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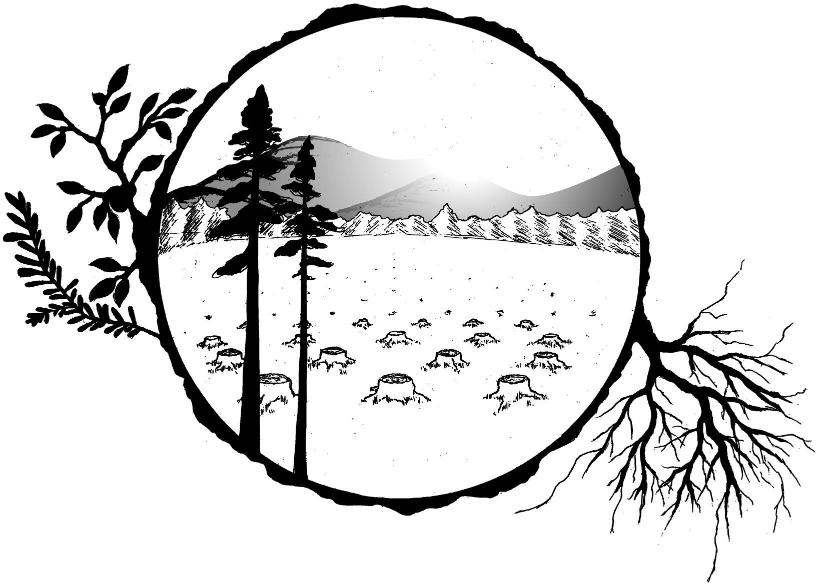
Effects of climate change and disrupted tree continuity on boreal forest productivity

ANDREAS LUNDGREN



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Abstract

The boreal forest biome is a valuable carbon sink as well as a producer of several ecosystem services. In recent years, forests around the boreal biome have exhibited declining productivity in terms of tree growth. The declining growth may be a consequence of a variety of factors. In this thesis, I use the findings from four studies (I-IV) to explore forest growth in relation to two specific factors: climatic variables and clearcut forestry, as well as the interaction between the two. In the first study (I), I use data collected by the Swedish National Forest Inventory to show that tree growth-responses to climatic variables differ depending on local climatic factors. Specifically, trees growing in already warm regions are likely to decrease in growth with increasing temperature while the opposite is true for those growing in colder regions. Areas of high soil moisture may slightly mitigate the detrimental temperature-effect in warm regions. In the second study (II), I compare tree growth-responses to climatic variables between forests that were clearcut ~60 years earlier and forests that likely have never been clearcut. Tree growth in previously clearcut forests revealed to be more unstable between years and respond stronger to climatic variability. As an example, during the extreme drought year of 2018, the clearcut forests experienced worse growth declines than the non-clearcut forests. In the third study (III), I used a soil incubation experiment and found that the respiration rate from soils of recent clearcuts are more sensitive to warming than that of mature forests. However, the increase in respiration rate due to warming was highly transient, and the effect disappeared as the incubation proceeded, likely indicating differences in labile and recalcitrant substrates as a potential driver of the temperature sensitivity. The fourth study (IV) shows long-term differences between clearcut and non-clearcut forests in soil microbial communities important for decomposition, but these differences do not seem to correlate with aggravated nutrient limitations or long-term productivity declines. In conclusion, both climatic variables and clearcutting likely affect growth in the boreal forest, yet their effects are not unidirectional.

Keywords: boreal, climate, clearcut, tree growth, decomposition

Effekter av klimatförändringar och avbruten trädkontinuitet på boreal skogsproduktivitet

Sammanfattning

Den boreala skogen är en värdefull kolsänka samt en producent av flera ekosystemtjänster. Under de senaste åren har boreala skogar uppvisat en minskad tillväxt. Den avtagande tillväxten kan vara en följd av en rad olika faktorer. I denna avhandling använder jag resultaten från fyra studier (I–IV) för att undersöka skogstillväxt i relation till två specifika faktorer: klimatvariabler och trakthyggesbruk, samt samspelet mellan dessa. I den första studien (I) använder jag data insamlade av Riksskogstaxeringen för att visa att träds tillväxtrespons till klimatvariabler skiljer sig beroende på lokala klimatförhållanden. Mer specifikt är det sannolikt att träd som växer i redan varma regioner minskar i tillväxt vid stigande temperaturer, medan det motsatta gäller för träd som växer i kallare regioner. Områden med hög markfuktighet kan i viss mån mildra den negativa temperatureffekten i varma regioner. I den andra studien (II) jämför jag träds tillväxtrespons till klimatvariabler mellan skogar som kalavverkades för cirka 60 år sedan och skogar som sannolikt aldrig har kalavverkats. Tillväxten i tidigare kalavverkade skogar visade sig vara mer instabil mellan år och reagera starkare på klimatvariation. Som exempel uppvisade de kalavverkade skogarna större tillväxtminskningar än de icke-kalavverkade skogarna under torkåret 2018. I den tredje studien (III) använde jag ett inkubationsexperiment som visar att markrespirationen i nyligen kalavverkade områden är mer känslig för uppvärmning än i äldre skogar. Ökningen i respiration till följd av uppvärmning var dock övergående och avtog under experimentets gång, vilket sannolikt indikerar skillnader mellan lätt- och svårnedbrytbara substrat som en möjlig drivkraft bakom temperaturkänsligheten. Den fjärde studien (IV) visar långsiktiga skillnader mellan kalavverkade och icke-kalavverkade skogar gällande markens mikrobiella samhällen som är viktiga för nedbrytning, men att dessa skillnader inte tycks korrelera med förvärrade näringsbegränsningar eller långsiktiga minskningar i produktivitet. Sammanfattningsvis påverkar både klimatvariabler och kalavverkning sannolikt tillväxten i den boreala skogen, men påverkans riktning är inte universell.

Keywords: boreal, klimat, trakthyggesbruk, kalavverkning, trädtillväxt, nedbrytning

“*Being dimly aware that human beings had learned to tell the age of a tree by counting the rings, the original Counting Pines decided that this was why humans cut trees down. Overnight every Counting Pine readjusted its genetic code to produce, at about eye-level on its trunk, in pale letters, its precise age. Within a year they were felled almost into extinction by the ornamental house number plate industry.*”

Terry Pratchett

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Lundgren A., Strengbom J., Edvardsson J. & Granath G. 2025. Unpacking climate effects on boreal tree growth: an analysis of tree-ring widths across temperature and soil moisture gradients. Biogeosciences 22, 6427-6443. https://doi.org/10.5194/bg-22-6427-2025

II. Lundgren A., Granath G. & Strengbom J. 2026. Disrupting tree continuity through clearcut forestry can alter the climate sensitivity of future tree growth in northern Sweden. Forest Ecology and Management 599. https://doi.org/10.1016/j.foreco.2025.123295

III. Lundgren A., Clemmensen K. & Strengbom J. Temperature sensitivity of soil CO_2 respiration can be aggravated through clearcut forestry (*Manuscript*).

IV. Gangiah T., Lundgren A., Clemmensen K., Granath G., Strengbom J. & Lindahl B. Clearcutting alters mycorrhizal communities but does not reduce long-term productivity (*Manuscript*).

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List of tables

List of figures

Abbreviations

BAI	Basal Area Increment
DBH	Diameter at Breast Height (1.3 m)
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
MS	Mean Sensitivity
NFI	National Forest Inventory
PLFA	Phospholipid Fatty Acid
RH	Relative Humidity
RWI	Ring Width Index
SMHI	Swedish Meteorological and Hydrological Institute
SOC	Soil Organic Carbon
SOM	Soil Organic Matter
SPEI	Standardized Precipitation Evapotranspiration Index
TRW	Tree Ring Width
VPD	Vapour Pressure Deficit

AI declaration

In this thesis, generative AI (in the form of ChatGPT (prior to OpenAI's DoD-deal), Perplexity, Elicit, and ResearchRabbit) have been used as discussion partners, sources of inspiration, literature-finders, sanity-checkers, and coding-instructors.

1. Introduction

1.1 The Boreal Forest

The boreal forest (Figure 1) is one of the largest forest biomes of the world (FAO 2020). It is characterised by forests of relatively low productivity and low species diversity (Brandt et al 2013). However, the boreal forest constitutes roughly one third of the entire global terrestrial carbon stock and accounts for about a fifth of all the global forest carbon sequestration every year (Pan et al 2011), making it a vitally important asset in the perspectives of climate change mitigation. Other than acting as a carbon sink, the boreal forest can provide large quantities of renewable resources, such as lumber and paper (Mery et al 2010), further adding to its societal importance.

Lately, the boreal forest has been facing a number of problems (e.g. heat waves (Rao et al 2023), droughts (Wolf et al 2023), insect outbreaks (Jaime et al 2024), and oligotrophication through declining nitrogen (N) availability (Bassett et al 2026)) and the possibility for sustained growth of the forest has been called into question (Rao et al 2023). In fact, in many regions of the boreal biome, forests have experienced ecosystem-wide growth declines in the recent past (Matsala et al 2026; Jin et al 2016; Piao et al 2011; Parent & Verbyla 2010). Following this, the carbon sink potential of the boreal forest has greatly decreased in recent years (Naturvårdsverket 2025; Pan et al 2024; see also Li et al 2025 for carbon losses in temperate ecosystems during the last decade). There are, however, some exceptions to the general pattern. For example, increase in growth trends throughout the recent past has been reported from parts of the Russian boreal forest (Lapenis et al 2005). In contrast, from the Fennoscandian boreal forest, a productivity decline has been observed from ~2015 onwards (Breidenbach et al 2024; Henttonen et al 2024; Laudon et al 2024). Since a declining productivity of the boreal forest could have widespread negative effects on climate change mitigation and resource acquisition, it is important to know what causes growth increases and declines so that appropriate measures can be taken to ensure a sustained growth of the boreal forest.

Figure 1. Map of a portion of the northern hemisphere, projected through an arctic polar stereographic coordinate system. The geographical range of the boreal forest biome is highlighted in green. Geographical data retrieved from Olson et al 2001.

1.2 Climatic controls

The climate of the boreal forest is characterised by low mean annual temperatures, strong seasonality, and short growing seasons. These conditions require a number of morphological and physiological adaptations of the organisms. Plants in this region typically have leaves with higher proportions of structural components in relation to photosynthetic components (González-Zurdo et al 2016). Moreover, they often have physiological adaptations such as the downregulation of photosynthesis during periods of low temperature (Chang et al 2021). While these adaptations enable boreal vegetation to function under harsh climatic conditions, their growth is nevertheless constrained by climate (Jarvis & Linder 2000).

1.2.1 Climate change in the boreal biome

At the time of writing this thesis, the world experiences a warming climate at a global average of 1.1 °C compared to pre-industrial temperatures, and future predictions range from 1.5 to 4 °C warming at the turn of the century (IPCC 2023). However, the high latitudes are expected to experience an even greater warming than the global average (IPCC 2023), and parts of the boreal region already experienced an average increase of 2 °C during the start of the 21st century compared to pre-industrial temperatures (Price et al 2013). Other than increased temperature in the boreal biome, the global warming is expected to bring a number of indirect ramifications. Precipitation will likely increase when viewed as an annual sum (IPCC 2019). However, the majority of the precipitation is expected to be temporally constricted to short bouts of heavy rainfall or snowfall, leaving long stretches of time completely devoid of precipitation. Due to this, extreme events, such as droughts or wildfires, might become far more common than what they are today (Collins et al 2024). Depending on the climate change scenario, the predicted increase in extreme droughts in the boreal region range from 2 to 4 occurrences per decade (IPCC 2019).

1.2.2 Climatic effects on forest productivity

The growth of the boreal forest is generally thought to be tightly connected to temperature (Brandt et al 2013). However, while some have anticipated an increasing growth trend due to warming temperatures (Pan et al 2011), observational studies have found growth declines to be a more common reaction to climate change (Reich et al 2022). If growth declines can be assumed to be a proxy for stress responses in a tree, these persistent growth declines might precede more catastrophic events, such as increased mortality risk (Dobbertin 2005) or decreasing resistance to other stressors such as pests (Reyer et al 2015). Empirical analyses of the recent past have shown that previous positive growth responses to temperature have become increasingly negative in certain regions, creeping northward from the southern boreal borders (Piao et al 2014). A current, albeit highly uncertain, prediction states that the boreal forest may start experiencing whole-forest dieback events at a warming of 1.5 to 5 °C (Armstrong et al 2022).

Increasing temperatures have the potential to stimulate tree growth mediated through increasing rates of photosynthesis (Kellomäki & Wang 1996). For example, in the boreal forest many tree species are assumed to be relatively dormant when temperatures are low, only to increase photosynthetic rates exponentially with warmer temperatures (Crous et al 2022). However, this increase in photosynthesis, and consequently growth, will sometime reach a temperature optimum (Sendall et al 2015). If the surrounding environment surpasses the trees' temperature optimum, the outcome will rather be a steep growth decline with increasing temperatures (Gagne et al 2020), due to heat stress from e.g. atmospheric water demands that force stomata closure and reduced photosynthetic rates. Rather than just growth declines, when temperatures far exceed those of a tree's temperature optimum, risks for mortality events become increasingly higher (Huang et al 2015) (Figure 2).

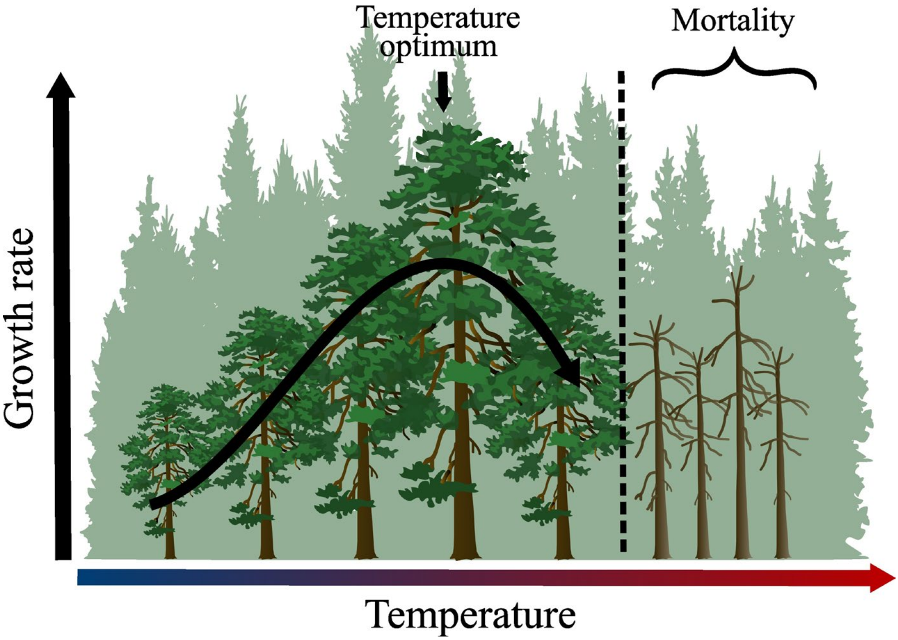

Figure 2. Conceptual graph showing increasing tree growth rates with increasing temperature until a temperature optimum is reached, after which growth declines and, in extreme temperatures, reach a point of mortality.

As mentioned, it is not only the direct effect of global warming that is expected to hit the boreal forest, and with further climate change, extreme weather events such as droughts are considered to become increasingly common. Throughout the boreal forest, much of the recently observed growth declines have been attributed to such droughts (Laudon et al 2024; Chen et al 2017). The ultimate effect of growth declines through drought is increased risks for tree mortality (Cailleret et al 2017). Drought induced tree mortality is increasing worldwide (Allen et al 2010), and in Europe the death of ~0.5 million hectares of trees has been attributed to increases in drought conditions alone throughout the last thirty years (Senf et al 2020). Compared to other biomes, the boreal forest has historically been relatively spared of these drought-impacts (Christian et al 2021). However, as the global warming is exacerbated in the boreal biome (IPCC 2023), the risks are increasing rapidly (Wang et al 2023). Therefore, it is vital for boreal forest longevity to ensure that there are ample conditions to survive the imminent increases in drought conditions.

1.2.3 Climate refuge through site- and species characteristics

A potential path to adapting forests to the changing environment is to make sure that more vulnerable tree species are growing in areas where the warming effects are milder. General patterns reveal that growth responses to temperature are increasingly positive in colder areas (Klesse et al 2018; Ols et al 2018) and higher latitudes (D'Orangeville et al 2016; Li et al 2020). Despite the knowledge of these patterns, in the Fennoscandian region, a common practice is to plant *Picea abies* in warmer, southern regions, and *Pinus sylvestris* in the colder, northern regions (SLU 2025), even though *P. abies* is generally the more drought-sensitive of the two (Gutierrez Lopez et al 2021; Treml et al 2022). While *P. abies* may have prominent growth rates, it generally has a shallow root system (Puhe 2003) which may limit water uptake during droughts. Furthermore, compared to deciduous species, both *P. abies* and *P. sylvestris* utilise a more isohydric strategy (Leo et al 2014), meaning that they are more conservative in the water usage and shut down their photosynthetic activity at earlier signs of water deficiency.

Areas of high soil moisture could act as potential refuges for species such as *P. abies* that are highly drought sensitive. Trees growing at such sites may be less influenced by drought events (Pau et al 2022). In contrast, for trees growing at already dry sites, the negative effects of dry spells may be aggravated (Gagne et al 2020). It is already a common argument among practitioners that *P. abies* should be planted on wet soils while e.g. *P. sylvestris* may handle the dry soils better. However, soil moisture is dynamic and the water content of boreal forest vegetation has recently been declining (Wang et al 2023). In fact, in some areas of the boreal forest, diminishing soil moisture may have been a driving force in reducing potential growth advantages from increasing temperatures (D'Orangeville et al 2016). For example, in the Fennoscandian region, ditching has long been a common practice to reduce the soil water content to enhance growth rates in water-saturated forest soils (Laudon et al 2022). However, in light of the current changing climate, these practices may have adversely affected the forests' ability to withstand droughts (Laudon et al 2024). To make informed decisions on climate-adaptations in forest management, it is important to know if and where there are refuges from negative climate-induced impacts on tree growth. Furthermore, it is important to know if and how some species can maintain their growth rates in dry conditions while others are in more dire need of these refuges.

1.2.4 CO_2 feedback

There is current evidence that the boreal forest may be transitioning from being a carbon sink to a carbon source (Bradshaw & Warkentin 2015). Decomposition, and thereby heterotrophic soil respiration, is the source of the largest CO_2 efflux in forest ecosystems (Lorenz & Lal 2010) and is tightly connected to the soil temperature (Bond-Lamberty & Thomson 2010). Plenty of studies have found either increases of soil respiration (Fierer et al 2006; Kirschbaum 2006) or decreases of soil carbon stocks (Davidson & Janssens 2006; Kirschbaum 1995) when temperatures increase. Although soil respiration generally increases with increasing temperature simply due to an intrinsic metabolic relationship with enzyme kinetics (Jin & Bethke 2007), the exact relationship is not entirely clear. The inability to accurately predict the temperature sensitivity of soil respiration has been mentioned as a great concern in regard to our understanding of climate change (Fierer et al 2006).

These changes in soil carbon dynamics under global warming may further increase CO_2 emissions from forest ecosystems, generating a feedback that reinforce the warming. Such positive climate feedbacks are expected to be comparatively large in the boreal forest (Johnston & Sibly 2018) as the soil respiration coupling to temperature is especially strong in higher latitudes (Niklinska et al 1999). Furthermore, since the soil constitutes the majority of the boreal forest carbon stock (Bradshaw & Warkentin 2015), coupled with the fact that soil respiration (i.e. outflux of CO_2) is thought to be more temperature-dependent than photosynthesis (i.e. influx of CO_2) (Fierer et al 2006), the feedback may be highly detrimental to the carbon storage ability of boreal forests. Additionally, if tree growth declines due to increasing temperatures, and the forest C sink potential is reduced (Simons-Legaard et al 2025), the warming feedback would be further exacerbated (Figure 3).

For this reason, knowledge about the factors influencing the climate-feedback potential of soil respiration in the boreal region is essential to maintain the climate benefits provided by the forest.

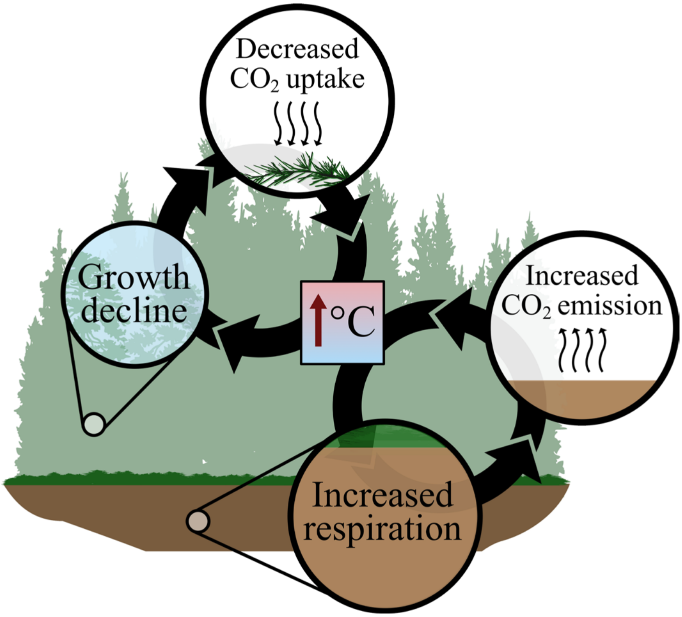

Figure 3. Conceptual graph showing potential feedback loops. Upper loop represents the positive feedback loop from increased temperature leading to reduced tree growth, which in turn leads to decreased CO2 uptake, and further increases of temperature. Note that this would only occur when temperatures are already above the tree growth's temperature optimum. Lower loop represents the positive feedback loop from temperature leading to increased respiration and CO2 emissions, which further increases temperature.

1.3 Disruptions of forest continuity

1.3.1 Clearcut forestry

Historically, the disturbance regimes in the boreal forest have been dominated by forest fires, windstorms, and insect outbreaks (Girona et al 2023). With these natural disturbances, stand-replacing events were rare (Girona et al 2023) and, when they occurred, left most of the remnants still within the forest ecosystem as deadwood and debris (Seedre et al 2011). Prior to the 20th century, forestry was generally limited to low-intensity selective logging (Lundmark et al 2013). However, starting at the turn of the last century, anthropogenic influences through clearcut forestry have taken over as the dominant disturbance in the boreal forest (Ahlström et al 2022). Clearcut forestry practices (or rotational forestry) forces a stand-replacing regeneration of the forest's tree populations (Duncker et al 2012). Current Swedish legislation

(2025) allows a stand-replacing regeneration every 45-100 years depending on the geographical location (SFA 2023), which is a relatively short rotation compared to the average return time of natural disturbances (Girona et al 2023).

Clearcut forestry provide great benefits to the forest sector. The management method delivers large quantities of timber and generally creates good conditions for the regeneration of new tree generations, especially for shade-intolerant species such as *P. sylvestris* (Kärenlampi & Riekkinen 2004). In addition, it may also provide fertile conditions that stimulate tree growth and thereby increase revenue (Duncker et al 2012). Soil processes that are vital to plant nutrient uptake may become affected for a long time after the disruption event (Ouimet et al 2021). As an example, clearcutting may disrupt the fungal community (Kyaschenko et al 2017), which has an important role in the forest nutrient dynamics. At first, this disruption may release saprotrophic fungi from competition (Bödeker et al 2016), which can accelerate their decomposition and cause a pulse of increased nutrient availability. However, other functional groups, such as mycorrhizal decomposers which makes generally inaccessible N available to trees (Bödeker et al 2014), may have a difficult time to recover from clearcutting (Kyaschenko et al 2017) which could potentially obstruct the vegetation's nutrient acquisition once the initial nutrient pulse diminishes. This could, in turn, lead to an aggravated N limitation in these forests and, ultimately, to a decreased productivity in the long term. Despite the relatively short existence of the clearcutting practice, the mentioned benefits and drawbacks have sparked a debate concerning its continuance. However, studies on long-term effects of clearcutting are lacking and, for the sake of an informed discussion on the matter, this knowledge gap needs to be filled.

1.3.2 Interactions with climate change

In the face of climate change, climate adapted forestry has become increasingly important. Much of the current advice regarding climate adaptations involve diversification of tree species to spread the risks of potential climatic effects (Felton et al 2016; Gamfeldt et al 2013). However, a potential effect of the clearcut practice on forests' climate sensitivity seems elusive. A few scientific studies have been conducted on the subject of clearcut-climate interactions, albeit these are mainly carried out in temperate regions (Mausolf et al 2018; Oheimb et al 2014; But see Wolf et al 2023 for satellite derived data in the Swedish boreal forest) and may not be generalizable to the boreal biome. Clearcut forestry may amplify negative climatic effects on tree growth in the boreal forest through a number of ways (Figure 4). For example, high growth rates early on, as may be expected following a clearcutting, can increase trees' sensitivity to extreme weather events such as droughts (Alfaro-Sánchez et al 2019; Bigler 2016; Rose et al 2009; But see also Cailleret et al 2017 for variability in research conclusions). The regeneration of forests itself, as follows from a clearcutting event, may also increase a forest's susceptibility to climate change as younger trees tend to be more affected by fluctuations in temperature and precipitation (Musavi et al 2017). Furthermore, reductions of soil organic matter (SOM) following clearcutting may lead to reduced water storage capacities which is likely to result in more detrimental impacts of drought conditions (Oheimb et al 2014). Lastly, despite rapid early growth in above-ground woody biomass, trees growing from a clearcut may exhibit diminished root systems, which is coupled with reduced water access and thereby an increased potential for drought impacts, compared to those that grow slowly in an already established forest (Mausolf et al 2017).

Other than climate change interactions affecting tree growth, forest management practices may also interact with a warming climate to alter the soil C dynamics. Clearcutting may result in decreased SOM quality, with increasing C:N ratios (Ouimet et al 2021), a loss of soil carbon and nitrogen (Pennock & Kessel 1997), and a lowered accumulation of labile compounds (Roth et al 2023). Furthermore, following a clearcutting event, the soil microbial biomass and diversity may decrease (Bowd et al 2021; Holden & Treseder 2013). Reduced SOM quality has a tendency to increase the temperature sensitivity of soil respiration (i.e. to which degree soil respiration increases with increasing temperature) (Karhu et al 2010; Fierer et al 2006). Similarly, while the temperature sensitivity of soil microbial communities are varied among taxonomic groups (Bölscher et al 2020; Van Nuland et al 2020), changes to the soil microbial community can have large effects on the soil respiration's response to warming (Sáez-Sandino et al 2023). Therefore, the alterations to SOM quality and soil microbial communities following clearcutting have the potential to drive changes in the temperature sensitivity of soil respiration. The potential of an increasingly positive climate feedback makes it important to understand in what direction, and to what extent, disruption events interact with climate change in their effect on soil C dynamics.

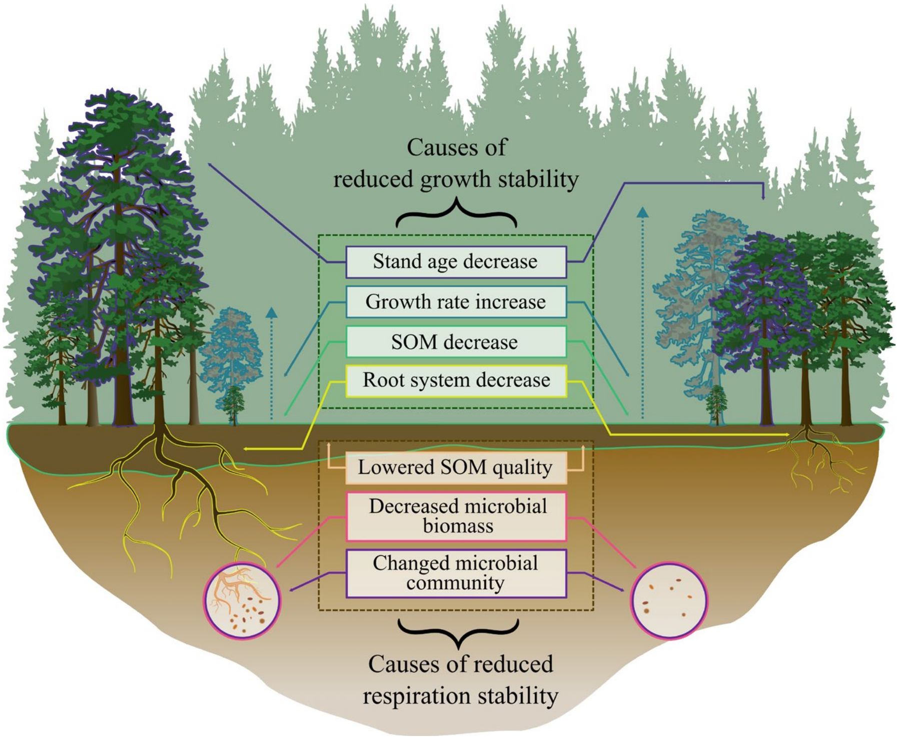

Figure 4. Conceptual graph showing potential mechanisms through which clearcutting can reduce tree growth stability and soil respiration stability in response to warming. The forest to the left and right are meant to symbolize forests that have never been clearcut and forests that have been clearcut, respectively.

The potential interactions between disrupted forest continuity, and the looming threat of climate change to forests in the boreal region, makes it vital to understand how younger, homogenized forests that regenerate from clearcutting are affected. If climate adapted forestry is to be able to handle the coming changes, practitioners and policy-makers need to know if the current paradigm of forest management is sustainable or detrimental to the longevity of forest growth.

