This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Repo, Anna; Eyvindson, Kyle J.; Halme, Panu; Mönkkönen, Mikko

Title: Forest bioenergy harvesting changes carbon balance and risks biodiversity in boreal forest landscapes

Year: 2020

Version: Accepted version (Final draft)

Copyright: © Canadian Science Publishing, 2020

Rights: In Copyright

Rights url: <http://rightsstatements.org/page/InC/1.0/?language=en>

Please cite the original version:

Repo, A., Eyvindson, K. J., Halme, P., & Mönkkönen, M. (2020). Forest bioenergy harvesting changes carbon balance and risks biodiversity in boreal forest landscapes. *Canadian Journal of Forest Research*, 50(11), 1184-1193. <https://doi.org/10.1139/cjfr-2019-0284>

Forest bioenergy harvesting changes carbon balance and risks biodiversity in boreal forest
landscapes

Anna Repo^{1,2*}, Kyle Eyvindson^{1,3}, Panu Halme^{1,3} & Mikko Mönkkönen^{1,3}

¹ Department of Biological and Environmental Science, P.O. Box 35, FI-40014, University of
Jyväskylä, Finland

² Natural Resources Institute Finland (Luke), P.O. Box 2, 00791 Helsinki, Finland

³ School of Resource Wisdom, University of Jyväskylä, P.O. Box 35, FI-40014, University of
Jyväskylä, Finland

*corresponding author anna.repo@luke.fi

Keywords: climate change mitigation, biodiversity, deadwood, logging residues, habitat
requirements

15 **Abstract**

16 Climate solutions relying on forest bioenergy may be in conflict with carbon sequestration and
17 storage by forests as well as conservation of biodiversity. We quantified effects of forest residue
18 harvesting for bioenergy on both forest carbon balance and biodiversity in a boreal forest
19 landscape. Through a modeling framework we simulated forest development in four real
20 watersheds with three scenarios: i) with and ii) without forest residue harvesting, and iii) set
21 aside to study the conservation potential of these landscapes in the future without management.
22 We simulated changes in the forest carbon stocks, and in the quality and the quantity of
23 deadwood resources for 100 years and combined this information with the information on
24 species habitat associations based on expert judgements. In this study current practices of slash
25 and stump harvesting reduced forest carbon stocks and deadwood volumes at the landscape
26 scale, and consequently halved the emissions savings that can be obtained with bioenergy. In
27 addition, logging residue harvesting reduced 15-21% the combined species conservation capacity
28 of the landscape for red-listed, saproxylic species compared to forest management without
29 bioenergy harvesting. Furthermore, the results indicated a potential conflict between areas of
30 high bioenergy potential and high conservation potential.

Introduction

Climate solutions relying on forest bioenergy may be in conflict with carbon sequestration and storage by forests as well as conservation of biodiversity. Intensifying biomass harvests for bioenergy production may cause significant net losses of carbon from forests which may partly or entirely offset the emission savings from replacing fossil fuels with bioenergy (Schulze et al. 2012). In addition, the intensification of forest biomass harvests to meet the climate goals has raised concerns on adverse effects on forest biodiversity (EASAC 2017).

Logging residues, such as branches, treetops, and stumps, are an increasingly important source of bioenergy in northern temperate and boreal forests. While biomass from other side streams and waste from forest industry are already used for energy production (Szabó et al. 2011), many studies have identified a large, unused bioenergy potential of logging residues (e.g. de Wit and Faaij 2010). As a result of policies promoting bioenergy and concerns about climate change, extraction rates of these previously unharvested residues are expected to further increase in the future (Mantau et al. 2010). This development can already be seen in Sweden (de Jong and Dahlberg 2017) and in Finland (Peltola 2014). In Finland, bioenergy production from forest chips made mainly from logging residues has multiplied by eight times since the year 2000, and placed forest chips as the most important solid wood fuel in Finland (Peltola 2014). Logging residues are an attractive source of bioenergy because the use of residues does not involve a change in land use nor cause a direct competition for land with food production. Hence, unlike

the use of agricultural biomass, the use of logging residues is not capped in the EU Renewable Energy directive and use of logging residues will likely expand (COM 2016).

Large-scale logging residue harvesting may pose a conflict with conservation efforts to protect deadwood-dependent species (Bouget et al. 2012, Ranius et al. 2018). In Fennoscandia approximately one quarter of forest species depend on deadwood (Siitonen 2001). Approximately half of the threatened forest species in Finland require forests rich in decaying wood (Hyvärinen et al. 2019). While national initiatives have been set to preserve and increase the amount of deadwood in forests to improve the state of biodiversity (Hjältén et al. 2010), simultaneous large-scale forest residue harvesting may result in further losses in already scarce deadwood resources and additional detrimental effects on deadwood-dependent species (e.g. Ranius et al. 2014, Johansson et al. 2016).

Previous studies indicate that logging residue harvesting for bioenergy causes habitat reduction and destruction and changes in the temporal availability of habitats of deadwood-dependent species, but the long-term impacts remain uninvestigated (Ranius et al. 2018). Previous empirical studies investigating the effects of forest bioenergy on biodiversity have focused mainly on short-term effects at the stand-level (de Jong & Dahlberg, 2017) or provided a snapshot field data at landscape level (Hiron et al. 2018). Modeling approaches have been introduced to investigate longer term impacts of logging residue extraction on deadwood (Verkerk et al. 2014; Hof et al. 2018a) or deadwood-dependent species (Geijer et al. 2014; Ranius et al. 2014; Johansson et al. 2016; Snäll et al. 2017). These modelling studies have either considered single forest stands or theoretical or real landscapes, and as response variables they have used the amount of dead

wood, the population development of real or theoretical model species, or the habitat amount for a wide range of saproxylic organisms based on their specialization to deadwood types. Studies investigating deadwood dynamics or changes in different deadwood types over time on larger landscapes with variation in initial, measured conditions are scarce. The information on deadwood types is important when assessing long-term impacts of logging residue harvesting, because both volume and diversity of deadwood affect the long-term sustainability of populations of deadwood-dependent species (Tikkanen et al. 2007). Hence, despite the large body of empirical research, little is still known about how forest biodiversity would respond to a large-scale removal of logging residues in the long term, and at the landscape scale. The lack of long-term studies limit our ability to predict the effects of harvesting logging residues on deadwood in two ways. First, only long-term studies are sufficient to capture the relatively slow process of wood decay dynamics. Second, year to year fluctuations in the deadwood diversity and abundance are common, and these fluctuations may mask the effects in short-term field experiments (Riffell et al. 2011).

The question whether bioenergy from logging residues truly mitigates climate change has been substantially debated both in public (Kangas et al. 2018) and in scientific forums (Agostini et al. 2013). An increasing number of studies show that logging residue extraction decreases the carbon stock and the sink capacity of forests, which reduces the climate benefits of replacing fossil fuels with bioenergy for years and decades (Agostini et al. 2013). However studies based on single stands may not reflect carbon dynamics in larger landscapes. While the carbon loss due to logging residue removal on individual stands is acknowledged, it may have not been considered problematic because other stands in the landscape could act as carbon sinks

95 compensating the carbon loss (Lamers and Junginger 2013). The initial age structure of the forest
96 stands affects the carbon balance of forest landscape (e.g. Routa et al. 2012). Hence, analyses on
97 larger landscapes are needed to investigate the effects of large-scale logging residue harvesting
98 on carbon dynamics.

