Growth response of *Pinus sylvestris* L. and *Picea abies* [L.] H. Karst to climate conditions across a latitudinal gradient in Sweden

Friday N. Ogana [a,d,*], Emma Holmström [a], Jorge Aldea [b], Mateusz Liziniewicz [c]

[a] *Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Alnarp, Sweden*
[b] *Instituto de Ciencias Forestales (ICIFOR-INIA), CSIC, Ctra. La Coruña, Km 7,5, Madrid 28040, Spain*
[c] *The Forestry Research Institute of Sweden (Skogforsk), Ekebo, Sweden*
[d] *Department of Forest Resources and Environmental Conservation, West Campus Dr., Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA*

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ABSTRACT

Pinus sylvestris L. (Scots pine) and *Picea abies* [L.] H. Karst. (Norway spruce) are the most important economic tree species in Sweden. However, like every other tree species, they are affected by climate change, especially drought conditions. In this study, we analysed the effect of climate variability on the radial growth of Scots pine and Norway spruce in Sweden. Sixteen sites of pairwise monospecific stands of Scots pine and Norway spruce distributed across latitudinal gradients in Sweden (55 – 67 ° N) were used. In each site, we sampled at least 15 dominant/codominant Scots pine and Norway spruce trees without any defect in the sampled plots' buffer zone (3 – 5 m wide). We performed a correlation analysis between climate variables and the radial growth of the species using different timescales; and regressed the coefficients with latitudes. Thereafter, important climate variables for both species were identified. Our results showed that temperature is the main climate factor affecting the radial growth of Scots pine while Norway spruce is more sensitive to early summer precipitation. The impact of summer precipitation on the radial growth of both species transitioned from a positive to a negative trend across a latitudinal gradient. Conversely, a contrasting pattern was noted in the relationship with summer temperature. The radial growth of both species responded positively to spring temperature, particularly at lower latitudes. The resistance of pine and spruce to drought showed a clear linear increase with latitude ($p < 0.001$). Compared to spruce, pine showed a better capacity to attain pre-drought growth levels (i.e., resilience) and was independent of latitude. Our findings contribute to the understanding of the spatial patterns of the growth-climate relationship of Scots pine and Norway spruce in Sweden; and could offer useful guidance on adaptive forest management in the face of climate change.

1. Introduction

The boreal-temperate forest ecosystems are adapted to varying degrees of disturbances from frost, snow, windthrow, fire, fungus infestation, activities of defoliating insects, drought, etc. (Esseen et al., 1997; Hansson et al., 1997; Mäkinen et al., 2001; Peh et al., 2015). These disturbances are connected to climate change in many ways. For example, a prolonged period of drought in a Norway spruce (*Picea abies* [L.] H. Karst.) stand heavily reduces its growth, increases mortality (Sedmáková et al., 2019), and predisposes the tree to bark beetle attack (Bolte et al., 2010; Swedish Forest Agency, 2020; Vitas, 2004). Similarly, drought could trigger the activities of pathogenic fungi in the needles of Scots pine (*Pinus sylvestris* L.), which can decrease photosynthetic

capability and result in early needle cast, which lowers growth (Millberg et al., 2015). Under the snow, Scots pine saplings face the threat of damage from *Phacidium infestans*, while above the snow, there is a risk of browsing by ungulates (Hansson et al., 1997). Regional findings strongly indicate that climatic fluctuations play a significant role in driving both growth disparities and variations in tree mortality (Mäkinen et al., 2001, 2002; Raitio, 2000). Tree growth in the northern boreal forest zone is limited by temperature and in the southern parts by precipitation (Cook and Peters, 1997; Zunde et al., 2008).

Several studies abound on the growth response of trees to climate conditions, especially in boreal-temperate forests (Aakala and Kuuluvainen, 2011; Brichta et al., 2024; Mensah et al., 2021; Boisvenue and Running, 2006; Bose et al., 2021, 2020; Cailleret et al., 2019; Goude

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et al., 2022). Tree response to weather conditions varies with species and site conditions (Aakala et al., 2018). In Central Europe, spring drought has been reported to affect the growth of Norway spruce (Mikulenka et al., 2020). In addition, warm summers and soil moisture deficits have also affected Norway spruce and Scots pine in Finland (Aakala et al., 2018). Furthermore, Metslaid et al. (2016) found that high precipitation in June-July and spring temperature positively influence the growth of Scots pine on mined land in Estonia, whilst a high temperature in August negatively affected wood production. Precipitation in June has been reported as the most important climate variable influencing radial growth in Norway spruce in the same country (Läänelaid and Eckstein, 2003). The key climate signal in Norway spruce in southern Sweden has also been noted to be precipitation in June of the current year (Grundmann et al., 2011; Linderson, 1992). Norway spruce's sensitivity to precipitation is not surprising given its shallow root system (Metslaid et al., 2016). Growing season (May-August) temperatures have been observed to influence the growth of Scots pine in the central Scandinavian mountains (Linderholm, 2001). In northern Sweden, temperatures between June and July are favourable for Norway spruce, while the growth of Scots pine is particularly influenced by July temperatures compared to other months (Björklund, 2009). Generally, temperature is a growth limiting factor in northern Sweden.

In Sweden, Norway spruce and Scots pine collectively constitute the dominant tree species, comprising approximately 40.3 % and 39.3 % of the standing timber volume, respectively (Swedish Forest Agency, 2020), which makes them invaluable to the economy of the country. However, with rising concern for the future climate, the growth of these species could be threatened; which may impose heavy economic consequences (Hanewinkel et al., 2013; Petersson et al., 2022). The current predictions of the mean annual temperature for Sweden based on the Representative Concentration Pathways scenario 4.5 (RCP4.5) indicate ca $+2$ °C and $+4$ °C increase in the southern and northern parts, respectively, for a reference period from 1995 – 2014 (Claesson et al., 2015). Similarly, precipitation is expected to rise between 10 and 30%, especially in northern Sweden (Claesson et al., 2015). This rise will occur primarily in the winter and less so in the summer and autumn (Zheng et al., 2002). The southern part of Sweden has experienced a longer period of drought in summer in recent times and there are indications that this trend may continue because of the impact of climate change (IPCC, 2021). The growth processes, especially of Norway spruce in southern Sweden are known to be significantly influenced by precipitation in the summer months (Grundmann et al., 2011; Linderson, 1992).

Previous studies of climate-related growth response on Norway spruce and Scots pine demonstrate a positive correlation between increased mean temperature and increased dominant height (Brichta et al., 2024; Mensah et al., 2021; Stankova et al., 2024) but also a correlation between reduced growth during years with summer drought (Aldea et al., 2022; Suvanto et al., 2016; Mäkinen et al., 2001). Monitoring data gives robust evidence of the ongoing global warming and response to the growing forests in the northern hemisphere (Aldea et al., 2021; del Río et al., 2022). However, conclusions for future tree species selection based on survey studies of managed forests should be done with precaution, since site selection has been practiced for centuries, giving bias for tree species regarding interactions of soil type, rooting depth and soil moisture type. Since interactions of drought tolerance and site type have been proven on tree species-specific data (Bose et al., 2020; Cedro et al., 2022; Klisz et al., 2023; Pardos et al., 2021), comparisons between tree species must be done in studies without management bias.

