



## Partly decoupled tree-ring width and leaf phenology response to 20th century temperature change in Sweden



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### ABSTRACT

The recent warming trend, and associated shifts in growing season length, challenge the principle of uniformitarianism, i.e., that current relations are persistent over time, and complicates the uncritical inferences of past climate from tree-ring data. Here we conduct a comparison between tree-ring width chronologies of *Pinus sylvestris* L. (Scots pine), *Picea abies* (L.) Karst. (Norway spruce) and *Betula pubescens* Ehrh. (Downy birch) and phenological observations (budburst and leaf senescence) of *Fagus sylvatica* L. (European beech), *Quercus robur* L. (European oak), *Betula* sp. (Birch), Norway spruce and Scots pine) in Sweden to assess to what extent the tree-ring width–temperature relationship and the timing of phenological phases are affected by increased temperature. Daily meteorological observations confirm a prolongation of the thermal growing season, most consistently observed as an earlier onset of around 1–2 weeks since the beginning of the 20th century. Observations of budburst closely mimic this pattern, with budburst of the deciduous trees occurring 1–2.5 weeks earlier. In contrast to the changes seen in phenology and observational temperature data, the tree-ring width–temperature relationships remain surprisingly stable throughout the 20th century. Norway spruce, Scots pine and Downy birch all show consistently significant correlations with at least one 30 day-long window of temperature starting in late June–early July season. Norway spruce displays the largest degree of stability, with a consistent 60 day-long temperature window with significant correlation starting around Julian calendar day 150. Thus, our results suggest that the principle of uniformitarianism is not violated during the period covered by modern meteorological observations. Further research is needed to determine at what thresholds the temperature sensitivity of these species may alter or deteriorate as a consequence of the ongoing climate change.

### 1. Introduction

The growing season temperature is the most critical factor for tree growth in high latitude and altitude forests, which are characterized by short, and often cool, growing seasons. Near the tree line, the temperature during just a few weeks around summer solstice can explain up to half of the ring-width variance for species like *Pinus sylvestris* L. (Scots pine) and *Picea abies* (L.) Karst. (Norway spruce) (Kaczka et al., 2015;

Linderholm et al., 2010; Rocha et al., 2021; Vaganov et al., 1999). It is thus a reasonable assumption that the projected climate warming (IPCC, 2021) would lead to increased growth as a general tendency, or alternatively, that an altered temperature sensitivity may emerge (Peltier and Ogle, 2020; Wilmking et al., 2020), complicating the uncritical use of tree-ring data for climate reconstructions. This may, also, have consequences for the ecology of the tree line habitats, where the tree line likely will climb with longer and/or warmer growing seasons (Esper and

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(Schweingruber, 2004; Kullman, 2015). Indeed, the past century, have seen a consistent rise of tree lines for pine, spruce and birch averaging 70–90 m in the southern Swedish Scandes (c. 63–65° N).

Meteorological measurements of high quality are prevalent in northern Europe extending back to the 19th century (Brönnimann et al., 2019). Some of the longest daily temperature observations in the world derive from this region (e.g., Central England 1659– CE, De Bilt, the Netherlands 1706– CE, and Uppsala, Sweden 1722– CE). From these and other records, we know that surface air temperature has increased in the region, as in most other parts of the world, since the end of the Little Ice Age (c. 1850), and in particular since the 1980s (IPCC AR6). This warming has been stronger in winter and spring than in summer and autumn in northern Europe (Twardosz et al., 2021). The warming trends in winter and spring are to a large degree determining the increase in the annual mean temperature (Pfister and Wanner, 2021). These trends are steeper in northern Europe than the global average as a result of the Arctic amplification effect (Hind et al., 2016; Serreze and Barry, 2011). Regional annual mean temperature is now around 2 °C higher than it was in the mid-19th century, corresponding to a rate of warming approximately twice as large as the global average (SMHI, 2022; IPCC, 2021). Fennoscandia is moreover home of some of the most prominent tree-ring width-based temperature reconstructions covering the entire, or most of, the Common Era (Grudd et al., 2002; Helama et al., 2002; Kirchhefer, 2001, Linderholm and Gunnarson, 2005, Svarva et al., 2018). The combination of long high-quality meteorological observations recording a pronounced and persistent warming, together with some of the most summer temperature-sensitive trees in the world (Esper et al., 2016; St. George, 2014) makes tree line forests of this region suitable, as well as relevant, testing grounds to study the stability of the temperature response of trees.

The timing of spring events in mid- to high-latitude plants, such as budding, leafing and flowering, is mainly regulated by temperatures after the dormancy is released, and several studies have found significant correlations between spring phases and air temperatures (Chmielewski and Rötzer, 2002; Chmielewski et al., 2004; Menzel and Fabian, 1999; Sparks and Menzel, 2002; Wielgolaski, 1999). As a result of the recent temperature increase, the season warm enough for plant growth is prolonged. The climatological growing “season” can be viewed as the entire period in which growth can theoretically take place, and should be distinguished from the growing “period”, which is the period of actual growth (Carter, 1998). There are a number of ways to define the growing season length, one definition is the period between the date of the last spring frost and first autumn frost (e.g. Robeson, 2002). Other investigations have used threshold temperatures in a predefined number of days to start and end the growing season. In this study, we adopt the latter approach, the start/end of the growing season is here determined from the first/last four consecutive days of the year when the daily mean temperature has remained above/below 5 °C (a definition frequently used by the Swedish Meteorological and Hydrological Institute, SMHI). The start date of the growing season is thus the first day and the end date is the last day of these four days long periods. The physiological significance of this period naturally differs among plant types, but is at high latitudes, likely relevant to perennial plants that are exposed to the weather throughout the year (e.g., trees and shrubs) (Carter, 1998).

The thermal growing season has been prolonged considerably since the beginning of the 1900s. Walther and Linderholm (2006) found that the thermal growing season has extended in Sweden and regions at similar latitudes surrounding the Greater Baltic Area over the 20th century, with, on average, a 12 days earlier onset and an 8 days delayed end. Furthermore, direct observations of plant seasonal activity (i.e., the phenology) has a long history in Sweden as well as in the rest of Europe. Documented observations of budburst and leaf coloring exist episodically from the end of the 19th century throughout the study area. These and other phenological evidence have been used in prior studies to demonstrate a close coherence between recent changes in leaf phenology and observed tendencies in climatological growing season

changes (e.g., Abu-Asab et al., 2001, Chmielewski et al., 2004, Olsson et al., 2013, Rötzer and Fm, 2001). However, during recent decades an apparent reduced temperature sensitivity of spring leaf phenology of temperate deciduous trees has emerged. A diminishing effect of additional increase in temperature, suggests that other constraints, such as photoperiod, instead increasingly acts as limiting factor (Fu et al., 2015).

In high-latitude forests where trees are dormant during winter, reactivation of the cambium occurs in spring when new cells start to form, followed by expansion of the cells, giving rise to radial growth of the trees. The rate of radial growth and the duration of cambial activity will determine tree-ring the width the annual tree-ring. The radial growth rate starts slowly and then gradually increases, typically following an s-shaped curve, where maximum growth is obtained around summer solstice (Carrer et al., 2017; Henttonen et al., 2009). Cell division ends for the season when the temperature still is relatively high, several degrees higher than for which it was initiated, hence the secondary growth are skewed towards the early part of the thermal growing season (Cuny et al., 2015, Rossi et al., 2008). Importantly, the timing of xylogenesis in relation to leaf phenology varies substantially for different species. Ring-porous species initiate its growth early in the season, where oak trees, for instance, build up much of its tree-ring even before budburst (Zweifel et al., 2006). For diffuse porous species (e.g., *Fagus sylvatica* (European beech), *Betula* sp. (Birch)) the start of xylogenesis is more synchronized with budburst and the duration of growth is considerable shorter than for both ring-porous and the non-porous (e.g., Scots pine and Norway spruce). As growth before budburst indicate, trees exhibit varying degrees of ecological memory where growth may be influenced by conditions of the previous season and may even be affected by conditions several years back in time (e.g. Zweifel and Sterck, 2018).

