Coupling carbon sequestration of forests and croplands with ecosystem service assessments

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Abstract

The carbon (C) cycle of forests and croplands contributes to human wellbeing by regulating climate, producing food, timber and energy, and providing habitats for species. In the future, climate change and the increasing use of natural resources may threaten the availability of these ecosystem services (ES). Sustainable environmental management requires spatially explicit information on the impacts of human activity on ES. Mapping C stocks and changes using overly simplified, land cover -based proxies might cause inaccuracy to the ES estimates.

This dissertation introduces different approaches to quantify the C budget of terrestrial ecosystems in boreal and temperate regions. The overall objectives were to couple the estimates of C sequestration with ES assessments and to investigate the spatial variation of climate regulation in relation to other ES indicators. The specific objectives were 1) to examine the drivers of C sequestration of forests and croplands using process-based models, 2) to develop a framework for mapping the current status of forest C budget across boreal landscapes and 3) to identify and map synergies and trade-offs between regulating and provisioning ES in response to alternative forest management practices and climate change.

Reasons for the observed decline in the C concentration of Finnish croplands on mineral soils in 1974-2009 were investigated in paper I. The soil C model applied was able to estimate the changes in the C stock of soil reliably based on information about the climatic conditions and the chemical composition of litter. The soil C stock of Finnish croplands declined in 1974-2009 because they produced less litter than the pre-cropland forests and this agricultural litter decomposed more rapidly. According to the sensitivity analysis, climate warming has not been a significant reason for the observed C loss yet.

The effects of different climate change and forest management scenarios on the growth and C budget of forests were examined across a long latitudinal gradient in Europe in paper II. The simulated productivity of forests increased substantially in 2005-2095 throughout the studied gradient. Whole-tree harvesting caused a loss of soil C independent of the model used, demonstrating this pattern to be robust. Biomass growth was unexpectedly enhanced as a result of harvest residue extraction, revealing that the post-harvest microbial controls of stand productivity require further research. The results indicated that in the short-term, forest management affected the C budget more than climate change.

An approach to quantify the C budget of boreal forested landscapes was developed in paper III by combining simulation modelling with extensive information on stand characteristics. The mapping framework produced reliable estimates of the current status of C budget in the study region in southern Finland. It was developed further in paper IV to map projections of climate regulation, biomass production and dead wood production in response to alternative forest management practices. Regular harvesting, affecting the stand age class distribu tion, was a key driver

of the C stock changes in the studied catchment during the simulation period 2012-2100. Extracting branches and stumps enhanced energy-wood production but caused trade-offs for climate regulation, dead wood production and, consequently, forest biodiversity.

The mapping framework developed in this dissertation allows for visualizing ES related to C cycling as high-resolution maps to support sustainable land use planning. It contributes to bridging the gap between ecosystem service assessments and simulation modelling. In addition, the simple structure of the approach is an advantage in comparison with some detailed simulation models. The modular structure of the mapping framework enables its flexible development with new data and models in the future.

Acknowledgements

This dissertation was mainly funded by Maj and Tor Nessling Foundation through the project "Coupling carbon sequestration of forests and croplands with ecosystem service assessments". The work was also supported by the Academy of Finland through Strategic Research Council project "Integrating biodiversity conservation and carbon sequestration in the changing environment", the Life+ Instrument of the European Union through "Climate Change Indicators and Vulnerability of Boreal Zone - Applying Innovative Observation and Modeling Techniques" and the Ministry of Agriculture and Forestry through project "Development of a calculation method for carbon stock changes in agricultural soils".

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Helsinki, August 2020
Anu Akujärvi

Contents

List of original publications

This thesis is based on the following publications, referred to in the text by their roman numerals:

I Akujärvi, A., Heikkinen, J., Palosuo, T. & Liski, J. 2014. Carbon budget of Finnish croplands – effects of land use change from natural forest to cropland. Geoderma Regional 2: 1-8.*

II Akujärvi, A., Shvidenko, A. & Pietsch, S.A. 2019. Modelling the impacts of intensifying forest management on carbon budget across a long latitudinal gradient in Europe. Environmental Research Letters 14: 3.

III Akujärvi, A., Lehtonen, A. & Liski, J. 2016. Ecosystem services of boreal forests – Carbon budget mapping at high resolution. Journal of Environmental Management 181: 498-514.

IV Akujärvi, A., Repo, A., Akujärvi, A.M. & Liski, J. 2020. Bridging mapping and simulation modelling in the ecosystem assessments of boreal forests: effects of bioenergy production on carbon dynamics. Manuscript in review.

* This publication has been previously used in: Heikkinen, J. 2016. Carbon storage of Finnish agricultural mineral soils and its long-term change. Department of Agricultural Sciences Publications 44.

Contributions

I AA and JL designed the study. AA and JH prepared the data. AA conducted the model simulations with the support of co-authors. AA was responsible on the preparation of the manuscript, with all authors commenting and contributing to writing.

II All authors designed the study. AA prepared the data, with the support of co-authors. AA conducted the model simulations and data analysis. AA prepared the manuscript, with all authors commenting.

III AA and JL designed the study. AA prepared the data with the support of AL. AA was responsible on the preparation of the manuscript, with all authors commenting.

IV AA, AR and JL designed the study. AA prepared the data with the support of AMA. AA analysed the results, with AR and JL contributing. AA prepared the manuscript, with AR and AMA commenting and contributing to writing.

Abbreviations

BGC-MAN	BioGeoChemistry Management Model
C	Carbon
CICES	Common International Classification of Ecosystem Services
CH_4	Methane
CO_2	Carbon dioxide
CWD	Coarse Woody Debris
ES	Ecosystem Services
GPP	Gross Primary Production
IPCC	Intergovernmental Panel on Climate Change
MS-NFI	Multi-Source National Forest Inventory
MOTTI	A statistical forest stand simulator
N	Nitrogen
NEP	Net Ecosystem Production
NIR	National Inventory Report under the UNFCCC and the Kyoto Protocol
NPP	Net Primary Production
RCP	Representative Concentration Pathway
R_a	Autotrophic Respiration
R_h	Heterotrophic Respiration
SOC	Soil Organic Carbon
SOH	Stem-only harvest
SOM	Soil Organic Matter
UNEP	United Nations Environment Programme
WTH	Whole-tree harvesting
Yasso	Litter and soil carbon model

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1 Introduction

1.1 Background and motivation

Forests and croplands provide an array of goods and services that are essential for human well-being. They are commonly called ecosystem services (denoted hereafter as ES) (Costanza et al., 1997). In the future, climate change and the increasing use of natural resources may threaten the availability of ES in the boreal and temperate regions (Foley et al., 2005). The growing demand for renewable energy is associated with intensifying forest management practices, which might risk the long-term carbon (C) sink capacity and productivity of forests (Harmon et al., 1990; Hudiburg et al., 2011; Lamers et al., 2013). Increasing biomass removal also reduces the amount of dead wood, vital for several endangered species (Bouget et al., 2012). To manage ecosystems sustainably, spatially explicit information on the impacts of human activity on the state and trends on ES is called for (Maes et al., 2012a). This dissertation first introduces different approaches to estimate the C budget of croplands and forests on mineral soils. Second, it presents a mapping framework to couple C sequestration with ES assessments.

Terrestrial ecosystems are the largest storage of organic C on earth and sequester about 30% of the annual CO_2 emissions globally (Le Quéré et al., 2018). A part of the C stored in forests and croplands is used as food, raw materials and renewable energy. Ecosystems regulate climate by exchanging CO_2 between the atmosphere, biomass and soil. Increasing the C stocks of biomass and soil by avoiding deforestation and improving agricultural and forest management practices is a means of mitigating climate change (Freibauer et al., 2004; Nabuurs et al., 2017). There is growing evidence that management practices enhancing C sequestration and storage might also benefit biodiversity conservation (Griscom et al., 2017; Jantke et al., 2016). Human activities often cause spatial and temporal trade-offs or synergies between ES and biodiversity (Rodriguez et al., 2006). To support sustainable land use planning, approaches to quantify the effects of alternative land management practices on ES at the landscape level are needed.

