









LETTER

A fingerprint of climate change across pine forests of Sweden

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Abstract

Climate change has likely altered high-latitude forests globally, but direct evidence remains rare. Here we show that throughout a ≈ 1000 -km transect in Scots pine (*Pinus sylvestris* L.) forests in Sweden, mature trees in ≈ 2015 had longer needles with shorter lifetimes than did trees in ≈ 1915 . These century-scale shifts in needle traits were detected by sampling needles at 74 sites from 2012 to 2017 along the same transect where needle traits had been assessed at 57 sites in 1914–1915. Climate warming of $\approx 1^\circ\text{C}$ all along the transect in the past century has driven this temporal shift in foliage traits known to be physiologically critical to growth and carbon cycling processes. These century-scale changes in Scandinavian Scots pine forests represent a fingerprint of climate change on a fundamental biological element, the leaf, with repercussions for productivity and sensitivity to future climate, which are likely to be mirrored by similar changes for evergreen conifers across the boreal biome.

Keywords

Boreal forests, climatic drivers, functional traits, needle longevity, *Pinus sylvestris*.

Ecology Letters (2020) **23**: 1739–1746

INTRODUCTION

Observations, experiments and theory all show that climate and climate change influence the location, composition, structure and function of forests in many parts of the world, including the high-latitude forests dominated by boreal species (Körner, 1998; Barber *et al.*, 2000; Lloyd *et al.*, 2011; Henttonen *et al.*, 2014; Henttonen *et al.*, 2016; Reich *et al.*, 2018; Hisano *et al.*, 2019). However, direct evidence of a fingerprint of climate change on trees and forests is scarce, complex and often prone to conflicting interpretation, in part because of the challenge of disentangling changes among multiple synchronous drivers (Körner, 1998; Barber *et al.*, 2000; Lloyd *et al.*, 2011; Henttonen *et al.*, 2014; Henttonen *et al.*, 2016; Hogg *et al.*, 2017; Reich *et al.*, 2018; Hisano *et al.*, 2019). For example, evidence from North America, Europe and Asia suggests both increased and decreased forest growth as a result of a changing climate, with growth often trending higher in colder regions, whereas increasing drought associated with increasing temperature has suppressed growth elsewhere (Barber *et al.*, 2000; Reich and Oleksyn, 2008; Lloyd *et al.*, 2011; Henttonen *et al.*, 2014; Henttonen *et al.*, 2016; Hogg *et al.*, 2017; Reich *et al.*, 2018; Hisano *et al.*, 2019). Similarly, there is considerable evidence of treeline expansion globally, including in regions with cold winter climates, but changing land use (e.g. vegetation management, grazing pressures), and rising CO_2 and nitrogen deposition complicate the interpretation of such patterns in many if not all areas (Harsch *et al.*, 2009; Cudlín *et al.*, 2017; Weiser *et al.*, 2019).

The size and longevity of leaves influence forest function (Schoettle, 1990; Reich *et al.*, 2003; Pensa and Jalkanen, 2005), are influenced by climate (Jalkanen *et al.*, 1995; Reich

et al., 2003; Pensa and Jalkanen, 2005; Reich *et al.*, 2014; Ľupek *et al.*, 2015; Wright *et al.*, 2017) and in turn shape responses to climate (Nicotra *et al.*, 2010; Gornish and Prather, 2014; Reich *et al.*, 2014). For example, in boreal conifers conditions that restrict tree growth also alter needle traits associated with growth: reduce needle length, increase longevity, decrease nutrient concentrations and photosynthetic rates (Schoettle, 1990; Reich *et al.*, 2003; Pensa and Jalkanen, 2005); those modifications in turn co-regulate tree growth (Schoettle, 1990; Reich *et al.*, 2003; Pensa and Jalkanen, 2005). Hence, changing environmental conditions over the past century may have impacted tree needle traits, with consequences for forest growth and productivity (Gornish and Prather, 2014; Reich *et al.*, 2014).

Herein we provide evidence of a climate change fingerprint on the foliage of Swedish Scots pine (*Pinus sylvestris* L.) forests, based on needle sampling along a ≈ 1000 km latitudinal transect (Fig. 1) early in the 20th century (1914–1915) and repeated early in the 21st century (2012–2017), when all sites had warmed by $\approx 1^\circ\text{C}$ (see Figs S1 and S2 in Supporting Information). Scots pine is the most prevalent tree species in Europe and one of the most widespread conifer species on Earth, and plays a considerable role in temperate and boreal carbon cycling as well as in providing vast ecosystem and economic services. In 2012, 2016 and 2017, we sampled Scots pine trees along the transect at 74 sites (Fig. 1 and Table S1). At each site we measured the average length and longevity of needles on mature trees (mean tree height ≈ 17 m, mean tree age ≈ 150 years old). We chose those sites and measures because a Swedish scientist, Nils Sylvén, measured those same

climate-sensitive traits at 57 sites along the same transect in 1914–1915 (Sylvén, 1917; Fig. 1 and Table S1). We hypothesised that the temperature rise over the 100-year interval

