Site carrying capacity of Norway spruce and Scots pine stands has increased in Germany and northern Europe

Harri Mäkinen [a,*], Helena M. Henttonen [b], Ulrich Kohnle [c], Christian Kuehne [d], Pekka Nöjd [a], Chaofang Yue [c], Joachim Klädtke [c], Jouni Siipilehto [b]

[a] Natural Resources Institute Finland, Tietotie 2, 02150 Espoo, Finland
[b] Natural Resources Institute Finland, Latokartanonkaari 9, 00790 Helsinki, Finland
[c] Forest Research Institute Baden-Württemberg, Wonnhaldestr. 4, 7100 Freiburg i. Br., Germany
[d] Norwegian Institute of Bioeconomy Research, Division of Forestry and Forest Resources, P.O. Box 115, 1431 Ås, Norway

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ABSTRACT

The maximum size-density relationship describes site carrying capacity, i.e., the maximum number of trees of a given size that can be stocked per unit area (self-thinning line). We analysed whether the self-thinning lines of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) have remained unchanged over time in South Germany, Norway and Finland, i.e., over a wide climatic gradient from Central Europe up to the Arctic circle. The analyses are based on long-term growth and yield experiments measured on individual tree basis over several decades, the oldest experiments established during the early 20th century. The stochastic frontier analysis was used to analyse changes in the species-specific self-thinning lines. The results show that the self-thinning lines have shifted upwards over time in all the regions. Thus, currently stands sustain higher stand densities than in the past. The increase of the maximum density for a given average stem size was more pronounced for pine than for spruce, but similar in all studied geographical regions. In addition, increasing site index was associated with increasing site carrying capacity for spruce and pine in all regions. The results imply that environmental changes have altered site properties in similar fashion across the whole study region. In practical forestry, increased site carrying capacity will reduce mortality and loss of growing stock.

1. Introduction

Growing stock has shown an increase in many developed countries (e.g., Köhl et al., 2015), which is also reflected in increasing forest carbon stocks (Pan et al., 2011). In Central and Northern Europe, this increase is partly attributable to improved site productivity and enhanced forest growth as indicated by empirical results. Part of the observed increase in growth rates can be linked to environmental changes such as increased growing season temperature (Pretzsch et al., 2014b; Henttonen et al., 2017). Moreover, model predictions forecast a future enhancement of growth rates in some regions (e.g., Xia et al., 2014; Kellomäki et al., 2018).

The maximum size-density relationship (also called as self-thinning line) has been used to identify the capacity of biomass storage for a given species and site (Reineke, 1933; Yoda et al., 1963). It describes site carrying capacity, i.e., the maximum number of trees of a given size that can be stocked per unit area ("packing space"). It is often estimated as a

line fit to the tree size and stand density using static data on quadratic mean diameter and number of trees per unit area. Stands self-thin at different density levels following different size-density trajectories depending on species, regions and site fertility. On fertile sites, mortality due to competition occurs at higher stand densities than on infertile sites (Bi, 2004; Zhang et al., 2013; Weiskittel and Kuehne, 2019). In addition, the slope may not be a constant and it may vary between species and environmental conditions (e.g., Brunet-Navarro et al., 2016; Aguirre et al., 2018).

There are indications that forest sites are becoming increasingly fertile as shown for example in the Boreal region (Salemaa et al., 2008; Dirnböck et al., 2014). Such changes are likely to be reflected in natural mortality patterns. Up to now, results on this process have been contradictory. Zeide (2001) demonstrated that the environmental change over time has increased the number of Jack pines (*Pinus banksiana* Lamb.) of the same diameter and age per unit area in Northern Ontario. Accordingly, in Southern and Central Germany and Western Poland,

* Corresponding author.
 E-mail address: harri.makinen@luke.fi (H. Mäkinen).

[Pretzsch et al. (2014a)](#) showed that the carrying capacity of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) stands increased in terms of the number of living trees at a given tree size per unit area. In contrast, the maximum number of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.) trees per unit area has not changed over time in Southern Germany ([Pretzsch et al., 2014b](#)).

Several studies have shown that stands growing under different climatic conditions differ in terms of the relationship between tree density per unit area and average tree size in fully stocked stands (e.g., Hynynen, 1993; Brunet-Navarro et al., 2016; Condés et al., 2017; Aguirre et al., 2018; Kimsey et al., 2019). Even though such studies based on different growing conditions do not consider time explicitly, their results have been assumed to indicate the responses of current stands to future climate conditions. Clearly, our knowledge about the long-term changes in stand dynamics is limited and the underlying processes and the driving factors behind it have not been studied adequately.

