Author(s): Peura, Maiju; Burgas Riera, Daniel; Eyvindson, Kyle; Repo, Anna; Mönkkönen, Mikko

Title: Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia

Year: 2017

Version:

Please cite the original version:

Peura, M., Burgas Riera, D., Eyvindson, K., Repo, A., & Mönkkönen, M. (2017). Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia. Biological Conservation, 217, 104-112. https://doi.org/10.1016/j.biocon.2017.10.018

Title: Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia

Authors: Maiju Peura[*a], Daniel Burgas[a,b], Kyle Eyvindson[a], Anna Repo[a,c], Mikko Mönkkönen[a]

Affiliations:

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

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

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

* Corresponding author

E-mail addresses: maiju.peura@jyu.fi, daniel.burgasriera@helsinki.fi, kyle.eyvindson@jyu.fi, anna.m.repo@jyu.fi, mikko.monkkonen@jyu.fi

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 forest. 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.

Key words: biodiversity, ecosystem service, even-age, set aside, sustainability, uneven-age

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 (O'Hara, 2002; Kuuluvainen et al., 2012; 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 group of trees, are removed from the forest usually every 15-20 years (Pommerening & Murphy 2004; Laiho, Lähde & Pukkala 2011; Kuuluvainen, Tahvonen & Aakala 2012). 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 hectares. 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 more than 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: Figure 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; Figure 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: Figure 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; Figure 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; Figure 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).

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 (Peltola 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, 2016, 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 myrtillys*) 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 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

$$SMF_i = \frac{obsSMF_i - minSMF_i}{maxSMF_i - minSMF_i},$$

where SMF_i 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* indicates the observed value of a single biodiversity or ecosystem service measure in a stand, *minSMF* and *maxSMF* 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 (Figure 1a,2a; Appendix S2: Table S1,S2). Carbon storage was moderately higher and sequestration remarkably higher in landscapes consistently managed using CCF in comparison with RFM (Figure 1a; Appendix S2: Figure S1). In terms of the regulating services, CCF outperformed RFM in approximately 75% of the stands (Figure 1b). Bilberry yields and scenic beauty were higher with CCF (Figure 1a) and CCF outperformed RFM in 70–90% of the stands (Figure 1b). In contrast, cowberry and marketed mushroom yields were higher in RFM (Figure 1a) and it outperformed CCF in approximately 90% of the stands (Figure 1b).

RFM provided more harvested timber (Figure 2a; Appendix S2: Table S1) outperforming CCF in 60% of the stands (Figure 2b). There were differences in the shares of sawlogs and pulpwood between CCF and RFM (Appendix S2: Figure 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 (Figure 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% (Figure 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 S2, Figure S3c).

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

SA forests provided higher values than CCF, RFM or their combination particularly for the climate regulating services but also for scenic beauty (Figure 1). Managed forests tended to provide a higher delivery of collectable goods 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 (Figure 3a; Appendix S2: Table S3). For three biodiversity indicators (Lesser spotted woodpecker, Long-tailed tit and number of large diameter trees) CCF outperformed RFM in almost 100% of stands (Figure 3b) and the difference in favour of CCF was remarkably large (Figure 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 (Figure 3a) providing higher habitat suitability index in between 50% to 97% of the stands (Figure 3b).

In five cases, a combination of CCF and RFM provided higher scores than either of them separately (Figure 3a). 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 (Figure 3b) yielded 55% larger HSI value than consistent application of CCF and 30% larger than consistent application of RFM (Figure 3a). For the Hazel grouse, the combination (Figure 3b) yielded 65% larger HSI value than consistent application of RFM and 20% larger than consistent application of CCF (Figure 3a).

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

The frequency of unsuitable habitats varied among species (Figure 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 Long-tailed tit 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 (Figure 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 RMF 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 sequestrate 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 RMF 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, Lähde & Pukkala 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 provided 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 m^3 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 multi-functionality 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, Pukkala & Kurttila 2016; Tahvonen & 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 60-90 $m^3\ ha^{-1}$ (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.

ACKNOWLEDGEMENTS

We are grateful to Jenny and Antti Wihuri (to M.P.) and Kone foundations (project #46-10588 to M.M.) as well as the Academy of Finland (project #275329 to M.M.) for funding. We thank T. Heinonen for help in putting together the forest simulator.

