

**This is an electronic reprint of the original article.
This reprint *may differ* from the original in pagination and typographic detail.**

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>

All material supplied via JYX is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the repository collections is not permitted, except that material may be duplicated by you for your research use or educational purposes in electronic or print form. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone who is not an authorised user.

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

3

4 **Authors:** Maiju Peura^{*a}, Daniel Burgas^{ab}, Kyle Eyvindson^a, Anna Repo^{ac}, Mikko Mönkkönen^a

5

6 **Affiliations:**

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

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

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

13 * Corresponding author

14

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

17

18 **Abstract:**

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

37

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

39 **1. INTRODUCTION**

40 Forests are crucial in delivering ecosystem services for human wellbeing. During the last decades many
41 forests in the boreal zone have been managed for intensive timber production applying conventional even-
42 aged rotation forest management (hereafter RFM) while largely disregarding management effects on
43 biodiversity and other forest ecosystem services (Burton et al., 2010; Gauthier et al., 2015; Vanhanen et
44 al., 2012). Solely focusing on timber production, RFM has resulted in a biodiversity decline in production
45 forests (Bradshaw et al., 2009; Siitonen, 2001; Östlund et al., 1997). Moreover, RFM can disturb nutrient
46 cycling, increase land erosion and decrease water quality (Laudon et al., 2011). The role of boreal forests
47 in climate regulation is well known as they contain about one third of the global terrestrial carbon stock
48 (Bradshaw and Warkentin, 2015; Pan et al., 2011). However, the common practice of RFM focusing
49 solely on timber production reduces carbon storage in boreal forests compared with optimal forest
50 management (Triviño et al., 2016). Focusing on timber production can also be in conflict with other
51 economically beneficial forest uses, such as recreation and harvest of non-timber forest products (e.g.,
52 berries and mushrooms) (Peura et al., 2016). Earlier research has shown that diversifying forest
53 management is a cost-efficient tool for enhancing ecosystem services (Miina et al., 2016; Triviño et al.,
54 2015) and biodiversity (Mönkkönen et al., 2014) in production forest landscapes. In addition, previous
55 studies indicate that alternative silvicultural practices are needed to ensure the delivery of multiple
56 benefits of forests (Puettmann et al. 2015, Felton et al. 2016).

57 Continuous cover forestry (henceforth CCF) has a long history throughout the world, however
58 has been widely replaced by RFM for decades (O'Hara, 2002; Kuuluvainen et al., 2012; Pommerening
59 and Murphy, 2004). Recently, CCF is returning as an important silvicultural alternative to RFM (Diaci et
60 al., 2011). In CCF, single trees, or small group of trees, are removed from the forest usually every 15-20
61 years (Pommerening & Murphy 2004; Laiho, Lähde & Pukkala 2011; Kuuluvainen, Tahvonen & Aakala
62 2012). Trees regenerate naturally, and the structure of forests is often uneven-aged. Such forest
63 management practice has been called 'near natural forestry' since it may mimic a natural forest state and
64 natural disturbances better than RFM (Kuuluvainen et al., 2012).

65 Previous research in boreal forests has shown that CCF is better than RFM from the perspective
66 of berry production, the amenity of forest landscape, carbon balances and resistance against wind
67 (Pukkala, 2016a; Pukkala et al., 2016, 2011). Moreover, CCF may be economically more profitable than
68 rotation forest management for forest owners (Pukkala, 2016a; Tahvonen, 2016; Tahvonen et al., 2010;
69 Tahvonen and Rämö, 2016). However, there are also contradictory results, regarding the economic
70 profitability (Andreassen and Øyen, 2002) as well as the effects on climate regulation (Lundmark et al.
71 2016) and resistance against disturbances (Hanewinkel et al., 2014). Consequently, the debate on the
72 usefulness of CCF is still ongoing (Diaci et al., 2011). Even though CCF may often outperform RFM at
73 the stand level, we do not know the relative performance of these management practices at a large
74 landscape scale nor do we know the potential benefits a combination of these practices may have for
75 ecosystem services and biodiversity across the landscape.

76 In general, CCF may provide more habitats and resources for species living in mature or late
77 successional forests compared with RFM (Calladine et al., 2015; Kuuluvainen et al., 2012; Pukkala et al.,
78 2012). In boreal forests, CCF has been found to be less harmful than RFM, for example, for understorey
79 vegetation (Jalonen and Vanha-Majamaa, 2001), some invertebrate species (Matveinen-Huju and
80 Koivula, 2008), and soil fauna (Siira-Pietikäinen and Haimi, 2009). Moreover, in comparison to RFM,
81 CCF may provide more resources for dead wood dependent species (Atlegrim and Sjöberg, 2004) as well
82 as for herbivores (Atlegrim and Sjöberg, 1996). However, because different species require differing
83 habitats and resources, it is obvious that no single management can be the best for all species and
84 biodiversity aspects (Calladine et al., 2015; Mönkkönen et al., 2014). Thus, it is important to understand
85 how the different silvicultural practices promote different types of forest structures and species (Felton et
86 al., 2016).

87 Even though there is evidence that CCF is better than RFM for several forest purposes (Pukkala,
88 2016a), their relative performance of ecosystem service provisions and of biodiversity is not well known
89 when compared with unmanaged forests (but see Pukkala, 2016b; Sharma et al., 2016). Even if there is a
90 seemingly large difference between the two silvicultural alternatives, they may both appear equally poor

91 relative to forests in a more natural state. If so, then CCF may not be the solution to declining biodiversity
92 and ecosystem services. Therefore, comparing both practices with unmanaged forests generates valuable
93 knowledge about their actual effects on the ability of forest landscapes to provide goods and benefits to
94 humankind.