Several statistical approaches have been proposed for fitting size-density relationships. Zhang et al. (2005) and Salas-Eljatib and Weis-kittel (2018) compared alternative approaches. Zhang et al. (2005) favoured the stochastic frontier analysis and Salas-Eljatib and Weiskittel (2018) quantile regression, although in both studies the approaches performed nearly equally well.

The aim of this study was to quantify the effects of the changing environment on tree mortality in South Germany, Norway and Finland, i.e., over a wide climatic gradient from Central Europe up to the Arctic circle. We analyzed whether stand carrying capacity has changed over a period of 100 years. Specifically, we analysed whether the self-thinning lines of two common tree species (Norway spruce and Scots pine (*Pinus sylvestris* L.) have remained unchanged over time at differing locations. Our hypothesis is that self-thinning occurs at higher stand densities today than in the past. Due to different environmental conditions, i.e. temperate climate in Central Europe, maritime climate in Norway and more continental subarctic climate in Finland, it is plausible that a divergent trend in site carrying capacity has occurred in the different regions.

2. Materials and methods

2.1. Study material

The analyses are based on long-term growth and yield experiments measured on individual tree basis over several decades in Finland, Norway and Germany, the oldest experiments established during the early 20th century. Successive tree-size measurements and recording of living and dead trees form the basis for analysing mortality patterns and the resulting stand dynamics.

The Finnish data set consists of 148 plots from long-term experiments with Norway spruce ("spruce", N = 39) and Scots pine ("pine", N = 109), established to investigate the effects of varying thinning intensities on the growth and yield of the stands (Table 1). Most of the experiments were located in South and Central Finland, but the northernmost experiments were located north of the Arctic circle (Fig. 1). The experiments were originally established in pure or almost pure even-aged spruce and pine stands with high initial densities on mineral soils. Most of the experiments were established in young stands near the first thinning stage, but some experiments were in older stands. The experiments were measured 2–11 times between 1928 and 2016 (Fig. 2). Only the unthinned control plots of the experiments were used for our study. On each plot, stem diameter at breast height (1.3 m), as well as tree status (living/dead), of all the trees were measured. In addition, the height of sample trees randomly selected across a stand's diameter range (~30 per plot) was measured. Site index, i.e., mean height of the 100 thickest trees ha^{-1} at stand age 100 years (H_{100}), was calculated based on a measurement around 1990 (or the last measurement if the experiment was terminated earlier) using the models by Vuokila and Väliaho (1980) for artificially regenerated stands and the models by Gustavsen

Table 1

Characteristics of the Norway spruce and Scots pine plots in Finland, Norway and Germany.

Parameter	Unit	Mean	Std	Min.	Max.
Finland, Norway spruce					
No of plots		39			
Plot size	ha	0.12	0.03	0.05	0.25
No of measurements	N/plot	5.7	2.2	2	11
Period length	years	6.2	2.3	2	14
H_{100}*	m	32.0	2.3	27.0	36.4
Elevation	m, asl	122	28	80	200
Tsum	d.d.	1200	69	1033	1275
Finland, Scots pine					
No of plots		109			
Plot size	ha	0.11	0.04	0.01	0.25
No of measurements	N/plot	4.3	1.9	2	11
Period length	years	9.1	3.5	2	26
H_{100}*	m	24.3	4.1	15.6	32.0
Elevation	m, asl	150	54	35	280
Tsum	d.d.	1099	177	744	1332
Norway, Norway spruce					
No of plots		114			
Plot size	ha	0.09	0.03	0.02	0.25
No of measurements	N/plot	7.5	2.2	3	13
Period length	years	5.8	2.3	1	20
H_{40}*	m	20.6	4.1	10.1	28.8
Elevation	m, asl	149	87	15	400
Tsum	d.d.	1045	236	560	1406
Norway, Scots pine					
No of plots		65			
Plot size	ha	0.12	0.06	0.04	0.28
No of measurements	N/plot	9.3	4.0	4	22
Period length	years	6.4	2.5	1	15
H_{40}*	m	13.8	4.5	3.5	21.8
Elevation	m, asl	168	83	20	340
Tsum	d.d.	918	236	539	1331
Germany, Norway spruce					
No of plots		13			
Plot size	ha	0.18	0.08	0.10	0.33
No of measurements	N/plot	7.6	2.1	3	10
Period length	years	4.3	1.4	1	7
H_{100}	m	37.7	3.0	32.3	40.7
Elevation	m, asl	750	233	421	1087
Tsum	d.d.	1479	238	1007	1757

* H_{40} and H_{100} are site indices, i.e., mean height of the 100 thickest trees ha^{-1} at stand age 40 and 100 years, respectively; Period length is the number of years between the successive measurements; *Tsum* is temperature sum.

