Department of Ecology, Environment and Geoscience

Patterns and drivers of carbon cycling in old-growth boreal forests

Hanna Axén

UMEÅ UNIVERSITY

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The truth is

that nature can be our saviour

– but only if we save it first.

Inger Andersen

I am the wilderness locked in a cage

I am the growing force you kept in place

I am the tree reaching for the sun

Please don't hold me down

Release me

Oh Laura

Abstract

Old-growth forests, defined by minimal human disturbance, provide natural baselines for understanding forest carbon (C) cycling, especially in the face of climate change. Although boreal forests are important C sinks that mitigate climate change, the climate benefits of old-growth forests remain debated. Declining boreal C sink strength makes understanding the processes sustaining C uptake increasingly urgent. Yet detailed measurements of these processes remain scarce, particularly in old-growth forests, limiting our ability to predict their future C balance.

To address these knowledge gaps, we established a network of 12 boreal old-growth forests spanning a broad climate gradient and varying hydrological conditions, where we measured key C cycling components.

The first study examined stem growth responses to warming and drought. Norway spruce in southern Sweden emerged as vulnerable to both, although wetter conditions buffered growth declines following the major 2018 drought.

The second study quantified belowground C stocks, inputs, and respiratory losses. Unexpectedly low root-associated inputs coincided with comparatively low soil respiration, resulting in a neutral C balance - indicating stable soil C stocks. We link the low soil respiration to cool soil temperatures, possibly maintained by insulating and water-retaining old-growth features such as dense understory vegetation and dead wood. Wetter parts held substantial belowground C stocks and further suppressed respiratory losses.

The third study integrated C fluxes into a budget, to estimate the net ecosystem production as a proxy for C balance. All studied old-growth forests were C sinks, sustained by high tree growth and low soil heterotrophic respiration. Net primary production increased more than respiratory losses across the climate gradient, suggesting that moderate climate warming may strengthen these sinks.

Together, these findings establish boreal old-growth forests as natural baselines that reveal ongoing C sequestration and show how species composition, soil wetness, and forest structure may shape its persistence in a warming climate.

Sammanfattning

Gammelskogar, präglade av låg mänsklig påverkan, kan ge insikt i skogarnas naturliga kolprocesser. Den boreala skogens förmåga att ta upp och lagra in kol är välkänd, men gammelskogarnas klimatnytta är omdebatterad. När den boreala kolinlagringen nu minskar blir det allt viktigare att förstå de upprätthållande processerna. Detaljerade mätningar av dessa processer är dock få, särskilt i gammelskogar, vilket begränsar vår förmåga att bedöma skogarnas framtida klimatnytta.

För att undersöka gammelskogarnas kolbalans och vad som styr den etablerade vi ett nätverk av 12 gammelskogar längs klimat- och markfuktighetsgradienter i Sverige. Där mätte vi centrala kolprocesser och kolförråd.

I första studien undersökte vi hur trädtillväxten påverkas av temperatur och torka. Gran i södra Sverige framstod som känslig mot båda, även om de negativa effekterna av torka uteblev i våtare områden. Tall påvisade i viss mån ökad tillväxt vid högre temperaturer.

I andra studien riktade vi blicken under markytan. Vi undersökte markens kolflöden, kolförråd och vilka miljöfaktorer som påverkade dessa. Oväntat låga inflöden från rötter sammanföll med låg kolförluster genom respiration, vilket resulterade i en neutral kolbalans. Dessa låga kolförluster tycks bero på låga marktermperturer, möjligen tack vare gammelskogens isolerande och vattenhållande strukturer: tät undervegetation, ett varierat trädskikt och död ved.

I den tredje studien sammanfogade vi alla kolflöden för att kunna beräkna skogarnas kolbalans. Alla underökta gammelskogar agerade som kolsänkor under studieperioden, de lagrade alltså in mer kol än de släppte ut. Kolsänkan var starkare i varmare klimat, där biomassaproduktionen, främst trädtillväxten, ökade mer än kolförlusterna genom respiration.

Sammantaget tyder resultaten på att boreala gammelskogar kan agera som kolsänkor som kan stärkas i ett varmare klimat. Bevarande av gammelskogar ser ut att kunna förena hög biologisk mångfald med klimatnytta.

List of Papers

This thesis is based on the following papers:

I: *Species and soil wetness shape tree growth responses to warming and drought in boreal old-growth forests.*
Hanna Axén, Daniel B. Metcalfe, Anders Ahlström and Micael Jonsson
Environ. Res. Commun. 8 065045

II: *The balanced soil carbon budget in boreal old-growth forests is sustained by temperature-restricted CO_2 effluxes*
Hanna Axén, Micael Jonsson, Ulrika Ervander, Karina Clemmensen, Robert Björk, Anders Ahlström, and Daniel B. Metcalfe
Manuscript in preparation

III: *Boreal old-growth forests as carbon sinks across climatic and hydrological gradients: patterns and drivers*
Hanna Axén, Micael Jonsson, Anders Ahlström, and Daniel B. Metcalfe
Manuscript in preparation

Author Contributions

I: The study was designed by HA and DBM. AA supported the site selection. Field work was carried out by HA and DBM. HA performed the statistical analyses and wrote the manuscript with contributions from DBM, MJ and AA.

II: The study was designed by HA, DBM and UE. AA supported the site selection. Field work was carried out by HA, UE and DBM. Laboratory work was done by HA, UE, RB and KC. HA, DBM, UE and KC processed the data. HA performed the statistical analyses and wrote the manuscript with contributions from DBM, MJ, UE, RB, KC and AA.

III: The study was designed by HA and DBM. AA supported the site selection. Field work was carried out by HA and DBM. Laboratory work was done by HA. HA and DBM processed the data. HA performed the statistical analyses and wrote the manuscript with contributions from DBM, MJ and AA.

Authors: HA: Hanna Axén, DBM: Daniel B. Metcalfe, MJ: Micael Jonsson, AA: Anders Ahlström, UE: Ulrika Ervander, RB: Robert Björk, KC: Karina Clemmensen.

Additional Papers

Additional co-authorships not included in the thesis:

1. *Patterns and environmental drivers of root traits across hydrological gradients in old growth boreal forests.*
   Naomi Vöhringer, **Hanna Axén**, Anders Ahlström, Gesche Blume-Werry, and Daniel B. Metcalfe
   Oikos e11955. https://doi.org/10.1002/oik.11955
2. *Understory production in boreal forests: species differences, disturbance responses and climatic drivers.*
   Aleanor Lewis, Timon Callebaut, **Hanna Axén**, Michael Gundale, Marie-Charlotte Nilsson, Maja K. Sundqvist, Anders Ahlström, Daniel B. Metcalfe
   Submitted to Ecology

Disclosing the use of Artificial Intelligence

In this thesis ChatGPT (OpenAI) was used to assist with R coding (including figure creation and statistical analyses), to create conceptual graphics, and to suggest edits for proofreading and improving clarity of the manuscript text. All outputs were critically reviewed and approved by the authors.

Preface

I found a place to cross the river, balancing the fallen tree. Tried to read the wetland maze - which turfs connect and how deep would I sink? Met a stand scarred by recent fire - not what I was looking for. Pushed through a denser patch, the boulder field, over and under fallen logs. Eyes on the next point on the map.

Then all of a sudden.

Ahead of me stood a giant. Painted black by time, draped in white lichen. Shimmering as light scattered in water drops from rain that just stopped. Below the clearest of cold springs emerged. Time stood still.

I was on a measuring quest, and here I found myself struck by the moment. By something.

Some things cannot be measured. Should not be measured. A measurement would make the entirety collapse into a reduced point on my data sheet. Like a quantum-mechanical system - where all possible states collapse into one, if measured.

With the roots in physics, my fascination for nature and concern for climate change made me evolve into a physical geographer. Somewhere along the way, I got caught by Arctic and alpine environments.

But somehow doubt grew in me.

What difference does it make to know how fast glaciers melt, permafrost thaws, or methane is being released, if political and societal action remains highly inadequate?

Path-changing.

While spending five years in teaching, mountain leader training, and guiding, the forest debate grew stronger in Sweden. It puzzled me. How could conservation and production advocates, despite fundamentally different views on the role of forests in climate change mitigation, both claim scientific support?

The puzzlement and curiosity brought me back to science. Eventually.

I've now spent the past five years measuring things we can measure. Or that's what we tell ourselves. While trying to find representative areas, sampling strategies, frequencies, and gradients. Capturing entities that should give meaning. And trying to make sense of the resulting patterns. Time after time being struck by nature's complexity.

I've been on a quest for the carbon story in old-growth forests. Trying to bridge the knowledge gaps in the forestry debate. Because there are things we've forgotten to measure over the years. Measurements that can give meaning.

Here, I will tell you what I found. So find yourself a comfy place, sit back, and join me to glance at the old-growth forests through a carbon lens. But keep in mind that we're walking the world of giants, and log dragons. And when you get out there, allow yourself to be filled with awe.

Hanna Axén
October 17, 2026
Umeå

Part I

Introduction

Notes of urgency

Planetary emergency

At the time of writing, the *World scientists' warning to humanity: a third notice* has collected more than 11,500 signatures by scientists from over 140 countries (Ripple et al., in press). Collectively reaching out, from the perceived moral obligation that may come with knowledge. Concluding how human pressures and current activities are threatening life on Earth. Including ours. An attempt to communicate the planetary emergency that we are in.

Climate change is largely a story of carbon. Of intricate biological, chemical, and physical processes, intertwined with complex feedbacks which we are still working to unravel. At its base lies one of the largest scientific collaborations that the world has ever seen. The Intergovernmental Panel of Climate Change (IPCC) was established two years before I was born, in 1988, and has since produced six assessment reports. As an example, the last report involved nearly 800 experts, reviewing more than 66,000 scientific articles, and addressing 200,000 comments (Lidskog, 2024). Kimberly Nicholas (2021) summarised its conclusions well:

It's warming. It's us. We're sure. It's bad.