Until now, there are no studies established yet on a pairwise country-scale representative analysis of the radial growth response of Norway spruce and Scots pine to climatic factors in Sweden. It will be worthwhile to investigate the growth responses of these invaluable species to climate change on a large scale. It has been reported that both species respond differently to precipitation and temperature at varying periods

of the year in southern Sweden (Aldea et al., 2022; Tufvesson, 2018). Such studies are limited in scope, thus, cannot be generalised for the entire country, because the climate conditions vary across latitudinal gradients in Sweden. A common trend in weather conditions from lower to high latitudes decreasing temperature, increasing moisture, short growing season and longer duration of snow period (Fraver et al., 2014). Delineating the spatial patterns and the relative strength in the way Scots pine and Norway spruce respond to climate conditions in Sweden would guide forest owners and practitioners on the choice of species, especially with the paradigm shift of increasing spruce stands in the southern part of the country. Thus, proffering answers to the past, present, and future conditions of the Norway spruce and Scots pine forests in Sweden.

Therefore, the objectives of this study were to: investigate the influence of temperature and precipitation on the radial growth of Scots pine and Norway spruce across latitudinal gradients, and (2) evaluate the impact of extreme drought year(s) on the species, but without management bias. We hypothesized that the response of Scots pine and Norway spruce to climatic factors differs, and thereby not uniform across the country. To achieve this, we carried out a site-to-site assessment of the growth response of Scots pine and Norway spruce to precipitation and temperature variables across the Swedish landscape. All sites used were carefully chosen from the database of the long-term forest experiments, where Scots pine and Norway spruce were randomly established in stands side by side.

2. Materials and methods

2.1. Study sites and sample collection

This study used sixteen sites of pairwise stands of Norway spruce and Scots pine distributed across latitudinal gradients in Sweden (55 – 67 ° N) (Fig. 1). From north to south, the sites included were Storlandet, Kloten BB2, Kulbäcksliden, Svedje, Lomåsen, Fillsta, Östbodarna SSK 24, Siljansfors BB 80 2, Siljansfors BB 80 1, Siljansfors BB 80 3, Rippestorpsvägen, Råda, Förarp, Lessebo, Tönnersjö and Tomelilla (Table 1). The first seven sites are situated at high latitudes ($\geq 62°$ N), whereas the other sites are at low latitudes ($\leq 61°$ N). The minimum distance between the sites was > 80 km (large enough to show weather variations between sites), except for Siljansfors BB 80 2, Siljansfors BB 80 1, and Siljansfors BB 80 3 which are relatively close. The type of experiments/ trials established on the sixteen sites could be categorised as tree species comparison, thinning and fertilization, and planting and soil/site preparation. Stand age varies between the sites (40 – 77 years) but not between the species on the same site or within pairs. Site productivity varied between 3 and 16 m^3 ha^{-1} yr^{-1}, with the southernmost sites exhibiting higher productivity (Table S1). For details on site-specific information, see Table S1. The experiments consist of treatment net plots sized between 0.05 – 0.1 hectares where all trees are numbered for individual revised measurements, and buffer zones between treatment net plots where the trees are not measured or numbered but undergo the same management. The years of establishment vary across the sites. The average climate conditions at those locations revealed rising temperatures and decreasing yearly precipitation, especially in southern Sweden in the last decade (Fig. 2). For information on the monthly climate at the sites, see Fig. S1.

In each site, we purposively sampled at least 15 Scots pine (hereinafter referred to as pine) and 15 Norway spruce (hereinafter referred to as spruce) trees outside the net plots i.e., trees in the buffer zone (3 – 5 m wide). This is because we could only core trees outside the net plots. We sampled only dominant/codominant trees with a minimum diameter size of > 12.0 cm and without any form of defect. The diameter at breast height (1.3 m above the ground) of the trees was measured with a calliper to an accuracy of 0.1 cm, and one core sample per tree was extracted with the Haglöf increment borer. Height was measured with a Vertex IV for every second tree to an accuracy of 0.1 m. The core samples
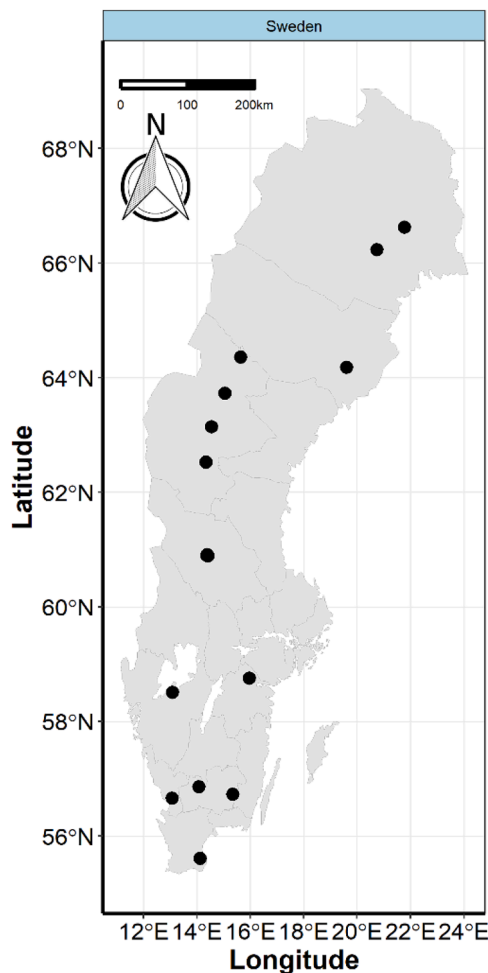
Fig. 1. The distribution of the studied sites across latitudinal gradients in Sweden.

were labelled by site name, species and tree number before being taken to the dendrochronology laboratory for analysis.

We mounted the core samples on a wooden core mount with water-soluble glue and then dried them at ambient temperature for some days. Thereafter, sanded with an electric sander to fine grit until the ring architecture was well noticeable. The core samples were scanned to a resolution of 2400 dpi with Epson Perfection V330 Photo. The tree rings were cross-dated, and measured to an accuracy of 0.01 mm using CooRecorder integrated with CDendro 9.1 program by Cybis™ (Maxwell and Larsson, 2021).

2.2. Construction of tree-ring chronology

Before the construction of the tree-ring chronology, detrending was performed on the tree-ring series to remove the effect of age-related trends and other non-climatic signals. We use the spline function from *dplR* package (Bunn, 2008) implemented in R (R Core Team, 2021) to detrend the tree-ring series. The degree of smoothing was set to 50% frequency response at 30 years (Cook et al., 1990). The detrended series (ring-width indices, RWI) were further pre-whitened using autoregressive moving average modelling to remove serial autocorrelation and thereby improve the "common signal" (Cook et al., 1990). Thereafter, we averaged the individual ring-width indices for each site per species using Tukey's bi-weight robust mean – a method where the mean is not affected by outliers (Bunn, 2008) to get the tree-ring chronology.

We assessed the quality and strength of the chronologies of pine and spruce for each site using basic chronology statistics such as series inter-

correlation (SIC), expressed population signal (ESP), mean sensitivity (MS), first-order autocorrelation (AR1) and signal-to-noise ratio (SNR) (Briffa and Jones, 1990). The SIC defines the strength of the common signal in the chronology, whilst ESP measures how well the common signal is expressed in the chronology. The AR1 quantifies the degree of correlation between consecutive tree rings i.e., how the tree growth in one year is closely related to its growth in the previous year. The SNR refers to the ratio of meaning information (the signal) contained in the tree ring to the random variation (the noise). An ESP value > 0.85 threshold implies that the common signal is adequately expressed in the chronology (Wigley et al., 1984). Mean sensitivity is a measure of the relative change in the annual ring width variations (Aakala and Kuu-luvainen, 2011). For climate-growth analysis, an MS threshold > 0.09 is considered adequate (Villalba et al., 1994).

