

JYU DISSERTATIONS 204

Maiju Peura

Continuous Cover Forestry, Biodiversity and Ecosystem Services



UNIVERSITY OF JYVÄSKYLÄ
FACULTY OF MATHEMATICS
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Editors

Jari Haimi

Department of Biological and Environmental Science, University of Jyväskylä

Ville Korkiakangas

Open Science Centre, University of Jyväskylä

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ABSTRACT

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More sustainable silvicultural approaches are needed to stop the loss of biodiversity and ecosystem services. Most boreal forests are managed with rotation forestry, and continuous cover forestry has been suggested to be a method to reduce the negative impacts of forestry on nature. In the thesis, I studied the impacts of continuous cover forestry on biodiversity and ecosystem services in boreal forests in Finland. I used long-term forest simulations in commercial forest landscapes and empirical methods in streamside key habitats. Simulations showed that continuous cover forestry could be a cost-efficient method to retain ecosystem services and, for example, habitats of species dependent on deciduous trees or mature forest structure. However, at the landscape scale, diverse use of regimes from both continuous cover forestry and rotation forestry was the best in terms of both biodiversity and ecosystem services. Moreover, the amount of dead wood was low in both silvicultural approaches. Empirical studies, on the other hand, showed that the selective loggings of continuous cover forestry disturbed the natural features in streamside key habitats and therefore are not a sustainable method to manage these habitats. The area of unmanaged forests needs to be increased to stop the biodiversity decline. Scenario simulations revealed that from both ecological and economic perspectives, it could be effective to allocate strict protection and conservation measures in commercial stands jointly into specific landscapes. Together, the studies of my thesis suggest that increasing the share of continuous cover forestry in commercial forest landscapes could alleviate the negative impacts of forestry on biodiversity and ecosystem services. However, more protection, careful landscape-scale planning, and retention of essential biodiversity features, such as dead wood or key habitats, are still needed irrespective of the silvicultural approach. Moreover, both rotation forestry and continuous cover forestry can be done more or less intensively. Therefore, instead of strongly contrasting the approaches, more attention should be paid into the amount of harvested timber in commercial forests.

Keywords: Conservation; empirical research; simulation; spatial planning; uneven-aged forestry.

Maiju Peura, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

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Peura, Maiju

Jatkuvapeitteinen metsänkasvatus, monimuotoisuus ja ekosysteemipalvelut

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Diss.

Monimuotoisuuden ja ekosysteemipalvelujen hupenemisen pysäyttämiseksi tarvitaan kestävämpiä metsänkäsitelymenetelmiä. Suurinta osaa borealisista metsistä käsitellään jaksollisen kasvatuksen menetelmin, ja jatkuvapeitteistä kasvatusta on ehdotettu menetelmäksi, joka vähentää metsienkäsitelyn negatiivisia vaikutuksia metsäluontoon. Väitöskirjassani tutkin jatkuvapeitteisen kasvatuksen vaikutuksia boreaalisiin metsiin Suomessa. Käytin sekä pitkän aikavälin simulaatiomenetelmiä metsämaisematasolla että empiirisiä tutkimusmenetelmiä puronvarsimetsien avainbiotoopeissa. Simulaatiot osoittivat, että jatkuva kasvatus voisi olla kustannustehokas tapa säilyttää talousmetsien ekosysteemipalveluja ja esimerkiksi lehtipuuta ja varttunutta metsää vaativien lajien elinympäristöjä. Maisematasolla kuitenkin monipuolinen yhdistelmä jatkuvaa ja jaksollista kasvatusta oli paras sekä monimuotoisuuden että ekosysteemipalveluiden näkökulmasta. Lisäksi lahoppuun määrä oli vähäinen molemmissa käsittelymenetelmissä. Empiiriset tutkimukset osoittivat, että poimintahakkuut häiritsivät puronvarsien avainbiotooppien ominaispiirteitä eivätkä siten ole ekologisesti kestävä tapa käsitellä kyseisiä avainbiotooppeja. Monimuotoisuuden hupenemisen pysäyttämiseksi myös suojelupinta-alaa tulisi nostaa merkittävästi. Simulaatioskenaariot osoittivat, että suojelualueet ja talousmetsien suojelutoimet voisi olla sekä taloudellisesti että ekologisesti kustannustehokasta keskittää tiettyihin maisemiin. Yhdessä tutkimukset ehdottavat, että jatkuvan kasvatuksen lisääminen maisemassa voisi lieventää metsänkäsitelyn negatiivisia vaikutuksia monimuotoisuuteen ja ekosysteemipalveluihin. Suojelupinta-alan nostoa, maisematason suunnittelua ja monimuotoisuudelle tärkeiden rakennepiirteiden, kuten lahoppuun ja avainbiotooppien, säilyttämistä tarvitaan kuitenkin yhä käsittelytavasta riippumatta. Sekä jaksollista että jatkuvaa kasvatusta voi tehdä enemmän tai vähemmän intensiivisesti. Siksi niiden jyrkkää vastakkainasettelua tulisi välttää, ja sen sijaan olisi tärkeämpää tarkastella talousmetsiin kohdistuvaa hakkuupainetta.

Avainsanat: Empiirinen tutkimus; eri-ikäisrakenteinen metsätalous; simulaatio; spatiaalinen suunnittelu; suojelu.

Maiju Peura, Jyväskylän yliopisto, Bio- ja ympäristötieteiden laitos, PL 35, 40014 Jyväskylän yliopisto

Author's address Maiju Peura
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
maiju.h.peura@jyu.fi

Supervisors Professor Mikko Mönkkönen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Professor Janne Kotiaho
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

PhD Daniel Burgas
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Docent Kyle Eyvindson
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Reviewers Docent Eva-Maria Nordström
Department of Forest Resource Management
Swedish University of Agricultural Sciences
SE-901 83 Umeå
Sweden

Docent Timo Kuuluvainen
Department of Forest Sciences
P.O. Box 27
FI-00014 University of Helsinki
Finland

Opponent Professor Anne Tolvanen
Natural Resources Institute Finland
FI-90014 Oulu
Finland

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LIST OF ORIGINAL PUBLICATIONS

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- I Peura M., Burgas D., Eyvindson K., Repo A. & Mönkkönen M. 2018. Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia. *Biological Conservation* 217: 104-112.
- II Oldén A., Peura M., Saine S., Kotiaho J. S. & Halme P. 2019. The effect of buffer strip width and selective logging on riparian forest microclimate. *Forest Ecology and Management* 453: 117623.
- III Peura M., Oldén A., Elo M., Kotiaho J., Mönkkönen M. & Halme P. 2020. The effect of buffer strip width and selective logging on streamside polypore communities. *Canadian Journal of Forest Research* (accepted).
- IV Peura M., Eyvindson K., Mönkkönen M., Burgas D., Raatikainen K. & Kotiaho J. 2020. Cost-effective biodiversity protection through multiuse-conservation landscapes. Manuscript.

Table shows the contributions of authors to the original papers.

	I	II	III	IV
Planning	MP, MM, DB, KE	AO, JK, PH, MP	JK, PH, MP, AO	MP,JK,MM, KE,DB, KR
Data	KE, MP	AO, MP, SS	MP, JK	KE, MP
Analyses	MP, KE, DB, AR	AO, MP	MP, AO, ME, PH	MP, KE
Writing	MP, MM, KE, DB, AR	AO, MP, SS, JK, PH	MP, AO, JK, MM, PH, ME	MP, JK, MM, KE, DB, KR

MP=Maiju Peura, MM=Mikko Mönkkönen, JK=Janne Kotiaho, DB=Daniel Burgas, KE=Kyle Eyvindson, PH=Panu Halme, AO=Anna Oldén, ME=Merja Elo, KR=Kaisa Raatikainen, SS=Sonja Saine, AR=Anna Repo

1 INTRODUCTION

1.1 Declining biodiversity and ecosystem services

1.1.1 Current trend

Biodiversity, which includes diversity within species, between species and of ecosystems, is declining rapidly (CBD 2010, Butchart *et al.* 2010, IPBES 2019). Declining biodiversity can be interpreted, for example, as a decrease in genetic variability within a population, a decrease in the number of species within a species community, or a decrease in a variation among species communities (Walker 1992). In general, biodiversity loss is often easiest to measure and observe as a decreased number of species (Butchart *et al.* 2010). According to the latest estimation, every fourth species is at risk of extinction, and the rate of global species extinction is tens to hundreds of times higher than the average over the last 10 million years (IPBES 2019). The decline in biodiversity threatens the human wellbeing as well, as biodiversity maintains the functioning of crucial ecosystem services (Naeem *et al.* 1994, The Millennium Ecosystem Assessment 2005, Cardinale *et al.* 2012). Despite this, humans are actually the main cause of massive biodiversity loss.

Land-use and land-use change are one of the greatest direct factors that negatively impact nature (Foley 2005, IPBES 2019). In forest ecosystems, forest land has been converted to another land type (i.e., deforestation), such as agricultural land, and forests are managed for commercial timber production (Butchart *et al.* 2010). During the past 5000 years, the global forest cover has decreased by 50% (FAO 2016) and nowadays, the share of intact forest cover from the total forest cover has been estimated to be less than 25% (Potapov *et al.* 2008, Hansen *et al.* 2013). Thus, humans have destroyed a large share of natural forests and are continuing to disturb most of the remaining forest land.

The most important direct methods to reduce the loss of biodiversity and ecosystem services are changes in land-use management (IPBES 2019). Global agreements (e.g., Aichi Biodiversity targets) guide to increase the share of

protected areas and develop more sustainable methods for land-use management (CBD 2010). These actions are urgently needed in forests as well (Foley 2005, Butchart *et al.* 2010).

1.1.2 The persistence of species populations

The viability of species populations is one of the most critical aspects when the aim is to alleviate the biodiversity decline. The structure and dynamics of populations result from birth and death rates and by immigration and emigration (Begon *et al.* 2006). These processes, on the other hand, are driven by factors such as resource availability and species interactions, for example, through predation and competition. Habitat availability is the fundamental factor determining the viability of species populations (Fischer and Lindenmayer 2007). A suitable habitat is characterized by its abiotic features, such as microclimatic conditions, and biotic features, such as food availability. Again, the different attributes of habitat, such as area, quality, and connectivity, influence the persistence of species population (Hodgson *et al.* 2011). While the relative importance of these attributes on population viability is species-specific, in general, the area and quality of habitat are considered to be the most important ones (Doerr *et al.* 2011, Hodgson *et al.* 2011).

Habitat loss and degradation are the main factors decreasing the viability of populations and eventually driving species locally extinct in managed landscapes (Fischer and Lindenmayer 2007, Hodgson *et al.* 2011). In addition, when the remaining habitat cover is low and sparsely distributed, suitable habitat patches are often poorly connected (*i.e.*, isolated) and small, which is the case in habitat fragmentation. The independent effects of habitat loss and habitat fragmentation are challenging to separate as the amount of fragmentation typically increases with decreasing habitat cover (Fahrig 2010, Hanski 2011). In general, fragmentation *per se* can decrease the viability of a population through limited movement or dispersal between suitable habitat patches (Haddad *et al.* 2015). It has been suggested that the effect of fragmentation is likely small when the habitat cover is more than 30% of the original state (Andr en and Andr en 1994, Pardini *et al.* 2010, Hanski 2011).

Moreover, habitat fragmentation can divide large populations into isolated subpopulations, and if these subpopulations interact at some level they can be defined as a metapopulation (Hanski 1999). Although metapopulations are also inherent in pristine landscapes, the consequences and applications derived from metapopulation theory become especially important in managed landscapes (Hanski 2011, Rybicki and Hanski 2013). The basic idea in metapopulation dynamics is that local subpopulations can go extinct but the metapopulation can persist if colonizations compensate local extinctions (Hanski 1999).

1.1.3 The persistence of species communities

A group of interacting populations of several different species living within a particular area forms a community (Begon *et al.* 2006). Thus, the changes in the

viability of species population reflect to changes in the local community structure. Community structure can be described by its species richness (the number of species) and species diversity, which is a measure of both species richness and relative species abundance in the community (Magurran 2013). For example, a decline in local species richness originates from local population extinctions, and before species richness decreases, species relative abundances typically change.

Several ecological theories aim to explain the variation in local species richness, and these theories are applicable when the goal is to find more sustainable land-use methods (Fischer and Lindenmayer 2007). The emphasis in ecological research has been in studying the effects of area, energy, and habitat heterogeneity on local species richness (Honkanen *et al.* 2010). For example, larger areas are expected to have more resources and support larger population sizes and thus suffer lower extinction rates (MacArthur and Wilson 1967). Moreover, larger areas could contain more different kinds of resources and habitats and thus support more different kinds of species varying in their habitat requirements. It has been suggested that the primary reason why area promotes species richness is that larger area contain more energy (Wright 1983). For example, a larger amount of productive energy can support a larger number of trophic levels and result in more complex resource availability (Honkanen *et al.* 2010). Thus, both species-area and species-energy relationships are tightly linked with habitat heterogeneity. One of the main mechanisms why habitat heterogeneity promotes species richness is that resource complexity can increase the available niche space when more species can co-exist (Stein *et al.* 2014).

At a larger spatial scale, on the other hand, species diversity is a function of both local species diversity and variation in community composition among local communities (Magurran 2013). Thus, regional species diversity, for example, the species richness in regional species pool, can decrease even if the species richness in local communities is retained but they became more similar in species composition. The increasing similarity in communities between local sites is a process known as biotic homogenization (Olden 2006). In managed landscapes, homogenization originates typically from local extinctions of specialist species and from colonizations of generalist species (Clavel *et al.* 2011).

1.2 Boreal forests

1.2.1 Biome

Boreal forest is the largest land-biome globally (Saucier *et al.* 2015). It covers over 1 billion hectares of forest, mostly located in Russia, Canada, Alaska, Finland, and Sweden (Brandt *et al.* 2013). Boreal forests grow in high latitudes where freezing temperatures last several months, the growing season is relatively short, and trees grow slowly. These forests are dominated by relatively few tree species, mainly coniferous such as *Abies*, *Picea*, and *Pinus* species with deciduous-mixture

of species such as *Alnus*, *Betula*, and *Populus* (Burton *et al.* 2010). Boreal forest soils consist of different types of mineral and peat soils, and due to coniferous trees, the soil is often acid and poor in nutrient levels. Very dry and nutrient-poor sites are dominated by lichens (Esseen *et al.* 1997). Dry to moderately moist (i.e., mesic) and moderately nutrient-rich sites are dominated by dwarf shrubs and mosses. The share of vascular plants is often relatively small but it typically increases with soil productivity.

Different kinds of disturbances, varying in intensity, frequency, and range, shape the natural dynamics and succession in boreal forests (Esseen *et al.* 1997, Angelstam 1998, Shorohova *et al.* 2011, Kuuluvainen *et al.* 2016). Although in nature, different kinds of dynamics are a part of a larger continuum but at least three types of dynamic types have been separated in natural boreal forests: even-aged dynamics, cohort dynamics, and gap dynamics, which are driven by a different type of disturbance factors (Kuuluvainen and Aakala 2011). The most severe stand-replacing disturbances due to fire and storms drive even-aged forest dynamics, which take place in the early phases of natural forest succession. Low and intermediate level partial disturbances, for example, due to insects and small-scale fires and storms, drive cohort dynamics by opening tree canopy when a younger tree cohort can regenerate. In the late successional phase, small scale disturbances, for example, due to senescence and fungi, drive fine-scale gap dynamics. When only individual trees or a small group of trees die, the structure of old forest patch develops eventually towards an uneven-aged forest structure. In the directional succession, a forest develops through even-aged dynamics, cohort dynamics and gap dynamics into old-growth forest. However, the existence of disturbance factors determines whether directional succession really occurs (Kuuluvainen *et al.* 2016).

Moreover, the occurrence of different kinds of disturbances varies among boreal regions and site types. For example, in Canada, stand-replacing fires are common and lead to relatively short succession cycles and even-aged dynamics (Venier *et al.* 2014). In contrast, in Fennoscandia, fine scale disturbances have been more common than large scale disturbances, and thus gap dynamics have been typical in natural forest landscapes (Kuuluvainen and Aakala 2011). Then again at a smaller spatial scale, cohort dynamics are typical for dry and fire-resistant pine dominated forests, whereas gap dynamics are more common in mesic and spruce dominated forests (Kuuluvainen and Aakala 2011). This overall variation in natural disturbances and succession together with underlying environmental factors, such as soil type and topography, create much variation in the forest structure (Kulha *et al.* 2018). At the forest patch scale, different tree species and trees of different ages and sizes create a heterogeneous forest structure. At the larger spatial scale, on the other hand, natural boreal forest landscapes consist of a mosaic of forest patches at different successional phases and under different forest dynamics (Esseen *et al.* 1997, Kuuluvainen *et al.* 2012).

Finnish boreal forests cover 20.3 million hectares, which is 73% of the total land area in Finland (Vaahtera 2018). Two coniferous species dominate Finnish boreal forests: pine (*Pinus sylvestris*) mainly in dry sites and spruce (*Picea abies*)

mainly in mesic sites. Deciduous tree mixture consists of species such as birches (*Betula pendula* and *Betula pubescens*) and aspen (*Populus tremula*). In natural forests, most typical disturbance factors have been estimated to be fine-scale wind and insect outbreaks and low-severity surface fires (Kuuluvainen and Aakala 2011). Thus in Finland, the share of old-growth forests in natural forest landscapes has been relatively large (Kuuluvainen and Aakala 2011).

1.2.2 Biodiversity

Species in boreal forests have adapted to forest succession and disturbances, which produce a diverse set of resources and habitats for forest-dwelling species (Esseen *et al.* 1997). Especially many specialized species are dependent on specific disturbances, such as fire or specific successional stage of forest. Moreover, productive sites, such as swamps (Zackrisson *et al.* 1998) and forests near water bodies (Naiman and Décamps 1997), are typical biodiversity hot-spots in boreal forests and provide habitat for many specialized species.

In general, a large share of above-ground biomass is allocated in trees, litter, and shrub-layer, and thus these provide essential resources for forest-dwelling species (Esseen *et al.* 1997). Moreover, a large share of tree biomass is typically in dead trees in natural forests. The typical amount of dead wood in natural boreal forests can be even 60-120 m³ ha⁻¹ (Siitonen 2001). Dead trees provide a very diverse set of resources and habitats because multiple factors, such as tree species, size, growth rate, cause of mortality, decay rate, and decay stage generate large heterogeneity (Stokland *et al.* 2012). For example, snags provide substrate for fungi as well as nest and feeding habitats for bird species while fallen logs provide resources for invertebrates, fungi, and bryophyte species. In Finnish boreal forests, approximately one fourth of the forest-dwelling species are dependent on dead wood (Esseen *et al.* 1997). Moreover, for example, bilberry (*Vaccinium myrtillus*) is one of the most important keystone species in the shrub layer and provides resources for several bird and invertebrate species.

Compared with other forest biomes, the species richness in boreal forests is relatively low (Saucier *et al.* 2015). Nevertheless, the boreal forest has been estimated to host even 100,000 species, most of which are arthropods, microorganisms, and fungi (Burton *et al.* 2010). According to current knowledge, the number of forest-dwelling species in Finland is approximately 20,000 species (Hyvärinen *et al.* 2019). More than half of the species are invertebrate species belonging to orders like Hymenoptera and Coleoptera. The number of fungal and lichen species is also relatively large.

1.2.3 Ecosystem services

Boreal forest biodiversity and functioning maintain several crucial benefits for human-wellbeing (Burton *et al.* 2010). These services can be divided into regulating, provisioning, and cultural services (Haines-Young and Potschin 2011). The economically most valuable provisioning service is timber production, as nearly half of the global stock of growing timber is contained in boreal forests

(Burton *et al.* 2010, Vanhanen *et al.* 2012). Especially in Fennoscandia, most boreal forests are managed for timber production, whereas the largest intact forest areas are located in Russia and Alaska (Potapov *et al.* 2008). Non-timber provisioning services in boreal forests are, for example, berries and mushrooms (Burton *et al.* 2010). One of the most important regulating services in boreal forests is climate regulation, as boreal forests have been estimated to contain a large share of the global forest carbon storage and sinks (Bradshaw and Warkentin 2015). In addition, boreal forests, for example, support freshwater resources and provide several cultural services such as recreational options (Burton *et al.* 2010, Saastamoinen *et al.* 2014).

The role of the forest industry for Finnish economy and welfare is notable (Vanhanen *et al.* 2012). Wood products, such as paper, paperboard, and sawnwood, are among the most significant export products in Finland. The share of forest sector from the total gross domestic product is 4.4%, and the forest sector employs nearly 60,000 people (Vaahtera 2018). Moreover, timber revenues are the source of income for private forest owners, and for example in Central and Southern Finland even 70% of forests are privately owned (Vaahtera 2018). In addition to timber benefits, Finnish forests also provide other economically valuable services (Kettunen *et al.* 2012). Berries, such as bilberry and cowberry (*Vaccinium vitis-idaea*) and edible mushrooms, are collected for sale and household consumption (Saastamoinen *et al.* 2000, Vaara *et al.* 2013). In addition, Finnish forests are valuable carbon storages, and they have been estimated to sink even half of Finland's total carbon emissions (Ministry of Agriculture and Forestry 2018).

1.2.4 Forest management

The human impact on boreal forests is long (Esseen *et al.* 1997, Brandt *et al.* 2013). Boreal forest land was converted for cattle grazing and agricultural land already thousand years ago. Between the 17th and 19th century, for example, the mining industry, burn beating, and potash and tar production have changed the cover and structure of boreal forests. Forest industry developed in the late 19th century, and the number of sawmills started to increase rapidly in boreal regions (Esseen *et al.* 1997, Burton *et al.* 2010, Brandt *et al.* 2013). Timber was harvested by selective logging, when mainly the largest and healthiest trees were removed.

In the beginning of 20th century, harvesting methods started to intensify and clear-cut harvesting (i.e., rotation forestry) eventually replaced selective logging as a forest management method (Esseen *et al.* 1997, Brandt *et al.* 2013). To maximize economic revenues, timber production forests are typically managed to maximize tree growth (Hynynen *et al.* 2005). This leads to relative short rotation cycles and young forest structures. Moreover, natural disturbances, such as fire and insect outbreaks, are often controlled or prevented to limit economic loss for timber production (Thom and Seidl 2016). Trees can be even logged for protection against a pest (i.e., sanitation logging), and if a natural disturbance occurs, damaged trees are often removed to reduce the economic loss (i.e., salvage logging).

Selective logging was the most common forest management method also in Finland until the mid of the 20th century (Esseen *et al.* 1997, Siiskonen 2007). However, selective loggings did not produce enough timber for the forest industry, and the quality of growing stock was suspected to decrease due to selective logging when forest management started to be strongly directed towards rotation forestry with clear-cuts (Siiskonen 2007, Laiho *et al.* 2011). Nowadays, the most commercial forests are managed with rotation forestry (Äijälä *et al.* 2014). The economically optimal rotation length is about 60-90 years, depending on the region. Regeneration is based on artificial regeneration through planting and seeding or natural regeneration through retained seeding trees. Mechanical land modification is applied to enhance the success of artificial regeneration. Tree breeding is used to boost the growth and quality of new trees. The growth of young stands is often improved by management, for example, by removing grasses around saplings. Thinnings from below (the smallest tree removed) are typically conducted to boost the growth of the remaining trees. At the stand scale, rotation forestry creates single species monocultures having quite even-aged forest structure (Kuuluvainen 2009). At the landscape scale, on the other hand, rotation forestry creates a mosaic of forest patches at different development stages.

1.3 Negative impacts of forest management

1.3.1 Biodiversity

Natural disturbances create resources for forest-dwelling species and increase structural heterogeneity in forests, whereas anthropocentric disturbances via loggings remove resources from forest-dwelling species and homogenize the forest structure at multiple spatial scales (Franklin and Forman 1987, Kuuluvainen 2009). Even if timber extraction does not destroy the forest area permanently, it changes the forest structure and disturbs the natural forest dynamics and succession for a very long time into the future (Muurinen *et al.* 2019). Moreover, as loggings make gaps to the canopy, they change microclimatic conditions in forests, for example, by decreasing humidity and increasing temperature (Zheng *et al.* 2000, Kovács *et al.* 2017). Moreover, forest management creates sharp edges to forest landscapes. Edge effect, for example, due to clear-cut logging can spread even 50-200 m into the contiguous forest and change both abiotic and biotic conditions (Murcia 1995, Ylisirniö *et al.* 2016).

In general, managed forests lack several structural features typical for natural forests and thus important for natural biodiversity. At the stand scale, managed boreal forests lack natural structural features, such as deciduous trees, large and old trees, dead wood, and structural within-stand heterogeneity (Esseen *et al.* 1997, Siitonen *et al.* 2000, Nilsson *et al.* 2002, Venier *et al.* 2014). At the landscape scale, on the other hand, managed forests typically lack continuity in forest cover, old-growth forests, and young forests at early successional stages

with a large amount of dead wood and deciduous trees (Esseen *et al.* 1997, Kuuluvainen and Gauthier 2018). Due to changed forest structure and removed resources, it is evident that many forest-dwelling species have difficulties in finding resources and habitat from managed forests.

In Finland, forest management is one of the main drivers of biodiversity decline (Tikkanen *et al.* 2006, Hyvärinen *et al.* 2019). According to the latest estimation, nearly one third of all threatened species are forest-dwelling species, and forests are the main habitat for 833 threatened species (Hyvärinen *et al.* 2019). These species live mainly in herb-rich forests and old-growth heath forests. For example in Southern Finland, only 9% of forests are over 100 years old, and 1.4% of forests are over 140 years old (Vaahtera 2018). The remaining cover of real old-growth forest is fragmented and often located in small and isolated patches (Kouki *et al.* 2001). About 30% of threatened forest-dwelling species are dependent on dead wood (Hyvärinen *et al.* 2019). The average level of dead wood in commercial forests is less than 5 m³ ha⁻¹, which means that even 95% of the dead wood resources have been lost due to forest management (Siitonen 2001). Other main causes of threat are changes in the tree species composition, such as lack of deciduous trees (Tikkanen *et al.* 2006, Hyvärinen *et al.* 2019).

1.3.2 Ecosystem services

In addition to biodiversity, altered forest structure and dynamics cause changes also in other benefits boreal forests provide for human-wellbeing. Altered abiotic and biotic conditions can disturb the important forest functions and eventually impact the final benefits forests provide (Haines-Young and Potschin 2011). In general, timber production is often in conflict with non-timber benefits (Pohjanmies *et al.* 2017b). Timber harvesting decreases, for example, carbon storages in tree biomass and soil (Triviño *et al.* 2015, Pukkala 2018), recreational and cultural forest values (Miina *et al.* 2016) and the quality of soil and water (Laudon *et al.* 2011). Reconciling the conflicting demands of forests is challenging, especially in areas where the timber harvesting pressure is high, as in Finnish boreal forests (Pohjanmies *et al.* 2017b).

1.4 Methods to alleviate the negative impacts of forest management

Efforts to reduce the loss of biodiversity and ecosystem services are needed at multiple spatial scales (Lindenmayer *et al.* 2006). Large protected areas outside commercial forest landscapes represent the most traditional conservation methods. The current target is to protect 17% of land area (CBD 2010). However, this target has not been reached in all boreal forest regions, and managed forests often dominate boreal forest landscapes (Potapov *et al.* 2008, FAO 2016). This means that a large share of biodiversity and ecosystem services also exists in

commercial forests, and therefore, conservation efforts are needed within commercial forests as well (Lindenmayer *et al.* 2006). In practice, for example, legislations and forest certifications guide to preserve biodiversity also in commercial forests.

