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Unpacking climate effects on boreal tree growth: An analysis of tree-ring widths across temperature and soil moisture gradients

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Abstract. The effect of climate change on tree growth in boreal forests is likely mediated by local climate conditions and species-specific responses that vary according to differences in traits. Here, we assess species-specific tree growth responses to climate along gradients of mean annual temperature (MAT) and soil moisture (SMI).

We assessed growth-climate relationships by using tree-ring width data in Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) from the Swedish National Forest Inventory in relation to climatological data along MAT and SMI gradients.

Trees growing in warmer areas responded more negatively to high temperature and more positively to high precipitation. Site-specific SMI only showed an effect on the growth responses in areas of high MAT. The growth-climate response differed between the species; specifically, the growth response to high temperature varied more along the MAT gradient for *P. abies* than for *P. sylvestris*. Growth responses to extreme weather events did not deviate from non-extreme events along the climatic gradients.

Our study suggests that tree growth responses to climate change will depend on tree species, and that the response will be more sensitive to site-specific temperature variations than to local soil moisture conditions. High soil moisture may mitigate the adverse effects of climate change on tree growth in areas with a high mean annual temperature. Although the matching between extreme tree growth and extreme temperature or precipitation years was consistently higher than expected if the two variables were independent, an extreme year is unlikely to cause a tree growth response that markedly diverges from predictions based on linear relationships. Thus, the amplification of negative growth-climate responses during extreme years is likely of limited importance for long-term growth, as such events are inherently rare. However, extreme years may still significantly impact forest productivity by influencing tree mortality, which was beyond the scope of this study. In the face of climate change, forest management should consider site-specific climate conditions and species differences to sustain future forest productivity.

1 Introduction

The boreal forests constitute 27% of the global forest area (FAO, 2020) and play a significant role for global carbon storage (Pan et al., 2024). Presently, about two-thirds of the boreal forest area is managed (Gauthier et al., 2015), and since the growing forest stock in the boreal region as of 2020 corresponds to 24% of the global stock (FAO, 2024), its tree growth also represents

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a significant economic value. However, under global warming, the delivery of these ecosystem services is at stake. The boreal forests and their tree growth may be particularly vulnerable (Babst et al., 2019), as the rate and impact of climate change are predicted to be more pronounced at higher latitudes (IPCC et al., 2019), and there are indications that the boreal biome's continued ability to assimilate and sequester carbon will be at stake by the mid of this century (Rao et al., 2023). There are already indications that global warming has reduced the geographical distribution of the boreal biome, by contraction of forested area in the southern parts of the biome and limited expansion in the north (Rotbarth et al., 2023). Given its global importance, predicting the response of boreal forests to climate change becomes of vital importance.

With ongoing and projected warming of the climate (IPCC, 2023), tree growth is expected to increase in the boreal region (Kauppi et al., 2014; Pau et al., 2022), due to the positive relationship between temperature and photosynthetic activity (Saxe et al., 2001). However, increasing temperature also cause an increase in atmospheric vapour pressure deficit (VPD) which has the potential to reduce plant growth rates (López et al., 2021; Yuan et al., 2019). The temperature-growth response is, however, complex as an increase in growth due to increasing temperature can be expected until a certain point after which the stress from high VPD induces growth decreases instead (Grossiord et al., 2020). Assuming that tree growth has a temperature optimum (Sendall et al., 2015), it is expected that growth in colder regions will increase under global warming, while growth in warmer regions likely will decrease as the temperature optimum may be surpassed. This effect will likely be amplified by a longer growing season resulting from increasing temperature that can enhance tree growth in cold areas, but may have a negative impact in warmer areas due to increasing water demands (Gao et al., 2022). Therefore, it can be hypothesized that a warmer climate is likely to increase tree growth in relatively cold regions, but decrease tree growth in warmer regions.

Tree growth is often influenced by small temperature changes (Reich et al., 2022), and early growth declines may signal more severe impacts, such as dieback (Popa et al., 2024). Extreme events such as droughts may have a far more detrimental effect than the direct effect of increased temperature (Peng et al., 2011), and sometimes affect the tree growth over multiple years (Babst et al., 2012). Years characterized by unusually high temperature may also increase tree mortality and therefore decrease forest productivity (Barber et al., 2000; Peng et al., 2011). Furthermore, the growth response of species that typically exhibit a positive response to elevated temperature can undergo a shift and become adversely impacted by excessively high temperature (Reich et al., 2022). These extreme weather events are predicted with high certainty to become more frequent in the boreal region (IPCC, 2021). For example, an increased global mean temperature of 1.5 °C is predicted to increase the frequency of extreme temperature events by 4.1 per decade compared with levels prior to 1900 (IPCC, 2021). The more frequent extreme events make it vital to understand if these exacerbate the overall effects of climate change on tree growth, and if such events can be predicted based on the same relationship as changes in mean temperature.

Due to the significant impact of local factors, the response to climate change vary widely across geographical locations (D'Orangeville et al., 2016; Ols et al., 2018; Pedlar & McKenney, 2017; Perret et al., 2024), highlighting the necessity to acknowledge the effects of local factors to make reliable predictions of climate change impacts on tree growth. For instance, the potential adverse impacts of rising temperature on tree growth may be mitigated by soil moisture conditions, as studies have shown that the positive correlations between tree growth and temperature is enhanced at sites with high soil moisture

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(Pau et al., 2022). Similarly, increased temperature may aggravate the effects of drought on tree growth more in dry sites (Gagne et al., 2020). The opposing influences of soil moisture might have restrained the influence of rising temperature on tree growth in the boreal region. Nonetheless, recent findings of reduced water content in boreal forest vegetation (Wang et al., 2023) could indicate a diminishing mitigating effect of soil moisture. Correspondingly, there have been suggestions that alterations in soil moisture alone may have neutralized the potential advantages of warming on forest growth in certain areas (D'Orangeville et al., 2016). Therefore, to reliably predict future tree growth, it is important to understand how site-specific characteristics, such as soil moisture, interact with a changing climate.

Tree species may show different responses to climate change, and the response to climate change is expected to vary even among different species of conifers (Jevšenak & Saražin, 2023). While both *Picea abies* and *Pinus sylvestris* adopt a relatively isohydric strategy (Leo et al., 2014), *P. abies* has often been found to be more sensitive to drought than *P. sylvestris* (Gutierrez Lopez et al., 2021; Treml et al., 2022). Furthermore, the differences in drought response between species may be linked to site specific conditions (Feng et al., 2019). For example, in pine trees, the sensitivity to drought may increase at higher elevations, whereas in spruce trees it may decrease (Gutierrez Lopez et al., 2021). Variation in sensitivity and responses to local conditions among tree species may lead to altered species composition, potentially impacting the ecosystem services they provide, such as wood production (Huuskonen et al., 2021). Hence, increased understanding of how tree growth responses interact with local conditions is crucial not only for comprehending ecological responses to global warming but also for practical implications, e.g. for management practices.