2.3. Climatic data

Gridded daily temperature and precipitation data from 1961 to 2021 were downloaded for each site from the website of the Swedish Meteorological and Hydrological Institute (SMHI) (www.smhi.se/data). We obtained the monthly minimum temperature (TMIN), maximum temperature (TMAX) mean temperature (TMEN) and precipitation sum. Furthermore, the data was used to compute the Standardised Precipitation Evapotranspiration Index (SPEI) with timescales of one and three months (Vicente-Serrano et al., 2010). Standardised Precipitation Evapotranspiration Index integrates the impact of both temperature and precipitation, making it one of the most significant indices frequently used to evaluate drought (Bose et al., 2020; Hoffmann et al., 2018; Schwarz et al., 2020; Zhang et al., 2022). To get the SPEI for the 16 sites, first, we calculated the potential evapotranspiration (PET) with the '*thornthwaite*' function in the SPEI package (Beguería and Vicente-Serrano, 2017) using the monthly mean temperature and latitude. The water balance was then calculated by subtracting the PET values from the monthly precipitation sum. Thereafter, the *spei* function was used to obtain the SPEI values from the water balance.

For identifying moderate, severe and extreme drought years for the 16 sites, we used SPEI: -1.0 to -1.5, -1.5 to -2.0 and < -2.0, respectively.

### 2.4. Growth-climate relationships

To analyse the relationships between the tree-ring chronologies and climatic variables, we applied correlation analysis in the *treeclim* package (Zang and Biondi, 2015) implemented in R. We used monthly mean temperature (TMEN) and precipitation sum (PRCP) over the RWI year from September of the current year to previous August. We used one-, two- and three-month timescales in this study. Weather extremes such as minimum (TMIN) and maximum temperature (TMAX) were also considered since it is the extremes that are likely to change in the future (Marquis et al., 2020). Previous year variables were included because conifer growth is generally influenced by both previous and current conditions (Aakala and Kuuluvainen, 2011). Specifically, conifer trees allocate carbohydrates in the fall of the previous year to be used in the spring of the following year to start the "growth flush." (Grundmann et al., 2011; Metslaid et al., 2016). We carried out site-to-site analysis for both pine and spruce across the 16 sites as defined above. Furthermore, following the procedure of Ni et al. (2023), we regressed the correlation coefficients obtained from RWI and climate variables with latitude to see whether the site's climatic conditions were indicative of the growth sensitiveness of pine and spruce to local climate variability. All the relationships were analysed for a common period (1993 – 2021) at a 5% level of significance.

Since our analysis was based on one-, two- and three-month timescales climate variables (large explanatory variables) with high interrelations, we used the random forest algorithm to select the most important climate variables affecting the radial growth of pine and

Table 1
Site characteristics, tree-ring information and chronological statistics (obtained from detrended rings) at decreasing latitudes (North to South). N: number of trees cored; dbh: diameter at breast height (1.3 m); h: tree height; MRW: mean ring width; SIC: series inter-correlation; EPS: expressed population signal; MS: mean sensitivity; AR1: first-order autocorrelation; SNR: signal-to-noise ratio. To differentiate the species, bold text was used for pine.