2. Research aims

This thesis explores the effects of climate change and disruption of forest continuity through clearcutting, as well as the interaction between these two factors, on tree growth and soil respiration in the boreal forest. Specifically, I have aimed to bring clarity to the following questions:

- Do local temperature and soil moisture regimes affect tree growth responses to climate change? (Project I)
- Does clearcutting alter trees’ growth sensitivity to climate change? (Project II)
- Does clearcutting alter the feedback of soil respiration from increasing temperatures? (Paper III)
- What are the long-term effects of clearcutting on soil microbial communities, N dynamics, and forest productivity? (Project IV)

In Project I, I explored whether tree growth responses to climatic factors differ depending on: (I) the MAT of the growth site; (II) the soil moisture of the growth site; and (III) the tree species. Furthermore, I explored (IV) the effects of extreme years in terms of high temperature or low precipitation on tree growth.

In Project II, I explored the effects of clearcutting on: (I) the long-term tree growth stability; (II) drought resistance of the tree growth; as well as (III) possible pathways through which clearcutting could affect growth stability and drought resistance.

In Project III, I explored the short-term and long-term effects of clearcutting on: (I) soil quality; (II) soil respiration; and (III) the temperature sensitivity of soil respiration.

In Project IV, I explored the effects of clearcutting on: (I) soil microbial communities; (II) the forests’ N limitation; and (III) the overall forest productivity.

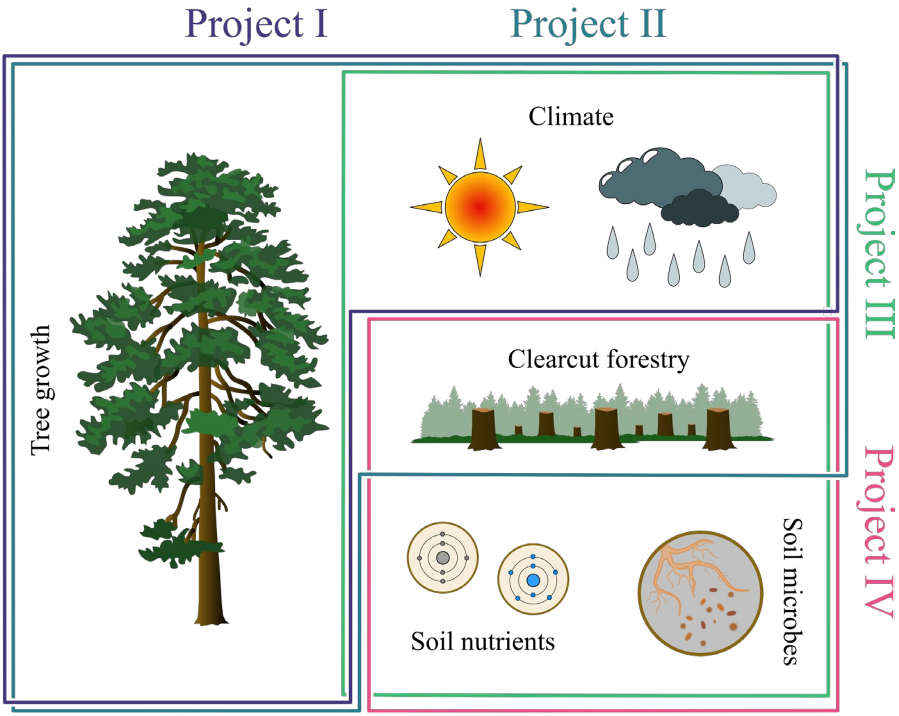

Figure 5. Conceptual graph showing the overarching themes of each project in the thesis. Colours indicate project-affiliation.

3. Methods

3.1 Overview of methods

In Project I, to test for tree growth-climate responses on a large spatial scale, I used data on tree-ring widths (TRW) and climatological parameters on a national level.

In Project II, to test the effect of clearcutting on tree growth-climate responses, I collected data on TRW and compared these with local climate parameters. Furthermore, to test for potential mechanisms behind the differences in tree growth-climate responses, I collected data on tree characteristics (height and DBH), and soil characteristics (SOM and soil temperature).

In Project III, to test the effect of clearcutting on soil respiration temperature sensitivity, I subjected soil samples to an incubation experiment. Furthermore, to explore soil characteristics that had the potential to be linked to changes in temperature sensitivity, I collected data on soil quality parameters through hydrolysis, as well as C and N measurements.

In Project IV, to test the long-term effects of clearcutting on ecosystem functionality coupled with productivity, data on fungal communities, C and N stocks, as well as productivity indicators (tree growth and understorey vegetation composition) was studied.

Here follows a description on how all data has been collected and analysed. For simplicity, Table 1 shows all the metrics analysed in this thesis as well as which sub-sections of the methods section explain the process of obtaining those metrics.

Table 1. List of variables (response, explanatory, and mediator) used in analyses throughout the thesis. The Project column indicates which project the variables have been used in, and the Section column indicates which sub-section of the methods section explains the production of the data. Note that covariates used to ensure site similarities in Projects II – IV are excluded but can be found in Table 2.

Variable	**Unit**	**Project**	**Section**
MAT	°C	I	3.2
SMI	Index	I	3.2
DBH	cm	II	3.3
Tree height	m	II	3.3
Soil temp.	°C	II	3.3
Veg. biomass	kg m^{-2}	IV	3.3
Veg. cover	% (area)	IV	3.3
Soil resp. *III*	µmol CO_2 h^{-1} m^{-2}	IV	3.3
TRW	mm	I – II	3.4
RWI	Index	I – II	3.4
MS (ind.)	Index	II	3.4 *
MS (stand)	Index	II	3.4 *
Growth rate	kg $year^{-1}$	II	3.4
Tree age	years	II	3.4
Resistance	Index	II	3.4 *
Recovery	Index	II	3.4 *
Resilience	Index	II	3.4 *
Temperature	°C	I – II	3.5 *
Precipitation	mm	I – II	3.5 *
SPEI	Index	I – II	3.5 *
VPD	kPa	I	3.5 *
Soil resp. *IV*	µmol CO_2 h^{-1} $gSOM^{-1}$	III	3.6
SOM	kg m^{-2}; % (mass)	II – IV	3.7
Soil C & N	% (mass)	III – IV	3.7
Needle C & N	% (mass)	IV	3.7
Hydrolysable C	% (mass C)	III	3.7
PLFA	µmol g $soil^{-1}$	IV	3.7
Fungal groups	% (fungal PLFA)	IV	3.7

* Data manipulation prior to analysis further explained in the Data analysis section (3.8).

3.2 Study sites

The data used in Project I has been collected on a national level by the Swedish NFI, and constitutes 544 sites around Sweden. These sites are all located in productive forests (wetland and mountainous forests excluded). For each site, I also acquired data on soil moisture index (SMI) based on readily available topographical models (Ågren et al 2021) and the mean annual temperature (MAT) based on modelled temperature data (see section 3.5 for details).

For Project II and IV, I collected data from a set of 18 forests in the north of Sweden. Nine of these forests were unforested, likely following a clearcut, in the early 1960's (hereafter referred to as Clearcut; CC_{60}), while the other nine have, to my knowledge, never been clearcut (Non-clearcut; NC). To ensure that the forests were correctly categorized as either clearcut or non-clearcut, I made use of a database produced by the forestry company Sveaskog, in which they had classified non-clearcuts as forests in which at least 30% of the trees were >140 years old. From the forests that could accurately be classified, I made a selection of sites based on similarities in geographical position (latitude, altitude, slope and aspect of slope), as well as a number of metrics reported by Sveaskog: annual temperature sums, soil moisture and grain size, and estimated productivity prior to clearcutting. To further correct for underlying differences other than the clearcutting, I estimated soil acidification levels through analyses on mineral soil Al and Ca (Table 2). The area in which these forests grow has a MAT of ~0 °C, ranging from -15 °C in January to 13 °C in July, and a MAP of ~500-600 mm. The forests' tree populations are dominated (>50 %) by *P. sylvestris*, but also contain *P. abies* and *Betula spp*. The understory is dominated by *Vaccinium* and *Empetrum* species, and the forest floor by feather mosses. In each of these forests, I established three circle plots (⌀ = 20 m) based on their representative nature of the forest as a whole, in terms of vegetation composition, slope and distance from non-forest areas. All further data analyses in Project II – IV are based on samples collected from these plots.

For Project III, I used a subset of the abovementioned 18 forests (5 clearcut and 5 non-clearcut forests, chosen based on having similar averages of the variables presented in Table 2). However, to also include effects experienced more recently after clearcutting, I added another 5 clearcuts that had been clearcut <10 years prior to the study (Young clearcuts; CC_{10}). The new sites were geographically close to the other study sites and were dominated by *P. sylvestris* saplings.

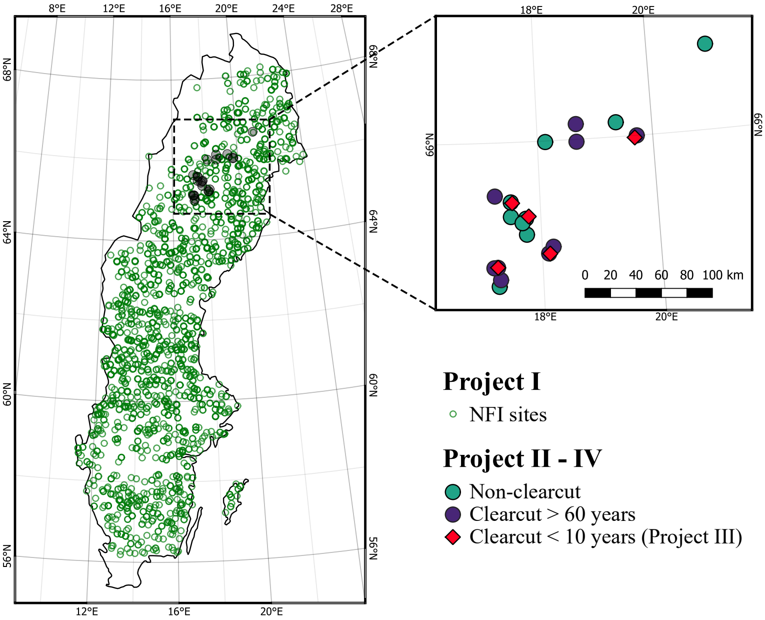

Figure 6. Map of study sites. Left: Map of all NFI sites used in the analyses of Project I; as well as study sites of Project II – IV highlighted in grey. Right: Study sites used in Project II – IV where: green circles indicate Non-clearcut forests; purple circles indicate forests that have been clearcut ~60 years ago; and red squares indicate forests that have been clearcut <10 years ago (note that data from the young clearcuts have only been used in Project III).

Table 2. Variables used to ensure similarities beyond clearcutting between the two forest types (60-year old clearcut forest (CC_{60}) and non-clearcut forests (NC)) studied in Projects II and IV. Values are reported as means ± SE (based on 9 replicates for each forest type). Note that soil moisture and soil grain size do not have quantitative data but all sites have been deemed intermediate by Sveaskog. The quantitative variables are also used as covariates in a number of statistical analyses (see section 3.8).

Variable	**Unit**	**CC_{60}**	**NC**
Altitude	masl	399 ± 14	375 ± 14
Slope	Degrees °	4.8 ± 1.7	3.1 ± 0.7
Temperature sum	°C	695 ± 15	729 ± 13
Estimated productivity	m^3 ha^{-1} $year^{-1}$	2.6 ± 0.13	2.5 ± 0.15
Mineral soil Ca:Al	Ratio	0.22 ± 0.04	0.25 ± 0.04
Soil moisture	Estimation	Intermediate	Intermediate
Soil grain size	Estimation	Intermediate	Intermediate

3.3 Field sampling (Project II – IV)

For Projects II – IV, I conducted field measurements. Here is a brief explanation of the reasoning behind all sample collections, followed by a more detailed description of the samplings.

For Project II, I collected tree cores to be analysed for growth pattern differences between clearcut and non-clearcut forests. The cores were collected from all trees with a DBH >5 cm using a 5 mm ⌀ tree borer. I also measured the sizes of all these trees to establish size diversity in the plots, as trait diversity has been found to increase stability when viewed at a stand-wide level (Anderegg et al 2018). I measured size through both circumference at breast height using a tape measurer, and height using a Vertex IV and Transponder T3. Further, I made use of soil samples to explore differences in organic matter contents as the water retention potential of thicker soil organic layers has been suggested to buffer against dry spells (Mausolf et al 2018; Oheimb et al 2014). I collected the organic soil layer from 15 soil samples in each plot using a 2.5 cm ⌀ soil corer. I also used temperature loggers to explore differences in microclimatic stability. To get an estimate of the soil microclimate and its fluctuations, I buried temperature loggers in all plots, roughly 10 cm into the soil for ~1 year.

For Project III, I collected the soil samples to be used in an incubation experiment, using the organic layer of twelve 135 cm^2 subplots divided between three plots in each forest.

For Project IV, I used a variety of measurements to explore potential differences in growth-related factors and C dynamics ~60 years after clearcutting. I made use of the tree size measurements in Project II to get an estimate of the amount of tree biomass present in each plot (see Eq. 1 for conversions to biomass). To get a further estimate of the total biomass in the stands, I estimated the aboveground biomass of the understorey in each plot. As the understorey can be telling of the productivity in the forest, I estimated the areal cover of the most dominating vegetation (*Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Empetrum sp*.). To explore the N availability of the forests, I estimated C and N in pine-needle- and soil samples. To explore the soil microbial community, PLFA- and DNA analyses on the soil samples were used. Finally, to get an estimate of soil microbial activity and soil CO_2 efflux, I conducted field-based soil respiration measurements using a portable infra-red gas analyser (IRGA) connected to a closed chamber.

3.4 Tree rings (Project I – II)

The use of TRW is a common and well-established method to study growth patterns of trees, as well as the trees' growth responses to changes in the growth environment (Girona et al 2023). Here, I made use of TRW in Project I and II to explore the geographical differences as well as the effects of disrupted forest continuity on growth-climate responses, respectively.

In Project I, the tree cores used to establish TRW series have been obtained by the Swedish NFI between the years 2018-2022. One to three trees of each present tree species were cored in each NFI plot, chosen through unequal probability systematic sampling based on probabilities proportional to basal area (see Fridman et al 2014 for details on the NFI sampling). In this project, I have only made use of TRW series from *P. abies* and *P. sylvestris*.

In Project II, I measured TRW from tree cores collected from the study sites. In each plot, I sampled every tree with a DBH >5 cm for analysis. Due to difficulties in determining TRW, I excluded all deciduous trees (140 trees) and two pine trees from further analysis. In total, I used the TRW series of 1107 trees for analysis on growth patterns and climate responses.

As TRW is only representative of the radial stem growth of a tree, indices are often used to get a more accurate estimation of growth patterns. Here, I use basal area increments (BAI) to portray growth rates, as well as biomass conversions (Eq. 1) through allometric functions to estimate standing stocks of tree biomass.

$$\text{Eq. 1: } Biomass_t = e\left(-2.2 + 11.4\left(\frac{\varnothing}{\varnothing + 14}\right)\right)$$

Where $Biomass_t$ *= stemwood biomass (for full tree biomass calculations, see Marklund 1988), and* $\varnothing$ *=* $diameter_t$ *calculated as 2 * (*$TRW_{1:t} - TRW_{1:t-1}$*).*

In order to accurately assess tree growth responses to inter-annual changes in climatic factors, long-term age-related growth patterns need to be accounted for. To remove the long-term growth patterns prior to growth-climate response analyses, I detrended the growth data using a spline with a 50% cutoff after 30 years. This produces time series of ring width indices (RWI) where the long-term trends have been removed (Figure 7).

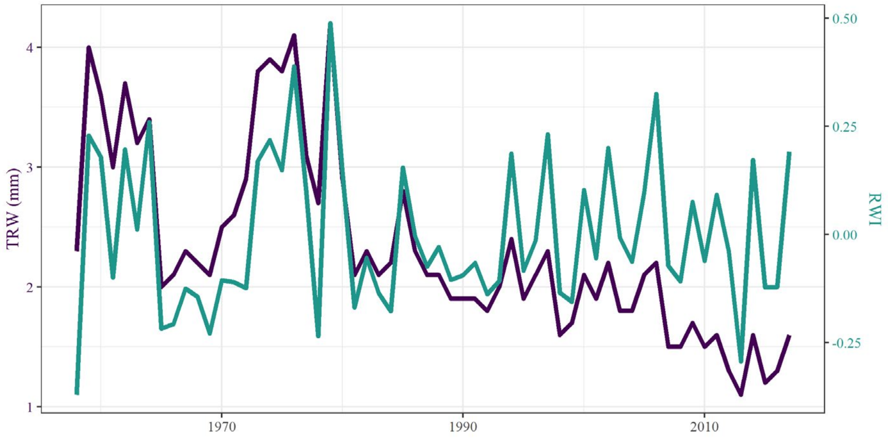

Figure 7. Example of the effects of detrending for time-series data. Purple line (left y-axis) represents the true TRW values of a single tree time-series. Cyan line (right y-axis) represents detrended data (RWI) from the same time-series. Note that the long-term decline in growth is removed while short-term variations are kept in the RWI.

Using RWI series to study growth-climate responses is highly sensitive to accurate dating of each individual tree ring. To ensure that the RWIs studied in Project I and II accurately represent the years I assign to them, I carried out quality assessments in the form of inter-series correlations, where RWI series with correlation values below a certain threshold were excluded. In Project I, I carried out the inter-series correlations between all trees within the same NFI site. In Project II, I carried out the inter-series correlations between all trees within their respective plot. In both Projects, I excluded data from tree cores that failed to reach an inter-series correlation of 0.33. This resulted in datasets of 4578 trees across 1979 sites in Project I, and 1036 trees across the 18 clearcut and non-clearcut sites in Project II.

A useful metric to study a tree's growth stability, i.e. how much the growth varies from year to year, is mean sensitivity (MS). The MS is calculated from the growth differences between one year to the next (Eq. 2) such that a low value indicates high growth stability. The calculation produces a value between 0 – 1, but in the boreal forest, values generally range between 0.1 – 0.2 (Linderholm & Linderholm 2004).

$$\text{Eq. 2:}\, MS = \frac{1}{N}\sum_{i=1}^{N}\frac{|RWI_i - RWI_{i-1}|}{RWI_i + RWI_{i-1}}$$

Where RWI = Ring Width Indices (detrended TRW values), and N = the length of the RWI series in years.

To explore the effect of extreme drought years on growth, I have used disturbance indices (first described by Lloret et al 2011) to calculate the growth response to drought in terms of resistance, recovery and resilience (Eq. 3). Resistance indicates how much the growth declines during the year of drought compared to the years prior to the drought. Recovery indicates the ability to increase growth after the drought. Resilience indicates the ability to return to "normal" growth rates after the drought (Figure 8).

$$\text{Eq. 3:}\, Resistance = \overline{RWI_{t-3:t-1}}/RWI_t$$

$$Recovery = RWI_t/\overline{RWI_{t+1:t+3}}$$

$$Resilience = \overline{RWI_{t+1:t+3}}/\overline{RWI_{t-3:t-1}}$$

Where t = the year of drought.

For both Project I and II, the tree ring widths produced the following metrics which I used for data analysis: TRW (mm year^{-1}); RWI (index); and Drought resilience indices (index). For Project II, I also used the following metrics: Tree age (years); Growth rates during the first 20 years (kg year^{-1}); and MS (index).

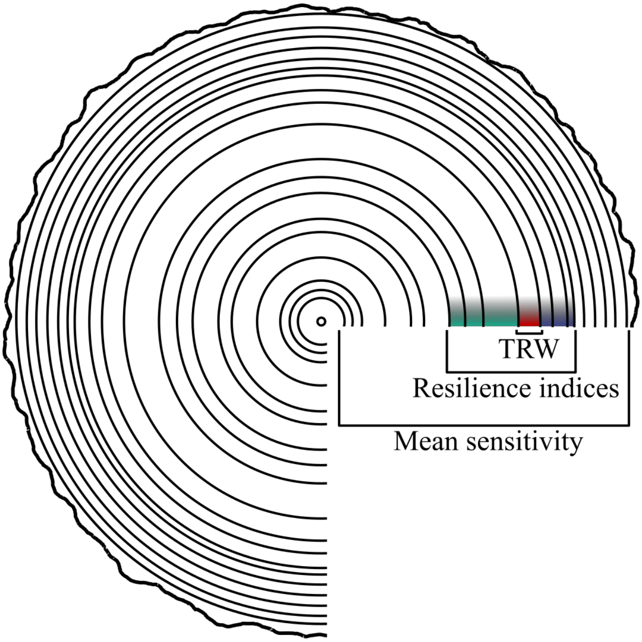

Figure 8. Conceptual illustration of a cross-section of a tree depicting the annual rings. Colored rings indicate rings used to calculate resilience indices regarding a focal year (marked in red): cyan rings indicate the three years prior to the focal year which are used to calculate resistance values; purple rings indicate the three years following the focal year which are used to calculate recovery values. Both cyan and purple rings are used to calculate resilience values. All rings from pith to bark are used to calculate the mean sensitivity (MS).

3.5 Climate variables (Project I – III)

To analyse tree growth-climate responses in Project I, I made use of climate data retrieved from SMHI’s modelled data for the Fennoscandian region (Andersson et al 2021). The dataset is modelled on a 2.5 km grid on a daily basis during the period 1961-2018, and contains data on temperature (mean, maximum, and minimum), precipitation, and RH. From these data, I calculated drought estimations based on daily values of VPD, and monthly values of SPEI. VPD is a measure of atmospheric water demand and is generally used to infer how much water a tree needs to sustain photosynthesis (Howell & Dusek 1995). VPD is expressed as kPa and can, theoretically, reach any value >0, but studies on coniferous trees in the boreal forest have shown that values exceeding 1.5 kPa generally force stomatal closure and a steep reduction of photosynthetic activity (Kurjak et al 2012) (Eq. 4). SPEI is the difference between accumulated precipitation and potential evapotranspiration inferred from temperature and solar radiation (Eq. 5). The resulting value is unitless but generally ranges from -2 to 2, where lower values indicate worse drought conditions.

To analyse tree growth-climate responses in Project II, I used temperature and precipitation data obtained from the Arjeplog weather station (N: 66.0513, E: 17.8396). I further used data from the Arjeplog station to inform correct ambient temperatures to be used for the incubation experiment in Project IV.

$$\text{Eq. 4:}\, VPD = \left(1 - \frac{RH}{100}\right) * \frac{611e^{(17*T)/(T+237)}}{1000}$$

Where VPD = Vapour Pressure Deficit, RH = relative humidity, and T = mean temperature in °C.

$$\text{Eq. 5:}\, SPEI = P - PET$$
$$PET = 0.0023 * (T_{mean} + 17.8) * (T_{max} - T_{min})^{0.5} * R$$

Where P = precipitation, and PET = Potential Evapotranspiration calculated through the Hargreaves method, where T = temperature in °C, and R = incoming radiation estimated through latitude.

For Project I and II, the climate variables produced the following metrics which I used for data analysis: Temperature (°C); Precipitation (mm); and SPEI (index). For Project I, I also made use of the VPD (kPa). Furthermore, for Project III, I used the temperature data to inform the correct ambient temperatures to be used in the incubation experiment (see section 3.6).

3.6 Incubation (Project III)

In Project III, to test whether there are differences in how the soil respiration from clearcut and non-clearcut forests respond to warming, I used a lab incubation setup and heated the soils collected from the different forests.

I took the twelve samples collected from each forest, homogenized these and removed any coarse roots (>2 mm ⌀). After homogenization, I divided the soils between twelve samples again. One of the samples from each forest was freeze-dried and used to analyse initial conditions of soil properties. One of the samples was weighed, oven-dried, and weighed again, to get an estimate of water content in the samples. These samples were also used for SOM measurements. I calculated the mean water content among all forests and manipulated the remaining 10 samples from each forest to gain the same water content (either by allowing them to dry, or by adding deionized water, until the mean water content was reached).

After homogenization and water content standardization, I placed the 10 remaining samples from each forest into plastic boxes and into climatically controlled chambers for 4 weeks. Half of the samples were exposed to mean summer temperatures (night temperatures of 9 ºC and day temperatures of 15 ºC, which correspond to the WMO reference period in the area (EEA 2024)), and half were exposed to 5 ºC warming (in line with the SSP5-8.5 scenario in the study area). I standardized the air humidity to 80 RH during night hours and 65 RH during day hours, and the light regime to complete darkness, for all samples.

Once every week, I conducted respiration measurements by closing the plastic boxes with a lid connected to an IRGA, and measuring the CO_2 every 15 seconds for 2 minutes per sample. The development of CO_2 concentration in ppm was then converted to amount of CO_2 emitted through Eq. 6.

$$\text{Eq. 6: } \mu mol\ CO_2 = \frac{\Delta ppm * p * v}{R * T}$$

Where p = pressure (~1 atm), v = volume of the enclosed system, R = gas constant (8.21x10^{-5}), T = temperature in Kelvin.

For Project III, the incubation experiment produced the following metrics which I used for data analysis: Soil respiration (µmol CO_2 s^{-1}).

3.7 Lab analyses (Project II – IV)

In Projects II-IV, I compared SOM between the different forest types. I measured the SOM content of dried soil samples through loss on ignition where the soils were heated to 550 ºC for six hours, for all organic matter to be incinerated. I then estimated the SOM as the proportion of the soil samples' weight that was lost after heating.

In Project III, the C, N, ^{13}C, and ^{15}N of soil samples was estimated using an elemental analyser (EA-IRMS). I also analysed the hydrolysable (easily decomposable) fraction of the soil by subjecting the soil samples to hydrochloric acid, and calculated the hydrolysable C as the proportion of C lost after hydrolysis.

In Project IV, I analysed the C and N content of individually ball-milled and homogenized soil- and needle samples using an elemental analyser. Furthermore, to get an estimate of the microbial abundance in the soil samples, I analysed the PLFA content. I attributed the following PLFAs to be biomarkers for bacteria: tetradecanoate (14:0) pentadecanoate (15:0); hexadecanoate (16:0); and heptadecanoate (17:0). I attributed the PLFA octadecenoate (18:2ω6) to be a biomarker for fungi (Yao et al 2000; modified from Frostegård et al 1991). To gain more detailed insights into the soil fungal community composition, DNA was extracted from the soil samples, PCR amplified using fungal-specific primers, and sequenced. Sequences were taxonomically assigned and classified into ectomycorrhizal fungi (ECM), ericoid mycorrhizal fungi (ERM), or saprotrophic fungi.

For Project II, I used the SOM calculated per area (kg m^{-2}) as a mediator variable in the data analysis. For Project III, the lab analyses produced the following metrics which I used for data analyses: SOM (% soil mass); Soil C (% soil mass), N (% soil mass), ^{13}C ($\delta^{13}C$), and ^{15}N ($\delta^{15}N$); and the soil hydrolysable C fraction (% soil C). For Project IV, the lab analyses produced the following metrics which I used for data analyses: SOM (% soil mass); Soil- and needle C and N (% soil or needle mass); PLFA (μmol g $soil^{-1}$); Proportions of ECM, ERM, and saprotrophic fungi (% of total fungal community).

3.8 Data analyses

3.8.1 Project I

Prior to statistical analyses, I aggregated the climatic variables (temperature, precipitation, SPEI, and VPD) to growing season averages. In this case, I used the meteorological definition of growing season such that the season begins on the first day of the first four-day period with a daily mean temperature >5 ºC and ends when the daily mean temperature has been <5 ºC for four consecutive days. With this aggregation, the climatic variables are spatially dynamic and site-specific.

To explore the effect of MAT, SMI, and tree species (*P. abies* and *P. sylvestris*) on the tree growth response to climatic factors, I used linear mixed models with RWI as a response variable and the respective climatic variable, MAT, SMI, and tree species as explanatory variables, and the NFI site as a random variable. With this approach, the interaction effects of the climatic variable and the other explanatory variables represent how the tree growth response to the climatic variable varies along MAT and SMI gradients and between species.

To explore the effects of extreme years in terms of high temperature or low precipitation on tree growth, I identified climatically extreme years as those with the 10% highest temperature or 10% lowest precipitation, and the extreme growth years as those with lowest 10% RWI. To explore if the climatically extreme years coincided with extreme growth years, I calculated the coincidence rates as the number of coincidences (i.e. the number of years that was extreme in high temperature/low precipitation *and* low RWI) divided by the maximum number of possible coincidences (i.e. 10% of the RWI series length). The coincidence rate produces a value between 0 – 1, where 0 indicates no coincidences, and 1 indicates that all years of low RWI coincides with a climatically extreme year. Furthermore, I calculated the resistance values (Eq. 3) of RWI to the extreme climatic years.

3.8.2 Project II

In all the following linear mixed effects models, I have used plot (3 plots within each of the 18 forests) as a random variable, and geographical variables (latitude and altitude), and the proportion of non-pine trees in the RWI data, as covariates.

To explore the effects of clearcutting on long-term tree growth stability, I calculated the MS (Eq. 2) on two scales: for RWI of individual trees; and for stand-wide average RWI. I then analysed the differences in MS using linear mixed models with MS as the response variable and the forest type (CC_{60} and NC) as the explanatory variables. With this approach, the effects of forest type represent the difference in MS caused by clearcutting. Furthermore, any changes in results from individual tree MS to stand-wide average MS may be informative of complementary growth patterns - similar MS in individual trees and stand-wide averages would indicate that all trees grow exactly the same; while a high decrease in MS from individual trees to stand-wide averages would indicate that one tree exhibits high growth in a year when a second tree exhibits low growth.