REFERENCES

Andreassen, K., Øyen, B.H., 2002. Economic consequences of three silvicultural methods in unevenaged mature coastal spruce forests of central Norway. Forestry 75, 483–488. doi:10.1093/forestry/75.4.483

Atlegrim, O., Sjöberg, K., 2004. Selective felling as a potential tool for maintaining biodiversity in managed forests. Biodivers. Conserv. 13, 1123–1133. doi:10.1023/B:BIOC.0000018148.84640.fd

Atlegrim, O., Sjöberg, K., 1996. Effects of clear-cutting and single-tree selection harvests on herbivorous insect larvae feeding on bilberry (*Vaccinium myrtillus*) in uneven-aged boreal Picea abies forests. For. Ecol. Manage. 87, 139–148. doi:10.1016/S0378-1127(96)03830-3

Boncina, A., 2011. History, current status and future prospects of uneven-aged forest management in the Dinaric region: an overview. Forestry 84, 467–478. doi:10.1093/forestry/cpr023

Bradshaw, C.J.A., Warkentin, I.G., 2015. Global estimates of boreal forest carbon stocks and flux. Glob. Planet. Change 128, 24–30. doi:10.1016/j.gloplacha.2015.02.004

Bradshaw, C.J.A., Warkentin, I.G., Sodhi, N.S., 2009. Urgent preservation of boreal carbon stocks and biodiversity. Trends Ecol. Evol. 24, 541–548. doi:10.1016/j.tree.2009.03.019

Brazee, R.J., 2003. The Volvo Theorem: From myth to behavior model, in: Helles, F., Strange, N., Wichmann, L. (Eds.), Recent Accomplishments in Applied Forest Economics Research. Springer Netherlands, Dordrecht, pp. 39–48. doi:10.1007/978-94-017-0279-9_3

Burton, P.J., Bergeron, Y., Bogdanski, B.E.C., Juday, G.P., Kuuluvainen, T., McAfee, B.J., Ogden, A., Teplyakov, V.K., Alfaro, R.I., Francis, D.A., Gauthier, S., Hantula, J., 2010. Sustainability of boreal forests and forestry in a changing environment. For. Soc. responding to Glob. drivers Chang. 247–282.

Calladine, J., Bray, J., Broome, A., Fuller, R.J., 2015. Comparison of breeding bird assemblages in conifer plantations managed by continuous cover forestry and clearfelling. For. Ecol. Manage. 344, 20–29. doi:10.1016/j.foreco.2015.02.017

Couture, S., Cros, M.-J., Sabbadin, R., 2016. Risk aversion and optimal management of an uneven-aged forest under risk of windthrow: A Markov decision process approach. J. For. Econ. 25, 94–114. doi:10.1016/j.jfe.2016.08.002

Diaci, J., Kerr, G., O’hara, K., 2011. Twenty-first century forestry: integrating ecologically based, uneven-aged silviculture with increased demands on forests. Forestry 84, 463–465. doi:10.1093/forestry/cpr053

Felton, A., Gustafsson, L., Roberge, J.M., Ranius, T., Hjältén, J., Rudolphi, J., Lindbladh, M., Weslien, J., Rist, L., Brunet, J., Felton, A.M., 2016. How climate change adaptation and mitigation strategies can threaten or enhance the biodiversity of production forests: Insights from Sweden. Biol. Conserv. 194, 11–20. doi:10.1016/j.biocon.2015.11.030

Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. Ecol. Indic. 57, 420–434. doi:10.1016/j.ecolind.2015.05.028

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. Science (80-.). 349, 819–822. doi:10.1126/science.aaa9092

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lohmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: A world perspective. Bioscience 62, 633–645. doi:DOI 10.1525/bio.2012.62.7.6

Haines-Young, R., Potschin, M., 2011. Common international classification of ecosystemservices (CICES): 2011 Update. Expert Meet. Ecosyst. Accounts … 1–17.

Hanewinkel, M., Kuhn, T., Bugmann, H., Lanz, A., Brang, P., 2014. Vulnerability of uneven-aged forests to storm damage. Forestry 87, 525–534. doi:10.1093/forestry/cpu008

Hanski, I., 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio 40, 248–55.

