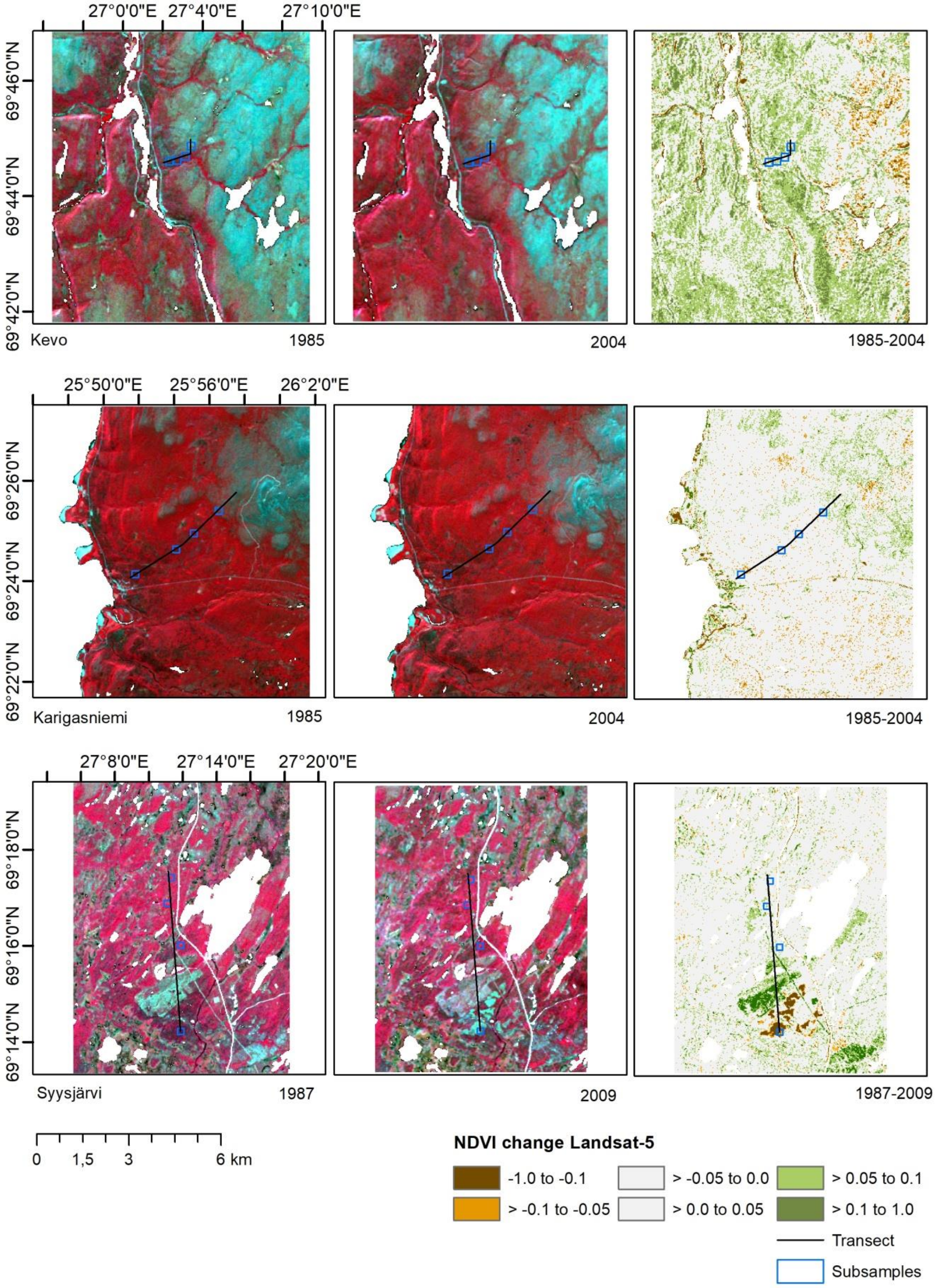


Figure 5a. False-colour images of Landsat-5 (first and second image) and NDVI change detection (third image) with subsamples (blue squares; used in Fig. 4) and transects (red line; used in Fig. 7) for all sites.

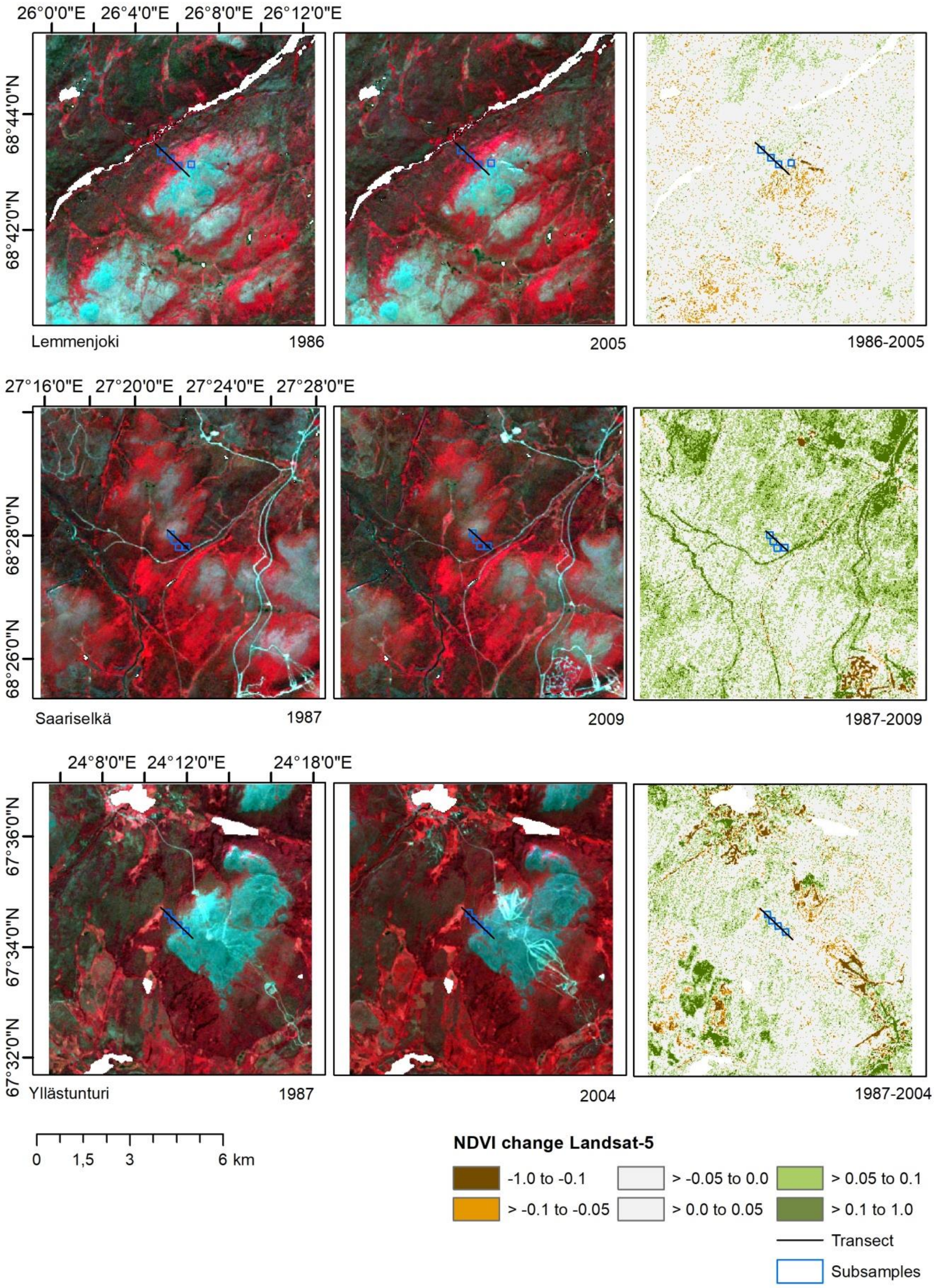


Figure 5b. False-colour images of Landsat-5 (first and second image) and NDVI change detection (third image) with subsamples (blue squares; used in Fig. 4) and transects (red line; used in Fig. 7) for all sites.