However, the planetary emergency is not only about climate change, but how resource use and expansion of the human species are pushing beyond the life-sustaining planetary boundaries, such as biodiversity, freshwater use, nutrient cycling, and ocean acidification (Richardson et al., 2023). The call of the scientists articulates how the solutions moving forward must take all these boundaries into account, but also how these sought-after solutions can bring opportunities and synergies to restore a prosperous planet and enhance human well-being.

The window of opportunity to act is about to close. As years of insufficient action pass, we risk triggering self-reinforcing climate feedbacks, irreversible within human time scales. Leaving the corridor of life behind (Rockström et al., 2021).

Instead of a collaborative action to ensure a future for humanity, distrust flourishes. Misinformation is all over (Rockström, 2026). Polarization tears us apart.

Yet, 89% of the world's population want stronger climate regulations, and a clear majority are even willing to contribute economically (Andre et al., 2024). But we think we are alone (Andre et al., 2024).

It's a story about us. A species whose success builds on collaboration (Bregman, 2020). It's time to get that collaboration going before the opportunity is lost.

Loss

Loss may be a part of life. But right now, we are losing life. Habitats. Lifeforms. Species. Individuals. In evolution, species evolve and go extinct. The current extinction rate could exceed the natural background by a factor 100 - 1000 (Pimm et al., 2014; Ceballos et al., 2015). And we are starting to see the consequences. Loss of biodiversity, driven by human disturbance and fragmentation of ecosystems, increase the risk of zoonotic diseases (Gibb et al., 2020; Karesh et al., 2012), undermine pollination and natural pest control, threatening food production (Dainese et al., 2019), and constrain natural water purification (Cardinale, 2011). As degradation of nature proceeds, ecosystem functions become constrained or lost (Hooper et al., 2012), resulting in major economic losses and financial risks (Karesh et al., 2012; Agarwala et al., 2026). Nature is complex, immensely complex - and we are playing a game, in which only future generations will be able to tell the ultimate consequences.

In Sweden, 40% of threatened species are connected to forests (Artdatabanken, 2026). The great majority of these species depend on large old coarse-barked trees that make you think of childhood sagas, or dead trees whose lives may have begun before the borders of this country were even drawn. Heterogenous structures that feature old-growth forests. Those few that scarcely have seen a human axe, let alone a harvester.

While forest cover most of Sweden, yet less than one twentieth of the forest area remain old-growth forests. Outside the mountain region, the proportion falls to just 0.3% (Volle et al., 2026; Figure 2). Tiny islands in a managed landscape.

Figure 1: Nothing in the forest is more alive than dead wood.
"Död ved är det mest levande i skogen." (okänd).

Figure 2: Distribution of remaining old-growth forests in Sweden, based on data from Ahlström et al. (2020). Outlines are widened for visibility, and old-growth forest areas therefore appear larger than they are.

Nevertheless, we are losing the last fragments of unprotected, old, previously uncut forests at a rate by which they may be gone well before the end of this century (Ahlström et al., 2022).

This interface, between the climate crisis and biologically invaluable old-growth forests, is where my thesis unfolds. Can old-growth forests offer one of those sought-after synergies between biodiversity conservation and climate change mitigation?

Forests in the global carbon cycle

Anthropogenic CO_2 emissions and the terrestrial carbon sink

When the industrial revolution took off in the 17th century and our carbon dioxide (CO_2) emitting era begun, ecosystems responded. As the level of atmospheric CO_2 rose, so did the CO_2 uptake by the world's vegetation. Up to this day, land vegetation has captured as much as 24% of the CO_2 we have emitted (Friedlingstein et al., 2026), acting as a so-called carbon (C) sink. For this uptake, the world's forests have been key players (Pan et al., 2011), thereby greatly counteracting climate change. But can we trust our branchy co-habitants on this planet to continue this service as the effects of climate change progress? Worryingly, we can see signs of reduced C sink strength as forest ecosystems are stressed by intensified disturbances, land-use change, and fragmentation (Pan et al., 2024). Understanding the processes underlying the C sink and its drivers is fundamental to predicting the effects of future global change scenarios and to build the foundation for us to act upon. But before continuing this story, we need to disentangle a few fundamental concepts.

Introducing key concepts

An ecosystem's role as a C sink depends on the balance between its incoming and outgoing C. When inputs exceed outputs, C is gained and the ecosystem acts as a C sink. We say such systems sequester C. When outputs instead exceed inputs, the ecosystem loses C and acts as a C source. In some ecosystems inputs and outputs can be approximately equal, and those are referred to as C neutral (Figure 3, Table 1).

Vegetation takes up C through photosynthesis (gross primary production, GPP). Some of the C returns quickly to the atmosphere through maintenance respiration (autotrophic respiration, RA). The remaining C mostly goes to biomass production (net primary production, NPP), although a portion is transported to symbiotic

Table 1: Abbreviations and definitions of carbon-cycle concepts and climate variables.

Term	Name	Description
C	Carbon	Essential building block of life. Highly problematic if too much is in the atmosphere.
C flux	Carbon flux	Rate of C transfer between compartments or between the ecosystem and atmosphere.
C stock	Carbon stock	Amount of C stored in an ecosystem compartment (vegetation, organisms, or soil).
C budget	Carbon budget	Accounting of ecosystem C inputs, outputs, and changes in stocks.
C balance	Carbon balance	The total rate of C stock accumulation or loss.
GPP	Gross primary production	Total photosynthetic C uptake; GPP = NPP + RA.
NPP	Net primary production	C remaining after plant respiration; NPP = GPP - RA.
R	Respiration	Release of C through respiration.
RA	Autotrophic respiration	Respiration by plants.
RH	Heterotrophic respiration	Respiration by heterotrophic organisms.
R_{eco}	Ecosystem respiration	Total ecosystem respiration; R_{eco} = RA + RH.
NEP	Net ecosystem production	Proxy for net ecosystem C balance; NEP = GPP - R_{eco} = NPP - RH.
C sink	Carbon sink	Net ecosystem C gain; NEP $>$ 0.
C neutral	Carbon neutral	No net ecosystem C gain or loss; NEP = 0.
C source	Carbon source	Net ecosystem C loss; NEP $<$ 0.
Climate variables		
MAT	Mean annual temperature	Average annual air temperature.
GDD	Growing degree days	Cumulative daily temperatures above 5 °C; measure of growing-season warmth.
SPEI	Standardized precipitation-evapotranspiration index	Climatic water balance index; negative values indicate dry conditions and positive values wet conditions.

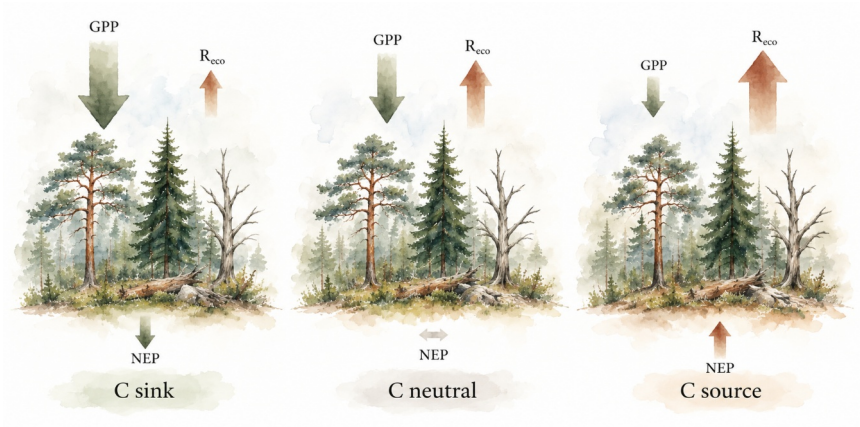


Figure 3: Conceptual illustration describing the different states of forest C balance. When photosynthetic inputs (GPP) are larger than outputs from ecosystem respiration (R_{eco}), the forest is a C sink and accumulates C. If GPP equals R_{eco}, the forest is C neutral and the C stocks are in equilibrium. Where R_{eco} is larger than GPP, the forest is a C source and loses C to the atmosphere. Generated using ChatGPT (OpenAI, 2026).

mycorrhizal fungi or released into the rhizosphere (exudation). As biomass is shed or dies, decomposition starts and C is, at least partly, respired back to the atmosphere, a process called heterotrophic respiration (RH). RA and RH combine into ecosystem respiration (R_{eco}). The balance between CO_2 uptake and release is called net ecosystem production (NEP) and can be calculated either as GPP - R_{eco}, or as NPP - RH, because both GPP and R_{eco} includes RA (Table 1). NEP largely reflects the full C balance of the ecosystem, and positive values indicate a C sink while negative values indicate a C source (Figure 3), although C losses through processes like leaching, or emissions of methane and volatile organic compounds can also contribute to the C balance (Chapin et al., 2011).

A positive C balance sustained over time leads to C sequestration and increasing C stocks. However, large C stocks reflect past C sequestration and do not necessarily indicate a contemporary C sink: an ecosystem can have high or low C stocks while either gaining of losing C (Figure 4). Ecosystems with large C stocks but low C sequestration rates are however not less important, because of their potential to either keep C locked up or,

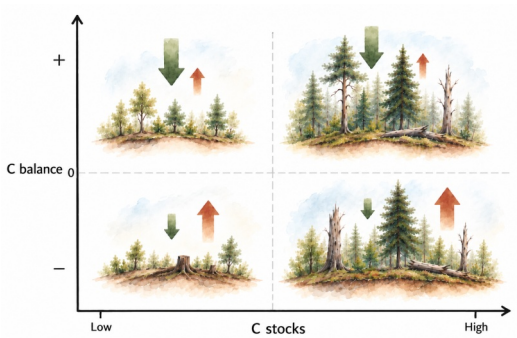


Figure 4: Conceptual illustration showing how a forest can encompass either combination of C balance: from positive C sink to negative C source, and C stocks: from high to low. Generated using ChatGPT (OpenAI, 2026).

if destabilized, cause substantial C release to the atmosphere. We need to understand C cycling processes that govern both continued C sequestration and the stability of existing stocks to predict their response to future global changes.

