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Direct and indirect pressures of climate change on nutrient and carbon cycling in northern forest ecosystems

Dynamic modelling for policy support

Lucander, Klas

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PO Box 117
221 00 Lund
+46 46-222 00 00

Direct and indirect pressures of climate change on nutrient and carbon cycling in northern forest ecosystems

Dynamic modelling for policy support

KLAS LUCANDER

CENTRE FOR ENVIRONMENTAL AND CLIMATE SCIENCE (CEC) | LUND UNIVERSITY



Direct and indirect pressures of climate change on nutrient and carbon cycling in northern forest ecosystems

Dynamic modelling for policy support

Klas Lucander



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DOCTORAL DISSERTATION

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Abstract Northern forest ecosystems play an important role in mitigating climate change by sequestering carbon (C), while additionally providing and regulating other ecosystem services. A majority of the Swedish environmental quality objects (EQOs) that guide Swedish environmental policy and management are associated with the forest, and they have proven difficult to achieve. Several of them relate to the biogeochemical cycling of C and nutrients. Climate change increases the direct pressure on the forest ecosystems, and affects the C and nutrient cycling through direct pressures such as increasing temperatures and the risk of droughts, and through indirect pressures caused by an increasing demand of renewable energy from forests. Dynamic forest ecosystem models can be a useable tool for holistically studying, understanding and predicting the effects of increasing pressures, as a basis for policy support. This thesis aimed to compare, quantify and analyze the effects of direct and indirect pressures of climate change on forest soil and vegetation processes, and indicators related to nutrient and C cycling in forests, focusing on three of the EQOs that relate to forests, Natural Acidification Only, Zero Eutrophication and Reduced Climate Impact. The dynamic ecosystem model ForSAFE was applied on sites in different climate regions in Sweden, with different exposure to deposition. First, the effect of historical land use change on nitrogen (N) leaching and the risk of eutrophication was studied. Then, effects of intensified forest management on tree growth and concentrations of base cations (BC) and N in the soil solution were investigated. Finally, ForSAFE was used to study the effect of climate change on weathering of BC, which is an important process for providing vegetation with nutrients and for buffering against acidification. Using a combined approach with empirical data and the ForSAFE model, we could conclude that present environmental conditions alone are not enough to predict the risk of N leaching from two geographically close and comparable forest sites. Information about previous land use and moisture conditions was required to be able to correctly model the current dynamics of the soil organic matter. The effect of N fertilization on tree growth and N leaching was studied at three sites in areas with high, intermediate and low nitrogen deposition. The tree growth was the largest at the low deposition site, whereas the effect on N leaching was more pronounced at the high deposition site. These results support the Swedish Forest Agency's current recommendations for N fertilization, which differ between regions depending on historical and present N deposition. Whole-tree harvesting (WTH), i.e. harvesting of not only stems but also branches and tops at final felling, led to a temporary reduction (20-30 years) of BC concentrations in the soil solution compared to stem only harvesting, in a study on six sites all over Sweden. This could not be explained by higher weathering rates after WTH, which has been suggested in earlier studies. Instead, it could be explained by higher BC leaching and BC uptake in trees during a period after stem only harvesting. Direct effects of climate change led to an increase in weathering rates in all of Sweden, with increased weathering rates year around in southern Sweden but not in winters in Northern Sweden. Future droughts may reduce weathering due to reduced soil moisture, and the risk is the highest in southern Sweden, where low soil moisture during summers already inhibits weathering. The study also highlighted the importance of soil texture and mineralogy for predicting weathering throughout Sweden, moderating the strong effect of temperature on weathering. The results highlighted the potential of using process-based models with high temporal resolution on well-investigated sites, for increasing the process knowledge and providing results useful for policy makers. An important message to policy makers is that site history and soil properties should be taken into account when planning for future forest management recommendations to reach the EQOs.		
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Klas Lucander



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Author contributions

- I KL conceptualised the study with guidance from the other authors. KL together with other authors developed the model version, prepared the model inputs and model parameterizations. KL performed the model simulation and data analysis. KL wrote the paper with contributions from the other authors.
- II KL was involved in the design of the study. KL prepared the model inputs and model parameterizations supported by the other authors. KL performed the model simulation and data analysis. KL wrote the paper with contributions from the other authors.
- III KL was involved in preparing the model inputs for the sites, model parameterizations and validating the results. KL contributed with feedbacks in the reviewing process.
- IV KL was involved in preparing the model inputs for the sites, bias correcting the climate data, developing the model and validating the results. KL contributed to writing the paper.

Abstract

Northern forest ecosystems play an important role in mitigating climate change by sequestering carbon (C), while additionally providing and regulating other ecosystem services. A majority of the Swedish environmental quality objects (EQOs) that guide Swedish environmental policy and management are associated with the forest, and they have proven difficult to achieve. Several of them relate to the biogeochemical cycling of C and nutrients. Climate change increases the direct pressure on the forest ecosystems, and affects the C and nutrient cycling through direct pressures such as increasing temperatures and the risk of droughts, and through indirect pressures caused by an increasing demand of renewable energy from forests. Dynamic forest ecosystem models can be a useable tool for holistically studying, understanding and predicting the effects of increasing pressures, as a basis for policy support.

This thesis aimed to compare, quantify and analyze the effects of direct and indirect pressures of climate change on forest soil and vegetation processes, and indicators related to nutrient and C cycling in forests, focusing on three of the EQOs that relate to forests, *Natural Acidification Only*, *Zero Eutrophication* and *Reduced Climate Impact*. The dynamic ecosystem model ForSAFE was applied on sites in different climate regions in Sweden, with different exposure to deposition. First, the effect of historical land use change on nitrogen (N) leaching and the risk of eutrophication was studied. Then, effects of intensified forest management on tree growth and concentrations of base cations (BC) and N in the soil solution were investigated. Finally, ForSAFE was used to study the effect of climate change on weathering of BC, which is an important process for providing vegetation with nutrients and for buffering against acidification.

Using a combined approach with empirical data and the ForSAFE model, we could conclude that present environmental conditions alone are not enough to predict the risk of N leaching from two geographically close and comparable forest sites. Information about previous land use and moisture conditions was required to be able to correctly model the current dynamics of the soil organic matter. The effect of N fertilization on tree growth and N leaching was studied at three sites in areas with high, intermediate and low nitrogen deposition. The tree growth was the largest at the low deposition site, whereas the effect on N leaching was more pronounced at the high deposition site. These results support the Swedish Forest Agency's current recommendations for N fertilization, which differ between regions depending on

historical and present N deposition. Whole-tree harvesting (WTH), i.e. harvesting of not only stems but also branches and tops at final felling, led to a temporary reduction (20-30 years) of BC concentrations in the soil solution compared to stem only harvesting, in a study on six sites all over Sweden. This could not be explained by higher weathering rates after WTH, which has been suggested in earlier studies. Instead, it could be explained by higher BC leaching and BC uptake in trees during a period after stem only harvesting. Direct effects of climate change led to an increase in weathering rates in all of Sweden, with increased weathering rates year around in southern Sweden but not in winters in Northern Sweden. Future droughts may reduce weathering due to reduced soil moisture, and the risk is the highest in southern Sweden, where low soil moisture during summers already inhibits weathering. The study also highlighted the importance of soil texture and mineralogy for predicting weathering throughout Sweden, moderating the strong effect of temperature on weathering.

The results highlighted the potential of using process-based models with high temporal resolution on well-investigated sites, for increasing the process knowledge and providing results useful for policy makers. An important message to policy makers is that site history and soil properties should be taken into account when planning for future forest management recommendations to reach the EQOs.

Sammanfattning

Nordliga skogsekosystem spelar en viktig roll för att mildra klimatförändringarna genom att binda kol, samtidigt som de tillhandahåller och reglerar andra viktiga ekosystemtjänster. En majoritet av de svenska miljö kvalitetsmålen som vägleder svensk miljöpolitik och miljöförvaltning är knutna till skogen men har visat sig svåra att uppnå. Flera av dem relaterar till det biogeokemiska kretsloppet av kol och näringsämnen. Klimatförändringarna ökar det direkta trycket på skogarnas ekosystem, och påverkar kol och näringsämnenas kretslopp direkt genom stigande temperaturer och risk för torka, och genom indirekta tryck orsakade av ökad efterfrågan på förnybar energi från skogen. Dynamiska skogsekosystemmodeller kan vara ett användbart verktyg för att holistiskt studera, förstå och förutsäga effekterna av ökat tryck, som underlag för beslutsfattande. Särskild uppmärksamhet har i denna avhandling givits åt att lyfta fram kunskap och behov hos avnämare som är ansvariga för miljö kvalitetsmålen genom att fokusera de valda studierna på vilken typ av kunskapsluckor de uppfattar och policystöd de behöver.

Denna avhandling syftar till att jämföra, kvantifiera och analysera effekterna av direkta och indirekta tryck från klimatförändringar på skogsmark och växtlighetsprocesser, och indikatorer relaterade till näringsämnes- och kolkretslopp i skogar, med fokus på tre av de miljö kvalitetsmål som relaterar till skogar: *Bara naturlig försurning*, *Ingen övergödning* och *Begränsad klimatpåverkan*. Med den dynamiska ekosystemmodellen ForSAFE modellerades skogsytor i olika klimatregioner i Sverige, med olika exponering för atmosfärisk deposition. I avhandlingens första artikel studerades effekten av historisk markanvändningsförändring på kväveutlakning och risken för övergödning. I den andra och tredje artikeln undersöktes effekter av intensifierat skogsbruk på träd tillväxt, kolinlagring och koncentrationer av baskatjoner och kväve i markvattnet. Slutligen användes ForSAFE för att studera effekten av klimatförändringar på kemisk vittring av baskatjoner, vilket är en viktig process för att förse vegetationen med näringsämnen och för att buffra mot försurning av marken.

Genom att använda ett kombinerat tillvägagångssätt med empirisk data och ForSAFE-modellen kunde vi dra slutsatsen att det inte räcker att bara ha kunskap om klimat och hur mycket kväve som skogen har fått genom kvävedeposition för att förutsäga risken för kväveläckage från två geografiskt nära och jämförbara

skogsytor. Information om tidigare markanvändning och fuktförhållanden krävdes för att korrekt modellera den aktuella dynamiken i markens organiska material.

Effekten av kvävegödsling av skogen på träd tillväxt och kväveläckage studerades genom att simulera skogsgödsling på tre skogsytor i områden med hög, medelhög och låg kvävedeposition i Sverige. Effekten av gödsling på träd tillväxten var störst i den skog som hade utsatts för låg kvävedeposition, medan effekten på kväveläckage var mer uttalad på skogen som utsatts för hög kvävedeposition. Dessa resultat stödjer Skogsstyrelsens nuvarande rekommendationer för kvävegödsling, som skiljer sig mellan regioner beroende på historisk och nuvarande kvävedeposition.

Skörd av inte bara stammar, utan även grenar och toppar vid skogsavverkning, så kallat helträdsuttag, för att använda som biobränsle, ledde till en tillfällig minskning (20-30 år) av baskatjonhalter i markvattnet jämfört med enbart stamskörd, i en studie på sex skogsytor över hela Sverige. Detta kunde inte förklaras av högre vittringshastigheter efter helträdsuttag, vilket har föreslagits i tidigare studier. Istället kan det förklaras av högre baskatjonläckage från marken och högre upptag av baskatjoner av träden under en period efter stamskörd.

Direkta effekter av klimatförändringarna ledde till en ökad vittringshastighet i hela Sverige, med ökad vittringshastighet året runt i södra Sverige men inte under vintrarna i norra Sverige. Framtida torka kan minska vittringen på grund av minskad markfuktighet och risken är högst i södra Sverige där låg markfuktighet under somrarna redan hämmar vittringen. Studien lyfte också fram betydelsen av markens kornstorleksfördelning och vilka mineraler som dominerar i marken, för att förutspå vittring i hela Sverige, då dessa faktorer dominerar över temperaturens inverkan på vittring.

Dessa resultat belyser potentialen i att använda processbaserade modeller med hög tidsupplösning på väl undersökta platser, för att öka processkunskapen och ge användbara resultat för beslutsfattare. Ett viktigt budskap till beslutsfattare är att skogsytans tidigare markanvändning och markegenskaper bör beaktas när man planerar för framtida skogsbruksrekommendationer för att nå miljö kvalitetsmålen.

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List of Abbreviations

ANC	Acid neutralizing capacity
BC	Base cations
C	Carbon
C:N	Carbon to Nitrogen ratio
Ca ²⁺	Calcium ion
Cl ⁻	Chloride ion
CO ₂	Carbon dioxide
DOC	Dissolved organic carbon
EQO	Environmental Quality Objective
K ⁺	Potassium ion
Mg ²⁺	Magnesium ion
N	Nitrogen
Na ⁺	Sodium ion
NH ₄ ⁺	Ammonium
NO ₃ ⁻	Nitrate
SO ₄ ²⁻	Sulphate
SOC	Soil organic carbon
SOM	Soil organic matter
SON	Soil organic nitrogen

Introduction

Forests cover 31 % of the total land surface area or almost four billion ha globally (UNEP, 2020). The total global carbon (C) stock in forests is estimated to 861 \pm 66 gigatonnes (Gt) C, with 42 % of the C found in living biomass, 8 % in dead wood, 5 % in litter and 44 % in soil (to 1 m depth). The boreal forest is the second largest global forest biome (after the tropical forest), covering around 30 % of the global forest area (Brandt *et al.*, 2013), and is estimated to contain approximately 32% of the global forest stocks of C (272 \pm 23 Gt C in live and dead biomass and soils). The third largest forest biome, the temperate forest, covers 16 % of the global forest area and estimated to contain 14 % of the stored C in forests or 119 Gt C (Pan *et al.*, 2011). While tropical and boreal forests store the most C there are large differences in how the C is distributed in the forest; in the tropical forest 56 % of the C is stored in biomass, 12 % in dead wood and litter and 32 % in the soil, while in the boreal forest only 20 % is stored in the biomass, 20 % in dead wood and litter and 60% in the soil. Both the boreal forest and the temperate forest have been estimated to be C sinks, sequestering 0.5 \pm 0.08 Gt C year⁻¹ and 0.72 \pm 0.08 Gt C year⁻¹, respectively, on average during the years 1990-2007. The total global forest C sink is estimated to be 2.4 \pm 0.4 Gt C year⁻¹, or 1.1 \pm 0.8 Gt C year⁻¹ taking into account global C losses from deforestation and land-use, primarily in the tropical regions (Pan *et al.*, 2011). In comparison, according to the latest published assessment of the global carbon budget, total carbon dioxide (CO₂) emissions from fossil fuels and cement production for the last decade available (2010-2019), was 9.6 \pm 0.5 Gt C year⁻¹ (Friedlingstein *et al.*, 2020). Thus, the forest ecosystems play an important role in the global C cycle and mitigating climate change by sequestering atmospheric CO₂, in order to meet the Paris Agreement by limiting global warming to well below 2, preferably 1.5 degrees Celsius, compared to pre-industrial levels (Paris Agreement 2015). However, there is uncertainty about how the interaction between climate change, pressures from human activities and natural ecosystem processes, such as aging of the forest and disturbance, affect the ability of forests to sequester and store C over the long term (Nabuurs *et al.*, 2013; Girardin *et al.*, 2016).

How the forest is to be used (or not used) most efficiently in sequestering C is debated (Bellassen and Luysaert, 2014; Berndes *et al.*, 2018). Bastin *et al.* (2019) emphasized the importance of global afforestation to counter historical deforestation. In managed forests there is a debate about intensifying forest management for increased production of wood and bioenergy (e.g. Canadell and

Raupach (2008), Lundmark *et al.* (2014)) or leaving forest as a carbon sink (e.g. Naudts *et al.* (2016)).

Additionally, the forest ecosystem provides multiple other critical and diverse services and values to human society, i.e. ecosystem services (Hansen and Malmaeus, 2016). The forest is home to most of the global terrestrial biodiversity, supporting its maintenance and conservation. The forest offers a diverse set of habitats for plants, animals and micro-organisms. Forests provides a multitude of benefits for humans serving as a place of aesthetic, recreational, and spiritual value (Thurfjell *et al.*, 2019). Furthermore, the forest provides economic values by providing food, energy, fibre, timber and other forest product (FAO 2010). The forest is of important economic value for countries in the boreal region, such as Canada, Russia, Finland and Sweden and more than 33 % of lumber and 25 % of paper exported comes from the boreal forest (Burton *et al.*, 2010). Healthy forest ecosystems are important for climate regulation, water supply and regulation (FAO, 2021), and act as a buffer for air pollution from ending up in the surface waters, which is especially important as boreal forest contains more surface freshwater than any other land biome (Brandt, 2009). The forest and the water cycle are interlinked as the trees regulate the water quantity in soil through growth and transpiration, and regulate the water quality by effecting the soil water chemistry through different processes e.g. uptake and decomposition of plant litter, just to name a few. The runoff water from forests affects in turn water chemistry in streams, lakes and eventually in the oceans.

Sweden, with a large area in the boreal and hemiboreal zone, is in focus in this thesis. 70 % (28 million ha) of Sweden is covered by forest, and almost 85 % (23,6 million ha) of it is productive forest land, dominated by the coniferous species Norway Spruce and Scots Pine (Skogsdata, 2020). A large part of southern Sweden is in the hemiboreal vegetation zone, with its intermediate position between the proper coniferous forests and the true temperate deciduous forest in the temperate vegetation zone. Parts of Scania and the southwest coast is in the temperate vegetation zone (nemoral) (Ahti *et al.*, 1968). For Sweden as for the whole boreal region, the forest is one of the most important natural resources, where the forest products industry accounted for approximately 2 % of the annual gross domestic product, in year 2014 (Swedish Forest Agency 2014).

The forest in Sweden is connected to a number of environmental quality objectives (EQOs), guiding Swedish environmental policy and management since 1999. Objectives associated with forests are *Natural Acidification Only, Sustainable Forests, Flourishing Lakes and Streams, Zero Eutrophication, A Balanced Marine Environment, Good-Quality Groundwater, Thriving Wetlands, A Magnificent Mountain Landscape, A Rich Diversity of Plant and Animal Life and Reduced climate impact*. Thus, a majority of the objectives are associated with the forest, entailing multiple values. In the latest annual follow-up, none of the objectives were

predicted to be reached and all objectives but *Natural Acidification Only* had a negative or uncertain development (Naturvårdsverket, 2021).