At the stand scale, retention forestry aims to retain structural complexity within forest stand and retain critical structural features such as snags, cavity trees, deciduous trees, and dead wood resources (Gustafsson *et al.* 2012). Also, retention trees are spared, for example, near water bodies to buffer them from the negative impacts of forest management. However, the amount of retention trees is often relatively small, and the ecological function of retention trees stays vague (Kuuluvainen *et al.* 2019). At larger spatial scales, retention of biodiversity hotspots has been suggested to be a cost-effective method to reduce biodiversity loss (Timonen *et al.* 2010, 2011). In boreal forests, for example, forests near water bodies have high biodiversity values as they provide habitat for many rare and endangered species (Naiman and Décamps 1997). Thus, leaving them outside of forest management practices could alleviate the biodiversity loss at the landscape scale. However, as in the case of retention forestry, the ecological function of preservation of small habitat patches in fragmented landscapes is uncertain, as these patches are often too small to support viable populations of species (Hylander and Weibull 2012, Ylisirniö *et al.* 2016). Moreover, these habitats are often prone to edge effects due to loggings in adjacent forests.

In addition, logging regimes mimicking natural disturbances are expected to retain more natural forest structure and thus alleviate the negative impacts of forest management on nature (Lindenmayer *et al.* 2006). Rotation forestry can emulate even-aged dynamics, but forest management regimes mimicking other dynamics are typically lacking (Kuuluvainen 2009). Possible regimes are, for example, selective logging (a type of continuous cover forestry, section 1.5) emulating gap dynamics and modified thinnings emulating cohort dynamics. For example, longer rotation lengths or modifications in the thinning schedule have been shown to be possible methods to alleviate the negative impacts of rotation forestry on biodiversity and ecosystem services (Liski *et al.* 2001, Miina *et al.* 2010, Mönkkönen *et al.* 2014, Triviño *et al.* 2015, Felton *et al.* 2017b). In general, the diversification of forest management regimes at a landscape scale could increase the heterogeneity of commercial forest landscapes and thus support the existence of different kinds of habitats. Furthermore, previous research suggest that multiobjective optimization methods and landscape-level planning can help to alleviate the conflicts among various forest benefits (Mönkkönen *et al.* 2014, Felton *et al.* 2017a, Pohjanmies *et al.* 2017a, Eyvindson *et al.* 2018).

However, current conservation targets and suggested methods to reduce forestry-related biodiversity loss may not be enough to stop the decline of biodiversity in boreal forests (Hanski 2011). The current target to protect 17% of the area may not be sufficient to retain viable populations of specialized species that can find suitable habitat only from unmanaged forests (Hanski 2011, Kotiaho 2017). The reason for this insufficiency results from the negative impact of habitat

fragmentation on the viability of populations when the habitat cover is low (Hanski 2011) (see 1.1.2). To reduce the negative impact of fragmentation, it has been suggested to split forest landscapes into production landscapes and multiuse-conservation landscapes where different conservation efforts are allocated (Hanski 2011, Kotiaho 2017). For example, if 17% of the area was protected and these protected areas were allocated to the half of landscapes (i.e., defined as multiuse-conservation landscape), protected areas would cover 33% of the area in multiuse-conservation landscapes (Kotiaho 2017). In that case, the negative impact of fragmentation would likely be small (Hanski 2011, Kotiaho 2017). Moreover, methods that aim to retain biodiversity and ecosystem services in commercial forests, such as less intensive forest management, could be allocated to the remaining 67% of the multiuse-conservation landscapes to support biodiversity protection and ecosystem services. However, systematic approaches to incorporate diverse economic, ecological, and social perspectives have not been tested. (Ranius and Roberge 2011, Vauhkonen and Packalen 2019).

In Finland, the share of protected forests from the total forest land is 12% (2.7 M ha) (Vaahtera 2018). However, most of the protected forests are located in Northern Finland, while only 4.8% of forest land is protected in Southern Finland. Statutory protected areas such as national parks and strict nature reserves encompass 89% of the protected forest area, while conservation areas in commercial forests encompass 11%. For example, the Finnish forest act (*Forest act* 2013) defines specific types of key habitats, such as streamside forest, which has to be retained from forest management. Most of the Finnish forests belong to either PEFC (Programme for the Endorsement of Forest Certification) or FSC (Forest Stewardship Council) certification system, which require, for example, to leave 10 retention trees per ha in final clear-cut. Nevertheless, these conservation efforts have not been sufficient to stop the biodiversity decline in Finnish boreal forests, and more efficient methods to alleviate the biodiversity loss are needed, especially in Southern Finland (Hyvärinen *et al.* 2019).

1.5 Continuous cover forestry

Continuous cover forestry generally refers to a silvicultural approach that maintains uninterrupted tree canopy cover and in which clear-cuts are avoided (Pommerening and Murphy 2004). The definition varies over regions, and there is much variation within the approach. Terms, such as uneven-aged forestry or selective logging, are often used as synonyms for continuous cover forestry (Pommerening and Murphy 2004, Diaci *et al.* 2011, Boncina 2011). The largest trees are typically removed, and regeneration usually occurs through natural regeneration (Pommerening and Murphy 2004). The stand structure in a forest under continuous cover forestry is often diverse, having multiple cohorts of trees in different sizes, heights, and tree species. The knowledge of environmental problems and the negative impacts of clear-cuts on forest ecosystems has revived the interest towards this alternative silvicultural approach for rotation forestry

(Diaci *et al.* 2011, Puettmann *et al.* 2015, Sharma *et al.* 2016, Felton *et al.* 2017a, Sténs *et al.* 2019).

A review comparing rotation forestry and continuous cover forestry approaches at the stand-scale in boreal Fennoscandia showed that continuous cover forestry may retain species living in mature forests and late successional stages better than rotation forestry with clear-cuts at least in the short term (Kuuluvainen *et al.* 2012). Empirical evidence suggests that, for example, soil fauna (Siira-Pietikäinen *et al.* 2003, Siira-Pietikäinen and Haimi 2009) can recover from the continuous cover forestry with selective loggings better than from the rotation forestry with clear-cuts. Similarly, a common forest species, bilberry (*Vaccinium myrtillus*), was disturbed less due to continuous cover forestry with selective loggings than due to rotation forestry with clear-cuts (Atlegrim and Sjöberg 2004). After the review of Kuuluvainen *et al.* (2012) more empirical research with longer follow-up times (up to 15 years) have been published. These studies have explored responses of saproxylic beetles (Joelsson *et al.* 2017, 2018b, a), Coleoptera (Jokela *et al.* 2019, Koivula *et al.* 2019), Carabidae (Koivula *et al.* 2019) and understorey vegetation (Vanha-Majamaa *et al.* 2017). The findings of recent research are mainly in line with the conclusion of Kuuluvainen *et al.* (2012): continuous cover forestry approach disturbs the natural species diversity and assemblages often less than rotation forestry with clear-cuts.

In studies considering saproxylic beetles, stands under continuous cover forestry were also compared to thinned stands under rotation forestry. Saproxylic beetles diversity (Joelsson *et al.* 2017) or assemblages (Joelsson *et al.* 2018a) did not differ between these treatments. Moreover, some studies exploring the long-term impacts of selective logging on biodiversity in boreal forests also exist (Bader *et al.* 1995, Sippola *et al.* 2001, 2004, Lommi *et al.* 2010), and these can provide valuable insights on the possible long-term impacts of continuous cover forestry. In these studies, forests that were selectively logged 50-100 years ago were compared to unmanaged old-growth forests (Bader *et al.* 1995, Sippola *et al.* 2001, 2004). Selective logging can disturb the continuity of dead wood resources and dead wood dependent species richness decades after loggings (Bader *et al.* 1995, Sippola *et al.* 2001, 2004). But on the other hand, lichen species richness was as high in selectively logged stands as in unmanaged stands (Lommi *et al.* 2010). Nevertheless, studies covering the total rotation period of rotation forestry and comparing the effects of continuous cover forestry and rotation forestry are lacking. Such long-term studies are needed to fully understand the effects of different silvicultural approaches.

The recent global review comparing continuous cover forestry and rotation forestry concluded that the combination of them is likely the best strategy to retain biodiversity in commercial forests (Nolet *et al.* 2018). Neither continuous cover forestry nor rotation forestry was superior over the other in terms of different biodiversity features. An empirical study from beech forests in Central Europe found that the mosaic of rotation forestry stands at different ages was better for regional biodiversity than the high stand-level heterogeneity of continuous cover forestry stands (Schall *et al.* 2018). However, the effects of

combining continuous cover forestry and rotation forestry have not been explored in boreal settings, where forest management regimes differ from those in temperate deciduous forests. Therefore, the results of Nolet *et al.* (2018) and Schall *et al.* (2018) studies cannot be directly extrapolated to boreal forest ecosystems. Thus, landscape-level impacts of continuous cover forestry in the boreal deserve more research as well.

The impacts of continuous cover forestry and rotation forestry on ecosystem services are mainly studied using modelling and simulation methods. Continuous cover forestry has been suggested to be economically as profitable as or even more profitable than rotation forestry (e.g., Tahvonen *et al.* 2010, Pukkala *et al.* 2011, Kuuluvainen *et al.* 2012, Tahvonen and Rämö 2016, Parkatti *et al.* 2019). On the other hand, many studies have also questioned the economic profitability of continuous cover forestry (Shanin *et al.* 2016, Vauhkonen and Packalen 2019, Kellomäki *et al.* 2019). Uncertainty in the success of natural regeneration (Eerikäinen *et al.* 2014, Nygren *et al.* 2017, Kellomäki *et al.* 2019), decreased growth responses of remaining trees (Hynynen *et al.* 2019) and increased harvesting costs (Vauhkonen and Packalen 2019) can decrease the economic profitability of continuous cover forestry. Moreover, the development stage and structure of stand affect the profitability when shifting to continuous cover forestry (Tahvonen *et al.* 2010, Juutinen *et al.* 2018).

In terms of ecosystem services other than timber revenues, continuous cover forestry has been suggested to be a better option than rotation forestry for carbon storage and sequestration (Pukkala 2016a, Sinha *et al.* 2016), recreational forest values (Pukkala *et al.* 2011, Díaz-Yáñez *et al.* 2019) and wind disturbance resistance (Pukkala *et al.* 2016, Nevalainen 2017). In general, continuous cover forestry could be a better silvicultural approach than rotation forestry if the aim is to maintain multifunctional production forests (Nordström *et al.* 2013). However, at the larger spatial scale, the combination of continuous cover forestry and rotation forestry is likely a better option for non-timber ecosystem services than either silvicultural approach alone (Nolet *et al.* 2018).

When the Finnish forest act changed in 2014, practising continuous cover forestry became again a practicable management in the country. At the moment, less than 5% of forest cuttings are reported as continuous cover forestry ('Finnish forest centre' 2018). The interest towards this silvicultural approach has increased rapidly during recent years, but it is still unclear to what extent continuous cover forestry can contribute to alleviating the biodiversity loss while simultaneously providing ecosystem services in boreal forest landscapes in the long term.

1.6 Aims of the thesis

In the thesis, I study the potential of continuous cover forestry to alleviate the forestry-related loss of biodiversity and ecosystem services in forest landscapes in Finland. First, I compare the long-term impacts of continuous cover forestry and rotation forestry on different kinds of biodiversity features and ecosystem

services at the landscape scale by applying forest simulations and modelling tools (I). Second, I explore the mid-term impacts of continuous cover forestry on natural biodiversity features in streamside key habitats where selective logging was a factor in an experimental set-up (II, III). Finally, I return to the forest simulations and test the suggested approach of multiuse-conservation landscapes (IV).

In the first study (I), I compare the impacts of continuous cover forestry and rotation forestry on biodiversity and ecosystem services in commercial forest stands over a 100-years period. In both continuous cover forestry and rotation forestry, harvesting treatments follow the recommended practices for sustainable forest management in Finland (Äijälä *et al.* 2014). Thus, management in neither of these silvicultural approaches are optimized from the perspective of biodiversity or ecosystem services. Previous research has mainly compared the immediate impacts of clear-cutting and selective logging activities on biodiversity. However, it is essential to understand the effects alternative silvicultural approaches have in the long term, which covers all development stages of rotation forestry. The study (I) aims to answer the following question:

1. What biodiversity features and ecosystem services can be retained better in continuous cover forestry than in rotation forestry, and vice versa?

In the empirical studies of my thesis (II & III), I study the impacts of selective logging on natural features in streamside key habitats defined by the Finnish forest act. Streamside forests have naturally closed forest structure, and cool and moist microclimate, and they provide habitat for many specialized and endangered species (Naiman and Décamps 1997, Selonen and Kotiaho 2013). In Finnish forests landscapes, where nearly all forests are managed with rotation forestry, streamside key habitats are retained by leaving a forested buffer strip between a stream and a clear-cut area. To reduce the economic loss of preserving streamside key habitats, Finnish forest act allows selective logging within the forested buffer strip if it does not alter natural features in streamside habitat. However, the impacts of selective logging are still poorly known. Therefore, we studied the effects of buffer strip width (15 m or 30 m) and selective logging within a strip on microclimatic conditions (II), the formation of dead wood, and polypore communities (III) in streamside key habitats 12 years after loggings. These studies aim to answer the following question:

2. Do buffer strip width and selective logging affect microclimatic conditions in streamside habitat (II)?

3. Do buffer strip width and selective logging affect the formation of dead wood and the succession of polypore communities in streamside habitat (III)?

In the last study (IV), I test the suggested approach of multiuse-conservation landscapes and explore its effects on ecological, climatic, and economic benefits

in forests. We created different management scenarios for the landscapes varying in their share of allocation to timber production, biodiversity protection (i.e., set aside) and forest multiuse as well as whether set aside, multiuse or both were aggregated to specific landscapes (i.e., multiuse-conservation landscapes). In this study, both rotation forestry and continuous cover forestry included more management regime options than in the first study (I). The allocation of management regimes in timber production and multiuse was optimized to maximize specific targets. The study (IV) aims to answer the following questions:

4. What are the impacts of set asides, managing forest for multiuse, and their aggregations on economic, climatic, and biodiversity benefits in forests?
5. What is the contribution of continuous cover forestry in relation to rotation forestry while maximizing timber production and forest multiuse?

Together, the results from these studies can help to better understand for which targets and under which circumstances, continuous cover forestry could be a profitable management option.

2 METHODS

2.1 Simulations vs empirical studies

To find sustainable land-use management practices, the impacts of different management should be evaluated in the long term and over large areas (Felton *et al.* 2017a). However, the slow succession of boreal forests poses a challenge for research. Forest modelling and simulation approaches provide useful tools for studying different land-use methods and their impacts from multiple perspectives simultaneously (Hynynen *et al.* 2005, Felton *et al.* 2017a). Growth models predicting the development of forest under rotation forestry are highly developed (Hynynen *et al.* 2002). In recent years, the growth models predicting the development of forest under continuous cover forestry have become available as well (Pukkala *et al.* 2013). The structural data from simulations can be used to predict different proxies for biodiversity and ecosystem services, such as the amount of dead wood or timber revenues (e.g., Hynynen *et al.* 2005, Mönkkönen *et al.* 2014). Further, these can be used as responses to assess the impacts of different planning scenarios or as targets to find optimal forest management actions.

However, uncertainty exists within simulations and predictions, for example, due to natural variation in forest growth (Eyvindson and Kangas 2015). Moreover, stochastic events, such as the occurrence of natural disturbances, are challenging to predict and are not typically included in predictions. Furthermore, the ecological complexity of nature makes it challenging to predict biological responses, especially over long time periods. For example, due to the complex interactions among species (Ovaskainen *et al.* 2016), the impacts of management actions on species communities are hard to predict. However, empirical studies are typically specific case studies with a relatively short follow-up time, and they cannot be directly applied, for example, to study different landscape-scale scenarios (Felton *et al.* 2017a). Therefore, I have used both empirical and simulation methods in the thesis.

2.2 Study forests

The study forests of long-term modelling studies (I, IV) consist of 31,489 forest stands (i.e. planning units) located in 17 different watersheds (i.e., landscapes) in Southern-, Eastern-, and Central-Finland (Fig. 1). The total size of the study area is 47,561 ha (IV), and the mean size of forest stands is 1.5 ha. The initial forest data, based on forest laser-scanning, originates from the local forest authority. The forest data contain stand-level characteristics, such as forest soil and site type, tree species composition, and size distribution of trees. Mineral soils cover 77% (I, IV) and peatlands 23% (IV) of the total area. Study I included only the stands on the mineral soil. Forests are mainly mesic heath, herb-rich heath, sub-xeric heath, and xeric heath sites mainly dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) with varying amount of deciduous mixture. Forests vary in terms of their initial development stage and age (Pohjannies *et al.* 2017a).

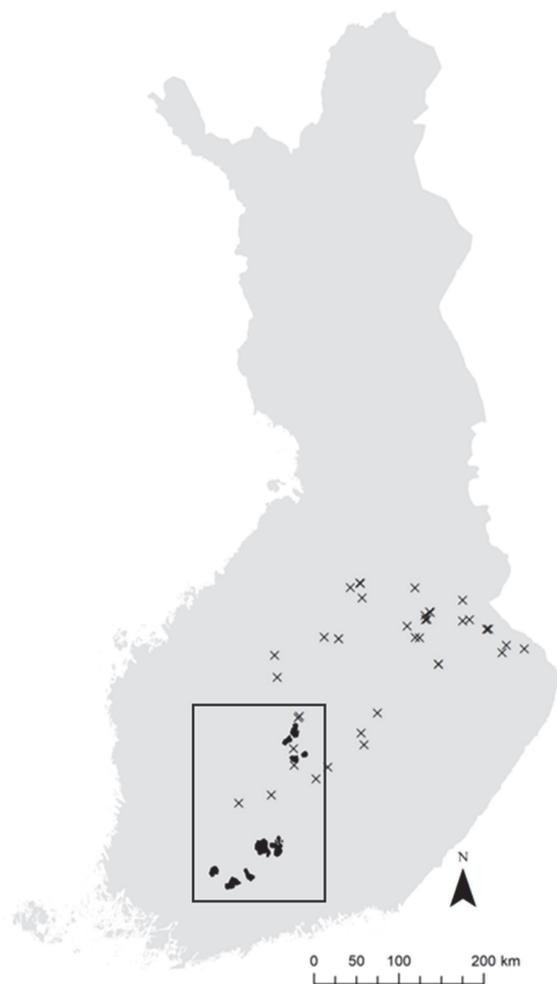


FIGURE 1 Study forests. Dark areas inside the box indicate the location of forests in simulation studies (I, IV). Crosses indicate the location of study forests in empirical studies (II, III).

Study forests of empirical studies (II, III) are located in Central Finland, Eastern Finland, Western Finland, and North-Karelia (Fig. 1). These 35 forest sites are streamside key habitats defined by the Finnish Forest Act (*Forest act* 2013). Streamside forests are spruce dominated mature forests mainly on the mineral soil, and they represent mesic heath forests. At the beginning of the study (2004), the forests were 80-100 years old, and clear-cuttings had not been conducted in adjacent forest stands.

2.3 Forest management regimes

2.3.1 Simulations

The development of forest stands in studies I and IV was simulated 100 years into the future under alternative forest management practices. The development under rotation forestry was modelled using the model set of Hynynen *et al.* (2002), which consists of species-specific individual-tree models for ingrowth, growth, and mortality. The development under continuous cover forestry was first predicted using the same models (Hynynen *et al.* 2002), and after the first harvesting of continuous cover forestry, the models from Pukkala *et al.* (2013) were applied (I). The model set of Pukkala *et al.* (2013) consists of species-specific individual-tree diameter increment and survival models, and a stand-level model for ingrowth. Growth models of Hynynen *et al.* (2002) are based on a larger amount of data than the growth models of Pukkala *et al.* (2013). Therefore, more uncertainty exists within the growth models applied for continuous cover forestry.

Rotation forestry included artificial regeneration for spruce or pine, tending of seedlings, one to three commercial thinnings from below and clear-cut where 10 retention trees were left (Fig. 2). In continuous cover forestry, mainly harvesting from above was conducted for every 15-20 years, and regeneration was based on natural regeneration (Fig. 2). A small share of largest trees were retained as seeding trees, but specific retention trees were not left.

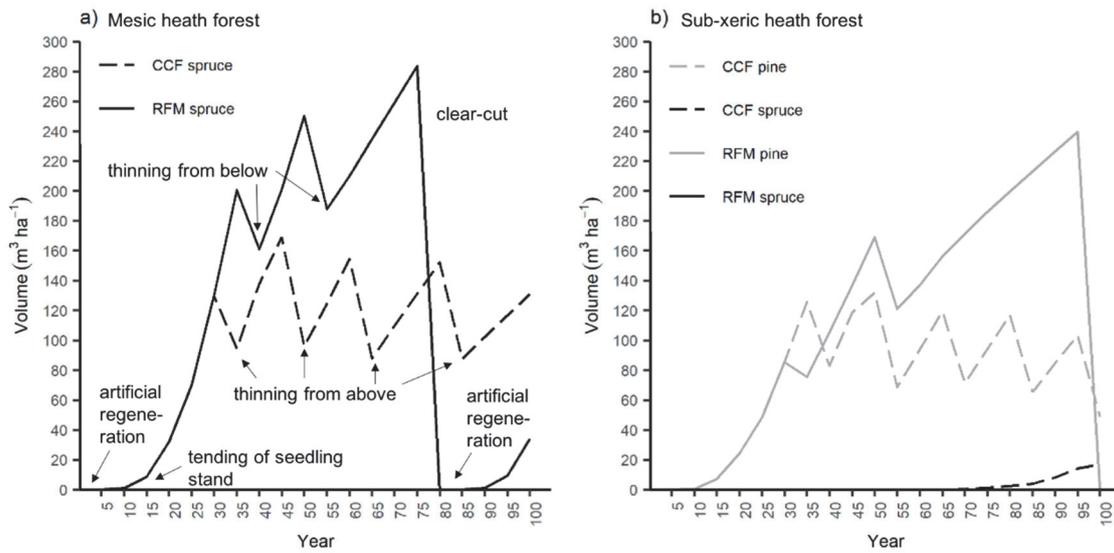


FIGURE 2 Typical stand-level development of tree volume under continuous cover forestry (CCF) and rotation forestry (RFM) in a) spruce-dominated mesic heat site and b) pine-dominated sub-xeric heat site. Silvicultural treatments follow the recommendations (Äijälä *et al.* 2014).

Only the recommended management regimes of silvicultural approaches were followed in the first study (I), whereas multiple modified regimes were simulated in the other simulation study (IV). In rotation forestry, the length of rotation, the amount of retention trees, and the timing of thinnings were modified. In continuous cover forestry, the harvesting interval was modified by decreasing and varying the pre-harvest basal area (i.e., the basal area when harvesting was conducted). In addition, forests were simulated into the future without management when they were set aside from timber production (I, IV). The models of Hynynen *et al.* (2002) were used for set asides.

2.3.2 Streamside forests

In streamside forests, the width of the buffer strip between a stream and a clear-cut area and selective logging on a buffer strip were manipulated in four buffer strip treatments (Fig. 3a). In each buffer strip treatment, a clear-cut was conducted on the one side of a stream during the winter 2005-2006, and one type of forested buffer strip was retained between a stream and a clear cut: 15-m or 30-m wide buffer strips with or without selective logging (II, III). In selective logging, 30% of the basal area was logged evenly from the whole width of the buffer strip, and the largest trees were mainly removed. In addition, eight sites were unmanaged control sites.

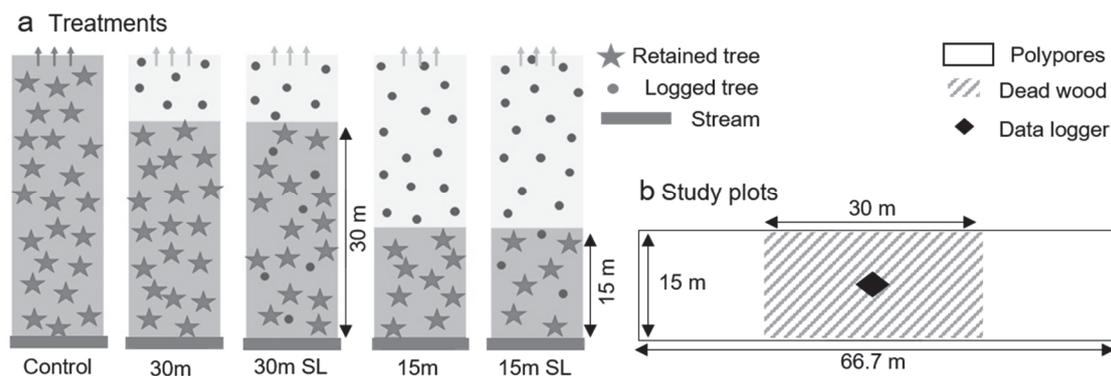


FIGURE 3 a) Study design of treatments modified from the paper III. Streams are at the bottom of the figure, arrows above indicate continuous forest cover in the controls and continuing clear-cut area in buffer strip treatments. SL indicates selective logging. b) The study plots for dead wood, polypores and microclimatic conditions.

2.4 Measures of biodiversity and ecosystem services

2.4.1 Indicators of biodiversity and ecosystem services (I, IV)

Forest simulations produce structural forest data with 5-year time steps. The structural forest data and other stand-level information were used to model stand-level indicators for each of the 20 time steps under each forest management regime. Biodiversity indicators were habitat availabilities of six indicator species (I, IV) and dead wood resources (I, IV). Ecosystem services indicators were timber net present value (NPV) (I, IV) and the amount of harvested timber (I), carbon storage (I, IV) and sequestration (I), yields of collectable goods (I), and scenic beauty of forests (I). Moreover, one watershed-level indicator, a metacommunity capacity of dead wood dependent species, was used (IV).

Habitat availabilities were calculated for a selected set of umbrella or indicator species which require different kind of structural features (Mönkkönen *et al.* 2014). Habitat availability for species measures the capacity of the forests to maintain species populations and takes into account the area and quality of habitat patches (connectivity not included). For each species, a habitat availability across the study forests was calculated as the sum of products between a stand specific habitat suitability index (HSI, between 0 and 1) value and the area of a stand. The species were: Capercaillie (*Tetrao urogallus*) lekking sites representing availability of pine-dominated forests, Hazel grouse (*Bonasa bonasia*) representing an adequate level of deciduous mixture, Lesser-spotted woodpecker (*Dryobates minor*) representing old deciduous trees and deciduous snags, Long-tailed tit (*Aegithalos caudatus*) representing mature deciduous trees, Siberian flying squirrel (*Pteromys volans*) representing a high volume of spruce and deciduous mixture, and Three-toed woodpecker (*Picoides tridactylus*) representing a high volume of fresh dead wood (I, IV).

Dead wood resources were estimated as the volume of dead wood multiplied by the diversity of dead wood species (Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, and birches *Betula pendula* and *Betula pubescens*) and 5 decay stages (Mäkelä et al. 2006) (I, IV). In study IV, based on dead wood resources, habitat availability and metacommunity capacities of dead wood dependent species were also estimated (IV). For this, we applied the metapopulation capacity measure from Hanski (Hanski 1999). In addition to habitat availability, metacommunity capacity takes into account the amount of habitat connectivity and the dispersal ability of species. Metacommunity capacities were calculated for each watershed separately. As dispersal ability of dead wood dependent species varies (Komonen and Müller 2018), the following dispersal abilities were used: 500 m and 1 km representing short-distance dispersers and 3 km and 6 km representing mid-distance dispersers.