Hanski, I., 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87, 209–219.

Hara, K.L.O., 2002. The historical development of uneven-aged silviculture in North America 75.

Holopainen, M., Talvitie, M., 2006. Effect of data acquisition accuracy on timing of stand harvests and expected net present value. Silva Fenn. 40, 531–543. doi:10.14214/sf.335

Hynynen, J., Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H., Haapala, P., 2002. Models for predicting stand development in MELA System. Research Paper 835. Finnish Forest Research Institute, 116 pp.

Jalonen, J., Vanha-Majamaa, I., 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. For. Ecol. Manage. 146, 25–34. doi:10.1016/S0378-1127(00)00446-1

Junninen, K., Komonen, A., 2011. Conservation ecology of boreal polypores: A review. Biol. Conserv. 144, 11–20. doi:10.1016/j.biocon.2010.07.010

Klapwijk, M.J., Bylund, H., Schroeder, M., Björkman, C., 2016. Forest management and natural biocontrol of insect pests. Forestry 89, 253–262. doi:10.1093/forestry/cpw019

Kurttila, M., Pykäläinen, J., Hujala, T., 2013. Metsätieteen aikakauskirja Optimoinnin käyttö yksityismetsien tilatason metsäsuunnittelussa 61–70.

Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fenn. 36, 97–125. doi:10.1579/08-A-490.1

Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-Aged and Uneven-Aged Forest Management in Boreal Fennoscandia: A Review. Ambio 41, 720–737. doi:10.1007/s13280-012-0289-y

Laiho, O., L??hde, E., Pukkala, T., 2011. Uneven-vs even-aged management in Finnish boreal forests. Forestry 84, 547–556. doi:10.1093/forestry/cpr032

Laudon, H., Sponseller, R.A., Lucas, R.W., Futter, M.N., Egnell, G., Bishop, K., Ågren, A., Ring, E., Högberg, P., 2011. Consequences of more intensive forestry for the sustainable management of forest soils and waters. Forests 2, 243–260. doi:10.3390/f2010243

Liski, J., Palosuo, T., Peltoniemi, M., Sievänen, R., 2005. Carbon and decomposition model Yasso for forest soils. Ecol. Modell. 189, 168–182. doi:10.1016/j.ecolmodel.2005.03.005

Liski, J., Pussinen, A., Pingoud, K., Mäkipää, R., Karjalainen, T., 2001. Which rotation length is favourable to carbon sequestration? Can. J. For. Res.-Rev. Can. Rech. For. 31, 2004–2013.

Lundmark, T., Bergh, J., Nordin, A., Fahlvik, N., Poudel, B.C., 2016. Comparison of carbon balances between continuous-cover and clear-cut forestry in Sweden. Ambio 45, 203–213. doi:10.1007/s13280-015-0756-3

Lundqvist, L., Chrimes, D., Elfving, B., Mörling, T., Valinger, E., 2007. Stand development after different thinnings in two uneven-aged Picea abies forests in Sweden. For. Ecol. Manage. 238, 141–146. doi:10.1016/j.foreco.2006.10.006

Maltamo, M., Korhonen, K.T., Packal??n, P., Meht??talo, L., Suvanto, A., 2007. Testing the usability of truncated angle count sample plots as ground truth in airborne laser scanning-based forest inventories. Forestry 80, 73–81. doi:10.1093/forestry/cpl045

Mastrangelo, M.E., Weyland, F., Villarino, S.H., Barral, M.P., Nahuelhual, L., Laterra, P., 2014. Concepts and methods for landscape multifunctionality and a unifying framework based on ecosystem services. Landsc. Ecol. 29, 345–358. doi:10.1007/s10980-013-9959-9

Matveinen-Huju, K., Koivula, M., 2008. Effects of alternative harvesting methods on boreal forest spider assemblages. Can. J. For. Res. 38, 782–794. doi:10.1139/X07-169

Miina, J., Hotanen, J.P., Salo, K., 2009. Modelling the abundance and temporal variation in the production of bilberry (*Vaccinium myrtillus* L.) in Finnish mineral soil forests. Silva Fenn. 43, 577–593. doi:10.14214/sf.181

Miina, J., Pukkala, T., Kurttila, M., 2016. Optimal multi-product management of stands producing timber and wild berries. Eur. J. For. Res. 1–14. doi:10.1007/s10342-016-0972-9

Mönkkönen, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Salminen, H., Tikkanen, O.P., 2014. Spatially dynamic forest management to sustain biodiversity and economic returns. J. Environ. Manage. 134, 80–89. doi:10.1016/j.jenvman.2013.12.021

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G., Ranius, T., 2002. Densities of large living and dead trees in old growth temperate and boreal forests. For. Ecol. Manage. 161, 189–204.