A good forest soil status (e.g. not nitrogen (N) saturated nor acidic) and good-quality runoff water (low on N and not acidic) is important for several of the objectives. The soil status and runoff water quality are affected by atmospheric deposition, climate change and forest management. In the end of the last century, acidic atmospheric N and Sulphur (S) deposition mainly caused by burning of fossil fuels (S) and traffic and agriculture (N) was seen as the greatest threat for northern forest soils and surface water, leading to acidification of soils and waters in the forest ecosystems (Grünewald, 1988) and contributing to eutrophication. S deposition has since then decreased substantially but N deposition is still on a high level (Akselsson *et al.*, 2010), although decreasing (Karlsson *et al.*, 2022). However, it has been shown that the ecosystem response is slower. The recovery from acidification in forest soils, which is required for full recovery of the surface waters, is slow compared to reduction in emissions (Akselsson *et al.*, 2013), leaving the ecosystem still vulnerable for changes hindering the recovery.

Climate change increases the direct pressure on the forest ecosystem and on the already demanding task of reaching the EQOs. Climate change induces temperature increase and more frequent weather extremes (e.g. severe droughts), changed precipitation patterns and water stress (IPCC, 2007), resulting in increased threats for the forests health and productivity (Kellomäki *et al.*, 2008; McDowell *et al.*, 2011; Restaino *et al.*, 2016). Northern forest ecosystems are predicted to be at particular risk due to the especially large temperature increase and changing precipitation patterns in the boreal region (IPCC, 2013), with projected increase in drought occurrence (Kellomäki *et al.*, 2018).

Sweden has adopted a national climate policy framework (proposition 2016/17:146), with the long term climate goal of zero net emissions of greenhouse gases by 2045 and negative emissions after that. In order to reach these goals, the share of renewable energy, including bioenergy from the forests, will have to increase (Börjesson *et al.*, 2017). Furthermore, the framework stipulates that greenhouse gas emissions from activities in Sweden should be at least 85 percent lower than in 1990 while the remaining 15 percent can be reached by supplementary measurements, such as increased C sequestration in forest and land. This means allocating land for planting forest (afforestation), decreasing the amount of forest harvested or increasing tree growth, thus binding more C in forest biomass and soil. Global greenhouse emissions have not started to decline and powerful efforts are needed to reach the goals set by the Paris agreement. The forest becomes increasingly important as a solution to reach the goals, with high expectations on the forest as both a major raw material for the expected increase in biofuel demand and as a sink for sequestering C, which further increases the pressure on the forest ecosystem.

Today climate change and the political mitigation measures, or direct and indirect pressures due to climate change, can be seen as the biggest threat to reaching these objectives. Direct pressures of climate change are e.g. increased temperatures leading to increased rates of processes such as tree growth, mineralization and weathering or droughts, instead leading to potential decreased rates of processes. Indirect effects are the changes in forest management due to a higher demand of biomass and forest fuels.

This thesis aims to compare, quantify and analyze the effects of direct and indirect pressures of climate change on forest soil and vegetation processes and indicators related to nutrient and C cycling in forests, focusing on three of the EQOs objectives that relate to forests, *Natural Acidification Only*, *Zero Eutrophication* and *Reduced Climate Impact*. This will be done by applying the dynamic ecosystem model ForSAFE (Wallman *et al.*, 2005; Belyazid *et al.*, 2006a) in different climate regions in Sweden, and will be used as a basis for management policies.

In the following section, C, N and base cation (BC) cycle in the forest soil, soil water and vegetation are presented, as they are important for understanding the effects of climate change pressures on the EQOs. The emphasis is on the N cycle being so central for reaching the EQOs in focus. Then follows a section on the increasing direct and indirect pressures due to climate change on the nutrient and C cycle in the northern forest ecosystems. In the final part of the introduction, dynamic modelling for policy and decision making support is introduced.

Nutrient and carbon cycle in the forest ecosystem

Nitrogen cycling in the forest

Nitrogen (N) is a key element in forest ecosystems, as it is an essential plant nutrient that often limits tree growth in boreal forests (Tamm, 1991). Therefore, N governs how much C that gets sequestered in biomass and in the soil. Furthermore, N is the main governing factor controlling soil C response to climate change in N-limited ecosystems as boreal forests (Diaz and Grime (Diaz and Grime, 1993; Ineson *et al.*, 1995), 1993; Ineson *et al.*, 1995). The global N cycle (the movement of N between the atmosphere, biosphere and geosphere in different N forms) has been drastically altered by humans, with severe effects on the ecosystems and biodiversity (Galloway James *et al.*, 2008). The accelerated increase of N input to the ecosystems through deposition from pollution and N fertilization has increased the productivity of the ecosystems, but at the same time, excess N has contributed and continue to contribute to loss of biodiversity (Bobbink *et al.*, 2010), and eutrophication in aquatic ecosystems (Cowling *et al.*, 2001). At the end of the last century, atmospheric N and S deposition were seen as the greatest threats for northern forest

ecosystems, leading to acidification and contributing to eutrophication. Today, when S deposition levels have decreased to low levels, whereas N deposition remains at relatively high levels, the N cycling is of key importance for the future of the forest ecosystem, by affecting tree growth, C sequestration, biodiversity and water quality. It is thus important to be able to predict how the N cycling will develop in a future climate.

N is the most abundant element in the earth's atmosphere, where it exists mainly in the form of N gas, (N₂) that makes up about 78 % of the earth's atmosphere. N₂ is however inert and not available for plants. For organisms/plants to use N, it has to be in the form of reactive N (N compounds that support, or are products of, cellular metabolism and growth) (Stein and Klotz, 2016), mainly in the forms of ammonium (NH₄⁺) or nitrate (NO₃⁻) (Gundersen *et al.*, 2006). The natural interchange between inert N and reactive N is almost completely controlled by microbial activities.

N inputs to the forest ecosystem

The transformation of inert N to reactive N is naturally governed by two processes - biological N-fixation by certain specialized microorganisms and to a lesser extent by lightning (Gundersen *et al.*, 2006). During the last century, another large input of reactive N is through atmospheric deposition of N from anthropogenic sources (as NO_x, HNO₃, NH₃, NH₄⁺ or NO₃⁻) (Vitousek *et al.*, 1997). Deposition of organic N also occurs (Neff *et al.*, 2002). In boreal forests N fixation is conducted by moss-associated cyanobacteria and contribute with reactive N to the soil N pool (DeLuca *et al.*, 2002). This process is difficult to quantify but have been seen to contribute with up to 7 kg N/ha/year to forest-level N budgets (Lindo *et al.*, 2013). Deposition of N can fall either as wet deposition where N enters the system with precipitation, or as dry deposition, where N particles get caught in the canopy and end up in the soil with throughfall (Howarth and Ramakrishna 2005). Some of the N deposition can also be taken up directly by the canopy of the tree before it reaches the ground (Kreutzer *et al.* 2009; Korhonen *et al.* 2013). The input of inorganic N through deposition to the ecosystem varies throughout Sweden, ranging from 20 kg per hectare and year in the south to less than 2 kg per hectare a year in the north (Karlsson *et al.*, 2019). In production forests reactive N may also be added as fertiliser (NH₄⁺ and NO₃⁻).

Internal N cycling

The annual input of new N through the natural processes to the pools of organic N bound in plants and soils is relatively small compared to the annual N demand of the plants (trees take up 15–50 kg N ha⁻¹ year⁻¹ in a growing boreal production forest (Binkley and Högberg, 1997; Korhonen *et al.*, 2013). The main source of N that meets the demand in the boreal forest ecosystem is instead N released through mineralization of litter and SOM that have accumulated over time. The N soil pool is the largest N pool in the boreal forest ecosystem. 70 – 90 % of added N ends up

bound in the SOM (Kauppi *et al.*, 1995; Tietema, 1998; Nadelhoffer *et al.*, 1999). Boreal soils can store between 1000 and 8000 kg N ha⁻¹ (Hyvönen *et al.*, 2008), compared to 200 – 600 kg N ha⁻¹ in trees (Sponseller *et al.*, 2016). Despite the huge N pool in the forest soil, plant growth in boreal forests is usually N limited (Tamm, 1991). This is because soil N gets bound to complex organic structures that are recalcitrant to decomposition and too large for uptake by plants or microbes (Vitousek *et al.*, 2002). Without input of N through deposition, the N cycle in boreal forest stand would be fairly ‘closed’, characterized by an almost internal cycle between primary producers and the large pool of N in SOM, with relative limited input of inorganic reactive N and small losses of N through leaching or volatilisation, relative to input and internal cycling. The important processes governing this internal N cycle is: litter production (foliage and roots), decomposition, mineralization and nitrification, immobilisation, and plant uptake.

In the internal N cycle, N enters the soil with litter from plants and decaying microbial biomass. The litter, composed of large organic N compounds, then gets decomposed or depolymerized by microorganisms in the soil to low molecular weight dissolved organic N (LDON; e.g., amino acids). This depolymerisation through the action of extracellular enzymes is considered the key rate-limiting process in the forest N cycle (Schimel and Bennett, 2004). LDON can then be immobilised by bacteria and fungi if they are N limited. If not N limited, soil microbes may metabolise (i.e., mineralise) LDON to meet energy demands (consuming C), producing NH₄⁺. N mineralization can be low in boreal forests with rates varying between -5 to 15 kg ha⁻¹ year⁻¹ in the organic rich surface soil layer (Sponseller *et al.*, 2016). N mineralization rates are higher deeper down in the mineral soil layers where microbial N limitation is lower (Wild *et al.*, 2015). pH, moisture, temperature, and in particular soil C and N concentrations and the C:N ratio of the litter material, seems to have the biggest effect on the mineralization rates (Attiwill and Adams, 1993). Furthermore, LDON may be taken up by plants directly. Historically, it has been assumed that N is only available for the plants in the inorganic N forms of NH₄⁺ and NO₃⁻, but more recent studies have pointed out the importance of the direct uptake of LDON by plants, possibly in symbiosis with mycorrhiza (Nasholm *et al.*, 1998; Sponseller *et al.*, 2016). The importance of this pathway is not clear, but it may be most important in nutrient poor forest ecosystems (Jones *et al.*, 2005). In those, it may even be the dominant N source for forest trees (Nasholm *et al.*, 2009).

Once NH₄⁺ is formed, it may be taken up by plants or microbes (immobilised) or be further oxidised to NO₃⁻ through nitrification. It may also be immobilised abiotically by being held on exchange complexes or enter the interlayer portion of clays.

N is absorbed by plants in three distinct forms: NH₄⁺ and NO₃⁻ and amino acids. At which rate the plants take up N depends on both the concentration in the environment and the demand of the plant, the latter being at least partly determined by the growth rate of the plant (Larcher, 2003). Most terrestrial plants absorb N

primarily via their roots from the soil. However, leaves are also capable of N uptake (Sutton *et al.*, 1995).

N outputs

NO₃⁻ is highly mobile in the soil and easily gets taken up by plants, immobilised by soil microbes or lost by leaching from the soil solution. Northern forest ecosystems are generally N limited and capable of retaining N in the soil with low leaching of NO₃⁻ (Tamm, 1991). Usually, dissolved organic N (DON) dominates N leaching from these forest ecosystems (Smolander *et al.*, 2001). However, leaching of NO₃⁻ from these systems might be induced by disturbances such as clear-cutting (Futter *et al.*, 2010) or after decades of elevated N deposition, making the forest N saturated (Akselsson *et al.*, 2010). NO₃⁻ is highly mobile in the soil and is easily leached, therefore the nitrification process is the gateway to major N losses from forest soils (Gundersen *et al.*, 2006).

NO₃⁻ can also be volatilised to the atmosphere by denitrification, a process in which NO₃⁻ is reduced to NO, N₂O, N₂ or NH₃. Denitrification is usually low in most well-drained and aerated forest (<2 kg ha⁻¹ a⁻¹) (Gundersen *et al.*, 2006). However, in anoxic wet forests (with high ground water table) and in riparian zones along rivers, where nitrate and C substrate are available, denitrification can be of importance (Gundersen *et al.*, 2006).

Base cation cycling in the forest

Base cations (BC) are important both for tree nutrition (Ca, Mg, K) and for buffering against acidification (Ca, Mg, K and Na). A key parameter for the soil's resistance to acidification is base saturation, which is the percentage of BC on the cation exchange position on soil particles (CEC). BC are added to the forest ecosystem through atmospheric deposition and weathering of minerals in the soil. Weathering rates are affected by water chemistry, soil moisture, temperature and physical properties of the soil (Sverdrup and Warfvinge, 1995). In the soil, desorption and adsorption of BC between the soil matrix and soil solution happens through ion exchange. Acidification accelerates the desorption process, which leads to decreased base saturation. BC leave the soil through leaching and uptake by trees, but re-enter the soil with litter, becomes part of the soil SOM and decomposes and enters the soil solution again. If biomass is harvested, incorporated BC are lost from the system permanently, as is the case for leached BC.

Carbon cycling in the forest

Forests sequester CO₂ through photosynthesis, and the energy of sunlight is trapped in the C in organic molecules. These are then either used as a source of energy, via respiration, by the plants themselves, with C being returned back to the atmosphere as CO₂. The rest of C is stored temporally as part of the standing vegetation. Some of plant material may be eaten by animals, exposed to fire or harvested and burned, in which case part of the C also is returned to the atmosphere as CO₂. The rest of the C in the plant eventually ends up in the soil as plant litter, root exudates or excrement from grazing animals. In the soil, the litter is metabolized by soil organisms through the process of decomposition, which gradually returns the C to the atmosphere as CO₂ (Weil and Brady, 2017). The rate of this decomposition and the stability of SOM in the soil depends on environmental factors (Strawn *et al.*, 2015), and how SOM in forest soils will react to a changing climate is uncertain, i.e. if climate change will accelerate loss of C from soil to the atmosphere (Bradford *et al.*, 2016). As discussed in the beginning of the thesis, forest ecosystems contain large amounts of C and thus contribute to significant annual C exchanges with the atmosphere (Denman *et al.*, 2007). Furthermore, boreal forest stores a large proportion of the C in the soils as SOC, making them extra important in the forest C cycling.

Eutrophication

The EQO “Zero Eutrophication” states that: “Nutrient levels in soil and water must not be such that they adversely affect human health, the conditions for biological diversity or the possibility of varied use of land and water.”

The increased input of N in areas subjected to high N deposition has led to forest ecosystems shifting from N-limited to N-saturated (Aber *et al.*, 1989; Aber *et al.*, 1998; Aber *et al.*, 2003), and increasing the risk of N leaching from forest soils (Akselsson *et al.*, 2004; Akselsson *et al.*, 2010). Forests risk turning from N limited to limited by other factors such as water or nutrients, such as phosphorus (Aber *et al.*, 1989; Akselsson *et al.*, 2008), limiting the potential increase in tree growth, thus leading to excess N being leached from the forest soil.

Increased input of N to the ecosystems may lead to terrestrial eutrophication that contribute to change of species composition and to loss of biodiversity (Bobbink *et al.*, 2010). Leached N will eventually end up in the coastal system, causing eutrophication in marine aquatic ecosystems, that are often N limited (Driscoll *et al.*, 2003).

As mentioned earlier, forests in Sweden are generally N limited and capable of retaining N in the soil (Tamm, 1991), and consequently leaching of N is generally low from undisturbed growing forests in Sweden. There is, however, a strong N deposition gradient across Sweden, ranging from 20 kg per hectare a year in the

South to less than 2 kg per hectare a year in the north. In southwesternmost Sweden, elevated N concentrations in forest soil water has been detected from undisturbed forests. However, how the forest reacts to N deposition can not only be predicted on the basis of historic N deposition, and previous land use has been shown to have a major impact on how the forest responds to N deposition (Aber *et al.*, 1998).

Acidification

The EQO “Natural Acidification Only” states that: “*The acidifying effects of deposition and land use must not exceed the limits that can be tolerated by soil and water. In addition, deposition of acidifying substances must not increase the rate of corrosion of technical materials located in the ground, water main systems, archaeological objects and rock carvings.*”

At the end of the 1960s, attention was drawn to acidification as a serious environmental threat in Scandinavia (Odén, 1968). Deposition of sulfate (SO_4^{2-}) and nitrate (NO_3^-) was understood to be the main drivers of acidification, as it forms acid rain containing sulphuric acid (H_2SO_4) and nitric acid (HNO_3). However, nitrate is only directly acidifying the soil if it is not taken up by the plant, as uptake leads to release of a negatively charged ion (OH^- or HCO_3^-). If nitrate is not taken up but leaches out of the soil, acidification is increased since nitrate leaches out together with a cation, usually base cations, which are important for buffering short-term changes in soil acidity. Deposition of ammonium (NH_4^+), originating mainly from agriculture, does not have a direct acidifying effect in the soil unless it is taken up by the tree, releasing a positively charged ion (H^+) is released. If ammonium undergoes nitrification, producing nitrate and releasing two H^+ , it risks a bigger contribution to acidification, if not nitrate is taken up by the plant, which could happen if N saturated forests where available N exceeds the plant’s need (Galloway, 1995). Uptake of base cations leads to the same acidifying effects as uptake of ammonium.

Soils have a significant buffering capacity to acidification (i.e. the soil base saturation) as H^+ ions are exchanged with BC (Ca^{2+} , K^+ , Mg^{2+} , Na) on soil particles, leading to loss of BC from the soil by leaching. This leads to lower base saturation and decreased resistance to further acidification.

Forest growth is naturally a soil acidifying process since trees take up more positive than negative ions, releasing H^+ ions in exchange. If biomass is harvested, BC are not recycled back to the soil through litter and mineralization of the litter, acidification persists. Harvesting and removal of branches and tops (with a high concentrations of BC) increases the acidification effect of forestry (Nilsson *et al.*, 1982). The acidifying effect of whole-tree harvesting of spruce (removal of branches, tops and stumps) has been estimated to be 114-263% of that of acid deposition (Iwald *et al.*, 2013).

Mitigate climate change

The EQO “Reduce Climate Impact” states that: *“In accordance with the UN Framework Convention on Climate Change, concentrations of greenhouse gases in the atmosphere must be stabilised at a level that will prevent dangerous anthropogenic interference with the climate system. This goal must be achieved in such a way and at such a pace that biological diversity is preserved, food production is assured and other goals of sustainable development are not jeopardised. Sweden, together with other countries, must assume responsibility for achieving this global objective.”*

This EQO directly relates to the C cycle. The impact forests have on C cycle is described in previous section Carbon cycling in the forest.