The economic value of forests was estimated by calculating a timber net present value (NPV in €) (I, IV). The timber NPV consists of three components: the revenues from harvesting (clear-cuts, thinnings from below, and thinnings from above), the value of standing timber in the end of simulations, and the value of spare land in the end of simulations (Pukkala 2005). In addition, timber NPV takes into account costs resulted from silvicultural actions related to regeneration and young stands in rotation forestry (I, IV). The timber revenues and costs during the 100-year period were discounted with varying interest rates (1-5% in I, 1% in IV).

The carbon storage was calculated as the amount of carbon in tree biomass and in soil. The amount of carbon in biomass was estimated by multiplying the total tree biomass by 0.5. The carbon in soil was modelled using Yasso07 model (Tuomi et al. 2011) for mineral soils (I, IV) and carbon lux model for peatlands (Ojanen et al. 2014) (IV). The carbon sequestration was estimated from differences in the total carbon storage between consecutive time steps (I). The yields of two most common berries, bilberry and cowberry, and the scenic beauty were estimated using model approximations (Pukkala et al. 1988, Miina et al. 2009, 2016, Turtiainen et al. 2013) (I).

2.4.2 Microclimate (II)

Microclimate was measured from streamside forests in 2017, 12 years after the treatment loggings. Data loggers were used to measure relative humidity and air temperature at 5-minute time intervals for a month in the summer 2017. Two data loggers were placed on a trunk of a mature spruce tree located at a distance of about 7.5 meters from the stream (Fig. 3b). From the data of each logger, the following response variables were calculated: the mean relative air humidity, the mean of daily minimum relative air humidity, the standard deviation of all of the relative air humidity values, the mean air temperature, the mean of daily maximum air temperatures, and the standard deviation of all of the temperature values.

2.4.3 Dead wood resources and polypore communities (III)

Dead wood and polypores were inventoried before the loggings in the autumn 2004 and after the loggings in the autumn 2017. Dead wood was measured from 0.045 ha study plots and polypores from 0.1 ha plots at the distance of 0 to 15 m from a stream, which was assumed to be the main key habitat (Fig. 3b). The lengths, diameter, tree species, and decay stages (Renvall 1995) of whole trunks and fragments were recorded. From the dead wood data following response variables were calculated for each stand: the change in the volume of fresh dead wood (decay stages 1, 2) between 2004 and 2017 and the change in the volume of old dead wood (decay stages 3, 4, 5) between 2004 and 2017. Polypores were surveyed by observing their fruiting bodies from the dead and living trees. From the polypore data, the following response variables were calculated for each stand: change in the number of individuals between 2004 and 2017, and change in the number of species between 2004 and 2017. Moreover, Bray-Curtis dissimilarity measure was used to estimate the composition of polypore communities between sites and years.

2.5 Analyses

2.5.1 Comparisons between continuous cover forestry and rotation forestry (I)

First, the levels of biodiversity and ecosystem services measures under continuous cover forestry, rotation forestry, and set aside were calculated at landscape scale across 100 years (I). Set asides were used as a reference level for the comparison between different silvicultural approaches. Thus, to estimate the relative performance of continuous cover forestry and rotation forestry compared to set aside forests in the delivery of different biodiversity and ecosystem services, their values were divided by the values in set aside forests (except in the case of timber benefits). Moreover, the share of stands when continuous cover forestry outperforms rotation forestry and vice versa was calculated (I).

Afterwards, I also explored whether the initial stage of the stand or site type could explain the optimal allocation of continuous cover forestry and rotation forestry. I explored only one timber-provisioning service and three indicator species. In the cases of indicator species, I studied the optimal allocation of silvicultural approaches only in site types that were likely able to provide suitable habitat for a species. Indicators were timber NPV with 1% discount rate for herb-rich heath, mesic heath, sub-xeric heath, and xeric heath sites, Hazel grouse for herb-rich heath, mesic heath and sub-xeric heath sites, Siberian flying squirrel for herb-rich heath and mesic heath sites, and Capercaillie for sub-xeric and xeric heath sites. For each indicator and stand class, I calculated the mean and the standard deviation and visually explored whether the superiority of either silvicultural approach depended on the site type or the initial stage of stand.

2.5.2 Microclimate, dead wood and polypore communities (II, III)

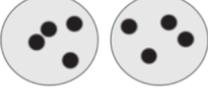
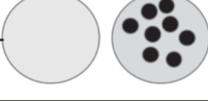
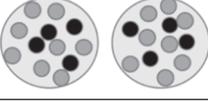
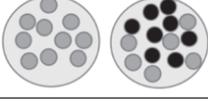
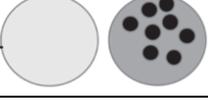
Multivariate analysis methods were mainly used in empirical studies. First, each of four logging treatments (30m or 15m wide buffer strip without or with selective logging) was compared with a control treatment. Second, the effect of buffer strip width (30m or 15m) and selective logging on a strip (yes or no) and their interaction were analysed without the controls. Multivariate Analyses of Variance (Manova) was used to analyse microclimate data and separate Manovas were performed for humidity and temperature. Kruskal-Wallis One-way Analyses of Variance was used to analyse the amount of change in fresh and old dead wood, polypore species richness, and the number of polypore individuals. Each treatment was compared to control with the Dunn's test. Permutational Manova (Permanova) was used to analyse the mean composition of polypore community data, and Betadisper was used to analyse the dispersion of polypore community data. Permanova and Betadisper were performed separately for years 2004 and 2017 and then simultaneously for both years to analyse the change.

2.5.3 Scenario analyses (IV)

Six scenarios were built where commercial forest landscapes were transformed towards multiuse-conservation landscapes step by step (from S1 to S6 in Table 1a). Scenarios varied in their share of allocation to timber production (100%, 83% or 50% of the total area), set aside (0% or 17% of the total area) and multiuse (0% or 33% of the total area) as well as whether set aside, multiuse or both were aggregated (Table 1a). In forests managed for production, the optimal allocation of the management regimes was targeted to maximize timber NPV with 1% discount rate. Set asides were selected to maximize dead wood resources. In forests managed for multiuse, the optimal allocation of management regimes was targeted to maximize carbon storage, dead wood resources, and habitat availabilities of six indicator species. Set aside was not allowed as a management regime in production or multiuse.

Optimizations were run separately for all six scenarios (Table 1a), and the results from the scenarios were compared to evaluate the effects of multiuse-conservation landscapes and to separate the effects of different management types and their aggregations (Table 1b) on different forest benefits. These were: timber NPV to indicate economic benefits, carbon storage to indicate climate benefits, and habitat availability of dead wood dependent species and metacommunity capacities of dead wood dependent species with different dispersal abilities to indicate biodiversity benefits. Finally, the optimal allocations of management regimes to maximize timber production and multiuse were evaluated.

TABLE 1 a) Different scenarios and their management objectives, share of area allocated to each management objective, and aggregation of set aside or multiuse. In figures, light grey indicates production, black indicate set aside and dark grey indicates multiuse. YES/NO in the aggregation column indicates that the management in question is or is not aggregated to half of the landscapes. b) Comparisons between scenarios which reveal the effects of management objectives and their aggregations. From paper IV.

a)	Scenario	Management objective of stands	Share (%) of allocation	Aggregation
S1		Production	100	
		Set aside	0	NO
		Multiuse	0	NO
S2		Production	83	
		Set aside	17	NO
		Multiuse	0	NO
S3		Production	83	
		Set aside	17	YES
		Multiuse	0	NO
S4		Production	50	
		Set aside	17	NO
		Multiuse	33	NO
S5		Production	50	
		Set aside	17	YES
		Multiuse	33	NO
S6		Production	50	
		Set aside	17	YES
		Multiuse	33	YES

b) Scenario comparisons

Effect over all the landscapes

S1 vs S6	Effect of 50% multiuse- conservation landscapes.
S1 vs S2	Effect of 17% set aside.
S2 vs S3	Effect of aggregation of set asides.
S2 vs S4	Additional effect of 33% multiuse on top of the effect of 17% set asides.
S4 vs S5	Effect of aggregation of 17% set asides when 33% multiuse located anywhere.
S5 vs S6	Additional effect of aggregation of 33% multiuse on top of 17% aggregated set asides.

3 RESULTS AND DISCUSSION

3.1 Continuous cover forestry in commercial forest landscapes

3.1.1 Comparisons between continuous cover forestry and rotation forestry (I)

Long-term simulations where forest management in both silvicultural approaches followed the recommendations (Äijälä *et al.* 2014), revealed that continuous cover forestry provided higher habitat availabilities for Hazel grouse, Lesser-spotted woodpecker, Long-tailed tit and Three-toed woodpecker, bilberry yields, carbon storage and sequestration, and scenic beauty than rotation forestry (I). On the other hand, rotation forestry provided higher habitat availabilities for Capercaillie and Siberian flying squirrel, and cowberry yields than continuous cover forestry. In the cases of Capercaillie, Siberian flying squirrel, Three-toed woodpecker, and carbon indicators, the levels in both forest management approaches were clearly lower than the levels in set asides. The amount of dead wood resources was also low in both approaches. Moreover, in terms of timber benefits, the superiority of continuous cover forestry or rotation forestry depends on the considered perspective (i.e., forest industry or forest owner).

Typically, indicator species that got more habitat under continuous cover forestry than under rotation forestry require mature forest structure and deciduous trees (Mönkkönen *et al.* 2014). Deciduous mixture was maintained in continuous cover forestry (Fig. 4c), whereas coniferous species monocultures were created in rotation forestry. However, it should be noted that deciduous mixture could also be maintained in rotation forestry, which would likely increase the habitat availability of deciduous trees dependent species in forests under rotation forestry.

The share of spruce increased in pine-dominated forests under continuous cover forestry (Fig. 2b, Fig. 4c). This explains the increased potential of rotation forestry to provide habitat for Capercaillie in pine-dominated forests (I). For example, to promote the natural regeneration of light-demanding pine in

continuous cover forestry, tree density should be likely lower than currently recommended (Parkatti *et al.* 2019).

In the case of Siberian flying squirrel, the larger habitat availability under rotation forestry than under continuous cover forestry can be explained by the low volume of standing trees in forests under continuous cover forestry (Fig. 2a). The habitat model of flying squirrel assumes that in order for forest to provide any habitat, the volume of spruce has to be more than $140 \text{ m}^3\text{ha}^{-1}$ (Mönkkönen *et al.* 2014). The volume of spruce was often smaller or just slightly more than this limit in forests under continuous cover forestry when the current recommendations were followed (Fig. 2a). In contrast, forests at late development stages under rotation forestry fulfilled the habitat requirements of a flying squirrel.

Including habitat connectivity to predictions could change some results as, for example, in the case of Siberian flying squirrel, clear-cuts can prevent the movement between suitable habitat patches (Selonen and Hanski 2004). Nevertheless, these results highlight the importance of long-term and landscape-level comparisons. Most studies exploring different silvicultural approaches have compared the effects of clear-cut and selective logging events. These comparisons cannot be directly applied to compare continuous cover forestry and rotation forestry approaches over long time periods. The negative impacts of clear-cuts are evident, but during 100-years, rotation forestry can include only one clear-cut and two thinnings from below, whereas continuous cover forestry can include four thinnings from above (Fig. 2). Thus, even though the intensity of one harvesting event can be lower in continuous cover forestry than in rotation forestry, the harvesting frequency can be higher, and this could potentially have some effects on species.

Even though the quantity of harvested timber obtained from continuous cover forestry was smaller than from rotation forestry, continuous cover forestry provided higher timber NPV than rotation forestry with discount rates above 2% (I). This can be explained by the sole use of natural regeneration in continuous cover forestry (no costs from artificial regeneration) as compared to artificial regeneration methods used with rotation forestry, by more even flow of income, and by a larger share of logwood in continuous cover forestry (79% in continuous cover forestry vs 65% in rotation forestry, see I). Similar results have also been found earlier (e.g., Laiho *et al.* 2011, Pukkala 2016b, Tahvonen and Rämö 2016). Thus, these results suggest that rotation forestry could meet better the requirements of forest industry, while continuous cover forestry could be more profitable for private forest owners (I).

In general, the results are in line with previous research showing that continuous cover forestry could be an economically profitable method to retain multifunctional commercial forests (e.g., Pukkala 2016b, Shanin *et al.* 2016). In terms of carbon benefits, the largest differences between continuous cover forestry and rotation forestry were in soil (I). Young stands in rotation forestry were carbon sources even 15-30 years after clear-cuts, whereas changes in soil carbon were smaller after loggings in continuous cover forestry. Bilberry is

sensitive to clear-cuts (Miina *et al.* 2009, Hedwall *et al.* 2013), which mainly explains the larger bilberry yields in continuous cover forestry than in rotation forestry. In contrast, cowberry is less sensitive to clear-cuts than bilberry and can produce high yields in young stands (Turtiainen *et al.* 2013).

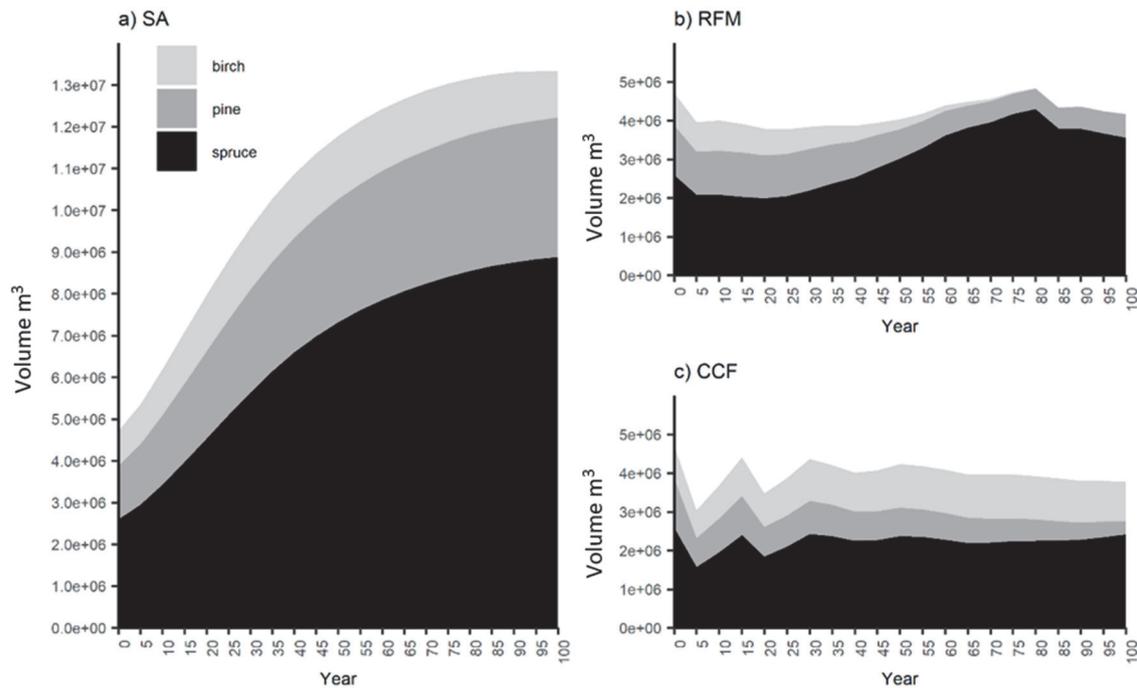


FIGURE 4 The development of total tree volume (birch, spruce and pine) over all of the study forests (I) during the 100-year period under a) set aside (SA), b) rotation forestry (RFM) and c) continuous cover forestry (CCF).

3.1.2 Impacts of initial stage of stand and site type

Neither of the silvicultural approaches was superior over the others in terms of most studied indices (I). For example, when the interest rate was 1% continuous cover forestry was more profitable option than rotation forestry in about 50% of stands and vice versa (I). More detailed comparisons showed that the relative economic profitability of continuous cover forestry tended to increase with decreased site fertility (Fig. 5a-d). Moreover, continuous cover forestry tended to be more profitable than rotation forestry if the stand was initially at early or intermediate development stage. Managing initially mature stand with continuous cover forestry likely results in lowered timber NPV because less timber will be harvested in near future than under rotation forestry (Tahvonon *et al.* 2010, Pukkala *et al.* 2011). In the case of Siberian flying squirrel and Capercaillie, rotation forestry was a better option than continuous cover forestry in 70-80% of forest stands (I) but continuous cover forestry tended to be better option than rotation forestry if the stand was initially mature (Fig. 5e-h). Also in the case of Hazel grouse, continuous cover forestry tended to be a better option,

especially if the stand was initially mature (Fig. 5i-k). Therefore, even though continuous cover forestry could be on average more profitable than rotation forestry and could be on average less bad option for biodiversity than rotation forestry (I), more detailed comparisons show that the conflict between economic and ecological benefits still clearly exists (Fig. 5). Thus, like rotation forestry, continuous cover forestry alone cannot maximize the economic and ecological benefits simultaneously at the forest stand scale.

At the landscape scale, instead, increasing the share of continuous cover forestry could alleviate the negative impacts of forestry on biodiversity and ecosystem services (I) (Eyvindson *et al.* 2018). The allocation of both approaches to the landscape would also mimic more natural landscape structure with different kinds of forest dynamics and, as shown, it can increase habitat heterogeneity (I). Moreover, the low amount of dead wood in both approaches shows that the preservation of important structural features for biodiversity, for example, through retention trees, needs to be considered irrespective of the silvicultural approach (I) (Gustafsson *et al.* 2019).

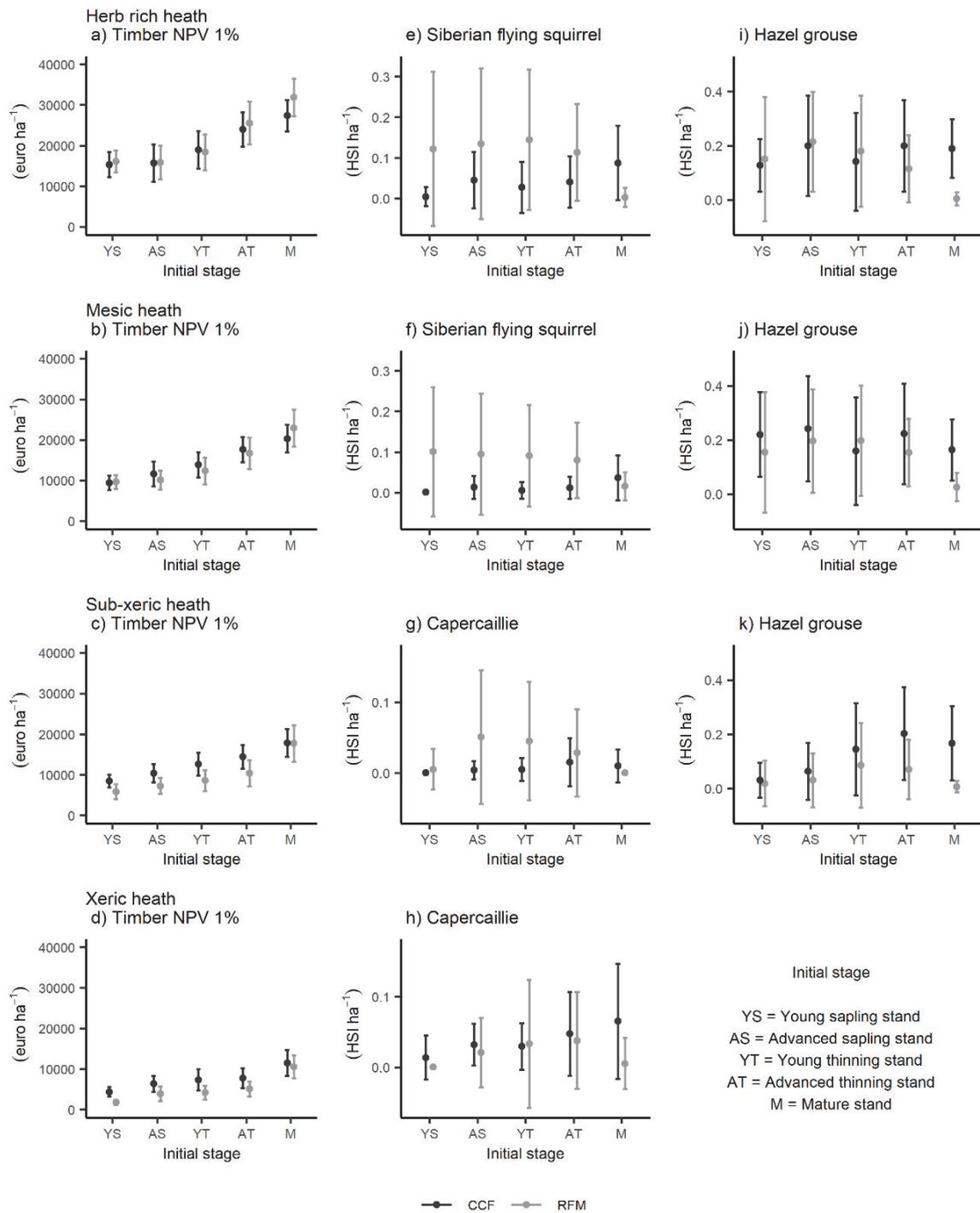


FIGURE 5 The average timber NPV (a-d), habitat suitability (HSI) of Siberian flying squirrel (e-f), Capercaillie (g-h) and Hazel grouse (i-k) over 100 years under continuous cover forestry (CCF) and rotation forestry (RFM) categorized based on the initial development stage of stand and site type. Timber NPV is shown for all site types (herb-rich, mesic, sub-xeric and xeric heath site type) but HSI-values only for site types mainly suitable for the considered species.

3.2 Selective logging in streamside key habitats (II, III)

Compared with unmanaged streamside forests, microclimatic conditions in managed sites were typically drier and warmer, and their microclimatic conditions were less constant 12 years after loggings (II). The effect of buffer strip width on microclimatic conditions was strong, and thus the effect of selective logging remained small (II). This was not surprising as clear-cuts change the within-stand microclimatic conditions remarkably (Zheng *et al.* 2000), and due to edge effect, these impacts of clear-cuts can influence even 50 m into forest interior of an adjacent stand (Murcia 1995, Ylisirniö *et al.* 2016). However, selective logging tended to have some additional impacts on microclimatic conditions, which was expected as logging creates gaps to the canopy and thus, for example, increases the amount of direct solar radiation (Zheng *et al.* 2000, Gray *et al.* 2002).

The formation of fresh dead wood had increased in most sites 12 years after loggings (III). The increase in dead wood formation was not surprising as spruce-dominated and mature study forests were assumed to develop slowly towards old-growth conditions, in which case the formation of dead wood, for example due to senescence- and fungi-related tree mortality, is likely (Kuuluvainen and Aakala 2011). On the other hand, buffer strips next to clear-cuts are also prone to wind disturbances (Murcia 1995), and sites with 15 m wide buffer strips had a large number of windthrows (Mäenpää *et al.* unpublished). Thus, wind disturbance was likely the main driver for the formation of dead wood in sites with 15 m wide buffer strips. Streamside forests with 30 m buffer strips were not exposed to wind disturbances as much as those with 15 m buffer strips (Mäenpää *et al.* unpublished). Within these sites, weak evidence was found that selective logging may have reduced the natural formation of dead wood and thus may have disturbed the natural forest succession already during 12 years (I). Strong evidence exists that selective logging disturbs the natural formation of dead wood in the long term (Bader *et al.* 1995, Sippola *et al.* 2001). The finding also supports the long-term projections, which showed that compared with set asides, the availability of dead wood resources was smaller in continuous cover forestry (I).

The numbers of polypore individuals and species tended to increase similarly in unmanaged and managed streamside forests (III). This was not surprising as the polypore species diversity increases typically with forest succession and after disturbances (Selonen *et al.* 2005, Junninen and Komonen 2011). Nevertheless, the responses in polypore community composition suggest that the adjacent clear-cut and selective logging disturbed natural polypore communities (III). The polypore community succession seemed to be disturbed especially in sites with 15 m wide buffer strips. Their community composition started to resemble the composition typically found in commercial forests, and many generalist species favouring edges became more abundant (Snäll and Jonsson 2001, Siitonen *et al.* 2005). Although, the additional impacts of selective logging were small, selective logging tended to homogenize polypore

communities among managed sites. This suggests that selective logging disturbed the natural diversity in polypore communities (Abrego *et al.* 2014), which supports earlier findings about negative impacts of selective logging on polypores (Sippola *et al.* 2001, 2004).

In summary, the responses in microclimatic conditions (II), dead wood and polypore communities (III) showed that the negative impact of clear-cuts was larger than that of selective logging. If forests near streamside habitats are managed with rotation forestry, the width of the buffer strip between a stream and a clear-cut should be at least 30 m wide to preserve natural features in streamside key habitat (II, III). Selective logging (30% of the basal area removed) seemed to disturb the natural microclimatic conditions, natural biodiversity and its succession in streamside forests and, therefore, it is not recommended as a management option to reduce the economic loss of preserving streamside key habitats.

However, applying continuous cover forestry instead of rotation forestry in forests near streamside habitats could retain more natural forest structure without sharp forest edges (Angelstam 1998, Braithwaite and Mallik 2012). The edge effect of continuous cover forestry would be likely smaller than the edge effect of rotation forestry when the width of the unmanaged strip could be perhaps narrower than the suggested 30 m (II, III). Furthermore, as continuous cover forestry could also be economically profitable management option (I), managing forest stands next to a key habitat under continuous cover forestry could be an economical method to diminish the negative impacts of adjacent loggings on streamside habitats. In this case, long-term planning would be required to secure the profitability because the shift to continuous cover forestry is economically profitable to do before the forest stand becomes mature (I). Future studies should tackle these issues more carefully.

3.3 Continuous cover forestry and multiuse-conservation landscapes (IV)

3.3.1 Effects of multiuse-conservation landscapes

Multiuse-conservation landscapes were an efficient tool to increase biodiversity and climate benefits in forests but simultaneously incurred high economic costs (IV). The largest management impacts emerged from setting aside 17% of forest area, whereas the additional impacts of managing 33% of the area for multiuse were clearly smaller.

The overall impacts of management aggregations were smaller than the impacts of set asides and multiuse management (IV). Measured over all the landscapes, aggregations decreased the habitat availability of dead wood dependent species slightly (due to decreased quality of some habitats) but increased the metacommunity capacities of dead wood dependent species

somewhat more (due to increased connectivity of habitats). From the metacommunity capacity perspective, results suggest that the benefit of increased habitat connectivity was larger than the slight cost of habitat quality. Especially species with short-distance dispersal ability seemed to benefit from the aggregations of set asides and multiuse to multiuse-conservation landscapes.

These aggregations did not have impacts on forest climatic benefits. However, the aggregations of set asides and multiuse stands to multiuse-conservation landscapes decreased their economic cost. Thus, partitioning landscapes into intensively managed production landscapes and multiuse-conservation landscapes could alleviate the conflicts between ecological and economic benefits, which supports earlier findings about the profits of spatial planning (e.g., Côté *et al.* 2010, Pohjanmies *et al.* 2017a, Mönkkönen *et al.* 2018).