95 As forests provide multiple services and benefits, the capabilities of alternative forest
96 management practices should be assessed from a multifunctionality perspective, i.e., their relative
97 performance to provide bundles of services simultaneously (Mastrangelo et al., 2014; van der Plas et al.,
98 2016). Although earlier results demonstrate the high potential of CCF to simultaneously provide multiple
99 services (Pukkala, 2016a), the concept of multifunctionality has not been commonly applied.
100 Multifunctionality of forests can be considered as an index, which highlights the number of services
101 which exceed a specified level of those services (van der Plas et al., 2016). Therefore, when estimating
102 the capacity of different silvicultural practices to provide multiple benefits simultaneously, the effect of
103 desired level of services should be taken into account.

104 We use a dataset describing a large forest landscape where we apply three alternative
105 management practices —CCF, RFM and set aside (no management)— simulated for 100 years into the
106 future to estimate their relative performance to provide forest ecosystem services and maintain
107 biodiversity. We address the following questions: 1) Which ecosystem services and biodiversity measures
108 benefit more from CCF compared with RFM and vice versa? 2) What are the levels of biodiversity and
109 ecosystem services under two alternative forest management practices as well as their optimal
110 combination compared with unmanaged forests? 3) Which silvicultural practice provides the greatest
111 forest multifunctionality across large forest landscapes?

112

113 **2. METHODS**

114 **2.1 Forest data and simulations**

115 The study areas are located in central and southern Finland, encompassing 39,979 hectares. Data consist
116 of 26,024 commercial forest stands on mineral soils with the average size of stands being 1.5 ha. The

117 initial forest data was provided by the Finnish Forest Centre, and are based on laser scanned data with
118 ground-truthing (Maltamo et al., 2007). The data contain forest characteristics, such as forest site type,
119 age, or tree species compositions. In the initial data, Scots pine (*Pinus sylvestris*) was the dominant tree
120 species on 23% of the stands, Norway spruce (*Picea abies*) on 63% of the stands and birches (*Betula*
121 *pendula* and *B. pubescens*) on 14% of the stands. Mixed stands, i.e., where none of the tree species
122 accounted for more than 75% of the total volume, represent 45% of all the stands. The variation in the
123 site type and initial age of stands are given in Appendix S1: Figure S1.

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

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

140 RFM is currently the recommended and the most common forest management practice in
141 Fennoscandia (Äijälä et al., 2014). In Finland RFM includes several silvicultural actions: soil preparation,
142 seeding or planting trees, one to three thinnings, and the final clear cut, where approximately five

143 retention trees per hectare are retained (according to the good practice guidance for forestry from Äijälä et
144 al., 2014). The management rules for regeneration cutting are given in Appendix S1: Table S2. The
145 average rotation length of RFM is approximately 80 years in our study region (Appendix S1; Figure S2).
146 RFM creates forest stands, which are often very homogenous in tree species composition as well as in the
147 age structure. The growth models of Hynynen et al. (2002) for even-aged stands were applied for this
148 regime.

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

154

155 **2.2 Ecosystem services and biodiversity indicators**

156 **2.2.1. Ecosystem services**

157 Different ecosystem categories (provisioning, regulating, and cultural) were considered with a set of
158 ecosystem services (Table 1). Timber production is the economically most important provisioning service
159 in boreal forests (Vanhanen et al., 2012). The net present value (NPV, €) of sawlogs and pulpwood for
160 each tree species across 100 years was estimated. *The timber NPV* consists of three components: the
161 revenues from harvesting (clear-cuts, thinnings, selective loggings; Appendix S1: Table S3), the value of
162 standing timber at the end of simulations, and the value of spare land at the end of simulations (Pukkala,
163 2005). In addition, timber NPV accounted for costs resulting from silvicultural actions related to
164 regeneration and young stand (Appendix S1: Table S4). The stumpage prices of harvest revenue
165 components and the prices for the silvicultural costs were calculated from the historical averages in
166 Finland (Peltola 2014, Appendix S1: Table S3). The stumpage prices included costs from harvesting. The
167 harvesting costs are higher in partial cuttings in CCF than in final fellings in RFM (e.g., Pukkala, 2016,
168 Tahvonen et al., 2010) so the prices from second thinnings (also called intermediate felling) were used for

169 CCF. The interest rate varied between 1% and 5% in discounting the timber revenues and costs during the
170 100-year period. In addition, to study the sensitivity of timber NPV with different costs and prices in CCF
171 and RFM, we calculated NPV without regeneration costs in RFM and using the same prices for CCF and
172 RFM. Timber revenues can be seen as a service for private forest owners, and thus, we also estimated the
173 amount of harvested timber biomass separately for pulpwood and sawlogs, which can be considered as a
174 provisioning service for the whole society since the forest industry is dependent on biomass.

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

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

189

190 **2.2.2. Biodiversity**

191 Biodiversity is a multi-faceted phenomenon, which can be measured using indices derived from forest
192 structural data (Table 1). Dead wood is a critical resource in boreal forests (Siitonen, 2001). In boreal
193 Fennoscandia, 20-25% of the forest-dwelling species are dependent on dead-wood habitats, and species
194 dependent on dead wood constitute 60% of the red-listed species (Rassi et al., 2010). Association between

195 dead-wood volume and biodiversity is well established (Gao et al., 2015). The capacity of a stand to
196 maintain populations of dead-wood associated species was estimated by multiplying total dead-wood
197 volume by the diversity of deadwood across tree species, diameter and decay stage categories (Triviño et
198 al., 2016). Thus, a stand with large total deadwood volume distributed evenly across deadwood types will
199 receive high values of deadwood availability. In addition, large diameter living trees are an essential
200 structural feature in boreal forests that has become a limiting factor for biodiversity in production forests
201 (Nilsson et al., 2002). Therefore, the number of large diameter (>40 cm) trees was also calculated.