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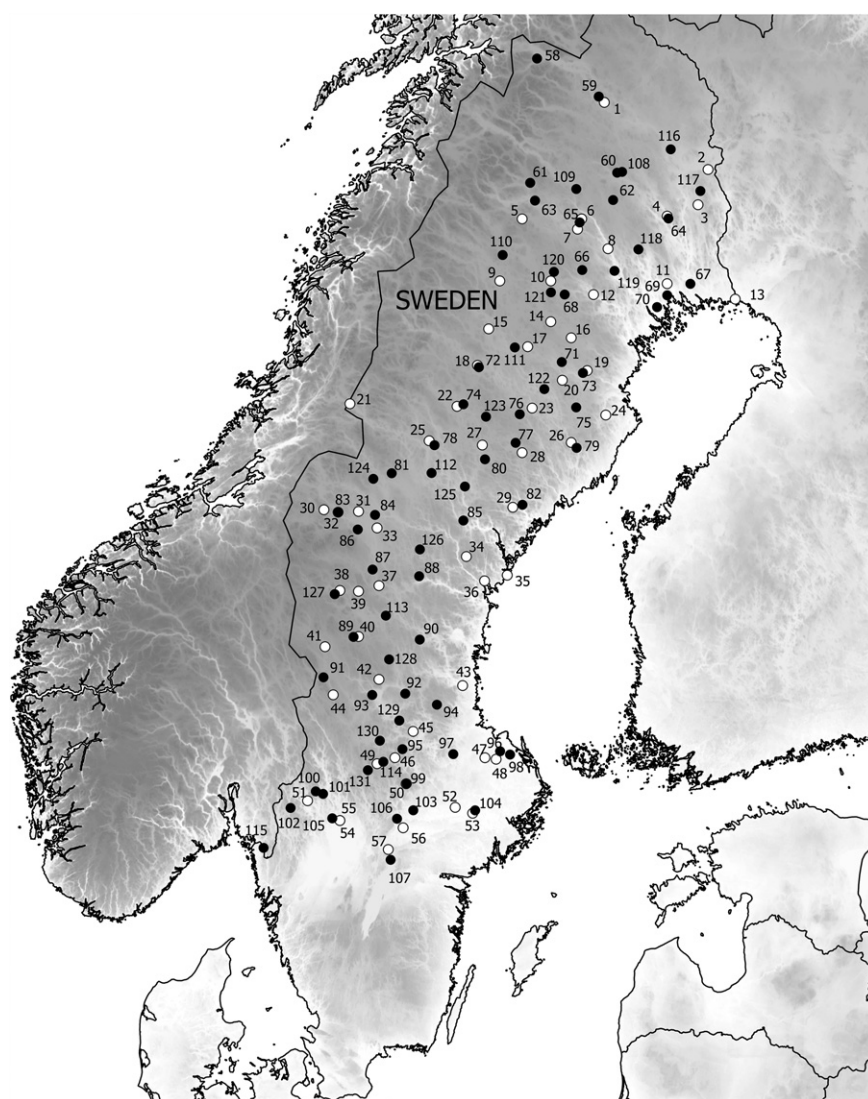


Figure 1 Map showing sites in Sweden sampled for needle traits in 1914–1915 (white) and 2012–2017 (black). See Table S1 for information about each site.

separating the sampling campaigns would increase needle length and reduce needle longevity, reflecting and reinforcing the stimulating effect of warming on tree growth at high latitudes.

METHODS

Field sampling strategy

In 2012–2017 we conducted three field sampling campaigns in Sweden, during which we visited 74 sites spaced over a ≈ 1000 -km transect. These sites were located in the vicinity of the 57 historical locations where in winter of 1914–1915 Scots pine branches were harvested for the assessment of needle length and longevity (Sylvén, 1917). Our goal was to compare the data from the two studies in relation to latitude and climate, therefore we recorded geographical coordinates (latitude, longitude and elevation) of all our sites based on GPS data and obtained coordinates for Sylvén's sites based on locality of the nearest church town (Sylvén, 1917). During

each trip, sites at different latitudes and longitudes were sampled in July and/or August (2012: day of year (DOY) 208–240, $n = 50$ sites; 2016: DOY 186–204, $n = 8$ sites; and 2017: DOY 222–239, $n = 16$ sites). The median sampling DOY was 225 (August 12). Autumn senescence of the oldest needle cohorts had not begun by any of those dates.

Tree growth measurement

In 2012 only, a 20 m by 20 m plot was established at each site and tree height was determined at each plot using the optical height meter PM-5/1520 (Suunto, Vantaa, Finland). Wood cores were extracted from two opposite directions at breast height from 18 trees per stand at 48 of the 50 stands using the Pressler's borer. Tree age was determined in laboratory along with the measurements of annual increment. Width of 30 most recent annual increments was taken to calculate annual radial growth rate (mm/year). Trees were on average older towards the north ($P = 0.015$, $R^2 = 0.11$) but age varied considerably among sites at any latitude. For example, southern

(< 58 °N) sites ranged from a mean of 75 to 250 years old and northern sites (> 66 °N) ranged from 80 to 330 years old. Height also varied geographically, with significant latitudinal decrease ($P = 0.0004$, $R^2 = 0.24$). Mean height averaged ≈ 22 m at the southernmost sites and ≈ 14 m at northernmost sites.

Determination of needle traits

Pole-pruners were used in 2012, 2016, and 2017 to cut branches (one 1–2 m long branch per tree) from sun-lit parts of the mid-crown of 25 mature trees at each site. The number of needle cohorts was counted on 10 twigs in each branch, with the fraction of the oldest cohort estimated to the nearest tenth. Needle length was measured for all needle age classes on each sampled branch, except the current-year needles. Needle length measurements were taken in the field shortly after collection using a computer-operated desktop scanner and a WinSeedle (Regent Instruments, Quebec, Canada) software, using 20 randomly picked needles from each cohort. Twenty-first century data on needle longevity and length from 14 of the 131 sites represented herein were included in a prior study (Jankowski *et al.*, 2017) as two of 30 morpho-anatomical needle traits.