3.3.2 The optimal allocations of management regimes

The optimal allocation of management regimes to maximize timber production (NPV with 1% discount rate) included about 60% of continuous cover forestry and 40% of rotation forestry (Fig. 6a S1, S2, S3, Fig. 6b timber production landscapes). Within continuous cover forestry, regimes with delayed harvest timing dominated (i.e., increased pre-harvest basal area criteria, depending on the site type 16–22 m²ha⁻¹ +3 and +6 m²ha⁻¹), while the share of the unmodified regime was approximately 25%. Within rotation forestry, regimes without thinnings and shorter rotation lengths dominated while the share of the unmodified regime was approximately 10%. These results suggest that the current recommendations (Äijälä *et al.* 2014) do not guide to economically maximal timber production, and more variation within both approaches is desired. Therefore, as previous research has shown (e.g., Hynynen *et al.* 2005, Tahvonen *et al.* 2010, Rämö and Tahvonen 2014), careful forest management planning at a stand level can bring economic benefits. Moreover, the result that continuous cover forestry could be economically more profitable than rotation forestry in many forests (I) tends to hold also when a larger amount of management regimes exists within both approaches (IV).

The optimal combination of management regimes to maximize forest multiuse included about 40% of continuous cover forestry and 60% of rotation forestry (Fig. 6b multiuse-conservation landscapes). Within continuous cover forestry, the regime with the delayed harvest timing dominated (depending on the site type 16–22 m²ha⁻¹ +6 m²ha⁻¹). Within rotation forestry, 40% of forests were managed with the increased amount of retention trees (30 trees ha⁻¹) and 60% of forests with longer rotation lengths (mainly 30 years longer rotation length than recommended). The share of continuous cover forestry in the optimal allocation of regimes for multiuse was smaller than what could have been expected (I) (Pukkala 2016b, Shanin *et al.* 2016). However, several reasons can explain this.

Firstly, timber revenues were not a target in multiuse management when economically less intensive and less profitable rotation forestry regimes were favoured. For example, rotation forestry with 30 years longer rotation length can benefit carbon storages and biodiversity remarkably, but simultaneously it leads

to decrease in the economic performance (Liski *et al.* 2001, Triviño *et al.* 2015). Secondly, more less-intensive regime options were available within rotation forestry than within continuous cover forestry. In continuous cover forestry, for example, the post-harvest basal area was not modified, and it could be increased.

Thirdly, the share of management regimes can be explained through an evaluation of the forest stand structure (3.1.2). Set asides were allocated to stands with the highest potential of dead wood resources, and this allocation was done before the allocation of multiuse (IV). The amount of dead wood strongly correlates with the structure of the forest (Mäkinen *et al.* 2006), so many set asides were mature and old stands at the beginning of the planning period. This means that forests available for multiuse management were on average younger than all forests on average. From the biodiversity perspective, the benefit of continuous cover forestry tended to be the largest for initially mature forest stands (Fig. 5). Therefore, as the amount of mature stands available for multiuse was smaller, it likely decreased the share of continuous cover forestry in the optimal allocation of management regimes for multiuse. This impact can be seen when comparing the share of management regimes in scenarios S5 and S6 (Fig. 6a). The share of continuous cover forestry was larger in the scenario where set asides were aggregated and multiuse forests were allowed to locate anywhere (Fig. 6a S5) than in the scenario where both set asides and multiuse forests were aggregated in multiuse-conservation landscapes (Fig. 6a S6). In the scenario with multiuse anywhere (S5), the initially mature stands in landscapes without set asides were available for multiuse, when the share of continuous cover forestry was larger.

Nevertheless, in all these cases, the potential of different silvicultural approaches to reduce the negative impacts of forestry on biodiversity and carbon storages mainly emerge from the decreased amount of harvested timber during the simulated period. Moreover, the largest positive impact of set asides on biodiversity and climatic benefits (IV) indicates that instead of contrasting continuous cover forestry and rotation forestry approaches, the amount of unmanaged forests and the amount of harvested timber within managed forests needs to be considered. This is also supported by earlier research showing that both continuous cover forestry and rotation forestry approaches were included in the optimal allocation of management regimes to mitigate the negative impacts of forestry on biodiversity and ecosystem services, but that mitigation became more difficult when the harvesting level increased (Eyvindson *et al.* 2018).

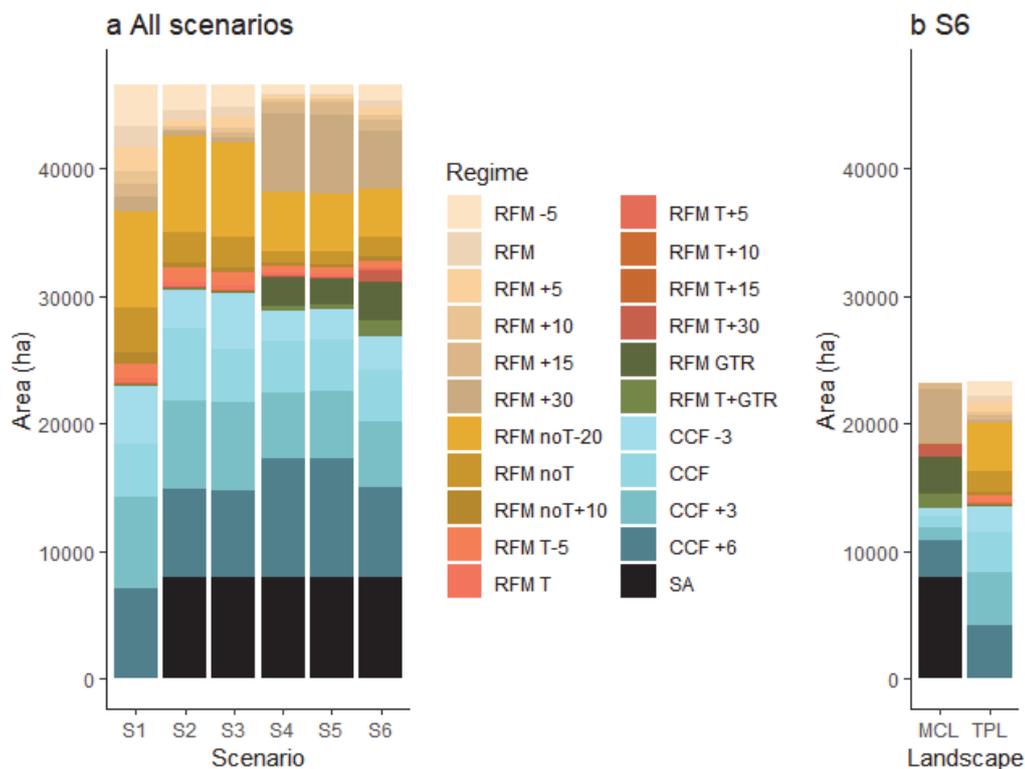


FIGURE 6 The optimal allocation of management regimes for a) each scenario and b) different landscapes in scenario S6. In b), MCL indicates multiuse-conservation landscapes where 33% of stands was set aside and 67% of stands were managed for multiuse, and TPL indicates landscapes where all stands were managed for timber production. RFM indicates rotation forestry and the number of years shorter or longer rotation length, noT is no thinnings, T is thinnings before and after clear-cut, and GTR is 30 retention trees instead of 10 per ha. CCF indicates continuous cover forestry and the number refers to smaller or larger pre-harvest basal area ($\text{m}^2 \text{ha}^{-1}$). SA indicates set asides. From paper IV.

4 CONCLUSIONS

Continuous cover forestry has been suggested to be an economically cost-efficient method to reduce the loss of biodiversity and ecosystem services in boreal commercial forests (e.g., Kuuluvainen *et al.* 2012, Pukkala 2016b). However, its possible long-term impacts at the landscape scale have been poorly studied from diverse perspectives. Thus, in the thesis, I used long-term simulation methods and empirical methods to explore what are the possibilities of continuous cover forestry to alleviate the negative impacts of forestry on boreal forests in Finland.

Long-term simulations suggest that continuous cover forestry could be a cost-efficient method to retain ecosystem services and some important biodiversity features, such as deciduous trees and tree cover continuity, in commercial forests landscapes (I). However, the combination of continuous cover forestry and rotation forestry was the best from the perspectives of both biodiversity and ecosystem services (I, IV). Moreover, dead wood is one of the most critical resources in Fennoscandia (de Jong and Dahlberg 2017, Hyvärinen *et al.* 2019), and the amount of dead wood was small in the recommended versions of both silvicultural approaches (I). Nevertheless, as previous research has also shown, continuous cover forestry could be a cost-efficient method to increase multiuse potential in commercial forests (Pukkala 2016b).

In reality, management in both silvicultural approaches can vary a lot. The intensity can be reduced, for example, by increasing the pre-harvest basal area in continuous cover forestry or increasing the rotation length in rotation forestry (IV). When more management regimes were available in both silvicultural approaches, the optimal allocations of regimes for timber production and forest multiuse included a remarkable share of modified regimes from both approaches (IV). Thus, it is not reasonable to put continuous cover forestry and rotation forestry against each other but instead to consider how flexibly they are used in commercial forest landscapes and how carefully their allocation is planned. Recent research has also shown that categorizing continuous cover forestry and rotation forestry is not necessarily straightforward as, in reality, it is possible to change the silvicultural approach within the planning period (Díaz-Yáñez *et al.*

2019). For example, thinning from above can be also done in rotation forestry and thus postpone the clear-cut, which often disturbs the forest the most (e.g., Siira-Pietikäinen and Haimi 2009, Hedwall *et al.* 2013).

The responses of microclimate (II), dead wood, and polypore communities (III) in streamside forests showed, on the other hand, that selective logging (i.e., a type of continuous cover forestry) is not an ecologically feasible option to reduce the financial cost of preserving streamside key habitats. Even though the impacts of selective logging were smaller than the impacts of adjacent clear-cut, results showed that selective logging also disturbed the natural biodiversity in streamside key habitats. Thus, important biodiversity features in commercial forest landscapes, such as key habitats and dead wood (I), needs to be considered irrespective of silvicultural approach. However, managing the forest stand next to key habitat under continuous cover forestry instead of rotation forestry would likely reduce the negative impacts of sharp forest edges on the key habitat (e.g., Braithwaite and Mallik 2012, Pukkala *et al.* 2016).

In addition, leaving forest unmanaged is likely the best option to preserve many specialized and sensitive species, such as many dead wood dependent species (I-IV). The targeted 17% protection level has not yet been reached in Finland, and the need for protection is especially urgent in Southern Finland (Hyvärinen *et al.* 2019). To allocate limited conservation resources efficiently, additional protected areas and conservation efforts in commercial forests could be aggregated jointly to specific landscapes designated as multiuse-conservation landscapes (Hanski 2011, Kotiaho 2017). Evidence was found that the aggregations of conservation efforts could decrease the negative impacts of forest fragmentation on biodiversity (IV). However, as most forests in Finland are privately owned, putting this kind of approach into practice can be very challenging, and some kind of compensation system would be likely needed to treat forest owners equally.

Finally, I did my best to consider the impacts of continuous cover forestry from diverse perspectives. However, for example, the uncertainty in the success of natural regeneration (Kellomäki *et al.* 2019) and the growth models, which are used for continuous cover forestry and rotation forestry, can both influence predictions about their relative profitability (Parkatti *et al.* 2019). Moreover, as the results from empirical studies showed, the negative effects of forest edges on biodiversity can be strong, and they were not considered in the simulation predictions. Furthermore, for example, climate change can cause new challenges to forest ecosystem, and both silvicultural approaches can have their risks (Nevalainen 2017). There are still several other aspects, which can affect the profitability of continuous cover forestry and rotation forestry, and more research is needed.

In summary, the results of my thesis support earlier research and show that increasing the share of continuous cover forestry in commercial forest landscapes could alleviate the negative impacts of forestry on biodiversity and ecosystem services. Nevertheless, as previous research has shown, timber production is in strong conflict with other forest benefits (Pohjanmies *et al.* 2017b), and mitigating

conflicts becomes more difficult with increased harvesting levels (Eyvindson *et al.* 2018). Timber harvesting removes resources from forest-dwelling species and disturbs the natural succession and dynamics in forests. Therefore, more attention should be paid on the amount of protected areas and the amount of harvested timber in commercial forest landscapes, rather than the cutting method with which the resources are removed. If harvesting pressure is decreased, there are several less-intensive options to manage forests more sustainably.

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ORIGINAL PAPERS

I

CONTINUOUS COVER FORESTRY IS A COST-EFFICIENT TOOL TO INCREASE MULTIFUNCTIONALITY OF BOREAL PRODUCTION FORESTS IN FENNOSCANDIA

by

Maiju Peura, Daniel Burgas, Kyle Eyvindson, Anna Repo & Mikko Mönkkönen
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Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia

Maiju Peura^{a,*}, Daniel Burgas^{a,b}, Kyle Eyvindson^a, Anna Repo^{a,c}, Mikko Mönkkönen^a

^a University of Jyväskylä, Department of Biological and Environmental Sciences, P.O. Box 35, FI-40014, Finland

^b University of Helsinki, Department of Forest Sciences, P.O. Box 27, FI-00014, Finland

^c Finnish Environment Institute (SYKE), Climate Change Programme, P.O. Box 140, FI-00251 Helsinki, Finland

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ABSTRACT

Earlier research has suggested that the diversification of silvicultural strategies is a cost-efficient tool to ensure multifunctionality in production forests. This study compared the effects of continuous cover forestry and conventional rotation forestry on ecosystem services and biodiversity in boreal forests in Finland. We simulated over 25,000 commercial forest stands for 100 years under continuous cover and rotation forest management. Forests without management were used as a reference. We compared the effects of silvicultural practices over space and time on ecosystem services, biodiversity indicators and multifunctionality. Our results revealed that continuous cover forestry was better than rotation forest management in terms of timber net present value, carbon sequestration, bilberry production, scenic beauty and the number of large trees. It provided higher habitat availability for indicator species dependent on deciduous trees and mature forest structure. Rotation forest management was better than continuous cover forestry in terms of harvested tree biomass, cowberries, mushrooms, and species dependent on high tree volume. In general, multifunctionality was higher in continuous cover forests than in rotation forests. Therefore, continuous cover forests may have a greater potential to produce simultaneously multiple benefits from forests. However, unmanaged forests often provided the highest levels of services and biodiversity making their role indispensable in delivering forest related ecosystem services and, especially, in the maintenance of biodiversity. Continuous cover forestry does not itself guarantee the maintenance of all ecosystem services and biodiversity in commercial forests but it can be an important part of a successful progression towards more sustainable forestry.

1. Introduction

Forests are crucial in delivering ecosystem services for human wellbeing. During the last decades many forests in the boreal zone have been managed for intensive timber production applying conventional even-aged rotation forest management (hereafter RFM) while largely disregarding management effects on biodiversity and other forest ecosystem services (Burton et al., 2010; Gauthier et al., 2015; Vanhanen et al., 2012). Solely focusing on timber production, RFM has resulted in a biodiversity decline in production forests (Bradshaw et al., 2009; Siitonen, 2001; Östlund et al., 1997). Moreover, RFM can disturb nutrient cycling, increase land erosion and decrease water quality (Laudon et al., 2011). The role of boreal forests in climate regulation is well known as they contain about one third of the global terrestrial carbon stock (Bradshaw and Warkentin, 2015; Pan et al., 2011). However, the common practice of RFM focusing solely on timber production reduces

carbon storage in boreal forests compared with optimal forest management (Triviño et al., 2016). Focusing on timber production can also be in conflict with other economically beneficial forest uses, such as recreation and harvest of non-timber forest products (e.g., berries and mushrooms) (Peura et al., 2016). Earlier research has shown that diversifying forest management is a cost-efficient tool for enhancing ecosystem services (Miina et al., 2016; Triviño et al., 2015) and biodiversity (Mönkkönen et al., 2014) in production forest landscapes. In addition, previous studies indicate that alternative silvicultural practices are needed to ensure the delivery of multiple benefits of forests (Puettmann et al., 2015; Felton et al., 2016).

Continuous cover forestry (henceforth CCF) has a long history throughout the world, however has been widely replaced by RFM for decades (Kuuluvainen et al., 2012; O'Hara, 2002; Pommerening and Murphy, 2004). Recently, CCF is returning as an important silvicultural alternative to RFM (Diaci et al., 2011). In CCF, single trees, or small

* Corresponding author.

E-mail addresses: maiju.peura@jyu.fi (M. Peura), daniel.burgasriera@helsinki.fi (D. Burgas), kyle.eyvindson@jyu.fi (K. Eyvindson), anna.m.repo@jyu.fi (A. Repo), mikko.monkkonen@jyu.fi (M. Mönkkönen).

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group of trees, are removed from the forest usually every 15–20 years (Laiho et al., 2011; Kuuluvainen et al., 2012; Pommerening and Murphy, 2004). Trees regenerate naturally, and the structure of forests is often uneven-aged. Such forest management practice has been called ‘near natural forestry’ since it may mimic a natural forest state and natural disturbances better than RFM (Kuuluvainen et al., 2012).

Previous research in boreal forests has shown that CCF is better than RFM from the perspective of berry production, the amenity of forest landscape, carbon balances and resistance against wind (Pukkala, 2016a; Pukkala et al., 2016, 2011). Moreover, CCF may be economically more profitable than rotation forest management for forest owners (Pukkala, 2016a; Tahvonen, 2016; Tahvonen et al., 2010; Tahvonen and Rämö, 2016). However, there are also contradictory results, regarding the economic profitability (Andreassen and Øyen, 2002) as well as the effects on climate regulation (Lundmark et al., 2016) and resistance against disturbances (Hanewinkel et al., 2014). Consequently, the debate on the usefulness of CCF is still ongoing (Diaci et al., 2011). Even though CCF may often outperform RFM at the stand level, we do not know the relative performance of these management practices at a large landscape scale nor do we know the potential benefits a combination of these practices may have for ecosystem services and biodiversity across the landscape.

In general, CCF may provide more habitats and resources for species living in mature or late successional forests compared with RFM (Calladine et al., 2015; Kuuluvainen et al., 2012; Pukkala et al., 2012). In boreal forests, CCF has been found to be less harmful than RFM, for example, for understorey vegetation (Jalonen and Vanha-Majamaa, 2001), some invertebrate species (Matveinen-Huju and Koivula, 2008), and soil fauna (Siira-Pietikäinen and Haimi, 2009). Moreover, in comparison to RFM, CCF may provide more resources for dead wood dependent species (Atlegrim and Sjöberg, 2004) as well as for herbivores (Atlegrim and Sjöberg, 1996). However, because different species require differing habitats and resources, it is obvious that no single management can be the best for all species and biodiversity aspects (Calladine et al., 2015; Mönkkönen et al., 2014). Thus, it is important to understand how the different silvicultural practices promote different types of forest structures and species (Felton et al., 2016).

Even though there is evidence that CCF is better than RFM for several forest purposes (Pukkala, 2016a), their relative performance of ecosystem service provisions and of biodiversity is not well known when compared with unmanaged forests (but see Pukkala, 2016b; Sharma et al., 2016). Even if there is a seemingly large difference between the two silvicultural alternatives, they may both appear equally poor relative to forests in a more natural state. If so, then CCF may not be the solution to declining biodiversity and ecosystem services. Therefore, comparing both practices with unmanaged forests generates valuable knowledge about their actual effects on the ability of forest landscapes to provide goods and benefits to humankind.

As forests provide multiple services and benefits, the capabilities of alternative forest management practices should be assessed from a multifunctionality perspective, i.e., their relative performance to provide bundles of services simultaneously (Mastrangelo et al., 2014; van der Plas et al., 2016). Although earlier results demonstrate the high potential of CCF to simultaneously provide multiple services (Pukkala, 2016a), the concept of multifunctionality has not been commonly applied. Multifunctionality of forests can be considered as an index, which highlights the number of services which exceed a specified level of those services (van der Plas et al., 2016). Therefore, when estimating the capacity of different silvicultural practices to provide multiple benefits simultaneously, the effect of desired level of services should be taken into account.

We use a dataset describing a large forest landscape where we apply three alternative management practices — CCF, RFM and set aside (no management) — simulated for 100 years into the future to estimate their relative performance to provide forest ecosystem services and maintain biodiversity. We address the following questions: 1) which

ecosystem services and biodiversity measures benefit more from CCF compared with RFM and vice versa? 2) what are the levels of biodiversity and ecosystem services under two alternative forest management practices as well as their optimal combination compared with unmanaged forests? 3) which silvicultural practice provides the greatest forest multifunctionality across large forest landscapes?

2. Methods

2.1. Forest data and simulations

The study areas are located in central and southern Finland, encompassing 39,979 ha. Data consist of 26,024 commercial forest stands on mineral soils with the average size of stands being 1.5 ha. The initial forest data was provided by the Finnish Forest Centre, and are based on laser scanned data with ground-truthing (Maltamo et al., 2007). The data contain forest characteristics, such as forest site type, age, or tree species compositions. In the initial data, Scots pine (*Pinus sylvestris*) was the dominant tree species on 23% of the stands, Norway spruce (*Picea abies*) on 63% of the stands and birches (*Betula pendula* and *B. pubescens*) on 14% of the stands. Mixed stands, i.e., where none of the tree species accounted for > 75% of the total volume, represent 45% of all the stands. The variation in the site type and initial age of stands are given in Appendix S1: Fig. S1.

The development of each stand was simulated 100 years into the future using SIMO-forest simulator (Rasinmäki et al., 2009) under three different forest management regimes: CCF, RFM, and no silvicultural management (set aside, SA). We chose a time scale of 100 years since it is long enough to cover an entire rotation, and thereby to reveal the long-term impacts of silvicultural practices. The forest simulations create forest structural data at 5 year intervals.

In CCF, a selection of the largest trees is removed from the forests approximately every 15 years. Through natural regeneration, the composition of tree species becomes more mixed (Appendix S1; Fig. S2). Over time, CCF changes the forest age structure to uneven-aged containing different age classes of trees. No retention trees were left (trees retained permanently through 100 years). The management rules for cuttings are given in Appendix S1: Table S1 (according to the good practice guidance for forestry in Finland from Äijälä et al., 2014). For CCF regime, the growth models of Hynynen et al. (2002) were used until the first cutting and then the growth models of Pukkala et al. (2013) for uneven-aged forests were used (Appendix S1: Fig. S3). The model set of Hynynen et al. (2002) consists of species-specific individual-tree models for ingrowth, growth and mortality. The model set of Pukkala et al. (2013) consists of species-specific individual-tree diameter increment and survival models, and a stand level model for ingrowth.

RFM is currently the recommended and the most common forest management practice in Fennoscandia (Äijälä et al., 2014). In Finland RFM includes several silvicultural actions: soil preparation, seeding or planting trees, one to three thinnings, and the final clear cut, where approximately five retention trees per hectare are retained (according to the good practice guidance for forestry from Äijälä et al., 2014). The management rules for regeneration cutting are given in Appendix S1: Table S2. The average rotation length of RFM is approximately 80 years in our study region (Appendix S1; Fig. S2). RFM creates forest stands, which are often very homogenous in tree species composition as well as in the age structure. The growth models of Hynynen et al. (2002) for even-aged stands were applied for this regime.

In SA regime, forests are allowed to grow without human intervention (Appendix S1; Fig. S2). In SA, forests are denser, grow slower and there is more tree competition compared with managed forests resulting in higher self-thinning and tree mortality. The models of Hynynen et al. (2002) were applied to simulate forest growth without management actions since they predict better the development of old-growth forests than the models of Pukkala et al. (2013).

Table 1
Ecosystem services and biodiversity indicators in the study.

	Abbreviation	Description
Ecosystem services		
Timber NPV	NPV	Timber net present value (€ ha ⁻¹) at different discount rates 1–5%
Harvested timber	HARV	Total harvested timber volume (m ³ ha ⁻¹ , over 100 years)
Carbon storage	CSTOR	Carbon stored in the soil and in the biomass of living and dead trees (t C ha ⁻¹ , average over 100 years)
Carbon sequestration	CSEQ	Change in carbon storage between consecutive time steps (t C ha ⁻¹ year ⁻¹)
Bilberry	BILB	Bilberry yield (kg ha ⁻¹ year ⁻¹)
Cowberry	COWB	Cowberry yield (kg ha ⁻¹ year ⁻¹)
Mushroom	MM	Marketed mushrooms yield (kg ha ⁻¹ year ⁻¹)
Scenic beauty	SB	Scenic beauty of forest (ha ⁻¹ , average over 100 years); increases with the size and age of trees, with a share of pines and deciduous trees, and with decreasing number of stems.
Biodiversity		
HSI Capercaillie	CC	Game bird with social and economic value, associated with pine volume (min 60 m ³ ha ⁻¹) with intermediate spruce mixture and steam density (ha, average over 100 years)
HSI Hazel grouse	HG	Game bird species indicating adequate levels of deciduous mixture (20–40%) with spruce (> 20%) (ha, average over 100 years)
HSI Lesser spotted wood pecker	LSWP	Indicator species associated with old deciduous trees (min 60 years) and deciduous snags (ha, average over 100 years)
HSI Three-toed woodpecker	TTWP	Indicator species associated with high volume of trees (min 60 m ³ ha ⁻¹) and fresh deadwood (ha, average over 100 years)
HSI Long-tailed tit	LTT	Indicator species associated with mature forests (min 30 years) deciduous trees (20–60%) (ha, average over 100 years)
HSI Siberian flying squirrel	SFS	Red-listed species associated with high volume of spruce (min 140 m ³ ha ⁻¹) with deciduous mixture (min 12 m ³ ha ⁻¹) (ha, average over 100 years)
Dead wood	DWD	Volume of dead wood weighted by diversity (m ³ ha ⁻¹ , average over 100 years)
Large trees	N40	Number of trees with diameter > 40 cm (ha ⁻¹ , average over 100 years)

2.2. Ecosystem services and biodiversity indicators

2.2.1. Ecosystem services

Different ecosystem categories (provisioning, regulating, and cultural) were considered with a set of ecosystem services (Table 1). Timber production is the economically most important provisioning service in boreal forests (Vanhanen et al., 2012). The net present value (NPV, €) of sawlogs and pulpwood for each tree species across 100 years was estimated. The timber NPV consists of three components: the revenues from harvesting (clear-cuts, thinnings, selective loggings; Appendix S1: Table S3), the value of standing timber at the end of simulations, and the value of spare land at the end of simulations (Pukkala, 2005). In addition, timber NPV accounted for costs resulting from silvicultural actions related to regeneration and young stand (Appendix S1: Table S4). The stumpage prices of harvest revenue components and the prices for the silvicultural costs were calculated from the historical averages in Finland (Pelto, 2014, Appendix S1: Table S3). The stumpage prices included costs from harvesting. The harvesting costs are higher in partial cuttings in CCF than in final fellings in RFM (e.g., Pukkala, 2016a; Tahvonen et al., 2010) so the prices from second thinnings (also called intermediate felling) were used for CCF. The interest rate varied between 1% and 5% in discounting the timber revenues and costs during the 100-year period. In addition, to study the sensitivity of timber NPV with different costs and prices in CCF and RFM, we calculated NPV without regeneration costs in RFM and using the same prices for CCF and RFM. Timber revenues can be seen as a service for private forest owners, and thus, we also estimated the amount of harvested timber biomass separately for pulpwood and sawlogs, which can be considered as a provisioning service for the whole society since the forest industry is dependent on biomass.

