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Long-term implications of climate change and forest management for ecosystem services and ecosystem functioning

Exploring the decision-making space in Swedish production forests

JOHN BERGKVIST

DEPARTMENT OF PHYSICAL GEOGRAPHY AND ECOSYSTEM SCIENCE | LUND UNIVERSITY

Long-term implications of climate change and forest management for ecosystem services and ecosystem functioning: Exploring the decisionmaking space in Swedish production forests

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John Bergkvist

DOCTORAL DISSERTATION

By due permission of the Faculty of Science, Lund University, Sweden. To be publicly defended on the 13th September at 13.00 in Pangea Auditorium, Geocentrum II, Sölvegatan 12, Lund, Sweden.

> *Faculty opponent* Assistant professor Rasoul Yousefpour

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Title and subtitle: Long-term implications of climate change and forest management for ecosystem services and ecosystem functioning: Exploring the decision-making space in Swedish production forests

Abstract: Climate change is expected to affect temperate and boreal forests, potentially causing profound changes to the functioning and the structure of ecosystems. This calls for assessments of the plausible long-term outcomes of a range of climate change scenarios to increase the knowledge base for decision making in forestry. Forest owners need to consider whether current silvicultural management practices remain suitable also in the future. Contemporary decisions will determine the future landscape composition of production forests and have implications for the provisioning of ecosystem services. In this thesis, we analysed the varying preferences for maintaining ecosystem services among a sample of non-industrial private forest owners in Sweden. The findings demonstrated positive perceptions of 10 forest ecosystem services, with the highest rankings of biodiversity, timber quality, water quality and recreation. Differences in prioritization between ecosystem services largely depended on whether the owners were certified and if they were members of a forest owner association. These findings also revealed a consistent and broad agreement regarding a preferred expansion of mixed-species and deciduous stands in the landscapes, in line with current recommendations for climate change adaptation. The process-based ecosystem model LPJ-GUESS was evaluated to determine its skill in simulating managed production forests in Sweden through comparisons of model projections of standing volume against observations derived from the Swedish National Forest Inventory. New vegetation parameters were suggested for Norway spruce and Scots pine, which better represented observed growth rates in even-aged monocultures. Additionally, the evaluations provided insight into potential model improvements, specifically regarding the early phase of stand growth. The evaluated model was applied to study the long-term outcomes of altered management practices and climate change on forests in Sweden. Three alternative future trajectories of landscape development were visualized as changes in forest policy. In the first policy scenario current management practices were maintained, whereas the second emphasized risk-spreading and adaptation, and the third a transitioning towards conservation-focused practices with reduced management intensity. The simulations projected consistent increases in net primary productivity towards the end of the 21st century that were of greater magnitude in the higher emission scenarios, and with the largest changes occurring in northern Sweden in all three policies. The increases were mediated by higher N mineralization in combination with increased water use efficiency, driven by higher air temperatures and atmospheric CO₂ concentrations. The model indicated consistent increases in storm damage vulnerability in central and northern Sweden, regardless of simulated forest policy. However, storm damage vulnerability was lower at the end of the century compared to in the time period 2001-2020 in the conservation-oriented policy in southern Sweden. The model results also indicated that there may be long-term benefits associated with implementing a forest policy of riskspreading and adaptation. Compared to the scenario representing a continuation of current management practices, the risk-spreading and adaption policy provided similar or higher gains for net primary productivity, net ecosystem productivity, soil nitrogen availability, and provisioning of wood, and also showed a generally lower vulnerability of forests to storm damage in southern and central Sweden. The provisioning of wood, and also shorted a generally conditionalized to consider a consideration and robustness of the results. Site-scale simulations provided additional insight into the effects of climate change on the net carbon exchange in an unmanaged set-aside forest in the southern boreal zone in Sweden. These simulations showed clear short to medium-term mitigation benefits of retaining the unmanaged set-aside stand compared to clear-felling and replanting with either Scots pine or Norway spruce. However, the model results also indicated a decrease in the net carbon sink with increased age of the unmanaged stand over the long term, where a higher climate impact led to an earlier and more pronounced loss of carbon uptake. The findings of this thesis confirm the value of utilizing process-based models enabled with advanced representations of forest management to study long-term changes in ecosystems. It has advanced the knowledge of the implications of changing climate conditions and altered management for production forests in Sweden.

Key words: Ecosystem modelling, boreal forest, net primary productivity, ecosystem services, nonindustrial private forest owners, ecosystem functioning, Norway spruce, Scots pine Supplementary bibliographical information:

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Abstract

Climate change is expected to affect temperate and boreal forests, potentially causing profound changes to the functioning and the structure of ecosystems. This calls for assessments of the plausible long-term outcomes of a range of climate change scenarios to increase the knowledge base for decision making in forestry. Forest owners need to consider whether current silvicultural management practices remain suitable also in the future. Contemporary decisions will determine the future landscape composition of production forests and have implications for the provisioning of ecosystem services.

In this thesis, we analysed the varying preferences for maintaining ecosystem services among a sample of non-industrial private forest owners in Sweden. The findings demonstrated positive perceptions of 10 forest ecosystem services, with the highest rankings of biodiversity, timber quality, water quality and recreation. Differences in prioritization between ecosystem services largely depended on whether the owners were certified and if they were members of a forest owner association. These findings also revealed a consistent and broad agreement regarding a preferred expansion of mixed-species and deciduous stands in the landscapes, in line with current recommendations for climate change adaptation.

The process-based ecosystem model LPJ-GUESS was evaluated to determine its skill in simulating managed production forests in Sweden through comparisons of model projections of standing volume against observations derived from the Swedish National Forest Inventory. New vegetation parameters were suggested for Norway spruce and Scots pine, which better represented observed growth rates in even-aged monocultures. Additionally, the evaluations provided insight into potential model improvements, specifically regarding the early phase of stand growth.

The evaluated model was applied to study the long-term outcomes of altered management practices and climate change on forests in Sweden. Three alternative future trajectories of landscape development were visualized as changes in forest policy. In the first policy scenario current management practices were maintained, whereas the second emphasized risk-spreading and adaptation, and the third a transitioning towards conservation-focused practices with reduced management intensity. The simulations projected consistent increases in net primary productivity towards the end of the $21st$ century that were of greater magnitude in the higher emission scenarios, and with the largest changes occurring in northern Sweden in all three policies. The increases were mediated by higher N mineralization in combination with increased water use efficiency, driven by higher air temperatures and atmospheric $CO₂$ concentrations. The model indicated consistent increases in storm damage vulnerability in central and northern Sweden, regardless of simulated forest policy. However, storm damage vulnerability was lower at the end of the

century compared to in the time period 2001-2020 in the conservation-oriented policy in southern Sweden. The model results also indicated that there may be longterm benefits associated with implementing a forest policy of risk-spreading and adaptation. Compared to the scenario representing a continuation of current management practices, the risk-spreading and adaption policy provided similar or higher gains for net primary productivity, net ecosystem productivity, soil nitrogen availability, and provisioning of wood, and also showed a generally lower vulnerability of forests to storm damage in southern and central Sweden. The applied approaches were also discussed in terms of model uncertainty, which influenced the interpretation and robustness of the results.

Site-scale simulations provided additional insight into the effects of climate change on the net carbon exchange in an unmanaged set-aside forest in the southern boreal zone in Sweden. These simulations showed clear short to medium-term mitigation benefits of retaining the unmanaged set-aside stand compared to clear-felling and replanting with either Scots pine or Norway spruce. However, the model results also indicated a decrease in the net carbon sink with increased age of the unmanaged stand over the long term, where a higher climate impact led to an earlier and more pronounced loss of carbon uptake.

The findings of this thesis confirm the value of utilizing process-based models enabled with advanced representations of forest management to study long-term changes in ecosystems. It has advanced the knowledge of the implications of changing climate conditions and altered management for production forests in Sweden.

Sammanfattning

Klimatförändringarna förväntas påverka skogar i de tempererade och boreala zonerna och leda till omfattande förändringar i ekosystemens struktur och funktion. Därför behövs analyser av sannolika utfall av olika scenarier av ökad klimatpåverkan på lång sikt, för att förbättra kunskapsunderlaget och stödja beslutsfattande inom skogssektorn. För skogsägare innebär klimatförändringarna ett behov att överväga om den nuvarande skogsskötseln även är lämplig i fortsättningen. Samtida skötselbeslut kommer att avgöra det framtida skogslandskapets sammansättning och påverka tillhandahållandet av ekosystemtjänster.

I denna avhandling analyserades småskaliga privata skogsägares preferenser för att bibehålla ekosystemtjänster i produktionsskogar i Sverige. Svaren indikerade generellt positiva värderingar av 10 ekosystemtjänster, med högst värdering av biodiversitet, virkeskvalitet, vattenkvalitet och rekreation. Skillnader i prioritering mellan ekosystemtjänster länkades till om skogsägaren hade certifierat sin fastighet och om hen vad medlem i en skogsägarförening. Skogsägarna visade preferenser för ökad etablering av blandskog och lövskog i landskapet, i linje med samtida rekommendationer för klimatanpassning.

I detta arbete utvärderades även den dynamiska vegetationsmodellen LPJ-GUESS. Utvärderingen syftade till att avgöra modellens kapacitet att simulera skötta produktionsskogar genom jämförelser av modellsimuleringar av stående volym mot observationer från Riksskogstaxeringen. Nya vegetationsparametrar föreslogs för gran och tall som bättre fångade observerad tillväxttakt hos trädarterna i monokulturer. Utvärderingen bidrog även till kunskap om potentiella modellförbättringar för simulering av unga bestånd.

Den utvärderade modellen applicerades sedan för att studera utfall av förändrad skogsskötsel och klimatpåverkan på produktionsskogar i Sverige. Tre scenarier av alternativa framtida förändringar i skogslandskapets sammansättning modellerades. I det första scenariot bibehölls nuvarande sammansättning av skogstyper i landskapen fram till slutet av århundradet. Det andra scenariot motsvarade en ökad fokus på riskspridning och klimatanpassning, och det tredje en gradvis övergång till mer naturnära skogsbruk och ökad skydd av skog. LPJ-GUESS föreslog en ökad nettoprimärproduktion vid slutet av århundradet i samtliga tre scenarier vid både hög och låg klimatpåverkan. Nettoprimärproduktionen ökade mer vid högre klimatpåverkan, med de största relativa förändringarna i norra Sverige.

Nettoprimärproduktionen stimulerades av en ökad kvävemineralisering till följd av en högre marktemperatur, och av en ökad vatteneffektivitet på grund av en högre koldioxidhalt i atmosfären. Modellen indikerade en ökad stormkänslighet i Svealand och i Norrland i alla tre alternativa skötselscenarier. Skogslandskapets känslighet för stormskador var lägre i slutet av århundradet jämfört med 2001-2020 i södra Sverige i scenariot med ökat fokus på naturnära skogsbruk och skydd av skog.

Riskspridnings- och klimatanpassningsscenariot gav liknande eller högre nettoprimärproduktion, kolupptag, kvävemineralisering och tillhandahållande av biomassa som scenariot som motsvarade en fortsättning av nutidens skogsbruk. Även stormkänsligheten var lägre i Götaland och i Svealand. Metoderna som användes för att nå modellresultaten diskuterades i förhållande till modellosäkerheter och antaganden, vilket påverkar tolkningen och robustheten i simuleringarna.