To compare our data collected early in the 21st century (2012–2017) with data from 100 years earlier (Sylvén, 1917), a number of issues involving methodology and appropriate climate data were addressed. As noted above, our protocol was to count cohorts and measure needle length on branches in mid-canopy in mid- to late summer (July or August) whereas Sylvén's measurements were taken on branches harvested in mid- to late winter, when trees were harvested (Sylvén, 1917). As the needles of the oldest cohort typically senesce annually and the majority are shed in autumn (Portillo-Estrada *et al.*, 2013; Ukonmaanaho, 2013), we adjusted our measurements to account for the shedding of oldest cohort that would have occurred between our summertime sampling and the mid-winter sampling of Sylvén. Data for seven sites across Finland (roughly matching the climate span among our Swedish sites) show that an average of 57% of needles shed in the last 4 months of the year, with surprisingly negligible variation in this value among sites (minimum = 55%, max = 59%; Portillo-Estrada *et al.*, 2013; Ukonmaanaho, 2013). As the precise sampling date for Sylvén's samples is unknown, we therefore subtracted 0.57 from our needle cohort counts to account for this autumnal senescence and shedding. As another 8–10% of needles fall in the first two calendar months each year (Portillo-Estrada *et al.*, 2013; Ukonmaanaho, 2013; prior to mid-winter which is most likely date of sampling for Sylvén), but are not included in our adjustment, our adjustment is conservative.

Climate data

Given the role of climate in determining needle traits, we compare data from both surveys to recent site- and time-specific climate data. All climate data were collected by the Swedish Meteorological and Hydrological Institute. We obtained data for all weather stations north of 56 °N for all years from 1890 to 2018. To relate needle traits to climate, we use 5-year mean annual temperature (MAT_{5y}) and mean

annual precipitation (MAP_{5y}) data for each sampled site (numbers of weather stations varied somewhat from period to period, and for temperature versus precipitation, but averaged > 50). We use 5-year climate metrics as trees sampled in any given year would bear needles that were produced in a number of years (with needle length set the year the needle was produced) and the number of cohorts present in any given year also likely represents a multi-year response (Schoettle, 1990; Reich *et al.*, 2003; Pensa and Jalkanen, 2005; Reich *et al.*, 2014; Ľupek *et al.*, 2015). For data from 1914–1915 we use climate data for 1911–1915; for needle data sampled in 2012 we use climate data for 2008–2012; for data sampled in 2016 we use climate data for 2012–2016, etc.

Data analysis

We first developed regressions of weather station MAT_{5y} as a function of latitude, longitude and elevation, which we then applied to the sites sampled in the relevant time period. Note: we only use climate data for sites that had at least 3 years of full data of the relevant 5-year period. The relationships of MAT_{5y} to latitude, longitude and elevation were strong (R^2 averaged 0.97) for all four time periods (1911–1915, 2008–2012, 2012–2016 and 2013–2017), hence this appears to be a robust method of estimating site- and time-specific MAT_{5y} . MAP does not vary strongly in relation to latitude in Sweden, and thus regressions of MAP_{5y} on latitude, longitude and elevation explained at best a quite modest (R^2 averaged ≈ 0.25) amount of spatial variation in MAP_{5y} . Hence, instead of using those to predict MAP_{5y} we assigned each site where needle sampling occurred to the nearest weather station (average distance 34 km). We use these latter data for MAP_{5y} .

The 1000-km transect represents a striking temperature gradient in both time and space (Figs S1–S3). Precipitation varies weakly with geography (Fig. S4) and has increased over time (Fig. S1). Across the transect, MAT varies closely with latitude and elevation, and very weakly with longitude (Fig. S3), whereas MAP varies modestly with longitude, but not with latitude or elevation (Fig. S4). In our analyses we first related needle traits to site geography and time, and then explained those relations as a function of variation in space and time of climate drivers (MAT_{5y} and MAP_{5y}) that shape needle traits. Results were similar if different time periods were used to represent local climate (e.g. 10 years) or if different metrics (e.g. temperature and precipitation of the warmest quarter) were used (data and analyses not shown).

Several analyses of covariance models were applied to evaluate the effects and interactions of subsets of the following factors on needle length and longevity: time period (historical vs., modern), latitude, longitude, elevation, MAT_{5y} , MAP_{5y} , radial growth, tree height and stand age. \log_{10} transformations were used as they improved normality and the distributions of residuals, and linearised relations with geographic and climate data. All calculations were performed using the JMP Pro 14.2 software (SAS Institute, Cary, NC, USA).

RESULTS

Contrasts across time demonstrate a major shift in needle traits. Analyses of data from 1914–1915 and 2012–2017 (hereafter ≈ 1915 and ≈ 2015 for brevity) show that at any given latitude, modern plants growing in $\approx 1^\circ\text{C}$ warmer conditions have longer needles and shorter needle longevity than those a century ago (Fig. 2, Table 1). For example (and based on overall latitudinal regressions), at the mid-point in the transect, 64°N , modern plants have needle longevity that is shorter by 1.7 years, a decrease of 31%, and needle length that is longer by 4.7 mm, an increase of 14%. The change in needle longevity was similar (decrease $\approx 31\%$) along the transect, whereas needle length increase was smaller further south (increase of 9% at 59°N) and larger to the north (increase of 19% at 68°N).