202 Habitat availability for species measure the overall capacity of the forests to maintain species
203 populations. Habitat suitability indices (HSI) were calculated for a selected set of umbrella or indicator
204 species representing habitat associations as well as social and conservation values: Capercaillie (*Tetrao*
205 *urogallus*), Hazel grouse (*Bonasa bonasa*), Lesser spotted woodpecker (*Dryobates minor*), Long-tailed tit
206 (*Aegithalos caudatus*), Three-toed woodpecker (*Picoides tridactylus*), and Siberian flying squirrel
207 (*Pteromys volans*) (Table 1, Mönkkönen et al. 2014). Earlier research has shown that these species
208 indicate forest characteristics important for many other species (please see Mönkkönen et al. 2014 for the
209 detailed motivation to focus on these taxa). Our main focus is on late successional species due to their
210 severe conservation need in Fennoscandia (Rassi et al., 2010). Habitat suitability is a function of a set of
211 sub-utility functions based on expert knowledge and known species habitat that translate characteristics of
212 each stand into a habitat suitability index between 0 (unsuitable habitat) and 1 (the most suitable habitat).
213 For each species, we calculated habitat availability across the entire landscape as a sum of products
214 between stand specific HSI-values and the area of a stand.

215

216 **2.2.3 Comparison between silvicultural practices**

217 To estimate the performance of silvicultural practices in maintaining ecosystem services and biodiversity
218 (Table 1), their levels under CCF and RFM at a landscape scale across 100 years were calculated.
219 Moreover, the share of stands when CCF outperforms RFM and vice versa was calculated. To estimate
220 the maximum achievable levels of ecosystem services and biodiversity under the combination of CCF and

221 RFM, the practice that provided a larger value was applied for each stand. To estimate the relative
222 performance of silvicultural strategies compared with unmanaged forests in the delivery of ecosystem
223 services and biodiversity, their values under CCF, RFM, and their optimal combination (CCF+RFM)
224 were divided by the values in SA forests. In the cases of timber net present value and harvested timber
225 biomass, the optimal values (CCF+RFM) were used as a reference state since the value of SA regime was
226 zero.

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

232

233 **2.2.4 Multifunctionality**

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

$$237 \quad SMF_i = \frac{obsSMF_i - minSMF_i}{maxSMF_i - minSMF_i}$$

238 where SMF_i indicates a scaled multifunctionality value (between 0 and 1) of a single ecosystem service or
239 biodiversity measure i in a stand over 100 years (Table 1), $obsSMF$ indicates the observed value of a
240 single biodiversity or ecosystem service measure in a stand, $minSMF$ and $maxSMF$ indicate the minimum
241 and the maximum values of a single biodiversity or ecosystem service measure in the whole study area.

242 The ecosystem services and biodiversity measures were divided into four groups according to the
243 ecosystem service categories they represent (Haines-Young and Potschin, 2011): provisioning services
244 (timber NPV and harvested timber biomass), regulating services (carbon storage and sequestration), and
245 cultural services (scenic beauty and the combined yield of bilberries and cowberries). In addition, a

246 category representing biodiversity consisted of dead wood diversity and combined habitat suitability
247 index—a combination of six habitat suitability indices (Triviño et al., 2016). Grouped SMF (GMF) takes
248 value 1 if either of the SMF in a group was larger than the threshold value t . Finally, multifunctionality
249 score of a stand was calculated as the sum GMFs that had a value above a threshold t as follows:

$$250 \quad MF = \sum_{i=1}^n \begin{cases} 1 & GMF_i \geq t \\ 0 & GMF_i < t \end{cases}$$

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

260

261 **3. RESULTS**

262 **3.1. Ecosystem services**

263 CCF provided higher values than RFM for five out of eight ecosystem services at the landscape scale on
264 average over 100 years (Figure 1a,2a; Appendix S2: Table S1,S2). Carbon storage was moderately higher
265 and sequestration remarkably higher in landscapes consistently managed using CCF in comparison with
266 RFM (Figure 1a; Appendix S2: Figure S1). In terms of the regulating services, CCF outperformed RFM
267 in approximately 75% of the stands (Figure 1b). Bilberry yields and scenic beauty were higher with CCF
268 (Figure 1a) and CCF outperformed RFM in 70–90% of the stands (Figure 1b). In contrast, cowberry and
269 marketed mushroom yields were higher in RFM (Figure 1a) and it outperformed CCF in approximately
270 90% of the stands (Figure 1b).

271 RFM provided more harvested timber (Figure 2a; Appendix S2: Table S1) outperforming CCF in
272 60% of the stands (Figure 2b). There were differences in the shares of sawlogs and pulpwood between
273 CCF and RFM (Appendix S2: Figure S2). In CCF, 79% of the harvested timber was sawlogs and 21%
274 pulpwood, whereas in RFM the share of sawlogs was 65% and the share of pulpwood 35%.

275 The discount rate affected the economic performance of CCF and RFM (Figure 2a; Appendix S2:
276 Table S2). With a 1% discount rate, the NPV of both strategies was the same. The timber NPV was
277 greater in CCF than in RFM when the discount rate was 2% or larger. The optimal share of CCF and
278 RFM was 50% of each when the discount rate was 1% (Figure 2b). The optimal share of CCF increased
279 with the discount rate and was 80% at 5% discount rate. Only when the costs related to regeneration and
280 young stands were not taken into account and the discount rate was 1%, the NPV was greater in RFM
281 than in CCF (Appendix S2, Figure S3c).