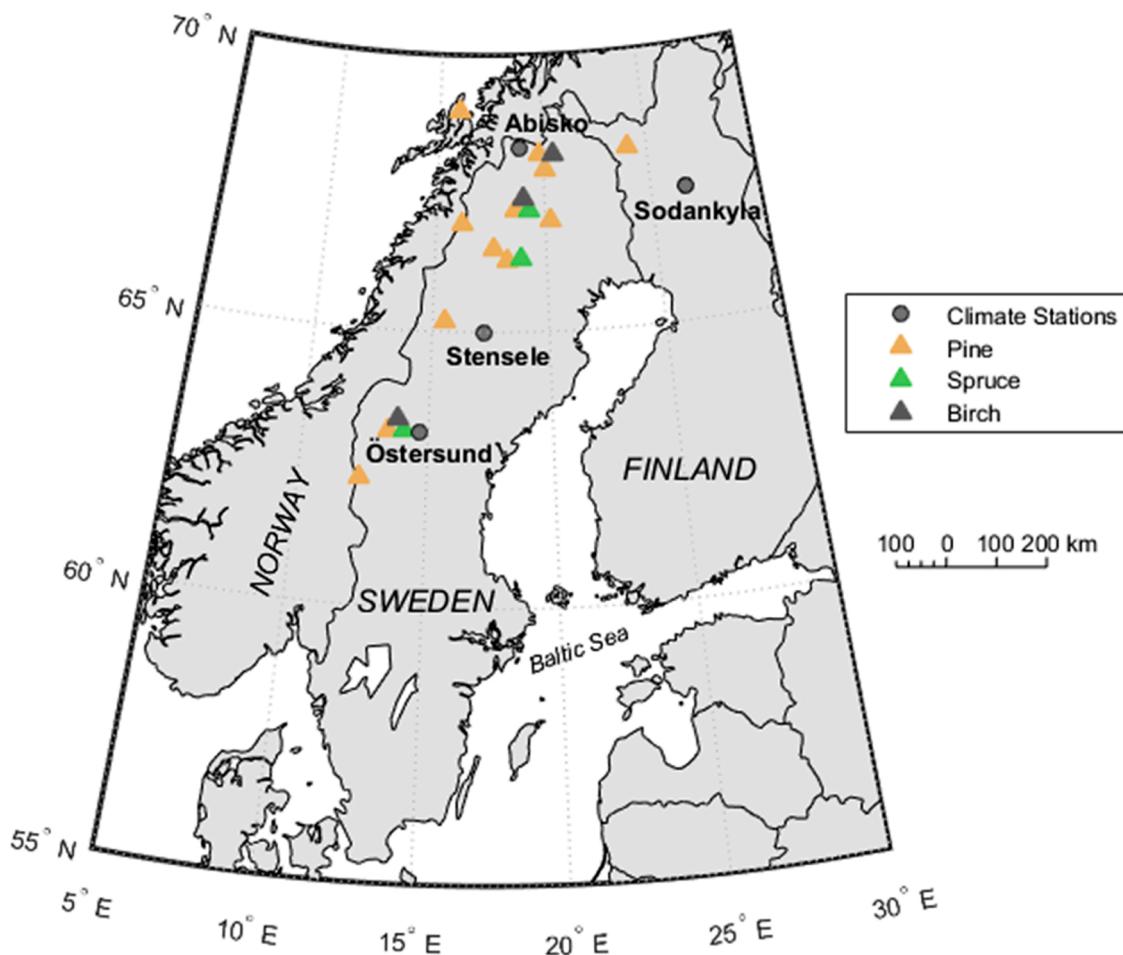
In this study we build on prior studies by making a synthesis of dendrochronological ring-width measurements and a regional-scale network of phenological observations in order to examine to what extent the observed changes in temperature and leaf phenology since the late 19th century are mirrored in the tree-ring increments of Scots pine and Norway spruce, and Downy birch. In particular, we will focus on the period of the year when tree-ring width correlates most strongly with temperature. We use tree-ring dataset from sites from high-latitude and/or tree-line locations, where growing season temperatures constitute the main limiting factor to tree growth. Thus, the strongest imprint of temperature will occur during the summer months regardless of the species. Specifically, we will focus on the following four questions: (i) Are there any changes in the seasonality and the strength of the tree-ring width response to temperature over the 20th century? And if so, (ii) are there any changes between the three tree species, and (iii) how does this relate to changes in leaf phenology and thermal growing season?

## 2. Method

### 2.1. Study region

Most of Sweden has a tempered and relatively mild climate considering its latitudinal location (c. 55–69°N), which is largely due to its proximity to the Gulf Stream in the North Atlantic and the prevailing westerlies in the region. In the south, where the maritime influence is most pronounced, mean winter temperatures hover around 0 °C and in the north around –15 °C. During summer, the north–south temperature gradient is more modest; the warmest month (July) ranging between 15 and 18 °C for the whole country except the mountains. Annual mean precipitation in Sweden varies from less than 400 mm to up to 2000 mm. A wide variety of deciduous trees thrives in the south, including beech and oak, which grows up until approximately 60°N. Scots pine, Norway spruce and various types of birch trees grow throughout most of the country.

Most available temperature-sensitive tree-ring width chronologies from Sweden, that have previously been used to reconstruct past



**Fig. 1.** Map of the study region showing the location of the climate stations used in the study and the sampling sites, for each tree species.

temperature variability, have been sampled in or near the Scandes mountain range. The Scandes stretches in a south–north direction through eastern Norway and western Sweden, and creates a kind of natural border between Sweden and Norway from around 60°N up to the northernmost tip of Sweden (69°N), where it bends eastwards toward Finland. For the most part, the range reaches up to 1000–2000 m a.s.l., although around 62–64°N, the topography is less pronounced. The Scandes forms a barrier against the marine influences from the North Atlantic and contributes to a more continental character of the climate in northern Sweden, marked by relatively large differences between summer and winter temperature and with moderate precipitation compared to the Norwegian side of the mountain range. The Scandes region falls in the boreal, alpine, and Arctic alpine ecotones with the treeline ranging between approximately 1100 m a.s.l. in the south and 600 m a.s.l. in the north.

## 2.2. Meteorological data

Daily air temperature data were used. We specifically selected observation records for the climate-response analysis and the examination of thermal growing season changes that (1) extended as far back in time as possible, and (2) were located in a near proximity to the tree-ring sampling sites. Four meteorological stations fulfilled these criteria and were included: Östersund (1918–), Stensele (1891–), Abisko (1913–), and Sodankylä (1908–) (Fig. 1). The coordinates and the elevation of the stations are provided in Table 1. We note that all the stations are located less than 200 km from the tree-ring sites, which is well within the decorrelation decay distance for temperature in the area (i.e., the temperature at the sampling sites are strongly correlated with

the temperature at the climate stations) (Büntgen et al., 2010; Jones et al., 1997). In cases where the sites are located midway between two climate stations an arithmetic mean of these temperature series has been used (Table 1).

## 2.3. Ring-width chronologies

Ring-width chronologies were compiled from the three most common tree species in the mountainous region of Sweden: Scots pine, Norway spruce and Downy birch. Data from 11 different sites ranging from the geographical center of Sweden (latitude 62.2°N) to the northernmost parts of Sweden, Norway and Finland (latitude 68.9°N), were included in the assessment (Table 1).

Previously unpublished ring-width data were measured using a stereomicroscope and a Lintab measurement table connected to the Time Series Analysis Program (TSAP) software (RinnTech, Heidelberg, Germany). Prior to measurements, the samples were prepared and cross-dated according to standard dendrochronological procedures (Stokes and Smiley 1968). The crossdating of the ring-width measurements was later checked statistically in the COFECHA software (Holmes, 1983).

Trends in the tree-ring data were removed by first-differencing the data before creating chronologies as arithmetic means of the tree-ring indices. Statistics such as Expressed Population Signal (EPS) (Wigley et al., 1984) were used to assess robustness of each chronology during the relevant period of analysis. EPS values for all the retained chronologies were > 0.85 during the period of analysis. A preliminary climate calibration furthermore confirmed that all the chronologies correlated positively and significantly ( $p < 0.05$ ) with temperature during one or several months during the summer season and were thus relevant to

**Table 1**

Location and altitude of tree-ring width sites and climatic stations with daily data used in the study. If two stations are specified for the same tree-ring site (i.e., as for the NScan PISY chronology), the climate response analysis for this site has been based on an arithmetic mean of these two stations.