O’Hara, K.L., Nagel, L.M., 2006. A functional comparison of productivity in even-aged and multiaged stands: A synthesis for *Pinus ponderosa*. For. Sci. 52, 290–303.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world’s forests. Science 333, 988–93. doi:10.1126/science.1201609

Peltola, A. (Ed.), 2014. Finnish Statistical Yearbook of Forestry. Finnish Forest Research Institute.

Peura, M., Triviño, M., Mazziotta, A., Podkopaev, D., Juutinen, A., Mönkkönen, M., 2016. Managing boreal forests for the simultaneous production of collectable goods and timber revenues. Silva Fenn. 50. doi:10.14214/sf.1672

Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77, 27–44. doi:10.1093/forestry/77.1.27

Puettmann, K.J., Wilson, S.M., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G., Harvey, B.D., Knoke, T., Lu, Y., Nocentini, S., Putz, F.E., Yoshida, T., Bauhus, J., 2015. Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? For. Ecosyst. 2, 1–16. doi:10.1186/s40663-015-0031-x

Pukkala, T., 2016a. Which type of forest management provides most ecosystem services? For. Ecosyst. 3, 9. doi:10.1186/s40663-016-0068-5

Pukkala, T., 2016b. Does management improve the carbon balance of forestry? Forestry 1–11. doi:10.1093/forestry/cpw043

Pukkala, T., 2014. Does biofuel harvesting and continuous cover management increase carbon sequestration? For. Policy Econ. 43, 41–50. doi:10.1016/j.forpol.2014.03.004

Pukkala, T., 2005. Metsikön tuottoarvon ennustemallit kivennäismaan männiköille, kuusikoille ja rauduskoivikoille. Metsätieteen Aikakausk. 3/2005, 311–322.

Pukkala, T., Kellomäki, S., Mustonen, E., 1988. Prediction of the amenity of a tree stand. Scand. J. For.

Res. 3, 533–544.
Pukkala, T., Laiho, O., Lähde, E., 2016. Continuous cover management reduces wind damage. For. Ecol. Manage. 372, 120–127. doi:10.1016/j.foreco.2016.04.014
Pukkala, T., Lähde, E., Laiho, O., 2013. Species interactions in the dynamics of even- and uneven-aged Boreal Forests. J. Sustain. For. 32, 371–403. doi:10.1080/10549811.2013.770766
Pukkala, T., Lähde, E., Laiho, O., Salo, K., Hotanen, J.-P., 2011. A multifunctional comparison of even-aged and uneven-aged forest management in a boreal region. Can. J. For. Res. 41, 851–862. doi:10.1139/x11-009
Pukkala, T., Sulkava, R., Jaakkola, L., Lähde, E., 2012. Relationships between economic profitability and habitat quality of Siberian jay in uneven-aged Norway spruce forest. For. Ecol. Manage. 276, 224–230. doi:10.1016/j.foreco.2012.04.006
Ranius, T., Eliasson, P., Johansson, P., 2008. Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. Biodivers. Conserv. 17, 2371–2381. doi:10.1007/s10531-008-9387-3
Rasinmäki, J., Mäkinen, A., Kalliovirta, J., 2009. SIMO: An adaptable simulation framework for multiscale forest resource data. Comput. Electron. Agric. 66, 76–84. doi:10.1016/j.compag.2008.12.007
Rassi, P., Hyvärinen, E., Juslén, A., Mannerkoski, I., 2010. The 2010 red list of Finnish species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki 685.
Redon, M., Luque, S., Gosselin, F., Cordonnier, T., 2014. Is generalisation of uneven-aged management in mountain forests the key to improve biodiversity conservation within forest landscape mosaics? Ann. For. Sci. 71, 751–760. doi:10.1007/s13595-014-0371-7
Shanin, V., Valkonen, S., Grabarnik, P., Mäkipää, R., 2016. Using forest ecosystem simulation model EFIMOD in planning uneven-aged forest management. For. Ecol. Manage. 378, 193–205. doi:10.1016/j.foreco.2016.07.041
Sharma, A., Bohn, K., Jose, S., Dwivedi, P., 2016. Even-aged vs. uneven-aged silviculture: implications

for multifunctional management of southern pine ecosystems. Forests 7, 86. doi:10.3390/f7040086