Numerous studies have shown an impact of ongoing climate change on forest growth (Aldea et al., 2024; Babst et al., 2019; Boisvenue & Running, 2006; Perret et al., 2024; Popa et al., 2024). However, significant uncertainties remain regarding the interaction between local factors and growth-climate relationships. Without knowledge of how growth-climate responses differ among species and site-specific climate, we risk extrapolating unrepresentative growth trends based on one area or species to those that are governed by different factors. To address this knowledge gap, we quantified the impact of temperature and precipitation on the growth of two boreal tree species, namely Norwegian spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), along a 1450 km climate gradient in Sweden. Specifically, we tested five hypotheses. (H1) Tree growth response to high temperature is negative in regions with high mean annual temperature, but becomes increasingly positive in colder regions. Furthermore, we tested how the tree growth response to other climate predictors (precipitation, VPD, and SPEI) varied along the mean annual temperature gradient. (H2) Increasing soil moisture, as a result of local topography, mitigates the negative impacts of increased temperature and lower precipitation on tree growth. (H3) The growth response and its interaction with mean annual temperature and soil moisture will differ among tree species, with greater responsiveness in *P. abies* than for *P. sylvestris*. (H4) Extreme years in terms of high temperature or low precipitation coincide with years of exceptionally low tree growth more often in regions of high mean annual temperature or low soil moisture. (H5) Tree growth in regions of high mean annual temperature, or low soil moisture is less resistant to temperature and precipitation extremes.

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2 Methods

2.1 Tree core data

We used radial growth data extracted from tree cores collected by the Swedish National Forest Inventory (NFI) between 2018 and 2022 at sites throughout Sweden (SLU, 2022). Similar radial growth data collected by the Swedish NFI has previously been used to examine the impact of oceanic dynamics (Ols et al., 2018) and drought (Aldea et al., 2023) on tree growth. Study areas of 0.25 - 1 km2 squares are systematically chosen through a grid design (Ranneby et al., 1987). Within each area, 6-10 survey plots are randomly distributed. In each plot, all trees within a 7 m radius are identified and the diameter at breast height (DBH) is measured. One to three trees are chosen for a single coring through unequal probability systematic sampling based on probabilities proportional to basal area (see detailed explanation in Fridman et al., 2014). The tree cores are cut with a microtome, treated with zinc paste and tree ring widths (TRW) are analysed through a camera microscope. TRW are measured for the latest sixty annual growth rings of each tree core. Where < 60 annual rings are detected, TRWs for all rings are measured. To minimize significant age-related variations, we exclusively analyzed trees aged > 40 years in our study. Furthermore, we excluded trees growing in wetlands, and on peat soils (organic layer > 30 cm) from the analysis. Prior to analyses, we created ring-width indices (RWI) by detrending each tree's TRW series with a spline function through the R package dplR (Bunn et al., 2023), using a 50% cutoff after 30 years. Nine time-series produced unreasonable RWI with the last year's RWI reaching values magnitudes higher than the rest and were removed from further analysis. We conducted a quality assessment of the RWI series by performing inter-series correlations using the R package dplR (Bunn et al., 2023) for all trees of the same species within the same study area. We excluded trees with an inter-series correlation below the critical confidence level of 0.3281 commonly used in COFECHA (Holmes, 1983). Further, we excluded all study areas containing < 5 trees above the inter-series correlation threshold. The resulting dataset compiled RWI series from 4578 trees (out of 9062) nested in 1979 plots (out of 2970) (Fig. 1).

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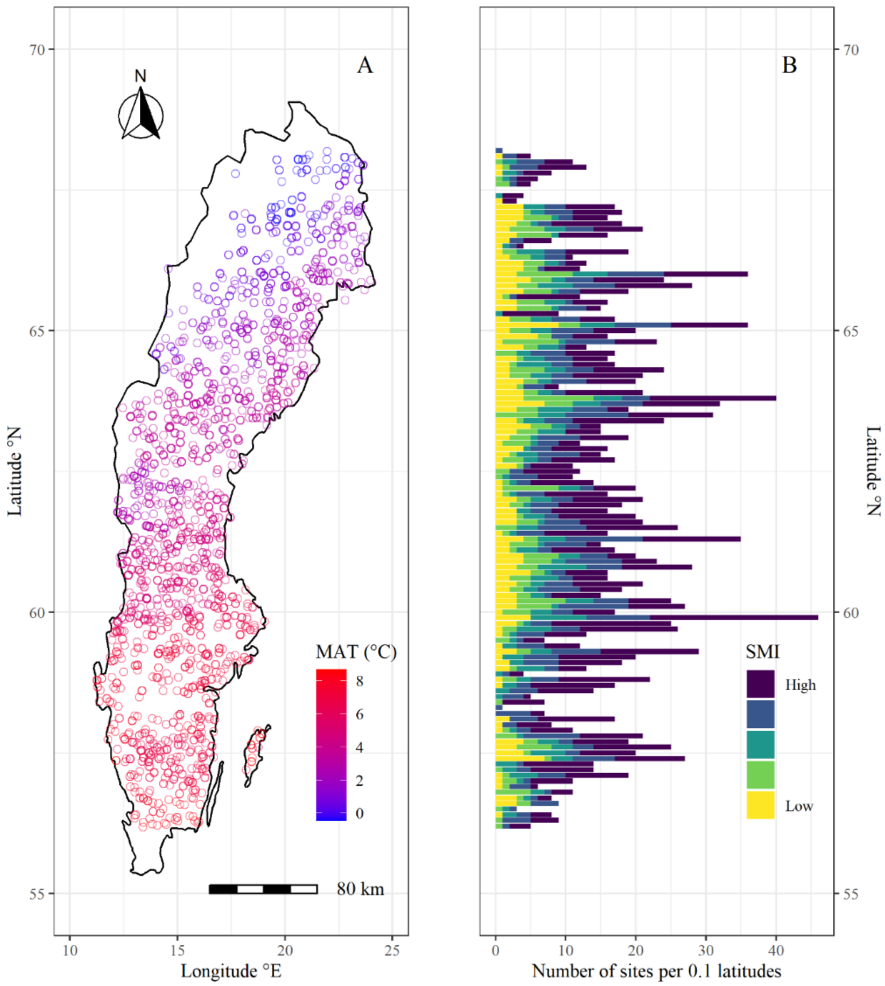

Figure 1. Map of the National Forest Inventory (NFI) sample sites used in this study. (A) shows geographical distribution of plots along a mean annual temperature (MAT) gradient. (B) shows latitudinal distribution of plots along a soil moisture (SMI) gradient, where the x-axis indicates the number of plots per 0.1 latitude.

2.2 Climate and soil moisture data

Data on mean, maximum, and minimum daily temperature, mean daily relative humidity and daily precipitation sum were retrieved for each study site from nationwide modeled data on a 2.5 km resolution grid (Andersson et al., 2021). In addition, we calculated a Standardized Precipitation-Evapotranspiration Index (SPEI) for each month using the R package SPEI (Beguería & Vicente-Serrano, 2023). A necessary component in the SPEI calculation is potential evapotranspiration, which was calculated using the Hargreaves function (Vicente-Serrano et al., 2010), where net radiation was inferred from latitude. Furthermore, we calculated the vapour pressure deficit (VPD) through relative humidity and saturated vapour pressure based on mean temperature (Howell & Dusek, 1995). We also calculated the number of days that the threshold of VPD > 1.5 kPa had been exceeded by calculating the VPD based on maximum daily temperature, because it has been suggested as a threshold

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value to force stomata closure (Kurjak et al., 2012). However, the number of days exceeding the threshold correlated strongly with the mean growing season VPD, and we therefore removed this variable from further analysis. Prior to analysis, data on mean temperature, precipitation sum, SPEI, and VPD were aggregated to growing season means, or sums for precipitation. The growing season for each site and year was calculated by assuming that the growing season starts at the first of four consecutive days with a daily mean temperature > 5 °C and ends after four consecutive days with a daily mean temperature < 5 °C (SMHI, 2011). To avoid anomalies in growing season length, a limit was set where the growing season could not start before March 1st and could not end until September 1st. Prior to analyses, we followed the recommendation of Ols et al (Ols et al., 2023) and detrended each climatic time-series data similarly to the detrending we used for TRW. As some SPEI values were negative, and the detrending function we used cannot handle this, we added the lowest value from all SPEI values so that they were all be positive prior to detrending.