Simuleringar på beståndsnivå bidrog till kunskap om klimatförändringens effekt på kolupptag och utbyte i en avsatt skog i den södra boreala zonen i Sverige. Modellen indikerade en klimatnytta på kort till medellång sikt med att öka andelen avsatt skog jämfört med alternativet att avverka och återplantera granskog eller tallskog. Dock minskade kolupptaget i den avsatta skogen över tid och med ökad ålder, med en mer markant minskning av kolupptaget i ett scenario av väldigt hög klimatpåverkan.

Resultaten av denna avhandling bekräftar betydelsen av processbaserade dynamiska vegetationsmodeller med funktionalitet att simulera skogsskötsel som viktiga redskap för att studera trender över tid i ekosystem. Detta har bidragit till mer kunskap om effekterna av klimatförändringar och ändrad skogsskötsel i svenska skogar.

List of papers

Paper I

Bergkvist, J., Nikoleris, A., Fors, H., Jönsson, A.M. (2024) Maintenance and enhancement of forest ecosystem services: a non-industrial private forest owner perspective. *European Journal of Forest Research*, *143*, 169-185.

Paper II

Bergkvist, J., Lagergren, F., Finnander Linderson, M-L., Miller, P., Lindeskog, M., & Jönsson, A. M. (2023). Modelling managed forest ecosystems in Sweden: An evaluation from the stand to the regional scale. *Ecological Modelling*, *477*, 110253.

Paper III

Bergkvist, J., Lagergren, F., Islam, R. M., Wårlind, D., Miller, P., Finnander Linderson, M-L., Lindeskog, M., Jönsson, A.M., Quantifying the impact of climate change and forest management on Swedish forest ecosystems using the dynamic vegetation model LPJ-GUESS. (*Under review in Earth's Future*).

Paper IV

Islam, R.M., Jönsson, A.M., **Bergkvist, J.**, Lagergren, F., Lindeskog, M., Mölder, M., Scholze, M., Kljun, N. (2024). Projected effects of climate change and forest management on carbon fluxes and biomass of a boreal forest. *Agricultural and Forest Meteorology*, *349*, 109959.

Author's contribution to the papers

Paper I

AMJ, HF and AN conceptualized the study. **JB**, AN, HF and AMJ designed the methodology. **JB** performed the statistical analysis of the survey data and visualized the findings. **JB** wrote the initial draft. All authors contributed to revisions of the manuscript.

Paper II

FL and AMJ conceptualized the study. **JB**, FL, and AMJ designed the methodology. **JB**, FL, PM and ML contributed with code and setup of the model. MFL provided observational data. **JB** ran the simulations. **JB** performed formal analysis of the data. **JB** visualized the findings. **JB** wrote the initial draft. All authors contributed to revisions of the manuscript.

Paper III

FL, AMJ and **JB** conceptualized the study. **JB**, FL, AMJ designed the methodology. JB, DW and ML contributed with code and setup of the model. **JB** ran the simulations. **JB** and MFL performed the formal analysis of the data. **JB** and RI visualized the findings. **JB** wrote the initial draft. All authors contributed to revisions of the manuscript.

Paper IV

AMJ and NK conceptualized the study. AMJ, FL, and NK designed the methodology. RI, **JB**, AMJ, FL, and ML contributed with code and setup of the model. MM and NK provided observational data. RI ran the simulations, performed the formal analysis of the data and visualized the findings. RI wrote the initial draft. RI, AMJ, **JB**, FL, MS and NK contributed to revisions of the manuscript.

Abbreviations

Glossary

Ecosystem services is a concept which highlights the benefits that ecosystem structures and processes provide to humans. They involve the provision of goods and services of direct or indirect value, but do not involve processes in nature with no clear benefit to humans. Ecosystem services are classified into provisioning services, which can include biomass, water, or food. Regulating ecosystem services include erosion prevention, carbon sequestration and storage, storm damage regulation or pest and disease regulation. Supporting services include pollination, seed dispersal and habitat provisioning, as well as cycling of nutrients. Cultural ecosystem services include aesthetic beauty, recreation and spiritual values of landscapes.

Ecosystem functioning describes the activities of all living organisms in an ecosystem and their collective effects on the physical, biological and chemical environment in the system. At the ecosystem scale, these can be jointly referred to as ecosystem processes, which depend directly on the biodiversity of the system.

Continuous cover forestry (CCF) is a classification of forest management strategies which involve practices of reduced intensity compared to the clear-felling system. In CCF, felled areas may not be larger than 0.25 ha, which ensures that the forest soil is never completely exposed and the canopy cover is continuously retained. Management ranges from shelterwood systems to single tree selection with target diameter harvesting of tree individuals.

Dynamic vegetation models (DVMs) are computer-based models which simulate the evolution of vegetation and changes in biogeochemical cycles over time. They require time series of climate data as input. DVMs are constructed from a theoretical understanding of key processes in nature (for example photosynthesis, respiration, mineralization) and include mechanistic representations of them.

Earth system models are computer-based simulation tools which represent processes in the biosphere, oceans, land and sea ice as well as in the atmosphere. Whereas DVMs only account for processes on land, and climate models only account for processes in oceans and in the atmosphere, in ESMs these are coupled. The coupling also allows for studying the feedbacks between the vegetation and the atmosphere.

Certification is a market-based instrument which intends to ensure that forest management is performed at a certain level of sustainability. Several certification standards exist, which provide a set of guidelines which must be followed by the forest owner to ensure that environmental and social values are maintained on the certified property. In return, the owner gains legitimacy and is often also able to sell the timber produced from certified forests at a slightly higher price.

Non-Industrial Private Forest (NIPF) is a classification of forest properties which are owned by private individuals rather than companies or the state. The properties are often small: in Sweden 52% of all owners hold properties smaller than 50 ha (Table 2 in **Paper I**). NIPF owners tend to not only prioritize timber production, but often also retain a strong emotional connection to their forests, and prefer recreational use, such as hunting and berry picking.

Forest owner association (FOA) are associations which provide members with advice regarding forestry-related matters, but also buy wood from the owners, offer aid in its extraction, and provide additional services such as regeneration and thinning. In Sweden, about one-third of all NIPF owners were members of an FOA in 2014.

Thesis rationale and structure

Changes in temperature and precipitation in Sweden resulting from climate change will lead to altered growth and decomposition rates, changes in vegetation cover and distribution of species, and will also amplify abiotic and biotic damage to forests. Forest owners will have to make decisions with limited knowledge of potential future outcomes and impacts of climate change. The management decisions of forest owners will at the same time have long-term implications for the provisioning of forest ecosystem services (ES), and it is therefore important to understand their intentions and preferred practices. Societal demands for bio-based products are also expected to increase, which is likely to put additional pressures on forests to provide timber, pulp and biofuels. This thesis has studied how climate change and altered management affects the provisioning of forest ES.

Paper I explored how preferences for maintaining forest ES varies among a sample of non-industrial private forest (NIPF) owners in Sweden. Their chosen forest management practices and preferences for future changes in forest composition were also assessed. This study aimed to provide an overview of the contemporary and future intentions of small-scale forest owners.

Paper II provided an evaluation of the DVM LPJ-GUESS which determined its capacity to recreate observed forest structure in Sweden. Additionally, this modelling study intended to highlight the ability of the model to capture seasonal and interannual variation in net ecosystem carbon exchange, gross primary productivity and ecosystem respiration for two sites in the southern boreal and nemoral zones.

In **Paper III**, the ecosystem model LPJ-GUESS was used to generate information on plausible future outcomes for forests in Sweden for three different climate change trajectories. It intended to provide new and relevant knowledge to decision makers within Swedish forestry regarding the impacts of climate change and the direction of ecosystem responses.

In **Paper IV**, LPJ-GUESS was utilized to assess the impacts of climate change and a range of different reforestation practices on the NEE of a southern boreal forest site in central Sweden. This study provided valuable information to stakeholders on potential management alternatives for enhancement of carbon uptake, both over the short term as well as the long term.

Introduction

Times of uncertainty

A changing climate

Climate change will lead to alterations in the functioning and structure of forests (Gauthier et al., 2015). These changes will require forest owners and managers to reconsider forestry practices which have been suitable in the past and adapt their management to new climate conditions. The long rotations in forestry implies that the consequences of decisions last for several decades. At the same time, the uncertainty regarding the magnitude of climate change will remain large, as it depends both on the sensitivity of the climate to increased emissions (Zelinka et al., 2020), and on the continued rate of emissions at the global scale (IPCC, 2021). The current growth rate of atmospheric $CO₂$ is higher than previously observed during any year of the past $800\,000$ years, and the observed $CO₂$ concentrations which reached 417 ppm in 2022 have not occurred for two million years (Friedlingstein, 2023). This has caused global average air temperatures to increase with $1.09 \degree C$, when comparing the decade 2011-2020 to pre-industrial conditions (IPCC, 2021).

In Sweden, the average annual air temperature has increased with about $1.7 \text{ }^{\circ}\text{C}$ (mean 1991-2019) when compared to 1861-1900 (Kjellström et al., 2022). Climate model projections of future warming agree on an unevenly distributed temperature increase with a proportionally greater warming in northern Sweden compared to in southern Sweden. Depending on emission scenario, the northern boreal and subarctic regions could experience a climate warming ranging from 2.5 (RCP 2.6) to 6 \degree C (RCP 8.5) when comparing 2071-2100 to 1971-2000, with a more pronounced increase during winter than during summer (Kjellström et al., 2022). In southern Sweden, the mean annual temperature increase will likely range from 1 °C (RCP 2.6) to 5 \degree C (RCP 8.5), which will yield a gradual lengthening of the vegetation season: a warming corresponding to RCP 4.5 could result in a prolonging of 2 months or more at the end of the century. The agreement between climate models on future changes in precipitation for Sweden is lower when compared to changes in temperature, but most models suggest consistent precipitation increases which are, similarly to projected changes in air temperature, proportionally greater in northern Sweden compared to in southern Sweden. Increases in

evapotranspiration, as an outcome of higher air temperatures, are projected to lead to lower near-surface soil moisture content during the vegetation season, with more pronounced decreases in southern and central Sweden in high emission scenarios (Ruosteenoja et al., 2018).

Changes in forest productivity and growth

Findings regarding changes in productivity in the boreal and temperate forest zones as an outcome of changing climate conditions differ between published studies, but most studies show consistent productivity increases in boreal forests. Wang et al. (2023) used a machine learning algorithm to model the effects of changes in climate corresponding to RCP 4.5 and RCP 8.5 on tree growth across the boreal zone of Canada. The study found gains in growth across the studied regions ranging from 20.5 to 22.7% by 2050, with the greatest positive responses in eastern boreal Canada. D'Orangeville et al. (2018) modelled changes in forest growth in Quebec, Canada, and found a strong dependency of the net change in productivity on soil water availability. Similarly to Wang et al. (2023), the study found larger growth increments in areas north of 50 $^{\circ}$ N, at temperature increases of 2 and 4 $^{\circ}$ C. However, they also found general declines in growth in areas south of 50 °N, due to the effects of drier soil conditions.