Increasing climate pressures on the nutrient and carbon cycle in the northern forest ecosystems

Climate change affects forest ecosystems, both directly, through increasing CO₂ concentrations, increasing temperatures and changed precipitation patterns, and indirectly, through changed management to sequester more carbon and/or to produce renewable energy. Both direct and indirect pressures have the potential to affect the forest ecosystem substantially, and the combined effects may be difficult to predict.

Direct pressures

Over the past decades, the climate change induced temperature increase has been faster in the boreal forest than in other forest regions globally, and the trend is predicted to continue (Gauthier *et al.*, 2015). Together with changed precipitation patterns and more frequently occurring extreme heat episodes, the risk of drought increases as well (Kellomäki *et al.*, 2008; Ruosteenoja *et al.*, 2018). In Scandinavia, the extreme summer of 2018 is an example of such an event (Toreti *et al.*, 2019). Drought, here meaning moisture limitation due to below average precipitation and/or high temperature, with periods of low moisture content in forest soils, might affect multiple processes such as tree growth, tree mortality and weathering (Hartmann *et al.*, 2018).

Next, the environmental factors with the largest influence on weathering are summarised, as they are relevant for the studies on direct pressures of climate change in this thesis. In ForSAFE the effects on more processes are taken into account (see Methods), and can provide a help in predicting the combined effect of pressures on multiple processes.

Weathering rates increase with temperature, and also with soil moisture (Weil and Brady, 2017). Increasing temperature due to climate change affects the weathering rates directly by increasing it, due to the temperature dependence of the weathering but also indirectly as temperature increase the evapotranspiration, which may lead to drying of the soils, decreasing the weathering rates. Additionally, changed precipitation patterns may affect soil moisture, and thus also weathering rates. In sites with soils with coarser texture this effect becomes more dominant as the soils dries up faster, or in sites with already dry summers. A relationship between total exposed surface and texture has been shown (White and Brantley, 1995). It looks different for different soils and mineralogies, but generally, the finer the soil texture the larger the total exposed area of the mineral grains (mineral surface area) in the soil. As the weathering of minerals takes place on the surface of the mineral grain, the larger the exposed area of the mineral the larger the weathering rates. Soil moisture in coarse texture soils is more sensitive to an increase in temperature or drought as these soils dry up faster. As weathering happens on the water film on the mineral grain, weathering rates increase with increases in soil moisture. Soil moisture can thus limit the effect of climate change on increasing weathering rates.

Indirect pressures

To meet the demand of renewable energy and biomass production, changes in managements have been suggested, such as expanding the area of managed lands, the use of different or genetically improved tree species, and/or more intense forest management. Whole tree harvesting and fertilization have been put forward as options that can potentially increase biomass production (Sponseller *et al.*, 2016) and the focus in this thesis is on those management options.

Nitrogen fertilization

N fertilization has been suggested as a forest management option that can potentially increase forest growth and produce more biomass while at the same time sequestering C (Sathre *et al.*, 2010). However, the effect of N fertilization on both biomass growth and C sequestration can be expected to depend on the N status of the ecosystems, i.e. if they are capable of retaining the N or if there is N in excess (Aber *et al.*, 1989). Excess N will risk leading to elevated N leaching. Substantially elevated concentrations of N after fertilization has been detected in soil solution (Högbom *et al.*, 2001; Ring *et al.*, 2006) and in surface water (Binkley *et al.*, 1999) during the first few years after treatment. Fertilization has been proposed to increase N leaching also after final felling (Gundersen *et al.*, 2006), but different responses have been reported from experiments: higher (Ring, 1996), lower (Ring *et al.*, 2003) and unaltered (Hedwall *et al.*, 2013) N concentrations in soil solution in the fertilized sites compared to the control plots.

Whole-tree harvesting

Whole-tree harvesting (WTH) following final felling is increasingly promoted as a method to extract biomass for energy purposes. WTH is usually defined as harvesting of stems, branches and tops. WTH has increased in Sweden over the last decades and was notified on 35-41 % of the notified final fellings during the years 2015-2019 (Akselsson *et al.*, 2021). When WTH is performed in a forest, N and other nutrients contained in the branches and tops are removed from the system, with the result that they are permanently lost from the ecosystem. Two to three times more N is removed by harvesting slash compared with harvesting stems (Olsson *et al.*, 1996). Because harvest slash can act as a ‘slow release fertilizer,’ the removal of this material during WTH may lead to reduced rates of forest growth during the subsequent rotation period (Egnell and Ulvcróna, 2015). One question is whether the removal of N at harvest will be sustainable over multiple future rotation cycles and if it will need additional N to keep up with increasing demand on forest production. In N saturated forest soils, the increased N removal with WTH might lead to a ‘N relief’ that may be positive from a eutrophication point of view (Akselsson and Westling, 2005), by leading to less N leaching after clear-felling and less N accumulation in the soils (de Jong *et al.*, 2017). Whole-tree harvesting also means loss of base cations (BC), which has an acidifying effect (Nilsson *et al.*, 1982). Taking account of the negative effects of WTH on the forest BC budget, de Jong *et al.* (2017) assessed that biomass extraction of harvest residues could increase 2.5 times and still be sustainable, but only if ash recycling is applied, to compensate for the loss of nutrient losses with the removal of branches and tops from the forest. The study takes into account that ash production is only sufficient to cover 50 % of the clear felled area in Sweden.

Dynamic modelling for policy and decision making support

Increasing pressure on the forest by climate change and intensified management, leads to a risk of far-reaching effects that takes time to observe and possibly takes time to recover from. Therefore, it is important to be able to predict the effects on forest soils and runoff water in the future, so that decision makers can optimize decisions about forest management to reach the EQOs.

There are many different types of environmental models. Some are physical models, like chemical experiments in the lab, some are purely conceptual, based on a simplified representation of processes regulating the system, some are empirical, simulating ecosystem responses based on the analysis of observations, and some are deterministic or process based (Slingerland and Kump, 2011). Dynamic models are the latter type and are based on equations that provide a physical explanation to the

system processes. The simulation of processes is usually process-based, but it can be integrated with conceptual or empirical model components when the principles regulating the process are not fully understood (Zanchi, 2016). When pressures affect different variables at the same time it is important to analyze the system holistically. Dynamic ecosystem models can be important tools for increased understanding of processes and feedback mechanisms, and for predicting combined effects of climate change, past land use and forest management on the forest nutrient cycle.

Dynamic models are based on the methodology of system analysis, by which complex problems can be approached and studied (Haraldsson and Sverdrup, 2004). It is based on causal relationships between the variables creating a system. The causal chains can form closed loops, or feedbacks, meaning that the effect of one variable on another may affect the original variable as well. This concept of feedback is central to system thinking, and by combining the causal relationships and the feedbacks between the various variables in the system, it is possible to reconstruct the structure of an entire system. With this constructed system, the mechanisms that drive or limit the system can be identified, and if the system is reconstructed successfully, you can use it to predict the future behaviour of the system (Belyazid, 2006).

Dynamic modelling is an important complement to experiments and environmental monitoring, as experiments are often limited to a specific location (e.g. climate, N status), or to a few selected variables and they are often not carried out over a sufficient period of time. With dynamic models, you have the potential to simulate effects in the future and to scale up to the regional or national level. Together with experiments, it is possible to evaluate opportunities and risks with different pressures on the forest in areas with different conditions, as a basis for management recommendations.

Dynamic global vegetation models (DGVMs), design for regional or global studies, have dynamic response to future changes and integrated processes, taking into account feedback mechanism. Furthermore, they can be individual based model (e.g. LPJ-GUESS (Smith *et al.*, 2001)), providing a higher resolution of ecological processes such as succession and competition for light and water between plants. These models are important in predicting climate feedbacks on future vegetation change and the global C cycle and further the feedbacks of vegetation change on climate. But what they gain in spatial expansion they lose in local variability and process description detail.

Site-level dynamic models such as ForSAFE can be used to test and increase our process understanding and gives the opportunity to scale up in space and time in a way that is often difficult to do with experiments. ForSAFE includes biological, biochemical and hydrological processes simultaneously simulating the biogeochemical cycles of several elements and their interdependencies, instead of

focusing on a specific ecosystem component. ForSAFE offers high resolution in process descriptions, which allows the model to deal with feedback mechanisms and non-linear responses, which we need when we understand the effects of indirect and direct pressures of climate change on the complex biogeochemical cycles in the forest ecosystem. On the other hand, the model demands a fair amount of input data.

Given that there are multiple EQOs to be achieved, the knowledge that dynamic models can provide is important as policy support - it can help understand goal conflicts and how trade-offs between goals can be found.

This thesis focuses on C, N and BC cycles that are linked to EQOs *Natural Acidification Only*, *Zero Eutrophication* and *Reduced Climate Impact*. These EQOs are important for national agencies working with the Swedish forests, see further the Materials and methods section.

Aims and objectives

The overarching aim of my thesis was to compare, quantify and analyze effects of direct and indirect pressures of climate change on forest soil and vegetation processes and indicators related to nutrient and carbon cycling in soils and focusing on the environmental objectives *Natural Acidification Only*, *Zero Eutrophication* and *Reduced Climate Impact*, for different climate regions in Sweden, as a basis for management policies.

To achieve this a combined empirical and modelling approach was used, where the dynamic ecosystem model ForSAFE was applied on well-investigated forest sites within the Swedish Throughfall Monitoring Network (SWETHRO).

The specific objectives were:

- To find a potential explanation for the different ecosystem responses for N and DOC leaching to almost identical atmospheric N deposition and climate, and to increase the understanding about key factors controlling N retention in forests with intermediate N deposition (Paper I).
- To test if the ForSAFE model is able to correctly simulate the effects of N fertilization on biomass, N leaching and SOC when considering different levels of N availability in the forest, and if so to describe the process interactions behind ecosystem responses to N fertilization (Paper II).
- To investigate the effects of forest residue extraction on tree growth and base cation (Ca, Mg, K) concentrations in soil water in different climatic regions in Sweden (Paper III).
- To describe how weathering of base cations (Ca, Mg, K and Na) would develop in a future climate (the A1B scenario), investigate how it would further be affected by five consecutive years of warm summer drought, and discuss the implications on base cation cycling (Paper IV).

Materials and Methods

To meet the objectives of the thesis, a combination of dynamic modelling and empirical site-specific observations was used (Paper I-IV). The process-based model ForSAFE (Wallman *et al.*, 2005; Belyazid *et al.*, 2006a) was applied at forest site level on long-term monitored managed spruce sites throughout Sweden within the Swedish Throughfall Monitoring Network (SWETHRO) (Pihl Karlsson *et al.*, 2011). The modelled sites represent different conditions and behaviours (such as different growth rates, retention or leaching of N and different acidification status). The sites are located in different climate regions (Figure 4) and in areas with different historical, present and future atmospheric depositions, and are expected to be exposed to future pressures to varying degrees. Furthermore, as the sites are managed forests, ecosystem responses of forest management are also observed.

As part of this PhD project, interviews and workshops with representatives from the different agencies in charge of following up the EQOs concerning the Swedish forest were conducted at an early stage. The aim was to increase the prerequisites for using the full potential of dynamic models in research and decision making. The meetings ended up in participants highlighting a number of indicators and scenarios that they saw as important and prioritized from their respectable point of views and that could be possible to model in ForSAFE. The outcomes from the stakeholder interactions were taken into account in the design of the studies, e.g. through the choice of scenarios and indicators.

In paper I, two adjacent managed spruce sites in the southernmost part of Sweden, Hissmossa (HM) and Västra Torup (VT), were studied (Figure 1). The sites show very different responses to the high historical N deposition in the area. Elevated concentrations of inorganic N are measured in HM, seemingly without disturbance, while in VT, elevated N concentrations were not detected until after the forest was cut down (Figure 1). Concentrations of dissolved organic carbon (DOC) below the rooting zone are also almost twice as high in HM compared to VT. Furthermore, measured C and N concentrations from the soil samples collected at the two sites showed a lower C:N-ratio in all soil layers in HM compared to VT. The C:N-ratio in the organic layer was 24% lower in HM compared to VT. Total SOC in the soil profile was 45 % higher in HM compared to VT while soil organic nitrogen (SON) pool was twice as large, according to measurements.

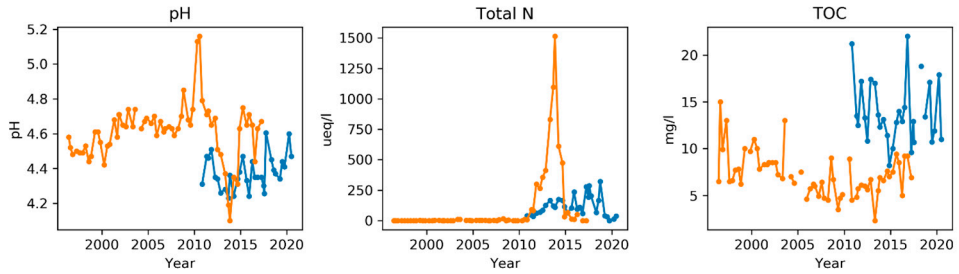


Figure 1. Properties of the soil solution at 50 cm depth in Hissmossa (blue line) and Västra Torup site (orange line).

With the help of available historical maps from the beginning of the 19th century, aerial photographs and personal communication with land owners, we could determine that both sites had been forested pastures before spruce was planted, but the conversion was more recent in HM. Other dissimilarities are that the HM site is surrounded by wet parts that has historically been described as marsh peat and today there is least one ditch running along one side of the plot. VT is located on a drier site and has previously been a heath with birch trees. From this we conclude that the soil in HM probably has been wetter than in VT.

The two sites were simulated with the ForSAFE model to further investigate the key factors determining different N concentrations in the soil solutions at the sites. As the sites are located so close to each other, climate and atmospheric deposition input data are similar, but with differences in soil texture, soil mineralogy and forest management practices.

In paper II, ForSAFE was used to study the effects of N fertilization on tree biomass, N leaching and soil organic carbon (SOC) in the organic layer, from the time of first fertilizer event to 20 years after the final felling. The simulations were performed on three managed SWETHRO forests sites, each located in one of the three zones with different recommendations for N fertilization according to the recommendation by the Swedish Forest agency (Agency, 2007, 2014): a site in Northern Sweden with an N deposition close to background levels, a site in Central Sweden with intermediate N deposition and a site in Southern Sweden, with the highest historical and present N deposition of the sites (Figure 2). An N fertilization scenario was applied to each site ($3 \cdot 150$ kg/ha in the future forest rotation), and compared to an identical scenario but without N fertilization.

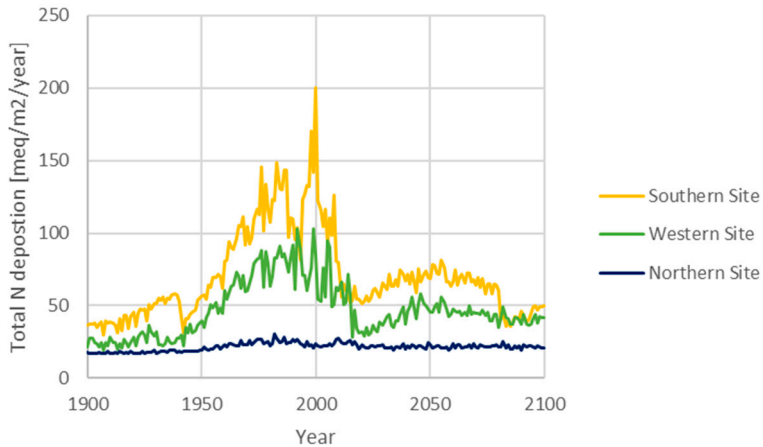


Figure 2. Total nitrogen (N) deposition input to the model for the three sites in paper II.

In paper III, ForSAFE was applied on six SWETHRO forest sites, to study the effects after whole-tree harvesting (WTH) on temporal development of tree biomass and BC and N concentrations in soil solution, under different climatic conditions in Sweden. Three SWETHRO sites were added to the three used in paper II, to represent more climate regions (Figure 3). The climate regions have their basis in SMHI's 19 forecast regions, which have been merged in a way that is intended to integrate information on climate change, change in deposition, forest properties and forestry, as well as effects on EQOs (Akselsson *et al.*, 2021). The climate region in the northwest was excluded, since WTH is not a realistic option there.

In paper IV, the fate of future BC input through weathering under climate change and extreme droughts, and its implications on BC availability and acidification, was studied. The climate change scenario A1B and a scenario with five consecutive years of extreme summer drought were simulated with ForSAFE on seven SWETHRO sites, one in each climate region, to analyze the different response throughout Sweden.

The ForSAFE model, the studied sites used for simulation and the data required for running and validating the model used in each paper are presented below.

The dynamic ecosystem model ForSAFE

ForSAFE is a dynamic, process-based biogeochemical model developed to simulate the dynamic responses of environmental change on tree growth, C and nutrient cycling and soil and soil water chemistry in the forest ecosystems (Wallman *et al.*, 2005; Belyazid *et al.*, 2006b). The model includes C, N and BC (calcium, magnesium and potassium) that are essential for growth, and sodium, chlorine, sulphur, dissolved organic carbon (DOC) and aluminium that are related to the acidity of the soil and soil water (together with N and BC). ForSAFE comprises four established models: the tree growth model PnET (Aber and Federer, 1992), the soil chemistry model SAFE (Alveteg *et al.*, 1995), the decomposition model Decom (Walse *et al.*, 1998; Wallman *et al.*, 2006), and the hydrology model PULSE (Lindström and Gardelin, 1992). Next follows a short, simplified description of what drives growth and cycling of elements in the forest ecosystem as presented in the ForSAFE model.

Biomass growth is driven by available light through photosynthesis and limited by available water and nutrients. In the model, potential photosynthesis is first simulated based on leaf area index (the size of the trees canopy), the N content in foliage, solar radiation exposing the leaves and air temperature. Actual photosynthesis is then calculated based on the actual availability of water. C captured through photosynthesis is stored in a C pool in the tree. C is then allocated to different parts of the tree where needed, followed by allocation of nutrients. The allocated C is then used in the model for respiration or growth. Based on the C pool the need for nutrients is calculated and allocated from the trees nutrient pool. As a consequence, the trees nutrient pool gets depleted which leads to a nutrient deficiency which drives the uptake of nutrients from the soil. The uptake of nutrients is restricted by nutrient availability in the soil, which is given by the nutrient availability in the soil solution.

Nutrient content in the soil solution is determined and affected by several processes. Atmospheric deposition, fertilization and increased mineralization together with weathering (only for BC) and desorption (only for BC) increases the nutrient amount in the soil solution. In contrast, uptake of nutrients by the tree and adsorption of BC to the soil matrix decreases the nutrient content. Furthermore, nutrient content is affected by water and nutrients flowing in from the soil layers above and by leaching to the layers below.