Data on soil moisture for each individual site were retrieved from a Swedish soil moisture model that is largely based on topography and ground water data, and validated by NFI permanent plots (Ågren et al., 2021). The modeled data consist of values ranging from 0 to100, which indicates theprobability of being classified as the “wet” category in the NFI inventory field plots at a 2 m resolution raster grid. We calculated a soil moisture index (SMI) based on mean soil moisture values in a buffer of 25 m around individual trees using zonal statistics in QGIS (QGIS Association, 2021).

2.3 Data analysis

To test our first three hypotheses on how tree growth responses to climatic variables vary along a MAT gradient, an SMI gradient, and between *P. abies* and *P. sylvestris*, we fitted linear mixed models using the R package nlme (Pinheiro et al., 2025). We fitted one model for each climatic variable (temperature, precipitation, SPEI, and VPD) to test the four-way interaction effect of the climatic variable x MAT x SMI x tree species on RWI, as well as the effects of all lower order terms. To account for spatial autocorrelation within the models, we added plot as a random variable. We also estimated variograms at multiple time points to explore the possibilities to include a more complex spatial process. However, we did not find any shape in these variograms, regardless of the model used (exponential, spherical, Gaussian) and this approach was abandoned. To account for temporal autocorrelations, we added a continuous-time autoregressive factor of order 1 (AR1). With this approach, the interaction term between each respective climatic variable and MAT, SMI, or species, represents how the tree growth response to the climatic variable varies along the gradients and between species.

To test our fourth hypothesis that extremely warm or dry years coincide with years of low tree growth more often in regions of high MAT or low SMI, we calculated coincidence rates and tested these along the MAT and SMI gradients as well as between species. To calculate the coincidence rates, we counted the number of extreme events that the RWI series and temperature series have in common (Rammig et al., 2015). We identified extreme years in terms of high temperature as those inside the top 10% of mean growing season temperature for each site. We then identified the years with the lowest 10% of RWI for each tree. We counted the number of coincidences for each tree as the number of years that appeared both among the 10% highest temperature years and 10% lowest RWI years. Finally, we normalized the coincidence rate for each tree by

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dividing the number of coincidences with the total number of extreme years (i.e. 10% of the tree's time series). With this approach, any coincidence rate above 0.1 indicates that years of extremely high temperature coincide with years of extremely low growth on more occasions than can be expected if the two variables are uncorrelated. Any coincidence rate below 0.1 indicates that these years coincide more rarely than can be expected from independence, i.e., a negative correlation between the two variables. We then used linear mixed models to test the three-way interaction effect of MAT x SMI x tree species on the coincidence rates, as well as the effects of all lower order terms. To account for spatial autocorrelation within the models, we added plot as a random variable. We used the same approach for testing coincidence rates with extreme years in terms of low precipitation.

To test our fifth hypothesis that tree growth in regions of high MAT or low SMI is less resistant to extremes, we calculated resistance values for the extreme years and tested these along the MAT and SMI gradients as well as between species. Using the same years of high temperature as those used for calculating the coincidence rates, we determined the resistance values (Lloret et al., 2011) for each tree by dividing the RWI of the target year by the mean RWI of the three preceding years. With this approach, any value < 1 indicates a decrease in growth during the extreme years, and any value > 1 indicates an increase in growth during the extreme years. We then used linear mixed models to test the three-way interaction effect of MAT x SMI x tree species on the resistance values, as well as the effects of all lower order terms. Since we used 10% of each tree's time series (i.e. several years per tree), we added tree identity nested within plot as a random variable to make up for within-tree dependency.

All data analyses were conducted in R (R Core Team, 2021).

3. Results

3.1 Influence of mean annual temperature, soil moisture, and tree species on RWI

Averaged across the entire dataset, temperature and VPD had a positive effect on RWI while precipitation and SPEI had a negative effect (Table A1). However, the direction of these effects was highly dependent on site-specific characteristics. In support of our first hypothesis (H1), we found that the tree growth response to temperature was negative in regions with relatively high MAT, but became increasingly positive in colder regions (Fig. 2; Table 1). The growth response to VPD followed a similar pattern throughout the MAT gradient. The growth response to precipitation and SPEI became increasingly positive with increasing MAT (Fig. A2; Table 1).

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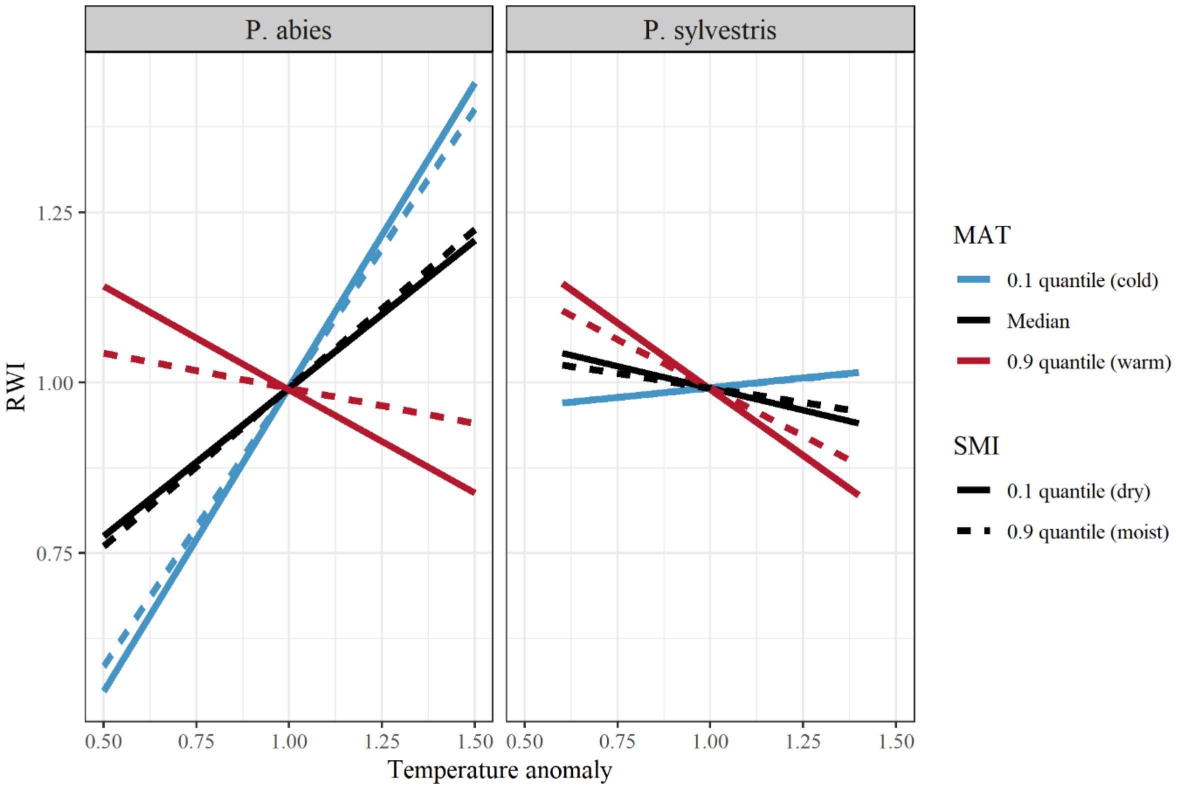