Within both time periods, Scots pine needle length and needle longevity were strongly related to latitude (Fig. 2, Table 1), as predicted (Jalkanen *et al.*, 1995; Reich *et al.*, 2003; Pensa and Jalkanen, 2005; Reich *et al.*, 2014; Ľupek *et al.*, 2015). Needles in warmer, more southern locations were longer and had shorter lifetimes during both time periods (Fig. 2); likely in response to temperature (Table S2), and consistent with the parallel shifts in temperature and needle traits across the 100-year period.

Examining needle traits in relation to climate (Fig. 3) rather than latitude shows that for both needle traits recently experienced temperatures (MAT_{5y}) and time period (i.e. early 20th vs. early 21st century) were both highly significant ($P < 0.0001$; Table S2). Additionally, the effect of temperature on needle traits was similar across space and time, as the interaction of $\text{MAT}_{5y} \times \text{time}$ (period) was not significant (Table S2). MAP_{5y} was not significant as a main effect for either needle trait, although responses to MAT_{5y} were modestly influenced by MAP_{5y} (Table S2). The changes over time in needle length and longevity were coordinated; needle length and longevity were inversely correlated in both 1915 and 2015 (Fig. S5). Trees in 2015 tended to occupy positions of higher needle length and shorter longevity along a similar trait–trait axis as trees in 1915.

DISCUSSION

Our results indicate the importance of temperature as a driver of both needle traits. The overall temperature effect likely

Table 1 Analysis of covariance model of impacts of century (Time), latitude (Lat), elevation (Elev) and interactions on needle length and longevity (full model $R^2 = 0.740$ and 0.818 respectively)

Source of variance	(Needle length)		(Needle longevity)	
	<i>F</i>	<i>P</i> > <i>F</i>	<i>F</i>	<i>P</i> > <i>F</i>
Time	96.77	<0.0001	217.77	<0.0001
Lat	99.01	<0.0001	195.77	<0.0001
Elev	37.85	<0.0001	23.34	<0.0001
Time \times Lat	0.58	0.4493	1.22	0.2714
Time \times Elev	4.07	0.0457	0.36	0.5493
Lat \times Elev	11.99	0.0007	0.77	0.3818
Time \times Lat \times Elev	5.65	0.0190	3.22	0.0750

A model including longitude showed similar results and explained slightly more of the variance, but due to poorer values vis-à-vis AIC and BIC criteria, and inflated variance (latitude and longitude co-vary), that more complex model was not selected.

incorporates both direct (through temperature-mediated physiological responses) and indirect (e.g. variation in soil nutrient availability associated with temperature in boreal ecosystems) mechanisms (Reich and Oleksyn, 2004; van Sundert *et al.*, 2018). However, if temperature alone drove needle traits we would expect that recent 5-year temperatures would fully explain variance, eliminating time (century) as a significant variable (i.e. data for 2015 would migrate to higher temperatures along a shared regression relationship with 1915 data). In fact, responses to century-scale temperature rise were larger than would be predicted based on spatial responses to temperature, especially for needle longevity. This suggests that other factors (e.g. rising CO_2 levels, forest management, etc.) may play a role in the changes in needle trait values over the past century (see below).

Much of the observed spatial and temporal variation in needle traits is likely associated with variation in tree growth, because climatic influences on needle traits likely influence growth, and in turn, climate effects on growth also influence needle traits in a parallel direction (Schoettle, 1990; Reich *et al.*, 2003; Pensa and Jalkanen, 2005; Reich *et al.*, 2014). Needle traits that contribute to faster growth (Reich *et al.*, 2003; Reich *et al.*, 2014) tend to be enhanced in a warmer climate (Schoettle, 1990; Reich *et al.*, 2003; Pensa and Jalkanen,

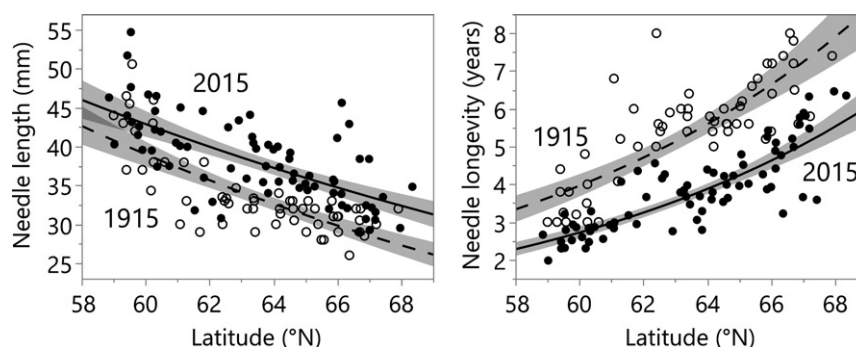


Figure 2 Needle traits versus latitude for data collected in 1914–1915 (1915, open circles, dashed lines) and 2012–2017 (2015, filled circles, solid lines). Fits are shown for logarithmic (ln basis) relationships of needle traits versus latitude, with accompanying 95% confidence intervals. R^2 ranged from 0.47 to 0.71 ($P < 0.0001$; equations shown in Table S3).