Carbon storage and sequestration are important climate regulating services (Pan et al., 2011). Carbon storage was calculated as the amount of carbon in tree biomass and in soil. Total tree biomass (aboveground and belowground biomass) was estimated within the forest simulator and the amount of carbon in biomass was calculated by multiplying the total tree biomass by 0.5. Carbon in litter and soil was modelled using Yasso07 model (Liski et al., 2005; Tuomi et al., 2011, 2009). Carbon sequestration was calculated based on differences in the total carbon storage between consecutive time steps.

Non-timber forest products are economically valuable provisioning

services as well as recreationally valuable cultural services in boreal forests (Vaara et al., 2013). The yields of two most common berries, bilberry (*Vaccinium myrtillus*) and cowberry (*V. vitis-idaea*), were estimated using models of Miina et al. (2009) and Turtiainen et al. (2013) following the methods of Miina et al. (2016). The marketed mushroom yields for spruce dominated stands were calculated using the model of Tahvanainen et al. (2016). In addition, scenic beauty of forests was estimated to describe their recreational values. The scenic beauty index was calculated based on forest age, density and tree species composition according to Pukkala et al. (1988) (Table 1).

2.2.2. Biodiversity

Biodiversity is a multi-faceted phenomenon, which can be measured using indices derived from forest structural data (Table 1). Dead wood is a critical resource in boreal forests (Siitonen, 2001). In boreal Fennoscandia, 20–25% of the forest-dwelling species are dependent on dead-wood habitats, and species dependent on dead wood constitute 60% of the red-listed species (Rassi et al., 2010). Association between dead-wood volume and biodiversity is well established (Gao et al., 2015). The capacity of a stand to maintain populations of dead-wood associated species was estimated by multiplying total dead-wood volume by the diversity of deadwood across tree species, diameter and decay stage categories (Triviño et al., 2016). Thus, a stand with large total deadwood volume distributed evenly across deadwood types will receive high values of deadwood availability. In addition, large diameter living trees are an essential structural feature in boreal forests that has become a limiting factor for biodiversity in production forests (Nilsson et al., 2002). Therefore, the number of large diameter (> 40 cm) trees was also calculated.

Habitat availability for species measure the overall capacity of the forests to maintain species populations. Habitat suitability indices (HSI) were calculated for a selected set of umbrella or indicator species representing habitat associations as well as social and conservation values: Capercaillie (*Tetrao urogallus*), Hazel grouse (*Bonasa bonasa*), Lesser spotted woodpecker (*Dryobates minor*), Long-tailed tit (*Aegithalos caudatus*), Three-toed woodpecker (*Picoides tridactylus*), and Siberian flying squirrel (*Pteromys volans*) (Table 1, Mönkkönen et al., 2014). Earlier research has shown that these species indicate forest characteristics important for many other species (please see Mönkkönen et al., 2014 for the detailed motivation to focus on these taxa). Our main focus is on late successional species due to their severe

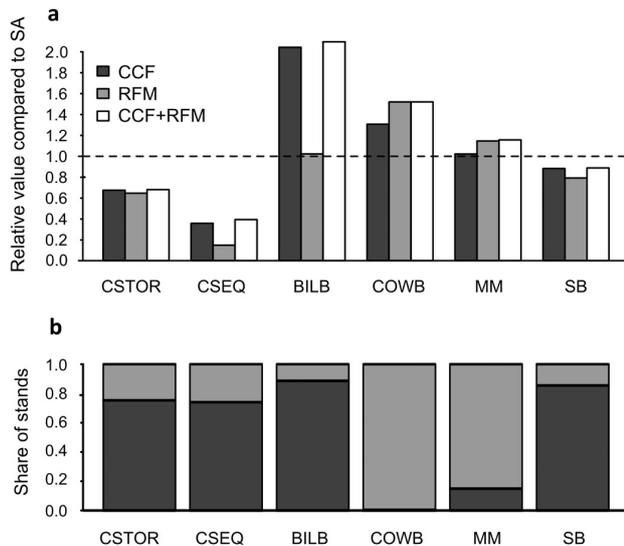


Fig. 1. a) Relative ecosystem service values for carbon storage (CSTOR) and sequestration (CSEQ), bilberry (BILB), cowberry (COWB), marketed mushrooms (MM), and scenic beauty (SB) under continuous cover forestry (CCF), rotation forest management (RFM), and their optimal combination (CCF + RFM) compared to set aside (1, the dashed line). Absolute values are given in Appendix S2: Table S1. b) Optimal share of stands to maximize the provision of ecosystem service in the study area under CCF and RFM.

conservation need in Fennoscandia (Rassi et al., 2010). Habitat suitability is a function of a set of sub-utility functions based on expert knowledge and known species habitat that translate characteristics of each stand into a habitat suitability index between 0 (unsuitable habitat) and 1 (the most suitable habitat). For each species, we calculated habitat availability across the entire landscape as a sum of products between stand specific HSI-values and the area of a stand.

2.2.3. Comparison between silvicultural practices

To estimate the performance of silvicultural practices in maintaining ecosystem services and biodiversity (Table 1), their levels under CCF and RFM at a landscape scale across 100 years were calculated. Moreover, the share of stands when CCF outperforms RFM and vice versa was calculated. To estimate the maximum achievable levels of ecosystem services and biodiversity under the combination of CCF and RFM, the practice that provided a larger value was applied for each stand. To estimate the relative performance of silvicultural strategies compared with unmanaged forests in the delivery of ecosystem services and biodiversity, their values under CCF, RFM, and their optimal combination (CCF + RFM) were divided by the values in SA forests. In the cases of timber net present value and harvested timber biomass, the optimal values (CCF + RFM) were used as a reference state since the value of SA regime was zero.

Especially in the cases of habitat and ecological resources, their uninterrupted availability is important for species persistence (Hanski, 1999; Ranius et al., 2008). Therefore, to estimate the temporal continuity of habitats at a stand scale, we calculated the number of cases across stands and time steps under each management practice when the habitat availability index was zero, i.e., when a stand is totally unsuitable for a given species.

2.2.4. Multifunctionality

To estimate the potential of different silvicultural strategies to provide different services and biodiversity simultaneously the forest multifunctionality was estimated. The forest stand multifunctionality value was calculated using the formula from the study of van der Plas et al. (2016) as

$$SMF_i = \frac{obsSMF_i - min SMF_i}{max SMF_i - min SMF_i}, \text{ where } SMF_i \text{ indicates a scaled}$$

multifunctionality value (between 0 and 1) of a single ecosystem service or biodiversity measure i in a stand over 100 years (Table 1), $obsSMF_i$ indicates the observed value of a single biodiversity or ecosystem service measure in a stand, $minSMF_i$ and $maxSMF_i$ indicate the minimum and the maximum values of a single biodiversity or ecosystem service measure in the whole study area.

The ecosystem services and biodiversity measures were divided into four groups according to the ecosystem service categories they represent (Haines-Young and Potschin, 2011): provisioning services (timber NPV and harvested timber biomass), regulating services (carbon storage and sequestration), and cultural services (scenic beauty and the combined yield of bilberries and cowberries). In addition, a category representing biodiversity consisted of dead wood diversity and combined habitat suitability index — a combination of six habitat suitability indices (Triviño et al., 2016). Grouped SMF (GMF) takes value 1 if either of the SMF in a group was larger than the threshold value t . Finally, multifunctionality score of a stand was calculated as the sum GMFs that had a value above a threshold t as follows:

$$MF = \sum_{i=1}^n \begin{cases} 1 & GMF_i \geq t \\ 0 & GMF_i < t \end{cases}$$

where GMF_i indicates a scaled multifunctionality value (between 0 and 1) of a grouped ecosystem (provisioning, regulating and cultural) or biodiversity measure i in a stand where threshold t was continuous between 0 and 1. The maximum multifunctionality score is 4 when a stand is able to provide all services and biodiversity above the threshold level, and minimum is 0 indicating that all indicators remain below the threshold. We calculated average multifunctionality score over time and space in the data. The threshold was varied between 0 and 1 to see if the relative utility of alternative management regimes from multifunctionality perspective changes with the desired level of functionality. High threshold values denote situations where the society aspires for high levels of all ecosystem services and biodiversity, while low value refers to a low societal need for multifunctionality.

3. Results

3.1. Ecosystem services

CCF provided higher values than RFM for five out of eight ecosystem services at the landscape scale on average over 100 years (Figs. 1a, 2a; Appendix S2: Tables S1, S2). Carbon storage was moderately higher and sequestration remarkably higher in landscapes consistently managed using CCF in comparison with RFM (Fig. 1a; Appendix S2: Fig. S1). In terms of the regulating services, CCF outperformed RFM in approximately 75% of the stands (Fig. 1b). Bilberry yields and scenic beauty were higher with CCF (Fig. 1a) and CCF outperformed RFM in 70–90% of the stands (Fig. 1b). In contrast, cowberry and marketed mushroom yields were higher in RFM (Fig. 1a) and it outperformed CCF in approximately 90% of the stands (Fig. 1b).

RFM provided more harvested timber (Fig. 2a; Appendix S2: Table S1) outperforming CCF in 60% of the stands (Fig. 2b). There were differences in the shares of sawlogs and pulpwood between CCF and RFM (Appendix S2: Fig. S2). In CCF, 79% of the harvested timber was sawlogs and 21% pulpwood, whereas in RFM the share of sawlogs was 65% and the share of pulpwood 35%.

The discount rate affected the economic performance of CCF and RFM (Fig. 2a; Appendix S2: Table S2). With a 1% discount rate, the NPV of both strategies was the same. The timber NPV was greater in CCF than in RFM when the discount rate was 2% or larger. The optimal share of CCF and RFM was 50% of each when the discount rate was 1% (Fig. 2b). The optimal share of CCF increased with the discount rate and was 80% at 5% discount rate. Only when the costs related to regeneration and young stands were not taken into account and the discount rate was 1%, the NPV was greater in RFM than in CCF (Appendix

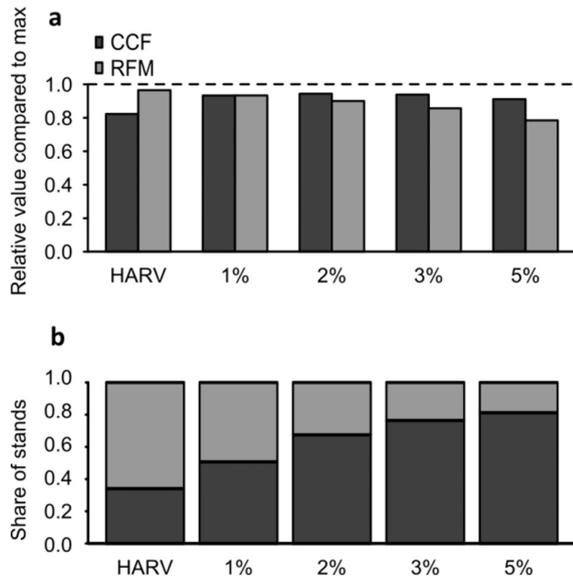


Fig. 2. a) Relative harvested timber biomass (HARV) and revenues (NPV) with different discount rates (1–5%) in the study area under continuous cover forestry (CCF) and rotation forest management (RFM) compared to their optimal combination (CCF + RFM, the dashed line). Absolute values are given in Appendix S2: Tables S1, S2. b) Optimal share of stands under CCF and RFM to maximize harvested timber and timber revenues in the study area.

S2, Fig. S3c).

The optimal combination of CCF and RFM provided slightly higher levels of ecosystem services than either of them separately in all cases except in cowberry yields (Figs. 1, 2). The benefit of applying both regimes in landscapes was the largest for timber NPV (Fig. 2).

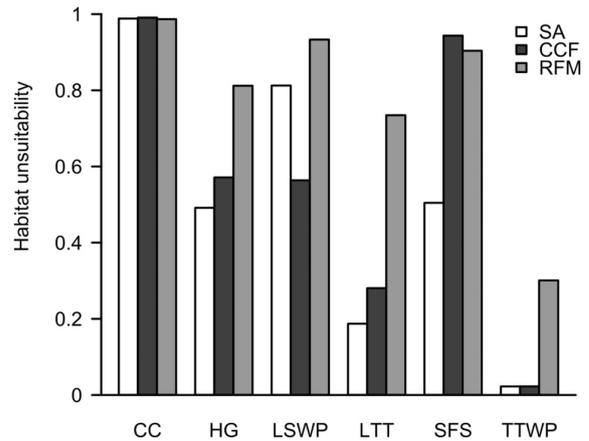


Fig. 4. Relative frequency of cases when habitat suitability index was zero for the Capercaillie (CC), Hazel grouse (HG), Lesser spotted woodpecker (LSWP), Long-tailed tit (LTT), Siberian flying squirrel (SFS), and Three-toed woodpecker (TTWP), under set aside (SA), continuous cover forestry (CCF) and rotation forest management (RFM).

SA forests provided higher values than CCF, RFM or their combination particularly for the climate regulating services but also for scenic beauty (Fig. 1). Managed forests tended to provide a higher delivery of non-timber forest products than SA forests. However, SA performed as well as CCF in marketed mushroom production and as well as RFM in bilberry production.

3.2. Biodiversity

Consistent application of CCF in landscapes yielded higher values than RFM for five out of eight biodiversity indicators (Fig. 3a; Appendix S2: Table S3). For three biodiversity indicators (Lesser spotted

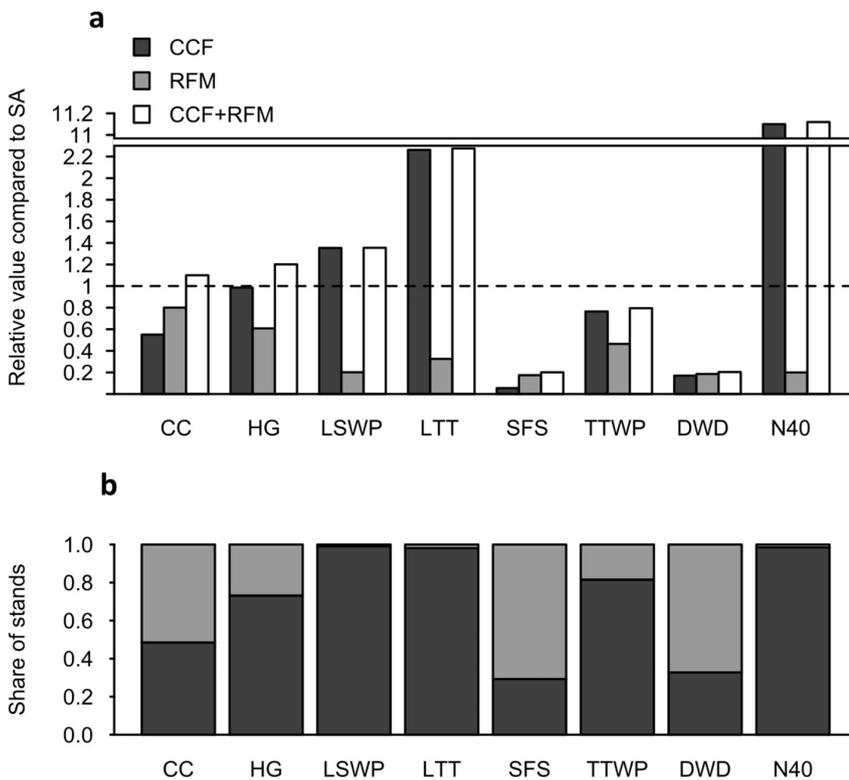


Fig. 3. a) Relative biodiversity indicator values in the study area for Capercaillie (CC), Hazel grouse (HG), Lesser spotted woodpecker (LSWP), Long-tailed tit (LTT), Siberian flying squirrel (SFS), Three-toed woodpecker (TTWP), deadwood availability (DWD), and number of large diameter trees (N40) under continuous cover forestry (CCF), rotation forest management (RFM), and their optimal combination (CCF + RFM) compared to set aside (1, the dashed line). Please note that there is a break in the y-axis between values 2.2 and 11. Absolute values are given in Appendix S2: Table S3. b) Optimal share of stands under CCF and RFM to maximize biodiversity measures in the study area.

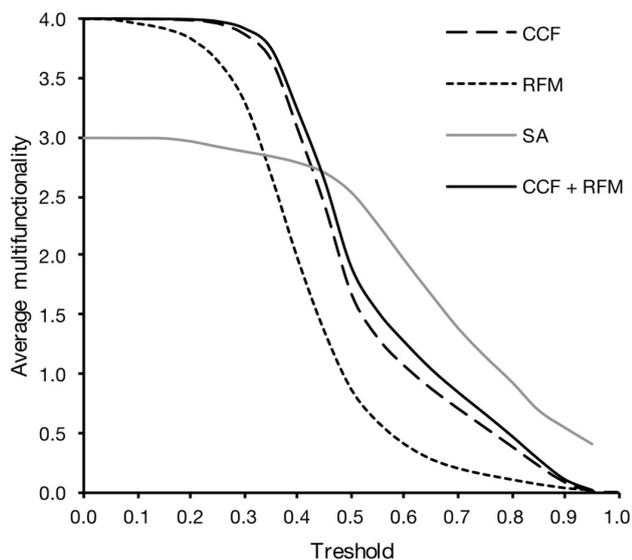


Fig. 5. Average forest multifunctionality values for 100 years in the study area under different threshold values for continuous cover forestry (CCF), rotation forest management (RFM), their optimal combination (CCF + RFM), and set aside (SA).

woodpecker, Long-tailed tit and number of large diameter trees) CCF outperformed RFM in almost 100% of stands (Fig. 3b) and the difference in favour of CCF was remarkably large (Fig. 3a). CCF also yielded clearly higher values than RFM in the cases of Hazel grouse and Three-toed woodpecker when CCF outperformed RFM in between 70% to 80% of the stands. In contrast, RFM yielded slightly higher dead wood indicator values outperforming CCF in 67% of the stands. Moreover, for the Capercaillie and flying squirrel consistent application of RFM clearly performed better than CCF (Fig. 3a) providing higher habitat suitability index in between 50% to 70% of the stands (Fig. 3b).

In five cases, a combination of CCF and RFM provided higher scores than either of them separately (Fig. 3). The benefits of combining the two management practices in landscapes were particularly pronounced for the Capercaillie and the Hazel grouse. For the Capercaillie, the combination of CCF and RFM (Fig. 3b) yielded 55% larger HSI value than consistent application of CCF and 30% larger than consistent application of RFM (Fig. 3a). For the Hazel grouse, the combination (Fig. 3b) yielded 65% larger HSI value than consistent application of RFM and 20% larger than consistent application of CCF (Fig. 3a).

From biodiversity perspective, SA was always clearly better than RFM (Fig. 3a). For one biodiversity indicator (habitat availability for the Hazel grouse), CCF and SA performed equally well, while in three cases CCF outperformed SA: CCF provided slightly higher habitat availability for Lesser spotted woodpecker, more than two times higher habitat availability for Long-tailed tit, and ten times higher number of large trees than SA (Appendix S2: Table S3).

The frequency of unsuitable habitats varied among species (Fig. 4). For the Capercaillie, practically all stands were unsuitable at some point of time irrespective of the management regime. For other species except the Siberian flying squirrel, the frequency of total unsuitability was the highest under RFM. SA showed the lowest frequency of total unsuitability for all other species except the Lesser spotted woodpecker when CCF performed the best.

3.3. Multifunctionality

At all threshold levels, the average forest multifunctionality was larger when forests were managed with CCF than forests managed with RFM (Fig. 5) indicating a larger capacity of CCF to simultaneously provide services from different categories. An optimal combination of

CCF and RFM always produced higher multifunctionality scores than RFM alone, and slightly higher scores than CCF alone when the threshold was larger than 0.4. This indicates that even though CCF in general is better from the multifunctionality point of view, there are some stands where RFM has higher potential to provide multifunctionality. SA provided the lowest multifunctionality below 0.4 threshold levels, which is primarily due to the lack of timber harvesting. When the demand for multifunctionality is high (threshold > 0.6) SA forests provided the highest multifunctionality scores. This means that when high levels of ecosystem services and biodiversity are simultaneously desired, leaving forests unmanaged (set aside) is more desirable than managing forests (both CCF and RFM).

4. Discussion

Our results show that CCF has the potential to deliver ecosystem services and maintain biodiversity in commercial forests better than conventional RFM. In general, the results of this study are in line with previous research (Pukkala, 2016a; Shanin et al., 2016; Sharma et al., 2016). However, CCF was not better than RFM in terms of all ecosystem services or biodiversity indicators. Moreover, the optimal combination of CCF and RFM provided higher values of ecosystem services and biodiversity measures than either CCF or RFM applied consistently in all stands. Previous studies have also shown the benefit of using a diverse set of silvicultural practices in forest landscapes (Mönkkönen et al., 2014; Redon et al., 2014; Triviño et al., 2016, 2015). Thus, the relative utility of silvicultural practice depends on site characteristics; an aspect that should be further studied.

In terms of regulating services, while there were no large differences between CCF and RFM in carbon storage, CCF outperformed RFM in carbon sequestration. In RFM, a stand is periodically a source of carbon after the clear-cut. This is mainly because the decomposing forest harvest residues release carbon more than is sequestered in the biomass growth. In CCF, changes in soil carbon stock are smaller after harvests than in RFM because the litter input from harvest residues is smaller. The carbon balance of forests critically depends on the final use of timber biomass after it is removed from the forest ecosystem (Lundmark et al., 2016; Pukkala, 2016b) but we did not take into account the carbon storage in wood products or emissions from the procurement chain. However, as the proportion of sawlogs compared with pulpwood is higher in CCF than in RFM, the carbon retention time would be longer for timber produced in CCF (Pukkala, 2014). Therefore, inclusion of carbon storage in the wood products would not change the main findings. The superior capacity of unmanaged forests to sequester carbon is explained by the initial state of the forest stands and their management history. Intensively managed forest landscapes in Finland have a high proportion of young stands holding large potential for carbon sequestration. Although in SA the rate of carbon sequestration decreases with the increasing age of the forest (Pukkala, 2016b), we show that unmanaged forests can have a remarkable role in climate change mitigation for several decades.

Our results considering timber NPV support earlier findings (Pukkala et al., 2011; Tahvonen et al., 2010) where discount rates larger than 1% make CCF more profitable than RFM. Higher profitability of CCF is related to the higher price of sawlogs versus pulpwood (CCF provides more sawlogs) as well as the large costs of regeneration and thinnings in RFM. However, in some cases RFM provided also larger economic profits than CCF. This is the case, for stands that are mature, i.e. ready for final harvesting at the beginning of 100 year time period (Tahvonen et al., 2010). CCF is not commonly applied in Fennoscandia because of the uncertainty in regeneration success, lower timber quality and higher total harvesting costs (Laiho et al., 2011). The potential for lower timber quality and higher harvesting costs were accounted for by applying a lower price for timber originating from CCF. In addition, we estimated the NPV with and without taking regeneration costs into account for RFM. In contrast to NPV, RFM

produced more harvested timber biomass, which is also supported by earlier studies (Lundqvist et al., 2007; Pukkala et al., 2011; Tahvonen et al., 2010). Thus, CCF may be more profitable for private forest owners while RFM may better meet the industry's current needs.

For four out of the six umbrella and indicator species, CCF produced higher habitat availability than RFM. This is not surprising since many species in this study are dependent on tree cover and deciduous trees, which CCF provides. Moreover, the frequency where the stands were totally unsuitable for the species was often highest in RFM. Thus, one benefit of CCF for mature forest species is the less severe temporal fluctuations in habitat quality. However, for early successional species RFM may actually provide more habitats (Calladine et al., 2015). Nevertheless, habitat availability for species dependent on high tree volume and dead wood availability in forests under both CCF and RFM were far from those in unmanaged forests. Thus, some species habitat availability and dead wood availability more critically depend on the amount of harvested timber than on the silvicultural practice used in harvesting (Atlegrim and Sjöberg, 2004). For many deadwood dependent species, the desirable minimum level of dead wood is approximately $20 \text{ m}^3 \text{ ha}^{-1}$ (Junninen and Komonen, 2011) while both CCF and RFM provided only about 25% of that. To further improve the ability of CCF to promote biodiversity we recommend a similar kind of green tree retention that is applied in RFM (leaving permanently behind, at least, 5 trees per ha) to be included in the CCF management regime. Interestingly, CCF provided the greatest number of large trees resulting from the larger resource availability of individual trees (space and light). In contrast, for unmanaged forests, tree growth is lower. This is likely due to the development and transition of very young and planted stands at the beginning of the simulation. For these stands, transition to uneven aged stands will take longer than 100 years and the large trees will likely be harvested during the next (or following) CCF cutting. However, if the simulation time had been longer than 100 years, the number of large diameter trees would have been larger in SA regime and on the other hand smaller in CCF since the transition from even-aged to uneven-aged forestry allows large diameter trees in our CCF simulations.

In general, our multifunctionality results indicate that CCF has greater potential than RFM to simultaneously produce multiple benefits in forests, which supports earlier findings (Pukkala, 2016a; Sharma et al., 2016). With a moderate demand level for services (threshold value 40%), CCF simultaneously provided services from all categories when RFM provided services only from three categories. Moreover, the relative multifunctionality performance of SA increased with the demanded level of services. Therefore, when discussing the delivery of ecosystem services and maintaining biodiversity, their demanded levels should be taken into account. If society demands high multifunctionality in forest landscapes, more resources must be allocated to unmanaged set aside forests since their role in delivering high levels of biodiversity and regulating services is often indispensable.

In the simulation process, all management options were based on decision rules instead of optimizing the specific management at stand level. Both management alternatives that we used could be changed substantially by altering the specific decision rules (i.e. delaying final felling, restricting the frequency of harvests, or requiring green tree retention following a clear felling) to increase the delivery of multiple benefits in forest stands (e.g., Liski et al., 2001; Gustafsson et al., 2012). Optimizing the management at a stand level can improve the economic and ecological performance of a stand (e.g., Miina et al., 2016; Tahvonen and Rämö, 2016). However, stand level optimizing is problematic for several reasons. First, there is high uncertainty, e.g., because of errors in inventory estimates and in inaccuracies in growth models resulting only in crude approximations. As a consequence, the actual performance of a stand level optimized management plan could fall short of the management plan following decision rules (Holopainen and Talvitie, 2006). Second, optimizing at the stand level is a time consuming and data intensive activity, and consequently not often

practicable (Kurttila et al., 2013). Third, in practice management decisions depend on the choices of the forest owner, whose preferences may more likely be based on the personal economic situation rather than on specific stand characteristics (Brazee, 2003). In such cases, simple decision rules may better provide guidance to decisions than knowledge about stand level optimal management.

Our comparison among CCF, RFM and unmanaged forests has some limitations. Even though the planning horizon was long (100 years), even set-aside forests do not provide a natural-state benchmark for managed forests. For example, the amount of dead wood in the natural forest state is approximately $60\text{--}90 \text{ m}^3 \text{ ha}^{-1}$ (Siitonen, 2001) but in our data the amount of dead wood under set-aside was significantly lower. Moreover, our simulation did not include natural disturbances, such as storms and diseases, which may substantially change the forest characteristics, e.g. dead wood volumes (Kuuluvainen, 2002). Therefore, our simulations probably underestimate the delivery of some ecosystem services and biodiversity values in all management regimes, and on the other hand, overestimate timber production in both CCF and RFM. Disturbances do occur in forests regardless of management but their intensity and effects vary depending on management of the stand itself and its surrounding forests. Since CCF maintains natural tree species and more natural structure of forests it may be more resistant against the disturbances, such as wind damages (Couture et al., 2016; Pukkala et al., 2016), and insect pathogens (Klapwijk et al., 2016). We leave it as a challenge for future studies to accommodate disturbance effects on ecosystem services and biodiversity in forests under different management regimes. This would inevitably require a spatially explicit landscape level approach.