Global change, and the onset of the C sink

So, what has shaped the forest C sink since the industrial revolution? Several interacting drivers, collectively termed global change, have influenced its trajectory, but their relative importance varies among biomes (Keenan and Williams, 2018; Ruehr et al., 2023). Elevated atmospheric CO_2 concentrations increase photosynthesis (Farquhar et al., 1980), an effect often referred to as CO_2 fertilization or CO_2 enrichment. Furthermore, combustion of fossil fuels releases nitrous oxides causing elevated nitrogen (N) deposition, which can boost productivity (Norby, 1998), particularly in N-limited ecosystems (Guo et al., 2026). Warmer temperatures and longer growing seasons, resulting from the increasing CO_2 concentration, contribute to enhanced productivity, at least in temperature-limited biomes (Zhu et al., 2016). Finally, land-use changes, such as forests re-establishing on previous agricultural land, have also further contributed to increased C sequestration (Keenan and Williams, 2018). The combination of these factors has altered the conditions in which ecosystems exist, promoting the increasing C sinks (Ruehr et al., 2023).

Boreal forests

Boreal forests, characterised by both low temperatures and N-limitation, have responded to a combination of the global changes (Hyvönen et al., 2007). This large forest belt, making up a third of the world's forested area (FAO, 2020) and spanning much of the Eurasian and North American northern latitudes, has been considered the most important terrestrial C sink (Tagesson et al., 2020). But also here, the C sink strength has declined (Pan et al., 2024). This alarming not only because of the reduced C sequestration, but also because boreal forests store large quantities of C that could be released if these ecosystems are destabilized (Bradshaw and Warkentin, 2015). These high latitudes are also warming faster than the global average (IPCC, 2021), enhancing the risk of destabilization. Of the large C stocks in boreal forests, a disproportionate amount is stored belowground, particularly in wetter areas (Bradshaw and Warkentin, 2015; Crowther et al., 2019). Despite their importance as C sinks and exposure to climate change, boreal forests remain under-represented when it comes to C cycling measurements (Anderson-

Teixeira et al., 2021) - limiting our understanding of the future C sink of boreal forests.

Old-growth forests

While much of the boreal forests is managed with practices aiming to increase stem-wood production, e.g., drainage, plant breeding programs, monocultures, and fertilization, boreal old-growth forests, defined by minimal human influences, can serve as natural baselines for understanding how C cycling processes respond to environmental conditions and change. A strict tree age limit for old-growth forests does not exist, partly because the age concept becomes complicated in uneven-aged forests (Hilbert and Wiensczyk, 2007). Some old pines may have survived an otherwise stand-replacing fire, while age-related mortality can reduce the mean age as time passes. Boreal old-growth forests are instead characterized by trees of varying species, ages, and size, gap dynamics, and large amounts of dead wood (Buchwald, 2005).

Historically, late-successional forests were often assumed to be C neutral – hence of little climate benefit. This assumption followed Odum's hypothesis of ecosystem development (Figure 5; Odum, 1969). During development, photosynthetic C uptake exceeds respiratory losses, causing biomass to accumulate in the ecosystem. As the ecosystem matures, photosynthesis declines as nutrients become increasingly locked up in biomass, while respiratory losses continue to increase with higher biomass. Eventually, Odum hypothesised, respiration should approach photosynthesis, resulting in C neutrality, but high C stocks.

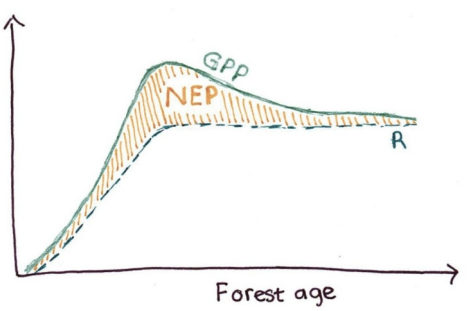


Figure 5: Illustration of the hypothetical model of ecosystem succession by Odum (1969). GPP: gross primary production or photosynthesis, R: respiration, NEP: net ecosystem production, reflecting the C balance. Drawn based on Odum (1969).

Old-growth forests do store large quantities of C (Pascual et al., 2026), but they have primarily been valued for supporting high biodiversity and multiple ecosystem services (de Assis Barros et al., 2022; Watson et al., 2018), and their conservation has sometimes been framed as conflicting with climate change mitigation (Jansons et al., 2025). However, evidence that old-growth forests act as C sinks is accumulating (Luyssaert et al., 2008; Peichl et al., 2022; Besnard et al., 2025),

although the debate is not yet settled (Gundersen et al., 2021). Whether, where and for how long old-growth forests act as C sinks remains uncertain, as does their response to future global change. It is also unclear whether their apparent C sequestration reflects a (transient) response to global change or challenges Odum's hypothesis of C neutrality in late-successional forests (McGrath et al., 2024).

Carbon processes in boreal old-growth forests

Understanding forests through carbon budgets

Different methods to quantify the NEP or C balance of forests exist, all with their strengths and weaknesses. Eddy-covariance towers, estimating forest - atmosphere gas exchange from CO_2 concentrations and turbulent air motion at multiple vertical positions, may capture diurnal, seasonal, and annual patterns in C exchange between forests and the atmosphere (Baldocchi, 2003). Recurring C stock inventories can provide information about the net C balance over longer time periods, and thus confidently assess C sequestration or losses (Chapin et al., 2011). Although these approaches can prove informative data on C stocks and C exchange, they present limited opportunity to understand underlying processes. Here, biometric methods, aiming to quantify the individual C budget components, can be a powerful tool (Xu et al., 2014). Not only can biometric methods give us an estimate of NEP, but the patterns and relative distribution among the C components can inform us about C cycling processes underlying the C balance.

The C budget of a forest is much like the economic budget of a company; describing the inflow, outflow, and net balance of money, but also where the investments go and transfers through the organisation. But here we are dealing in the C currency. As for the company's budget, we can learn about the functioning of the forest, and potentially its preparedness for unforeseen events. As we shall see, allocation patterns shift with ecosystem characteristics, reflecting their functioning, and largely controlling their C sequestration.

C allocation under resource limitation

C allocation varies among plant groups and species, as plants invest their photosynthetically fixed C to maximize their success (survival and reproduction). More needles and leaves enhance photosynthesis, whereas stem-wood growth enables reaching the light and, together with coarse roots, offers structural stabil-

ity. Neither is possible unless the plant has enough water and nutrients. When such resources are scarce, as they may be in old-growth forests (Wardle et al., 2004), belowground allocation may become increasingly important (Litton et al., 2007). Investments in fine roots (diameter $\leq$ 2mm), largely responsible for resource acquisition, enhance nutrient and water uptake. Roots can also release soluble organic compounds to the soil to stimulate nutrient mineralization and facilitate nutrient uptake, a process called root exudation (Oburger and Jones, 2018). To overcome nutrient limitation, most boreal plants form mycorrhizal symbiosis with fungi, where they trade photosynthetically fixed C for nutrients. Mycorrhizal fungi can access nutrients by a combination of extensive mycelia providing an enormous surface area for nutrient uptake, but these fungi can also produce various exo-enzymes which they release into the surrounding soil to help degrade organic matter that enable further nutrient acquisition (Read and Perez-Moreno, 2003; van der Heijden et al., 2015). Under nutrient-poor conditions, understory vegetation, mainly consisting of ericaceous dwarf shrubs and mosses, can contribute as much as trees to aboveground production (Nilsson and Wardle, 2005; Turetsky et al., 2010). Thus, if nutrient limitation strongly controls boreal old-growth forest functioning, we expect a greater relative investment in belowground resource acquisition and a greater contribution of understory vegetation to production.

From C allocation to C sequestration

Plants' C allocation patterns influence how long C remains in the ecosystem. Greater allocation to a compartment does not necessarily increase C sequestration: its contribution also depends on tissue lifespan, the fate of its residues, and its effects on decomposition. Allocation into compartments with long residence-times, such as stem-wood or coarse roots, lock up C in the forest over long periods and thereby promote C sequestration (Sierra et al., 2021). Leaves and needles are more short-lived and decompose relatively quickly, making the C return to the atmosphere faster. However, mosses and dwarf shrubs produce litter with relatively high levels of lignin or phenolic compounds and low nutrient concentration, making them more resistant to decomposition (DeLuca and Boisvenue, 2012; Hobbie et al., 2000; Nilsson and Wardle, 2005), and can therefore contribute more to soil C sequestration (Hilli et al., 2010). In addition, fine roots and some mycorrhizal mycelia may, despite having relatively short lifetime, promote soil C accumulation by forming recalcitrant necro-mass (Adamczyk et al., 2019; Clemmensen et al., 2013). However, other mycorrhizal fungi abundant in late-successional forests

overcome nutrient limitation by acting like saprotrophic fungi (i.e., decomposers) and thereby restrict soil C accumulation (Lindahl et al., 2021). Similarly, exudation of labile C compounds may stimulate microbial activity and enhance decomposition rates and C loss (Kuzyakov, 2002; Jones et al., 2009). Overall, C allocation patterns control how long the recently fixed C stays in the ground, but can also stimulate loss of older C.