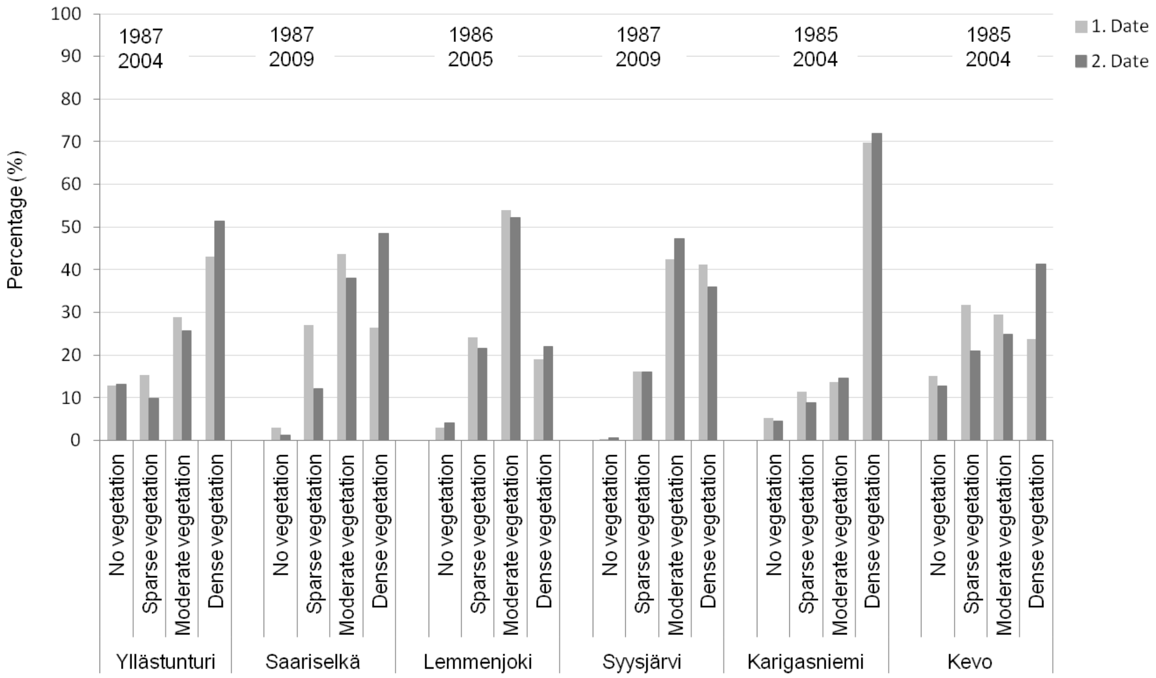


Figure 6. NDVI change detection for the studied sites between two acquisition dates (years of acquisition given above the bars). Each pixel was classified by NDVI to no vegetation (≤ 0.5), sparse vegetation (> 0.5 – 0.65), moderately dense vegetation (> 0.65 – 0.75) or dense vegetation (> 0.75). The percentage of each class was plotted by site and acquisition date.

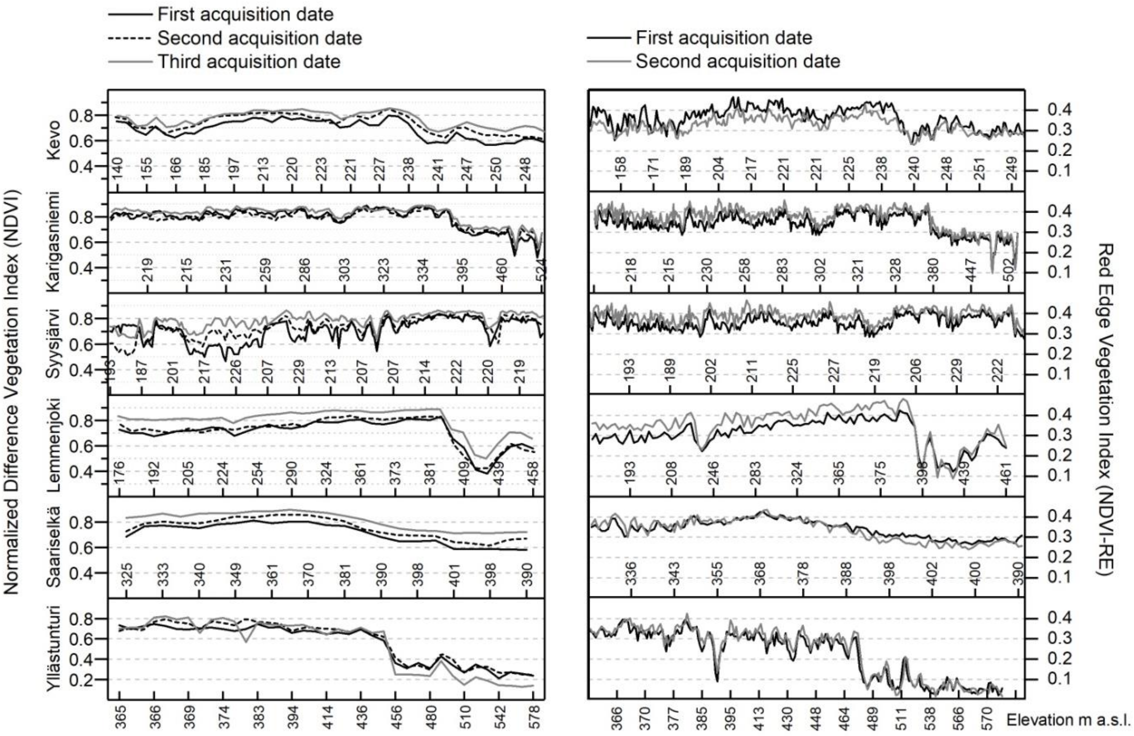
3.4 Variations of the tree-line position

By using NDVI profiles, we aimed to examine whether the increasing NDVI values were the result of a relocation of the tree-line position between three different dates. The profiles in Yllästunturi, Lemmenjoki, Karigasniemi and Kevo indicated the border from closed to sparse vegetation towards the fell tops by a clear drop in NDVI values with increasing altitude (Fig. 7). In these sites, except of Kevo, NDVI indicated only minor differences between the first and second acquisition date of Landsat-5 and no remarkable relocation of the tree-line position during 1985−2017. The NDVI was slightly higher in the scenes of Landsat-8 in Kevo, Karigasniemi and Lemmenjoki, but constant or even lower in Yllästunturi. These findings recurred in the NDVI-RE profiles of Rapid-Eye, while the NDVI increase of the recent years occurred mostly in the lower elevations below the tree line.

In Saariselkä and Syysjärvi no sharp tree line was detected in the profiles (Fig. 7). The NDVI values of the profiles increased in Saariselkä and Syysjärvi during the studied time span, while the NDVI-RE profile remained unchanged or slightly decreased for the recent years in Saariselkä. In Syysjärvi, we found strongly changing values in the lower half of the profile, while the upper half remained more stable. The lower half was positioned in disturbed areas, where signs of clear-cuttings occurred in the images.