The C cycling of terrestrial ecosystems has been studied extensively in the recent decades (e.g. Karhu et al., 2014; Luyssaert et al., 2007; Malhi et al., 1999). Although the biogeochemical and human drivers of the C cycling are rather well known this knowledge has not been fully implemented in the mapping and assessment of ES. C storage and fluxes are often mapped based on simple land cover -based proxies (Adhikari and Hartemink, 2016; Eade and Moran, 1996; Kareiva et al., 2011; Naidoo et al., 2008; Nelson et al., 2009; Sutton and Costanza, 2002). They have been shown to fit poorly to primary data on ES, with a risk to mislead management strategies (Eigenbrod et al., 2010; Stephens et al., 2015). Moreover, ignoring the complex feedbacks of management interventions and environmental conditions to the C cycling (Birkhofer et al., 2015; Boerema et al., 2017; Smith et al., 2013) as well as the fine-scale characteristics of landscapes (Hou et al., 2013) may add uncertainty to the estimates. The ES assessments could be improved significantly by combining scientifically sound information on climate regulation with high-resolution data on landscape characteristics (Ausseil et al., 2013; Crossman et al., 2013). This dissertation introduces a novel approach for quantifying the C budget of boreal forests and croplands at the landscape level, compatible with the assessment of other ES and biodiversity.

1.2 The concept of ecosystem services

ES are defined as the direct and indirect contributions of ecosystems to human wellbeing (Costanza et al., 1997; MA, 2005). The term ES was first introduced in the early 1980s (Erlich and Erlich, 1981). Scientific research, applications and policy of ES has expanded enormously since the outcome of two seminal publications by Daily (1997) and Costanza et al. (1997) about the value of the world's natural capital (Costanza et al., 2017). The concept of ES has received global attention e.g. in the UNEP supported projects Millennium Ecosystem Assessment (MA, 2005) and The Economics of Ecosystems and Biodiversity (TEEB, 2010). It has also been adopted in global and continental policy pursuing the goals of sustainable development and halting the biodiversity loss (CBD, 2010; EC, 2006; EC, 2011).

ES can be classified to four broad types: provisioning, regulating and maintenance services, cultural services and supporting services (MA, 2005). It is noteworthy that biodiversity and primary production are ecosystem functions that underlie all services (Costanza et al., 2017). A "cascade" from ecosystem structures to functions and then to benefits and values has been proposed as a framework to conceptualise ES (Potschin and Haines-Young, 2017). Costanza et al. (2017) criticised the cascade model of a too narrow definition of value and an oversimplification of the complex connections between ecosystem processes, functions and benefits to humans. They argued that services equal benefits and that the social and ecological systems interact non-linearly and dynamically to produce ES (Costanza et al., 2017). The Common International Classification of Ecosystem Services (CICES) has been developed to enable uniform accounting of the natural capital. In Finland, a national ES indicator framework was developed by modifying the common typologies to apply better in the national conditions (Mononen et al., 2016).

This dissertation studied ES linked to C cycle: crop, timber and energy-wood production, climate regulation, provisioning of dead wood and primary production (Table 1). These ES were selected because they could be derived from the basic C budget outputs of the models used.

Table 1. The studied ecosystem functions and services related to C cycle according to the typology by Costanza et al. (1997) in Papers I-IV.

SECTION	ECOSYSTEM FUNCTION	ECOSYSTEM SERVICE	PAPER
Provisioning	The portion of gross primary production extractable as food	Crop production	I
Provisioning	The portion of gross primary production extractable as raw materials	Timber and energy-wood production	II-IV
Regulating	Regulation of global temperature and precipitation	Greenhouse gas / climate regulation	I-IV
Supporting	Provisioning of habitat, biodiversity	Habitat for dead wood dependent populations	IV
Supporting	Storage, internal cycling, processing, and acquisition of nutrients	Nutrient cycling, primary production	II

1.3 Contributions of carbon cycle to human wellbeing

Terrestrial ecosystems regulate climate through C sequestration and storage to biomass, litter and soil (Fig. 1). The cycling of C contributes to human wellbeing also directly because part of the gross primary production (GPP) is extracted as food and raw materials. The C stock of biomass, and the change in this stock, is determined by the balance between C uptake from the atmosphere in photosynthesis and the release through autotrophic respiration (R_a), natural mortality and biomass harvesting. In croplands, a remarkable proportion of the biomass is extracted annually in harvest which reduces the amount of dead organic matter entering the soil compared with forests (Hay, 1995). In forest ecosystems, natural disturbances, such as storms and bark beetle outbreaks cause natural mortality and the generation of coarse woody debris (CWD). Dead wood is an important habitat for several threatened forest species, like birds (Virkkala et al., 2016), insects (Martikainen et al., 1999) and fungi (Penttilä et al., 2004), thereby safeguarding biodiversity. In managed forests, harvest residues and retention trees are the main source of CWD. The amount of CWD is substantially higher in natural forests than in managed forests (Siitonen, 2001).

Soil organic carbon (SOC) consists of the litter and soil C pools which can be classified to chemical compound groups according to their decomposition rates (Trofymow et al., 1995). SOC is strongly correlated with soil nutrient availability and water holding capacity, supporting agricultural productivity in dry conditions (Williams and Hedlund, 2014). The soil C stock and change depend on the balance between the C input from plant residues, root exudates and organic amendments, and the output from decomposition, erosion and leaching. In decomposition, C is released from the soil through heterotrophic respiration (R_h) and transferred between the chemical compound groups, resulting to the formation of recalcitrant humus (Prescott, 2010). On mineral soils, decomposition produces CO_2 through aerobic soil respiration. On moist or-

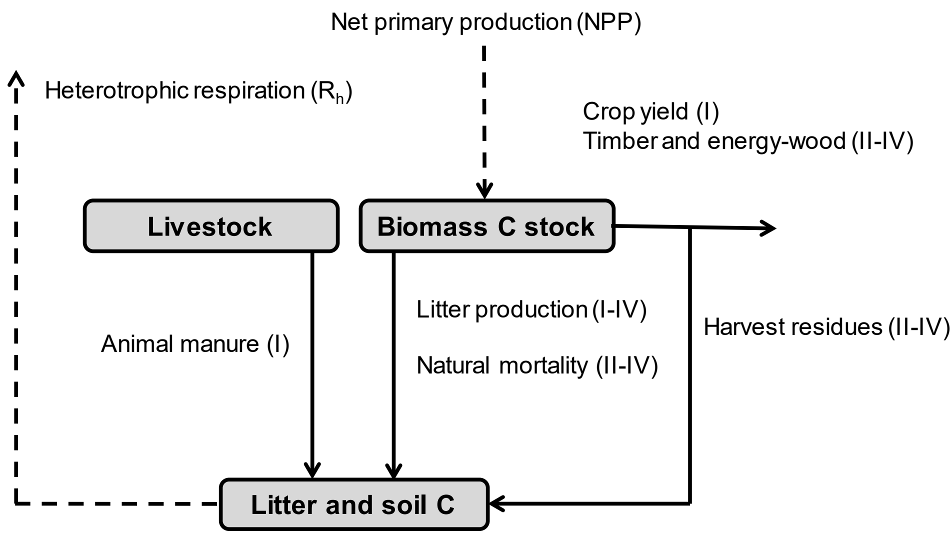

Figure 1. The pools and fluxes of carbon in forest and agricultural ecosystems studied in Papers I-IV. The gaseous and material fluxes are denoted with dashed and solid lines, respectively.

ganic soils, such as drained peatlands, methane (CH_4) is produced through an anaerobic pathway. Methane is a strong greenhouse gas having 28 times the global warming potential of CO_2 over a 100-year time horizon (Myhre et al., 2013). Net ecosystem production (NEP) is the net C uptake of ecosystem after subtracting R_h from GPP. Climate, land use changes and management practices all drive the changes in the C budget (i.e. stocks and changes) of terrestrial ecosystems (Bonan, 2008; Kasimir et al., 2018; Luyssaert et al., 2007).