Sites Coordinates Elevation	Species	References	Meteorological station Coordinates Elevation
Torneträsk BEPU 68.33°N, 18.8°E 350–450 m.a.s.l.	<i>Betula pubescens</i> Ehrh. (Downy birch)	Hoogesteger (2008) (updated for this study)	Abisko 68.36°N, 18.82°E 388 m.a.s.l.
Torneträsk PISY 68.2°N 19.6°E 350–450 m.a.s.l.	<i>Pinus sylvestris</i> L.	Unpublished	Abisko 68.36°N, 18.82°E 388 m.a.s.l.
NScan PISY 66–69°N, 19–32°E 140–450 m.a.s.l.	<i>Pinus sylvestris</i> L.	Esper et al. (2012)	Abisko/Sodankyla 68.36°N, 18.82°E/ 67.4°N, 26.6°E 388/179 m.a.s.l.
Forfjordalen PISY 68.79°N, 15.73°E 40–160 m.a.s.l.	<i>Pinus sylvestris</i> L.	Kirchhefer (2001); McCarroll et al. (2013)	Abisko
Ultevis PISY 67.2°N 18.6°E c. 600 m.a.s.l.	<i>Pinus sylvestris</i> L.	Unpublished	Stensele/Abisko 68.36°N, 18.82°E/ 65.2°N, 17.2°E 388/325 m.a.s.l.
Ultevis PCAB 67.2°N 18.6°E c. 600 m.a.s.l.	<i>Picea abies</i> L. Karst	Unpublished	Stensele/Abisko
Ultevis BEPU 67.2°N 18.6°E C. 600 m.a.s.l.	<i>Betula pubescens</i> Ehrh.	Unpublished	Stensele/Abisko
Muddus PISY 66.5°N 20.2°E, C. 450 m.a.s.l.	<i>Pinus sylvestris</i> L.	Unpublished	Stensele/Abisko
Tjeggelvas PISY 66.6°N 17.6°E 460–580 m.a.s.l.	<i>Pinus sylvestris</i> L.	Gunnarson et al. (2012)	Stensele/Abisko
Arjeplog PISY 66.3°N 18.2°E 500–700 m.a.s.l.	<i>Pinus sylvestris</i> L.	Unpublished	Stensele
Arjeplog PCAB 66.2°N 18.1°E 500–700 m.a.s.l.	<i>Picea abies</i> (L.) H. Karst.	Unpublished	Stensele
Ammarnäs PISY 65.9°N 16.1°E 400–600 m.a.s.l.	<i>Pinus sylvestris</i> L.	Unpublished	Stensele/Abisko
Kittelfjäll PISY 65.2°N 15.5°E 530–600 m.a.s.l.	<i>Pinus sylvestris</i> L.	Unpublished	Stensele
Jämtland PISY 63.2°N 13.5°E c. 700 m.a.s.l.	<i>Pinus sylvestris</i> L.	Rocha et al. (2021)	Östersund 63.2°N, 14.5°E 376 m.a.s.l.
Jämtland PCAB 63.2°N 13.5°E c. 700 m.a.s.l.	<i>Picea abies</i> (L.) H. Karst.	Rocha et al. (2021)	Östersund
Jämtland BEPU 63.2°N 13.5°E C. 700 m.a.s.l.	<i>Betula pubescens</i> Ehrh.	Unpublished	Östersund
Rogen PISY 62.2°N, 12.2°E 900 m.a.s.l.	<i>Pinus sylvestris</i> L.	Fuentes et al. (2017)	Östersund

include in the more detailed daily-resolved analyses described below.

#### 2.4. Phenological observations

In the study we also used data on leaf phenology. Phenology can be defined as: “the study of the timing of recurring biological phases, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species” (Lieth, 1974). The data used in this study is compiled by the Swedish National Phenology Network (SWE-NPN) (<http://www.swe-npn.se>), coordinated

by the Swedish University of Agricultural Sciences (Langvall & Dahl, 2019). The most recent version of this data set extends to the year 2021, and has been obtained for this study by the Superintendent of the Unit for Field-based Forest Research at Swedish University of Agricultural Sciences (personal communication, Langvall, 2021–10–27).

Observations included the timing (day of the year, DOY) of budburst and autumn-colored leaves observed for the following species: *Betula pendula* (Silver birch), *Betula pubescens* (Downy birch), European beech, Norway spruce, Scots pine and European oak. In large parts of the dataset no distinction is made between different subspecies, and it is common with hybrids in the genus of *Betula* (Olsson et al., 2013). For our analyses, we combined the observations of Downy birch, Silver birch and unspecified subspecies of birch, which are henceforth denoted as *Betula* sp. The dataset consists of a longer historical subset (1873–1951) and a shorter modern subset (2008–2021). The historical dataset comprises a total of 13,633 observations from 634 unique locations throughout Sweden, with a majority of the observations made in the 19th century, and a sharp decline of observations in the 1920 s. The modern-day observations consist of 18,555 observations from 6867 unique locations. These modern-day data are more specific as the observers also have estimated how much of the tree was budded or had autumn-colored leaves. The phenological observations are to a large extent conducted by volunteers, which may raise concerns regarding uncertainties and errors in the data. However, as we used averages of large amounts of data in our analysis, the issue of random errors should be mitigated and reflect “true” central tendencies in terms of long-term trends in the phenological phases (henceforth phenophases).

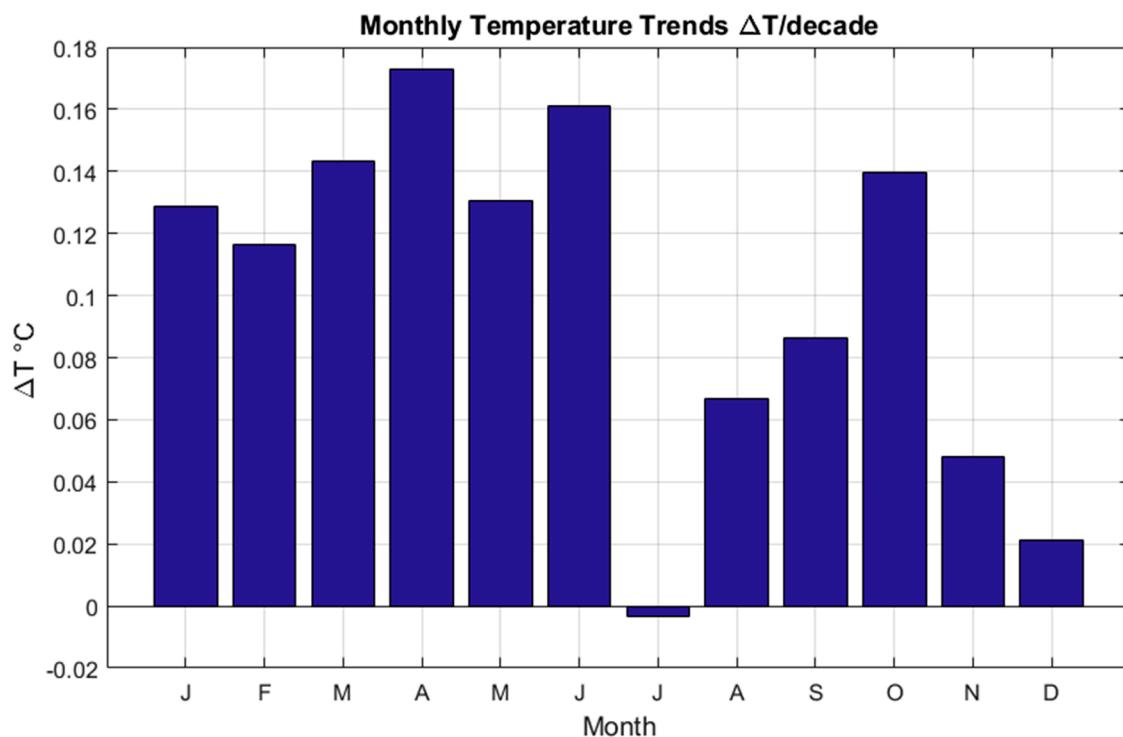
#### 2.5. Statistical analysis

Information of growing season changes for the last century were obtained by using (i) calculations based on meteorological measurements, and (ii) phenological observations of budburst and leaf coloring. These results were compared to temperature signals of the tree-ring width series, and possible changes in their strength and temporal stability.

The tree-ring sites are in most cases located at higher altitude than the climate stations used in this study (on average approximately 150 m higher). A correction (spanning the range 0.6–1 °C/100 m), based on the altitudinal difference between each individual tree-ring site and the corresponding meteorological station, was applied to the temperature data before determining the thermal growing season trends for individual sites (Fig. A3). While this correction does not affect the correlation analysis, it is crucial to consider when examining absolute temperatures and the length of the thermal growing season.