Siira-Pietikäinen, A., Haimi, J., 2009. Changes in soil fauna 10 years after forest harvestings: Comparison between clear felling and green-tree retention methods. For. Ecol. Manage. 258, 332–338. doi:10.1016/j.foreco.2009.04.024

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Tahvanainen, V., Miina, J., Kurttila, M., Salo, K., 2016. Modelling the yields of marketed mushrooms in Picea abies stands in eastern Finland. For. Ecol. Manage. 362, 79–88. doi:10.1016/j.foreco.2015.11.040

Tahvonen, O., 2016. Economics of rotation and thinning revisited: The optimality of clearcuts versus continuous cover forestry. For. Policy Econ. 62, 88–94. doi:10.1016/j.forpol.2015.08.013

Tahvonen, O., Pukkala, T., Laiho, O., Lähde, E., Niinimäki, S., 2010. Optimal management of uneven-aged Norway spruce stands. For. Ecol. Manage. 260, 106–115. doi:10.1016/j.foreco.2010.04.006

Tahvonen, O., Rämö, J., 2016. Optimality of continuous cover vs . clearcut regimes in managing forest resources. Can. J. For. Res. 901, 1–26. doi:10.1139/cjfr-2015-0474

Triviño, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Mönkkönen, M., 2015. Managing a boreal forest landscape for providing timber, storing and sequestering carbon. Ecosyst. Serv. 14, 179–189. doi:10.1016/j.ecoser.2015.02.003

Triviño, M., Pohjanmies, T., Mazziotta, A., Juutinen, A., Podkopaev, D., Le Tortorec, E., Mönkkönen, M., 2016. Optimizing management to enhance multifunctionality in a boreal forest landscape. J. Appl. Ecol. 54, 61–70. doi:10.1111/1365-2664.12790

Tuomi, M., Laiho, R., Repo, A., Liski, J., 2011. Wood decomposition model for boreal forests. Ecol. Modell. 222, 709–718. doi:10.1016/j.ecolmodel.2010.10.025

Tuomi, M., Thum, T., Järvinen, H., Fronzek, S., Berg, B., Harmon, M., Trofymow, J.A., Sevanto, S., Liski, J., 2009. Leaf litter decomposition-Estimates of global variability based on Yasso07 model. Ecol. Modell. 220, 3362–3371. doi:10.1016/j.ecolmodel.2009.05.016

Turtiainen, M., Miina, J., Salo, K., Hotanen, J.P., 2013. Empirical prediction models for the coverage and yields of cowberry in Finland. Silva Fenn. 47, 3. doi:10.14214/sf.1005

Vaara, M., Saastamoinen, O., Turtiainen, M., 2013. Changes in wild berry picking in Finland between 1997 and 2011. Scand. J. For. Res. 28, 586–595. doi:10.1080/02827581.2013.786123

van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Hector, A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Berthold, F., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Coomes, D., Coppi, A., Bastias, C.C., Muhie Dawud, S., De Wandeler, H., Domisch, T., Finér, L., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Jucker, T., Koricheva, J., Milligan, H., Müller, S., Muys, B., Nguyen, D., Pollastrini, M., Raulund-Rasmussen, K., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Zielínski, D., Fischer, M., 2016. Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. Nat. Commun. 7, 11109. doi:10.1038/ncomms11109

Vanhanen, H., Jonsson, R., Gerasimov, Y., Krankina, O.N., Messier, C., 2012. Making boreal forests work for people and nature.. IUFRO's special project on world forests, society and environment. https://archive.today/o/OiEG/http://www.iufro.org/download/file/8354/133/wfse-pol-brief-boreal-forests_pdf/