Respiratory pathways and their drivers

Loss of C from forests mainly occur via soil respiration and dead wood decomposition. The largest output flux, soil respiration (Janssens et al., 2001), is highly variable spatially and temporally (Phillips and Nickerson, 2015), making it challenging to quantify. Soil temperature and moisture are often the main drivers of soil respiration magnitude (Walkiewicz et al., 2026; Davidson et al., 2002), even if other factors such as organic matter input quality (Hobbie et al., 2000), soil microbial community (Karhu et al., 2014), and vegetation composition (Raich and Tufekciogul, 2000) also can be important. In boreal forests, increasing temperatures generally result in higher soil respiration, although low soil moisture can constrain this effect (Dong et al., 2026). Also, high soil moisture can reduce soil respiration, as oxygen limitation can suppress decomposition rates (Moyano et al., 2013), explaining the large C stocks found in wet parts of boreal forests (Bradshaw and Warkentin, 2015; Crowther et al., 2019). The fate of these large soil C stocks under warming may therefore depend on whether wet conditions continue to constrain decomposition.

Soil respiration is not only the result of microbial decomposition, but also maintenance respiration of roots and mycorrhizal fungi. Partitioning soil respiration into its components is therefore important to understand the effects of soil C stability. The respiratory components from roots and fungi typically increase in more productive ecosystems, because of higher GPP (Litton et al., 2007), which should not be confused with loss of soil C. On the other hand, the proportion of photosynthesis used for maintenance respiration is higher when resources are scarce (Hagenbo et al., 2019) - the organisms having to use more energy to get their resources. This proportion reflects the Carbon Use Efficiency (CUE) of an organism. High CUE means that a large proportion of GPP is used for growth instead of respiration, and vice versa (Manzoni et al., 2018). CUE can be a useful metric for assessing C sequestration potential, describing the proportion of GPP that goes into biomass instead of being lost.

To summarize, studying C allocation patterns and respiratory pathways under

varying climatic and hydrological conditions can provide insights into the underlying mechanisms for C sequestration. The lack of C cycling component measurements in boreal, old-growth forests (Anderson-Teixeira et al., 2021) thereby limits our understanding of their potential for C sequestration, now and under future global change.

Objectives

The overall aim of this project was to describe C cycling and allocation in boreal old-growth forests, and how these patterns vary over climatic and hydrological gradients. By measuring the main components of the forest C budget in old-growth forests sites across Sweden, I have addressed the following research questions:

i How does tree growth respond to warming and drought in boreal old-growth forests, and how is this response mediated by soil wetness?

ii What are the main drivers of C cycling and allocation in old-growth forests?

iii What is the net ecosystem production (NEP) of boreal old-growth forests across climatic and hydrological gradients, and which C budget components drive variation in this balance?

Part II

Methodology

Study areas

All studies for this doctoral thesis were based on the same network of 12 old-growth forests sites. At the start of the project, we established this network to cover a broad latitudinal (57 - 67 °N) and climatic (MAT: -0.4°C to 6.6°C) gradient (Figure 6). We selected sites from a national map of primary forests (Ahlström et al., 2020; Volle et al., 2026) based on criteria excluding both forests < 0.25 km^2, and those with markedly greater elevation than their surroundings (Pascual et al., 2026). To ensure old-growth forest characteristics, we selected forests rating ≥ 6 on the Buchwald naturalness index (Buchwald, 2005). This classification encompasses forests with minimal known or visible human disturbance, and characterized by trees of varying ages and sizes, typically mixed tree species composition, multiple canopy layers, gap dynamics, well-developed understory vegetation, and large amounts of dead wood.

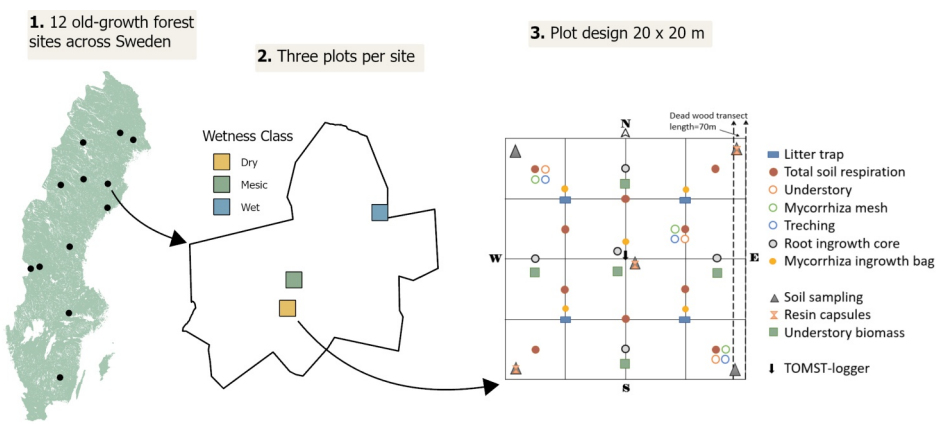


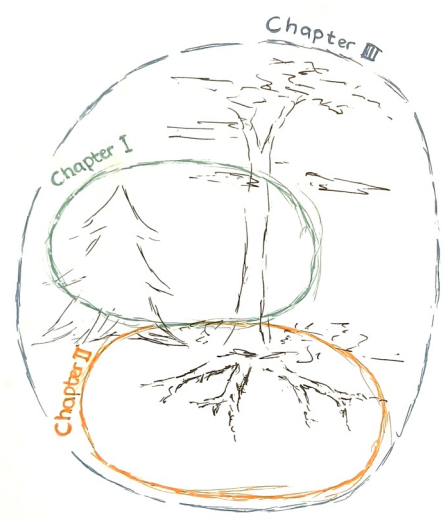
Figure 6: The map of Sweden (1.) shows the distribution of the 12 old-growth forest sites. In each forest (2.), we established three 20 $\times$ 20 m plots at varying soil wetness class (dry, mesic, and wet), as illustrated by the map in the middle. The right-most illustration (3.) provides an overview of the main plot-level installations and measurements.

In each forest site, we established three 20 × 20 m plots, one in each of three soil wetness classes; dry, mesic, and wet. These wetness classes were based on Topographic Wetness Index, which provides a proxy for soil moisture based on the combination of soil properties, topography, and depth to water (The Swedish Environmental Protection Agency, 2019; Pascual et al., 2026). Across all plots, the dominating tree species were Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst.), and birch (*Betula* spp.), but to varying extent. The understory vegetation was dominated by mosses, *Sphagnum* in most wet plots; *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis* in dry and mesic plots, and ericaceous dwarf shrubs, mostly *Vaccinium myrtillus* although *V. vitis-idaea*, *Empetrum nigrum*, and *Calluna vulgaris* were also present in many plots. The dry and mesic plots were mostly located on podzol soil, except in the two southernmost which were on cambisols. The wet plots were mostly located on histosols, although podzols were present in parts of some plots.

Measurements

Overview

The chapters address different parts of the C budget (Figure 7), and therefore measurements of C stocks, net primary production (NPP) and respiratory losses (R) lay the foundation for this thesis. We estimated these components from measurements within representative sampling areas and, for fluxes, over selected time periods. We then scaled the estimates to tonnes of C per hectare (Mg C ha^{-1}), and annual fluxes to tonnes of C per hectare (Mg C ha^{-1} yr^{-1}), using C content, mostly literature-based, to convert biomass measurements to C when needed.



The chapters focus on:

I: Tree growth reconstructed from tree cores.

II: Belowground C cycling, including C stocks, inputs, and losses.

III: Whole-ecosystem C cycling, integrating C fluxes into a full C budget.

Figure 7: Focus area of each chapter.

Capturing the C budget

C stocks

Trees
To estimate tree biomass, we measured the diameter at breast height (dbh) and height of all trees with dbh $>$ 10 cm, within the 20 $\times$ 20 m plots. We then relied on species-specific biomass functions to estimate the biomass of foliage, branches, stems, and coarse roots (Marklund, 1988; Petersson and Ståhl, 2006). To convert biomass into C stocks, we applied species and compartment-specific C contents from Mensah and Petersson (2024).

Understory
We estimated understory C stocks based on destructive biomass harvest of five 38 $\times$ 38 cm subplots. The biomass was separated into dwarf shrubs, mosses, annuals, and perennials, dried, weighed and converted to C stocks using plant group-specific C contents (Ma et al., 2018; Woziwoda et al., 2014).

Fine roots
We estimated fine root (diameter $<$ 2 mm) C stocks by manually retrieving roots from five soil cores (diameter = 6.7 cm, maximum depth = 30 cm). The roots were separated by organic and mineral soil horizons. From the dry root biomass and horizon depths, we calculated root density which was upscaled to plot level based on mean horizon depth for the entire plot from 20 probings (see *Soil C*). The conversion from biomass to C stocks was based on the plot and horizon-specific C content from the work by Vöhringer et al. (2026).

Dead wood
Coarse dead wood C stocks were estimated based on two different inventories; (i) using a 70 $\times$ 1 m transect (Fraver et al., 2018) and (ii) a full inventory of the 20 $\times$ 20 m plot. We included both methods because of the stochastic nature of dead wood, and because of uncertainty whether the transect would accurately reflect the plot wetness class. In both methods we recorded dbh and height of all standing and downed dead wood with dbh $\geq$ 10 cm and classified them into five decay classes (Sandström et al., 2007). We estimated the C stocks combining the allometric biomass functions (Marklund, 1988; Petersson and Ståhl, 2006), decay class- and species-specific densities and C concentrations (Sandström et al., 2007). Finer dead wood, with diameter $<$ 10 cm, was estimated from the transect only. We sampled and weighed all fine dead wood in the transect separately by decay

class (Sandström et al., 2007). Subsamples of approximately 100 g per decay class were dried and weighed to obtain a wet-dry-conversion factor for each plot. We thereby converted the wet weights to C stocks using the conversion factor and decay class-specific C concentrations (Sandström et al., 2007). Total dead wood C stocks were calculated as the mean of the two coarse dead wood inventories plus the fine dead wood.