3.5 Random Forest classification

The accuracy assessment of the Random Forest land-cover classification indicated a high Overall Accuracy and low error rates (Table A2 in Appendix). The classification results revealed minor variations in vegetation patterns of the southern sites but more distinct changes towards the North (Fig. 8; Fig. A2a/b in Appendix). In Yllästunturi, the abundance of conifers decreased slightly while the sparse vegetation slightly increased. In Lemmenjoki, sparse vegetation was most likely replaced by deciduous vegetation while the abundance of conifers remained stable. The changes in these two sites were, however, of minor degree. Vegetation class changes were more frequent in Saariselkä, pointing to a vegetation shift from sparse and deciduous to coniferous vegetation. The class size of fell tops showed only slight variations. In the northern sites, Syysjärvi and Karigasniemi indicated increasing class size in the sparse vegetation while deciduous and coniferous vegetation decreased. This decline was, however, only minor until 2004/2009 but major until 2014/2016. In Kevo, the area of sparse vegetation was clearly replaced by deciduous and partly even coniferous forest, pointing towards the establishment of higher plants in previously open alpine tundra.



Location	NDVI			REVI	
	1. acqu. Date	2. acqu. Date	3. acqu. Date	1. acqu. Date	2. acqu. Date
Kevo	1985	2004	2015	2013	2015
Karigasniemi	1985	2004	2014	2009	2013
Syysjärvi	1987	2009	2016	2011	2015
Lemmenjoki	1986	2005	2017	2009	2013
Saariselkä	1987	2009	2014	2011	2015
Yllästunturi	1987	2004	2017	2010	2013

Figure 7. NDVI profiles along elevation gradients from closed forest in lower elevations towards open fell tops in higher elevations. The profiles are plotted for three acquisition dates during the high growing season in Landsat-5 and Landsat-8 (left panels), and for two acquisition dates in RapidEye (right panels). The NDVI values of Landsat-5 were corrected for Landsat-8. Strong increase in NDVI indicates vegetation densification or vegetation expansion near the tree-line, which is indicated by an abrupt drop of NDVI.

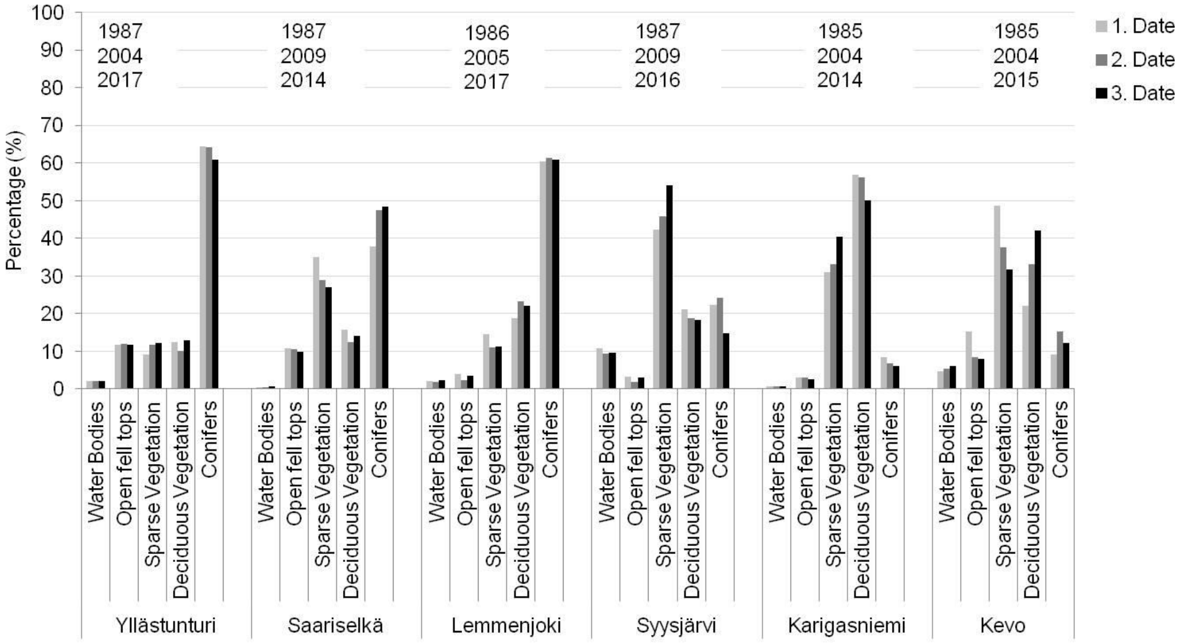


Figure 8. Frequency of five land cover classes in the Random Forest classification result. The percentage of pixels in each class were plotted by site and acquisition date. The first and second scenes were taken by Landsat-5 (grey bars), the third scene by Landsat-8 (black bars).

4 Discussion

We found evidence for a densification of open forest stands in the southern sites by NDVI change detection, while no greening was detected in the fell area of the higher elevation belts. Neither the NDVI profiles nor the land-cover classification showed clear trends for rising and expanding higher vegetation towards alpine tundra. Prominent changes in vegetation patterns originated in the southern sites from human impact, appearing as recent roads or infrastructure constructions in skiing areas, e.g. in Saariselkä and Yllästunturi in Fig. 5b. In Yllästunturi, we found evidence for clear-cuttings and land-use change from forested lands to parcels of other use (lower left quarter of Fig. 5b and A2b in Appendix). These patterns were identified by land-cover change from deciduous and coniferous vegetation to sparse vegetation, followed by a revegetating of deciduous vegetation in the disturbed areas over the years (Fig. A2b in Appendix).

In the northern sites, we found evidence for increasing stand densities as well, occurring mostly in sparsely covered areas around the fell tops. NDVI change detection and land cover classification indicated an extending deciduous forest belt in Kevo, and a greening of the fell tops in Karigasniemi and Syysjärvi by increasing sparse vegetation. However, trends of advancing or expanding forest vegetation were quite unspecific in Karigasniemi and Syysjärvi, showing even less pixel classified as deciduous or coniferous forest over the study period. Strong NDVI decline with subsequent greening was also in the northern sites primarily caused by human impact (Syysjärvi in Fig. 5a) or river terrace erosion (Karigasniemi and Kevo in Fig. 5a), but also by biotic disturbance events. During the past two decades moths, such as Autumnal moth (Epirrita autumnata) or Winter moth (Operophtera brumata) have been defoliating mountain birch stands extensively in northern Lapland (Jalkanen 2007; Jepsen et al. 2009; Jepsen et al. 2013; Neuvonen and Viiri 2017) as to be seen in the extensive decline in deciduous vegetation detected in Karigasniemi in the northern part of the scenes during 2009 and 2013 (Fig. A2a in Appendix), and in Syysjärvi in 2016 (Fig. A2a in Appendix).

Our results hence indicate rather a densification of already established open forest stands, whereas no clear signals for up-rising tree lines were detected. This is in accordance with the findings of the monitoring and dendroecological study conducted previously on the same sites (Franke et al. 2015; Franke et al. 2017). The monitoring revealed increasing tree biomass of pine in all sites and elevations zones, while the stem numbers remained stable or even decreased. The pine radial growth increased in juvenile pines in the southern part of the study region, while mature and northernmost trees did not show any response to warming climate (Franke et al. 2017). This leads to the assumption that the current environmental conditions promote the maturation of established pine forest stands, particularly in the southern region, which then contribute to increasing NDVI values and a more closed forest canopy in previously open stands (see also Masek 2001; Hofgaard et al. 2012; Franke et al. 2015; Franke et al. 2017).