99 A central question in the discussion on the effects of logging residue extraction is if landscape
100 level processes could counteract the adverse effects of residue extraction on carbon balance or
101 deadwood. Hence, even in landscapes where large-scale logging residue harvesting takes place,
102 different types of deadwood could be abundant or increasing in other parts of the landscape
103 where logging residue harvesting is not practiced (Lamers and Junginger 2013). This implies that
104 logging residue harvesting would not decrease deadwood availability for saproxylic species at
105 the landscape level. Similar arguments have been presented for forest carbon balance (Lamers
106 and Junginger 2013). Yet, studies quantifying both changes in forest carbon balance resulting
107 from logging harvesting and subsequent effects on the habitat availability of deadwood-
108 dependent species on larger landscapes are missing. In addition, it has not been investigated to
109 what extent forest stands that have a high bioenergy potential also have a high conservation
110 potential for red-listed, deadwood-dependent species. Evaluating this potential overlap in forest
111 values is important from the forest planning perspective.

112 The objectives of this study were to i) investigate how large-scale stump and slash harvesting for
113 bioenergy affects forest carbon balance and the quality and quantity of deadwood in a landscape,
114 ii) study how the changes in the deadwood affect the amount of suitable habitats of deadwood-
115 dependent species and iii) explore the overlap between areas of high bioenergy potential and
116 high conservation potential for selected deadwood-dependent species. To address these questions,

we modeled the forest carbon dynamics and the availability of different types of deadwood in a landscape over 100 years.

Material and Methods

Approach

To study the effect of large-scale forest residue harvesting on forest carbon balance and the habitat availability on deadwood-dependent species we simulated the development of forest stands in central Finland. Our study landscape consisted of four watersheds that differed in their productivity and age distribution (Table 1). The modelled landscape encompassed of ca. 11 000 hectares and was derived from 6 800 forest stands on mineral soils (Table 1). Measured forest data was provided by the Finnish Forest Center. Our simulation combined modelling of forest carbon budget, deadwood quality and quantity with information of species habitat associations. Species habitat associations modelled with habitat suitability indices were based on expert judgements (Tikkanen et al. 2006, 2007). Combining expert judgements with forest models has been used also in previous studies, but on individual stands (Dahlberg et al. 2011; Ranius et al. 2014). In addition, instead of a snapshot of time, our approach provided dynamic estimates of bioenergy resource, forest carbon balance, and the formation and the decay of different types of deadwood in larger forest landscapes

135 We simulated three scenarios i) with (BIO) and ii) without (BAU) forest residue harvesting for
 136 bioenergy, and iii) set aside (SA), which was used to study the conservation potential of these
 137 landscapes without management. In the BIO and BAU scenarios forest stands were managed
 138 according to the current forest management recommendations in Finland where forests were
 139 clear-cut at the age of 70-90 years (Äijälä et al. 2014). After final felling stands were artificially
 140 regenerated by planting or seeding. Stands were tended and thinned two to three times before the
 141 final felling. In the BIO scenario branches and treetops were harvested from thinnings and final
 142 fellings. In addition, stumps were extracted from all clear-cuts. We assumed that 70% of all
 143 available residues were harvested, which was consistent with the extraction percentage reported
 144 in field studies (Dahlberg et al. 2011), and with good practice guidance for forest residue
 145 harvesting in Finland (Koistinen et al. 2016). We assumed that logging residue harvesting
 146 increased the destruction and removal of snags and downed logs by 30% based on the
 147 observations of field studies (Hautala et al. 2004; Rudolphi and Gustafsson 2005; Rabinowitsch-
 148 Jokinen and Vanha-Majamaa 2010). To define the increase in destruction and removal in the
 149 modelling framework we used an iterative approach where we first estimated the baseline
 150 reduction in the annual deadwood input to be 60% in the BAU scenario. The rate of destruction
 151 and removal resulted deadwood pool values consistent with the measured values in the National
 152 Forest Inventory (Peltola 2014). High rate of deadwood destruction and removal are partly
 153 explained collection of firewood by forest owners. Foliage was assumed to be left in stands to
 154 prevent nutrient loss and corrosion in power plants (Alakangas et al. 2016). We assumed no
 155 effect on the growth of the next tree generation.

We predicted the forest growth and yield for each stand with a SIMO forest simulator for 100 years. The SIMO modelling framework consists of several models for describing natural processes, such as growth and mortality, and forestry operations. These models are documented in detail in the scientific literature (Kangas and Rasinmäki 2008). The growth and yield predictions were made using growth models by Hynynen et al. (2002), which were developed based on extensive data of field measurements in the National Forest Inventory. Therefore, the models based on this data cover all main tree species and forest site types in Finland (Hynynen et al. 2002). To predict the development of total biomass, simulated stem wood volumes were converted to estimates of total aboveground and belowground biomass through biomass models by Repola et al. (2007) within the SIMO framework. The SIMO model has been shown to produce equally good estimates of forest growth as another widely used Finnish forest simulator MOTTI (Mäkinen et al. 2008).

To estimate changes in litter and soil carbon stocks resulting from forest harvest residue extraction, the litter input from SIMO was used as input to the soil carbon model Yasso07 (Tuomi et al. 2011). Litter input to soil included input from thinnings and final fellings (Kangas and Rasinmäki 2008), natural mortality (Hynynen et al. 2002), and litter input from living trees (Liski et al. 2002). In addition, litter input from understory vegetation to soil was accounted for (Muukkonen and Mäkipää 2006). In the Yasso07 model the decomposition of organic matter depends on climate, litter type and litter diameter (Tuomi et al. 2011). We applied 2 cm diameter for all fine woody litter and an average diameter of 10 cm for coarse woody litter (Raumonen et al. 2011). The Yasso07 model calculates carbon stocks separately for each input type and the sum of these carbon stocks is the total litter and soil carbon stock. We used the carbon stock,

178 calculated from the coarse woody litter without the humus fraction, as a proxy for coarse woody
 179 debris.

180 The initial litter and soil carbon stocks were calculated by running the Yasso07 model to a steady
 181 state with an average litter input of current recommended rotation periods (Äijälä et al. 2014). To
 182 account for the different stand ages in the landscape in the initialization, the simulated steady-
 183 state carbon stocks were adjusted to match the site type and initial age. For this, soil carbon pools
 184 were estimated for different stand ages using the information about annual litter input of
 185 recommended rotation period. These values were assigned for stands based on stand age, site
 186 type and dominant species.

187 We estimated the potential of the forest landscape consisting of four watersheds to provide net
 188 CO₂ emissions reductions with bioenergy while taking into account the changes in forest carbon
 189 balance. Bioenergy potentials was calculated by applying net calorific values of 19.3 MJ kg dry
 190 biomass⁻¹ for stumps and 19.6 MJ kg dry biomass⁻¹ for branches and treetops (Alakangas et al.
 191 2016). The net caloric values were averages of different deciduous and coniferous species. The
 192 effect of bioenergy harvesting on the forest carbon balance was the difference between BAU and
 193 BIO scenarios. To show the magnitude of possible net emission reductions with bioenergy from
 194 forest harvest residues we applied the emission factor of 93 kg CO₂ GJ⁻¹ to coal (Statistics
 195 Finland 2019).