Both biogeochemical cycles such as photosynthesis and respiration (Law et al., 2002) and biophysical mechanisms such as evapotranspiration, the formation of biogenic volatile organic compounds (BVOCs) and surface albedo (Anderson-Teixeira et al., 2012; Naudts et al., 2016) affect the climate regulation of terrestrial ecosystems. Forest evapotranspiration and albedo were accounted for by the biogeochemical model used in paper II. They were not included in the structure of the empirical forest productivity model used in papers III-IV. In this dissertation, the climate regulation service was quantified in terms of the C budget of mineral soils. Organic soils are, however, a large source of greenhouse gas emissions in Finland (see section 3.1). Organic soils were excluded because the soil C models used were applicable only on mineral soils. In addition, estimating a complete greenhouse gas budget of forests and croplands would have been out of the scope of this study.

Environmental conditions such as climate, nitrogen deposition and soil type, as well as the ecophysiology of individual plant species affect the responses of ecosystems to management interventions (Thornley and Cannell, 2000). Climate warming has been predicted to enhance biomass growth and the production of dead organic matter especially in the northern latitudes of Europe, given adequate soil moisture and nutrient availability (Lindner et al., 2010). It is, however, uncertain whether the net C uptake of ecosystems would rise. Heterotrophic respiration could increase because of higher soil temperature which would partly offset the C gain from the higher productivity of forests (Davidson and Janssens, 2006; Frey et al., 2013; Pries et al., 2017). In croplands, the C loss from the soil could accelerate (Schlesinger and Andrews, 2000; Wiesmeier et al., 2016).

Land use changes and management interventions influence the biogeochemical cycles of forests and croplands (Jandl et al., 2007; McLauchlan, 2006). For example, converting forest to cropland reduces the C stock of soil substantially (Guo and Gifford, 2002). Tillage has effects on the soil temperature and, consequently, on the decomposition rate of soil organic matter (SOM) (Reicosky et al., 1997). Crop rotation, avoiding bare fallow and adding organic manure to the soil are means to increase the C stock of soil (Freibauer et al., 2004; Smith et al., 2008). In forests, increasing the harvest intensity through shorter rotations (Harmon et al., 1990), or biomass extraction for bioenergy production (Hudiburg et al., 2011) reduce the input of C and nutrients to the soil. This soil degradation might lead to diminishing site productivity and C sink capacity (Schlamadinger et al., 1995; Schulze et al., 2012). In this dissertation, the impacts of land use change and alternative management practices on climate regulation were investigated using simulation models (Papers I, III and IV). Process-based models enable the simulation of complicated feedbacks between the atmosphere, plants and soil, accounting for various site and climate conditions (Landsberg, 2003; Mäkelä et al., 2000).

1.4 Quantifying ecosystem services in landscapes

Mapping is defined as "the organisation of spatially explicit quantitative information" (Englund et al., 2017). Mapping serves as a decision-support tool in monitoring and managing the spatial and temporal flows of ES, efficient resource allocation and supporting governance and management (Crossman et al., 2013; Hauck et al., 2013). According to recent reviews, the methodologies of mapping can be divided into two broad categories: ecological production function and benefit transfer methods (Andrew et al., 2015; Crossman et al., 2013; Englund et al., 2017). Ecological production function methods encompass direct mapping (e.g. geographical survey and census), empirical models, simulation and process-based models and logical models. They enable the estimation of ES supply at a specific location with varying biotic and abiotic conditions. Benefit transfer methods include extrapolation and data integration. The latter two methods are proxy-based; e.g. they estimate the value of ES at one context based on its value in a different context (Andrew et al., 2015).

Landscapes have been studied primarily in the scientific fields of landscape ecology, geography and spatial planning (Conrad et al., 2011). The field of landscape ecology has traditionally had a nature-centred view on landscape. The relationships between ecological processes and patterns have been in the focus of landscape ecology (Pickett and Cadenasso, 1995; Turner, 1989), and people have been long seen as a cause of landscape change (Termorshuizen and Opdam, 2009). In spatial planning, however, people are acknowledged as a part of the landscape and it is supposed that landscape change should benefit them (Termorshuizen and Opdam, 2009). In the emerging field of ES, both the intrinsic value of nature and the various benefits it has for human society are recognized (Potschin and Haines-Young, 2017). In the recently proposed ES glossary, landscape was defined as a mosaic of land cover viewed at a scale depending on its ecological, social, cultural-historical or economic importance (Potschin et al., 2016). In this dissertation, region was defined as an area of land that has a common climate and vegetation type (Papers I-II). Landscape level is referred to as a mosaic of forest types whose spatial scale is kilometres to tens of kilometres (Papers III-IV).

Climate regulation and biomass provisioning were the two most common ES mapped according to a recent review about mapping ES at the landscape level (Englund et al., 2017). This probably reflected the perceived importance or the ease of mapping these ES. Logical and empirical models and extrapolation were the most commonly used mapping methods. Only twelve percent of the cases mapping biomass provisioning and six percent of the ones mapping climate regulation were validated with empirical data. The poor calibration of the models and lack of validation seriously limit their applicability in land use planning (Boerema et al., 2017; Englund et al., 2017; Seppelt et al., 2011). Nevertheless, integrated modelling has become increasingly popular in ES mapping in recent years (e.g. Bagstad et al., 2013; Boumans et al., 2015; Turner et al., 2016). Integrated modelling utilises spatially explicit data on landscape characteristics and process-based modelling of the social-ecological system. According to Costanza et al. (2017), it addresses the complex and dynamic interactions between the ecosystems and human activity that lead to ES production.

1.5 Thesis objectives and scope

The aims of this dissertation were 1) to couple the C sequestration of boreal forests and croplands with ES assessments and 2) to estimate the spatial variation of climate regulation in relation to other ES and biodiversity. The specific objectives were to

1. Investigate the impacts of land use change and land management on the C cycle of forests and croplands at a regional scale (I and II),
2. Identify synergies and trade-offs between regulating and provisioning ES in response to alternative forest management practices and climate change (II),
3. Develop a framework for mapping the current status of forest C budget across boreal landscapes (III),
4. Map projections of ES and biodiversity in response to alternative forest management practices (IV),
5. Evaluate the suitability of this approach for assessing ES at the landscape level (IV).

Paper I presents an approach to study the impacts of land use change on the litter and soil C stock of boreal croplands on mineral soils. The approach is applied to estimate the C budget of these croplands at a regional scale. Paper II investigates the impacts of management intensification on the C and N cycles of forest across a long latitudinal gradient in Europe. Paper III introduces a spatially explicit framework to map the C stocks and changes of boreal forested landscapes, and to couple them with ES assessments. Paper IV builds upon Paper III and presents projections of ES in response to changing forest management practices at the landscape level. The suitability of this mapping framework for ES assessments is discussed in this dissertation.

2 Materials and methods

2.1 Study areas

The study areas of this dissertation (Fig. 2) were in Finland (Papers I, III and IV) and across a long latitudinal gradient in Europe (Paper II). The study areas in Finland represent the boreal zone which is dominated by coniferous and mixed forests. The main tree species are Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst) and Silver birch (*Betula pendula* Roth). Forest land covers about 20 million ha which is nearly 70% of the total land area in Finland. Peatlands cover about 34% of the forestry land and their growing stock is 23% of the total growing stock volume in Finland (Peltola, 2014). Forest land was a net sink of -17.5 mill. t CO_2 eq. in 2018. However, drained peatlands acted as a source, emitting altogether 6.9 mill. t CO_2 eq. to the atmosphere (Statistics Finland, 2020).

Finnish croplands cover 2.2 million ha and are mainly located in the southern and western coasts of the country. The country was divided into four geographical regions (south, west, east and north) to estimate the C stock of agricultural soils on mineral soils (Paper I). The main crop varies depending on the region; annual crops are mainly grown in south and west and perennial crops in east and north, respectively. Organic soils cover less than 10% of the total cropland area. However, they were responsible for about 50% of the greenhouse gas emissions reported in the whole land use, land use change and forestry (LULUCF) sector in 2018 (Statistics Finland, 2020).