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Figure 2. Model output of the effects of temperature on RWI (ring width index) when separated between low (10% quantile; blue lines), median (black lines), and high (90% quantile; red lines) MAT (mean annual temperature). Lines show the differences between low (10% quantile; solid line), and high (90% quantile; dashed line) SMI (soil moisture index). Facets show differences between species (left = P. abies; right = P. sylvestris). Note that quantiles represent different values for the different species. SMI values for
195 **P. abies (and P. sylvestris in parentheses) are 2.7 (1.9) and 85 (87), for low and high values, respectively. MAT values are 0.9 (1.1), 3.4 (3.7), and 7.4 (7.4), for low, median, and high values, respectively.**

Table 1. Output (t- and p-values) of linear mixed effects models testing the interaction effects of each respective climatic variable (temperature, VPD, precipitation, and SPEI during the growing season), mean annual temperature (MAT), soil moisture (SMI), and tree species (TS), on RWI. Sample size of each model is 1979. Note that main effects are not shown (see Table A1-A4 for main and
200 **random effects values of each model).**

Interaction term	t	p
Temperature x MAT	-17.9	< 0.01
Temperature x SMI	-0.57	0.57
Temperature x TS	32.5	< 0.01
Temperature x MAT x SMI	2.26	0.02
Temperature x MAT x TS	-18.3	< 0.01
Temperature x SMI x TS	-1.81	0.07
Temperature x MAT x SMI x TS	2.22	0.03

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VPD x MAT	-21.8	< 0.01
VPD x SMI	-1.88	0.06
VPD x TS	25.1	< 0.01
VPD x MAT x SMI	4.32	< 0.01
VPD x MAT x TS	-15.1	< 0.01
VPD x SMI x TS	-1.46	0.14
VPD x MAT x SMI x TS	2.24	0.02
Precipitation x MAT	19.7	< 0.01
Precipitation x SMI	0.67	0.50
Precipitation x TS	-8.83	< 0.01
Precipitation x MAT x SMI	-2.47	0.01
Precipitation x MAT x TS	3.39	< 0.01
Precipitation x SMI x TS	0.11	0.91
Precipitation x MAT x SMI x TS	-1.57	0.12
SPEI x MAT	13.0	< 0.01
SPEI x SMI	0.76	0.45
SPEI x TS	-6.79	< 0.01
SPEI x MAT x SMI	-2.81	< 0.01
SPEI x MAT x TS	5.34	< 0.01
SPEI x SMI x TS	-0.04	0.97
SPEI x MAT x SMI x TS	0.33	0.74

Except for a small but significant interaction between SMI and VPD, SMI did not have any effects on the tree growth responses to the studied climatic variables (Fig. 2; Table 1). However, SMI did have interactive effects with MAT in all variables. Although the effects were small, there is an indication that increasing SMI in regions of high MAT mitigates some of the negative effects of high temperature (and VPD) and low precipitation (and SPEI) on tree growth. Hence, our second hypothesis (H2) that increasing SMI mitigates the negative impacts of increased temperature or decreased precipitation, is only partly supported as the effect of SMI is dependent on the site specific MAT.

In support of our third hypothesis (H3), there were clear differences between species in growth response to all studied variables. Mainly, *P. abies* had a stronger interactive effect of temperature on growth compared to *P. sylvestris*. The opposite was true for precipitation, but the interaction effects were smaller. Furthermore, there was a significant MAT x species interaction in all studied variables, where the effect of MAT on the temperature response was stronger for *P. abies*, and weaker for *P.*

sylvestris, while the opposite was true for precipitation. There were no interaction effects between species and SMI for any of the studied variables.

3.2 Impacts of extreme years

Averaged across the entire dataset, the years of high temperature or low precipitation showed low coincidence with years of low RWI (coincidence rate = 0.12 and 0.11 for high temperature and low precipitation, respectively). However, the coincidence rates depended on site-specific characteristics (Table 2). Again, SMI did not have any intrinsic effects on the coincidence rates, while MAT and species did. However, for both species, higher MAT increased the probability of low growth years coinciding with years of extremely high temperature. The same pattern was true for years of low precipitation, although the increase along the MAT gradient was smaller. Furthermore, *P. abies* had lower coincidence rates than *P. sylvestris*, in regards to both high temperature and low precipitation. However, there was an interaction effect between MAT and species where the coincidence rates increased along the MAT gradient more for *P. abies* than for *P. sylvestris* (Fig. 3). In fact, the coincidences with low precipitation hardly increased at all along the MAT gradient for *P. sylvestris*. Again, we observed a minor interaction effect between MAT and SMI, where high SMI decreased the coincidence rates somewhat in warmer regions.