If we assume, that a warming climate is causative for increasing stand volumes, it might then appear surprising that no signs of expanding coniferous tree lines by natural regeneration were detected in any of the sites. However, our findings correspond with results from other studies in the polar tree-line ecotone, where greening trends beyond the polar-alpine tree line were found to arise from expanding birch forest and shrub vegetation (Fig. A2a/b in Appendix; Fig. 8) (Sturm et al. 2001; Wielgolaski 2005; Forbes et al. 2010; Goetz et al. 2011), while very limited advance of conifers to higher elevations was detected (Masek 2001; Bunn and Goetz 2006; Holtmeier and Broll 2011; Hofgaard et al. 2012). An invasion of pine beyond the current tree line would require both the production of sufficiently big seed crops and a successful seed establishment in open tundra sites. Holtmeier et al. (1996) found that seedling establishment increased in close proximity to healthy seed trees and under open canopies in sheltering stands. In greater distance to the seed tree in open unsheltered areas, as well as in dense forest stands with a closed canopy, the seedling density decreases rapidly (Holtmeier and Broll 2011).

In the tree-line ecotone, pine seedlings underlie a high mortality rate in the open sites before reaching tree size. When uncovered from the snow pack by strong winds, seedlings are stressed by wind, winter desiccation, and ice abrasion and were found to die on exposed ground (Repo et al. 1996; Gu et al. 2008; Middleton et al. 2008; Holtmeier and Broll 2011; Salminen and Jalkanen 2015). A varying snow pattern and warm spells during warming late winters enhance the risk of frost-induced damage. Seedlings established near the forest line or in less wind-eroded depressions grow more sheltered from climatic disturbances (Bolli et al. 2007), but are at higher risk to suffer from snow blight (Phacidium infestans P. Karst) under deep, wet snow coverage (Jalkanen 2007; Holtmeier and Broll 2011), especially when large cohorts of pine seedlings occur. Since current warming has taken place mostly during winter and spring in northern Finnish Lapland (Klein Tank et al. 2002; Mikkonen et al. 2014), the listed disturbances are likely to increase the mortality rate of pine. High seed crops by seed-producing old pines would be necessary to enhance the survival rate of seedlings in open sites (Juntunen and Neuvonen 2006; Danby and Hik 2007; Holtmeier and Broll 2011).

Shrubs and lichens are better adapted to the harsh conditions of the tree-line ecotone and better able to establish as pioneers on bare ground. They are less sensitive to snow loads, spring frosts and nutrient-poor substrates of the fell tops and e.g. the mountain birch is able to grow larger seed crops under adverse conditions (Wehberg 2007). Increasing temperatures and moisture conditions during summer promote growth and germination of deciduous species in the sub-arctic biome (Tømmervik et al. 2005; Wielgolaski 2005; Forbes et al. 2010; Weijers et al. 2018). We found increasing NDVI values in the upper elevations in the northern sites, where shrubs and mountain birch dominate the landscape. In Kevo and Lemmenjoki in particular, the mountain birch belt expanded during the study period as indicated by NDVI and the Random Forest classification. Positive NDVI trends in Kevo result from extending mountain birch coverage and expansion of lichen and shrub-dominated vegetation (Tømmervik et al. 2005).

A dense understory of shrubs and mosses hinders successful tree seedling establishment (Holtmeier 2003, Hyppönen et al. 2013), but may also provide shelter in open birch stands for young pines invading into the tundra (Holtmeier and Broll 2011). In the shelter of birch, pine may grow up to tree size, forming prospective seed trees if persisting under the harsh conditions of the tree-line ecotone. According to Aakala et al. (2014), tree recruitment advanced rapidly in the 1970s and 1980s, but returned to low recruitment levels in the 1990s. Since conifers in the alpine and polar tree-line ecotone grow rather slow and an expansion of coniferous forest might happen with time delay, it is possible, that recently established young, scattered pine cohorts are not yet distinguishable from the deciduous vegetation in the satellite data. When deciduous vegetation suffers from drought stress (Dalen and Hofgaard 2005; Bunn and Goetz 2006; Danby and Hik 2007; Langer 2010; Tuomenvirta 2010) or moth outbreaks (Kullman 2007), it is possible that conifers gradually follow the birch forest belts and replace the deciduous vegetation (Middleton et al. 2008).

Conclusions

We found evidence for greening in the polar-alpine biome in Finnish Lapland derived from NDVI and a Random Forest land cover classification. We found these changes to arise primarily from increasing stand densities in lower elevations and from an expansion of deciduous trees and shrub communities towards open fell tops. While we observed densification of the forest stands in the pine-dominated southern parts of the study region, we did not find evidence for greening of the fell tops there. In contrast, in the northern parts of the study region the upper elevations were found to become greener during the observation period. Based on our results, an instantaneous establishment of new pine stands beyond the current tree-line under global warming is not likely, but a gradual expansion of mountain birches and shrub communities into currently open fell areas is already ongoing.

Acknowledgements

This work was made possible by USGS & NASA, Luke/EFINORD and the National Land Survey of Finland who provided the database of satellite and background data freely available for scientific research. High resolution RapidEye data have been kindly provided by the RapidEye/Blackbridge Science Archive (RESA) through data grant Project-ID 997. The Terra MODIS MOD13Q1 data was retrieved from the NASA Earthdata Search, courtesy of the NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota, https://search.earthdata.nasa.gov/. We thank one anonymous reviewer for providing helpful comments and improvements on earlier drafts of the manuscript.

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Table A1. Standard deviation (std) for the scene-specific NDVI used in Figure 3 and standard deviation for the sample-specific NDVI used in Figure 4. The samples in Figure 4 covered the forest zone (F), the forest-line zone (FL), the tree-line zone (TL) and the Fell tops (FT).

Kevo						
Sensor	Year	Scene	Sample plots			
		std	std: F	std: FL	std: TL	std: FT
Landsat-5	1985	0.12	0.05	0.03	0.04	0.04
	1986	0.12	0.06	0.04	0.04	0.04
	1987	0.12	0.05	0.03	0.04	0.04
	1988	0.13	0.05	0.03	0.04	0.04
	1989	0.13	0.05	0.03	0.04	0.04
	1991	0.13	0.06	0.03	0.04	0.04
	1994	0.13	0.05	0.03	0.03	0.05
	1996	0.13	0.05	0.03	0.03	0.05
	1998	0.13	0.05	0.02	0.03	0.03
	2004	0.13	0.05	0.02	0.03	0.04
	2005	0.14	0.05	0.03	0.03	0.04
	2006					
	2007	0.13	0.05	0.03	0.03	0.05
	2009	0.12	0.05	0.03	0.03	0.03
Landsat-8	2013	0.12	0.05	0.02	0.03	0.03
	2015	0.12	0.05	0.02	0.03	0.03
	2016	0.12	0.04	0.01	0.02	0.03
RapidEye	2013		0.05	0.04	0.03	0.04
	2015		0.04	0.03	0.03	0.03