No.	Site	Latitude	Elevation	Species	N	dbh	h	Ring Span	MRW	Chronology statistics				
			(m)			(cm)	(m)		(mm)	SIC	EPS	MS	AR1	SNR
1	Storlandet	66.626	236	**Pine**	**17**	**28.2**	**19.7**	**1963 - 2022**	**2.382**	**0.575**	**0.925**	**0.148**	**0.392**	**14.076**
				Spruce	15	18.5	14.9	1964 - 2022	1.706	0.595	0.900	0.204	0.192	10.778
2	Kloten BB 52	66.233	194	**Pine**	**14**	**27.3**	**21.7**	**1965 - 2022**	**2.215**	**0.573**	**0.895**	**0.166**	**0.296**	**9.086**
				Spruce	18	16.0	14.5	1964 - 2022	1.414	0.660	0.947	0.211	0.226	20.600
3	Svedje	64.356	297	**Pine**	**15**	**27.9**	**24.1**	**1950 - 2022**	**1.687**	**0.538**	**0.873**	**0.167**	**0.373**	**7.199**
				Spruce	13	16.6	16.8	1956 - 2022	1.270	0.612	0.883	0.194	0.279	8.372
4	Kulbäcksliden	64.179	233	**Pine**	**15**	**27.2**	**22.5**	**1960 - 2022**	**2.008**	**0.495**	**0.838**	**0.161**	**0.390**	**5.598**
				Spruce	14	15.7	14.0	1964 - 2022	1.314	0.623	0.889	0.191	0.237	8.706
5	Lomåsen	63.727	364	**Pine**	**15**	**26.3**	**21.0**	**1965 - 2022**	**1.994**	**0.588**	**0.902**	**0.191**	**0.379**	**10.01**
				Spruce	16	18.9	16.6	1961 - 2022	1.569	0.571	0.904	0.180	0.320	11.467
6	Fillsta	63.143	358	**Pine**	**15**	**28.7**	**24.0**	**1958 - 2022**	**1.820**	**0.552**	**0.892**	**0.165**	**0.329**	**8.533**
				Spruce	17	17.9	16.2	1961 - 2022	1.484	0.590	0.907	0.179	0.248	11.332
7	Östbodarna SSK 24	62.524	435	**Pine**	**14**	**22.3**	**16.2**	**1988 - 2022**	**2.979**	**0.595**	**0.902**	**0.159**	**0.361**	**10.066**
				Spruce	14	18.3	13.9	1993 - 2022	3.336	0.588	0.886	0.176	0.192	7.797
8	Siljansfors BB 80_2	60.911	389	**Pine**	**19**	**21.3**	**29.0**	**1974 - 2022**	**2.702**	**0.506**	**0.909**	**0.192**	**0.532**	**10.710**
				Spruce	15	19.1	19.1	1976 - 2022	1.891	0.535	0.895	0.175	0.398	9.112
9	Siljansfors BB 80_1	60.900	247	**Pine**	**14**	**22.6**	**24.6**	**1971 - 2022**	**1.956**	**0.532**	**0.879**	**0.169**	**0.369**	**7.626**
				Spruce	15	17.6	16.8	1973 - 2022	1.578	0.555	0.904	0.190	0.418	10.025
10	Siljansfors BB 80_3	60.890	278	**Pine**	**16**	**17.5**	**21.2**	**1984 - 2022**	**2.371**	**0.571**	**0.956**	**0.184**	**0.640**	**23.576**
				Spruce	14	12.6	13.3	1984 - 2022	1.517	0.574	0.879	0.214	0.254	7.715
11	Rippestorpsvägen	58.756	89	**Pine**	**15**	**23.1**	**27.6**	**1965 - 2022**	**2.009**	**0.518**	**0.924**	**0.212**	**0.421**	**12.945**
				Spruce	15	28.2	23.4	1965 - 2022	2.358	0.642	0.918	0.213	0.431	11.894
12	Råda	58.505	92	**Pine**	**14**	**25.0**	**19.9**	**1990 - 2022**	**3.378**	**0.601**	**0.909**	**0.250**	**0.298**	**5.573**
				Spruce	15	21.7	18.2	1992 - 2022	3.512	0.633	0.905	0.213	0.418	2.394
13	Förarp	56.863	157	**Pine**	**15**	**25.7**	**19.5**	**1986 - 2021**	**3.327**	**0.542**	**0.886**	**0.247**	**0.284**	**6.625**
				Spruce	15	21.9	17.0	1991 - 2021	3.617	0.653	0.954	0.285	0.339	5.966
14	Lessebo	56.730	190	**Pine**	**15**	**23.8**	**19.8**	**1986 - 2021**	**2.983**	**0.562**	**0.924**	**0.227**	**0.413**	**12.566**
				Spruce	14	25.6	20.0	1984 - 2021	3.562	0.581	0.884	0.244	0.293	8.257
15	Tönnersjö	56.659	66	**Pine**	**15**	**28.5**	**20.8**	**1982 - 2021**	**3.129**	**0.624**	**0.927**	**0.271**	**0.451**	**13.462**
				Spruce	15	23.2	18.7	1981 - 2021	2.568	0.584	0.940	0.286	0.337	16.601
16	Tomelilla	55.608	115	**Pine**	**15**	**28.4**	**19.7**	**1985 - 2021**	**3.460**	**0.606**	**0.919**	**0.297**	**0.216**	**12.160**
				Spruce	15	32.2	20.9	1986 - 2021	5.136	0.692	0.936	0.299	0.282	8.498
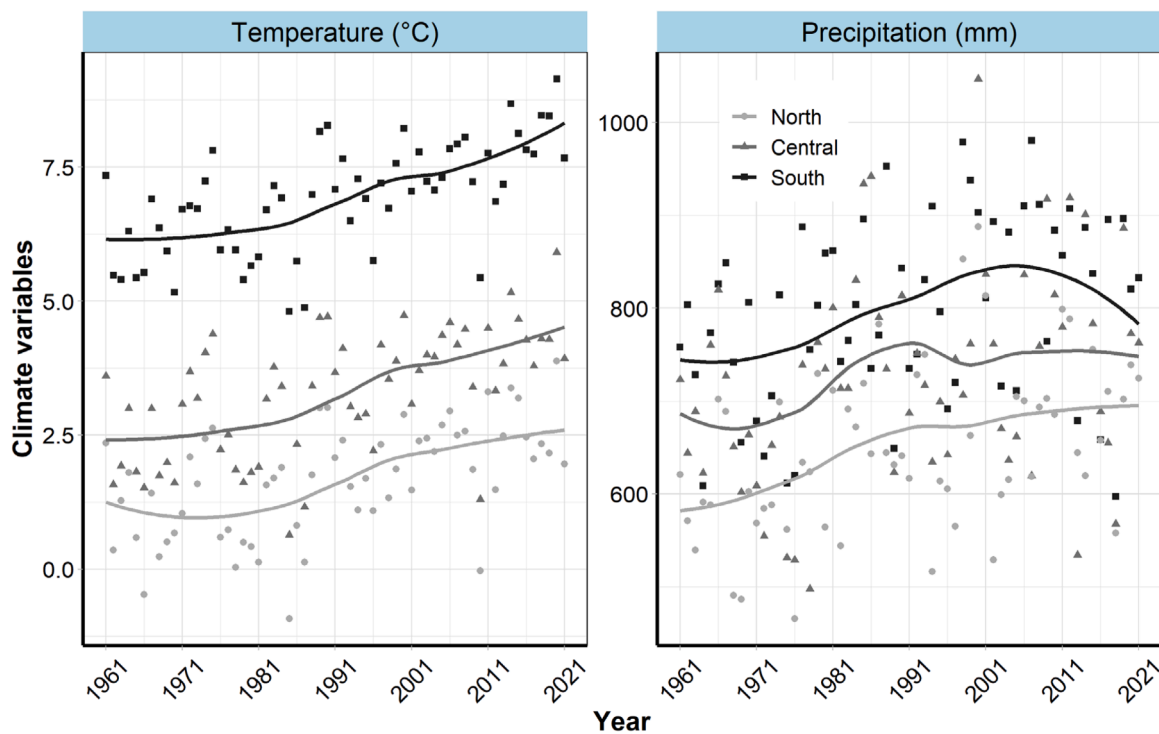
Fig. 2. Mean annual temperature and yearly precipitation sum of the study area (northern, central and southern Sweden).

spruce. To determine the number of variables to retain in the random forest model, we applied a nested cross-validation technique with five folds to reduce the number of predictors based on variable importance. This technique allows for the detection of the most important variables as well as the direct evaluation of the algorithm. Thereafter, we used a partial dependency plot to describe the influence of the selected climate variables on the radial growth of pine and spruce. We used the *randomForest* package (Liaw and Wiener, 2002) in R.

2.5. Tree growth resilience

We used Lloret's resilience components – resistance, recovery and resilience (Lloret et al., 2011) to obtain indices that quantify the impact of drought based on the RWI. We used the SPEI values to identify drought year(s) and restricted our analysis to extreme drought years common to the 16 sites. The Lloret's resistance index gives the intensity of growth decrease during the drought year with respect to the pre-drought period i.e., the growth ratio between the drought year and pre-drought period (Eq. (1)). The recovery index measures growth after the drought year against growth during the drought year (Eq. (2)). It quantifies the size of the growth rise; a value of < 1 denotes a sustained drop in growth following the drought year (Hoffmann et al., 2018; Lloret et al., 2011). Resilience is the capacity to attain pre-drought growth levels, as measured by the ratio of growth after and before the drought (Eq. (3)).

$$Resistance = \frac{Growth\ during\ drought\ (G_{drought})}{Growth\ before\ the\ drought\ (G_{pre-drought})} \quad (1)$$

$$Recovery = \frac{Growth\ after\ the\ drought\ (G_{post-drought})}{Growth\ during\ drought\ (G_{drought})} \quad (2)$$

$$Resilience = \frac{Growth\ after\ the\ drought\ (G_{post-drought})}{Growth\ before\ the\ drought\ (G_{pre-drought})} \quad (3)$$

The two-year mean growth before and after a drought, respectively, were used to determine the pre- and post-drought growths (Hoffmann et al., 2018; Knutzen et al., 2017; Schwarz et al., 2020). We obtained Lloret's resilience components for pine and spruce trees across the sites using the *pointRes* package (van der Maaten-Theunissen et al., 2021). Finally, we assessed how the resilience components change along latitudinal gradients (55 - 67° N).

3. Results

3.1. Tree sizes and radial growth pattern of the tree-ring chronologies

The average diameters of the sampled spruce trees at high latitudes were comparatively smaller (dbh < 20) than those observed at sites located in lower latitudes (Table 1). The sizes for the dominant/codominant trees of pine were less variable across the sites with an average dbh > 20 cm. The ring span of the standardized chronologies of pine and spruce in the 16 sites varied from 1990 to 1950 (i.e., 32 to 72 years) and 1993 to 1956 (i.e., 29 to 66 years), respectively (Table 1). The mean ring width (ARW) of pine varied between 1.68 and 3.46 mm, while for spruce, it ranged from 1.27 to 5.13 mm, with the highest values observed at lower latitudes for both species. The population signal was effectively captured in the chronologies, exhibiting an EPS exceeding the threshold of 0.85, except for pine at Kulbäcksliden, which is located at a higher latitude. The strength of the common signal (SIC) in the chronologies was high for pine and spruce. The relative change in the annual ring width variations (MS) of pine and spruce exceeded 0.09 (threshold) in all 16 sites, thus, confirming the reliability of the chronologies. Additionally, the signal-to-noise ratio (SNR) was relatively large for both pine and spruce.