Soil C

We excavated five soil pits at each plot, to a maximum depth of 1 meter, or until reaching bedrock or large rocks. We estimated C concentration of each horizon based on soil samples taken at the middle of each soil horizon (5 cm long, 21 mm diameter), processed by standard procedures and analysed with EA-IRMS (SLU, Umeå). These C concentrations were upscaled to plot level based on the mean horizon depths from 20 probe depth measurements, and a correction of stoniness fraction in the mineral layer Eriksson and Holmgren (1996).

NPP components

Trees

We estimated tree growth from increment cores taken from a subset of trees of different species and sizes at each plot. For **Chapter I**, we used basal area increment (BAI) as a proxy for tree growth over the years 2012 – 2021. BAI of year j (BAI_j) was calculated based on the difference between dbh of that year (dbh_j) and the preceding year (dbh_{j-1}) according to Equation 1. We obtained the annual dbh-estimates by subtracting the rings widths from the tree census dbh.

$$BAI_j = \frac{\pi}{4} \cdot (dbh_j^2 - dbh_{j-1}^2) \tag{1}$$

For **Chapter II and III**, we combine the increment core data with the tree census to estimated total biomass growth of the compartments foliage, stem, branches and coarse roots (Marklund, 1988; Petersson and Ståhl, 2006). Based on plot- and species-level growth-biomass relationships we estimated the growth on uncored trees. Then we applied species and compartment-specific C concentrations (Mensah and Petersson, 2024) to obtain NPP estimates.

These NPP estimates only encompass tree expansion and were complemented by estimates annual production of foliage and small branches (diameter $<$ 10 cm) from litterfall traps and the revisit of the dead wood transect.

Understory

Growth of dwarf shrubs and mosses were estimated from shoot:total ratios of 20

individuals of each species per plot, following Nilsson and Wardle (2005). These ratios were applied to the understory C stocks to obtain aboveground understory NPP, and combined with the NPP of annuals, which equals their C stocks.

Fine roots
We estimated fine root growth from five cylindrical in-growth mesh cores per plot. They were retrieved two years after installation, and we estimated the fine root NPP following the same procedure as the fine root C stocks.

Mycorrhizal mycelia
To estimate growth of mycorrhizal mycelia we used five in-growth mesh bags per plot (mesh size = 50 µm, diameter = 2 cm, length = 10 cm, Wallander et al., 2013). The bags were retrieved after one year, and living biomass was estimated based on ergosterol concentration analysed by our collaborators at Gothenburg University following established protocols (Nylund and Wallander, 1992; Salmanowicz and Nylund, 1988), and assuming a C content of 43 % (Montgomery et al., 2000).

Exudation
We estimated exudation indirectly based on established relationships to (i) total tree NPP (Finzi et al., 2015), (ii) root NPP (Abramoff and Finzi, 2016), and (iii) root respiration (Sun et al., 2021). Following Riutta et al. (2021), we based our estimate of exudate production on the mean of these methods.

Respiratory components

Total soil respiration
We measured the soil respiration using the closed chamber approach, 1-2 times annually (summer and autumn) over the years 2022 – 2024. Additionally, we took monthly respiration measurements at one site between October 2022 and June 2023. When snow depth exceeded 40 cm, we used the gradient method (Björkman et al., 2010; McDowell et al., 2000), which assumes diffusive flux through the snowpack according to Fick's first Law (Sommerfeld et al., 1993) based on measurements of CO_2 concentrations at the top and bottom of the snowpack. In 2022 and 2023 measurements were done at 10 positions in each plot, but in 2024 at 3 positions. We recorded soil temperature next to each respiration measurement.

The instantaneous respiration rates were upscaled to annual estimates using a Q_{10}-modelling approach based on soil temperature (Equation 2; Chen and Tian, 2005). The parameters R_{10} (reference respiration at 10 °C) and Q_{10} (the relative change in respiration for every 10 °C, i.e., the temperature sensitivity)

were estimated based on the instantaneous respiration rates and paired soil temperatures. We estimated a shared Q_{10} but plot-level specific R_{10}. The upscaling was based upon plot-level 15-minute-frequency soil temperature recording, from TMS-4 loggers (TOMST s.r.o, Praha, Czech Republic) installed at the centre of each plot.

$$R(T) = R_{10} \cdot Q_{10}^{(T-10)/10} \tag{2}$$

Partitioning of soil respiration

To partition the soil respiration into the contribution from aboveground understory vegetation, roots, mycorrhizal mycelium and soil heterotrophs, we installed exclusion treatments (following e.g., Riutta et al., 2021; Ryhti et al., 2021). In each plot, three partitioning clusters installed in paired setups with total soil respiration controls. The clusters comprised four treatments (Figure 8):

(1) Unmodified control.

(2) Removal of aboveground understory vegetation.

(3) Removal of aboveground understory vegetation; trenching and enclosure with a 50 μm mesh that excluded roots but allowed mycorrhizal mycelia to penetrate.

(4) Removal of aboveground understory vegetation; trenching and enclosure with a plastic tarp that excluded both roots and mycelia.

All modifications were done in a 20-cm-diameter circular plot, and we trenched down to maximum 30 cm depth.

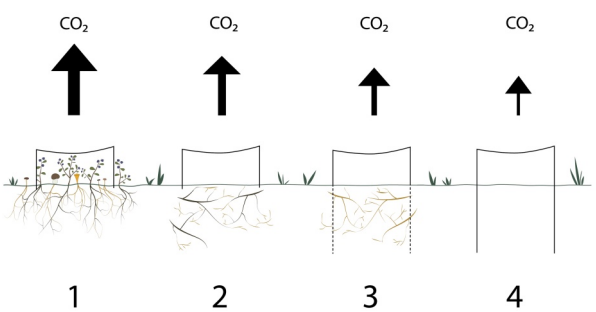


Figure 8: Experimental removal and exclusion treatments used to partition ground-surface CO_2 efflux into contributions from understory vegetation, roots, mycorrhizal fungi, and saprotrophic organisms. Graphic design: Ella Axén.

Table 2: Derivation of surface CO_2 efflux components from the four partitioning treatments.

Component	Interpretation	Calculation
R_{us}	Aboveground understory vegetation	1 – 2
R_{root}	Root respiration	2 – 3
R_{myc}	Mycorrhizal mycelia respiration	3 – 4
$R_{H,soil}$	Soil heterotrophic respiration	4

We measured the respiratory fluxes from all treatments in July and September two years after installation, following the same methods used for total soil respiration. The respiratory contributions of each component were then calculated according to Table 2. We then calculated each component's proportional contribution to the total soil respiration in the control treatment and applied this ratio to the annual soil respiration to obtain annual estimates of each component.

Dead wood respiration
We estimated the dead wood respiration by applying a species-specific decay constant (Shorohova et al., 2008) to the dead wood C stocks.

Carbon Use Efficiency and residence time

We estimated carbon use efficiency (CUE: the proportion of total C available allocated to biomass growth) for aboveground understory, fine roots, and mycorrhizal fungi according to Eq 3 (DeLucia et al., 2007).

$$CUE = \frac{NPP}{NPP + R} \tag{3}$$

We estimated residence time (RT) for fine roots and SOC according to Eq 4 (Finér et al., 2011; Ostonen et al., 2005). This calculation builds on the assumption of steady-state, where NPP equals R over longer timescales and broad spatial scales (Sierra et al., 2017). Compartments in late-successional systems such as old-growth forests would be broadly expected to meet this assumption (Harmon et al., 2004; Odum, 1969).

$$RT = \frac{stock}{NPP} \tag{4}$$

Lloret's resilience indices

To assess the drought response in tree growth using Lloret's resilience indices (Lloret et al., 2011), which compares growth during the drought year (*Dr*) to pre-drought growth (*PreDr*). We modified this metric to also evaluate growth in the first, second, and third year after the drought (*PostDr1*, *PostDr2*, and *PostDr3*, respectively), to disentangle legacy (gradually diminishing) effects and lagged (delayed) responses (Kannenberg et al., 2020; Schwarz et al., 2020).

$$Immediate = \frac{Dr}{PreDr}, \quad Lag1yr = \frac{PostDr1}{PreDr}, \quad Lag2yr = \frac{PostDr2}{PreDr}, \quad Lag3yr = \frac{PostDr3}{PreDr} \tag{5}$$

Environmental data

Climate

We downloaded gridded (4×4 km resolution) monthly temperature data for all sites and the years 1994 - 2023 (SMHI, 2025). Based on this, we calculated the 30-year mean annual temperature (MAT) to represent our gradient in **Chapter II and III**. For **Chapter I**, we also calculated the annual Growing Degree Days (GDD) by summing daily mean temperatures (T_{daily}) above T_{base} = 5 °C (McMaster and Wilhelm, 1997), Equation 6. In this chapter, we chose GDD as the temperature metric as it summarizes growing season warmth and length.

$$\sum max(T_{daily} - T_{base}, 0) \tag{6}$$

For **Chapter I** we used Standardized Precipitation-Evapotranspiration Index (i.e., SPEI; Vicente-Serrano et al., 2010) as a drought indicator. We downloaded monthly SPEI (0.5° resolution) from the Global SPEI database (`https://spei.csic.es/database.html`) and calculated the mean value for the growing season (May-September).

Soil nutrients

In **Chapter II** we used total available soil N (the sum of NH_4^+ and NO_3^-) as a proxy for nutrient status. This was measured with ionic exchange resin capsules (PST-1 capsule, Unibest, Kennewick, WA, USA), installed 12 months at three positions in each plot, at the middle of the organic layer (but maximum 15 cm depth).

Microbial community

In **Chapter II**, we calculated metrics to describe the soil microbial composition to evaluate its control over belowground C cycling. We took organic layer soil samples from each of the control partitioning treatments. The soil samples were analysed to characterize fungal community composition using ITS2 metabarcoding (Lindahl et al., 2013). We used the first axis of principal component analysis (PCA) on the relative abundance of the 30 most frequent and abundant species as a metric for the fungal community composition. To estimate fungal biomass, bacterial biomass, and gram-positive:gram-negative bacterial ratio the soil samples were also analysed for phospholipid fatty acid (PLFA) (Joergensen, 2022).