Previous findings regarding productivity changes in Scandinavia and Sweden similarly show a general productivity increase in boreal forests in scenarios of higher climate impact. Jönsson & Lagergren (2018) modelled coniferous forests with the dynamic vegetation model LPJ-GUESS at three sites in the temperate and boreal zones in Sweden, and assessed the influence of RCP 8.5 and differing soil properties on NPP and soil water availability. Their findings show increases in NPP of 10-15% in response to the changed climate conditions, but also emphasize the drought sensitivity of southern Swedish Norway spruce forests. Subramanian et al. (2019) applied the hybrid Heureka-3PG model to a county in southern Sweden. When storm damage was not included in the modelled scenarios, they found a net change of 8.6% and 21% in annual volume increment for 2080-2100 for RCP 4.5 and RCP 8.5, respectively, when compared to a historical baseline simulation. Inclusion of storm damage events however, caused a reduction in the positive change in volume increment. Pilli et al. (2022) utilized a hybrid modelling approach combining output from LPJ-GUESS with an empirical growth model, and found gains in NPP in deciduous forests of 15 to above 25% for RCP 2.6 and 6.0 in Sweden. However, they also found no net change or small losses in NPP in coniferous forests in southern Sweden for these emission scenarios. In line with these results, Belyazid & Giuliana (2019) found a gradual decline in carbon storage in both biomass and soil in south Swedish forests when applying the ForSAFE model with a simulated climatic change corresponding to the A2 scenario. Their results also suggested an increased carbon storage in biomass in northern boreal regions of Sweden.

Changes in disturbance rates

Gradual warming will also amplify climatic extremes, and severe droughts are predicted to become more frequent in northern Europe, with adverse effects on forest carbon sequestration capacity (Ruosteenoja et al., 2018). Reductions in the carbon uptake was observed in central and western Europe during the dry and hot summer of 2003 (Reichstein et al., 2007). Similarly, eddy-covariance data from Sweden showed decreased NEP during the drought year 2018 for several sites (Lindroth et al., 2020). Droughts also have the potential to reduce the resistance of trees to additional disturbance factors. In southern Sweden, droughts have predisposed Norway spruce (*Picea abies L. Karst.*) to damage from the European Spruce bark beetle (*Ips typographus*). Bark beetles have been estimated to have caused 17% of all registered disturbance losses of timber during 1950-2019 in European forests, with gradually increasing losses after 2000 (Patacca et al., 2023). Conditions for development of *I. typographus* will become more favorable in the future, and an earlier spring swarming more likely to occur in all parts of Sweden with gradual warming. Jönsson et al. (2009) modelled the temperature dependent activity and development of *I. typographus* in Sweden, utilizing a process model forced with climate data corresponding to both low and high emission scenarios (A2, A1B and B2). They showed that the likelihood of initiation of a second beetle generation in southern Sweden was 63-81% at a warming of 2.4-3.8 °C at the end of the century. Climate warming is also expected to increase damage in the forestry sector from the fungal pathogen *Heterobasidion spp.* which causes decay in the roots and stems of a range of commercially important tree species in Sweden, including Scots pine (*Pinus sylvestris L.*), Norway spruce and birch (*Betula spp.*) (Berglund, 2005). *Heterobasidion spp.* may exacerbate both bark beetle damage and storm damage in stands through its reduction of tree vigor and supportive strength.

Modelled estimations of changes in mean wind speed and in maximum wind gust strength show no changes at a warming of 1.5 to 2 °C either in southern, central or northern Sweden (Kjellström et al., 2021), suggesting no direct effects of a limited climatic change on storm damage in forests. However, storm vulnerability can indirectly result from gradual warming, due to loss of ground frost during winters in boreal forests, which reduces tree root anchoring and stability during winter storms. Storms are currently the primary cause of volume loss in European forests and observed damage levels are expected to increase (Seidl et al., 2014; Patacca et al., 2023). Changes in forest storm vulnerability therefore has implications for the long-term mitigation capacity of forests, as well as the potential economic income from timber production and the provisioning of a range of other ES.

Maintenance of the forest carbon sink and storage capacity

As forests form important components of the terrestrial carbon sink, they exert a negative influence on climate forcing by regulating the atmospheric $CO₂$ content (Pan et al., 2011; Harris et al., 2021). The C stored in biomass is sourced from the atmospheric pool, which implies that the utilization of forest products for materials and energy has a lower imprint on the size of the atmospheric pool when compared to utilizing fossil-based fuels and materials. Sustainable forestry and harvesting is for this reason promoted in Sweden as important to mitigating climate change over the long term (SNFP, 2018). However, high harvesting intensities have been shown to reduce the carbon sink capacity of forests, as well as to reduce carbon stocks (Soimakallio et al., 2022). The challenge of balancing the preservation of forest carbon storage capacity and simultaneously utilizing biomass as a renewable material is well understood in the scientific community. A range of studies have provided differing results regarding suitable harvesting intensities and its subsequent benefits for climate mitigation. Skytt et al. (2021) found that increased harvesting is counterproductive and provides reduced mitigation capacity both over short and long timescales. Gustavsson et al. (2021) similarly showed that setting aside more forest land may result in improved mitigation in the near future, but that forest management which increases productivity leads to greater climate benefits when longer timescales are considered.

Uncertainty in key parameters which determine the carbon footprint of wood products, and consequently the benefit of substitution, is often a major reason for disagreement and diverging results between studies. Substitution factors need to consider the whole life-cycle of the wood product, including emissions from harvesting, transport, combustion losses, and end-use effective emission factors for benefits to be determined (Leturcq, 2020). Uncertainty in the substitution benefits also relate to potential changes in future productivity, growth and sequestration capacity of re-growing forest stands on harvested sites, which may result from future altered climate conditions in Sweden. Drought and poor regeneration may challenge an effective compensation of emissions from combustion of harvested biomass, which highlights the importance of directly measuring the carbon uptake in forests for a range of different conditions (Reichstein et al., 2007). Peichl et al. (2023) measured the NEP of a forested landscape in Västerbotten, northern Sweden, and found that the cumulative NEP remained at an optimum up to stand ages of 138 years. This indicates that shorter rotation periods, which may be economically motivated, would not necessarily result in additional positive mitigation outcomes. However, the benefits of longer rotations also need to be considered in relation to risk management, as the predisposition to storm and bark beetle damage generally is higher in older stands for some tree species, including the commercially important Norway spruce.

International and national climate and environmental targets

In 2019 the European Commission launched the Green Deal, a strategy consisting of multiple policies intending to gradually transform European society. It emphasizes a shift towards a circular economy, protection of biodiversity, sustainable food production, reduced pollution, improved resource use efficiency in construction, renewable energy production, and mitigation of climate change (Cifuentes-Faura, 2022). The core of the Green Deal is the European Climate Law, where the member states of the EU are required to reach net-zero emissions by 2050, with an intermediate goal of 55% lower emissions by 2030 compared to 1990. The Land Use, Land Use Change and Forestry (LULUCF) sector has been highlighted as a key component to reaching this target, as forests are important sinks of $CO₂$. Their value for continuous carbon uptake and storage are also outlined in the EU Forest Strategy 2030 and EU Biodiversity Strategy 2030. The harvesting rates within member states of the EU increased during 2016-2018 compared to 2011-2015, most likely due to changed demands for bio-based materials and products or altered management practices (Ceccherini et al., 2020). The increase in harvests, in combination with changes in natural mortality rates, have in most countries been detrimental to carbon uptake and storage and have caused reductions in the LULUCF net sink, including in Sweden (Hyyrynen et al., 2023). As a result, the EU net $CO₂$ uptake in 2021 of -230 Mt $CO₂e$ was considerably lower than the uptake in $2016-2018$ of -276 Mt CO₂e. Apart from the long-term climate goals for 2050 , the EU targets include binding commitments for member states to maintain or increase the LULUCF sink, to reach a net sink of -310 Mt CO₂e within the EU by 2030 (Korosuo et al., 2023).

Sweden has, similar to 194 other parties of the UNFCCC, ratified the Paris Agreement with the intention to limit global warming to far below 2 °C. The voluntary mitigation commitments of Sweden are formally determined in the Climate Act, which contains a long-term target of transitioning to net-zero $CO₂$ emissions in 2045, milestone targets of 63% lower emissions in 2030 than in 1990, and 75% lower emissions in 2040 than in 1990. The Climate Act favors reductions in national emissions foremost through the development of new and more efficient technologies, as well as substituting fossil-based materials and fuels with bioenergy and bio-based materials (Andersson et al., 2022). The strategy had an effect on emissions within the territorial boundaries of Sweden up to 2022, with reduced emissions of 37% compared to 1990 (Swedish Climate Policy Council, 2024). The Climate Policy Framework has had the beneficial effects of clearly communicating the need to reach the climate goals to Swedish industrial actors, and has also led to a stronger consensus of prioritizing mitigation actions within the Swedish parliament. It has however also been criticized for not clearly outlining the policy tools required for reaching the climate goals (Matti et al., 2021).

Forestry in Sweden

Swedish forest management is regulated in the Swedish Forestry Act (SFS, 1979), but also in the Swedish Environmental Code (SFS, 1998) within the Environmental Quality Objective "Sustainable Forests" (Lindahl et al., 2017). In 1993 the Forestry Act was revised, which marked a significant change with a deregulation of the forest sector. The previous strong focus on timber production was reduced and environmental protection was emphasized as an equally important goal within the revised policy, known as 'the Swedish forestry model', in order to improve the depauperate state of many forests at the time. The deregulation allowed greater management freedom among forest owners (Bush, 2010). In its current form, the Swedish forest policy encourages forest owners to improve environmental and social forest values by making voluntary commitments beyond the legal minimum requirements. Certification exists as a market-driven option to forest owners which objectively verifies that environmental, social and economic values are maintained at a high standard. The two most common certification bodies in Sweden are the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC) which are recognized by the state as valuable instruments for progress towards improved environmental concern in forests, for example through setting-aside forest land (SFA, 2019). Set-asides aim to preserve elements important for biodiversity, as well as regulating ecosystem functions and values relating to cultural heritage and recreation. Beyond the formally protected area of 6.1% on productive forest land in 2023, voluntary set-asides represented an additional 5.7% (Statistics Sweden, 2024).

Sweden is the fifth largest exporter of forest products in the world, with only 1% of the global forested area. The majority of the contemporary productive forest land area is occupied by stands younger than 60 years (SNFI, 2024a). Due to its predictable outcomes in terms of harvest levels and low intervention requirements, even-aged forest management with clear-felling has been the preferred practice on the vast majority of productive forest land in Sweden since the 1950s (Ekelund $\&$ Hamilton, 2001). Annual harvests constitute about 94% of the annual net increment on managed forest land, which in 2015 produced 73 million $m³$ of roundwood, more than any of the other member states within the EU (Forest Europe 2020).

The demand for renewable forest-based materials is expected to increase in the future as Sweden transitions to carbon-neutrality, as the requirements for substitutes to fossil-based materials grow (Lodin et al., 2020). At the same time, improvements to forest habitat quality and size will be necessary for further progress towards the stated targets within the Environmental Quality Objective *'Sustainable forests'*. Recent evaluations of '*Sustainable forests*' show ongoing losses of old-growth forests and habitat fragmentation (SFA, 2022). In order for conservation goals to be effective, they also need to be considered in relation to climate change, in order to determine any potential effects of changing climate conditions on the habitats of

sensitive species (Lagergren et al., 2024). In the worst-case scenario, protected areas may become unsuitable for a range of species of conservation interest (Arneth et al., 2020). The IPCC and the IPBES have therefore emphasized the need for policies which simultaneously address climate change and biodiversity loss.