The annual fluctuations in the ring-width index (RWI) of pine and

spruce exhibited a trend of increasing amplitude as latitude decreased across the sites (see Fig. S2). The year 2018 marked a drought year for the majority of the sites, particularly those situated at lower latitudes, where a noticeable decrease in growth was evident.

3.2. Site-specific climate-growth relationship

Analysis across different sites revealed that at higher latitudes, the radial growth of pine exhibited a positive correlation ($p < 0.05$) with current July temperatures (TMEN, TMAX, and TMIN) across all sites (Fig. 3). However, for spruce, this relationship was most prominent in June and July, with correlations becoming negative at lower latitudes during these months. In contrast, current March temperatures showed a significant positive correlation ($p < 0.05$) with the growth of both pine and spruce in most sites at lower latitudes. On the other hand, correlations between current May to August precipitation (PRCP) and Standardised Precipitation Evapotranspiration Index (SPEI) with the radial growth of pine in higher latitudes were generally weak, with some cases exhibiting negative and non-significant associations. For spruce, the radial growth of the species across the 16 sites exhibited a positive correlation with current June precipitation (PRCP) except for Östbodarna situated at latitude 62.5° N with an elevation above 400 m. Additionally, the SPEI of current June showed a significant positive correlation with the radial growth of spruce in most sites spanning latitudes from 55.6° N to 60.9° N.

Furthermore, using two- and three-month timescales also showed that the spring temperature correlated positively with the radial growth of pine and spruce (see Figs. S3–S4). However, the correlation was negative in the summer, except for those sites in higher latitudes where significant positive correlations were observed ($p < 0.05$), particularly with the radial growth of spruce. Precipitation and SPEI in summer correlated positively with pine and spruce from latitudes 55.6° N to 60.9° N. Climate conditions during autumn and winter had minimal impact on the radial growth of pine and spruce. Nonetheless, PRCP and SPEI during autumn and winter showed significant negative correlations ($p < 0.05$) with spruce radial growth at certain sites in higher latitudes, specifically the northernmost locations.

The correlation coefficients between summer month temperatures and the radial growth of pine and spruce displayed a linear increase with latitude, transitioning from negative to positive associations (Fig. 4). Conversely, correlations with spring month temperatures decreased, with a significant trend observed only in TMIN for both species. Similarly, the effects of summer PRCP and SPEI on the radial growth of pine and spruce shifted from positive to negative along latitudinal gradients. The effects of PRCP and SPEI in other seasons on the species appear to be independent of latitude.

3.3. Important climate variables affecting the radial growth of pine and spruce

The results from the random forest regression showed that the current temperature in March, June, July, May – June, summer (June – August), and SPEI in July – September, were the six most important climate variables affecting the radial growth of pine (Table S2 and Fig. S5). For spruce, SPEI in June, precipitation (PRCP) in June, June – July, and temperature in May – June, June – July and May – July were the six most important climate variables selected.

The partial dependency plots between the six most important variables and the radial growth of pine and spruce are presented in Fig. 5. Among the selected climate variables for pine, the temperature in July (TMEN.JUL) had the greatest impact on the radial growth of the species (Fig. 5 and Table S2). At mean temperatures ≤ 16.5°C, TMEN.JUL had a positive effect on the radial growth of pine but became negative above the threshold. Summer mean temperature (June – August, TMEN.JUN-AUG) had a weak effect on pine, but at higher TMEN.JUN-AUG, there was a substantial decline in the radial growth of pine. A similar pattern
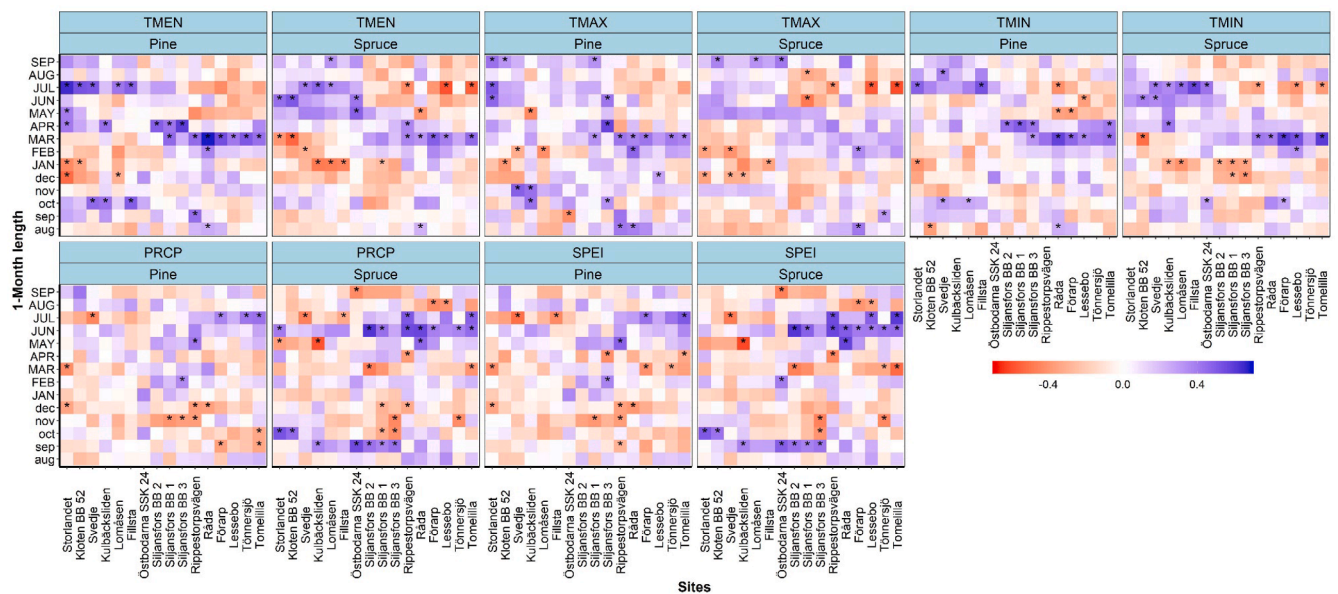
Fig. 3. Correlation between ring width index (RWI) and climate data for the sites (north to south). Climate data include mean (TMEN), maximum (TMAX) and minimum temperature (TMIN), precipitation (PRCP), and Standardised Precipitation Evapotranspiration Index (SPEI). Correlations were calculated for a 14-month window from the current September to the previous August. The lowercase and uppercase letters represent the previous and current year's months, respectively. Scale bars show the ranges of correlation coefficients; asterisks indicate significance at $p < 0.05$ level.

was also observed with the mean temperature of May-June. The mean temperature in June had a minimal impact on pine but contributed to decreasing growth at very high temperatures. The radial growth of pine increased gradually with increased mean temperature in March (TMEN. MAR), and at temperatures $> 0°C$, a sharp growth rise was observed. Pine growth increased with increased SPEI in July-September (SPEI. JUL-SEP), but no significant increase was observed at values > -1.

The radial growth of spruce was closely related to precipitation in June (PRCP.JUN), and it increased approximately linearly with the PRCP.JUN up to 160 mm. Low precipitation in June-July (PRCP.JUN-JUL) decreased growth. Spruce was very sensitive to dry conditions i.e., negative SPEI in June produced low growth. When the mean temperature in May – July (TMEN.MAY-JUL) was less than 13°C, spruce was positively related to the increase in TMEN.MAY-JUL. Increased in the mean temperature in May – June (TMEN.MAY-JUN) and June – July (TMEN.JUN-JUL) up to 14.2°C and 15.4°C, respectively brought about a marginal increase in the growth of spruce.