Vegetation composition

We also used PCA-based metrics to describe tree and understory species composition for **Chapter II and III**. The PCAs were based on relative biomass proportions of all tree species and understory the dwarf shrub species *V. myrtillus*, *V. vitis-idaea*, *V. uliginosum*, *E. nigrum*, *C. vulgaris*, mosses, annuals and perennials, respectively. Again, we used the first PCA axis to represent the community compositions. For the tree composition this broadly aligned between Norway spruce and birch-dominated stands (positive values) and Scots pine dominated stands (negative values). For understory composition, positive values were associated with moss-dominance and negative values with dwarf shrub-dominance.

Statistical models

Linear mixed models

To account for the hierarchical study design, in which plots representing different wetness classes within forest sites, we used Linear Mixed Effects Models (LMEs, using the lmer-function from Bates et al., 2015) for most statistical analyses. For analyses with one observation per plot (**Chapter II and III**), forest site was included as a random intercept to account for the non-dependence of plots within the same forest. The exception was the estimation of the R_{10}-parameter used in Q_{10}-modelling. Because respiration was measured repeatedly within each plot, plot was included as the random intercept, allowing plot-specific R_{10} estimate.

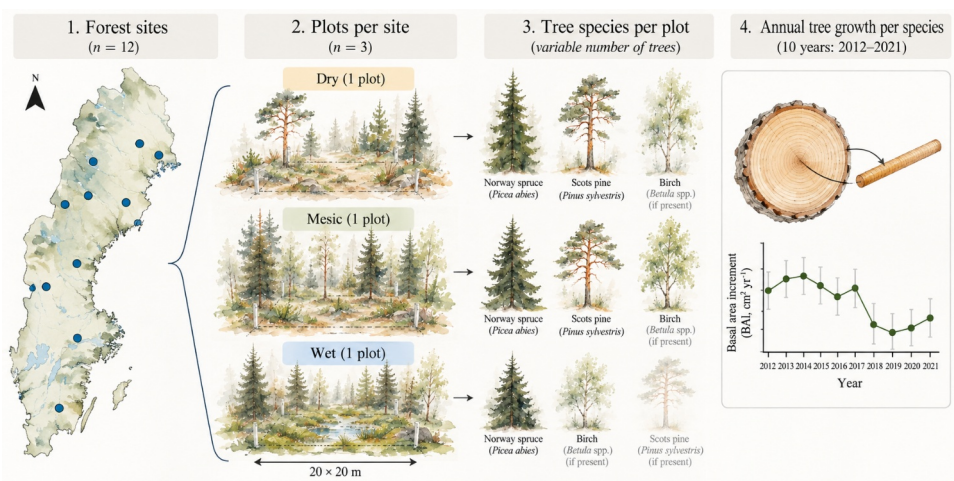


Figure 9: Illustration of the hierarchical study design in **Chapter I**: plots representing three wetness classes were nested within forest sites, with up to three tree species per plot and 10 years (2012–2021) of annual mean growth per species. Generated using ChatGPT (OpenAI, 2026).

The tree growth analyses in **Chapter I** had a more complex hierarchical and

temporal structure. Each forest site contained plots representing different wetness classes, each plot contained multiple tree species, and each tree species had repeated annual growth measurements. Random intercepts were therefore fitted for tree-species nested within wetness class and forest, specified as

```
random = 1 | Forest/Class/Species
```

in the lme-function (nlme-package; Pinheiro et al., 2021). In addition, temporal autocorrelation, with tree growth adjacent years being more similar, had to be accounted for by adding a first-order autoregressive correlation structure, specified as

```
correlation = corAR1(form = Year | Forest/Class/Species))
```

Model selection

Initial models were formulated based on our hypotheses, which sometimes required multiple interactions. For example, we expected soil wetness to modify the drought response in tree growth, with this buffering effect differing among species and between colder and warmer forests. Mathematically, this translates to a 4-way interaction:

$y \sim species \times Class \times climate \times drought$

To reduce the risk of over-parametrization, e.g., fitting more parameters than the data can reliably support, we simplified the models. The simplification was informed by small sample corrected AIC (AICc), which evaluates model fit against complexity by penalizing additional parameters, with the lowest value reflecting model fit and parsimony.

The models were fitted with maximum likelihood (ML) during the fixed effect model selection and then refitted with restricted maximum likelihood (REML) to estimate parameters.

Singularity

Some models had singularity-issues related to zero variance in the site random intercept. This meant that random intercepts could not be computed, and essentially that the LME was fitted as a linear model (LM). For parameter estimation, this is not problematic, because there is simply no support for clustering. For hypotheses testing, or model selection process however, the overestimated sample sizes will cause underestimated standard error and increase the risk of Type I

errors (false positives). In those cases, we therefore fitted separate LM for each wetness class.

Part III

Key findings and discussion

Chapter I: Tree growth responses to warming and drought

In Chapter I, we focused on the most familiar and striking component of forests: trees and their growth. Although aboveground tree measurement alone provides an incomplete picture of ecosystem C cycling, tree growth adds C to woody biomass, one of the most long-lived C pools which can contribute to forest C sequestration (Sierra et al., 2021). Recent reductions in boreal tree growth (e.g., Henttonen et al., 2024; Laudon et al., 2024) may therefore contribute to the weakening C sink. More frequent and intense droughts have been proposed as a driver of the growth reductions (Anderegg et al., 2022; DeSoto et al., 2020; Laudon et al., 2024), although these studies mainly rely on data from managed forests. As a contrast, old-growth forests appear less sensitive to droughts (Wolf et al., 2023), but it remains uncertain if this resistance also includes tree growth. We therefore investigated stem-growth trends in old-growth forests and how this growth varied with temperature and drought based on our tree ring data spanning the years 2012 – 2021.

1. Overall growth trend

We found no overall decline in tree growth for the period when growth reductions have been reported (2013 – 2021, Laudon et al., 2024). This indicates some intrinsic stability or resistance to the underlying driver of the decline previously reported. However, we found a species-specific growth decline for Norway spruce in the warmer part of our climate gradient. Although this is consistent with reported vulnerability of Norway spruce to warm and dry conditions (Aldea et al., 2022; Ogana et al., 2024), our results confirm that this vulnerability also exists for naturally regenerated trees in unmanaged forests.

2. *Response to major drought*

Because drought has been proposed as key driver for the reported growth decline, we set out to explore the tree growth responses to the major 2018-drought. We showed how growth responses vary by species over the climate gradient and plot wetness. By assessing the growth for up to three years after the drought, compared to pre-drought growth, we could also display how the temporal dynamics in responses vary by species.

Again, southern Norway spruce was identified as particularly vulnerable to drought. However, the strongest growth decline appeared with a delay, the year following drought. The response was clearly buffered by plot wetness with the strongest decline in dry plots, where growth was reduced for at least three years, while no growth decline compared to pre-drought conditions was detected in wet plots (Figure 10). The growth decline increased in warmer climates, while Norway spruce in the coldest portion of our climate gradient showed no growth decline.

Scots pine was generally less affected by drought and only showed growth

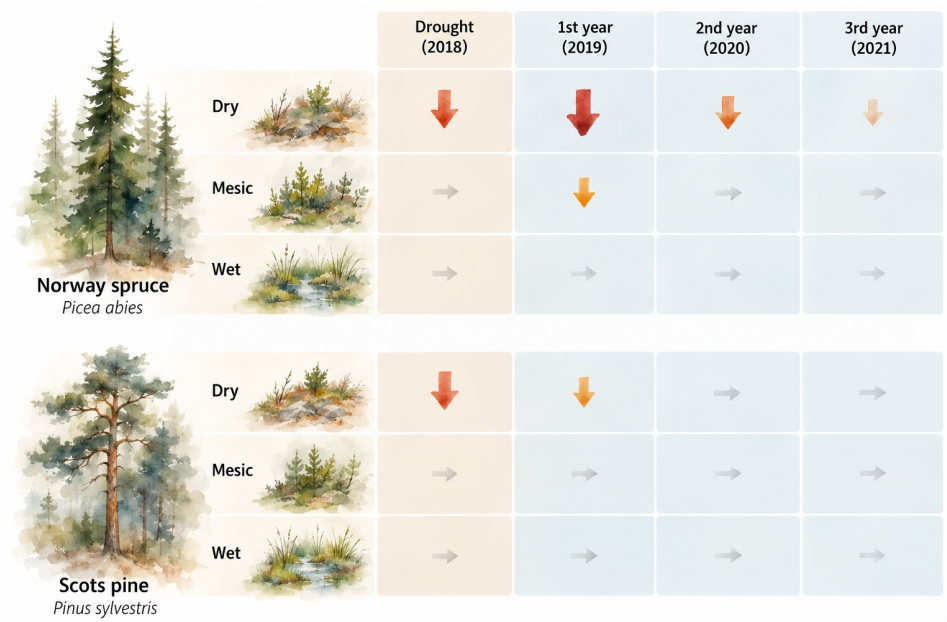


Figure 10: Graphics showing temporal dynamics in growth response for Norway spruce and Scots pine over the wetness classes. The down-wards arrows denote growth reductions relative to pre-drought growth, sized and coloured by the reduction magnitude. Gray horizontal arrows indicate no growth change compared to pre-drought conditions. These growth dynamics represent the response in the warmer part of our climate gradient. Created with help from ChatGPT (OpenAI, 2026).

reductions in dry plots. In contrast to Norway spruce, the strongest decline for Scots pine occurred during the drought year and persisted only for one year. But also, for Scots pine, the response varied with climate and growth reductions were only seen in the warmest portion of the climate gradient.

3. Climatic controls

In a second step and to understand the detailed drivers of tree growth, we analysed how tree growth responded to temperature (GDD) and drought (SPEI) over all individual years 2012 – 2021. This allowed us to investigate the effect of interactions between drought and temperature.