About half of all productive forest land in Sweden is owned by NIPF owners with differing values, preferences and management intentions. Many of the ES provided in their forests, such as carbon sequestration, carbon storage, and a range of cultural ES, are considered public goods on privately owned land. Changing environmental conditions, disturbance rates, and biodiversity loss have increased the complexity of forest management in Sweden. Awareness of the need to adapt forests to increase resilience and limit damage from climate-induced natural disturbances seem to be increasing among forest owners and stakeholders. In the largely deregulated Swedish forest policy, which relies on voluntarism as the mode of governance, the responsibility of adaptation falls on the individual owner (Eriksson & Sandström, 2022). However, the agency of the forest owner may be limited by a lack knowledge or capacity to adapt (Blennow & Persson, 2009). The outcomes of forest owner decisions will nevertheless have major implications for the future forest composition at the regional scale as well as for the provisioning of ES.

Aims

This thesis intended to determine potential future impacts of forest owner choices, management practices and changing climate conditions on forest ecosystems in Sweden. Both modelling and empirical research methods were used. Specifically, the aims were to:

- Determine the perceived importance of forest ES among NIPF owners and the associated forest management practices at present, and preferred practices in the future (**Paper I**).
- Evaluate the forestry-enabled dynamic vegetation model (DVM) LPJ-GUESS for its capacity to simulate managed forest ecosystems in Sweden, for forest structure at the regional scale and the net exchange of carbon at the stand scale (**Paper II** & **Paper III**).
- Assess how future plausible emission trajectories and large-scale shifts in forest management influence the direction of ecosystem responses and provisioning of forest ES (**Paper III**).
- Determine the effects of different management decisions and climate change on the carbon uptake potential of a southern boreal site (**Paper IV**).

Materials and Methods

Overview

The findings of this thesis were produced through utilizing a range of different scientific tools and research methods. The approach in **Paper I** relied on empirical methods for data collection such as the stratified sampling approach, and on a set of different statistical models for analysis. The DVM LPJ-GUESS was used to generate the results for **Paper II, III** & **IV**.

Ecosystem model

Model description

LPJ-GUESS (Lund-Potsdam-Jena General Ecosystem Simulator) is a DVM which simulates terrestrial vegetation by representing processes which govern ecosystem structure and functioning (Smith et al., 2001; Smith et al., 2014). The model was originally designed to simulate potential natural vegetation (PNV), where the given climate, environmental and soil conditions determine the vegetation composition within the considered area. Since then the model has undergone continuous revisions and now incorporates advanced representations of human land use and land use change, including forest, pasture, and cropland management (Lindeskog et al., 2021; Lindeskog et al., 2013). It has been utilized in a wide range of studies to explore aspects of the carbon and nitrogen cycle within past, present and projected future climates on local to global spatial scales (Gustafson et al., 2021; Pugh et al., 2019; Ahlström et al., 2012; Miller et al., 2008).

The vegetation in forestry-enabled LPJ-GUESS is represented by plant functional types (PFTs), which for the European adapted PFT set (24 PFTs) are distinguished as tree species or represent a generalized grass/shrub layer (Hickler et al., 2012). The characteristics of each PFT is defined through a set of parameters which govern traits including climatic and shade tolerance limits, stem allometry, life span, phenology, leaf size, leaf longevity and leaf shape (Hickler et al., 2012). The traits of each PFT influence its competitive strength for resources such as light, water and nutrients.

The LPJ-GUESS model dynamically generates ecosystems via input of climate and environmental data. It requires daily or monthly data on precipitation (mm), air temperature (\degree C) and surface downwelling short-wave radiation (W m⁻²) and yearly data on atmospheric carbon dioxide concentration and nitrogen deposition. Additionally, input data on soil texture is required. Ecosystem processes which are mechanistically represented include photosynthesis, respiration, stomatal regulation, phenology, and the cycling of soil carbon and nitrogen, which are computed at a daily time step (Sitch et al., 2003; Smith et al., 2014). The total yearly photosynthesis (gross primary production, GPP) minus removals from losses due to autotrophic respiration (Ra) results in the yearly sum of net primary production (NPP). The accrued carbon of each individual is allocated to growth at the end of each year and partitioned into stem wood, leaves or roots according to the defined allometric constraints of each PFT. Competition between individuals within each stand for resources such as light, water and nutrients also determine the growth and mortality rates. During periods of water stress more of the accumulated carbon is assigned to root growth. Mortality can also occur as an outcome of stochastic patchdestroying disturbances (when enabled) which represent the influence of storms or fires on vegetation (Smith et al., 2014).

Soil processes such as mineralization and nitrogen fixation are also modelled mechanistically. Decomposition of soil organic matter and N mineralization occurs within 11 different pools with varying decay rates. The decomposition rates depend on soil moisture, soil temperature and the resistance to decay of each pool (Smith et al., 2014). The fixation of N in the soil depends on the modelled rate of evapotranspiration.

Managed or unmanaged forests are dynamically simulated in the model as tree individuals in patches (1000 m^2) where competition for resources, establishment and mortality occurs (Figure 1). At the patch level, all tree individuals of the same age are identical in size. A simulated forest stand can be represented with a number of patches. When simulating natural forests, patches provide a means to capture potential heterogeneity, for example through the destruction of some patches from stochastic disturbances. Stands are simulated within grid cells, which set the boundary conditions for growth through the specified climate, soil and nitrogen deposition data provided as input to the model. The temporal and spatial resolution of the input data defines the size of the grid cell and the resolution of the model output.

Forest management module

All papers in this thesis which included LPJ-GUESS are based on simulations with the forestry-enabled version of the model. **Paper II** used *forestry* version 4.0 whereas version 4.1 was used in **Paper III** & **IV**. The forest management module provides the user with a wide range of options to simulate both even-aged and

uneven-aged silvicultural systems. An important concept is the *stand type*, which defines the boundary rules and sets the intended outcomes of management (Figure 1). A stand type contains instructions on the management type, including any potential transition from one type of management to another (for example from clear-felling to continuous cover forestry). Multiple stands can be assigned to a stand type, and will then be managed according to those specified set of rules (Lindeskog et al., 2021).

A managed forest stand can be initiated as a direct transition from PNV or from bare ground. The latter case is preferred when simulating even-aged forest management. The initiation of a stand then involves defining the establishment year of the stand and its regeneration method (planting or natural regeneration). Tree species of PFTs can be established in this way even outside of their natural climatic boundaries. Continuous emergence of regenerating seedlings throughout the rotation period of the stand can also be enabled or disabled.

The user may also define the timing of thinning interventions and strength of removals within each stand. Options include thinning from below, where individuals in the cohort with the lowest diameter values are targeted, whereas thinning from above removes trees with the largest diameter. The length of the rotation period can be set manually, and is then defined as the final age of the stand at the time of felling, or it can be automatically triggered based on stand density through an alternative setting. Transitions between different silvicultural systems may also be set to occur following a clear-felling (Lindeskog et al., 2021).

Each stand can be simulated either as a monoculture or as a mixed stand consisting of several defined PFTs/species. Multiple stands can be initialized simultaneously at a given simulation year. Monocultures managed as even-aged stands allows intraspecific competition only among the individuals within the stand (which are of the same size and age) but not between stands. Age class distributions within the wider forest landscape is achieved by initializing stands at different points in time. Uneven-aged forest management may also be initialized, and this alternative management implies a varied age and size structure within the stand. Forests can then be managed as continuous cover with cuttings at a given target diameter. A continuous removal of tree individuals above the set threshold can then take place at user-defined intervals (commonly 5-20 years) with no set end year of management (Lindeskog et al., 2021).

Figure 1. Overview of a grid cell in the forestry-enabled version of LPJ-GUESS presenting the two land cover types 'natural forest' and 'managed forest' (adapted from Figure 1 in Lindeskog et al., 2021).

Apart from the above-mentioned silvicultural options, vegetation growth may be modified further through fertilization, which can be set as an annual rate of nitrogen addition (kg N ha⁻¹ year⁻¹). Moreover, irrigation of the stand can also be enabled which inhibits any occurrence of drought stress in the stand. The forest management module is described in full in Lindeskog et al. (2021).

Methodological overview of included publications

Paper I

The aim of **Paper I** was to gain information on how NIPF owners in Sweden perceive ES in their forests, and to find out which ES they rank most highly. Since this category of owners holds about half of all forest land in Sweden, their decisions regarding which ES to prioritize also have considerable implications for the status of forest ES in Sweden in general. The study is based on data gathered from a survey which was distributed to small scale private forest owners in Sweden. The survey itself was designed through the web-based tool *Sunet Survey* which is available through Lund University. The access to the survey, which was only available in online form, was distributed by postcard with a printed QR-code on it. Following the proportionate stratified sampling approach, 750 owners in each of the four Swedish bioclimatic zones were selected as recipients (nemoral, boreonemoral, southern boreal and northern boreal).

The data analysis determined whether sociodemographic or other factors could explain the choices or behaviors of the NIPF owners regarding how they value ES. Additionally, their preferred forest management activities and views on the future forest landscape were also assessed. In order to do this, a set of statistical tests and analyses were used, including the Kruskal-Wallis test with Dunn's Multiple Comparison test, chi-square tests, and principal component analysis. A complete description of the method is available in **Paper I**.

Paper II

In **Paper II**, observational data from the Swedish National Forest Inventory (NFI) and from ICOS Sweden (Heiskanen et al., 2021) were used to evaluate the performance of forestry-enabled LPJ-GUESS. The landscape scale evaluation, where Swedish NFI data were utilized, intended to determine if the observed standing volume of production forests could be recreated by the model for observed age classes in southern, central and northern Sweden (Figure 2). This study was important for determining the potential for improvements when simulating the structure of forest types and to provide more information on the potential bias of simulations.

For this reason, the model was set up to produce output at the regional scale for the four most common forest types in Sweden. Observational data from the CRU-NCEP dataset with a spatial resolution of $0.5 \times 0.5^{\circ}$ and a monthly temporal resolution were used as input to generate the productive forest landscape. As the model output for Norway spruce and Scots pine monocultures deviated from the observed, a local sensitivity analysis (LCA) was performed in order to suggest new values for a set of parameters which govern growth, allometry and productivity. The model output generated with the new set of vegetation parameters were evaluated against the NFI data alongside model output based on the original parameters. **Paper II** also included an evaluation at the site-scale where the ecosystem properties of a boreonemoral site (Hyltemossa, 56°06' N, 13°25' E) and of a boreal site (Norunda, $60^{\circ}05'$ N, $17^{\circ}29'$ E) were assessed (Figure 2). Site-level observational input data with a daily temporal resolution derived from ICOS Sweden were utilized to simulate the forest structure and exchange of carbon between the atmosphere and the forest at these sites. Additional details in the set-up of forest management can be found in **Paper II**. This study was produced with *forestry* version 4.0 (Table 1).

Figure 2. Overview of the study area in Paper II, including both regions and sites for which the model was evaluated.