The role of unmanaged forests is central in delivering ecosystem services and maintaining biodiversity, and unmanaged forests should exist in commercial forested landscapes. One suggested way to protect biodiversity, habitats and ecosystems is the third-of-third approach (Hanski, 2011) where a third of the landscapes are managed as multi-use conservation landscapes within which a third of the land area is protected. Because CCF provides a cost-efficient option to manage forests for multiple purposes it could be applied in multi-use landscapes. Moreover, because CCF has the potential to maintain habitat connectivity (Pukkala et al., 2012) and may better provide corridors and stepping stones for species living in protected areas, it may well promote species persistence in managed landscapes if augmented with adequate levels of set-asides.

5. Conclusion

Our results indicate that continuous cover forestry has greater potential than rotation forest management to maintain multifunctional forests. However, continuous cover forestry was not the best for all ecosystem services or biodiversity indicators. Furthermore, the combination of different forest management practices provided higher levels of services and indicators than single practices applied consistently over the landscape. Moreover, we show that commercially managed forests, if set aside, may provide important resources for biodiversity and regulating services. Thus, it is not reasonable to rely on one single practice and careful landscape planning is needed. Continuous cover forestry does not itself guarantee the maintenance of all ecosystem services and biodiversity in commercial forests but it can be an important part of a successful progression towards more sustainable forestry.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2017.10.018>.

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APPENDIX S1 to “Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia” Peura et al.

Supplementary material: Methods

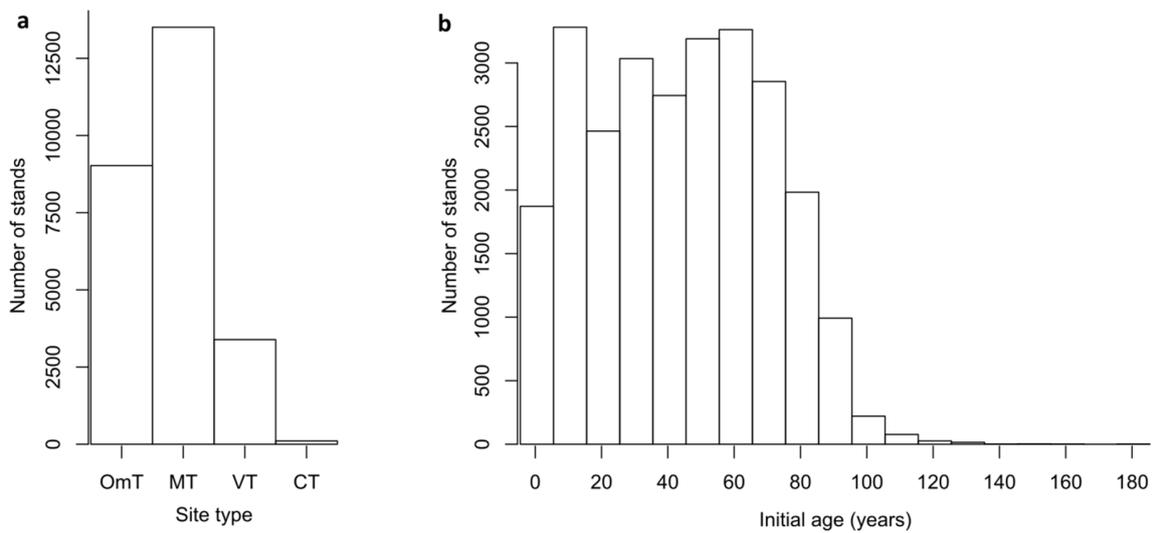


Figure S1. a) The number of stands belonging to site types (from the most fertile to the poorest): herb-rich heath (OmT), mesic heath (MT), sub-xeric heath (VT) and xeric heath (CT) forest type in our study area. **b)** The distribution of initial age of stands in the study.

Table S1. The cutting rules for CCF (Äijälä et al. 2016). Site types are the same as above in Figure S1. *Cutting limit* indicates stand basal area (BA, all trees with a height gt 1.3 m contribute to the stand level BA measurement) above which cutting is allowed and *lower limit* indicates stand BA after the cutting. In addition to BA limit, there is a minimum number of trees remaining (50 trees ha⁻¹). This rule means that when very few large trees exist on the stand, it is possible to have higher BA than the lower BA limit.

Site type	Cutting limit (m ² ha ⁻¹)	Lower limit (m ² ha ⁻¹)
OmT	22	12
MT	20	11
VT	19	10
CT	16	10

Table S2. The regeneration rules for RFM (Äijälä et al. 2016). *Main species* is the dominating tree: spruce (*Picea abies*), pine (*Pinus sylvestris*), silver birch (*Betula pendula*) or downy birch (*Betula pubescens*). Site types are same as above in Figure S1. *Regeneration BA lower* and *-upper* indicate lower and upper limits in stand basal area (BA) and *Regeneration age lower* and *-upper* indicate lower and upper limits in stand age when regeneration cutting is allowed.

Main species	Site type	Regeneration	Regeneration	Regeneration age lower (years)	Regeneration age upper (years)
		BA lower (m ² ha ⁻¹)	BA upper (m ² ha ⁻¹)		
Spruce	OmT	24	28	80	100
Spruce	MT	24	28	80	100
Spruce	VT	23	27	90	110
Spruce	CT	22	25	100	130
Pine	OmT	26	30	70	90
Pine	MT	25	28	80	100
Pine	VT	25	28	80	100
Pine	CT	25	28	80	100
Silver birch	OmT	27	30	60	70
Silver birch	MT	26	28	60	70
Silver birch	VT	26	28	60	70
Silver birch	CT	26	28	60	70
Downy birch	OmT	22	25	60	70
Downy birch	MT	22	25	60	70
Downy birch	VT	22	25	60	70
Downy birch	CT	22	25	60	70

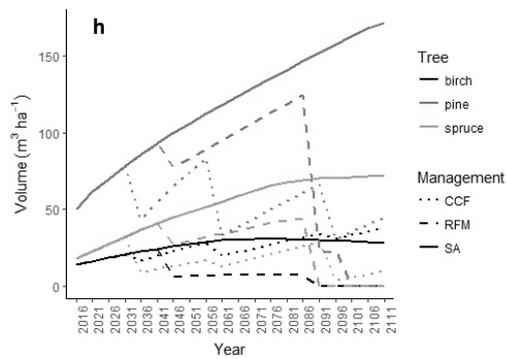
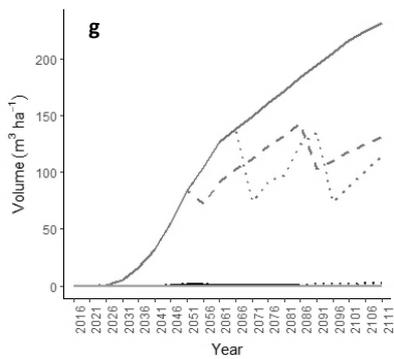
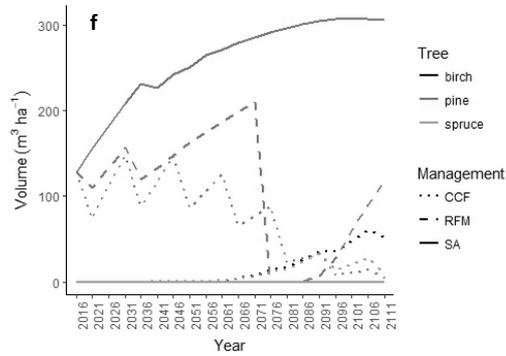
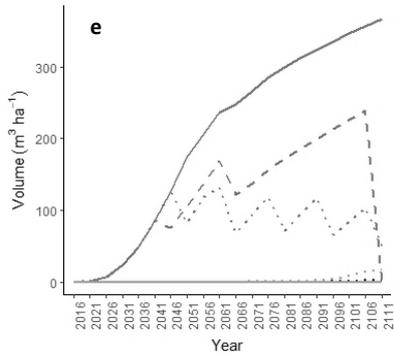
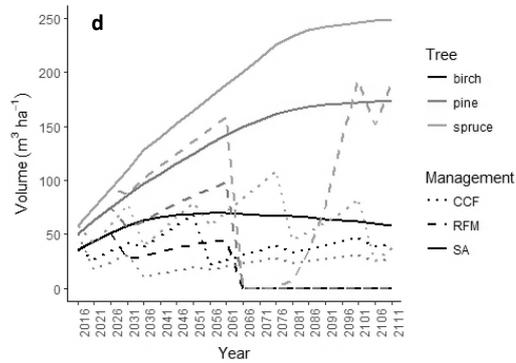
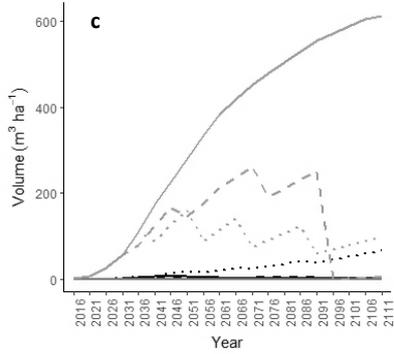
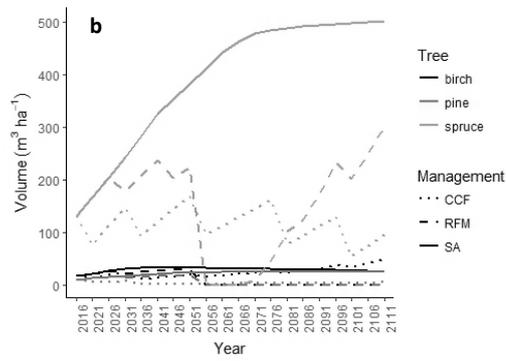
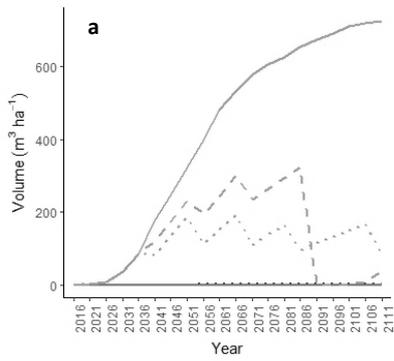


Figure S2. The development of volume of three main tree species: birches (○), Scots pine (○) and Norway spruce in the simulations under continuous cover forestry (CCF), rotation forest management (RFM) and set aside (SA) for 8 different example stands (a-h). Stands are herb-rich heath forests (a,b), mesic heath forests (c,d), sub-xeric heath forests (e,f) and xeric heath forests (g,h). The stands on the left side are young sapling stands in the beginning of the simulation, and the stands on the right side are 40 years old stands in the beginning of the simulation. Please note that the scale of y-axis varies between figures.

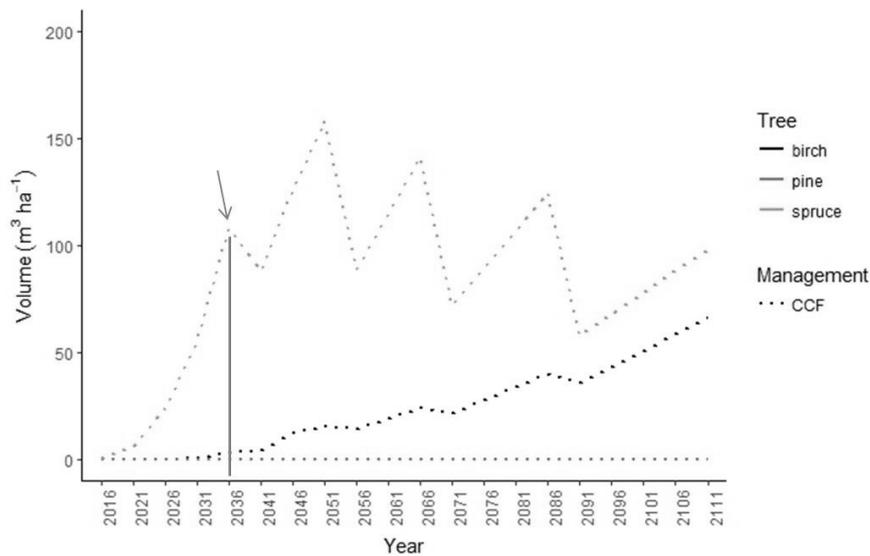


Figure S3. An example of a stand under CCF simulation. The models of Hynynen et al. (2002) were used until the first CCF cutting in year 2036 (the arrow in the figure). After the year 2036, the models of Pukkala et al. (2013) for uneven-aged stands were applied.

Table S3. Stumpage prices (€ m⁻³) for different tree species and wood assortments (averages over the last 10 year period, Natural Resource Institute Finland, 2017a).

Assortment	Clearcut	First thinning	Second thinning
Pine log	55	40	50
Pine pulp	17	11	13
Spruce log	55	42	50
Spruce pulp	25	19	21
Birch log	43	35	38
Birch pulp	15	10	11
Other	10	7	8

Table S4. Costs related to regeneration and young stands (€ ha⁻¹) in RFM. In planting, there are different prices for different tree species (averages over the last 10 year period, Natural Resource Institute Finland, 2017b)..

Planting	Scarification	Mounding	Harrowing	Early tending of seedling stand	Tending of seedling stand
Pine 627	250	280	125	220	250
Spruce 510					
Birch 813					

References

Natural Resource Institute Finland. 2017a. Stumpage prices of roundwood by year and by region.

<http://statdb.luke.fi/PXWeb/pxweb/en/LUKE/>

Natural Resource Institute Finland. 2017b. Total costs of silvicultural and forest improvement work.

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APPENDIX S2 to “Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia” Peura et al.

Supplementary material: Results

Table S1. The average values of ecosystem services in the study area under set aside (SA), continuous cover forestry (CCF) and rotation forest management (RFM).

Variable	SA	CCF	RFM	Unit
Harvested timber	0	537	629	m ³ ha ⁻¹ (across 100 years)
Carbon storage	285	192	183	tC ha ⁻¹ (average across 100 years)
Carbon sequestration	1.88	0.68	0.23	tC ha ⁻¹ yr ⁻¹ (average across 100 years)
Bilberry yield	9.5	18.1	9.6	kg ha ⁻¹ yr ⁻¹ (average across 100 years)
Cowberry yield	28.0	36.6	42.5	kg ha ⁻¹ yr ⁻¹ (average across 100 years)
Marketed mushrooms yield	17.1	16.7	18.8	kg ha ⁻¹ yr ⁻¹ (average across 100 years)
Scenic beauty	6.9	6.1	5.5	ha ⁻¹ (average across 100 years)

Table S2. The average timber net present values (NPV, € ha⁻¹) with different discount rates in the study area under continuous cover forestry (CCF) and rotation forest management (RFM).

Management	Discount rate			
	1 %	2 %	3 %	5 %
CCF	18446	11918	8586	5522
RFM	18453	11368	7839	4754

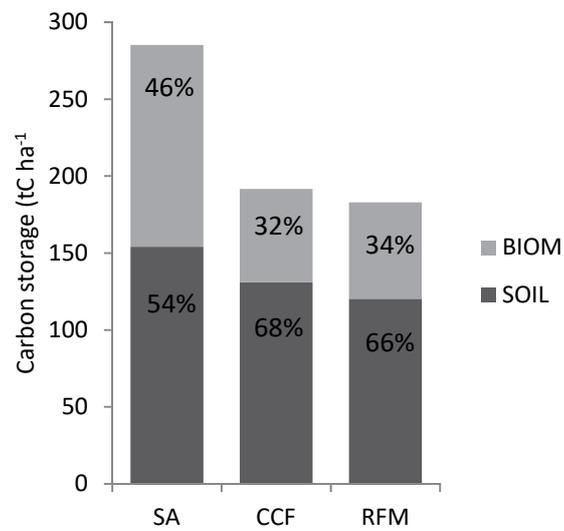


Figure S1. The average carbon storages and the shares of carbon stored in litter and soil (SOIL) and in living biomass (BIOM) across space and time under set aside (SA), continuous cover forestry (CCF) and rotation forest management (RFM).

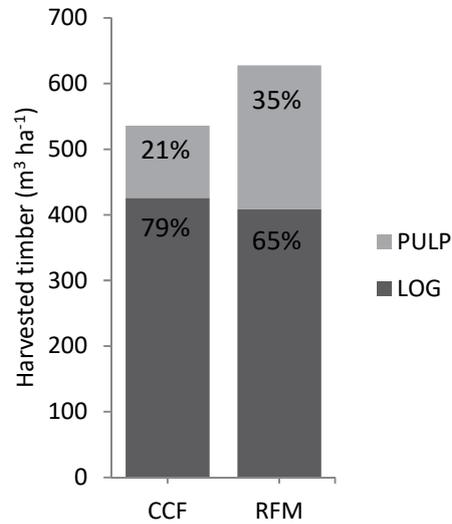


Figure S2. The average harvested timber in the study area over 100 years separately for pulpwood (PULP) and logwood (LOG) under continuous cover forestry (CCF) and rotation forest management (RFM).

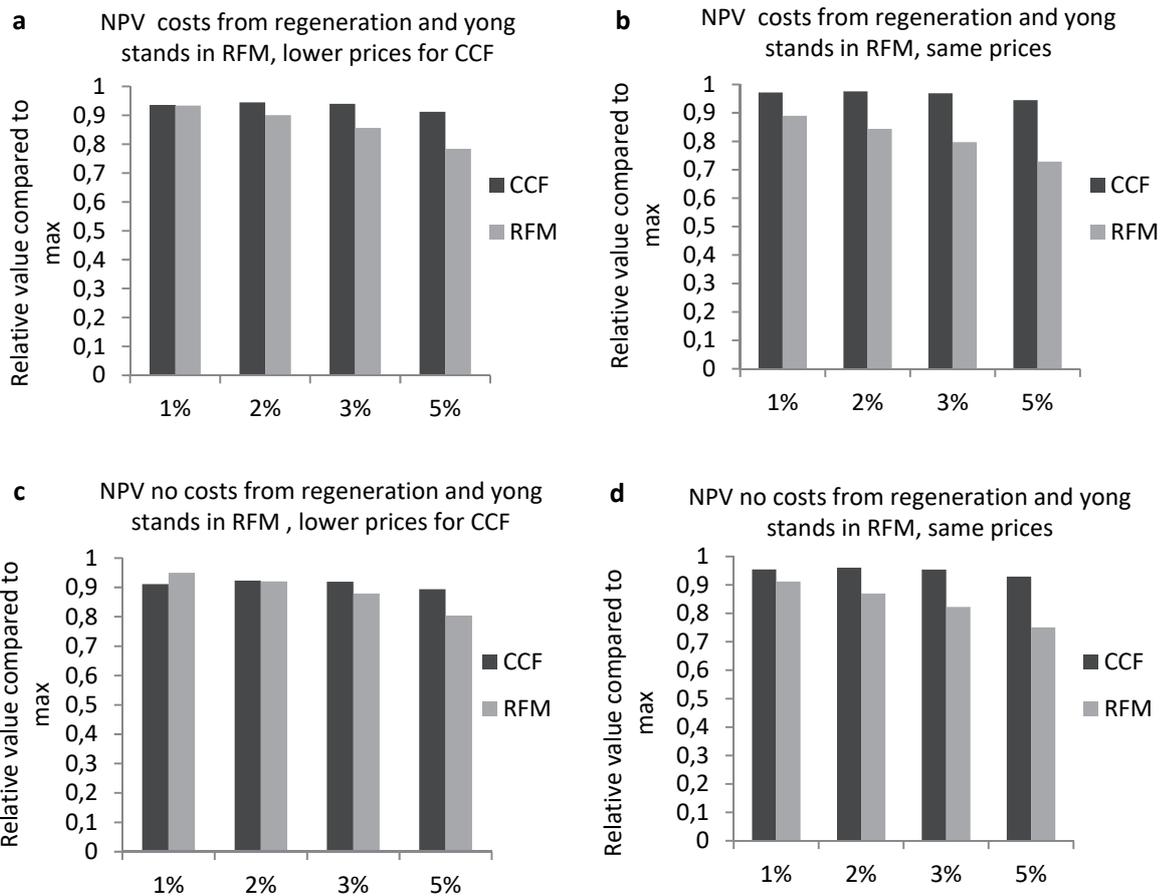


Figure S3. The relative timber NPV values across the study area with different prices and costs: a) costs related to regeneration and young stands in RFM taken into account but lower price for CCF applied, b) costs related to regeneration and young stands in RFM taken into account and same price for CCF and RFM applied, c) no costs related to regeneration and young stands in RFM taken into account and lower price for CCF applied, and d) no costs related to regeneration and young stands in RFM taken into account and same price for CCF and RFM applied.

Table S3. The average values of biodiversity indicators in the study area under set aside (SA), continuous cover forestry (CCF) and rotation forest management (RFM).

Variable	SA	CCF	RFM	Unit
HSI Capercaillie	356	197	333	ha (average across 100 years)
HSI Hazel grouse	7756	8313	4821	ha (average across 100 years)
HSI Lesser spotted woodpecker	7075	10493	1513	ha (average across 100 years)
HSI Long-tailed tit	1925	5167	673	ha (average across 100 years)
HSI Siberian flying squirrel	16954	1048	3066	ha (average across 100 years)
HSI Three-toed woodpecker	20858	15579	9723	ha (average across 100 years)
Number of large diameter trees	1.2	13.8	0.1	ha ⁻¹ (average across 100 years)
Dead wood diversity	16.8	2.9	3.1	m ³ ha ⁻¹ (average across 100 years)
Dead wood volume	22.4	4.1	4.4	m ³ ha ⁻¹ (average across 100 years)



II

THE EFFECT OF BUFFER STRIP WIDTH AND SELECTIVE LOGGING ON RIPARIAN FOREST MICROCLIMATE

by

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The effect of buffer strip width and selective logging on riparian forest microclimate

Anna Oldén^{a,b,*}, Maiju Peura^{a,b}, Sonja Saine^{a,c}, Janne S. Kotiaho^{a,b}, Panu Halme^{a,b}

^a Department of Biological and Environmental Science, P.O. Box 35, FI-40014, University of Jyväskylä, Finland

^b School of Resource Wisdom, P.O. Box 35, FI-40014, University of Jyväskylä, Finland

^c Organismal and Evolutionary Biology Research Programme, University of Helsinki, P.O. Box 65, Helsinki FI-00014, Finland

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ABSTRACT

Riparian forests have cool and humid microclimates, and one aim of leaving forested buffer strips between clear-cut areas and streams is to conserve these microclimatic conditions. We used an experimental study set up of 35 streamside sites to study the impacts of buffer strip width (15 or 30 m) and selective logging within the buffer strips on summer-time air temperature, relative air humidity and canopy openness 12 years after logging. The buffer strip treatments were compared to unlogged control sites. We found that 15-meter buffer strips with or without selective logging and 30-meter buffer strips with selective logging were insufficient in maintaining temperature, relative humidity and canopy openness at similar levels than they were in control sites. In contrast, 30-meter buffer strips differed only little from control sites, although they did have significantly lower mean air humidity. Microclimatic changes were increased by southern or southwestern aspect of the clear-cut, and by logging on the opposite side of the stream. We also tested how the cover of three indicator mosses (*Hylocomium splendens*, *Pseudobryum cinclidioides* and *Polytrichum commune*) had changed (from pre-logging to 12 years post-logging) in relation to post-logging air temperature, relative air humidity and canopy openness. We found that each of the species responded to at least one of these physical conditions. Air humidity was the most significant variable for explaining changes in the cover of the indicator moss species, suggesting that the changes in this microclimatic component has biological impacts. We conclude that to preserve riparian microclimatic conditions and species dependent on those, buffer strips should exceed 30 m in width, and not be selectively logged. Wider buffer strips are required if the clear-cut is towards south or southwest, or if the two sides of the stream are logged at the same time or during subsequent years.

1. Introduction

Streamside riparian zones consist of the ecotone between the stream and upland forest. They host high biodiversity due to the complexity in soil conditions, topography and microclimate (Hylander et al., 2005; Naiman and Décamps, 1997). In addition to many species typical to upland forests, the riparian zones host species that are adapted to moist soil and flooding (MacDonald et al., 2014; Naiman and Décamps, 1997). Although the area of riparian forests is small in the boreal landscape (a few percent), they form a habitat network of high connectivity, which may enhance the dispersal of organisms (Johansson et al., 1996; Naiman and Décamps, 1997). Thus, protecting the integrity of the riparian forests surrounding watercourses should be a high priority of biodiversity conservation in managed forest landscapes (Fries' et al., 1998; Naiman et al., 1993). However, riparian forests and

their biodiversity are threatened by intensive forestry, and in North America and Europe > 80% of riparian corridors have already been disturbed or destroyed (Naiman et al., 1993). Nowadays, buffer strips are left between streams and clear-cuts, but it is still uncertain what width is enough to conserve the microclimatic conditions and species in the riparian zones (e.g Hylander, 2014; Moore et al., 2005; Selonen and Kotiaho, 2013; Sweeney and Newbold, 2014).

Compared to intact forest, the forest edge adjacent to a clear-cut has higher daytime temperatures (but slightly lower at night), lower daytime relative air humidity, higher soil temperature, higher wind speed and more solar radiation (Chen et al., 1995; Moore et al., 2005). In upland forests, solar radiation and soil temperature acclimate to interior forest levels at about the distance of one tree length, while it takes a longer distance for air temperature, wind speed and, especially, relative air humidity (Chen et al., 1995; Moore et al., 2005). The depth

* Corresponding author at: Department of Biological and Environmental Science, P.O. Box 35, FI-40014, University of Jyväskylä, Finland.
E-mail address: anna.m.olden@jyu.fi (A. Oldén).

of the edge effects is affected by several factors, with aspect being of large importance: in the northern hemisphere, edge effects are largest and deepest on south- or southwest-facing edges (Chen et al., 1995; Heithecker and Halpern, 2007; Moore et al., 2005). It is not well known how the edge effect is affected if the retained forest is selectively logged. When the canopy becomes less dense, it results in a longer, less steep edge effect (Heithecker and Halpern, 2007). On the other hand, it has been suggested that a feathered edge with a dense understory is more resistant to physical edge effects (Chen et al., 1995), and better mimics the edges created by e.g. wildfires (Braithwaite and Mallik, 2012).

Results on the depth of the edge effect in upland forests do not necessarily apply in riparian forests, where logging may have smaller effects on the microclimate and communities because the naturally moister and cooler microclimate may buffer against the changes (Dynesius et al., 2009; MacDonald et al., 2014; Rykken et al., 2007). The study of Brososke et al. (1997) suggested that buffer strips should be at least 45 m wide to protect the natural riparian microclimate, while in the study of Rykken et al. (2007) buffer strips of 30 m were sufficient. In terms of species, the buffer width should be at least 30 m in order to protect communities of vascular plants and mosses that grow in the riparian habitat next to the stream (Elliott and Vose, 2016; Oldén et al., 2019; Selonen and Kotiaho, 2013) as well as aquatic species (Sweeney and Newbold, 2014). Selective logging in the buffer strip increases the density of stream macroinvertebrates (Carlson et al., 1990), increases the regeneration of saplings in the buffer (Mallik et al., 2014; Zenner et al., 2012), and decreases the amount of decaying wood in the long-term (Lundström et al., 2018). It also causes changes in moss communities in 15-m wide buffers but not in 30-m wide buffers (Oldén et al., 2019). However, studies on the effects of selective logging on riparian microclimate are lacking.