(1980) for naturally regenerated stands. Such a static site index accounts for differences between site types and geographical regions but retains potential changes in the site carrying capacity over time. The mean annual temperature ranges from slightly over +5 °C in South-West Finland to about −2 °C in Northern Finland, and annual precipitation sums range from about 500 mm to 650 mm with the highest sums in Southern Finland. The average temperature sum (*Tsum*, 1971–2000) was calculated for each plot according to Ojansuu and Henttonen (1983). Most of the experiments have been used in previous studies and a more detailed description of the experiments and measurements is provided in Mäkinen and Isomäki (2004a,b) and Mäkinen et al. (2017).

The Norwegian data set derives from 179 plots in pure or almost pure spruce (N = 114) and pine stands (N = 65) on mineral soil with varying initial density (Fig. 1, Table 1). About 62% of the plots were unthinned and 38% had been thinned at the time of establishment, but left unthinned thereafter. The oldest measurements dated back to the early 1920s, but only a few plots were that old, and the most resent measurements were from 2014 (Fig. 2). Later on, the number of plots consistently increased especially in the 1960s and thereafter. The plots were measured as in the Finnish data set, but site index was calculated as the mean height of the 100 thickest trees at breast height age 40 years (H_{40}) using the models by Tveite (1977) and Tveite and Braastad (1981). Mean annual temperature for the Norwegian plots analysed here varies between little under −2 °C in northern Norway to about 7 °C in western

Fig. 1. Location of the sample plots in Finland, Norway and Germany; Norway spruce square, Scots pine circle.

Norway while annual precipitation ranges from circa 350 mm in the far north to slightly over 2500 mm in the west. The average temperature sum for each plot was calculated as annual degree days >5 °C (1961–1990) using climate data obtained from the Meteorological Institute of Norway. The plots are described in Næsset (1995), Øyen and Nes (1997), Braastad and Tveite (2001).

The German data set comprises repeated measurements of 13 spruce experimental plots at nine different locations (stands) in Baden-Würt-temberg, Southwestern Germany (Fig. 1, Table 1). The plots were measured 3–10 times between 1964 and 2018, the longest measurement period being 38 years (Fig. 2). In the course of the experiments, the plots were left unthinned or almost unthinned, i.e., thinning was restricted only to the removal of dying and dead trees. The site indices (H_{100}) were calculated using the model by Sloboda (1971). All stands were single-species and even-aged. The mean annual temperatures range from 4.7 to 8.2 °C, and precipitation from about 800–1800 mm. During the vegetation period (April-September), temperatures range from 10.1 to 14.6 °C and precipitation from about 370–750 mm (the source of the climate data: Deutscher Wetterdienst).

The early development of the plots before the onset of self-thinning was removed from the data, if the plot exhibited no mortality. In addition, plots exhibiting an increase in the number of stems ha^{-1}, as well as a decrease in mean stem diameter, in subsequent measurements were removed.

2.2. Self-thinning line

The stochastic frontier analysis (SFA) was used to analyse changes in the species-specific maximum size-density relationships over time in the different regions. SFA has been adopted to forestry and ecological research from economics (e.g., Coelli et al., 1998; Bi, 2004). The analysis renders production frontier, i.e., the maximum asymptotic stand density as a function of tree size. SFA is able to evaluate changes in production frontier over time when panel data is used.

The basic equation used to illustrate the size-density trajectories was:

$$\ln(N_{it}) = \alpha_0 + \alpha_1 \ln(Dq_{it}) + v_{it} + u_{it} \tag{1}$$

where N_{it} is the number of stems ha^{-1} of measurement t on plot i, Dq_{it} is the quadratic mean diameter, v_{it} is a random error and u_{it} is a one-sided error ($u_{it} \geq 0$) capturing the technical inefficiency in production, i.e., the shortfall of N_{it} from the frontier.