Changes in the phenophases have been examined for three sub-regions based on latitude: southern (<60°N), central (60–64°N) and northern (>64°N) Sweden. The number of data points and its geographical location varies considerably over time, which may affect year-to-year variability. Therefore, the data are averaged into 5-year segments, which gives a more accurate representation of the general tendencies and also provides a better visual overview of temporal and geographical characteristics. Moreover, 5-year segments based on less than 15 data points have been excluded from the analysis, while the linear trends are based on all data points (Fig. 3). A t-test was conducted to determine if there are any significant differences in the timing of the two phenophases between the historical data (1873–1951 period) as a whole, compared to the recent (2008–2021) period. Moreover, spatial variations in the timing of the two phenophases, and changes between the historical and modern time data were also examined by mapping (0.1 × 0.1° resolution) and spatially interpolating the phenological data. As the historical period after c. 1925 has few observations, the period 1926–1951 was excluded prior to spatial interpolation. All calculations were conducted in the MATLAB software.

Running correlations are frequently used to explore the stability of climate signals in tree-ring chronologies. Conventionally, this would be



**Fig. 2.** Linear trends of monthly temperature, over the 1918–2015 period, from the Abisko, Sodankyla, Stensele and Östersund stations. The station observations have been averaged prior to trend computation. For temperature series from each climate station, see Fig. A4 in the Appendix.

**Table 2**

Changes in the thermal growing season (defined as four consecutive days with daily mean temperature =  $> 5^{\circ}\text{C}$ ), were estimated by fitting a linear regression to all thermal growing season start and end dates between 1918 and 2015. The difference between the endpoints were considered as the change in the growing season start and end. The column to the right refers to the change in days in the length of the growing season (LGS).

Station	Start	End	Change LGS
	1918	2015	1918–2015
Abisko	140	132	267
Sodankyla	132	124	266
Stensele	130	117	276
Östersund	114	107	288

done on individual or aggregated calendar months. However, the timing of the growing season is a dynamical phenomenon that closely reflects the environmental conditions. Thus, limiting the analysis to a monthly timescale may limit the possibilities to discern any potential changes. Therefore, instead of using fixed calendar months, we conducted a moving window correlation analysis of the tree-ring time-series with daily temperature data averaged into 30-day segments (31-years in length) where the start date of the aggregation was moved one day at a time throughout the year (*sensu* Jevšenak and Levanič, 2018). This methodology allowed us to distinguish temporal shifts in the tree-ring width–temperature relationship on a weekly-scale, which would not be possible to detect using the coarser monthly data. First-differences were consistently applied on time series of tree-ring data as well as temperature data for trend removal in order to minimize spurious correlations.

### 3. Results

#### 3.1. Leaf phenophases versus the thermal growing season

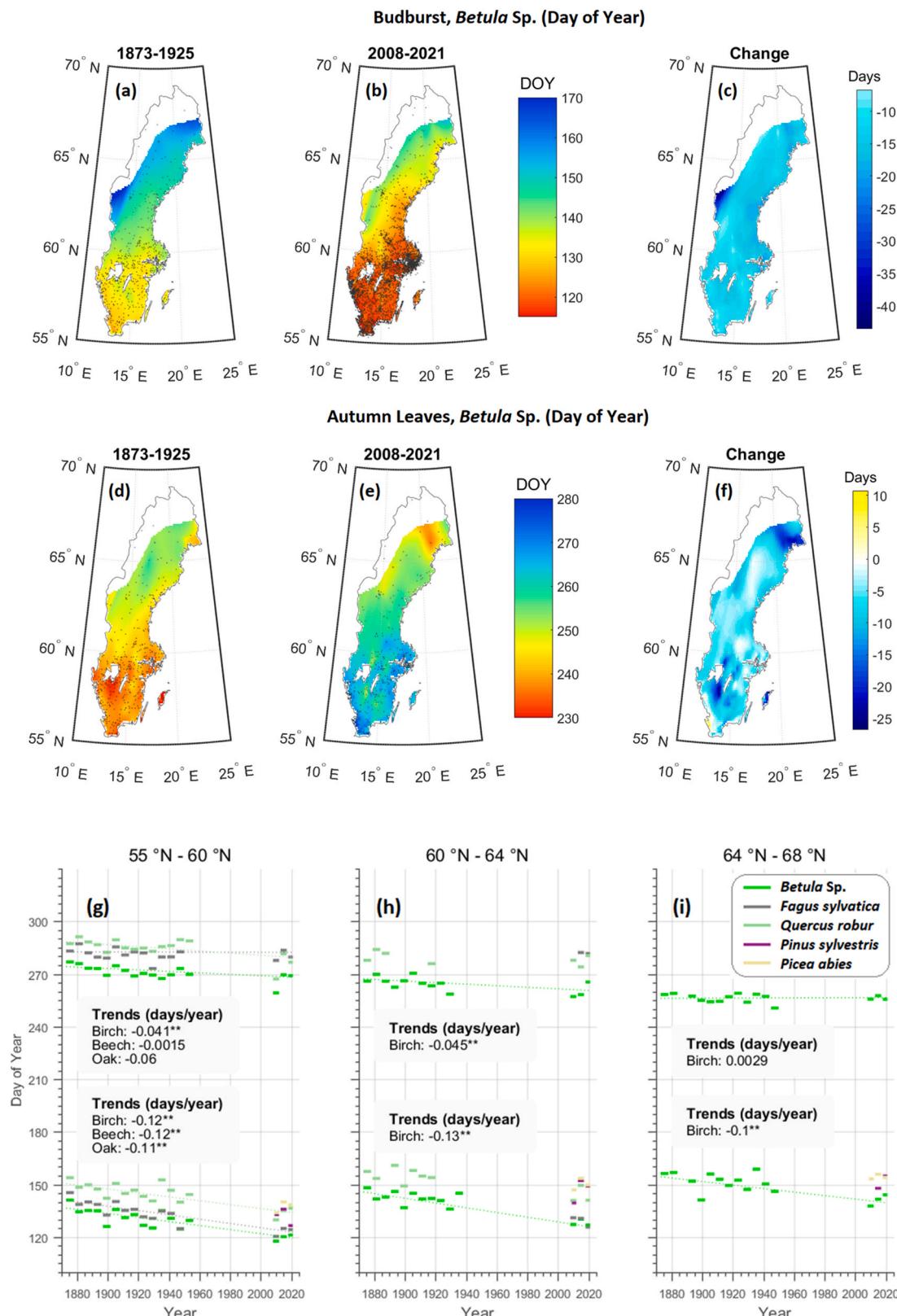
Fig. 2 shows the long-term trends computed on monthly temperature

data from the Östersund, Stensele, Abisko, and Sodankylä meteorological stations. Data from the four stations have been averaged over their common 1918–2015 period prior to the trend calculation. We found the steepest temperature trends in the first half of the year (January–June), when monthly trends varied between  $0.12$  and  $0.17^{\circ}\text{C}/\text{decade}$  over the period 1918–2015. The most noticeable deviation from the general temperature increase was for July, which had a negligible temperature trend.