Bryophytes (mosses and liverworts) are excellent bioindicators for studying the possible responses of species to changed microclimatic conditions in riparian buffer strips (Hylander et al., 2005, 2002; Stewart and Mallik, 2006). They are poikilohydric, i.e. they cannot regulate their water loss and are dependent on moisture from the soil and air to retain growth (Proctor, 1990). Many species, especially those adapted to grow under forest canopy, are very sensitive to logging-induced changes in moisture and light conditions (Busby et al., 1978; Dynesius and Hylander, 2007; Hylander et al., 2005, 2002; Stewart and Mallik, 2006). Studies have shown that bryophyte growth, cover, species richness and community composition change soon after clearcutting or logging with narrow buffers, indicating low resistance to change (Hylander et al., 2005, 2002; MacDonald et al., 2014; Oldén et al., 2019; Stewart and Mallik, 2006). Small populations may survive in microclimatic refugia on the northern side of objects, such as boulders or stumps (Schmalholz and Hylander, 2011).

In Finland, those riparian streamside habitats that are in natural or nearly natural condition are protected by law, the Forest Act. The Act states that it is not allowed to alter their characteristic features, which are specified as the special growing conditions and microclimate that result from the proximity of water and the tree and shrub layers (Forest Act, 2013). However, the width of buffer strips has been on average 15 m in streamside habitats classified as Forest Act Habitats (Ahonen, 2017), while the latest recommendation is that the buffer width should equal the average length of the trees (Metsäkeskus, 2018), i.e. around 20 m, which is probably also insufficient to conserve the microclimate and growing conditions. Thus, there is a contrast between the > 30 m suggested by earlier studies, the reality in the field, and the law.

In this paper, we study the impact of buffer strip width (15 or 30 m) and selective logging (30% of tree basal area removed from the buffer or not) on summer-time microclimatic conditions and canopy openness in streamside habitats. We compare the conditions in the logged sites to unlogged control sites 12 years after the logging treatments in order to answer the following questions: 1. What kind of buffer strips in our set up, if any, are able to maintain relative air humidity, air temperature

Table 1

The study sites: Municipality of the location, North and East coordinates in decimal degrees, width of the stream and the total basal area of trees before logging treatments. The sites are listed based on their treatments.

Site ID	Municipality	N	E	Stream width (m)	Tree basal area (m ² /ha)
Control					
6	Vieremä	63.94052	26.66638	1.0	36
21	Lieksa	63.23884	30.75467	1.6	32
27	Leivonmäki	61.90145	25.92199	1.5	27
28	Leivonmäki	62.02793	26.18217	0.6	24
31	Kuhmoinen	61.71589	24.93035	0.4	13
35	Sotkamo	63.93125	28.22158	3.2	32
45	Rautavaara	63.59531	28.48888	2.1	26
47	Rautavaara	63.63822	28.44861	0.8	32
30 m without selective logging					
4	Vieremä	63.98945	26.8938	0.3	35
16	Lieksa	63.46902	29.8989	0.5	25
25	Kivijärvi	63.20412	24.90234	1.9	27
34	Uurainen	62.54641	25.48799	2.5	25
40	Rautavaara	63.66626	28.57471	0.2	27
30 m with selective logging					
15	Kaavi	63.11614	28.73192	0.6	37
18	Lieksa	63.46808	29.94605	0.3	37
23	Äänekoski	62.56329	25.51531	1.2	23
26	Korpilahti	62.04014	25.42641	1.1	31
33	Karstula	62.97202	24.97654	1.7	22
39	Rautavaara	63.67432	28.56051	0.4	30
42	Nurmes	63.56566	29.33364	0.6	29
43	Nurmes	63.57713	29.50002	0.3	26
15 m without selective logging					
1	Vieremä	63.83188	26.94863	0.3	37
2	Pieksämäki	62.39258	26.93276	1.5	33
29	Korpilahti	62.21604	25.39608	0.8	31
32	Orivesi	61.6162	24.20887	0.6	23
38	Rautavaara	63.40632	28.20288	0.7	32
15 m with selective logging					
3	Vieremä	63.98682	26.90886	0.5	40
8	Pielavesi	63.39579	26.39757	0.2	37
17	Lieksa	63.46600	29.89691	1.6	33
20	Lieksa	63.28729	30.34200	1.1	36
22	Lieksa	63.21131	30.22918	0.4	37
24	Pihtipudas	63.41049	26.05685	0.8	34
48	Rautavaara	63.59369	28.45654	0.7	36
49	Nurmes	63.78579	29.35355	0.7	38
56	Pieksämäki	62.26919	26.99563	2.2	46

and canopy openness at similar levels than in unlogged sites? 2. How are air humidity and temperature affected by buffer width, selective logging and the aspect of the clear-cut? 3. Are the differences in humidity and temperature smaller on the northern side of a tree than on the southern side, i.e. can objects like trees create small microclimatic refugia? In addition, we compare the effects of air humidity, air temperature and canopy openness on the changes that have happened in the cover of three common indicator moss species between pre-logging and 12 years post-logging in order to answer the question: 4. Which physical conditions drive the changes in the cover of the three mosses?

2. Material and methods

2.1. Study sites

The study area is located in Central and Eastern Finland, on southern and middle boreal vegetation zones (Ahti et al., 1968). The mean annual air temperature in the area is 2–4 °C and precipitation 600–700 mm year⁻¹ (average from 1981 to 2010) (Pirinen et al., 2012). We studied 35 streamside sites in the area (Table 1). Each site was located on a separate stream. Before the logging treatments, all study sites were dominated by even-aged spruce (*Picea abies* (L.) H. Karst.), and the dominant trees were at least 80 years old. The sites

were completely forested, i.e. spruce trees grew close to the stream and there were no extensive treeless riparian zones. The water channels were small streams or rivulets with regular, year-round flow. The width of the water channels varied from 0.2 to 3.2 m (Table 1). The sites did not have extensive regular flooding, but occasional flooding could occur especially near the stream. All of the sites had been classified as Forest Act Habitats by Finnish forest authorities.

2.2. Treatments

During the winter 2005–2006, logging treatments were applied on 27 of the sites, while 8 sites were left as unlogged controls. The logging treatments included clear-cutting in the upland forest, and one of the following types of buffer strips next to the stream:

1. 30-meter wide buffer strip without selective logging (5 sites),
2. 30-meter wide buffer strip with selective logging (8 sites),
3. 15-meter wide buffer strip without selective logging (5 sites),
4. 15-meter wide buffer strip with selective logging (9 sites).

In the selective logging, 30% of the basal area of trees was logged from the buffer strip, focusing on the largest trees of the stand. Trees were logged within the whole width of the buffer. Additional information on the treatments can be found in Oldén et al. (2019). The treatments were allocated randomly to the sites.

Originally, the logging treatment was performed on only one side of the stream, and mature forest was left standing on the opposite side. If by the year 2017 logging had also happened on the opposite side of the stream, we measured the distance from the stream to the edge of the clear cut, and sites where the distance was < 40 m were recorded as logged on the opposite side. In these 15 sites the opposite buffers had not been selectively logged, but the buffer width varied both within sites and between sites from about 10 to 40 m (mean of site means was 23 m). In the 20 unlogged sites there were no buffer strip loggings within 50 m distance from the study area, but in some of them there were clear-cuts further than 50 m away. Since these clear-cuts were mostly tens or hundreds of meters away, it was considered that they did not impact the microclimate of the study area considerably.

2.3. Data collection: Microclimate and canopy openness

On each study site there was a rectangular 10 m * 15 m study area next to the stream. One of the 10-m sides of the study area followed the stream shoreline. The study area was placed in the center of the treatment area, i.e. the logged area was on the same side of the stream.

We used data loggers (Lascar EL-USB-2) to measure relative humidity and air temperature at 5-minute time intervals for a month between 18th of July and 18th of August 2017. Each data logger contains one sensor for relative humidity (accuracy 2.25%) and temperature (accuracy 0.55 °C). Two data loggers were placed on a trunk of a mature spruce tree located at a distance of about 7.5 m from the stream, and as near to the center of the 10-meter wide study area as possible (Fig. 1). The loggers were placed at 50 cm height from the ground, on the opposite sides, south and north, of the tree. From the data of each logger, we calculated the following values: the mean relative air humidity (%), the mean of daily minimum relative air humidities (%), the standard deviation (SD) of all of the relative air humidity values, the mean air temperature (°C), the mean of daily maximum air temperatures (°C), and the standard deviation of all of the temperature values.

To measure canopy openness in 2017, we took fisheye-photos and calculated the proportion of visible sky from the pixels. Four photos were taken (one towards each cardinal direction) at both of the lowest corners of the study area at the shoreline (Fig. 1). The average proportion of visible sky in these eight photos was used to approximate the openness at 0-m distance from the stream. Similarly, four photos were taken at a distance of 10 m from the stream, along both of the edges of

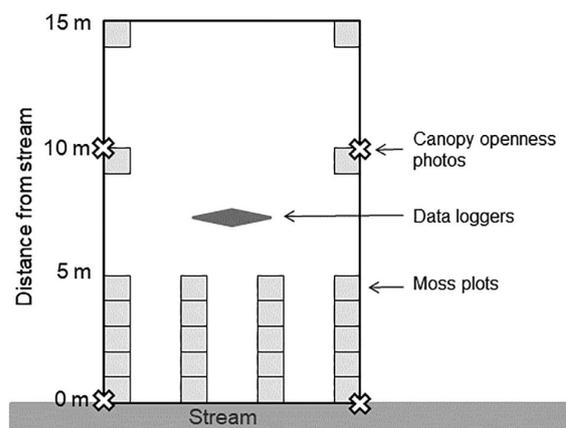


Fig. 1. The location of canopy openness photos, data loggers and moss plots within the study area next to the stream.

the study area, and these eight photos were used to approximate the openness at 10-m distance. The photos were taken with a digital camera and a fish-eye converter that allows for photos with 120° angle of view. For each photo, the camera was held vertically so that the upper edge was upright. The proportion of sky pixels out of all pixels in the photo was calculated with ImageJ 1.45 s (a more detailed description of the method given in Oldén et al., 2017).

2.4. Data collection: mosses

2.4.1. Indicator mosses

In order to test for the ecological significance of the physical conditions (humidity, temperature and canopy openness), we followed the change in the cover of three common indicator moss species. *Hylocomium splendens* (Hedw.) Schimp., *Pseudobryum cinclidioides* (Huebener) T.J.Kop., and *Polytrichum commune* Hedw. differ in their ecology from each other, but are known to require moist microhabitats and to respond to microclimatic changes:

1. *H. splendens* is a feather moss that forms loose wefts (intertwining branched layers) on boreal forest floors. *H. splendens* dries out quickly in dry conditions, so it thrives in relatively constant, shaded habitat conditions, where trees provide high humidity and low temperatures (Callaghan et al., 1978). The growth of *H. splendens* has been shown to decrease due to logging-induced microclimatic edge effects (Caners et al., 2013; Hylander, 2005; Stewart and Mallik, 2006).
2. *P. cinclidioides* is a large-leaved moss that grows as turf (vertical stems with little or no branching). It grows on mesotrophic, waterlogged soil in springs, swamps, flooded mires, flood meadows and stream banks (Darell and Cronberg, 2011; Ulvinen et al., 2002). *P. cinclidioides* has been observed to decrease in retention patches after the surrounding forest is logged (Perhans et al., 2009).
3. *P. commune* is a tall turf moss that grows commonly on peat in mires and in paludified spots in forests (Ulvinen et al., 2002). It has an underground stem, internal water-conducting tissues and complex leaves that are resistant to water loss (Bayfield, 1973). Due to these properties *P. commune* is able to grow also in periodically dry and exposed conditions (Callaghan et al., 1978).

2.4.2. Cover change

The percentage cover of each of the three study species was estimated (by eye estimation) in 2004 (before logging) and in 2017 (12 years after logging) on 1 m² plots within the study area. Twenty plots were located within the first five meters from the stream (distance

0–5 m) and four additional plots were located at 10 and 15 m from the stream (Fig. 1). The sampling was focused on the first five meters from the stream because the primary aim of leaving buffer strips is to conserve the species growing in the immediate vicinity of the stream.

In 2017, several plots were discarded on many of the sites due to the following reasons: 1) the plot markings had been lost and the plot could not be placed with certainty in the same place than in 2004, 2) the microhabitats in the plot had changed substantially due to windfalls (there was a root mound, a log or a pile of branches on the plot), or 3) the stream had meandered and the shoreline had moved. These plots were not included in the data of either year.

For each species, we calculated the mean cover on the studied plots in 2004 and in 2017, and then calculated the relative change in the cover as $(Cover_{2017} - Cover_{2004}) / (Cover_{2004} + Cover_{2017})$. When the change in the cover is divided by the sum, the relative change gets a maximum value of 1 (colonization) and a minimum value of -1 (extinction).

2.5. Statistical analyses

We used Multivariate Analysis of Variance (MANOVA) to analyze the data where several response variables were affected at the same time and were correlated with each other. MANOVA is used to test whether the explanatory variables affect the response variables simultaneously in their global model. All analyses were performed in R (R Core Team, 2017). Function `lm` was used to build the separate linear models for each response variable, and function `Anova` from package “car” (Fox and Weisberg, 2011) was used to perform the Analysis of Variance with type III sums of squares (suitable for unbalanced designs).

The response variables in the models were

- 1) Relative humidity: mean humidity, mean daily minimum humidity and the standard deviation of humidity (mean values from the two data loggers on a site),
- 2) Temperature: mean temperature, mean daily maximum temperature and the standard deviation of temperature (mean values from the two data loggers on a site),
- 3) Canopy openness: canopy openness at 0 m from stream and canopy openness at 10 m from stream (means of the eight canopy openness photos taken at that distance in a site).

First, we tested how each of the four different kinds of buffer strips (the treatments) differed from the unlogged controls, i.e. whether one or more of the buffer strip types could provide similar microclimatic conditions as unlogged sites. We used three MANOVAs, one for the humidity variables, one for the temperature variables and one for the canopy openness variables. Prior to analysis, both of the canopy openness values were log₁₀-transformed to improve the model fit. In each model, the explanatory variables were the treatment (controls compared to the four buffer treatments: 30 m without selective logging, 30 m with selective logging, 15 m without selective logging, and 15 m with selective logging), logging on the opposite side of the stream (yes or no), and east coordinates of the geographic location. North coordinates could not be added in the model because they correlated with logging on the opposite side (more sites had been logged in south than north of the geographic area) and with east coordinates (the sites were located within the geographic area so that those that were more in north also tended to be more in east).

Second, we used four MANOVAs to test how relative humidity and temperature were affected by buffer width, selective logging and southern or southwestern aspect in the buffer strip treatment sites. Control sites were not included in these analyses as aspect is not relevant without a clear-cut, and there was no buffer width or selective logging in the controls. The compass point of the treatment clear-cut from the stream was transformed into an index of southern aspect,

which has a value of 180 if the clear-cut is towards south, decreases continuously through 90 in east and west, and is 0 if the clear-cut is towards north. Similarly, southwestern aspect is 180 if the clear-cut is towards southwest, and 0 if the clear-cut is towards northeast. Separate models were built for southern and southwestern aspects. Each model included the following explanatory variables: Buffer width (15 or 30), selective logging (yes or no), southern or southwestern aspect (0–180), logging on the opposite side of the stream (yes or no) and east coordinates. We also included the interactions buffer width * selective logging and buffer width * southern/southwestern aspect, but these did not have significant impacts in any of the models, and we excluded them from the final models.

Third, to test whether microclimatic changes are smaller on the northern side of a tree than on the southern side of the tree, we built two similar MANOVAs separately for the south- and north-facing data loggers. Separate models were built for relative humidity and temperature. Only the logging treatment was included as an explanatory variable in these MANOVAs, and we compared the strength of the treatment effects on the models of south-facing loggers and north-facing loggers.

Fourth, we used three MANOVAs to test for the effect of humidity, temperature and canopy openness on the changes in the cover of the three moss species. In all of the three models, the response variables were the same: the relative change in *H. splendens*, relative change in *P. cinclidioides* and relative change in *P. commune*. In the humidity model, the explanatory variable was mean humidity, and in the temperature model, it was mean temperature (means of the two loggers on the site). In the canopy openness model, the explanatory variable was the mean of the canopy openness values at 0 and 10 m.

For those readers who are interested in the impacts of the treatments, buffer width, selective logging and logging on the opposite side of the stream on the relative changes of the three indicator mosses, we provide these analyses in Appendix A.

3. Results

3.1. Impact of logging on physical conditions

The treatments had a strong impact on the humidity variables, and logging on the opposite side and the east coordinate also had an impact in the global MANOVA model (Table 2). When compared to the control sites, all of the four types of buffer strips had lower mean humidity (Fig. 2A), and mean humidity was also lowered by logging on the opposite side of the stream (Table 3). In terms of the mean daily minimum humidity, the 30-meter buffers without selective logging did not differ significantly from control sites, while all other treatments had significantly lower values (Fig. 2B), and the minimum humidity values were also lowered by logging on the opposite side of the stream (Table 3). All buffer strips, except for the 30-meter buffers without selective logging, had higher variation (standard deviation) in humidity (Fig. 2C). The standard deviation was also increased by logging on the opposite side and by an eastern location in the geographic area (Table 3).

The treatments and logging on the opposite side had significant impacts on the temperature values in their global model, but east coordinate did not (Table 2). Mean temperature was increased on the logged treatments, but only the 15-meter buffer strips (with or without selective logging) differed significantly from controls (Fig. 2D). Mean temperature was also increased by logging on the opposite side of the stream (Table 3). In terms of the mean daily maximum temperature and the standard deviation of temperature, all treatments except the 30-meter buffers without selective logging had significantly higher values than the controls (Fig. 2E and F). In addition, logging on the opposite side also increased the daily maximum and the standard deviation of temperature (Table 3).

Canopy openness was affected by both the treatments and by the

Table 2

Results from the three MANOVAs on the impact of treatments (unlogged control vs. buffer strip treatments), logging on the opposite side and east coordinate on relative air humidity (mean, daily minimum and standard deviation), temperature (mean, daily maximum and standard deviation) and canopy openness (at 0 and 10 m from stream). Pillai test statistic, approximate F-statistic, hypothesis and error degrees of freedom, and p-value.

Response	Explanatory	Pillai	F	Hypoth. df	Error df	p	Sign.
Humidity	Treatment logging	0.94	3.2	12	84	0.001	***
	Opposite logging	0.26	3.1	3	26	0.043	*
	East coordinate	0.29	3.5	3	26	0.029	*
Temperature	Treatment logging	0.82	2.6	12	84	0.005	**
	Opposite logging	0.30	3.8	3	26	0.022	*
	East coordinate	0.19	2.1	3	26	0.129	.
Canopy openness	Treatment logging	0.59	3.0	8	56	0.008	**
	Opposite logging	0.37	8.1	2	27	0.002	**
	East coordinate	0.11	1.6	2	27	0.213	.

Significance: *** $p < .001$, ** $0.001 < p < .01$, * $0.01 < p < .05$, . $0.05 < p < .1$.

logging on the opposite side, but not by the east coordinate (Table 2). At the stream shoreline, only the 15-meter buffer strips with selective logging had significantly higher canopy openness than control sites (Fig. 2G). Logging on the opposite side increased canopy openness at stream shoreline (Table 3). At the distance of 10 m, all buffer strips, except for the 30-meter buffers without selective logging, had significantly higher canopy openness than control sites (Fig. 2H). Logging on the opposite side increased canopy openness as well (Table 3).

3.2. Impact of buffer width, selective logging and aspect on microclimate

Buffer width (15 or 30 m) had significant impacts on the humidity and temperature variables (Table 4). Selective logging (yes or no) did not have significant impacts, although it did have a nearly significant impact on humidity when modelled together with southern aspect (Table 4). Both southern and southwestern aspects impacted the humidity variables significantly, but the temperature variables were not affected by southwestern aspect and southern aspect had a nearly significant impact (Table 4).

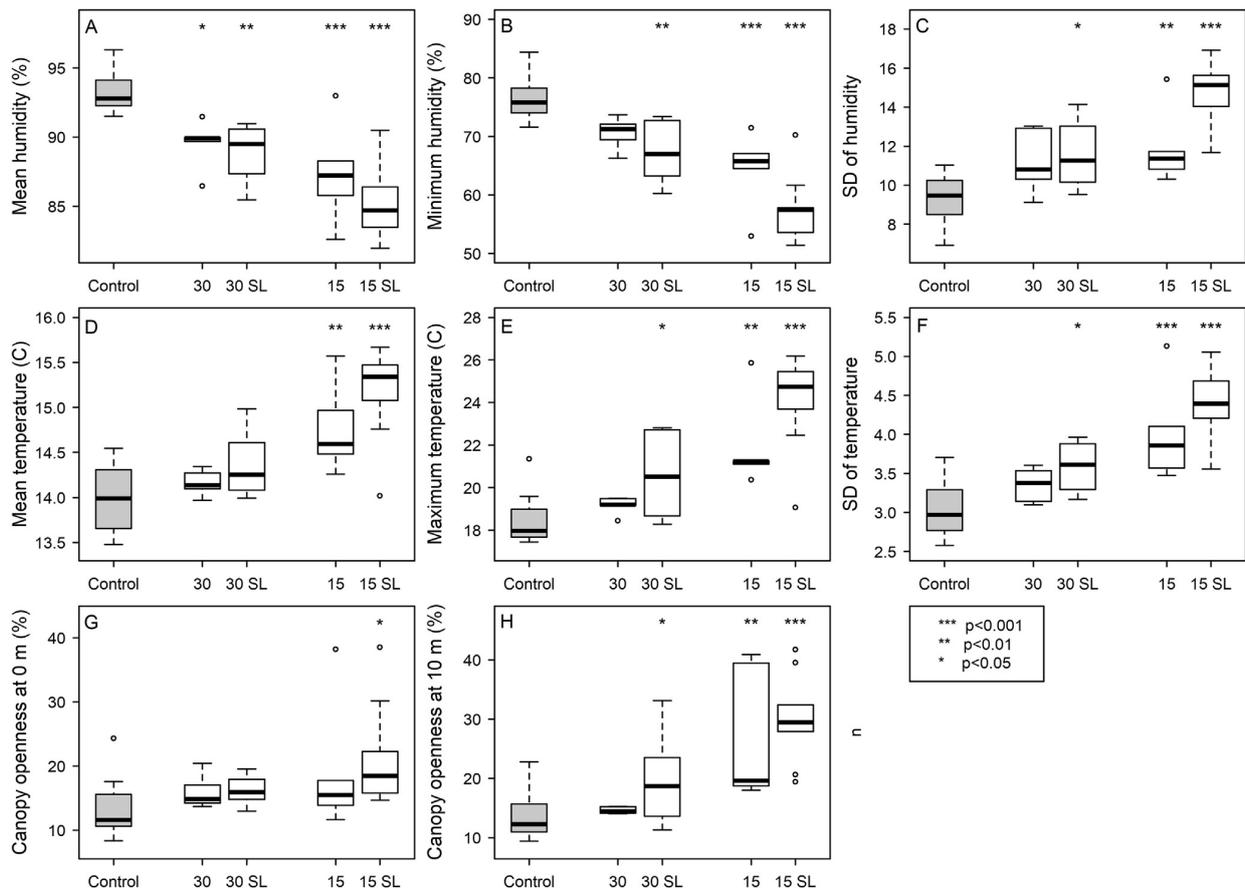


Fig. 2. The differences between unlogged control sites and the sites with buffer strips (30-meter without or with selective logging [SL] and 15-meter without or with selective logging) in their physical conditions: A) mean relative humidity, B) mean daily minimum humidity, C) standard deviation of humidity, D) mean temperature, E) mean daily maximum temperature, F) standard deviation of temperature, G) canopy openness at stream shoreline, an H) canopy openness at 10-meter distance from stream.

Table 3

Results from the eight linear models on the effects of logging on the opposite side of the stream and east coordinate on the humidity, temperature and canopy openness variables. Opposite logging and east coordinates were modelled together with the effects of treatment loggings (results in Fig. 2).

Response	Explanatory					
	Logging on opposite side			East coordinate		
	Estimate	p	Sign.	Estimate	p	Sign.
Mean humidity	-2.47	0.012	*	-9.6E-06	0.066	.
Minimum humidity	-5.80	0.005	**	-2.1E-05	0.054	.
SD of humidity	1.87	0.004	**	1.0E-05	0.005	**
Mean temperature	0.36	0.037	*	7.0E-07	0.440	.
Maximum temperature	1.85	0.014	*	4.4E-06	0.264	.
SD of temperature	0.54	0.002	**	1.9E-06	0.033	*
Canopy openness at 0 m	0.17	< 0.001	***	4.6E-07	0.079	.
Canopy openness at 10 m	0.12	0.024	*	1.9E-07	0.490	.

Significance: *** $p < .001$, ** $0.001 < p < .01$, * $0.01 < p < .05$, . $0.05 < p < .1$.

3.3. Microclimatic refugia on northern side of trees

Air humidity was affected by the treatments on both the southern and northern sides of the trees (Table 5). Air temperature was affected more strongly on the southern than on the northern side, but the effect was significant on the northern side as well (Table 5).

3.4. Impact of physical conditions on mosses

Mean humidity, mean temperature and mean canopy openness each explained significantly the changes in the cover of the three moss species, and mean humidity had the strongest effect among the three variables (Table 6).

The relative change in the cover of *H. splendens* was affected by humidity, which had a significant positive impact, while temperature

and canopy openness did not have significant impacts on this species (Fig. 3A–C). Similarly, the relative change of *P. cinclidioides* was significantly and positively affected by humidity, while temperature and canopy openness did not have significant effects (Fig. 3D–F). In contrast, the relative change in *P. commune* was significantly affected by all three variables: negatively by humidity, and positively by temperature and canopy openness (Fig. 3G–I). Canopy openness had the largest impact on *P. commune* (Fig. 3I).

4. Discussion

4.1. Impact of logging on physical conditions

We found strong impacts of logging on the measured microclimatic variables of air temperature and relative humidity. As expected, the divergence from control site microclimates was in the order 15-meter selectively logged > 15-meter without selective logging > 30-meter selectively logged > 30-meter without selective logging. The effects were similar for canopy openness at 10 m from the stream, while right at the stream shoreline only the most intensive logging (15 m selective logging) resulted in significant difference from controls.

The 15-meter wide buffers, both those with and without selective logging, differed from control sites in their microclimate. They had lower humidity and higher temperature, and both humidity and temperature varied more. These logging-induced changes in microclimate are well known near clear-cut edges in upland forests (Chen et al., 1995; Moore et al., 2005). Obviously, 15-meter buffers do not fulfil the criteria of no changes in microclimate and are therefore illegal in Finnish Forest Act habitats (Forest Act, 2013), although they have been common in practice (Ahonen, 2017). Our measurements were made 12 years after logging, when the newly regenerated trees already provided some protection, but there had also been abundant windfalls in many sites with 15-meter buffers, which had resulted in more microclimatic changes by the time of our measurements.