Äijälä, O., Koistinen, A., Sved, J., Vanhatalo, K., Väisänen, P., 2014. Metsänhoidon suositukset. Metsätalouden kehittämiskeskus Tapion julkaisuja. [in Finnish]

Östlund, L., Zackrisson, O., Axelsson, a-L., 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Can. J. For. Res. 27, 1198–1206. doi:10.1139/x97-070

TABLES

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 (kgC ha^{-1}, average over 100 years)
Carbon sequestration	CSEQ	Change in carbon storage between consecutive time steps (kgC ha^{-1} $year^{-1}$)
Bilberry	BIL	Bilberry yield (kg ha^{-1} $year^{-1}$)
Cowberry	COW	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	DW	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)

FIGURES

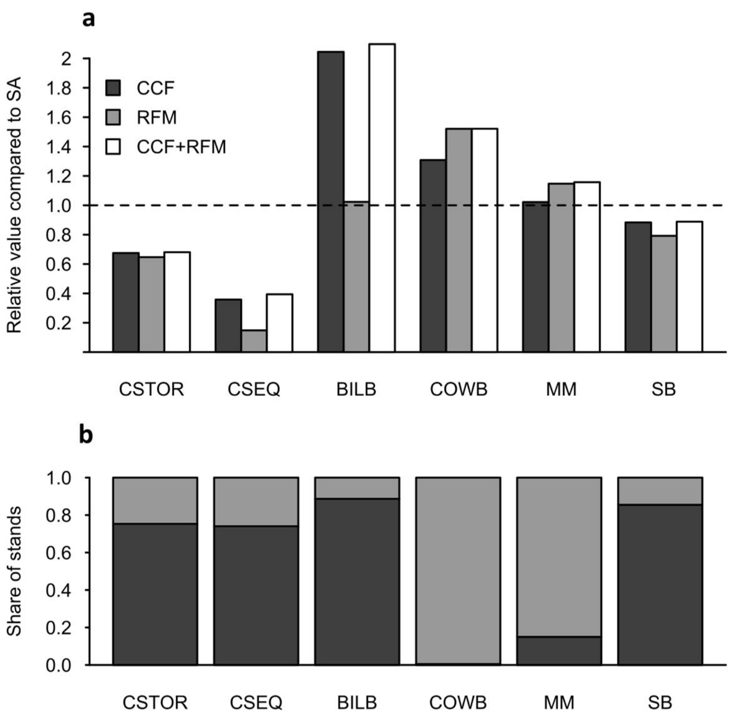

Figure 1 a) Relative ecosystem service values for carbon storage (CSTOR) and sequestration (CSEQ), bilberry (BILB), cowberry (COWB), marketed mushrooms (MM), and scenic beauty (SB) under continuous cover forestry (CCF), rotation forest management (RFM), and their optimal combination (CCF+RFM) compared 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.

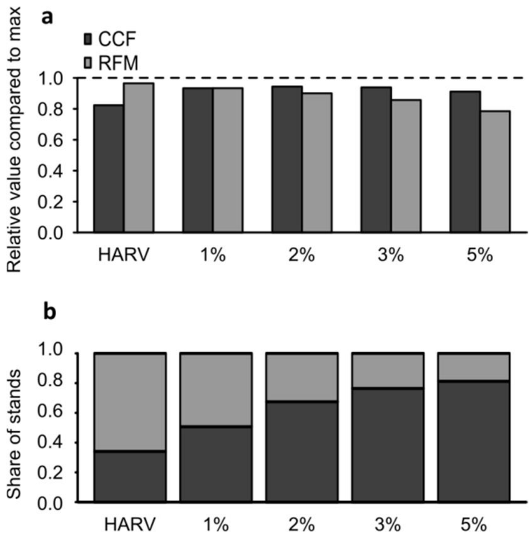

Figure 2 a) Relative harvested timber biomass (HARV) and revenues (NPV) with different discount rates (1-5%) in the study area under continuous cover forestry (CCF) and rotation forest management (RFM) compared to their optimal combination (CCF + RFM, the dashed line). Absolute values are given in Appendix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