The latitudinal gradient studied in Paper II ranged from northern Finland to middle Ukraine. The annual mean temperature ranged from -0.9 °C in the north to 8.4 °C in the south, and the annual mean precipitation from 619 to 811 mm, respectively, during 1971–2005. The vegetation zones comprised of boreal and temperate coniferous forest. The ten study sites represented typical planted or semi-natural, even-aged Scots pine and Norway spruce stands. In order to maximize the comparability of the results with measurement-based estimates, the sites were selected among the most common forest types, with over 90% dominance of the studied species, growing in similar geomorphological conditions, having the same age (90 years in 2005) and without visible consequences of natural disturbances.

In the study area in southern Finland (Papers III-IV), the annual mean temperature was 4.2 °C and the annual precipitation 637 mm during 1970-2012. The proportion of peatlands is 12-17% of the forestry land which is less than at the national level. Most of the forests, around 95%, are managed by planting or natural regeneration, regular thinning and clear-cutting. In 2013, about 14% of the harvest removal consisted of energywood, of which 30% was spruce. Protected areas cover altogether 3% of the area. They represent a wide range of habitats regionally important for biodiversity conservation.

2.2 Mapping framework

In this dissertation, a framework to map the C budget of forests and croplands, compatible with the assessment of other ES and biodiversity, was developed. The mapping framework consists of the simulated estimates of C stocks and spatially explicit information on land cover. Papers I and II present approaches to study the C budget of forests and croplands at a regional level. Similar approaches were applied at a landscape level for forests in Papers III and IV.

The C budget of croplands was estimated using Yasso with litter input data from agricultural statistics (Paper I). The C budget was quanti-

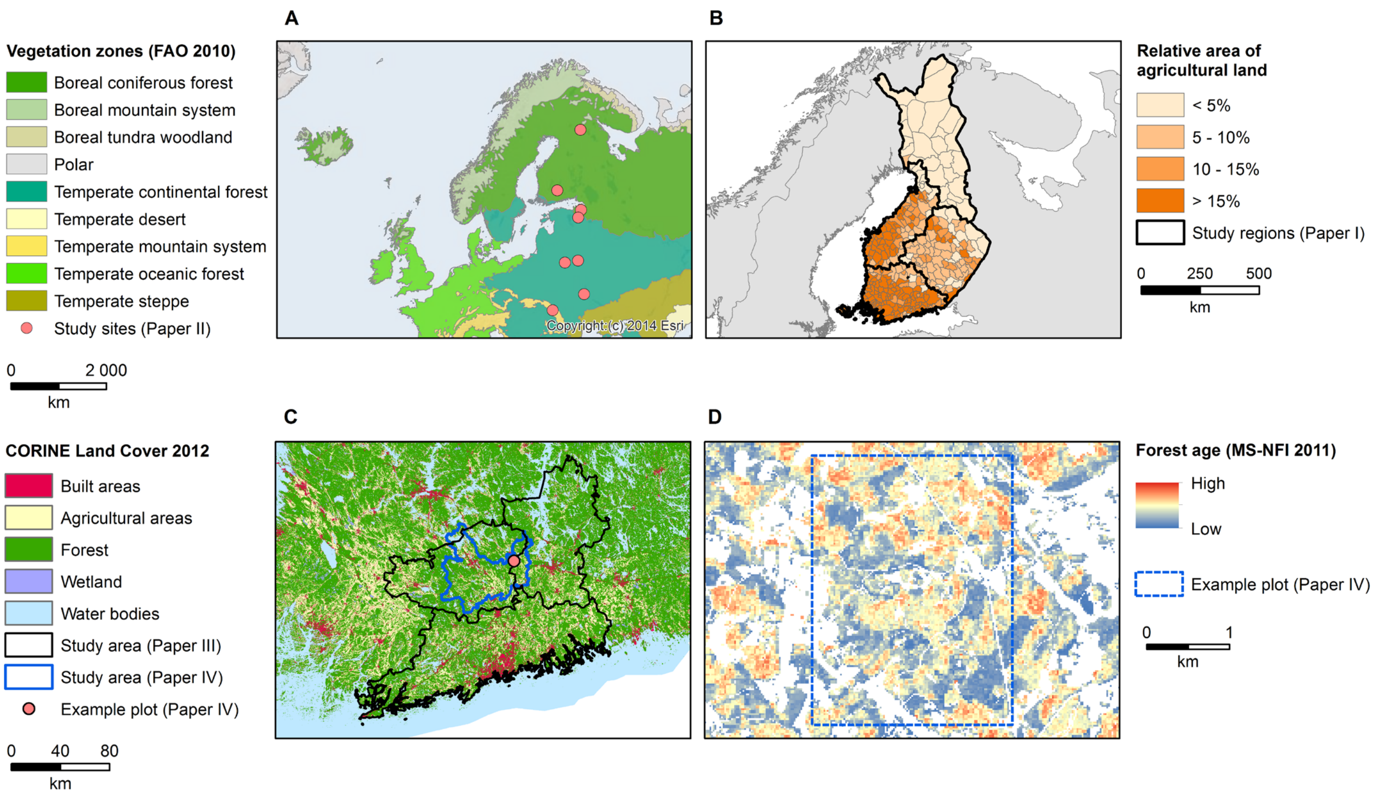

Figure 2. The location of the study areas in north-eastern Europe. Panel A shows the study sites of Paper II in relation to the extent of global vegetation zones. Panel B presents the relative area of agricultural land in Finland in 2011 and the four study regions the country was divided into in Paper I. Panel C shows the main land cover classes in the study areas of Papers III-IV. The fine-scale variation of forest stand age, used as an input data for the mapping framework in Papers III-IV, is illustrated for an example plot in Panel D.

fied at the regional level based on site level estimates representing typical crops and climatic conditions in Finland. Organic soils were excluded because Yasso is applicable on mineral soils only. The croplands were assumed to have been established in the early 1900s from fertile, fully-stocked forests. To investigate the potential reasons for the observed C stock changes on mineral soils a sensitivity analysis was carried out. Four input variables were changed: The C input to the soil of the pre-cropland forest, the C input to the soil of the studied croplands, an upward trend in the C input and increasing trends in the annual mean temperature over the simulation period 1900-2011. The temperature trends, 0.5 and 1.0 °C linear warming, were based on observed warming in Finland (Tietäväinen et al., 2010).

The impacts of forest management practices on C budget under changing climate were studied at the regional level in Eastern Europe (Paper II). The C budget of biomass, litter and soil was simulated using BGC-MAN. To compare the litter and soil C stock estimates, BGC-MAN and Yasso were coupled by using the litter production output of the former as input to the latter model. The studied management practices were whole-tree harvesting (WTH), shortened rotation length and even-aged management as a reference. In even-aged management, planting and regular thinning followed the best practices in the studied regions (Koistinen et al., 2016; Sved and Koistinen, 2015; Lesiv, 2007; MPR RF, 2017). The climate change scenario applied was IPCC's representative concentration pathway (RCP) 4.5 which represents a moderate, less than 2°C global warming by the late 21st century (van Vuuren et al., 2011).

A spatially explicit framework was developed to map the current status of the C budget of forested landscapes (Paper III). Stand level estimates of C stocks and changes were scaled up for the landscape level using the multisource national forest inventory (MS-NFI) data. It includes thematically detailed and regularly updated information on forest characteristics countrywide (Tomppo et al., 2014). The forest resource maps of MS-NFI are produced using k Nearest Neighbours estimation based on the NFI field plot data, satellite images and digital maps (Katila and Tomppo, 2001; Tomppo et al., 2008; 2014). The data represented year 2011 and had a spatial resolution of 20x20 meters. The stand age layer of the MS-NFI data was classified and given an identifier (ID) containing information about forest site type, main tree species (based on biomass) and stand age. The empirical growth model MOTTI was coupled with Yasso to estimate the litter input from tree biomass to soil. The current C budget was then mapped by joining the simulated estimates of biomass, litter and soil C stocks and changes to the classified stand age layer based on the given ID. In the model simulations, forest management was assumed to follow the national recommendations (Sved and Koistinen, 2015). The mapping framework is illustrated in Fig. 3.