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

285 SA forests provided higher values than CCF, RFM or their combination particularly for the climate
286 regulating services but also for scenic beauty (Figure 1). Managed forests tended to provide a higher
287 delivery of collectable goods than SA forests. However, SA performed as well as CCF in marketed
288 mushroom production and as well as RFM in bilberry production.

289

290 **3.2 Biodiversity**

291 Consistent application of CCF in landscapes yielded higher values than RFM for five out of eight
292 biodiversity indicators (Figure 3a; Appendix S2: Table S3). For three biodiversity indicators (Lesser
293 spotted woodpecker, Long-tailed tit and number of large diameter trees) CCF outperformed RFM in
294 almost 100% of stands (Figure 3b) and the difference in favour of CCF was remarkably large (Figure 3a).
295 CCF also yielded clearly higher values than RFM in the cases of Hazel grouse and Three-toed
296 woodpecker when CCF outperformed RFM in between 70% to 80% of the stands. In contrast, RFM

297 yielded slightly higher dead wood indicator values outperforming CCF in 67% of the stands. Moreover,
298 for the Capercaillie and flying squirrel consistent application of RFM clearly performed better than CCF
299 (Figure 3a) providing higher habitat suitability index in between 50% to 97% of the stands (Figure 3b).

300 In five cases, a combination of CCF and RFM provided higher scores than either of them separately
301 (Figure 3a). The benefits of combining the two management practices in landscapes were particularly
302 pronounced for the Capercaillie and the Hazel grouse. For the Capercaillie, the combination of CCF and
303 RFM (Figure 3b) yielded 55% larger HSI value than consistent application of CCF and 30% larger than
304 consistent application of RFM (Figure 3a). For the Hazel grouse, the combination (Figure 3b) yielded
305 65% larger HSI value than consistent application of RFM and 20% larger than consistent application of
306 CCF (Figure 3a).

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

312 The frequency of unsuitable habitats varied among species (Figure 4). For the Capercaillie,
313 practically all stands were unsuitable at some point of time irrespective of the management regime. For
314 other species except the Siberian flying squirrel, the frequency of total unsuitability was the highest under
315 RFM. SA showed the lowest frequency of total unsuitability for all other species except the Long-tailed
316 tit when CCF performed the best.

317

318 **3.3. Multifunctionality**

319 At all threshold levels, the average forest multifunctionality was larger when forests were managed with
320 CCF than forests managed with RFM (Figure 5) indicating a larger capacity of CCF to simultaneously
321 provide services from different categories. An optimal combination of CCF and RFM always produced
322 higher multifunctionality scores than RFM alone, and slightly higher scores than CCF alone when the

323 threshold was larger than 0.4. This indicates that even though CCF in general is better from the
324 multifunctionality point of view, there are some stands where RFM has higher potential to provide
325 multifunctionality. SA provided the lowest multifunctionality below 0.4 threshold levels, which is
326 primarily due to the lack of timber harvesting. When the demand for multifunctionality is high (threshold
327 >0.6) SA forests provided the highest multifunctionality scores. This means that when high levels of
328 ecosystem services and biodiversity are simultaneously desired, leaving forests unmanaged (set aside) is
329 more desirable than managing forests (both CCF and RFM).

330

331 **4. DISCUSSION**

332 Our results show that CCF has the potential to deliver ecosystem services and maintain biodiversity in
333 commercial forests better than conventional RFM. In general, the results of this study are in line with
334 previous research (Pukkala, 2016a; Shanin et al., 2016; Sharma et al., 2016). However, CCF was not
335 better than RFM in terms of all ecosystem services or biodiversity indicators. Moreover, the optimal
336 combination of CCF and RFM provided higher values of ecosystem services and biodiversity measures
337 than either CCF or RFM applied consistently in all stands. Previous studies have also shown the benefit
338 of using a diverse set of silvicultural practices in forest landscapes (Mönkkönen et al., 2014; Redon et al.,
339 2014; Triviño et al., 2016, 2015). Thus, the relative utility of silvicultural practice depends on site
340 characteristics; an aspect that should be further studied.

341 In terms of regulating services, while there were no large differences between CCF and RFM in
342 carbon storage, CCF outperformed RFM in carbon sequestration. In RFM, a stand is periodically a source
343 of carbon after the clear-cut. This is mainly because the decomposing forest harvest residues release
344 carbon more than is sequestered in the biomass growth. In CCF, changes in soil carbon stock are smaller
345 after harvests than in RFM because the litter input from harvest residues is smaller. The carbon balance of
346 forests critically depends on the final use of timber biomass after it is removed from the forest ecosystem
347 (Lundmark et al., 2016; Pukkala, 2016b) but we did not take into account the carbon storage in wood
348 products or emissions from the procurement chain. However, as the proportion of sawlogs compared with

349 pulpwood is higher in CCF than in RFM, the carbon retention time would be longer for timber produced
350 in CCF (Pukkala, 2014). Therefore, inclusion of carbon storage in the wood products would not change
351 the main findings. The superior capacity of unmanaged forests to sequester carbon is explained by the
352 initial state of the forest stands and their management history. Intensively managed forest landscapes in
353 Finland have a high proportion of young stands holding large potential for carbon sequestration. Although
354 in SA the rate of carbon sequestration decreases with the increasing age of the forest (Pukkala, 2016b),
355 we show that unmanaged forests can have a remarkable role in climate change mitigation for several
356 decades.