Paper III

Paper III was produced with an updated version of the *forestry* module (version 4.1.2) and utilized the optimized vegetation parameters produced in **Paper II** for Norway spruce and Scots pine. The shift from version 4.0 to 4.1 led to new possibilities to model managed forests through additional implementations of model code, but it also changed productivity and growth rates to some extent. An additional short evaluation of model performance was therefore included in **Paper III** to determine the extent of these changes, as well as to validate the new set of parameters developed in **Paper II** in terms of simulated height, diameter, volume and stand density. The concise evaluation also addressed some of the suggestions of improvements produced in **Paper II**. Two allometric parameters governing the relationship between diameter and height were calibrated for the five most common forest species in Sweden. In the second part of this study, forest management was set up to recreate the forest landscape in Sweden in 2020 based on the observed structure, including both managed forests and protected areas. Simulated daily climate data from the three Earth System Models (ESMs) MRI-ESM2.0, EC-Earth3-Veg, and GFDL-ESM4 provided input to the model in **Paper III** with a spatial resolution of $0.5 \times 0.5^{\circ}$.

Table 1. General themes of included papers which utilize LPJ-GUESS in the thesis.

Paper IV

Paper IV focused on the site Norunda in the boreal bioclimatic zone (Figure 2). This site is home to a monitoring station of the exchange of carbon between the vegetation and the atmosphere which is managed and run by ICOS Sweden. The forest at the site was clear felled in 2022. At the time of felling it consisted of a mixture of Scots pine and Norway spruce with smaller proportions of birch. The clear-felling of the forest at Norunda gave the opportunity to utilize LPJ-GUESS to model future alternative pathways of development of the re-growing forest stand. Hence, the model was set up to recreate the historical stand composition for the period 1901-2022. Following the clear cut in 2022, the model was set up to produce several plausible alternative options of reforestation, including a monoculture of Norway spruce, a monoculture of Scots pine, and a mixed stand of Norway spruce and Scots pine. An additional option where no clear-felling takes place, where the stand is retained as a set-aside, was also included. The influence of climate change on forest growth and carbon exchange was represented through two alternative trajectories (RCP 4.5 and RCP 8.5). The climate data input was derived from EC-Earth-SMHI-RCA4. For a complete description of the methods, see **Paper IV**.

Results

NIPF owner preferences for ES and future landscape development (Paper I)

Paper I showed that NIPF owners ranked the ES biodiversity, recreation, water quality and timber quality highly, indicating that these services were broadly considered valuable and important among all respondents. Differing preferences for maintaining ES among the respondents largely depended on factors such as certification of the estate and membership within a forest owner association. The analysis also showed that these factors were important for explaining differences among NIPF owners in preferred management practices (Figure 3).

Paper I also revealed that the majority of the respondents favor a future landscape development where mixed species stands and deciduous stands increase at the expense of monocultures in Sweden. This preferred transition was consistent with a generally high awareness of the need for climate change adaptation. 61.9% of the respondents had indicated undertaking some adaptive measures to reduce the sensitivity of their properties to climate-related damage. Certified forest owners who were also members of a forest owner association (CMs) more frequently made active management decisions to establish mixed and broadleaved stands (Figure 3).

Forest owners who lacked a certification of their property and who also were not part of a forest owner association (NCNM) were less interested in achieving outcomes associated with timber production, such as sustaining high forest growth rates, when compared to other owners in the sample (Figure 3). This category of owners also had lower preferences for utilizing forest-derived biomass as substitution for fossil-based materials when compared to CMs, indicating differences among forest owner categories in their preferred means of mitigating climate change.

When the rankings of all ES were considered simultaneously for each respondent in **Paper I** within the principal component analysis of *Theme: Ecosystem services,* forest owners within the NCNM category were more associated with higher rankings of recreation, biodiversity, berries & mushrooms, cultural heritage & water quality (Figure 2 in **Paper I**). The higher preferences of NCNMs for these ES were also consistent with their opinions of the future forest landscape composition. The PC analysis of *Theme: Future outlook* showed that NCNMs more strongly preferred less intensive management practices and maintenance of the natural characteristics of forests, when asked to consider the future forest landscape development. The PC analysis showed higher rankings of more old forest, more recreational forest, more set-asides, more retention forestry, more broadleaf forest, more mixed forest and more CCF in the future forest landscape among NCNMs when compared to the other categories of owners (Figure 5 in **Paper I**)

Figure 3. *Theme Ecosystem services*: Significant differences between four classifications of forest owners. **NCNM** = non-certified forest owners with no membership in a forest owner association. **NCM** = non-certified members, **CNM** = certified non-members, **CM** = certified members. A one step deviation toward the center indicates a significant lower rating of the ES, whereas a one-step deviation toward the edge indicates a significant higher rating. *Theme Forest management*: significant differences between the total sample frequency and four classifications of forest owners regarding performing management activities. A one step deviation from the green line indicates a significant difference between the group compared to the total sample. A deviation one step toward the edge indicates significantly more of the NIPF owners within the groups had taken the activity, and a deviation one step toward the center indicates that significantly fewer of the respondents had taken such an action. *Theme Future outlook*: significant differences are visualized as in *Theme Ecosystem services*.

The capacity of LPJ-GUESS to recreate managed forests of Sweden (Paper II & III)

LPJ-GUESS version 4.0 was evaluated in **Paper II** with the aim to determine the model potential for simulating managed forest structure at the regional scale in Sweden. In this study, the approach utilized a setup of management where the four most common forest types in Sweden were simulated, in order to assess the

deviation of modelled age-dependent standing volume from observed. For Norway spruce monocultures, the findings showed a simulated value of half of the observed for age classes within the age range of 21-80 years in southern and central Sweden (Table 4 & 5 in **Paper II**). For Scots pine monocultures, the simulated standing volume was higher than observed in all three regions of Sweden, with an overestimation ranging from 21-63% depending on region.

These findings motivated a sensitivity analysis of a set of parameters governing tree respiration, carbon allocation, and allometry, in order to determine if the speciesspecific settings for growth and development could be improved for Scots pine and Norway spruce. The sensitivity analysis was performed for four parameters, and settings were changed based on available literature references for two additional parameters. This resulted in a suggestion of new sets of parameters for both Scots pine and Norway spruce. The optimization resulted in improvements for Norway spruce monocultures with a deviation of simulated volume to observed of -4 to -5% in southern Sweden, and of 0.2 to 2% in central Sweden (Table 5 in **Paper I**). The updated parameters did however not improve estimated standing volume for Norway spruce in northern Sweden.

Similarly to Norway spruce monocultures, the capacity of the model to represent Scots pine monocultures improved with deviations from observed standing volume ranging from 9-13% in southern and 2-4% in central Sweden with the updated parameters. A positive bias of 30% for northern Sweden also indicated an improvement compared to the positive bias of 63% resulting from the original parameter settings (Table 4 in **Paper I**). The updated parameters did not result in consistent improvements for mixed coniferous forests, and produced an overestimation of standing volume for each given age class in each of the three regions. Simulated volume for the mixed spruce-birch forest was similarly higher than observed in southern Sweden, but similar to observations for the youngest age class in central and northern Sweden.

Paper III provided a complementing evaluation to **Paper II** with an updated model version (4.1.2). The evaluation was performed to determine the extent of changed productivity and growth resulting from the update to version 4.1.2, as well as to address the suggested improvement of calibrating two allometric parameters governing tree height and diameter development in the model. Five stand variables were assessed along a latitudinal gradient in Sweden: simulated stand height, diameter, stand density, standing volume and height to diameter ratio. In addition to Scots pine and Norway spruce monocultures, simulated birch, Pedunculate oak (*Quercus robur L.*) and beech (*Fagus sylvatica*) monocultures were also evaluated. Simulated height correlated well with observed across the range of forest types and locations, and ranged from 0.77 to 0.95 (Figure A5 in Appendix A, **Paper III**). The model tended to underestimate stand height at high observed heights, which was most noticeable for Scots pine in Dalarna and Skellefteå.

Simulated stand diameter correlated well with observed in Scots pine and Norway spruce monocultures, but the correlation was lower in birch stands, where it ranged from 0.54 in Dalarna to 0.74 in Västra Götaland (Figure A3 in Appendix A, **Paper III**). For birch monocultures, the model tended to overestimate simulated stand diameter and standing volume for most stands and areas. Oak monocultures were well represented both in terms of height and diameter, whereas the simulated height in beech monocultures were lower than observed.

The evaluation of simulated NEE in **Paper II** showed a lower simulated carbon uptake than observed for a middle-aged Norway spruce monoculture at the Hyltemossa site in southern Sweden (Figure 5 in **Paper II**). The high observed site productivity at Hyltemossa was challenging for the model to capture, as simulated average GPP for 2015-2019 was 15% lower than observed. However, simulated Reco was only 5% lower than observed. The model was also applied to the southern boreal forest site Norunda for 2015-2019 in **Paper II**, where it produced an average annual simulated GPP for the studied period which was 9% higher than the observed (Figure 5 in **Paper II**). Modelled Reco was 6% lower than the observed average for 2015-2019, hence also showing good agreement. However, the modelled NEE indicated the site to be a net C sink, whereas the observations showed consistent annual net C losses.

Future changes in ecosystem functioning and ecosystem service provisioning (Paper III)

The modelled emission scenario SSP1-2.6 in **Paper III** indicated future higher rates of NPP in 2081-2100 ranging from 4% (BAU) to 8% (EUPOL) at the national scale, with large variations depending on the region considered. NPP increased the most in northern Sweden, as did Rh, which showed significant gains in this region of 7- 12% (Figure 6). When considering the whole of Sweden, the forest policies AR and EUPOL indicated a significant positive net change in NEP in SSP1-2.6 (Table 2). The air temperature in this emission scenario showed peaks in each region around 2060, and higher air temperature and $CO₂$ during mid-century contributed to stimulating growth and productivity in stands which were ready for felling in 2081- 2100. This resulted in a significant gain in C biomass in all three policies (BAU, AR, and EUPOL) when compared to 2001-2020 (Table 2). Additionally, the stimulating effects of temperature and $CO₂$ on growth caused a higher vegetation demand for N, which reduced the soil N content, causing a reduction in leached N for all forest policies in SSP1-2.6 (Figure 4).

Paper III also showed that major changes in the functioning of ecosystems can be expected at the end of the century in the higher emission scenarios SSP3-7.0 and SSP5-8.5 in Sweden (Figure 5 $\&$ 6). The NPP increase ranged from 21-25% in

SSP3-7.0 to 25-29% in SSP5-8.5, with more pronounced gains in northern Sweden than in southern Sweden (Figure 6 & Figure B2 in **Paper III**). Greater rates of N mineralization and an improved water use efficiency contributed to enhancing NPP in these emission scenarios (Table 2). WUE was on average 30-34% higher in SSP3- 7.0 and 33-39% higher in SSP5-8.5 in 2081-2100 compared to in 2001-2020. CUE, indicating the efficiency with which atmospheric carbon is converted into biomass, changed over time in both scenarios of low, high and very high emissions. Despite the positive change in the magnitude of NPP in SSP3-7.0 and in SSP5-8.5, CUE was reduced in these emission scenarios, indicating that less carbon was retained in biomass relative to the amount taken up through photosynthesis (GPP) over the course of a year (Figure 5).