Karigasniemi						
Sensor	Year	Scene	Sample plots			
		std	std: F	std: FL	std: TL	std: FT
Landsat-5	1985	0.12	0.02	0.03	0.01	0.04
	1986	0.11	0.02	0.02	0.01	0.05
	1987	0.12	0.02	0.03	0.02	0.05
	1989	0.12	0.02	0.03	0.02	0.05
	1992	0.12	0.02	0.03	0.02	0.05
	1995	0.13	0.03	0.03	0.02	
	1997	0.12	0.02	0.02	0.02	0.05
	1998	0.11	0.02	0.02	0.01	0.05
	2004	0.12	0.02	0.02	0.01	0.05
	2005	0.12	0.01	0.02	0.01	0.06
	2006	0.11	0.02	0.02	0.01	0.04
	2009	0.11	0.02	0.02	0.02	0.04
Landsat-8	2014	0.11	0.01	0.02	0.01	0.04
	2016	0.11	0.01	0.01	0.01	0.03
RapidEye	2009		0.03	0.03	0.02	0.04
	2013		0.03	0.03	0.02	0.04
	2014		0.02	0.02	0.02	0.03
	2015		0.02	0.02	0.01	0.03

Syysjärvi						
Sensor	Year	Scene	Sample plots			
		std	std: F	std: FL	std: TL	std: FT
Landsat-5	1985	0.07	0.03	0.02	0.03	0.01
	1986	0.07	0.02	0.02	0.03	0.01
	1987	0.07	0.02	0.02	0.03	0.02
	1989	0.07	0.02	0.02	0.03	0.02
	1991	0.07	0.02	0.02	0.03	0.02
	1994	0.07	0.02	0.02	0.02	0.01
	1996	0.07	0.02	0.03	0.02	0.02
	1997	0.09	0.02	0.02	0.02	0.01
	1998	0.08	0.02	0.02	0.02	0.02
	2005	0.06	0.02	0.02	0.02	0.01
	2009	0.07	0.05	0.02	0.02	0.01
Landsat-8	2015	0.05	0.04	0.01	0.01	0.01
	2016	0.04	0.04	0.01	0.01	0.01
RapidEye	2011		0.03	0.03	0.02	0.02
	2015		0.03	0.03	0.02	0.02

Lemmenjoki						
Sensor	Year	Scene	Sample plots			
		std	std: F	std: FL	std: TL	std: FT
Landsat-5	1985	0.08	0.02	0.04	0.03	0.09
	1986	0.08	0.03	0.04	0.02	0.05
	1987	0.08	0.03	0.04	0.02	0.05
	1991	0.09	0.03	0.03	0.02	0.06
	1994	0.09	0.04	0.02	0.03	0.06
	1995	0.09	0.03	0.04	0.03	0.06
	1997	0.09	0.03	0.04	0.03	0.11
	2005	0.09	0.03	0.04	0.02	0.08
Landsat-8	2013	0.08	0.02	0.03	0.02	0.06
	2014	0.07	0.02	0.02	0.01	0.05
	2017	0.07	0.02	0.02	0.01	0.06
RapidEye	2009		0.03	0.03	0.02	0.04
	2012		0.04	0.04	0.03	0.06
	2013		0.04	0.04	0.03	0.05
	2015		0.03	0.03	0.02	0.05

Saariselkä						
Sensor	Year	Scene	Sample plots			
		std	std: F	std: FL	std: TL	std: FT
Landsat-5	1985	0.09	0.03	0.02	0.04	0.03
	1986	0.09	0.02	0.02	0.05	0.03
	1987	0.09	0.02	0.02	0.04	0.03
	1991	0.09	0.03	0.02	0.05	0.03
	1993	0.09	0.03	0.01	0.05	0.03
	1994	0.09	0.04			
	1997	0.09	0.04	0.02	0.04	0.03
	2005	0.09	0.03	0.02	0.05	0.03
	2007	0.08	0.02	0.02	0.06	0.02
	2009	0.08	0.03	0.02	0.05	0.03
Landsat-8	2013	0.09	0.02	0.01	0.04	0.02
	2014	0.08	0.02	0.01	0.04	0.01
	2015		0.02	0.01	0.05	0.01
	2017	0.10	0.02	0.01	0.05	0.02
RapidEye	2011		0.03	0.02	0.02	0.02
	2013		0.03	0.02	0.03	0.02
	2015		0.03	0.02	0.04	0.02

Yllästunturi						
Sensor	Year	Scene	Sample plots			
		std	std: F	std: FL	std: TL	std: FT
Landsat-5	1984	0.16	0.02	0.02	0.04	0.06
	1987	0.17	0.02	0.03	0.05	0.08
	1988	0.17	0.02	0.03	0.05	0.05
	1992	0.16	0.03	0.04	0.04	0.08
	1994	0.17	0.02	0.03	0.04	0.06
	1995	0.17	0.02	0.02	0.05	0.07
	2004	0.18	0.02	0.03	0.06	0.09
	2006	0.18	0.04	0.07	0.05	0.07
	2011	0.18	0.04	0.06	0.06	0.07
Landsat-8	2013	0.18	0.04	0.07	0.06	0.07
	2014	0.18	0.03	0.05	0.06	0.09
	2015	0.18	0.03	0.06	0.06	0.10
	2017	0.21	0.05	0.06	0.08	0.12
RapidEye	2010		0.04	0.05	0.04	0.06
	2013		0.04	0.05	0.04	0.07

Table A2. Accuracy Assessment of the Random Forest land-cover classification, providing Producr’s Accuracy (PA), User’s Accuracy (UA), Overall Accuracy (OAC) and out-of-bag estimate of error rate.

Study site	Land-cover class	1985		2004		2015	
		PA%	UA%	PA%	UA%	PA%	UA%
Kevo	Water Bodies	100	100	100	100	100	100
	Open fell tops	100	79	100	100	100	100
	Sparse Vegetation	100	100	100	86	100	100
	Deciduous Vegetation	87	100	100	100	100	100
	Conifers	83	96	83	100	100	100
	OAC	94.0 %		96.7 %		100.0 %	
	OOB estimate of error rate	0.49 %		0.74 %		0.25 %	
		1985		2004		2014	
		PA%	UA%	PA%	UA%	PA%	UA%
Karigasniemi	Water Bodies	75	100	75	100	75	100
	Open fell tops	100	82	100	88	100	90
	Sparse Vegetation	100	100	100	100	100	100
	Deciduous Vegetation	100	100	100	100	100	94
	Conifers	90	81	93	79	93	81
	OAC	92.4 %		92.9 %		92.9 %	
	OOB estimate of error rate	0.00 %		0.24 %		0.00 %	
		1987		2009		2016	
		PA%	UA%	PA%	UA%	PA%	UA%
Syysjärvi	Water Bodies	100	83	100	97	100	82
	Open fell tops	100	100	67	100	33	100
	Sparse Vegetation	100	100	100	100	83	100
	Deciduous Vegetation	100	100	97	75	77	100
	Conifers	73	94	97	75	87	45
	OAC	94.7 %		92.0 %		76.0 %	
	OOB estimate of error rate	0.00 %		0.46 %		3.63 %	
		1986		2005		2017	
		PA%	UA%	PA%	UA%	PA%	UA%
Lemmenjoki	Water Bodies	100	100	97	100	100	100
	Open fell tops	100	100	100	100	100	88
	Sparse Vegetation	100	100	97	100	87	100
	Deciduous Vegetation	90	100	93	97	100	100
	Conifers	100	91	100	91	100	100
	OAC	98.0 %		97.3 %		97.3 %	
	OOB estimate of error rate	0.32 %		0.33 %		0.32 %	
		1987		2009		2014	
		PA%	UA%	PA%	UA%	PA%	UA%
Saariselkä	Water Bodies	97	100	90	100	93	93
	Open fell tops	100	97	98	77	92	72
	Sparse Vegetation	100	100	100	100	93	97
	Deciduous Vegetation	100	100	83	100	80	100
	Conifers	100	100	100	100	97	100
	OAC	99.4 %		94.4 %		91.2 %	
	OOB estimate of error rate	0.00 %		0.25 %		0.25 %	