In the model, the three BC calcium, magnesium and potassium are lumped together in the adsorption process and in the soil solution, but deposition and weathering are modelled for all base cations separately.

In the decomposition sub-model, SOM accumulation and decomposition is driven by tree growth and a reinforcing loop is formed: more tree growth gives more litter, more litter gives more SOM and more SOM increases the decomposition, which in

turn increases the amount of available nutrients in the soil solution, enabling more nutrient uptake by the tree. This reinforcing loop is regulated mainly by balancing loops e.g.: (1) the more SOM the more decomposition, the more decomposition the less SOM and (2) the more decomposition, the higher DOC, the higher DOC the lower pH. The lower pH the lower decomposition. Furthermore, decomposition rates are affected by temperature, soil moisture content and aluminium concentration in the soil solution.

Litter from the tree is decomposed in the decomposition module (Wallman *et al.*, 2006). The model classifies the litter into four different substrate quality classes with different decomposition rates. As the litter is decomposed, part of the C is respired, part produces DOC and part is redirected into less decomposable SOM and ultimately recalcitrant C in the SOM. The mineralization of nutrients in the litter follows a simpler path as C, with parts ending up in the soil solution through mineralization and parts of the mineralised nutrients are immobilised into a less decomposable SOM compartment. The product of net nutrient mineralization ends up in the soil solution making the nutrients available for the tree again.

A fraction of the mineralised N can be re-immobilised into the SOM depending on a function of the C:N ratio of the SOM, with higher N immobilisation when the SOM N to SOM C ratio decreases and lower N immobilisation when SOM N to SOM C increases. This function is based on the degree of N limitation on microbial production, and the effectiveness of microbial demand for N in competition with plants for mineral N (Aber *et al.*, 1997). The function is reparametrized in this thesis, to better simulate the behaviour of microbes in nutrient rich environments, with the basis in updated empirical data.

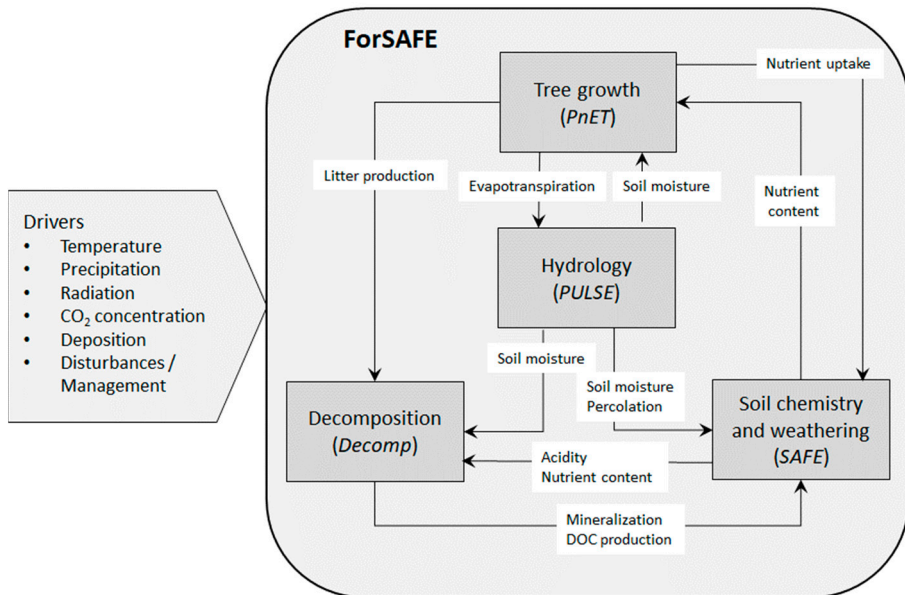


Figure 3. Schematic illustration of the different model components included in the ForSAFE model and their interactions, from Zanchi and Brady (2019). The names of the original models combined in ForSAFE are reported in brackets. The factors driving model processes are listed on the left of the figure.

Choice of indicators and scenarios

ForSAFE can be a useful tool to model scenarios of indirect and direct pressures of climate change and study their effects on indicators related to the EQOs. We further based the choice of focus on what kind of knowledge gaps and policy support forest actors perceive and need. This we found out through interviews and workshops.

During the fall of 2017 and spring of 2018 a set of interviews and workshops were held with three Swedish agency stakeholders, responsible for different EQOs related to the Swedish forest. The participants came from three national agencies, the Environmental Protection Agency, responsible for the EQO *Natural Acidification Only*, the Forest Agency, responsible for the EQO *Sustainable Forests* and for recommendations about forest management methods and the Agency for Marine and Water Management, responsible for the EQOs *Zero Eutrophication*, *Flourishing Lakes and Streams* and *A Balanced Marine Environment*. They all had a scientific background.

First, individual semi-structured interviews were conducted at the stakeholder's work place with the purpose to get a picture of how the stakeholders are looking at, and using, dynamic models in their work, how they look at model based results

compared with other types of results, how they handle uncertainties and what they see for limitations and opportunities with dynamic models.

To the next meeting, in the spring of 2018, all the interviewed stakeholders were invited. The purpose of the workshop was to get input on what indicators and scenarios would be interesting to model in ForSAFE from their perspectives.

Issues discussed during the workshops were e.g. water stress (estimating the risk of water stress and how climate change together with topographic and site specific properties affect the forest water supply), run off water quality, effects on biodiversity, climate adaptation of the forest, ground water - soil water dynamics and issues about how intensified forestry and N fertilization will effect water supply and vice versa.

Prioritized issues and knowledge gaps that came up during the workshops that stakeholders considered most important now, and in the future, and would like to see addressed, were further compiled into scenarios and their effect on indicators of interests to be modelled with the ForSAFE model. Based on this, we chose to proceed with climate change and drought, N fertilization, Intensified forest residue extraction scenarios, as they are important from a scientific point of view and there was a knowledge gap that we saw we could strive to answer, but also important for the stakeholders.

Study sites – SWETHRO sites

To answer the research questions, sites from The Swedish Throughfall Monitoring (SWETHRO) network was chosen for investigation, as they deliver unique long-term observations on well-investigated sites (Pihl Karlsson *et al.*, 2011), offering a range of data, some suitable for model input and other data suitable for validation. The network was established in 1985, with the purpose to study the effects of acid deposition caused by air pollution, on managed forest ecosystems across Sweden. Today there are around 60 active sites in mature, even-aged forest stands with varying length of observations, some over 30 years. Most of the sites are in productive managed forests stands, most stands consisting of coniferous trees, *Picea abies* or *Pinus sylvestris*.

At the SWETHRO sites, atmospheric deposition is measured in the forest stand under the canopy, i.e. throughfall deposition (TF). In the forest stand the soil solution chemistry is also measured. In some of the sites, bulk deposition (BD) is measured at a nearby open area, sometimes together with measurements of air concentrations. For deposition, the standardized repeated measurements are performed every month, and for soil water chemistry three times per year, with lysimeters at a depth of 50 cm, to represent the conditions before, during and after

the vegetation period. Chemical analyzes of the samples are performed at laboratories accredited for chemical analyzes. As the monitoring is meant to take place in managed forests, sites are moved to a nearby forest stand after final felling or large storm damages. Soil water chemistry observations are however sometimes kept at the site, giving important information on ecosystem response after disturbance or final felling.

Four of the forest sites in this thesis are also included in the Level II of ICP forests, which is the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests operating under the UNECE Convention on Long-range Transboundary Air Pollution. These sites provide additional data on tree biomass, soil chemistry and parameters such as defoliation and foliage chemistry.

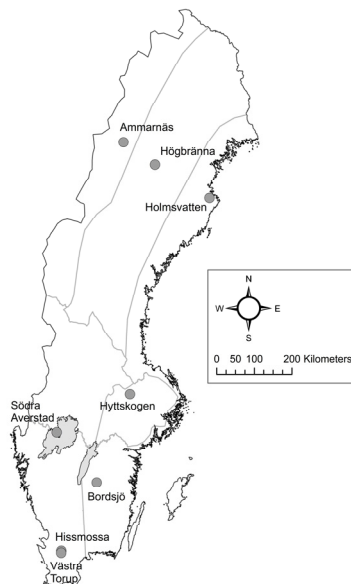


Figure 4. Location of the SWETHRO sites (gray dots) simulated in this study, distributed in 7 different climatic regions in Sweden (grey line).

This thesis is built on studies performed on eight SWETHRO sites covering all climate regions in Sweden (Table 1): Västra Torup, Hissmossa, Bordsjö, Södra Averstad, Hyttskogen, Holmsvatten, Högbränna and Ammarnäs. These sites were also part of a campaign during the years 2010 - 2011, where soil samples were collected to analyze soil texture, bulk density, soil chemistry and total elemental composition for mineralogy estimation for 4-5 layers down to a soil depth of around 50 cm. An ocular assessment of stoniness and soil moisture together with other site observations that might be relevant were documented. Multiple samples of the

organic layer were also collected. Moreover, each tree in the 30 x 30 m plot was marked and measured to measure and follow up tree growth.

Table 1. The SWETRHO sites investigated in this thesis and their properties. Climate: mean annual temperature (Tm) and annual precipitation (P) as yearly averages for the time period 1990–2019 to the left and projected climate for the A1B scenario for the time period 2070–2099 to the right. Management: PL = planting year, CC = last reported clearfelling; Productivity: mean annual increment calculated from tree diameter data converted to stem biomass with equations by Marklund (1988); n.a.: data not available

Site	Climate 1990-2019	Climate 2070-2099	Soil Type	Soil texture	Productivity (m ³ ha ⁻¹ yr ⁻¹)	Forest management
Ammarnäs	Tm: -0.4 °C P: 778 mm	Tm: 3.0 °C P: 916 mm	No developed Podzol	Silt	n.a.	n.a. (PL) n.a. (CC)
Högbränna	Tm: 0.4 °C P: 723 mm	Tm: 5.0 °C P: 871 mm	Podzol soil	Sand	1.3	n.a. (PL) n.a. (CC)
Holmsvatten	Tm: 2.8 °C P: 698 mm	Tm: 7.0 °C P: 851 mm	Podzol soil	Sand	n.a.	n.a. (PL) 2011 (CC)
Hyttskogen	Tm: 5.9 °C P: 650 mm	Tm: 9.7 °C P: 738 mm	Brown earth	Sand	1.6	1957 (PL) n.a. (CC)
Södra Averstad	Tm: 6.8 °C P: 744 mm	Tm: 10.7 °C P: 832 mm	Brown podzolic soil	Loamy sand	n.a.	1931 (PL) 2016 (CC)
Bordsjö	Tm: 6.0 °C P: 722 mm	Tm: 9.6 °C P: 824 mm	Brown earth	Sand	4.2	1952 (PL) n.a. (CC)
Hissmossa	Tm: 7.6 °C P: 871 mm	Tm: 10.5 °C P: 969 mm	Brown podzolic soil	Loamy sand	7.7	1972 (PL) n.a. (CC)
Västra Torup	Tm: 7.6 °C P: 871 mm	Tm: 10.5 °C P: 969 mm	Brown podzolic soil	Sandy loam	6.7	1940 (PL) 2010 (CC)

Input data for ForSAFE

With the ForSAFE model effects of changes in climate, forest management and deposition can be simulated. These changes are given to the model as input data of time series. The first two are obtained from results from external regional climate and deposition models, downscaled based on local observational data. Forest management scenarios are based on information from historical records and communication with land owners. Additionally, ForSAFE requires data on soil mineralogy, soil chemistry and soil texture that are obtained from the measurements at the forest site level, and information on the dominant tree species (Table 2). Data on current base saturation are used for backcasting of historical base saturation. Finally, to evaluate the simulations, simulated forest growth, SOM and soil water chemistry is evaluated against measurements.

The direct and indirect pressures of climate change were studied with the model by running simulation with different input data as time series of climate (Papers I-IV), and management scenarios (Paper II and III) (Table 2).

Table 2. Input data to the ForSAFE model

Input data	Source
Climate	Climate input consists of data series of daily average, minimum and maximum temperature, precipitation and photosynthetically active radiation (PAR) for the years 1900-2100.
Temperature (daily) and precipitation	Temperature and precipitation used in the model runs (Papers I-IV) originates from the regional climate model RCA3 downscaled to Europe (Kjellström <i>et al.</i> , 2005), from the global climate model ECHAM5-r3 (Roeckner <i>et al.</i> , 2006) with emission scenario A1B (Nakicenovic, 2000). Daily average temperature and precipitation, for each site, where obtained from a database on bias corrected data based on distribution-based scaling towards climatic observations from nearby SHMI stations (Johansson, 2000; Yang <i>et al.</i> , 2010). Daily minimum and maximum temperatures were not provided by the database. Instead they were obtained from uncorrected climate data which were bias corrected on observed climate data for the period 1981–2010 that was downloaded from the Swedish Meteorological and Hydrological Institute (SMHI) and interpolated over Sweden. The bias correction was based on an algorithm (Hempel <i>et al.</i> , 2013) that ensures that in the historical period, the mean distance between the maximum/minimum daily temperature value and the daily average temperature is preserved.
Photosynthetic active radiation (PAR), i.e. the portion of the incoming solar radiation that can be used by plants to photosynthesising.	Data for daily PAR was obtained from the ECLAIRE project (Effects of Climate Change 30 on Air Pollution and Response Strategies for European Ecosystems; ECLAIRE 2021).
Atmospheric CO ₂ (daily)	Trends from the A1B scenario modified to daily values based on a schematic inter-annual variation. In A1B, CO ₂ levels in the atmosphere reaches 720 ppm in 2100.
Deposition	Yearly deposition data was given as input to the model and in the model distributed to days with precipitation from the climate input data.
Atmospheric deposition (yearly)	Deposition data of sulphate (SO ₄ ²⁻), nitrate (NO ₃ ⁻) and ammonium (NH ₄ ⁺) were obtained from simulations with the MATCH atmospheric dispersion model. Measurements of precipitation chemistry from the study sites (as they are part of the SWETHRO network) were used to estimate the average deposition of chloride (Cl ⁻) and base cations (Ca ²⁺ , K ⁺ , Mg ²⁺ , Na ⁺) which were assumed constant over the simulation period. Modelled deposition was replaced with deposition data from the study sites, when available.
Soil	Soil samples collected 2010-2011 provided information on soil texture, organic matter content, BC, CEC, bulk density and total elemental contents for 4-5 soil layers, down to about 50 cm soil depth. Soil mineralogy based on the total element contents was estimated with the A2M model (Posch and Kurz, 2007).
Vegetation	A set of vegetation parameters is used to describe the dominant tree type at the modelled site. For Norway spruce that was the dominant tree type at all the sites parameters were obtained from previous studies.
Forest management	Historical forest management at the sites, perpetrated also in the future. Information from historical records and communication with land owners.
Increased pressure scenarios	
Nitrogen fertilization	Developed by the authors based on existing recommendations, see Paper II
WTH	Developed by the authors based on existing practices, see Paper III
Drought	Developed by the authors based on a former drought event, see Paper IV

Results and Discussions

History regulates N and DOC leaching (Paper I)

In Paper I, two monitored managed spruce forest sites, 5 km apart, were compared. They showed very different response to the high historical N deposition in the area. One site (Hissmossa) was leaching N, seemingly without disturbance, while the other site (Västra Torup) was not. Furthermore, measured dissolved organic carbon (DOC) concentrations in soil water in Hissmossa (HM) were twice as high as in Västra Torup (VT). The model could reproduce the different levels of soil water N concentrations at the sites only if the impact from previous land use was taken into account.

In the baseline simulations with a standard model set-up, the model was able to reproduce the tree biomass at both sites, but highlighted some interesting disagreements between model results and observations (simulation A for HM in Figure 5). The model underestimated the soil organic carbon (SOC) and soil organic nitrogen (SON) levels and overestimated the carbon to nitrogen (C:N) ratio levels in both sites, but much more so in HM. Also DOC concentrations were underestimated at both sites, more so in VT. The acid neutralizing capacity (ANC), which is an indicator of the acidity of the soil solution (Strawn *et al.*, 2015), was overestimated at HM, which is consistent with the underestimation of N leaching. At VT however, ANC was well reproduced but for the wrong reason. The overestimation of DOC was balanced out by the underestimation of N leaching and the overestimation of BC concentrations. The overestimation of BC concentrations can be explained by an underestimation of BC uptake due to underestimation of biomass, and uncertainties in initial BC content in SOM. To our surprise, the model did not predict any elevated N concentrations in the soil solution at HM, even after the last thinning event after a storm, as seen in measurements.