To explore the effects of clearcutting on the drought resistance of tree growth, I first investigated the general effect of climatic variables (temperature, precipitation, and SPEI) on the tree growth in the different forest types. I used linear mixed models with RWI as the response variable and the respective climatic variable and forest type as the explanatory variables. With this approach the interaction effect of the climatic variable and forest type represents the effect of clearcutting on the tree growth-climate response. Furthermore, I calculated the drought indices (Eq. 3) with 2018 as the focal year, as this has been noted as a year of extreme drought (SMHI 2019; Toreti et al 2019; Wolf et al 2023). I then analysed the differences in drought indices through linear mixed effects models with the respective drought index as the response variable and forest type as the explanatory variable. With this approach the effects of forest type represent the difference in drought response between the forest types.

To explore the possible pathways through which clearcutting affects the growth stability and the drought resistance, I used mediation analyses (Eq. 7) on the models concerning drought indices with both tree variables and soil variables as potential mediators of the effects of clearcutting. With this approach, it is possible to discern which stand characteristics that explains the difference in the response variables (drought indices) between the forest types. The values produced from the mediation analysis range from -1 to 1, where a high positive number indicates that much of the observed difference in the response variable is *due to* the mediator variable (mediation). Conversely, a high negative number indicates that the observed difference in the response variable exists *despite* differences in the mediator variable (suppression) (see Figure 9 for conceptual examples of mediating/suppressing effects).

$$\text{Eq. 7: } Mediation = \frac{\beta_{my} * \beta_{xm}}{\beta_{xy}}$$

Where β_{my} *= regression coefficient of the mediator variable on the response variable,* β_{xm} *= regression coefficient of the predictor variable on the mediator variable,* β_{xy} *= regression coefficient of the predictor variable on the response variable.*

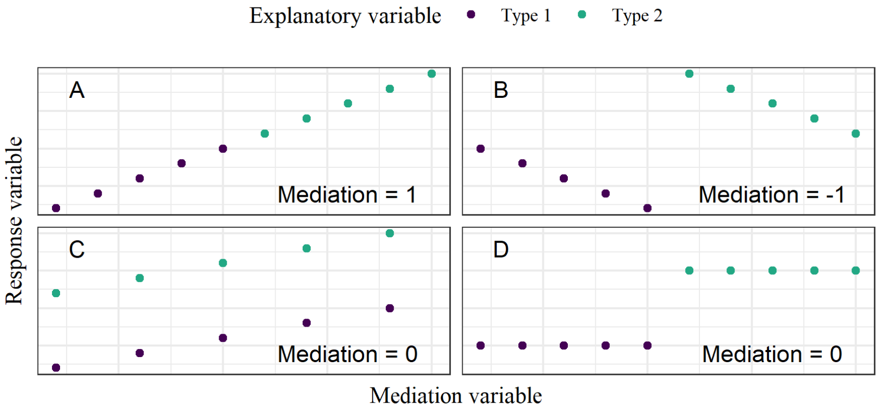

Figure 9. Examples of mediation effects. Figure A shows a perfect mediation (mediation value = 1) where the difference in the Response variable between the two types of the Explanatory variable can be explained entirely by the difference in the Mediation variable. Figure B shows a perfect suppression (mediation value = -1) where the difference in the Response variable would have been larger if the Mediation variable did not differ between the two types. Figure C shows a scenario of no mediation due to the two types having no difference in the Mediation variable. Figure D shows a scenario of no mediation due to the Mediation variable having no effect on the Response variable when the Explanatory variable is accounted for.

3.8.3 Project III

To explore the effects of clearcutting on soil characteristics (SOM, hydrolysable fraction, C:N ratio, $\delta^{13}C$ and $\delta^{15}N$), as well as soil respiration, I used ANOVAs (SS Type II) with the respective soil parameter as the response variable and the forest type (NC, CC_{60}, CC_{10}) as the explanatory variable.

To explore the effects of clearcutting on the temperature sensitivity of the soil respiration, I estimated the proportional change in soil respiration due to warming as the quotient of the soil respiration (CO_2 g^{-1} h^{-1}) in the warmed samples divided by that of the samples exposed to ambient temperatures. I then used ANOVAs with the proportional change as the response variable and the forest types as the explanatory variable.

3.8.4 Project IV

To explore the effects of clearcutting on the soil microbial communities, C and N concentrations of soils and needles, as well as forest productivity indicators, I used linear mixed effects models with forest type (NC and CC_{60}) as the explanatory variable and the response variables: total PLFA of soil samples; fungi:bacteria ratios based on soil PLFA; G+:G- bacterial ratios based on PLFA; soil respiration rates; C and N concentrations and C:N ratios in soil- and needle samples; the mean BAI of the last five years; the proportion of the understorey covered in either *Vaccinium* or *Empetrum* species.

Since the data on fungal communities (proportions of ECM, ERM, and saprotrophic fungi) were pooled within sites (i.e. having no within-site variation based on plots), I used ANOVAs (SS Type II) to test for differences between the forest types.

4. Results and discussion

4.1 Tree growth – climate responses

The results in this chapter are based on linear mixed effects models (3.8.1) using data on TRW (3.4) and climate variables (3.5) collected from all over Sweden (3.2).

When I examined the datasets regarding TRW, climate variables, and soil moisture, throughout the Swedish forest landscape, I found three interesting patterns. (I) Site-specific MAT corresponds to substantial variation in tree growth correlations to climate variables, and this pattern differs clearly between *P. abies* and *P. sylvestris*. (II) On the contrary, site-specific soil moisture shows little association with tree growth responses, except for a slight tendency toward weaker responses in areas of high MAT. (III) Extreme years, in terms of high temperature or low precipitation, follow similar patterns along MAT and soil moisture gradients as that of changes in average growing season temperature or precipitation.

4.1.1 Along a MAT gradient

The analysis of tree growth-climate responses throughout Sweden revealed that these differ strongly depending on the MAT of the growth site (Figure 10). In warm regions, tree growth in both *P. abies* and *P. sylvestris* responded negatively to high temperatures and high VPD, while colder regions revealed opposite patterns (i.e. positive correlations to high temperature and VPD on tree growth). The positive effects of temperature in the colder regions are likely due to the temperatures reaching levels that promote increased photosynthetic rates (Saxe et al 2001; Kellomäki & Wang 1996) without overshooting the temperature optimum and causing heat stress (Gagne et al 2020). Additionally, increasing temperatures may prolong the growing season (Gustafson et al 2024), and further add to the positive growth-temperature relationship. On the contrary, in regions that are already relatively warm, the negative effects of increasing temperatures may be due to the temperatures overshooting the trees' temperature optimum (Gantois 2022), causing heat stress and stomata closure which results in reduced growth (López et al 2021; Yuan et al 2019). Furthermore, the difference in growth-climate responses between warm and cold regions was greater in *P. abies* than *P. sylvestris* (Figure 10). This suggests that, with future warming, *P. abies* may benefit more from having their growth-sites adjusted to colder regions, while *P. sylvestris* may be less affected by the ambient temperatures of their growth-sites.

The growth-response to precipitation and SPEI revealed an opposite pattern to that of temperature and VPD (i.e. positive growth-responses to high precipitation or SPEI in warm regions but negative responses in cold regions) (Figure 11). Possibly, high amounts of precipitation may alleviate drought stressors in warm regions, while it may lead to soil water saturation and subsequent growth declines in colder regions (Laudon et al 2024). As climate models predict increased future precipitation in this study area (IPCC 2023), this pattern could be expected to mitigate potential negative effects of future climate change on tree growth in warmer regions. However, as precipitation is also projected to occur as intermittent heavy rainfall events interspersed with periods of droughts, this mitigating effect may be reduced. Positive growth-precipitation relationships may become increasingly negative if the precipitation occurs as infrequent heavy rains (Land et al 2017), and intervening drought periods risk causing severe growth declines (Huang et al 2015). Interestingly, the differences between *P. abies* and *P. sylvestris* are also reversed for precipitation and SPEI compared with temperature and VPD, and the growth-responses in *P. sylvestris* reveal greater contrasts between warm and cold regions than that of *P. abies*.

These findings indicate that there are clear differences in growth-climate responses along a MAT gradient, and that regional temperature acts as an important factor when adapting forests to climate change. For example, of the two most common species in these forests, *P. abies* can be thought to benefit more from growing in currently cold regions where they can make use of the coming temperature increases without exceeding their temperature optimum, while *P. sylvestris* may be able to handle the warming better in already warm regions.

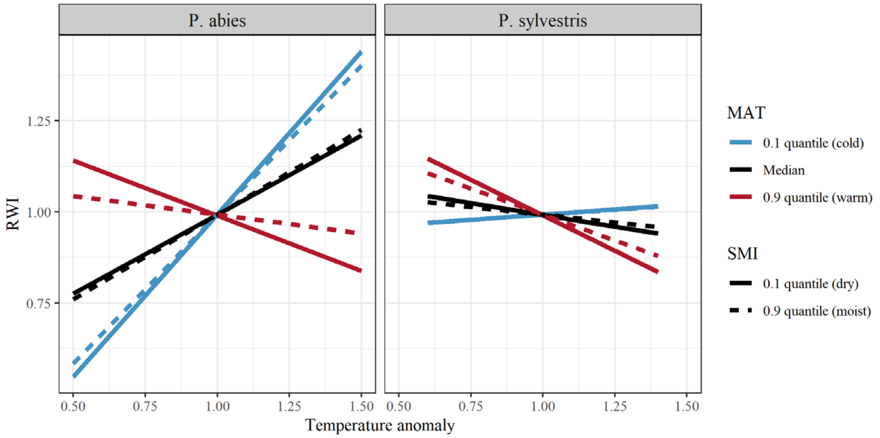

Figure 10. Model output of the effects of temperature on RWI (ring width index) when separated between low (10% quantile; blue lines), median (black lines), and high (90% quantile; red lines) MAT (mean annual temperature). Lines show differences between low (10% quantile; solid lines), and high (90% quantile; dashed line) SMI (soil moisture index). Facets show differences between species (left = *P. abies*; right = *P. sylvestris*).

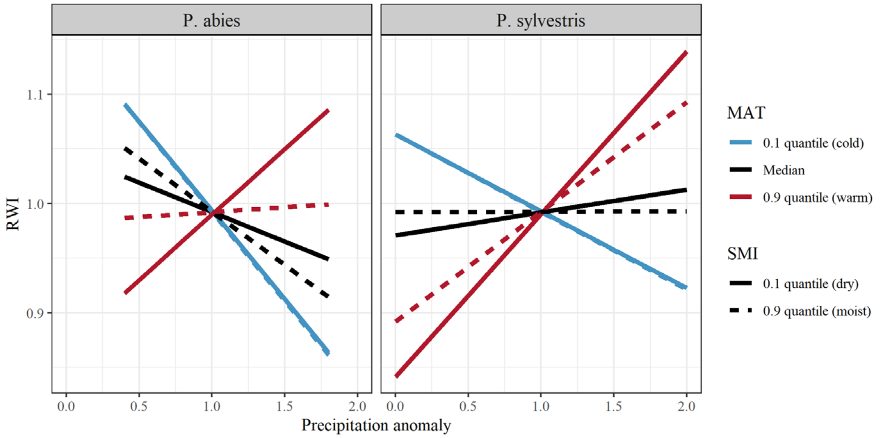

Figure 11. Model output of the effects of precipitation on RWI (ring width index) when separated between low (10% quantile; blue lines), median (black lines), and high (90% quantile; red lines) MAT (mean annual temperature). Lines show differences between low (10% quantile; solid lines), and high (90% quantile; dashed line) SMI (soil moisture index). Facets show differences between species (left = *P. abies*; right = *P. sylvestris*).

4.1.2 Along a soil moisture gradient

Compared to MAT, the analysis of soil moisture did not reveal as clear differences in tree-growth responses (Figure 10). However, there were interaction effects with MAT, where high soil moisture showed a potentially mitigating effect against high temperature, or low precipitation, in the warmer regions while it had no effect in colder regions. It seems logical that areas of high soil moisture can only mitigate negative effects from climate change in regions where high temperature or low precipitation is detrimental for tree growth (i.e. areas of high MAT in this study system). The water requirement to sustain photosynthesis increases with temperature (Reich et al 2018), and in colder regions the water availability may be sufficient to sustain tree growth even in times of relatively high temperatures. On the contrary, in warm regions the trees may experience an atmospheric water demand that surpasses the water availability in dry areas. However, it is important to note that future climate change may force currently cold regions into warmer states, in which soil moisture may become an increasingly important factor to consider for sustained tree growth. Furthermore, the refuge effect of soil moisture in warm regions seems to be more prevalent in *P. abies* than *P. sylvestris*. This possibly reflects reduced water demands in *P. sylvestris* (Sutinen & Middleton 2020) following their deeper roots (Puhe 2003) and higher root:leaf ratio (Helmisaari et al 2007).

These findings indicate that soil moisture is currently only influencing growth-climate responses in warm regions but that it, under global warming, may become a more important factor in other regions. With recent declines in forest water contents (Wang et al 2023), considerations of soil moisture may become increasingly important for climate change-adapted forest management. For example, reduced cleaning of old ditches (Laudon et al 2024), or carefully considering where to plant different tree species, may enhance the effects of soil moisture refuges in terms of growth stability.

4.1.3 Divergence of extreme anomalies

The analysis regarding coincidence rates revealed differences along the MAT gradient in the coincidences between high temperature or low precipitation and low RWI. Years of extremely high temperature or low precipitation coincided with years of extremely low RWI more often in warm regions than in cold regions (Figure 12). Similarly, the analysis regarding resistance values revealed differences along the MAT gradient in the growth resistance to the extreme years, where growth in warm regions was reduced more than growth in cold regions (Figure 13). In fact, in many sites in the colder regions, the extreme years in terms of high temperature or low precipitation were not detrimental to RWI, but rather positive. Furthermore, the effect of soil moisture was small and only apparent in warm regions. Hence, the patterns of extreme years' effects on growth seems to largely reflect those observed when studying the overall climatic effects.

Interestingly, the most detrimental factor for growth was different between the species. While *P. abies* reacted most severely to extreme years in terms of low precipitation, *P. sylvestris* was more negatively affected by extreme years in terms of high temperature.

While the climatic extremes observed in this study did coincide with growth declines in the warm regions, the coincidences are comparatively infrequent (e.g. Zhang et al 2023 found coincidence rates as high as 0.7). The small effect sizes, coupled with the fact that extremes (according to the definition in this thesis) are inherently rare, suggest that any amplification of negative growth-climate responses due to extreme events of this type is likely of limited importance. However, it is important to note a few caveats regarding the analysis of extremes. First, the extremes studied here are not necessarily representative for those that may come with future climate change (IPCC 2021). For example, an extreme drought observed in northern Europe in 2018 may become a new norm in the near future (Toreti et al 2019), thereby making the events currently defined as extreme more common. Secondly, it is possible that the definition of extremes used here does not capture biologically relevant climatic extremes. Thirdly, compound effects (i.e. years that are both extremely hot and with extremely low precipitation) are not incorporated, which may have amplifying effects on the growth responses (Zhang et al 2023).

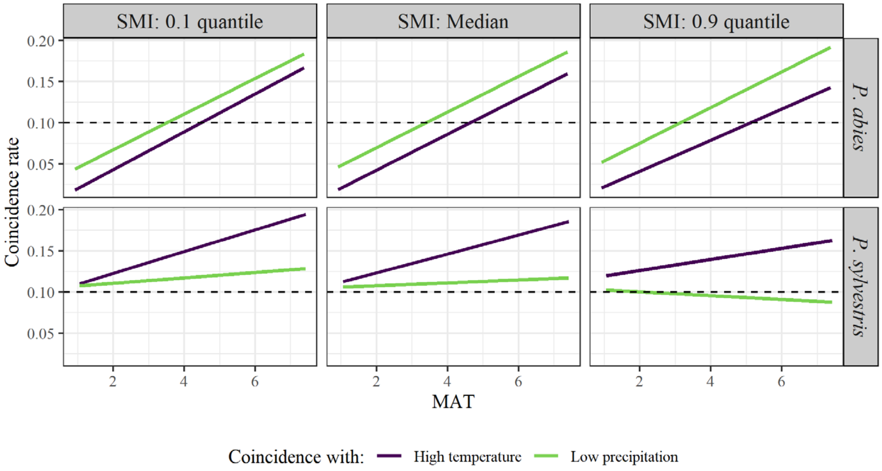

Figure 12. Model output on the effects of MAT on rate of coincidence between years of low growth and high temperature (purple lines) or low precipitation (green lines). Facets show the differences between low (10% quantile; left graphs), median (middle graphs), and high (90% quantile; right graphs) SMI, as well as between species (upper = *P. abies*; lower = *P. sylvestris*). The dashed lines indicate the 0.1 threshold, above which the years coincide more often than can be expected from random coincidences.

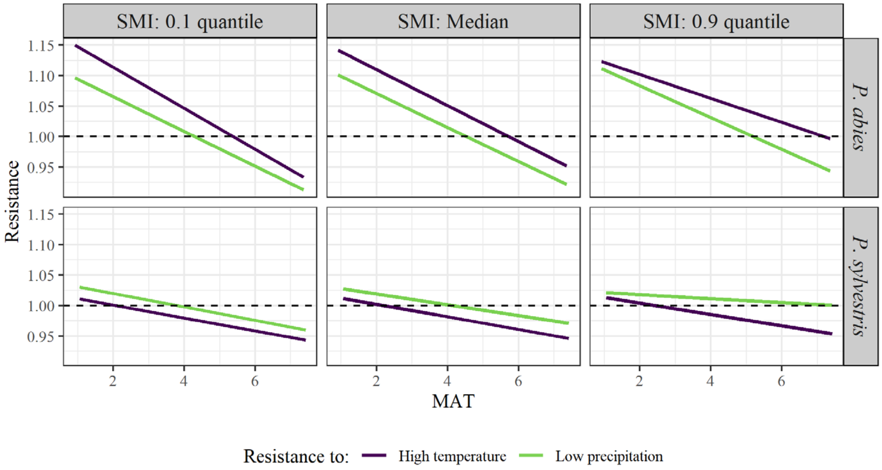

Figure 13. Model output of the effects of MAT on tree growth resistance to years of high temperature (purple lines) or low precipitation (green lines). Facets show the differences between low (10% quantile; left graphs), median (middle graphs), and high (90% quantile; right graphs) SMI, as well as between species (upper = *P. abies*; lower = *P. sylvestris*). The dashed lines indicate the 1.0 threshold, below which the extremes have a negative impact on tree growth.

4.1.4 Chapter summary

Do local temperature and soil moisture regimes affect tree growth responses to climate change? Yes, I found clear evidence that tree growth responds differently to climatic variables depending on the conditions of their growth site. In particular, trees growing in already warm regions are more sensitive to increasing temperatures than those growing in cold regions. Furthermore, trees growing in areas of higher soil moisture contents within the warmer regions may be somewhat alleviated from the negative effects of increasing temperatures, although the effect is currently quite small. Lastly, there are distinct differences in how trees of *P. abies* and *P. sylvestris* respond to different climatic factors.

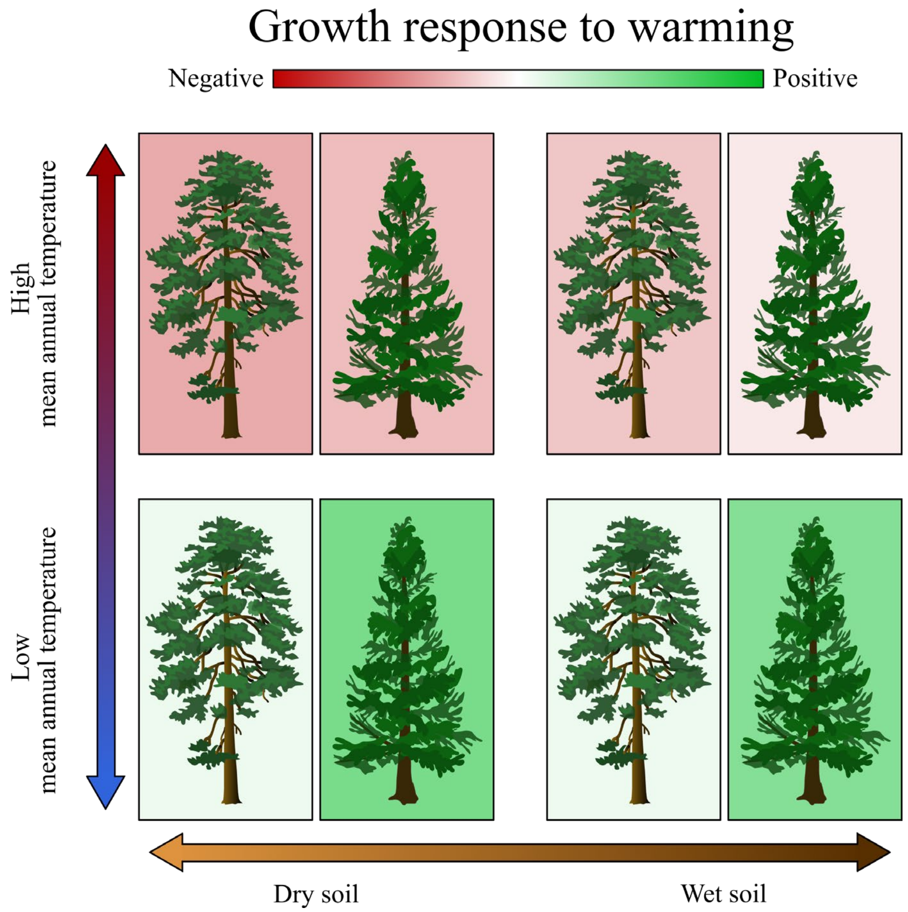

Figure 14. Conceptual graph of the findings in Chapter 4.1: Showing that the growth response to warming depends on local mean annual temperature and that soil moisture has a slight alleviating effect in warm areas.

4.2 Effects of clearcutting on tree growth – climate responses

The results in this chapter are based on linear mixed effects models and mediation analyses (3.8.2) using data on TRW (3.3 - 3.4) and climate variables (3.5) collected from the study sites in northern Sweden (3.2).

Given the effect of climatic variability on tree growth, as seen in Chapter 4.1, coupled with recent observations of increasing climatic sensitivity following forest continuity disruptions (Wolf et al 2023; Mausolf et al 2017; Oheimb et al 2014), this chapter is dedicated to exploring the effects on growth-climate responses from clearcutting in the Fennoscandian boreal forest. Here, I give (I) further evidence to the pattern of higher climatic sensitivity in clearcut forests. To further bring clarity as to why this pattern exists, I also present (II) an exploration of mechanistic explanations to the higher climatic sensitivity through tree- and soil characteristics.

4.2.1 Growth patterns

The TRW data from the study sites in Project II (Figure 6) reveal clear differences in growth patterns between trees growing in previously clearcut forests (CC_{60}) and trees growing in forests that have not been clearcut (NC) (Figure 15). In early life, the trees in clearcut forests have much higher growth rates than those of non-clearcut forests. This elevated growth rate may be positive from a short-term productivity perspective. However, the fast growth of the clearcut forests may force decreased root:leaf ratios in the trees (Lim et al 2015) and thereby produce forests that have reduced access to water and are more sensitive to drought conditions (see section 4.2.3). Therefore, the long-term productivity and growth stability of the clearcut forests may be adversely affected by the enhanced early growth rates.

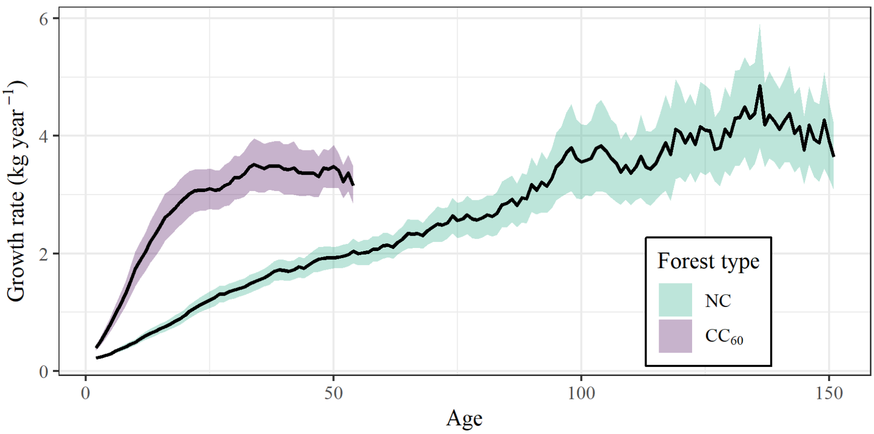

Figure 15. Annual biomass gain of individual trees in clearcut forests (CC$_{60}$; purple) and non-clearcut forests (NC; green). Note that lines are cut when one of the sites of the respective category contains no trees above the age of the cut point (i.e. at age 54 for CC$_{60}$, and 151 for NC).

Indeed, the growth stability in clearcut forests seems to be somewhat lower in comparison to that of non-clearcut forests. On an individual tree level, the MS (a measure of inter-annual growth variability) of the different forest types is quite similar (Figure 16). This means that from one year to the next, the individual trees of both forest types vary in similar magnitudes. However, when the growth variability is studied on a basis of stand-wide mean averages, the pattern is different. The stand-wide growth varies more from year to year in clearcut forests than non-clearcut forests. This discrepancy suggests that trees in non-clearcut forests have more complementary growth rates, so that when one tree experiences low growth, another experiences high growth. On the contrary, in clearcut forests, all trees are more similar in their experience of high or low growth years. Interestingly, the mediation analyses (as seen in section 4.2.3) revealed that none of the studied variables that create complementarity through trait diversity (age and size variation) explained the differences in the stand-wide MS between clearcut and non-clearcut forests. Hence, I have been unable to find a good mechanistic explanation as to why the complementary pattern in non-clearcut forests arise.

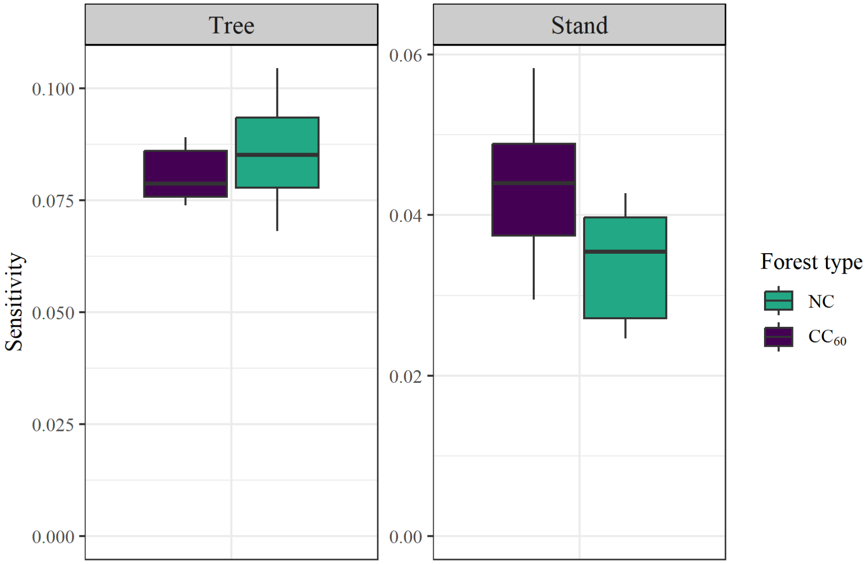

Figure 16. Mean sensitivity (MS; inter-annual growth variability) in clearcut forests (CC_{60}; purple) and non-clearcut forests (NC; green). On the left, the data is presented as the MS calculated first for individual trees and then averaged for each forest. On the right, the data is presented as the MS calculated for the stand-wide mean growth.

4.2.2 Climate responses

The growth-responses to climatic variables were generally more moderate in non-clearcut forests than clearcut forests. This is unsurprising, although not a certainty, following the lower inter-annual variability of the non-clearcut forests. Importantly, tree growth in clearcut forests was more negatively affected by high temperatures during the summer months, and more positively affected by high precipitation and SPEI (Figure 17), than that of non-clearcut forests. A dependency on high precipitation while simultaneously being adversely affected by high temperatures may create poor conditions for sustaining growth during drought periods.

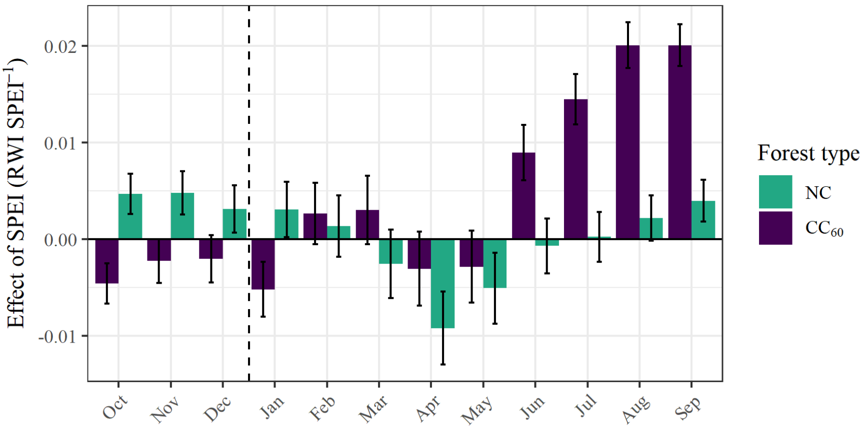

Figure 17. Model output of the effects of monthly SPEI on annual RWI in clearcut forests (CC$_{60}$; purple) and non-clearcut forests (NC; green).