3.4. Tree growth resilience

The 2018 extreme drought effects on the radial growth of pine and spruce were more visible in the south of Sweden. The resistance index of pine and spruce was relatively the same and showed a clear linear increase with latitude ($p < 0.001$) with R^2 of 0.86 and 0.72, respectively (Fig. 6). Pine had a greater recovery index than spruce at low latitudes. Their recovery indices decreased linearly with increasing latitude because drought impact was lower in the north. Additionally, compared to spruce, pine showed a better capacity to attain pre-drought growth levels (i.e., resilience) and was independent of latitude ($p = 0.800$). The resilience of spruce to extreme drought increased with latitude ($p = 0.03$). The site-to-site analysis of the pre-drought, drought and post-drought growth of the two species is presented in Fig. S6.

4. Discussion

This study evaluated the growth response of Scots pine and Norway spruce to climate conditions in Sweden along latitudinal gradients (55 - 67° N). Using 16 sites of pairwise comparison of Scots pine and Norway spruce, we showed that the effect of temperature and precipitation on

the radial growth of these species varied across Sweden. By only using sites where stands with spruce or pine was established on the same site, we could here rule out management bias within the pairs, e.g., stand age differences or site properties. Our hypothesis of different climate-growth responses of Scots pine and Norway spruce across Sweden was confirmed, and these responses varied spatially.

4.1. Climate-growth relationship

At lower latitudes ($\leq 61°$ N), the radial growth of both pine and spruce respond positively to early spring (March) temperature, and the association tends to be weaker beyond this latitudinal limit. However, late spring (May) temperature influenced the radial growth of spruce more than pine at higher latitudes. The importance of warm springs to the growth of these species has been documented in previous studies e. g., spring temperature has been shown to influence the radial growth of pine in Estonia (Metslaid et al., 2016) and spruce in Central Europe (Mikulenka et al., 2020). Pine and spruce need warm springs to initiate cambial activities after the winter dormancy and before the growing season (Metslaid et al., 2016; Svystun et al., 2021).

Following spring, the majority of the growth (both apical and lateral growths) in pine and spruce occurs during the summer months (June – August), and as such summer conditions are germane in the life of the species. Our results showed that precipitation in June (early summer) is the main climate variable affecting the growth of spruce in Sweden (Figs. 3 and 5). Using a one-month timescale, precipitation in June had a positive association with the radial growth of spruce in most of the sites except in Östbodarna. When the timescale was increased to two and three months (i.e., precipitation sum for two- and three-months length), only those sites at lower latitudes showed significant positive correlations with precipitation in June (sum for May – June) and July (sum for June – July) (Figs. S3 and S4). Our result is in line with previous studies in southern Sweden and other parts of Europe where early summer precipitation was reported as the main climate signal influencing spruce (D'Andrea et al., 2023; Grundmann et al., 2011; Helama et al., 2016; Läänelaid and Eckstein, 2003; Linderson, 1992). The partial dependency plot also revealed that the radial growth of spruce would continue to increase with the rise in June precipitation up to 160 mm. Surprisingly the average precipitation sum in June from the 16 sites has been ≤ 125
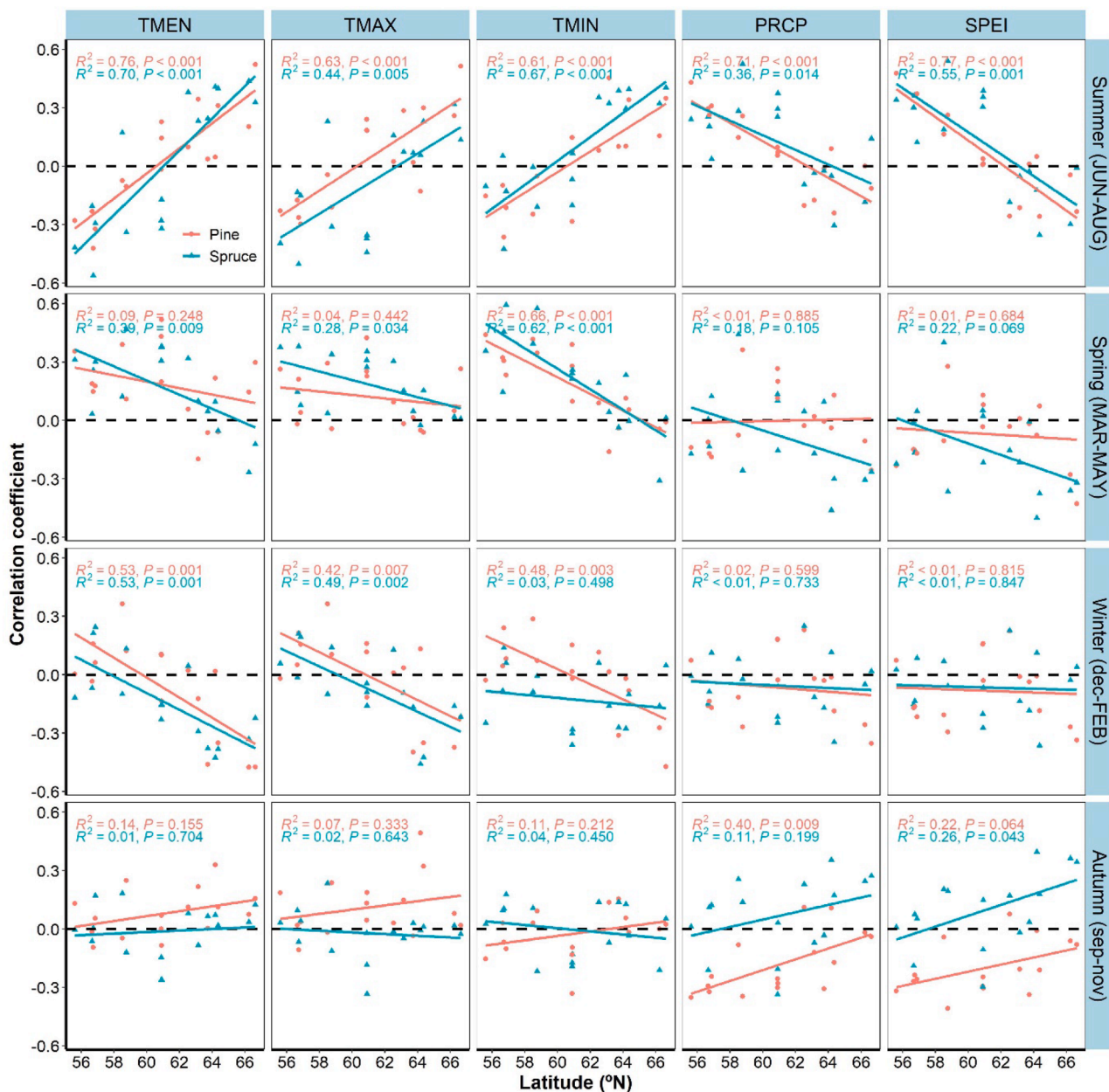
Fig. 4. Relationship between latitude and the correlation coefficient of RWI (pine: red and spruce: blue) and climate variables in four seasons during the common period (1993 – 2021). R^2: coefficient of determination, $P < 0.05$ indicates a significant linear trend. The black dashed line showed the transition from positive to negative correlation and vice versa, along latitude.

mm in the last two decades with a decreasing pattern (Fig. S1). Drier early summer may continue especially in lower latitudes (southern Sweden) due to the impact of climate change (SMHI, 2022). Though current prediction shows that precipitation would increase particularly at higher latitudes in Sweden (northern part), such a rise is expected in the winter and less so during the summer months (Claesson et al., 2015; Zheng et al., 2002). Compared to spruce, precipitation had less effect on the radial growth of pine.