The mapping framework presented in Paper III was further developed in Paper IV to identify synergies and trade-offs between ES and biodiversity across a forested landscape over the study period 2012-2100. Varying levels of harvest residue extraction in the final felling were compared to a situation where they were left on site to decompose. Energy-wood harvest from thinning was not simulated because the growth response to nutrient removal was not accounted for by the MOTTI model. The stand age was updated annually for each grid cell of the MS-NFI data to produce annual C budget maps. The forests were regenerated stochastically based on normally distributed, site-type and species -specific rotation lengths with a standard deviation of 10 years. The ES indicators studied were annual timber and energy-wood production, climate regulation

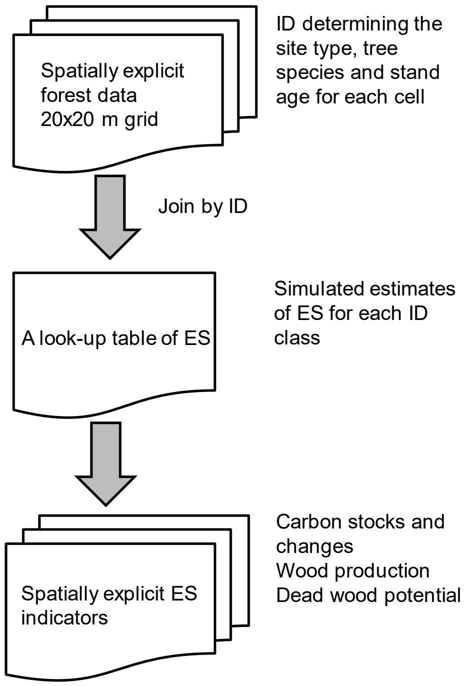

Figure 3. The mapping framework of ecosystem services applied in Papers III and IV.

through C sequestration and coarse woody litter production, used as a proxy for dead wood production. The indicators were derived from the C budget outputs and calculated as annual means for the simulation period. Coarse woody litter production represented the potential production of fresh dead wood without taking into account decomposition. The amount of dead wood is strongly correlated with the richness of several threatened forest species (Martikainen et al., 1999; Penttilä et al., 2004; Virkkala, 2016) which makes it a good biodiversity indicator.

2.3 Model simulations

The C budget of biomass, litter and soil was estimated using existing, scientifically validated simulation models: a statistical forest stand simulator MOTTI (Hynynen et al., 2002; Salminen et al., 2005), a biogeochemistry management model BGC-MAN (Pietsch, 2014) and a dynamic litter and soil C model Yasso (Liski et al., in preparation; Tuomi et al., 2011a; 2011b; 2009). In papers III and IV, forest stand development was simulated using the MOTTI v.3.3 simulator. It applies statistical forest growth and yield models that describe forest structure, growth and management at a stand level (Hynynen et al., 2002). These models cover the most typical site types and tree species in Finland. They have been evaluated nationally based on long time-series of forest inventories and field experiments (Matala et al., 2003).

In paper II, forest stand development was simulated using a process-based ecosystem model BGC-MAN. It estimates the effects of management interventions on C, N and water cycles in terrestrial ecosystems at a daily time-step (Petritsch et al., 2007; Pietsch and Hasenauer, 2006; Pietsch et al., 2005). The model is a modified version of Biome-BGC which has been applied in estimating the impacts of whole-tree harvesting (Merganicova et al., 2005) and thinning (Gautam et al., 2010) on forest C and N stocks at a regional scale. In BGC-MAN, leaf and fine root litter is divided into three pools based on the species-specific weight fractions of lignin, cellulose and labile compounds (see Thornton et al., 2002). The decomposition rate of these pools depends on temperature and soil moisture, and results in the formation of more recalcitrant SOM. Before entering the lignin and cellulose pools, woody litter passes through CWD that is subject only to physical degradation. Decomposition of litter and SOC also depends on the availability of soil mineral N subject to microbial immobilisation. The model has been parameterised for common tree species growing in Europe based on field data and published literature (Pietsch et al., 2005).

Yasso is a dynamic litter and soil C model that can be operated on an annual or monthly time-step. It has five state variables representing the chemical fractions of soil organic carbon (SOC); compounds soluble in a non-polar solvent, ethanol or dichloromethane (denoted using E), soluble in water (W), hydrolysable in acid (A) and neither soluble nor hydrolysable at all (N). The decomposition rate of these fractions depends on temperature and precipitation, and results in the formation of more recalcitrant humus (H). The decomposition of woody litter depends additionally on its diameter (Tuomi et al., 2011a). The decomposition rates are independent of the origin of the litter. The parameter values were estimated with Bayesian inference based on a large set of litter-bag experiments worldwide (Liski et al., in preparation; Tuomi et al., 2011b; 2009). Two model versions were used in this dissertation: Yasso07 (Paper I) and the improved Yasso15 (Papers II-IV). The simulated soil C stock estimates represented the soil layers above the depth of 1 meter. The validity of Yasso07 has been tested at global (Goll et al., 2015; Thum et al., 2011; Tuomi et al., 2009), regional (Lehtonen and Heikkinen, 2015; Ortiz et al., 2013; Rantakari et al., 2012; Wu et al., 2015) and site (Karhu et al., 2011; Lu et al., 2013) scales.

Litter production of biomass was used as input to the litter and soil C model in all papers. In croplands, the litter production consisted of manure, crop residues and root exudates (Fig. 1). It was estimated based on agricultural statistics by applying national conversion coefficients (Bolinder et al., 2007; Statistics Finland, 2020). In forests, the annual litter input consisted of the litter production of living trees, harvest residues and natural mortality. It was estimated either based on growth and yield tables representing the pre-cropland forests (Paper I) or the output of the stand growth model applied (Papers II-IV). The C stocks of biomass, litter and soil were readily included in the output of BGC-MAN (Paper II). The annual estimates of the growing stock, harvest residues and natural mortality were transformed to biomass using allometric equations (Repola, 2008; Repola, 2009) (Papers I, III and IV). The annual litter production of the living trees was estimated by multiplying the biomass components (stems, branches, foliage, stumps, coarse roots and fine roots) with species-specific turnover rates (Liski et al., 2006; Pietsch et al., 2005). The litter production of ground vegetation was estimated following the methods of the national greenhouse gas inventory of Finland (Muukkonen and Mäkipää, 2006).

The EWANH fractions of litter applied in the Yasso simulations were the same that are used in the national greenhouse gas inventories of Finland and Sweden (Ortiz et al., 2013; Sievänen et al., 2014). The chemical quality of crop residues and manure was derived from a previous study on agricultural soil (Karhu et al., 2012)(Paper I). In Papers II-IV, the diameter of branch and root litter was 2 cm and that of stem residues and stumps 10 cm, similarly to the national greenhouse gas inventory (Statistics Finland, 2020). In Paper I, the stem diameters were calculated based on the growth and yield tables (Koivisto, 1959). The soil C stock was assumed to be in a steady state with average climate and the litter input from forest covering the land before establishing the croplands (Paper I) or the mean litter production over forest rotation (Papers II-IV). The climate observations and scenarios were provided by the Finnish Meteorological Institute (Papers I, III and IV), and the Inter-Sectoral Impact Model Intercomparison Project (Paper II).

2.4 Model evaluation

The validity of the simulated estimates of C stocks and changes was tested by comparing them with measurement-based empirical estimates. In Paper I, the simulated soil C stock estimates of the pre-cropland forest were compared with measurement-based estimates taken in forests adjacent to croplands today (Karhu et al., 2011). The simulated estimates of the cropland soil C stock in 2009 and the decrease rate in 1974-2009 were compared to the results of extensive national soil inventories (Heikkinen et al., 2013). A direct comparison of the estimates was, however, difficult because the model simulations covered soil layers down to one meter while the measurements were taken only from a 15 cm deep topsoil layer.