One of the worst drought years in the near past was that of 2018 (Toreti et al 2019). And indeed, the tree growth of clearcut forests was more negatively affected during 2018 than the tree growth of non-clearcut forests (Figure 18). While both forest types showed declines in growth between 2017 and 2018, the average growth decline in clearcut forests was 19% while the non-clearcut forests experienced an average growth decline of 11%. However, as both forest types returned to relatively normal growth rates after the drought, the recovery of clearcut forests was greater than that of non-clearcut forests.

It is important to note that the region in which these trees grow was particularly affected by the 2018 drought (as seen from vegetation indices in Wolf et al 2023), which may suggest that these results are exacerbated compared to the average impact throughout the boreal forest. However, if future climate change causes extreme droughts to become more common (IPCC 2021; Toreti et al 2019), these results may be relevant for a larger scale as well. Nevertheless, the resistance values in this study suggest that forest management is of importance for forests' drought resistance and that actions can be taken to mitigate negative drought effects on forest productivity.

Another important note is that even though clearcut forests experienced a greater growth decline in 2018, the growth was still greater than that of non-clearcut forests (i.e. the decline did not decrease the clearcut forests' growth to levels below that of non-clearcut forests). However, the increased sensitivity to drought may be indicative of future growth declines to levels below that of non-clearcut forests if these are to become more common or more severe (IPCC 2021; Toreti et al 2019). Furthermore, a greater sensitivity may precede more severe drought responses, such as mortality events (Dobbertin 2005), which could be far more detrimental for the forest productivity.

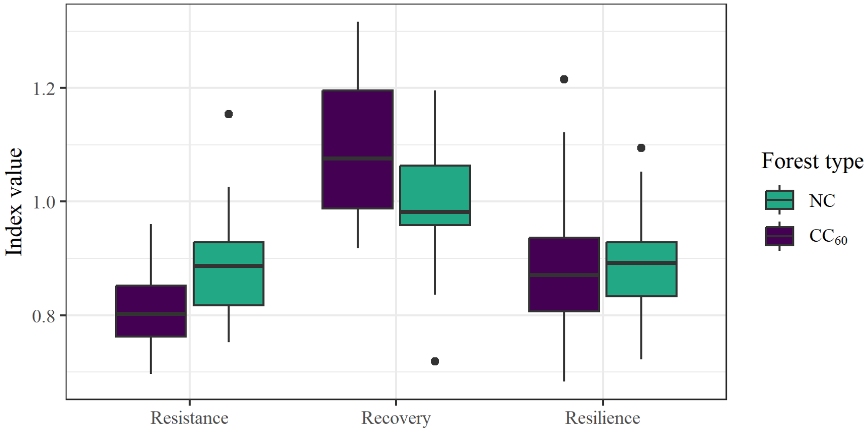

Figure 18. Index values of resistance, recovery, and resilience (see equation 3) to the 2018 drought, based on RWI data for clearcut forests (CC_{60}; purple) and non-clearcut forests (NC; green).

4.2.3 Mechanistic explanations to drought responses

To adapt the forest to the potentially more frequent and severe droughts of the future, it will be important to understand which mechanisms that drive the differences between forest management types in drought resistance. I investigated a number of tree- and soil characteristics that may have been influenced by the clearcutting and, in turn, have impacted the trees' drought resistance (Figure 19 lower). The mediation analyses revealed that among the most prevalent mediating characteristics were: a decreased mean tree age (Figure 19 upper); increased early growth rates; and, to a lesser extent, a decrease of tree age heterogeneity.

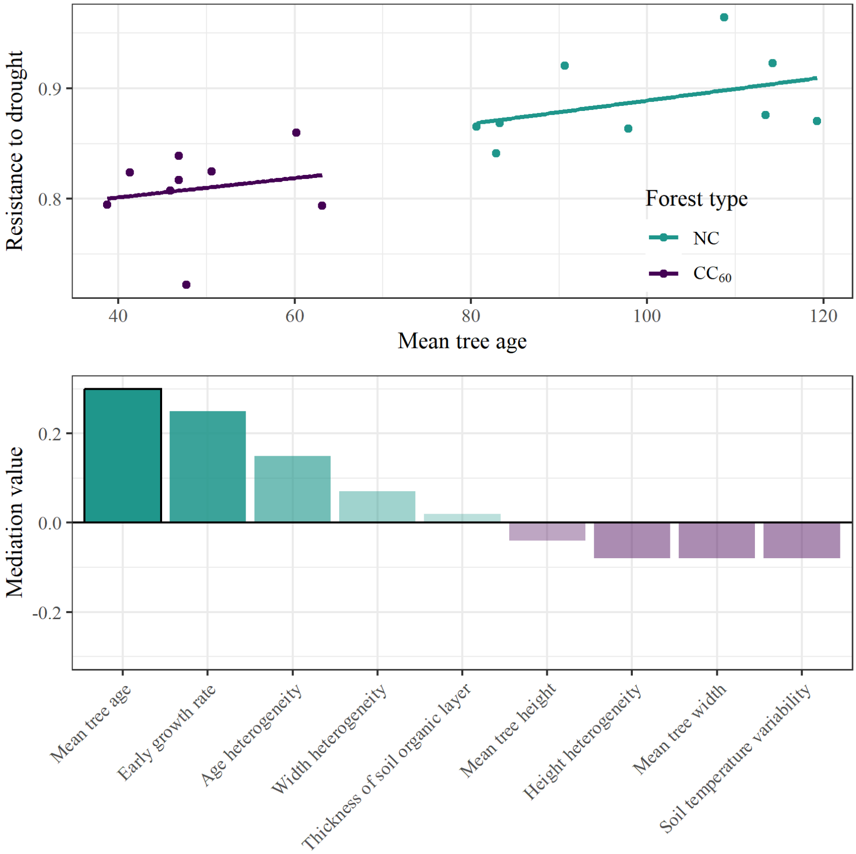

Figure 19. Results from mediation analyses of the effect of disrupted forest continuity through clearcutting on resistance to the 2018 drought. The upper graph shows the effect of the variable with greatest mediation values (mean tree age) on drought resistance, separated between clearcut forests (CC_{60}; purple) and non-clearcut forests (NC; green). The lower graph shows the mediation values for all studied mediating factors.

While younger trees may experience less hydraulic constraints compared to older and taller trees (Ryan & Yoder 1997), older trees may have a more developed root system, which enables their water uptake even during relatively drier periods (Zhang et al 2022). In these study systems, older age indicated higher resistance to droughts, which suggests that the benefits to water uptake may be more prevalent. This is also consistent with the fact that high early growth rates proved detrimental for drought resistance, as trees with faster growth may allocate less resources to below-ground growth (Lim et al 2015), and thereby have a lower water uptake capacity.

The soil characteristics did not reveal much of a mediating effect in this study. This may seem surprising as highly dense, or poorly developed, organic soil layers may lower the soil water retention capacity (Cartwright et al 2020; Oheimb et al 2014). However, in this study, the difference in soil characteristics between clearcut and non-clearcut forests was small, and thereby could not mediate the observed differences in drought resistance. Thus, any general importance of soil characteristics cannot be ruled out through these analyses.

Interestingly, as a side-effect of tracking the soil moisture levels during the incubation experiment in Project III, I found that the water retention capacity was greater in non-clearcut forests than clearcut forests (i.e. the soil moisture did not decline as fast in non-clearcut forest soils) (see Appendix 1). Although the sample size was reduced in Project III, this could add another potential mechanistic pathway through which the non-clearcut forests are more drought tolerant. However, since the soils of the non-clearcut and clearcut forests in Project III did not differ much in regard to the measured soil metrics, we cannot say *why* the pattern of greater water retention capacity occurred in the non-clearcut forests.

4.2.4 Chapter summary

Does clearcutting alter trees' sensitivity to climate change? Yes, I found evidence that hints at forests having a decreased growth stability ~60 years after clearcutting compared to those that have never been clearcut. The decreased growth stability also seems to have led to a reduced capability of sustaining growth during drought. Lastly, the reduced drought resistance seems to have been mediated to some extent by differences in the mean tree age, where forests containing older trees react less severely to drought.

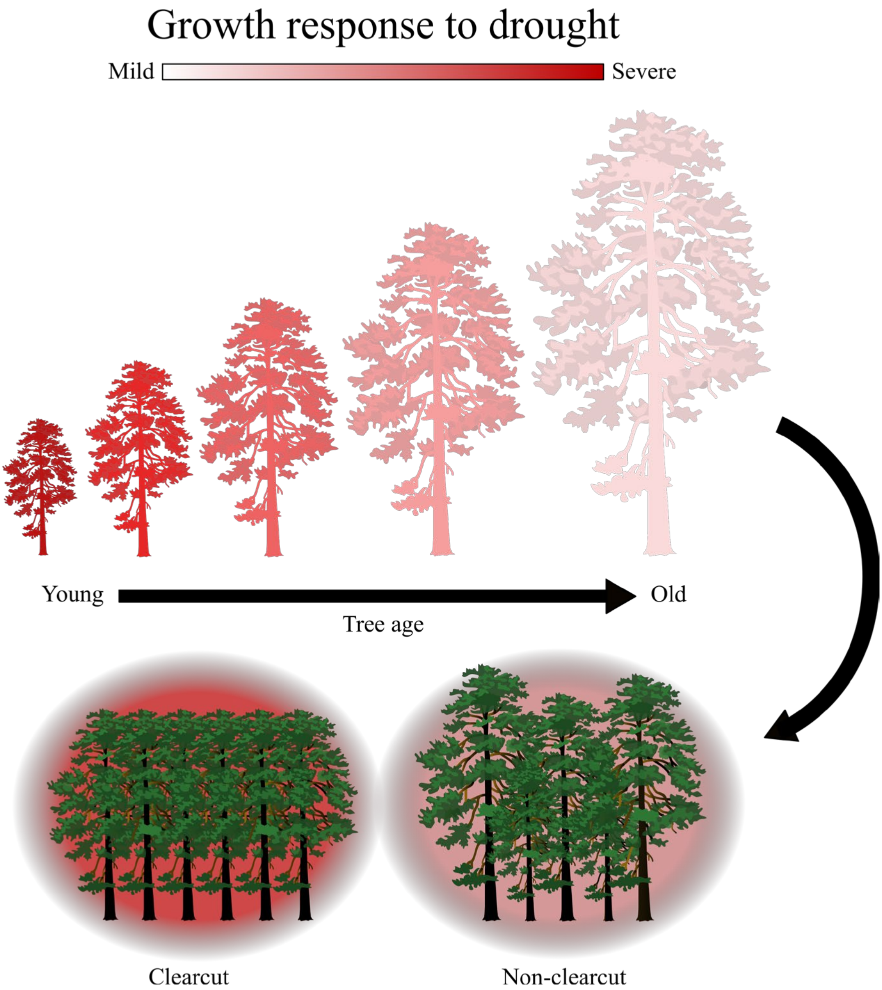

Figure 20. Conceptual graph of the findings in Chapter 4.2: Showing that stands with younger trees revealed more severe growth responses to drought, which partly explains the finding of reduced drought-resistance in clearcut forests.

4.3 Effects of clearcutting on soil – climate responses

The results in this chapter are based on linear mixed effects models (3.8.3) using data on soil characteristics collected through lab analyses (3.7) and respiration measurements carried out through the incubation experiment (3.6).

Other than tree growth, a forest ecosystem may hold other compartments whose functions are equally sensitive to rising temperatures. Generally, the soil of a boreal forest stores carbon at levels comparable to, or higher than, that of trees. If the soil respiration, i.e. the outflux of CO_2 from the soil to the atmosphere, increases, the ecosystem service of carbon storage could be diminished. Clearcutting may cause a reduction in several indicators of SOM quality, and such a quality reduction could in turn lead to increased temperature sensitivity of the soil respiration. Here, I show that clearcutting may be followed by a slight increase in soil respiration temperature sensitivity. I provide observations from an experiment where I found that (I) soil characteristics were slightly different in recent clearcuts compared with ~60 year old clearcuts and forests that have never been clearcut. Furthermore, I found that (II) soil respiration was lower in young clearcuts, and that (III) the temperature sensitivity of the soil respiration was higher in young clearcuts, but both respiration and the temperature sensitivity were similar between ~60 year old clearcuts and non-clearcuts.

4.3.1 Soil characteristics

The comparison of soil properties (SOM, hydrolysable C, C:N ratio, $\delta^{13}C$ and $\delta^{15}N$) only revealed slight differences between forest types (Figure 21). Mainly, the soils of young clearcuts (<10 years old) exhibited slightly smaller fractions of easily decomposable material (hydrolysable C), as well as slightly higher $\delta^{13}C$ values. Interestingly, the young clearcuts also exhibited the highest level of variability in all soil properties, suggesting more between-stand heterogeneity when it comes to soil characteristics.

The differences in both the hydrolysable fraction and the $\delta^{13}C$ may reflect a shift from labile to more recalcitrant substrates in the young clearcuts' soils (Roth et al 2023; Bol et al 2003). The lower amount of labile SOM in the young clearcuts may be a consequence of continued decomposition post-clearcutting while input of new labile material ceased (Roth et al 2023). This is further supported by the higher $\delta^{13}C$, where litter input generally decreases $\delta^{13}C$ while decomposition increases $\delta^{13}C$ due to discrimination against ^{13}C in microbial degradation (Natelhoffer & Fry 1988). Lastly, the similarity in labile SOM between non-clearcuts and older clearcut forests (~60 years old) may suggest that the increased litter input as the forest matures post-clearcutting increases the labile SOM fraction until it reaches an equilibrium of input and decomposition (i.e. converges with the levels of non-clearcut forests).

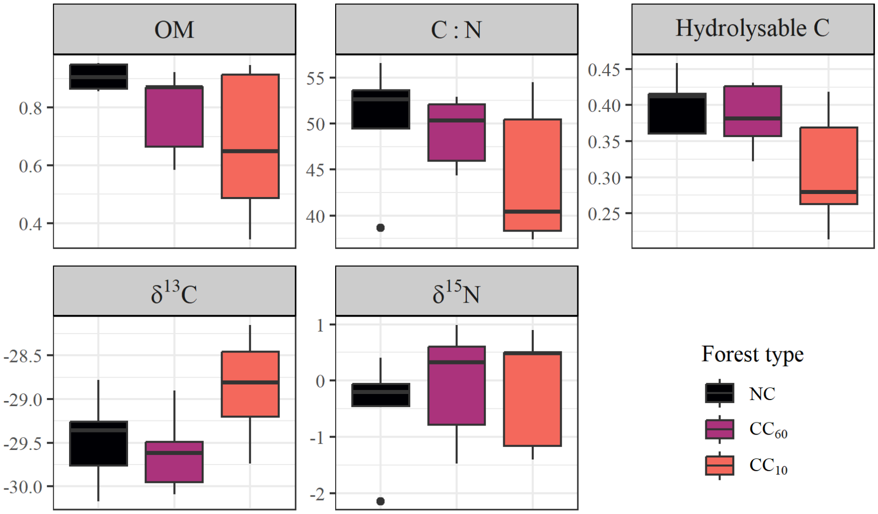

Figure 21. Soil properties (organic matter (OM); C:N ratio; hydrolysable fraction of soil carbon; δ^{13}C and δ^{15}N) in non-clearcut (NC; black), old clearcut (CC_{60}; purple), and young clearcut (CC_{10}; orange) forests.

4.3.2 Soil respiration

The soil respiration differed somewhat between the different forest types prior to the incubation of the soil samples, with the highest levels in the older clearcut forests and the lowest levels in the young clearcuts. Although slightly lower, the soil respiration of the non-clearcut forests was similar to that of the older clearcuts – a pattern that was consistent with the soil respiration measurements in the field (as seen in Chapter 4.4). This suggests an early decrease in soil respiration following clearcutting, and a later increase to levels that may surpass that of non-clearcut forests. However, the low temporal resolution of the data makes it difficult to know if the soil respiration levels are still increasing 60 years after clearcutting, or if they have reached a peak and are now converging with the levels found in the non-clearcut forests, or if they simply plateau at higher levels.

A decrease in soil respiration following clearcutting may be due to altered microclimatic conditions (Guo et al 2010), or a decrease in autotrophic respiration due to the removal of trees (Moroni et al 2009; Striegl & Wickland 1998). However, due to the experimental setup in this study, the microclimate and the autotrophic respiration should be accounted for (i.e. the soils are incubated at similar temperature and moisture conditions, and all plant material has been removed). Therefore, while these parameters may still be important for a general decrease in soil respiration, there are other factors that play a part. Likely, the changes in substrate quality (increased recalcitrance) forces the observed lower respiration rates in the young clearcuts (Wang et al 2018; Karhu et al 2010).

4.3.3 Soil respiration temperature sensitivity

The initial differences between forest types regarding soil respiration remained similar throughout the incubation period (i.e. young clearcuts had lower respiration than older clearcuts and non-clearcut forests) (Figure 22). During the first days of incubation, the warmed soils of all forest types exhibited much higher respiration rates (~20-40%) than the ambient soils. However, as the incubation period progressed, the difference between warmed and ambient soils decreased until a convergence after 15-20 days. At the time of termination, the ambient soils even exhibited slightly higher respiration levels than that of the warmed soils.

The increased respiration levels following warming was anticipated, due to the positive relationship between temperature and microbial metabolism (Jin & Bethke 2007), and has been observed in many previous studies (e.g. Vogel et al 2014; Bond-Lamberty & Thomson 2010; Fierer et al 2006). However, the later decrease of soil respiration in the warmed soils, to levels below that of ambient soils, is more surprising. Possibly, the reduction is merely a consequence of a decrease of labile substrates during the earlier period of the incubation (Birge et al 2015) – that is to say, due to the increased respiration early on, the warmed soils may have depleted more of the labile, easily decomposable, substrates which later on may have caused a more severe decrease in soil respiration.

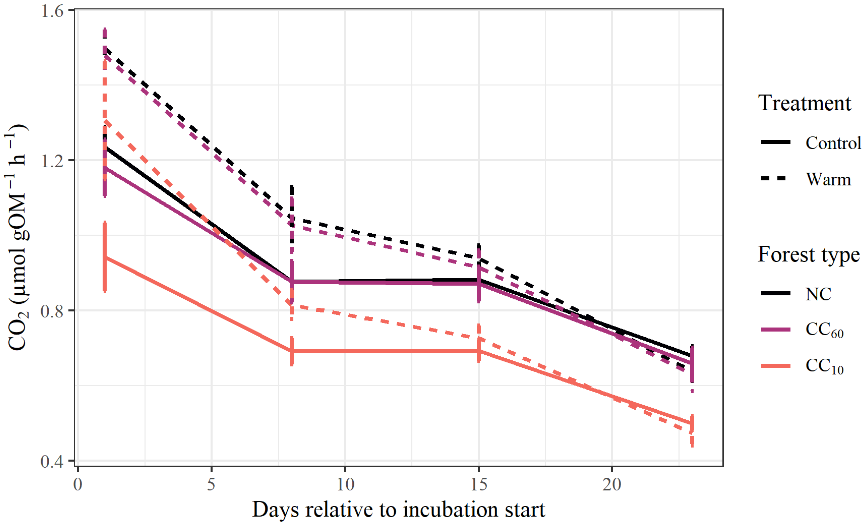

Figure 22. Soil respiration (CO_2) during the incubation period separated between control and warmed (+5 C) treatments, and between non-clearcut (NC; black), old clearcut (CC_{60}; purple), and young clearcut (CC_{10}; orange) forests.

In the first few days of the incubation, the increase in respiration due to warming was slightly stronger in the young clearcuts than the other forest types (38±9% compared to 26±7% and 22±4% in old clearcuts and non-clearcuts, respectively). This suggests that the soil respiration in the young clearcuts is more sensitive to increasing temperatures than that of mature forests. Again, this may be a consequence of the increased recalcitrance following clearcutting, where more recalcitrant material requires higher activation energy for microbial enzymes to decompose (Davidsson & Janssens 2006). Importantly, the difference between the forest types faded throughout the incubation period (i.e. there was no difference in the proportional increase of soil respiration due to warming between the forest types in later measurements). However, if the increase in temperature sensitivity in the young clearcuts, as observed in the first measurement, is indicative of an increase in a “real” system, this has implications for the soil respiration-warming feedback. Increasing temperatures would then lead to an increased production of CO_2 in the clearcuts which would potentially elevate the temperatures even more, and around it goes. Furthermore, the soils in clearcuts will likely experience higher temperature increases than those of forests

(Starck et al 2025), potentially leading to even higher respiration-warming feedback due to differences in microclimatic conditions coupled with the observed differences in intrinsic soil respiration temperature sensitivity.

However, when comparing forests regenerated after clearcutting with non-clearcut forests in Project II, I found that there seems to be little difference in terms of soil temperature regimes. Therefore, it seems like the difference in soil temperature diminishes over time, much like the difference in soil respiration temperature sensitivity. This suggests that the elevated temperature sensitivity following clearcutting is transient. Furthermore, soil respiration responses to varying degrees of temperature increases are difficult to predict (Lloyd & Taylor 1994), and the respiration (and thereby the positive feedback loop) is unlikely to increase interminably with higher temperatures (Liu et al 2018). Nevertheless, if increasing soil respiration, even up to a point, is coupled with declining, unchanging, or even less increasing, growth, the end result is likely to be reduced forest carbon stocks.

4.3.4 Chapter summary

Does clearcutting alter the feedback of soil respiration from increasing temperatures? Yes, to some extent. I found that recent clearcuts (<10 years) exhibited slightly higher soil respiration temperature sensitivity. However, in older clearcuts (~60 years) the increased temperature sensitivity was no longer present.

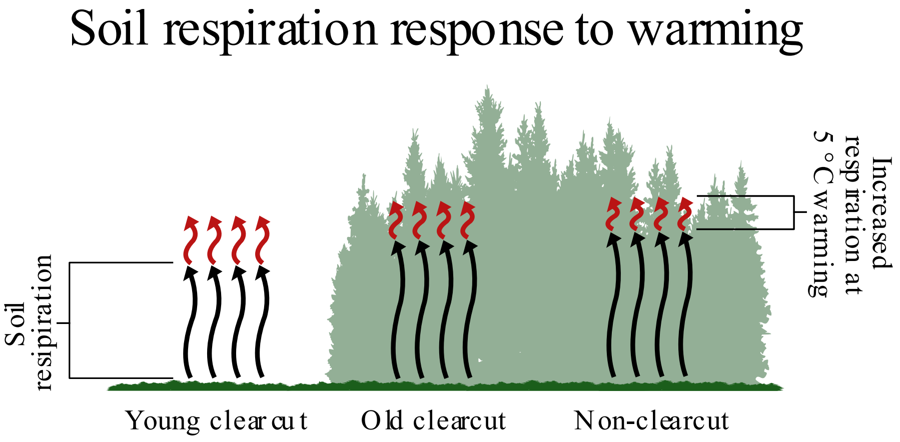

Figure 23. Conceptual graph of the findings in Chapter 4.3: Showing a lower but more temperature-sensitive soil respiration rate in young clearcuts.

4.4 Effects of clearcutting on long-term productivity

The results in this chapter are based on linear mixed effects models (3.8.4) using data collected through a variety of field- and labwork (3.3 & 3.7) from the study sites in northern Sweden (3.2).

While climate change has an effect on forests, the productivity of forests also affects climate change, e.g. through C sequestration and the provision of relatively renewable resources. In the short term, clearcutting can be thought to reduce the C stocks of forests, while it simultaneously enhances productivity and C uptake. However, as clearcutting is a young practice (on a forest generational scale), long-term changes to ecosystem functions that are vital to productivity remain relatively unexplored. Here, I provide evidence that, relative to non-clearcut forests, forests ~60 years after clearcutting (I) exhibit different soil microbial communities important for nutrient cycling, (II) but a very small difference in N limitation, and (III) substantially higher productivity.

4.4.1 Soil microbial communities

The PLFA analysis revealed that the clearcut forests hosted a larger abundance of PLFA than the non-clearcut forests. The clearcut forests' PLFA had a higher fungi:bacteria ratio, and an overall higher abundance of fungal PLFA.

The soil bacterial PLFA was relatively similar between the two forest types, with only slight differences in the G+ and G- bacterial proportions. The clearcut forests had higher amounts of PLFA biomarkers for both G+ and G- bacteria, but the increase was more prominent for G- bacteria which often are more associated with decomposition of labile C compounds (Fanin et al 2019).

The soil fungal communities revealed some differences between the forest types (Figure 24). The ectomycorrhizal (ECM) fungi, important for tree N acquisition through symbiotic relationships (Smith & Read 2008), had slightly higher biomass in the clearcut forests compared to the non-clearcuts. However, at finer taxonomic resolutions, this difference revealed more details: The higher ECM fungal biomass was mainly driven by *Atheliales* taxa, which generally lack oxidative decomposition capabilities important for nutrient cycling (Bödeker et al 2014); The biomass of oxidative decomposers (*Cortinarius* and *Russula* taxa), on the other hand, were slightly lower in the clearcut forests.

The biomass of ericoid mycorrhizal (ERM) fungi, which produces generally recalcitrant necromass (Clemmensen et al 2015), was proportionally lower in the clearcut forests than in the non-clearcuts. If soils from the clearcuts contain less recalcitrant organic matter, as a result of the lower abundance of ERM, the need for microbes that can decompose such litter may be limited. This could explain why fungi with such decomposing capabilities are less common in the clearcuts. However, as seen in Chapter 4.3.1, I did not find any strong evidence to suggest that there are differences in substrate recalcitrance between the ~60 year old clearcuts and non-clearcuts, suggesting that there are factors other than the ERM-induced input of recalcitrant organic matter that cause the differences in ECM decomposers.

The respiration rates in the clearcut forests were consistently higher than that of non-clearcut forests, which may indicate greater soil microbial activity and higher rates of decomposition (Hanson et al 2003). While this difference was relatively small, it is important to note that soil respiration represents both heterotrophic respiration, produced by soil microorganisms during decomposition of SOM (Kuzyakov 2006), and autotrophic respiration, produced by plant roots (Tang et al 2019). Autotrophic respiration may be further partitioned into growth respiration and maintenance respiration (Hirano et al 2022). In this study, the non-clearcut forests showed substantially higher amounts of vegetation biomass (see Appendix 3), potentially indicating higher amounts of autotrophic respiration due to increased maintenance load. On the other hand, the clearcut forests revealed higher growth rates (Figure 26), which may indicate higher amounts of autotrophic respiration as well. Given the difficulty in assigning the autotrophic proportion of the soil respiration, and thereby the heterotrophic counterpart, it is difficult to extrapolate the respiration values to differences in decomposition. Therefore, it is difficult to say with any certainty if either forest type has a higher rate of decomposition but with the evidence that I do have, in terms of total soil respiration data, it seems likely that the organic matter of clearcut forests decompose faster than that of non-clearcut forests.

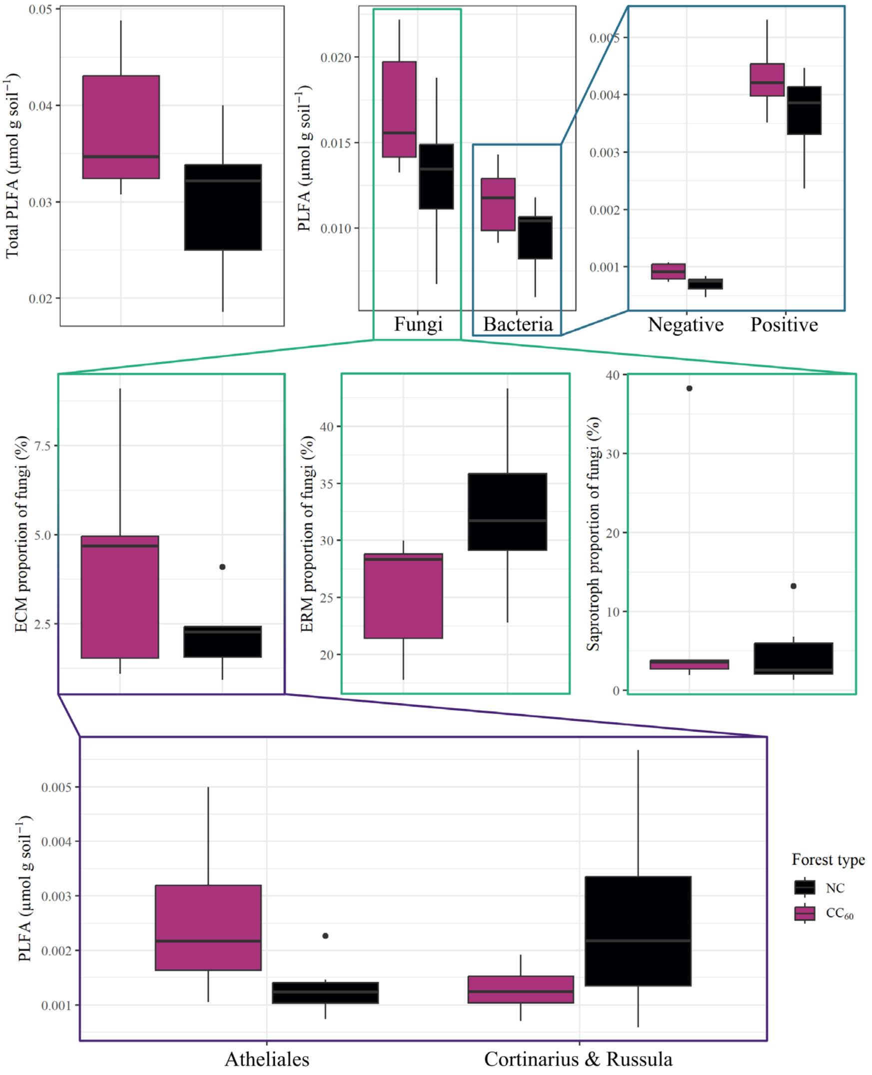

Figure 24. Chart of the microbial communities with descending taxonomic resolution in non-clearcut (NC; black) and clearcut (CC$_{60}$; purple) forests. Y-axes on the upper row represent PLFA abundance in soil samples (separated between the total amount of identified PLFA; biomarkers for fungi and bacteria; as well as for G- and G+ bacteria). Y-axes on the middle row represent the proportion of fungal sequences belonging to ECM, ERM, and Saprotrophic fungi. The y-axis on the bottom row is calculated by multiplying the proportion of fungal sequences belonging to *Atheliales* or *Cortinarius* and *Russula* by the fungal PLFA. Note the independent scales.