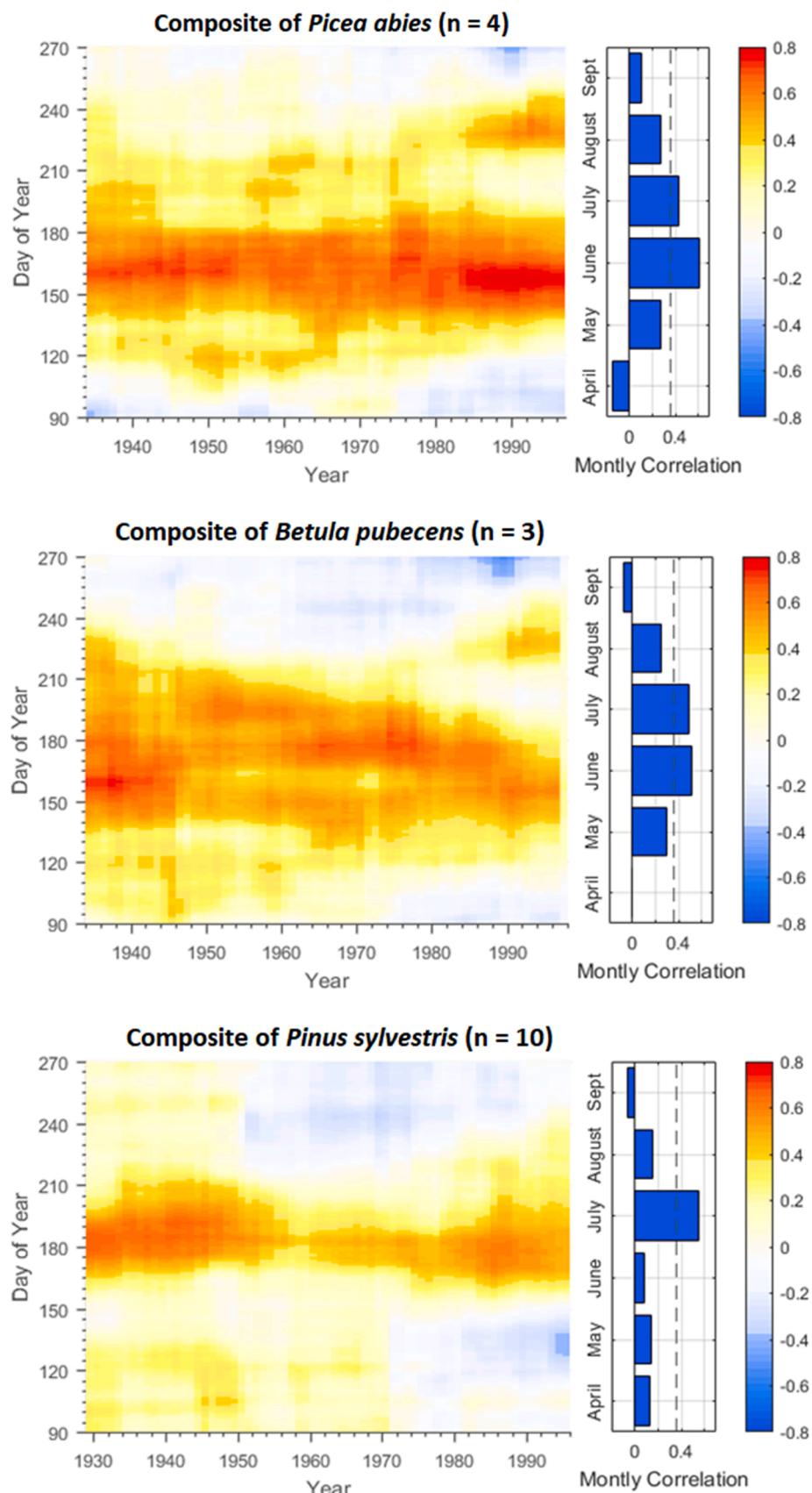
The thermal growing season has, according to all four meteorological stations, Östersund (1918–), Stensele (1891–), Abisko (1913–), and Sodankylä (1909–), been prolonged since the early 20th century. The earlier onset and later termination shifted on average 1–2 weeks, with Östersund being an exception exhibiting a negligible end-date shift (Table 2).

There is a clear tendency towards earlier budburst for all tree species through Sweden, similar to changes in the thermal growing season (Fig. 3). The linear trends are in the range of 10–13 days per century ( $p < 0.01$ ). Interestingly, also the leaf coloration shows a tendency to occur earlier in the year. However, this pattern is less consistent than the spring phenology. Amongst all species, only *Betula* sp. in southern and central Sweden exhibited a significant autumn leaf coloration trend (4–5 days/century). Although these changes are modest, they contrast to the trend in the thermal growing season end. Further, our results indicate that leaf buds appear almost always first on birch, followed by beech and then oak. The same species-order applies for the leaf coloration in the autumn. Hence, the length of the period with green leaves is similar for all the tree species. For Norway spruce and Scots pine, phenological data were limited to the recent 2008–2021 period, so the long-term trends could not be determined. Nevertheless, the observations for the 2008–2021 period indicate that the budburst on the conifers occur later than for the deciduous trees. This tendency is most consistent for spruce, which buds last of all the five species and up to three weeks after birch. Although limited in time, the observations of budburst in the conifers also provide a context for the ring width *versus* temperature correlations, which primarily are made with pine and spruce.

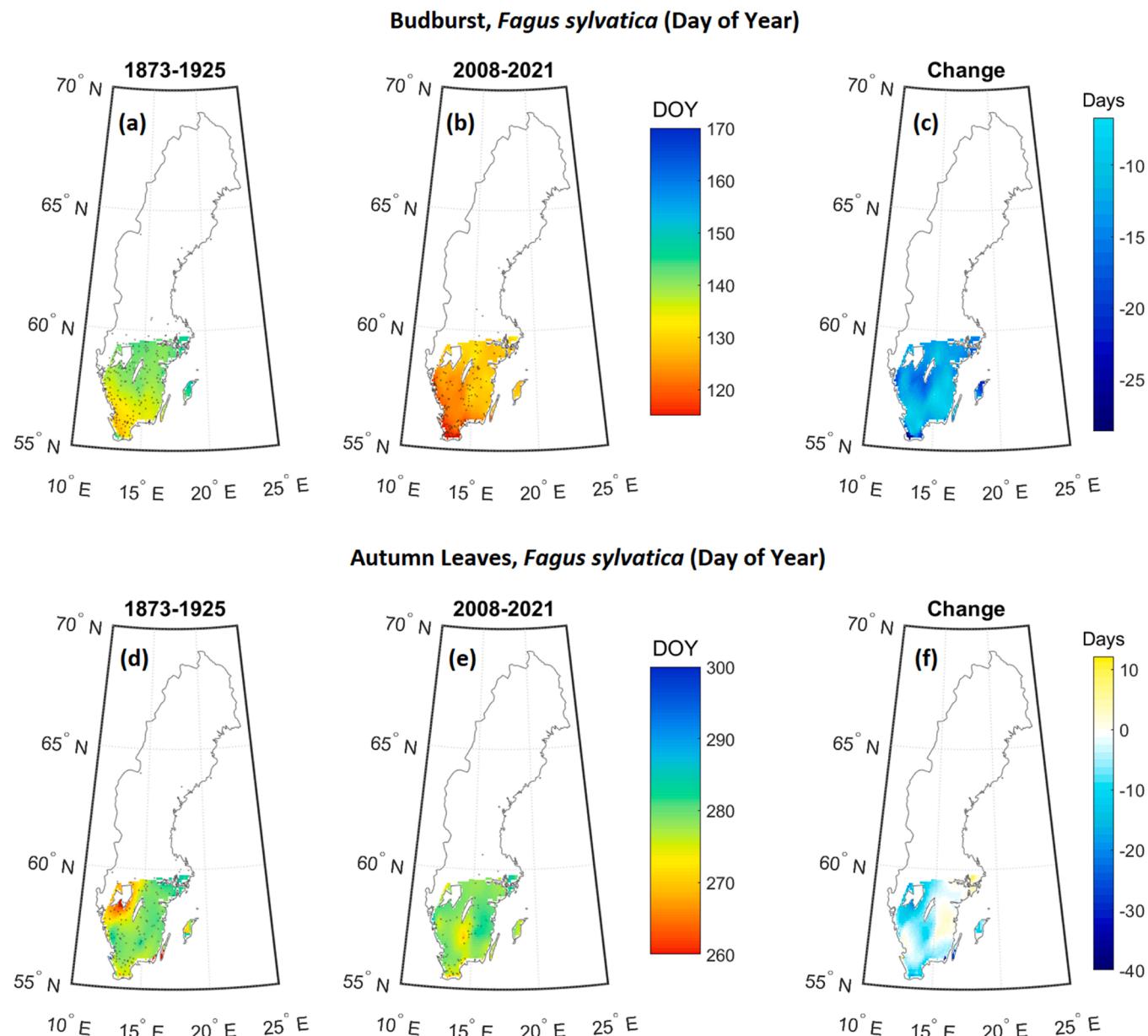
In birch, for which we have spatial data coverage over most of



**Fig. 3.** Day of budburst and leaf coloring in Julian Calendar Day of Year. Interpolated maps covering Sweden of budburst and leaf coloring for *Betula* sp. (birch) with averaged data for (a,d) historical and (b,e) modern times, and (c,f) difference between modern time and historical data (phenological sites marked as black dots). The lower plates (g-i) show time series of phenological observations (*Betula* sp., *Fagus sylvatica* (European beech), *Quercus robur* (European oak), *Pinus sylvestris* (Scots pine) and *Picea abies* (Norway spruce)) averaged across three latitudinal regions (<60°N, 60–64°N and >64°N). Data are averaged into 5-year blocks (less than 15 observations for each 5-year segment were excluded).



**Fig. 4.** 31-years running correlation between tree-ring width and 30 days mean temperatures for composites of (a) *Picea abies* (Norway spruce) (4 chronologies), (b) *Betula pubescens* (Downy birch) (3 chronologies), (c) *Pinus sylvestris* (Scots pine), (10 chronologies) for the 1918–2015 period. Day of Year on the y-axis correspond to the start of each 30-day period. Insignificant correlations ( $p > 0.05$ ) are displayed with pale color. The bar charts display monthly correlation for the entire 1918–2015 period. For individual tree-ring width chronologies, see Fig. A3 in the Appendix.