The temperature in July seems to be one of the key climate variables affecting the radial growth of pine. The radial growth of pine will increase with the rise in current summer temperatures, particularly in July but only up to a certain limit. Our result showed that a further rise in temperature in July beyond 16.5℃ will cause a decrease in the radial growth of pine. Growing season temperatures have been reported to influence the growth of pine in northern Europe (Brichta et al., 2024; Mensah et al., 2021; Linderholm, 2001; Metslaid et al., 2016).

Previously, it has also been shown that only July temperature enhances the growth of pine in northern Sweden, whilst June and July temperatures positively influence the growth of spruce (Björklund, 2009). The impact of summer temperature on spruce showed obvious differences between lower and higher latitudes. At higher latitudes ($\geq 62°$ N, i.e., northern Sweden), summer temperature had a positive influence on the radial growth of spruce irrespective of the timescale (1-, 2-, or 3-month length), whereas the reverse effect was the case at lower latitudes. The radial growth of spruce will increase if the mean temperatures in summer do not exceed around 14 – 15℃ (Fig. 5). Interestingly, the average summer temperature in northern and southern Sweden in the last decade (2011 – 2021) was around 13.2℃ and 16.3℃, respectively. This indicates that both pine and spruce could still be benefiting from warmer summers in northern Sweden but not in southern Sweden (14 – 15 < 16.3℃). However, the decreasing summer precipitation and rising temperature (Fig. S1), indicate an increasing water deficit in the active
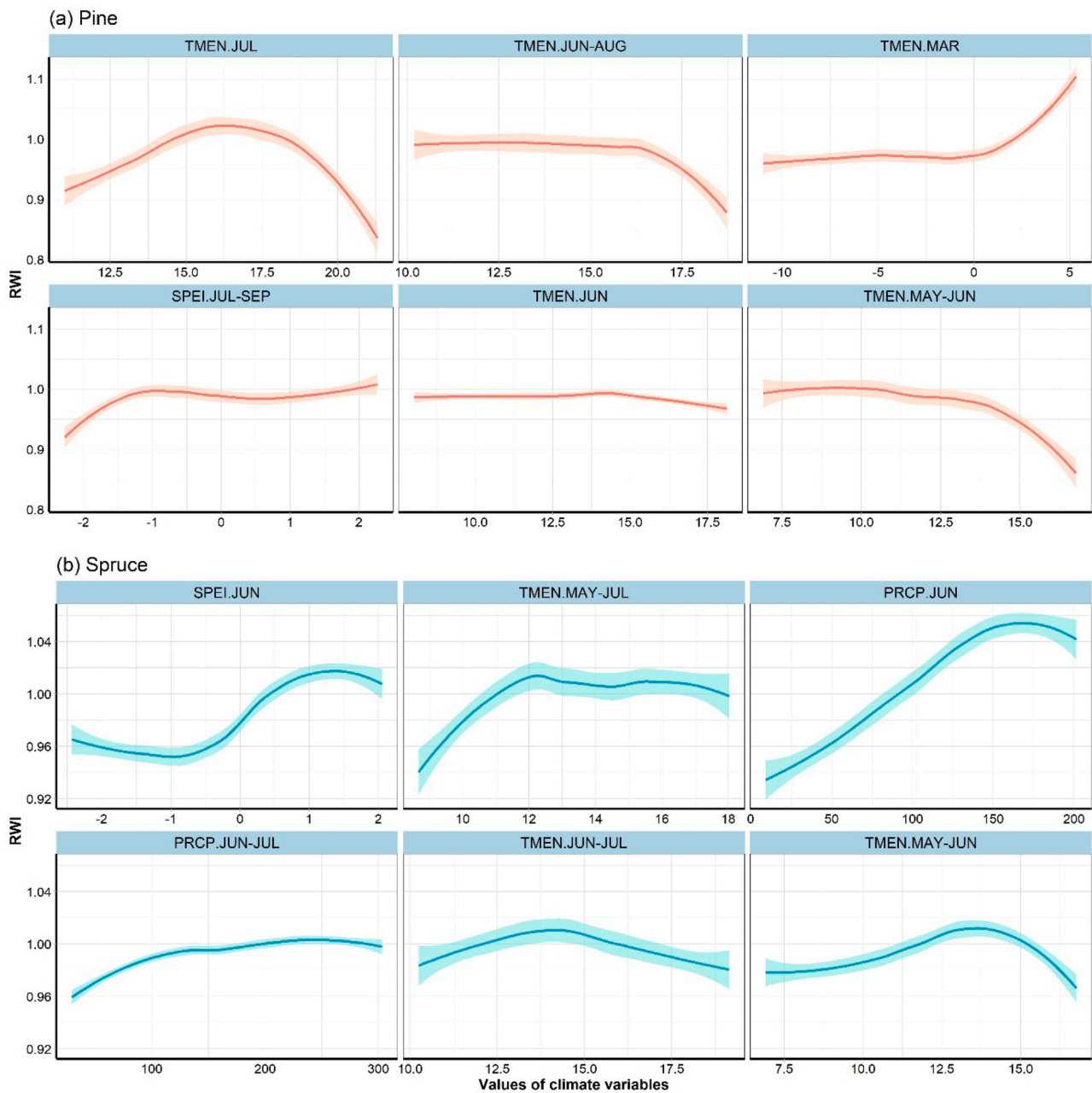
Fig. 5. Partial dependencies between the predicted RWI and the important climate variables with 95% confidence intervals for (a) pine and (b) spruce. Arranged according to their levels of importance (from left to right). When the target variable changes, the other variables remain constant.

growing period for both species, particularly at lower latitudes due to evapotranspiration. Soil moisture deficit (i.e., drought condition) in summer decreases the radial growth of both pine and spruce (Aakala et al., 2018; Aakala and Kuuluvainen, 2011), but spruce tends to suffer more (Aldea et al., 2022; Gutierrez Lopez et al., 2021; Treml et al., 2022). Our results show strong positive associations between the radial growth of spruce and the Standardized Precipitation-Evapotranspiration Index (SPEI) in summer compared to pine.

4.2. Tree growth resilience

Drought conditions either moderate, severe, or extreme in early summer resulted in the decline of the radial growth of spruce. Conversely, the radial growth of pine was sensitive only from a certain threshold of negative SPEI value. Extreme drought conditions were found to affect both spruce and pine annual diameter growth (Aldea

et al., 2022; Pardos et al., 2021). For example, we found that the 2018 extreme drought year affected both species in Sweden but pine showed better recovery and was able to bounce back (resilience) than spruce. Generally, spruce is typically regarded as one of the species with the least resistance and resilience to droughts in Europe (Vitasse et al., 2019).