Overall and as expected, warming increased growth in the colder portion of the climate gradient, while the response at the warmer end was more variable. Our findings gave further support to the vulnerability of southern Norway spruce to warming and drought, while Scots pine appears to benefit from warming at least during wetter years.

From a modelling perspective, our results show that accounting for the temporal autocorrelation alone was insufficient to capture the delayed drought response identified in **part 2**. Without a lagged drought variable, the model even suggested that Norway spruce growth would benefit from the combination of warming and drought, contradicting both previous studies and our own results in **part 2**. Including the previous years' drought conditions allowed the model to capture this response. This illustrates the difficulty in linking growth specifically, and C allocation in general, to dynamic drivers such as climatic conditions. The observed responses may reflect a mixture of current conditions, delays and legacies from previous events (Kannenberg et al., 2020; Anderegg et al., 2015).

Overall, tree growth in old-growth forests appeared relatively stable over the period 2012 – 2021. Even the major 2018-drought caused no overall decline in tree growth. However, throughout the study Norway spruce emerged as particularly vulnerable to warming and drought, although the negative effects were partly buffered by wetter areas in the landscape.

Chapter II: Drivers of belowground C cycling

For this chapter, we left the forests as most of us know them and headed into the world belowground. We explored the pathways for C into soils; litter from trees and understory vegetation, but also growth and senescence of roots, mycorrhizal mycelia, and attempted an estimate of the elusive root exudates. We quantified the amount of C stored belowground, as soil organic matter, in the coarse roots anchoring trees, and in finer roots responsible for nutrient uptake. We measured C leaving the soil surface as respired CO_2, and installed an experimental setup to partition this efflux by its source; decomposition by free-living organisms (heterotrophs), roots, mycorrhizal fungi, and aboveground understory vegetation.

We investigated how efficiently fine roots, mycorrhizal fungi, and understory vegetation produce biomass, i.e., carbon-use-efficiency, CUE. From the inputs and stocks, we estimated how long C of fine roots and soil organic matter stays in the system, i.e., residence time, RT. Finally, we quantified the most important drivers of the fluxes, stocks, CUE, and RT.

Magnitude of fluxes

We found that belowground inputs roughly balanced the respiratory outputs. The main input was aboveground tree litter, although the relative contribution of understory litter inputs dominated in some plots. Our estimated root-associated inputs were relatively low compared to previous studies (e.g., Anderson-Teixeira et al., 2021; Peichl et al., 2022; Martínez-García et al., 2022), and on average representing 24% of the total inputs. However, the low root-associated inputs were balanced by comparatively low total soil respiration. Given its spatial and temporal variability, soil respiration is challenging to capture and model. However, our respiration rates at a common reference temperature were similar

to comparable studies. We instead attribute the relatively low soil respiration to low soil temperatures.

Decomposition by soil heterotrophs accounted for the largest share of soil respiration, contributing almost 50%. We suspect that this proportion could be overestimated due to enhanced decomposition in the experimental setup, but nevertheless, it is within the relatively wide range reported in comparable studies and similar to Högberg et al. (2001) and Mielke et al. (2022). The estimated contribution from roots to soil respiration, on the other hand, appears relatively low (Ryhti et al., 2021; Anderson-Teixeira et al., 2021). Although methodological biases may influence the low fine root growth and respiration, the combination could also indicate relatively low C investments in root growth and metabolism (Högberg et al., 2002). Instead, our results suggest that fine root growth occurs at relatively constant CUE of around 34%, while the CUE of aboveground understory vegetation was substantially larger (64%), and for mycorrhizal fungi only 9%. Further, we show that fine root C can remain in old-growth forests for over 10 years, which is substantially longer than previously estimated (e.g., Solly et al., 2018). Moreover, estimated residence times for soil C in wet areas were in some cases over a century, highlighting the C sequestration potential in these undrained areas.

Drivers of belowground C components

Both total inputs, particularly tree litter, and soil respiration were higher in warmer climates, with a slight indication that inputs increase more than respiration with warming (Figure 11). We also found the highest soil C stocks at the warmest end of our climate gradient. If we allow our climate gradient to be representative of a space-for-time substitution (Pickett, 1989), our results suggest stable belowground C stocks which may even increase in response to future warming.

Soil wetness controlled soil C stocks and soil respiration, although the latter less strongly so, with higher C stocks and lower soil respiration in wet plots. Such a response could be explained by higher water tables restricting oxygen availability, reducing decomposition rates and causing soil C to accumulate. Thus, effects of warming must consider potential alterations in local hydrology which may enhance soil respiration and destabilise the large soil C stocks (Bradshaw and Warkentin, 2015).

We note that components of belowground C cycling varied greatly in their drivers, often interactively so with soil wetness class. As an example, fungal community composition was associated with both soil C balance and total soil

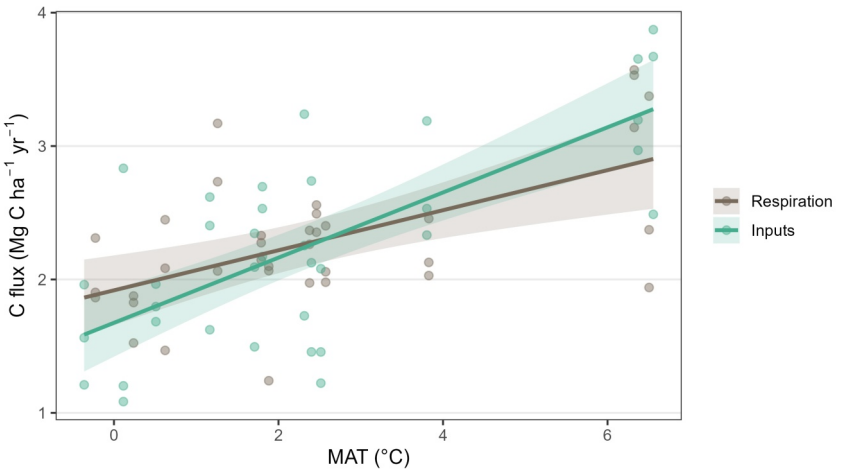


Figure 11: Temperature (MAT) responses of total C inputs and total soil respiration. Points represent plot-level estimates, lines show model predictions, and shaded areas indicate 95% confidence intervals. The slope for C inputs was steeper than that for respiration, although evidence for this difference was weak ($p = 0.08$).

C stocks, but at the same time at least partly confounded by wetness, making it hard to disentangle if the communities drive C sequestration or mainly reflect the hydrological conditions. The combined results highlight the complex interplay among environmental conditions, vegetation and belowground communities in shaping belowground C cycling.

Overall, across these boreal old-growth forests high soil wetness was associated with large belowground C stocks and low soil respiration. In fact, soil respiration rates were in general comparatively low, thereby limiting C losses from the system. We attribute the low soil respiration to low soil temperatures, which may be associated with insulating and water-retaining structures such as dense understory vegetation (Kovács et al., 2017; Porada et al., 2016; Turetsky et al., 2010), high dead wood stocks (Dhar et al., 2022), and thick organic layers (Yi et al., 2009; Keith et al., 2010; Harden et al., 2006). The future stability of the belowground C may be dependent on whether these structures continue to insulate against high temperature, and whether the increasing inputs associated with higher temperatures can be stabilised as soil C or represent a high turnover pool that quickly returns to the atmosphere.

Chapter III: Old-growth forests as C sinks

In the third chapter, we combined the belowground fluxes with the remaining tree net primary production (NPP) components and dead wood heterotrophic respiration, to attain the total NPP and heterotrophic respiration (RH). This enabled us to estimate the C balance from NEP = NPP - RH. Finally, we could assess C allocation patterns from the relative proportions of the NPP components.

C fluxes

All our old-growth forest sites acted as C sinks, sequestering C from the atmosphere. Their C sink strength (NEP) was approximately twice that previously reported from mature boreal forests (Anderson-Teixeira et al., 2021) and older forests (131-211 years) in northern Sweden (Peichl et al., 2022). NPP estimates were broadly consistent with those studies, but our lower RH resulted in the stronger C sink.

Tree foliage and woody NPP were the dominating C inputs and each contributed around 30% of the total NPP. Understory NPP contributed on average 20% of total NPP, although its contribution was as high as 50% in some plots. The proportion of NPP allocated belowground to fine roots and mycorrhizal fungi, was on average 16%, which is substantially lower than comparable boreal estimates (Anderson-Teixeira et al., 2021; Gower et al., 2001). Total RH was dominated by soil RH (73%), although dead wood RH contributed more than some other Fennoscandian estimates (Peichl et al., 2022), probably reflecting the higher dead wood C stocks characteristic for old-growth forests, such as ours.

Drivers

C inputs (NPP) increased more strongly in warmer climate (MAT) than C losses (RH) (Figure 12), reflected in the positive relationship between C sink strength (NEP) and MAT - suggesting higher C sequestration in warmer climate. The

positive temperature response of NPP was particularly strong for stem-growth. Increasing allocation to such long-lived C pools is particularly important for C sequestration (Sierra et al., 2021). We found the opposite climate-pattern for relative production of understory vegetation, which was highest in the coldest climates.