**Fig. A1.** Day of budburst and leaf coloring in Julian Calendar Day of Year. Interpolated maps covering Sweden of budburst and leaf coloring for *Fagus sylvatica*, with averaged data for (a,d) historical, (b,e) modern time and (c,f) difference between modern time and historical data (observation sites are marked as black dots).

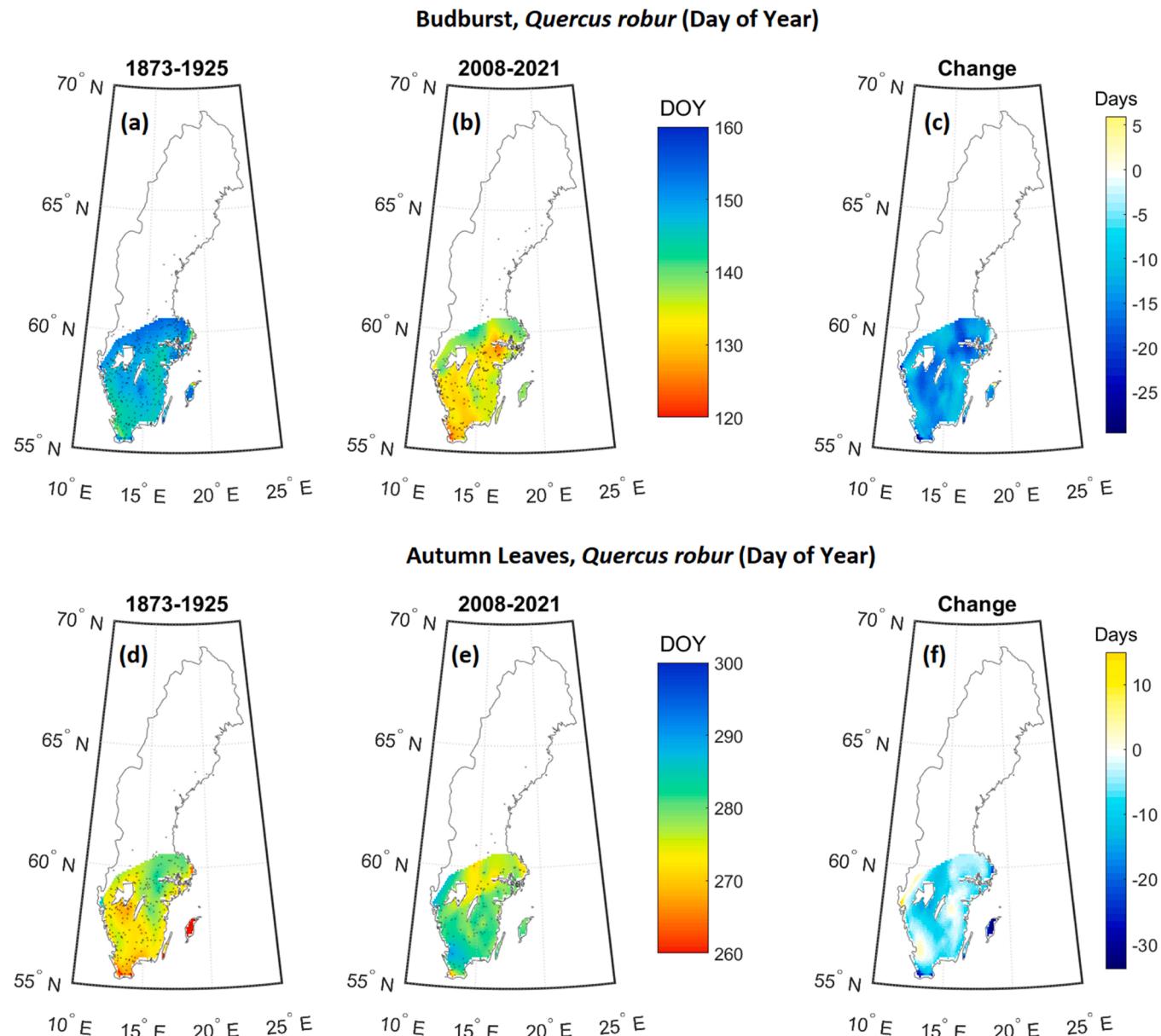
Sweden, the phenophases for historical and recent times are shown in Fig. 3a–f. Our results indicate consistent south–north gradients for both budburst and leaf coloring, with a successively shorter growing season further north. The same tendency associated to temperature can be observed at higher altitudes, especially for budburst in the central western region. We note, however, that parts of the Scandinavian mountains lack sufficient phenological data coverage for further interpretations. Mapping of the data shows that the early onset of budburst in the recent data, in comparison with historical data, is relatively homogeneous across the country (Fig. 3c), with an average change in budburst around –14 days, and with local extremes over a month. Leaf coloring, as well, tends to appear earlier, but with large local variations, ranging from +10 to –25 days and with no clear gradients.

### 3.2. Trends and patterns in tree-ring width–temperature response

Moving-window correlations between daily temperatures and ring-width chronologies of Scots pine, Norway spruce and Downy birch

over the 1918–2015 period are shown in Fig. 4. For each species, correlations have first been computed for each individual site chronology (see the list of sites in Table 1). These site-level responses to temperature have then been averaged on a species-level to highlight the general tendency for each species across a broader region. Our results show that for the 1918–2015 period, each species correlates significantly and positively with temperatures in a >30-day long window. All three species share a month-long window of significant correlations with temperature starting at around day 180 (i.e., end of June). Except for this, there are substantial differences amongst the three species in terms of the timing, strength and temporal changes in the tree-ring width–temperature relationship during the 1918–2015 period.

The temperature response of Scots pine and Downy birch become statistically significant early in the season, already in the last weeks of the spring (DOY 130–140). The composite of Scots pine on the other hand, reveals a much later temperature signal, appearing around DOY 170, at the end of June, and extends through the month of July, coinciding with the warmest period of the year. In the late summer, the link



**Fig. A2.** Day of budburst and leaf coloring in Julian Calendar Day of Year. Interpolated maps covering Sweden of budburst and leaf coloring for *Quercus robur*, with averaged data for (a,d) historical, (b,e) modern time and (c,f) difference between modern time and historical data (observation sites are marked as black dots).

between tree growth and temperature appears to be temporarily unstable for all species. In particular, Scots pine and Downy birch significantly correlate with temperature all through August in the early 20th century, but the late summer temperature signal is not consistent over time.

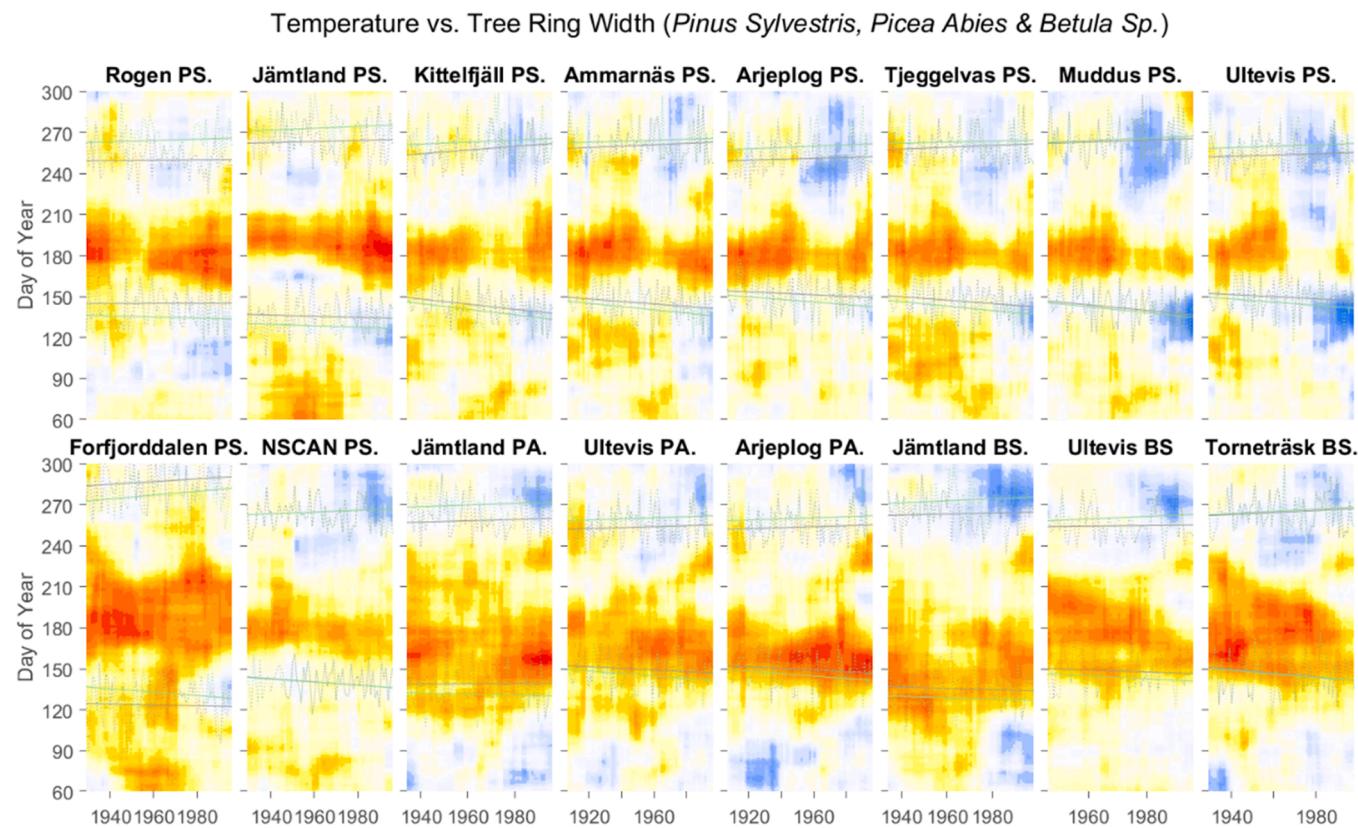
For Downy birch the window of significant correlation substantially shortens over the 1918–2015 period by gradually bringing the end date earlier, from early September to late July over the course of the century. This is truly the most striking deviation from the trend in the thermal growing season. Furthermore, the strength of the correlation appears to vary more for Downy birch than for the other species. Note that the Downy birch composite is based on fewer chronologies ( $n = 3$ ). Similarly, the August temperature signal detected for Scots pine fades in the mid-century, but notably reemerges in the recent decades. Another noteworthy observation, for the last few decades, is the emergence of a brief period with significant positive correlation in the early autumn (for both Norway spruce and *B. pubescens*). This time window ought to be too late in the season for wood formation, and at this moment, we have no