Higher annual air and soil temperatures, along with similar or higher annual precipitation amounts also stimulated soil C decomposition, which caused a gradual loss of C from soils to the atmosphere over time (Figure 4). The losses were significant in BAU, AR and EUPOL in both SSP3-7.0 and SSP5-8.5, despite the higher annual inflow of CWD. The resulting shift in carbon storage from belowground soil C to living biomass C was most pronounced in EUPOL in SSP5- 8.5. Despite the major changes in ecosystem functioning and the resulting higher rates of respiration, the net ecosystem production (NEP) increased in all parts of the country, with similar outcomes across forest policies for each given emission scenario. In SSP3-7.0 the NEP gains ranged from 20-30 $\rm g \, C \, m^2 \, year^{-1}$, and in SSP5-8.5 they were 20 g C m⁻² year⁻¹ (Table 2).

Higher N leaching rates occurred in the SSP3-7.0 and SSP5-8.5 emission scenarios, regardless of modelled forest policy (Figure 4). In these scenarios, enhanced N leaching resulted from increased soil N due to higher rates of N mineralization. Higher soil water percolation rates in areas which experienced increased precipitation may also have contributed to greater N losses.

As exemplified above, **Paper III** showed that the outcomes for EF and the provisioning of several ES strongly depended on the magnitude of climate change. However, changes in the forest landscape composition through altered management practices, manifested as alternative forest policies, influenced the forest landscape storm sensitivity. At the national scale, the increase in predisposition to storm damage in 2081-2100 ranged from 47% (SSP1-2.6) to 54% (SSP5-8.5) in BAU. For AR it ranged from 26% (SSP1-2.6) to 28% (SSP5-8.5) and for EUPOL from 20% (SSP1-2.6) to 24% (SSP5-8.5). Differences in forest landscape storm sensitivity between policies were most pronounced in southern Sweden, where EUPOL showed a reduction in predisposition to storm damage ranging from -12% (SSP1- 2.6), to -7% (SSP5-8.5). The higher proportions of Norway spruce monocultures in BAU contributed to an increased sensitivity in 2081-2100 of between 60% (SSP1- 2.6) to 76% (SSP5-8.5). The shift towards increased proportions of mixed-species and deciduous stands in the AR policy led to more modest increases in predisposition to storm damage, ranging from 4% (SSP1-2.6) to 11% (SSP5-8.5).

Table 2. Average values for 6 indicators of ecosystem functioning and 8 indicators of ecosystem services in Sweden. BAU = business as usual, $AR =$ Adaptation & Resilience, EUPOL = EU-policy. Historical = average for 2001-2020. Results for emission scenarios SSP1-2.6, SSP3-7.0, SSP5-8.5 represent averages for 2081-2100. Values in bold for SSP1-2.6, SSP3-7.0 or SSP5-8.5 are significantly different from historical values at a significance level of 5%. Note that significant differences between emission scenarios and forest policies in 2081-2100 are not shown.

Indicator	Histo rical	SSP1-2.6			SSP3-7.0			SSP5-8.5		
	BAU	BAU	AR	EUPOL	BAU	AR	EUPOL	BAU	AR	EUPOL
NPP (kg C m^{-2} year ¹)	0.51	0.53	0.55	0.55	0.62	0.64	0.64	0.64	0.65	0.66
Rh (kg C m^{-2} year ⁻¹)	0.43	0.44	0.45	0.46	0.51	0.52	0.54	0.53	0.54	0.56
NEP (kg C m^{-2} year ⁻¹)	0.09	0.09	0.10	0.09	0.11	0.11	0.11	0.10	0.11	0.10
CUE	0.45	0.44	0.44	0.45	0.40	0.40	0.41	0.39	0.39	0.40
Biomass C (kg C m ⁻²)	5.56	6.73	6.80	7.32	7.47	7.54	8.07	7.62	7.68	8.21
Potential harvest C $(kg C m-2)$	4.43	5.67	5.67	5.00	6.04	6.05	5.32	6.13	6.14	5.39
Soil C (kg C m^{-2})	12.2	11.9	11.9	11.8	11.8	11.8	11.7	11.8	11.7	11.6
Biomass C to soil C ratio	0.51	0.64	0.65	0.71	0.72	0.73	0.79	0.74	0.75	0.81
Rh to litter C input ratio	1.48	1.46	1.45	1.43	1.47	1.47	1.45	1.49	1.49	1.47
CWD C input (kg C m^{-2} year ¹)	0.07	0.08	0.07	0.08	0.09	0.09	0.10	0.10	0.09	0.10
Leached N (kg N ha ⁻¹ year ¹	6.26	5.21	5.09	5.15	6.79	6.63	6.66	7.41	7.17	7.21
Net N mineralization $(kq N ha^{-1} year^{-1})$	17.9	19.6	22.2	25.8	24.4	27.9	32.4	26.3	29.7	34.5
Predisposition to storm damage $(m-3)$ ha^{-1})	27.3	40.2	34.3	32.9	40.8	34.3	33.5	42.0	34.9	33.8
Water Use Efficiency $(g C kg-1 H2O)$	8.0	8.7	8.8	8.6	10.7	10.7	10.3	11.1	11.0	10.6

Plausible changes in C uptake in a southern boreal forest stand (Paper IV)

In **Paper IV** LPJ-GUESS was utilized to model future changes in C uptake for the most common forest types at a southern boreal site in Sweden. Two alternative emission scenarios, one moderate (RCP 4.5) and one very high (RCP 8.5) were considered for 2022-2100. The establishment and simulation of four alternative reforestation options enabled the comparison of their performance in terms of growth and carbon uptake over the course of the 21st century.

The findings of **Paper IV** indicated a higher C uptake in all of the four forest types in the emissions scenario RCP 4.5 when compared to in RCP 8.5 (Table 3 in **Paper IV**). The model also indicated that set-asides may remain carbon sinks for the majority of the 21st century, but that the continued carbon sequestration capacity for this forest type strongly depends on the magnitude of climate change, where a trajectory similar to RCP 8.5 is more likely to turn old forests carbon neutral or into C sources (Table 4 in **Paper IV**).

Figure 4. Long-term trends in the provisioning of 8 ES in production forests in Sweden, comparing annual averages for 2081-2100 to 2001-2020. BAU = business-as-usual, AR = Adaptation & Resilience, EUPOL = EU-Policy. SSP1-2.6 represents a low emission scenario, SSP3-7.0 a high, and SSP5-8.5 a very high emission scenario. Arrows pointing upwards indicate significant increases, horizontal arrows no significant change, and arrows pointing downwards show significant decreases at a significance level of 5%. The magnitude of the change is indicated by arrow size, and was estimated using Cohen's d. Small arrows indicate an effect size of < 0.2 , medium arrows an effect size between 0.2 and 0.8, and large arrows an effect size > 0.8.

Paper IV also provided information on the outcomes of clear-felling versus setting aside a forest stand, of relevance to stakeholders and forest owners who are considering the potential effects on mitigation and carbon sequestration. The results showed that the time required for the total cumulative C uptake to balance

cumulative C emissions at the clear-felled and regenerated site varied between 12- 16 years, depending on forest type and emission scenario. The Scots pine monoculture regenerated in 2022 required 56 years under RCP 8.5 and 61 years under RCP 4.5 in order for the cumulative NEE to match that of the alternative unfelled forest stand (estimated from 2022 onwards). This point of carbon parity was similarly reached after 73 years in the Scots pine-Norway spruce mixture, but was not reached for any of the remaining forest types in the study during the simulation period (2022-2100) (Figure 5 in **Paper IV**). In this case, the comparison was made assuming that 33% of the harvested C from the clear-felling ends up in long-lived wood products.

With the original parameter settings, Scots pine monocultures offered the highest C uptake of all alternative management strategies, with an average annual NEE of - 140 g C m^2 year⁻¹ given RCP $\overline{4.5}$ for the simulation period (2022-2100), and with -125 g C m-2 year-1 given RCP 8.5 (Table 3 in **Paper IV**). The Norway spruce monoculture option provided a lower C uptake compared to the Scots pine monoculture, with a NEE of -78 g C m⁻² year⁻¹ for RCP 4.5, and of -70 g C m⁻² year ¹ for RCP 8.5, which also resulted in a lower C biomass gain at the end of the century when compared to the Scots pine monoculture.

Figure 5. Long-term trends for six indicators of ecosystem functioning in productive forests in Sweden, comparing annual averages for 2081-2100 to 2001-2020. BAU = business-as-usual, AR = Adaptation & Resilience, EUPOL = EU-Policy. SSP1-2.6 represents a low emission scenario, SSP3-7.0 a high, and SSP5-8.5 a very high emission scenario. Arrows pointing upwards indicate significant increases, horizontal arrows no significant change, and arrows pointing downwards show significant decreases at a significance level of 5%. The magnitude of the change is indicated by arrow size, and was estimated using Cohen's d. Small arrows indicate an effect size of < 0.2, medium arrows an effect size between 0.2 and 0.8, and large arrows an effect size > 0.8.

Figure 6. Projected relative changes in net primary production (NPP), heterotrophic respiration (Rh), net ecosystem productivity (NEP), and in net nitrogen mineralization (N min), comparing 2081-2100 to 2001- 2020. BAU = business as usual, AR = Adaptation & Resilience, EUPOL = EU-policy. Due to the high similarities between SSP3-7.0 and SSP5-8.5, only results for SSP5-8.5 are presented. For heatmap visualizations for SSP3-7.0, see Figure B2 in Appendix B, Paper III.

Discussion

Future developments linked to NIPF owner preferences (Paper I & III)

Forest owners and managers will have to make decisions with limited knowledge of the magnitude of climate change. The available management alternatives need to be carefully considered to determine whether the management intentions are likely to be fulfilled given the realization of any plausible emission scenario (Yousefpour et al., 2017). **Paper I** indicated consistent preferences among the respondents of the survey for more mixed-species and broadleaf stands in the landscape. Establishment of mixtures are promoted by the Swedish Forest Agency (SFA) as a measure for risk-spreading, but such strategies also need to consider whether the species in the mixture remain suitable throughout the entire expected rotation period for the considered area (Wessely et al., 2024). The optimal annual air temperature for growth of Norway spruce saplings for high soil moisture conditions has been estimated to 7-9 °C (Marchand et al., 2023). These annual mean air temperatures will be exceeded by mid-century in southern Sweden in SSP3-7.0 and in SSP5-8.5 (Figure 4 in **Paper III**). Simultaneously, 61.9% of all respondents in **Paper I** indicated that they had taken some efforts to adapt their estates to climate change. This percentage is higher than previously found in other studies of climate change adaptation among NIPF owners in Sweden (Blennow et al., 2012), and seems to indicate that awareness of adaptation is increasing. However, it should also be considered in relation to the sample size of the study $(n = 232)$ which limits any firm conclusions regarding the national population of NIPF owners.

Paper I revealed that CMs more frequently established mixed species and deciduous stands on their properties compared to other owners in the sample, consistent with their stated preferences for the future. This category also showed a greater interest in taking part in the SFA meetings for forest owners, and hence might be more exposed to information about the benefits of establishing mixed and broadleaf stands. The findings of **Paper I** also indicated that factors such as membership in an FOA and certification were important for explaining differences among the respondents regarding preferences for ES relating to timber production, as has also been shown in earlier research (Johansson & Lidestav, 2011).

A transition towards more mixed and deciduous stands, at the expense of Norway spruce or Scots pine monocultures, would also be beneficial for a range of ES, including water quality, biodiversity, as well as for aesthetic and recreational values (Felton et al., 2016). The stated desires for change in forest landscape composition of the NIPF owners were also consistent with the stated rankings for these ES.