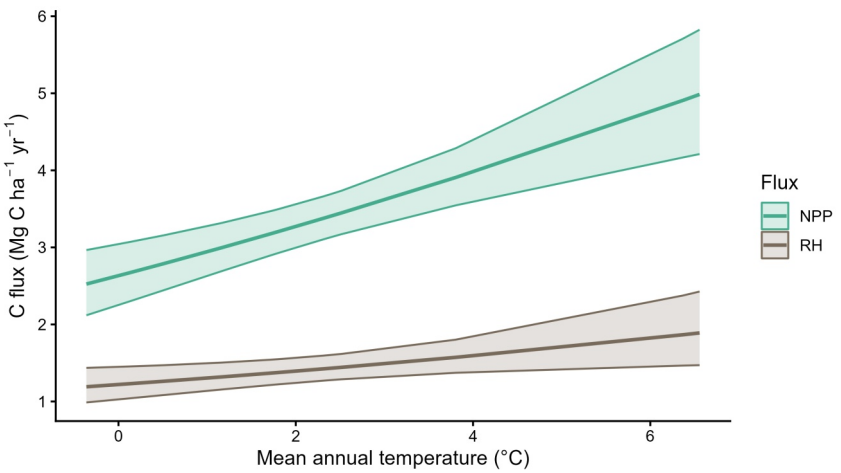


Figure 12: NPP increased more strongly with temperature (MAT) than total RH. Lines show model predictions, and shaded areas indicate 95% confidence intervals.

Contrary to our expectations, soil wetness affected neither NEP, NPP, nor RH. We had expected higher soil wetness to cause a stronger C sink in wet plots. We see two methodological choices that could overestimate RH at wet plots. First, water tables fluctuate and oxygen availability with them, while our soil respiration measurements cover temporally limited periods, and because we were unable to use continuous soil moisture data in our upscaling model, we may not represent these particularly wet periods very well - potentially overestimating soil respiration in wet plots. Second, while dead wood RH may decline under high soil wetness (Bond-Lamberty et al., 2002), we applied the same decay constant across all sites and wetness classes - probably causing our estimates to be overestimated in wet plots and cold climates, at least in relative terms. Nevertheless, these results may also reflect true patterns, if the water tables in our wetter areas were not high enough to substantially reduce decomposition rates. To resolve these uncertainties, we suggest increased frequency of respiration measurement over variable temperature and soil moisture conditions, and for dead wood, direct respiration measurements from dead wood of different decay classes, species, sizes and moisture levels.

Further, we found species compositional effects on some components. Norway spruce-dominated stands were associated with higher stem NPP, lower understory NPP, and weakly so with higher belowground allocation. We had not expected such overarching positive association between Norway spruce and stem NPP, because Scots pine often outperforms in colder and less fertile conditions (Nilsson et al., 2012; Holmström et al., 2018). While both species were present across our climate gradient, it is still possible that Norway spruce dominates in more fertile plots - causing the higher stem NPP. We also found indications of higher relative belowground allocation for Norway spruce-dominated stands. Generally, higher relative belowground allocation can be expected under lower nutrient availability (Litton et al., 2007; Poorter et al., 2012), which may seem contradictory to the higher stem NPP. However, Norway spruce may respond more strongly to nutrient limitation and thereby allocate more resources to roots and mycorrhizal fungi to overcome this limitation (Blaško et al., 2020).

The main finding in this chapter was the consistent C sink across all the old-growth forests studied. The C sink resulted from a combination of high tree NPP, mainly foliage and stem wood, and low soil heterotrophic respiration. The total NPP, particularly stem growth, increased more strongly towards warmer climate than the respiratory losses, suggesting that the C sink could strengthen, at least in moderate warming scenarios.

Discussion

We found substantial C sinks across all studied boreal old-growth forests. This C sink was primarily driven by the combination of high C allocation to tree stem-growth and low soil respiration.

Higher productivity in warmer climates, particularly for tree stem growth (**III**), suggests that warming could strengthen the old-growth C sink. Because stems represent a long-lived C pool, greater allocation may have positive effects on C sequestration (Sierra et al., 2021). However, faster growth may involve allocation trade-offs. As trees allocate more C to stem wood less may be invested in defence compounds (Herms and Mattson, 1992). Further, higher growth rates have been associated with lower wood density (Chave et al., 2009; Pretzsch et al., 2018), reducing the amount of C stored per unit of wood volume and possibly structural stability. Overall, faster tree growth is associated with shorter tree lifespan (Brienen et al., 2020; Begović et al., 2023). These trade-offs may therefore partially offset the increased C sequestration from higher stem growth (Pretzsch et al., 2018).

Future climate change comes not only with warming, but also with increased frequency of extreme events such as droughts (IPCC, 2021). In **Chapter I**, Norway spruce was particularly vulnerable to warming and drought, although wetter conditions buffered drought-related declines. This vulnerability matters because greater stem C allocation was associated with spruce-dominated stands (**III**), making the temperature response more uncertain. Moreover, the positive relationship between temperature and stem growth may partially reflect higher N deposition in southern Sweden (Karlsson et al., 2022). Additional N can relieve nutrient limitation and shift allocation from belowground compartments to tree growth, potentially strengthening NEP (Guo et al., 2026). However, reduced investments in fine roots and mycorrhizal fungi could also limit water uptake (Lehto and Zwiazek, 2011) and increase drought vulnerability. The combination of drought-vulnerability in spruce and potential allocation shift from N deposition, could make an extrapolation of the positive temperature-relationship of stem growth

into a warming scenario misleading. Whether greater stem growth strengthens the future C sink of old-growth forests will depend on how species composition and soil wetness mediate drought impacts, and whether faster growth comes at the expense of tree longevity.

Low soil respiration helped sustain both the old-growth C sink and balanced soil C stocks. We mainly attribute these low respiratory rates to low soil temperatures, possibly maintained by old-growth features such as understory vegetation and dead wood (**II**). However, litter chemistry may also constrain decomposition. Mosses and ericaceous dwarf shrubs contributed substantially to total productivity in colder climates (**III**), and their decomposition-resistant litter may support soil C (DeLuca and Boisvenue, 2012; Hobbie et al., 2000; Nilsson and Wardle, 2005; Turetsky et al., 2010). Ericaceous dwarf shrubs may also contribute indirectly through their ericoid mycorrhizal fungi, who's persistent necromass has been linked to soil C accumulation in late-successional forests (Clemmensen et al., 2015). More generally, root-associated inputs, including fine roots and mycorrhizal mycelia, are more likely to stabilize as soil C compared to aboveground inputs (Jackson et al., 2017; Adamczyk, 2021). Thus, even their relatively low production in our studied forests (**II, III**) may contribute to soil C accumulation (Clemmensen et al., 2013, 2015; Adamczyk et al., 2019).

Across this thesis project, soil wetness emerged as an important influence on forest C cycling: wetter conditions buffered drought-related growth declines (**I**), supported larger belowground C stocks (**II**), and suppressed soil respiration (**II**). These findings reinforce the importance of local hydrology for boreal forest C storage (Larson et al., 2023). The future C balance of boreal old-growth forests will therefore depend not only on warming, but also how it interacts with - and alters - local hydrological conditions.

Future directions

To reduce uncertainties about C allocation trade-offs and variation in C cycling across space and time, collaborative monitoring networks should be expanded. Simultaneous, long-term measurement of multiple C cycling components would help reveal how allocation patterns respond to dynamic environmental drivers. However, as shown in **Chapter I: part 2**, delayed responses and legacy effects can complicate attribution to underlying conditions. Combining monitoring with experimental manipulations, such as drought treatments, would help disentangling such effects. Unmanaged, natural forests provide essential baselines, helping assess the consequences of forest management and the conservation and

restoration efforts that lie ahead of us (Convention on Biological Diversity, 2022). Understanding these natural baselines would help us identify when protecting and restoring forests can sustain C sequestration alongside biodiversity and guide forest management towards both goals.

Part IV

Conclusions

Scientific summary

Old-growth forests can act as C sinks across large climate gradients and varying hydrological conditions. This sink is mainly driven by tree growth and low soil respiration. Our results suggest that the C sink could strengthen with warming, because productivity showed a stronger positive relationship with mean annual temperature than respiratory losses. However, the intricate response of tree growth to warming and drought demonstrates how allocation patterns can be a mix of contemporary effects, delays, and legacies. Further complicating the case, we show the multitude of different environmental, vegetation and microbial community drivers that interactively shape C cycling processes in old-growth forests. To move forward, we call for scientific collaboration and funding enabling monitoring networks of boreal forests over large climate gradients, measuring C cycling processes over longer time periods. By doing so we could establish how old-growth C sink varies spatially and temporally, its potential response to future warming, but also provide a baseline for which forest management options can be assessed.

A new story

This thesis is about the carbon flowing through old-growth forests. Although the drama could be representative for much of the boreal region, the plot has been set in Sweden. A land of forests. And forestry. Beyond the mountainous areas, old-growth forests only exist as islands in a managed landscape.

Those before me have shown how these fragments act as havens for biodiversity, and the many species dependent on forest continuity. Supported by structures that developed over centuries.

Extensive evidence shows how diverse systems can support ecosystem functioning, increase resistance, and resilience to disturbances (Isbell et al., 2026; Loreau and de Mazancourt, 2013; Hautier et al., 2015). Much like human organisations benefit from individuals with different skills, backgrounds, and perspectives, diverse ecosystems with a multitude of species, ages, and environmental conditions may be better adapted to the challenges we face. Possibly allowing for continued C sequestration in old-growth forests under increasing pressure from global changes.

While we need to acknowledge the values of the few remaining natural forests and find socially acceptable and just ways to protect them - we also need another story for the landscape in which they are scattered. To move beyond polarized extremes.

It is about a larger toolbox, and managing forests for multiple goals.

For C sequestration and truly long-lived products. For reindeer husbandry and tourism. For thriving rural communities. For clean water, water retention, and pollination. For the immeasurable values providing us with inspiration, connection, and meaning. While preparing for an uncertain future with increasing temperatures, extreme weather events, and pests.

Sometimes doing less may give more.

Our current situation may be one of these times. Emitting less greenhouse gases,

consuming less resources, and losing fewer natural ecosystems should be our starting point. Embrace that we live with limited resources. Like old-growth forests.

Maybe this also needs a new story of us. Our apparent need for being lead actors and actresses. A story where we recognize the complexity and power of natural ecosystems, take a step back and let them rewild. Allow them to be saved, and be saviours.

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Jag kan ha fel.

Björn Natthiko Lindeblad

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