357 Our results considering timber NPV support earlier findings (Pukkala et al., 2011; Tahvonen et
358 al., 2010) where discount rates larger than 1% make CCF more profitable than RFM. Higher profitability
359 of CCF is related to the higher price of sawlogs versus pulpwood (CCF provides more sawlogs) as well as
360 the large costs of regeneration and thinnings in RFM. However, in some cases RFM provided also larger
361 economic profits than CCF. This is the case, for stands that are mature, i.e. ready for final harvesting at
362 the beginning of 100 year time period (Tahvonen et al., 2010). CCF is not commonly applied in
363 Fennoscandia because of the uncertainty in regeneration success, lower timber quality and higher total
364 harvesting costs (Laiho, Lähde & Pukkala 2011). The potential for lower timber quality and higher
365 harvesting costs were accounted for by applying a lower price for timber originating from CCF. In
366 addition, we estimated the NPV with and without taking regeneration costs into account for RFM. In
367 contrast to NPV, RFM produced more harvested timber biomass, which is also supported by earlier
368 studies (Lundqvist et al., 2007; Pukkala et al., 2011; Tahvonen et al., 2010). Thus, CCF may be more
369 profitable for private forest owners while RFM may better meet the industry's current needs.

370 For four out of the six umbrella and indicator species, CCF provided higher habitat availability
371 than RFM. This is not surprising since many species in this study are dependent on tree cover and
372 deciduous trees, which CCF provides. Moreover, the frequency where the stands were totally unsuitable
373 for the species was often highest in RFM. Thus, one benefit of CCF for mature forest species is the less
374 severe temporal fluctuations in habitat quality. However, for early successional species RFM may

375 actually provide more habitats (Calladine et al., 2015). Nevertheless, habitat availability for species
376 dependent on high tree volume and dead wood availability in forests under both CCF and RFM were far
377 from those in unmanaged forests. Thus, some species habitat availability and dead wood availability more
378 critically depend on the amount of harvested timber than on the silvicultural practice used in harvesting
379 (Atlegrim and Sjöberg, 2004). For many deadwood dependent species, the desirable minimum level of
380 dead wood is approximately $20 \text{ m}^3 \text{ ha}^{-1}$ (Junninen and Komonen, 2011) while both CCF and RFM
381 provided only about 25% of that. To further improve the ability of CCF to promote biodiversity we
382 recommend a similar kind of green tree retention that is applied in RFM (leaving permanently behind, at
383 least, 5 trees per ha) to be included in the CCF management regime. Interestingly, CCF provided the
384 greatest number of large trees resulting from the larger resource availability of individual trees (space and
385 light). In contrast, for unmanaged forests, tree growth is lower. This is likely due to the development and
386 transition of very young and planted stands at the beginning of the simulation. For these stands, transition
387 to uneven aged stands will take longer than 100 years and the large trees will likely be harvested during
388 the next (or following) CCF cutting. However, if the simulation time had been longer than 100 years, the
389 number of large diameter trees would have been larger in SA regime and on the other hand smaller in
390 CCF since the transition from even-aged to uneven-aged forestry allows large diameter trees in our CCF
391 simulations.

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

401 In the simulation process, all management options were based on decision rules instead of
402 optimizing the specific management at stand level. Both management alternatives that we used could be
403 changed substantially by altering the specific decision rules (i.e. delaying final felling, restricting the
404 frequency of harvests, or requiring green tree retention following a clear felling) to increase the delivery
405 of multiple benefits in forest stands (e.g., Liski et al. 2001; Gustafsson et al. 2012). Optimizing the
406 management at a stand level can improve the economic and ecological performance of a stand (e.g.,
407 Miina, Pukkala & Kurttila 2016; Tahvonen & Rämö 2016). However, stand level optimizing is
408 problematic for several reasons. First, there is high uncertainty, e.g., because of errors in inventory
409 estimates and in inaccuracies in growth models resulting only in crude approximations. As a consequence,
410 the actual performance of a stand level optimized management plan could fall short of the management
411 plan following decision rules (Holopainen and Talvitie, 2006). Second, optimizing at the stand level is a
412 time consuming and data intensive activity, and consequently not often practicable (Kurttila et al., 2013).
413 Third, in practice management decisions depend on the choices of the forest owner, whose preferences
414 may more likely be based on the personal economic situation rather than on specific stand characteristics
415 (Brazeel, 2003). In such cases, simple decision rules may better provide guidance to decisions than
416 knowledge about stand level optimal management.

417 Our comparison among CCF, RFM and unmanaged forests has some limitations. Even though the
418 planning horizon was long (100 years), even set-aside forests do not provide a natural-state benchmark for
419 managed forests. For example, the amount of dead wood in the natural forest state is approximately 60-90
420 $\text{m}^3 \text{ha}^{-1}$ (Siitonen, 2001) but in our data the amount of dead wood under set-aside was significantly lower.
421 Moreover, our simulation did not include natural disturbances, such as storms and diseases, which may
422 substantially change the forest characteristics, e.g. dead wood volumes (Kuuluvainen, 2002). Therefore,
423 our simulations probably underestimate the delivery of some ecosystem services and biodiversity values
424 in all management regimes, and on the other hand, overestimate timber production in both CCF and RFM.
425 Disturbances do occur in forests regardless of management but their intensity and effects vary depending
426 on management of the stand itself and its surrounding forests. Since CCF maintains natural tree species

427 and more natural structure of forests it may be more resistant against the disturbances, such as wind
428 damages (Couture et al., 2016; Pukkala et al., 2016), and insect pathogens (Klapwijk et al., 2016). We
429 leave it as a challenge for future studies to accommodate disturbance effects on ecosystem services and
430 biodiversity in forests under different management regimes. This would inevitably require a spatially
431 explicit landscape level approach.