Modelling the changes in the available habitat for red-listed deadwood-dependent species

To simulate changes in the amount and the quality of snags and downed logs we linked predictions of the natural mortality (Hynynen et al. 2002) and decomposition through decay stages (1-5) of deadwood (Mäkinen et al. 2006). These models predict 1) initial wood density of the dead tree, 2) probability of dead tree being a snag or a downed log and 3) the change to successive decay class. Initial values for snags and downed deadwood were set to be consistent with the Finnish National Forest inventory data, which provided average volumes per hectare of snags and downed deadwood for tree species for Southern Finland (Peltola 2014). The initial values for snags and downed logs together ranged from 3.1 to 4.5 m³ ha⁻¹, and the values were assigned as initial values based on the dominant tree species on studied stands (Cajander 1949).

To study the effects of the scenarios on the availability of the habitats of selected red-listed deadwood dependent species we applied models for habitat suitability indices (HSIs) to calculate species conservation capacity (SCC). This resource-focused approach was chosen as the reduction of deadwood along with reduction of old-growth forests and decreasing number of large trees is the primary cause of threat to threatened forest species, and the second most important cause of regional extinctions in Finland (Hyvärinen et al. 2019). We applied HSI models that connect forest stand characteristics with habitat requirements of red-listed species. The HSI models developed by Tikkanen et al. (2006, 2007) have been created using expert opinion assessment in which Finnish experts in various taxa assessed the habitat preferences of the red-listed forest species in relation to predefined structures of forest stands and trees within stands. Then a total of 98 species were grouped to 27 groups according to their shared habitat requirements, which can be connected to stand characteristics modelled with a forest simulator

(Tikkanen et al. 2007). Each group is represented by one red-listed species that typifies the group (Tikkanen et al. 2007). The type species cover 11 fungi, 15 insect and one lichen species. The stand specific HSI of a type species is a product of deadwood resources, microclimate and temporal continuity of the resource (see Tikkanen et al. 2007 for equations). We estimated the combined SCC in different scenarios for each stand s for different HSIs describing stand quality for type species k (eq 1, Pakkala et al. 2002). The combined SCC is the weighted average of HSIs, in which the HSIs give the weights. The combined SCC was used as a proxy for a conservation capacity of a stand for all 27 type species for each year. Then the average combined SCC across landscape for each year was calculated for BAU, BIO and SA to compare scenarios. In addition, to study the effect of residue harvesting on HSIs of different type species, we calculated type species-specific vulnerability to residue harvesting with the methodology introduced by Mazziotta et al. (2016). Type species-specific SCC were calculated to form a proxy for the conservation capacity of all stands for each type species and year in BIO and BAU scenarios. Vulnerabilities were calculated as the differences in the species-specific SCC across stands between BIO and BAU scenarios for each year. These vulnerabilities were summarized across landscape and time for different combinations of species requirements for deadwood resource and microclimate.

$$SCC_s = \sum_{k=1}^{27} ((HSI_s)^2)_k / \sum_{k=1}^{27} (HSI_s)_k \quad (1)$$

Relationships between areas of high bioenergy potential and high potential conservation capacity

We identified stands with high bioenergy potential and high conservation capacity by classifying stands by combined SCC values in the set aside scenario, and by bioenergy potential in the bioenergy scenario to top 10 % quantiles. This threshold was chosen because the 10% quantiles have been used to identify important sites for conservation planning and ecosystem service hotspots (Schröter et al. 2017). The stands were classified to the highest class if the value was over the highest-class threshold at any point of the simulation period.

Results

Changes in forest carbon stocks and balance

Forest residue harvesting for bioenergy reduced litter and soil carbon stocks on average 3.5 tC ha⁻¹ the beginning of the simulation period and up to 12 tC ha⁻¹ after 100 years. This carbon loss corresponded to a 3-9% decrease in the size of litter and soil carbon stock. Logging residue harvesting reduced the average amount of coarse woody debris 15-31% per hectare. Development of total carbon stocks varied across watersheds in response to initial age distribution and site productivity. Nevertheless, the reduction in the litter and soil carbon stocks resulting from residue harvesting was of the same order of magnitude in all watersheds, hence the results were presented for all four watersheds together.

Producing bioenergy from forest residues reduced fossil fuel emissions, but also reduced the forest carbon sink compared to scenario where residues were left in place (Figure 1). The annual average bioenergy potential to replace fossil fuels in the landscape of four watersheds ranged from 323 to 1100 TJ year⁻¹ depending on timber harvests in different years. Harvesting stumps, branches and treetops for bioenergy reduced the carbon sink of the landscape (Figure 1, white

bars). Although bioenergy reduced fossil fuel emissions (Figure 1 grey bars), the decrease in the carbon sink reduced the net emission savings. Since the logging residues would release CO₂ even if left to decompose in the forest, the negative effect on the forest sink decreased over time. Hence, after ten years the decrease in the carbon sink reduced the net emission savings 53%, 12% after 50 years and 2% after 100 years (Figure 1, grey and black bars).

Changes in deadwood and the habitat availability for deadwood-depended species

The destruction and removal of snags and logs resulting from logging residue extraction reduced the average amount of deadwood in the landscape 1 – 3.7 m³ ha⁻¹ during the simulation period, and changed the quality of deadwood, especially reducing the amount of recently killed logs or snags of coniferous species (Figure 2) compared to management without residue harvesting. The average relative reduction in the BIO scenario compared to BAU was the largest in recently died spruce logs and snags (-43, and -41%), recently died deciduous logs (-38%) and the smallest in almost totally decayed pine logs (-19%) during the study period. Residue harvesting caused bottlenecks in the availability of at least one deadwood type (volume < 0.001 m³ ha⁻¹) on 185–2724 forest stands, which corresponds to 0.07 – 1.7% increase in bottlenecks compared to the BAU scenario. Deadwood was generally a scarce resource in the simulated landscapes with the average total amount of deadwood ranging from 2.2 to 10.1 m³ ha⁻¹ in the BAU scenario. In the set aside scenario, average total amount of deadwood in the landscape was 6 –73 m³ ha⁻¹. Hence, the set aside landscape had 2.5 – 33 times more deadwood per hectare than the same landscapes managed according to the current recommendations. Logging residue harvesting further increased this difference.

Logging residue extraction reduced the combined species conservation capacity of the landscape for the selected deadwood-depended type species on average by 15 – 21% compared to BAU and 32-54% compared to the set aside scenario (Figure 3). The species-specific vulnerabilities to residue harvesting were up to 8% during the simulation period. No large differences in the vulnerability to residue harvesting were observed between different type species (Figure 4). Consequently, irrespective of the specific resource or microclimatic associations of the species, bioenergy harvesting reduced the ability of the landscape to provide habitats for the studied red-listed species.

Relationships between high bioenergy and conservation potential

In the data 17% of stands had both the greatest conservation capacity and the greatest potential for bioenergy exploitation when threshold for the highest potentials were set to top 10% quantile (Figure 5). However, 31% of the forest stands had high bioenergy potential but low conservation potential. Herb-rich heath forests, with Norway spruce as the dominant species, had both the highest bioenergy and the highest conservation potential. Alternatively these characteristics applied also to stands with the highest bioenergy and the lowest conservation potential (Figure 5). Hence, simple forest characteristics such as site type or stand age did not identify stands with high bioenergy potential and high/low conservation potential.