The resilience of pine to drought is independent of latitude, which implies that the species could occupy a wider geographical range in Sweden than spruce. Bose et al. (2020) similarly observed that the resilience of Scots pine to drought is not dependent on latitude, but rather on the growth performance before the drought. In our analysis, we did not observe a significant decline in growth for pine and spruce during the pre-drought period (i.e., before the extreme drought year of 2018) in most of the sites located at lower latitudes in the southernmost regions (Fig. S6). The timing and duration of drought have been identified as significant factors influencing the growth resilience of pine and
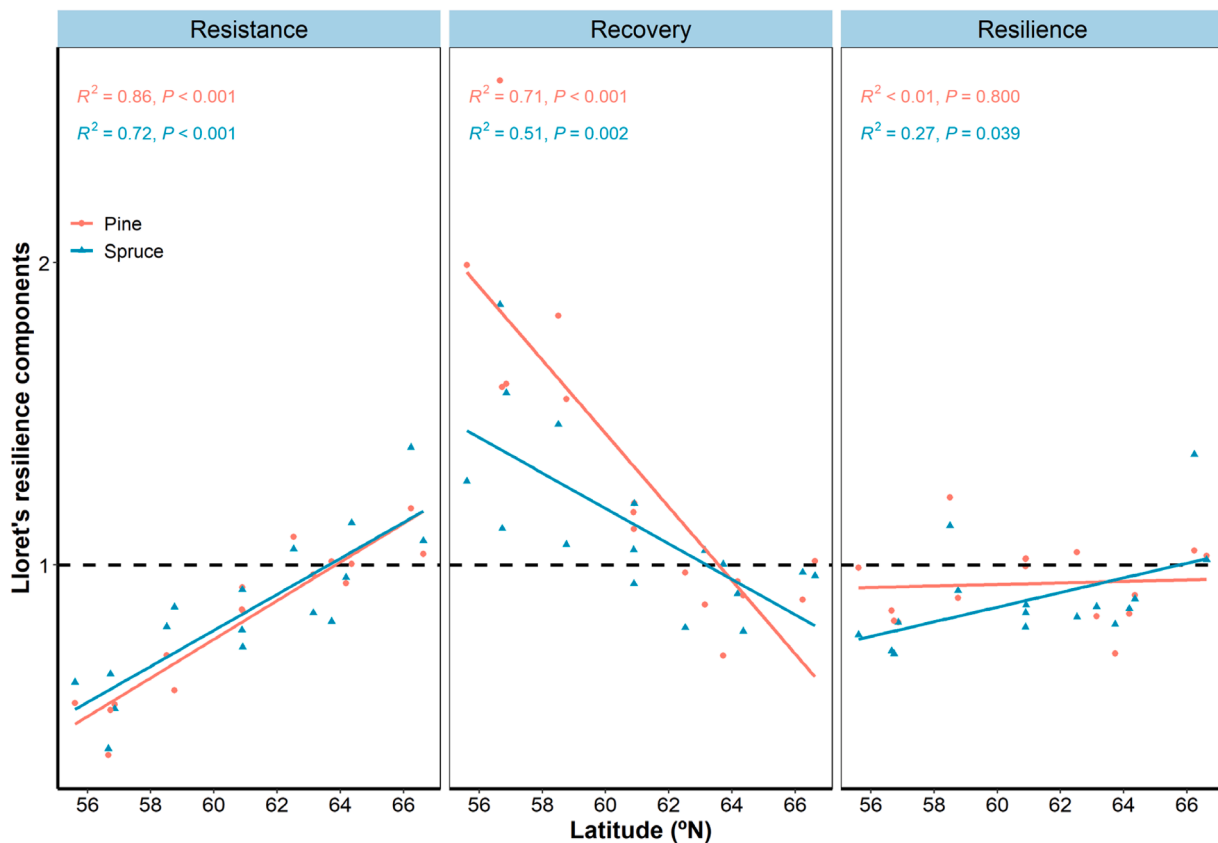
Fig. 6. The Lloret's growth resilience components (average) of pine (red) and spruce (blue) to the extreme drought year of 2018 across latitudinal gradients. The black dashed line means that Lloret's resilience indices are equal to one. R^2: Coefficient of determination, $p < 0.05$ indicates a significant linear trend.

spruce, with spruce showing greater susceptibility to summer drought (Aldea et al., 2022; Lévesque et al. 2014; Gutierrez Lopez et al., 2021), particularly in southern Sweden (Aldea et al., 2023). Though both species exhibit an isohydric physiological property that enables them to regulate transpiration through stomata closure during drought (Belokopytova et al., 2021; Rötzer et al., 2017), the shallow rooting system of spruce makes it more vulnerable to drought conditions (Metslaid et al., 2016). In addition, the late termination of shoot elongation and radial growth in spruce predisposes it to drought compared to pine (Zang et al., 2012). Besides growth reduction caused by decreased photosynthetic activities during drought, repeated and prolonged drought conditions could increase the susceptibility of the species to disease infection (Bolte et al., 2010; Millberg et al., 2015), and potentially exceed the capacity for acclimation i.e., ability to cope with new conditions (Bose et al., 2020).

As the current climate projection predicts drier years during the growing seasons, it would be necessary to adapt the species composition of forest stands, particularly in southern Sweden. Since spruce is more sensitive to drought compared to pine, replanting spruce stands in southern Sweden with spruce without changing stocking and stand management, might not be an optimal choice in the context of predicted climate changes. Greater use of pine should be advocated both planted as monocultures and as mixed forests. A higher resistance to summer drought conditions was found in surveyed pine and spruce mixtures, without a substantial decrease in forest productivity compared to survey monoculture stands in central Europe and the Scandinavian regions (Aldea et al., 2022). The type of species composition affects their growth resistance to drought (Fichtner et al., 2020), with conifers-broadleaves admixture showing greater resistance (Pardos et al., 2021). The drought resistance in pine-spruce admixture would diminish with prolonged drought durations, especially in drought-prone sites (Aldea et al., 2022). As per a recent investigation, mixing species can potentially

alleviate the adverse effects of climate on stand growth, offering a feasible nature-based climate solution (del Río et al., 2022).

Previous research has indicated that local stand conditions, such as density, age, site type and size, significantly influence the growth response of species to drought (Aldea et al., 2023; Gutierrez Lopez et al., 2021; Klisz et al., 2023; Pardos et al., 2021; Pretzsch et al., 2018). In our study, trees had the same age within (even-aged stands) and inter (species) plots on each site. Additionally, the plots were situated within proximity to each other, less than 1 km apart on each site, thereby eliminating the site effect. We did not evaluate the effect of density and size in our study, and as such, this information may be compounded in the analysis. Exploring this aspect is worthwhile, especially in stands without management bias.

5. Conclusion

This study has evaluated and compared the annual growth response of Scots pine and Norway spruce to climate conditions along a latitudinal gradient using pairwise stands distributed throughout Sweden. We showed that both species respond differently to climate conditions, particularly during summer (the growing season). The July temperature of the current growing season was identified as one of the key climate variables affecting the radial growth of pine. The radial growth of spruce is affected by early summer precipitation and standardized precipitation-evapotranspiration index. Though spruce showed high sensitivity to drought conditions, particularly at lower latitudes, under extreme drought, both species could be affected negatively. However, pine has better resilience following extreme drought compared to spruce. While the resilience of spruce varies with latitude, pine showed stability across a latitudinal gradient. Understanding the relationship between climate and growth in the two leading species in Sweden may offer useful guidance on adaptive forest management in the face of

climate change.

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CRediT authorship contribution statement

Friday N. Ogana: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Emma Holmström:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing. **Jorge Aldea:** Data curation, Methodology, Supervision, Writing – review & editing. **Mateusz Liziniewicz:** Conceptualization, Writing – review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2024.110062.

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