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

441

442 **5. CONCLUSION**

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

452

453 **ACKNOWLEDGEMENTS**

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

457 **REFERENCES**

- 458 Andreassen, K., Øyen, B.H., 2002. Economic consequences of three silvicultural methods in unevenaged
459 mature coastal spruce forests of central Norway. *Forestry* 75, 483–488.
460 doi:10.1093/forestry/75.4.483
- 461 Atlegrim, O., Sjöberg, K., 2004. Selective felling as a potential tool for maintaining biodiversity in
462 managed forests. *Biodivers. Conserv.* 13, 1123–1133. doi:10.1023/B:BIOC.0000018148.84640.f0
- 463 Atlegrim, O., Sjöberg, K., 1996. Effects of clear-cutting and single-tree selection harvests on herbivorous
464 insect larvae feeding on bilberry (*Vaccinium myrtillus*) in uneven-aged boreal *Picea abies* forests.
465 *For. Ecol. Manage.* 87, 139–148. doi:10.1016/S0378-1127(96)03830-3
- 466 Boncina, A., 2011. History, current status and future prospects of uneven-aged forest management in the
467 Dinaric region: an overview. *Forestry* 84, 467–478. doi:10.1093/forestry/cpr023
- 468 Bradshaw, C.J.A., Warkentin, I.G., 2015. Global estimates of boreal forest carbon stocks and flux. *Glob.*
469 *Planet. Change* 128, 24–30. doi:10.1016/j.gloplacha.2015.02.004
- 470 Bradshaw, C.J.A., Warkentin, I.G., Sodhi, N.S., 2009. Urgent preservation of boreal carbon stocks and
471 biodiversity. *Trends Ecol. Evol.* 24, 541–548. doi:10.1016/j.tree.2009.03.019
- 472 Brazee, R.J., 2003. The Volvo Theorem: From myth to behavior model, in: Helles, F., Strange, N.,
473 Wichmann, L. (Eds.), *Recent Accomplishments in Applied Forest Economics Research*. Springer
474 Netherlands, Dordrecht, pp. 39–48. doi:10.1007/978-94-017-0279-9_3
- 475 Burton, P.J., Bergeron, Y., Bogdanski, B.E.C., Juday, G.P., Kuuluvainen, T., McAfee, B.J., Ogden, A.,
476 Teplyakov, V.K., Alfaro, R.I., Francis, D.A., Gauthier, S., Hantula, J., 2010. Sustainability of boreal
477 forests and forestry in a changing environment. *For. Soc. responding to Glob. drivers Chang.* 247–
478 282.
- 479 Calladine, J., Bray, J., Broome, A., Fuller, R.J., 2015. Comparison of breeding bird assemblages in
480 conifer plantations managed by continuous cover forestry and clearfelling. *For. Ecol. Manage.* 344,
481 20–29. doi:10.1016/j.foreco.2015.02.017
- 482 Couture, S., Cros, M.-J., Sabbadin, R., 2016. Risk aversion and optimal management of an uneven-aged

483 forest under risk of windthrow: A Markov decision process approach. *J. For. Econ.* 25, 94–114.
484 doi:10.1016/j.jfe.2016.08.002

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

488 Felton, A., Gustafsson, L., Roberge, J.M., Ranius, T., Hjältén, J., Rudolphi, J., Lindbladh, M., Weslien, J.,
489 Rist, L., Brunet, J., Felton, A.M., 2016. How climate change adaptation and mitigation strategies can
490 threaten or enhance the biodiversity of production forests: Insights from Sweden. *Biol. Conserv.*
491 194, 11–20. doi:10.1016/j.biocon.2015.11.030

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

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

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

500 Haines-Young, R., Potschin, M., 2011. Common international classification of ecosystem services
501 (CICES): 2011 Update. *Expert Meet. Ecosyst. Accounts ...* 1–17.

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

504 Hanski, I., 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *Ambio* 40,
505 248–55.

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

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

- 509 Holopainen, M., Talvitie, M., 2006. Effect of data acquisition accuracy on timing of stand harvests and
510 expected net present value. *Silva Fenn.* 40, 531–543. doi:10.14214/sf.335
- 511 Hynynen, J., Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H., Haapala, P., 2002. Models for
512 predicting stand development in MELA System. Research Paper 835. Finnish Forest Research
513 Institute, 116 pp.
- 514 Jalonen, J., Vanha-Majamaa, I., 2001. Immediate effects of four different felling methods on mature
515 boreal spruce forest understorey vegetation in southern Finland. *For. Ecol. Manage.* 146, 25–34.
516 doi:10.1016/S0378-1127(00)00446-1
- 517 Junninen, K., Komonen, A., 2011. Conservation ecology of boreal polypores: A review. *Biol. Conserv.*
518 144, 11–20. doi:10.1016/j.biocon.2010.07.010
- 519 Klapwijk, M.J., Bylund, H., Schroeder, M., Björkman, C., 2016. Forest management and natural
520 biocontrol of insect pests. *Forestry* 89, 253–262. doi:10.1093/forestry/cpw019
- 521 Kurttila, M., Pykäläinen, J., Hujala, T., 2013. Metsätieteen aikakauskirja Optimoinnin käyttö
522 yksityismetsien tilatason metsäsuunnittelussa 61–70.
- 523 Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological
524 diversity in boreal Fennoscandia. *Silva Fenn.* 36, 97–125. doi:10.1579/08-A-490.1
- 525 Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-Aged and Uneven-Aged Forest Management in
526 Boreal Fennoscandia: A Review. *Ambio* 41, 720–737. doi:10.1007/s13280-012-0289-y
- 527 Laiho, O., Lohde, E., Pukkala, T., 2011. Uneven-vs even-aged management in Finnish boreal forests.
528 *Forestry* 84, 547–556. doi:10.1093/forestry/cpr032
- 529 Laudon, H., Sponseller, R.A., Lucas, R.W., Fitter, M.N., Egnell, G., Bishop, K., Ågren, A., Ring, E.,
530 Högberg, P., 2011. Consequences of more intensive forestry for the sustainable management of
531 forest soils and waters. *Forests* 2, 243–260. doi:10.3390/f2010243
- 532 Liski, J., Palosuo, T., Peltoniemi, M., Sievänen, R., 2005. Carbon and decomposition model Yasso for
533 forest soils. *Ecol. Modell.* 189, 168–182. doi:10.1016/j.ecolmodel.2005.03.005
- 534 Liski, J., Pussinen, A., Pingoud, K., Mäkipää, R., Karjalainen, T., 2001. Which rotation length is