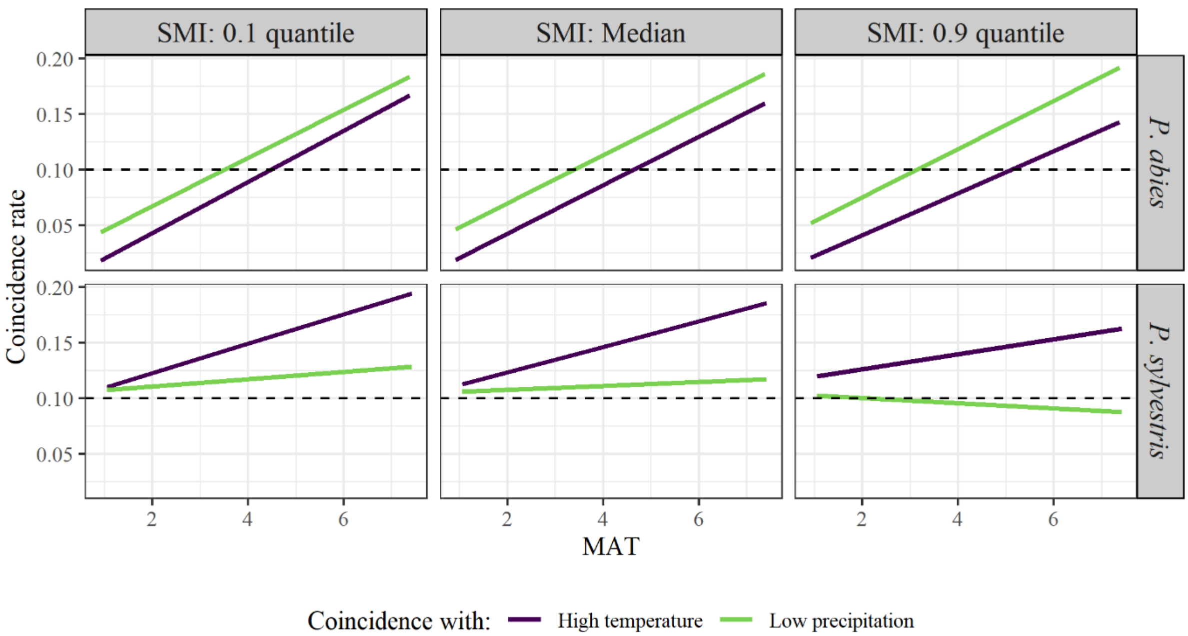

Figure 3. Model output of the effects of MAT on rate of coincidence between years of low growth and high temperature (purple line) or low precipitation (green line). Facets show the differences between low (10% quantile; left graphs), median (middle graphs), and high (90% quantile; right graphs) SMI, as well as between species (upper = P. abies; lower = P. sylvestris). Note that quantiles represent different values for the different species. SMI values for P. abies (and P. sylvestris in parentheses) are 2.7 (1.9), 27 (26), and 85 (87), for low, median, and high values respectively, Dashed line represents the 0.1 threshold, above which the years coincide more often than can be expected from random coincidences.

Table 2. Output (t- and p-values) of linear mixed effects models testing the effects of mean annual temperature (MAT), soil moisture (SMI), and tree species (TS), on coincidence rates between the years of 10% lowest RWI and years of either 10% highest temperature or 10% lowest precipitation. The sample size of both models is 1979.

Term	High temperature		Low precipitation	
	t	p	t	p
SM	1.22	0.22	0.14	0.89
TS	-8.42	< 0.01	-6.75	< 0.01
MAT	8.57	< 0.01	2.25	0.02
SM x TS	-0.45	0.65	0.35	0.72
SM x MAT	-2.25	0.02	-2.00	0.05
TS x MAT	3.86	< 0.01	7.08	< 0.01
SM x TS x MAT	0.49	0.62	1.28	0.20

The results of coincidence rates were largely reflected in the resistance values (Table 3). The resistance values to the years of high temperature ranged between 0.02 and 4.54, while the values to the years of low precipitation ranged between 0.02 and 4.44. The resistance values decreased along the MAT gradient for both species, while SMI did not have any intrinsic effects. There were clear differences between the species, where *P. abies* generally had higher resistance values than *P. sylvestris*. Interestingly, *P. abies* was more resistant to years of high temperature than to years of low precipitation while the opposite was true for *P. sylvestris* (Fig. 4). In fact, in wet areas across the MAT gradient, individual *P. sylvestris* trees rarely dropped below a resistance value of 1 to years of low precipitation. This indicates that no observed lack of precipitation during the study period was detrimental to *P. sylvestris* in areas of high SMI.

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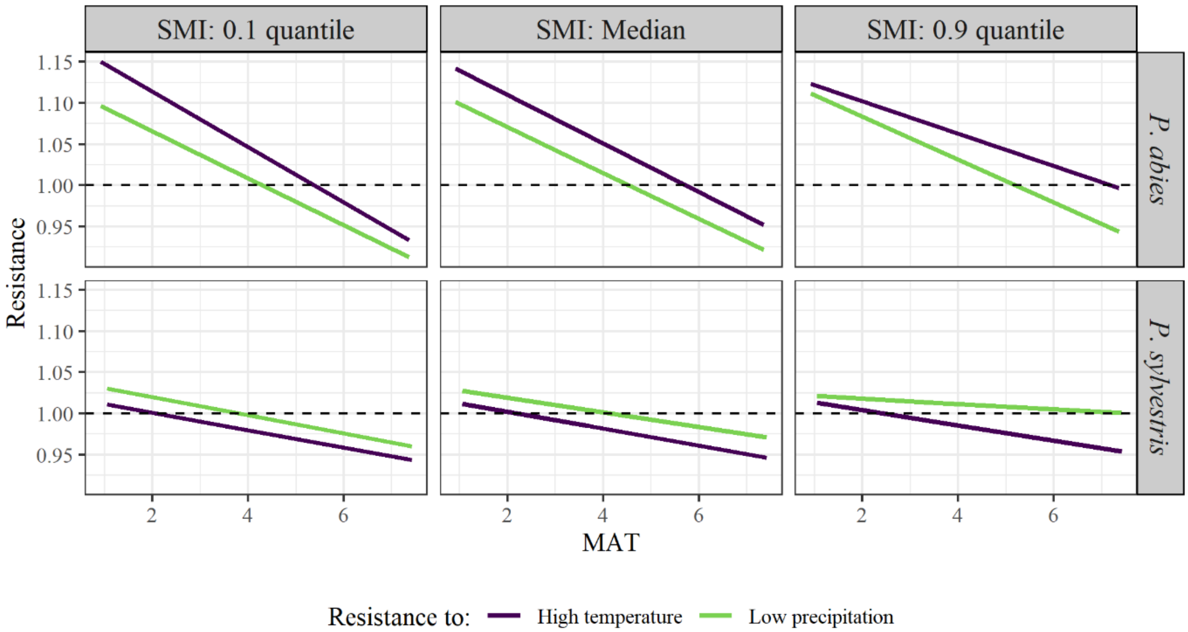

Figure 4. Model output of the effects of MAT on tree growth resistance to years of high temperature (purple line) or low precipitation (green line). Facets show the differences between low (10% quantile; left graphs), median (middle graphs), and high (90% quantile; right graphs) SMI, as well as between species (upper = P. abies; lower = P. sylvestris). Note that quantiles represent different values for the different species. SMI values for P. abies (and P. sylvestris in parentheses) are 2.7 (1.9), 27 (26), and 85 (87), for low, median, and high values respectively, Dashed line represents the 1.0 threshold, below which the extremes have a negative impact on tree growth.

Table 3. Output (t- and p-values) of linear mixed effects models testing the effects of mean annual temperature (MAT), soil moisture (SMI), and tree species (TS), on resistance values to the years of either 10% highest temperature or 10% lowest precipitation. The sample size of both models is 1979.

	High temperature		**Low precipitation**	
	t	**p**	**t**	**p**
SM	0.06	0.95	-1.30	0.19
TS	13.8	< 0.01	6.73	< 0.01
MAT	-6.99	< 0.01	-6.87	< 0.01
SM x TS	-2.04	0.04	1.41	0.16
SM x MAT	0.49	0.62	2.66	< 0.01
TS x MAT	9.50	< 0.01	-6.76	< 0.01
SM x TS x MAT	2.77	< 0.01	-1.11	0.27

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4. Discussion

In this study, we examined the regional differences in tree growth responses to climatic variables and found that the growth response to temperature and precipitation is dependent on the site-specific mean annual temperature (MAT). Furthermore, we found that while soil moisture (SMI) has an insignificant intrinsic effect, it can somewhat mitigate negative effects of changing temperature and precipitation on growth in areas of high MAT.