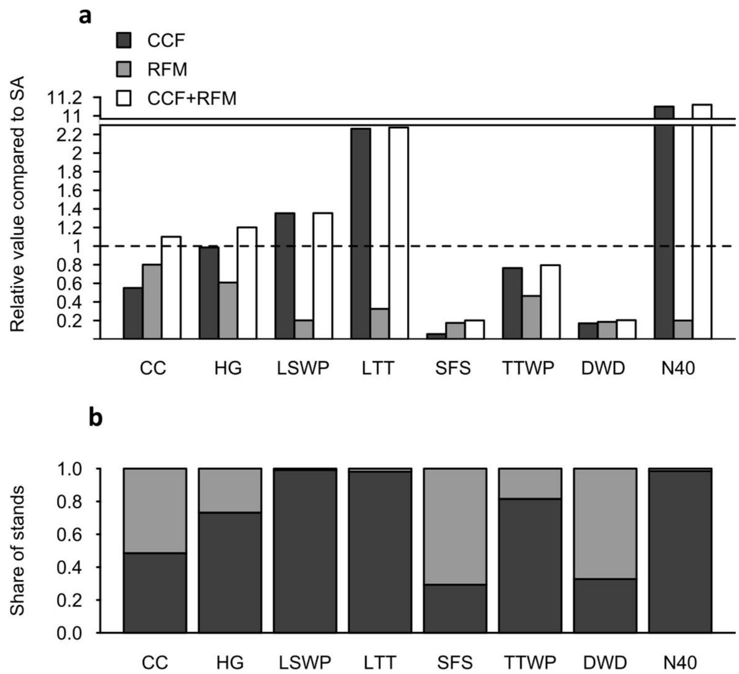

Figure 3 a) Relative biodiversity indicator values in the study area for Capercaillie (CC), Hazel grouse (HG), Lesser spotted woodpecker (LSWP), Long-tailed tit (LTT), Siberian flying squirrel (SFS), Three-toed woodpecker (TTWP), deadwood availability (DWD), and number of large diameter trees (N40) under 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 timber revenues in the study area.

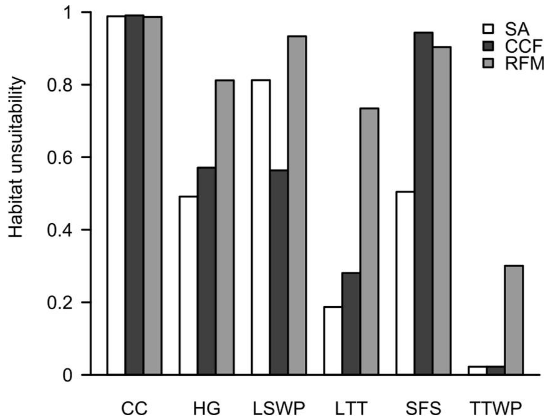

Figure 4 Relative frequency of cases when habitat suitability index was zero for the Capercaillie (CC), Hazel grouse (HG), Lesser spotted woodpecker (LSWP), Long-tailed tit (LTT), Siberian flying squirrel (SFS), and Three-toed woodpecker (TTWP), under set aside (SA), continuous cover forestry (CCF) and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

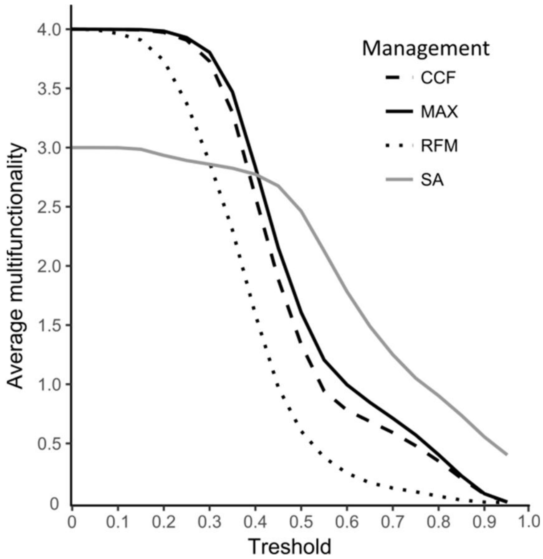

Figure 5 Average forest multifunctionality values for 100 years in the study area under different threshold values for continuous cover forestry (CCF), rotation forest management (RFM), their optimal combination (MAX), and set aside (SA).