		1987		2004		2017	
		PA%	UA%	PA%	UA%	PA%	UA%
Yllästunturi	Water Bodies	100	97	100	91	100	97
	Open fell tops	100	100	100	100	100	100
	Sparse Vegetation	90	100	63	100	83	100
	Deciduous Vegetation	100	91	100	79	100	88
	Conifers	97	100	100	100	100	100
	OAC	97.3 %		92.7 %		96.7 %	
	OOB estimate of error rate	1.98 %		0.99 %		2.52 %	

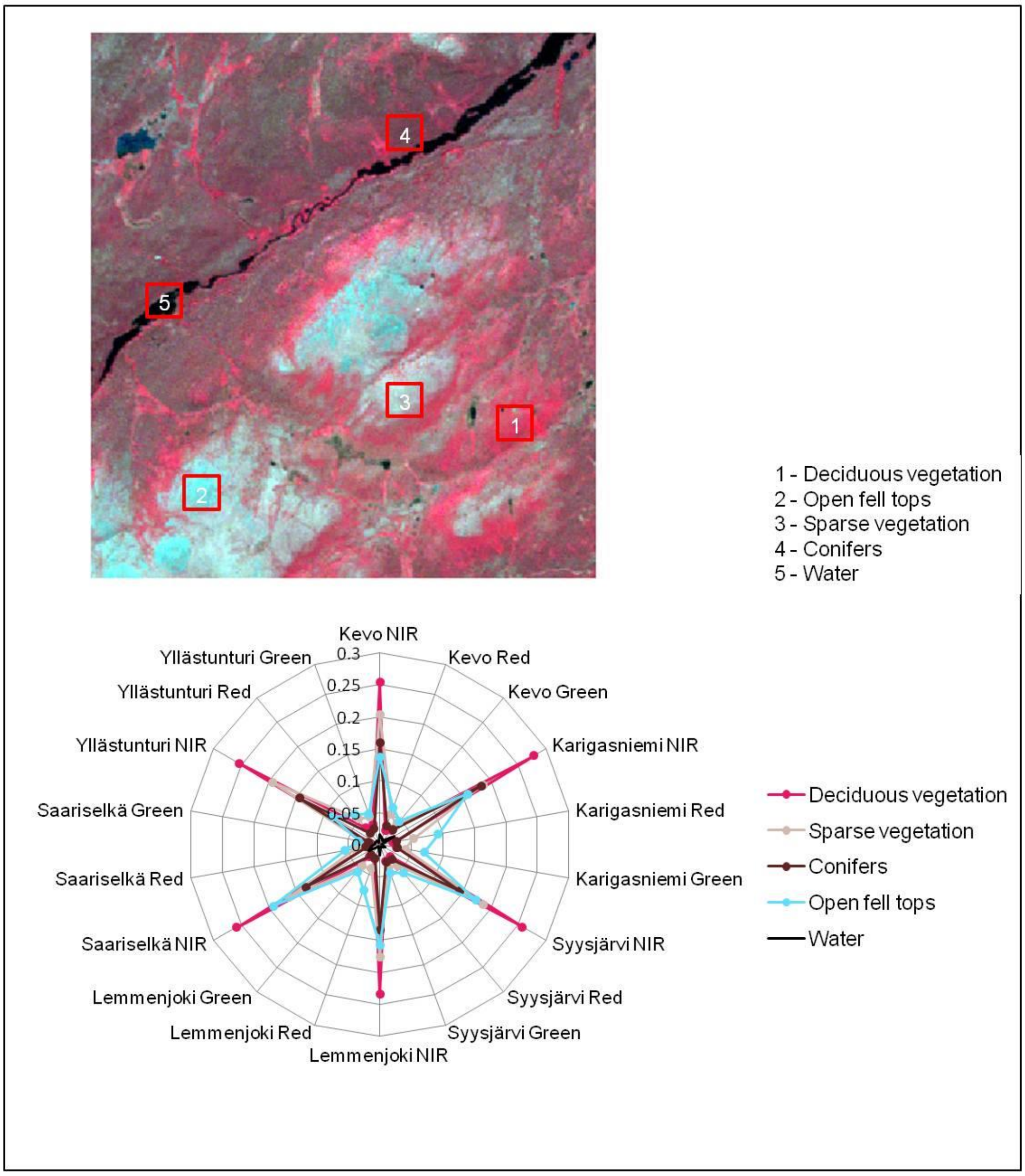


Figure A1. Example of class separation for the RandomForest land-cover classification. Five broad land-cover classes can be distinguished visually (e.g. satellite image of Lemmenjoki above) and by spectral signatures using near-infrared (NIR), red and green channel (Figure below). In some locations, the spectral signatures are clearly distinguishable (e.g. Yllästunturi, Lemmenjoki), while some locations are characterized by open stands with mixed vegetation in the pixel values (e.g. Karigasniemi, Syysjärvi).