4.1 The influence of local temperature on tree growth responses to environmental changes

We found support for our first hypothesis (H1) that the response of tree growth to temperature and precipitation shifts along a gradient of site-specific MAT (Fig. 2; Table 1). In terms of growth responses to temperature, similar results have been observed in earlier studies, showing progressively negative correlations to temperature along gradients of increasing mean growing season temperature (Klesse et al., 2018; Ols et al., 2018), or positive along latitudinal gradients (D'Orangeville et al., 2016; Li et al., 2020). As photosynthetic rates increase with temperature (Kellomäki & Wang, 1996), this likely underlines the positive growth response to temperature observed in the colder regions of our study. However, in the warmer regions, the positive effects of increased temperature might be outweighed by heat-stress resulting from temperatures exceeding an optimum threshold (Gantois, 2022). Such heat-stress will eventually reach a critical point, resulting in tree mortality (Huang et al., 2015). Even if this critical threshold is not surpassed, the interplay between heat stress and other disturbances, such as pest infestations, has the potential to intensify stress levels and induce significant changes well before reaching the critical temperature threshold (Reyer et al., 2015). The divergent responses to increased temperature observed in our study can, therefore, have significant implications for the functioning and management decisions of boreal forest ecosystems. Hence, our findings need to be considered when developing future management strategies aimed at ensuring the health of these ecosystems. This will be particularly important in parts of the boreal biome where forestry is important for the economy and the implications for tree growth have societal significance.

For precipitation, we found that colder regions respond more negatively to increased precipitation. The effect of precipitation along our temperature gradient is geographically inconsistent with studies suggesting that precipitation is consistently positively correlated to tree growth, regardless of site-specific temperature or latitude (Li et al., 2020; Restaino et al., 2016; Walker et al., 2015). However, our results are in accordance with studies by D'Orangeville et al. (2016) and Babst et al. (2013) that have demonstrated an increasingly negative correlation with latitude. The studies conducted by Walker et al. (2015) and D'Orangeville et al. (2016) both investigated black spruce in North America, but reported different results regarding the impact of precipitation. However, the study by Walker et al. (2015) is a comparison of north- and south-facing slopes rather than large geographical areas. This suggests that variation in growth responses to precipitation becomes evident on larger spatial scales rather than the smaller scale variation generated by for example slope aspect. However, a positive growth response to precipitation across a large spatial scale is not uniform among all tree species and has not been observed for species in genera such as *Larix*, *Pinus* (Li et al., 2020) and *Pseudotsuga* (Restaino et al., 2016). Thus, the growth responses to precipitation

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across large spatial scales seems to be complex, and future studies need to confirm whether our results are general or only representative for the Fennoscandian boreal forest. Climate models generally predict increased precipitation across our study area (IPCC, 2023), which might mitigate the negative effect of increasing temperature on tree growth in the warmer parts of the boreal forest. However, the increased precipitation is expected to come as heavy rainfalls rather than a temporally even increase (IPCC, 2021), and the mitigating effect from changed precipitation may therefore be smaller than expected. In fact, a positive tree growth-precipitation correlation can be weakened if the precipitation occurs as infrequent heavy rains (Land et al., 2017). Therefore, while increased precipitation as an average during the growing season is positive in the warmer regions of our study, an increase in precipitation through intermittent heavy rainfall may show less positive effects.

4.2 The effect of soil moisture on tree growth responses to environmental changes

Our second hypothesis (H2) was only partly supported, trees' growth response to temperature and precipitation was weakly affected by local soil moisture, and only in warmer regions (Fig. 2; Table 1). This weak effect is surprising as an earlier study from Canada found that trees growing in already wet areas showed a weak response to drought, while tree growth in drier areas was reduced to zero during drought (Huang et al., 2015). However, our results are in line with Lange et al's (2018) finding that the effect of small scale site-specific conditions are weak in comparison to larger scale climate regimes. While the intrinsic effect of SMI in our study was small, it did interact with MAT so that the negative effects of high temperature was mitigated by high soil moisture values in warmer areas (Fig. 2). The photosynthesis of several tree species has previously been found to be more affected by low soil moisture when exposed to warming (Reich et al., 2018). Possibly, in our study system, only trees growing in warm areas experienced an atmospheric water demand that was high enough for soil moisture to actually limit the tree growth. Future climate change may push previously cold areas into warmer states, making the buffering effect of soil moisture relevant in more locations and increasingly critical in the region covered by our study. This may complicate climate change adaptations of forest management, as site-specific soil moisture should be considered in warm areas, while other factors such as MAT or VPD should take precedence when adapting management to climate change in relatively cold areas.

4.3 Differences between species

We found contrasting results in regard to our third hypothesis (H3) that *P. abies* would exhibit a greater growth response to climatic factors than *P. sylvestris* (Fig. 2; Table 1). While *P. abies* indeed showed a generally more positive response to increasing temperature than *P. sylvestris*, the opposite was true for increasing precipitation where *P. sylvestris* showed a more positive response compared to *P. abies*. This is surprising as *P. sylvestris* has been shown to physiologically benefit more from warming than *P. abies* (Kivimäenpää et al., 2017). Furthermore, *P. sylvestris* has a higher root:leaf ratio than *P. abies* (Helmisaari et al., 2007), which ought to make them less dependent on sufficient precipitation and less detrimentally affected by increasing temperature. However, *P. sylvestris* may act more isohydric than *P. abies*, at least based on sapflow responses to drought conditions (Leo et al., 2014). This may explain the differences seen in our study as high temperature would force a stronger growth decline through increased atmospheric water demand, and increasing precipitation may alleviate such stress more for *P. sylvestris* than for *P. abies*. Interestingly, we did not find any interactive effects between species and soil moisture, even though they are known to separate their distribution based on soil water contents (Sutinen & Middleton, 2020). On the contrary, the differences in growth-climate responses between our studied species was more dependent on MAT. Our results indicate that climate adaptation in forest management needs to consider the tree species, where the growth of *P. abies* likely tolerate larger temperature increases, especially in colder regions, whereas *P. sylvestris* may benefit from increased precipitation in warmer regions.

4.4 The effect of extreme years on tree growth

Extreme events have been noted to be important indicators for tree growth, where e.g. drought events inferred by SPEI or climatic water deficit (Wu et al., 2022), or persistent extreme heat waves (Yang et al., 2023) might cause growth reductions. Extreme weather conditions may also be more influential than changes of the growing season averages for trees in a specific site (Sanginés de Cárcer et al., 2018). We did find support for our fourth and fifth hypotheses (H4 and H5) that climatically extreme years would coincide with weakened tree growth more often in warm areas (Fig. 3; Table 2), and that the resistance to these extremes would follow a MAT and SMI gradient (Fig. 4; Table 3). However, the coincidence rates and resistance values calculated here followed much the same pattern as for the growth response models conducted on the whole dataset. Furthermore, while the mean coincidence rates observed in our study are consistently larger than what we could expect if extreme events and growth were uncorrelated, the rates are relatively low (Zhang et al., 2023). Given these values, it is unlikely that a year of extreme temperature or precipitation sum would have an extreme effect on tree growth that deviate from predictions based on linear relationships across climate variable space. Therefore, amplification of negative growth-climate responses during extreme years may be of limited importance for long-term growth as these events are inherently rare. However, the extremes of our studied time series might not be representative of those that may come with further climate change (IPCC, 2021). Furthermore, it is possible that the extremes in our study, based on high or low temperature or precipitation sums during the growing season, are too blunt to capture biologically important extreme weather conditions. Climate change may also affect forests in more ways than what we have presented here due to, for example, more frequent forest fires and insect outbreaks. As our analyses consider only living trees, it is possible that there are effects of extreme years on mortality rates that we have not captured here. However, these effects are not within the scope of our study. Therefore, our results showing that extremes affect growth-climate responses similarly to that of a growing season average, should be considered with caution.