The potential change over time in the size-density relationship was tested by first including calendar year (*Year*), its interaction with *Dq*, and site index ($H_{100,i}$, $H_{40,i}$ was used in the Norwegian data) to the model:

$$\ln(N_{it}) = \alpha_0 + \alpha_1 \ln(Dq_{it}) + \alpha_2 H_{100,i} + \alpha_3 Year_t + \alpha_4 Year_t$$
$$\times \ln(Dq_{it}) + \alpha_5 Tsum_i + v_{it} + u_{it} \tag{2}$$

The interaction term *Year* × ln(*Dq*) was not significant and it was excluded. The average temperature sum of plot i ($Tsum_i$) was then added to the model for describing geographical differences (latitude, altitude) between the plots. However, it was not statistically significant when site index (H_{40} or H_{100}) was included in the model. Moreover, the interaction terms *Year* × H_{100}, H_{100} × ln(*Dq*) and *Tsum* × ln(*Dq*) were not significant and were not included. The maximum likelihood estimates of the parameters of Eq. (2) were calculated using the QLIM procedure in SAS (version 9.4, SAS Institute Inc. 2017). To distinguish whether the results are method dependent (Zhang et al., 2005; Salas-Eljatib and Weiskittel, 2018), we calculated the size-density relationships also based on the quantile regression approach using the QUANTREG procedure in SAS.

Even though new plots have been established over the study period, there is a lack of young stands in recent years (Fig. 2). In order to counterbalance the shift towards older ages, we also calculated the results by fixing the age span to 40–85 years.

3. Results

In all regions, stand density decreased with increasing stem diameter (Fig. 3). The decrease was fastest for spruce in Finland and slowest for spruce in Norway (parameter α_1, Table 2). No consistent pattern was found for the tree species, i.e., in Finland the decrease was faster for spruce than for pine, but in Norway vice versa.

Increasing site index (H_{40}, H_{100}) was associated with increasing site carrying capacity for spruce and pine in all regions (parameter α_2, Table 2). As it was the case with stem diameter, no coherent order was found for the coefficient of site index for spruce and pine in Finland and Norway, where both species were available in the data. The temperature sum ($Tsum_i$) was not significant in any country when site index was included in the model.

The maximum density for a given average stem size increased over time in all regions (Table 2). The increase appeared to be slightly larger for pine than for spruce both in Finland and Norway (Table 2, Fig. 3).

The results were also calculated by fixing the age span to 40–85 years. However, narrowing the age span resulted in no major changes to the results (Supplementary material, Table S2).

The maximum size-density relationships were also derived using quantile regression to further evaluate whether findings are sensitive to the statistical approach. The results revealed no major differences between the two evaluated approaches. Findings for the stochastic frontier analysis are reported here, and those derived from quantile regression in the supplementary material (Table S1).
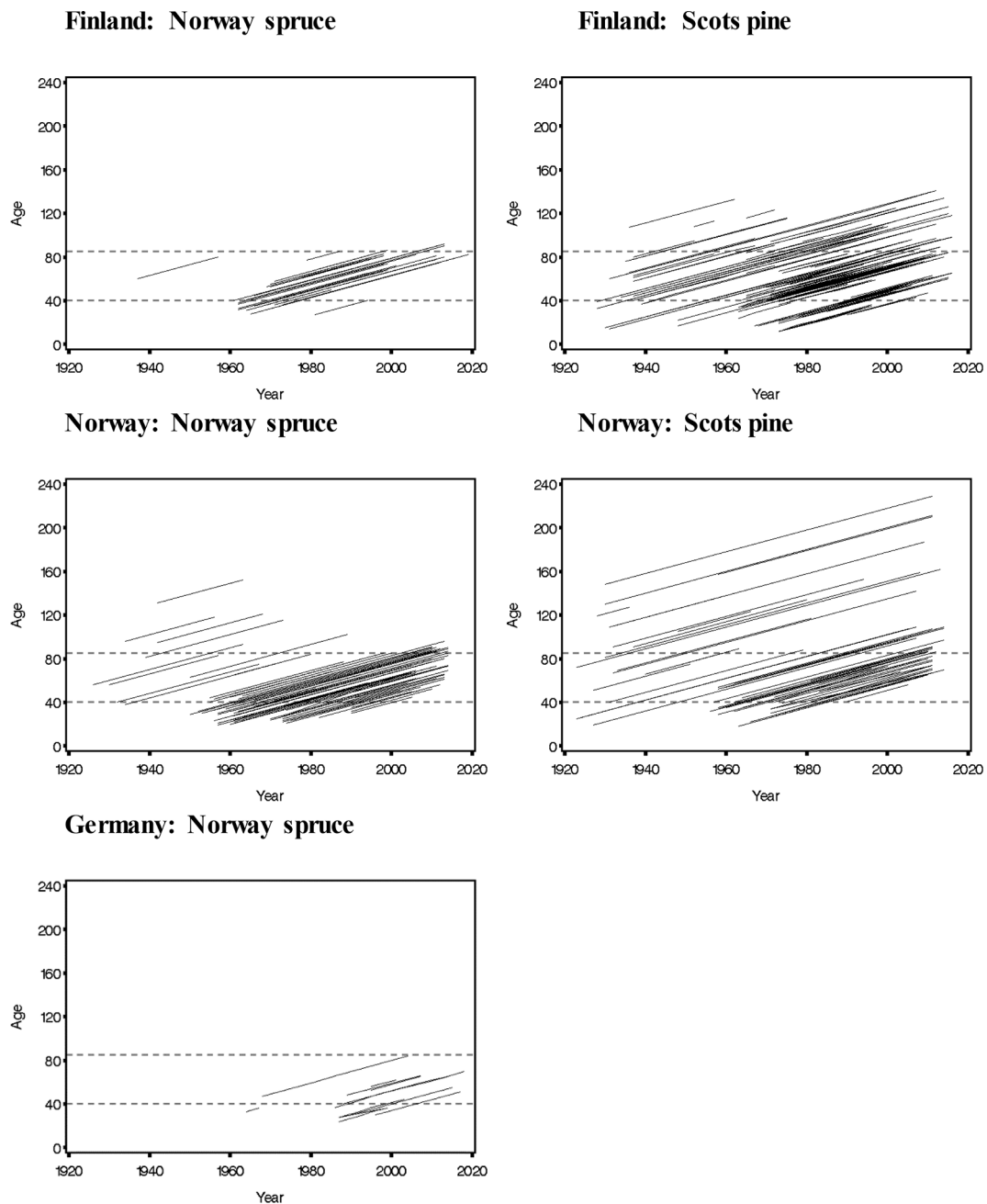
Finland: Norway spruce