535 favourable to carbon sequestration? *Can. J. For. Res.-Rev. Can. Rech. For.* 31, 2004–2013.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

587 Res. 3, 533–544.

588 Pukkala, T., Laiho, O., Lähde, E., 2016. Continuous cover management reduces wind damage. *For. Ecol.*
589 *Manage.* 372, 120–127. doi:10.1016/j.foreco.2016.04.014

590 Pukkala, T., Lähde, E., Laiho, O., 2013. Species interactions in the dynamics of even- and uneven-aged
591 Boreal Forests. *J. Sustain. For.* 32, 371–403. doi:10.1080/10549811.2013.770766

592 Pukkala, T., Lähde, E., Laiho, O., Salo, K., Hotanen, J.-P., 2011. A multifunctional comparison of even-
593 aged and uneven-aged forest management in a boreal region. *Can. J. For. Res.* 41, 851–862.
594 doi:10.1139/x11-009

595 Pukkala, T., Sulkava, R., Jaakkola, L., Lähde, E., 2012. Relationships between economic profitability and
596 habitat quality of Siberian jay in uneven-aged Norway spruce forest. *For. Ecol. Manage.* 276, 224–
597 230. doi:10.1016/j.foreco.2012.04.006

598 Ranius, T., Eliasson, P., Johansson, P., 2008. Large-scale occurrence patterns of red-listed lichens and
599 fungi on old oaks are influenced both by current and historical habitat density. *Biodivers. Conserv.*
600 17, 2371–2381. doi:10.1007/s10531-008-9387-3

601 Rasinmäki, J., Mäkinen, A., Kalliovirta, J., 2009. SIMO: An adaptable simulation framework for
602 multiscale forest resource data. *Comput. Electron. Agric.* 66, 76–84.
603 doi:10.1016/j.compag.2008.12.007

604 Rassi, P., Hyvärinen, E., Juslén, A., Mannerkoski, I., 2010. The 2010 red list of Finnish species.
605 Ympäristöministeriö & Suomen ympäristökeskus, Helsinki 685.

606 Redon, M., Luque, S., Gosselin, F., Cordonnier, T., 2014. Is generalisation of uneven-aged management
607 in mountain forests the key to improve biodiversity conservation within forest landscape mosaics?
608 *Ann. For. Sci.* 71, 751–760. doi:10.1007/s13595-014-0371-7

609 Shanin, V., Valkonen, S., Grabarnik, P., Mäkipää, R., 2016. Using forest ecosystem simulation model
610 EFIMOD in planning uneven-aged forest management. *For. Ecol. Manage.* 378, 193–205.
611 doi:10.1016/j.foreco.2016.07.041

612 Sharma, A., Bohn, K., Jose, S., Dwivedi, P., 2016. Even-aged vs. uneven-aged silviculture: implications

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

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

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

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

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

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

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

628 Triviño, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Mönkkönen, M.,
629 2015. Managing a boreal forest landscape for providing timber, storing and sequestering carbon.
630 *Ecosyst. Serv.* 14, 179–189. doi:10.1016/j.ecoser.2015.02.003

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

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

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

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

641 Vaara, M., Saastamoinen, O., Turtiainen, M., 2013. Changes in wild berry picking in Finland between
642 1997 and 2011. *Scand. J. For. Res.* 28, 586–595. doi:10.1080/02827581.2013.786123

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

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

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

659 Östlund, L., Zackrisson, O., Axelsson, a-L., 1997. The history and transformation of a Scandinavian
660 boreal forest landscape since the 19th century. *Can. J. For. Res.* 27, 1198–1206. doi:10.1139/x97-
661 070

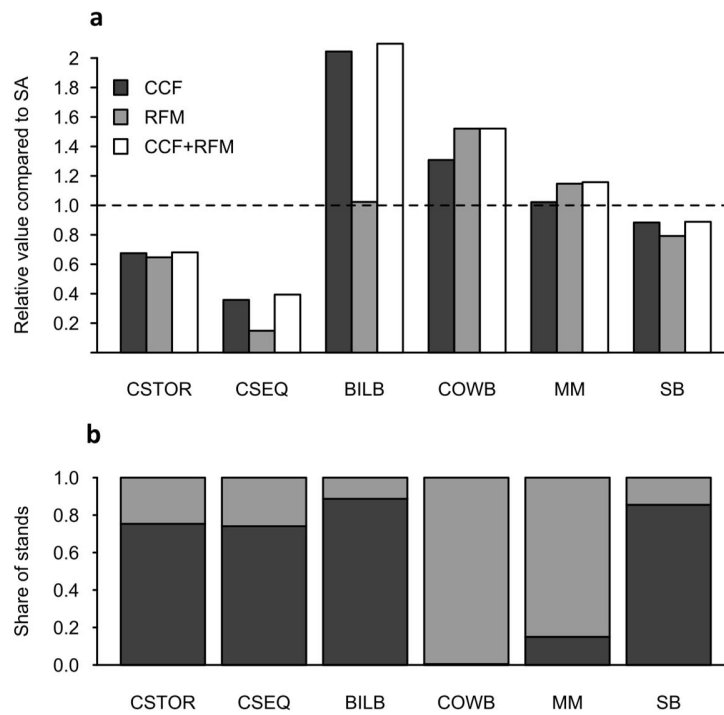
662

663

665 **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)