In Paper II, the validity of the simulated estimates was tested by comparing them with measurement-based estimates and inter-model comparison for the historical simulation period 1915-2005. The simulated estimates of stem C stock were converted to merchantable timber volume to make them comparable with the measurement-based estimates derived from empirical growth and yield tables. These tables represented average Scots pine and Norway spruce stands growing in the studied latitudinal gradient (Koivisto, 1959; Shvidenko et al., 2008). The reliability of the simulated estimates of soil C stock was evaluated by comparing the outputs of BGC-MAN and Yasso15 for each study site. In addition, the uncertainty caused by inter-annual weather variation was estimated by running Monte Carlo simulations (n=100) for each site.

In Paper III, the simulated estimates of biomass C stock in the study area in 2011 were compared to extensive inventory-based estimates derived from the MS-NFI 2011 dataset. The soil C measurements were derived from a previous study and national soil inventory results from the same region (Liski and Westman, 1995; Rantakari et al., 2012). The biomass extracted in harvests was used as a measure of the biomass C stock change. The simulated estimates of harvests were compared with harvest statistics provided by the Natural Resources Institute Finland. The estimates of biomass C stock and harvest were stratified according to municipality and those of soil C stock according to forest site type. The model performance was estimated using a regression analysis of the measured mean vs. model predicted mean values. In Paper IV, the scenarios of ES for 2012-2100 were built upon the results reported in Paper III. The reliability of the results was evaluated by comparing the mean estimates of carbon stocks and harvest removals in the study region in 2012 to measurement-based estimates.

3 Results and discussion

3.1 Drivers of soil organic carbon in boreal croplands (I)

Paper I investigated the causes for the observed loss of soil C from Finnish croplands on mineral soil. The simulated mean soil C stock in the studied croplands was 9.2-12.4 kg m^{-2} in 2009 among the four regions the country was divided into (Paper I, Fig. 2). It was comparable with the inventory-based estimates derived from the repeated national soil inventories. The measured mean soil C stock in a 15 cm deep mineral soil layer was 5.1-6.2 kg m^{-2} depending on the study region (Heikkinen et al., 2013). The 15–100 cm soil layer has been estimated to contain 50-67% of the amount of C in the 0–100 cm soil layer (Yli-Halla et al., 2000). Based on this assumption, the 100 cm deep soil layer, used in the model simulations, would contain approximately 7.1-11.2 kg C m^{-2}. This range is comparable with the variability of the simulated estimates in the study regions and the sensitivity analysis, supporting the validity of the modelling approach (Paper I, Fig. 4).

The simulated soil C stock of Finnish croplands declined in the whole country in 1900-2009. During the last 35 years, the mean decrease rate was 0.029-0.036 kg m^{-2} $year^{-1}$ depending on the region (Paper I, Fig. 2). The simulated decrease rates were in general higher than the average inventory-based estimate 0.022 kg m^{-2} $year^{-1}$ (Heikkinen et al., 2013). It is about 30-60% lower than the simulated mean estimates. A direct comparison of the simulated and measured estimates was challenging because they represented partly different soil layers. However, the soil C stock changes in the 100 m deep soil layer are probably greater than those reported for the 15 cm layer because of a higher C content. In conclusion, both the simulated soil C stocks and changes were reasonable in comparison with measurements. This supports the use of the modelling approach in analysing reasons for the observed decline in the soil C stock of Finnish croplands.

The results showed that the soil C stock declined because croplands produced less litter than the pre-cropland forests and this agricultural litter decomposed more rapidly (Paper I, Tables 1-4). Croplands produce less litter than forests because a large proportion of the NPP, often 40-60%, is extracted as harvest (Hay, 1995). In addition, the NPP of croplands today was on average 36% lower than that of the pre-cropland forests (Paper I). Like these results, Leifeld (2013) suggested the high harvested fraction of organic matter from croplands as the major reason for the decline in soil C. The crop residues and manure decomposed faster than forest litter because of lack of the slowly decomposing woody litter and a lower concentration of the recalcitrant lignin-like compounds.

Based on the sensitivity analysis, climate warming has not been a significant reason for the observed loss of C from mineral cropland soils yet (Paper I, Fig. 3). Similarly, Smith et al. (2007) found that changes in agricultural management practices affected the soil C stock of croplands more than climate change. Decreased organic manure application, increased residue removal, and historical land use change were identified as the main reasons for the observed decline in the soil C stock of croplands in England and Wales (Smith et al., 2007). Similar findings have been made also in Belgium (Sleutel et al., 2006). Based on the results, application of organic manure and avoiding bare fallow could slow down the loss of C from Finnish croplands on mineral soils. Tillage and fertilisation may also affect the cycling of C in cropland soils (Mikha and Rice, 2004; West and Post, 2002). However, these management practices have a limited capacity to improve the greenhouse balance of Finnish croplands as a whole because of the large emissions from cultivated organic soils. The results indicate that a simulation model together with information on the C input and climate was a suitable approach for detecting the drivers of change in the soil C stock of boreal croplands on mineral soils (Paper I).

3.2 Effects of forest management on carbon sinks under climate change (II)

Paper II examined the impacts of alternative forest management practices and climate change on C sequestration in 2005-2095 across a long latitudinal gradient in Europe. The biogeochemical model BGC-MAN estimated the historical stand development similarly to measurement-based estimates, supporting the validity of the modelling framework (Paper II, Fig. 3). The simulated productivity of Scots pine and Norway spruce stands increased drastically over the study period as a result of climate warming (Paper II, Fig. 5 and Appendix B in the electronic supplementary material). The results suggest that forest growth will be enhanced with continuing climate change throughout the environmental gradient studied, given the availability of water and nutrients. This is supported by previous studies which predicted increased forest growth as a result of climate change especially in the temperate and boreal regions (Hlasny et al., 2011; Lindner et al., 2010). The expected increasing frequency of drought periods, however, adds a great uncertainty to these predictions (Babst et al., 2013; Shvidenko et al., 2017; Zang et al., 2014).

The simulated responses of the soil C stock to climate change were less clear among the ten study sites. The soil C stock increased in most of the sites due to the enhanced biomass growth and litter production (Paper II, Fig. 5 and Appendix B). The N stock of soil also increased in these sites, creating a positive feedback to stand growth. In some sites, the decomposition of SOM accelerated and led to the decline of soil C stock compared with the historical simulation period. This was supported by experimental and modelling studies which found a decreasing soil C stock as a result of climate warming (Karhu et al., 2010; Mäkipää et al., 2014). Overall, the above- and belowground C stocks increased by 24-76% in 2005-2095 indicating an enhanced C sink capacity of forests as a result of climate change (Paper II, Appendix B). It must be noted, however, that the model applied did not account for the risks of natural disturbances adding uncertainty to the estimates.

The biogeochemical model predicted a positive response of the biomass C stock to whole-tree harvesting (WTH). Biomass growth slowed down temporarily after stem-only harvest (SOH) because the immobilisation of N by microbes exceeded its uptake by trees (Paper II, Fig. 5 and Appendix D). WTH caused lower microbial immobilization of mineral N together with higher plant uptake than SOH because of smaller input of dead organic matter to the soil. This might be related to the non-linear feedbacks in the nutrient allocation among decomposers and plants (Kuzyakov and Xu, 2013), or the different C/N ratios of litter on the forest floor after SOH and WTH. The growth enhancement related to WTH was stronger and more long-lasting than found in another modelling study (Merganicova et al., 2005). Earlier modelling (Mäkipää et al., 2014; Palosuo et al., 2008) and experimental studies (Achat et al., 2015; Egnell, 2017) have observed growth reductions after WTH in the boreal and temperate zones, contrary to the result. Further research on the post-harvest microbial controls of stand productivity is thus required to improve the nutrient dynamics in the model. Shortened rotation length reduced the C stock of biomass (Paper II, Fig. 5), similarly to previous modelling studies (Zanchi et al., 2014).

As a result of WTH, the litter and soil C and N stocks decreased by 7-13% compared with SOH (Paper II, Appendix B). The result was in the range of the measurement-based estimates reported in previous studies (Johnson and Curtis, 2001; Kaarakka et al., 2014). The C loss was the highest immediately after harvest. It declined as the stands grew older because also the harvest residues left on site in SOH started to decompose. The result was consistent with previous studies applying different process-based models in temperate (Merganicova et al., 2005) and boreal forests (Mäkipää et al., 2014; Ortiz et al., 2014). The response of the soil C stock to harvest residue removal and rotation length was independent of the model used demonstrating this pattern to be robust.