Finland: Scots pine

Norway: Norway spruce

Norway: Scots pine

Germany: Norway spruce

Fig. 2. Age-calendar year trajectories of the Norway spruce and Scots pine plots in Finland, Norway and Germany.

4. Discussion

Using repeated measurements spanning over time periods of up to 96 years, we quantified whether stand dynamics and mortality have changed in three climatically different countries from Central Europe up to Northern Fennoscandia. The results showed that the self-thinning line has shifted upwards over time and self-thinning occurs at higher stand densities today.

Contrary to our prior expectations, no major differences were found between Germany, Norway and Finland. The results imply that environmental changes have altered site properties in a similar fashion across the whole study region. The similar changes in the maximum size-density relationship suggest that one large-scale factor has played a driving role, but the possibility that several changing environmental determinants have resulted in parallel shifts in the site carrying capacity cannot be excluded. There are many possible causes for changes in site

carrying capacity, including rising temperature, eutrophication due to nitrogen deposition and atmospheric CO_2 enrichment. While a combined effect of all these drivers might have caused the observed changes in carrying capacities irrespective of studied species and region, individual contributions by each driver are likely to vary between regions. Based on the results of this study, it is, however, difficult to quantify the individual effects and the considerations about potential driving factors remain rather speculative.

The growth of the Finnish forests has steadily increased since the early 1970s (Peltola et al., 2019). In a recent study, we showed that environmental changes explain as much as 37% of the shift (Henttonen et al., 2017). In Finland, nitrogen deposition is very low compared to most regions in Europe (Dirnböck et al., 2014; Ruoho-Airola et al., 2014) and the monotonous temporal trend in the atmospheric CO_2 does not resemble with the observed growth trend. Furthermore, the mean annual temperature has risen by more than 2 °C during 1847–2013 in