4.4.2 N limitation

Needle N concentrations ranged from 0.66-1.13% in both forest types, a range consistent with N-limited forests (Major & Mosseler 2021; Sikström et al 1998). The clearcut forests showed slightly higher needle C:N ratios than the non-clearcut forests (Figure 25). Such higher ratios can either indicate stronger N limitation (Sheng et al 2021; Xu et al 2020) or improved N use efficiency (Zhang et al 2020) (i.e. gaining more C for each unit of N). Because the elevated C:N ratios were partly due to lower needle N concentrations, trees in the clearcut forests likely experienced reduced N access compared to those in the non-clearcut forests. Interestingly, the clearcut forests exhibited slightly lower soil C:N ratios, driven mainly by somewhat higher soil N concentrations. This potentially points towards higher N availability in the soils of the clearcut forests (Cote et al 2000). Thus, the lower needle N concentrations more likely reflect a reduced N uptake capacity rather than a limited soil N supply. Overall, difference in needle N concentrations was minor and highly variable among sites. On average, needle N concentrations in the clearcut forests were only ~4% lower than in the non-clearcut forests. This is a small difference compared with changes observed after N fertilization (17% increase; Palvi et al 2025) or CO_2 fertilization (17% decrease; Major & Mosseler 2021).

Hence, these results indicate a relatively small intensification of N limitation in the clearcut forests. This is not surprising given the changes in the soil microbial community. The lower relative abundance of ERM fungi may have resulted in more labile soil organic matter due to a lower proportion of highly recalcitrant fungal necromass (Clemmensen et al 2015). Simultaneously, the ECM community has likely maintained the function of oxidative decomposition as the proportional reduction of such taxa was very small. Similarly, the clearcuts' soil bacterial community only revealed a slightly lower proportion of G+ bacteria (as seen in Project III), which are generally adapted to decompose more complex substrates (Wang et al 2018). Possibly, the slight differences in oxidative decomposing fungi and G+ bacteria were too small to reinforce the N limitation. Alternatively, the limitation may have been compensated by other N pathways, such as increased fine root biomass, as observed following clearcutting in other studies (Yuan & Chen 2012; Makkonen & Helmisaari 2001), or the general increase in ectomycorrhizal fungi to promote N access. Regardless of the mechanism, the aggravated N limitation following clearcutting was relatively mild in these forests.

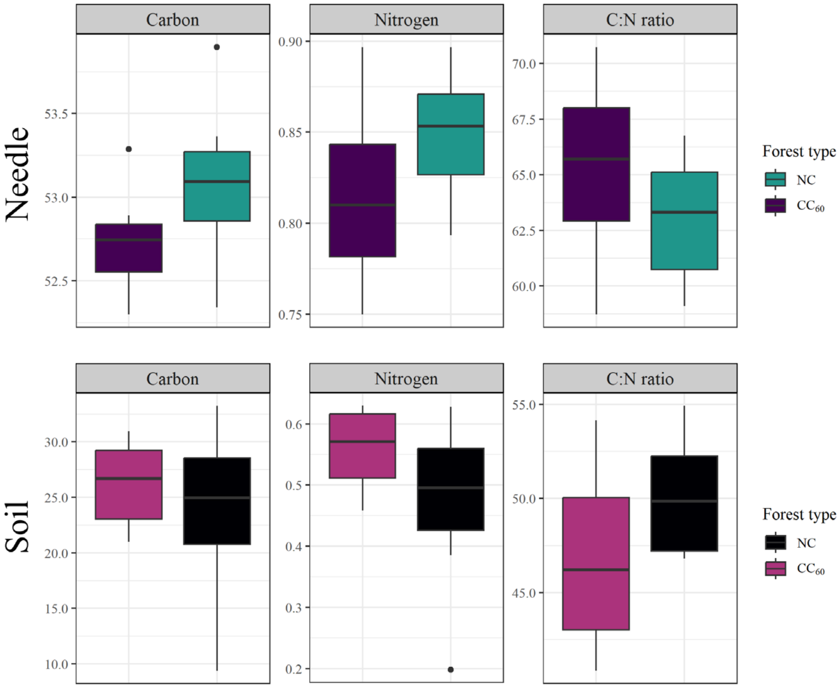

Figure 25. Carbon and nitrogen concentrations (ω %), and C:N ratio, in needle samples and soil samples from non-clearcut (NC) and clearcut (CC_{60}) forests.

4.4.3 Long-term productivity

The clearcut forests had much higher BAI during the last five years of the study period than the non-clearcut forests (on average ~60% higher). The higher BAI has been present for more than 40 years among those trees that are still alive today (Figure 26), but it is important to note that the further back in time we look, the more data we are missing from trees that may have died during the studied time. In other words, the BAI may have been higher for both forest types, but we lack data for the trees that have not survived until today. Since the trees in the clearcut forests still, after ~60 years, had not accumulated the same biomass as that of trees in non-clearcut forests, it is likely that they still benefit from the alleviation in light- and nutrient competition that follow a disturbance event (Lapointe et al 2006; Vitousek 1981).

However, it remains to be seen if the clearcut forests retain a higher productivity even when the same biomass has been accumulated, and thereby result in an increased aboveground C-stock. Furthermore, productivity and aboveground C-stocks may be assumed to reach a maximum in middle-late successional stages before declining to a lower equilibrium (Gao et al 2018). Hence, the clearcut forests may grow to achieve slightly higher biomass levels than that of non-clearcut forests before dropping to similar levels if they are allowed to transition into later successional stages.

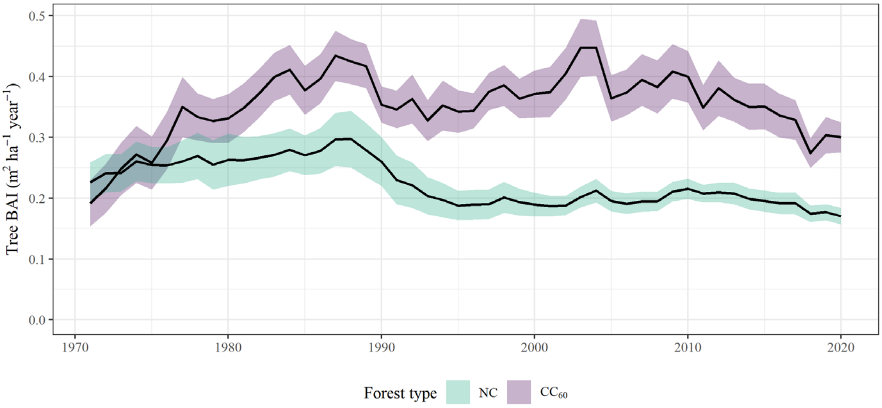

Figure 26. Tree basal area increments (BAI) over a 50-year period in clearcut forests (CC_{60}; purple) and non-clearcut forests (NC; green). Data represents only trees alive at the time of sampling.

A difference in productivity of the understorey was less apparent. *Vaccinium* species are proposed to indicate higher site productivity than *Empetrum* species (Nilsson & Wardle 2005), both of which were highly abundant in both forest types. However, while the clearcut forests did contain a slightly higher relative cover of *Vaccinium* species, and lower relative cover of *Empetrum* species, than the non-clearcut forests, these differences were very small. Hence, the large increase in productivity observed from the higher BAI in the clearcut forests is only somewhat reflected in the understorey vegetation.

4.4.4 Chapter summary

What are the long-term effects of clearcutting on forest productivity? About 60 years after clearcutting, these forests seem to maintain a higher productivity than non-clearcut forests. In parallel, soil nutrient cycling showed modest differences between the forest types. While nitrogen stocks and C:N ratios were rather similar, the microbial community in clearcut forests exhibited traits indicative of adaptation to decomposition of labile substrates. Whether these functional shifts persist throughout a full rotation (~90 years in the studied area) is unclear, but I have found no indication that clearcutting would negatively affect productivity even in the long-term.

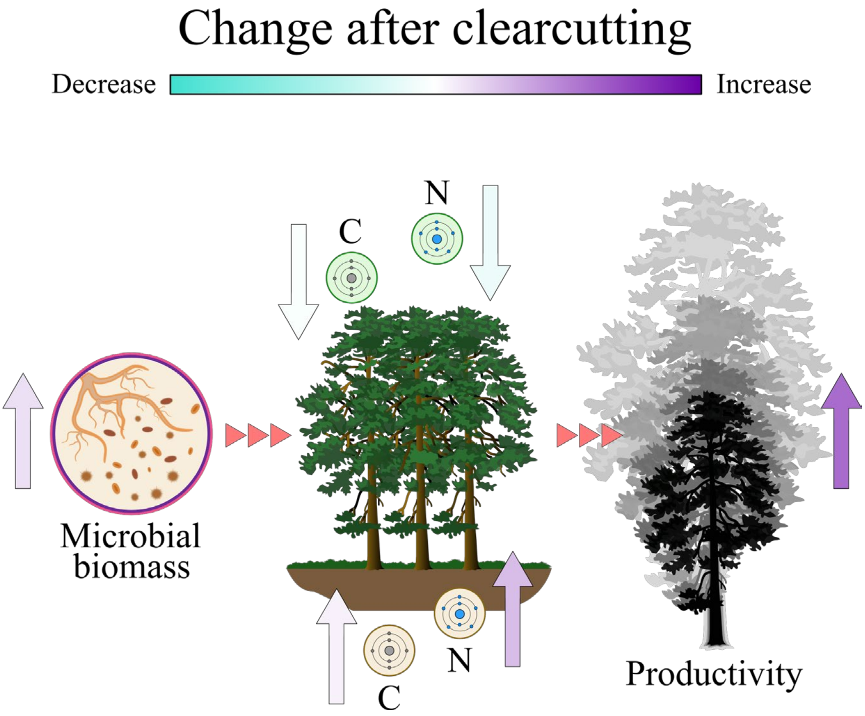

Figure 27. Conceptual graph of the findings in Chapter 4.4: Showing that forests ~60 years after clearcutting exhibit slightly elevated soil microbial biomass (as proxied by PLFA; see section 4.4.1 for more details on the changes to soil microbial communities), very minor changes to soil- and needle N, and a heavily increased productivity.

5. Concluding remarks

A brief search in Web of Science reveals that studies regarding Forest * Management * Climate (the three cornerstones of this thesis) in the last decade number in ~22,000. If I would have read 10 of these studies every day (which I have not), including weekends and holidays, for the last four years of my PhD, I would have read slightly more than 66% of everything published on this topic during the last ten years (excluding synonyms in the original search). Thus, even if I would have banked the memory of everything I had read (which I would not have), there would still be a substantial amount of information that I would have missed. What I want to say with this paragraph is that this thesis should not be considered the work of an expert, which PhD theses so often are, but rather the retelling of a few results that I have found interesting. While academical dogma requires some more or less speculative conclusions to be drawn, I would prefer for readers to first take the results of this thesis at face value and adopt a cautious perspective before drawing too general conclusions from the findings. An exaggerated will for inference and grand statements could have dire consequences when extrapolation reaches implementation and policymaking.

That being said, here is what I would conclude regarding the future management of the boreal forest based on the findings in this thesis.

First of all, the careful consideration of species-specific responses may be important for adapting forests to a future climate. For example, the most common species in Sweden (*P. abies* and *P. sylvestris*) exhibit differences in their growth-climate responses. While *P. abies* seems to be more affected by low precipitation, *P. sylvestris* seems to be more influenced by high temperature. Similarly, the growth responses of *P. abies* depend more on soil moisture. Hence, planting *P. abies* in primarily moister soils will likely mitigate some of the detrimental effects of climate change on the forest productivity.

Secondly, it is important to remember that things will likely change in the future. The effect of climate change on boreal forest ecosystems seems to act as a great equalizer (as opposed to the effects it has on socioeconomics (WMO 2023)). For example, currently highly productive, warm regions will likely become less productive with climate change, while currently low-productive, cold regions may become more productive. Similarly, highly productive and heavily managed forests may become more vulnerable for climate change-induced droughts than low-productive "natural" forests. And finally, the respiration rates of low-activity soils can be presumed to increase more due to warming than that of already highly active soils, diminishing the gap between systems. Whether such a homogenization of ecosystems is desirable is, of course, a matter of opinion, but from a functional- and management perspective it implies a loss of differentiation among systems, which could constrain the adaptive capacity to further disturbances.

Converging growth- and respiration patterns between high- and low-productivity forests bring to mind the question of scale. Management through clearcutting will, on a large scale, leave the landscape with both relatively old and young forests. Old clearcut forests seem to maintain a high CO_2 uptake (tree growth) and similar CO_2 efflux as that of non-clearcut forests. In contrast, young clearcut forests seem to have a highly reduced CO_2 uptake and a more temperature sensitive respiration rate (CO_2 efflux) than that of non-clearcut forests. Hence, old clearcuts can likely be thought to be positive from a climate change mitigation perspective, while young clearcuts can be thought to be negative. This becomes important for the management of the boreal forest as, for example, increased rotation times could help maintain high productivity and CO_2 uptake through the large-scale increase in old compared to young clearcuts.

Importantly, the positive/negative effects of clearcutting on climate change mitigation are conditional on what happens to the C that was stored in the pre-clearcut forests. This takes into account questions on societal resource usage and substitution effects that I am not qualified to answer. However, it does shed some light on the importance of differentiating the net C sink/source potential between CO_2 uptake (tree growth) and CO_2 efflux (soil respiration). Recent observations from the Canadian boreal forest show that the net ecosystem productivity in 2023, one of the warmest years to date, increased due to a massive decline in soil respiration rates (Dong et al 2026). This caused a temporary amplification of the forest net carbon uptake and thereby a negative climate feedback. While an increase in net ecosystem productivity is generally beneficial for climate mitigation, there is some complexity that needs to be considered: if the negative feedback is caused by decreased CO_2 efflux, rather than increased CO_2 uptake, other connected functions may still be detrimentally affected. For example, the forests' substitution effects, as well as the amount of carbon stored in long-lived woody products, can only increase when the forest productivity increases, but would be unaffected by decreased soil respiration. Hence, the climate mitigation benefit from an enhanced net C uptake is limited when it is a consequence of decreased respiration rather than increased growth.

Lastly, can the effects of climate change and clearcutting help explain the recent growth declines in the boreal forest?

The effects of climate change (i.e. changes in temperature, precipitation, and drought regimes) have not had a uniform effect throughout my study area (section 4.1). While increasing temperatures have been correlated with decreasing growth in the south, growth increases in the north may have offset this decline. Similarly, extreme years (in terms of high temperatures or low precipitation) may have aggravated the growth response somewhat in the south, but even such extremes have been positive for growth in the north. Recent decreases in forest water resources may have aggravated the negative effects of warming somewhat in the south, but the effects do not seem to have been substantial.

Clearcutting places forests in temporary growth declines, as young forests need time to accelerate their growth rate (section 4.2 and figure 15), as well as temporary growth increases, as the more mature forests grow better than their non-clearcut counterparts (section 4.4 and figure 26). Hence, without a scaled-up management plan, widespread clearcutting could force an apparent overall growth decline for a few years or even decades if too many forests are harvested at the same time. However, the growth decline experienced in the boreal forest has been observed for stands and even individual trees of different ages, suggesting that the problem is more complex and exists on a smaller scale (Henttonen et al 2024). I found that clearcut forests are more responsive to climatic changes, e.g. drought years, which may provide a part of the explanation of growth decline as previously non-clearcut forests are progressively replaced by a clearcut counterpart. However, the difference in growth responsiveness is relatively small and I doubt that it would be the only explanation for the recent growth decline.

Therefore, I will end with an unsatisfactory conclusion: Climate change and clearcutting may both have contributed in a non-uniform part to changes in productivity, but there is likely other, or more complex, drivers of the recent growth declines.

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Popular science summary

The boreal forest is one of the largest forest biomes in the world. Situated in the far north, it runs through northern Europe, Asia, and North America, but it provides a global service in terms of carbon uptake and storage. For the boreal forest to function as a carbon sink, and thereby a positive contribution in the fight against climate change, it needs to maintain a relatively high carbon uptake from the atmosphere while producing relatively low carbon emissions. However, recently the boreal forest has been observed to experience a decline in its most important carbon uptake function – tree growth. If tree growth is reduced while the carbon output from the forests remains steady or even increases, the boreal forest may risk turning from a carbon sink to a source (i.e. emitting more carbon into the atmosphere than it takes up). The observed growth decline has occurred conveniently in time of a changing climate where increased temperature, a prolonged growing season, and increased frequency of extreme events such as droughts are known to affect plant-life. Simultaneously, a large portion of the current boreal forest has grown following a clearcutting event, a stand-replacing disturbance with a magnitude that likely has been rare before the 20th century. Therefore, it does not seem farfetched to think that the current growth declines are in some way related to climate change or ecosystem changes induced by clearcutting. In this thesis, I have explored how tree growth is influenced by climate change, clearcutting, and the combination of the two.

Firstly, I made use of tree growth data collected all over Sweden to get a sense of how growth patterns differ geographically. Comparing this data with that of climate models for the last 60 years, I have investigated what kind of climate the forests in different parts of Sweden "like". The pattern that emerged is that trees growing in relatively warm areas have, during the last half century, grown more during cold years than warm years while the opposite has been true for trees in relatively cold areas. This hints at a temperature optimum that has been breached, forcing a stressor onto the trees in warmer regions. Further exploring this pattern with models on soil characteristics, I found that this temperature-induced stress can be somewhat alleviated by higher soil moisture levels. With the regional disparity in climatic effects, I am not convinced that climate factors alone can have forced the recent growth declines.

Secondly, I have explored the differences between forests that were clearcut ~60 years ago and those that likely have never been clearcut. The clearcut forests, even after sixty years and when they have started to physically resemble non-clearcut forests, seem to favor "early" microbial characteristics. These microbes, fungi and bacteria, are important for the nutrient cycles to work efficiently within a forest ecosystem. Favoring only one set of organisms over another could mean that important functions are lost. However, the de-prioritization of certain microbial functions in the clearcut forests does not seem to have led to any exceptional growth declines. On the contrary, after a short initial period of poor growth, the productivity in clearcut forests seems to be much higher than that of non-clearcut forests. Hence, the recent growth declines are unlikely to be the consequences of any long-term ecological changes forced by clearcutting.

Then, what about a combination of climatic factors and clearcutting? I explored if the clearcutting practice forced forests into a state where they were more susceptible to the effects (both positive and negative) of climate change. My findings suggest that trees growing in clearcuts respond more strongly to variations in temperature and precipitation. As an example, the extreme drought year of 2018 reduced the growth of all studied trees quite a lot, but the reduction was much greater in clearcuts (19% reduction compared to 11% reduction in non-clearcuts). Although this hints at greater sensitivity in the clearcuts, which may have more dire consequences, it is important to note that these growth reductions did not force the clearcuts into a state of lower productivity than the non-clearcuts. That is to say, even if every year was as extreme as 2018, the productivity of clearcuts may remain higher than that of non-clearcuts. Hence, the combined effect of climatic factors and clearcutting, as studied here, does not seem to explain the growth decline.

Accepting that the growth declines exist, I also examined the combined effects of temperature and clearcutting on soil respiration (the main source of carbon emissions from the forests) to get a sense of the carbon source/sink potential in these forests. By subjecting soils collected from clearcuts and non-clearcuts to a warming experiment, I found that higher temperature consistently increased the soil respiration rate. This increase in soil respiration rate following warming was slightly elevated in young clearcuts (<10 years old) compared with older clearcuts (~60 years old) and non-clearcuts. Hence, if the forests will experience higher temperature due to climate change, we can expect an increase in CO_2 emissions from their soils – and even more so if those soils have recently been subjected to clearcutting.

All these findings combined suggest that climate change and clearcutting, at least as studied here, are not the sole perpetrators in the recent boreal forest growth declines. However, the interplay between climatic factors and clearcutting may have consequences for the forest ecosystem functionality – with clearcutting, we may expect fast-growing forests whose carbon cycle is more sensitive to climatic variations.

Populärvetenskaplig sammanfattning

Den boreala skogen är ett av de största skogsbiomen i världen. Den är belägen långt i norr och sträcker sig genom norra Europa, Asien och Nordamerika, men den tillhandahåller en global tjänst i form av kolinlagring. För att den boreala skogen ska fungera som en kolsänka, och därmed bidra positivt i kampen mot klimatförändringar, behöver den upprätthålla ett relativt högt kolupptag från atmosfären samtidigt som den producerar relativt låga koldioxidutsläpp. På senare tid har man dock observerat en minskning i den boreala skogens viktigaste kolupptagsfunktion – trädens tillväxt. Om trädens tillväxt minskar samtidigt som skogarnas kolutsläpp förblir stabila eller till och med ökar, riskerar den boreala skogen att gå från att vara en kolsänka till att bli en kolkälla (dvs. släppa ut mer kol i atmosfären än den tar upp). Den observerade tillväxtminskningen har skett samtidigt som klimatet förändras, där ökade temperaturer, en förlängd växtsäsong och en ökad frekvens av extrema händelser såsom torka kan påverka växtlivet. Samtidigt har en stor del av dagens boreala skog vuxit upp efter kalavverkning, en beståndsersättande störning av en omfattning som sannolikt varit ovanlig före 1900-talet. Det verkar därför inte långsökt att tänka sig att de nuvarande tillväxtminskningarna på något sätt är relaterade till klimatförändringar eller till ekosystemförändringar orsakade av kalavverkning. I denna avhandling har jag undersökt hur trädens tillväxt påverkas av klimatförändringar, kalavverkning och kombinationen av dessa.

Till att börja med använde jag tillväxtdata insamlade över hela Sverige för att få en uppfattning om hur tillväxtmönster skiljer sig geografiskt. Genom att jämföra dessa data med klimatmodeller för de senaste 60 åren har jag försökt fastställa vilket slags klimat skogarna i olika delar av Sverige ”föredrar”. Mönstret som framträdde är att träd som vuxit i relativt varma områden under det senaste halvseklet har gynnats av kalla år snarare än varma år, medan det motsatta har gällt för träd i relativt kalla områden. Detta tyder på att ett temperatur-optimum har överskridits, vilket utsätter träden i varmare regioner för stress. Vidare analys av detta mönster med modeller över markegenskaper visade att denna temperaturinducerade stress delvis kan mildras av högre markfuktighet. Med de regionala variationerna i klimateffekter är jag inte övertygad om att enbart klimatfaktorer kan ha orsakat de aktuella tillväxtminskningarna.

Jag har även undersökt om kalavverkning kan ha varit ett upphov till tillväxtminskningarna. Detta gjorde jag genom att granska skillnader mellan skogar som kalavverkades för cirka 60 år sedan och sådana som sannolikt aldrig har kalavverkats. De kalavverkade skogarna, även efter sextio år och när de utseendemässigt har börjat likna icke-kalavverkade skogar, tycks gynna "tidiga" mikrobiella egenskaper. Dessa mikroorganismer, svampar och bakterier, är viktiga för att näringscykler ska fungera effektivt i ett skogsekosystem. Att gynna endast en grupp organismer framför en annan kan innebära att viktiga funktioner går förlorade. Nedprioriteringen av vissa mikrobiella funktioner i de kalavverkade skogarna verkar dock inte ha lett till några exceptionella tillväxtminskningar. Tvärtom tycks produktiviteten i kalavverkade skogar, efter en kort initial period av svag tillväxt, vara mycket högre än i icke-kalavverkade skogar. De senaste tillväxtminskningarna är därför sannolikt inte en följd av långsiktiga ekologiska förändringar orsakade av kalavverkning.

Vad gäller då för en kombination av klimatfaktorer och kalavverkning? Jag undersökte om kalavverkning försatte skogarna i ett tillstånd där de blev mer mottagliga för klimatförändringarnas effekter. Resultaten tyder på att träd som växer i kalhyggen reagerar starkare på variationer i temperatur och nederbörd. Som exempel minskade tillväxten hos alla studerade träd ganska mycket under det extrema torkåret 2018, men minskningen var betydligt större i kalavverkade skogar (19% minskning jämfört med 11% minskning i icke-kalavverkade skogar). Även om detta tyder på en större känslighet hos kalhyggen, vilket kan få mer allvarliga konsekvenser, är det viktigt att notera att dessa tillväxtminskningar inte förde de kalavverkade skogarna till en lägre produktivitetsnivå än de icke-kalavverkade skogarna. Med andra ord kan produktiviteten i kalhyggen förbli högre än i icke-kalavverkade skogar även om varje år skulle vara lika extremt som 2018. Den kombinerade effekten av klimatfaktorer och kalavverkning, såsom den studerats här, verkar därför inte förklara tillväxtminskningen.

Med utgångspunkt i att tillväxtminskningarna existerar undersökte jag också de kombinerade effekterna av temperatur och kalavverkning på markrespiration (den huvudsakliga källan till skogarnas koldioxidutsläpp) för att få en uppfattning om dessa skogars potential som kolkälla eller kolsänka. Genom att utsätta jordar från kalavverkade- och icke-kalavverkade skogar för ett uppvärmningsexperiment fann jag att högre temperatur konsekvent ökade markrespirationen. Denna ökning efter uppvärmning var något större i unga kalhyggen (där träden var yngre än 10 år) jämfört med äldre kalhyggen (~60 år) och icke-kalavverkade skogar. Om skogarna upplever högre temperaturer till följd av klimatförändringar kan vi därför förvänta oss ökade CO_2-utsläpp från skogsmarken – framförallt om dessa nyligen har kalavverkats.

Sammantaget tyder dessa resultat på att klimatförändringar och kalavverkning, åtminstone såsom de studerats här, inte ensamma ligger bakom tillväxtminskningarna i den boreala skogen. Samspelet mellan klimatfaktorer och kalavverkning kan dock få konsekvenser för skogsekosystemens funktionalitet – med kalavverkning kan vi förvänta oss snabbväxande skogar vars kolcykel är mer känslig för klimatvariationer.

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Appendix 1: Soil water retention

During the incubation experiment in Project III, I kept the moisture levels standardized in each sample (gravimetric soil moisture = 58%; based on average initial conditions) by adding deionized water to the samples between all CO_2 measurements. Although it was not an intent with the study, I was able to track the water loss over time and how this differed between soils of different forest types (NC, CC_{60}, CC_{10}). Below is a brief analysis of the water retention during the last measurement (it reflects the water retention over the entire incubation period).

Both forest type and soil warming affected the soil water loss, with clearcutting and warming forcing a faster water loss. However, the effect of warming on the soil water loss was unaffected by clearcutting (i.e. there were no interaction effects) (see Table A1 and Figure A1).

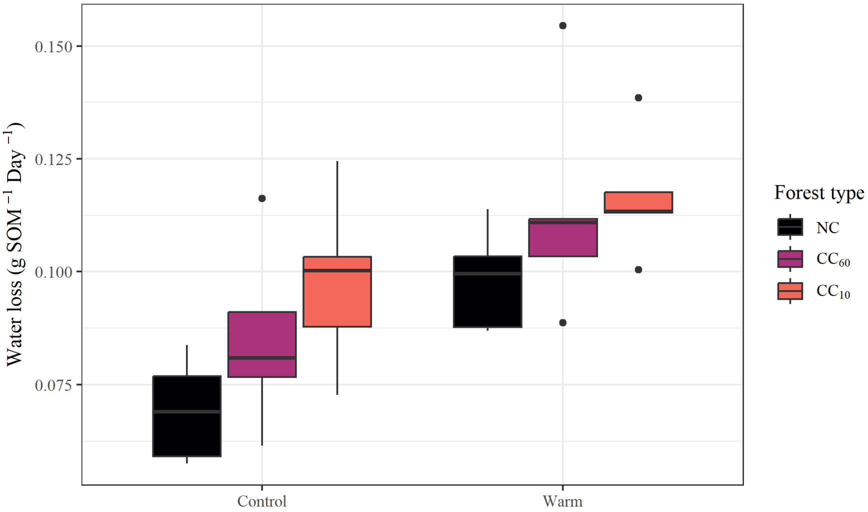


Figure A1. Daily water loss (standardized per organic matter content) from soil samples during the incubation experiment in non-clearcut (NC; black), old clearcut (CC_{60}; purple), and young clearcut (CC_{10}; orange) forests. Data is divided between incubation treatments (control samples (left), and warmed soil samples (right)).

Table A1. Output of pairwise ANOVAs (SS Type II) from a linear model testing the effects of Forest type (non-clearcut (NC); 60-year old clearcuts (CC_{60}); and clearcuts < 10 years old (CC_{10})) and Treatment (Warm; and Ambient) on soil water retention. The sample size of each combination of Forest type and Treatment = 5 (full sample size of each model = 20). The output of a full (non-pairwise) model resulted in: Forest type (F = 4.66; p = 0.02), Treatment (F = 15.98; p < 0.01), and their interaction (F = 0.27; p = 0.77).