5. Conclusion

We found that warmer areas (higher MAT) in the studied geographic region exhibited more negative growth responses to high temperature and more positive responses to high precipitation. Contrary to the effects of MAT, SMI only mitigated negative

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climatic effects in areas of high MAT. We also found that on average *P. abies* responds more positively to high temperature than *P. sylvestris*, but that the difference in response is highly dependent on local MAT. Moreover, growth responses to extreme weather events, although sometimes co-occurring with years of low growth, followed similar patterns to those observed during non-extreme conditions along the MAT and SMI gradients. This consistency suggests that climate change-adapted management to mitigate extreme events does not require different considerations than managing for general climate change. Overall, our study suggests that management practices tailored to site-specific and species-specific requirements are crucial to maintaining high tree growth and the overall health of boreal forests.

Appendix A

Effect tables

Table A1. Output (t- and p-values) of linear mixed effects models testing the effects of temperature, mean annual temperature (MAT), soil moisture (SMI), and tree species (TS), on RWI. For main-effect terms, the variance inflation factor (VIF) is given (computed from the r-package *car* on a model containing only the main effects). Model sample size is 4578 RWI nested in 1979 plots. Phi-value of the AR1 temporal autocorrelation = 0.40. Plot intercept variance = 2.77×10^{-11}. Tree nested within plot variance = 1.14×10^{-11}.

Term	t	p	VIF
Temperature	6.74	< 0.01	1.000
SMI	0.54	0.59	1.008
TS	-32.1	< 0.01	1.006
MAT	17.6	< 0.01	1.013
Temperature x SMI	-0.57	0.57	-
Temperature x TS	32.5	< 0.01	-
SMI x TS	1.77	0.08	-
Temperature x MAT	-17.9	< 0.01	-
SMI x MAT	-2.19	0.03	-
TS x MAT	18.0	< 0.01	-
Temperature x SMI x TS	-1.81	0.07	-
Temperature x SMI x MAT	2.26	0.02	-
Temperature x TS x MAT	-18.3	< 0.01	-
SMI x TS x MAT	-2.17	0.03	-
Temperature x SMI x TS x MAT	2.22	0.03	-

Table A2. Output (t- and p-values) of linear mixed effects models testing the effects of precipitation, mean annual temperature (MAT), soil moisture (SMI), and tree species (TS), on RWI. For main-effect terms, the variance inflation factor (VIF) is given

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(computed from the r-package *car* on a model containing only the main effects). Model sample size is 4578 RWI nested in 1979 plots. Phi-value of the AR1 temporal autocorrelation = 0.40. Plot intercept variance = 5.57×10^{-12}. Tree nested within plot variance = 5.10×10^{-11}.

Term	t	p	VIF
Precipitation	-14.0	< 0.01	1.000
SMI	-0.69	0.49	1.008
TS	8.29	< 0.01	1.006
MAT	-18.9	< 0.01	1.013
Precipitation x SMI	0.67	0.50	-
Precipitation x TS	-8.83	< 0.01	-
SMI x TS	-0.13	0.90	-
Precipitation x MAT	19.7	< 0.01	-
SMI x MAT	2.45	0.01	-
TS x MAT	-3.32	< 0.01	-
Precipitation x SMI x TS	0.11	0.91	-
Precipitation x SMI x MAT	-2.47	0.01	-
Precipitation x TS x MAT	3.39	< 0.01	-
SMI x TS x MAT	1.53	0.13	-
Precipitation x SMI x TS x MAT	-1.57	0.12	-

Table A3. Output (t- and p-values) of linear mixed effects models testing the effects of SPEI, mean annual temperature (MAT), soil moisture (SMI), and tree species (TS), on RWI. For main-effect terms, the variance inflation factor (VIF) is given (computed from the r-package *car* on a model containing only the main effects). Model sample size is 4578 RWI nested in 1979 plots. Phi-value of the AR1 temporal autocorrelation = 0.40. Plot intercept variance = 2.27×10^{-11}. Tree nested within plot variance = 7.59×10^{-11}.

Term	t	p	VIF
SPEI	-8.48	< 0.01	1.000
SMI	-0.78	0.44	1.008
TS	6.52	< 0.01	1.006
MAT	-12.5	< 0.01	1.013
SPEI x SMI	0.76	0.45	-
SPEI x TS	-6.79	< 0.01	-
SMI x TS	0.02	0.99	-
SPEI x MAT	13.0	< 0.01	-
SMI x MAT	2.77	< 0.01	-

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TS x MAT	-5.17	< 0.01	-
SPEI x SMI x TS	-0.04	0.97	-
SPEI x SMI x MAT	-2.81	< 0.01	-
SPEI x TS x MAT	5.34	< 0.01	-
SMI x TS x MAT	-0.28	0.78	-
SPEI x SMI x TS x MAT	0.33	0.74	-

380 **Table A4. Output (t- and p-values) of linear mixed effects models testing the effects of VPD, mean annual temperature (MAT), soil moisture (SMI), and tree species (TS), on RWI. For main-effect terms, the variance inflation factor (VIF) is given (computed from the r-package *car* on a model containing only the main effects). Model sample size is 4578 RWI nested in 1979 plots. Phi-value of the AR1 temporal autocorrelation = 0.40. Plot intercept variance = $1.72x10^{-11}$. Tree nested within plot variance = $5.63x10^{-11}$.**

Term	t	p	VIF
VPD	12.7	< 0.01	1.000
SMI	1.77	0.08	1.008
TS	-24.3	< 0.01	1.006
MAT	21.0	< 0.01	1.013
VPD x SMI	-1.88	0.06	-
VPD x TS	25.11	< 0.01	-
SMI x TS	1.40	0.16	-
VPD x MAT	-21.8	< 0.01	-
SMI x MAT	-4.11	< 0.01	-
TS x MAT	14.6	< 0.01	-
VPD x SMI x TS	-1.46	0.14	-
VPD x SMI x MAT	4.32	< 0.01	-
VPD x TS x MAT	-15.1	< 0.01	-
SMI x TS x MAT	-2.15	0.03	-
VPD x SMI x TS x MAT	2.24	0.02	-

Appendix B

Correlations among explanatory variables

The explanatory variables used in our study can be divided into two sections: The temporally static variables of mean annual temperature (MAT) and soil moisture (SMI); and the temporally dynamic climatic variables or Temperature, Precipitation, VPD, and SPEI. The autocorrelation between our static variables, MAT and SMI, when calculated through the entire dataset

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is -0.16. The autocorrelation among our dynamic variables, Temperature, Precipitation, VPD, and SPEI, varies but never exceeds 0.7 (Figure A1).