Finland: Norway spruce

Finland: Scots pine

Norway: Norway spruce

Norway: Scots pine
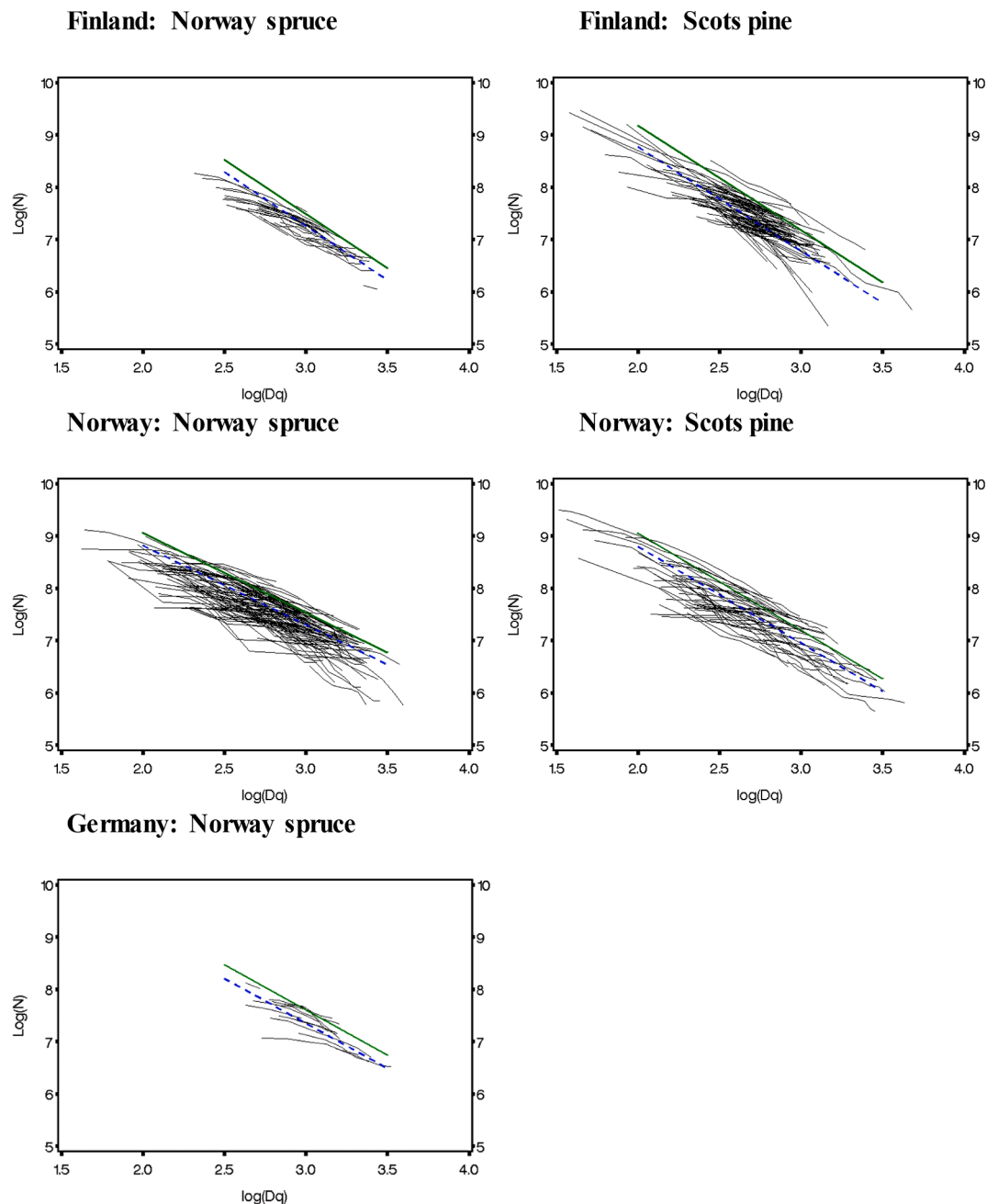
Germany: Norway spruce

Fig. 3. Size-density trajectories of the individual plots (black thin lines). The dashed blue and continuous green lines show the SFA estimates (Eq. (2)) of the trajectories for years 1970 and 2015, respectively, using the average site index on each data set.

Finland, the warming being more rapid after the late 1960s (Mikkonen et al., 2015). Comparisons with temperature sums suggested similarities between summer temperatures and the environment-induced increment change in Finland (Henttonen et al., 2017) and Sweden (Mensah et al., 2021). Thus, it is likely that increasing temperature has been a major contributing factor also for the observed change in the site carrying capacity. Low nitrogen content available to trees is typical of boreal forest soils (e.g., Saarsalmi and Mälkönen, 2001; Saarsalmi et al., 2014). Even though nitrogen influx is an implausible contributing factor, increasing soil temperature enhances organic matter decomposition and thus nutrient availability and uptake by trees (e.g., Lahti et al., 2005; Hedwall and Brunet, 2016).