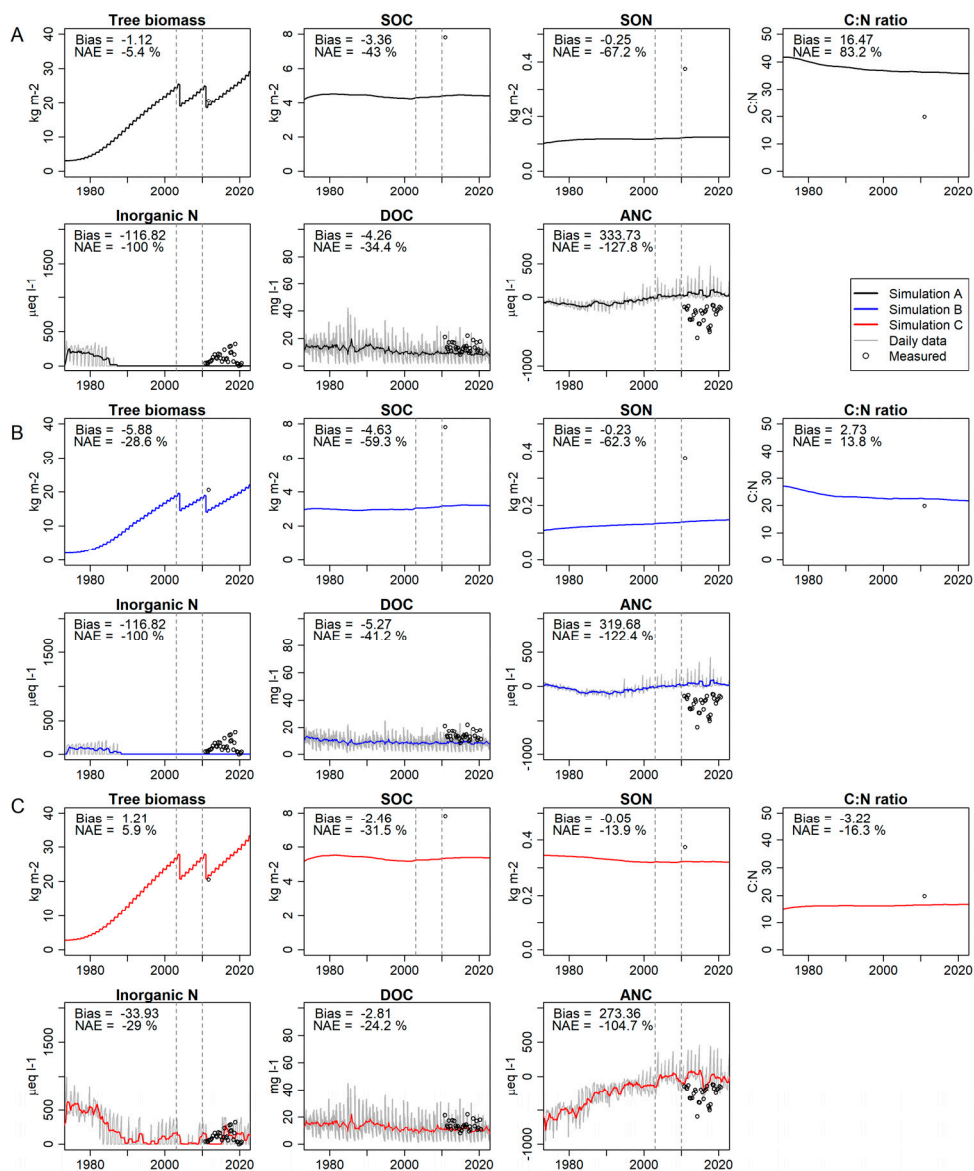


Figure 5. Comparison of modeled data (lines) to measured data (dots) in Hissmosa for tree biomass (above-and belowground), data on soil organic matter in the topsoil (soil organic carbon, SOC, and nitrogen, SON and C:N ratio) and soil water chemistry at 50–cm-depth. The black line represents daily modeled results for tree biomass, SOC and C:N and the moving average on a yearly basis for soil water chemistry (inorganic N, DOC and ANC). Grey vertical lines represent the years when forest management events occurred (final felling by a solid line and thinning by dotted lines). A: Simulation A (BAS scenario); B: Simulation B; C: Simulation C.

A new model run, where more realistic land use histories prior to the forestation were considered, led to noticeably improved model performance compared to measurements (simulation C in Figure 5). In the new model run, the facts that the forest is first generation spruce and that the previous land use was forested pasture were considered in the modelling setup process for the two sites, by assuming higher N content and thereby lower C:N ratio in the soil as compared to forest land (Xu *et al.*, 2013). The revised history, taking into account that at HM land use change had occurred more recently and the wet conditions at the site, created an initial state, at the start of the simulation, that contained significantly more N stored as SON at HM, more than double that at VT, which led to significantly improved agreement between simulated and measured SON and C:N ratio at both sites. Most importantly, a new pattern of N leaching emerged at HM, whereby the simulation predicted consistently reoccurring N leaching events throughout the simulation period, leading to a better agreement between simulation and measurement that was not reached without taking land use history into account. This consideration also affected the ANC at HM, where a clear recovery was simulated. The ANC was, however, still overestimated by the model, partly due to still underestimated N leaching and partly due to a combination of low SO₄ and high modelled BC concentrations.

When comparing the outcome of the new initialization due to the reconstructed histories (simulation C), we see that SOC and SON were significantly higher at HM than VT (Figure 6). Therefore, more N was available at the start of the simulations at HM which in turn is reflected in higher N leaching. In HM, N leaching was higher in simulation C than in simulation A despite the higher N retention, which may seem illogical. But the reason for higher N leaching despite that more N is retained is that there is more SON building up as a consequence of higher N retention together with a more realistic site history, resulting in more N to be mineralized and potentially leached. VT has not had as high historical SON and therefore lower N mineralization leading to less N leaching.

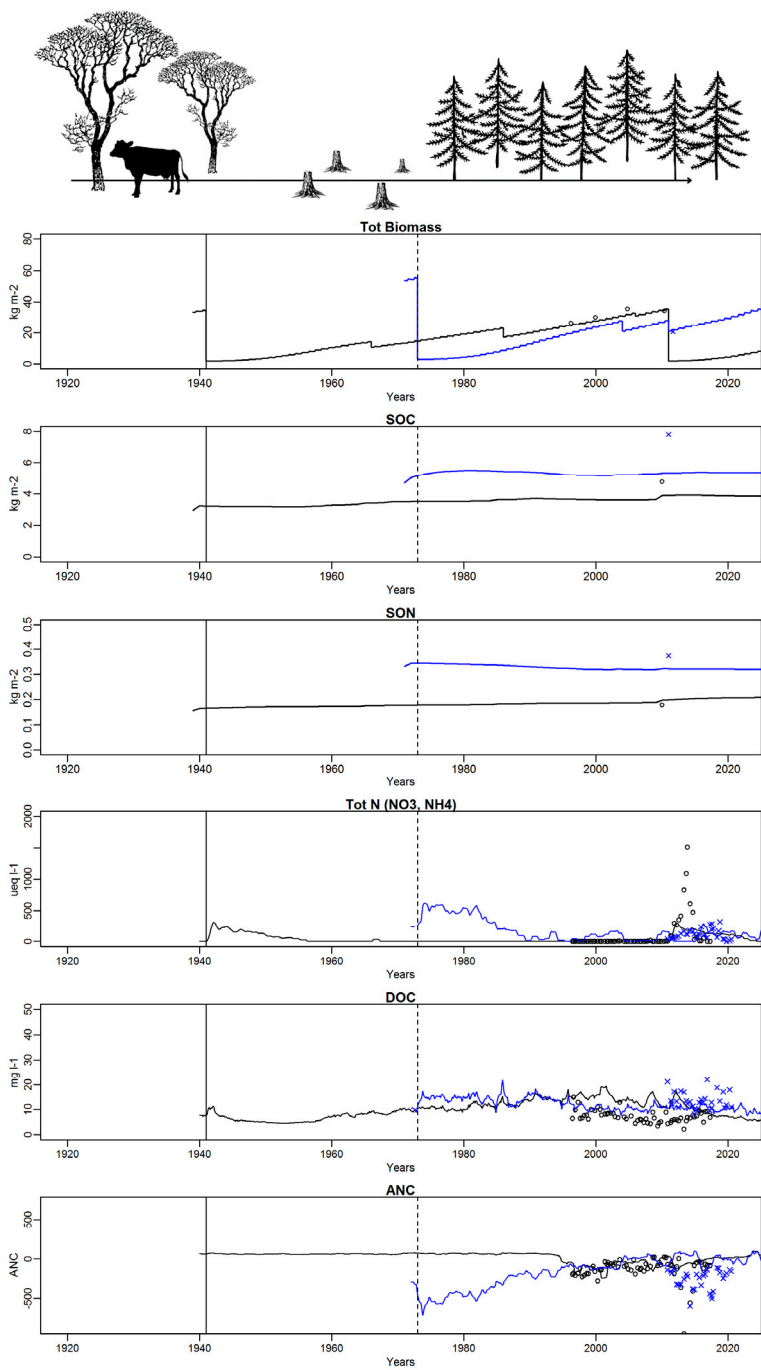


Figure 6. Comparison of model simulations from simulation C and measurements for HM (blue lines and crosses) and VT (black lines and circles). Vertical lines represent time of forest plantation (black solid line for VT and dashed line for HM).

Effects of indirect pressures - intensified forest management (Papers II and III)

In paper II and III we investigated the effects of two types of forest management intensifications on tree growth and nutrient concentrations in the soil solution across Sweden. The studied interventions were N fertilization and whole-tree harvesting (WTH), here defined as removal of not only stems but also branches and tops. N fertilization has the potential to increase productivity of the forest and increase harvest (Mälkönen, 1990; Tamm *et al.*, 1999; Nohrstedt, 2001; Bergh *et al.*, 2014) but it also entails a risk of enhanced N leaching from the forest soil and nutrient depletion (Högbom *et al.*, 2001; Ring *et al.*, 2006). WTH is a management strategy to produce renewable energy from forests for climate mitigation, with potential negative effects in long-term loss of base cations that can lead to soil acidification (Kimmins, 1976; Kreuzweiser *et al.*, 2008; Johnson *et al.*, 2015; Clarke *et al.*, 2021).

Nitrogen Fertilization (Paper II)

In paper II, N fertilization effects on tree biomass, SOC in organic layer and N leaching was simulated with the ForSAFE model on three managed forest sites, representing different deposition and climate conditions in Sweden.

The study showed that the effect of N fertilization on tree growth was largest in the Northern site with historically low N deposition, whereas the effect on sites with medium (Central site) to high deposition (Southern site) was limited (Figure 7). The fertilization effect, i.e. % difference in biomass before the final felling between the base scenario and the N fertilization scenario, was 21% in the Northern site and 6% and 5% for the Central and Southern site, respectively. A fertilization effect of 5-6 %, is here considered insufficient for it to be profitable to fertilise.

These effects are in line with the N saturation theory (Emmett, 2007) stating that in N saturated forests, growth is no longer limited by N and adding N to the system will not increase net primary productivity (NPP). Instead, NPP has shifted to being limited by other nutrients. Growth in N saturated terrestrial ecosystems could then become phosphorus limited instead (Vitousek *et al.*, 2010). Phosphorous (P) limitation was indicated for another SWETRHO forest site in southwestern Sweden, that had been exposed to high N deposition (Yu *et al.*, 2018). In a site in Hubbard Brook Experimental Forest calcium limitation was suggested as an explanation for the observed forest growth decline after large quantities of BC were lost from soils due to inputs from acid deposition and decline in BC deposition (Likens *et al.*, 1996). In the Southern site in Paper II, BC has leached in large amounts due to high sulphur deposition, thus growth could potentially become BC limited if the site would be N fertilised.

The findings are, however, in contrast to views stating that N fertilization can be beneficial to forest growth all over Sweden (Högberg *et al.*, 2014), and to a study showing growth effect both in northern and southern Sweden (Nohrstedt, 2001). In contrast to those results but in line with our present study, a more recent study including 13 fertilization experiments in Norway spruce stands in the southern part of Sweden showed no response in growth to N fertilization (Bergh *et al.* 2014). Our study also showed a residual effect of N fertilization in the following rotation period (up to 20 years after final felling) at the northern site, which is in agreement with a study by From (2015) on a site with similar N deposition.

The effect of N fertilization on simulated SOC in the organic layer in the concurrent forest rotation was small at all sites (1-2 % higher in the fertilization scenario just before final felling), suggesting limited effects of N fertilization on SOC in the short term. There was however a clearer long term effect in the Northern site where the simulations showed a 4 % increase in SOC 20 years after final felling, in the fertilization scenario (Figure 7). The effect in the following forest rotation can be explained by the relatively larger biomass and consequently larger woody litter input after clear felling of an N fertilized stand. Therefore, we simulate a higher increase in SOC after final felling. In the model, growth increase due to N fertilization resulted in a slight increase in woody litter production, but no increase in leaf litter production. SOC increase was therefore highest after clear felling in the northern site, with highest growth increase. After a clear felling, more woody litter, which have slower decomposition rates, is being left on the forest floor. This leads to long term rather than a short term effect on SOC accumulation (Zhang *et al.*, 2019). This effect is also seen in previous studies (Peltoniemi *et al.*, 2004; Fahey *et al.*, 2005), but compared to our study the peaks in SOC increase were shorter, and after the increase the SOC decreased after the residues had decomposed.

The results support the hypothesis that fertilization can lead to an increase in primary production and litter production on nutrient poor sites (Johnson and Curtis, 2001). This means a potential long term positive effect on SOC at such sites. But the uncertainties for SOC are larger than for the biomass and N leaching, and a review and revision of the process descriptions governing the simulated responses to N fertilization on SOC is required to reduce uncertainties.

As seen in paper II, N fertilization leads to increased N leaching risk at all sites, regardless climate or deposition zone, before final felling in the model simulations (Figure 1). The effect was largest in the Southern site where 39 % of applied N leached, compared to the central site where 34 % leached and the northern site were 20 % leached. These results indicate a higher N retention with decreasing N atmospheric deposition from the South to the North of Sweden.

The modelled N concentrations following the fertilization events (data not shown) are in agreement with experimental studies in central Sweden (Binkley *et al.*, 1999; Högbon *et al.*, 2001), showing similar patterns of N concentrations in the soil

solution directly after N fertilization and similar heightened concentrations in the following years. However, none of the sites show any effect of fertilization on N leaching in the 20 first years in the next rotation period, contrary to previous views (Gundersen *et al.*, 2006). In the model simulations the missing fertilization effect on N leaching after final felling can be attributed to the fact that the fertilization had effects mainly on woody biomass, which decomposes slowly and it is less N rich than foliage litter.

We could with the model largely confirm the different effects of N fertilization on tree growth and N leaching in areas with high or low N deposition. Clear and long-term effects on tree growth were seen only in the least N-rich site in the north. Enhanced leaching of N as an effect of N fertilization occurred at all sites, but the largest fraction leached of applied N was at the Southern site (39%). Effects on SOC were more uncertain. A long term positive effect on N-poor sites was indicated, but further research on N fertilization effects on C sequestration in soils is needed. These results show that the model ForSAFE can be a useful tool in assessing effects of N fertilization on tree growth and N leaching.

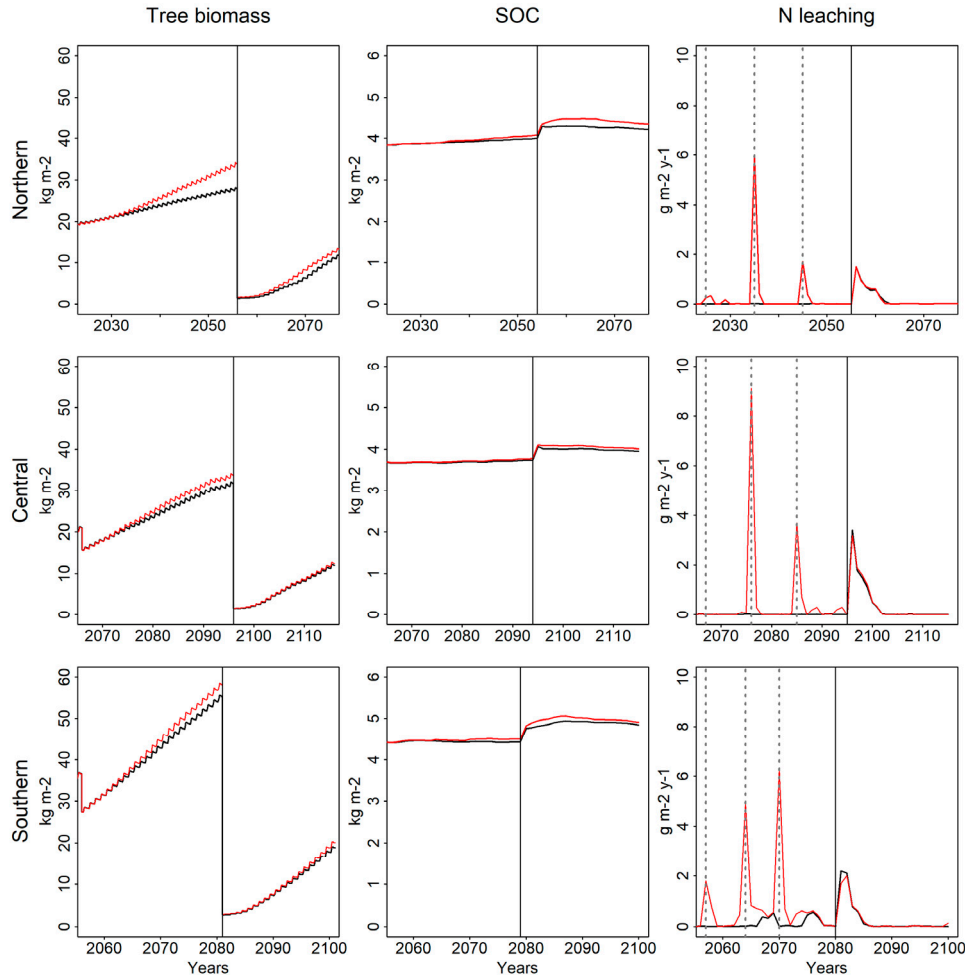


Figure 7. Modelled tree biomass (a), SOC in the organic layer (b) and N leaching (c) according to a fertilization scenario (red line) and a baseline scenario (black line). Vertical lines represent management activities: final felling (black solid line) and N fertilization events before final felling (grey dashed lines).

Whole-Tree Harvesting (Paper III)

In paper III, the future effects of forest management intensification were evaluated by comparing tree biomass and soil water chemistry under two alternative forest management scenarios: A Stem Harvesting scenario (SH) and a Whole-Tree Harvesting scenario (WTH). The study was performed at six sites representing different climate zones, the same three sites as in the previous study and additionally three SWETHRO-sites.

WTH had a negative effect on tree growth on the two most northern sites, Holmsvattnet and Högbränna, where simulated tree biomass was 27% and 16% lower 30 years after clear-felling under WTH. In both of the sites the effect was caused by the low N availability, which explains that there was no growth response at the southern sites with higher N deposition. The effect at the northern sites decreased with time, and after 40 years from final felling the difference was 7% lower in Högbränna and 18% in Holmsvattnet. In the end of the simulation period the difference in biomass was close to zero.

The results suggested that over a rotation period, other limiting factors might level up the earlier difference in tree growth under stem and whole-tree harvesting. On the other hand, there is a concrete risk that prolonged extraction of forest residues will progressively deplete nutrient pools in the forest ecosystems and increase the period of slower tree growth after whole-tree harvesting. As a consequence, the biomass difference could become permanent.