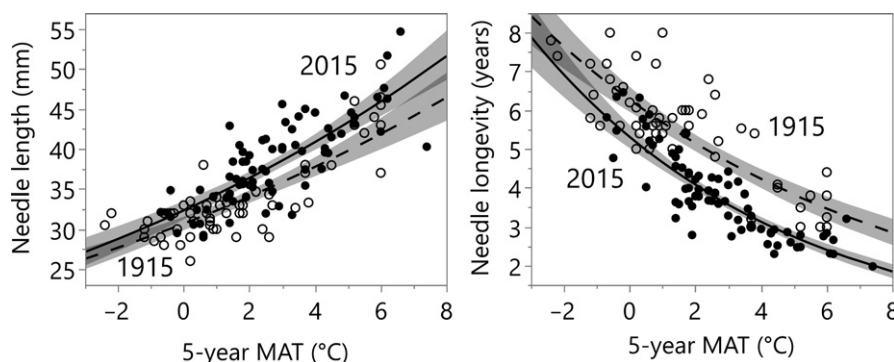


Figure 3 Needle traits versus most recent 5-year mean annual temperature (MAT_{5y}) relative to the year of sampling, for data collected in 1914–1915 (1915, open circles, dashed lines) and 2012–2017 (2015, filled circles, solid lines). Fits are shown for logarithmic (ln basis) relationships of needle traits versus MAT_{5y} , with accompanying 95% confidence intervals. R^2 ranged from 0.62 to 0.76 ($P < 0.0001$; equations shown in Table S3).

2005; Reich *et al.*, 2014; Ľupek *et al.*, 2015), and when trees grow faster, as is typical for boreal trees in warmer climates (Pensa and Jalkanen, 2005; Reich *et al.*, 2008; Henttonen *et al.*, 2014; Henttonen *et al.*, 2016), they replace needles more frequently, leading to reduced needle longevity and higher levels of associated traits like length or nitrogen concentration (Schoettle, 1990; Reich *et al.*, 2003; Pensa and Jalkanen, 2005; Reich *et al.*, 2014). Results of our study are consistent with these ideas. For trees sampled in 2012, the height and radial growth of trees decreased with latitude (data not shown) and temperature (Fig. S6), but were unrelated to variation in precipitation (data not shown). The higher growth rate in warmer sites is consistent with the greater needle length and shorter longevity at those sites as well. Moreover, for the data in this study, needle length and longevity were significantly related to both tree height and 30-year radial increment, both using raw data (Fig. S7) and also in analyses of covariance models after accounting for variation in stand age. The strong co-variation between needle traits, climate and growth rate, however, makes it difficult to disentangle their independent effects. Nonetheless, we posit that it is likely that warmer temperatures lead to higher growth rates, and that both contribute to longer needle length and faster turnover rate in southern than northern sites at any point in time and in 2015 than in 1915 at any given site; moreover, those shifts in needle traits in turn likely contribute to higher growth rates in more southerly than northerly sites and in 2015 versus 1915.

It is important to note that although shorter needle longevity can indicate stress, such as from air pollution (Kozlov and Niemelä, 1999), the typically shorter longevity of needles on faster growing trees in more favourable conditions is associated with a less conservative growth strategy and is an indication of the rate of whole-plant and foliar metabolism (Reich *et al.*, 2003; Ľupek *et al.*, 2015); for instance, climatic factors impact needle production, and it is thought that needle longevity varies in order to maintain constancy in the overall number of needles or length of foliated shoots (Schoettle, 1990; Pensa and Jalkanen, 2005). Thus reduced needle longevity over space or time in this study should not be considered a negative attribute or a stress response.

As noted above, if changing temperatures were entirely responsible for the large shifts over time in needle traits

documented in Fig. 2 – and assuming that relationships to temperature were identical across time as across space – the data from both time periods would be predicted to occupy a similar trait envelope in their relationship of traits to 5-year recent MAT. That is not the case (Fig. 3): even at a common experienced MAT, modern plants have slightly longer needles with considerably shorter lifetimes than plants in 1915. Thus, Scots pine needles have changed more in a century than would be expected solely due to rising temperatures. Other global and regional environmental change factors, and forest management, could have contributed to these century-scale changes in needle traits.

For example, rising CO_2 , increasing precipitation and nitrogen deposition could have simultaneously increased tree growth, needle length and needle turnover (decreasing needle longevity) beyond shifts attributable to temperature. That is because in addition to 21st century Sweden being warmer than in ≈ 1915 , it has also experienced higher nitrogen deposition and higher CO_2 as well as become rainier. Collectively, this environmental transformation would encourage higher pace-of-life traits and faster tree growth, potentially contributing to larger changes in needle length and needle longevity than predicted based solely on rising temperatures.

First, nitrogen deposition has increased in Sweden (Karlsson *et al.*, 2012), which could increase growth and needle N concentrations, both likely to be associated with longer needles and shorter needle lifespans (Schoettle, 1990; Reich *et al.*, 2003; Pensa and Jalkanen, 2005; Reich *et al.*, 2014). However, nitrogen deposition has not increased uniformly across Sweden (Karlsson *et al.*, 2012). Its highest levels and greatest geographic variation are in southern Sweden, largely outside the location of the region surveyed in our report, whereas the levels of nitrogen deposition are relatively low, with modest spatial variation, in northern Sweden. Thus, if nitrogen deposition was the main driving factor in increased growth and associated needle trait changes over the century, differences from ≈ 1915 to ≈ 2015 should have been negligible in the far north, and large further south, which was not the case (see Fig. 2). This suggests a modest role for nitrogen deposition in the century-scale changes observed in needle traits.