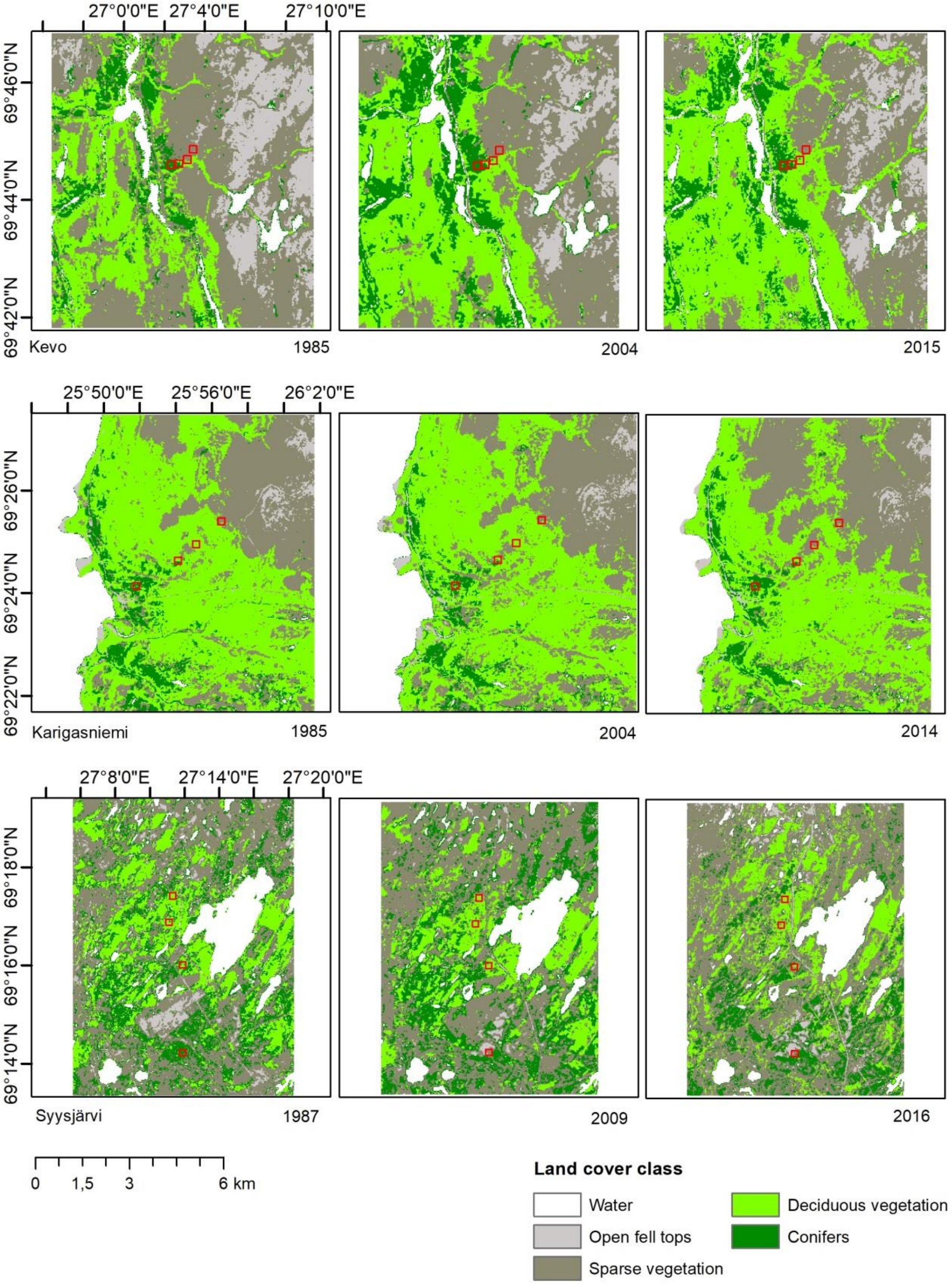


Figure A2a. Random Forest land-cover classification with subsamples (used in Figure 4) for all sites during three acquisition dates of Landsat-5 (1. and 2. images) and Landsat-8 (3. image) during the peak growing season.

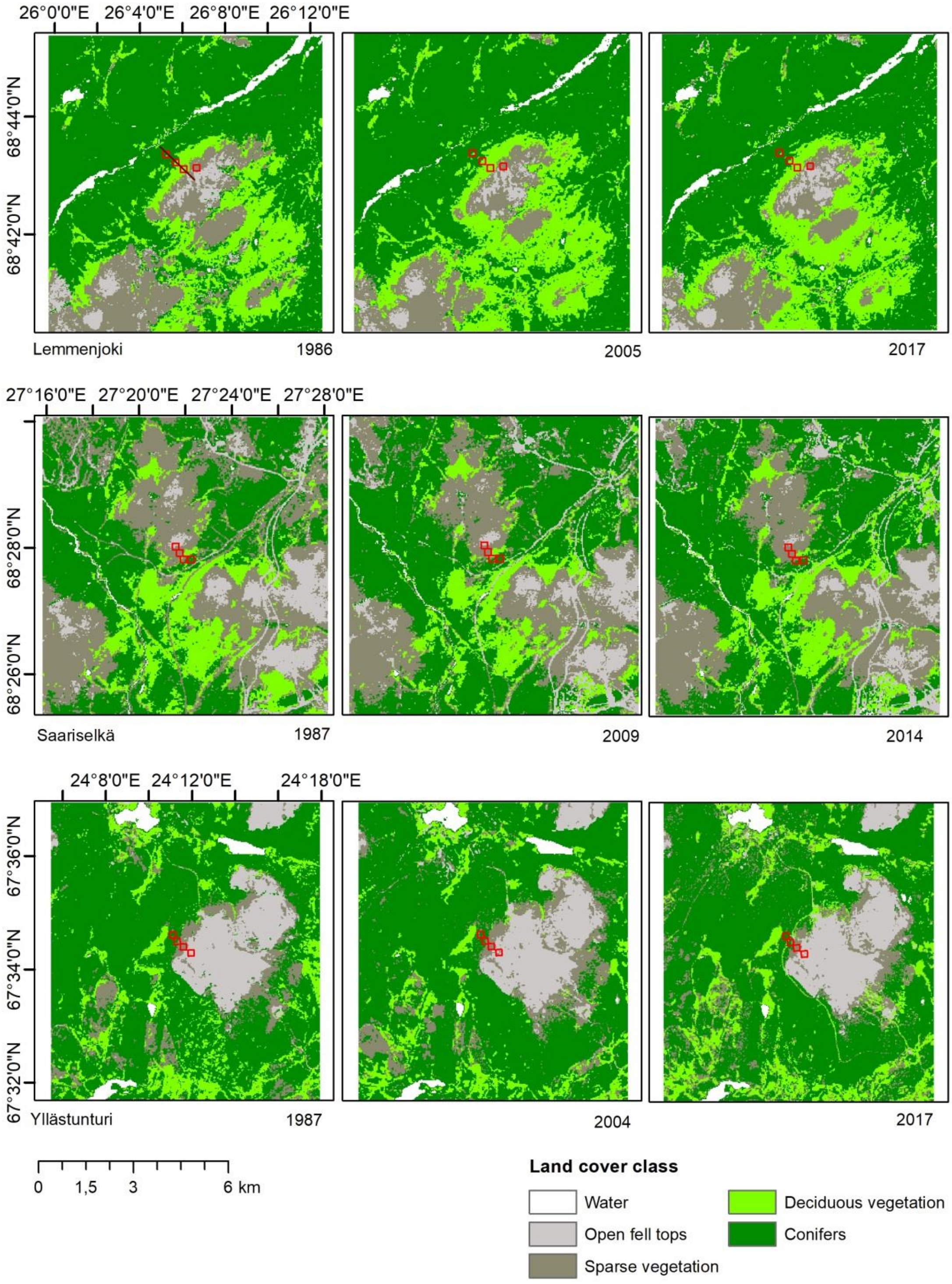
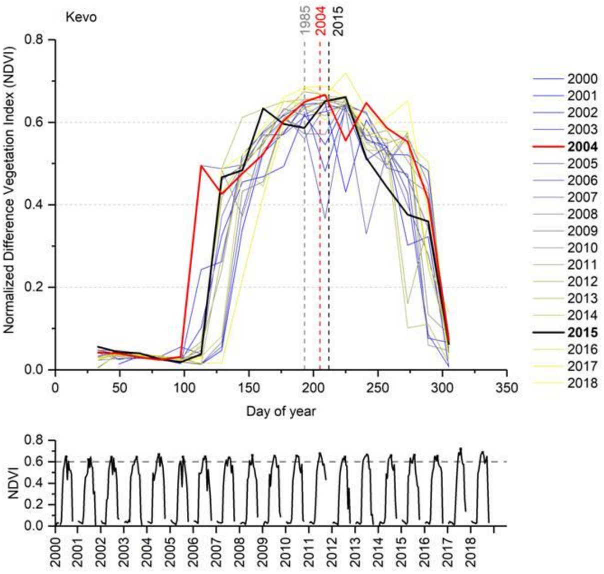
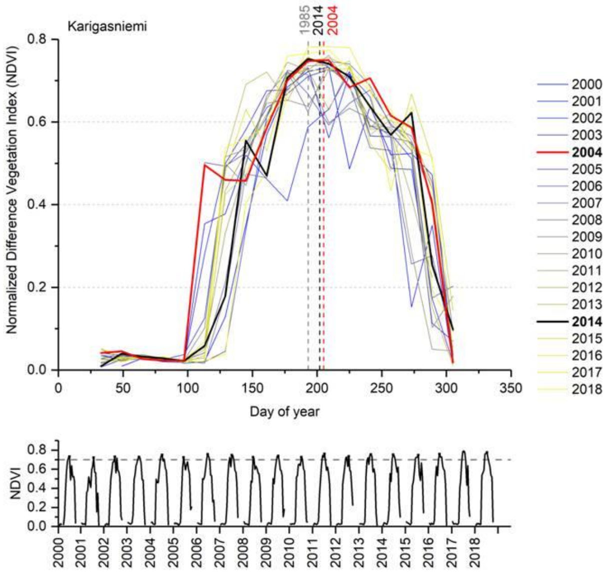
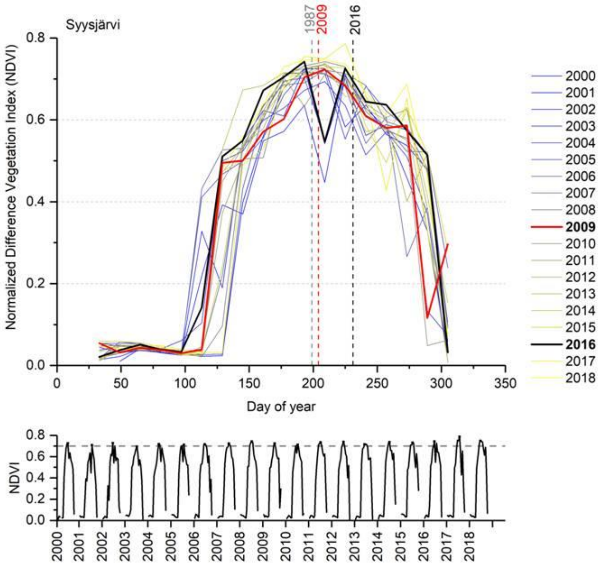
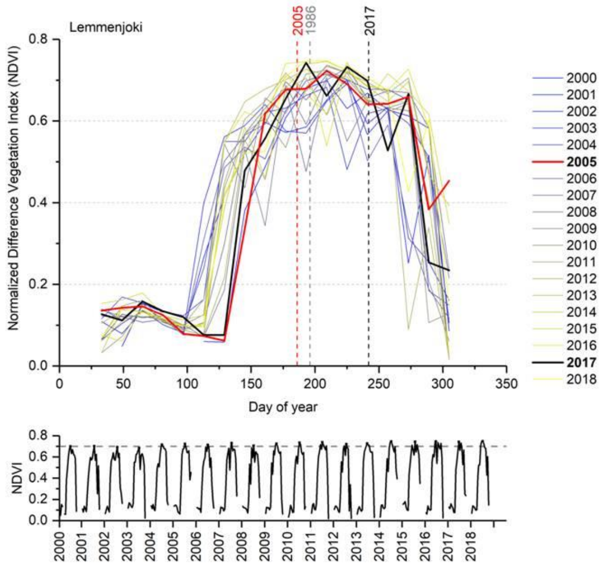