Discussion

In this study logging residue harvesting reduced both forest carbon stock and carbon sink capacity of forest landscapes, and decreased deadwood compared to business as usual management without bioenergy harvesting. Logging residue harvesting reduced the amount of snags and logs in different decay stages at landscape scale faster than these deadwood resources

were formed, and the same applied to litter and soil carbon stocks. Hence, large-scale logging residue harvesting increased the outflow of carbon and deadwood from the system compared to business as usual management. Our results show that logging residue harvesting decreases carbon stocks and deadwood availability for saproxylic species even when carbon dynamics are analyzed on landscape level instead of individual stands. These findings corroborate the findings of other studies on stand (e.g. Ranius et al 2011) and landscape level (e.g. Johansson et al. 2016, Hiron et al. 2018)

Changes in the forest carbon balance resulting from logging residue harvesting reduced the climate benefits of bioenergy and resulted in delayed emissions savings. The results support the earlier studies on different scales ranging from forest stands (Zanchi et al. 2012) to forest landscapes (McKechnie et al. 2011) and countries (Repo et al. 2015a) showing that bioenergy from logging residues is not carbon or climate neutral, and that emission savings with bioenergy come with a delay. In our study after the first decade of residue harvesting changes in carbon balance reduced the net emissions savings by half compared to fossil carbon savings. Reductions of similar magnitude in emission savings were reported by Forsius et al. (2016) in their study conducted in the same region. During the simulation period, the forest carbon stock of the landscape increased in all scenarios because of initial conditions of the studied landscape. Although initial age distribution and site productivity affected the forest carbon dynamics (Routa et al. 2012), accounting for these factors did not compensate for the reduction in the carbon stocks due to bioenergy harvesting. We assumed that logging residue harvesting does not affect the growth of the next tree generation. Field experiments on whole-tree harvesting report no effect and negative effects of tree growth after final felling (Thiffault et al. 2011) and growth

losses after repeated whole-tree harvesting (Kaarakka et al. 2014). If forest residue harvesting caused growth loss, the effects on carbon balance would be more pronounced.

Logging residue harvesting, and the associated destruction of snags and downed logs, halved the amount of some decay classes of logs and snags, and reduced the amount of coarse woody debris for up to one third. Field studies have reported an additional damage, or an immediate loss of deadwood, due to logging residue harvesting ranging from 25 to 88% depending on the definition of deadwood (Eräjää et al. 2010; Rabinowitsch-Jokinen and Vanha-Majamaa 2010). Some field studies have highlighted the destruction of moderately and well-decayed coarse woody debris (Rabinowitsch-Jokinen and Vanha-Majamaa 2010, Work et al. 2014), while in the current study the largest relative reduction was in the fresh deadwood. In general, in our study the average reduction in the coarse woody debris was lower than reported in field studies. The use of different definitions for deadwood and decay classes make direct comparisons to other studies challenging.

Logging residue harvesting and the associated destruction of snags and downed deadwood reduced the combined species conservation capacity of the landscape for deadwood-dependent red-listed species by one fifth compared to the general effect of forest management. The result may be an under- or overestimation because of limited empirical data on the on additional effect of residue harvesting on destruction and removal of large-diameter deadwood. However, our results highlight the importance of considering this potential loss of large-diameter deadwood in bioenergy harvesting operations. In Finland and Sweden, the majority of declining and red-listed deadwood-dependent species are associated with coarse woody debris rather than with fine

346 woody debris (Siitonen 2001). As none of the red-listed species in Sweden is primarily
347 associated with branches and tree tops of Norway spruce, a review study by de Jong and
348 Dahlberg (2017) suggested that harvesting logging residues of conifers has small to negligible
349 additional impacts on species of conservation interests in Sweden with current extraction levels.
350 However, our study suggests that the long-term impacts of extensive residue harvesting, and the
351 associated removal and destruction of large-diameter deadwood are important. Since the
352 investigated species are largely red-listed because of the reduction in deadwood (Hyvärinen et al.
353 2019), a further reduction of suitable habitats because of bioenergy harvesting operations may
354 have detrimental effects on these species.

355 Our study indicates that combating climate change with bioenergy makes halting biodiversity
356 loss increasingly difficult. In a study by Snäll et al. (2017), stump harvesting for bioenergy
357 caused a rapid decline in lichen metapopulations rendering many currently common lichen
358 species red-listed within two to three decades in Sweden. However, since the lichen
359 metapopulations stabilized at lower equilibrium levels of the stump resource after few decades
360 and climate benefits of stump bioenergy increased with time, Snäll et al. (2017) argued that the
361 trade-off between biodiversity conservation and climate change mitigation with stump bioenergy
362 is transient. This conclusion may result from the assuming a sudden increase in stump harvesting
363 from zero to 50% (Snäll et al. 2017). A slower increase in harvest levels might result in a
364 different conclusion. However, concluding that the trade-off is transient would mean accepting
365 permanently lower population levels for common species. Even if somewhat lower population
366 size does not cause high risk to the common species themselves, it may potentially cause losing
367 some of the specialist species that are dependent on the presence of the common ones. Many

saproxyllic species are, for example, dependent on the so-called priority effects, where a preceding species changes the physiochemical conditions of the deadwood suitable for successor species (Weslien et al. 2011). It has been shown that the successor suffers more of the reduced availability of the resources (Abrego et al. 2017).

Moreover, permanently lower resource availability may be detrimental for species that are already red-listed or depend on specific deadwood types. Our study indicates that logging residue harvesting, and the associated additional deadwood destruction may increase temporal breaks in the availability of the deadwood resources at the landscape scale. These breaks may make the effects of bioenergy harvesting more severe because deadwood continuity has been shown to affect deadwood-dependent biodiversity (Nordén et al. 2014). If such a break happens on a large enough area, some of the specialist species may be totally lost. Johansson et al. (2016) showed that harvesting stumps on 20% of the clear-cuts of the landscape increases extinction risk of rare specialist species to 50%, and further increasing stump extraction to 30% of the clear-cuts negatively affects common species. Thus, extensive logging residue harvesting not only makes halting biodiversity loss less likely, but also increases the likelihood of extinctions of currently threatened species and may put currently common species under risk of becoming threatened.