Fewer NIPF owners indicated that they had retained set-asides in southern Sweden, which might be related to the higher value of forest land in this region due to higher productivity (SNFI, 2022). Changes in the price of forest land may also occur in the future, as an outcome of the suggested changes in productivity due to climate change (**Paper III**), as well as due to changed demands for biomass (Lodin et al., 2020), potentially affecting the willingness of forest owners to retain voluntary set-asides. However, studies show that small-scale forest owners in Sweden generally value environmental and social values more highly than economic values (Lidestav & Westin, 2023) which suggests that at least in some areas, it is unclear whether this would translate into reductions in protected areas. Contemporary certification arrangements, as well as the EU Law of Nature Restoration which was passed in 2024, is also likely to hinder further intensification.

The principal component analysis for the theme *Ecosystem Services* in **Paper I** indicated significantly higher preferences for the ES biodiversity, recreation, berries & mushrooms, cultural heritage and water quality among the NCNM category. However, NCNMs also simultaneously had made lower efforts to retaining setasides, dead wood, forest edges, and establishing deciduous stands, which seems to indicate a more passive approach to forest management in general. This indicated that their expressed preferences for ES and for the future were not sufficiently strong motivating factors for achieving their stated desires for the future.

Model evaluation, LPJ-GUESS version 4.0 (Paper II)

The evaluation of the DVM LPJ-GUESS in **Paper II** based on model version 4.0 provided indications of the model performance in terms of its ability to recreate managed forest structure for productive forest land in Sweden. The optimization focused specifically on Norway spruce and Scots pine, which represent 79.4% of the stock on productive forest land (SNFI, 2024b). The optimized parameters were not developed for simulating unmanaged forests or set-asides, as the sensitivity analysis was made against observational data from production forests. Hence the new parameter settings for Norway spruce can be said to represent selectively bred varieties, used in contemporary production-oriented management in Sweden due to their higher growth rates, rather than unimproved material of Swedish origin (Liziniewicz et al., 2019). For Norway spruce monocultures, productivity was consistently increased, with improvements primarily in southern and central

Sweden, but with overestimation of standing volume in northern Sweden. For Scots pine monocultures, the suggested vegetation parameters improved the representation of forests across the country compared to the original parameter settings.

When the model was applied to the Hyltemossa site 2015-2019, the simulation with updated parameters for Norway spruce indicated a representative CUE of 0.41 for the period, consistent with findings for Norway spruce in the boreal zone (Harkonen et al., 2010). A re-simulation utilizing the original model parameters for Norway spruce reduced CUE to 0.30 , indicating that more of the C gained through annual photosynthesis was lost to respiration with the original parameter settings (*data not shown*). A station-based climate data set and detailed soil information was used as input to generate model estimates for GPP for the Hyltemossa site between 2015- 2019. The model underestimation of observed GPP by 15% was linked to the high site productivity of Hyltemossa, indicated by an estimated site index of 38.0 m at 100 years. Model results for the Norunda site further highlighted the challenge of capturing variation in site conditions based on climate and soil texture data input alone. The observed annual average NEE for 2015-2019 was 343 $g \text{ C m}^2$, which differed from the modelled estimate of -103 g C $m⁻²$. One of the main suggested causes for the observed continuous high C emissions from the site is a low soil N content, causing microbial decomposition of old soil organic matter, resulting in elevated Rh (Shahbaz et al., 2022). As stands age, reductions in litter quality have also been observed, which may decrease N mineralization and reduce stand photosynthesis, contributing to a higher NEE (Gower et al., 1996).

Model evaluation, LPJ-GUESS version 4.1 (Paper III)

The outcomes of the site-level evaluation of the coniferous mixture of Norway spruce-Scots pine at Norunda and the Norway spruce monoculture at Hyltemossa suggested a potential for calibration of the two allometric parameters kallom2 and kallom3, which was subsequently performed in **Paper III**, improving the height to diameter ratio primarily in Norway spruce monocultures.

The additional evaluation in **Paper III** was performed following the productivity changes presented in version 4.1. It indicated agreement of simulated standing volume with observations in Scots pine monocultures in the central Swedish county Dalarna, up to volumes of 300 m^3 ha⁻¹ given the optimized parameters. The volume was generally underestimated at volumes over 200 m^3 ha⁻¹ in the county. Despite the high correlation of simulated to observed height along the latitudinal gradient for forest types in **Paper III**, simulated height and volume was overestimated in young stands, as was also found in **Paper II**. This suggests a potential for further model improvement, which could include exploring establishment parameter values

related to initial planting size in the model, to determine their implications for early height and diameter development for a range of different sites. Implementation of growth-reducing abiotic or biotic disturbances, including browsing damage, bud frost damage, pest or pathogen damage in regenerations could also be options to consider (Bergqvist et al., 2014; Wallertz & Petersson, 2011; Holmström et al., 2018). Additionally, parameter values governing competition between young trees and grasses, herbs and shrubs can also be further explored.

The decision to disable patch-destroying disturbances during the transient simulations (2001-2100) in **Paper III** is likely to have increased historical modelled NEP, which was estimated for Sweden to 0.09 kg C m^2 . This can be compared to estimates for Scandinavia generated by an ensemble of 16 DVMS in the Global Carbon Project, where NEP ranged from 0.02-0.08 kg C $m²$ (Friedlingstein et al., 2022). However, the modelled average annual NEP for northern Sweden (2001- 2020) of 0.070 kg m⁻² agreed well with the two-year mean NEP of 0.087 kg C m⁻² $(2016-2018)$ of a forest landscape of 68 km² in northern Sweden (Chi et al., 2019). The changes in biomass C generated with LPJ-GUESS in **Paper III** ranged from 2.1 to 2.7 kg C in the very high emissions scenario SSP5-8.5 at the end of the century, which also agreed well with the estimated increase of 3 kg C m^2 provided by Anderegg et al. (2022) for boreal forests in Scandinavia under SSP5-8.5.

Benefits and risks of projected changes (Paper III & IV)

In the cold-limited boreal forests, the joint positive effects of higher temperatures and higher $CO₂$ has been shown to enhance carbon assimilation. Photosynthesis benefits from higher air temperatures through a stimulation of the enzymatic activity at the leaf-scale (Dusenge et al., 2019). The positive effects of increased $CO₂$ on photosynthesis can however be limited by low nutrient availability (Curtis & Wang, 1998). The model results in **Paper III** indicated reduced N limitations on growth in all emission scenarios due to the stimulating effects of temperature on decomposition and N mineralization (Figure 4). A higher N availability and associated productivity increase in SSP3-7.0 and in SSP5-8.5, found to be consistent across all forest policies, can lead to denser and darker forests (Gustafson et al., 2021). This can limit the occurrence of light-demanding dwarf-shrubs and negatively impact the provisioning of berries and food for ungulates (Hedwall et al., 2019).

The nemoral forest zone in Sweden will experience increased evapotranspiration due to higher air temperatures, which will limit soil moisture availability during the warmest parts of the year (Ruosteenoja et al., 2018). LPJ-GUESS accounts for potential effects of drought through stomatal closure during periods of low soil water content, resulting in downregulation of photosynthesis (Smith et al., 2014).

Despite the higher air temperatures and the implications for evapotranspiration in southern Sweden in SSP3-7.0 and SSP5-8.5, LPJ-GUESS did not indicate long-term reductions in NPP for BAU in this region, but showed consistent increases ranging from 14-16% for SSP3-7.0 and from 16-18% for SSP5-8.5, but with a gradient with low increases in the southernmost parts of the region (Figure 6 & Figure B2 in **Paper III**). This may partly be due to a higher WUE in these emission scenarios (Table 2). Additionally, a prolonged vegetation season may also have compensated for transient reductions in photosynthesis during periods of low soil moisture content. The SPEI index in **Paper IV** quantified for the Norunda site indicated an increased occurrence of severe drought years at the end of the century in the very high emission scenario RCP 8.5, which is likely to adversely affect forest growth in this area. This assessment also highlights the need for further analysis of the modelled influence of drought on productivity for additional areas of boreal and nemoral forests in LPJ-GUESS, to determine whether the model underestimates the limiting effects of drought on growth.

The higher NPP indicated by LPJ-GUESS produced higher estimated potential harvests, with similar suggested gains in the BAU and AR policies at the end of the century. However, the predisposition to storm damage increased more in the BAU policy, primarily due to higher proportions of storm-sensitive conifers such as Norway spruce in the forest landscape. In SSP1-2.6, AR provided a significantly higher mean annual NPP, mean annual NEP, and rate of nitrogen mineralization at the end of the century (2081-2100) when compared to 2001-2020, whereas BAU did not (Figure 4 $\&$ Figure 5). AR provided similar or higher values for these ES indicators also in SSP3-7.0 and in SSP5-8.5. This indicates that the preferred future increase in deciduous and mixed forests stated by forest owners in **Paper I** would benefit ecosystem functioning and ES provisioning at the regional scale, and may provide an important risk-spreading option through a decrease in the landscape storm sensitivity.

The importance of set-asides and protected forests (Paper III & IV)

Paper IV indicated that the cumulative NEE of several regenerated reforestation alternatives did not match the cumulative NEE of the set-aside forest stand over the course of the 21st century. The Scots pine monoculture reached the point of carbon parity by 2078 in the emissions scenario RCP 8.5 and by 2083 in RCP 4.5 under the assumption that 33% of harvested C ended up in long-lived wood products. The lower noted modelled NEE for the Norway spruce monoculture can partly be explained by the parameter settings governing growth and tree C allocation, which were not based on the optimized settings derived in **Paper II**. Peichl et al. (2023) showed that stand or landscape NEE is mainly determined by tree NPP. Few longterm measurements of NEE in Norway spruce stands exist in Sweden, and no data is available covering a full rotation. More research measuring the net C exchange of specific forest types would provide further insight into the carbon uptake in setasides and in reforestation alternatives and its dependency on stand age, local climate, soil conditions, N deposition and management decisions, and would also be valuable for model evaluation and optimization.

The findings of **Paper IV** suggest that policies and steering which motivate the retention of set-asides during the 2020s would potentially not only benefit habitat provisioning and conservation (Häkkilä et al., 2021; Gustafsson et al., 2020), but would also benefit carbon uptake over the short- to medium term, due to a reduction in the clear-felled area. The Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC) both require forest owners to retain 5% of the productive forest land on their properties as set-asides (FSC, 2020; PEFC, 2017). The FSC certification standard was revised in 2020, adding a requirement that an additional 5% of the certified property should be managed for the gradual development of environmental and social values. This could include transformation of stands to CCF, as well as further increasing the set-aside area, which would translate into short-term benefits for both carbon sequestration and storage (Law et al., 2018).

Paper IV also showed that the long-term response of set-asides to gradual warming results in higher respiration losses during the course of a year, which may completely offset the ecosystem carbon uptake or cause the stand to shift into a carbon source. The EUPOL alternative in **Paper II** represented a landscape development where the area of set-asides and unmanaged forests increased from between 9-12% (BAU, 2001-2020) to 18-24% (2081-2100) depending on the region considered. Despite this increase, the NEP of EUPOL at the end of the century was similar to the alternatives BAU and AR, which represented forest landscapes managed with higher intensity. The NEP for EUPOL was significantly higher in 2081-2100 when compared to BAU in 2001-2020 both in SSP1-2.6, SSP3-7.0 and in SSP5-8.5.