	Parameter	Difference (mg)	F	p
NC – CC_{60}	Forest type	-15.79	3.93	0.06
	Treatment	28.79	13.08	< 0.01
	Interaction		< 0.01	0.98
NC – CC_{10}	Forest type	-23.37	13.38	< 0.01
	Treatment	23.94	14.04	< 0.01
	Interaction		0.63	0.44
CC_{60} – CC_{10}	Forest type	-7.57	0.73	0.41
	Treatment	23.70	7.14	0.02
	Interaction		0.30	0.59

Appendix 2: Field- and lab CO_2

Soil respiration was measured on three occasions (July 2023, June 2024, and August 2024) in all field sites (see sections 3.2 and 3.3). Below are scatterplots showing how the measurements correlate between the time points. In general, there is a positive correlation between the different measurements, with somewhat more variation in sites of higher soil respiration.

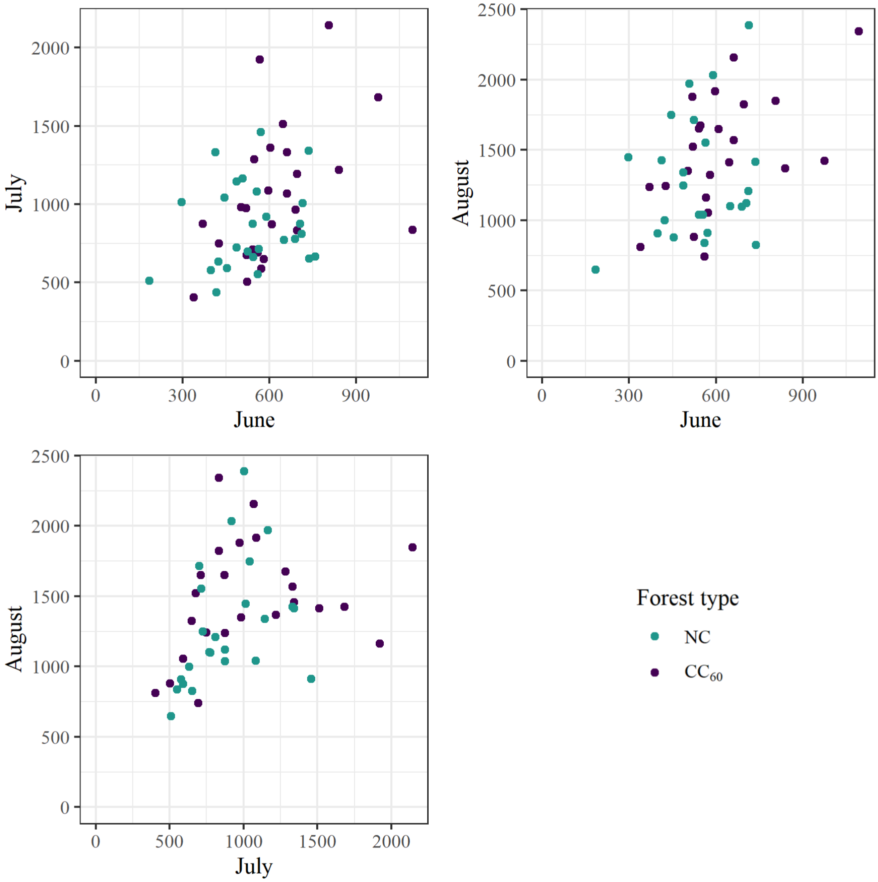


Figure A2:1. Comparison of soil respiration between the times of measurement. Data is divided between non-clearcut forests (NC; green) and old clearcut forests (CC_{60}; purple).

The soil respiration was also measured both in the field (for Project IV) and in a lab setting (during Project III). Below is a plot showing the correlation between field- and lab measurements. Note that only sites that occur in both projects (i.e. 5 per forest type) are presented. Also note that the soil respiration is expressed in different units: Field = µmol CO_2 h^{-1} m^{-2}; and Lab = µmol CO_2 h^{-1} $gSOM^{-1}$. Hence, differences in organic matter per unit area may skew the relationship.

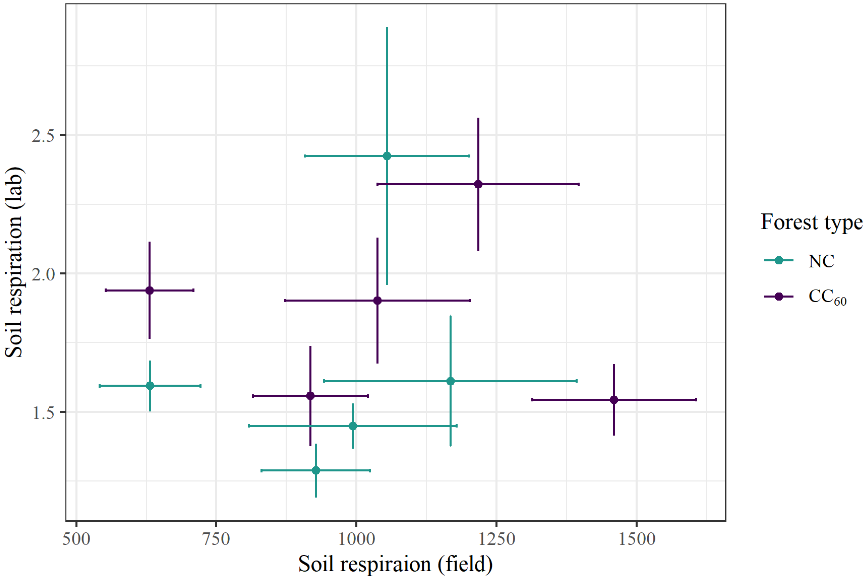


Figure A2:2. Comparison of soil respiration measured in the field (µmol CO_2 h^{-1} m^{-2}) and from samples used in the incubation experiment (µmol CO_2 h^{-1} $gSOM^{-1}$). Data is divided between non-clearcut forests (NC; green) and old clearcut forests (CC_{60}; purple). Error bars for field measurements are based on 9 samples per site; and error bars for lab measurements are based on 12 samples.

Appendix 3: Mass of forest compartments

Data on mass (weight) was gathered from all forest sites (see section 3.3). Tree biomass was estimated through allometric functions (see Eq. 1) with data on tree diameter and height. Understorey biomass was estimated through drying and weighing clipped vegetation from five 30 cm diameter subplots in each site. Soil dry weigh was estimated through the drying and weighing of the organic soil layer from fifteen 3 cm diameter soil cores. In general, the previously clearcut forests had similar soil dry weight (on average 6% higher soil dry weight) and understorey biomass (on average 4% lower understorey biomass) as that of non-clearcut forests. However, the tree biomass was substantially lower in the clearcut forests than the non-clearcut forests (on average 28% lower tree biomass).

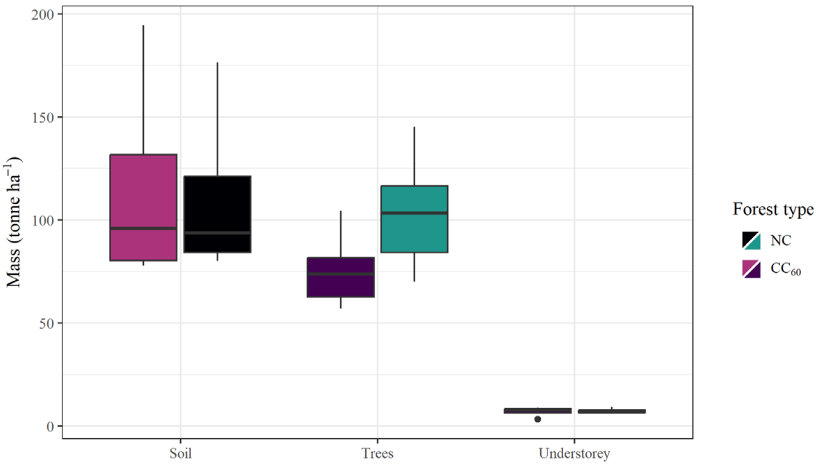
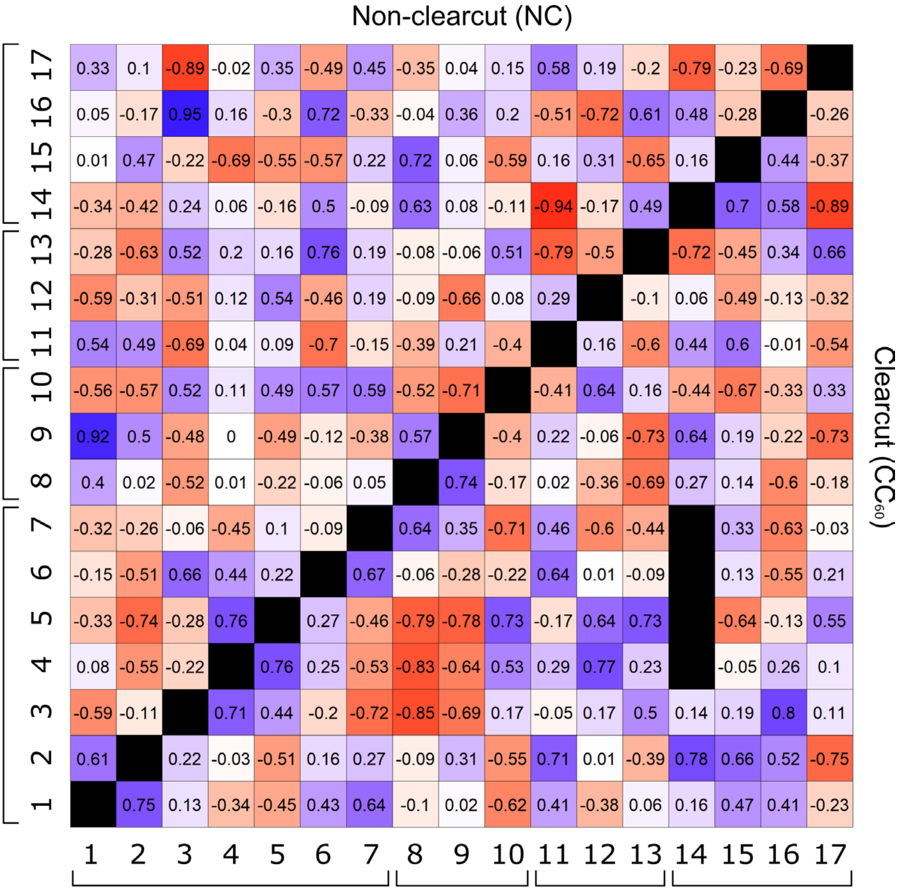


Figure A3. Comparison of mass (tonne ha^{-1}) of soil, trees, and understorey. Data is divided between non-clearcut forests (NC; black and green) and old clearcut forests (CC$_{60}$; purple). Difference in colours (black/green and shades of purple) indicate below- and above-ground compartments.

Appendix 4: Correlations between variables

A large number of variables were collected in the non-clearcut forests (NC) and the 60-year old clearcuts (CC_{60}). Below is a correlogram exploring most of the site-level data from Projects II and IV. As some variables differ substantially between the forest types (e.g. BAI is on average 66% larger in CC_{60} than NC) the correlations are presented for each forest type individually.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
17	0.33	0.1	-0.89	-0.02	0.35	-0.49	0.45	-0.35	0.04	0.15	0.58	0.19	-0.2	-0.79	-0.23	-0.69	
16	0.05	-0.17	0.95	0.16	-0.3	0.72	-0.33	-0.04	0.36	0.2	-0.51	-0.72	0.61	0.48	-0.28		-0.26
15	0.01	0.47	-0.22	-0.69	-0.55	-0.57	0.22	0.72	0.06	-0.59	0.16	0.31	-0.65	0.16		0.44	-0.37
14	-0.34	-0.42	0.24	0.06	-0.16	0.5	-0.09	0.63	0.08	-0.11	-0.94	-0.17	0.49		0.7	0.58	-0.89
13	-0.28	-0.63	0.52	0.2	0.16	0.76	0.19	-0.08	-0.06	0.51	-0.79	-0.5		-0.72	-0.45	0.34	0.66
12	-0.59	-0.31	-0.51	0.12	0.54	-0.46	0.19	-0.09	-0.66	0.08	0.29		-0.1	0.06	-0.49	-0.13	-0.32
11	0.54	0.49	-0.69	0.04	0.09	-0.7	-0.15	-0.39	0.21	-0.4		0.16	-0.6	0.44	0.6	-0.01	-0.54
10	-0.56	-0.57	0.52	0.11	0.49	0.57	0.59	-0.52	-0.71		-0.41	0.64	0.16	-0.44	-0.67	-0.33	0.33
9	0.92	0.5	-0.48	0	-0.49	-0.12	-0.38	0.57		-0.4	0.22	-0.06	-0.73	0.64	0.19	-0.22	-0.73
8	0.4	0.02	-0.52	0.01	-0.22	-0.06	0.05		0.74	-0.17	0.02	-0.36	-0.69	0.27	0.14	-0.6	-0.18
7	-0.32	-0.26	-0.06	-0.45	0.1	-0.09		0.64	0.35	-0.71	0.46	-0.6	-0.44		0.33	-0.63	-0.03
6	-0.15	-0.51	0.66	0.44	0.22		0.67	-0.06	-0.28	-0.22	0.64	0.01	-0.09		0.13	-0.55	0.21
5	-0.33	-0.74	-0.28	0.76		0.27	-0.46	-0.79	-0.78	0.73	-0.17	0.64	0.73		-0.64	-0.13	0.55
4	0.08	-0.55	-0.22		0.76	0.25	-0.53	-0.83	-0.64	0.53	0.29	0.77	0.23		-0.05	0.26	0.1
3	-0.59	-0.11		0.71	0.44	-0.2	-0.72	-0.85	-0.69	0.17	-0.05	0.17	0.5	0.14	0.19	0.8	0.11
2	0.61		0.22	-0.03	-0.51	0.16	0.27	-0.09	0.31	-0.55	0.71	0.01	-0.39	0.78	0.66	0.52	-0.75
1		0.75	0.13	-0.34	-0.45	0.43	0.64	-0.1	0.02	-0.62	0.41	-0.38	0.06	0.16	0.47	0.41	-0.23

Figure A3. Correlation plot of most variables used in Projects II and IV (see Table A3 for list of variables). The bottom right half of the correlations are based on data gathered from clearcut forests, and the top left half is based on data gathered from non-clearcut forests. Only correlations with at least 5 shared observations are shown.

Table A4. List of variables used for the correlation calculations in Figure A4.

Category	ID	Variable
Tree variables	1	Tree biomass
	2	BAI
	3	Needle C:N
	4	MS (stand)
	5	MS (tree)
	6	Resistance (drought)
	7	Recovery (drought)
Understorey variables	8	Understorey biomass
	9	Vaccinium
	10	Empetrum
Soil geochemical variables	11	Soil pH
	12	Soil Ca:Al
	13	Soil C:N
Soil biological variables	14	Soil respiration
	15	ECM
	16	ERM
	17	Saprotrophic fungi

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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 and soil moisture.

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 gradients in mean annual temperature and soil moisture.

Trees growing in warmer areas responded more negatively to high temperature and more positively to high precipitation. Site-specific soil moisture only showed an effect on the growth responses in areas of high mean annual temperature. The growth-climate response differed between the species; specifically, the growth response to high temperature varied more along the gradient of mean annual temperature 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 site-specific climate conditions. In warmer areas, high soil moisture may mitigate the adverse effects of warming on tree growth mainly for *P. abies*. In colder areas, *P. abies* is likely to benefit more from warming than *P. sylvestris*. 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. Nevertheless, extreme years may influence forest productivity by affecting tree mortality, an aspect that was beyond the scope of this study. In the face of climate change, our results emphasize that 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 a significant economic value. However, under global warming, the delivery of these ecosystem services is at risk. Boreal forests and their tree growth may be particularly vulnerable (Babst et al., 2019), as the rate and impact of increasing temperature are predicted to be more pronounced at higher latitudes (IPCC, 2018). This has raised concerns that the boreal biome's capacity to assimilate and sequester carbon could be at stake by the mid of this century (Rao et al., 2023). Moreover, there are already indications that global warming has reduced the biome's geographical range, with forest contraction in its southern areas and limited expansion in the north (Rotbarth et al., 2023). Given its global importance, predicting the response of boreal forests to global warming 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), attributable 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 (Novick et al., 2024; López et al., 2021; Yuan et al., 2019). The temperature-growth response is complex as growth may increase with rising temperatures to a certain threshold, beyond which high VPD leads to a reduction in growth (Grossiord et al., 2020). Assuming that tree growth has a temperature optimum (Sendall et al., 2015), growth in colder regions is expected to increase under global warming, whereas growth in warmer regions may decline if the temperature exceeds the optimum. This effect can be further amplified by a longer growing season, as anticipated with an extension of the snow free period (Gustafson et al., 2024), as rising temperatures are likely to enhance tree growth in colder regions but limit growth in warmer areas due to increased water stress (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 growth declines may act as early warning signals for more severe impacts, such as forest dieback (Popa et al., 2024; Gazol et al., 2020). In addition, warming may also increase the frequency and intensity of extreme disturbances (Gustafson et al., 2024; Gauthier et al., 2015). 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 (Peng et al., 2011) due to hydraulic failure or prolonged photosynthetic inactivity following stomatal closure in response to the drought conditions (Klein et al., 2014) and therefore decrease forest productivity (Barber et al., 2000). Furthermore, species that normally show a positive growth response to elevated temperatures may exhibit the opposite response and become negatively affected when temperatures become excessively high (Reich et al., 2022). Such 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 high probability of more frequent extreme events makes it vital to understand if droughts and heat spells exacerbate the overall effects of climate change on tree growth, and if the impact of such extreme events can be predicted based on the same relationship as changes in mean temperature.

Local factors strongly influence tree growth responses to rising temperatures, causing substantial variation across geographical locations (D'Orangeville et al., 2016; Ols et al., 2018; Pedlar and McKenney, 2017; Perret et al., 2024). Accounting for such local effects is essential for accurately predicting the impacts of climate change 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 (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, it has been suggested 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 increasing temperature.

Tree species may show different responses to warming, and the response to increasing temperature is expected to vary even among different species of conifers (Jevšenak and Saražin, 2023; Klein, 2014). While both *Picea abies* and *Pinus sylvestris*, the two most common tree species in the Fennoscandian boreal forest (SLU, 2025b), 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). This difference may be partly explained by the higher root-to-leaf ratios in *P. sylvestris* which likely provide greater access to water during drought (Helmisaari et al., 2007). However, species-specific drought responses can also be shaped by site-specific environmental conditions (Feng et al., 2019). Projections of 21st-century tree growth suggest that *P. sylvestris* will be more strongly influenced by local climate, with growth increasing in colder regions but declining in warmer ones, whereas *P. abies* is expected to show a more uniform growth response (Martinez del Castillo et al., 2024). Furthermore, since *P. sylvestris* generally thrives on drier soils than *P. abies* (Sutinen and Middleton, 2020), it may be less affected by adverse conditions in dry areas. 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 and carbon sequestration (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 and 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 relatively high mean annual temperature, i.e. the southern range of the studied gradient, 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. Specifically, we anticipate that *P. sylvestris* has a more positive response to increased temperature in relatively cold areas and more negative response to increased temperature in relatively warm areas compared to *P. abies*. Furthermore, we anticipate that *P. sylvestris* has a more positive response to increased temperature in dry areas compared to *P. abies*.
- (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.

2 Methods

2.1 Site description

For our study, we used data on tree radial growth and climatic variables from the entire range of the boreal forest region in Sweden. The forests are dominated by *P. abies* and *P. sylvestries* which constitute $\sim 40\,\%$ each of the total growing stock (SLU, 2025a). Within the Swedish boreal forest there are some regional differences, with *P. sylvestris* being more common in the north than in the south, constituting $\sim 50\,\%$ and $\sim 30\,\%$ of the total growing stock in the northernmost and the southernmost regions, respectively. Conversely, *P. abies* is more common in the south than in the north, constituting $\sim 30\,\%$ and $\sim 40\,\%$ of the total growing stock in the northernmost and the southernmost regions, respectively.

The mean annual temperature in our study area during 1991–2020 ranged from 10 °C in the south to −2 °C in the north (SMHI, 2025). According to meteorological observations, the mean annual temperature has increased by 0.5–2 °C compared to the period of 1961–1990. The temperature increase has not shown a clear north–south gradient. The mean annual precipitation during 1991–2020 ranged from 400 to 1200 mm, although without a clear difference along the north–south gradient (SMHI, 2025). Meteorological observations throughout the study area have shown that the mean annual precipitation has increased by 20–200 mm compared to the period of 1961–1990, with the greatest increase in the south-west. A few relatively small areas in the middle of our latitudinal range have experienced a reduced mean annual precipitation of 20–60 mm. The annual maximum snow depth during 1991–2020 ranged from < 10 cm in the south to 200 cm in the north (SMHI, 2025). The maximum snow cover has decreased by 5–25 cm compared to the period of 1961–1990 in the south and in the middle of the study area, while remaining stable or experiencing a slight increase in the northernmost parts.

2.2 Tree core data

In order to explore tree growth responses to climatic variables, 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., 2024) on tree growth. The NFI study areas consist of 0.25–1 km^2 squares that 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 analyzed 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, to limit our study to trees growing in productive forests (mean annual tree growth rate $> 1\,\mathrm{m}^3\,\mathrm{ha}^{-1}$), 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 % cut-off after 30 years. Nine time-series produced unreasonable RWI with the last year's RWI reaching a value 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 from further analyses. The choice of confidence level was based on what is commonly used in the dendrochronological software 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).

2.3 Climate and soil moisture data

Data on mean, maximum, and minimum daily temperature, mean daily relative humidity and daily precipitation sum for the period 1961–2018 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 and 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. SPEI centers around 0, where negative values indicate drier conditions and positive values indicate wetter conditions. Furthermore, we calculated the vapour pressure deficit (VPD) through relative humidity and saturated vapour pressure based on mean temperature (Howell and 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. The threshold level was justified as it has been proposed as the value at which stomata closure is triggered (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 1^{st} and could not end until after 31 August. Prior to analyses, we followed the recommendation of 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 to 100 at a 2 m resolution raster grid, where values indicate the probability of being classified as the "wet" category in the NFI inventory field plots. The NFI classification of "wet" indicates water-saturated soil with visible surface water originating from groundwater (SLU, 2025b). Using the modeled soil moisture data, we calculated a soil moisture index (SMI) based on mean soil moisture values in a buffer of 25 m radius around individual trees using zonal statistics in QGIS (QGIS Association, 2021).

2.4 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 × MAT × SMI × 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 se-

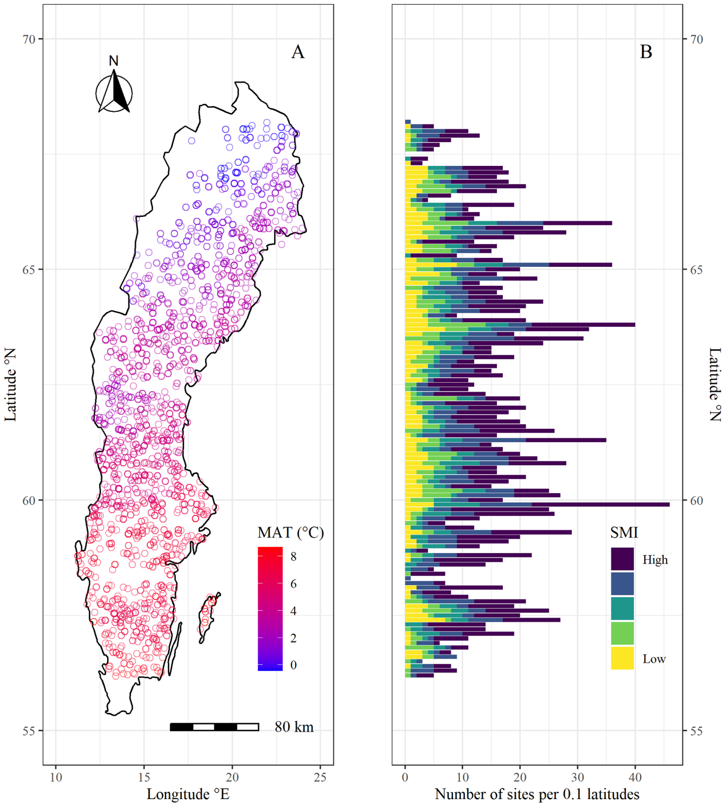

Figure 1. Map of the National Forest Inventory (NFI) sample sites used in this study. **(A)** shows geographical distribution of plots along a mean annual temperature (MAT) gradient. **(B)** shows latitudinal distribution of plots along a soil moisture (SMI) gradient, where the x axis indicates the number of plots per 0.1 latitude and the color gradient indicates the probability of a site being classified as "wet" in increments of 20 % (yellow = 0 %–20 %, light green = 21 %–40 %, dark green = 41 %–60 %, blue = 61 %–80 %, purple = 81 %–100 %). For more information on the SMI classification (see Sect. 2.3).

ries 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 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 × SMI × 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 × SMI × 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.

For all linear mixed effects models, we tested the fixed effects of the models with Type II Wald Chi-square tests from the R package car (Fox and Weisberg, 2019).

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, RWI increased with increasing temperature and VPD but decreased with increasing precipitation and SPEI (Tables A1 and A2). 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).

SMI had modest effects on the tree growth responses to the studied climatic variables and had interactive effects with MAT in all growth responses (Fig. 2; Table 1). Although the effects were minor, 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.

Regarding our third hypothesis (H3), there were clear differences between species in growth response to all studied variables. Mainly, the response to increased temperature was more pronounced for *P. abies* than for *P. sylvestris*. The opposite was true for precipitation, but the effects were more modest. Furthermore, there was a significant MAT × species interaction in all studied growth responses to climatic 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 growth responses.

Table 1. Output (χ^2 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 Tables A1–A4 for main and random effects values of each model).

Interaction term	χ^2	p
Temperature × MAT	2669	< 0.001
Temperature × SMI	11.0	< 0.001
Temperature × TS	2558	< 0.001
Temperature × MAT × SMI	22.0	< 0.001
Temperature × MAT × TS	618	< 0.001
Temperature × SMI × TS	0.03	0.870
Temperature × MAT × SMI × TS	5.01	0.025
VPD × MAT	2696	< 0.001
VPD × SMI	24.7	< 0.001
VPD × TS	1417	< 0.001
VPD × MAT × SMI	53.0	< 0.001
VPD × MAT × TS	403	< 0.001
VPD × SMI × TS	0.78	0.378
VPD × MAT × SMI × TS	5.04	0.025
Precipitation × MAT	1324	< 0.001
Precipitation × SMI	24.3	< 0.001
Precipitation × TS	371	< 0.001
Precipitation × MAT × SMI	19.0	< 0.001
Precipitation × MAT × TS	10.9	< 0.001
Precipitation × SMI × TS	4.84	0.028
Precipitation × MAT × SMI × TS	2.52	0.112
SPEI × MAT	712	< 0.001
SPEI × SMI	14.6	< 0.001
SPEI × TS	42.5	< 0.001
SPEI × MAT × SMI	10.6	0.001
SPEI × MAT × TS	67.7	< 0.001
SPEI × SMI × TS	0.22	0.636
SPEI × MAT × SMI × TS	0.10	0.755

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 coinci-

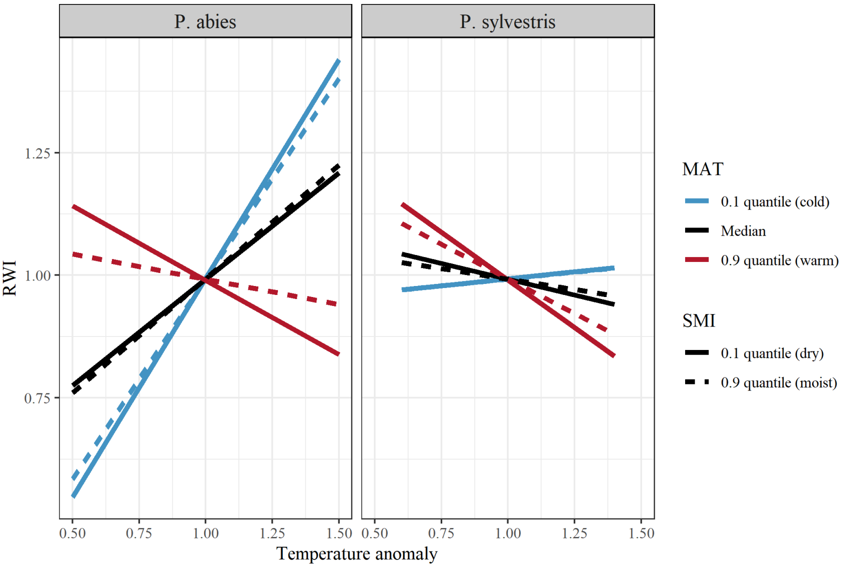

Figure 2. Model output of the effects of temperature on RWI (ring width index) when separated between low (10 % quantile; blue lines), median (black lines), and high (90 % quantile; red lines) MAT (mean annual temperature). Lines show the differences between low (10 % quantile; solid line), and high (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 *P. abies* (and *P. ylvestris* 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.

dence rates than *P. sylvestris* concerning high temperature. 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 marginally decreased the coincidence rates in warmer regions.