We assessed the reliability of our results by comparing estimates of different modelling steps to independent data. The changes in the carbon balance due to logging residue harvesting result from changes in the litter and soil carbon pool, and the size of the soil carbon pool is determined by litter input and the decay rate of organic matter decomposition. The annual litter input estimates ranged from 1.4 – 3.9 tC ha⁻¹ year⁻¹, which is consistent with other estimates for

Southern Finland based on net primary production (Härkönen et al. 2010), litter measurements
 (Ukonmaanaho et al. 2008; Ilvesniemi et al. 2009), and with other modelling frameworks (Repo
 et al. 2015a; Lehtonen et al. 2016). The soil carbon stock estimates were within the range 40–
 149 tC ha⁻¹ reported for Southern Finland in other studies (Rantakari et al. 2012; Repo et al.
 2015a; Lehtonen et al. 2016). The annual changes in the litter and soil carbon pool were
 modelled with a soil carbon model, which produced stock change estimates and uncertainty
 estimates of similar magnitude as other models or soil measurements (Rantakari et al. 2012;
 Ortiz et al. 2013). The average logging residue potentials per hectare were consistent with
 previous modelling and field studies (Eräjää et al. 2010; Repo et al. 2015b). The quantitative
 estimates of net emission savings that can be obtained with forest bioenergy depend on the
 diameters of residues harvested, time scales studied, energy content of forest chips and the fossil
 fuel replaced (Repo et al. 2012; Alakangas et al. 2016). However, this study shows the
 magnitude and time dynamics of the emission savings at landscape scale when forests are
 managed and residues extracted following the current recommendations. It is important to note
 that species conservation capacity was derived from potential availability of suitable habitats
 produced by model and habitat preferences based on expert judgment and our model predictions
 would benefit from validation in field. However, the main findings were consistent with results
 from a field study in Sweden (Hiron et al. 2018)

Setting safe thresholds for forest residue harvesting requires answering three questions: 1) Where
 to extract logging residues? 2) Which residues to harvest? 3) How much to harvest? To
 minimize negative impacts on biodiversity logging residue harvesting should be targeted in
 stands with low ecological values and avoided in stands with high ecological values (Bouget et

al. 2012). In this study, approximately every sixth stand had both high conservation potential and high bioenergy potential indicating a potential conflict between bioenergy and biodiversity objectives. However, almost one third of stands were characterized by high bioenergy but low conservation potential. Identifying these stands would be a useful way to avoid the conflict. However, our results suggest that stand characteristics, such as the main tree species, stand age and site type alone cannot separate high and low biodiversity potential. Therefore, more precise proxies will be needed for planning sustainable bioenergy harvesting. Regarding which residues to harvest, extracting fast decomposing, small diameter branches for bioenergy has shown to have smaller climate warming impact than producing bioenergy from slowly decaying stumps (Repo et al. 2012). While from the perspective of climate change mitigation focusing residue harvesting on fast decomposing branches might be beneficial, also small diameter branches have been shown to host specialist species (Juutilainen et al. 2014). Generally, de Jong et al. (2014) suggested that extracting branches and tops of Norway spruce is less problematic from biodiversity perspective than harvesting stumps. However, in this study the stumps constituted 27–55% of the bioenergy potential. Hence, meeting the increasing bioenergy demand needs with only branches requires more hectares for logging residue extraction, which may cause additional destruction of large diameter deadwood from larger areas. The intensity of residue extraction can be considered at the level of individual forest stands and at the level landscapes (Root and Betts 2016). Root & Betts (2016) argued that the question of intensity of residue extraction should be addressed at the landscape scale, since it is not possible to maintain all biodiversity and ecosystem functions at the stand scale. A Swedish expert group concluded that extracting slash on more than 50% or stumps on more than 10-30% of the harvested stands increases

species extinction risk (de Jong et al. 2017), and consequently pointed out a need for landscape level planning of residue extraction.

Logging residue harvesting is in conflict with the ongoing efforts to increase the amount of deadwood in forests to ensure the favorable state for biodiversity. In the short-term bioenergy from forest residues does not result in deep emission reductions, and it puts a small, but additional, pressure on species already at risk with current forest management practices. Global studies show that biodiversity is likely suffer, if cropland expansion for bioenergy is a major component of climate change mitigation (Hof et al. 2018b). Our study together with previous studies (e.g. Hiron et al. 2018), indicates that biodiversity may be at risk because of bioenergy even without land-use change when forest land stays as forest land but the harvesting intensity is increased. While guidance to good practices in energy wood harvesting along with forest certification and legislation offer tools to minimize negative effects of forest bioenergy harvesting on biodiversity and forest carbon balance, they are likely insufficient in preventing further losses. Landscape level forest management and residue extraction planning, avoiding additional destruction or removal of large-diameter deadwood, setting aside land for conservation and new schemes for compensating deadwood or soil carbon loss may offer ways forward.

Acknowledgements

The work was supported by the Finnish Ministry of Agriculture and Forestry, and by European Union through the ERA-NET SumForest program (FutureBioEcon - Sustainable future of European Forests for developing the bioeconomy, Dnro 302/03.02.06/2017), the Strategic

454 Research Council (SRC) at the Academy of Finland (n:o 312559), Kone Foundation (KOMET,
455 no 087124) and the Academy of Finland (n:o 322066). We thank anonymous reviewers for their
456 valuable comments.

References

- Abrego, N., Dunson, D., Halme, P., Salcedo, I., and Ovaskainen, O. 2017. Wood-inhabiting fungi with tight associations with other species have declined as a response to forest management. *Oikos* (126): 269–275. doi:10.1111/oik.03674.
- Agostini, A., Giuntoli, J., and Boulamanti, A. 2013. Carbon accounting of forest bioenergy. *In* JRC Technical Report. Joint Research Centre of the European Commission, Ispra. doi:10.2788/29442.
- Äijälä, O., Koistinen, A., Sved, J., Vanhatalo, K., and Väisänen, P. 2014. Metsänhoidon suositukset. [The good practice guidance to forestry, (in Finnish)]. Metsäkustannus Oy, Forestry Development Centre Tapio, Helsinki.
- Alakangas, E., Hurskainen, M., and Raatikainen-Luntama, J. & Korhonen, J. 2016. Properties of indigenous fuels in Finland. *VTT Technol.* **272**: 222. Available from <http://www.vtt.fi/inf/pdf/technology/2016/T272.pdf>.
- Bouget, C., Lassauce, A., and Jonsell, M. 2012. Effects of fuelwood harvesting on biodiversity — a review focused on the situation in Europe. *Can. J. For. Res.* **42**(8): 1421–1432. doi:10.1139/x2012-078.
- Cajander, A.K. 1949. Forest types and their significance. *Acta For. Fenn.* **56**: 1–71.

- COM. 2016. Proposal for a directive of the European Parliament and the of the Council on the promotion of the use of energy from renewable sources. Available from <http://eur-lex.europa.eu/legal-content/EN/TXT/HTML/%3Furi%3DCELEX:52016PC0767%26from%3DEN>.
- Dahlberg, A., Thor, G., Allmér, J., Jonsell, M., Jonsson, M., Ranius, T., Allmé, rJohan, Jonsell, M., Jonsson, M., Ranius, T., Allmér, J., Jonsell, M., Jonsson, M., and Ranius, T. 2011. Modelled impact of Norway spruce logging residue extraction on biodiversity in Sweden. *Can. J. For. Res.* **41**(6): 1220–1232. NRC Research Press. doi:10.1139/x11-034.
- EASAC. 2017. Multi-functionality and sustainability in the European Union’s forests. EASAC policy Rep. 32. April 2017. (April): 51.
- Eräjää, S., Halme, P., Kotiaho, J.S., Markkanen, A., and Toivanen, T. 2010. The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. *Silva Fenn.* **44**(2): 203–211.
- Forsius, M., Akujärvi, A., Mattsson, T., Holmberg, M., Punttila, P., Posch, M., Liski, J., Repo, A., Virkkala, R., and Vihervaara, P. 2016. Modelling impacts of forest bioenergy use on ecosystem sustainability: Lammi LTER region, southern Finland. *Ecol. Indic.* **65**: 66–75. doi:10.1016/j.ecolind.2015.11.032.
- Geijer, E., Andersson, J., and Bostedt, G. 2014. Safeguarding species richness vs . increasing the use of renewable energy — The effect of stump harvesting on two environmental goals. *J.*