The total C stock of forest was 5-27% higher with WTH than with SOH over the simulation period 2005-2095, suggesting a positive feedback of WTH to the C sequestration capacity of forest (Paper II, Appendix B). This is a highly uncertain result due to the limited description of the N dynamics in the model. However, when combined with shortened rotation length, WTH produced a remarkably lower total C stock than SOH. With this scenario, the total C stock was 19-50% lower compared with SOH because the C loss from soil exceeded the C gain of biomass. The result demonstrates that very intensive harvests may deteriorate the climate change mitigation potential of forests, which is in line with previous studies (e.g. Harmon et al., 1990). The results showed that in the decadal scale, forest management affected the C sink capacity more than climate change.

3.3 Mapping the carbon budget of boreal forested landscapes (III)

Paper III introduced a framework for mapping the C budget of boreal forested landscapes at a high spatial resolution. Simulated estimates of the C stocks of biomass and soil, and their annual changes were combined with detailed, spatially explicit information on forest characteristics. The simulated mean C stock of biomass was 6.6 kg m^{-2} and that of soil 7.9 kg m^{-2} across the studied landscape in 2011 (Paper III, Fig. 3 a, b). The simulated mean change rates of these C stocks were 0.032 and 0.022 kg m^{-2} $year^{-1}$, respectively (Paper III, Fig. 3 c, d). The spatial patches of C stock changes were smaller and more heterogeneous than those of C stocks. The fine-scale variation in the C stocks was related to the distribution of forest site type, main tree species and stand age in the landscape, affecting forest growth and the decomposition of litter (Tupek et al., 2015). The patches of C stock changes illustrated more the distribution of harvests in the landscape, depending on stand age (Sievänen et al., 2014).

The simulated and measurement-based estimates of the biomass C stock were highly correlated (Paper III, Fig. 5 a). It was expected because they were based on partly similar inventory data on Finnish forests (Tomppo et al., 2014). The simulated estimates of the soil C stock (Paper III, Fig. 5 b) were also very similar to measurements (Liski and Westman, 1995; Rantakari et al., 2012). The slight tendency for overestimation was expected because the simulated estimates included also dead wood unlike the measurements. Moreover, the simulated estimates of harvests, used as a measure of the C stock changes, correlated well with the observed harvests (Paper III, Fig. 5 c; see also a corrected version on page 36 in the summary). The simulated estimates of the biomass C stock and harvests were, however, somewhat overestimated. The main reasons for the discrepancies between the simulated and observed values were the overly optimistic assumptions related to forest management: regular thinning, the regeneration of only mature stands and the absence of natural disturbances. Based on the good mapping framework performance in general, it was suitable for quantifying the impacts of forest management on climate regulation at the landscape level (Paper III).

Land cover -based proxies have been shown to fit poorly to primary data on C stocks and changes (Eigenbrod et al., 2010). The developed mapping framework produced more accurate and reliable estimates of climate regulation than simple, land-cover based proxies for three reasons. Firstly, the time-series of C stocks and stock changes were produced using reliable models of forest growth and soil C cycling, based on several validity tests (e.g. Karhu et al., 2011; Matala et al., 2003). Secondly, the soil C and stand growth models were coupled. As a result, the status of both biomass and soil C stocks, as well as the feedbacks from trees to soil, could be estimated. Thirdly, the maps had a high spatial resolution because the simulated C budget estimates were combined with extensive, high-resolution data on forest characteristics.

A broad spatial coverage and comprehensive information on forest characteristics are the strengths of the MS-NFI data compared with other land use and land cover maps. Beside the main tree species, it includes estimates of the site type, mean stand age and tree size (Kangas et al., 2018). However, MS-NFI is more accurate on medium and large spatial scales rather than on individual grid cells. This is because the k Nearest Neighbour method averages stand volumes levelling off extremes (Haakana, 2017; Katila, 2006). Furthermore, errors in the MS-NFI data are spatially autocorrelated (Katila and Tomppo, 2001). Despite the limitations in the MS-NFI data the mapping framework performed well in quantifying the C budget at the landscape level. The developed mapping framework can be applied to identify hotspots of C storage and sinks, as well as to identify synergies and trade-offs between climate regulation and other ES (Paper IV). Due to the modular structure of the framework, different models, such as the ones used in Papers I and II, can be connected to it to respond to varying information needs.

3.4 Multi-scale impacts of forest management on ecosystem services (IV)

Paper IV explored the impacts of forest management on ES in a boreal catchment in 2012-2100 applying the mapping framework introduced in Paper III. In the studied scenarios, forests were managed following the national recommendations with varying levels of harvest residue removal for bioenergy production. The studied ES were climate regulation, timber and energy-wood production and coarse woody litter production, used as a proxy for dead wood abundance important for biodiversity conservation. In this scenario application of the mapping framework, the relationships between ES could be examined in multiple scales: from individual patches to the catchment level, and in a time-span reaching from single years to a century.

The simulated mean C stock of biomass fluctuated between 5.4 and 7.3 kg m^{-2} over the simulation period 2012-2100, independent of the bioenergy scenario studied (Paper IV, Fig. 2). Its change rate varied between -0.07 and 0.07 kg m^{-2} $year^{-1}$. The litter and soil C stock remained relatively stable over the simulation period, varying between 8.5 and 8.8 kg m^{-2}. Its change rate varied between -0.003 and 0.017 kg m^{-2} $year^{-1}$. The forests acted as a sink of C in the studied catchment for as long as stand growth exceeded harvest removal (Paper IV, Fig. 3). The more biomass was extracted for bioenergy production, the slower was the accumulation of soil carbon. Extracting branches, tree tops and stumps in the final felling reduced the catchment-level means of soil C stock change as much as 59% compared with conventional SOH in 2012. The changes in the total carbon stock of forest were, however, mainly driven by regular harvesting rather than the bioenergy scenarios. The results indicated that the landscape level estimates were highly sensitive to the changes in stand age class distribution over time, depending on the assumed harvest regime (Paper IV, Fig. S1 in the supplementary material).

Both the simulated mean timber and energy-wood production peaked in the late 2050s as more stands reached maturity, and decreased afterwards (Paper IV, Fig. 5). The mean annual timber production from the final felling sites varied between 0.73 and 1.1 mill. m^3 $year^{-1}$, and that of energy-wood production between 0.02 and 0.15 mill. m^3 $year^{-1}$, depending on the bioenergy scenario. The extraction of stumps multiplied the energy-wood potential nearly three-fold compared with the extraction of only branches and tree tops. The simulated mean annual production of coarse woody litter remained at a stable level during the simulation period, following loosely the trend of the total harvest removal in the study area. Extracting branches, tree tops and stumps in the final felling reduced the catchment-level means of coarse woody litter production by 4.6% compared with the reference scenario (Paper IV, Fig. 5). It is noteworthy, that the amount of dead wood in managed forests is substantially lower than in natural forests (Siitonen, 2001). Therefore, even small reductions in the volume of dead wood could threaten the survival of endangered species (Juutilainen et al., 2014; Virkkala, 2016). To conclude, timber and energy-wood production were synergetic in the studied scenarios. However, producing energy from forest harvest residues had a trade-off relationship with climate regulation and maintaining the habitats for dead wood-dependent species (Paper IV).

The simulated estimates of C stock s were somewhat higher than inventory-based estimates in southern Finland in 2012 (Peltola, 2014; Rantakari et al., 2012). The estimates of timber and energy-wood production were also generally higher than the inventory-based estimates in a larger area (Peltola, 2014). The simulated estimate of energy-wood production, 0.4 m^3 ha^{-1}, was, however, much lower than a previous model-based estimate, 1.1 m^3 ha^{-1}, which included also other tree species and the thinning stands (Forsius et al., 2016). These deviations were mainly related to the relatively high proportion of fertile site classes in the studied catchment. Another explanation could be the optimistic assumptions about forest growth in the model simulations (Paper III, see section 3.3), and A direct comparison of the simulated and inventory-based estimates of coarse woody litter production was not possible for two reasons. First, the simulated estimates represented the potential post-harvest production of fresh dead wood without considering its accumulation or decay. Second, the inventory-based estimates of dead wood only account for the fragments of wood exceeding the diameter of 10 cm and the length of 1.3 m. Therefore, it was not meaningful to compare the simulated estimates of dead wood production to operative targets of CWD in managed forests.