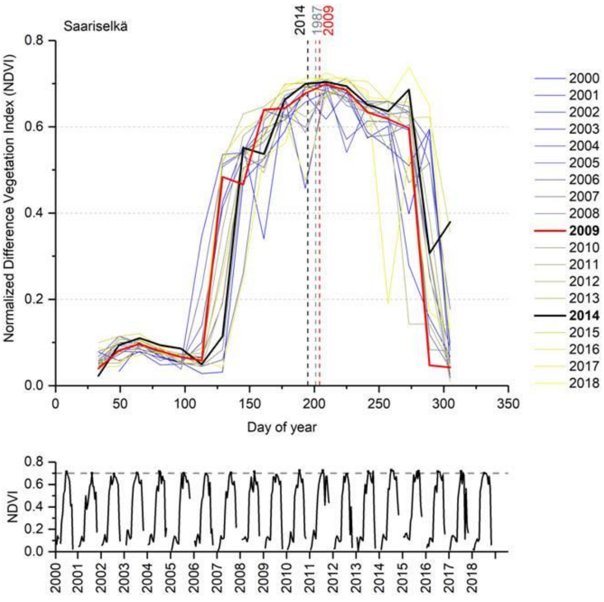
Figure A2b. Random Forest land-cover classification with subsamples (used in Figure 4) for all sites during three acquisition dates of Landsat-5 (1. and 2. images) and Landsat-8 (3. image) during the peak growing season.


Kevo
1985
2004
2015
Normalized Difference Vegetation Index (NDVI)
0.0
0.2
0.4
0.6
0.8
0
50
100
150
200
250
300
350
Day of year
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
NDVI
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018


Karigasniemi
1985
2014
2004
Normalized Difference Vegetation Index (NDVI)
0.0
0.2
0.4
0.6
0.8
0
50
100
150
200
250
300
350
Day of year
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
NDVI
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018


Syysjärvi
1987
2009
2016
Normalized Difference Vegetation Index (NDVI)
0.0
0.2
0.4
0.6
0.8
0
50
100
150
200
250
300
350
Day of year
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
NDVI
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018


Lemmenjoki
2005
1986
2017
Normalized Difference Vegetation Index (NDVI)
0.0
0.2
0.4
0.6
0.8
0
50
100
150
200
250
300
350
Day of year
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
NDVI
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018


Saariselkä
2014
1987
2009
Normalized Difference Vegetation Index (NDVI)
0.0
0.2
0.4
0.6
0.8
0
50
100
150
200
250
300
350
Day of year
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
NDVI
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018

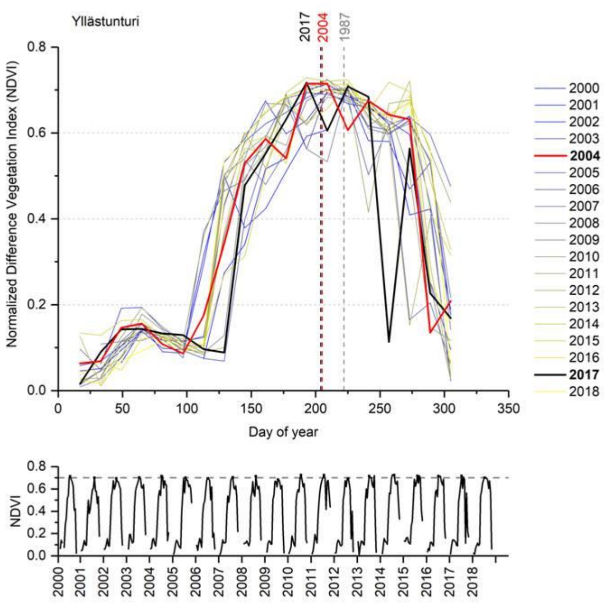

Yllästunturi
2017
2004
1987
Normalized Difference Vegetation Index (NDVI)
0.0
0.2
0.4
0.6
0.8
0
50
100
150
200
250
300
350
Day of year
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
NDVI
2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018

Figure A3. Phenology curves during 2000–2018 based on the maximum NDVI derived from Terra MODIS datasets (MOD13Q1) for each location. Years which were part of the vegetation change analysis (Fig. 5–8; Fig. A2) are marked as thick lines in black and red colour. The analyzed day of year is marked with a dashed vertical line to display the current phenological stage of the vegetation. The lower panels display the course of NDVI during 2000–2018. By integrating a horizontal line at value 0.6 or 0.7 increasing or decreasing trends in the annual maximum NDVI are demonstrated.

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Declaration of originality

I, Anna Katharina Franke, declare that this thesis titled "Climate-induced growth responses and tree-line shifts of boreal conifers in the alpine and polar tree-line ecotone in Finnish Lapland" and the work presented in it are my own. I confirm that: All references and data sources that were used in the thesis have been appropriately acknowledged. I furthermore declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure. I certify that the manuscripts presented are written by me as first author.

Nuremberg, 01.07. 2019

A.K. Franke

Anna Katharina Franke

Maailmaa on jos jonnekin päin, sanoi akka, kun kepillä saunanluukusta koitti.