Second, rising CO_2 might also be increasing tree growth (Norby and Zak, 2011), which could contribute to the

observed shifts towards faster pace-of-life traits. However, elevated CO₂ tends to cause declining needle N concentration (Laitinen *et al.*, 2000), and common, strong inverse relationships between needle longevity and N concentration (Reich *et al.*, 2003; Reich *et al.*, 2014) suggest that rising CO₂ might indirectly increase, not decrease, longevity. In fact, the very few studies of leaf longevity with rising CO₂ (albeit with angiosperms, not gymnosperms) do suggest longer lifespan (Craine and Reich, 2001). Hence CO₂ might influence longevity in two off-setting ways, by increasing growth (which would tend to reduce needle longevity) and by decreasing N concentration (which would increase needle longevity). Whether these mechanisms were at work for Swedish pine and if so, which of these two mechanisms had greater impact are uncertain.

Third, increasing precipitation over the past 100 years hypothetically might have contributed to faster growth rate and thus to increasing needle length and decreasing longevity. In a drier region in Switzerland, irrigation resulted in increased needle length in Scots pine but had no effect on needle longevity (Feichtinger *et al.*, 2015). In our study, the nearly complete insensitivity of needle traits and tree growth to spatial or temporal variation in precipitation suggests that if important at all, precipitation was likely a very minor contributor to the observed century-scale changes in needle traits. This likely resulted from the study focus on a cold-limited and mesic biome; we do not suggest such effects would be immaterial in drier regions.

Finally, changes in forest management, including the use of genetically improved seed material (possibly included in our samples from Southern Sweden), higher stocking rates, improved drainage, less reliance on selective harvesting and improved regeneration techniques (Elfving and Tegnhammar, 1996; Henttonen *et al.*, 2016), have likely also increased productivity on average in Sweden over the past century, with those shifts in productivity potentially contributing to century-scale shifts in needle traits being larger than predicted based solely on spatial relations to temperature. For instance, analyses of Swedish and Finnish historical inventory data show increasing tree growth (Elfving and Tegnhammar, 1996; Henttonen *et al.*, 2016), with changing climate as well as changing management considered to have played important roles. However, as the trees we sampled were generally relatively old, in stands with modest, if any, active management, and were likely self-sown, impacts on changing forest management may have been limited in our data.

Uncertainty about the impacts of additional drivers suggests that interpretation of these results must be done carefully. The evidence clearly indicates that across Sweden, pine needles in the current era (≈ 2015) are longer and live shorter lifetimes than in ≈ 1915 , similar to needle traits of trees in warmer vs. colder regions during both periods. Evidence from within the two time periods, and across them, showing strong relations of needle traits to temperature, strongly suggests that spatial and temporal temperature variation likely is a major driver of the observed variation in both needle traits. Environmental changes in other drivers, such as nitrogen deposition, CO₂ and precipitation may have further increased (in the same direction) the magnitude of the changes in length and

longevity of pine needles, but the roles of each potential driver, and the magnitude of their impact, are uncertain.

Climate change-induced modification of the traits, growth rates and vitality of forests globally is almost certain, and as shown for Swedish pine forests, has begun in documentable fashion in high-latitude conifer forests. Needle traits, and how they adjust to changing climate, will help determine future forest productivity and carbon cycling (Gornish and Prather, 2014; Reich *et al.*, 2014). The century-scale shifts we observed in needle length and longevity likely correspond to parallel shifts in needle nitrogen concentration and photosynthetic and growth capacity that might enable trees and forests in high latitudes with generally cold climates and short growing seasons to grow faster and be more productive under today's elevated temperatures and CO₂ levels (Lloyd *et al.*, 2011; Reich *et al.*, 2003; Pensa and Jalkanen, 2005; Reich *et al.*, 2008; Reich *et al.*, 2014). Note, however, that such shifts are both less likely to have occurred and less likely to enhance Scots pine productivity in warmer areas of its range (Martínez-Vilalta *et al.*, 2008; Reich *et al.*, 2008; Lloyd *et al.*, 2011; Büntgen *et al.*, 2013; Hogg *et al.*, 2017). That is because increased drought and negative effects of heat associated with a changing climate can offset positive benefits of a longer growth season or warmer temperatures on Scots pine performance in locations in Spain and central Europe (Martínez-Vilalta *et al.*, 2008; Reich *et al.*, 2008; Büntgen *et al.*, 2013), and can be confounded by direct effects of rising CO₂. Hence, we should not presume that the needle trait shifts of conifers observed in cold, high-latitude forests (towards longer needles with short lifetimes) would parallel those in warmer, mid-latitude forests; if any prediction is supported, it is the opposite that slower growth and greater stress would lead to shorter needles with long lifetimes. We hope such evidence can be obtained by those working in such regions.

Historical data, as in the case described herein, can be invaluable for quantifying forest change and associated consequences for critical ecosystem services such as carbon storage, but is a rare resource, especially going back more than a few decades. Looking forward for the rest of this century, deploying all tools possible to detect forest change and to understand the underlying mechanisms, will be required to enable knowledge generation that can transfer to management at a rate that can keep up with the pace of environmental change and help maintain sustainable forests.