Maximum daily temperature and minimum daily humidity differed more from the values found in control sites than did the means of temperature and humidity. For example, in the sites with 15-meter selectively logged buffers, mean temperature was on average 1.2 °C

Table 4

Results from four MANOVAs on the effects of buffer width, selective logging and aspect (southern or southwestern) on the humidity (mean, SD and mean daily minimum) and temperature (mean, SD and mean daily maximum) on sites with buffer strips. Logging on the opposite side of the stream and east coordinates were also included as additional explanatory variables. Pillai test statistic, approximate F-statistic, hypothesis and error degrees of freedom, and p-value.

Response	Explanatory	Pillai	F	Hypoth. df	Error df	p	Sign.
Humidity	Buffer width	0.49	6.0	3	19	0.005	**
	Selective logging	0.30	2.8	3	19	0.071	.
	Southern aspect	0.46	5.4	3	19	0.008	**
	Logging on opposite side	0.38	3.9	3	19	0.026	*
	East coordinate	0.45	5.1	3	19	0.009	**
	Buffer width	0.46	5.3	3	19	0.008	**
	Selective logging	0.25	2.1	3	19	0.136	.
	Southwestern aspect	0.33	3.2	3	19	0.049	*
	Logging on opposite side	0.23	1.9	3	19	0.161	.
	East coordinate	0.28	2.4	3	19	0.099	.
Temperature	Buffer width	0.58	8.7	3	19	0.001	***
	Selective logging	0.27	2.3	3	19	0.111	.
	Southern aspect	0.28	2.4	3	19	0.097	.
	Logging on opposite side	0.38	3.8	3	19	0.027	*
	East coordinate	0.28	2.4	3	19	0.098	.
	Buffer width	0.54	7.5	3	19	0.002	**
	Selective logging	0.23	1.9	3	19	0.167	.
	Southwestern aspect	0.09	0.7	3	19	0.589	.
	Logging on opposite side	0.32	3.0	3	19	0.059	.
	East coordinate	0.23	1.9	3	19	0.161	.

Significance: *** $p < .001$, ** $0.001 < p < .01$, * $0.01 < p < .05$, . $0.05 < p < .1$.

Table 5

Results from the four MANOVAs on the impact of treatments on air humidity (mean, daily minimum and standard deviation) and temperature (mean, daily maximum and standard deviation) on the southern and northern sides of trees. Pillai test statistic, approximate F-statistic, hypothesis and error degrees of freedom, and p-value.

Response	Explanatory	Pillai	F	Hypoth. df	Error df	p	Sign.
Humidity in south-facing loggers	Treatment logging	0.89	3.2	12	90	< 0.001	***
Humidity in north-facing loggers	Treatment logging	0.97	3.6	12	90	< 0.001	***
Temperature in south-facing loggers	Treatment logging	0.81	2.8	12	90	0.003	**
Temperature in north-facing loggers	Treatment logging	0.69	2.2	12	90	0.016	*

Significance: *** $p < .001$, ** $0.001 < p < .01$, * $0.01 < p < .05$, $0.05 < p < .1$.

Table 6

Results from the three MANOVAs on the impacts of mean humidity, mean temperature and mean canopy openness on the change in the cover of three moss species (*H. splendens*, *P. cinclidioides* and *P. commune*). Pillai test statistic, approximate F-statistic, hypothesis and error degrees of freedom, and p-value.

Response	Explanatory	Pillai	F	Hypoth. df	Error df	p	Sign.
Mosses	Mean humidity	0.39	6.7	3	31	0.001	**
Mosses	Mean temperature	0.24	3.3	3	31	0.033	*
Mosses	Mean canopy openness	0.31	4.7	3	31	0.008	**

Significance: *** $p < .001$, ** $0.001 < p < .01$, * $0.01 < p < .05$, $0.05 < p < .1$.

higher while mean daily maximum temperature was 5.6 °C higher than in controls, and mean humidity was 8.1% lower while mean daily minimum humidity was 19.0% lower. This is because at night unlogged forests are somewhat warmer than logged areas, and the stream humidifies the surrounding air (Moore et al., 2005; Rykken et al., 2007). The changes in the heat and dryness of the hottest time of the day may be detrimental to sensitive organisms.

The differences in mean and maximum temperatures are comparable to the expected effects of climate change in the area (mean temperature increases by 2–3 °C and the mean temperature of the annual hottest day increases by 1.5–2 °C if global warming is limited to 1.5 °C; Hoegh-Guldberg et al., 2018). However, climate change happens over several decades, while logging changes the microclimate immediately (or in a time span of a few years if there are subsequent windfalls), leaving very little time for sensitive organisms to adapt or migrate. It is

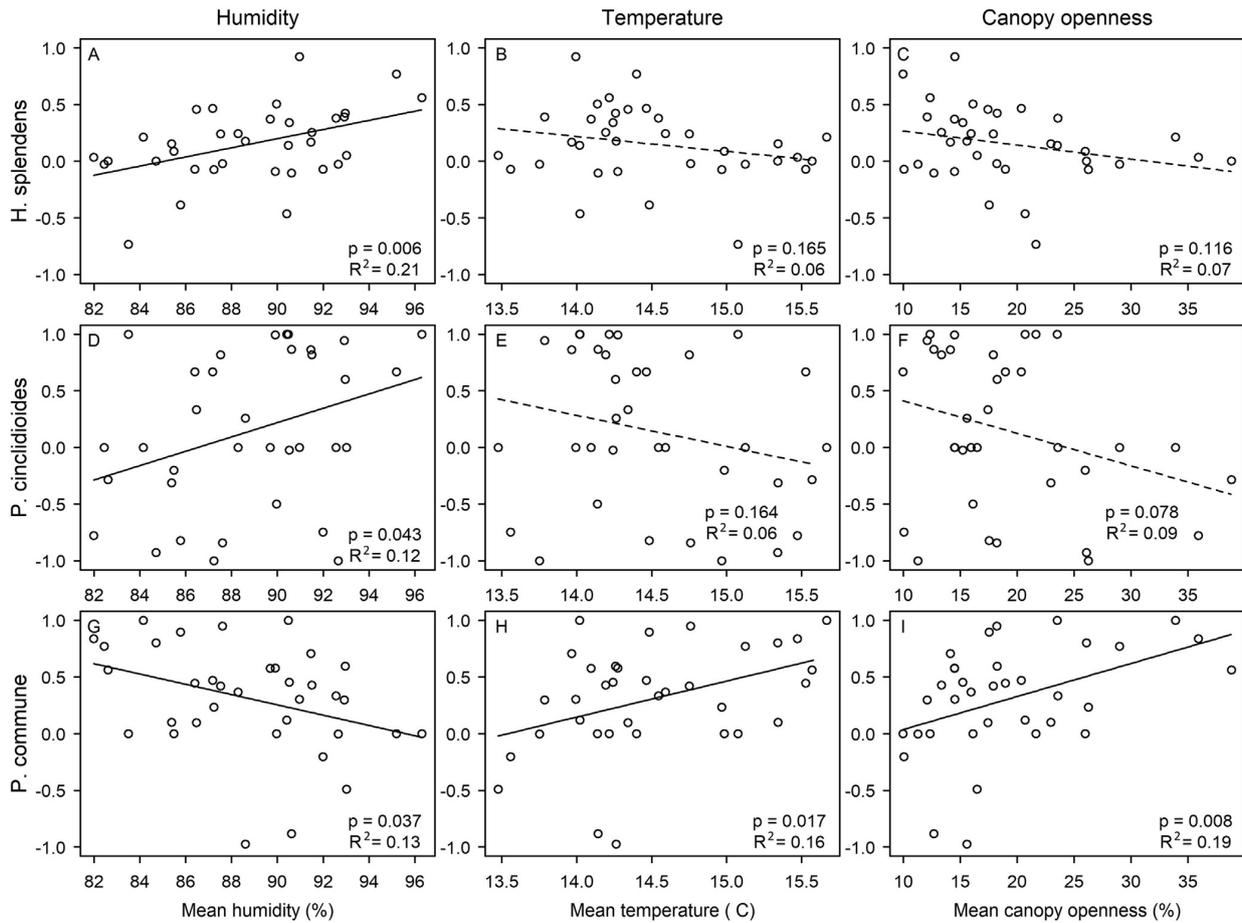


Fig. 3. The impacts of mean relative humidity, mean temperature and mean canopy openness on the relative changes that have occurred in the cover of the three moss species (from pre-logging to 12 years post-logging): A-C) *Hylocomium splendens*, D-F) *Pseudobryum cinclidioides*, and G-I) *Polytrichum commune*. Solid regression lines indicate significant relationships ($p < .05$) and dashed lines indicate non-significant relationships ($p > .05$).

likely that within a few decades, the joined effect of climate change and logging causes peak temperatures of the logged streambanks to increase by several degrees compared to present values. In addition, logging with narrow buffers destroys the possibilities of cool and humid streambanks to function as microclimatic refugia or dispersal corridors during climate change (see Ashcroft, 2010; Fremier et al., 2015; Isaak et al., 2015). All this adds pressure to secure wide buffer strips.

Microclimatic changes were smaller in 30-meter buffers. On average, both the selectively logged and the non-selectively logged 30-meter buffers were warmer and drier and had more variation than did the unlogged controls, but the difference from controls was mostly significant for only the selectively logged ones. However, in the case of mean relative humidity also the 30-meter buffers without selective logging were drier than control sites. Thus, based on our data, 30-meter wide buffers are nearly wide enough to retain microclimatic conditions in streamside forests, but the buffers should not be selectively logged. Our results are supported by Brosfoske et al. (1997) who found that 45-meter buffers are mostly sufficient to protect riparian microclimatic gradients, and by the study of Rykken et al. (2007) where 30-meter buffers were sufficient to retain similar microclimate as unlogged forests. Thus, buffer width should exceed 30 m when the aim is to conserve microclimatic conditions in valuable habitats. Probably the buffer width should be about 40–50 m, but more studies are needed to confirm this suggestion. On the other hand, if the primary aim of leaving a buffer strip is not to conserve the microclimate, narrower or selectively logged buffer strips can be sufficient. Selective logging within buffers may provide better emulation of natural disturbances and increase habitat diversity and tree regeneration (Kreutzweiser et al., 2012; Mallik et al., 2014). Therefore, selective logging could be applied in sites where microclimatic protection is not considered necessary, thus increasing habitat heterogeneity at the landscape-scale.

Logging on the opposite side of the stream had significant impacts on all of the measured temperature, humidity and canopy openness variables. This implies that a wider buffer should be left if the other side has been logged recently, or there is a risk that it will be logged before the currently logged area has reached high enough growing stock for resisting edge effects (in Finnish conditions we expect this to happen in about three decades). Finally, additional variables such as topography, hydrology or the sensitivity of the species communities, should be considered wherever possible to modify buffer width case-by-case. For example, streambanks with groundwater discharge or frequent flooding may be especially sensitive and may require wider buffers (Kuglerová et al., 2014). If the retained buffer is too narrow to retain the microclimate and specific biodiversity values in the particular streamside, it is not cost-efficient at all, because it incurs economic costs but the most sensitive species are lost anyway.

4.2. Impact of buffer width, selective logging and aspect on microclimate

Buffer width exerted a much stronger impact on relative air humidity and temperature than did selective logging within the buffer. This is not surprising as the two buffer strip treatments (15 or 30 m) differed by 50% tree removal, while selective logging removed 30% of tree basal area. The buffer width causes so much microclimatic changes that additional changes caused by selective logging are smaller. However, the selectively logged sites differed more from controls than those that were not selectively logged (see Fig. 2). Thus, although buffer width seems to be the most important factor determining microclimatic conditions, selective logging does exert some additional changes. This is most likely due to canopy gaps resulting in increased solar radiation and increased air temperature (Gray et al., 2002). In upland forests, forest density is the main driver of summer temperature minima and maxima (Greiser et al., 2018), and selective logging results in clear microclimatic changes (Zheng et al., 2000). In addition, microclimatic edge effects reach deeper into the forest when the forest is more open (Heithecker and Halpern, 2007; Schmidt et al., 2017). On the other

hand, selective logging within the riparian buffer results in increased regeneration of tree saplings and shrubs (Mallik et al., 2014; Zenner et al., 2012), which may provide microclimatic protection (Kovács et al., 2017). As our sites had been logged 12 years before the measurements, the shrubs and saplings can be already quite large, which may explain why the impact of selective logging seems to be relatively small. In our study, the trees were removed evenly from the whole width of the buffer strip, but the microclimate might be better protected by uneven logging where more trees are removed closer to the clear-cut edge.

Southern or southwestern aspect of the clear-cut increased the impacts of the logging actions on relative air humidity, and southern aspect also caused a small impact on air temperature. These results are mostly in accordance with earlier results on the effects of aspect in upland forest edges (Chen et al., 1995; Heithecker and Halpern, 2007; Moore et al., 2005). However, buffer width and logging on the opposite side did cause larger impacts than aspect, especially on temperature. Therefore, we recommend leaving buffer strips of > 30 m on all aspects, but protecting air humidity requires even wider buffers if the clear-cut will be towards south or southwest.

4.3. Microclimatic refugia on northern side of trees

We did not find evidence that the northern side of spruce trunks could provide small-scale microclimatic refugia. Both humidity and temperature variables were affected by the logging treatments on both the northern and southern sides of the trees. For the humidity variables, the northern side of the trees did not provide any protection compared to the southern sides. Thus, for species that are sensitive to changes in air humidity, there are no refugia on northern sides of trees in riparian forests. For the temperature variables, the treatments caused larger differences on the southern sides of trees than on northern sides of trees. This is most likely due to more sunlight on the southern side, which heats up the tree bark as well as the data logger, and respectively the organisms on it. Therefore, for those species that suffer from logging-induced increases in radiation or temperature, there is a higher chance of survival on the northern sides of trees. However, on the northern sides of the trees there were still differences in temperature between control sites and treatment sites, which weakens the refugia.

Schmalholz and Hylander (2011) found that the northern sides of boulders and stumps provided refugia for forest floor bryophytes on clear-cuts, where the microclimate changes more drastically than in riparian buffers. It may be that the base of large boulders or large stumps provide more constant microclimatic conditions also in riparian buffers. In addition, organisms that grow on the forest floor, especially in concave depressions, are better protected than those on convex substrates such as tree bases (Hylander et al., 2005).

4.4. Impact of physical conditions on mosses

The relative change in the cover of the three model moss species was affected by each of the physical factors: mean relative humidity, mean temperature and canopy openness. Thus, the logging-induced changes in the microclimatic conditions do result in changes in sensitive species communities, which is in accordance with earlier studies from riparian buffer strips of various widths (Elliott and Vose, 2016; Hylander et al., 2005; Oldén et al., 2019). The most significant of the three variables was air humidity, which had a significant impact on the relative change of each of the three moss species. This shows that changes in humidity must be avoided to prevent changes in moss communities.

The relative change in the cover of the forest floor moss *Hylocomium splendens* was affected by humidity: the cover of the species had increased in sites with high humidity and decreased or stayed at the same level in sites with low humidity. Earlier studies have shown that the growth of *H. splendens* decreases due to microclimatic edge effects, in both riparian buffers (Stewart and Mallik, 2006) and in retained upland

forest patches (Caners et al., 2013; Hylander, 2005). Water is the major limiting factor for the growth of *H. splendens*, because it does not have an internal water conducting system and under dry conditions it dries out quickly (Callaghan et al., 1978). Busby et al. (1978) showed that the growth of *H. splendens* was affected positively by precipitation frequency and negatively by evaporation stress. Light and temperature were not significant factors in controlling growth rates (Busby et al., 1978), which is in accordance with our results of no significant impacts of temperature or canopy openness on the change in the species cover. Callaghan et al. (1978) showed that the photosynthesis of *H. splendens* is positively affected by higher temperatures, but in high temperature respiration exceeds gross photosynthesis, and therefore the growth of the species is favored by low temperature.

Similarly to *H. splendens*, the relative change in the cover of *Pseudobryum cinclidioides* was also positively affected by mean air humidity. This exemplifies that even the riparian species that grow on the inundated soil right next to the stream may suffer from changed air humidity due to logging 15–30 m away from the stream. The decline in the abundance of *P. cinclidioides* in retention patches has been recorded also by Perhans et al. (2009). The large leaves of the species may be efficient in photosynthesizing in moist and humid conditions, but they are likely to dry out if air humidity decreases, and even high soil moisture may not be able to buffer against this. Therefore, *P. cinclidioides* could be used as an indicator species when studying microclimatic changes in riparian communities. However, in our study sites the species often had low cover, and therefore even small changes in cover results in large changes in relative cover, causing much variation in the data. *P. cinclidioides* typically grows beside the stream in the zone that is inundated for a short period during spring and then is waterlogged during the rest of the growing season (Darell and Cronberg, 2011). For this reason, a better study setup for this species would have more study plots right next to the stream.

Polytrichum commune showed an opposite response to increasing changes in microclimate: the relative cover increased in sites with low humidity, high temperature and high canopy openness. *P. commune* has an underground stem system, internal water conducting tissues and complex leaves that are able to resist water loss, which enables the species to photosynthesize in dry conditions (Bayfield, 1973). Instead of water availability, the growth of *P. commune* is limited by light availability, and for this reason it grows fast in habitats where there is little shadow from other vegetation (Callaghan et al., 1978). In addition, *P. commune* spreads efficiently to bare soil patches via both sexual reproduction and vegetative reproduction from underground stems (Callaghan et al., 1978). Thus, the death of other mosses due to damage from logging machinery or microclimatic stress creates suitable habitats for this opportunistic moss.

We do not have pre-logging microclimatic data from the sites and therefore it is not possible to analyze the effects of the treatments on changes that have happened in microclimate from pre-logging to post-logging. The fact that the moss changes from pre-logging to post-logging correlate well with the post-logging microclimatic data implies that there have indeed been logging-induced changes in the buffer strip sites. Also, the results show that the microclimatic conditions, which were measured in only one point at the height of 0.5 m, caused changes in mosses that respond to the conditions in their immediate surroundings at the ground-level. This indicates that moist soil conditions or field layer vegetation were not enough to protect the ground-dwelling mosses against the larger microclimatic changes within the site. On the other hand, only 15-meter buffers trips resulted in significant changes in the relative covers of the mosses, while the impacts were more varied for sites with 30-meter buffers trips (see Appendix A). More comprehensive studies with more sites, more plots and more species are needed to confirm the minimum buffer width that is adequate to conserve mosses.

5. Conclusions

We compared the microclimatic conditions in four different buffer strip treatments and unlogged controls, and found that all the treatments affected some or all of the microclimate variables. The conditions in 15-meter buffer strips (with or without selective logging) or in 30-meter buffer strips with selective logging were so different from controls that they clearly do not meet the requirements for no change in microclimate set by the Finnish Forest Act (Forest Act, 2013).

The 30-meter buffer strips without selective logging differed only little from controls, but they did have significantly lower mean air humidity. The differences in mean air humidity between all of the sites correlated with the responses of the three indicator moss species, suggesting that the changes in this microclimatic component has biological impacts. In addition, we found no evidence of the possibility of the northern side of large trees (or other similar objects) to provide microclimatic refugia for species that are sensitive to changes in air humidity, although species sensitive to high radiation and temperature might survive better on the northern side of the trees.

We conclude that to preserve riparian microclimatic conditions and species dependent on those, buffer strips between the stream and the clear-cut should exceed 30 m. We do not recommend evenly distributed selective logging (of about 30% basal area) even within wide buffer strips. Extra wide buffer strips should be considered if the aspect of the clear-cut is towards south or southwest, or if the two sides of a stream are logged at the same time or during subsequent years. It is preferable to avoid logging both sides during subsequent decades.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

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Appendix A for “The effect of buffer strip width and selective logging on riparian forest microclimate”

Authors: Anna Oldén, Maiju Peura, Sonja Saine, Janne S. Kotiaho & Panu Halme

The effects of the buffer strip treatments on the three indicator mosses

Methods

We built one MANOVA to test how the buffer strip treatments and logging on the opposite side of the stream impact the relative changes in the cover of the three indicator mosses. The response variables were the relative change of *H. splendens*, relative change of *P. cinclidioides* and relative change of *P. commune*. The explanatory variables were the treatment (each of the four buffer strip treatments compared to controls) and logging on the opposite side of the stream (yes or no).

Second, we used another MANOVA to test how the changes in the covers of the three indicator mosses were affected by buffer width (15 or 30), selective logging (yes or no) and logging on the opposite side of the stream (yes or no). Control sites were excluded from this analysis. We also tested for the effect of the interaction buffer width * selective logging, but it did not have significant impacts and was excluded from the reported models.

Results

In the global MANOVA model that combines the responses of the three moss species, treatments had an impact on the relative changes, but logging on the opposite side did not (Table 1).

Table 1. Results from the MANOVA on the impact of treatments (unlogged control vs. buffer strip treatments) and logging on the opposite side on the relative changes in the cover of *H. splendens*, *P. cinclidioides* and *P. commune*. Pillai test statistic, approximate F-statistic, hypothesis and error degrees of freedom, and p-value.

Explanatory	Pillai	F	Hypoth. df	Error df	p
Treatment logging	0.62	1.9	12	87	0.048
Opposite logging	0.16	1.8	3	27	0.175

The treatments impacted the three mosses differently. For the relative change of *H. splendens*, the treatments had a negative impact in relation to the controls, but only the 15-meter buffer strips with selective logging differed significantly (Figure 1 A). The relative change of *P. cinclidioides* was more varied and none of the treatments differed significantly from controls (Figure 1 B). The relative change of *P. commune* was more positive in the 15-meter buffer strips with selective logging (significantly) and in the 15-meter buffer strips without selective logging (nearly significantly) (Figure 1 C). Logging on the opposite side of the stream did not impact any of the species significantly, but it did have a nearly significant negative impact on *P. cinclidioides*.

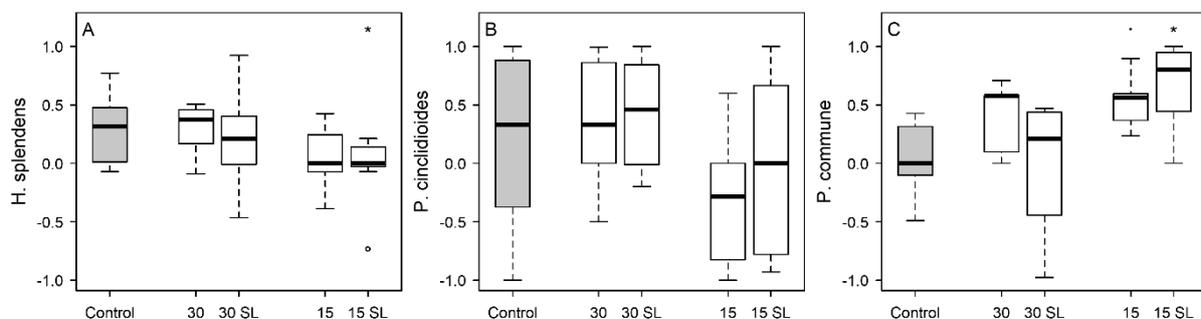


Figure 2. The relative changes of the indicator moss species in sites of the five treatments. The asterisks indicate the statistical difference between unlogged control sites and the sites with buffer strips (30-

meter without or with selective logging [SL] and 15-meter without or with selective logging): * $p < 0.05$, . $0.05 < p < 0.1$. A) *Hylocomium splendens*, B) *Pseudobryum cinclidioides*, and C) *Polytrichum commune*.

In the global MANOVA model on the impacts of buffer width, selective logging and logging on the opposite side of the stream, only buffer width showed a significant impact on the responses of the three mosses (Table 2). Selective logging did not have an impact, and logging on the opposite side had a nearly significant impact (Table 2).

Table 2. Results from the MANOVA on the impacts of buffer width, selective logging and logging on the opposite side of the stream on the relative changes in the cover of *H. splendens*, *P. cinclidioides* and *P. commune*. Pillai test statistic, approximate F-statistic, hypothesis and error degrees of freedom, and p-value.

Explanatory	Pillai	F	Hypoth. df	Error df	p
Buffer width	0.49	6.7	3	21	0.002
Selective logging	0.03	0.2	3	21	0.886
Opposite logging	0.27	2.6	3	21	0.082

Again, the three species differed in their responses (Table 3). *H. splendens* showed a nearly significant positive response to the wider buffer width of 30 meters. *P. cinclidioides* responded positively to wider buffer width and negatively to logging on the opposite side of the stream. *P. commune* responded negatively to the wider buffer width. Selective logging did not have significant impacts on any of the species (Table 3).

Table 3. Results from the three linear models on the impacts of buffer width, selective logging and logging on the opposite side of the stream on the relative changes in the cover of *H. splendens*, *P. cinclidioides* and *P. commune*. Estimates, standard error, t-value and p-value.

Response	Explanatory	Estimate	SE	t	p
<i>H. splendens</i>	Buffer width	0.25	0.12	2.07	0.050
	Selective logging	-0.04	0.13	-0.35	0.728
	Opposite logging	0.16	0.12	1.32	0.199
<i>P. cinclidioides</i>	Buffer width	0.49	0.22	2.26	0.033
	Selective logging	0.07	0.23	0.33	0.748
	Opposite logging	-0.58	0.22	-2.64	0.015
<i>P. commune</i>	Buffer width	-0.47	0.17	-2.72	0.012
	Selective logging	-0.14	0.18	-0.79	0.440
	Opposite logging	-0.05	0.18	-0.30	0.766

Discussion

The changes that had occurred from the pre-logging to 12 years post-logging in the cover of the three moss species were affected mostly in the 15-meter buffer strips, and especially in those with selective logging. The 30-meter buffer strips seem sufficient to maintain the cover of these species near the stream, and selective logging within them did not cause changes in the moss covers. However, it is worth noting that closer to the clear-cut there is likely to be changes, and other species may respond more strongly. For a more comprehensive understanding of the impacts of each treatment on mosses, a dataset with more species, more plots, and more sites per treatment would be needed. The changes in individual species can be large due to random variables that are not related to the treatments, especially for rare species with low cover. This can be seen in the relative changes of *P. cinclidioides* that tended to have very low cover, and thus large relative changes have happened in sites of each kind of treatment.

Logging on the opposite side of the stream had only weak effects, mostly on *P. cinclidioides* that grows in the immediate vicinity of the stream, and thus is more exposed to changes on the other side of the stream.

The treatments had stronger impacts on the microclimatic variables than on the three moss species. This is expected as the treatments impact the microclimate directly, and the mosses only indirectly via the microclimate. The post-logging microclimatic variables reflect the combined effects of the original tree composition, topography, soil moisture and the impacts of the treatment, possible logging on the other side of the stream and possible windthrows. Thus, a continuous microclimatic variable summarizes the conditions for the mosses, and for this reason it has a stronger impact on the moss covers than that of the two class variables, i.e. the treatment and logging on the opposite side.



III

THE EFFECT OF BUFFER STRIP WIDTH AND SELECTIVE LOGGING ON STREAMSIDE POLYPORE COMMUNITIES

by

Maiju Peura, Anna Oldén, Merja Elo, Janne Kotiaho, Mikko Mönkkönen
& Panu Halme 2020

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IV

COST-EFFECTIVE BIODIVERSITY PROTECTION THROUGH MULTIUSE-CONSERVATION LANDSCAPES

by

Maiju Peura, Kyle Eyvindson, Mikko Mönkkönen, Daniel Burgas, Kaisa Raatikainen
& Janne Kotiaho 2020

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