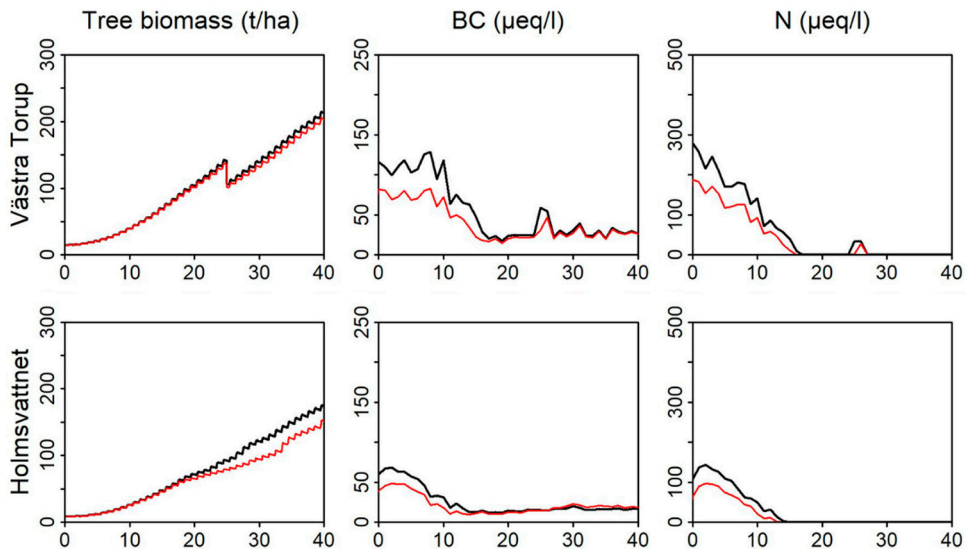


Figure 8. Effects of Whole-Tree Harvesting (red line) and Stem-Only Harvesting (black line) on biomass, base cation concentration in soil water and nitrogen concentration in soil water during the first 40 years following clear-felling. The figure is modified from paper III, with only two sites presented, one site in Southern Sweden and one in Northern Sweden.

Furthermore, the study showed that WTH temporarily reduced the simulated elevated base cation (BC) and N concentration in soil solution after clear-felling, compared to SH, at all the sites. The model results showed an agreement with data from long-term experiment, unlike previous modelling studies that have shown longer negative effects of WTH on the BC pools in the soil and on the acidity of surface waters (e.g. Zetterberg *et al.* (2014)). BC concentrations in soil solution was

lower after WTH than after SH for 20-30 years, with the lowest concentrations for the first 10 years, which is in agreement with experimental data (Zetterberg *et al.*, 2013; Achat *et al.*, 2015; Ring *et al.*, 2017). The negative effect followed a south to north gradient, with the longest lasting effect in southern Sweden, which is in agreement with a study showing more effect of WTH in warmer climate (Clarke *et al.*, 2021). The peak in N concentrations, which naturally occurs after disturbances such as final fellings (Akselsson *et al.*, 2004), was lower after WTH compared to after final felling in the SH scenario. The reason for these differences is the higher simulated BC and N mineralization from the soil organic matter pool under the SH scenario, caused by the decomposition of nutrient rich branches and needles left on the site (Figure 8). After WTH, more BC were removed by harvest and therefore giving rise to lower concentrations of BC. After SH, the higher BC concentration in soil solution lead to higher leaching of BC from the soil with runoff water. This was partially the reason for the diminishing difference in BC concentrations with time. Another reason for the diminishing difference between SH and WTH was the larger tree uptake of BC after SH in northern Sweden, that also removed BC from the soil.

Effects of direct pressures of climate change (Paper IV)

The effects of droughts on BC weathering rates were investigated in Paper IV. Weathering of minerals in the soil is the main input of BC to the forest ecosystem (Brantley *et al.*, 2008), and increases with temperature, but also with soil moisture.

Firstly, the modelling study showed that weathering rates depend strongly on the seasons, with lower and less variable rates during winter and higher and more variable rates during summer, due to higher summer temperatures, and higher variability in summer temperatures and soil moisture. In the south, the variability of weathering rates during the summer was more prominent as it is regulated by both temperature and soil water shortage, while in the north soil moisture is mostly sufficient, and weathering mainly follows the temperature.

Secondly, the study showed that there was a strong geographical variation but no geographical gradient between sites, as the weathering rates depend strongly on soil texture and mineralogy, which show no large-scale geographical gradient in Sweden. These two factors regulate how weathering is affected by simulated climate change induced temperature increase, changed precipitation patterns and drought across Sweden.

Results from the model simulations with the climate change scenario A1B indicated that annual weathering rates will increase in the future, in all the climate regions in Sweden. The modelled increase varies between the sites, from 5 to 17% per degree of yearly average warming. The differences between the sites' response depended

more on the differences in soil mineralogy and texture than on which climate region they belonged to.

The future temperature induced increase of weathering rates will generally be highest during the summer months when the weathering rates are the highest. Furthermore, the study showed that seasonal dynamics of weathering rates were affected differently across sites. In Västra Torup in southern Sweden, the largest relative increase in weathering rates will occur during the spring because of the dry conditions during summer and autumn, restricting weathering. In the north, there will be little increase during the winter months as the temperature will stay below zero, under which conditions no weathering occurs. In the dry and coarse textured site Hyttskogen, weathering during summer will increase by 26 %, because of less dry conditions in the future than today.

The implications of increased weathering rates outside the growing season on nutrient availability for trees may become more significant in the future when the growing season is also expected to lengthen (Jin et al., 2019). Potential negative effects on tree growth during summers, due to more frequently occurring summer droughts, might thus partially be compensated for.

The model simulation with climate scenario A1B did not result in further decreased soil moisture in the southern sites and therefore the model didn't simulate an increase in water limitation on tree growth, i.e. no more water limitation than today. In another simulation with ForSAFE, with a more extreme climate scenario, the forest growth in Southern Sweden was predicted to become water limited due to increased periods of waters stress (Belyazid and Zanchi, 2019).

In a simulation of five consecutive years with drought, weathering rates decreased in all the climates regions, compared to the base scenario A1B. This happened because of drastically decreasing levels of soil moisture during the summer, due to less precipitation and higher temperature compared to the base scenario. The simulated average weathering rates decreased in the drought scenario, despite the fact that the sites in southern Sweden already showed signs of drought to some degree in the scenario without droughts. The decrease was seen in northern Sweden as well, despite the fact that the soils there didn't dry up so much in the drought scenario due to lower evapotranspiration.

The modelling study highlighted the importance of soil texture for the soils' response to precipitation and drought. A finer textured soil dries up slower than a coarser textured soil, leading to a slower decrease in weathering rates. On the other hand, a coarse textured soil rewets faster than a finer textured soil, as a response to rainfall after a drought period, with the weathering rates going back to normal faster.

The extreme drought scenario was based on the drought of 2018, with high temperature and low precipitation in May to July, but normal precipitation prior and after this period, making the soils ability to react and recover important. Therefore,

in this study the soil moisture was back to normal levels at the start of every growing season during the drought event. If a future drought events would imply low precipitation during the whole year, it could have larger negative effects on soil moisture and ground water, leading to larger reductions in weathering rates and a more extensive negative effect on vegetation growth.

The potential of increased weathering rates when the temperatures increase is often discussed in relation to increased biomass mass harvesting, as higher release of base cations could counteract parts of the losses (Akselsson *et al.*, 2016). This study highlights, however, the risk of decreased weathering rates due to drought, which instead would increase the risk of BC depletion from the forest soil and nutrient imbalances in trees. This can in turn decrease their capacity to cope with droughts (Hartmann *et al.*, 2018), and risk reduced growth in the future due to BC limitation.

Opportunities and limitations with dynamic models

Dynamic models can, as shown by the ForSAFE modelling studies in this thesis, provide opportunities beyond empirical material. But there are also limitations and potential risks, and the models need to be continuously developed to be adapted to the emerging knowledge status. In this section I will demonstrate a few examples of the opportunities discovered in this thesis, as well as point towards limitations one needs to be aware of, and finally discuss possible development that could further increase the usage of ForSAFE as a tool for policy making.

Opportunities

One of the main purposes of using ForSAFE is to increase process knowledge. Modelling multiple sites in different regions in Sweden with minimal site specific adjustments of model parameters, gives us the opportunity to see when the process descriptions on which the model is based succeed in describing reality correctly, and when the process descriptions need to be developed. The purpose of using the model is thus not to achieve total agreement between measurements and simulations, but instead to increase the knowledge about the ecosystem processes. In paper I the lack of agreement between modelled and measured soil and soil solution chemistry led to increased understanding of the importance of the effects of different land use histories. We could show that ForSAFE could be used to explain local variability between sites by studying two nearby sites with different N concentrations in the soil solution. This led to the conclusion that the effect of past land use on the soil nutrient conditions regulates the current N leaching at the sites. The difficulties that emerged when we tried to model the two sites opened up for an increased understanding of what factors play a role in whether the forest will leak

N or not, and how the sites can be expected to respond to increased input of N in the future.

Another opportunity is the model's ability to simulate the dynamics at local, small scale systems with detailed soil input data, such as grain size distribution and mineralogy, to capture the dynamics, the processes and their feed-backs. By doing that, we could see effects that cannot be seen with models that are run on a larger scale and thus are more basic in their process descriptions and dynamics. For example, in paper III we were able to explain the effects of whole-tree harvesting at final felling on BC concentrations. According to experiments the effect decreases over time, which has not been captured with models before but could be reproduced and explained by ForSAFE, due to its capacity to dynamically model key processes such as nutrient uptake, weathering and decomposition, and the feedbacks in between.

Thirdly, in this thesis, we have for the first time used the model ForSAFE with daily time step to catch the processes that happen on a high temporal scale on well-documented SWETHRO sites in seven climate regions in Sweden. In paper IV we were able to point out the importance of seasonal variability in weathering rates due to the high temporal resolution. We could see how increased temperature leads to increased weathering to 2100, but also how the increase is distributed differently over the seasons and over Sweden. Furthermore, the model simulations indicated that there will be almost no change in winter weathering in northern Sweden although the temperature change is highest in the winter. This is due to the fact that the winter temperatures in the future continue to be below zero. The study also showed that, although there are differences in effects of climate change on weathering between regions, the differences between sites due to soil properties are dominating. Those results are dependent on a model with high resolution in time and space.

By taking advantage of these opportunities with the model, we have been further able to highlight a few processes and parameters in the model that are important in controlling the carbon and nutrient cycle in the forest ecosystem, but where further development is required to increase the model performance, which will be discussed next.

Limitations and future development

The studies in this thesis pointed out some limitations that need to be handled in order to reduce uncertainties in the simulations of the C and nutrient cycle in the forest ecosystem, and supply more reliable management strategies to policy makers.

Hydrology

In the model validation process in the studies, discrepancy between simulated and measured tree growth and SOM in the organic layer at some of the sites emerged,

that could be attributed to the under- or overestimation of soil moisture at the sites. This led to mismatch between actual and simulated water limitation in the case of Västra Torup and Hyttskogen, and mismatch between modeled and measured SOM sequestration in Södra Averstad.

In Paper II, the capability of the model to correctly estimate biomass accumulation was dependent on the application of different water use efficiency values at different sites. For Västra Torup, this meant the constant for calculating water use efficiency was set 50% higher than the original value, to match the forests ability to more efficiently make use of the available water at the southern site. This highlights the importance of water availability as a regulating factor of forest growth.

In Hyttskogen (Papers III-IV), where the coarse soil texture (sandy soil with a large fraction of gravel and stones), as well as the limited number of valid measurements of soil chemistry due to lack of enough water at many measurement occasions, were indications on dry conditions. This is also reflected in the low observed biomass, which however the model could not fully simulate, probably as it failed to fully capture the extent to which such extreme soil conditions can affect tree growth.

According to simulations at Södra Averstad (Papers II-IV) in central Sweden, the site is experiencing recurring periods of drought. But according to field observations on site, the site is slightly wet. SOM was therefore significantly underestimated in the model compared to the measured value.

Therefore, future research should focus on improving soil water simulations, e.g by further development of parameters and functions regulating water use of trees under water stress, in order to improve simulations of forest ecosystem processes such as tree growth, decomposition and weathering. Soil moisture measurements at the sites would be highly beneficial for model validation. Expanding the SWETHRO measurement scheme with soil moisture measurements could be a well-invested measure to validate the model.

SOM dynamics

While ForSAFE is able to reproduce the buildup / dynamics of SOM in the organic layer obtained from measurements, the simulated SOM in the mineral soil is significantly lower compared to measurements, at all sites. As large part of C and N is stored in the mineral soil in boreal forests (STINSON *et al.*, 2011), total future sequestration of C in forest soils cannot be predicted completely unless the mineral soil C can be modeled correctly. This fact also has consequences when simulating land use change, as the soil might not have been built up in the same way in previous land use, e.g. under crop field or pasture where no distinct organic layer is developed.

To address the limitation in the modelling of mineral soil SOM further, development of vertical transport of SOM is suggested. The role of bioturbation needs to be

further investigated, and processes currently in ForSAFE that contribute to SOM input to different layers need to be further developed e.g. vertical movement of DOC, C allocation to roots in different layers and C exudation from roots.

Furthermore, in ForSAFE, the formation of soil layers is not taken into account, as soil layer thickness is static, which is usually not a problem during our simulation time scales, but can be problematic when reconstructing longer site histories and changes in land use or land cover. Dynamic soil layer thickness should be implemented to allow simulations buildup of organic layers due to afforestation and / or changes of environmental conditions such as rewetting of ditches, forests or mires.

Modelling of BC cycle

Underestimation of BC concentrations in soil water at the northern sites (paper III) indicated some uncertainties in BC cycling in ForSAFE. A potential reason is that the SOM-BC sink has been shown to be of the same size or larger than the exchangeable pool (Erlandsson Lampa *et al.*, 2019), but the uncertainties in the modelling of the organic pool are large. Predicting the size and behaviour of that pool depends on past deposition of BC, uptake of BC, the amount of BC ending up in the litter, BC content in the organic matter, decomposition rates, and BC retention in soil organic matter.

Data requirements

Finally, for process-based models to provide reliable management/policy support, they need to continuously be developed, as the process knowledge increases. This also requires data for validation. Networks like SWETHRO offer this, with well-investigated sites across the country. The thesis highlights the importance of well-investigated sites and long time-series, for development and use of dynamic models, as well as continuous investments in model development. This requires continued resources in the form of staff, scientists and funding.

Implications for policy

In this section I will demonstrate how the model studies carried out in this thesis, that echoed interests and questions raised in the workshops with stakeholders, can contribute to knowledge on topics that are central for several of the environmental goals. If this knowledge can be communicated in a way that it can be usable to stakeholders involved in developing policies, it can contribute to reaching the EQOs. A few topics stood out during the stakeholder workshops.

Hydrology in a changing climate

Hydrology linked to forest management, and the implications and risks of future droughts, was one of the concrete suggestions for areas where the models could contribute with increased knowledge, and be useful as support for stakeholders. Water is central as it is regulating most of the processes related to the EQOs. In paper IV, we modeled the effect of recurring droughts on weathering, and one of the conclusions was that the drought effect was largely controlled by the soil texture, i.e. the grain size distribution of the soil. The soil texture affects soil moisture and regulates how the soil water is affected by precipitation change and drought. This can have implications on how sensitive the forest will be to different management options such as WTH, and if the forest can take advantage of future forest N fertilization or if the growth will be water limited. In paper I, we also point out the importance of considering soil properties and local conditions in addition to regional conditions, in order to be able to calculate the risk of N leaching. The study showed that both site history and local soil moisture conditions were important for the N leaching behaviour. An important message to policy makers is that site history and soil properties should be taken into account when planning for future forest management recommendations to reach the EQOs.

N fertilization

N fertilization of forests was another suggestion for an area where dynamic models could be useful, and where increasing process understanding and prediction of effects was requested. N fertilization is a politically debated issue and there is a need for a scientific basis underpinning the guidelines regarding N fertilization. Dynamic models could be useful to predict fertilization effects on soil water and run off water quality.

At the moment, it is not recommended to N fertilise the forest in southern Sweden (Agency, 2007, 2014), but there are indications that this recommendation may change due to pressure from both research and industry. A clear indication of this was the commission in July 2022, from the government to Swedish University of Agriculture (SLU), to produce a preliminary study on environmentally adapted forest fertilization for increased forest growth, where SLU must make proposals on how the forms of forest fertilization can be developed so that a greater proportion of the forest land can be fertilized than is done today (Näringsdepartementet 2022). Many experimental studies have been done on the effects of nitrogen fertilization on growth (Sikström, 1997; Bergh *et al.*, 2014), but there are fewer studies on the effect on N concentrations in soil water, especially in southern Sweden. Different studies point to different responses. The different response may be due to a combination of site fertility, soil vegetation, historical N input and forestry. To assess the combined effect of N fertilization and climate change on forest sites in

the future on different climate regions, with different historical N input and on different soil types would require burdensome and long-lasting experiments. Here, dynamic models can contribute with important knowledge as a basis for recommendations for forestry.

In paper II, simulated N fertilization showed no effect on tree growth in the Southern and Central sites, but instead a pronounced effect on N leaching. Consequently, the combined results in paper II support the Swedish Forest Agency's current recommendations for N fertilization, which differ between regions depending on historical and present N deposition. Although decreasing, N deposition is still elevated in southwestern Sweden, where also the total deposition exceeds the critical load for coniferous forest, 5 kg N per ha and year. An increase in N fertilization of these forests would further increase the risk of these forest to leach N, and would further compromise reaching the goal *Zero Eutrophication*. The direct effect on soil water acidification was not studied explicitly in paper II, but should theoretically be small, as forest fertilization is added with base cations as well as N. But, the nitrification process releases hydrogen ions, which in cases of excessive nitrification may lead to increased acidification, thus affecting the EQO *Natural Acidification Only*.

The model has been shown to adequately simulate the effects of N fertilization, and supports the current recommendations, but in order to be able to draw more general conclusions on the role of the soil properties on the effects, and the interaction with climate change, more sites from a wider range of climate and soil conditions should be modelled. Also, the effects of N fertilization on ground vegetation and biodiversity should be taken into account, which is not done in this study.

Whole-tree harvesting

Another issue that arose during the discussions with the stakeholders was the combined effects of more intensive forestry and climate change. For example for the EQO *Natural Acidification Only*, indirect effects of climate change are often seen as the major threat, as the increased demand for biofuels has the potential to affect acidification more than the atmospheric acidic deposition, now when the acidifying emissions have declined substantially (Iwald *et al.*, 2013). Stakeholders were interested to know how much forest can be sustainably harvested in the future and how it affects acidification of forest soils and water. One of the stakeholders mentioned that there is a mismatch between models and monitoring regarding the acidifying effect of the WTH, and experienced that it affects their confidence in modeling studies in that matter.