- 494 For. Econ. **20**(2): 111–125. Elsevier GmbH. doi:10.1016/j.jfe.2014.01.001.
- 495 Härkönen, S., Pulkkinen, M., Duursma, R., and Mäkelä, A. 2010. Estimating annual GPP, NPP
496 and stem growth in Finland using summary models. For. Ecol. Manage. **259**: 524–533.
- 497 Hautala, H., Jalonen, J., Laaka-Lindberg, S., and Vanha-Majamaa, I. 2004. Impacts of retention
498 felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland.
499 Biodivers. Conserv. **13**(8): 1541–1554. Kluwer Academic Publishers-Plenum Publishers.
500 doi:10.1023/B:BIOC.0000021327.43783.a9.
- 501 Hiron, M., Jonsell, M., Kubart, A., Thor, G., Schroeder, M., Dahlberg, A., Johansson, V., and
502 Ranius, T. 2017. Consequences of bioenergy wood extraction for landscape-level
503 availability of habitat for dead wood-dependent organisms. J. Environ. Manage. **198**: 33–42.
504 doi:10.1016/j.jenvman.2017.04.039
- 505 Hjältén, J., Stenbacka, F., and Andersson, J. 2010. Saproxylic beetle assemblages on low stumps,
506 high stumps and logs: Implications for environmental effects of stump harvesting. For.
507 Ecol. Manage. **260**(7): 1149–1155. doi:10.1016/j.foreco.2010.07.003.
- 508 Hof, A.R., Löfroth, T., Rudolphi, J., Work, T., and Hjältén, J. 2018a. Simulating long-term
509 effects of bioenergy extraction on dead wood availability at a landscape scale in Sweden.
510 Forests **9**(8). doi:10.3390/f9080457
- 511 Hof, C., Voskamp, A., Biber, M.F., Böhning-Gaese, K., Engelhardt, E.K., Niamir, A., Willis,
512 S.G., and Hickler, T. 2018b. Bioenergy cropland expansion may offset positive effects of

- climate change mitigation for global vertebrate diversity. *Proc. Natl. Acad. Sci. U. S. A.* 115(52): 13294–13299. doi:10.1073/pnas.1807745115.
- Hynynen, J., Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H., and Haapala, P. 2002. Models for predicting stand development in MELA system. *Metsäntutkimuslaitoksen Tied.* **835**.
- Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., and Liukko, U.-M. 2019. The 2019 Red List of Finnish Species. *Ympäristöministeriö & Suomen ympäristökeskus, Helsinki*.
- Ilvesniemi, H., Levula, J., Ojansuu, R., Kolari, P., Kulmala, L., Pumpanen, J., Launiainen, S., Vesala, T., and Nikinmaa, E. 2009. Long-term measurements of the carbon balance of a boreal Scots pine dominated forest ecosystem. *Boreal Environ. Res.* **14**: 731– 753.
- Johansson, V., Felton, A., and Ranius, T. 2016. Long-term landscape scale effects of bioenergy extraction on dead wood-dependent species. *For. Ecol. Manage.* **371**: 103–113. Elsevier B.V. doi:10.1016/j.foreco.2015.10.046.
- de Jong, J., Akselsson, C., Berglund, H., Egnell, G., Gerhardt, K., Lönnberg, L., Olsson, B., and von Stedingk, H. 2014. Consequences of an increased extraction of forest biofuel in Sweden Summary of the synthesis report. : 38. doi:IEA Bioenergy Task 43, Report 2014:TR01.
- de Jong, J., Akselsson, C., Egnell, G., Löfgren, S., and Olsson, B.A. 2017. Realizing the energy potential of forest biomass in Sweden – How much is environmentally sustainable? *For. Ecol. Manage.* **383**: 3–16. doi:10.1016/j.foreco.2016.06.028.

- de Jong, J., and Dahlberg, A. 2017. Impact on species of conservation interest of forest harvesting for bioenergy purposes. *For. Ecol. Manage.* **383**: 37–48. Elsevier B.V. doi:10.1016/j.foreco.2016.09.016.
- Juutilainen, K., Mönkkönen, M., Kotiranta, H., and Halme, P. 2014. The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *For. Ecol. Manage.* **313**: 283–291. Elsevier B.V. doi:10.1016/j.foreco.2013.11.019.
- Kaarakka, L., Tamminen, P., Saarsalmi, A., Kukkola, M., Helmisaari, H.-S.S., and Burton, A.J. 2014. Effects of repeated whole-tree harvesting on soil properties and tree growth in a Norway spruce (*Picea abies* (L.) Karst.) stand. *For. Ecol. Manage.* **313**(0): 180–187. Elsevier B.V. doi:10.1016/j.foreco.2013.11.009.
- Kangas, A., and Rasinmäki, J. 2008. SIMO - Adaptable Simulation and Optimization for Forest Management Planning. University of Helsinki, Department of Forest Resource Management Publications 41.
- Kangas, H.-L., Lyytimäki, J., Saarela, S.R., and Primmer, E. 2018. Burning roots: Stakeholder arguments and media representations on the sustainability of tree stump extraction in Finland. *Biomass and Bioenergy* **118**(May): 65–73. Elsevier Ltd. doi:10.1016/j.biombioe.2018.08.006.
- Koistinen, A., Luiro, J.-P., and Vanhatalo, K. 2016. Metsänhoidon suositukset energiapuun

korjuuseen, työopas [Good practice guidance for energywood harvesting (in Finnish)].
Tapio.

Lamers, P., and Junginger, M. 2013. The ‘debt’ is in the detail: A synthesis of recent temporal
forest carbon analyses on woody biomass for energy. *Biofuels, Bioprod. Biorefining* **7**:
373–385. doi:10.1002/bbb.1407.

Lehtonen, A., Linkosalo, T., Peltoniemi, M., Sievänen, R., Mäkipää, R., Tamminen, P., Salemaa,
M., Nieminen, T., Ľupek, B., Heikkinen, J., and Komarov, A. 2016. Forest soil carbon stock
estimates in a nationwide inventory: evaluating performance of the ROMULv and Yasso07
models in Finland. *Geosci. Model Dev.* **9**(11): 4169–4183. doi:10.5194/gmd-9-4169-2016.

Liski, J., Perruchoud, D., and Karjalainen, T. 2002. Increasing carbon stocks in the forest soils of
western Europe. *For. Ecol. Manage.* **169**(1–2): 159–175. doi:10.1016/S0378-
1127(02)00306-7.

Mäkinen, A., Kangas, A., Kalliovirta, J., Rasinmäki, J., and Välimäki, E. 2008. Comparison of
treewise and standwise forest simulators by means of quantile regression. *For. Ecol.
Manage.* **255**(7): 2709–2717. doi:10.1016/j.foreco.2008.01.048.