Forest growth has displayed a considerable increase during the latter part of the 20th century also in several Central European countries (e.g., Pretzsch et al., 2014a,b). Also, site productivity of spruce stands

described by site index has increased after the mid-1950s in Southwest Germany, i.e., in the area covered by this study (Yue et al., 2014). The results of this study show that a corresponding change has also taken place in the site carrying capacity of spruce stands. In contrast, Pretzsch et al. (2014b) found that spruce and European beech stands grew faster but the number of trees per unit area at a given mean diameter had remained the same. Their data came from Southeast and Central Germany, i.e., from adjacent geographical regions. Our results apply to sites in the plains and low - to mid-elevation mountain ranges with altitudes of 421–1087 m above sea level, and those by Pretzsch et al. (2014b) to altitudes of 330–843 m. Their plots were also unthinned or only slightly thinned and the site conditions comparable. Even though the observed change in the site carrying capacity in Germany was coincident with Norway and Finland, our German data contained only 13 plots, which makes the results less conclusive. In a parallel study with data from

Table 2

Parameter values and their standard errors of the size-density trajectory (Eq. (2)) for Norway spruce and Scots pine in Finland, Norway and Germany.

Variable	Estimate	Std Err	t-value	P > t
Finland: Norway spruce				
α_0	11.714	0.150	78.29	0.001
α_1, $\ln(Dq)$	−2.039	0.056	−36.52	0.001
α_2, H_{100}	0.037	0.003	11.87	0.001
α_3, *Year*-1920	0.008	0.001	8.20	0.001
v	0.051	0.009	5.93	0.001
u	0.134	0.014	9.67	0.001
Finland: Scots pine				
α_0	11.630	0.176	65.92	0.001
α_1, $\ln(Dq)$	−1.989	0.066	−30.15	0.001
α_2, H_{100}	0.027	0.004	7.47	0.001
α_3, *Year*-1920	0.009	0.002	5.56	0.005
v	0.156	0.012	13.00	0.001
u	0.146	0.019	7.53	0.001
Norway: Norway spruce				
α_0	11.505	0.091	125.75	0.001
α_1, $\ln(Dq)$	−1.517	0.035	−43.64	0.001
α_2, H_{40}	0.004	0.002	1.55	0.121
α_3, *Year*-1920	0.005	0.001	8.31	0.001
v	0.210	0.014	15.45	0.001
u	0.166	0.022	7.51	0.001
Norway: Scots pine				
α_0	11.817	0.105	112.57	0.001
α_1, $\ln(Dq)$	−1.847	0.035	−53.29	0.001
α_2, H_{40}	0.029	0.003	11.26	0.001
α_3, *Year*-1920	0.006	0.001	11.80	0.001
v	0.211	0.014	15.08	0.001
u	0.138	0.024	5.71	0.001
Germany: Norway spruce				
α_0	11.024	0.488	22.60	0.001
α_1, $\ln(Dq)$	−1.720	0.126	−13.68	0.001
α_2, H_{100}	0.032	0.006	5.24	0.001
α_3, *Year*-1920	0.006	0.002	3.66	0.001
v	0.080	0.019	4.11	0.001
u	0.134	0.029	4.60	0.001

Dq is the quadratic mean diameter, H_{40} and H_{100} are site indices and *Year* is the calendar year (1920 was subtracted from it to provide intelligible coefficients).

Southeast and Central Germany, as well as from Western Poland, Pretzsch et al. (2014a) found that the carrying capacity of oak stands had indeed increased. Thus, the differences between our results and those by Pretzsch et al. (2014b), as well as those between Pretzsch et al. (2014a,b), are hard to explain.

Throughout central Europe mean temperatures have increased during the past decades (Schöpp et al., 2003; Wellbrock et al., 2005) and the increasing temperatures correspond to some extent with increasing forest growth and site indices (Kohnle et al., 2014; Yue et al., 2014). Simultaneously, nitrogen deposition has increased considerably (Schöpp et al., 2003; Wellbrock et al., 2005) associated with increases in soil nitrogen concentrations and availability of nitrogen (e.g., Phoenix et al., 2012). Consequently, several studies have suggested that elevated nitrogen supply is a factor of major importance for net primary productivity and higher stand-level growth during the late 20th century (e.g., Kahle et al., 2008; Phoenix et al., 2012; Yue et al., 2016).

Site productivity has increased also in Norway and the site indices of recently established stands tend to exceed those in older stands (Nilsen and Larsson, 1992; Bøhler and Øyen, 2011; Sharma et al., 2012; Allen et al., 2020). Sharma et al. (2012) found a significant interaction of increasing site index trend and temperature sum. Moreover, Andreassen et al. (2006) found that warm and dry summers increased growth of spruce stands in coastal, northern and mountainous areas, but decreased growth in the lowlands of Southeast Norway. Sharma et al. (2012) concluded that that even though changing temperature and precipitation seem to contribute to the trends in site indices, increased nitrogen availability and atmospheric CO_2 levels may also be important factors. In Southern Norway, nitrogen deposition has possibly increased forest growth up to 25% (Solberg et al., 2004, 2009). However, there is a steep

nitrogen deposition gradient in Norway with a considerable input in the south and low input in the north. As the geographical trends in temperature and nitrogen deposition are highly correlated across Norway, it is difficult to quantify their separate effects on forest growth.