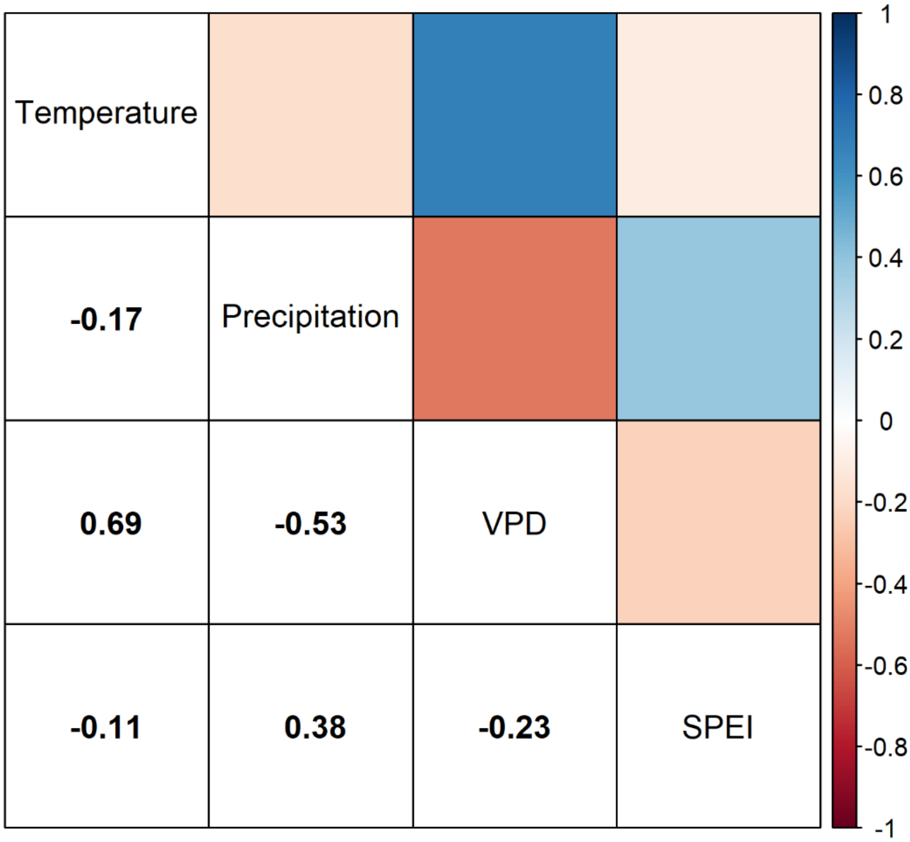

Figure A1. Correlation values among temporally dynamic explanatory climatic variables.

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Appendix C

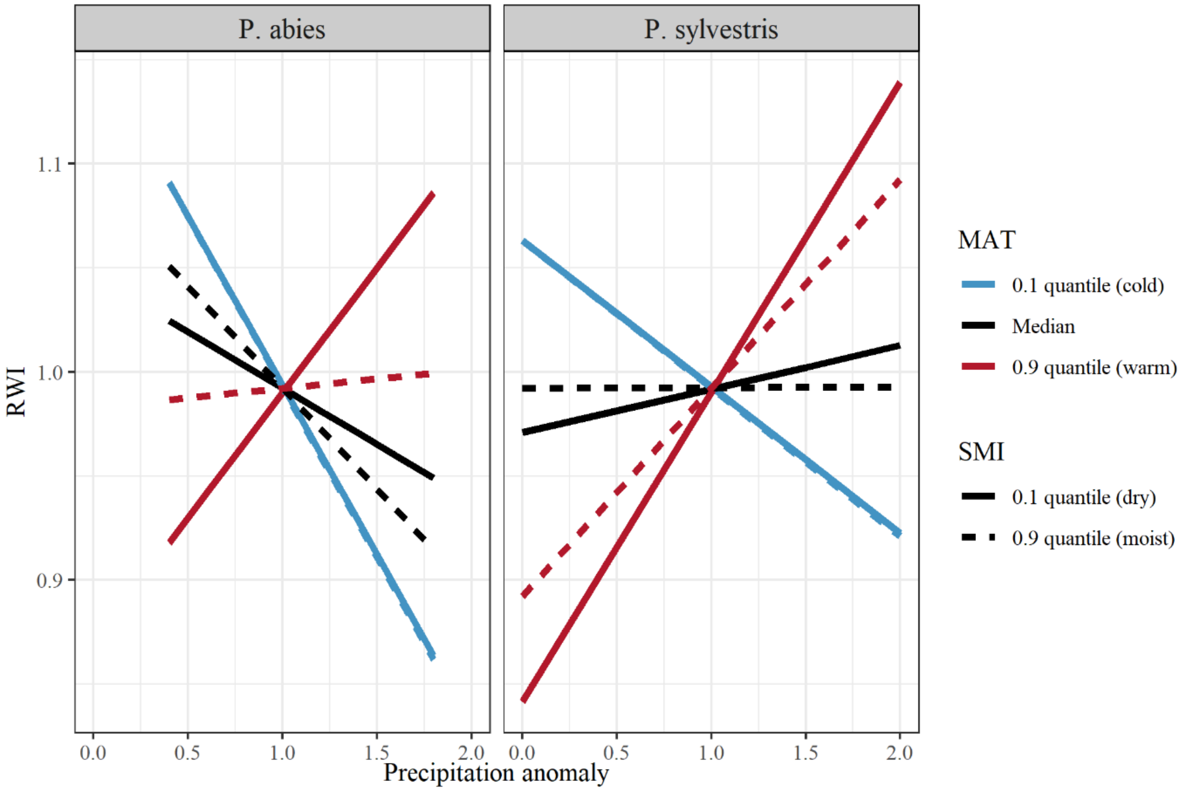

Figure A2. Model output of the effects of precipitation on RWI (ring width index) when separated between low (10% quantile; blue lines), median (black lines), and high (90% quantile; red lines) MAT (mean annual temperature). Lines show the differences between low (10% quantile; solid line), and high (90% quantile; dashed line) SMI (soil moisture index). Facets show differences between species (left = P. abies; right = P. sylvestris). Note that quantiles represent different values for the different species. SMI values for P. abies (and P. sylvestris in parentheses) are 2.7 (1.9) and 85 (87), for low and high values, respectively. MAT values are 0.9 (1.1), 3.4 (3.7), and 7.4 (7.4), for low, median, and high values, respectively.

Code availability

All code used in this study can be found at: https://github.com/LundgrenAndreas/Research/tree/main/Project_GeoTree

Data availability

Data on tree ring widths and forest characteristics are available for download at the Swedish National Forest Inventory website: https://www.slu.se/en/Collaborative-Centres-and-Projects/the-swedish-national-forest-inventory/foreststatistics/microdata-for-download/ (see Fridman et al., 2014 for details on the dataset).

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Data on climatic variables are available for download at the SMHI (Swedish Meteorological and Hydrological Institute) website: https://www.smhi.se/data/utforskaren-oppna-data/meteorologisk-ateranalys-smhigridclim-uerra-harmonie (see Andersson et al., 2021 for details on the dataset).

Data on modeled soil moisture are available for download at: https://www.slu.se/en/departments/forest-ecology-management/forskning/soil-moisture-maps/here-are-the-maps/.

All data used in this paper (except site coordinates) are available at: https://doi.org/10.5281/zenodo.12655494 (Lundgren et al., 2025).

Author contributions

AL: Conceptualization, methodology, investigation, validation, writing – original draft, project administration, and funding acquisition.

JS: Conceptualization, methodology, validation, writing – review and editing, project administration, and funding acquisition.

JE: Conceptualization, methodology, validation, writing – review and editing.

GG: Conceptualization, methodology, validation, writing – review and editing, and funding acquisition.

Competing interests

The authors declare that they have no conflict of interest.

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