Mäkinen, H., Hynynen, J., Siitonen, J., and Sievanen, R. 2006. Predictin the decomposition of
Scots Pine, Norway spruce and Birch stems in Finland. *Ecol. Appl.* **16**(5): 1865–1879.
doi:10.1890/1051-0761(2006)016[1865:PTDOSP]2.0.CO;2.

Mantau, U., Saal, U., Prins, K., Steierer, F., Lindner, M., Verkerk, H., Eggers, J., Leek, N.,

- 569 Oldenburger, J., Asikainen, A., and Anttila, P. 2010. EUwood - Real potential for changes
570 in growth and use of EU forests. Final report. EUwood (June): 106p. doi:TREN/D2/491-
571 2008.
- 572 Mazziotta, A., Triviño, M., Tikkanen, O.-P., Kouki, J., Strandman, H., and Mönkkönen, M.
573 2016. Habitat associations drive species vulnerability to climate change in boreal forests.
574 *Clim. Change* **135**(3–4): 585–595. Springer Netherlands. doi:10.1007/s10584-015-1591-z.
- 575 McKechnie, J., Colombo, S., Chen, J., Mabee, W., and MacLean, H.L. 2011. Forest bioenergy or
576 forest carbon? Assessing trade-offs in greenhouse gas mitigation with wood-based fuels.
577 *Environ. Sci. Technol.* **45**(2): 789–795. doi:10.1021/es1024004.
- 578 Muukkonen, P., and Mäkipää, R. 2006. Empirical biomass models of understorey vegetation in
579 boreal forests according to stand and site attributes. *Boreal Environ. Res.* **11**(5): 355–369.
580 Available from file:///000241915400003.
- 581 Nordén, B., Dahlberg, A., Brandrud, T.E., Fritz, Ö., Ejrnaes, R., and Ovaskainen, O. 2014.
582 Effects of ecological continuity on species richness and composition in forests and
583 woodlands: A review. *Écoscience* **21**(1): 34–45. Taylor & Francis. doi:10.2980/21-1-3667.
- 584 Ortiz, C.A., Liski, J., Gärdenäs, A.I., Lehtonen, A., Lundblad, M., Stendahl, J., Ågren, G.I., and
585 Karlton, E. 2013. Soil organic carbon stock changes in Swedish forest soils—A comparison
586 of uncertainties and their sources through a national inventory and two simulation models.
587 *Ecol. Modell.* **251**: 221–231. doi:10.1016/j.ecolmodel.2012.12.017.

- 588 Pakkala, T., Hanski, I., and Tomppo, E. 2002. Spatial ecology of the three-toed woodpecker in
589 managed forest landscapes. *Silva Fenn.* **36**(1): 279–288.
- 590 Peltola, A. 2014. Finnish Statistical Yearbook of Forestry 2014. Finnish Forest Research
591 Institute. : 428 p. doi:ISBN: 978-956-318-098-5.
- 592 Rabinowitsch-Jokinen, R., and Vanha-Majamaa, I. 2010. Immediate Effects of Logging,
593 Mounding and Removal of Logging Residues and Stumps on Coarse Woody Debris in
594 Managed Boreal Norway Spruce Stands. *Silva. Fenn.* **44**(1): 51–62.
- 595 Ranius, T., Caruso, A., Jonsell, M., Juutinen, A., Thor, G., and Rudolphi, J. 2014. Dead wood
596 creation to compensate for habitat loss from intensive forestry. *Biol. Conserv.* **169**: 277–
597 284. doi:10.1016/j.biocon.2013.11.029.
- 598 Ranius, T., Hämäläinen, A., Egnell, G., Olsson, B., Eklöf, K., Stendahl, J., Rudolphi, J., Sténs,
599 A., and Felton, A. 2018. The effects of logging residue extraction for energy on ecosystem
600 services and biodiversity: A synthesis. *J. Environ. Manage.* 209: 409–425. Elsevier Ltd.
601 doi:10.1016/j.jenvman.2017.12.048.
- 602 Rantakari, M., Lehtonen, A., Linkosalo, T., Tuomi, M., Tamminen, P., Heikkinen, J., Liski, J.,
603 Mäkipää, R., Ilvesniemi, H., and Sievänen, R. 2012. The Yasso07 soil carbon model –
604 Testing against repeated soil carbon inventory. *For. Ecol. Manage.* **286**: 137–147. Elsevier
605 B.V. doi:10.1016/j.foreco.2012.08.041.
- 606 Raumonen, P., Kaasalainen, S., Kaasalainen, M., and Kaartinen, H. 2011. Approximation of

- 607 volume and branch size distribution of trees from laser scanner data. *Int. Arch.*
 608 *Photogramm. Remote Sens. Spat. Sci.* **38(5/W12)**.
- 609 Repo, A., Böttcher, H., Kindermann, G., and Liski, J. 2015a. Sustainability of forest bioenergy in
 610 Europe: Land-use-related carbon dioxide emissions of forest harvest residues. *GCB*
 611 *Bioenergy* **7(4)**: 877–887. doi:10.1111/gcbb.12179.
- 612 Repo, A., Känkänen, R., Tuovinen, J.P., Antikainen, R., Tuomi, M., Vanhala, P., and Liski, J.
 613 2012. Forest bioenergy climate impact can be improved by allocating forest residue
 614 removal. *GCB Bioenergy* **4(2)**: 202–212. doi:10.1111/j.1757-1707.2011.01124.x.
- 615 Repo, A., Tuovinen, J.-P.J.-P., and Liski, J. 2015b. Can we produce carbon and climate neutral
 616 forest bioenergy? *Glob. Chang. Biol. Bioenergy* **7(2)**: 253–262. doi:doi:
 617 10.1111/gcbb.12134.
- 618 Repola, J., Ojansuu, R., and Kukkola, M. 2007. Biomass functions for Scots pine, Norway
 619 spruce and birch in Finland.
- 620 Riffell, S., Verschuyt, J., Miller, D., and Wigley, T.B. 2011. Biofuel harvests, coarse woody
 621 debris, and biodiversity – A meta-analysis. *For. Ecol. Manage.* **261(4)**: 878–887.
 622 doi:10.1016/j.foreco.2010.12.021.
- 623 Root, H.T., and Betts, M.G. 2016. Managing Moist Temperate Forests for Bioenergy and
 624 Biodiversity. *J. For.* **114(1)**: 66–74. Oak Ridge National Laboratory, Oak Ridge, TN.
 625 doi:10.5849/jof.14-114.