Pine is light-demanding early-successional species, whereas spruce is intermediate in shade tolerance and capable of occupying growing space below canopy. Pine typically grows on less fertile sites than spruce. Therefore, one would expect pine to benefit more from increasing temperature and resource supply, as indeed was the case according to the results of this study. Moreover, increasing drought periods have reduced productivity of spruce stands, especially in Central Europe but also in the boreal region due to the species' shallow root system (Allen et al., 2010; Lindner et al., 2010; Kellomäki et al., 2018).

In the early studies, the slope of the self-tinning line was considered a universal constant (Yoda et al., 1963; Weller, 1987). Later studies have suggested that the slope may not be a constant and it may vary between species and environmental conditions. For example, Aguirre et al. (2018) found for Scots pine in Spain that the intercept did not vary according to aridity, but the slope did, i.e., vice versa to our results. Brunet-Navarro et al. (2016) found that the slopes did not vary among different pine species growing in Spain, but Scots pine in colder conditions had a higher intercept and steeper slope. Our results are, however, consistent with the previous Finnish studies (Hynynen, 1993) suggesting that site index had an effect on the intercept but not on the slope of self-thinning line.

This study is based on periodically remeasured long-term experiments which include fully stocked plots representing maximum stand density. The data set from the long-term experiments provide insight into site carrying capacity over time. Using unthinned plots of permanent experiments ensures similar site conditions and helps to exclude several confounding factors that could impair the results. In contrast, if temporary plots under varying climatic conditions are used as database, it is hard to ensure that the range of space-time substitution exclusively represents changing climatic conditions over time. The effects of climate and other local site conditions may be coalesced and are difficult to differentiate. Other unknown differences, e.g., in tree genotype, represent additional sources of uncertainty.

Due to the broad variation of stand age (Fig. 2), the plots represent a wide range of stand developmental stages. Even though new plots have been established over the study period, the material from recent years includes few young stands. In order to counterbalance the shift towards older ages, we calculated the results also by fixing the age span to 40–85 years. The results remained essentially the same (Supplementary material, Table S2). Thus, although a more balanced data set would be desirable, we are confident that the identified trends are genuine.

5. Conclusions

While several recently published papers have demonstrated the enhancing effect of warmer climate on site carrying capacity, our work is one of the few that has shown changing maximum stand densities over time under similar site conditions. Based on observation periods spanning up to 100 years, the findings of this study reveal that the level of self-thinning line has risen within a century, i.e., current stands sustain higher stand densities. The increase in maximum density was slightly more pronounced for pine than for spruce, but similar in all three geographical regions. In practical forestry, increased site carrying capacity will reduce mortality and therefore loss of growing stock.

The maximum stand density on a given site is essential information for modelling and predicting stand dynamics and the effects of silvicultural treatments. Growth and yield simulators often base their predictions on data collected under a different climate, for the boreal zone a less favourable one. If the competition-related processes are being altered due to changing environmental conditions, simulators using the concept of maximum stand density for predicting tree mortality need to be tuned. Thus, the findings of this study stress the need for temporally

variant self-thinning models. A direct implementation of the results into growth simulators is not possible. However, they may help to quantify causal relationships between forest growth and site carrying capacity in order to develop environment-sensitive mortality models.

Even though the results imply that growing conditions are generally improving due to environmental changes, a causal analysis of changes in the site carrying capacity was explicitly not within the scope of the study. The question, which particular environmental changes have actually driven the increase in maximum stand density, requires a different approach. In particular, the finding that no major differences in the increase of stand carrying capacity existed between the regions appears to contradict some previous studies and calls for further elaboration.

CRediT authorship contribution statement

Harri Mäkinen: Conceptualization, Funding acquisition, Project administration, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft. **Helena M. Henttonen:** Conceptualization, Funding acquisition, Methodology, Writing - review & editing. **Ulrich Kohnle:** Data curation, Writing - review & editing. **Christian Kuehne:** Data curation, Methodology, Writing - review & editing. **Pekka Nöjd:** Conceptualization, Funding acquisition, Writing - review & editing. **Chaofang Yue:** Data curation, Writing - review & editing. **Joachim Klädtke:** Data curation, Writing - review & editing. **Jouni Siipilehto:** Data curation, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119214.

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