EUPOL provided the policy option which increased carbon storage the most in forests by 2081-2100 when compared to 2001-2020. The gain was on average 1.8 kg C m⁻² in SSP1-2.6 (increase of 32%), 2.5 kg C m⁻² in SSP3-7.0 (increase of 45%) and 2.7 kg C m⁻² in SSP5-8.5 (increase of 48%). In southern Sweden, the increase in biomass C in EUPOL was similar to BAU for all emission scenarios, but the storm sensitivity index indicated a lower risk of storm damage in this policy scenario at the end of the century. The expansion of set-asides and protected areas, where beech and lime (*Tilia cordata Mill.*) became more dominant, at the expense of storm-sensitive Norway spruce monocultures, contributed to a lowered storm index value in this region. Such a transition of tree species dominance suggests that setasides in southern Sweden would provide multiple benefits both in terms of increased carbon storage, sustained carbon sequestration, storm stability, and habitat provisioning (**Paper II** & **IV**).

Forest owners who lacked certification as well as membership in a forest owner association (NCNM) in **Paper I** stated higher preferences for forests similar to the modelled EUPOL alternative. They preferred the use of continuous cover forestry and increasing the area of old forest over time. However, the stated preferences of the NCNM category were not reflected in their survey responses regarding actual management practices. The results for *Theme: Forest management* in **Paper I** indicated that NCNMs had made less efforts towards retaining set-asides and dead wood on their estates and similar efforts in transforming stands to CCF when compared to the average owner in the sample.

Limitations of the approaches

Assumptions and limitations in Paper I

The proportional stratified sampling approach was used in **Paper I**, leading to the distribution of 750 invitations to partake in the questionnaire in each of the four bioclimatic zones of Sweden (nemoral, boreonemoral, southern boreal and northern boreal). Despite the relatively low sample size $(n = 232)$, the statistical analysis showed significant results within all three themes of the study. The trends which emerged indicated a spread in opinion where the two categories NCM and CNM showed greater similarities, and the two categories NCNM and CM were more polarized in their opinions. A larger overall sample size would have likely resulted in clearer trends also between the two categories NCM and CNM.

Assumptions and limitations of the modelling approaches (Paper II, III & IV)

Simulations in Paper II

The sensitivity analysis of **Paper II** was performed for the central Swedish county Örebro. It was based on a comparison of simulated standing volume against observed at the county level, which included changing the parameter values for a set of 4 parameters, one-at-a-time, to determine the influence of the change on the model output. The simulations performed in the optimization assumed that both Scots pine and Norway spruce monocultures retained one single dominant cohort in the even-aged stands. The optimization also assumed a change in the leaf to sapwood area ratio (k latosa) with latitude, resulting in more carbon stored in leaves compared to in stems for trees on higher latitudes. Hence, the setting for k_latosa

was raised one step for northern Sweden and lowered one step for southern Sweden. The basis for the changes to parameters not included in the sensitivity analysis and the range of the parameter values included is provided in Appendix A**, Paper II**. Patch-destroying disturbances were turned off in the simulations in **Paper II**, which implied that all forests were assumed to be undamaged. The Opt_w simulations provided a weighted mean standing volume for each forest type based on multiple simulations on different soils. The weighting of these results assumed that Scots pine is more frequently established on drier soils, and that Norway spruce is established on soils with higher water holding capacity, in line with contemporary silvicultural recommendations (Table A3 in Appendix A, **Paper II**).

Simulations in Paper III

The managed production forests which were simulated in **Paper III** were not influenced by naturally occurring disturbances, and for this reason we could not take losses of C and N resulting from such events in these systems into account. Our model simulations can therefore be said to represent an 'optimal outcome'. This also partly explains the higher estimated NEP for the historical period (2001-2020) compared to estimates for Scandinavia (Friedlingstein et al., 2022). A stochastic patch-destroying disturbance setting was enabled in set-aside and protected areas. However, this setting implies that all forest types have an equal likelihood of being destroyed. Stands which naturally exhibit greater resistance to disturbances, such as mixtures, would be equally affected compared to stands which are known to be more sensitive to damage, for example Norway spruce monocultures. Moreover, the setting does not represent an increased probability of damage when climate conditions become more extreme. For this reason, it was considered unsuitable for use in production forests, and we instead quantified potential damage from disturbances as the risk of storm damage, estimated as an index for storm predisposition.

The simulations performed in **Paper III** assumed that rotation periods were not altered over time in response to changes in productivity which result from a gradually changing climate in each emission scenario. Hence, the forest age structure did not shift towards younger or older stand ages as an outcome of forest management. The development and implementation of a setting where a stand is felled based on a threshold level for tree biomass C could provide a parsimonious solution which would result in an altered rotation period if the productivity rates change during the simulation.

Climate data originating from the three ESMs MRI-ESM2.0, EC-Earth3-Veg and GFDL-ESM4 were used as input to LPJ-GUESS, with averages of output from these model runs presented in the manuscript, in order to reduce climate-related uncertainty. Differences in the equilibrium climate sensitivity (ECS), in other words the temperature response to a doubling of atmospheric $CO₂$ at equilibrium, varied between the ESMs included. The ensemble mean ECS of the three included ESMs was close to the multi-model mean ECS of the CMIP5 and CMIP6 ensembles (Meehl et al., 2020).

In **Paper III**, all forest types were simulated one at a time in the grid cells were they naturally occur. In order to achieve the landscape composition representing the forest policy AR, the area of mixed forest and mixed coniferous forest received greater weight in 2081-2100. In EUPOL, the area of protected forest and Norway spruce managed with CCF received greater weight. The simulations assumed that the transitions of forest types hypothetically started in 2021 and were fully successful by 2081. Drössler et al. (2014) used an individual tree-based model to estimate the transition period length and changes in productivity, when converting Norway spruce monocultures to CCF, and found a plausible time period of 50 years in central Sweden, during which productivity can decrease by 30%.

Simulations in Paper IV

The simulations of Scots pine and Norway spruce in **Paper IV** were based on the original model parameters, but were performed with the updated model version 4.1, which has exhibited changes in productivity compared to model version 4.0. Despite these productivity changes, the simulated height and diameter at breast height of Scots pine in the mixed coniferous stand at Norunda in **Paper IV** was similar to the simulated height and diameter in **Paper II** where the optimized parameters were used. On the other hand, Norway spruce in the stand exhibited higher height and diameter also at higher stand densities. Similarly, to in **Paper II** and in **Paper III**, stochastic patch-destroying disturbances were turned off during these simulations.

Conclusions

This thesis has provided an in-depth analysis of the diverse opinions of NIPF owners in Sweden regarding the utilization of forests, an evaluation of LPJ-GUESS in simulating managed forest ecosystems, and model projections of the impacts of hypothetical forest policy changes and climate change on ES and ecosystem functioning. Additionally, it has offered insights into the outcomes of different reforestation strategies on carbon sequestration and storage in a southern boreal forest stand under alternative future climate scenarios.

Paper I found varied opinions among NIPF owners in Sweden regarding how forests should be utilized. However, the responses indicated a consensus for a high perceived value of the ES biodiversity, timber quality, water quality and recreation. Additionally, the respondents showed consistent preferences for more deciduous and mixed forest stands in the future. Differing opinions regarding which values should be prioritized were mainly related to whether the owners were certified and members of a forest owner association. These findings provided relevant information to stakeholders and policymakers on how NIPF owners differ in their opinions of which values matter, as well as their preferences for forest management. Further research could explore the link between stated preferences of NIPF owners and their knowledge of trade-offs and synergies between ES, as well as how opinions are influenced by risk awareness.

The capacity of LPJ-GUESS to recreate managed forest ecosystems was evaluated in two studies in this thesis, resulting in an enhanced understanding of the limitations and strengths of the model to simulate forest structure and carbon exchange in Sweden. The results of the first study indicated agreement between simulations and observations of standing volume for monocultures of Norway spruce and Scots pine in southern, central and northern Sweden, following an optimization of a set of vegetation parameters for both species. The site-scale evaluation of carbon uptake indicated an overestimation of modelled GPP of 9% compared to observed for a central Swedish site, and an underestimation of GPP of 15% for a southern Swedish site. A complementing evaluation in the second study of simulated diameter, height, standing volume and stand density for the five most common tree species in Sweden further confirmed the ability of the model to simulate the structure of managed production forests. However, the standing volume of young forests were generally overestimated for all PFTs, showing the need to revisit establishment parameter values governing planting size, as well as parameters governing competition between the field layer and regenerating trees.

The third study in this thesis provided insight into plausible outcomes for a range of ES and for ecosystem functioning in Sweden, considering both hypothetical changes in forest policy in Sweden and the influence of climate change at the end of the century. The three emission trajectories SSP1-2.6, SSP3-7.0 and SSP5-8.5 were modelled, representing a low, high and a very high climate impact, respectively. This study showed that trajectories corresponding to SSP3-7.0 and SSP5-8.5 would result in major changes in ecosystem functioning and ES provisioning in production forests in Sweden, with end-of-century increases in NPP ranging from 21-29%. NPP was mediated by higher air temperatures, causing a prolonged vegetation season, higher net N mineralization, as well as increases in WUE, on average between 30- 34% in SSP3-7.0 and of 33-39% in SSP5-8.5. The low emissions scenario SSP1- 2.6, where air temperatures peak by mid-century, indicated changes of lower magnitude, as well as decreases in N leaching across the country. The conservationoriented forest policy EUPOL resulted in the highest biomass C gains due to an expansion of set-asides and protected areas in all emission scenarios, with synergistic benefits for net N mineralization and habitat provisioning. EUPOL was the only policy which resulted in decreases in the predisposition to storm damage in southern Sweden when compared to the contemporary forest landscape in 2001- 2020. The predisposition to storm damage increased by between 61-76% in BAU and by 4-11% in AR for this region. Although the model projections rely on assumptions and are associated with uncertainties, the direction and magnitude of the changes can provide policymakers and stakeholders in forestry with valuable information. As these simulations were not able to account for the influence of disturbances on ES provisioning, they should be considered as an optimal outcome. Future studies with LPJ-GUESS should aim to further explore whether the model underestimates the effects of drought on productivity and mortality, and potential impacts of other disturbances on ecosystem C.

The fourth study of this thesis provided information on the plausible outcomes of establishment choices on C uptake and emissions in a southern boreal forest. The simulations performed at the site Norunda showed the impact of RCP 4.5 and RCP 8.5 on four alternative reforestation options, as well as on an uncut set-aside baseline. The findings indicated an increased C uptake in monocultural stands consisting of Norway spruce and Scots pine as well as in the mixed stand of sprucepine, when comparing the time periods 2022-2050 to 2076-2100. The net C sink was reduced towards the end of the 21st century in the uneven-aged Norway spruce stand and in the set-aside forest stand (NCNM). These reductions were more pronounced in the very high emission scenario RCP 8.5. These model projections have provided increased knowledge of the impacts of reforestation and climate change on carbon sequestration and storage in this region. This information can be of use to forest owners and stakeholders who are considering short and long-term effects of different management approaches.

Model projections can contribute to a broader understanding of how varying climatic and policy scenarios influence ES and carbon dynamics in forest ecosystems. This may offer valuable insights to policymakers and forest owners, aid in making informed decisions, and support sustainable forest management.

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