explanation for this pattern. Our results show that Norway spruce correlates ( $p < 0.05$ ) with temperatures during a two-month long window starting at the end of May, and that there are no discernible 20th century trends in its temperature response. The signal strengthens, however, in the last decades and the seasonal correlation maximum appear around midsummer (i.e., overlapping with the summer solstice).

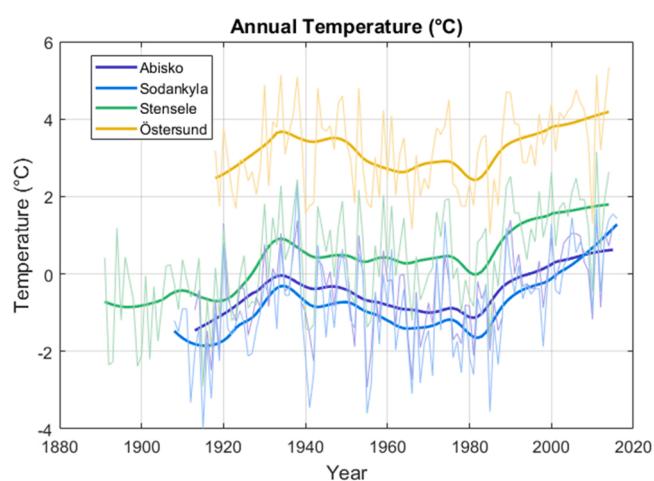
Summarizing, the climate response analysis conducted on a large network of tree-ring width chronologies of Scots pine, Norway spruce and Downy birch showed that, although there are some species-specific variations in regard to the timing of the temperature signal, the early-season (June and July) signal for all three species is noteworthy stable throughout the 20th century. The late summer temperature signal is however more elusive, showing a more pronounced instability throughout the entire century.

#### 4. Discussion

Fennoscandia is an important region seen from a



**Fig. A3.** Correlation coefficients between tree-ring growth and daily temperatures for individual tree ring series used in the study. Dotted lines: start and the end of the thermal growing season. Temperature is adjusted ( $0.6\text{--}1.0\text{ }^{\circ}\text{C}/100\text{ m}$ ), based on the altitudinal difference between each individual tree-ring site and the corresponding meteorological station. Green lines correspond to a lapse rate of  $0.6\text{ }^{\circ}\text{C}/100\text{ m}$  and grey lines  $1.0\text{ }^{\circ}\text{C}/100\text{ m}$ .



**Fig. A4.** Average annual temperature at Abisko (1913–2015), Sodankyla (1908–2016), Stensele (1891–2015) and Östersund (1918–2015).

dendroclimatological perspective, and a large number of temperature reconstructions have been developed from tree-ring data originating from this area (Linderholm et al., 2010). However, recent changes in temperature and potential shifts in the growing season may challenge the principle of uniformitarianism and the fidelity of the calibration exercises using tree-ring data in the area (Ljungqvist et al., 2020; Peltier and Ogle, 2020; Wilmking et al., 2020). Analysis of daily temperature data show that there is indeed a general shift in the thermal growing season in Fennoscandia (Walther and Linderholm, 2006). In our study, this tendency is confirmed by phenological observations, where we see

an earlier budburst in the spring, but also an earlier leaf coloring in the autumn (Fig. 3). Interestingly, these shifts are, in general, not fully reflected in the tree-ring width data. A visual assessment of the temperature signal in composite chronologies, consisting of multiple sites/species throughout Fennoscandia, reveals a reasonably stable temperature signal with only minor shifts in the peripheral ends of the target season. Some deviations occur from this general tendency when considering a local site level (Fig. A3), encouraging the use of multiple-site composites rather than individual site chronologies when reconstructing past temperatures across the region using tree-ring width.

Although it is clear that the time span when the temperature is high enough for trees to grow has theoretically been extended in the study area, it is less certain if this has actually led to a longer growing season period. Rather, the phenophases, which are indicative for a start and end of the growing season, shifted towards an earlier budburst and earlier leaf coloring. Thus, our results suggest only a modest extension in the length of the growing season. Despite the earlier onset of around two weeks, which is observed consistently in the phenology of deciduous trees throughout the region, the temperature signal obtained from the tree-ring width chronologies remain relatively stable during the first half of the summer. While some individual tree-ring chronologies have temperature growth signals which emerge earlier (Fig. S3), the overall tendencies illustrated in the composite charts show little change. In the cases where late summer temperature signals initially existed in the early 20th century, they tend to gradually fade away (Downy birch) or become unstable (Scots pine and Norway spruce) from the 1950's onward. An interesting, and maybe unexpected, observation is that although ring-porous and diffuse-porous plants differ significantly in their timing of xylogenesis, Scots pine, Norway spruce and birch all exhibit remarkably similar trends in leaf phenology.

**Table A1**

Average time of budburst in historical data (1873–1951) compared with recent data (2008–2021), for south (55–60°N), middle (60–64°N) and north (64–68°N) Sweden. Standard deviation ( $\sigma$ ) and number of observations for each subset is also included. Last column shows the difference between the recent and historical data set and the t-value,  $|t| \geq 1.96$  indicates a significant change.

		Historical data (1873–1951)			Recent data (2008–2021)			Change	
		DOY	$\sigma$ (days)	n	DOY	$\sigma$ (days)	n	Days	t-value
55–60°N	<i>Betula sp.</i>	134.2	10.1	2783	120.1	7.2	8423	-14.1	80.2
	<i>Fagus sylvatica</i>	138.2	10.0	1457	123.8	10.6	883	-14.4	33.0
	<i>Quercus robur</i>	148.2	8.9	2375	134.6	14.3	1288	-13.5	35.2
60–64°N	<i>Betula sp.</i>	142.9	9.8	699	126.5	10.5	1281	-16.4	34.0
	<i>Fagus sylvatica</i>	151.1	8.0	25	130.4	8.4	50	-20.8	10.3
	<i>Quercus robur</i>	155.6	8.6	156	145.9	14.7	109	-9.8	6.8
64–68°N	<i>Betula sp.</i>	151.9	10.7	329	139.9	13.7	325	-12.0	12.5

**Table A2**

Average time of leaf coloring in historical data (1873–1951) compared with recent data (2008–2021), for south (55–60°N), middle (60–64°N) and north (64–68°N) Sweden. Last column shows the difference between the recent and historical data set and the t-value,  $|t| \geq 1.96$  indicates a significant change.