668 **FIGURES**



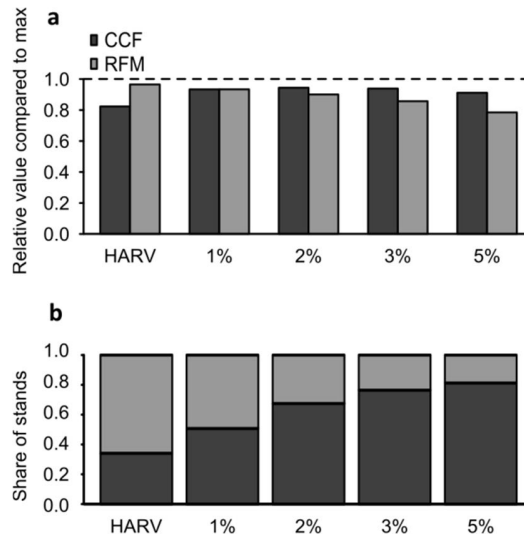
669

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

676

677

678



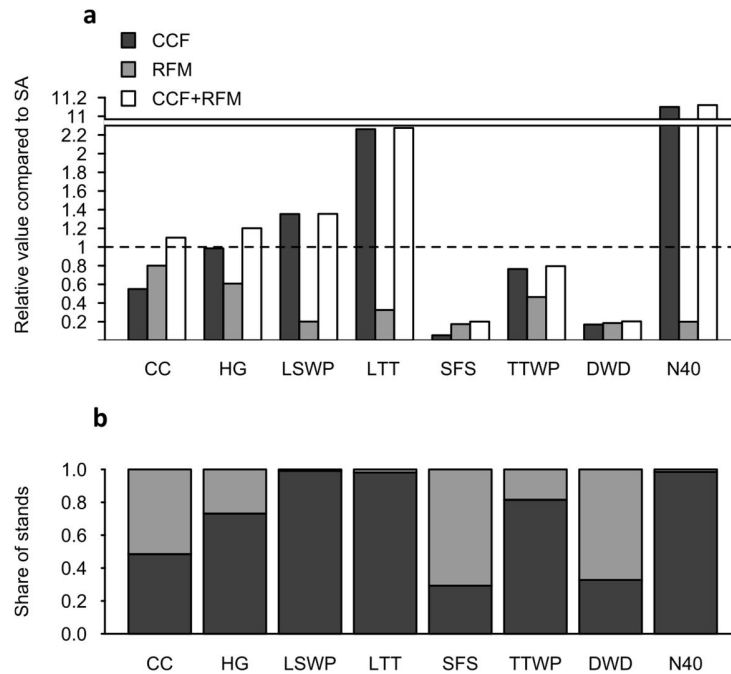
679

680 **Figure 2** a) Relative harvested timber biomass (HARV) and revenues (NPV) with different discount rates
681 (1-5%) in the study area under continuous cover forestry (CCF) and rotation forest management (RFM)
682 compared to their optimal combination (CCF + RFM, the dashed line). Absolute values are given in
683 Appendix S2: Table S1,S2. b) Optimal share of stands under CCF and RFM to maximize harvested
684 timber and timber revenues in the study area.

685

686

687

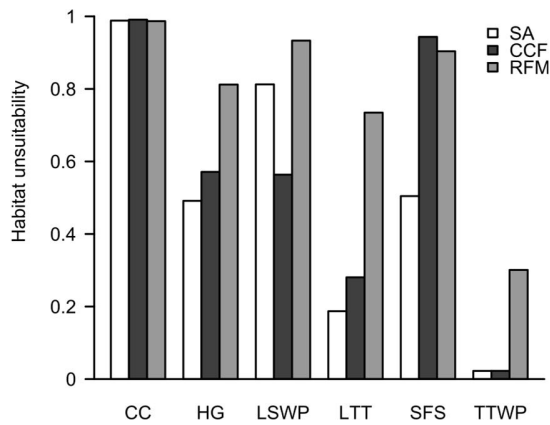


688

689

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

697



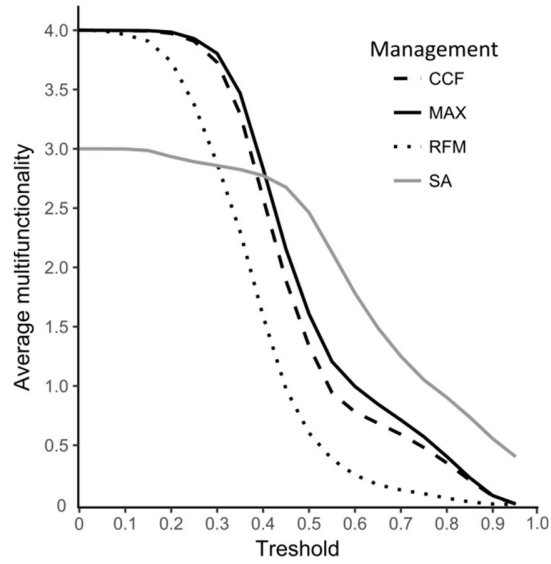
698

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

703

704

705



706

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

710