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. The resistance values to low precipitation increased marginally with increasing SMI. 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. Hence, we found no evidence that low

Table 2. Output (χ^2 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	
	χ^2	p	χ^2	p
SMI	3.28	0.070	3.14	0.077
TS	244	< 0.001	0.83	0.362
MAT	317	< 0.001	115	< 0.001
SMI × TS	0.01	0.935	7.91	0.005
SMI × MAT	5.98	0.014	2.40	0.121
TS × MAT	39.6	< 0.001	142	< 0.001
SMI × TS × MAT	0.21	0.644	1.54	0.215

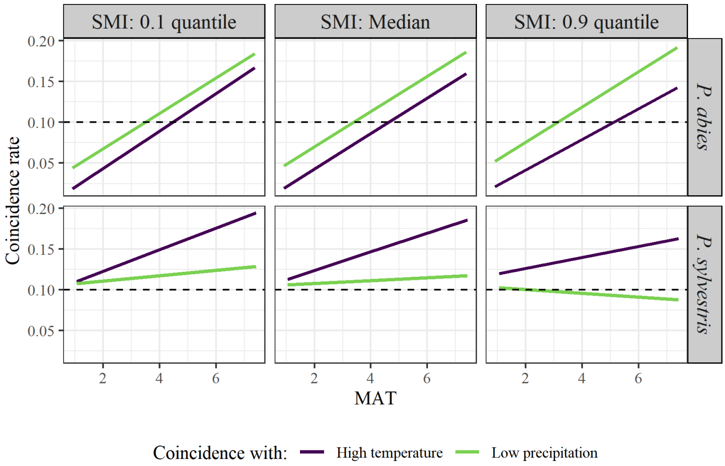

Figure 3. Model output of the effects of MAT on rate of coincidence between years of low growth and high temperature (purple line) or low precipitation (green line). Facets show the differences between low (10 % quantile; left graphs), median (middle graphs), and high (90 % quantile; right graphs) SMI, 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 3. Output (χ^2 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	
	χ^2	p	χ^2	p
SMI	2.60	0.107	9.24	0.002
TS	344	< 0.001	17.8	< 0.001
MAT	443	< 0.001	320	< 0.001
SMI × TS	0.42	0.515	0.81	0.369
SMI × MAT	7.28	0.007	6.15	0.013
TS × MAT	123	< 0.001	126	< 0.001
SMI × TS × MAT	7.68	0.006	1.28	0.258

precipitation during the study period impaired the growth of *P. sylvestris* in areas with high SMI.

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 throughout Europe, North America and northern Asia, 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). Although boreal forests experience relatively low temperature, similar patterns have also been observed in the tropical (Zuidema et al., 2022) and temperate (Charru et al., 2017) biomes. As photosynthetic rates increase with temperature (Kellomäki and 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

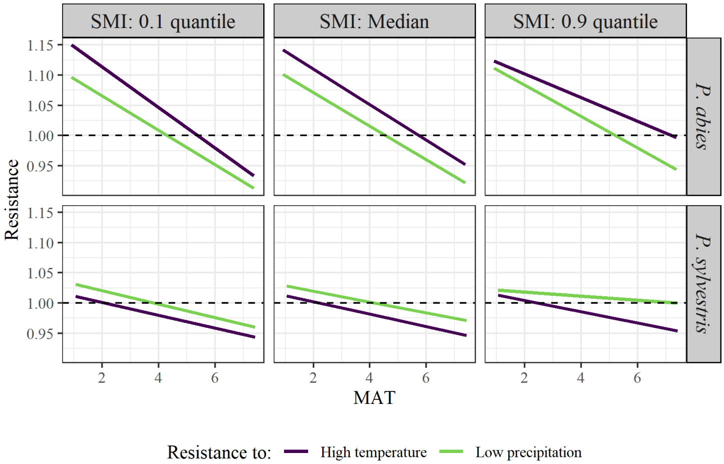

Figure 4. Model output of the effects of MAT on tree growth resistance to years of high temperature (purple line) or low precipitation (green line). Facets show the differences between low (10 % quantile; left graphs), median (middle graphs), and high (90 % quantile; right graphs) SMI, as well as between 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.

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 should 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. A potential mechanism of the negative effects of precipitation is that higher amounts of snowfall delays the start of the growing season (D'Orangeville et al., 2016). However, the negative response in our study is based on growing season precipitation sums only, thereby likely excluding snowfall unless a correlation exists between winter and summer precipitation. Another possible explanation for the negative effect of high precipitation on tree growth in the colder regions is that the forests in the north are already near water saturation and excess precipitation causes waterlogging (Laudon et al., 2024). The effect of precipitation along our temperature gradient is 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 comparisons over large geographical areas. This suggests that variation in growth responses to precipitation becomes evident at larger spatial scales rather than at smaller scale variations 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 across large spatial scales seem 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, whereas tree growth in drier areas was reduced to zero during drought (Huang et al., 2015). Notably, we excluded trees growing in wetlands in our study. The inclusions of such trees may have revealed a greater effect of soil moisture on the trees' growth response to drought conditions. However, our results are in line with Lange et al.'s (2018) finding that the effect of small-scale site-specific conditions is weak in comparison to larger scale climate regimes. Furthermore, Zweifel et al. (2006) found that even small amounts of rainfall could offset a negative relationship between soil water deficits and tree growth, and argued that it was the wetting of the crown rather than the soil that provided this benefit. Such an effect might diminish the importance of soil moisture content and explain the surprisingly weak effect that we observed. While the intrinsic effect of SMI in our study was small, it did interact with MAT, such that the negative effects of high temperature was mitigated by high soil moisture values in warmer areas (Fig. 2). This mitigating effect may be the consequence of retained stomatal conductance despite increasing temperature due to higher levels of soil water availability (Novick et al., 2024). Indeed, 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). Furthermore, the temperature optimum, beyond which VPD tends to negatively affect trees' growth rates, has been found to occur at higher temperature in areas of wetter soils (Novick et al., 2024). Possibly, only trees growing in warm areas experienced an atmospheric water demand high enough for soil moisture to actually limit the tree growth in our study system. 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 the growth response of *P. sylvestris* would be more dependent on local climatic factors than *P. abies* (Fig. 2; Table 1). While *P. abies* 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 and Middleton, 2020). On the contrary, the differences in growth-climate responses between our studied species were more dependent on MAT. Hence, our results indicate that climate adaptation in forest management needs to consider the tree species, where the growth of *P. abies* likely tolerate greater 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 drivers of tree growth, where for example, 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 our MAT and SMI gradients (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 deviates 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. It is also important to note that we have studied discrete extreme years, whereas extended periods of extreme conditions rather than single-year extremes may produce the most severe effects for tree growth (Gustafson et al., 2016). Climate change may impact forests in additional ways beyond what we have studied, such as more frequent forest fires and insect outbreaks, which may have greater influence on growth than the predictors we investigated. As our analyses consider only living trees, it is also possible that there are effects of extreme years on mortality rates that we have not captured here. These caveats suggest that our findings that extremes affect growth-climate responses similarly to growing season averages, should be viewed with some caution.

5 Conclusion

These results indicate that climate change adaptations in forest management must differ across the boreal biome and consider species selection. We found that warmer areas (higher MAT) in the studied region exhibited more negative growth responses to high temperature and more positive responses to high precipitation. On average, *P. abies* responded more positively to higher temperature than *P. sylvestris*, but the difference between the two species was strongly influenced by local MAT. In the warmer, southern range, sites with high soil moisture can mitigate the negative effects of higher temperatures on *P. abies*. By contrast, in the cooler, northern range, such local variation plays a more limited role; here, increasing temperatures are likely to enhance the growth of *P. abies* but not *P. sylvestris*. 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 (χ^2 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	χ^2	p	VIF
Temperature	323	< 0.001	1.000
SMI	0.09	0.763	1.008
TS	0.01	0.915	1.006
MAT	1.63	0.201	1.013
Temperature × SMI	11.0	< 0.001	–
Temperature × TS	2558	< 0.001	–
SMI × TS	< 0.01	0.966	–
Temperature × MAT	2669	< 0.001	–
SMI × MAT	0.30	0.584	–
TS x MAT	0.29	0.592	–
Temperature × SMI × TS	0.03	0.870	–
Temperature × SMI × MAT	22.0	< 0.001	–
Temperature × TS × MAT	618	< 0.001	–
SMI × TS × MAT	0.02	0.879	–
Temperature × SMI × TS × MAT	5.01	0.025	–

Table A2. Output (χ^2 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 (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	χ^2	p	VIF
Precipitation	217	< 0.001	1.000
SMI	0.10	0.757	1.008
TS	0.01	0.916	1.006
MAT	1.50	0.221	1.013
Precipitation × SMI	24.3	< 0.001	–
Precipitation × TS	371	< 0.001	–
SMI × TS	< 0.01	0.957	–
Precipitation × MAT	1324	< 0.001	–
SMI × MAT	0.28	0.599	–
TS × MAT	0.16	0.688	–
Precipitation × SMI × TS	4.84	0.028	–
Precipitation × SMI × MAT	19.0	< 0.001	–
Precipitation × TS × MAT	10.9	< 0.001	–
SMI × TS × MAT	0.02	0.902	–
Precipitation × SMI × TS × MAT	2.52	0.112	–

Table A3. Output (χ^2 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	χ^2	p	VIF
SPEI	1.12	0.291	1.000
SMI	0.10	0.755	1.008
TS	0.02	0.893	1.006
MAT	1.40	0.237	1.013
SPEI × SMI	14.6	< 0.001	–
SPEI × TS	42.5	< 0.001	–
SMI × TS	< 0.01	0.955	–
SPEI × MAT	712	< 0.001	–
SMI × MAT	0.29	0.592	–
TS × MAT	0.14	0.711	–
SPEI × SMI × TS	0.22	0.636	–
SPEI × SMI × MAT	10.6	0.001	–
SPEI × TS × MAT	67.7	< 0.001	–
SMI × TS × MAT	0.02	0.894	–
SPEI × SMI × TS × MAT	0.10	0.755	–

Table A4. Output (χ^2 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 = 1.72×10^{-11}. Tree nested within plot variance = 5.63×10^{-11}.

Term	χ^2	p	VIF
VPD	326	< 0.001	1.000
SMI	0.10	0.751	1.008
TS	0.01	0.911	1.006
MAT	1.68	0.195	1.013
VPD × SMI	24.7	< 0.001	–
VPD × TS	1417	< 0.001	–
SMI × TS	< 0.01	0.958	–
VPD × MAT	2696	< 0.001	–
SMI × MAT	0.26	0.608	–
TS × MAT	0.26	0.612	–
VPD × SMI × TS	0.78	0.378	–
VPD × SMI × MAT	53.0	< 0.001	–
VPD × TS × MAT	403	< 0.001	–
SMI × TS × MAT	0.01	0.910	–
VPD × SMI × TS × MAT	5.04	0.025	–

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 is −0.16. The autocorrelation among our dynamic variables, Temperature, Precipitation, VPD, and SPEI, varies but never exceeds 0.7 (Fig. B1).

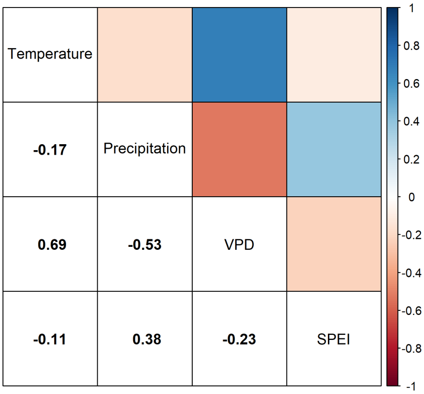

Figure B1. Correlation values among temporally dynamic explanatory climatic variables.

Appendix C: Precipitation effects on RWI

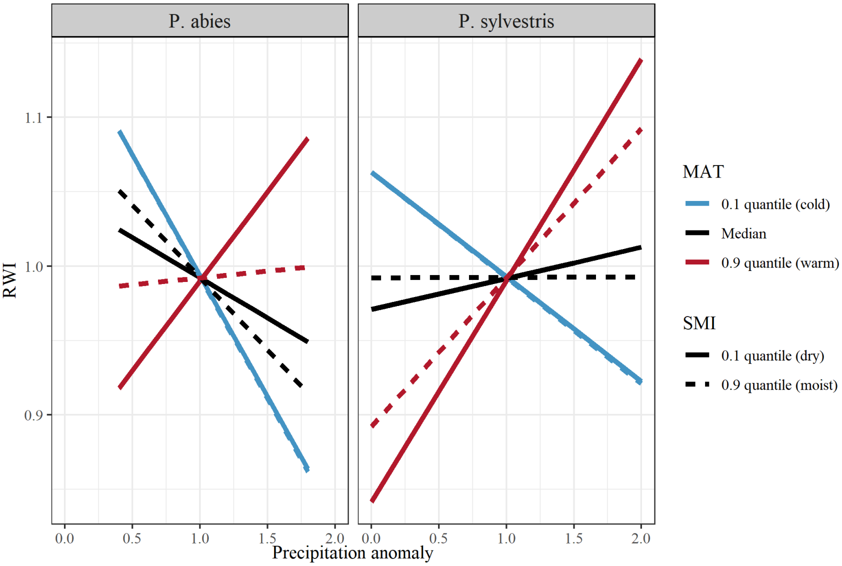

Figure C1. Model output of the effects of precipitation on RWI (ring width index) when separated between low (10 % quantile; blue lines), median (black lines), and high (90 % quantile; red lines) MAT (mean annual temperature). Lines show the differences between low (10 % quantile; solid line), and high (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 .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/blob/main/Project_Geotree (last access: 3 November 2025).

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/about-slu/organisation/departments/forest-resource-management/miljoanalys/nfi/our-data/ (last access: 3 November 2025) (see Fridman et al., 2014 for details on the dataset).

Data on climatic variables are available for download at the SMHI (Swedish Meteorological and Hydrological Institute) website: https://www.smhi.se/data/sok-oppna-data-i-utforskaren/meteorologisk-ateranalys-smhigridclim-uerra-harmonie (last access: 3 November 2025) (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/about-slu/organisation/departments/forest-ecology-management/research/themes/digital-landscapes/soil-moisture-map/here-are-the-maps/ (last access: 3 November 2025).

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

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Disrupting tree continuity through clearcut forestry can alter the climate sensitivity of future tree growth in northern Sweden

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ABSTRACT

Disrupting tree continuity through clearcut forestry is a widespread management practice across the boreal biome. However, concerns remain that forests regenerated after clearcutting may be more sensitive to climatic fluctuations. We examined how clearcutting affects tree growth responses to weather variability, focusing particularly on the extreme 2018 drought. We collected tree-ring width data from forests in northern Sweden that either were clearcut ~60 years prior to the study or never had been clearcut but exposed to past selective logging. We tested whether growth responses to interannual weather variations variables differed between these forest types and assessed how the differences were mediated by soil organic matter, soil temperature stability, and variations in tree age, size, and early growth rates. Forests regenerated after clearcutting showed greater responsive to interannual variation in weather, being more negatively affected by increasing temperature but more positively affected by precipitation. During the 2018 drought, clearcut forests exhibited a mean growth reduction of 19 %, compared to 11 % in non-clearcut forests. The higher drought resistance in non-clearcut forests was primarily associated with greater mean tree age and slower early growth rate. However, as these variables are strongly correlated with clearcutting history, their independent mediation effects are difficult to interpret. Our results suggest that clearcut forestry may increase the sensitivity of regenerating forests to climatic variability. Further research is needed to disentangle the underlying mechanisms and to determine how forest management practices can promote greater climatic resilience in boreal ecosystems.

1. Introduction

The boreal forest constitutes more than a quarter of the world's forested area (FAO, 2020). Despite its relatively low productivity, it provides wood products of global importance (Burton et al., 2010) and plays a key role in climate change mitigation, as a substantial portion of the world's terrestrial carbon is stored in boreal ecosystems (Gauthier et al., 2015). Consequently, changes in tree growth may have significant economic and climate-regulating implications, underscoring the importance of a deeper understanding of the factors that control tree growth.

Over the past century, the global temperature has increased by ~1.1 °C, and current climate change projections estimate a future increase ranging from 1.5 °C to as much as 4 °C (IPCC, 2023). In the boreal forest, the warming has been thought to result in accelerated tree growth (Zhu et al., 2016). However, recent observations of forest productivity declines in the Fennoscandian boreal forest contradict these predictions (Henttonen et al., 2024; Laudon et al., 2024; Breidenbach et al., 2024) and suggest that global warming may instead have a negative effect on tree growth. Even small shifts in temperature and precipitation can influence tree growth (Huang et al., 2010), while extreme environmental events, such as droughts, have the potential to significantly reduce growth and cause tree mortality (Spiecker and Kahle, 2023). However, considerable uncertainty remains regarding which factors interact with climate change to affect tree growth. For instance, tree response to rising temperatures vary among species (Huang et al., 2010) and across geographical regions (Jiang et al., 2016). Temporal tree continuity may be an equally important, yet understudied, factor influencing tree

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growth responses to climate change (Mausolf et al., 2018; Oheimb et al., 2014; Wolf et al., 2023).

The boreal forest contains some of the largest pristine forested areas (Potapov et al., 2008), but parts of the biome, such as northern Fennoscandia, are experiencing a rapid increase in disrupted tree continuity through clearcutting (Ahlström et al., 2022; SLU, 2023). Under natural disturbance regimes, northern Fennoscandian pine forests (*Pinus sylvestris*) generally regenerate under cohort or gap dynamics, while stand-replacing disturbances, similar to the type that follows after clearcutting, are less common (Kuuluvainen and Aakala, 2011). Clearcutting results in nutrient mobilisation (LeDuc and Rothstein, 2007) and relax competition from large trees (Kärenlampi and Riekkinen, 2004) and thereby promote the growth rate of the emerging tree regeneration. However, forests of long tree continuity may be more resilient to environmental changes than those that have undergone a disruption event (Oheimb et al., 2014). Indeed, impacts of the Europe-wide summer drought in 2018 suggest that primary forests may be less sensitive to droughts than secondary forests (Wolf et al., 2023). However, the underlying mechanisms driving this difference remain unknown.

One possible explanation as to why forests that have undergone clearcutting are more susceptible to weather variability and may be more sensitive to climate change is that they have a less stable soil climate. Longer continuity allows greater build-up of soil organic layers and provides greater water storage capacity (Oheimb et al., 2014), which in turn potentially alleviate trees from drought stressors during periods of high temperature and low precipitation. In addition to these soil-related changes, clearcutting may also affect tree-root dynamics. Disrupted tree continuity may reduce tree root production (Mausolf et al., 2018) and thereby decrease the root:shoot ratio (Lim et al., 2015), as increased nutrient availability (LeDuc and Rothstein, 2007) lowers the need for resource allocation to root growth (Poorter et al., 2012). A reduced root:shoot ratio limit water uptake in relation to transpiration (Chen et al., 2022) and will increase tree susceptibility to elevated temperatures and drought stress. These effects are further compounded by rising soil temperatures, which not only influence root function (Pregitzer et al., 2000) but may also aggravate tree water loss through increased transpiration (Wieser et al., 2015). Therefore, the belowground micro-climate may be of great importance for trees' ability to withstand climatic changes.

Aside from soil associations, factors intrinsic to the trees themselves may also influence the responsiveness to interannual weather variability following clearcut forestry. Clearcutting inherently lowers the average tree ages within a forest. Tree age can affect growth responses to weather variability. For instance, younger trees may be more resilient to drought due to lower hydraulic constraints compared to older, taller, trees (Ryan and Yoder, 1997). Conversely, younger trees may have shallower root systems, making them more drought sensitive (Zhang et al., 2022). Hence, it remains unclear if changed tree age, as a consequence of clearcutting, will increase or decrease the stand's overall drought resistance. Furthermore, the regeneration of a forest through clearcutting will likely cause a homogenization of the trees' ages and sizes. Such a reduction in functional diversity may decrease ecological redundancy, and possibly lower drought resistance at the stand scale (Anderegg et al., 2018). For instance, a stand with higher tree heterogeneity (age, size, species etc.) would have a higher probability of containing individuals that are highly resilient to a specific stressor (Mori et al., 2013). Therefore, tree traits and functional diversity may play a critical role in supporting a forest's resilience to climatic change.

Given that clearcut forestry is the dominant management practice across large areas of the boreal biome, and considering the biome's significant economic and climate-regulating importance, it is crucial to develop a deeper understanding of how this management approach influences tree growth and climate sensitivity. In this study, we investigate detailed growth patterns following a continuity disruption event in northern Sweden caused by clearcutting by examining tree ring widths. We hypothesize that (I) the stand-level growth in trees regenerated after clearcutting exhibits greater interannual variation due to the homogenization of tree characteristics, resulting in reduced functional diversity. Furthermore, we hypothesize that (II) clearcutting reduces drought resistance in tree growth by decreasing functional diversity and altering key tree and ecosystem attributes, such as tree age and soil organic layer thickness.

2. Methods

2.1. Study area

In order to explore the consequences of disrupted tree continuity, we compared 9 forests that had been clearcut ~60 years prior to the study (hereafter referred to as Clearcut forests) with 9 forests that have never been clearcut, but exposed to selective logging in the past (hereafter referred to as Non-clearcut forests) (Fig. 1). The studied forests are located in northern Sweden and spans a distance of approximately 250 km. The area has a mean annual temperature of ~0 °C, with monthly average temperatures ranging from −15 °C in January to 13 °C in July, and a mean annual precipitation of ~500–600 mm (SMHI, 2009). The studied forests are dominated (>50 % of trees) by pine (*P. sylvestris*), but also contain some spruce (*Picea abies*) and birch (*Betula pubescens*). The understory vegetation is dominated by ericaceous dwarf-shrubs, predominantly *Vaccinium* and *Empetrum* species, and the forest floor is dominated by feather mosses and ground-living lichens. The geology consists mainly of granite moraine, but is also scattered with glaciofluvial deposits (SGU, 2023). The 18 forests were selected from a dataset on stand characteristics compiled by the Swedish forestry company Sveaskog. To ensure that tree growth was not influenced by other underlying differences in site conditions than the management type, we made an effort to select stands with similar conditions in terms of annual temperature sums, altitude, latitude, and estimated site productivity prior to clearcutting. Information on the latter was derived from the forest company's stand database and based on the original forest owners' estimation of site productivity. To select Non-clearcut forests, we used information from the forest company Sveaskog's database on sites with long tree continuity. To ensure that sites with long tree continuity are not harvested (as part of the company's biodiversity conservation strategy), Sveaskog determines each stand's mean tree age by systematically coring trees in forests that might have long tree continuity. This involves coring trees at the base of the stem in a systematic grid until an average mean tree age is established. Sites where at least 30 % of the trees have an age greater than 140 years are classified as having long tree continuity and are subjected to special consideration if logging is planned. Our Non-clearcut forests were selected from this subset. Since a proportion of the trees in these forests predate the introduction of clearcutting in the area (Östlund et al., 1997), we can state with high confidence that the forests we identified as Non-clearcut have never been clearcut. To further verify our classification, we used aerial imagery from the 1960s that confirmed that the selected Non-clearcut forests had a continuous canopy, while the Clearcut forests were open, non-forested sites during the same period. Variation in tree age structure among the Non-clearcut forests, and the lack of such variation in the Clearcut forests, further indicates that these forests are regenerated following non-stand-replacing disturbances and stand-replacing disturbances, respectively (Figure S1). It is important to note that the Non-clearcut forests should not be regarded as pristine, as they all show evidence of past selective logging, such as the presence of old tree stumps. Although logging in some areas may have been relatively intensive, it was not stand-replacing in the way clearcutting is. Since the transition from selective logging to clearcut forestry, these forests have only experienced low-intensity management. In each forest, we randomly selected three circular plots (20 m ⌀) with at least 30 m distance between two adjacent plots. This resulted in a total of 54 plots across the 18 forests. To avoid the influence of edge-effects, we ensured that no plot was situated closer than 30 m to the edge of the stand.

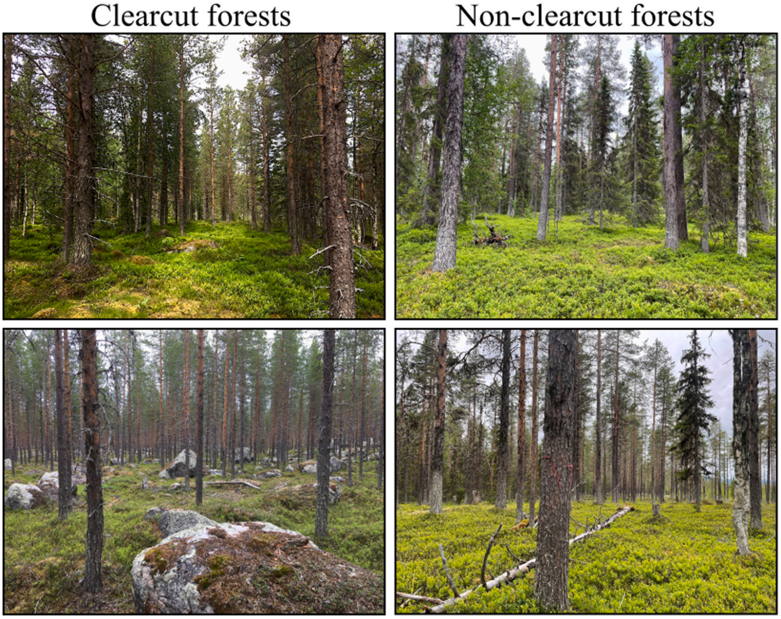

Fig. 1. Example images of the studied forests. Pictures to the left show forests that have been clearcut ~60 years ago. Pictures to the right show forests that have never been clearcut.

2.2. *Tree variables*

To study the growth patterns of the trees, we collected tree cores. In every plot, we cored all trees > 5 cm DBH (at 1.3 m) with a 5 mm tree borer in July-August 2022 (a total of 1249 trees). We dried the cores at 50 °C and then mounted and sanded them to enhance the ring visibility. Where tree rings were unclear, we treated the cores with zinc paste. We measured the tree ring widths (TRW) using the R package MtreeRing (Shi and Xiang, 2021). Due to difficulties in accurately assessing TRWs, all deciduous trees (2 aspen, 7 sallows, and 131 birches) as well as two pine trees, whose rings were too unclear to allow visual inspection of tree rings even after zink paste treatment, were excluded from analysis. Of the excluded trees, 83 belonged to the Clearcut category and 59 belonged to the Non-clearcut category. We detrended the TRW series to produce ring width indices (RWI) using a spline function from the dplR package in R (Bunn et al., 2025), in accordance with standard dendrochronological procedures (Frank et al., 2022). To ensure accurate assignment of growth years in the RWI series, we computed estimates of inter-series correlations (Rbar) and the Expressed Population Signal (EPS) for each of the 54 plots. We excluded a total of 71 RWI series (32 from Clearcut and 39 from Non-clearcut forests) with an inter-series correlation below the critical level of 0.3281 which is the recommended default value used in the dendrochronological software COFECHA (Holmes, 1983). Low correlations between individual RWI series and mean RWI series may be produced either by dating errors of individual year TRW, or due to individual trees producing growth patterns that differ from the mean. Because of this, we also conducted analyses on the dataset including the 71 RWI series and found the results to be similar. However, to present results that are as reliable as possible in terms of data quality, we present only the results based on analyses where we excluded the 71 RWI series of low inter-series correlations. The resulting rbar was on average 0.57 (±0.02) and 0.56 (±0.02) for Clearcut forests and Non-clearcut forests, respectively. Due to the high number of trees sampled (~20 per plot), the retained EPS-values were on average 0.96 (±0.05) and 0.95 (±0.06) for Clearcut forests and Non-clearcut forests, respectively. To illustrate growth patterns of the different forests, we transformed TRWs to biomass estimates using allometric functions for pine and spruce (Marklund, 1988). Since a tree's size traits are potential mediators of differences in drought resistance, we also measured all sampled trees for circumference at breast height using a tape measure, and height using a Vertex IV and Transponder T3.

2.3. *Soil variables*

To test if soil climatic stability is a potential mechanism that mediates differences in growth responses during extreme droughts, we collected data on variations in soil temperature. We placed temperature data loggers ~10 cm below the soil surface in all sample plots during June 2023 and retrieved them in June 2024. We used the coefficient of variance from each temperature logger's time series to examine the soil temperature variability. As the timing of placement and recovery of the temperature loggers differed somewhat among sites, we only used the period when all loggers were buried in the soil for further analysis (July 1st to May 15th). Data from one temperature logger in a Clearcut forest was excluded as it was deemed unreliable after showing a heat anomaly in March (reaching >20 °C and then remaining above 5 °C for a full month).

Further, to explore differences in the soil organic layer, we collected fifteen soil samples, 2.5 cm diameter each, of the organic soil layer from each plot. We estimated organic matter in the soil samples through loss on ignition (LOI) by drying and weighing samples and then burning them at 550 °C for 6 h to remove all organic matter. We calculated the organic matter as the fraction of weight lost after burning. As we are interested in the total amount of organic matter as a potential mediator of drought resilience, we extrapolated the fraction of organic matter to the total collected soil mass for each plot. Thus, we present the data here as organic matter in terms of kg per m^{-2}.

2.4. Weather data

To explore the effects of climatic variables on tree growth, we retrieved data on daily precipitation, maximum (T_{max}), minimum (T_{min}) and mean temperature (T_{mean}) from the Swedish Meteorological and Hydrological Institute's (SMHI) weather station in Arjeplog. The Arjeplog station is located in the centre part of the study area (N: 66.0513, E: 17.8396) and contains the most cohesive dataset of the nearby stations. Using this data, we also calculated Standardized Precipitation Evapotranspiration Index (SPEI) based on precipitation and temperature measurements of 6 months prior to the indexed month (e.g. Jevšenak, 2019), with potential evapotranspiration calculated through the Hargreaves method (Vicente-Serrano et al., 2010). To test the tree growth responses to an extreme drought year, here 2018, we analysed the growth changes during 2018 which has been noted as an extreme drought year in the region (Martín-Gómez et al., 2017; Toreti et al., 2019; Wolf et al., 2023; SMHI, 2019).

2.5. Data analysis

All statistical tests and descriptive statistics were done in R (version 4.4.1; R Core Team 2022).