		Historical data (1873–1951)			Recent data (2008–2021)			Change	
		DOY	$\sigma$ (days)	n	date	$\sigma$ (days)	n	Days	t-value
55–60°N	<i>Betula sp.</i>	273.2	11.7	2215	268.4	18.0	2261	-4.8	10.5
	<i>Fagus sylvatica</i>	282.3	11.8	973	282.6	18.2	548	0.3	-0.4
	<i>Quercus robur</i>	287.1	11.3	1716	279.8	16.9	1134	-7.3	13.8
60–64°N	<i>Betula sp.</i>	266.2	11.9	491	260.9	14.9	491	-5.3	6.1
	<i>Fagus sylvatica</i>	273.7	14.5	17	281.6	8.6	35	7.9	-2.5
	<i>Quercus robur</i>	279.1	10.6	96	278.5	13.0	64	-0.6	0.3
64–68°N	<i>Betula sp.</i>	256.1	8.4	293	256.7	12.0	186	0.6	-0.7

The strength of the correlation appears to vary more for Scots pine than the other species. Downy birch on the other hand, is periodically affected by moth outbreaks, a disturbance that may have effects on the correlation values. We observed several growth-rings that were white/pale, as well as extremely narrow. These rings were often occurring synchronized in time and are likely caused by moth outbreaks which defoliate trees and effectively impair tree growth (Olsson et al., 2017). Larch bud moth outbreaks have recently been less intense in the Alps (Büntgen et al., 2020), but this trend is most likely not mirrored in the Scandes, where outbreak frequency and duration may be intensified, exemplified with the widespread and long-lasting outbreaks around the turn of the millennium (Young et al., 2014). It is unclear if these disturbances have had any effect on the target season length, stability or correlation strength in the climate response analysis.

The earlier leaf coloring in recent years is in sharp contrast to the end of the thermal growing season trend. This counterintuitive observation is somewhat of a conundrum as the drivers of autumn leaf senescence are poorly understood. It has, however, been suggested that earlier leaf emergence and higher growing season temperature may accelerate carbon sink saturation and leaf senescence (Zani et al., 2020). In addition it has been questioned to what extent temperature still is the most limiting factor for tree growth in the northern boreal forests, or if the recent sharp increase in temperature has caused a decoupling between these previously strongly correlated parameters (e.g. Schreel, 2021).

A legacy effect between leaf phenology and tree-ring width has been indicated repeatedly from remote sensing measurements such as the Normalized Difference Vegetation Index (NDVI). NDVI is a measure a measure of photosynthetic activity and a number of studies have showed a positive association between NDVI for parts or whole summer and TRW in the northern forests (e.g. Kaufmann et al., 2004, Liang et al., 2005, Lopatin et al., 2006, Seftigen et al., 2018). Bhuyan et al. (2017) derived various phenological metrics from NDVI data and examined the relationship between these and TRW for 69 sites across the Northern Hemisphere. Although variation between space and tree types, on the whole they observed a clear legacy effect, there cumulative NDVI values for both previous year's spring and summer, and the end date of previous season had a positive influence on current year's TRW. Interestingly, the start date of the same year's season had negligible effect.

Furthermore, an interesting observation is that although ring-porous and diffuse-porous trees differ substantially in the timing of xylogenesis, the trends in the timing of leaf phenology are remarkably consistent for the different species of deciduous trees used in this study.

Our sites near the tree limit show a relatively strong and stable temperature signal during the first half of the summer, extending until July when the maximal annual temperature occur. Even more, we detected tendencies of an enhanced growth–summer temperature response in the last few decades for Norway spruce. We would argue that this stable temperature signal around the warmest time of the year, is in clear contradiction with the hypothesis that a threshold temperature has been surpassed at the high latitude and altitude sites. However, there may be indirect mechanisms, related to the temperature increase, that challenge the integrity of the temperature signal.

In regard to the hydrological cycles near the tree line, snowmelt takes place late in the spring, mostly in May. Consequently, a large part of the annual precipitation becomes available to plants and contributes to soil moisture in the early stage of the growing season. It is reasonable to assume that higher temperatures in the spring, driving earlier snow-thawing, have led to reduced water availability towards the end of the growing season. This, in turn, may lead to a weak temperature signal towards the latter part of the season if water becomes a limiting factor. In fact, recent studies exploring high-latitude forests reveal that previously temperature limited forests have become increasingly drought sensitive (Babst et al., 2019; Harvey et al., 2020). However, precipitation in climate response analyses sets higher requirements on proximity between sites and climate stations, as precipitation generally exhibits much larger local variability (Büntgen et al., 2010). A rapid but persistent change in environmental conditions can be challenging for plants to adapt to (Kijowska-Oberc et al., 2020). For instance, when the norm is an abundance of soil moisture, plants are less incentivized to invest in extensive root systems. If moisture conditions change, it is not a small feat to adapt the root systems to cope with more frequent moisture limitations and eventual droughts.

Unstable late summer temperature signals through the 20th century, particularly for Scots pine, could be a manifestation of this mechanism. Moisture limitation during the warmer 1930s and 1940s may have distorted the temperature signals at this time, but subsequently, the trees

may have adapted to the new conditions and overcome the new scarcer moisture conditions with expanded or developed root systems. The fact that Scots pine is better adapted to grow in mesic and dry sites than Norway spruce could be corroborating to this hypothesis. Habitats where Norway spruce is competitive are most often characterized by high levels of soil moisture even though snow melt and growing season rainfall are reduced.

Despite some instability at the edges of the correlation patterns, an intact target season with a stable core of temperature signal remains. This is encouraging for climate reconstructions from the region. Using 30-days aggregated periods of climate parameters rather than monthly data, gives a better chance to accurately determine the timing of the season for which tree growth can be used as a reliable climate proxy. At our tree ring chronology sites, all located near the tree line across the Scandinavian mountains, the period with significant correlation tends to end considerably earlier than when the thermal growing season ends. When aiming to reconstruct climate, applying a too wide target season, e.g., the entire summer season, could therefore be misleading. In particular if the temperature trends beyond the period of highest correlations greatly differ from the trends within. Moreover, we find a less pronounced warming in the summer compared to the spring and autumn, where July in particular stands out with a negligible temperature trend (Fig. 2). Using a too wide target season under those circumstances would lead to a deceptively steep positive trend in temperature, which may for good reasons be outstanding in a more appropriately timed and shorter target season.

Although this study did not compare trends of monthly-based target season with more tailor-made daily-aggregated target seasons, it is interesting to note that the Scots pine composite correlation patterns weakened in the 1960s (though reemerge in recent years), roughly coinciding with the well-known, but hard to explain emergence of the “divergence problem” (*sensu* D’Arrigo et al., 2008). The “divergence” in some high latitude tree-ring-based temperature reconstructions displaying a trend deviation, or deterioration in correlation, with target season temperatures, may simply relate to a drift or shortening of the daily-aggregated target season compared to a monthly-based compromise. However, further research is needed to address this problem and we recognize the many potential pitfalls in detection and attribution of divergence in tree-ring data (Esper and Frank, 2009).

The common tendency, particularly for Norway spruce, is a strong affinity to a midsummer temperature response, which also remains notable stable over time. As this time of the year coincides with seasonal maximum of solar angle rather than temperature, the question raises to what extent sunshine is a limiting factor, and whether it may emerge as a temperature signal as these two parameters are so strongly related (e.g., Park et al., 2018).

## 5. Summary and conclusions

In this study, we have employed daily meteorological temperature records, a comprehensive network of phenological observations and tree-ring width chronologies of some of the most wide-spread tree species in Scandinavia (Scots pine, Norway spruce and birch) to explore the thermal growing season and its relationship with tree-ring increments. Our most important findings include: (a) the thermal growing season has been extended, depending on location, with between one to three weeks over the 20th century as a result of the general temperature increase (b) phenological data of deciduous trees indicates that plant activity starts earlier but does not end later despite an in general later end of the thermal growing season (c) the 20th century tree-ring width–temperature relationship remains stable up until August despite the observed changes in the thermal growing season and in budburst phenology. (d) The Norway spruce and Downy birch temperature signals emerge at the end of May, whereas for Scots pine it emerges much later, in the middle of June.

Further studies are needed to (i) explore if the diminishing late

summer temperature signal is associated with changes in soil moisture/water availability, (ii) examine to what extent sunshine might be a limited factor rather temperature for the various species, and to (iii) quantify the magnitude of error in temperature reconstructions when using a target season that extends beyond the actual period for which a significant tree-ring width–temperature relationship exists.

## 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.

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## Appendix

See Appendix Fig. A1, Fig. A2, Fig. A3, Fig. A4, Tables A1 and A2.

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