With paper III and a prior study (Erlandsson Lampa *et al.*, 2019), we believe that we have come closer to an explanation for this discrepancy. Previous modeling studies, with less dynamic models, lacking e.g. a link between uptake from

vegetation and soil water concentrations, have shown a greater negative effect of WTH on the soil BC pools and ANC in the runoff water, and have not been able to recreate the gradually reduced difference in BC concentration in the soil solution between WTH and CH, that have been demonstrated in experiments (e.g. Zetterberg et al. 2017). Increased weathering due to lowered BC concentration in soil solution after WTH has been put forward as one possible reason, and lack of dynamic weathering has been suggested to be the cause of this discrepancy between models and measurements (Paré and Thiffault, 2016). However, when the ForSAFE model was applied on the sites, the hypothesis about gradually reduced difference due to increased weathering could be rejected as weathering of BC was not significantly affected by WTH and thus could not be the explanation for the discrepancy between models and measurements. The simulated difference between BC concentrations in the soil solution between WTH and SH was caused by a higher simulated BC mineralization from the SOM pool under SH, as there were more residues left on the forest floor to be decomposed. After about 20-30 years the BC concentrations of both scenarios were back to the same level and the diminishing difference between the treatments could be linked to reduced uptake and reduced leaching in the next rotation after WTH (described in more detail in the Results and Discussions section under Whole-Tree Harvesting).

The results from this study and from Erlandsson et al. (2019) confirm results from long-term experiments, that whole-tree harvesting leads to a temporary effect on base cation concentrations in soil solution (20-30 years), which can lead to consequences for acidification during that period. The studies also highlight the knowledge gaps about long-term effects, where e.g. the organic pool play an important role. The more intensive WTH is in terms of total biomass extracted and the frequency of extraction, the more reduced the BC availability will be by WTH, with possible consequences on acidification and long-term depletion of the BC stock. Increased knowledge about the dynamics of the organic pools are important to be able to predict the long-term effects of prolonged extraction of forest residues on soil nutrient pools, acidification and tree growth.

Interactions between researchers and stakeholders

It was mentioned during the workshops that in order for the research to be relevant and useful for stakeholders, it is helpful that they are involved early in the modeling process, to get a heads up about what kind of results or what type of studies they will need to take into consideration. All stakeholders understood that there are uncertainties in models and in predictions, but it was emphasized that it is important that the uncertainties are clearly communicated together with the results when they are presented to stakeholders.

An obstacle to the stakeholders' ability to assimilate emerging deeper knowledge is their often limited resources with tight deadlines and heavy work load. This means,

researchers cannot expect stakeholders in public authorities to seek out knowledge from the scientific community themselves. Researchers need to find ways to communicate their research findings to stakeholders in multiple ways as a way to push for a greater impact. According to the stakeholders, it is important to be up to date on which direction the research field develops, as part of their job is to keep an oblique view of the current state of knowledge and base their recommendations on that. One way to ease the knowledge intake of stakeholders, could be to improve the communication in both directions, meaning; If researchers include stakeholders earlier on in the research process, they can more efficiently target the areas that are topical to that specific stakeholder and in that way make scientific knowledge more usable. The stakeholders will benefit from this as well as they can keep up to date and in contact with the current state of knowledge and assimilate more knowledge than would otherwise be possible.

Conclusions

This thesis shows the need for dynamic modelling in high temporal and spatial scale, in studies of indirect and direct pressures of climate change on forest soil and vegetation processes, aiming at increasing process understanding and producing relevant and usable knowledge for policy support.

The effects of indirect and direct pressures of climate change were investigated in the four studies in this thesis and the following conclusions could be drawn:

- Present environmental conditions alone are not enough to predict the risk of N leaching from two geographically close and comparable forests. It is important to also include the site history, which in our case is reflected in the initial SOM-C and N pools. Since data from the time of the start of the simulations (usually in the first half of 1900s) are missing, we need to be able to reconstruct them. Information about site management history can help us reconstruct starting conditions, and enable us to better predict N leaching risks. Available data is promising (maps, aerial photography), and can be used for this purpose.
- The model simulations supported our hypotheses that N fertilization have different effects on tree growth and N leaching between areas with high and low N deposition, with low expected tree growth increase but increased risk of leaching in areas with historically high N deposition. These results support the Swedish Forest Agency's current recommendations for N fertilization, which differ between regions depending on historical and present N deposition.
- ForSAFE can be a useful tool in assessing the effects of N fertilization on tree growth and N leaching. There are, however, still uncertainties in how SOC respond to N availability and a review and revision of the processes governing this in the model is recommended.
- Whole-tree harvesting, or removal of branches and tree tops in addition to stems, can lead to temporarily reduced base cation concentrations in soil water up to 30 years after harvest, but not thereafter, compared to stem only harvest. We propose that the diminishing difference, that has been seen in experiments and in our modelling studies, but has not been reproduced in models without dynamic tree growth, is linked to reduced uptake in the next

rotation after whole-tree harvest and reduced leaching. The lower concentrations of BC in the first 30 years post-harvest is due to reduced input of organic material and consequently reduced nutrient mineralization in the soil, compared to stem only harvest.

- Growth was only temporally reduced due to whole-tree harvesting in our study but there is a concrete risk that prolonged extraction of forest residues will progressively deplete nutrient pools in the forest ecosystems and increase the period of slower tree growth after whole-tree harvesting. Further studies are needed to understand the mid- and long term effects of whole-tree harvesting on tree growth. As available long-term experiments do not exceed 50 years, dynamic modelling is a relevant tool for researching this further.
- Weathering rates are generally increasing with climate change throughout Sweden. The increasing effect is seen all year around in southern Sweden but not in winters in northern Sweden, as the winters are still projected to have temperatures mostly below zero, when weathering is very low.
- Future extreme climate change pressures like droughts may reduce weathering due to reduced soil moisture, and the risk is the highest in southern Sweden.
- The study highlights the importance of soil texture and mineralogy for predicting weathering, Despite the strong temperature dependency of weathering and the strong temperature gradient from southern Sweden to northern, in this study the differences in yearly average weathering rates between the forest sites had no geographical gradient. Instead the differences depended on the different soil properties.

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References

- Aber, J., McDowell, W., Nadelhoffer, K., Magill, A., Berntson, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L., Fernandez, I., 1998. Nitrogen Saturation in Temperate Forest Ecosystems. *BioScience* 48, 921-934.
- Aber, J.D., Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92, 463-474.
- Aber, J.D., Goodale, C.L., Ollinger, S.V., Smith, M.-L., Magill, A.H., Martin, M.E., Hallett, R.A., Stoddard, J.L., 2003. Is Nitrogen Deposition Altering the Nitrogen Status of Northeastern Forests? *BioScience* 53, 375-389.
- Aber, J.D., Nadelhoffer, K.J., Steudler, P., Melillo, J.M., 1989. Nitrogen Saturation in Northern Forest Ecosystems: Excess nitrogen from fossil fuel combustion may stress the biosphere. *BioScience* 39, 378-386.
- Aber, J.D., Ollinger, S.V., Driscoll, C.T., 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling* 101, 61-78.
- Achat, D.L., Deleuze, C., Landmann, G., Pousse, N., Ranger, J., Augusto, L., 2015. Quantifying consequences of removing harvesting residues on forest soils and tree growth – A meta-analysis. *For. Ecol. Manage.* 348, 124-141.
- Agency, S.F., 2007. Kvävegödsling av Skogsmark; Meddelande 2007:2. In, Jönköping, Sweden.
- Agency, S.F., 2014. Föreskrifter om Ändring i Skogsstyrelsens föreskrifter och allmänna råd (SKSFS 2011:7) till Skogsvårdslagen; SKSFS 2013:2. In.
- Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5, 169-211.
- Akselsson, C., Belyazid, S., Hellsten, S., Klarqvist, M., Pihl-Karlsson, G., Karlsson, P.-E., Lundin, L., 2010. Assessing the risk of N leaching from forest soils across a steep N deposition gradient in Sweden. *Environmental Pollution* 158, 3588-3595.
- Akselsson, C., Hultberg, H., Karlsson, P.E., Pihl Karlsson, G., Hellsten, S., 2013. Acidification trends in south Swedish forest soils 1986–2008 — Slow recovery and high sensitivity to sea-salt episodes. *Sci. Total Environ.* 444, 271-287.
- Akselsson, C., Kronnäs, V., Stadlinger, N., Zanchi, G., Belyazid, S., Karlsson, P.E., Hellsten, S., Karlsson, G.P., 2021. A Combined Measurement and Modelling Approach to Assess the Sustainability of Whole-Tree Harvesting—A Swedish Case Study. *Sustainability* 13, 2395.

- Akselsson, C., Olsson, J., Belyazid, S., Capell, R., 2016. Can increased weathering rates due to future warming compensate for base cation losses following whole-tree harvesting in spruce forests? *Biogeochemistry BECC: Biodiversity and Ecosystem services in a Changing Climate* 128, 89-105.
- Akselsson, C., Westling, O., 2005. Regionalized Nitrogen Budgets in Forest Soils for Different Deposition and Forestry Scenarios in Sweden. *Global Ecology and Biogeography* 14, 85-95.
- Akselsson, C., Westling, O., Alveteg, M., Thelin, G., Fransson, A.-M., Hellsten, S., 2008. The influence of N load and harvest intensity on the risk of P limitation in Swedish forest soils. *Sci. Total Environ.* 404, 284-289.
- Akselsson, C., Westling, O., Orlander, G., 2004. Regional mapping of nitrogen leaching from clearcuts in southern Sweden. *For. Ecol. Manage.* 202, 235-243.
- Alveteg, M., Sverdrup, H., Warfvinge, P., 1995. Regional assessment of the temporal trends in soil acidification in Southern Sweden, using the safe model. *Water, Air, and Soil Pollution* 85, 2509-2514.
- Attiwill, P.M., Adams, M.A., 1993. Nutrient cycling in forests. *New Phytologist* 124, 561-582.
- Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C.M., Crowther, T.W., 2019. The global tree restoration potential. *Science* 365, 76-79.
- Bellassen, V., Luysaert, S., 2014. Carbon sequestration: Managing forests in uncertain times. *Nature* 506, 153-155.
- Belyazid, S., 2006. Dynamic modelling of biogeochemical processes in forest ecosystems. Department of Chemical Engineering, Lund University.
- Belyazid, S., Westling, O., Sverdrup, H., 2006a. Modelling changes in forest soil chemistry at 16 Swedish coniferous forest sites following deposition reduction. *Environmental Pollution* 144, 596-609.
- Belyazid, S., Westling, O., Sverdrup, H., 2006b. Modelling changes in forest soil chemistry at 16 Swedish coniferous forest sites following deposition reduction. *Environ Pollut* 144, 596-609.
- Belyazid, S., Zanchi, G., 2019. Water limitation can negate the effect of higher temperatures on forest carbon sequestration. *European Journal of Forest Research* 138, 287-297.
- Bergh, J., Nilsson, U., Allen, H.L., Johansson, U., Fahlvik, N., 2014. Long-term responses of Scots pine and Norway spruce stands in Sweden to repeated fertilization and thinning. *For. Ecol. Manage.* 320, 118-128.
- Berndes, G., Goldmann, M., Johnsson, F., Lindroth, A., Wijkman, A., Abt, B., Bergh, J., Cowie, A., Kalliokoski, T., Kurz, W., Luysaert, S., Nabuurs, G.-J., 2018. Forest and the C climate. Manage for maximum wood production or leave the forest as a C sink? In, *kungl. skogs- och lantbruksakademiens tidskrift*.
- Binkley, D., Burnham, H., Lee Allen, H., 1999. Water quality impacts of forest fertilization with nitrogen and phosphorus. *For. Ecol. Manage.* 121, 191-213.

- Binkley, D., Högberg, P., 1997. Does atmospheric deposition of nitrogen threaten Swedish forests? *For. Ecol. Manage.* 92, 119-152.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20, 30-59.
- Börjesson, P., Hansson, J., Berndes, G., 2017. Future demand for forest-based biomass for energy purposes in Sweden. *For. Ecol. Manage.* 383, 17-26.
- Bradford, M.A., Wieder, W.R., Bonan, G.B., Fierer, N., Raymond, P.A., Crowther, T.W., 2016. Managing uncertainty in soil carbon feedbacks to climate change. *Nat. Clim. Chang.* 6, 751-758.
- Brandt, J., Flannigan, M., Maynard, D., Thompson, I.D., Volney, W.J.A., 2013. An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues INTRODUCTION. *Environ. Rev.* 21, 207-226.
- Brandt, J.P.B.P., 2009. The extent of the North American boreal zone. *Environ. Rev.* 17, 101-161.
- Brantley, S.L., Kubicki, J.D., White, A.F., 2008. Kinetics of water-rock interaction.
- Burton, P.J., Bergeron, Y., Bogdanski, B.E., Juday, G.P., Kuuluvainen, T., McAfee, B.J., Ogdén, A., Teplyakov, V.K., Alfaro, R.I., Francis, D.A., 2010. Sustainability of boreal forests and forestry in a changing environment. IUFRO (International Union of Forestry Research Organizations) Secretariat.
- Canadell, J.G., Raupach, M.R., 2008. Managing Forests for Climate Change Mitigation. *Science* 320, 1456-1457.
- Clarke, N., Kiær, L.P., Janne Kjønaas, O., Bárcena, T.G., Vesterdal, L., Stupak, I., Finér, L., Jacobson, S., Armolaitis, K., Lazdina, D., Stefánsdóttir, H.M., Sigurdsson, B.D., 2021. Effects of intensive biomass harvesting on forest soils in the Nordic countries and the UK: A meta-analysis. *For. Ecol. Manage.* 482, 118877.
- Cowling, E., Galloway, J., Furiness, C., Barber, M., Bresser, T., Cassman, K., Erisman, J.W., Haeuber, R., Howarth, R., Melillo, J., Moomaw, W., Mosier, A., Sanders, K., Seitzinger, S., Smeulders, S., Socolow, R., Walters, D., West, F., Zhu, Z., 2001. Optimizing Nitrogen Management in Food and Energy Production and Environmental Protection: Summary Statement from the Second International Nitrogen Conference. *TheScientificWorldJOURNAL* 1, 320976.
- de Jong, J., Akselsson, C., Egnell, G., Löfgren, S., Olsson, B.A., 2017. Realizing the energy potential of forest biomass in Sweden – How much is environmentally sustainable? *For. Ecol. Manage.* 383, 3-16.
- DeLuca, T.H., Zackrisson, O., Nilsson, M.C., Sellstedt, A., 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature* 419, 917-920.
- Denman, K., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P., Dickinson, R., Haugustaine, D., Heinze, C., Holland, E., Jacob, D., Lohmann, U., S, R., Silva Dias, P., Wofsy, S., Zhang, X., 2007. Couplings Between Changes in the Climate System and Biogeochemistry. In, pp. 499-587.

- Diaz, S., Grime, J.P., 1993. Evidence of a feedback mechanism limiting plant response to elevated carbon dioxide. *Nature* 364, 616.
- Driscoll, C.T., Whitall, D., Aber, J., Boyer, E., Castro, M., Cronan, C., Goodale, C.L., Groffman, P., Hopkinson, C., Lambert, K., Lawrence, G., Ollinger, S., 2003. Nitrogen Pollution in the Northeastern United States: Sources, Effects, and Management Options. *BioScience* 53, 357-374.
- Egnell, G., Ulvcröna, K.A., 2015. Stand productivity following whole-tree harvesting in early thinning of Scots pine stands in Sweden. *For. Ecol. Manage.* 340, 40-45.
- Emmett, B., 2007. Nitrogen Saturation of Terrestrial Ecosystems: Some Recent Findings and Their Implications for Our Conceptual Framework. *Water, Air & Soil Pollution: Focus* 7, 99.
- Erlandsson Lampa, M., Belyazid, S., Zanchi, G., Akselsson, C., 2019. Effects of whole-tree harvesting on soil, soil water and tree growth - A dynamic modelling exercise in four long-term experiments. *Ecological Modelling* 414.
- Fahey, T.J., Siccama, T.G., Driscoll, C.T., Likens, G.E., Campbell, J., Johnson, C.E., Battles, J.J., Aber, J.D., Cole, J.J., Fisk, M.C., Groffman, P.M., Hamburg, S.P., Holmes, R.T., Schwarz, P.A., Yanai, R.D., 2005. The Biogeochemistry of Carbon at Hubbard Brook. *Biogeochemistry* 75, 109.
- FAO, I., USDA, 2021. A guide to forest–water management. In, *FAO Forestry Papers*, Rome, Italy.
- Friedlingstein, P., O'Sullivan, M., Jones, Matthew W., Andrew, Robbie M., Hauck, J., Olsen, A., Peters, Glen P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Canadell, Josep G., Ciais, P., Jackson, Robert B., Alin, S., Aragão, Luiz E.O.C., Arneeth, A., Arora, V., Bates, Nicholas R., Becker, M., 2020. Global Carbon Budget 2020. *Earth System Science Data* 12, 3269-3340.
- Futter, M.N., Ring, E., Högbom, L., Entenmann, S., Bishop, K.H., 2010. Consequences of nitrate leaching following stem-only harvesting of Swedish forests are dependent on spatial scale. *Environmental Pollution* 158, 3552-3559.
- Galloway James, N., Townsend Alan, R., Erisman Jan, W., Bekunda, M., Cai, Z., Freney John, R., Martinelli Luiz, A., Seitzinger Sybil, P., Sutton Mark, A., 2008. Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions. *Science* 320, 889-892.
- Galloway, J.N., 1995. Acid deposition: Perspectives in time and space. *Water, Air, and Soil Pollution* 85, 15-24.
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. *Science* 349, 819-822.
- Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M., de Jong, R., Frank, D.C., Esper, J., Büntgen, U., Guo, X.J., Bhatti, J., 2016. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO₂ fertilization. *Proceedings of the National Academy of Sciences* 113, E8406-E8414.