- 626 Routa, J., Kellomäki, S., and Peltola, H. 2012. Impacts of Intensive Management and Landscape
627 Structure on Timber and Energy Wood Production and net CO₂ Emissions from Energy
628 Wood Use of Norway Spruce. *BioEnergy Res.* **5**(1): 106–123. doi:10.1007/s12155-011-
629 9115-9.
- 630 Rudolphi, J., and Gustafsson, L. 2005. Effects of forest-fuel harvesting on the amount of
631 deadwood on clear-cuts. *Scand. J. For. Res.* **20**(3): 235–242. Taylor & Francis.
632 doi:10.1080/02827580510036201.
- 633 Schröter, M., Kraemer, R., Ceaușu, S., Rusch, G.M., Ceaușu, S., and Rusch, G.M. 2017.
634 Incorporating threat in hotspots and coldspots of biodiversity and ecosystem services.
635 *Ambio* **46**(7): 756–768. doi:10.1007/s13280-017-0922-x.
- 636 Schulze, E.-D.D., Körner, C., Law, B.E., Haberl, H., and Luyssaert, S. 2012. Large-scale
637 bioenergy from additional harvest of forest biomass is neither sustainable nor greenhouse
638 gas neutral. *GCB Bioenergy* **4**(6): 611–616. doi:10.1111/j.1757-1707.2012.01169.x.
- 639 Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms:
640 Fennoscandian boreal forests as an example. *Ecol. Bull.* **49**: 11–41.
- 641 Snäll, T., Johansson, V., Jönsson, M., Ortiz, C., Hammar, T., Caruso, A., Svensson, M., and
642 Stendahl, J. 2017. Transient trade-off between climate benefit and biodiversity loss of
643 harvesting stumps for bioenergy. *GCB Bioenergy* **9**: 1751–1763. doi:10.1111/gcbb.12467.
- 644 Statistics Finland. 2019. Fuel classificaton 2019. Available from

- 645 https://www.stat.fi/tup/khkinv/khkaasut_polttoaineluokitus.html [accessed 25 February
646 2019].
- 647 Szabó, M., Jäger-Waldau, A., Monforti-Ferrario, F., Scarlat, N., Bloem, H., Quicheron, M.,
648 Huld, T., and Ossenbrink, H. 2011. Technical Assessment of the renewable energy action
649 plans. European Commission, Luxemburg. Available from
650 http://zotero.org/support/quick_start_guide.
- 651 Thiffault, E., Hannam, K.D., Paré, D., Titus, B.D., Hazlett, P.W., Maynard, D.G., and Brais, S.
652 2011. Effects of forest biomass harvesting on soil productivity in boreal and temperate
653 forests — A review. *Environ. Rev.* **19**(NA): 278–309. doi:10.1139/a11-009
- 654 Tikkanen, O.-P., Heinonen, T., Kouki, J., and Matero, J. 2007. Habitat suitability models of
655 saproxylic red-listed boreal forest species in long-term matrix management: Cost-effective
656 measures for multi-species conservation. *Biol. Conserv.* **140**(3–4): 359–372.
657 doi:10.1016/j.biocon.2007.08.020.
- 658 Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K., and Kouki, J. 2006. Red-listed
659 boreal forest species of Finland: associations with forest structure, tree species, and
660 decaying wood. *Ann. Zool. Fennici* **43**(4): 373–383.
- 661 Tuomi, M., Laiho, R., Repo, A., and Liski, J. 2011. Wood decomposition model for boreal
662 forests. *Ecol. Modell.* **222**(3): 709–718. doi:10.1016/j.ecolmodel.2010.10.025.
- 663 Ukonmaanaho, L., Merilä, P., Nöjd, P., and Nieminen, T.M. 2008. Litterfall production and

- 664 nutrient return to the forest floor in Scots pine and Norway spruce stands in Finland. *Boreal*
665 *Environ. Res.* **13**(SUPPL. B): 67–91. doi:10.1523/JNEUROSCI.2692-08.2008.
- 666 Verkerk, P.J.J., Mavsar, R., Giergiczny, M., Lindner, M., Edwards, D., and Schelhaas, M.J.J.
667 2014. Assessing impacts of intensified biomass production and biodiversity protection on
668 ecosystem services provided by European forests. *Ecosyst. Serv.* **9**: 155–165. Elsevier.
669 doi:10.1016/j.ecoser.2014.06.004.
- 670 Weslien, J., Djupström, L.B., Schroeder, M., and Widenfalk, O. 2011. Long-term priority effects
671 among insects and fungi colonizing decaying wood. *J. Anim. Ecol.* **80**(6): 1155–1162.
672 doi:10.1111/j.1365-2656.2011.01860.x.
- 673 de Wit, M., and Faaij, A.A. 2010. European biomass resource potential and costs. *Biomass and*
674 *Bioenergy* **34**(2): 188–202. Elsevier Ltd. doi:10.1016/j.biombioe.2009.07.011.
- 675 Work, T.T., Brais, S., and Harvey, B.D. 2014. Reductions in downed deadwood from biomass
676 harvesting alter composition of spiders and ground beetle assemblages in jack-pine forests
677 of Western Quebec. *For. Ecol. Manage.* **321**: 19–28. Elsevier B.V.
678 doi:10.1016/j.foreco.2013.06.021.
- 679 Zanchi, G., Pena, N., and Bird, N. 2012. Is woody bioenergy carbon neutral? A comparative
680 assessment of emissions from consumption of woody bioenergy and fossil fuel. *GCB*
681 *Bioenergy* **4**(6): 761–772. doi:10.1111/j.1757-1707.2011.01149.x.

Table 1. Characteristics of the watersheds. The high productivity site types are classified to herb-rich heath forest (OMT: see (Cajander 1949) for classification) and mesic heath forests (MT), while the lower productivity watersheds composed of pine dominated sub-xeric heath forests (VT) and pine dominated xeric heath forests (CT). The development stage “Young” refers to a stand with average diameter at breast height of 8-16 cm and “Mature” similarly average diameter greater than 16 cm but ready for final felling. “Ready to harvest” follows the timing of final felling according to the current forest management recommendations in Finland (Äijälä et al., 2014).

Site type [% of area]					Development class [% of area]				Stands [nro.]	Total area [ha]
OMT	MT	VT	CT	Clearing	Sapling	Young	Mature	Ready to harvest		
60	38	1	1	4	10	9	39	38	379	473
16	44	38	3	3	19	20	40	19	1142	1766
29	56	15	1	3	18	13	31	35	3258	4709
74	24	1	0	5	18	13	36	29	1923	4073

Figure 1. Changes in fossil emissions, forest carbon balance and net emissions ($\text{t CO}_2 \text{ a}^{-1}$) resulting from bioenergy production (BIO) compared to no bioenergy harvesting (BAU) in the landscape consisting of four watersheds. Positive values indicate a change in emissions whereas negative values a change in removals. Producing bioenergy from forest harvest residues reduces fossil carbon emissions through substitution (grey) but also cuts the forest carbon sink (white). The net change is the difference between fossil carbon emission reduction and carbon sink change (black).

Figure 2. Decrease in deadwood types resulting from logging residue harvesting for bioenergy compared to business as usual management without residue harvesting. Decay stages: 1 = recently died, 2 = weakly decayed, 3 = medium decayed, 4 = very decayed, 5 = almost decayed.

Figure 3. The development of the average combined species conservation capacity (SCC) in the landscape in with (BIO) and without (BAU) logging residue harvesting for bioenergy, and without any forest management actions (Set aside) in the landscape.

Figure 4. Type species-specific vulnerability to logging residue harvesting during the simulation period. The vulnerabilities were calculated as the differences in the type species-specific conservation capacity across stands between BIO and BAU scenarios for each year. The vulnerabilities are summarized as percentage values for different combinations of species requirements for deadwood (DS = decay stage) and microclimate.

716

Figure 5. The bioenergy potential and the conservation potential (SCC) of forest stands with different site types (OMT, MT, VT and CT, see Table 1). The conservation potential is the value of SCC if stands were set aside in the beginning of the simulation. The dashed lines indicate top 10% quantiles of SCC and bioenergy potential.