The mapping framework contributes to bridging the gap between mapping and simulation modelling in the ecosystem service assessments of boreal forests. It incorporated new features in comparison to some proxy-based tools for assessing ES (Maes et al., 2012b; Nelson et al., 2009). Firstly, the framework utilised integrated modelling of biomass and soil C cycling in combination with high-resolution spatial data on forest characteristics. As a result, the spatio-temporal dynamics of forest carbon cycle were described more accurately than in tools utilizing simple, land cover -based proxies (Eigenbrod et al. 2010). Secondly, the simple structure of the mapping framework is an advantage compared with some detailed, computationally intensive forest simulators (e.g. Rasinmäki et al. 2009; Redsven et al. 2004; Schelhaas et al. 2007) or process-based models (e.g. Bayer et al. 2015; Gutsch et al. 2018; Holmberg et al. 2019). The modular structure of the mapping framework enables its flexible development with new data and models in the future. Thirdly, the presented framework featured a stochastic development of forest age structure across the landscape, reflecting the variability of management regimes. This is a refinement in comparison with some decision-support systems applying fixed age classes (Frank et al. 2015).

3.5 Methodological issues

The major uncertainties in the simulated estimates of the soil C stock were likely caused by inaccurate information on the land use history, affecting the litter production estimates. The exact timing of the establishment of croplands (Paper I) or that of starting modern, even-aged forest management (Paper II) was not known. The historical forest management practices were also poorly known, adding uncertainty to the estimates of litter production before planting the current forests (Paper II). All model simulations were initialised by assuming a steady state of the soil C stock with average litter production (Papers I-IV). This assumption could be questioned because climate change and land management practices may have shifted the SOM pool from the steady state (Foereid et al., 2012).

In Paper I, the litter production of the pre-cropland forest was estimated based on old growth and yield tables of natural Norway spruce forests in Finland (Koivisto, 1959). According to the biomass estimates calculated based on these tables, the historical, fully-stocked forests produced more litter than the frequently thinned forests today. As a result, the estimates of the soil C stock in the pre-cropland forests were generally higher than the simulated or measured estimates today (Liski et al., 2006; Ortiz et al., 2013; Rantakari et al., 2012). The growth and yield tables represented, however, the best information on the historical forests in Finland.

Some of the factors regulating the C cycling in terrestrial ecosystems were not accounted for by the simulation models used in this dissertation. The effects of soil texture or management practices, such as soil preparation or fertilisation, were not directly accounted for by the Yasso model (Papers I-IV). However, according to previous validity tests of the model it is suitable for estimating the changes in the soil C stock based on the information on climate and litter input only (e.g. Karhu et al., 2012; Lehtonen et al., 2016). The BGC-MAN model simulated the biogeochemical feedbacks between the atmosphere, plants and soil but lacked some of the biophysical processes, such as BVOCs (Paper II). The uncertainties in the climate change scenarios and the post-harvest microbial controls of nutrient cycling also limited the reliability of the projected impacts of forest management in the changing climate (Paper II).

In addition to the historical factors, lack of knowledge about the actual forest management was a central source of uncertainty in the mapping framework for quantifying the C budget of boreal forests (Papers III-IV). The simulated estimates of C stocks showed a tendency for overestimation. The discrepancies with the simulated and measurement-based estimates of the C budget of forest did not imply inaccuracy in the models used as such. They resulted rather from the overly optimistic assumptions related to forest management, leading to high estimates of stand growth and litter production. In addition, the inventory data on forest characteristics was also partly inaccurate. The standard errors in the site fertility class, tree species and stand age variables of the MS-NFI data are quite high compared to that of stand volume. Using stand volume instead of stand age in mapping the simulated C budget estimates would therefore probably improve the accuracy of the estimates.

4 Conclusions and future perspectives

This dissertation provided new insights into the multi-scale patterns and drivers of C cycling across forests and croplands in boreal and temperate regions. It introduced a framework for quantifying the spatiotemporal variation of ES related to C cycling. The dynamic nature of C sequestration has often been ignored in ES assessments applying simplified land cover -based proxies for C stocks and changes (e.g. Nelson et al., 2009). This could potentially lead to significant inaccuracy in the C budget estimates (Eigenbrod et al., 2010; Stephens et al., 2015). Spatially explicit, detailed information on land characteristics is, however, equally important for upscaling stand level estimates of ES to the landscape level (Crossman et al., 2013). The mapping framework developed in this dissertation produced reliable estimates of the C budget of terrestrial ecosystems, accounting for the dynamic couplings between plants and soil. Therefore, it contributed to bridging the gap between process-based modelling and traditional ES assessments (Morales et al., 2005).

According to the results, both climate change and land management practices affect the C sink capacity of terrestrial ecosystems. Land use change from forest to cropland has been the main reason for the observed decline in the soil C stock of Finnish croplands on mineral soils. To date, climate change has not been a significant reason for the decline. The loss of C from these croplands could be mitigated by agricultural management practices that increase the amount of organic matter entering the soil. Climate change increased the C stock of forests substantially by the end of this century according to model simulations for several regions in Europe. However, intensive biomass removal with shortened rotation length caused loss of C from the soil, partly offsetting the benefits from accelerated growth. The results indicate that forest management has a crucial role in maintaining the C sink capacity of boreal and temperate forests in the changing climate. The study revealed that the microbial controls of post-harvest forest growth require further research. Based on the validity tests, the drivers of changes in the C sequestration of terrestrial ecosystems can be detected using process-based modelling.

The current status of the forest C budget was quantified across a boreal landscape by combining simulation models with extensive inventory data. The approach provided reliable estimates of the human influence on the C cycling in forested landscapes. The mapping framework was developed further for investigating the impacts of alternative bioenergy scenarios on climate regulation, timber and energy-wood provision and coarse woody litter production, used as a proxy for dead wood abundance. The extraction of branches, tree tops and stumps enhanced energy-wood production in the studied catchment. However, the soil C sink decreased diminishing the net emission savings from the use of forest bioenergy. The annual production of fresh dead wood also slowed down, causing potentially long-lasting negative impacts on forest biodiversity locally. Other modelling studies have predicted negative impacts of harvesting for example on the diversity of birds (Tremblay et al., 2018) saproxylic beetles (Hof et al., 2018) and lichens (Snäll et al., 2017). The results indicate that producing bioenergy from the small-diameter harvest residues instead of stumps would be more beneficial both regarding climate impacts and biodiversity. The projections of ES depended strongly on the assumed harvest regime, affecting the distribution of forest age classes across the landscape.

The mapping framework developed in this dissertation coupled C sequestration with estimates of provisioning and supporting services, enabling the analysis of their simultaneous responses to forest management actions. High-resolution maps of ES could support sustainable land use planning and environmental management (Koschke et al., 2012). They could also facilitate interaction with stakeholders in the natural resources sector. Information on ES should indeed be produced at the landscape level to visualise their responses to alternative land management decisions to land managers and decision makers. Combined with optimisation tools, these maps could also serve in the spatial prioritisation of habitats (Kukkala and Moilanen, 2017) and finding climate-smart solutions for forest management planning (Eyvindson et al., 2018). In the future, a wider variety of ES indicators could be integrated into the mapping framework depending on the specific information needs. In addition, including growth and yield models for old-growth and uneven-aged forests (Pukkala, 2014), as well as litter and soil C models for organic soils (Ojanen et al., 2014) would improve its applicability at broad spatial scales.

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Erratum

Paper III:

In Fig. 5 c, the simulated estimates of harvests should be corrected. When converting the dry biomass estimates to fresh volume, a density of 400 kg m^3 should be used (Alakangas et al., 2016). The corrected figure is shown below.