- Grünewald, U., 1988. J. O. Reuss and D. W. Johnson: Acid Deposition and the Acidification of Soils and Waters. = Ecological Studies 59.–119 pp., figs. New York, Berlin, Heidelberg, Tokyo: Springer-Verlag 1986. ISBN 3-540-96290-5. 94,-DM. Internationale Revue der gesamten Hydrobiologie und Hydrographie 73, 124-124.
- Gundersen, P., Schmidt, I.K., Raulund-Rasmussen, K., 2006. Leaching of nitrate from temperate forests – effects of air pollution and forest management. Environ. Rev. 14, 1-57.
- Hansen, K., Malmaeus, M., 2016. Ecosystem services in Swedish forests. Scand. J. Forest Res. 31, 626-640.
- Haraldsson, H., Sverdrup, H., 2004. Finding Simplicity in Complexity in Biogeochemical Modelling. In, pp. 211-223.
- Hartmann, H., Moura, C.F., Anderegg, W.R.L., Ruehr, N.K., Salmon, Y., Allen, C.D., Arndt, S.K., Breshears, D.D., Davi, H., Galbraith, D., Ruthrof, K.X., Wunder, J., Adams, H.D., Bloemen, J., Cailleret, M., Cobb, R., Gessler, A., Grams, T.E.E., Jansen, S., Kautz, M., Lloret, F., O'Brien, M., 2018. Research frontiers for improving our understanding of drought-induced tree and forest mortality. New Phytologist 218, 15-28.
- Hedwall, P.-O., Grip, H., Linder, S., Lövdahl, L., Nilsson, U., Bergh, J., 2013. Effects of clear-cutting and slash removal on soil water chemistry and forest-floor vegetation in a nutrient optimised Norway spruce stand.
- Hempel, S., Frieler, K., Warszawski, L., Schewe, J., Piontek, F., 2013. A trend-preserving bias correction – the ISI-MIP approach. Earth Syst. Dynam. 4, 219-236.
- Högberg, P., Larsson, S., Lundmark, T., Moen, J., Nilsson, U., Nordin, A., 2014. Effekter av kvävegödsling på skogsmark Kunskapssammanställning utförd av SLU på begäran av Skogsstyrelsen, Rapport 1: 2014. In.
- Högbom, L., Nohrstedt, H.-Ö., Nordlund, S., 2001. Nitrogen Fertilization Effects on Stream Water Cadmium Concentration. Journal of Environmental Quality 30, 189-193.
- Hyvönen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G.I., Linder, S., 2008. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. Biogeochemistry 89, 121-137.
- Ineson, P., Cotrufo, M.F., Bol, R., Harkness, D.D., Blum, H., 1995. Quantification of soil carbon inputs under elevated CO₂: C₃ plants in a C₄ soil. Plant and Soil: An International Journal on Plant-Soil Relationships 187, 345-350.
- IPCC, 2007. Climate Change 2007 : the physical science basis : contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.
- IPCC, 2013. Climate change 2013 : the physical science basis : Working Group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press.
- Iwald, J., Löfgren, S., Stendahl, J., Karlton, E., 2013. Acidifying effect of removal of tree stumps and logging residues as compared to atmospheric deposition. For. Ecol. Manage. 290, 49-58.

- Johansson, B., 2000. Areal Precipitation and Temperature in the Swedish Mountains: An Evaluation from a Hydrological Perspective. *Hydrology Research* 31, 207-228.
- Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology & Management* 140, 227.
- Johnson, J., Aherne, J., Cummins, T., 2015. Base cation budgets under residue removal in temperate maritime plantation forests. *For. Ecol. Manage.* 343, 144-156.
- Jones, D.L., Healey, J.R., Willett, V.B., Farrar, J.F., Hodge, A., 2005. Dissolved organic nitrogen uptake by plants—an important N uptake pathway? *Soil Biology and Biochemistry* 37, 413-423.
- Karlsson, P.E., Akselsson, C., Hellsten, S., Pihl Karlsson, G., 2022. Twenty years of nitrogen deposition to Norway spruce forests in Sweden. *Sci. Total Environ.* 809, 152192.
- Karlsson, P.E., Pihl Karlsson, G., Hellsten, S., Akselsson, C., Ferm, M., Hultberg, H., 2019. Total deposition of inorganic nitrogen to Norway spruce forests – Applying a surrogate surface method across a deposition gradient in Sweden. *Atmospheric Environment* 217, 116964.
- Kauppi, P.E., Tomppo, E., Ferm, A., 1995. C and N storage in living trees within Finland since 1950s. *Plant Soil* 168, 633-638.
- Kellomäki, S., Peltola, H., Nuutinen, T., Korhonen, K.T., Strandman, H., 2008. Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 363, 2341-2351.
- Kellomäki, S., Strandman, H., Heinonen, T., Asikainen, A., Venäläinen, A., Peltola, H., 2018. Temporal and Spatial Change in Diameter Growth of Boreal Scots Pine, Norway Spruce, and Birch under Recent-Generation (CMIP5) Global Climate Model Projections for the 21st Century. *Forests* 9, 118-118.
- Kimmins, J.P., 1976. Evaluation of the consequences for future tree productivity of the loss of nutrients in whole-tree harvesting. *For. Ecol. Manage.* 1, 169-183.
- Kjellström, E., Barring, L., Gollvik, S., Hansson, U., Jones, C., Samuelsson, P., Rummukainen, M., Ullerstig, A., Willén, U., Wyser, K., 2005. A 140-year simulation of European climate with the new version of the Rossby Centre Regional Atmospheric Climate Model (RCA3).
- Korhonen, J.F.J., Pihlatie, M., Pumpanen, J., Aaltonen, H., Hari, P., Levula, J., Kieloaho, A.-J., Nikinmaa, E., Vesala, T., Ilvesniemi, H., 2013. Nitrogen balance of a boreal Scots pine forest. *Biogeosciences* 10, 1083.
- Kreutzweiser, D.P., Hazlett, P.W., Gunn, J.M., 2008. Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: A review. *Environ. Rev.* 16, 157-179.
- Larcher, W., 2003. *Physiological plant ecology : ecophysiology and stress physiology of functional groups.* Springer.
- Likens, G.E., Driscoll, C.T., Buso, D.C., 1996. Long-Term Effects of Acid Rain: Response and Recovery of a Forest Ecosystem. *Science* 272, 244-246.

- Lindo, Z., Nilsson, M.-C., Gundale, M.J., 2013. Bryophyte-cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change. *Glob. Change Biol.* 19, 2022-2035.
- Lindström, G., Gardelin, M., 1992. Model structure. In: Sandén, P., Warfvinge, P. (Eds.), *Modelling Groundwater Response to Acidification*. SMHI, Norrköping, Sweden.
- Lundmark, T., Bergh, J., Hofer, P., Lundström, A., Nordin, A., Poudel, B.C., Sathre, R., Taverna, R., Werner, F., 2014. Potential Roles of Swedish Forestry in the Context of Climate Change Mitigation. *Forests* 5, 557-578.
- Mälkönen, E., 1990. Estimation of nitrogen saturation on the basis of long-term fertilization experiments. *Plant Soil* 128, 75-82.
- Marklund, L.G., 1988. Biomassfunktioner för tall, gran och björk i Sverige : Biomass functions for pine, spruce and birch in Sweden, Umeå.
- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in ecology & evolution* 26, 523-532.
- Nabuurs, G.-J., Lindner, M., Verkerk, P.J., Gunia, K., Deda, P., Michalak, R., Grassi, G., 2013. First signs of carbon sink saturation in European forest biomass. *Nat. Clim. Chang.* 3, 792-796.
- Nadelhoffer, K.J., Emmett, B.A., Gundersen, P., Kjonaas, O.J., Koopmans, C.J., Schleppi, P., Tietema, A., Wright, R.F., 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* 398, 145-148.
- Nakicenovic, N., Alcamo, J., Davis, G., de Vries, B., Fenhann, J., Gaffin, S., Gregory, K., Grübler, A., , 2000. Emission scenarios. A Special Report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.
- Nasholm, T., Ekblad, A., Nordin, A., Giesler, R., Högberg, M., Högberg, P., 1998. Boreal forest plants take up organic nitrogen. *Nature* 392, 914.
- Näsholm, T., Kielland, K., Ganeteg, U., 2009. Uptake of organic nitrogen by plants. *New Phytol* 182, 31-48.
- Naturvårdsverket, 2021. Miljömålen: Årlig uppföljning av Sveriges nationella miljömål 2021–Med fokus på statliga insatser. In.
- Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J., Luysaert, S., 2016. Europe's forest management did not mitigate climate warming. *Science* 351, 597-600.
- Neff, J.C., Holland, E.A., Dentener, F.J., McDowell, W.H., Russell, K.M., 2002. The origin, composition and rates of organic nitrogen deposition: A missing piece of the nitrogen cycle? *Biogeochemistry* 57, 99-136.
- Nilsson, S.I., Miller, H.G., Miller, J.D., 1982. Forest Growth as a Possible Cause of Soil and Water Acidification: An Examination of the Concepts. *Oikos* 39, 40-49.
- Nohrstedt, H.-Ö., 2001. Response of Coniferous Forest Ecosystems on Mineral Soils to Nutrient Additions: A Review of Swedish Experiences. *Scand. J. Forest Res.* 16, 555-573.

- Odén, S., 1968. Nederbördens och luftens försurning : dess orsaker, förlopp och verkan i olika miljöer. In, Bulletin / Ecological Research Committee. Ekologikommittén, Statens naturvetenskapliga forskningsråd, p. 86.
- Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J., Kaj, R., 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. For. Ecol. Manage. 82, 19-32.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A Large and Persistent Carbon Sink in the World's Forests. *Science* 333, 988-993.
- Paré, D., Thiffault, E., 2016. Nutrient Budgets in Forests Under Increased Biomass Harvesting Scenarios. *Current Forestry Reports* 2, 81-91.
- Peltoniemi, M., Tamminen, P., Mäkipää, R., Liski, J., 2004. Changes in soil carbon with stand age - An evaluation of a modelling method with empirical data. *Glob. Change Biol.* 10, 2078-2091.
- Pihl Karlsson, G., Akselsson, C., Hellsten, S., Karlsson, P.E., 2011. Reduced European emissions of S and N – Effects on air concentrations, deposition and soil water chemistry in Swedish forests. *Environmental Pollution* 159, 3571-3582.
- Posch, M., Kurz, D., 2007. A2M—A program to compute all possible mineral modes from geochemical analyzes. *Computers & Geosciences* 33, 563-572.
- Restaino, C.M., Peterson, D.L., Littell, J., 2016. Increased water deficit decreases Douglas fir growth throughout western US forests. *Proceedings of the National Academy of Sciences of the United States of America* 113, 9557-9562.
- Ring, E., 1996. Effects of previous N fertilizations on soil-water pH and N concentrations after clear-felling and soil scarification at a *Pinus sylvestris* site. *Scand. J. Forest Res.* 11, 7-16.
- Ring, E., Bergholm, J., Olsson, B.A., Jansson, G., 2003. Urea fertilizations of a Norway spruce stand: effects on nitrogen in soil water and field-layer vegetation after final felling. *Can. J. For. Res.* 33, 375-384.
- Ring, E., Jacobson, S., Jansson, G., Högbom, L., 2017. Effects of whole-tree harvest on soil-water chemistry at five conifer sites in Sweden. *Can. J. For. Res.* 47, 349-356.
- Ring, E., Jacobson, S., Nohrstedt, H.-Ö., 2006. Soil-solution chemistry in a coniferous stand after adding wood ash and nitrogen. *Can. J. For. Res.* 36, 153-163.
- Roeckner, E., Brokopf, R., Esch, M., Giorgetta, M., Hagemann, S., Kornbluh, L., Manzini, E., Schlese, U., Schulzweida, U., 2006. Sensitivity of Simulated Climate to Horizontal and Vertical Resolution in the ECHAM5 Atmosphere Model. *Journal of Climate* 19, 3771.
- Ruosteenoja, K., Markkanen, T., Venäläinen, A., Räisänen, P., Peltola, H., 2018. Seasonal soil moisture and drought occurrence in Europe in CMIP5 projections for the 21st century. *Climate Dynamics* 50, 1177-1192.
- Sathre, R., Gustavsson, L., Bergh, J., 2010. Primary energy and greenhouse gas implications of increasing biomass production through forest fertilization. *Biomass and Bioenergy* 34, 572-581.

- Schimel, J.P., Bennett, J., 2004. NITROGEN MINERALIZATION: CHALLENGES OF A CHANGING PARADIGM. *Ecology* 85, 591-602.
- Sikström, U., 1997. Effects of low-dose liming and nitrogen fertilization on stemwood growth and needle properties of *Picea abies* and *Pinus sylvestris*. *For. Ecol. Manage.* 95, 261-274.
- Skogsdata, 2020. Skogsdata Dept. of Forest Resource Management, Swedish University of Agricultural Sciences, Umeå.
- Slingerland, R., Kump, L.R., 2011. *Mathematical modeling of earth's dynamical systems : a primer*. Princeton University Press.
- Smith, B., Prentice, I.C., Sykes, M.T., 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography* 10, 621-637.
- Smolander, A., Kitunen, V., Mälkönen, E., 2001. Dissolved soil organic nitrogen and carbon in a Norway spruce stand and an adjacent clear-cut. *Biol. Fertil. Soils* 33, 190-196.
- Sponseller, R.A., Gundale, M.J., Futter, M., Ring, E., Nordin, A., Näsholm, T., Laudon, H., 2016. Nitrogen dynamics in managed boreal forests: Recent advances and future research directions. *Ambio* 45, 175-187.
- Stein, L., Klotz, M., 2016. The nitrogen cycle. *Current Biology* 26, R94-R98.
- STINSON, G., KURZ, W.A., SMYTH, C.E., NEILSON, E.T., DYMOND, C.C., METSARANTA, J.M., BOISVENUE, C., RAMPLEY, G.J., LI, Q., WHITE, T.M., BLAIN, D., 2011. An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. *Glob. Change Biol.* 17, 2227-2244.
- Strawn, D.G., Bohn, H.L., O'Connor, G.A., 2015. *Soil Chemistry*. Wiley Blackwell.
- Sutton, M.A., Fowler, D., Burkhardt, J.K., Milford, C., 1995. Vegetation atmosphere exchange of ammonia: Canopy cycling and the impacts of elevated nitrogen inputs. *Water, Air, and Soil Pollution* 85, 2057-2063.
- Sverdrup, H., Warfvinge, P., 1995. Critical Loads of Acidity for Swedish Forest Ecosystems. *Ecological Bulletins*, 75-89.
- Tamm, C.O., 1991. Nitrogen in terrestrial ecosystems : questions of productivity, vegetational changes, and ecosystem stability. Springer-Vlg.
- Tamm, C.o., Aronsson, A., Popović, B., Flower-Ellis, J.G.K., 1999. Optimum nutrition and nitrogen saturation in Scots pine stands. In.
- Thurfjell, D., Rubow, C., Rimmel, A., Ohlsson, H., 2019. The Relocation of Transcendence. *Nature and Culture* 14, 190-214.
- Tietema, A., 1998. Microbial carbon and nitrogen dynamics in coniferous forest floor material collected along a European nitrogen deposition gradient. *For. Ecol. Manage.* 101, 29-36.
- UNEP, F.a., 2020. *The State of the World's Forests 2020*. In, *The State of the World's Forests (SOFO)*. FAO and UNEP, Rome, Italy, p. #214 p.

- Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H., Tilman, D.G., 1997. HUMAN ALTERATION OF THE GLOBAL NITROGEN CYCLE: SOURCES AND CONSEQUENCES. *Ecological Applications* 7, 737-750.
- Vitousek, P.M., Hättenschwiler, S., Olander, L., Allison, S., 2002. Nitrogen and nature. *Ambio* 31, 97-101.
- Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecological applications* 20, 5-15.
- Wallman, P., Belyazid, S., Svensson, M.G.E., Sverdrup, H., 2006. DECOMP – a semi-mechanistic model of litter decomposition. *Environmental Modelling & Software* 21, 33-44.
- Wallman, P., Svensson, M.G.E., Sverdrup, H., Belyazid, S., 2005. ForSAFE—an integrated process-oriented forest model for long-term sustainability assessments. *For. Ecol. Manage.* 207, 19-36.
- Walse, C., Berg, B., Sverdrup, H., 1998. Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity. *Environ. Rev.* 6, 25-40.
- Weil, R.R., Brady, N.C., 2017. *The nature and properties of soils*. Pearson.
- White, A.F., Brantley, S.L., 1995. *Chemical weathering rates of silicate minerals*. Mineralogical Society of America, Washington.
- Wild, B., Schnecker, J., Knoltsch, A., Takriti, M., Mooshammer, M., Gentsch, N., Mikutta, R., Alves, R.J.E., Gittel, A., Lashchinskiy, N., Richter, A., 2015. Microbial nitrogen dynamics in organic and mineral soil horizons along a latitudinal transect in western Siberia. *Global Biogeochemical Cycles* 29, 567-582.
- Xu, X., Thornton, P.E., Post, W.M., 2013. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Global Ecology and Biogeography* 22, 737-749.
- Yang, W., Andréasson, J., Phil Graham, L., Olsson, J., Rosberg, J., Wetterhall, F., 2010. Distribution-based scaling to improve usability of regional climate model projections for hydrological climate change impacts studies. *Hydrology Research* 41, 211-229.
- Yu, L., Zanchi, G., Akselsson, C., Wallander, H., Belyazid, S., 2018. Modeling the forest phosphorus nutrition in a southwestern Swedish forest site. *Ecological Modelling* 369, 88-100.
- Zanchi, G., 2016. *Modelling nutrient transport from forest ecosystems to surface waters : the model ForSAFE-2D*. Department of Physical Geography and Ecosystem Science, Faculty of Science, Lund University.
- Zanchi, G., Brady, M.V., 2019. Evaluating the contribution of forest ecosystem services to societal welfare through linking dynamic ecosystem modelling with economic valuation. *Ecosystem Services* 39, 101011.
- Zetterberg, T., Köhler, S.J., Löfgren, S., 2014. Sensitivity analyzes of MAGIC modelled predictions of future impacts of whole-tree harvest on soil calcium supply and stream acid neutralizing capacity. *Sci. Total Environ.* 494-495, 187-201.

Zetterberg, T., Olsson, B.A., Löfgren, S., von Brömssen, C., Brandtberg, P.-O., 2013. The effect of harvest intensity on long-term calcium dynamics in soil and soil solution at three coniferous sites in Sweden. *For. Ecol. Manage.* 302, 280-294.

Zhang, M., Cheng, X., Geng, Q., Shi, Z., Luo, Y., Xu, X., 2019. Leaf litter traits predominantly control litter decomposition in streams worldwide. *Global Ecology and Biogeography* 28, 1469-1486.

Web references:

Näringsdepartementet (2022): Miljöanpassad skogsgödsling för ökad takt i klimatomställningen [Press release], 7th of July
<https://www.regeringen.se/pressmeddelanden/2022/07/miljoanpassad-skogsgodsling-for-okad-takt-i-klimatomstallningen/> (last accessed 2022-08-22)

Paris Agreement, 2015 <https://unfccc.int/process-and-meetings/the-paris-agreement/the-paris-agreement> (last accessed 2022-08-22)

Regeringens Proposition 2016/17:146. Ett klimatpolitiskt ramverk för Sverige, Swedish Parliament 2017 https://www.riksdagen.se/sv/dokument-lagar/dokument/proposition/ett-klimatpolitiskt-ramverk-for-sverige_H403146 (last accessed 2022-08-22)



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