FUNDING INFORMATION

This research was supported by the National Science Center, Poland (2011/02/A/NZ9/00108).

ACKNOWLEDGEMENTS

The authors thank their home institutions for support in conducting this work. We thank A. Lisewska for assistance in the field.

AUTHORSHIP

JO and *PR* contributed equally but in distinct ways to this work. They jointly came up with the idea for this study. *JO* organised, supervised and participated in the field sampling and sample processing; *PR* analysed the data, and wrote the first and all subsequent drafts of the paper. *TW* participated in the field sampling and needle processing, and contributed to data analyses and interpretation, and to manuscript development and refinement. All the other authors participated in the field sampling and needle processing, and contributed to manuscript development and revision.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13587>.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: <https://doi.org/10.6084/m9.figshare.12622526.v1>

REFERENCES

- Barber, V.A., Juday, G.P. & Finney, B.P. (2000). Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, 405, 668–673. <https://doi.org/10.1038/35015049>.
- Büntgen, U., Martínez-Peña, F., Aldea, J., Rigling, A., Fischer, E.M., Camarero, J.J. *et al.* (2013). Declining pine growth in Central Spain coincides with increasing diurnal temperature range since the 1970s. *Global Planet. Change*, 107, 177–185. <https://doi.org/10.1016/j.gloplach.2013.05.013>.
- Craine, J.M. & Reich, P.B. (2001). Elevated CO₂ and nitrogen supply alter leaf longevity of grassland species. *New Phytol.*, 150, 397–403. (10.1046/j.1469-8137.2001.00116.x).
- Cudlín, P., Klop, M., Tognetti, R., Máliš, F., Alados, C.L., Bebi, P. *et al.* (2017). Drivers of treeline shift in different European mountains. *Clim. Res.*, 73, 135–150. <https://doi.org/10.3354/cr01465>.
- Elfving, B. & Tegnhammar, L. (1996). Trends of tree growth in Swedish forests 1953–1992: An analysis based on sample trees from the national forest inventory. *Scand. J. Forest Res.*, 11, 26–37. (10.1080/02827589609382909).
- Feichtinger, L.M., Eilmann, B., Buchmann, N. & Rigling, A. (2015). Trait-specific responses of Scots pine to irrigation on a short vs long time scale. *Tree Physiol.*, 35, 160–171. <https://doi.org/10.1093/treephys/tpu114>.
- Gornish, E.S. & Prather, C.M. (2014). Foliar functional traits that predict plant biomass response to warming. *J. Veg. Sci.*, 25, 919–927. <https://doi.org/10.1111/jvs.12150>.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.*, 12, 1040–1049. <https://doi.org/10.1111/j.1461-0248.2009.01355.x>.
- Henttonen, H.M., Mäkinen, H., Heiskanen, J., Peltoniemi, M., Laurén, A. & Hordo, M. (2014). Response of radial increment variation of Scots pine to temperature, precipitation and soil water content along a latitudinal gradient across Finland and Estonia. *Agr. Forest Meteorol.*, 198–199, 294–308. <https://doi.org/10.1016/j.agrformet.2014.09.004>.
- Henttonen, H.M., Nöjd, P. & Mäkinen, H. (2016). Environment-induced growth changes in the Finnish forests during 1971–2010 – An analysis based on National Forest Inventory. *Forest Ecol. Manag.*, 386, 22–36. <https://doi.org/10.1016/j.foreco.2016.11.044>.
- Hisano, M., Chen, H.Y.H., Searle, E.B. & Reich, P.B. (2019). Species-rich boreal forests grew more and suffered less mortality than species-poor forests under the environmental change of the past half-century. *Ecol. Lett.*, 22, 999–1008. <https://doi.org/10.1111/ele.13259>.
- Hogg, E.H., Michaelian, M., Hook, T.I. & Undershultz, M.E. (2017). Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. *Glob. Change Biol.*, 23, 5297–5308. <https://doi.org/10.1111/gcb.13795>.
- Jalkanen, R., Aalto, T. & Kurkela, T. (1995). Development of needle retention in Scots pine (*Pinus sylvestris*) in 1957–1991 in northern and southern Finland. *Trees*, 10, 125–133. <https://doi.org/10.1007/BF00192193>.
- Jankowski, A., Wyka, T.P., Żytkowiak, R., Nihlgård, B., Reich, P.B. & Oleksyn, J. (2017). Cold adaptation drives variability in needle structure and anatomy in *Pinus sylvestris* L. along a 1900 km temperate-boreal transect. *Funct. Ecol.*, 31, 2212–2223. (10.1111/1365-2435.12946).
- Karlsson, G.P., Hellsten, S., Karlsson, P.E., Akselsson, C. & Ferm, M. (2012). Kvävedepositionen till Sverige: jämförelse av depositionsdata från Krondroppsnätet, Luft- och nederbördskemiska nätet samt EMEP. IVL rapport B 2030, Svenska Miljöinstitutet.
- Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115, 445–459. <https://doi.org/10.1007/s004420050540>.
- Kozlov, M.V. & Niemelä, P. (1999). Difference in needle length - a new and objective indicator of pollution impact on Scots pine (*Pinus sylvestris*). *Water Air Soil Poll.*, 116, 365–370. (10.1023/A:1005213917615).
- Laitinen, K., Luomala, E.M., Kellomäki, S. & Vapaavuori, E. (2000). Carbon assimilation and nitrogen in needles of fertilized and unfertilized field-grown Scots pine in natural and elevated concentrations of CO₂. *Tree Physiol.*, 20, 881–892. <https://doi.org/10.1093/treephys/20.13.881>.
- Lloyd, A.H., Bunn, A.G. & Berner, L. (2011). A latitudinal gradient in tree response to climate warming in the Siberian taiga. *Global Change Biol.*, 17, 1935–1945. <https://doi.org/10.1111/j.1365-2486.2010.02360.x>.
- Martínez-Vilalta, J., López, B.C., Adell, N., Badiella, L. & Ninyerola, M. (2008). Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global Change Biol.*, 14, 2868–2881. <https://doi.org/10.1111/j.1365-2486.2008.01685.x>.
- Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U. *et al.* (2010). Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.*, 15, 684–692. <https://doi.org/10.1016/j.tplants.2010.09.008>.
- Norby, R.J. & Zak, D.R. (2011). Ecological lessons from Free-Air CO₂ Enrichment (FACE) experiments. *Annu. Rev. Ecol. Evol. Syst.*, 42, 181–203. <https://doi.org/10.1146/annurev-ecolsys-102209-144647>.
- Pensa, M. & Jalkanen, R. (2005). Variation in needle longevity is related to needle-fascicle production rate in *Pinus sylvestris*. *Tree Physiol.*, 25, 1265–1271. (10.1093/treephys/25.10.1265).
- Portillo-Estrada, M., Korhonen, J.F.J., Pihlatie, M., Pumpanen, J., Frumau, A.K.F., Morillas, L. *et al.* (2013). Inter- and intra-annual variations in canopy fine litterfall and carbon and nitrogen inputs to the forest floor in two European coniferous forests. *Ann. Forest Sci.*, 70, 367–379. (10.1007/s13595-013-0273-0).
- Reich, P.B. & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl Acad. Sci. U.S.A.*, 101, 11001–11006. (10.1073/pnas.0403588101).
- Reich, P.B. & Oleksyn, J. (2008). Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecol. Lett.*, 11, 588–597. <https://doi.org/10.1111/j.1461-0248.2008.01172.x>.
- Reich, P.B., Rich, R.L., Lu, X., Wang, Y.-P. & Oleksyn, J. (2014). Biogeographic variation in evergreen conifer needle longevity and impacts on boreal carbon cycle projections. *Proc. Natl Acad. Sci. USA*, 111, 13703–13708. <https://doi.org/10.1073/pnas.1421130111>.
- Reich, P.B., Sendall, K.M., Stefanski, A., Rich, R.L., Hobbie, S.E. & Montgomery, R.A. (2018). Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature*, 562, 263–267. <https://doi.org/10.1038/s41586-018-0582-4>.

- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. *et al.* (2003). The evolution of plant functional variation: traits, spectra, and strategies. *Int. J. Plant Sci.*, 164(3 Suppl.), S143–S164. <https://doi.org/10.1086/374368>.
- Schoettle, A.W. (1990). The interaction between leaf longevity and shoot growth and foliar biomass per shoot in *Pinus contorta* at two elevations. *Tree Physiol.*, 7, 209–214. (10.1093/treephys/7.1-2-3-4.209).
- Swedish Meteorological and Hydrological Institute. Available at: <https://www.smhi.se/data> Last accessed 01.07.2020.
- Sylvén, N. (1917). Den nordsvenska tallen. *Meddelanden från Statens Skogsförsöksanstalt*, 13–14, 9–110. https://pub.epsilon.slu.se/10288/1/medd_statens_skogsforskningsanst_013-14_bd1_03.pdf.
- Župek, B., Mäkipää, R., Heikkinen, J., Peltoniemi, M., Ukonmaanaho, L., Hokkanen, T., *et al.* (2015). Foliar turnover rates in Finland — comparing estimates from needle-cohort and litterfall-biomass methods. *Boreal Environ. Res.*, 20, 283–304. <http://hdl.handle.net/10138/165220>.
- Ukonmaanaho, L. (2013). Litterfall production and quality at Level II sites in Forest Condition Monitoring in Finland – National report. Editors Merilä, P., S. Jortikka, S. The Finnish Forest Research Institute. [Online report available at: <http://www.metla.fi/metinfo/forest-condition/intensive-monitoring/litterfall.htm>].
- Van Sundert, K., Horemans, J.A., Stendahl, J. & Vicca, S. (2018). The influence of soil properties and nutrients on conifer forest growth in

- Sweden, and the first steps in developing a nutrient availability metric. *Biogeosciences*, 15, 3475–3496. <https://doi.org/10.5194/bg-15-3475-2018>.
- Weiser, G., Oberhuber, W. & Gruber, A. (2019). Effects of climate change at treeline: lessons from space-for-time studies, manipulative experiments, and long-term observational records in the Central Austrian Alps. *Forests*, 10, 508. <https://doi.org/10.3390/f10060508>.
- Wright, I.J., Dong, N., Maire, V., Prentice, I.C., Westoby, M., Díaz, S. *et al.* (2017). Global climatic drivers of leaf size. *Science*, 35, 917–921. <https://doi.org/10.1126/science.aal4760>.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Josep Penuelas

Manuscript received 21 April 2020

First decision made 13 June 2020

Manuscript accepted 5 July 2020