To test our first hypothesis on whether there are differences in growth stability caused by clearcutting, we analysed the mean sensitivity of inter-annual variability in RWI (Fritts, 2012). In short, a high value of mean sensitivity indicates high growth variability and a low value indicates low growth variability. We used limited time series of 54 years since all forests had trees that were at least 54 years old (i.e. contained 54 annual rings at breast height). As the Clearcut forests are even-aged, increasing the length of the studied time series quickly decreases the number of Clearcut forest sites (e.g. from 9 forests to 3 forests between age 54 and age 61). Prior to analysis of mean sensitivity, we detrended the TRW series to RWI to avoid long-term intrinsic patterns of growth decline due to aging trees. The TRW series were detrended using a spline function with a 50 % cutoff after 36 years (2/3 of the studied 54 years). We used two separate analyses to study the growth variability of the different forest types on an individual tree level and on a forest stand level. To compare the growth variability of individual trees, we calculated mean sensitivity for individual trees prior to pooling the data in each plot for statistical analysis, so that the variability of the first 54 years was compared between individual trees of the different forest types. In the second analysis, we compared stand-wide growth sensitivity by calculating mean sensitivity during the 54 year study period based on the within-plot mean RWI. We then analysed tree-level and stand-level sensitivity statistically with linear mixed models from the lme4 package (ver. 1.1–35) in R (Bates et al., 2015) with sensitivity as the response variable and forest type as the explanatory variable and plot as a random variable. Given the extensive geographical spread of the sites, we added latitude and altitude as covariates to ensure that potential differences were not artefacts of geographical variation. Furthermore, to control for between stand variation in pine dominance, we included the proportion of cored trees that are not pine (i.e. spruce) as a covariate. We tested the fixed effects of the models with Type II SS ANOVAs using Kenward-Roger corrected degrees of freedom in the lmerTest package (ver. 3.1–3) in R (Kuznetsova et al., 2017).

To explore the forests' growth dependency on weather variability, we tested the effect of monthly values for precipitation, minimum temperature, mean temperature, maximum temperature, and SPEI on RWI. For each climatic variable and month, we used linear mixed models fitted with the nlme package (ver. 3.1–167) in R (Pinheiro and Bates, 2025) with RWI as the response variable and each respective climatic variable and forest type (Clearcut and Non-clearcut) as explanatory variables. Since the RWI and climatic variables are measured over multiple years, creating temporal autocorrelation in the data, we included an AR1 covariance structure in our model. To address the spatial autocorrelation primarily caused by multiple trees per plot, we added plot as a random variable.

To test our second hypothesis that clearcutting causes reduced drought resistance in tree growth, we focused on the year 2018 and analysed indices of resistance, recovery, and resilience (Lloret et al., 2011). Here, resistance is calculated as the ratio between the RWI of 2018 and the average RWI of three years prior; recovery is calculated as the ratio between the average RWI three years after the drought and the RWI of 2018; and resilience is calculated as the ratio between the RWI after drought and the RWI prior to the drought. Finally, we fitted linear mixed models using the lme4 package in R with the drought indices as response variables, forest type as the explanatory variable, plot as a random variable, and the aforementioned covariates. We tested the fixed effects of the models with Type II SS ANOVA using Kenward-Roger corrected degrees of freedom in the lmerTest package.

To explore potential mechanisms that explain the variation between the two forest types regarding the aforementioned drought indices, we conducted mediation analyses (Imai et al., 2010). A mediation analysis is a form of path analysis that examines the direct and indirect effects of a variable, in this case clearcutting, on the response variable through a mediator (Fig. 2). As mediator variables, we used mean tree age and age heterogeneity (calculated as the tree age coefficient of variance within each plot), mean tree height and height heterogeneity, mean tree circumference and circumference heterogeneity, early growth rates (calculated as the mean biomass (kg) gained during the first 20 years), soil temperature variability, and the mass of the soil organic layer. We here assume that the relative differences between forest types were the same during the drought year 2018 as when the data were collected in 2022–2023. We calculated the mediation of the effect from forest type as $\beta_{my} * \beta_{xm} / \beta_{xy}$, where β_{my} = regression coefficient of the mediator variable on the response variable when controlling for forest type; β_{xm} = regression coefficient of forest type on the mediator variable; and β_{xy} = regression coefficient of forest type on the response variable. While standardization of data is common within path analysis, it has no effect on the outcome of the mediation analyses. Therefore, we have chosen to report each coefficient in the mediation equation as based on raw data, so that the coefficients represent the change in the response variables per unit in the explanatory or mediator variable. With the mediation analysis approach, a high positive value indicates that much of the effect of clearcutting on the response variable is *because of* the mediator variable. A high negative value indicates that clearcutting affects the response variable *despite* directionally opposite differences in the mediator variable (i.e. the mediator variable has a weakening effect on

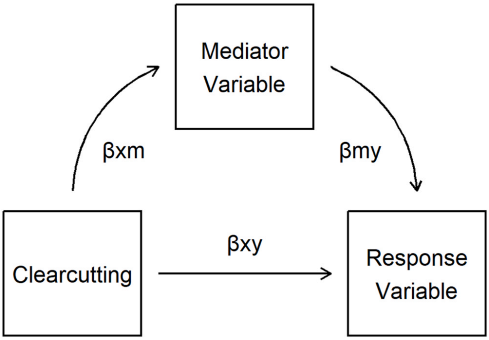

Fig. 2. Illustration of the parameters in a mediation analysis depicting the direct effect of clearcutting on a response variable where the mechanisms remain unidentified (βxy), and the effect mediated through a mediator variable (βxm x βmy), attributing the effect of clearcutting to a specific mechanism.

the differences between the forest types). A value close to 0 indicates that little of the clearcutting effect is mediated through the mediator variable, i.e. that the difference between the two forest types cannot be explained by variation in the particular variable.

Data are available at: https://doi.org/10.5281/zenodo.16037934

Code is available at: https://github.com/LundgrenAndreas

3. Results

3.1. Tree and soil characteristics

The mean tree age was higher in Non-clearcut forests than in Clearcut forests (Figure S1; Table 1). Likewise, the age heterogeneity (measured as tree age coefficient of variance) was greater in Non-clearcut forests than in Clearcut forests. The mean tree height and circumference were similar between the two forest types, but the size heterogeneity (measured as height and circumference coefficient of variance) was greater in Non-clearcut forests (Table 1). Trees growing in Clearcut forests had a higher rate of early biomass accumulation than those growing in Non-clearcut forests (Figure S2; Table 1). After 20 years, the growth rate in Clearcut forests plateaued at ~3 kg tree^{-1} year^{-1} while the trees in Non-clearcut forests continued to increase their growth rate until they reached a maximum of ~4.8 kg tree^{-1} year^{-1}. However, this maximum was reached after ~140 years, which extends well beyond the age of the oldest trees that we currently have data on from Clearcut forests.

Temperature variability (measured as temperature coefficient of variance) of the soil was somewhat lower in Clearcut forests than in Non-clearcut forests, but the difference was not statistically robust due to confounding effects of the geographical covariates (Table 1). The mean soil temperature throughout the measuring period (July 1st to May 15th) was 4.4 ± 0.1 and 4.1 ± 0.2 °C in Clearcut and Non-clearcut forests, respectively. The minimum soil temperature was −1.3 ± 0.3 and −3.1 ± 1.0 °C and the maximum soil temperature was 24.7 ± 1.0 and 25.4 ± 1.3 °C in Clearcut and Non-clearcut forests, respectively. There was no difference between the forest types in the amount of soil organic matter (Table 1).

Table 1

Descriptive statistics (mean ± standard error) of response and mediator variables, as well as mixed effects model statistics (F- and p-values) testing the effect of forest type. Latitude, altitude, percentage non-pine trees, and Al/Ca ratio are added as covariates (see Tables S2-S3 for details on full models). For the purpose of readability, mean sensitivity values have been multiplied by 100. Note that mean sensitivity is calculated from data over a time period of 54 years, while drought indices (Resistance, Recovery, Resilience) are calculated from the years around 2018 (2015–2021). CoV indicates the coefficient of variance for the given parameter. CC = Clearcut; NC = Non-clearcut. Sample sizes: n = 54 nested in 18 forests.

Response variable	***CC***	***NC***	***df***	***F***	***p***
Tree mean sensitivity (val x 100)	8.00 ± 0.2	8.87 ± 0.3	1, 12.5	0.91	0.36
Stand mean sensitivity (val x100)	4.43 ± 0.2	3.38 ± 0.2	1, 12.6	4.66	0.05
Resistance	0.88 ± 0.0	0.95 ± 0.0	1, 11.9	11.1	< 0.01
Recovery	1.17 ± 0.0	1.03 ± 0.0	1, 12.3	4.47	0.06
Resilience	1.03 ± 0.0	0.98 ± 0.0	1, 12.4	0.04	0.85
Mediator variables used for 2018 drought indices	***CC***	***NC***	***df***	***F***	***p***
Mean tree age (years)	49.0 ± 1.6	99.0 ± 4.3	1, 12.5	43.0	< 0.01
Age heterogeneity (CoV)	15.8 ± 1.6	40.2 ± 4.5	1, 12.8	8.96	0.01
Early growth rate (kg year^{-1})	1.77 ± 0.1	0.55 ± 0.0	1, 12.5	10.2	< 0.01
Mean tree height (m)	12.2 ± 0.4	12.8 ± 0.4	1, 12.7	0.41	0.53
Height heterogeneity (CoV)	22.1 ± 1.4	31.0 ± 2.2	1, 12.4	7.82	0.02
Mean tree circumference (cm)	51.7 ± 1.7	57.1 ± 2.4	1, 12.5	1.18	0.30
Circumference heterogeneity (CoV)	32.4 ± 1.9	48.2 ± 2.5	1, 12.5	13.1	< 0.01
Soil temperature variability (CoV)	138 ± 3.2	160 ± 6.2	1, 12.8	3.10	0.10
Soil organic matter (kg m^{-2})	12.9 ± 1.6	12.7 ± 1.1	1, 12.3	0.19	0.67

There were some correlations among the tree and soil characteristics (Figure S4). The mean tree age and tree age heterogeneity were both negatively correlated to early growth rates. Tree height was positively correlated to tree circumference, and the heterogeneity of tree height was positively correlated to the heterogeneity of tree circumference. Additionally, the soil temperature variability was positively correlated to the mean tree age and circumference.

3.2. Growth sensitivity

Patterns of mean sensitivity differed depending on whether it was expressed per individual tree or as stand-wide mean sensitivity (Fig. 3; Table 1). The mean sensitivity, when calculated for each individual tree, did not differ much between the two forest types. However, when mean sensitivity was calculated based on the stand's mean annual growth, Non-clearcut forests showed lower mean sensitivity than Clearcut forests.

3.3. Impact of weather variability

During the period 1970–2020, the mean annual temperature in the study region rose by an average of 0.033 °C year^{-1} (Figure S3; Table S1). Despite a large inter-annual variation in precipitation (ranging from 345 to 774 mm year^{-1}), there was no directional trend in annual precipitation over time while SPEI decreased by ~0.02 year^{-1} over the study period.

Tree growth of Clearcut forests showed greater responsiveness to weather variability than the tree growth of Non-clearcut forests (Fig. 4). The RWI of Clearcut forests was more affected by all temperature variables than those of Non-clearcut forests. Specifically, high temperatures in previous year autumn months (October, November) and current year August had a stronger negative effect, while high mean and minimum temperatures in current year September had a more positive effect on RWI in Clearcut forests compared to Non-clearcut forests. The effect of higher precipitation and SPEI on RWI was generally greater in Clearcut than Non-clearcut forests. Mainly, the precipitation and SPEI of current year summer months (June – September) had a greater positive effect on RWI in Clearcut forests than in Non-clearcut forests. In general, the effects of precipitation and SPEI on RWI were stronger than the effects of temperature.

3.4. Impact of the 2018 drought

The growth was greatly reduced in both forest types during the drought year of 2018 (TRW decline from the average growth of the three preceding years was 19 ± 1.3 % and 11 ± 1.3 % for Clearcut and Non-clearcut forests, respectively). Tree growth was more influenced by the 2018 drought in Clearcut than Non-clearcut forests, indicated by the reduced resistance values in the disturbance indices (Fig. 5; Table 1). Mediation analyses showed that the difference in resistance to the 2018 drought was mostly mediated by differences in mean tree age and early growth rate and, to a lesser extent, by age heterogeneity (Table 2). However, there was a strong correlation between the greatest mediating factors and forest type, leaving little variation explained by the mediating variables when forest type was accounted for (i.e. coefficient β_{my} was small for all mediating variables). Hence, the mediation analysis could not reveal if mean tree age, early growth rate, and age

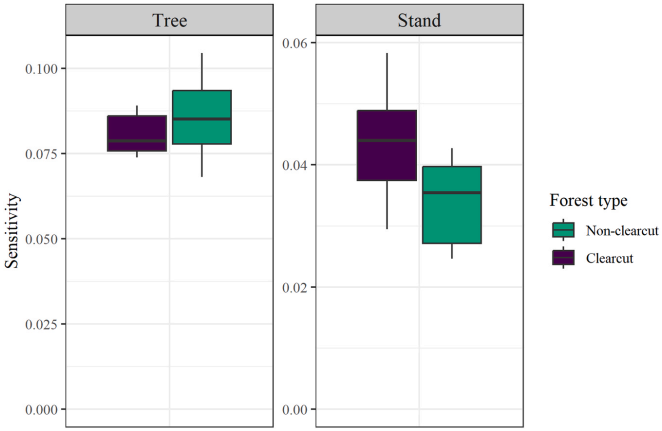

Fig. 3. Difference in mean sensitivity (inter-annual growth variability) between Clearcut forests and Non-clearcut forests. On the left, the data is presented for individual trees, and the mean sensitivity is calculated for each individual tree and then averaged per forest. On the right, the data is presented as a standwide mean average, and the mean sensitivity is calculated based on the forests' mean annual growth. Note the difference in scale between the two facets. In both cases, N = 18.

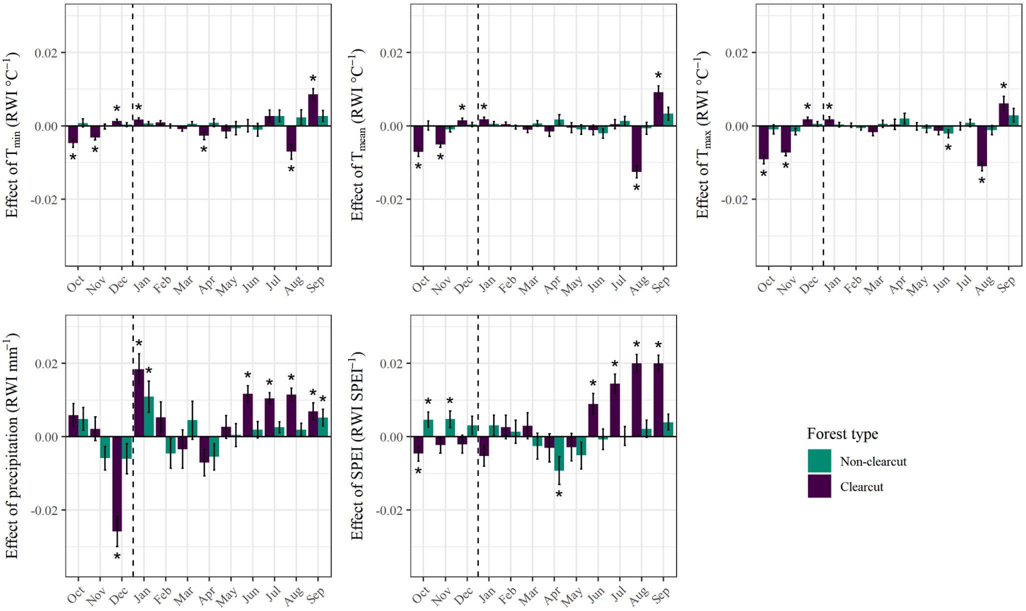

Fig. 4. Model output of the effects of climatic variables (maximum, mean, and minimum temperature, precipitation, and SPEI) on RWI in Non-clearcut forests (green) and Clearcut forests (purple). Asterisks indicate months where the main effect of the respective climatic variable on RWI in the indicated forest type shows a p-value < 0.05. In each month and climatic variable, N = 18.

heterogeneity, are true mediators of the effect of clearcutting or if their apparent effects resulted from multicollinearity with forest type.

Since the growth rates of both forest types returned to normal values in the years that followed the drought year of 2018, the recovery rate was greater in Clearcut forests due to their more substantial growth decline during the drought (Fig. 5). None of the studied variables mediated much of the differences in drought recovery (Table 2). Instead, the differences in mean age as well as heterogeneity in age, height, and circumference all weakened the differences in drought recovery.

The opposing directions of differences with greater resistance in Non-clearcut forests and greater recovery in Clearcut forests resulted in a similar resilience index for the two forest types (Fig. 5).

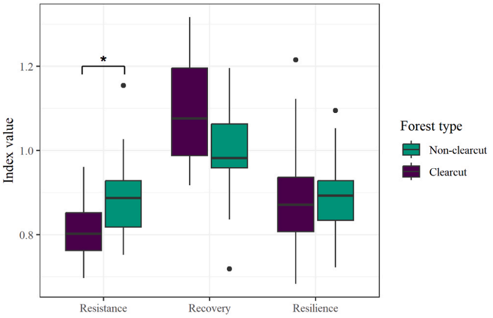

Fig. 5. Index values of resistance, recovery, and resilience, to the 2018 drought, based on RWI data for Clearcut forests (purple) and Non-clearcut forests (green). Asterisk indicates differences between forest types with a p-value < 0.05 (see Table 1 for detailed statistical output). In each index, $N = 18$.

4. Discussion

In this study, we examined the differences in tree growth sensitivity and response to weather variability between forests that had been clearcut ~60 years prior to the study and forests that have never been clearcut in northern Sweden. We found that disrupting tree continuity by clearcutting generally decreases the forests' ability to withstand extreme drought events. This is in accordance with similar findings from temperate forests (Alfaro-Sánchez et al., 2019; Mausolf et al., 2018; Oheimb et al., 2014), as well as recent findings from the Swedish boreal forest (Wolf et al., 2023). Our results further suggest that the increased drought sensitivity in forests regenerated after clearcutting is mediated through changes in tree characteristics such as decreased mean tree ages and increased early growth rates.

4.1. Growth sensitivity

We found modest support for our first hypothesis that tree growth stability would decrease following clearcutting. When examining the effect of clearcutting on tree growth stability, as measured by mean sensitivity scores, we found minor differences in mean sensitivity between Clearcut and Non-clearcut forests. Overall, the general mean sensitivity score in our study was slightly lower than those previously reported from forests in the region. For example, Linderholm and Linderholm (2004) showed mean sensitivity scores of 0.15 – 0.21 in pine trees, which is higher than the numbers we recorded (0.06 – 0.12). Interestingly, we found that the difference in mean sensitivity between Clearcut and Non-clearcut forests differed depending on whether it was expressed at the tree or stand level. When expressed as mean sensitivity at the individual tree level, the mean sensitivity score was slightly higher in Non-clearcut forests. Older trees may exhibit greater mean sensitivity (Carrer and Urbinati, 2004), which may explain our result, but the difference between forest types in our study was very small. In contrast, when we expressed mean sensitivity as the plot mean sensitivity across the stand, the mean sensitivity score was lower in Non-clearcut forests. Hence, the trees of the Non-clearcut forests showed more complementary growth patterns than the Clearcut forests, so that low growth for some trees was compensated by higher growth of other trees in the same plot.

Table 2
Mediation analyses of the effect of forest type mediated through mediator variables (mean tree age, age heterogeneity, mean tree height, height heterogeneity, mean circumference, circumference heterogeneity, early growth rate, soil temperature variability, and soil organic matter) on response variables (resistance to, and recovery from, the 2018 drought), based on detrended tree-ring series. Mediation values correspond to the proportion of the effect of clearcutting on the response variable that is explained by the mediator variable (calculated by: $\beta_{my} * \beta_{xm} / \beta_{xy}$). Note that negative mediation values indicate weakening effects. Path coefficient values are reported as mean (with standard deviation in parentheses), while the Mediation values are reported based on the means of the path coefficients.

	Response variable: Resistance to 2018 drought			
Mediator variable	β_{my}	β_{xm}	β_{xy}	***Mediation***
Mean tree age	4.9×10^{-4} (6.8×10^{-4})	49.4 (7.53)	0.08 (0.02)	0.30
Age heterogeneity	4.9×10^{-4} (7.2×10^{-4})	25.4 (8.50)	0.08 (0.02)	0.15
Early growth rate	-1.8×10^{-2} (1.5×10^{-2})	−1.12 (0.35)	0.08 (0.02)	0.25
Mean tree height	-4.9×10^{-3} (6.0×10^{-3})	0.63 (0.99)	0.08 (0.02)	−0.04
Height heterogeneity	-6.5×10^{-4} (1.4×10^{-3})	9.66 (3.46)	0.08 (0.02)	−0.08
Mean tree circumference	-1.2×10^{-3} (1.1×10^{-3})	5.12 (4.71)	0.08 (0.02)	−0.08
Circumference heterogeneity	3.7×10^{-4} (1.2×10^{-3})	15.9 (4.38)	0.08 (0.02)	0.07
Soil temperature variability	-3.2×10^{-4} (5.0×10^{-4})	18.8 (10.5)	0.08 (0.02)	−0.08
Soil organic matter	-1.7×10^{-4} (2.3×10^{-4})	−8.76 (20.3)	0.08 (0.02)	0.02
	Response variable: Recovery from 2018 drought			
Mediator variable	β_{my}	β_{xm}	β_{xy}	***Mediation***
Mean tree age	3.6×10^{-4} (9.4×10^{-4})	49.4 (7.53)	−0.09 (0.04)	−0.21
Age heterogeneity	9.1×10^{-4} (1.0×10^{-3})	25.4 (8.50)	−0.09 (0.04)	−0.27
Early growth rate	2.1×10^{-3} (2.0×10^{-2})	−1.12 (0.35)	−0.09 (0.04)	0.03
Mean tree height	-7.0×10^{-3} (8.4×10^{-3})	0.63 (0.99)	−0.09 (0.04)	0.05
Height heterogeneity	1.5×10^{-3} (2.0×10^{-3})	9.66 (3.46)	−0.09 (0.04)	−0.17
Mean tree circumference	8.8×10^{-4} (1.5×10^{-3})	5.12 (4.71)	−0.09 (0.04)	−0.05
Circumference heterogeneity	7.2×10^{-4} (1.7×10^{-3})	15.9 (4.38)	−0.09 (0.04)	−0.13
Soil temperature variability	2.2×10^{-5} (9.1×10^{-4})	18.8 (10.5)	−0.09 (0.04)	0.00
Soil organic matter	-3.5×10^{-4} (3.0×10^{-4})	−8.76 (20.3)	−0.09 (0.04)	−0.04

4.2. Impact of weather variability

We found that tree growth in Clearcut forests showed greater responsiveness to temperature and precipitation than tree growth in Non-clearcut forests. Generally, growth in Clearcut forests was more negatively affected by temperature (with the exception of September temperature which showed an opposite pattern) and more positively affected by precipitation and SPEI than growth in Non-clearcut forests. As both temperature and precipitation are expected to increase in the studied area as a result of global warming (IPCC, 2023 – and temperature data from the Arjeplog weather station in this study), it is difficult to predict if and how the forest types will diverge in their growth-weather response. Furthermore, we found temporal discrepancies revealing that summer precipitation (and SPEI) generally had a positive effect on growth while winter and spring precipitation had a more modest effect. This is possibly due to winter precipitation delaying the start of the growing season (Yun et al., 2018), and thereby limiting the otherwise positive effect of precipitation. Projected precipitation show an increase mainly during the winter months rather than the summer months (Alcamo et al., 2007). Such temporal dependency complicates the prediction of future tree growth responses as the differing effects of precipitation on tree growth was mostly apparent in summer months. Furthermore, while increased precipitation had a generally greater effect on growth than temperature in our study, future precipitation increases are predicted to be more unevenly distributed, featuring more distinct periods of heavy rainfall interrupted by droughts, rather than a uniform increase (IPCC, 2021). Periods of heavy rainfall generally weaken a tree's positive relationship with precipitation (Land et al., 2017), and droughts are generally negative for tree growth. Hence, the potential positive effects of increased precipitation in Clearcut forests may be double-edged. If droughts become more frequent between periods of heavy rainfall, the positive growth effects stimulated by higher precipitation may be offset, or even reversed, due to increased drought sensitivity during low precipitation periods.

4.3. *Impact of the 2018 drought*

We found support for our second hypothesis that forests regenerated after clearcutting would be less resistant to droughts. This reasonably follows from the Clearcut forests' greater responsiveness to temperature and precipitation, and is in line with previous studies, finding similar differences in the response to 2018 between old and more recently established forests in Sweden (Wolf et al., 2023), and in general drought responses in temperate regions (Alfaro-Sánchez et al., 2019; Mausolf et al., 2018; Oheimb et al., 2014). While the climatic data from the Arjeplog station did not reveal extreme values for 2018 in terms of annual mean temperature or precipitation (Figure S3), the year of 2018 has been noted as an extreme drought year in several previous studies (e.g. Martínez-García et al., 2024; Toreti et al., 2019). Importantly, the forest productivity of this study region was especially negatively affected by the 2018 drought (Wolf et al., 2023). Hence, the difference observed in our study may be exacerbated compared to a larger, biome-encompassing scale. However, if extreme droughts become more common in the boreal biome (Toreti et al., 2019; IPCC, 2021), the results of our study may be indicative of future drought effects on a larger scale.

There are many potential explanations to our observed differences in drought response between Clearcut and Non-clearcut forests. Here we have examined the mediation of the drought tolerance through differences in both tree and soil characteristics. Importantly, the mediators that appeared most influential (i.e. those that accounted for a large proportion of the effect of clearcutting on drought resistance) were strongly correlated with forest type. This indicates that the observed mediation partly reflects shared variance with forest type rather than independent effects. Keeping this in mind, one of the most important mediating factors in our study was early growth rate. This is consistent with previous studies that have found strong negative correlations between early growth and stress tolerance (Bigler, 2016; Bigler and Veblen, 2009; Di Filippo et al., 2015; Tao et al., 2024; Zang et al., 2014). Here, we found clear differences in growth patterns between forests that have been clearcut and those that have not. Most apparently, the early growth of Clearcut forests was substantially greater than that of Non-clearcut forests. This is not surprising, considering that clearcutting increases access to both nutrients and light (LeDuc and Rothstein, 2007), two of the most important growth-influencing factors in boreal forests (Kärenlampi and Riekkinen, 2004). Potentially, increased resource allocation to stem radial growth may come at the cost of reduced resource allocation to stress tolerance (Loehle, 1988) which could explain the detrimental effect of high early growth rates. Furthermore, the higher nutrient availability following clearcutting may have shifted the allocation patterns of trees in Clearcut forests, resulting in reduced resource allocation to belowground growth (Lim et al., 2015; Mausolf et al., 2018). This could lead to smaller root systems and, consequently, a reduced ability to access water during drought years.

Differences in soil properties have been shown to influence trees' drought tolerance, where drought sensitivity is generally higher in forests with greater soil bulk density (Cartwright et al., 2020), or poorly developed organic layers (Oheimb et al., 2014). Accordingly, drought tolerance in forests of disrupted continuity can be mediated by characteristics of the soil organic layer (Oheimb et al., 2014). However, the forests in our study exhibited minimal variation in soil organic mass, thereby disabling it as an important mediating factor in the observed reduced drought tolerance. Although we cannot rule out that the soil organic layer does play a role in drought tolerance even within our study system, we can show that similarities in soil organic layers do not equate to similar drought tolerance. Interestingly, in our study, the Non-clearcut forests had slightly more variable soil temperatures than Clearcut forests, while at the same time retaining greater drought resistance. Warmer soils have the potential to increase water loss in trees (Wieser et al., 2015), especially in isohydric species such as pine (Hu et al., 2024; Martín-Gómez et al., 2017). This may potentially explain why we found that the soil temperature variability had a weakening effect (although very minor) on the resistance values. In turn, this suggests that the Non-clearcut forests could potentially show even greater drought resistance if soil temperature variability would have been equal.

5. Conclusion

We found that trees growing in forests regenerated after clearcutting were more affected by temperature and precipitation patterns compared to stands that had been logged but never clearcut in northern Sweden. Further, we found that tree growth in forests regenerated after clearcutting was more severely affected by the extreme drought of 2018. The decrease in drought resistance was mainly mediated by a decrease in mean tree age as well as increased early growth rates in forests that have regenerated after clearcutting. It remains to be clarified whether the differences we have observed between clearcut forests and forests with long uninterrupted tree continuity represent an inherent effect of clearcutting, or whether they are primarily explained by the fact that clearcutting results in stands with lower average age and higher growth rates during the early stages of development, which generally make such forests more sensitive to weather variability. Nevertheless, our results demonstrate that clearcut forestry increases the responsiveness of tree growth to weather, which may be an important consideration for future forest management.

CRediT authorship contribution statement

Joachim Strengbom: Writing – review & editing, Writing – original draft, Conceptualization. **Gustaf Granath:** Writing – review & editing, Writing – original draft, Conceptualization. **Andreas Lundgren:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Andreas Lundgren reports financial support was provided by Swedish Research Council Formas. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123295.

Data availability

Data are available at: https://doi.org/10.5281/zenodo.16037934 and Code at: https://github.com/LundgrenAndreas

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Acta Universitatis Agriculturae Sueciae

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The growth of the boreal forest is an important function in the fight against climate change but lately that growth has dwindled. In this thesis, I explore the roles of climate change and clearcut forestry in altering boreal forest growth. I found that the growth-responses to climate change varies geographically, and that clearcutting, while increasing overall productivity, reduces growth stability.

Andreas Lundgren received his PhD education from the Department of Ecology, SLU, Uppsala.

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